# Status Review Report of Seven Giant Clam Species Petitioned Under the U.S. Endangered Species Act: *Hippopus hippopus, H. porcellanus, Tridacna derasa, T. gigas, T. mbalavuana, T. squamosa, and T. squamosina*

*Tridacna gigas* at Kwajalein Atoll, Marshall Islands. (Photo credit: Scott and Jeanette Johnson / CC BY-NC 4.0)

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# Executive Summary

This report was produced in response to a petition received on August 7, 2016 from Dwayne Meadows to list ten species of giant clams (Cardiidae: Tridacninae) as threatened or endangered under the Endangered Species Act (ESA). On June 26, 2017, we published a finding (82 FR 28946) announcing that the petition presented substantial scientific or commercial information indicating that the petitioned action may be warranted for seven of the ten species listed in the petition: *Hippopus hippopus* (horse's hoof, bear paw, or strawberry clam), *H. porcellanus* (porcelain or China clam), *Tridacna derasa* (smooth giant clam), *T. gigas* (true giant clam), *T. mbalavuana* (syn. *T. tevoroa*; devil or tevoro clam), *T. squamosa* (fluted or scaly clam), and *T. squamosina* (syn. *T. costata*; Red Sea giant clam), but that the petition did not present substantial scientific or commercial information indicating that the petitioned action may be warranted for the other three species (*T. crocea*, *T. maxima*, or *T. noae*). This report summarizes the best available scientific and commercial information regarding these seven species of giant clams and presents an evaluation of their respective status and extinction risk.

Giant clams are a small but conspicuous group of the planet's largest and fastest growing marine bivalves. Of the seven candidate species, *T. squamosa* has the broadest distribution, extending from the western Indian Ocean and Red Sea in the west to the central Pacific islands in the east. The most restricted ranges are those of *H. porcellanus*, *T. mbalavuana*, and *T. squamosina*, which occur only in relatively small areas of the Indo-Malay Archipelago, western Pacific, and the Red Sea, respectively. The other three species, *H. hippopus*, *T. derasa*, and *T. gigas*, occupy overlapping ranges centered in the Indo-Malay Archipelago and western Pacific regions. Abundance data and robust estimates of population trends are lacking for most locations where these species occur. However, available survey data and qualitative accounts consistently indicate that all species have suffered significant population declines over the last 50 years.

The most significant threats to all seven species are past and present overutilization and the inadequacy of existing regulatory mechanisms to address the threat of overutilization. The two largest species in particular, *T. derasa* and *T. gigas*, were targeted intensively by widespread commercial, and in many cases illegal, harvesting operations during the 1970s and 1980s to supply a high demand for their meat in Taiwan and Southeast Asia. There was little regulation regarding the harvest of giant clams during this time nor was their sufficient capacity to enforce existing regulations. As a result, these two species experienced severe population declines throughout their respective ranges. Several species have also been targeted extensively for the collection and sale of their shells, primarily *H. hippopus*, *H. porcellanus*, *T. derasa*, *T. gigas*, and *T. squamosa*. According to the best available information, these intense periods of commercial harvest, combined with longstanding and ongoing subsistence harvest of all species throughout their ranges, have led to widespread declines of all seven species.

In assessing the extinction risk of each species, we evaluated the current status, threats, and demographic risks to each species throughout the entirety of their respective ranges. In regard to *H. porcellanus*, *T. mbalavuana*, and *T. squamosina*, considering the species' highly restricted ranges, exceptionally low abundance, low natural productivity, the past and ongoing threats of harvest to all three species, and the likely threat of habitat degradation to *T. squamosina*, we concluded that all three species are in danger of extinction throughout the entirety of their respective ranges.

With respect to *H. hippopus*, *T. derasa*, and *T. gigas*, the most critical demographic risks to all three species are the low abundance and negative trajectory of populations throughout the majority of their respective ranges, as well as low natural productivity due to their inherent reliance on sufficient population density to facilitate reproductive success. For all three species, subsistence harvest still occurs and constitutes a significant threat in all locations of their respective ranges except Australia. These three species are reportedly still abundant in several locations—most notably the Great Barrier Reef; Palau, where *H. hippopus* and *T. derasa* are both considered frequent; and remote regions of Vanuatu and the Marshall Islands, where *H. hippopus* is reportedly still abundant. In contrast to other locations, Australia has effectively enforced a complete ban on the harvest of giant clams (including subsistence harvest), minimizing the threat of overutilization within its waters. Available reports indicate that populations of *H. hippopus*, *T. derasa*, and *T. gigas* are stable on the Great Barrier Reef. Based on this information, and considering that the Great Barrier Reef comprises a major proportion of the suitable habitat area within each species' respective range, we concluded that none of the three species are at moderate or high risk of extinction throughout its *entire* range.

However, under the ESA, a species warrants listing if it is in danger of extinction or likely to become so within the foreseeable future throughout all or a significant portion of its range. Thus, having determined that none of these three species is at moderate or high risk of extinction throughout *all* of its range, we conducted an additional analysis to assess whether each species is at a higher risk of extinction in a "significant portion of its range." A joint USFWS-NMFS policy (79 FR 37578, July 1, 2014) provided the agencies' interpretation of this phrase, and addressed how, in identifying possible "portions" of a species' range, a key part of the analysis is considering whether the threats to a species are geographically concentrated in some way. In this case, because we determined that the most significant threats to *H. hippopus*, *T. derasa*, and *T. gigas* are overexploitation and inadequacy of regulatory mechanisms to address overutilization, we focused our analysis on the portion of the range where these threats are most severe. Due to the effectiveness of strict harvest prohibitions in Australia we distinguished locations in Australia from all other locations in each species' range.

With respect to *H. hippopus*, we considered the species' low abundance, and in some cases extirpation, in 21 of the 24 countries and territories outside of Australia, its low natural productivity, and the ongoing threats of overexploitation and inadequate regulatory mechanisms in all 24 locations where it occurs. However, the species' current distribution encompasses a broad geographic area and variety of environmental conditions, and relatively healthy populations can still be found in the Marshall Islands, Palau, and Vanuatu. Based on this information, we conclude that, in the portion of its range that includes all locations outside of Australia, the species is on a trajectory that puts it at a high level of extinction risk within the foreseeable future, but that it is not at or near a level of abundance that places its continued persistence in question.

With respect to *T. derasa* and *T. gigas*, we again considered the low abundance, and in many cases extirpation, of each species in locations outside of Australia. Of the 16 locations where *T. derasa* naturally occurs outside of Australia, it is reportedly rare in 11 locations and extirpated (or reintroduced after extirpation) in 4. Of the 29 locations where *T. gigas* naturally occurs outside of Australia, it is rare in 11 locations, extirpated (or reintroduced after extirpation) in 14, and its occurrence is unconfirmed (likely exceptionally rare or extirpated) in 4. We also considered the low natural productivity of the two species, likely exacerbated by their low abundance, and the ongoing threats of subsistence harvest and the inadequacy of existing regulations to address it. Due to their large size, both species are still highly desired and targeted as a subsistence food item throughout their respective ranges. For these reasons, we conclude that, in the portion of each species' range that includes all locations outside of Australia, *T. derasa* and *T. gigas* are at or near a level of abundance that places their continued existence in question.

Having reached a positive answer with respect to the "status" question in the SPR analysis for all three species, we then considered several factors in determining whether the respective portion of each species' range is "significant." Given the similarity between the portions and general biology of the three species, we used the same rationale in answering the significance question for each. Each species was likely historically abundant in their respective portions, based on historical trade statistics. Additionally, given the reproductive strategy of giant clams, the populations in these portions likely played an important role in maintaining genetic connectivity throughout each species' range. Lastly, the geographic extent of each portion and varied habitats they encompass likely gave rise to significant genetic diversity and served as a critical demographic reserve, both of which may facilitate recovery following localized population declines. For these reasons, we find that the portion of each species' range defined as all locations outside of Australia is "significant," and serves a biologically important role in maintaining the long-term viability of *H. hippopus*, *T. derasa*, and *T. gigas*, respectively.

Lastly, with respect to *T. squamosa*, the best available scientific and commercial data indicate that, despite past and ongoing harvest, *T. squamosa* still occurs at relatively high abundance in several locations that constitute a major proportion of the suitable habitat within its range. This includes significant portions of South Asia and the Red Sea, two regions which notably have been subjected to a long history of subsistence harvest, and in the case of South Asia, intense commercial trade of *T. squamosa* shells throughout the 1980s. Considering the relatively high abundance of *T. squamosa* in major portions of its range as well as its expansive distribution (including 61 locations spanning the Indo-Pacific region from the central Pacific to southeast Africa and the Red Sea), we conclude that the species is at low risk of extinction throughout its entire range.

Having determined that *T. squamosa* is at low risk of extinction throughout all of its range, we again conducted an additional analysis to assess whether the species is at higher risk of extinction in a "significant portion of its range." In this case, we analyzed two different configurations of portions, both of which had a reasonable likelihood of meeting these conditions. Because we determined that the most significant threats to *T. squamosa* are overutilization and inadequacy of regulatory mechanisms to address that threat, we first based our analysis on the portion of the range where these threats are most severe, thus distinguishing locations in Australia from all other locations where *T. squamosa* occurs. In this portion, although harvest for subsistence purposes continues to occur in all locations outside of Australia and constitutes the most significant threat to *T. squamosa*, we found that the relatively high abundance of this species in locations such as the Philippines, Indonesia, Malaysia, and Saudi Arabia indicates that this threat likely does not place the continued persistence of the species in question now or in the foreseeable future. Thus, we concluded that *T. squamosa* is at low extinction risk in this portion of its range.

We then considered population genetics as a means of delineating alternative portions of the species' range. The best available population genetic data indicate at least four discrete subpopulations, which are located in the Red Sea, southeast Africa, Indo-Malay Archipelago, and Cenderwasih Bay in northern Papua. We identified these as four distinct portions of the species' range. Considering again the relatively high abundance of *T. squamosa* in the Red Sea and Indo-Malay regions, we concluded that the species is likely at low risk of extinction in these portions of its range. Lastly, with respect to the portions in southeast Africa and in Cenderwasih Bay, we took into account their genetic and likely demographic isolation from the majority of the species' range, as well as the relatively small geographic area they occupy. Based on this rationale, we did not find that these two portions could be considered "significant," or that they likely serve a biologically important role in maintaining the long-term viability of this species. As a result of this SPR analysis, we concluded that there are no portions within the range of *T. squamosa* for which it is true that both the portion is significant and that the species in the portion is at moderate or high risk of extinction.

Based on this information, and accounting for the current status, threats, and demographic risks to each species, we conclude that *H. porcellanus*, *T. mbalavuana*, and *T. squamosina* are in danger of extinction throughout the entirety of their respective ranges, *T. derasa* and *T. gigas* are in danger of extinction throughout a significant portion of their respective ranges, and *H. hippopus* is likely to be in danger of extinction within the foreseeable future throughout a significant portion of its range. We also find that *T. squamosa* is not currently in danger of extinction throughout all or a significant portion of its range, nor is it likely to become so within the foreseeable future.

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# 1.0 Introduction

On August 7, 2016, the National Marine Fisheries Service (NMFS, "we") received a petition to list 10 species of giant clams (Cardiidae: Tridacninae) as threatened or endangered pursuant to the U.S. Endangered Species Act (ESA) of 1973, as amended (16 U.S.C. 1531 *et seq.*) (Meadows, 2016). Section 4(b)(3)(A) of the ESA requires the Secretary to determine, to the maximum extent practicable, within 90 days of receiving a petition to list a species under the ESA, whether the petition presents substantial scientific or commercial information indicating that the petitioned action may be warranted. If a petition is found to present substantial scientific or commercial information that the petitioned action may be warranted, a status review shall be promptly commenced (16 U.S.C. 1533(b)(3)(A)). On June 26, 2017, we published a 90-day finding (82 FR 28946) stating that the petition presented substantial scientific or commercial information indicating that the petitioned action may be warranted for 7 of the 10 species of giant clams listed in the petition: *Hippopus hippopus* (horse's hoof, bear paw or strawberry clam), *H. porcellanus* (porcelain or China clam), *Tridacna derasa* (smooth giant clam), *T. gigas* (true giant clam), *T. squamosa* (fluted or scaly clam), *T. mbalavuana* (syn. *T. tevoroa*; devil or tevoro clam), and *T. squamosina* (syn. *T. costata*; Red Sea giant clam) and commenced a status review for these 7 species. We found that the petition did not present substantial scientific or commercial information indicating that the petitioned action may be warranted for the other three petitioned giant clam species (*T. crocea, T. maxima,* and *T. noae*).

There are two key tasks associated with conducting an ESA status review. The first is to delineate the taxonomic group(s) under consideration. To be considered for listing under the ESA, a group of organisms must constitute a "species", which according to the ESA also includes "any subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature." We address this question in **Section 2.1**. The second task is to conduct an extinction risk assessment to serve as the scientific basis for determining whether the candidate species are threatened or endangered. The ESA defines the term *endangered species* as "any species which is in danger of extinction throughout all or a significant portion of its range." The term *threatened species* is defined as "any species which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range." To make this assessment, we considered risks based on specific demographic factors of the species, such as abundance, productivity, spatial structure, and diversity, as well as specific threats faced by the species, as outlined in section 4(a)(1) of the ESA:

- the present or threatened destruction, modification, or curtailment of its habitat or range,
- overutilization for commercial, recreational, scientific, or educational purposes,
- disease or predation,
- the inadequacy of existing regulatory mechanisms, or
- other natural or manmade factors affecting its continued existence

This status review synthesizes the best available scientific and commercial information on the biology, population status and trends, and threats contributing to the extinction risk of each species. This includes a thorough review of relevant peer-reviewed articles, reports, gray literature, and data, which were gathered using Google Scholar, Reefbase, FishBase, Research

Gate, and the NOAA Central Library, as well as references provided by the petitioner. We also searched public websites for information (e.g., relevant trade web pages such as TRAFFIC), compiled Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) trade records, and consulted NMFS staff and academics with expert knowledge of these species. Lastly, we reviewed public comments which had been submitted in response to the published 90-day finding.

As this is a composite status review for these seven species of giant clam, the document is organized as follows. We first present information that is pertinent to all seven species under consideration, including taxonomy and phylogeny, general features of giant clam life history, ecology, distribution, and population genetics. Here, we also discuss the natural and anthropogenic factors threatening the survival and abundance of giant clams broadly. We then address species-specific information in subsequent sections. These include a brief description of distinguishing features of appearance, physiology, ecology and geographic range. Each species-specific section discusses available information on population status and trends for the respective species and concludes with two risk analyses. The first is a demographic risk analysis following the Viable Population approach outlined by McElhany et al. (2000). This approach addresses four biological descriptors of species status: abundance, productivity (i.e., population growth rate), spatial distribution, and diversity. The second is an extinction risk assessment, which evaluates the natural and anthropogenic threats specific to each species according to the five factors in section 4(a)(1) of the ESA.

Importantly, this document does not represent a decision by NMFS regarding whether these species should be proposed for listing as threatened or endangered under the ESA. That decision will be made by NMFS after reviewing this document, any efforts being made to protect the species, and all relevant laws, regulations, and policies. The result of the decision will be posted on the NMFS website and announced in the *Federal Register*.

# 2.0 Life History and Ecology of Giant Clams

## 2.1 Taxonomy and Phylogeny

Giant clams are a small but conspicuous group of the world's largest and fastest growing marine bivalves. They fall within the order Veneroida, family Cardiidae, and subfamily Tridacninae (Schneider, 1998). For many years, giant clams were considered to occupy their own family (Tridacnidae) sister to Cardiidae until molecular phylogenetics (Maruyama et al., 1998; Schneider & Foighil, 1999) and comparison of sperm ultrastructure (Keys & Healy, 2000) supported reclassifying the group as a subfamily within Cardiidae. This is the current, most widely accepted classification; however, Neo et al. (2017) note that others continue to argue that Tridacnidae should be retained as a full family based on its highly distinct morphology (Huber & Eschner, 2011; Penny & Willan, 2014). In fact, giant clam morphology does differ quite dramatically from that of cardiids (true cockles). Colloquially described as having 'upside down' orientation (Penny & Willan, 2014), giant clams lie with the hinge of their shell facing downwards, allowing their byssus (i.e., filamentous threads) to attach the organism to the substrate while orienting their enlarged mantle upwards toward the sunlight (Soo & Todd, 2014).

Additionally, most giant clam species employ an epifaunal lifestyle (i.e., situated on top of the substrate) in contrast to the largely infaunal lifestyle of their cardiid ancestors.

The subfamily Tridacninae is thought to have originated during the Paleogene on the western margin of the Tethys Sea (Newman & Gomez, 2000; Harzhauser et al., 2008). However, like many formerly Tethyan groups which now find their center of distribution in the Indo-Pacific, modern Tridacninae represents a “relic” subfamily, meaning that it is a survivor of an ancient radiation without any living ancestors (Newman & Gomez, 2000). Most genera of the subfamily went extinct prior to the Neogene likely as a result of major climatic changes concurrent with the breakup of Tethys (Newman & Gomez, 2000). Fossil evidence suggests that both extant genera, *Hippopus* and *Tridacna*, arose independently during the Miocene from a now-extinct *Byssocardium*-like ancestor, with *Hippopus* being considered the more primitive of the two (Stasek, 1962; Schneider, 1998).

The two genera are distinguished by several shell and mantle characteristics. In *Hippopus*, a very narrow byssal orifice is bordered by interlocking teeth, while *Tridacna* exhibits a well-defined byssal gape without teeth. Additionally, when the clam is completely open, the mantle of *Tridacna* extends laterally beyond the margin of the shell, whereas the mantle of *Hippopus* does not (Lucas, 1988). A result of this difference is that *Hippopus* species tend to gape their valves further apart than *Tridacna* species to expose a larger surface area of mantle in the space between (Lucas, 1994). *Tridacna* is further subdivided into three sub-genera: *Tridacna* sensu stricto, *Persikima* Iredale, 1937, and *Chametrachea* Herrmannsen, 1846.

There are currently 12 species of giant clams recognized in the literature, though this number changes often as advances in molecular phylogenetics resolve evolutionary relationships (including cryptic speciation) that had been overlooked by traditional morphology-based taxonomies. Joseph Rosewater’s seminal work in 1965 is widely cited as the authoritative material for early descriptions of giant clam species and includes six current species that remain valid to date: *Hippopus hippopus* (Linnaeus 1758), *Tridacna gigas* (Linnaeus 1758), *T. derasa* (Röding 1798), *T. maxima* (Röding 1798), *T. squamosa* (Lamarck 1819), and *T. crocea* (Lamarck 1819). He later added *H. porcellanus* to this list after re-examining its classification, having recognized that shell dealers had distinguished it in trade for many years (Rosewater, 1982).

At the time of the 1965 report, *T. mbalavuana* had only previously been formally described from fossils on Viti Levu, Fiji. However, Fijians had long known of this species occurring in local waters as 'tevoro', or devil clam. Thus, when Lucas et al. (1991) re-discovered the species in 1991, they described it as the new species *T. tevoroa*. It was not until 2000 that *T. mbalavuana* and *T. tevoroa* were re-classified as synonymous based on morphological similarities (Newman & Gomez, 2000). In this report, we refer to this species by its lectotype, *T. mbalavuana*. Additionally, Richter et al. (2008) described the new species *T. costata* in 2008, but upon further analysis, it too was found to be synonymous with a previously described species, *T. squamosina*, first discovered by Rudolf Sturany (1899) during the early Austro-Hungarian expeditions of the Red Sea (Huber & Eschner, 2011). In this report we refer to this species by its lectotype, *T. squamosina*.

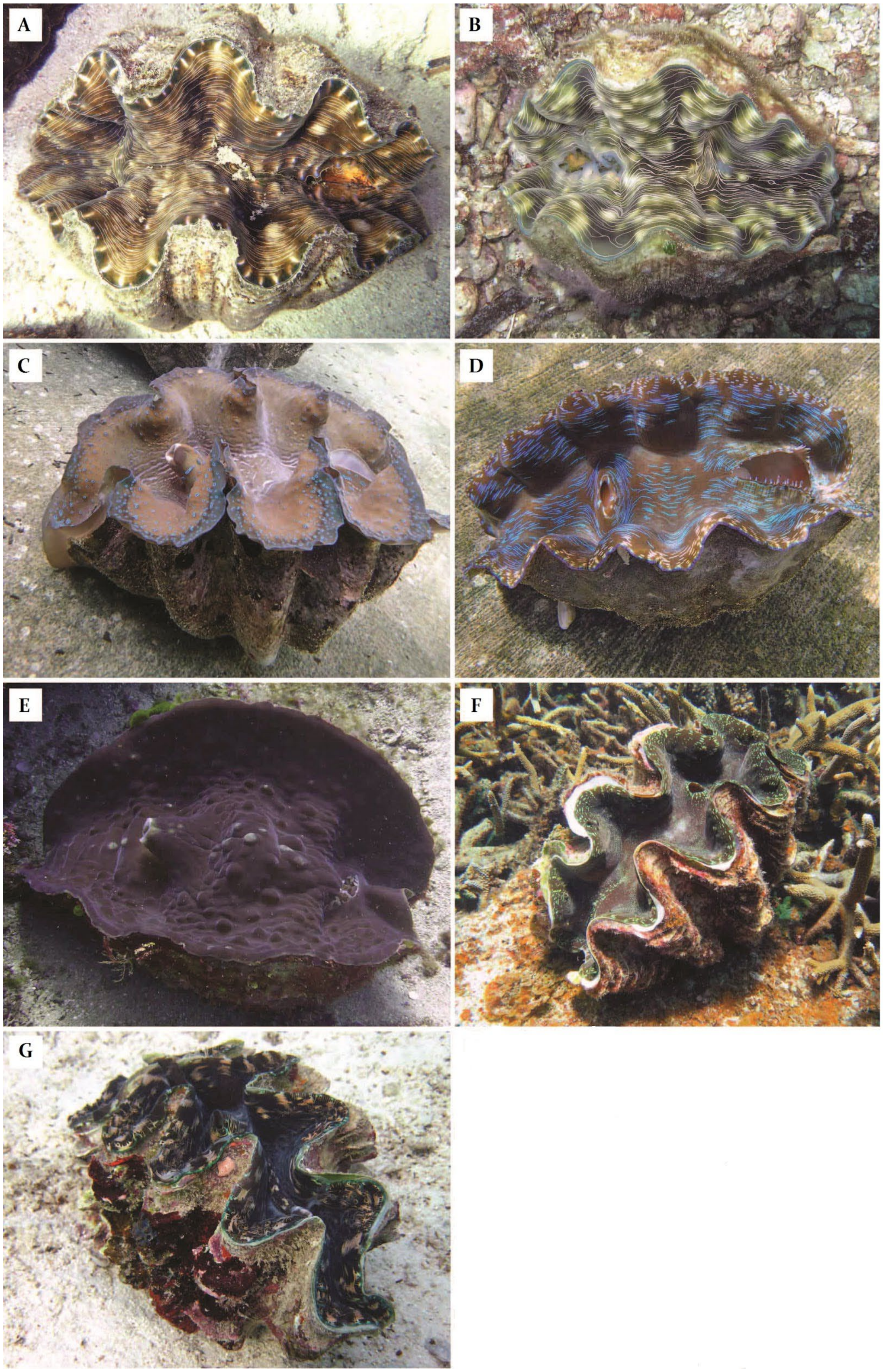


**Figure 1.** Photographs of giant clam species included in this status review report: (A) *H. hippopus*, (B) *H. porcellanus*, (C) *T. gigas*, (D) *T. derasa*, (E) *T. mbalavuana*, (F) *T. squamosa*, (G) *T. squamosina* (Source: Neo et al., 2017 / CC BY-NC-ND 4.0).

Several other species have been added in the years since, primarily based on molecular phylogenetic evidence; although, in most cases their validity is still a subject of debate. *T. noae*, for example, was recently resurrected from synonymy with *T. maxima* based on phylogenies constructed from two mitochondrial markers (Su et al., 2014). *T. elongatissima* (Bianconi, 1856) was similarly resurrected as a valid species based on molecular evidence (Fauvelot et al., 2020), which has subsequently been corroborated in two follow-up studies (Tan et al., 2021; Velkeneers et al., 2022). Lastly, as outlined by Tan et al. (2021), '*T. lorenzi*' was described as a new species from the outlying territories of Mauritius based on morphology (Monsecour, 2016) until more recent phylogenetic analysis concluded that it should in fact be considered a junior synonym of *T. rosewateri*, a rare Indian Ocean species with a restricted geographic range (Fauvelot et al., 2020).

The evolutionary relationship between these 12 species, including their placement within *Tridacna* subgenera, is depicted in Figure 3 of Tan et al. (2021). Moreover, representative photos of the seven species addressed in this status review (i.e., *H. hippopus*, *H. porcellanus*, *T. gigas*, *T. derasa*, *T. squamosa*, *T. mbalavuana*, and *T. squamosina*) are displayed in Figure 1 below.

## 2.2 Geographic Distribution

Giant clams are found along shallow shorelines and on coral reefs across the Indo-Pacific between 30°E and 120°W (i.e., from East Africa to French Polynesia) and between 36°N and 30°S (i.e., from Japan to Australia, excluding New Zealand and Hawaii). Additionally, three species of giant clam (i.e., *T. maxima*, *T. squamosa* and *T. squamosina*) can be found throughout the Red Sea. A recent review detailing the distribution, abundance, and status of giant clams identified a total of 66 locations (defined as countries, territories, or regions) where giant clams occurred historically or are currently present. Notably, giant clam distribution is not uniform—the highest diversity can be found in the western Pacific Islands and central Indo-Pacific, particularly in the "Coral Triangle" region encompassing Indonesia, Malaysia, Papua New Guinea, the Philippines, Solomon Islands and Timor-Leste (Pinca et al., 2010; Neo et al., 2017). Of the giant clam species covered in this report, *T. squamosa* has the most cosmopolitan distribution, while *T. squamosina*, *T. mbalavauna,* and *H. porcellanus* have the most restricted geographical ranges (bin Othman et al., 2010).

Four of the giant clam species assessed in this report naturally occur or have historically occurred within waters under the jurisdiction of the U.S. Additionally, several species have been introduced to locations where they did not otherwise occur naturally, typically with the aim of farming the introduced clams commercially or as a source of food for the local communities. Below, we describe the current distribution of giant clams in each territory, state, and region under U.S. jurisdiction where they have been reported to occur naturally or have been introduced by artificial means.

### ***American Samoa***

Giant clams have a "special significance" in American Samoan culture and are often used as offerings during family and community gatherings when available (Score, 2017). Two of the seven species in this report are native to American Samoa: *H. hippopus* and *T. squamosa*. Fossilized shells and anecdotal reports indicate that *H. hippopus* once occurred in American

Samoa but is likely now locally extinct (Munro & Heslinga, 1983; Newman & Gomez, 2000; Marra-Biggs et al., 2022; E. Brown, pers. comm., October 30, 2023). *T. squamosa* is still thought to occur in American Samoa but at very low abundance (Dawson, 1986; B. Smith, 1993; Green & Craig, 1999). A comprehensive assessment of giant clam abundance throughout the Samoan Archipelago is currently underway (P. Marra-Biggs, pers. comm., October 27, 2023).

In American Samoa, *T. derasa*, *T. gigas*, and *H. hippopus* have all been cultured at a government hatchery with the "main aim of establishing local farms to produce meat for local market" (S. Wells, 1997). As of September 1995, there were 6 lagoon nursery sites and 25 small-scale farms in operation. However, the current status of these operations is not clear. According to Marra-Biggs et al. (2022), the "stocks were harvested prior to reproduction and appear to be functionally extirpated."

Samoa gifted approximately 650 *T. derasa* juveniles to American Samoa in November 2023. The clams have been initially set out in protective cages in Faga'alu Bay off the main island of Tutuila and in Sa'ilele, where they will be monitored by the American Samoa Department of Marine and Wildlife Resources (DMWR) and local village partners to curb the threat of poaching. Similar to past giant clam farming operations, the goal of this initiative is to raise the clams to maturity at which point a portion of the population will be harvested and the remaining portion will be left to establish a sustainable food source for the community (American Samoa DMWR, 2024).

### ***Commonwealth of the Northern Mariana Islands (CNMI)***

There is very little information regarding the distribution and status of giant clams in CNMI. According to S. Wells (1997), *H. hippopus*, *T. derasa*, *T. gigas*, and *T. squamosa* are all native to CNMI, but all are very rare or extirpated, likely as a result of overutilization. Giant clams are traditionally valued by the CHamoru people, who live throughout the Mariana Islands, including CNMI and Guam (Cunningham, 1992). In 2017, a single observation of *T. gigas* and *T. squamosa* was recorded incidentally during a coral reef survey of Farallon de Medinilla, an uninhabited island of CNMI that is used by the Department of Defense for military and bombing exercises (SPAWAR Systems Center Pacific, 2018). However, we could not find any other reports describing the current abundance of these species in CNMI.

There have been efforts to reintroduce giant clams to CNMI using broodstock from the Palau Mariculture Demonstration Center (PMDC) and other mariculture facilities throughout the Pacific region. *H. hippopus*, *T. gigas*, and *T. squamosa* were reportedly reintroduced to Saipan in 1991, while *T. derasa* was reintroduced to Saipan on several occasions in 1986, 1987, 1988, and 1991 (Eldredge, 1994; Bearden et al., 2005). The main purpose of these reintroductions was to establish a local market for giant clam meat. However, according to Bearden et al. (2005), the efforts "failed to produce desired economic benefits" and were abandoned due to poaching (see also the CNMI Aquaculture Development Plan 2011-2015). The authors indicated that there were plans to initiate another mariculture venture in 2005 using the same four giant clam species, but the status of that initiative is not known. More recently, the CNMI Aquaculture Development Plan 2011-2015 identified giant clams as a "medium priority commodity" and expressed local interest in re-establishing giant clam culture in CNMI. However, the smaller species, *T. crocea* and *T. maxima*, seem to be the focus of this initiative, as their bright colors make them desirable for ecotourism as well as the ornamental aquarium trade.

### *Guam*

Historical reports and fossil evidence indicate that *H. hippopus*, *T. derasa, T. gigas,* and *T. squamosa* are all native to Guam (Collins et al., 1983; Newman & Gomez, 2000), but according to Neo et al. (2017), *T. squamosa* is the only one of the seven species in this report that still occurs there, albeit at very low abundance. The other three species are reportedly extirpated (Munro & Heslinga, 1983; Sant, 1995; S. Wells, 1997).

A giant clam hatchery was established at the Guam Aquaculture Development and Training Center and received several shipments of *T. derasa* broodstock from PMDC over three decades ago (S. Wells, 1997). However, many were lost due to damage from a cyclone in 1992, leaving approximately 100 specimens alive by 1994 (S. Wells, 1997). Heslinga et al. (1984) also noted that PMDC had shipped 500 *T. gigas* and 500 *T. squamosa* to the University of Guam Marine Laboratory "to explore the possibility of reintroducing giant clams to areas where they are now extinct or very rare." However, we could not find any information indicating the outcome of these reintroductions, and later reports consistently consider *T. gigas* to be extinct in Guam (Munro, 1994; Pinca et al., 2010; Neo et al., 2017).

More recently, the Division of Aquatic and Wildlife Resources in Guam initiated a community-led giant clam mariculture program in 2021, which is supported in part by funding from NOAA Fisheries. The primary goals of this program, like many others throughout the Pacific region, is to establish a sustainable source of food and income for local communities and revitalize cultural ties to giant clams as a natural resource. This program is specifically focused on *T. maxima* as the target species.

### *Pacific Remote Island Area (PRIA)*

The Pacific Remote Island Area (PRIA) consists of seven remote islands and atolls, which are managed cooperatively by NOAA, the U.S. Fish and Wildlife Service (USFWS), and the U.S. Department of Defense as part of the Pacific Remote Islands Marine National Monument. This includes Baker, Howland, and Jarvis Islands, Johnston, Wake, and Palmyra Atolls, and Kingman Reef. *T. squamosa* has been observed at Kingman Reef, although no estimates of species' abundance were provided (Maragos et al., 2008). The Integrated Natural Resource Management Plan for the Wake Atoll Airfield states that *T. squamosa* and *T. gigas* historically occurred in the waters around Wake Atoll. However, it seems that this assertion is based solely on the species range maps provided by Rosewater (1965). Wake Atoll was included within each species' range boundary, but there were no confirmed observations or archived specimens of either species from Wake Atoll in Rosewater (1965). Additionally, Brainard et al. (2019) reported seeing a single *T. gigas* just outside the lagoon at Johnston Atoll, but without any other reports confirming the presence of this species at Johnston Atoll, it is unclear if this is a natural occurrence of *T. gigas*, if it may have been introduced artificially, or if the specimen was misidentified. None of the seven giant clam species in this report have been reported in Baker, Howland, or Jarvis Islands, or in Palmyra Atoll.

### *Hawaii*

None of the seven giant clam species in this report are native to Hawaii. However, according to Heslinga (1996), *T. gigas* and *T. squamosa* were introduced to Keahole Point, Hawaii as part of a 5-year research project by Indo-Pacific Sea Farms to explore aquaculture of ornamental marine invertebrates for the aquarium trade. We are not aware of any efforts to outplant giant clams in Hawaii specifically for the purpose of establishing sustainable populations in the wild.

## 2.3 Reproduction and Growth

Giant clams are protandrous hermaphrodites, meaning they mature first as males and later develop ovaries to function as both male and female simultaneously (Wada, 1952; Rosewater, 1965). Size and age at maturity vary by species and geographic location, but generally giant clams are known to reach male phase maturity at around 2-3 years of age (Heslinga et al., 1984; Shelley, 1989) and female phase maturity as early as 3-5 years (Heslinga et al., 1984; Isamu, 2008). In larger species, such as *T. gigas*, female maturity typically occurs later at around 8-9 years of age (Gomez & Mingoa-Licuanan, 2006). Giant clams reproduce via broadcast spawning, in which sperm and eggs are released into the water column where external fertilization takes place (Wada, 1954). Sperm is released first, followed by eggs after a short interval (Munro, 1993a).

Giant clams are exceptionally fecund, with individuals producing by many estimates tens to hundreds of millions of eggs during a single spawning event (Lucas, 1988). This number varies by species; for example, estimates suggest that *H. porcellanus* can release around 5 million eggs (Alcázar et al., 1987), *H. hippopus* can release 25-60 million eggs (Jameson, 1976; Alcala et al., 1986), and *T. gigas* can release up to 500 million eggs (Crawford et al. 1986). However, despite their high fecundity, giant clams experience very high rates of mortality during early development (Jameson, 1976; Beckvar, 1981), resulting in very low levels of natural recruitment (Munro, 1993a). Reports suggest that less than 1% of all giant clam fertilized eggs survive larval development and progress to the juvenile phase (Jameson, 1976; Fitt et al., 1984; Crawford et al., 1986). As Lucas (1994) describes, “the extreme example is *T. gigas*, which being at or near the pinnacle of fecundity, must have near the lowest level of survival of potential recruits in the animal kingdom.”

Many scholars have described giant clam recruitment as “erratic” (McKoy et al., 1980; Adams et al., 1988; Lucas, 1994; Guest et al., 2008). For example, Braley (1988b) observed “extremely low” average recruitment on the Great Barrier Reef punctuated by a major recruitment event in 1987 yielding the largest population of *T. gigas* that had been recorded at the time. Together, these observations align with the concept of ‘sweepstakes’ reproduction, where intermittent bursts of reproductive success arise from the chance matching of reproductive activity with oceanographic conditions conducive to spawning, fertilization, dispersal, and recruitment (Hedgecock, 1994). The implication is that the reproductive success of a population varies significantly from one year to the next, and when it occurs, it is often dominated by a minority of individuals which randomly experience this sweepstakes chance, while most other individuals fail to reproduce. This can lead to sporadic waves of recruitment depending on the prevailing oceanographic conditions carrying a successful cohort of ‘sweepstakes’ larvae to a suitable settlement location. Importantly, for broadcast spawning organisms like giant clams, which primarily rely on the mixing of gametes with neighboring individuals, this reproductive strategy can be especially sensitive to changes in population density. In particular, low abundance and low population density severely reduces the likelihood of such sweepstakes success by minimizing the chance of fertilization. In effect, this negative relationship between population density and productivity, known as the Allee effect (Allee et al., 1949), can significantly hinder the recovery potential of populations that have been reduced by overexploitation.

There is considerable variation in the frequency and seasonality of spawning events among giant clam species. Table 1 provides reported spawning seasons for the seven species considered in this report. There is no evidence of reproductive seasonality in the central tropics, with some populations possessing ripe gametes year-round (Heslinga et al., 1984; Munro, 1993a; Lindsay et al., 2004). At higher latitudes, spawning is most often associated with late spring and summer months and can occur once per year (Shelley & Southgate, 1988), or in some cases periodically over the course of several months (Fitt & Trench, 1981; Heslinga et al., 1984; Roa-Quiaoit, 2005). The environmental cues that initiate gamete release are not fully known, but there is strong evidence that the lunar cycle may play a critical role. In Palau, for example, 76% of 55 observed spawning events by *T. gigas* occurred during the second quarter of the lunar cycle, while 24% occurred during the fourth quarter (Heslinga et al., 1984). Unlike many other broadcast spawning organisms, there is little evidence that temperature is important in the induction of spawning (Wada, 1954; Fitt & Trench, 1981).

Once one or more clams have begun to spawn, chemical cues associated with egg release have been shown to play a role in triggering the spawning of nearby individuals, which then release sperm for fertilization (Munro, 1993a). While a maximum distance between spawning individuals has not been quantified (Neo, Vicentuan, et al., 2015), *in situ* observations by Braley (1984) showed that 70% of the nearest spawning neighbors were within 9 m of one another, while only 13% were between 20-30 m of one another. Through laboratory trials, Neo, Vicentuan, et al. (2015) found that gametes of *T. squamosa* remained viable for up to 8 hours, but that viability decreased significantly with time. Because of these factors, maintaining sufficient population densities to facilitate fertilization among neighboring individuals is vital to the persistence of giant clam populations.

**Table 1.** *In situ* spawning observations for seven giant clam species included in this status review

| Species | Location | Latitude | Spawning Season | Reference |
|---|---|---|---|---|
| *Hippopus hippopus* | Palau | 6-8°N | Apr | Beckvar (1981) |
| | Palau | 6-8°N | Jun | Jameson (1976) |
| | Palau | 6-8°N | Jul | Yamaguchi (1977) |
| | N Great Barrier Reef, Australia | 16-17°S | Jan - Mar | Stephenson (1934) |
| | Orpheus Island, Australia | 18-19°S | Nov - Mar | Shelley and Southgate (19 |
| | Orpheus Island, Australia | 18-19°S | Mid-summer | Shelley (1989) |
| *Hippopus porcellanus* | *No in situ spawning records found* | | | |
| *Tridacna gigas* | Palau | 6-8°N | Year-long | Heslinga et al. (1984) |
| | Arlington Reef, Australia | 16-17°S | Jan - Mar | Nash et al. (1988) |
| | Michaelmans Reef, Australia | 16-17°S | Oct - Feb | Braley (1988b) |
| *Tridacna derasa* | Okinawa, Japan | 25-27°N | Mar - May | Iwai et al. (2006) |
| | Palau | 6-8°N | Yearlong | Heslinga et al. (1984) |
| | Michaelmans Reef, Australia | 16-17°S | Sep - Dec | Braley (1988b) |
| | Myrmidon Reef, Australia | 18-19°S | Oct - Feb | Braley (1984) |
| | Tonga | 21-22°S | Dec - Jan | McKoy (1980) |
| *Tridacna squamosa* | Gulf of Aqaba, Red Sea | 28-30°N | Jun - Nov | Roa-Quiaoit (2005) |
| | Gulf of Aqaba, Red Sea | 28-30°N | Jun - Nov | Richter et al. (2008) |
| | Okinawa, Japan | 25-27°N | Mar - Aug | Iwai et al. (2006) |
| | Eniwetok Atoll, RMI | 11-12°N | Feb - Mar | Rosewater (1965); (Schne & Foighil, 1999) |
| | Palau | 6-8°N | Feb | Hardy and Hardy (1969) |
| | Singapore | 1-2°N | Aug | Neo et al. (2011) |
| | Fiji | 17-18°S | Jun - Jul | LaBarbera (1975) |
| | Tonga | 21-22°S | Dec, Feb | McKoy (1980) |
| *Tridacna mbalavuana* | Fiji and Tonga | 17-22°S | ~ Oct | Ledua et al. (1993) |
| *Tridacna squamosina* | Gulf of Aqaba, Red Sea | 28-30°N | May - Jul | Roa-Quiaoit (2005) |
| | Gulf of Aqaba, Red Sea | 28-30°N | May - Jun | Richter et al. (2008) |

Importantly, there is also some evidence that giant clams are able to self-fertilize with variable fitness consequences among species. Alcazar (1988) observed the occurrence of self-fertilization in cultured *H. hippopus*, but found that it led to significantly reduced larval survival after seven months (0.09%) compared to cross-bred larvae (13.45%). Likewise, Benzie and Williams (1996) found that the genotype frequencies resulting from controlled crosses of *T. gigas* did not fit expectations of a pairwise mating, suggesting that self-fertilization likely occurred. Based on an observation that the end of sperm release can occasionally overlap with the beginning of egg release in some giant clams (see also Kurihara et al. (2010)), Murakoshi and Hirata (1993) experimentally induced self-fertilization in four species of giant clams

(*H. hippopus*, *T. crocea*, *T. maxima*, and *T. squamosa*) by removing the gonads and mixing gametes. They found that all four species are capable of self-fertilization, but that larval development of *H. hippopus* was significantly altered, and no *T. maxima* juveniles metamorphosed completely to the normal pediveliger stage. Juvenile *T. crocea* and *T. squamosa* survived up to a year post-fertilization, but the study was not long enough to evaluate possible effects on reproductive maturity or later-phase development. Most recently, Zhang et al. (2020) evaluated the fitness effects of self-fertilization in three species of giant clams (*T. crocea*, *T. derasa*, and *T. squamosa*) after one year of development. They found that there was no effect of self-fertilization on the fertilization rate or zygotic fertility in any species, and that larval survival and growth rate was significantly reduced in *T. crocea* and *T. squamosa*, but not *T. derasa*. The authors hypothesized that differing life histories may play a role in the variable success of self-fertilization. However, while self-fertilization may be possible in some species, numerous accounts of spawning in culture and *in situ* suggest that sperm and eggs are released successively without an overlap in timing in the vast majority of cases (LaBarbera, 1975; McKoy, 1980; Wada, 1954). It is likely that this limits the occurrence of self-fertilization in nature, and it likely plays only a marginal role in giant clam productivity.

Once an egg is fertilized, the life cycle of giant clams is typical of bivalve mollusks (Lucas, 1994; Soo & Todd, 2014). Fertilized eggs are approximately 90-130 µm in diameter (Jameson, 1976) and have a slightly negative buoyancy. They usually develop into swimming trochophores within 12-24 hours, at which time they are able to alter their depth distribution and begin searching for an eventual settlement site (Ellis, 1997; Neo, Vicentuan, et al., 2015). Based on feeding trials, giant clams are thought to initially rely on nutrition from egg yolk reserves during the trochophore stage (Fitt et al., 1984). Notably, Richter et al. (2008) hypothesize that differences in egg size between species may suggest that reliance on this embryonic food source can vary. Shell production in mollusks also begins at this early phase of development, following a thickening of epithelial cells that will define the future shell field (Gazeau et al., 2013). Primary mineralization occurs between this shell field and the outermost organic shell layer, known as the periostracum (Gazeau et al., 2013).

Within 36-48 hours after fertilization, larvae develop into shelled, swimming veligers, which use a ciliated velum for locomotion and feeding (Soo & Todd, 2014). The veligers are highly motile and begin feeding on microalgae of up to 10 µm in diameter (Munro, 1993a). Over the course of several days, the velum begins to degenerate and a foot develops as the larvae transition into the pediveliger stage (Soo & Todd, 2014). At this point, larvae alternate between swimming and crawling on the substrate, using their foot for sensing and feeding (Lucas, 1988; Soo & Todd, 2014). Pediveligers generally develop 6-14 days post-fertilization; however, Fitt and Trench (1981) noted considerable variation in the timing of this transition, where most took place by day 10 but others were observed up to 29 days post-fertilization.

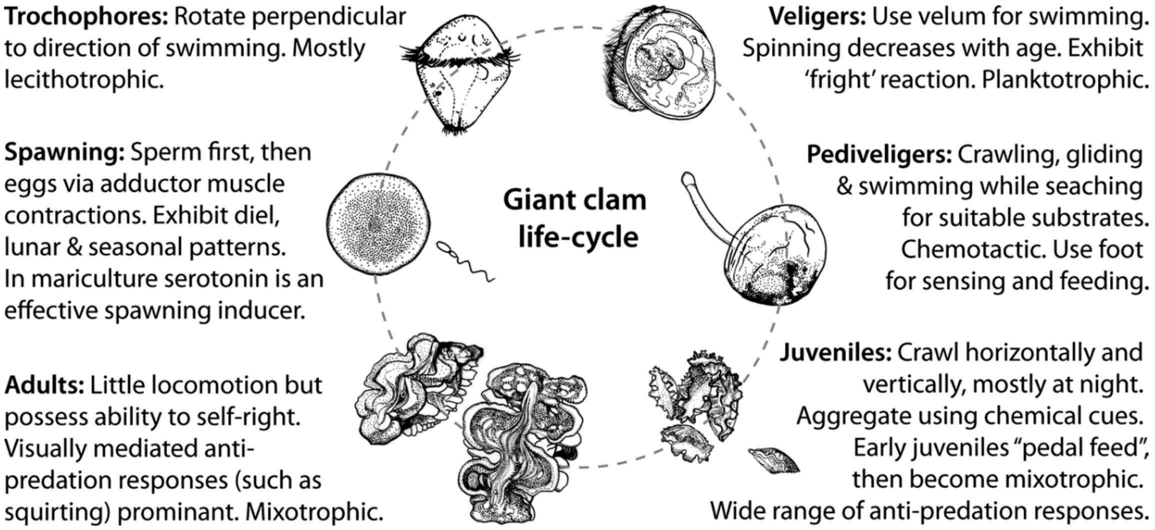


**Figure 2.** Giant clam life cycle and developmental behaviors (Source: Soo and Todd, 2014 / CC BY).

Larvae then metamorphose into juvenile clams at an approximate size of 200 μm (LaBarbera, 1975; Lucas, 1988; Soo & Todd, 2014). Juvenile clams remain mobile and are able to crawl both horizontally and vertically using their foot as they search for a settlement location (Soo & Todd, 2014). Giant clam larvae tend to settle on substrates that offer shelter in the form of grooves and crevices, highlighting the importance of habitat rugosity during this stage of development (Soo & Todd, 2014). Additionally, juveniles have been observed to move nonrandomly and clump towards conspecifics, which some hypothesize may be a behavioral adaptation to enhance reproduction and predator defense (Huang et al., 2007; Neo, 2020). Juvenile clams eventually attach themselves to the substrate by use of byssal threads, which in some species will remain in place throughout their lifetime. Larger species typically lose the byssal threads after reaching adulthood and are held in place only by their size and weight (Lucas, 1988). Figure 2 summarizes each phase of giant clam development and associated behaviors.

Growth rates vary among species, with larger species exhibiting more rapid growth than smaller species (Munro & Heslinga, 1983; Lucas, 1988). Growth rates after settlement generally follow a sigmoid ("S" shaped) curve, beginning slowly, then accelerating after approximately one year, and slowing again as the animals approach sexual maturity (Lucas, 1988; Ellis, 1997). Lucas (1994) provides examples of maximum rates of monthly shell growth for several species as recorded under culture conditions in the Philippines: *H. hippopus* – 5.3 mm, *T. squamosa* – 4.5 mm, *T. derasa* – 5.6 mm, and *T. gigas* – 9.1 mm (Calumpong, 1992; Gomez & Mingoa, 1993). Shell growth continues throughout the clam's lifespan (Lucas, 1994).

The maximum lifespan of giant clams is not known, but the oldest reliably aged individual was a large *T. gigas* determined to be 63 years old (Lucas, 1994). Similar aging studies based on the analysis of growth rings in the shell estimated a 43 cm long *T. squamosa* to be around 22 years old (Basker, 1991), a ~20 cm long *T. maxima* to be around 28 years old (Romanek et al., 1987), and a 93 cm long *T. gigas* to be around 60 years old (Watanabe et al., 2004). Using growth and mortality estimates, Dolorosa et al. (2014) predicted a lifespan of more than 20 years for *H. porcellanus*.

## 2.4 Feeding and Nutrition

As mentioned above, during the earliest stages of larval development, giant clams initially rely on nutrients stored in the egg yolk. Upon formation of the velum and hollow intestines within the first 2-3 days after fertilization, veliger larvae transition to planktivory and are able to actively ingest flagellates (~5 µm in diameter), zooxanthellae, and dissolved organic nutrients from the seawater via the mouth (Fitt et al., 1984; Soo & Todd, 2014). Like most bivalves, giant clams retain the ability to suspension feed into adulthood by pumping water into their mantle cavities via an inhalant siphon, filtering plankton through ciliated gills, and passing the water back out via an excurrent siphon (Hardy & Hardy, 1969). However, a defining characteristic of giant clams is their mutualistic relationship with dinoflagellates of the family Symbiodiniaceae, also known as zooxanthellae, which provide the primary source of nutrition to adult clams.

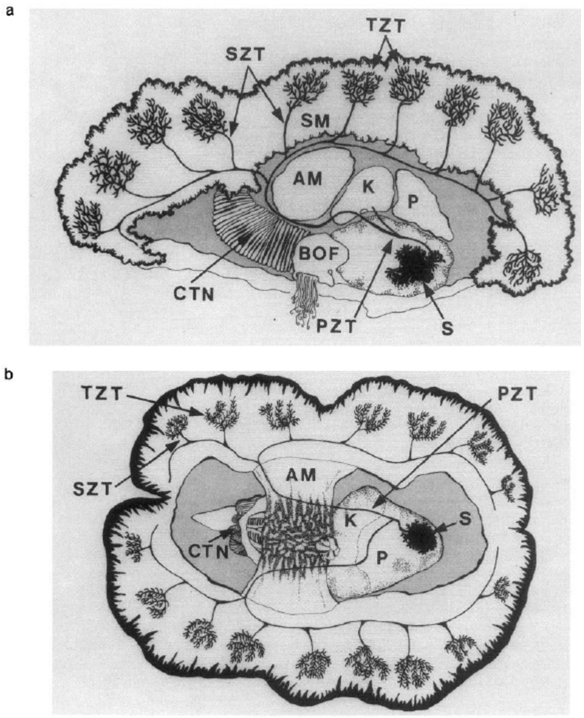


**Figure 3.** Diagram of the zooxanthellal tube structure via the medial (a) and dorsal (b) view of a bissected giant clam. The black, highly branched structure on the surface of the stomach (S) in both a and b is the mass of digestive diverticula. Note that the primary zooxanthellal tube (PZT) originates from one of the diverticular ducts. Abbreviations: AM – adductor muscle; BOF – byssal organ/foot; CTN –ctenidia; K – kidney; P – pericardium; PZT –primary zooxanthellal tube; S – stomach; SM –siphonal muscle; SZT – secondary zooxanthellal tube; TZT – tertiary zooxanthellal tube (Source: Norton et al., 1992).

These are the same dinoflagellate taxa that are well-known obligate symbionts of reef-building corals; however, the symbioses of giant clams and corals differ in two key details. Giant clams strictly acquire symbiotic algae from the seawater during larval development and therefore do not inherit symbionts via parental oocytes like many species of coral (Fitt & Trench, 1981; Hartmann et al., 2017). Furthermore, unlike in corals where zooxanthellae are established intracellularly within endodermal tissues, in giant clams zooxanthellae are housed extracellularly within a diverticular extension of the digestive tract (Norton et al., 1992). This 'tubular system' is spread throughout the upper levels of the mantle and is arranged as a dense network of tertiary canals branching off of secondary structures with no direct connection to the haemolymph of the clam (Figure 3) (Norton et al., 1992). Detailed scanning electron microscope images have shown that zooxanthellae are often stacked in pillars within these canals and are co-located with light-scattering iridocyte cells that enhance photosynthesis (L. Rehm, unpub.) and protect the algal cells from damaging UV radiation (Rossbach, Overmans, et al., 2020; Rossbach, Subedi, et al., 2020).

Symbiosis is thought to be established during metamorphosis from the pediveliger to juvenile phase. At this point, zooxanthellae can be observed migrating from the stomach to the tubular system (Fitt et al., 1986; Norton et al., 1992). Although, more recent studies have shown that genes known to be associated with symbiosis and glycerol synthesis are expressed in giant clam larvae, suggesting that symbiotic activity may be initiated earlier during larval development (Mies et al., 2016; Mies, Voolstra, et al., 2017).

Giant clams receive the majority of their metabolic carbon requirements via symbiotic autotrophy. They provide dissolved inorganic nutrients to support photosynthesis (e.g., $NH_4^+$, $NO_3^-$, $PO_4^+$) via direct absorption from the seawater and as an excretory byproduct of respiration (Hawkins & Klumpp, 1995; Toonen et al., 2011). They also actively enhance inorganic carbon supply to their zooxanthellae symbionts using a carbon-concentrating mechanism consisting of host-derived vacuolar-type $H^+$-ATPases (VHAs) and Carbonic Anhydrase 2-like proteins. These proteins are localized within the apical membrane of epithelial cells in the tubular gut system of the siphonal mantle (Ip, Koh, et al., 2017; Armstrong et al., 2018; Ip et al., 2018). Notably, the same proteins have been similarly convergently exapted in reef-building corals and significantly enhance zooxanthellae photosynthesis within their hosts (Armstrong et al., 2018; Barott et al., 2022). In return, zooxanthellae transfer photosynthetic carbon to the host in the form of glucose, glycerol, oligosaccharides, and amino acids (Griffiths & Streamer, 1988; Ishikura et al., 1999; Mies et al., 2016).

Under natural conditions, the contribution of autotrophy to giant clam nutrition tends to increase with body size and has been shown to vary between species (Klumpp & Griffiths, 1994; Klumpp & Lucas, 1994; Hawkins & Klumpp, 1995). This may in part be related to differences in their characteristic habitats. For example, *T. derasa* and *T. mbalavuana*, two species that occur predominantly in clear, oceanic environments, derive most (*T. mbalavuana*: 70% at 28 m, 105% at 15 m), if not all (*T. derasa*), of the carbon required for growth and respiration from autotrophy (Klumpp & Lucas, 1994). Notably, only *T. mbalavuana*, which is the deepest-occurring species of giant clam, increased its photosynthetic efficiency in the lowest light conditions (Klumpp & Lucas, 1994). *H. hippopus* and *T. gigas* exhibit a different strategy altogether, reflecting their natural occurrence in shallower intertidal and subtidal habitats, where there is often a higher concentration of suspended organics in the water column. Klumpp et al. (1992) showed that *T. gigas* is an efficient suspension-feeder and that heterotrophic carbon supplied significant amounts of the total carbon necessary for its respiration and growth (65% in ~43 mm individuals and 34% in ~167 mm individuals). In a follow-up study, Klumpp and Griffiths (1994) similarly found that ingested carbon provided 61 to 113% of total needs in 40 to 80 mm *T. gigas* and 36 to 44% in *H. hippopus*. Some have hypothesized that differences in energy acquisition and expenditure may in part explain the growth and size differences among giant clam species, and in particular the enormous size of *T. gigas*. At this point, however, no clear nutritional basis for these differences has been resolved (Klumpp & Griffiths, 1994).

Giant clams associate with several Symbiodiniaceae genera, which can vary by geographic location (Fitt et al., 1986). In the central Red Sea, for example, all sampled species (*T. maxima*, *T. squamosa*, *T. squamosina*) were found to exclusively harbor strains of *Symbiodinium* (formerly known as clade A) (Pappas et al., 2017). In Okinawa, Japan, the majority of *T. crocea* individuals also hosted *Symbiodinium* exclusively; however, *T. squamosa* hosted varying communities of *Symbiodinium*, *Cladocopium* (formerly clade C), and *Durusdinium* (formerly clade D) (Ikeda et al., 2017). Similarly, populations of *T. squamosa*, *T. maxima*, and *T. crocea* in eastern Indonesia were found to associate with mixed communities of these three genera (DeBoer et al., 2012). While certain symbiont genera have been shown to confer physiological benefits to *coral* hosts (e.g., greater tolerance to thermal stress or enhanced growth rate), there is no consistent evidence that these patterns translate directly to giant clams (reviewed in DeBoer et al., 2012).

## 2.5 Ecology

Giant clams inhabit coral reefs and a wide range of associated shallow-water habitats, including seagrass beds, intertidal reef flats, atoll lagoons, live coral, dead coral rubble, and sandy substrata (Munro, 1993a; Hernawan, 2010; Neo et al., 2017). The depth range varies considerably among species. The deep-adapted species, *T. mbalavuana*, is known to occur at depths over 30 m (Ledua et al., 1993), and the more wide-ranging *T. squamosa* has been observed up to 42 m deep (Jantzen et al., 2008; Neo et al., 2017), although its occurrence at this depth is unusual. On the other end of the spectrum, *H. hippopus* and *T. squamosina* are most often found at the shallowest depths, preferring sandy atoll lagoons and sandy rubble flats in their respective ranges (Purcell et al., 2020; K. K. Lim et al., 2021). *T. gigas* adults have even been found in intertidal areas and have been shown to survive up to ten hours of complete emersion (Lucas et al., 1989). The typical depth distribution and preferred habitat types vary among species and are outlined in each respective species-specific section.

It is commonly stated in the literature that giant clam larvae prefer settling on substrates of high rugosity, which offer adequate grooves and crevices for shelter; although, the support for these suggestions is quite limited. In one study, Neo et al. (2009) found that *T. squamosa* settlement was greater on the rough side of custom-made reef tiles than on the smooth side. Additionally, during two artificial spawning trials, juveniles of *T. maxima* were observed clumping on fragments of coral rubble and in the corners of raceways, while *H. hippopus* preferentially settled on coral fragments (42% of the time) but were observed in significant numbers on an array of substrates, including pebbles and stones (36%), coral rubble (14%), and several objects that were accidentally introduced to the tanks (e.g., a piece of wood, broken PVC pipe, and a leaf; 8%) (Alcala et al., 1986; Alcázar & Solis, 1986). Braley (1987b) also reported that *H. hippopus* juveniles preferentially settled on broken fragments of *Acropora* coral, as compared to a granite surface and clear rigid plastic of the aquarium with sparse sand grains. Thus, it is clear that giant clam larvae tend to avoid settling on smooth surfaces, but more research is needed to quantify the correlation between substrate rugosity and juvenile survival.

Chemotaxis is likely an important component of larval settlement behavior for giant clams. Larvae of *T. squamosa*, in particular, are attracted to substrates colonized by crustose coralline algae (CCA), a known settlement cue for a number of other benthic marine invertebrates (Courtois de Vicose, 2000; Neo et al., 2009; Neo, Vicentuan, et al., 2015). Additionally, Dumas et al. (2014) show that *T. maxima* can discriminate between the effluent of "favorable" and "unfavorable" settlement locations. Given the choice, larvae and juveniles more often than not settled in aquarium compartments adjacent to conspecifics, and in another trial, juveniles tended to move towards "healthy" reef effluent (i.e., live coral colony and CCA) rather than that of an "unhealthy" reef (i.e., cyanobacterial mat and sponge fragment).

Despite their close association with coral reefs, some species seem to actively avoid settling on live coral, perhaps due to allelopathic compounds or other competitive interactions. Comparing *T. squamosa* settlement preference on eight different substrate types, Calumpong et al. (2003) observed zero settlement on live coral but otherwise no significant difference between the other seven substrates. Likewise, giant clam abundance in Thailand was found to be inversely proportional to the percentage of live coral cover (Chantrapornsyl et al., 1996). Braley (1987b), however, reported the opposite pattern on the Great Barrier Reef, finding that *T. gigas* and *T. derasa* occurred preferentially among branching *Acropora* spp. and other hard corals; although, the author notes that groups of individuals were occasionally found on sand, coral rubble, and bare rock, generally close to beds of branching *Acropora* spp. Additionally, *T. maxima* and *T. crocea* can often be found boring into live bouldering corals (Klumpp & Griffiths, 1994; Su et al., 2014; Ramah et al., 2017), a behavior facilitated by the secretion of concentrated acid from the pedal mantle (Hill et al., 2018).

Thus, the association of giant clams with coral reefs may not be an obligate relationship with the corals themselves. Lucas et al. (1989) posit that it is likely a result of two conflicting environmental requirements for juvenile clams: 1) they must be exposed to high light levels to fuel the photosynthetic and nutritional requirements to support their rapid growth, and 2) they must also be sheltered and concealed from predators, as they remain quite vulnerable to predation for several years until they reach what is referred to in the literature as an 'escape size' (estimated to be around 15 cm to >20 cm for various species) (Heslinga et al., 1984; Calumpong, 1992; Gomez & Mingoa-Licuanan, 2006; reviewed in Waters, 2014). Coral reefs satisfy both conditions. However, this does not fully explain the distribution of species that are predominantly found in sand flats and seagrass beds (i.e., *H. hippopus*, *H. porcellanus*, and *T. squamosina*), where substrate rugosity is relatively low. It is possible that, for these species, high light exposure is the most important factor to drive rapid early growth, and their proximity to coral reefs is simply a matter of overlapping habitat requirements. On the other hand, it is also possible that they derive some other ecological benefit from their proximity to coral reefs or may rely on the cover of seagrass blades for concealment during early life stages. Unfortunately, the best available information is limited to that which is presented above, and therefore we cannot conclude one way or the other if larval settlement cues may vary between species in accordance with their observed habitat preferences.

Locomotion generally decreases soon after settlement (Jameson, 1976); although, there is evidence to suggest that giant clams are able to extend their pediveliger stage in cases where suitable substrates are unavailable (Soo & Todd, 2014). Juvenile clams also retain the ability to move short distances horizontally and vertically to continue searching for a habitat that will maximize their chance for survival (Soo & Todd, 2012; Dumas et al., 2014). Locomotive activity in juvenile *T. squamosa* tends to be greater at night and when they are grouped with conspecifics (Soo & Todd, 2012). This aligns with laboratory observations in which juveniles were found to move non-randomly towards conspecifics (Huang et al., 2007), as well as *in situ* reports indicating that "most undisturbed giant clams form dense aggregations of individuals" (Motoda, 1938; Salvat, 1972, as cited in Yamaguchi, 1977; McMichael, 1974; Braley, 1987b). Possible explanations for this clumping behavior include defense against predation, physical stabilization, and facilitation of reproduction (Huang et al., 2007). However, mobility of metamorphosed larvae and juveniles is quite limited, and aggregations of adults in the wild are most likely due to the grouped settlement of many larvae in the same location (R.D. Braley, pers. comm., September 25, 2019)

Giant clams play several important ecological roles in coral reef ecosystems (reviewed in Neo, Eckman, et al. (2015)). They provide a key food source for many predators and scavengers that consume their soft tissues, as well as opportunistic reef organisms that consume the materials expelled by giant clams (e.g., live zooxanthellae, feces, and gametes). Their shells and mantle cavities provide substratum and shelter for reef epibionts, including a wide array of burrowing and encrusting organisms (Vicentuan-Cabaitan et al., 2014). Furthermore, giant clams contribute to the topographical relief of coral reefs and produce significant quantities of calcium carbonate in their shells, which are eventually incorporated into the reef framework (Barker et al., 1988; Gilbert et al., 2006). Additionally, boring species such as *T. crocea* and *T. maxima* rank among the largest animals known to live fully ensconced within live bouldering corals and their abundance and size make them key contributors to reef bioerosion (Hamner & Jones, 1976). Giant clams also filter large volumes of seawater, drawing down and sequestering nutrients from the water column (Neo, Eckman, et al., 2015). With some estimates of water filtration as high as 28,000 L $ha^{-1}$ $h^{-1}$ (Pearson & Munro, 1991), giant clams play an important role in reducing the potential for eutrophication.

## 2.6 Population Genetics

Current literature indicates several consistent features of giant clam population genetics throughout their range. The first is significant genetic differentiation between giant clam populations of the central Pacific region, including Kiribati, Marshall Islands, Tuvalu, and Cook Islands, and the west Pacific region, including the Great Barrier Reef, Philippines, Solomon Islands, and Fiji (Benzie & Williams, 1995, 1997). The pattern is consistent across *T. gigas* and *T. maxima*, though there is some variability in the inferred level of connectivity between the Great Barrier Reef and Philippines in *T. derasa* (Macaranas et al., 1992). Interestingly, the patterns of genetic connectivity do not reflect oceanic currents as expected for a passively-dispersing organism like giant clams. Hence, Benzie and Williams (1997) hypothesize that "other mechanisms dominate present-day dispersal, or that [the observed patterns] reflect past connectivity which present-day dispersal along major surface currents has not altered over thousands of years."

All of the studies mentioned above that identify this particular biogeographic feature (i.e., genetic divergence between central Pacific and west Pacific giant clam populations) are based on allozyme variation, which relies on allelic differences in the encoded protein structure of functional genes. This approach was relatively common during the early stages of molecular population genetics, but follow-up studies based on mitochondrial or nuclear DNA sequencing often reveal discrepancies with allozyme data (reviewed in Hellberg et al., 2002). Some have argued that allozyme loci are subjected to stabilizing selection, and thus could be *underestimating* the magnitude of genetic subdivision. However, in the studies presented above, because the authors consistently identified significant differentiation between central Pacific and western Pacific giant clam populations, this detail in fact bolsters our confidence in the result.

Other studies describe a relatively consistent pattern of genetic structure within the Indo-Pacific region, often highlighting four or five genetic clusters distinguishing populations of the Red Sea, West Indian Ocean, East Indian Ocean, Indo-Malay Archipelago, and West Pacific. In every case, populations of *T. squamosa* and *T. maxima* in the Red Sea are found to be highly divergent from all other populations in their range (Nuryanto & Kochzius, 2009; Huelsken et al., 2013; Hui et al., 2016; Pappas et al., 2017; P. T. Lim et al., 2018). The same is true of West Indian Ocean populations, though to a slightly lesser extent (Hui et al., 2016; P. T. Lim et al., 2018). Additionally, there is a uniform pattern of differentiation between giant clam populations in the Indo-Malay Archipelago, in the western Pacific, and in the East Indian Ocean and Java Sea (Kochzius & Nuryanto, 2008; Nuryanto & Kochzius, 2009; Huelsken et al., 2013; Hui et al., 2016). This pattern is largely consistent across *T. squamosa*, *T. maxima*, and *T. crocea*, although some studies note variability between species with respect to certain genetic breaks identified in the Java Sea and in Cenderwasih Bay (Nuryanto & Kochzius, 2009; Huelsken et al., 2013).

On a smaller scale, giant clam populations within the northern and central Great Barrier Reef exhibit high genetic connectivity (Benzie & Williams, 1992, 1995, 1997). Evans and Jerry (2006) found tenuous evidence of isolation by distance in this region, suggesting that populations may be connected by the prevailing southward flow of the East Australian Current. In contrast, populations of *T. maxima* in the northern and southern Andaman Sea, Thailand were found to be genetically distinct despite relatively little geographic separation (Kittiwattanawong, 1997). The authors inferred that the lack of connectivity may be due to a divergent current pattern in the region. Kittiwattanawong et al. (2001) similarly found that *T. squamosa* in the Andaman Sea are genetically distinct from those in the Gulf of Thailand, again likely due to a physical or oceanographic barrier to dispersal. L. K. Lee et al. (2022) reported little genetic structure among populations of *T. squamosa* and *T. maxima* in the Perhentian Marine Park off the coast of peninsular Malaysia.

Overall, current knowledge on giant clam population genetics reaffirms the conclusion of Benzie and Williams (1997) that “neither high levels of anisotropic gene flow and therefore general exchange among Pacific [and other geographically distinct] populations, nor high levels of connectedness along present-day major surface currents, can be assumed.” Particularly for regions that have consistently been identified as genetically distinct (e.g., Red Sea, western Pacific, central Pacific, Indo-Malay Archipelago), it is evident that populations in one region cannot be reasonably relied upon to provide a significant influx of genetic diversity or immigration to sustain another.

# 3.0 Threats to Giant Clams

Giant clams face a number of natural and anthropogenic threats throughout their collective ranges. In the following section, we discuss each of these threats as they apply to giant clams broadly, within the framework of the five threat categories outlined in section 4(a)(1) of the ESA:

- the present or threatened destruction, modification, or curtailment of their habitat or range;
- overutilization for commercial, recreational, scientific, or educational purposes;
- disease or predation;

- the inadequacy of existing regulatory mechanisms; and
- other natural or manmade factors affecting their continued existence.

Specific information about the threats to each species individually is described as part of the species-specific risk assessments in **Section 4**.

## 3.1 Destruction, Modification or Curtailment of Habitat or Range

As discussed in **Section 2.5**, giant clams are often closely associated with coral reefs. They inhabit all types of shallow-water reef ecosystems (i.e., fringing, barrier, and atoll reefs), as well as various reef-adjacent habitats. However, it is important to re-emphasize that there is no conclusive evidence that giant clams directly rely on live, pristine corals for their survival. Certain species are habitat generalists (e.g., *T. squamosa*, *T. gigas*)—they are often observed among live corals but can also be found in other habitats that are not pristine coral reef (e.g., sand, rock, dead coral rubble, seagrass beds, macroalgae zones). Others are more specialized—*T. derasa* is most often found on offshore coral reefs, *T. mbalavuana* is found exclusively at depth on reef slopes, while *H. hippopus*, *H. porcellanus* and *T. squamosina* tend to prefer sandy areas, shallow lagoon flats and seagrass beds adjacent to coral reefs.

Available research on larval settlement preference offers some clues as to what may be driving the association with coral reefs. Several studies show that *T. squamosa* larvae prefer to settle on substrates of relatively high rugosity and are drawn to CCA, but actively avoid settling on live coral (Courtois de Vicose, 2000; Calumpong et al., 2003; Neo et al., 2009). Additionally, *T. maxima* has shown an ability to discriminate between “favorable” and “unfavorable” habitats, preferring to settle near the effluent of conspecifics and near the effluent of live coral and CCA, rather than cyanobacteria and sponges (Dumas et al., 2014). However, this information is limited to only two species, and there are no data for species that are predominantly found in sand flats and seagrass beds, where rugosity is especially low and settlement cues might differ.

Based on the known features of giant clam biology and larval development, Lucas et al. (1989) hypothesized that the proximity of giant clams to coral reefs is to some extent a result of two environmental requirements, which are maximized in shallow reef habitats: (1) high light conditions to support the photosynthetic nutrition that giant clams derive from their algal symbionts, and (2) substrate rugosity to provide cryptic settlement locations for vulnerable recruits and juveniles. While we cannot conclude that these factors are equally important to all species of giant clams, it is within the context of these two habitat requirements that we discuss the following threats to coral reef ecosystems and their potential impacts on giant clams.

### 3.1.1 Climate Change Impacts to Coral Reefs

This section addresses the major climate change-related threats to coral reefs, namely ocean warming and ocean acidification. Some of the information herein is summarized from our previous status review for 82 coral species (Brainard et al., 2011) and the associated final listing rule (79 FR 53851, September 10, 2014), both of which contain extensive discussion on climate change impacts on coral reefs. We also include updated information that has been published since the final listing rule in 2014. Note, while this section is focused on coral reefs as a key habitat for giant clams, the impacts of climate change on the clams themselves are discussed in **Section 3.5**.

### *Ocean Warming*

Reef-building corals typically occur in waters that range between 25°C–30°C and are highly sensitive to temperature excursions outside of this range (Brainard et al., 2011). Prolonged exposure to high-temperature anomalies can lead to coral bleaching, where the coral host expels its symbiotic zooxanthellae, leaving the tissue translucent and revealing its white skeleton underneath. As described in the final listing rule for corals (79 FR 53852, September 10, 2014), bleaching-associated mortality is quite variable and can depend on the duration and intensity of elevated temperatures, geographic location, bleaching history, species present, and other factors (Pandolfi et al., 2011; Putnam & Edmunds, 2011; van Hooidonk & Huber, 2012). Mild to moderate bleaching does not always lead to death; however, repeated and prolonged bleaching can cause widespread coral mortality on regional or global scales. Extreme summer temperature anomalies associated with strong El Niño events have led to three recognized global bleaching events in 1997-98, 2009-10, and 2014-17 (Hughes, Kerry, et al., 2017; Lough et al., 2018; Eakin et al., 2019). The 2014-17 event was the longest and most severe global bleaching event in recorded history. It affected every major coral reef region and led to the mortality of one third of the Great Barrier Reef in Australia (see Figure 4) (Couch et al., 2017; Hughes, Kerry, et al., 2017; Hughes, Kerry, et al., 2018). Many other regional-scale bleaching events since the 1980s have caused widespread coral mortality in reef communities throughout the Indo-Pacific (Brainard et al., 2011; Hughes, Anderson, et al., 2018).

While coral bleaching patterns can be complex, there is a general consensus that rising global ocean temperatures have led to more frequent and severe coral bleaching and mortality events during the last several decades (Hughes, Anderson, et al., 2018; Lough et al., 2018). Without drastic action to curb greenhouse gas emissions, this trend is projected to continue throughout this century (van Hooidonk et al., 2016). Additionally, several studies have shown that warming can significantly increase coral susceptibility to disease (Bruno et al., 2007; Sokolow, 2009; Brainard et al., 2011; Howells et al., 2020). The combination of these warming-related impacts has already caused dramatic declines in many coral species and changes to the composition and structure of coral reefs around the world (Brainard et al., 2011; Hughes, Barnes, et al., 2017; Hughes, Kerry, et al., 2018). During the major 2016 coral bleaching event on the Great Barrier Reef, for example, the fast-growing, structurally complex tabular and branching species suffered disproportionately (>75% mortality on heavily bleached reefs), shifting reef communities towards taxa with simpler morphological characteristics and slower growth rates (Hughes, Kerry, et al., 2018). Other studies similarly suggest that coral reef ecosystems, rather than disappear entirely as a result of warming, will likely persist, but with unpredictable changes to their community composition and ecological function (Pandolfi et al., 2011; Hughes et al., 2012).

Notably, several studies have identified much of the near-equatorial (~10°N-10°S) Indo-Pacific region from the central Indian Ocean to the central Pacific as an ocean warming "hot spot," where the rate of warming is higher than the global average or where future coral bleaching projections are most severe (Teneva et al., 2011; Lough, 2012; Meissner et al., 2012; van Hooidonk et al., 2013). This area encompasses the "Coral Triangle," which represents the center of giant clam abundance and diversity (Neo et al., 2017). Other areas of the Indo-Pacific have been identified as having lower than average warming (e.g., western Indian Ocean, Thailand, southern Great Barrier Reef, central French Polynesia, and the eastern equatorial Pacific). As such, the local and regional heterogeneity in ocean warming across the range of giant clams will likely result in highly variable impacts across spatial scales and among coral species.

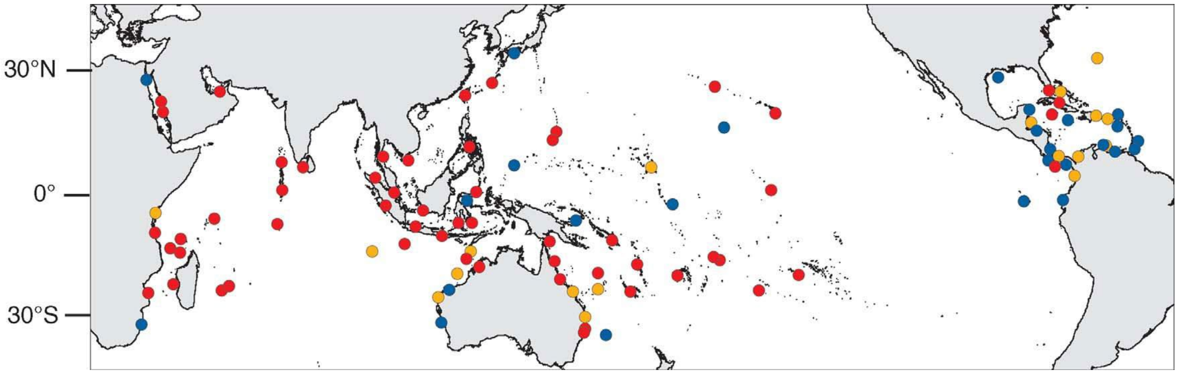


**Figure 4.** The global extent of mass bleaching of corals in 2015 and 2016. Symbols show 100 reef locations that were assessed: red circles, severe bleaching affecting >30% of corals; orange circles, moderate bleaching affecting <30% of corals; and blue circles, no substantial bleaching recorded (Source: Hughes, Anderson, et al., 2018. Reprinted with permission from AAAS).

### *Ocean Acidification*

Coral reefs are also facing increasing risk from ocean acidification, the process by which atmospheric carbon dioxide ($CO_2$) is absorbed into the surface ocean, resulting in reduced seawater pH and reduced availability of carbonate ions. Due to anthropogenic $CO_2$ emissions, average surface ocean pH (total scale, pHt) has already decreased by more than 0.1 pHt units below the pre-industrial average of 8.17, and is expected to fall up to an additional 0.42 pHt units by 2100 under IPCC's worst-case emissions scenario (Pörtner et al., 2014).

Such reductions in ocean pH could lead to drastic changes to the net calcification balance in many coral reef ecosystems. Numerous laboratory and mesocosm experiments have demonstrated a correlation between lower pH (or elevated partial pressure of $CO_2$, $pCO_2$) and decreased coral calcification rates (Anthony et al., 2008; Ries et al., 2009; Anthony et al., 2011; Gazeau et al., 2013; Albright et al., 2018). Brainard et al. (2011) provide a table summarizing the existing literature on the topic (Table 3.2.2 of the report), and for every species studied, the net calcification rate either declines, or in very few, there is no significant effect. In a pair of controlled mesocosm experiments, net community calcification of a small enclosed coral reef was found to increase under enhanced alkalinity and decrease after the addition of $CO_2$ (Albright et al., 2016; Albright et al., 2018), indicating that current levels of acidification are already impairing ecosystem-level calcification and will likely exacerbate this effect in the future. Coupled with dwindling coral cover due to warming-associated bleaching and mortality, continued acidification could transition many reef systems from net overall accretion to net erosion within this century (Eyre et al., 2018; Cornwall et al., 2021).

Others anticipate that ocean acidification will also weaken the structural integrity of coral reefs, both by promoting the efficiency of bioeroding organisms and by reducing reef cementation (i.e., secondary processes of carbonate precipitation that bind the reef framework). Coral reefs of the eastern Pacific have been studied as an illustration of these effects, as they occur in upwelling zones that cause naturally low pH conditions. Observations from these reefs reveal some of the highest rates of bioerosion documented globally, as well as poorly cemented, fragile, and unstable reef frameworks (Glynn, 1988; Eakin, 1996, 2001; Manzello et al., 2008). Crustose coralline algae (CCA) contribute significantly to reef cementation by consolidating loose rubble and sealing porous dead coral skeletons (Adey, 1998; Littler & Littler, 2013). However, there is major concern that CCA may be among the most sensitive taxa to declines in seawater pH, because they build their skeletons with magnesium-rich calcite, a highly soluble form of carbonate (Andersson et al., 2008). Recent studies suggest that early life stages of CCA may suffer reduced growth under reduced pH (Kuffner et al., 2007; Ordoñez et al., 2019), and that daily pH variability representative of natural conditions may exacerbate documented growth declines (Johnson et al., 2019).

### *Implications for Giant Clams*

In our previous status review for 82 species of corals, Brainard et al. (2011) concluded that “the combined direct and indirect effects of rising temperature, including increased incidence of disease, and ocean acidification […] are likely to represent the greatest risks of extinction to all or most of the candidate coral species over the next century.” They assessed the threat of continued ocean warming to be “highly certain” and graded the threat as “high” for most regions where the candidate corals are known to occur. Based on this assessment and the growing body of literature that has since become available regarding the impacts of climate change on coral reefs, we find it likely that live coral cover in general will continue to decline due to more frequent and severe bleaching events, and that ecosystem-scale calcification rates will decline as a result. Critically for giant clams, the negative impacts of warming are most pronounced in the fast-growing branching and tabular coral species, which are the primary contributors to the three-dimensional complexity of reef habitats. Thus, continued loss of live coral cover and of these species in particular will likely severely reduce the rugosity of future reef ecosystems. There is also evidence that ocean acidification will further inhibit calcification rates of living corals and weaken the structural integrity of the reef framework; although, the magnitude of these effects is not clear. As with ocean warming, the primary implication of these effects for giant clams will be reduced habitat rugosity.

Nevertheless, we must consider two important layers of uncertainty associated with these predictions, and especially their potential impacts on giant clam habitat. First, with respect to ocean acidification, carbonate chemistry is notoriously difficult to model precisely in open systems, as it relies on many physical and biological factors, including seawater temperature, proximity to land-based runoff and $CO_2$ seeps, proximity to sources of oceanic $CO_2$, salinity, nutrients, as well as ecosystem-level photosynthesis and respiration rates. The last factor, in particular, means that in many cases, daily fluctuations in pH or carbonate chemistry can significantly outweigh projected long-term changes to the average (Manzello et al., 2012; Johnson et al., 2019). Brainard et al. (2011) acknowledge this uncertainty in their report, concluding that “there is still much that we need to know to understand how [the threat of ocean acidification] will impact the particular species under consideration and various other important components of the reef ecosystem.” Secondly, as mentioned above, there is very little research establishing the degree to which giant clams rely on coral reef rugosity and thus might be impacted by any reduction thereof. The few larval choice experiments to date suggest that *T. squamosa* prefers rough to smooth surfaces and that *T. squamosa* and *T. maxima* are both attracted to CCA. However, most giant clam species can be found in an array of habitat types, and some even seem to prefer areas of low rugosity, such as sand flats and seagrass beds (e.g., *H. hippopus*, *H. porcellanus*, and *T. squamosina*). No studies have quantified how or if giant clams might be affected under varying levels of substrate complexity.

Without more information on the direct association between substrate rugosity and juvenile giant clam survival, it is difficult to estimate with any confidence the degree to which reef rugosity must decline to threaten the survival of giant clams. Likewise, given the lingering uncertainty in the dynamics and effects of ocean acidification, it is not possible to estimate a timespan over which such a risk to giant clams can be expected. Thus, while it is likely that continued ocean warming and acidification will drastically alter coral reef communities and reduce the rugosity of many reef habitats, the potential effect on the quality or suitability of giant clam habitat cannot be confidently assessed nor generalized across regions and species. However, if giant clams are sensitive to reductions in net ecosystem calcification and reef rugosity, the projected climate change-related impacts to coral reefs would likely pose a major threat to giant clams within the foreseeable future, and particularly those species that are known to reside preferentially within coral reef environments. We would expect decreased larval recruitment and juvenile survival across broad portions of their range. These early life stages are already known to suffer exceptionally high mortality rates naturally, and any further reduction in productivity would greatly threaten the viability of remaining giant clam populations.

### 3.1.2 Coastal Development

The physical degradation of nearshore habitats due to coastal development poses an additional threat to giant clams throughout much of their range. There is direct evidence of this impact in the Red Sea, where Roa-Quiaoit (2005) notes intense modification to the Jordanian coastline over “four decades of rampant development of ports, industrial and tourism areas, as well as extreme events such as oil spills.” Surveys of giant clam density in the area revealed an inverse relationship between the density of both *T. squamosa* and *T. maxima* and metrics of human impact and coastal use. The author goes on to argue that the observed 12-fold reduction of giant clam density in Jordan over three decades is in major part due to this intense habitat modification. Likewise, in the Egyptian Red Sea, Mekawy and Madkour (2012) report that large *T. maxima* specimens are more prevalent at sites that are further from human activity and development. In this case, it is unclear whether this is a function of coastal development, harvesting pressure, or a combination of both.

Similar examples of anthropogenic impacts on the coastal environment have also been documented in many areas of the Indo-Pacific region, although this is often discussed in relation to the health of coral reef ecosystems. In Singapore, approximately 60% of coral reef area has been lost during the 20th century due to land reclamation and associated sedimentation (Chou, 2006; Guest et al., 2008). On three specific Singapore reefs—Tanjong Teritip, Pulau Seringat, and Terumbu Bayan—Neo and Todd (2012a) note that giant clams were once found, but the areas have since been reclaimed (covered over) in their entirety. In addition, more than 20% of coral reefs in Indonesia, 35% of reefs in Malaysia, 25% of reefs in Papua New Guinea, and 60%

of reefs in the Philippines are threatened by the impacts of coastal development, including runoff from construction and waste from coastal communities (Burke et al., 2012). It is likely that the intense coastal pressure in these areas is causing a similar impact on the giant clam populations as has been reported in the Red Sea.

Sedimentation associated with the construction and maintenance of shipping ports and land-based runoff can reduce the amount of suitable substratum available for larval settlement. There is extensive evidence for such an effect on corals—increased sediment load has been shown to deter larval recruitment (Babcock & Davies, 1991), reduce settlement success and survival (Hodgson, 1990; Babcock & Smith, 2002), and decrease the effectiveness of CCA to induce settlement (Ricardo et al., 2017). We could not find any research directly investigating this effect in giant clams; however, similarities in the biology and behavior of giant clam larvae would suggest that comparable results can reasonably be expected. Like coral larvae, giant clam larvae prefer rough settlement surfaces and are likely deterred by unconsolidated, fine-grained sediment typical of anthropogenic sedimentation. Moreover, CCA provide a similarly important settlement cue for giant clams, and a reduction in effectiveness would likely decrease larval recruitment and settlement success.

Importantly, unlike habitat degradation due to climate change, coastal development poses a more localized threat to giant clam populations in specific regions. The impact is considerably greater, for example, in the areas mentioned above, near major population centers of the Red Sea and Indo-Pacific. In addition to undergoing intense coastal development activities over the past several decades, many of these areas are not well regulated with respect to coastal runoff and often do not prioritize sustainable management of the coastal environment (e.g., Gladstone et al., 1999; O. A. Lee, 2010). In contrast, the Great Barrier Reef in Australia and island nations of the central and western Pacific, two other important areas of giant clam distribution, likely do not suffer the same effects of coastal development. Australia strictly enforces an integrated management plan to protect the Great Barrier Reef from the effects of coastal land use change via numerous national and state regulations, and the relatively small populations of most Pacific island nations minimize the impact of coastal development on surrounding waters.

### 3.1.3 Tanmen Destructive Shell Harvesting

Despite a relatively small geographic scope, giant clam shell harvesting operations in the South China Sea have caused severe habitat destruction. In the last decade, the small fishing village of Tanmen in China's Hainan province became a regional epicenter for giant clam shell handicraft and trade (Hongzhou, 2016; Larson, 2016; Lyons et al., 2018). From 2012 to 2015, the number of retailers of giant clam shell handicrafts increased from 15 to more than 460, the number of shell carving workshops increased from 12 to more than 100, and by the end of this period, it was estimated that this industry supported the livelihood of nearly 100,000 Tanmen residents (Hongzhou, 2016; Bale, 2017; Wildlife Justice Commission, 2021).

As the industry grew, many Tanmen fishermen increasingly abandoned the traditional fishing industry and shifted focus to giant clam shells as their primary livelihood. With local stocks of giant clams having been depleted by a long history of overharvesting (see **Section 3.2**), many fleets resorted to destructive methods of digging out large portions of coral reef using their boat propellers to access the shells of long-dead clams that had been buried under the reef substrate (Wildlife Justice Commission, 2021). As reported by V. R. Lee (2016), harvesting boats are anchored with a long rope or chain against which the propeller holds tension as it carves an arc-shaped scar in the reef (see also Wingfield-Hayes, 2015). The majority of this activity has occurred in the South China Sea, and an analysis of satellite imagery revealed extensive damage in the Spratly Islands and Paracels, with an estimated 160 $km^2$ of coral reef in these areas completely destroyed by the combination of clam dredging and island-building activities (McManus, 2017).

In response to international pressures and following a 2016 arbitral tribunal ruling that China was aware of and responsible for "severe harm to the coral reef environment" in the South China Sea due in part to these activities (Permanent Court of Arbitration, 2016), steps were taken to crack down on destructive clam shell harvesting operations. President Xi Jinping began to enforce anti-corruption measures aimed at undermining demand for the expensive jewelry and statues carved from giant clam shells (Bale, 2017), and in January 2017 the Hainan Province People's Congress passed new regulations that effectively banned the commercial trade of all 10 giant clam species in Hainan (Wildlife Justice Commission, 2021). However, while giant clam shell harvesting operations were found to decline significantly between 2016 and 2018, the Wildlife Justice Commission (2021) has documented several lines of evidence suggesting that "illegal giant clam shell trade persists in China in a covert manner with one clear supply area" in Hainan Province, and that a new influx of clam harvesting boats have returned since 2018. Thus, while the extensive damage to the habitat in this region would likely take several decades or more to undo if the ecosystems were allowed to recover, the ongoing threat of illegal harvesting is likely to prevent any substantial recovery in the foreseeable future.

In the context of this status review, this threat of habitat loss is relevant to the species that are known to occur in this region and that are typically found in reef flat environments where the harvesting operations primarily occur. This includes *T. gigas*, *T. squamosa*, *H. hippopus*, and most critically *H. porcellanus*, which has a highly restricted range centered in the Sulawesi region of Indonesia but that extends northward into the Philippines and portions of the South China Sea (S. Wells, 1997; bin Othman et al., 2010; Neo et al., 2017).

However, the threat of overharvest associated with these activities is primarily relevant to *T. gigas*, as the larger shells are generally preferred for carvings and handicrafts (Lyons et al., 2018). This threat is addressed in **Section 3.2** below.

## 3.2 Overutilization for Commercial, Recreational, Scientific, or Educational Purposes

Subsistence fisheries, commercial harvest, international trade, and illegal poaching have contributed to extensive harvest, stock depletions, and local extirpations of giant clams throughout much of their collective ranges. Giant clams are easily collected given their typically shallow distribution, conspicuous appearance, and immobility. Additionally, as early as the 1970s, advancements in snorkeling and diving equipment led to the regular harvest of deeper, previously inaccessible stocks (Yamaguchi, 1977). Consequently, almost all tridacnine species have been exploited for meat as food, fish bait, or animal feed; for their shells which are sold to the curio trade or used for tools; and as live specimens in the aquarium trade (Sant, 1995; Kinch

& Teitelbaum, 2010; Neo et al., 2017). In addition to their easy collection, their late sexual maturity (Munro, 1989) and the density-dependence of their broadcast spawning reproductive strategy combine to increase giant clams' vulnerability to stock depletion. Intense fishing pressure can cause population densities to fall below undetermined thresholds required for successful reproduction and recruitment (Lucas, 1988; Munro, 1993a), which may hinder the natural recovery of stocks and cause populations to collapse (Neo & Todd, 2013). Declines and local extirpations of giant clam populations were observed in many countries as early as the 1980s (Copland & Lucas, 1988). Overutilization is likely the most significant threat to giant clams as a group, both historically and currently. Below we discuss three main categories that fall under the threat of overutilization: subsistence fisheries, commercial harvest and illegal poaching, and scientific research and education.

### 3.2.1 Subsistence Fisheries

Giant clams have long been, and continue to be, an important component of traditional livelihoods and culture throughout their geographic range (Craig et al., 2011). As described by Lindsay et al. (2004), "there are few locations within the Pacific where tridacnids are not gathered on a daily basis and found in local markets" (Munro, 1993a). Archaeological evidence from shell middens (piles of discarded shells), which can be found across the Indo-Pacific from as far back as 2000 years ago (Swadling, 1977), as well as anecdotal accounts and local fishing practices all point to the importance of giant clam in Indo-Pacific diets (Neo & Loh, 2014). The shells of giant clams are also frequently carved for use as tools, containers, and ornaments (Copland & Lucas, 1988; Lucas, 1994).

The relative importance of the different uses for giant clams varies geographically. In the Philippines, for example, giant clams are primarily harvested for their shells to be used as soap dishes, salad bowls, and ashtrays, whereas the meat is often considered a secondary food item (Gomez & Alcala, 1988). In Kiribati, giant clams are heavily exploited for food and may be cultured as pets (Taniera, 1988; Sant, 1995). The meat of giant clams was commonly consumed in Fijian villages until stock depletion led to low supply; clam shells have also had several subsistence uses including terracing Fijian 'bures' or houses, as ornaments and ash trays, serving dishes for pigs and chickens, for use in flower gardens, and to make fish fences (Vuki et al., 1991). In Indonesia, giant clam meat and shells have been used as a local food source and traditionally for a variety of purposes (e.g., ornaments, washbasins, etc.) (Pasaribu, 1988). Similarly in French Polynesia, giant clams have historically been harvested for their meat as well as for their shells which had uses as receptacles in religious ceremonies (Babadzan, 1992) and as adze blades for woodworking on low-elevation atolls where stones suitable for this use were otherwise unavailable (Radclyffe, 2015). Moreover, in Mauritius and the Dongonab area of Sudan, some local communities believe giant clams have medicinal properties and use them for such purposes (Shackour, 2004; Ramah et al., 2018).

Small clams are typically collected by reef gleaning (hand-collection on shallow reef flats) and opportunistically during other fishing activities, while large clams are usually collected by free-diving (Hviding, 1993; Sant, 1995) or with the use of hookah dive gear in deeper waters (Kinch & Teitelbaum, 2010). Where shells have little value or are exceedingly large, the clam's flesh (usually the adductor muscle) is removed from the shell and brought to the surface (Gomez & Alcala, 1988; Govan et al., 1988). Where shells have value, sticks and crowbars may be used to pry clams from the reef (Kinch, 2003). Clams located in deeper water may be hauled to the surface using ropes, winches, or chains (Lewis et al., 1988). Clams may be consumed on the boat, sea-ranched (or "re-planted" back in the sea) near the fisherman's house to be eaten on special occasions (Salamanca & Pajaro, 1996), or sold in the local market. In some places, clams are kept in 'gardens' close by as a reserve food supply (e.g., following cyclones) or for important traditional feasts (Lewis et al., 1988; Kinch, 2003). While subsistence gathering is typically conducted on an opportunistic basis, in places with high densities of giant clams, there may be an organized fishery targeting them. This is discussed further in **Section 3.2.2** in the context of commercial harvest.

Many historical subsistence fisheries were likely unsustainable, particularly in areas with large human populations (Lucas, 1994; Van Wynsberge et al., 2016). Quantitative data on past or present subsistence fisheries for giant clams are sparse, but it is clear from anecdotal reports and written history that subsistence consumption, even on its own, can severely deplete giant clam populations over time (Lewis et al., 1988; Lucas, 1994). In Kiribati, for instance, historical subsistence harvest placed such pressure on giant clam populations that a commercial fishery was deemed not viable (Munro, 1988a). As of the early 1990s, subsistence fisheries in the Cook Islands, Tokelau, and Tuvalu, were similarly deemed unsustainable (Lucas, 1994). Subsistence fisheries in Fiji depleted stocks of *T. derasa* and *H. hippopus* over generations (Lewis et al., 1988; Seeto et al., 2012), and the combination of subsistence fishing, commercial fishing, and poaching led to the local extinction of *T. gigas* in Fijian waters as of the early 1980s (Dawson, 1986). Subsistence fishing in the Cocos (Keeling) Islands has been deemed directly responsible for the decline of giant clam stocks (Neo et al., 2017), and similar depletions following long-term subsistence fishing have been reported in Cambodia, the Solomon Islands, Nauru, American Samoa, and the Cook Islands (Neo et al., 2017). Thus, poorly regulated or unregulated subsistence harvest has been a significant historical threat that likely continues to pose a major threat to giant clams globally.

Cultural preferences for certain giant clam species based on taste or texture, ease of collection, or workability for carving can vary geographically. These differences and overall species-specific threat assessments are addressed in more detail in **Section 4**.

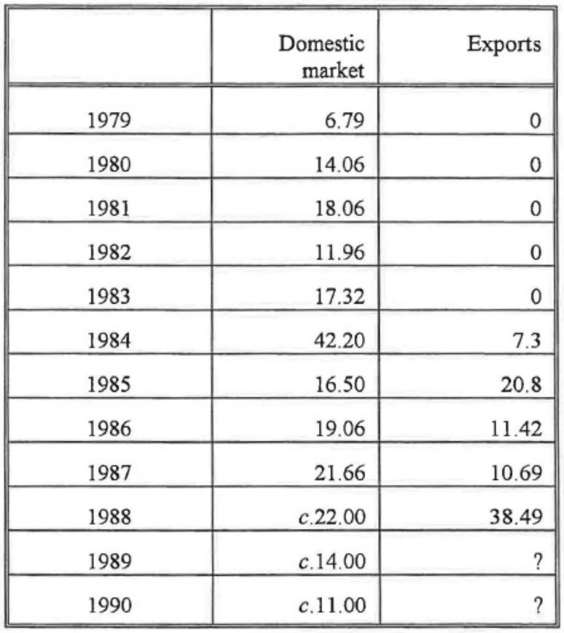
### 3.2.2 Commercial Harvest and Illegal Poaching

In addition to subsistence fisheries, historical overutilization of giant clams is also attributable to domestic commercial harvest, international trade in giant clam meat and shell-craft (e.g., carvings, ornaments, etc.), and extensive illegal harvest throughout the Indo-Pacific (Neo et al., 2017). In many areas with high densities of giant clams, commercial fisheries developed first for local consumption, and then for export. Although commercial exploitation of wild giant clams has now been banned in many countries in response to dwindling populations, large-scale poaching still poses a threat to remaining giant clam stocks (Neo et al., 2017; Neo, 2020). For example, in a recent report, the Wildlife Justice Commission (2021) found that Philippine authorities had made at least 13 seizures of giant clam shells since 2019, totaling over 120 million kilograms of contraband. Additionally, exploitation of giant clams has increasingly expanded into the aquarium trade, which has grown substantially over the last few decades (Wabnitz et al., 2003). While the traded clams are often of hatchery origin, wild specimens are still regularly collected and sold in many locations (Mies, Dor, et al., 2017).

Below, we discuss four main categories comprising the commercial harvest of giant clams: Domestic Markets (Meat and Shells), International Trade of Giant Clam Meat, International Trade of Giant Clam Shells and Shell-craft, and International Trade of Live Giant Clams for Aquaria. Within the context of these categories, we also address the historical and ongoing threat of illegal poaching to remaining giant clam populations.

### *Domestic Markets (Meat and Shells)*

As mentioned above, in areas where giant clams were abundant, commercial fisheries often developed alongside subsistence harvesting to supply the local demand for giant clam meat and shells. In Fiji, *T. maxima*, *T. squamosa*, and *T. derasa* were all harvested by small-scale commercial operations and sold in 11 municipal markets or other direct sales outlets (Lewis et al., 1988). From 1979-1987, the annual sale of giant clam meat in the domestic market ranged between 6 and 42 tons (Adams, 1988; Lewis et al., 1988; S. Wells, 1997; see Figure 5). With respect to both *T. squamosa* and *T. derasa*, Lewis et al. (1988) reported that commercial harvest had driven once abundant populations to low densities, particularly near major urban centers.



| | Domestic market | Exports |
|---|---|---|
| 1979 | 6.79 | 0 |
| 1980 | 14.06 | 0 |
| 1981 | 18.06 | 0 |
| 1982 | 11.96 | 0 |
| 1983 | 17.32 | 0 |
| 1984 | 42.20 | 7.3 |
| 1985 | 16.50 | 20.8 |
| 1986 | 19.06 | 11.42 |
| 1987 | 21.66 | 10.69 |
| 1988 | *c.*22.00 | 38.49 |
| 1989 | *c.*14.00 | ? |
| 1990 | *c.*11.00 | ? |

**Figure 5.** Domestic market and exports of giant clam meat in Fiji. Data represent mainly the weight of mantle and adductor muscle in tonnes, although in some cases (not specified) shell weight may be included. Subsistence consumption and poaching are not included. Data until 1987 from Lewis et al. (1988); data 1988-90 from Tisdell (1992), extrapolated from Figure 13.1. Export data were not available for the years 1989 and 1990. (Figure source: S. Wells, 1997).

Furthermore, the excerpt below from S. Wells (1997) summarizes a number of other domestic markets for giant clam meat throughout the Indo-Pacific:

> *"Local markets exist in a number of other Pacific countries, but there is little information beyond some data on prices which seem to be variable. In American Samoa, giant clam meat retails at about US$8/kg (Killelea-Almonte, 1992). In the Solomon Islands, clam meat (amounting to about 1 tonne a year) is occasionally sold in local markets for about*

> *US$1-2/kg, and there is some demand from restaurants and hotels in Honiara (Hambrey, 1991). There are local markets in the Marshall Islands (T. maxima, T. squamosa, H. hippopus) (Smith, 1992b), Niue (Dalzell et al., 1993), and [the Federated States of Micronesia] where, in 1990, 3.66 tonnes were sold in the main markets of Chuuk, at a total value of US$8900 (about US$2.2/kg) (Smith, 1992a). In Vanuatu, the main source of clam meat for the public market is north Efate (Bell and Amos, 1993). Clam meat is popular in Tonga. At the time of the study by Tacconi and Tisdell (1992a), data collected over a 10-week period suggested that annual landings for the domestic market might be 639-1,346kg, but it was thought that this might be an underestimate. Bell et al. (1994) estimate a total annual harvest of 52.8 tonnes in Tongatapu. There is a local market in Western Samoa but this is sporadic due to supply; clams of 40cm shell length sell for 20-25 WS$ in the Apia fish market (Tacconi and Tisdell, 1992a; Wright in litt. to S. Wells, 1994).*
>
> *In Indonesia, clam meat retailed for about US$1.5/kg (Panggabean, 1987). In Jepara, it is now normally sold dried; the lack of fresh meat may be due to local over-exploitation of stocks, so that meat has to come from more distant fishing grounds, possibly as a by-product of the shell trade for the tile industry (see section 3.2.2) (Firdausy and Tisdell, 1992). In Myanmar, clam meat is marketed fresh for local consumption (Munro, 1989).”*

Additional reports indicate that domestic markets have continued in many of these localities into at least the early 2000s. In 1998-1999, nearly six metric tonnes of giant clam products were sold at a single market in Samoa (Skelton et al., 2000). Giant clam meat was still reported to be sold openly at markets in Malaysia as of 2003 (Shau-Hwai & Yasin, 2003). Until bag limits were established in 2009, the declared commercial catch of giant clams in New Caledonia varied between 1.5 and 9 tonnes per year. This included *T. derasa*, *T. squamosa*, and *H. hippopus*, and the authors indicate that it is often the adductor muscle that is sold in stalls of local markets. In the decade since the bag limits were put in place, commercial catch has fallen below 2 tons per year (Purcell et al., 2020). Kinch and Teitelbaum (2010) report that a high demand for giant clams to supply the local market in Tonga “has resulted in the over-exploitation of giant clam stocks in some areas.” In Papua New Guinea, Kinch (2003, 2020) attributes sparse populations of giant clams to commercial harvest, particularly that of Brooker Islanders. From January to September 1999, the author recorded the total sales of giant clam adductor muscle from Brooker Islanders to a local fishing company, which included 551 kg (or 1,970 clams) of specimens under 400 g and 146 kg (or 170 clams) greater than 400 g. Notably, nearly one-third of the *T. gigas* individuals included in these sales were not full-grown adults, which likely had an effect on the future productivity of those populations. Similarly, harvesting of giant clams for sale and subsistence use in Vanuatu has led to severely reduced populations that are “now considered close to collapse in many locations despite the presence of suitable habitats for juveniles and adults” (Dumas et al., 2012).

Domestic markets for giant clam shells are often related to the tourism industry. In the Andaman and Nicobar Islands of India, Nandan et al. (2016) report that giant clams, including *T. squamosa* and *H. hippopus*, are fished for the tourism-based ornamental shell industry. Additionally, in Thailand, giant clams shells are usually first sold to local traders in Phuket, and then sold to tourists as ornamental shells or various shell crafts (e.g., ashtrays, soap trays, lamps) (Chantrapornsyl et al., 1996). Shells have also been a popular souvenir for tourists visiting the

Philippines and Indonesia (Tisdell, 1994). At the Pangandarin and Pasir Putah beach resorts in Java, Indonesia, as many as 39 and 35 giant clam shells, respectively, were available for sale in 2013, despite a prohibition on the harvest and sale of giant clams (except under "exceptional circumstances") under Indonesian law since 1987 (Nijman et al., 2015).

Prior to this prohibition, a major industry based on the use of giant clam shells for the production of floor tiles (a.k.a, 'teraso' tiles) led to the extensive harvest of giant clams in Indonesian waters. While much of the shell material was dead shells of *T. derasa* and *T. gigas* buried in reef flats, living specimens were known to be taken when found (Lucas, 1994). As described by Lucas (1994), there were tile production centers at Jakarta, Semarang, Bali, Manado, and likely Surabaya in the early 1980s, and clam shell trade routes had developed throughout the Indonesian islands to supply the industry. The best estimates of giant clam shell import to the Semarang tile production center from the nearby Karimun Jawa Islands varied between about 20 and 200 t per month over the period 1978-1983 (Brown & Muskanofola, 1985). At the Jakarta production center, the clam shell trade was estimated to reach at least 600 t per month in 1982 (Usher, 1984 cited in Lucas, 1994). This industry is no longer active in Indonesia as a result of the 1987 prohibition; however, it is likely that such intense demand, particularly for the largest specimens, severely depleted giant clam populations in Indonesian waters and limited the potential for recovery. Moreover, despite regulatory protection, all species of giant clams remain heavily exploited in Indonesia for their meat and shells, and some for the live aquarium trade (Neo et al., 2017). As a result of this overexploitation, the larger giant clam species are now thought to occur in only a few locations archipelago-wide (Hernawan, 2010).

### ***International Trade of Giant Clam Meat & Taiwanese Poaching***

While giant clam meat is consumed throughout the Indo-Pacific region, Taiwan has consistently had the largest market and demand for giant clams. Some of the earliest references indicate that giant clams around Taiwan were depleted many decades ago (Pearson, 1977; Tisdell & Chen, 1994). As local stocks were rapidly exhausted, Taiwanese vessels began to range farther from their home ports, and from the 1960s to the mid-1980s, a surge of Taiwanese fishing vessels began illegally entering the waters of other Pacific nations in search of giant clam meat, particularly from the larger species, *T. gigas* and *T. derasa* (Munro, 1993a; Kinch & Teitelbaum, 2010). Occasionally, these vessels operated under agreements with local communities in exchange for resources (Adams, 1988), but in the vast majority of cases, giant clams were harvested illegally and to an unsustainable degree (Lucas, 1994; Kinch, 2002). The clam poachers progressively worked their way through the Pacific, typically concentrating their efforts on uninhabited islands and reefs where giant clam stocks had been virtually untouched and where local surveillance was limited. Reports of Taiwanese poaching include areas of the Philippines, Micronesia, Indonesia, Papua New Guinea, the Solomon Islands, Australia (the Great Barrier Reef), Palau, Fiji, Kiribati, and the Marshall Islands (Dawson & Philipson, 1989; Sant, 1995).

Dawson (1986) described the typical Taiwanese giant clam harvesting vessel to be "a four to seventy tonne wooden junk, retired because of age from either long-lining or trawling." The vessel could carry a crew of 20, of whom all but a few would engage in diving and harvesting operations. Dawson (1986) estimated that an average giant clamming vessel would have been able to harvest one metric ton of adductor muscle per day and carry a full load of 10 metric tons, or approximately 11,000 giant clams.

Data on the landings of giant clam meat in Taiwan are generally unavailable due both to their illegal nature and because in the records, landings were combined with the meat of other marine mollusks and collectively referred to as ‘ganbei’ or ‘compoy’ (Lucas, 1994; Tisdell & Chen, 1994). Tisdell and Chen (1994) report that imports of ganbei ranged from 9 tons in 1977 to 621 tons in 1988. Other estimates of giant clam adductor muscle landings in the 1960s and 1970s range between 100 and 400 tons per year (Carlton, 1984; Dawson & Philipson, 1989). Dawson and Philipson (1989) estimated that during the peak of the Taiwanese fishery for giant clams, harvest likely did not exceed 100 tons of adductor muscle per year, though Munro (1989) regarded this to be an underestimate. Accounting for the harvesting of the smaller species, *T. derasa* and *H. hippopus*, which have an adductor muscle about one third the weight of *T. gigas*, those landings correspond to 300,000 to 450,000 clams per year. According to Dawson (1986), “it seems certain […] that the total illegal harvest of giant clams over the twenty-odd years that such activities have occurred in the region can safely be measured in the millions.”

Several other reports highlight the devastating impact of these activities on giant clam populations in certain areas of the Pacific. At Helen Reef in Palau, for example, a 1972 survey conducted by NMFS revealed a nearly untouched giant clam community with large populations of *T. gigas*, *T. derasa*, *H. hippopus*, and *T. maxima* (Hester & Jones, 1974). Conservative abundance estimates suggested approximately 49,800 *T. gigas*, 32,800 *T. derasa*, and 44,600 *H. hippopus*. Following repeated evidence of poaching by foreign fishing vessels, a second survey was conducted in 1975 revealing that systematic harvesting of the three largest species (*T. gigas*, *T. derasa*, and *H. hippopus*) had reduced populations to a fraction of their previous abundance (Bryan & McConnell, 1975). The remaining stock of *T. gigas* was estimated to be 8,600 individuals (17% of 1972 estimate), and the *T. derasa* population was estimated to be 12,900 individuals (39% of 1972 estimate). Moreover, the relative proportion of dead to living clams were 98.1 and 96.6%, respectively. While *H. hippopus* did not appear to suffer the same severe population declines, there was evidence that it was also heavily fished, as 95.4% of observed individuals were dead (Bryan & McConnell, 1975). A second follow-up survey was conducted in 1976 at the request of the Palau Marine Resources Office in response to continued reports of unauthorized fishing vessels in the vicinity of Helen Reef (Hirschberger, 1980). Because fewer transects were surveyed, comparison with previous results should be interpreted cautiously; however, rough estimates suggest that populations remained stable and may have even recovered to some extent (*T. gigas*: 4,700 – 22,900; *T. derasa*: 8,100 – 40,300; *H. hippopus*: 89,100 – 345,900; 80% confidence intervals) (Hirschberger, 1980).

As mentioned above, a similar scenario occurred in Marovo Lagoon of the Solomon Islands, where intensive Taiwanese harvesting of over 1,300 *T. gigas* specimens in late 1983 “seriously depleted largely untouched stocks” (Govan, 1989 cited in Hviding, 1993). In interviews, Solomon Islanders expressed their certainty that other instances of poaching by Taiwanese vessels had gone undetected and caused similar depletion in other areas (Hviding, 1993). On the Great Barrier Reef, 22 Taiwanese fishing vessels were apprehended between 1969 and 1976 while illegally poaching giant clams. Across all 22 vessels, a total of 72 tons of clam meat was confiscated, equating to over 500,000 clams (Pearson, 1977). Those ships were thought to represent only 10% of the fleet operating in the Great Barrier Reef at that time (Pearson, 1977).

Poaching by long-range Taiwanese vessels peaked in the mid-1970s and gradually declined during the 1980s as the extension of exclusive economic zones, improved surveillance of reef areas, boat seizures, and depleted stocks made the fishery less profitable (Lucas, 1994). In addition, growing pressure from many Indo-Pacific nations forced the Taiwanese government to take stricter actions against giant clam harvesters (Dawson, 1986). The last five 'compoy' (i.e., clam and other shellfish) fishing licenses were rescinded by the Taiwanese government in 1982, mainly due to pressure from the Australian government. Beginning in 1986, the Taiwanese government began rejecting all requests for approval of Taiwanese involvement in any clam fishing activities, regardless of whether foreign agreement or license documents were provided. There is evidence, however, that some poaching activities continued in remote locations. From 1982 to 1987, at least four Taiwanese vessels were apprehended on the outlying reefs of the Solomon Islands, in each case carrying meat from tens of thousands of giant clams (Govan et al., 1988). The authors note that the small size of the adductor muscles recovered indicates that large clams had likely already been harvested from the reef at an earlier date.

Even as Taiwanese poaching operations declined, the demand for giant clam meat in Taiwan persisted, incentivizing the development of legal commercial fisheries for export throughout the Indo-Pacific (Lewis et al., 1988; Basker, 1991; Lucas, 1994). It was estimated that imports of adductor muscle to Taiwan from these newly formed fisheries totaled approximately 30-40 tons in 1987 and 1988 (Tisdell & Chen, 1994). The fisheries, however, rapidly depleted local stocks and were in most cases short-lived, typically being shut down by local authorities in the span of a few years. In the Maldives, for example, commercial harvest of giant clams began in June 1990 and continued until early 1991. Two buyers were operating and collectively harvested over 90,000 individuals; one buyer exported 9.8 tons to a Taiwanese buyer (Basker, 1991). Concerned over the high exploitation rate, the Ministry of Fisheries and Agriculture conducted an assessment of the giant clam stocks and fishery, and the resulting report recommended closing off high density areas to further fishing and other restrictions (Basker, 1991). The commercial fishery was subsequently closed, and collection of giant clams remains prohibited in the Maldives. Likewise, a commercial fishery in Papua New Guinea reportedly removed at least 85 tons of adductor muscle over a 5 year period, equivalent to over 750 tons of total flesh weight, until it was closed due to depleted stocks (Munro, 1993a).

Adams (1988) described one example of the impact of extreme commercial harvesting pressure in Fiji when a ship named 'Vaea' intensively harvested giant clam stocks in 1985. Teams of two harvesters on hookah gear reportedly caught 50-250 clams per day. At one site, harvesters had taken approximately 80% of the standing stock of *T. derasa*, or nearly 15,000 individuals, from an area of 10 square miles down to a depth of 60 feet. Adams (1988) estimated that harvesting rates averaged 70% of the total living stock at each reef, less for scattered populations and more for denser ones. From 1984 to 1987, *T. derasa* catch rates in Fiji varied between 20 and 40 tons of flesh per year, half of which was exported (Adams, 1988). The Fijian fishery as a whole (including municipal markets, wholesale and retail outlets, and exports) landed over 149 tons during this period, with the largest annual harvest reaching 49.5 tons in 1984, the year in which exports began (Lewis et al., 1988).

By the early 1990s, pervasive stock depletions across the Indo-Pacific severely limited Taiwanese imports of giant clam meat (Tisdell and Chen, 1994). In the years since, many countries in the region have banned the commercial export of giant clams, some have imposed size and/or bag limits, and many have become signatories to the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES). The regulatory implications of CITES participation are discussed more thoroughly in **Section 3.4.2**, but one of its requirements is that Parties must submit an annual report of their trade in CITES-listed species, including the number and type of permits and certificates granted, the countries involved, and the quantities and types of specimens traded. All species of giant clams have been listed under Appendix II of CITES since 1985, and we can therefore rely to some extent on trade statistics from the CITES reporting database to characterize more recent patterns in the international market for giant clams. There are important caveats to this dataset, including inconsistencies in reporting quality and detail (see CITES (2013)), but the general trends in the dataset provide a useful indication as to the magnitude of past and ongoing trade.

The principal exporters of giant clam meat based on CITES reports are displayed in Figure 6. In most cases, countries have limited their reporting to the family or genus level, and outside of a few instances of trade reported for *T. derasa*, *T. gigas*, and *T. squamosa*, no other species were identified specifically (see also Kinch, 2021). Additionally, of all the transactions reported from 1983 to 2020, 50.4% and 39.5% were en route to New Zealand and the United States, respectively, while Japan, Singapore, and Australia comprised the remaining 10.1% of imports. United States imports that have been validated by the U.S. Fish and Wildlife Service for the period 2016-2020 (Table 2) indicate that nearly all of the imports of giant clam meat over the past five years were classified to be of 'Personal' nature, likely representing shipments intended for families or friends of Pacific islanders (Shang et al., 1994). Prior to 2000, there were several years in which countries reported significant export of meat from giant clams that had been born or bred in captivity. This includes 3,615 kg and 472 kg of *T. gigas* and *T. derasa* meat, respectively, exported from the Solomon Islands in the 1990s, 1,695 kg of *T. derasa* meat exported from Palau in 1990-1991, and 65 kg of *T. gigas* meat exported from Australia. Although the reporting from Papua New Guinea indicates the trade of 'Unknown' and 'Captive-Born' specimens, this reporting is known to be inaccurate. According to Kinch (2002), a local fishing company had misreported on CITES export permits that its products were from farmed clams when they were wild-caught. Kinch (2002) also reports several more instances of commercial export of giant clam meat from Papua New Guinea that are not included in the CITES trade database (Figure 7). Likewise, it can be reasonably assumed that the exports from the Philippines in the 1980s were all wild-caught, as there was no known mariculture operation at the time with the capacity to produce giant clam meat for commercial export (S. Wells, 1997).

A number of other countries have reported significant export of giant clam meat (species unknown) since the late 1990s, primarily to New Zealand and the United States. Nearly all of these exports are of wild-caught specimens, many of which have been seized or confiscated at the border due to improper or missing CITES export permits. The major exporters of giant clam meat in the last two decades include the Cook Islands, Kiribati, Marshall Islands, Federated States of Micronesia (FSM), and Tonga. At the higher end, Tonga has exported an average of 1210 kg giant clam meat per year since 2005, and at the lower end, FSM has averaged 58 kg per year during the same period.

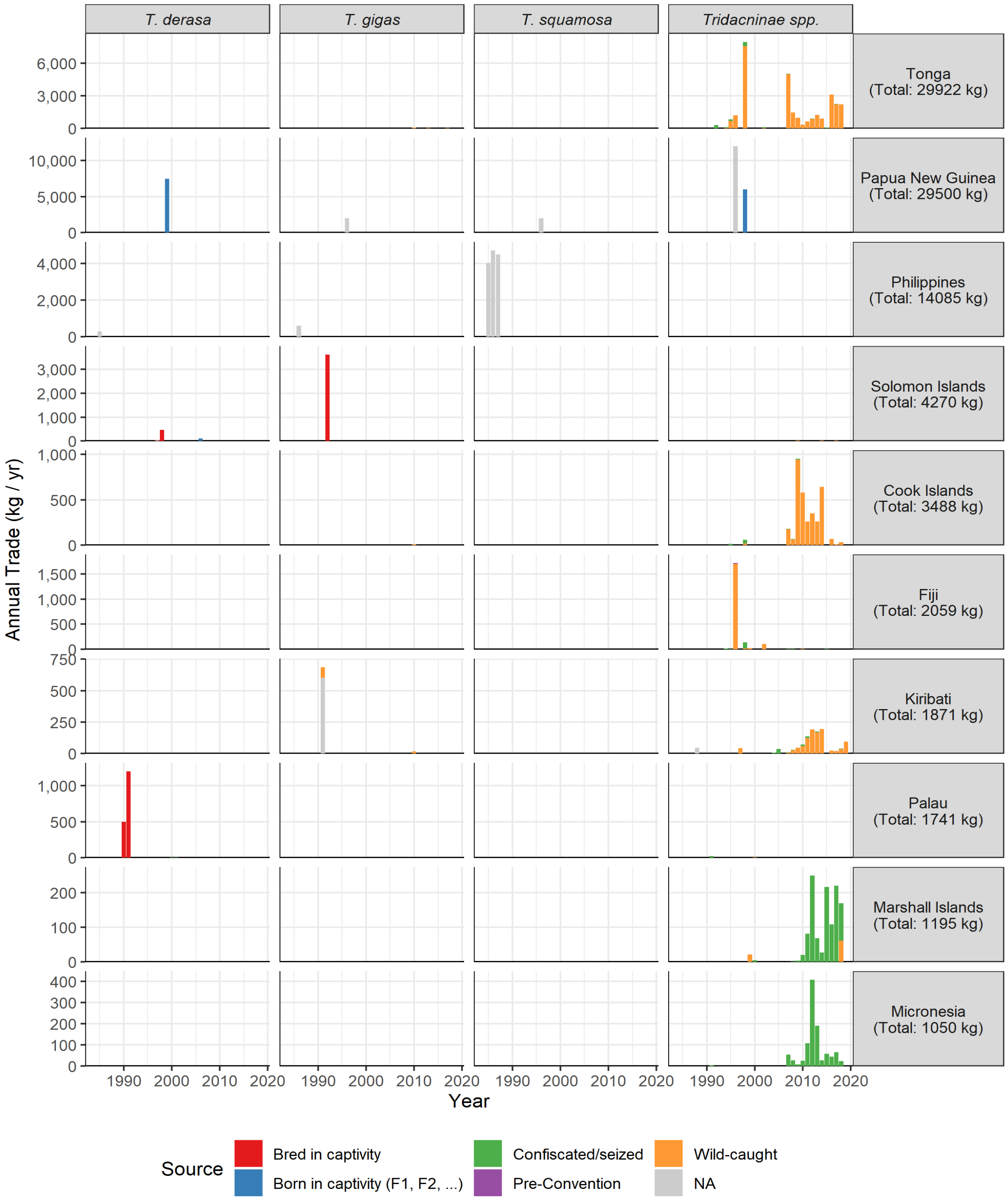
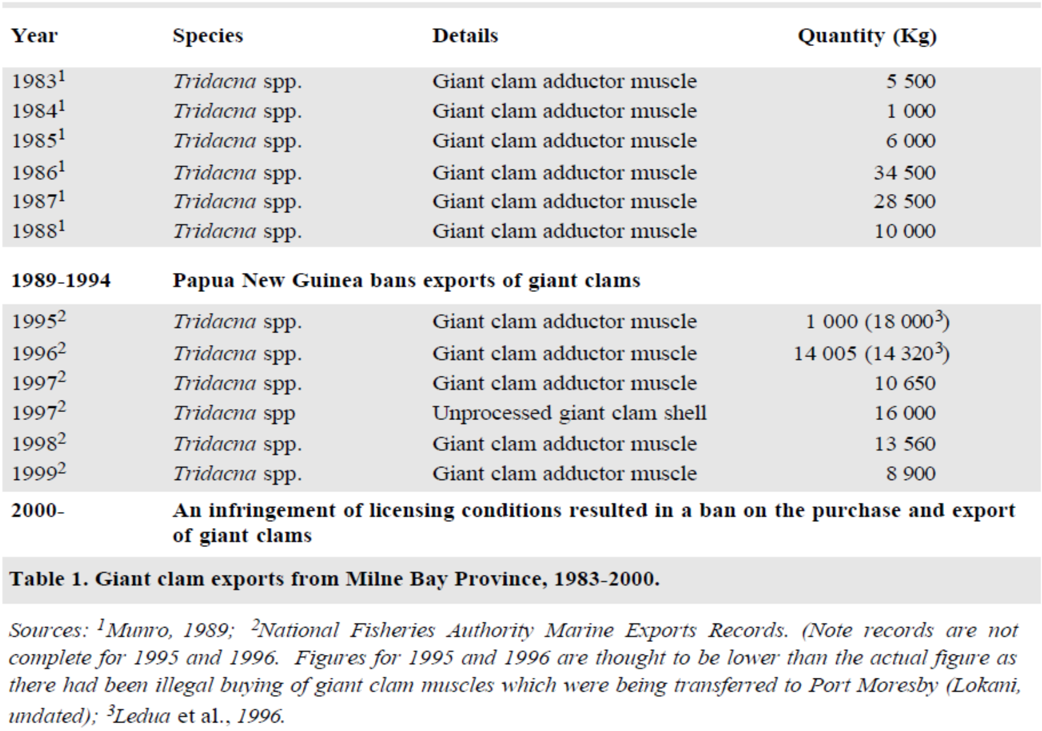


**Figure 6.** Annual exports of giant clam meat (recorded by weight) from the top ten exporting countries, based on CITES reports from 1983 to 2020. The total export volume over this period is included in parentheses under the country names. Values are derived from importers' data. NA indicates trade for which the source of the clam meat was not specified in CITES reports. Not visible in the figure are small quantities of pre-Convention trade of giant clam meat (unknown species) from Fiji (15 kg in 1996) and Tonga (2 kg in 2009). This figure also does not display trade of meat reported in terms of the number of specimens, of which there are significant quantities exported from the Marshall Islands and FSM from 2016 to 2020 (Source: CITES Trade Database, accessed 22 Mar 2022).

***<u>NOTE</u>: The y-axis scale has been allowed to vary by country for the purposes of visualization.***



| Year | Species | Details | Quantity (Kg) |
|---|---|---|---|
| 1983[1] | *Tridacna* spp. | Giant clam adductor muscle | 5 500 |
| 1984[1] | *Tridacna* spp. | Giant clam adductor muscle | 1 000 |
| 1985[1] | *Tridacna* spp. | Giant clam adductor muscle | 6 000 |
| 1986[1] | *Tridacna* spp. | Giant clam adductor muscle | 34 500 |
| 1987[1] | *Tridacna* spp. | Giant clam adductor muscle | 28 500 |
| 1988[1] | *Tridacna* spp. | Giant clam adductor muscle | 10 000 |
| **1989-1994** | **Papua New Guinea bans exports of giant clams** | | |
| 1995[2] | *Tridacna* spp. | Giant clam adductor muscle | 1 000 (18 000[3]) |
| 1996[2] | *Tridacna* spp. | Giant clam adductor muscle | 14 005 (14 320[3]) |
| 1997[2] | *Tridacna* spp. | Giant clam adductor muscle | 10 650 |
| 1997[2] | *Tridacna* spp | Unprocessed giant clam shell | 16 000 |
| 1998[2] | *Tridacna* spp. | Giant clam adductor muscle | 13 560 |
| 1999[2] | *Tridacna* spp. | Giant clam adductor muscle | 8 900 |
| **2000-** | **An infringement of licensing conditions resulted in a ban on the purchase and export of giant clams** | | |

**Table 1. Giant clam exports from Milne Bay Province, 1983-2000.**

*Sources: [1]Munro, 1989; [2]National Fisheries Authority Marine Exports Records. (Note records are not complete for 1995 and 1996. Figures for 1995 and 1996 are thought to be lower than the actual figure as there had been illegal buying of giant clam muscles which were being transferred to Port Moresby (Lokani, undated); [3]Ledua* et al.*, 1996.*

**Figure 7.** Giant clam exports from Milne Bay Province, 1983-2000 (Source: Kinch, 2002).

**Table 2.** Giant clam meat exported to the United States from 2016-2020. This includes species addressed in this report as well as products identified to the family or genus level. All data have been validated by the U.S. Fish and Wildlife Service.

| Year | Origin | Purpose | Source | Status | Unit | Quantity |
|---|---|---|---|---|---|---|
| 2016 | Marshall Islands | Personal | Unknown | Refused | kg | 14.2 |
| | | Personal | Unknown | Refused | # specimens | 1311 |
| | | Personal | Unknown | Seized | kg | 4 |
| | | Commercial/trade | Unknown | Refused | kg | 0.7 |
| | Federated States of Micronesia | Personal | Unknown | Refused | kg | 2.1 |
| | | Personal | Unknown | Seized | kg | 11.7 |
| | | Personal | Unknown | Seized | # specimens | 2530 |
| | Tonga | Personal | Unknown | Seized | kg | 2 |
| 2017 | Marshall Islands | Personal | Unknown | Refused | kg | 14.4 |
| | | Personal | Unknown | Refused | # specimens | 2366 |
| | | Personal | Unknown | Seized | kg | 6.0 |
| | Federated States of Micronesia | Personal | Unknown | Refused | kg | 1.4 |
| | | Personal | Unknown | Seized | kg | 3.3 |
| | Tonga | Personal | Unknown | Seized | kg | 5 |
| 2020 | Marshall Islands | Personal | Wild | Refused | kg | 7.7 |
| | Palau | Personal | Cultured | Cleared | # specimens | 40 |

It is important to note that most of the key countries in the trade of giant clam meat are not CITES contracting Parties (e.g., Cook Islands, Kiribati, Marshall Islands, FSM) or have only become so relatively recently (e.g., Palau in 2004, Solomon Islands in 2007, Tonga in 2016). Thus, any trade reported for these countries is based on values reported by the CITES Party involved, and any trade among two non-contracting nations is not included in this dataset.

### *International Trade in Giant Clam Shells and Shell-Craft*

The trade of giant clam shells and shell-craft has existed in some form for over two millennia (Neo et al., 2017). Artifacts made from giant clam shells date back at least 2,500 years and have been prominent in excavations around the world (Neo et al., 2017). In contemporary times, giant clam shells have been used for a variety of decorative and utilitarian purposes, including as beads, vases, lamps, ashtrays, and wash basins. *Hippopus hippopus* and *T. squamosa* are considered the most popular giant clam species for the shell trade (Shang et al., 1994) because of their unique physical characteristics (e.g., attractive colors, bowl-like shape, etc.); although, nearly all of the species (except *T. crocea*) have been harvested depending on the intended use, cultural preference, or geographic availability.

The Philippines has historically operated as the largest exporter of giant clam shells and shell-craft, accounting for over 95% of the global exports of giant clam products from 1983 to 2020 (Table 3; Figures 8, 9). During the peak of the shell trade from 1979 to 1992, total exports from the Philippines surpassed 4.2 million kg (Figures 10, 11; Juinio et al., 1987; S. Wells, 1997). While all species of giant clam that occur in the Philippines have been exploited, the two *Hippopus* spp. and *T. squamosa* were the most frequently used for ornamental purposes and handicrafts, and *T. gigas* was most frequently used for basins (Lucas, 1994). Juinio et al. (1987) noted that *T. derasa* may have also been harvested but was often not distinguished by shell dealers as a separate species; rather, it was known as a "heavier variety" of *T. gigas* or *H. porcellanus*.

Export records from the Philippines Bureau of Fisheries and Aquatic Resources indicate an initial peak in 1979, when 1,003 tonnes of giant clam shells were exported, corresponding to 895,000 shell pairs (Figure 10). Exports then declined to a minimum of 63 tonnes (or 67,000 shell pairs) in 1982, which was thought to reflect saturation of the international demand. Juinio et al. (1987) reported that the demand for giant clam shells could be met from existing stockpiles (except those of *H. porcellanus*, which was still considered to be highly marketable). However, exports began to increase again in the late 1980s and peaked in 1991 with nearly 1.2 million shells, over 460,000 carvings, and over 1,186 tonnes of shells (equivalent to about 825,000 shell pairs) (Figure 11; S. Wells, 1997). This occurred despite the government of the Philippines instituting a ban on the export of giant clams (except *T. crocea*) in 1990. In the following year, exports declined to 374,000 shells and 70,000 carvings, likely due to the issuance of CITES Notification No. 663 (16 January 1992) urging all CITES Parties to refuse trade permits for Tridacninae products from the Philippines, in accordance with Philippine legislation (S. Wells, 1997). In the 3 decades since 1992, reported exports of giant clam shells from the Philippines have been considerably lower (but not absent), totaling only 8,528 shells and 6,359 carvings (CITES Trade Database, accessed 22 Mar 2022).

Ultimately, widespread subsistence harvest in conjunction with heavy fishing pressure on giant clams to supply the commercial shell trade decimated populations of several giant clam species (e.g., *H. hippopus, H. porcellanus, T. gigas,* and *T. squamosa*), with local extinctions widespread throughout the Philippines (Juinio et al., 1987). S. Wells (1997) reported that exports until 1992 were dominated by *H. hippopus*, *T. squamosa*, and *H. porcellanus*, with *H. hippopus* comprising 53% of shell exports and 94% of carvings (see also Figures 8, 9). Even the few remaining locations thought to be the species' last strongholds in Philippine waters (e.g., in the Sulu Archipelago and Southern Palawan) were overharvested by the mid-1980s (Villanoy et al., 1988). Presently, eight species can still be found in the Philippines and they are all protected by Philippine law. Native *T. gigas* populations are restricted to reefs in Tubbataha in very low abundance; *T. derasa*, *H. hippopus,* and *H. porcellanus* are considered rare, and *T. squamosa* is considered frequent (only *T. maxima* and *T. crocea* are still considered abundant in the region; Neo et al., 2017).

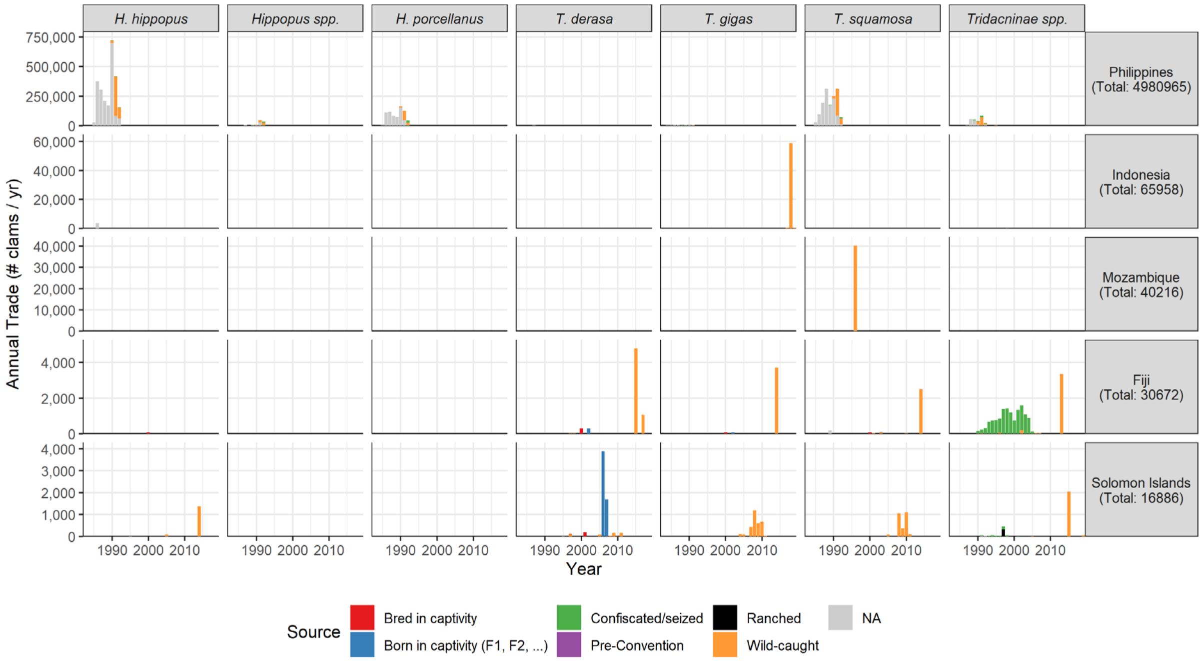


**Figure 8.** Annual exports of giant clam shells (# of specimens) from the top five exporting countries, based on CITES reports from 1983 to 2020. The total export volume over this period is included under the country names. Values are derived from importers' data and do not include trade recorded by weight, nor carvings or jewelry. NA indicates trade for which the source of the clam shells was not specified in CITES reports. Not visible in the figure are small quantities of pre-Convention trade from the Philippines (18 *H. hippopus*, 72 *H. porcellanus*, and 42 *T. squamosa* in 1998; 12 *T. derasa* in 1999; 1 *H. hippopus* in 2003; 1 *T. squamosa* in 2010; 1 *T. gigas* in 2018) and the Solomon Islands (1 *T. gigas* in 2014) (Source: CITES Trade Database, accessed 22 Mar 2022).

***NOTE*: *The y-axis scale has been allowed to vary by country for the purposes of visualization.***

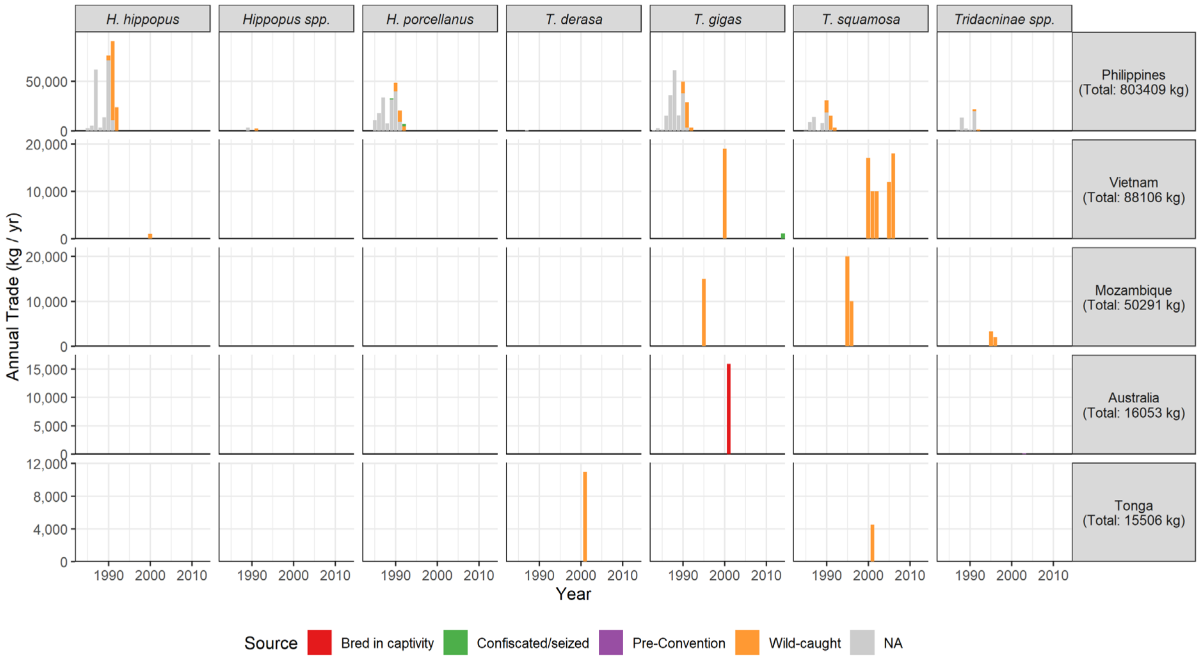


**Figure 9.** Annual exports of giant clam shells (recorded by weight) from the top five exporting countries, based on CITES reports from 1983 to 2020. The total export volume over this period is included under the country names. Values are derived from importers' data and do not include exports recorded by count, nor carvings or jewelry. NA indicates trade for which the source of the clam shells was not specified in CITES reports. Not visible in the figure are small quantities of pre-Convention trade of unknown species from Australia (100 kg in 2003; 22 kg in 2014) (Source: CITES Trade Database, accessed 22 Mar 2022).

***<u>NOTE</u>: The y-axis scale has been allowed to vary by country for the purposes of visualization.***

**Table 3.** Total exports of giant clam shell products from the Philippines (1983-2020), including the percentage of global trade that it represents. This includes species addressed in this report, as well as products identified to the family or genus level. Data are based on importers' reports. (Source: CITES Trade Database, accessed 22 Mar 2022).

| Product | Quantity | | Percent |
|---|---|---|---|
| Shells | 803,408 | kg | 81.3% |
| | 744,112 | pairs | 99.5% |
| | 4,234,016 | no. of specimens | 94.6% |
| Carvings | 112,245 | kg | 94.5% |
| | 23,094 | pairs | 100% |
| | 2,517,689 | no. of specimens | 98.5% |

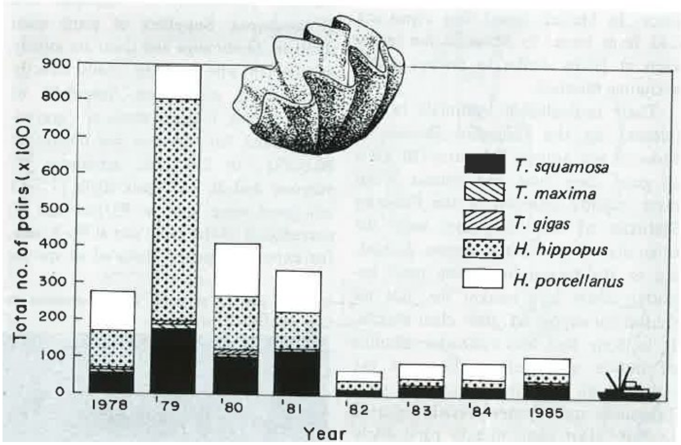
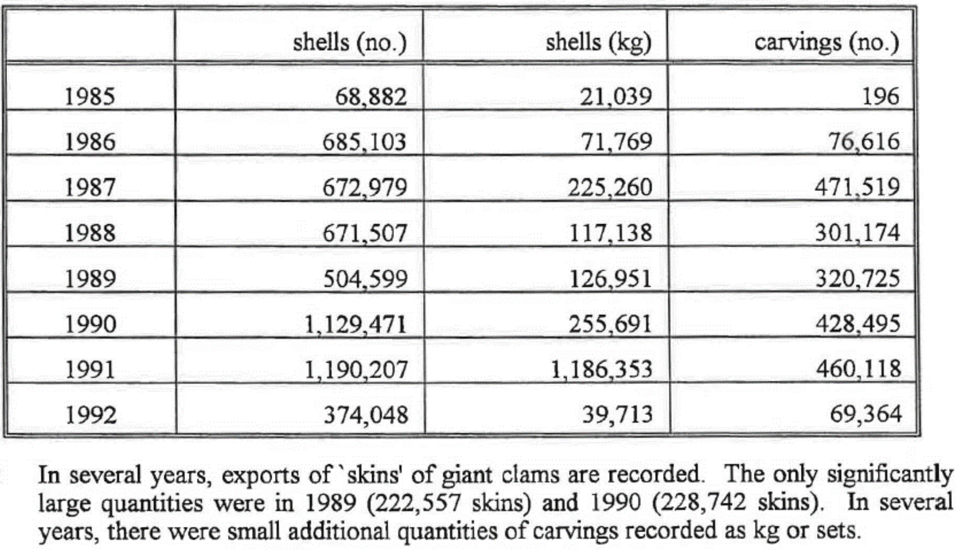


**Figure 10.** Giant clam shells exported from Zamboanga, Philippines from 1978-1985 based on records of export invoices from the Philippine Bureau of Fisheries and Aquatic Resources in Zamboanga (Source: Juinio et al., 1987, with permission from the author).



| | shells (no.) | shells (kg) | carvings (no.) |
|---|---|---|---|
| 1985 | 68,882 | 21,039 | 196 |
| 1986 | 685,103 | 71,769 | 76,616 |
| 1987 | 672,979 | 225,260 | 471,519 |
| 1988 | 671,507 | 117,138 | 301,174 |
| 1989 | 504,599 | 126,951 | 320,725 |
| 1990 | 1,129,471 | 255,691 | 428,495 |
| 1991 | 1,190,207 | 1,186,353 | 460,118 |
| 1992 | 374,048 | 39,713 | 69,364 |

NB: In several years, exports of `skins' of giant clams are recorded. The only significantly large quantities were in 1989 (222,557 skins) and 1990 (228,742 skins). In several years, there were small additional quantities of carvings recorded as kg or sets.

**Figure 11.** Annual net exports of giant clam shells (all species) from the Philippines, 1985-1992. Source: IUCN/TRAFFIC/WCMC (1996) (Figure source: S. Wells, 1997).

The United States, Japan, Australia and various European countries have historically been the largest importers of shells and shell-craft from the Philippines (Juinio et al., 1987; S. Wells, 1997). Table 4 displays the total import volume, based on CITES reports, for the top ten importing nations of giant clam shells and shell products (all species) from 1983 to 2020. The United States alone has accounted for over 50% of shells and over 60% of shell carvings imported over this time period. More recently, however, dwindling giant clam populations as well as greater regulatory protections in many countries have limited the shell trade among the traditional major importers of the 1980s. Instead, the majority of international trade has shifted increasingly to illegal means. From 2016 to 2020, the global trade in giant clam shells based on CITES reports totaled 65,129 shells and 221 shells carvings (primarily *T. gigas*), of which over 92% originated in Indonesia (see Figure 8) and over 97% were imported by China. This has occurred despite a prohibition on the harvest and export of giant clams under Indonesian law since 1987. While not at the same scale as the Philippines, Indonesia has participated in the trade of giant clam shells and shell products since the 1980s (Figure 8). Once giant clams were listed locally as protected species in 1987, Tisdell (1992) suggested that unrecorded exports of giant clam shells continued to occur from Indonesia to the Philippines. Likewise, several reports in the years since indicate that enforcement of the harvest and export ban remains grossly insufficient and, as is suggested by the CITES reports, substantial export of giant clam shells from Indonesia is ongoing (Allen & McKenna, 2001; Nijman et al., 2015; Harahap et al., 2018).

**Table 4.** Top ten importers of giant clam shell products from 1983 to 2020. This includes species covered in this report, as well as products identified to the family or genus level. Percent of the total global imports for each trade term is included in parentheses. (Source: CITES Trade Database, accessed 22 Mar 2022).

| Importer | Shells (no. specimens) | Shells (pairs) | Shells (kg) | Carvings (no. specimens) | Carvings (kg) |
|---|---|---|---|---|---|
| USA | 2,337,670 (52.2%) | 490,914 (65.6%) | 356,964 (36.1%) | 1,758,400 (68.8%) | 80,738 (68%) |
| Spain | 333,621 (7.5%) | 25,306 (3.4%) | 198,401 (20.1%) | 27,863 (1.1%) | 8,806 (7.4%) |
| Japan | 323,029 (7.2%) | 42,220 (5.6%) | 109,535 (11.1%) | 207,348 (8.1%) | 5,381 (4.5%) |
| UK | 281,027 (6.3%) | 17,929 (2.4%) | 29,193 (3%) | 107,521 (4.2%) | 1,885 (1.6%) |
| Germany | 255,505 (5.7%) | 7,607 (1%) | 13,461 (1.4%) | 141,905 (5.6%) | - |
| Netherlands | 221.891 (5%) | 13,191 (1.8%) | 27,210 (2.8%) | 110,201 (4.3%) | - |
| Italy | 148,410 (3.3%) | 25,391 (3.4%) | 129,660 (13.1%) | 11,379 (0.4%) | - |
| France | 139,841 (3.1%) | 19,774 (2.6%) | 22,025 (2.2%) | 120,811 (4.7%) | 3,810 (3.2%) |

Presently, the largest market for giant clam shells is in the city of Tanmen, in the southern Chinese Province of Hainan. As discussed in **Section 3.1.3**, a major shell-crafting industry developed in this region during the 2000s. At the time, fishing subsidies allowed local fishermen to travel well into the South China Sea, where they could find and harvest the shells of giant clams. Businesses carved the shells into decorative sculptures, jewelry, and other handicraft, and sold them at one of the many retail shops in the province or online on the major Chinese e-commerce sites, such as Taobao.com, Alibaba.com, and Aliexpress.com (Lyons et al., 2018). During the peak of the Tanmen shell-crafting industry in 2013-2014, there were an estimated 150 processing workshops supplying 900 craft shops with giant clam shell products in the province (Wildlife Justice Commission, 2021). The annual sales revenue of giant clam shell handicrafts in 2014 was estimated to be $75 million USD (Lyons et al., 2018; Kinch, 2021). In January 2017, the Hainan Province People's Congress passed new regulations banning the commercial trade of giant clams in Hainan. However, investigations conducted two years later by the Wildlife Justice Commission (2021) found that there were still more than 100 craft shops in Tanmen, although fewer than 20% were still in business. Giant clam shell products were also being sold openly in hundreds of stores in other parts of the Hainan Province, such as Haikou, Sanya, Guangdong, and Fujian provinces, and could be ordered on social media platforms, such as WeChat for delivery to other locations (Wildlife Justice Commission, 2021). This has been corroborated by first-hand news reporting from Scarborough Shoal in April 2019, which documented ongoing shell harvesting by fishing boats flying the Chinese flag (ABS-CBN News, 2019). The ABS-

CBN film crew captured many large piles of extracted giant clam shells around the harvesting area, some even extending above the water surface.

This industry primarily targets the shells of deceased clams embedded in the reef substrate; however, live clams are also taken whenever found. Large shells in particular are of the highest value, putting the remaining *T. gigas* populations in the area at the greatest risk. According to Lyons et al. (2018), "the more valuable [*T. gigas*] pieces come with a certificate of origin, specifying, for example, that it comes from Scarborough Shoal, Spratlys, or Paracels and, occasionally, even the specific reef concerned." This suggests that *T. gigas* shells have different grades or qualities depending on where they were harvested in the South China Sea. As a result of this intense market demand in combination with the destructive shell harvesting methods described in **Section 3.1.3**, Gomez (2015) noted that *T. gigas* is now "virtually extinct" in the center of the South China Sea, including the Paracels, the Macclesfield Banks, and the Spratlys.

### *International Trade of Live Giant Clams for Aquaria*

The largest current market for giant clams is that of live specimens for the aquarium trade and, to a lesser extent, to supply broodstock for mariculture operations. It can be difficult to distinguish the purpose of live specimen transactions from CITES reports alone, but S. Wells (1997) concluded "that the aquarium trade is now the main market for both wild-collected and mariculture clams." In the 25 years since that report, the market for giant clams as aquarium specimens has continued to grow, with giant clams now representing one of the most desired groups of invertebrates in the aquarium industry (Wabnitz et al., 2003; Teitelbaum & Friedman, 2008; Mies, Dor, et al., 2017). They are a sought-after commodity and have been described as a "must have" item by collectors and aquarium hobbyists (Lindsay et al., 2004). The smaller, more brightly colored species (i.e., *T. maxima* and *T. crocea* - not reviewed in this report) are by far the most popular in the marine ornamental trade, but *T. squamosa*, *T. gigas*, *T. derasa*, and *H. hippopus* are also traded in smaller numbers (Lindsay et al., 2004; Kinch & Teitelbaum, 2010).

As shown in Figure 12, CITES records indicate that the primary source countries for the species covered in this status review include Australia, Palau, Vietnam, Solomon Islands, and Marshall Islands, among others. Notably, the vast majority of giant clams exported from Australia, Palau, and the Marshall Islands have been bred/born in captivity and thus pose less risk to wild populations; however, much of the export volume from Vietnam, Solomon Islands, Tonga, and more recently, Cambodia, are of wild-sourced specimens. It is also likely that the significant exports of *H. hippopus* and *T. squamosa* from the Philippines in 1988 (>20,000 individuals of each species) were of wild origin, as this coincides with the peak of the shell trade in the Philippines when hundreds of thousands of giant clams were being harvested each year from local waters.

Of the species included in this status review, *T. derasa* and *T. squamosa* have been the most popular in the trade of live specimens, according to CITES reports (Figure 12). Comparing the two, exports of *T. derasa* have been higher from Pacific Island nations, such as Palau, Solomon Islands, Marshall Islands, Tonga, and FSM. Nearly all recent trade of this species is of captive-bred/born individuals, with wild harvest in these countries contributing minimally, if at all, by 2010. *T. squamosa*, by comparison, has been harvested more often by countries in Southeast Asia, such as Vietnam, Cambodia and Indonesia, and many of the recent exports from

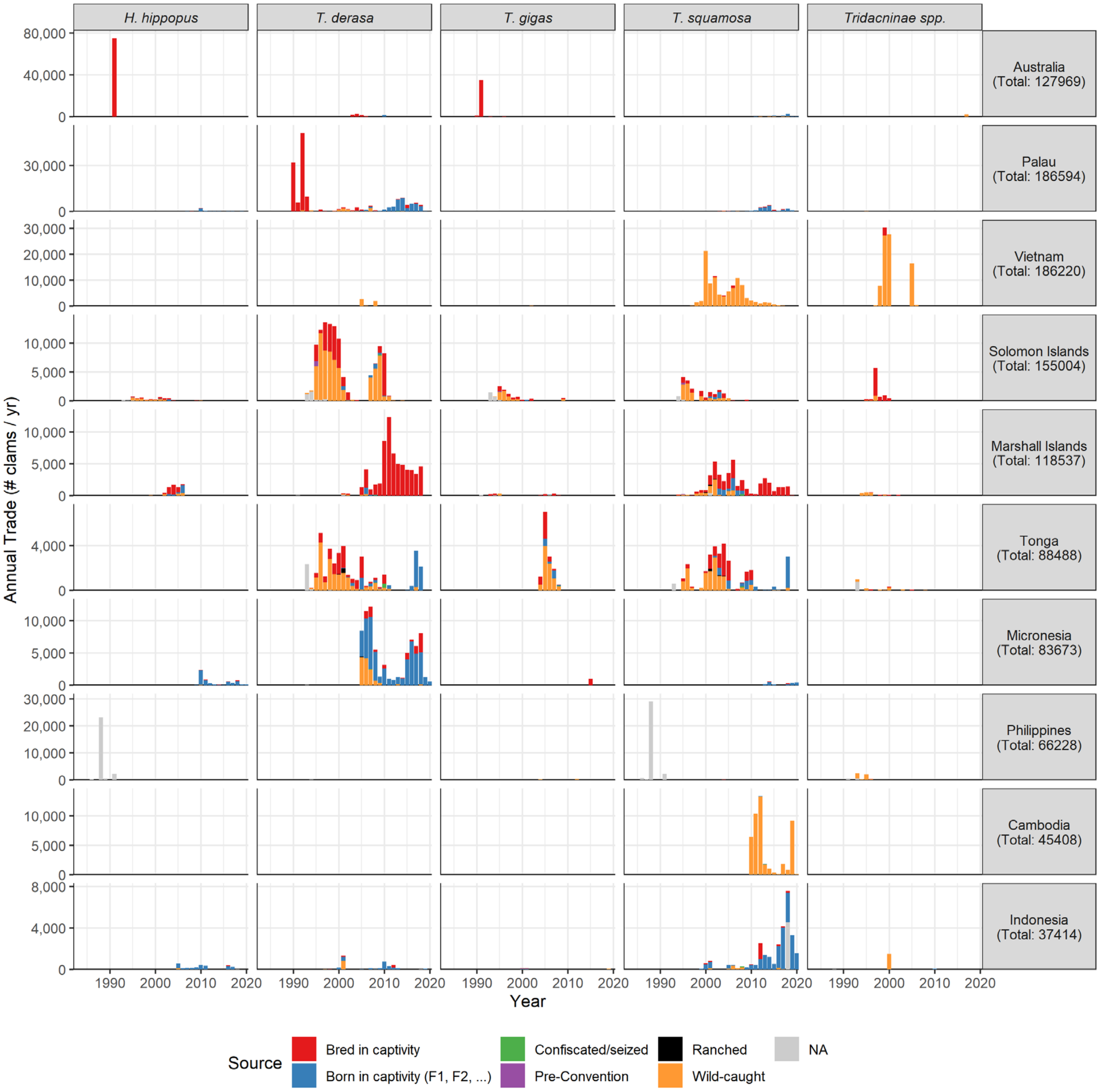


**Figure 12.** Annual exports of live giant clams for non-scientific purposes from the top ten exporting countries, based on CITES reports from 1983 to 2020. The total export volume over this period is included in parentheses under the country names. Values are derived from importers' data. NA indicates trade for which the source of the giant clam specimens was not specified in CITES reports. Not visible in the figure are small quantities of pre-Convention trade from Indonesia (6 *T. derasa* in 1995), Marshall Islands (20 *T. gigas* and 130 *T. squamosa* in 1995), Solomon Islands (57 *H. hippopus*, 862 *T. derasa*, 96 *T. gigas*, and 298 *T. squamosa* in 1995; 30 *T. derasa* in 2011), and Tonga (10 *T. derasa* in 1995) (CITES Trade Database, accessed 22 Mar 2022).

***NOTE: The y-axis scale has been allowed to vary by country for the purposes of visualization.***

**Table 5.** Top ten importers of live giant clams from 1983 to 2020. This includes species covered in this report, as well as specimens identified to the family or genus level. Percent of the total global imports for each trade term is included in parentheses. * indicates that all recorded imports to Samoa and Cook Islands were exported from Australia and are known to be for stock enhancement and mariculture programs. These numbers are not included in the total import for percentage calculations in parentheses (Source: CITES Trade Database, accessed 22 Mar 2022).

| **Importer** | ***H. hippopus*** | ***T. derasa*** | ***T. gigas*** | ***T. squamosa*** | **Tridacninae spp.** |
|---|---|---|---|---|---|
| USA | 13,243 (24.2%) | 296,201 (53%) | 22,064 (56%) | 140,172 (38.4%) | 18,502 (12.8%) |
| France | 1,902 (3.5%) | 13,256 (2.4%) | 1,927 (4.9%) | 54,286 (14.9%) | 90,954 (63%) |
| UK | 26,301 (48.2%) | 25,856 (4.7%) | 305 (0.8%) | 38,732 (10.7%) | 331 (0.2%) |
| Germany | 6,485 (11.9%) | 50,431 (9.1%) | 3,330 (8.5%) | 23,191 (6.4%) | 4,849 (3.4%) |
| Canada | 2,739 (5%) | 6,990 (1.3%) | 1,543 (3.9%) | 12,773 (3.5%) | 1,005 (0.7%) |
| Japan | 781 (1.4%) | 54,831 (9.9%) | 1,044 (2.7%) | 1,146 (0.3%) | 450 (0.3%) |
| Netherlands | 461 (0.8%) | 12,570 (2.3%) | 34 (0.1%) | 14,410 (4%) | 629 (0.4%) |
| Micronesia | 500 (0.9%) | 58,801 (10.6%) | - | 1,881 (0.5%) | - |
| Singapore | 112 (0.2%) | 2,180 (0.4%) | 3,784 (9.6%) | 6,259 (1.7%) | 426 (0.3%) |
| Hong Kong | 846 (1.5%) | 2,895 (0.5%) | 321 (0.8%) | 2,285 (0.6%) | 795 (0.6%) |
| Switzerland | 23 (0%) | 612 (0.1%) | 100 (0.1%) | 3,135 (0.9%) | 2,385 (1.7%) |
| Denmark | 50 (0.1%) | 3,811 (0.7%) | 404 (1%) | 3,972 (1.1%) | 400 (0.3%) |
| Vietnam | - | - | - | 29,750 (8.2%) | - |
| Cook Islands* | 25,000 | - | 10,000 | - | - |
| Samoa* | 50,000 | - | 26,000 | - | - |

Vietnam and Cambodia are of wild-sourced individuals. Exports from Vietnam peaked in the 2000s and have declined over the last decade, while exports from Cambodia have increased more recently, reaching nearly 10,000 *T. squamosa* specimens in 2019. Neo et al. (2017) notes that the decline in exports from Vietnam is related to trade restrictions implemented in response to concerns about sourcing wild specimens, and it is possible that some giant clams from Vietnam have been re-routed for export through Cambodia. In fact, CITES reports indicate that over 99% of the recorded *T. squamosa* exports from Cambodia were imported by Vietnam, implying a close trade connection between the two nations. According to J. Kinch (pers. comm., March 18, 2023), Vietnam has become a major entrepôt in the region facilitating the illegal smuggling of giant clam imports into China.

Neither *H. hippopus* nor *T. gigas* has been harvested consistently for the aquarium trade; although, with respect to *T. gigas*, Craig et al. (2011) attributed this to a lack of available supply rather than a decline in demand. Because of declining populations throughout much of its range, the majority of *T. gigas* specimens for the aquarium trade in the late 2000s were being sourced from just a few small island nations, primarily Tonga (Craig et al., 2011). However, according to CITES records, trade of *T. gigas* from Tonga has not occurred since 2011 (Figure 12). *Tridacna gigas* is not considered to be native to Tonga, but had reportedly been introduced as part of stock enhancement and aquaculture programs (Munro, 1993a; S. Wells, 1997). According to a CITES assessment in 2004, the introduced populations of *T. gigas* had by that point died out, so it is not clear where the exported specimens originated (CITES, 2004a).

The United States has consistently remained one of the top import markets for live giant clams, along with Canada, several countries in Europe, Japan, and Hong Kong (Wabnitz et al., 2003; Craig et al., 2011). In 2002, 70 percent of the giant clams exported for the aquarium trade went to the United States (Mingoa-Licuanan & Gomez, 2002 cited in Craig et al., 2011). According to CITES reports from 1983-2020, the United States has accounted for 24.2% of the total recorded imports of *H. hippopus*, 53% of imports of *T. derasa*, 56% of imports of *T. gigas*, 38.4% of imports of *T. squamosa*, and 12.8% of imports of Tridacninae specimens that were not identified to the species level (Table 5; CITES Trade Database, accessed 22 Mar 2022). Throughout the full record since 1983, 50.6% of the imports to the United States were recorded as captive-bred/born specimens, while 44.7% were recorded as wild-sourced; however, according to CITES records validated by the U.S. Fish and Wildlife Service for the period from 2016 to 2020, wild-sourced specimens now represent only 4% of imports, with captive-bred/born specimens accounting for the remaining 96%.

### 3.2.3 Scientific and Educational Use

There may be small markets for giant clams for scientific demonstration or research purposes (e.g., paleoclimatic reconstructions from clam shells or chemical extracts for health or medicinal purposes; see Tisdell, 1992; Lucas, 1994). We also note that many scientific publications on giant clams involve cultured specimens rather than individuals harvested from the wild. Although uncertain, there is little evidence to indicate that overutilization for scientific and/or educational purposes currently represents a threat to giant clams.

### 3.2.4 Conclusion

The pervasive harvest of giant clams for subsistence and domestic sale, and several periods of short-lived but intensive commercial harvest have severely depleted giant clam populations throughout their Indo-Pacific range. Once the center of giant clam diversity in the region, the Philippines saw commercial exploitation of giant clams for the international shell trade decimate populations of *H. hippopus*, *H. porcellanus*, *T. gigas*, and *T. squamosa*. Similar trends have been observed throughout Southeast Asia (i.e., Indonesia, Singapore, Thailand, Cambodia, Vietnam, and in the South China Sea), where each of these species except *T. squamosa* is now considered extremely rare or locally extinct (Neo et al., 2017). Likewise, illegal harvest of giant clams for the international clam meat trade, primarily by Taiwanese fishermen or to supply Taiwanese demand, severely reduced giant clam populations throughout the western and central Pacific. As a result, as in Southeast Asia, nearly all of the species (excluding *T. squamosa*) are now considered rare or extinct throughout most of their Pacific range (S. Wells, 1997; Neo et al., 2017). Although international demand (primarily for the aquarium trade) is increasingly met by the growing field of giant clam mariculture, wild-sourced clams are still observed in international trade, and the potential for laundering wild clams with mariculture-produced specimens cannot be discounted (Sant, 1995).

Ongoing harvest for subsistence or domestic market supply, as well as persistent poaching, continues to limit substantial population recovery of giant clams throughout much of their range. As broadcast-spawning organisms with little to no mobility, giant clams are reliant on sufficient population density to facilitate fertilization of their gametes. Thus, even if small populations of giant clams have survived the years of exploitation, in many cases individuals may be too dispersed to successfully reproduce. Furthermore, the largest individuals were often targeted for the meat and shell trade, leading to altered size structures in remnant giant clam populations. Juveniles and smaller adults are known to be more susceptible to predators and to exhibit lower reproductive output, which will likely continue to limit population recovery in the near future. It is for these reasons that we consider overutilization to be the most significant threat to all seven giant clam species.

## 3.3 Disease or Predation

### 3.3.1 Disease and Parasites

Most infectious diseases reported in giant clams have been either bacterial or protozoan in origin (Braley, 1992; Mies, Scozzafave, et al., 2017). Bacterial infections are most often caused by *Rickettsia* sp., which infect the ctenidia (gill-like respiratory organ) and the digestive lining of the clam (Norton et al., 1993; Mies, Scozzafave, et al., 2017). Protozoan infections are often caused by either *Marteilia* sp. or *Perkinsus* spp. Giant clams with *Marteilia* infections show no external symptoms, but the infection will eventually cause superficial lesions on the kidney (Mies, Scozzafave, et al., 2017).

Far more concerning due to its commonly fatal outcome and lack of treatment is Perkinsosis, also known as pinched mantle syndrome, which is caused by *Perkinsus* spp. Giant clams typically do not exhibit any symptoms of the infection until they become immunosuppressed due to some other environmental stress. At that point, the protozoan population is able to proliferate, and in some cases causes mortality of the host clam. Once the clam dies, trophozoites of *Perkinsus* spp. become waterborne and can infect nearby individuals (Mies, Scozzafave, et al., 2017). Perkinsosis is present in all ocean basins and has been implicated in the collapse of entire bivalve populations (Villalba et al., 2004; Dungan & Reece, 2006). A significant rate of infection by *Perkinsus* spp. was previously observed at several sites on the Great Barrier Reef, with 38 of 104 sampled individuals (including *T. gigas*, *H. hippopus*, *T. maxima*, and *T. crocea*) being infected (Goggin & Lester, 1987). Additionally, several *Perkinsus* infections were observed in association with a mass mortality of giant clams at Lizard Island in Australia in 1985; however, the cause of the death was never determined and the infections may have been coincidental (Alder & Braley, 1989). Unfortunately, more recent surveys of disease prevalence from these areas are not available for comparison. International shipments of giant clams infected with *Perkinsus* spp. have been reported (Sheppard & Phillips, 2008; Reavill et al., 2009). Freshwater dips (a treatment where the clam is placed in a freshwater bath to rid the clam of parasites) and antibiotics are not effective in addressing this disease. Perkinsosis is implicated as the cause of most unexplained deaths in captive giant clams (Mies, Scozzafave, et al., 2017).

Giant clams are also affected by external parasites, including snails, sponges, and algae. Pyramidellid snails are particularly invasive, exploiting the clams by inserting their proboscises (i.e., feeding appendage) into the clam tissue and consuming the haemolymph within the siphonal mantle (Braley, 1992). On rare occasions, the snails may prove fatal to juvenile clams, but they are unlikely to cause mortality in adult clams (Mies, Scozzafave, et al., 2017). Other external parasites (i.e., sponges and algae) are typically more of a nuisance to giant clams rather than fatal infestations. For instance, boring sponges (e.g., *Cliona)* may drill holes into the clam's shells, and algae (e.g., *Gracilaria* sp.) may overcrowd the shell and prevent the mantle from extending, but neither of these parasites typically cause mortality (Mies, Scozzafave, et al., 2017).

When disease is present, giant clams exhibit physical symptoms that are usually quite obvious, including a retracted mantle (typically the initial symptom), a gaping incurrent siphon (indicative of more advanced disease), and discarding of the byssal gland (Mies, Scozzafave, et al., 2017). While some diseases may respond to antibiotics, concentrations and dosages for giant clams have not been well studied. Overall, the prevalence and severity of disease likely varies across the extensive range of giant clams, but there is no information to indicate that disease is an operative threat to giant clams to the extent that it is significantly increasing the extinction risk of the species assessed here. Any species-specific information regarding disease prevalence will be discussed in more detail in the individual species accounts in **Section 4** of this report.

### 3.3.2 Predation

Much of what is known regarding the predation of giant clams has been learned from the ocean nursery phase of mariculture activities when juveniles are outplanted to their natural environment (Govan, 1992). Giant clams are widely exploited as a food source on coral reefs, with 75 known predators that employ a variety of attack methods (see Table 3 in Neo, Eckman, et al. (2015) for a comprehensive list). These predators are largely benthic organisms, including balistid fishes, octopods, xanthid crabs, and muricid gastropods (Govan, 1992). The fishes (e.g., wrasse, triggerfish, and pufferfish) prey on both juvenile and adult giant clams by biting the mantle edge, the exposed byssus, or the extended foot. Other predators (e.g., crabs, snails, and mantis shrimp) have been observed chipping, drilling holes into, and/or crushing the shells of smaller individuals (see review in Neo et al. 2015). Heslinga et al. (1984) observed several instances of predation firsthand in association with giant clam culturing operations in Palau. Large muricid snails (*Chicoreus ramosus*) were found to attack, kill, and eat *T. squamosa* specimens up to at least 300 mm shell length, and a single hermit crab was able to crush 26 *T. gigas* juveniles (20-30 mm) when inadvertently left in the culture tank. The authors also noted circumstantial evidence of predation by *Octopus* spp. in Palau based on the characteristically chipped shells of giant clams often observed outside of octopus dens.

Vulnerability to predation varies between species and size classes. For example, *H. hippopus* has been found to be less vulnerable to *Cymatium muricinum* than *T. gigas* and *T. derasa* (Heslinga et al., 1990 cited in Lucas, 1994). In fact, out of five species tested for their general resistance to predation, *H. hippopus* was the least vulnerable species, while *T. gigas* and *T. derasa* were the most vulnerable (Govan et al., 1993). Susceptibility to predation decreases as giant clams grow in size; although attacks on adult giant clams have been observed (Alcázar, 1986), they are relatively immune to predation (Heslinga & Fitt, 1987).

Giant clams employ a suite of defense mechanisms, both morphological and behavioral, to resist predatory attacks (Soo & Todd, 2014). For example, their large body size, small byssal orifice, and strong shells create physical barriers to predation. In addition, *T. squamosa* is equipped with hard, scaly projections on its shell known as scutes that have been shown to provide protection from crushing predators (Han et al., 2008). Giant clams also exhibit behavioral defense mechanisms, such as aggregation, camouflage, rapid mantle withdrawal (Todd et al., 2009), and squirting water from siphons (Neo & Todd, 2010). Defensive shell-closing has also been documented during all developmental stages (Soo & Todd, 2014). While the ability of giant clams to endure intense predation pressure and acclimate to repeated disturbance can have implications for their survival, these attributes have not been studied extensively (Soo & Todd 2014). Thus, the degree to which predation may be contributing to the extinction risk of giant clams cannot be confidently assessed. Where information is available, we discuss any species-specific information regarding the threat of predation in the individual species accounts in **Section 4** of this report.

## 3.4 Inadequacy of Existing Regulatory Mechanisms

Giant clams are protected to varying degrees by a patchwork of regulatory mechanisms implemented by the many countries, territories and tribal entities within their range. These local-scale measures are also supplemented by CITES international trade regulation, and in some areas, by multi-national initiatives aimed at supporting sustainable regional giant clam fisheries. We address each of these regulatory mechanisms in the following section and also include a brief discussion of international climate change regulations in the context of their potential effects on the extinction risk of giant clams.

### 3.4.1 Local Regulations

There is national legislation in place in more than 30 countries and territories specifically related to the conservation of giant clams (see Appendix 1). Many also provide indirect protection via marine parks and preserves or ecosystem-level management plans. In general, management of giant clam populations has been most effective in Australia, where early harvest prohibitions and strict enforcement have been largely successful in stabilizing giant clam population declines and limiting illegal poaching (S. Wells et al., 1983; Dawson, 1986; Lucas, 1994). Many Pacific Island nations have also implemented strict measures to mitigate fishing pressure on giant clams. These include total bans on commercial harvest and export of giant clams (e.g., Fiji, Papua New Guinea, Solomon Islands, Vanuatu, FSM, Guam, Republic of Kiribati and Palau), minimum size limits for subsistence harvesting (e.g., French Polynesia, Niue, Samoa, American Samoa and Tonga), harvest quotas or bag limits (e.g., New Caledonia and the Cook Islands), and gear restrictions on the use of SCUBA or certain fishing equipment (Andréfouët et al., 2013; Kinch & Teitelbaum, 2010; Neo et al., 2017). In many Pacific Islands, national legislation is also supplemented or enforced by way of customary fishing rights and marine tenure systems. This is the case in parts of Fiji, Samoa, Solomon Islands, Cook Islands, Papua New Guinea, and Vanuatu, where indigenous village groups hold fishing rights and regulate access to adjacent reef and lagoon areas (Govan et al., 1988; Fairbairn, 1992b, 1992a, 1992c; S. Wells, 1997; Foale & Manele, 2004; Chambers, 2007; UNEP-WCMC, 2012). The rights of each tribal group over its recognized fishing area include the right to carry out and regulate subsistence fishing activities. In certain circumstances, a local village or villages may impose temporary area closures to reduce harvesting pressure and allow giant clam stocks to recover (Foale & Manele, 2004; Chambers, 2007). The effectiveness of these measures, however, is variable, and with limited capacity for long-term monitoring programs in the region, it can be difficult to properly assess. In general, anecdotal reports indicate that giant clam populations throughout the Indo-Pacific region continue to face severe stress (Neo et al., 2017).

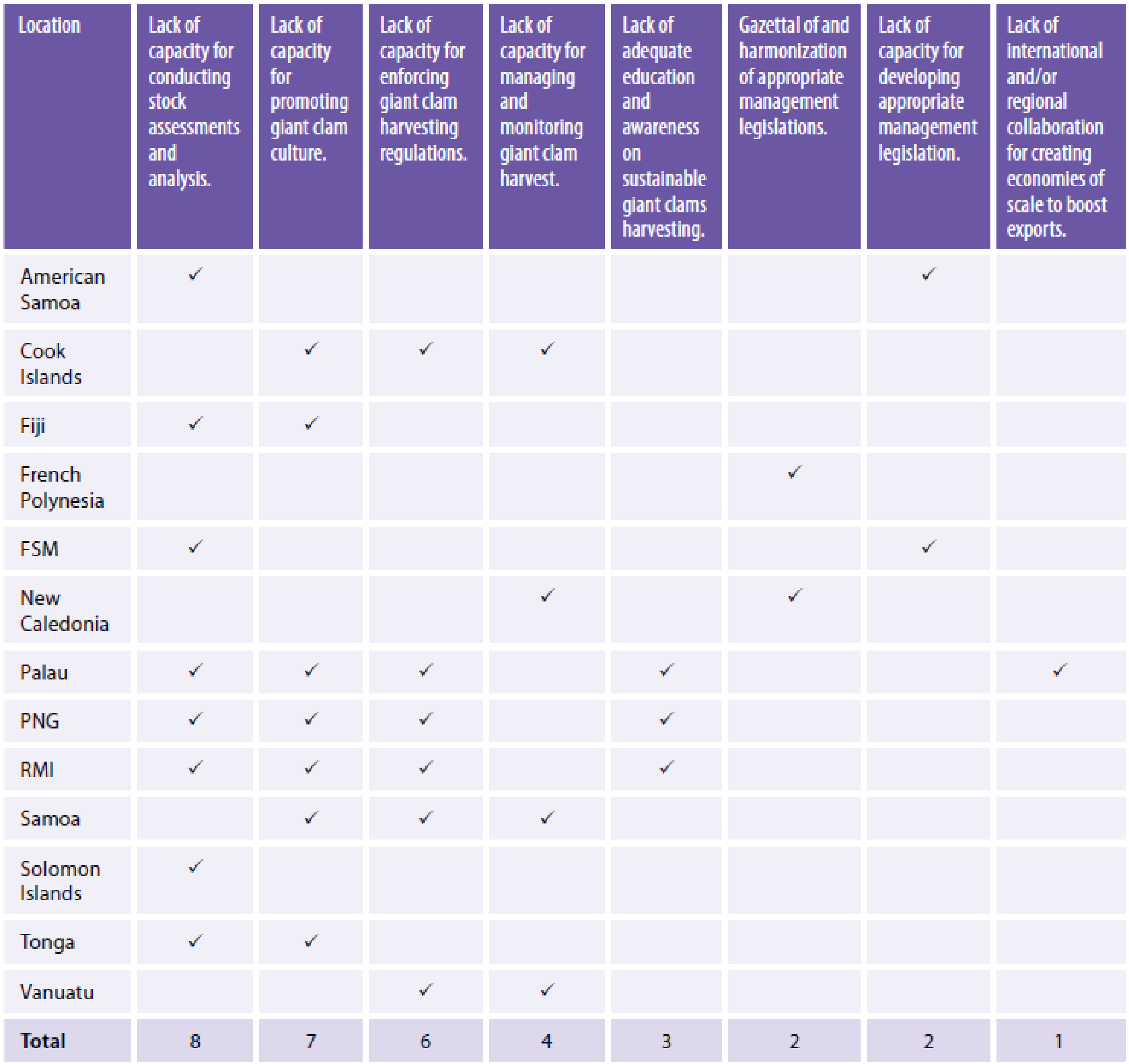
In the Philippines, for example, numerous reports following the giant clam export ban in 1990 suggested problems with enforcement, particularly within Badjao communities. The Badjao people live a predominantly seaborne lifestyle and are spread across the coastal areas of the southern Philippines, Indonesia, and Malaysia, with a total population estimated to be around one million (Government of the Philippines National Statistics Office, 2013; Rincon, 2018). Many in these communities were encouraged by buyers to collect and stockpile giant clam shells in the hope that the ban would eventually be lifted (Salamanca & Pajaro, 1996; S. Wells, 1997). Middlemen would reportedly advance money and provisions to fishermen on the condition that the shells be sold to them exclusively. The Badjaos would then harvest clams, consume or discard the meat and stockpile the shells (Salamanca & Pajaro, 1996). The non-compliance was exacerbated by inconsistent interpretations of the law by Philippine authorities, who issued numerous CITES export permits in 1991-1992 under the presumption that the law excluded ‘pre-ban stock’ (S. Wells, 1997). The ban was ultimately never lifted, and CITES reports indicate that the legal export of giant clams has ended in the Philippines. However, a recent report by the Wildlife Justice Commission (2021) found that authorities have continued to find stockpiles of giant clam shells throughout the country. They have made 14 seizures from 2016 to 2021, including that of a 132,000-ton stockpile in the southern Philippines in October 2019 and several stockpiles in the Palawan area, one of the centers of giant clam abundance in the region (Figure 13). It is unclear how many of the shells were collected prior to the ban in 1990 versus how many were collected illegally in the years since, but it suggests that the market for giant clam shells remains active more than 30 years after the ban was instituted. In an interview with ABS-CBN News (2021), Teodoro Jose Matta, executive director of Palawan Council for Sustainable Development, claimed that the clams are being smuggled to Southeast Asia and Europe and attributed the activities to a criminal syndicate operating across the Philippines, not just in Palawan. To our knowledge, these claims have not been corroborated by authorities.

**Figure 13.** Recent seizures of giant clam shell stockpiles in the Philippines. The **top** image is of a 132,000 ton stockpile seized in General Santos City, southern Philippines in October 2019 (Source: Jun Pulido via Philippine News Agency). The **bottom** image is of a 200 ton stockpile seized in the Palawan region in April 2021 (Source: Philippine Coast Guard via AP)

From recent surveys in Tubbataha Reefs Natural Park, an area near Palawan that had been intensively exploited in the 1980s, Mecha and Dolorosa (2020) report that "after 30 years of protection, […] eight individuals *T. gigas* [sic] were encountered between 2014 and 2018 […] and other medium-sized species such as *Tridacna derasa* and *Tridacna squamosa* also remained rare at TRNP (Dolorosa and Jontila, 2012; Dolorosa and Schoppe, 2005; Dolorosa et al. 2015)." In fact, given the limited success of existing regulations, the authors highlight "the essential contributions" of the hotel and resort industry in giant clam conservation based merely on the presence of 12 *T. gigas* individuals at four resorts in Palawan.

Similar confusion over giant clam harvesting regulations has impeded the effectiveness of management in Papua New Guinea. An initial ban on the purchase and export of wild-caught giant clams was put in place in 1988 by the Department of Environment and Conservation (DEC) (Kinch, 2002; UNEP-WCMC, 2011). It was then lifted in 1995 following the development of a management plan for sustainable harvest. However, Kinch (2002) noted that although the Milne Bay Province Giant Clam Fishery Management Plan had been drawn up by the National Fisheries Authority (NFA) – the CITES Scientific Authority for Papua New Guinea – it was never officially adopted "owing to confusion between the NFA and the DEC over responsibility for the enforcement of the plan and because of opposition from commercial and political interests." The ban was reinstated in 2000 following reports that a local fishing company had been mislabeling their exports of wild-caught specimens as captive-bred. Kinch (2002) suggested that further "conflict and confusion between the fisheries and environmental legislation" ensued and recommended that it be addressed to ensure the success of the regulation. According to J. Kinch (pers. comm., March 18, 2023), NFA regulations on the purchase and export of giant clams are still in place as of 2023. However, the last known monitoring survey in Papua New Guinea was conducted in 2001 (Skewes et al., 2003). Without more recent data, we cannot determine whether the regulatory actions have had any effect on the low abundance of giant clams in this region.

Furthermore, despite various levels of harvest and export prohibitions among many of the Pacific island nations, Kinch and Teitelbaum (2010) highlight a number of common challenges to ensuring sustainable giant clam management in these communities (Figure 14). This includes a lack of capacity for conducting stock assessments, promoting giant clam mariculture, enforcing harvesting regulations, and monitoring and actively managing giant clam harvest. The list also includes a lack of education and awareness among community members about sustainable giant clam harvest, an uncoordinated legislative structure, and a lack of international collaboration to promote a sustainable and scalable market for captive-bred giant clams. According to the assessment by Kinch and Teitelbaum (2010), each of the countries experiences these challenges to a different degree, but overall it highlights the difficulties in effectively managing giant clam populations for smaller island nations that may lack enforcement resources or expertise. This is compounded, in many cases, by the traditional importance of giant clams as a coastal resource, which may limit the willingness among indigenous communities to adopt the recommended practices (Neo et al., 2017).



| Location | Lack of capacity for conducting stock assessments and analysis. | Lack of capacity for promoting giant clam culture. | Lack of capacity for enforcing giant clam harvesting regulations. | Lack of capacity for managing and monitoring giant clam harvest. | Lack of adequate education and awareness on sustainable giant clams harvesting. | Gazettal of and harmonization of appropriate management legislations. | Lack of capacity for developing appropriate management legislation. | Lack of international and/or regional collaboration for creating economies of scale to boost exports. |
|---|---|---|---|---|---|---|---|---|
| American Samoa | ✓ |  |  |  |  |  | ✓ |  |
| Cook Islands |  | ✓ | ✓ | ✓ |  |  |  |  |
| Fiji | ✓ | ✓ |  |  |  |  |  |  |
| French Polynesia |  |  |  |  |  | ✓ |  |  |
| FSM | ✓ |  |  |  |  |  | ✓ |  |
| New Caledonia |  |  |  | ✓ |  | ✓ |  |  |
| Palau | ✓ | ✓ | ✓ |  | ✓ |  |  | ✓ |
| PNG | ✓ | ✓ | ✓ |  | ✓ |  |  |  |
| RMI | ✓ | ✓ | ✓ |  | ✓ |  |  |  |
| Samoa |  | ✓ | ✓ | ✓ |  |  |  |  |
| Solomon Islands | ✓ |  |  |  |  |  |  |  |
| Tonga | ✓ | ✓ |  |  |  |  |  |  |
| Vanuatu |  |  | ✓ | ✓ |  |  |  |  |
| **Total** | 8 | 7 | 6 | 4 | 3 | 2 | 2 | 1 |

**Figure 14.** Challenges facing Pacific Island countries and territories with ensuring sustainable giant clam management. FSM – Federated States of Micronesia, PNG – Papua New Guinea, RMI – Republic of the Marshall Islands (Source: Kinch and Teitelbaum, 2010).

In addition to the two examples above, there are a number of other reports highlighting the shortcomings of local regulations throughout the Indo-Pacific region. In Malaysia, and particularly in Borneo, illegal collection of giant clams was reported to occur despite a complete prohibition on the collection of giant clams (Ibrahim & Ilias, 2006). We could not find a more recent account of these activities, so it is unclear whether significant illegal harvest is still ongoing. In the Solomon Islands, commercial harvest and export was banned in 1998, but CITES records indicate that export of wild-sourced clams and shells from the Solomon Islands has continued to occur throughout the 2000s and as recently as 2015 (Figure 8, 12). S. Yusuf and Moore (2020) note that despite being fully protected under Indonesian law and widespread public awareness of associated harvest prohibitions, giant clams are still harvested regularly in the Sulawesi region of Indonesia, including mass collections for traditional festivals. When asked about enforcement of legal protections, locals explained that surveillance in certain areas was generally absent (or at best sporadic and ineffective), and throughout the region was "minimal, often perceived as misdirected and/or unfair, and mostly ineffective." Due in part to the ineffectiveness of the existing regulations, S. Yusuf and Moore (2020) have documented progressive declines in giant clam populations (except *T. crocea*) from 1999 to 2002, 2007, and 2015, with "some larger species (*Tridacna gigas*, *T. derasa*, *T. squamosa*, and *Hippopus porcellanus*) no longer found at many sites." A low abundance of *T. squamosa*, *T. derasa*, *T. gigas*, and *H. hippopus* has also been observed in the Anambas Islands of Indonesia, where Harahap et al. (2018) report ongoing harvesting and habitat destruction. In Mauritius, giant clams are protected under the Fisheries and Marine Resources Act of 2007, but a recent study shows continued population declines even within marine protected areas (Ramah et al., 2018). There are few studies highlighting the success of local regulations, but Rossbach et al. (2021) report based on interviews with local fishermen that giant clams are no longer targeted in Saudi Arabia since a harvest prohibition was imposed in the early 2000s. As noted above, a general lack of any systematic giant clam monitoring programs constrains our assessment to mostly anecdotal accounts. Those accounts, however, largely report declining populations of the seven giant clam species addressed in this status review.

## 3.4.2 International Regulations

***Regulations for International Trade***

CITES governs the international trade of Convention-listed species. Giant clams are listed under Appendix II of CITES, which consists of species that "are not necessarily now threatened with extinction, but may become so unless trade is closely monitored." This designation does not necessarily limit trade of the species, but instead requires that any species in trade has been legally acquired and a finding that trade is not detrimental to the survival of the species by the exporting Party's Scientific Authority. *Tridacna gigas* and *T. derasa* were the first giant clams listed in Appendix II in 1983. The remaining species were listed in 1985 due to difficulty in distinguishing between listed and unlisted species (S. Wells, 1997). CITES regulates all international trade in giant clams (including living or dead and captive-bred specimens) and requires the issuance of export permits and re-export certificates. Clams bred in captivity for commercial purposes (e.g., global marine aquarium trade) must have appropriate CITES permits issued for export as well (Kinch & Teitelbaum 2010). For each listing, a Party may take a reservation to that listing, meaning the Party will not be bound by the provisions of the Convention relating to trade in that species. While the reservation is in effect, the Party is treated as a non-Party regarding trade in the particular species. Currently, Palau has reservations on all of the giant clam listings. Parties with reservations or other non-Parties that trade with a CITES Party, are required to have documentation comparable to CITES permits. It is up to the Party state receiving the export whether to accept this documentation in lieu of CITES permits. Parties are advised only to accept documentation from authorities that are the equivalent of a Scientific Authority and are registered with the CITES Secretariat (Wells, 1997). To identify species that may be experiencing unsustainable levels of international trade and to identify problems and solutions concerning the implementation of CITES, a Review of Significant Trade may be conducted. A Significant Trade Review was conducted for several species of giant clam in 2004, and the associated results of that review are discussed in the individual species accounts.

Effective enforcement of CITES is largely dependent on whether the countries involved are signatories to the Treaty, as well as the accuracy of trade data supplied by the Parties (Wells, 1997). In the past, countries such as the Maldives were significantly involved in the giant clam trade, but were not Parties to the Convention, which hampered the implementation of CITES regulations (S. Wells, 1997). (The Maldives joined CITES in 2012.) In fact, even in instances where exporting countries are Parties to CITES, the trade data must be interpreted cautiously for reasons that include frequent discrepancies in recorded import and export quantities, inconsistencies in the terms or units used to describe the trade, occasional omissions of seized or confiscated specimens, erroneous data entry (e.g., wrong source code, submission of the number of permits issued instead of actual numbers of clams traded), and delays or failure to submit trade statistics to the Secretariat (UNEP-WCMC, 2012; CITES, 2013; Neo et al., 2017). Unsustainable trade is often caused by unauthorized or illegal trade occurring alongside legal trade, which happens when there are limited resources to sufficiently monitor the trade (Kinch & Teitelbaum 2010). Another common challenge affecting the effectiveness of CITES is a lack of knowledge and capacity to implement and enforce the provisions of the Treaty, especially in Pacific Island nations (Kinch & Teitelbaum 2010).

Based upon known seizures, refusals, and abandonments of shipments, illegal trade of giant clams to the United States from 2007-2016 involved 314 illegal exports from approximately 23 countries, totaling 4,562 clam specimens and mostly consisting of shells. This is likely a significant underestimate of the total amount of giant clam that is exported to and enters the United States, as many shipments likely make it past enforcement inadvertently (Keith Swindle, pers. comm., December 2017). Based on the continued shipments in spite of numerous seizures, it is possible that enough illegal shipments are successfully imported that it is profitable to risk the seizure of the shipment. In addition to regular illegal exports to the United States, similar shipments are sent to other countries, such as Australia and New Zealand (Keith Swindle, pers. comm., December 2017).

### ***Regulations to Address Climate Change***

In the final rule to list 20 reef-building corals under the ESA (79 FR 53851, September 2014), we assessed the adequacy of existing regulatory mechanisms to reduce global greenhouse gas (GHG) emissions and thereby prevent widespread impacts to corals and coral reefs. We concluded that existing regulatory mechanisms were insufficient to achieve this aim. Since the publication of that final rule, 197 countries and the European Union (EU) adopted the Paris Agreement on climate change, which set a goal of limiting the global temperature increase to below 2°C and optimally keeping it to 1.5°C above pre-industrial levels by 2100. Since the Agreement was entered into force on November 4, 2016, 191 countries and the EU have ratified or acceded to its provisions, and each Party has made pledges to decrease GHG emissions to achieve its goals (UNFCC, 2018). The United States, which currently accounts for one-fifth of the world's emissions, pledged to cut its emissions by 26-28%. However, according to a 2021 Synthesis Report published by the United Nations Framework on Climate Change, the current emissions trajectories and proposed climate actions by all 191 Parties are expected to lead to a 16% increase in GHG emissions by 2030 compared to 2010, rather than the 45% or 25% reduction necessary to limit the temperature increase to 1.5°C or 2°C, respectively. The current trajectory will lead to an estimated global temperature increase of around 2.7°C by the end of the century (UNFCC, 2021).

At this rate, unless emissions reduction goals are significantly strengthened, van Hooidonk et al. (2016) project that over 75% of coral reefs will experience annual recurrence of severe bleaching events before 2070. Even if implementation of the Paris Agreement successfully limits global warming to 1.5°C above pre-industrial by 2100 as intended (i.e., <0.5°C of additional warming above current levels), coral reefs will likely suffer substantial degradation, as additional warming would exacerbate the conditions that have led to their current downward trajectory (Hughes, Barnes, et al., 2017; Lough et al., 2018; IPCC, 2018, 2022). Thus, while meeting the objectives of the Paris Agreement would be a great improvement over current implementation, stronger action is necessary to potentially stabilize the trend of coral reef degradation and allow recovery.

As described in **Section 3.1.1,** while there is clear evidence that coral reefs, which are an important giant clam habitat, will undergo substantial changes as a result of ocean warming and acidification, it is unclear whether and to what degree the changes in coral reef composition and ecological function will affect the extinction risk of giant clams. Available research suggests that coral reef degradation will affect the ability of certain giant clam species (e.g., *T. squamosa*) to recruit to suitable habitats (see **Section 3.1.1**). In addition, as discussed in **Sections 3.5.1** and **3.5.2** below, it is likely that giant clams themselves will suffer physiologically as a result of climate change impacts. Ocean warming has been shown to reduce the symbiotic function of giant clams and can cause bleaching of the clam tissue (i.e., expulsion of their symbiotic algae). There is also limited evidence that giant clams (particularly juveniles) may suffer reduced growth due to ocean acidification, although experimental results at this point are not conclusive. Considering these potential impacts collectively and given the limited progress towards achieving the goals of the Paris Agreement, we conclude that current implementation of domestic and international climate regulations is insufficient to mitigate the cumulative threat of climate change to giant clam habitat and physiology.

## 3.5 Other Natural or Manmade Factors

There are several other natural or manmade factors that impact giant clams, such as ocean warming and acidification, coastal pollution and sedimentation, and stochastic mortality events. Below, we discuss each of these factors in detail, and where sufficient information is available, we evaluate the severity of the associated threat to giant clams.

### 3.5.1 Ocean Warming

As discussed in **Section 2.4**, giant clams associate symbiotically with a diverse group of dinoflagellates of the family *Symbiodiniaceae*. Known as zooxanthellae, these symbiotic algae reside within a network of narrow tubules that branch off the primary digestive tract and spread throughout the upper layers of the mantle (Norton et al., 1992). Giant clams provide dissolved inorganic nutrients to the zooxanthellae via direct absorption from the seawater or as an excretory byproduct of respiration. In return, they receive photosynthetic carbon in the form of glucose, glycerol, oligosaccharides and amino acids, comprising the majority of their metabolic carbon requirements (Klumpp et al., 1992; Hawkins & Klumpp, 1995). Exposure to stressful environmental conditions, however, can cause dysfunction in the symbiosis and, in extreme cases, can lead to a bleaching response wherein the zooxanthellae are expelled from the mantle tissue. When they bleach, giant clams lose a critical source of nutrition and experience drastic changes to their physiology, including decreased glucose and pH in the haemolymph, an increased concentration of inorganic carbon (e.g., $CO_2$ and $HCO_3^-$), and a reduced capacity for ammonium assimilation (Leggat et al., 2003).

Elevated temperatures, in particular, are known to induce bleaching in giant clams. Widespread bleaching of giant clams was observed in the central Great Barrier Reef, Australia in 1997-1998, when elevated water temperatures in conjunction with low salinity caused 8,000 of 9,000 surveyed *T. gigas* to experience varying levels of bleaching (Leggat, pers. comm., cited in Buck et al., 2002; Leggat et al., 2003). Some individuals suffered a complete loss of symbionts, while others were only affected in the central part or at the margins of the mantle tissue (Grice, 1999). A follow-up experiment designed to replicate the environmental conditions during this event demonstrated that elevated temperatures combined with high solar irradiance induced a consistent bleaching response in *T. gigas* (Buck et al., 2002). Populations of *T. squamosa* and *T. crocea* around Mannai Island, Thailand also suffered extensive bleaching in mid-2010 due to prolonged exposure to temperatures averaging 32.6°C (Junchompoo et al., 2013). Bleaching was recorded in every *T. squamosa* specimen observed (n = 12), of which only four individuals recovered while the remaining two-thirds died (Junchompoo et al., 2013).

While the appearance is similar to the bleaching response observed in corals (see **Section 3.1.1**), bleaching of giant clams is unique in two important ways. First, the mechanics differ on account of the zooxanthellae residing extracellularly in giant clams. Rather than being expelled from host cells, as is the case with corals, zooxanthellae are thought to be driven out of the giant clam tubular system via long cilia and expelled through the digestive tract (Norton & Jones, 1992; Norton et al., 1995). The expulsion of algal cells is associated with atrophy of the tertiary zooxanthellae tubes, which is thought to inhibit recovery (Norton et al., 1995). According to one account, some adult *T. gigas* have remained partially bleached for more than a year (R. Braley, pers. comm., cited in Norton et al., 1995). Second, there is evidence that giant clams are more resilient to bleaching than corals and can tolerate temperature stress for longer (Grice, 1999; Buck et al., 2002; Leggat et al., 2003). According to Leggat et al. (2003), of 6,300 *T. gigas* that bleached at Orpheus Island, Australia in 1998, over 95% completely recovered after 8 months. Similarly, at the Lakshadweep Islands in India, Apte et al. (2019) found that sustained mean summer temperatures above 30°C triggered bleaching in *T. maxima*, but that bleaching did not cause immediate mortality. Moreover, during the three global-scale coral bleaching events when anomalous warming caused widespread mortality of stony corals (see **Section 3.1.1**), reports of giant clam bleaching have been sparse and variable across species and geography. Neo et al. (2017) reported that in 2016, "*Tridacna maxima* did not bleach in Mauritius (R. Bhagooli, pers. comm., cited in Neo et al., 2017), but those in Singapore (M. L. Neo, pers. obs.), Guam (A. Miller, pers. comm., cited in Neo et al., 2017), and East Tuamoto (S. Andréfouët, pers. comm., cited in Neo et al., 2017) were bleached severely." At Lizard Island, Australia, *T. gigas* suffered "much lower" mortality than *T. derasa* and *T. squamosa* during the 2016 event (A. D. Lewis, pers. comm., cited in Neo et al., 2017). Actual mortality rates were not provided.

Even in the absence of bleaching, warming-related stress can profoundly impact the growth and reproduction of giant clams. Growth rate in giant clams tends to follow a standard thermal performance curve whereby growth is positively correlated with temperature up to a thermal optimum (Pearson & Munro, 1991; Hart et al., 1998; Schwartzmann et al., 2011; Van

Wynsberge et al., 2017). Beyond this point, further warming can cause shell growth to become erratic and slow down significantly (Schwartzmann et al., 2011; Syazili et al., 2020). Excessive warming has also been shown to lower fitness by reducing photosynthetic yield (Brahmi et al., 2021), altering the photosynthesis-respiration ratio (Braley et al., 1992; Blidberg et al., 2000; Elfwing et al., 2001), reducing the strength and carbonate content of the shells (Syazili et al., 2020), and reducing fertilization success (Armstrong et al., 2020). Early life stages are thought to be particularly sensitive to these impacts, as warming has been shown to speed up the progression through early development, leading to abnormal development, reduced settlement, and lower overall juvenile survival (Watson et al., 2012; Neo et al., 2013; Enricuso et al., 2019).

As discussed in **Section 3.1.1**, much of the equatorial western Pacific is projected to encompass ocean warming "hot spots," where the rate and intensity of rising temperatures will outpace the global average (Teneva et al., 2011; Lough, 2012; van Hooidonk et al., 2013). Many of these areas overlap the center of giant clam abundance and diversity in the Indo-Pacific, leaving populations that occur in these locations especially vulnerable to future temperature stress. The local and regional heterogeneity in projected ocean warming across the range of giant clams will likely result in highly variable impacts across spatial scales. Species restricted to areas where warming is predicted to be faster and more severe will likely be at a higher risk of warming-induced stress and potential mortality than other species.

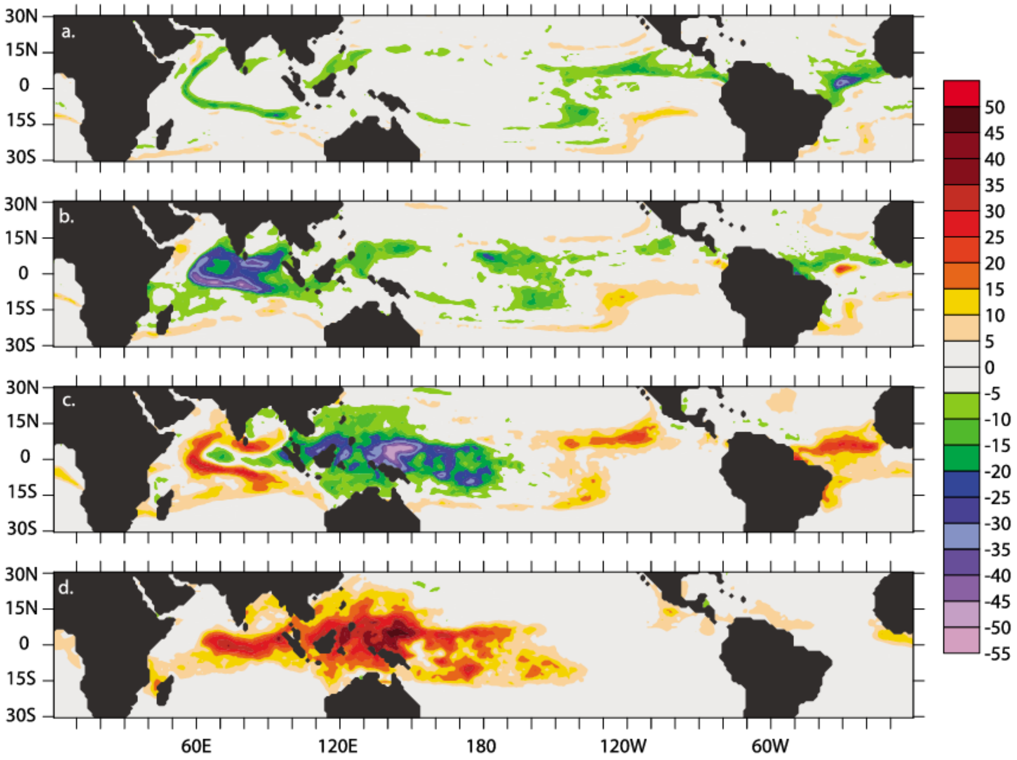


**Figure 15.** Percentage difference in months (1981–2011)–(1950–1980) within various SST ranges: (a) 26°C–27°C, (b) 27°C–28°C, (c) 28°C–29°C, and (d) 29°C–30°C. The percentage of months within each temperature range were first calculated for the two time periods, and the difference was then calculated to demonstrate a clear shift in the amount of time many areas of the Indo-Pacific are exposed to the highest temperatures. (Source: Lough, 2012).

Given the observed warming-induced impacts on giant clams, including altered growth and physiology, lower reproductive success, reduced juvenile survival, and in extreme cases, bleaching and mortality, we conclude that projected ocean warming will likely pose a significant threat to giant clams in general. Species-specific differences in susceptibility and the level of risk that ocean warming likely poses to each species will be addressed in **Section 4** of this report.

### 3.5.2 Ocean Acidification

Ocean acidification may also pose a significant risk to giant clams, based primarily on experimental evidence from other shelled mollusks. In two comprehensive literature reviews, both Parker et al. (2013) and Gazeau et al. (2013) concluded that the consequences of ocean acidification for calcifying marine organisms (and mollusks in particular) are likely to be severe, as they rely on the uptake of calcium and carbonate ions for shell growth and calcification. Yet, while many studies have demonstrated a negative effect on the growth of marine mollusks, some species have shown no response or even a positive growth response to ocean acidification (Ries et al., 2009; Gazeau et al., 2013; Parker et al., 2013). There is more consistent evidence that early life stages of shelled mollusks are highly sensitive to ocean acidification, with observed impacts including smaller-sized embryos and larvae, decreased shell thickness, increased larval development time, reduced survival, reduced metamorphosis, shell abnormalities, altered behavior, and alterations in the accumulation of heavy metals (reviewed in Parker et al., 2013; Gazeau et al., 2013). Fertilization success is largely unaffected except under the most extreme acidification scenarios (Gazeau et al., 2013; Parker et al., 2013).

With respect to giant clams specifically, experimental data on the effects of ocean acidification are limited and similarly inconclusive. Syazili et al. (2020) found that juvenile *T. squamosa* exhibited decreased growth and weaker shell structure under elevated $pCO_2$; however, Armstrong et al. (2022) found the opposite, that growth rates of juvenile *T. squamosa* were enhanced under acidification treatments. Watson et al. (2012) found that juvenile *T. squamosa* suffered greater mortality when exposed to elevated $pCO_2$ (see also Syazili et al., 2020), and fertilization success of *T. maxima* was found to be unaffected (Armstrong et al., 2020). Lastly, in comparing the growth and survival of four giant clam species in conditions approximating future ocean acidification scenarios, Toonen et al. (2011) found the responses to vary among species. *T. maxima* and *T. squamosa* had significantly lower growth rates in low pH, *T. derasa* had a significantly higher growth rate, and *T. crocea* was not significantly different between low pH and ambient seawater. The authors concluded that "such strong species-specific differences and interactions among treatment variables […] caution against broad generalizations being made on community effects of ocean acidification from single-species laboratory studies" (Toonen et al., 2011).

Research on marine mollusks generally suggests that the synergistic effects of ocean acidification and warming may be greater than the effect of acidification alone (Parker et al., 2013); however, for giant clams, the available information is again inconclusive. The results of Syazili et al. (2020) seem to show a synergistic effect between temperature and $pCO_2$ with respect to shell growth and survival of juvenile *T. squamosa*, but it is not clear whether their statistical analysis corroborates this conclusion. Additionally, neither Armstrong et al. (2020), Brahmi et al. (2021), nor Armstrong et al. (2022) found evidence for an interactive effect with respect to fertilization success of *T. maxima*, photosynthetic yield of *T. maxima*, or shell growth of *T. maxima* or *T. squamosa*. Thus, we cannot conclude that the potential effects of ocean acidification on the growth or survival of giant clams will be exacerbated by rising temperatures.

Lastly, to reiterate an important caveat addressed in **Section 3.1.1**, ocean acidification will likely not affect all regions uniformly, as seawater carbonate dynamics are highly dependent on many local-scale factors, such as temperature, proximity to land-based runoff, proximity to sources of oceanic $CO_2$, salinity, nutrients, as well as ecosystem-level photosynthesis and respiration rates. This makes it difficult to assess how ocean acidification is impacting giant clams currently or may impact them in the future. For this reason, and given the existing uncertainty regarding the effects of ocean acidification on giant clams, there is not sufficient information to further consider this potential threat in the extinction risk assessments for each species.

### 3.5.3 Land-Based Sources of Pollution

Giant clams are also susceptible to land-based sources of pollution, including sedimentation, elevated nutrients, salinity changes, and exposure to heavy metals. Together, these factors represent environmental conditions that giant clams may experience following heavy rains, particularly near coastlines that have been altered by human development. In its Sixth Assessment Report, the Intergovernmental Panel on Climate Change (IPCC) found that the frequency and intensity of heavy rainfall events have likely increased globally since the pre-industrial era and projected that this trend is “virtually certain” to continue with additional global warming (Seneviratne et al., 2021). The IPCC also found it “likely” that annual precipitation will increase over the equatorial Pacific and monsoon regions under a business-as-usual scenario, and projected with “medium confidence” that flooding and associated runoff will increase over parts of South and Southeast Asia by 2100 (Douville et al., 2021). Thus, it is likely that giant clams will face an increasing occurrence of heavy rain events, runoff, and associated changes to water quality throughout much of their range.

***Sedimentation***

Available evidence suggests that the impacts of sedimentation may vary between species. Reduced light levels associated with sedimentation have been shown to significantly decrease the growth rate of *T. squamosa* (Beckvar, 1981; Foyle et al., 1997; Guest et al., 2008), likely by limiting the photosynthetic potential of the symbiotic algae (Jantzen et al., 2008; Przeslawski et al., 2008). However, *in situ* observations from Pioneer Bay, Australia revealed that *T. gigas* grow faster in more turbid conditions compared to two offshore sites (Lucas et al., 1989). These contrasting results may be indicative of differences in nutritional strategy between species (Klumpp et al., 1992; see **Section 2.4**), suggesting that certain species can compensate for the reduction in photosynthetic yield by increasing the relative contribution of heterotrophy. Based on these differences in life history strategy, Braley (1987a) hypothesized that the observed distribution of *T. derasa*, which was restricted to clear, oceanic environments on the Great Barrier Reef, may reflect this species’ high sensitivity to turbidity.

Sedimentation can also lead to behavioral modification. Chronic exposure to sediment-laden water induced *T. squamosa* juveniles to partially or fully contract their mantle, and in some cases they have been observed expelling sediment from their mantle cavity by forcefully ejecting water using muscle contractions (Elfwing et al., 2001; Soo & Todd, 2014). These behavioral changes are likely detrimental to the fitness of giant clams—repeated mantle exhalations can be energetically costly, while chronic retraction of the mantle will limit its exposure to light and thereby inhibit photosynthesis. However, these potential effects have not been quantified in giant clams. Similarly, while some researchers assert that sedimentation may impede larval settlement, physically interfere with feeding, and result in damage to the gills (Neo & Todd, 2012a), these concerns are based on findings from other reef invertebrates; we could not find direct evidence of these effects in giant clams.

### *Salinity, Nutrients, and Heavy Metal Exposure*

Giant clams are also sensitive to variations in salinity, nutrients, and heavy metal concentrations. Blidberg (2004) showed that a reduction in salinity significantly decreased the survival rates of *T. gigas* larvae. Only 1.1% and 2.2% of larvae survived when exposed to salinities of 20‰ and 25‰, respectively, compared to a survival rate of 4.2% in the 32‰ control. Maboloc et al. (2014) also found that lower salinity (18‰ and 25‰ vs. 35‰) reduced the feeding capacity of juvenile *T. gigas* due to alteration of the digestive membrane. The same effects, however, were not observed for *T. squamosa*, as a milder salinity reduction (27‰ vs. 30‰) led to an increase in the survival of *T. squamosa* trochophores and no significant effect on the survival of *T. squamosa* embryos (Neo et al., 2013).

Extreme reductions in salinity have been shown to alter the behavior of early life stages. *T. squamosa* trochophores and veligers stopped swimming and sank to the bottom of an experimental tank when exposed to salinities of 9‰ and 12‰; although, once conditions returned to normal, the larvae resumed normal swimming functions within an hour (Eckman et al., 2014). Likewise, late-stage pediveligers withdrew their mantle tissues and siphons and closed their valves when inundated in freshwater, but recovered within 30 minutes of being returned to normal seawater (Eckman et al., 2014). These results provide some evidence that giant clams may be able to withstand temporary salinity fluctuations. However, it is unlikely that they would experience such extreme conditions *in situ*. For example, in October 2010, immediately after a week-long heavy rainfall in the Bolinao region of the Philippines brought by Typhoon Megi, salinity at a coastal giant clam nursery was measured to be 25‰ (Maboloc et al., 2014). Moreover, salinity at 2-m water depth recorded in June and July 2011, which coincided with two tropical depressions in the region, only fell to 27-32‰.

Regarding dissolved nutrients, there is consistent evidence that nitrogen enrichment increases the density of zooxanthellae in the clam tissue (Braley et al., 1992; Belda, Lucas, et al., 1993; Belda-Baillie et al., 1999) and, in most cases, enhances the growth rate of giant clams. The addition of inorganic nitrogen led to a near doubling of the growth rate of young juvenile *T. derasa* (< 1 cm) and a 20% increase in shell length in older juveniles over controls (Heslinga et al., 1990). Similarly, *H. hippopus* juveniles exhibited a 110% increase in growth per month when exposed to elevated nitrogen (Solis et al., 1988). Nitrogen enrichment has also been shown to enhance the shell and tissue growth of *T. gigas* (Belda, Cuff, et al., 1993; Belda, Lucas, et al., 1993). For *T. maxima*, growth in mean wet weight and shell length of older juveniles increased significantly when exposed to elevated ammonium, but decreased for the smallest size class (< 5 mm) (Grice & Bell, 1999). Responses to phosphate enrichment are not as straightforward. Belda, Cuff, et al. (1993) found that exposure to phosphate alone did not enhance the growth rate of *T. gigas* in the same way as nitrogen. In fact, in a combined treatment of nitrogen and phosphate enrichment, the authors attribute an increase in shell porosity to the inhibitory effect of phosphate in the deposition of calcium in skeletal structures.

Elevated heavy metals contribute to the environmental stress factors in contaminated waters near human development. For instance, in the Cook Islands, giant clams collected from the populated Pukapuka Atoll had significantly higher concentrations of iron, manganese, zinc, and lead than clams from the unpopulated Suvorov Atoll (Khristoforova & Bogdanova, 1981). Three related studies demonstrated that exposing *T. gigas*, *H. hippopus*, and *T. squamosa* to sub-lethal levels of copper (*T. gigas* and *H. hippopus*: 5 µg $l^{-1}$; *T. squamosa*: 50 µg $l^{-1}$) reduces photosynthetic activity and, in effect, significantly lowers the production-respiration ratio (Elfwing et al., 2001; Elfwing et al., 2002; Elfwing et al., 2003). This aligns with previous work showing that copper acts as an inhibitor in photosystem II (Cid et al., 1995 cited in Elfwing et al., 2001). In testing the limits of copper tolerance in *T. crocea*, Duquesne and Coll (1995) found that a copper concentration of 60 µg $l^{-1}$ induced bleaching, while 200 µg $l^{-1}$ caused 100% mortality. However, these levels are not realistic in a natural setting and simply demonstrate that the threshold of copper tolerance is quite high.

In most circumstances, however, it is unlikely that giant clams would experience only one of the aforementioned factors independent of the others. River outflows and runoff from heavy rain events will necessarily alter the salinity, and in most cases will also carry suspended sediments, dissolved nutrients, heavy metals, or a combination of the three to the nearshore environment. Blidberg (2004) suggests that synergistic effects of elevated heavy metal concentrations in combination with low salinity may be more detrimental to giant clams than either factor alone. At a relatively low dose of copper (2.5 µg $l^{-1}$), *T. gigas* larvae survival was not significantly altered, but combined with a moderate reduction in salinity (25‰ vs. 32‰), larval survival rate was decreased by nearly 75%. From these results, Blidberg (2004) hypothesized that chronically high copper concentrations and low salinity may explain the absence of giant clams near human settlements and river mouths. Likewise, in a global meta-analysis of *T. maxima* distribution, Van Wynsberge et al. (2016) found that, except for areas with very low human population density (<20 inhabitants per 10,000 $m^2$ of reef), *T. maxima* density decreased with increased human presence. A similar pattern was observed in the northern Red Sea, where the abundance of giant clams was higher at sites further away from human activity (Mekawy & Madkour, 2012).

Thus, while sedimentation, altered salinity, elevated nutrients, and heavy metals cause various impacts on giant clams independently, these results suggest that the collective changes to water quality associated with human activity are particularly detrimental to the survival of giant clams. It can be reasonably expected that any coastal development projects or land use change that alters one or more of these factors in nearshore waters will threaten the survival giant clams in general. Based on the available research presented above, we discuss any species-specific information regarding susceptibility or tolerance to these factors in **Section 4.**

### 3.5.4. Stochastic Events

Stochastic events include those events such as extreme weather and mass mortalities of unknown cause whose occurrence cannot be predicted with any precision.

### *Extreme Weather Events*

Extreme weather events such as typhoons and monsoons can cause widespread mortality of giant clams, particularly of smaller individuals in exposed environments. Lucas et al. (1989) found that storm surge and wave turbulence reduced the survival and growth rate of giant clams during the ocean-nursery rearing phase of a mariculture project in Queensland, Australia. Similarly, Barker and McKinnon (1993) reported heavy losses of captive-born juvenile clams from shallow, exposed portions of the Great Barrier Reef in Australia due to storms. In a giant clam restocking project conducted by Silliman University in the Philippines, the largest single cause of mortality was typhoons and monsoons at 35% (Lucas 1994). These reports from mariculture operations provide a plausible indication as to the potential impact of major storms on giant clams, but the degree to which storm damage affects natural populations is not apparent, as we could not find any surveys of natural populations following major storms. Self-righting behaviors have been described for both juvenile and adult giant clams, but the effects of repeated physical disturbances are unknown (Soo & Todd, 2014). Thus, while extreme weather events and storms can have significant effects on species with limited geographic ranges or may contribute to local extirpations of widespread species, the available data do not allow for a more detailed assessment of how this particular factor may be contributing to the extinction risk of the giant clam species addressed here.

### *Mass Mortalities of Unknown Cause*

Over the past few decades, there have been several reports of mass mortalities of giant clams without a definitive cause. For example, reports from Lizard Island, Great Barrier Reef indicated that 25% of *T. gigas* and *T. derasa* died during a 6-week period in mid-1985, and over the following 18 months, total mortality rates were 55-58% (Alder & Braley, 1988). The authors ruled out toxins, predators, environmental conditions, and old age as possible causes, and hypothesized that two pathogens that were observed (*Perkinsus* and an unknown protozoan) may be to blame. However, the findings were inconclusive, and the hypothesis was never confirmed. According to R. D. Braley (pers. comm., September 25, 2019), the occurrence of the initial mortality event during the austral winter is notable, as elevated mortality of cultured *T. gigas* was later observed during winter months at Orpheus Island Research Station. Extensive mortality was also reported in the early 1990s in the Solomon Islands, where *T. gigas* and *H. hippopus* were the main species affected (Gervis, 1992). Most recently, a mass mortality event involving *T. maxima* occurred at Tatakoto Atoll in French Polynesia, a site that had been known for its exceptional density of *T. maxima* (337 individuals per $m^2$). Following a survey in 2012, Andréfouët et al. (2013) determined (based on the age of juveniles that had settled inside dead shells) that a major mortality event had occurred approximately three years prior, which caused an 83% decline in *T. maxima* population density. The authors attributed the event to anomalous environmental conditions, including high temperatures and reduced water exchange within the atoll lagoon (Andréfouët et al. 2013)[1].

Importantly, although *T. maxima* is not under consideration in this status review, this mortality event highlights the unique environmental characteristics of semi-enclosed atoll lagoons, which are likely applicable to any species inhabiting these areas. Especially during calm

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[1] This information was discussed in the 90-day finding for 10 giant clam species, including *T. maxima* (82 FR 28946), in which we concluded that this event was an anomaly that did not, in and of itself, rise to the level of a threat that warranted further exploration in this status review.

summer weather, low wave conditions can isolate lagoon waters, leading to long residence times and low exchange with offshore water, while low wind speeds can shut down the wind-induced circulation, causing severe stratification and increasing the risk of hypoxia in subsurface waters (Andréfouët et al., 2015). These dynamics were thought to play a role in the mass mortality of *T. maxima* at Tatakoto Atoll and may elevate the risk of future mass mortality events at similar atolls that harbor other species of giant clams.

Mass mortality events represent a complex, unpredictable issue that can cause acute damage to giant clam populations with little forewarning. In each case, only certain giant clam species and certain areas were impacted by the mortality events, while other species, other bivalve mollusks, and other regions remained apparently unaffected (Lucas, 1994). In the context of this status review, the extinction risk associated with these stochastic events is likely most significant for species with a restricted range or with few remaining populations; although, their inherent unpredictability affords little confidence in any assessment regarding the time scale of this threat. Using available information, we address the threat of stochastic mortality events and these associated uncertainties on a case-by-case basis in the individual species accounts in **Section 4** of this report.

## 3.6 Summary of Threats

Giant clams face a wide variety of threats, both natural and anthropogenic. We agree with the conclusions of Neo et al. (2017) that historical and ongoing exploitation is likely the most important threat and conservation challenge for these species. Harvest for subsistence purposes or local sale is ongoing in many areas, and technological advancements in fishing, transport, and storage, combined with an increase in commercial demand for giant clams, have played a large role in the ongoing decline of wild populations (Neo et al., 2017). The best available information suggests that the largest species (*T. gigas* and *T. derasa*) have been selectively targeted for the commercial meat industry, which led to significant population declines and extirpations in many locations. The other smaller species have also been utilized for various purposes, including local consumption, and the commercial shell and aquarium trade, which has resulted in variable rates of decline. Moreover, existing regulations have failed to adequately protect giant clams from continued harvest in many countries and territories throughout their ranges, primarily due to poor enforcement and limited resources for monitoring. In the species accounts below, we discuss these threats in more detail as they pertain to each species and assess how each may be contributing to the species' extinction risk.

# 4.0 Individual Species Extinction Risk Assessments

In this section, we provide an assessment of each individual species' extinction risk. In determining the extinction risk of a species, it is important to consider both the demographic risks facing the species, as well as current and potential threats that may affect the species' status. To this end, we first conduct a demographic risk analysis following the Viable Population (VP) approach derived from McElhany et al. (2000), which addresses four biological descriptors of species status: abundance, productivity (i.e., population growth rate), spatial distribution, and diversity. The approach outlined in McElhany et al. (2000) reflects concepts that are well-founded in conservation biology and considers demographic factors that individually and collectively provide strong indicators of extinction risk. This analysis is designed to capture the biological symptoms of past threats that have contributed to the species' current status and provide insight into how the species may respond to present and future threats. Second, we synthesize the information provided in **Section 3** regarding the five threat categories listed in Section 4(a)(1) of the ESA, tailoring and supplementing each section with information that is pertinent to the respective species.

With respect to each demographic risk factor and each threat, we assign a qualitative score from 1 to 5 representing its estimated contribution to the species' extinction risk ("very low," "low," "moderate," "high," or "very high" risk). Definitions for each scoring level are included in Box 1 below. We also assign a confidence rating from 0 to 3, reflecting the quantity and quality of information used to assign the score, as follows:

0 = No confidence: No information.
1 = Low confidence: Very limited information
2 = Medium confidence: Some reliable information available, but reasonable inference and extrapolation required.
3 = High confidence: Reliable information with little or no extrapolation or inference required.

Lastly, all information from the demographic risk analysis and the threats assessment is synthesized to estimate the overall risk of extinction for each species. For this analysis, we use three reference levels of extinction risk ("low," "moderate," and "high"; see Box 2), which are consistent with those used in prior ESA status reviews (e.g., oceanic whitetip shark, Young et al., 2017; Pacific eulachon, Gustafson et al., 2010; five rockfishes, Drake et al., 2010). Importantly, these extinction risk categories are not meant to be a direct translation of the final listing determination for the species, as listing determinations must also consider ongoing conservation efforts of any State, foreign nation, or political subdivision thereof (16 U.S.C. §1533(b)(1)(A)) to determine whether the species meets the ESA's definition of an "endangered species" or "threatened species." Rather, this assessment represents the scientific conclusion about the overall risk of extinction faced by the species under present conditions and in the foreseeable future based on an evaluation of the species' demographic risks and assessment of threats.

| **Box 1. Demographic Factors and Threat Scores** | |
|---|---|
| **5 = Very High** | This factor by itself indicates a danger of extinction in the near future. |
| **4 = High** | This factor contributes significantly to the long-term risk of extinction and is likely to contribute to the short-term risk of extinction in the near future. |
| **3 = Moderate** | This factor contributes significantly to the long-term risk of extinction, but does not in itself constitute a danger of extinction in the near future. |
| **2 = Low** | It is unlikely that this factor contributes significantly to the long-term or near future risk of extinction by itself, but there is some concern that it may, in combination with other VP descriptors or threats. |
| **1 = Very Low** | It is unlikely that this factor contributes significantly to the risk of extinction, either by itself or in combination with other VP descriptors or threats. |

| **Box 2. Three Levels of Extinction Risk** | |
|---|---|
| **High** | A species with a high risk of extinction is at or near a level of abundance, productivity, spatial structure, and/or diversity that places its continued persistence in question. The demographics of a species at such a high level of risk may be highly uncertain and strongly influenced by stochastic or depensatory processes. Similarly, a species may be at high risk of extinction if it faces clear and present threats (e.g., confinement to a small geographic area; imminent destruction, modification, or curtailment of its habitat; or disease epidemic) that are likely to create imminent and substantial demographic risks. |
| **Moderate** | A species is at moderate risk of extinction if it is on a trajectory that puts it at a high level of extinction risk in the foreseeable future (see description of "High risk" above). A species may be at moderate risk of extinction due to current and/or projected threats or declining trends in abundance, productivity, spatial structure, or diversity. The appropriate time horizon for evaluating whether a species is more likely than not to be at high risk in the foreseeable future depends on various case- and species-specific factors (see **Defining the "Foreseeable Future"** below). |
| **Low** | A species is at low risk of extinction if it is not at moderate or high level of extinction risk (see "Moderate risk" and "High risk" above). A species may be at low risk of extinction if it is not facing threats that result in declining trends in abundance, productivity, spatial structure, or diversity. A species that is at low risk of extinction is likely to show stable or increasing trends in abundance and productivity with connected, diverse populations. |

### ***Defining the "Foreseeable Future"***

The appropriate time horizon for evaluating whether a species is more likely than not to be at a high level of risk in the "foreseeable future" depends on various case- and species-specific factors. For example, the time horizon may reflect certain life history characteristics (e.g., long generation time or late age-at-maturity) and may reflect the time scale over which identified threats are likely to impact the biological status of the species. In other words, the foreseeable future represents the period of time over which reliable projections can be made as to the specific threats facing the species as well as the species' response to those threats. It does not necessarily need to be limited to the period that the species' status can be quantitatively modeled or predicted within predetermined limits of statistical confidence. Reliable projections may be qualitative in nature.

With these criteria in mind, we determined that the "foreseeable future" for the following extinction risk analyses spans approximately ~50-60 years. Due to the species' life history traits, with longevity estimated to be at least 50 years (up to 60 years for *T. gigas*), maturity ranges from 3 to 9 years, and exceedingly low recruitment, it would likely take at least this amount of time (i.e., multiple generations) for the effects of any management actions to be realized and reflected in population abundance indices. Similarly, the impact of present threats to the species would be realized in the form of noticeable population declines within this timeframe, as has been demonstrated in the available literature. As the primary operative threat to giant clams is overutilization for subsistence and commercial harvest, this timeframe would allow for reliable predictions regarding the impact of current levels of harvest-related mortality on the biological status of all the species.

One important exception to this timeframe is in regard to the future impacts and threats related to climate change. Based on the current standard for climate projections, under which most available models are extended to the end of the century, we use the same timeframe (i.e., present day - 2100) to define the "foreseeable future" in assessing the likely future threat of climate-related habitat degradation and climate-related impacts to giant clam fitness.

### *Approach to Population Abundance Assessments*

Much of the information used to determine the status of each species throughout its range is derived from Table 4 of Neo et al. (2017), which we have supplemented or revised based on more recent survey data or reports. We have also adjusted the criteria used to define each qualitative abundance category, which Neo et al. (2017) defined as follows: Abundant: >100 individuals per hectare (ind $ha^{-1}$), Frequent: 1-10 ind $ha^{-1}$, Rare: <0.1 ind $ha^{-1}$. In doing so, we considered the reproductive ecology of giant clams, and in particular, the observations of Braley (1984) regarding the distance between nearest spawning *T. gigas* during a natural spawning event. Braley (1984) measured that 70% of nearest spawning individuals were within 9 m of one another, while only 13% were between 20-30 m of one another, suggesting that spawning synchrony decreases with distance. As broadcast spawning organisms, giant clams rely on sufficient population density to facilitate successful external fertilization of their gametes. Based on the distances above, we determined the minimum population density in a one hectare (10,000 $m^2$) square grid in which individuals could be evenly spaced at 9 and 30 m apart. Respectively, these distances represent populations that we consider to be "Abundant," where we expect relatively high reproductive success, and "Frequent," where we expect lower but moderate reproductive success. A "Rare" population in which individuals are spaced further than 30 m apart on average is likely to have infrequent, sporadic reproductive success. This approach led to the following criteria: Abundant: >100 ind $ha^{-1}$ (9-m distance), Frequent: 10-100 ind $ha^{-1}$ (30-m distance), and Rare: <10 ind $ha^{-1}$ (>30-m distance).

These categories are used to summarize the status of each species in each country, territory, or region throughout its range, but it is important to emphasize that they are meant as a rough guide. Precise quantitative assessments of abundance are not possible in most instances, as many regions lack current or comprehensive survey data or available survey data is reported in terms of population density (see Appendix 2 for all reported estimates of population density from specific surveys). Thus, where survey data are limited to only a few sites or where recent survey data are not available, we also take into account other available information, including qualitative descriptions of abundance or population trends, to reach a determination on the likely status of the species throughout each country, territory, or region *in its entirety*. In other words, although survey data from a single site may indicate a relatively abundant population, if the species is considered absent from all other areas, the species may be considered "rare" on average in that location. The benefit of this approach is twofold—it simplifies and maintains a degree of consistency between the assessments for each species, and it aligns the status assessment with national regulations that may be relevant to the protection of the species.

Additionally, it is important to note that, in the interest of simplicity, these categories are based on an assumption of uniform spacing between individuals. However, several studies report that giant clams often occur in a clumped distribution, where individuals are concentrated in a number of small, distantly-separated groups. In these cases, the abundance categories may underestimate the productivity of the respective population. In other words, if survey data indicates that a species occurs in some location at an average density of 9 ind $ha^{-1}$, reproductive success is more likely if the individuals are clustered in a few small groups, minimizing the distance between neighboring individuals, than if they are distributed uniformly.

# 4.1 *Hippopus hippopus*

## 4.1.1 Life History and Ecology

### 4.1.1.1 Taxonomy and Distinctive Characteristics

*Hippopus hippopus* was first described by Linnaeus in 1758. Commonly referred to as the horse's hoof clam or strawberry clam, *H. hippopus* has a heavy, thick shell that features prominent reddish blotches in irregular concentric bands (Rosewater, 1965). The shell interior is porcelaneous white, frequently flushed with yellowish orange on the ventral margin (Kinch & Teitelbaum 2010; Rosewater, 1965). The primary radial sculpture consists of 13 or 14 moderately convex rib-like folds over the surface of the valve, extending towards the ventral slope where they become obsolete (Rosewater, 1965). The mantle usually exhibits mottled patterns in green, yellow-brown or grey, and the incurrent siphon lacks guard tentacles (Neo et al., 2017; see Figure 16). Unlike *Tridacna* species, *Hippopus* species lack hyaline organs (i.e., small pinhole eyes) in their mantles, and the mantle does not project beyond the margins of the shell (Neo et al., 2017).

Juveniles and young, smaller adults are usually attached to coral rubble by their byssus, whereas older (larger, heavier) individuals are typically found unattached on the substratum being held in place by their weight (Rosewater, 1965; Neo et al., 2017). The largest reported shell length for *H. hippopus* is 50 cm, which was documented at the Bolinao Marine Laboratory in the Philippines (Neo et al., 2017).

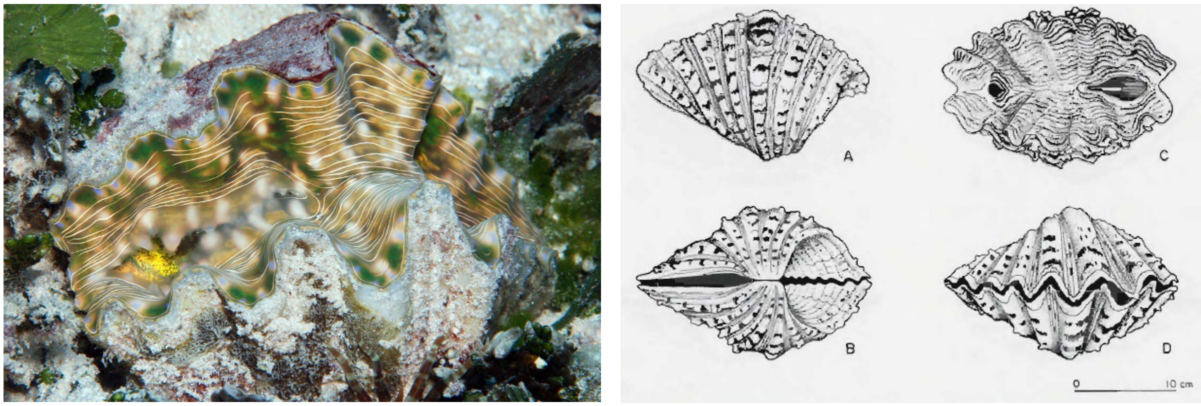

**Figure 16.** *H. hippopus* morphology. Left: Photograph of *H. hippopus* taken near Kwajalei Atoll, Marshall Islands. Right: Illustrations showing the lateral (A), ventral (B), mantle (C), and dorsal (D) view of a representative specimen. (Photo credit: Scott and Jeanette Johnson/iNaturalist, CC BY-NC 4.0; Diagram source: Calumpong, 1992).

### 4.1.1.2 Range, Distribution, and Habitat Use

*H. hippopus* is widely distributed throughout the Indo-Pacific, occurring from India in the west to the Republic of Kiribati in the east, and from New Caledonia in the south to the southern islands of Japan in the north (Figure 17; Neo et al., 2017). It has been recorded in 25 countries and territories across its range. This includes three U.S. territories (American Samoa, Guam, and CNMI); although, it is thought to have gone extinct in all three (Pinca et al., 2010; Neo et al., 2017). As is described in **Section 2.2**, *H. hippopus* was previously cultured at a government hatchery in American Samoa with the goal of establishing a local market for giant meat (S. Wells, 1997), but according to Marra-Biggs et al. (2022), the "stocks were harvested prior to reproduction and appear to be functionally extirpated." *H. hippopus* was also reintroduced to CNMI with a similar goal of establishing a local market for its meat, but according to Bearden et al. (2005), the efforts "failed to produce desired economic benefits" and were abandoned due to poaching.

According to Munro (1993), *H. hippopus* occurs in the widest range of habitat types of all the giant clam species. Most often, it is found in shallow, nearshore patches of reef, sandy areas and seagrass beds that can be exposed during low tides, but it can also be found on reefs as deep as 10 m (S. Andréfouët, pers. obs. cited in Neo et al., 2017). Based on a recent survey in New Caledonia, Purcell et al. (2020) found that *H. hippopus* "strongly preferred" lagoonal reefs. The authors hypothesized that the species may either prefer the siltier sediments and more turbid water of lagoon reef flats or alternatively may have low tolerance to the wave exposure of barrier reefs.

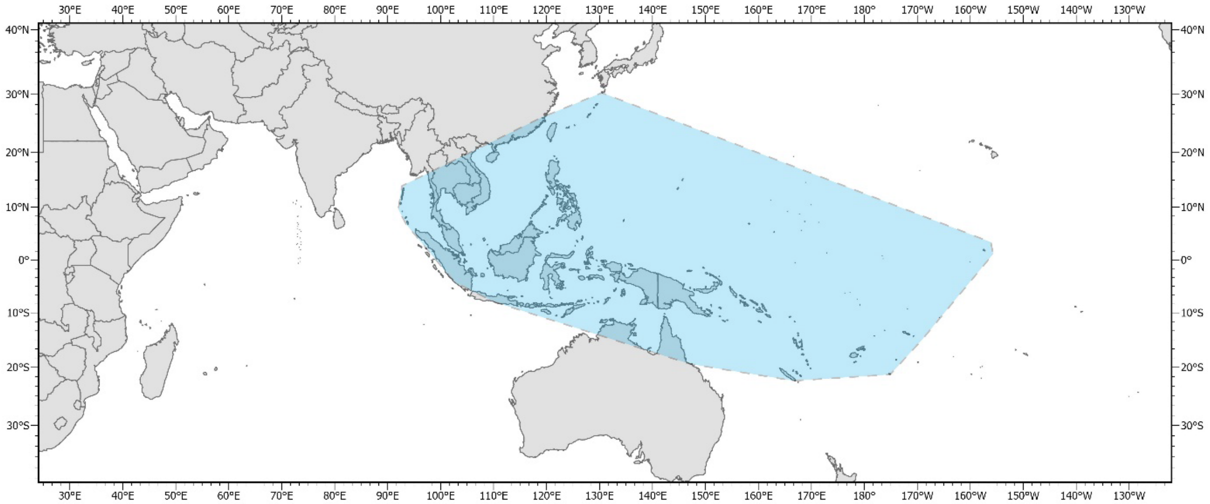

**Figure 17.** Approximate natural range of *H. hippopus* based on reported occurrences provided by Neo et al. (2017). The range does not include locations where *H. hippopus* has been introduced.

### 4.1.1.3 Reproduction and Growth

*H. hippopus* is estimated to reach sexual maturity at approximately two years of age for males and four years of age for hermaphrodites (Shelley, 1989; Alcázar et al., 1993). As outlined in **Section 2.3** (Table 1), *H. hippopus* tends to spawn annually during mid-summer months. On the Great Barrier Reef (16-19°S), evidence of spawning has been observed from November to

March (Stephenson, 1934; Shelley & Southgate, 1988; Shelley, 1989), and in Palau (6-8°N), it has been observed from April to July (Jameson, 1976; Yamaguchi, 1977; Beckvar, 1981). *H. hippopus* may also have a lunar spawning cycle, as 5 of 8 spawnings were on or near a new moon (Beckvar, 1981). It is likely that the energetic cost of reproduction in *H. hippopus* is quite significant, as Shelley and Southgate (1988) reported that individuals lost about 40% of tissue weight during spawning events, and Jameson (1976) estimated that an individual of 24.9 cm length spawned 25 million eggs.

Jameson (1976) described the early development of *H. hippopus* as following a pattern typical of bivalves. Trocophores developed 17 hours post-fertilization, pediveligers developed after 7 days, and settlement of *H. hippopus* larvae was 50% complete after 9 days (Jameson, 1976). Juveniles acquire their zooxanthellae continuously between 8 and 27 days post-fertilization (Jameson, 1976; Gula & Adams, 2018). Gula and Adams (2018) found that symbionts influence the early growth of *H. hippopus*, both by supporting faster growth and by increasing host cell proliferation in the immediate vicinity of symbionts, but that symbionts are not crucial for metamorphosis. There is also evidence that larger larvae metamorphose faster and have higher survival rates than smaller larvae (Jameson, 1976; Fitt et al., 1986).

Jameson (1976) also recorded shell growth rates after settlement and metamorphosis. Until day 27, growth rates for *H. hippopus* were low (0.9 µm/day), but growth increased significantly to 13.9 µm/day thereafter, corresponding to the time at which the majority of juveniles had acquired zooxanthellae. Beckvar (1981) measured average growth rates of 3-5 cm per year for *H. hippopus* during field growth studies in Palau and noted that instantaneous growth rates decreased with increasing shell length. Maximum rates of shell growth were reported under culture conditions in the Philippines as 5.3 mm per month (Lucas, 1994). Table 6 below provides available growth parameters for *H. hippopus* from the available literature.

**Table 6**. Recorded growth parameters for *H. hippopus*. Mean asymptotic size ($L\infty$) and growth coefficient (K) are for shell length and are based on Fabens or Wetberall plot estimates of parameters of the von Bertalanffy equation (adapted from Lucas, 1994).

| **Region** | **$L\infty$ (cm)** | **K (± SD)** | **Source** |
|---|---|---|---|
| Great Barrier Reef 1 | 34.7 | 0.205 | Shelley, 1989 |
| Great Barrier Reef 2 | 41. 5 | 0.155 | Shelley, 1989 |
| Papua New Guinea | 40 | 0.213 | Munro & Heslinga, 1983 |
| Palau | 40 | 0.100 (0.013) | Munro & Heslinga, 1983 |
| S. Philippines | 43.7 | 0.13 | Villanoy et al., 1988 |

#### 4.1.1.4 Feeding and Nutrition

In addition to the general information about giant clams provided in **Section 2.4**, Klumpp and Griffiths (1994) found that compared to *T. gigas* and *T. crocea*, *H. hippopus* was the least photosynthetically efficient, gaining an order of magnitude less nutrition from photosynthesis than *T. gigas*. Likewise, Blidberg et al. (2000) found that *T. gigas* and *T. derasa* respectively exhibited 3 and 2.5 times the maximal gross production rates of *H. hippopus*. Similar to other species of giant clams, suspension feeding decreases in importance with increasing size; however, it still provides 36-44% on average of the total nutritional requirements for

*H. hippopus*, second only to *T. gigas* in the proportion of carbon derived from heterotrophy. According to the calculations of Klumpp and Griffiths (1994), small *H. hippopus* (< 0.1 g) are unable to derive sufficient carbon from the combined intake of particulate matter and photosynthates to satisfy their growth and respiration requirements. It is unclear if this shortfall is made up by other sources of nutrition (e.g., dissolved organic matter or the digestion of zooxanthellae), or if it is due to an unidentified measurement error. Regardless, the finding suggests that early life stages of *H. hippopus* are likely particularly susceptible to disruptions in their nutritional regimen.

#### 4.1.1.5 Genetics and Population Structure

We could not find any species-specific information regarding the population structure or genetics of *H. hippopus.*

### 4.1.2 Abundance, Density and Population Status

Below, we synthesize the best available scientific and commercial information to assess the likely status of *H. hippopus* in each country, territory, or region where it has been observed or reintroduced. The status and abundance trends in each location are summarized in Table 7 and displayed in Figure 18 below.

***India (Andaman and Nicobar Islands) – RARE***

Rosewater (1965) included the Andaman and Nicobar Islands in the range of *H. hippopus*, and Nandan et al. (2016) mentioned *H. hippopus* as a resource in these locations, but neither source noted any specific records its occurrence. In the only known survey of these locations, Ramadoss (1983) did not encounter a single *H. hippopus*. It is likely that this species is extremely rare or extinct in the Andaman and Nicobar Islands.

***Japan – RARE***

Several sources have alluded to the occurrence of *H. hippopus* in Okinawa and the Ryukyu Islands (Hirase, 1954; Rosewater, 1965; S. Wells et al., 1983; Okada, 1997), but there is no information on its abundance nor is there recent evidence that *H. hippopus* still occurs in these locations. A recent survey by Neo et al. (2019) did not find any *H. hippopus* in the Ryukyu Islands. As assessed by Neo et al. (2017), it is likely that this species is extremely rare or extinct in Japan.

***Taiwan – LOCALLY EXTINCT***

Tisdell and Chen (1994) reported that *H. hippopus* once occurred in the Penghu Islands and waters around the Hengchu Peninsula. However, extensive harvest of giant clams by Taiwanese fishermen during the 1970s and 1980s, and demand for giant clam meat in Taiwan that continues today has posed a major threat to these populations. *H. hippopus* has not been recorded in the waters of Taiwan for the last three decades and is likely extinct from this area (Neo et al., 2017).

### *South China Sea – RARE*

*H. hippopus* is extremely rare in the island groups of the South China Sea (Neo et al., 2017). The most recent surveys from the region have encountered only one individual within a 0.36 ha survey area of Dongsha Atoll (Neo et al., 2018), one individual at each of two survey sites in the Spratly Islands (Calumpong & Macansantos, 2008), and one individual at Pulau Layang-Layang (Sahari et al., 2004). This species is likely extremely rare in the South China Sea.

### *Indonesia – RARE*

Historically, giant clams have been heavily exploited throughout Indonesia for subsistence and commercial purposes (see **Section 3.2**), and several reports indicate that giant clam populations continue to decline due to illegal harvest and habitat destruction (Nijman et al., 2015; Neo et al., 2017; Harahap et al., 2018). An early survey in Karimun Jawa found many small shells but no living specimens of *H. hippopus*, leading Brown and Muskanofola (1985) to conclude that the species was extirpated from the area. Eliata et al. (2003) documented an 84% decline in the population density of *H. hippopus* at Pari Island from 1984 to 2003 (from 19.2 down to 1.6 ind $ha^{-1}$). Moreover, only 5 *H. hippopus* were observed within a 1 ha survey area near Cenderwasih Bay, Papua (Tapilatu et al., 2021). Several recent surveys, however, have discovered a few relatively large *H. hippopus* populations in the Savu Sea, Kei Islands, and Raja Ampat. At the low end, estimates of population density in these areas fall between 4.5 and 16.3 ind $ha^{-1}$ (Hernawan, 2010; Naguit et al., 2012; Ode, 2017), and at the high end, one survey in Raja Ampat encountered 45 individuals within an area of 0.15 ha, equating to a population density of 300 ind $ha^{-1}$ (Wakum et al., 2017). Similarly, Triandiza et al. (2019) recorded 22 *H. hippopus* within a survey area of 0.25 ha in the Kei Islands, equating to a population density of 88 ind $ha^{-1}$. Based on the history of intense exploitation and recent reports of ongoing threats in this region, it is likely that these relatively abundant populations are an exception to the general scarcity of *H. hippopus* throughout Indonesia more broadly.

### *Malaysia – RARE*

Several sources note the occurrence of *H. hippopus* in Malaysia (S. Wells et al., 1983; Yasin & Shau-Hwai, 2000; Shau-Hwai & Yasin, 2003), but there is no information on its abundance nor is there recent evidence that *H. hippopus* still occurs there. Mamat et al. (2021) did not observe any *H. hippopus* in the Johor Islands. Likewise, L. K. Lee et al. (2022) did not observe *H. hippopus* in the Perhentian Islands. It is likely that this species is extremely rare or extinct in Malaysia.

### *Philippines – RARE*

The Philippines was historically a center of *H. hippopus* abundance in the Indo-Pacific region, but extensive harvest for the commercial shell trade severely reduced *H. hippopus* populations throughout the region. Villanoy et al. (1988) deemed *H. hippopus* overexploited in the Sulu Archipelago and Southern Palawan areas based on export volumes of giant clam shells from 1978-1985. During this 8-year period, a total of 413,230 giant clam shell pairs were exported, with *H. hippopus* comprising 22.4% of the export, or approximately 92,500 shell pairs. The authors emphasized that their findings had serious implications for the species, because these areas were thought to be the last stronghold for giant clams in the Philippines.

In 1984-1985, near the end of this period of intense commercial harvest, Alcala (1986) conducted a survey of giant clam populations at several coral reef areas of the Central Visayas, Western Visayas, Cagayan Islands, and Palawan. *H. hippopus* was observed in all regions except the Western Visayas, but only at Palawan was it found in the actual survey sites, likely due to low abundance elsewhere. Population density in the Palawan area was recorded as 13.8 ind $ha^{-1}$, or one individual every 725 $m^2$ on average. Juinio et al. (1989) also recorded low population density at several sites throughout Luzon and Palawan during this time. The highest density of *H. hippopus* in these regions was 7.8 ind $ha^{-1}$, or one individual every 1,282 $m^2$. Salazar et al. (1999) conducted a stock assessment of giant clams (including *H. hippopus)* in the Eastern Visayas region. Estimates of population density were not reported, but the authors noted that most of the populations consisted of juveniles and concluded that there were insufficient numbers of breeding adults to repopulate the region. Dolorosa and Schoppe (2005) reported a 97% decline in one population of *H. hippopus* in Tubbataha Reefs Natural Park from 1995-2005, leaving a density of 22.2 ind $ha^{-1}$; although, the data werefrom a single transect, and the authors noted that a more widespread assessment of giant clam abundance in the area (including *H. hippopus*) could not be confirmed. More recently, Dolorosa (2010) recorded 26 individuals of *Hippopus* spp. within an 0.83 ha survey area of Tubbataha Reefs Natural Park, but did not distinguish between the two *Hippopus* species. Across ten transects at Carbin Reef, Lebata-Ramos et al. (2010) found 67 *H. hippopus* within a 1 ha survey area. Taken together, these survey data reflect a drastic decline in the abundance of *H. hippopus* throughout the Philippines compared to the numbers that were once harvested and exported in the 1980s and 1990s (~10,000 per year). The most recent surveys in 2010 indicate that very few remaining locations host populations greater than 10 ind $ha^{-1}$. The current status of these populations is unknown, but ongoing illegal shell harvesting in the Philippines (see **Section 3.4.1**) continues to put them at risk of further decline.

### *Singapore – LOCALLY EXTINCT*

According to Neo and Todd (2013), *H. hippopus* reached the 50-year no-sighting criterion for proclaiming national extinction in 2013. There have been no reports of the species occurring in the waters of Singapore since.

### *Australia – FREQUENT (Great Barrier Reef); FREQUENT (NW Islands)*

The Great Barrier Reef in Australia is generally considered to have large, healthy stocks of giant clams relative to most other areas in their range (S. Wells, 1997; Neo et al., 2017). However, formal surveys and quantitative estimates of abundance are quite scarce, and those that are available from this region focus primarily on *T. gigas* and *T. derasa* (Braley, 1987a; Pearson & Munro, 1991). Braley (2023) recorded *H. hippopus* abundance at five sites in the far northern Great Barrier (near Lizard Island, Rachel Carson Reef, and Michaelmas Cay) in 2007-09. *H. hippopus* was recorded at four of the five sites with population densities ranging from 25.3 to 116.7 ind $ha^{-1}$ in survey areas of 0.022-0.73 ha. Braley (2023) revisited two of the five survey sites in 2017 and found that abundance had declined at both sites by 39.5 and 85.7%, leaving population densities of 31.5 and 3.6 ind $ha^{-1}$, respectively. Additionally, two unpublished reports to the Australian Government document the abundance of *H. hippopus* at two offshore marine reserves in the Coral Sea. In 2007-2008, Ceccarelli et al. (2008) recorded 150 *H. hippopus* within an approximate survey area of 15.3 ha in Coringa-Herald National Nature Reserve (NNR), while

Ceccarelli et al. (2009) recorded 33 individuals within an approximate area of 22 ha in Lihou Reef NNR.

Several other reports document *H. hippopus* density at a number of reefs in the Timor Sea off the northwestern coast of Australia. In a broad survey of seven reefs in the region, Skewes et al. (1999) recorded population densities of *H. hippopus* between 3 and 131 ind $ha^{-1}$, or one individual every 2941 to 76 $m^2$, respectively. Population density was significantly higher at shallow and shallow lagoon sites, and was particularly high at Ashmore (131 ind $ha^{-1}$) and Cartier Reefs (75 ind $ha^{-1}$). The report does not specify the total area surveyed, though it is clear that the survey design is quite comprehensive, comprising 765 sites spaced randomly on a 1-7 $km^2$ grid. In 2003, Rees et al. (2003) recorded population densities of 19 and 40 ind $ha^{-1}$, representing declines of over 85% and 47% at Ashmore and Cartier Reefs, respectively. Five years later, Z. Richards et al. (2009) reported only 2.7 and 1.0 *H. hippopus* $ha^{-1}$ at Ashmore and Cartier Reefs, respectively; although, the survey areas in this study were considerably smaller and covered only reef flat and reef slope habitats, leaving out lagoon areas where *H. hippopus* is typically more common. A small survey in 2010 also reports the occurrence of *H. hippopus* in Talbot Bay, but provides no estimates of population abundance or density (Wilson et al., 2011). It is difficult to evaluate the population trends at northwestern (NW) Australia reefs, as each study employs a different survey design and none of the surveys are deliberately focused on assessing giant clams; rather, they are designed to characterize the broad marine environment (e.g., demersal fish, corals, and commercially important invertebrates). However, two subsequent reports of reduced population density compared to Skewes et al. (1999) suggest that *H. hippopus* is facing some degree of population decline in the area. It is unclear what may be causing the decline, but it is likely not due to poaching, as the region has been actively managed by the Commonwealth Government of Australia with a "near-permanent enforcement presence" in protected areas since 1980s (Ceccarelli et al., 2011).

Despite the general lack of quantitative survey data, the strict enforcement of giant clam harvest prohibitions throughout the Great Barrier Reef and offshore reefs of NW Australia has likely prevented widespread declines of *H. hippopus* in Australia. Numerous sources from the 1980s reported relatively large, healthy stocks of giant clams generally on the Great Barrier Reef, and there is no evidence to suggest that these populations have declined significantly in the time since. Based on this information and the available survey data indicating average populations densities greater than 10 individuals per ha, we consider *H. hippopus* to be "frequent" in Australia.

### *New Caledonia – RARE*

Neo et al. (2017) assessed *H. hippopus* to be "frequent" in New Caledonia, referring to its importance as a subsistence resource. However, available survey data indicates that population density is quite low throughout the archipelago. In the most recent survey, Purcell et al. (2020) found only ten individuals across 50 sites spanning the archipelago, leading the authors to conclude that "*H. hippopus* can be considered at risk of extirpation in New Caledonia." As a result, we have determined the status of *H. hippopus* to be "rare" in New Caledonia.

### *Papua New Guinea – RARE*

Milne Bay Province has historically been the center of giant clam abundance and exploitation in Papua New Guinea. In an early giant clam stock assessment from the area, Chesher (1980) estimated that before commercial harvesting, unfished areas of southern Milne Bay Province contained an overall density of 39 ind ha$^{-1}$ for all giant clam species. A survey conducted in 1996 by the South Pacific Commission and the Papua New Guinea National Fisheries Authority at the Engineer and Conflict Islands (offshore of Milne Bay Province) found that *H. hippopus* was the most abundant species in the area at 20.1 ind ha$^{-1}$. However, Kinch (2003) noted that during a survey in 1999, *H. hippopus* was targeted preferentially by the inhabitants of Brooker Island (a small island near the Engineer and Conflict Island groups), as they could be collected opportunistically on nearshore reef flats. According to F. E. Wells and Kinch (2003), *Hippopus* spp. were the most commonly harvested clam in the area. Two years later, a stock assessment comprising 1,126 sites throughout the Milne Bay Province recorded only 4 *H. hippopus* and revealed that the average population density in the region had fallen to 0.4 ind ha$^{-1}$, which the authors estimated was equivalent to a total abundance of 195,543 (±55.9%) in the region (Skewes et al., 2003). F. E. Wells and Kinch (2003) noted that these findings aligned with other reports indicating that giant clam stock levels are very low and heavily depleted in the Milne Bay Province. We could not find more recent survey data from this region, nor any information on the status of *H. hippopus* in other areas of Papua New Guinea. Based on the available survey data and history of exploitation, it is likely that *H. hippopus* is rare throughout Papua New Guinea.

### *Solomon Islands – RARE*

According to Hviding (1993), *H. hippopus* could be found in “relatively large numbers” in the Solomon Islands, and at the time, locals did not voice any concerns regarding its abundance, despite it being the second most popular species as a food item. Local interviewees noted that it is the least conspicuous of the giant clams and “often lives in bad locations with muddy water […] so it is harder to find than the others, even though it does not hide among the corals” (Hviding, 1993). In the 1980s, high densities of *H. hippopus* had reportedly been observed in Marovo Lagoon and Ysabel (Govan et al., 1988); however, A. H. Richards et al. (1994) reported that *H. hippopus* had only a limited distribution in the Main Group Archipelago and that stock densities varied considerably between islands. In mid-1992, mass mortality of *H. hippopus* was observed in the eastern Solomon Islands and spread westerly through the archipelago over the following months (Lucas, 1994; A. H. Richards et al., 1994). In 2004, only four *H. hippopus* were recorded in a broad survey of the marine environment in Solomon Islands, which comprised 129 sites spanning 11.8 ha of the main islands (excluding the remote islands and atolls) (Ramohia, 2006). According to Neo et al. (2017), large populations of giant clams can be found within Arnavon Marine Conservation Area, but we could not find any information about *H. hippopus* specifically. Given the most recent survey data from 2004, coupled with ongoing harvest near areas of high population density (Neo et al., 2017), it is likely that *H. hippopus* is rare in the Solomon Islands.

### *Vanuatu – FREQUENT*

We could only find one survey estimating *H. hippopus* population density in Vanuatu in 1988 (Zann & Ayling, 1988). The survey included spot dives, manta tows, and belt transects at

29 sites on 13 islands, and documented densities of H. hippopus ranging from 1 to 25 ind $ha^{-1}$. Based on these findings, Zann and Ayling (1988) concluded that H. hippopus was “overfished on inhabited islands but secure on two remote reefs [Reef Islands, Pentecost and Cook’s Reef, Efate]” and recommended that these *H. hippopus* refuges be protected. Neo et al. (2017) note that giant clams, and especially *H. hippopus*, are still a prized subsistence food on most islands, and it is unclear if these more remote populations are subject to harvest.

### *Federated States of Micronesia (FSM) – RARE*

Dawson (1986) noted the occurrence of *H. hippopus* in FSM, but reported that all giant clam species were “under heavy pressure from local exploitation.” Noting the broad geographic extent of FSM, S. Wells (1997) elaborated on this point, suggesting that even the remotest reef areas may suffer from poaching. No formal quantitative surveys of giant clam stocks have been conducted in FSM. According to A. J. Smith (1992), *H. hippopus* is present throughout FSM, but at the time, the species occurred in very low numbers in Yap, Chuuk, and Pohnpei, and was rare in Kosrae. There are reports that all four states of FSM have received cultivated stocks of *H. hippopus* from Palau for the purpose of replenishing wild stocks (A. J. Smith, 1992; Teitelbaum & Friedman, 2008), but we could not find any information as to the success of these measures.

### *Republic of Kiribati – RARE*

Giant clam stocks of Abaiang, Abemama, Maiana, and Tarawa Atolls in the Central Gilbert Islands of Kiribati were surveyed in 1985 using manta tows that covered a total survey area of over 42.7 ha (Munro, 1988b). Across the four atolls, population densities of *H. hippopus* (at sites where they were observed) averaged between 0.2 and 13.1 ind $ha^{-1}$. We could not find any more recent data concerning the status of *H. hippopus* populations in Kiribati.

### *Marshall Islands – FREQUENT*

*H. hippopus* is thought to be widespread in the Marshall Islands, but to vary significantly in abundance among islands (S. Wells, 1997). Maragos (1994) reported “huge undisturbed” populations of *H. hippopus* in Bok-ak and Pikaar Atolls, and noted that *H. hippopus* was common in Akdup Atoll as well, but no quantitative estimates of abundance were provided. Similarly, Beger et al. (2008) reported *H. hippopus* to be abundant in Ailinginae Atoll, and present in Rongelap and Namu Atolls, but did not provide quantitative population estimates. According to Beger et al. (2008), the coral reef ecosystems of the Marshall Islands are “in excellent condition” and have been spared from many of the threats which are common in other Pacific islands.

### *Palau – FREQUENT*

Early surveys of giant clam abundance in Palau were focused on Helen Reef, a remote atoll in the Western Caroline Islands, and documented the impacts of an intensive illegal harvesting operation by Taiwanese fishing vessels in the early 1970s. In 1972, prior to the poaching, Hester and Jones (1974) estimated that the standing stock of *H. hippopus* at Helen Reef was 44,600 individuals. Following the poaching, unlike *T. gigas* and *T. derasa* which suffered severe population declines, Hirschberger (1980) estimated that the *H. hippopus* stock remained approximately stable at 47,400 individuals in 1975 and increased to over 70,500 individuals in

1976. These estimates were derived from observed population densities of 13.2, 8.9, and 40.7 ind ha$^{-1}$ in 1972, 1975, and 1976, respectively. We could not find more recent surveys of Helen Reef, so the current status of this population is unknown. Near more populated areas of Palau, an opportunistic survey of giant clam populations conducted by Rehm et al. (2022) documented 17 *H. hippopus* individuals within a survey area of 0.33 ha, which equates to an approximate population density of 51.5 ind ha$^{-1}$.

Notably, Palau is home to PMDC, which is one of the first (established in 1970) and most prolific institutions to successfully culture giant clams on a commercial scale. Cultured clams, including tens of thousands of *H. hippopus*, have been translocated as broodstock to many other countries for the purpose of natural stock enhancement (Kinch & Teitelbaum, 2010). Cultured clams from PMDC are also often distributed to local clam farmers to be later sold into the commercial meat and aquarium industry (Neo et al., 2017).

### *Fiji, Tonga, Samoa, American Samoa, Guam, and CNMI – REINTRODUCED*

According to numerous sources, *H. hippopus* is extirpated from Fiji, Tonga, Samoa, American Samoa, Guam, and CNMI, likely as a result of over-exploitation (Dawson, 1986; Munro, 1993a; Sone & Loto'ahea, 1995; Pinca et al., 2010). *H. hippopus* fossils from the late Pleistocene era are commonly recovered in Fiji, indicating its historical presence in the area (Lewis et al., 1988; Newman & Gomez, 2000). S. Lee et al. (2018) report that *H. hippopus* was recently rediscovered on Bukatatanoa and Navatu Reefs in southern Lau (N. Kuridrani, pers. comm., cited in S. Lee et al., 2018), but we could not find any data to corroborate this claim. Recent fossils of *H. hippopus* have also been found in Tonga (Dawson, 1986), but no living specimens were found during a survey in 1978-1979 and the species is presumed locally extinct (Langi & Aloua, 1988). Similarly, shell remains but no living specimens of *H. hippopus* have been found in Samoa (Skelton et al., 2000), and a large-scale survey in American Samoa found only *T. squamosa* and *T. maxima* (Green & Craig, 1999). According to Newman and Gomez (2000), *H. hippopus* is common in Holocene-era fossils in Guam, and one living *H. hippopus* had reportedly been found, but uncertainty regarding its origin led the authors to conclude that it was likely translocated to the area randomly. *T. maxima* is the only species known to still occur in CNMI (Dawson, 1986; Munro, 1989).

Cultured stocks of *H. hippopus* from other regions have been reintroduced to Fiji, Tonga, Samoa, Guam, and CNMI, primarily as broodstock from Palau and Australia (Munro, 1994; Neo et al., 2017; Teitelbaum & Friedman, 2008). Lindsay et al. (2004) also reported that Fiji, Tonga, Samoa, and American Samoa were engaged in local mariculture operations for the purpose of restocking *H. hippopus* in local waters. However, we could not find any information regarding the success or failure of these initiatives, and based on the documented challenges of giant clam restocking (see details below), we find it likely that *H. hippopus* remains extremely rare or absent in Fiji, Tonga, Samoa, American Samoa, Guam, and CNMI.

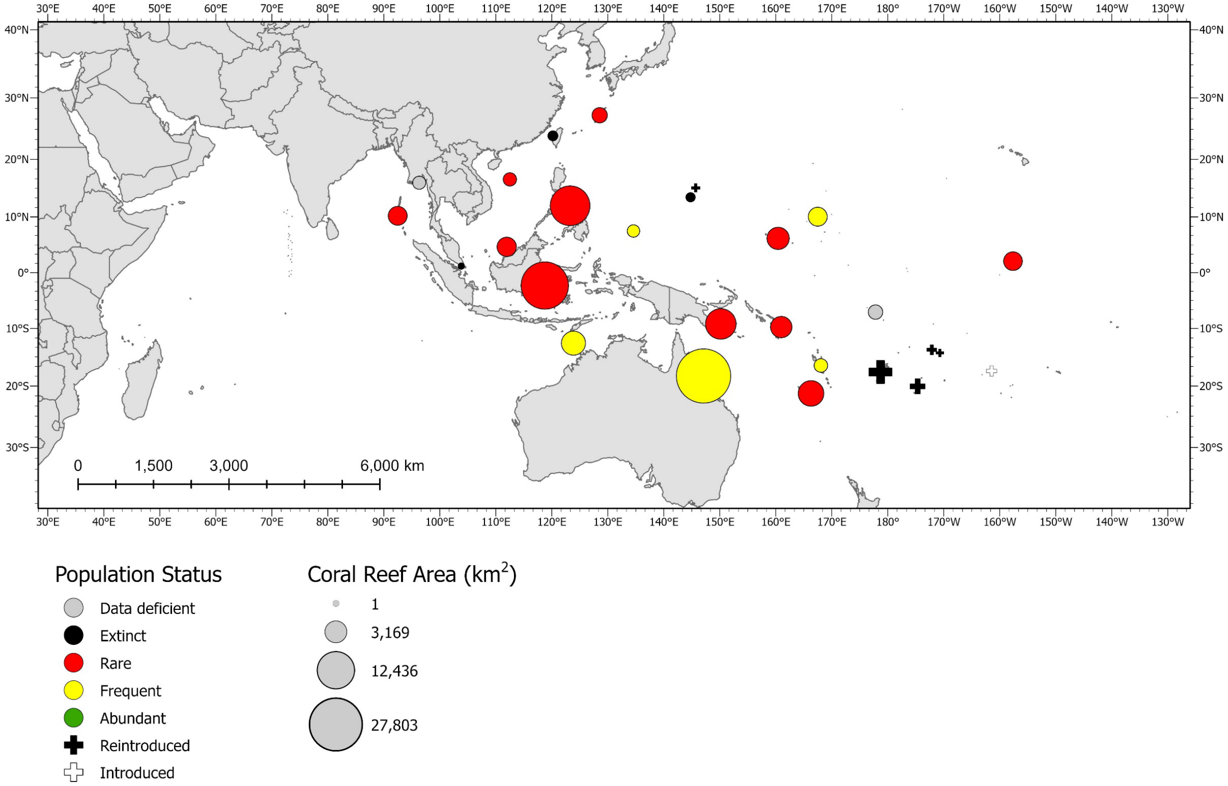

**Figure 18.** Qualitative abundance estimates for *H. hippopus* based on reported occurrence and survey data. Points are located at the approximate centroid of survey sites within each country, territory, or region from which data has been included in the abundance assessment. Abundance categories are based on those used by Neo et al. (2017), but have been revised as follows: Abundant (>100 ind ha$^{-1}$), Frequent (10-100 ind ha$^{-1}$), Rare (<10 ind ha$^{-1}$), Extinct, Introduced, Reintroduced (i.e., locations where the species was reportedly extirpated in the past but there have since been efforts to restore populations using cultured specimens; current presence/abundance may not be known), and Data Deficient (i.e., locations where reports of species occurrence have not been confirmed). The size of the points reflects the total estimated area of coral reefs within each location based on data compiled by the UN Environment World Conservation Monitoring Centre and the WorldFish Centre (UNEP-WCMC et al., 2021), increasing on a square-root scale. It is used here to roughly approximate the relative amount of giant clam habitat. However, the accuracy of this approximation likely varies between species based on their habitat preferences.

**Table 7.** Summary of *H. hippopus* population status across its geographic range (adapted from Table 4 in Neo et al. 2017 and supplemented with more recent information where available). Species abundance categories are as follows: Abundant (>100 ind ha$^{-1}$); Frequent (10-100 ind ha$^{-1}$); Rare (<10 ind ha$^{-1}$). Where the status has been revised from Neo et al. (2017), footnotes provide the data sources or rationale used to reach the respective status determinations.

| Location | Status | Notes |
|---|---|---|
| ***Indian Ocean*** | | |
| India | Rare | Occurrence in Andaman and Nicobar Islands is unconfirmed; giant clams are not subjected to extensive commercial exploitation, but area occasionally harvested for household consumption. |

| Location | Status | Notes |
|---|---|---|
| ***East Asia*** | | |
| Japan | Rare | No recent records of *H. hippopus*; second-most preferred species for domestic market. |
| South China Sea | Rare | Harvest of giant clams remains common but mostly for *T. gigas*. Recent surveys found only one *H. hippopus* at each of four sampling sites across several island groups. |
| Taiwan | Locally extinct | Not recorded in the last three decades and is likely locally extinct. |
| ***South Asia*** | | |
| Australia (NW islands) | Frequent | Initial surveys in 1999 reported population densities between 3 and 131 ind $ha^{-1}$. Subsequent surveys in 2003 and 2009 indicate that *H. hippopus* abundance has declined to some extent, but the cause is unknown. |
| Indonesia | Rare | Considered rare generally, but recent surveys have discovered few areas with abundant populations. All giant clam species remain heavily exploited for their meat (domestic market), shells, and some for live aquarium trade. Stock enhancement efforts have been in place since the 1990s, but no information regarding success of these efforts. |
| Malaysia | Rare | Rare and only reported in Johor Islands; giant clam populations in state of decline throughout Malaysia. |
| Myanmar (Burma) | Data deficient | No status information. |
| Philippines | Rare | Decimated by commercial exploitation (mainly for international shell trade). |
| Singapore | Locally extinct | *H. hippopus* reached the 50-year no-sighting criterion for proclaiming national extinction in 2013. |
| ***Pacific Ocean*** | | |
| American Samoa | Reintroduced | Heavily exploited, which led to local extinction. Species has been reintroduced, but latest surveys did not encounter *H. hippopus*. |
| Australia (Great Barrier Reef) | Frequent | Giant clam populations are considered relatively healthy in most locations, benefiting from strictly enforced harvest prohibitions, although there is minimal quantitative survey data from the Great Barrier Reef. |
| CNMI | Reintroduced | Reintroduced from Palau in 1986 but heavy exploitation resulted in local extinction. |
| FSM | Rare[1] | Anecdotal reports from early 1990s indicate *H. hippopus* occurs throughout FSM but at very low numbers. |
| Fiji | Reintroduced | Thought to be locally extinct; broodstock imported from Palau in 1985 and Australia in 1992. |
| Guam | Reintroduced[2] | Reintroduced from Palau in 1982 but may be locally extinct. |
| Marshall Islands | Frequent[3] | Anecdotal accounts suggest relatively abundant *H. hippopus* populations in several areas, but no quantitative estimates; giant clams generally heavily exploited near population centers. |

| Location | Status | Notes |
|---|---|---|
| New Caledonia | Rare[4] | Preferentially harvested for local consumption; recent survey in 2020 encountered only 10 individuals across 50 sites throughout the main island group. |
| Palau | Frequent[5] | Harvest of giant clams for subsistence and domestic sale is "very common"—many people target *T. crocea*, but *H. hippopus* and *T. derasa* are highly sought and collected when found (L. Rehm, pers. comm., May 26, 2022). Last known surveys of Helen Reef (1976) reported relatively high estimates of *H. hippopus* population abundance; more recent survey of populated islands reported a population density of 50.5 ind $ha^{-1}$. |
| Papua New Guinea | Rare | Local extinctions at sites and general low stocks attributed to unsustainable commercial fishing practices from unsustainable harvest, poaching, and long-standing exploitation. |
| Republic of Kiribati | Rare | No recent survey data; manta tows from 1985 found population densities 0.2-13.1 ind $ha^{-1}$. |
| Samoa | Reintroduced | Reintroduced after local extinction due to overexploitation. |
| Solomon Islands | Rare[6] | Mass mortality event in 1992. Most recent survey in 2004, including 129 sites and spanning 11.8 ha of survey area, indicates very low abundance in waters around the main islands. |
| Tonga | Reintroduced | Reintroduced after local extinction due to overexploitation. |
| Tuvalu | Data deficient | Noted as present by Munro (1989) but not documented elsewhere. |
| Vanuatu | Frequent | Prized subsistence food and collected for household consumption; heavily exploited near populated areas but relatively abundant at two remote reefs in 1988. No surveys since. |

Sources:
[1] Anecdotal reports of widespread poaching (S. Wells, 1997) and "very low numbers" (Smith, 1992)
[2] Mislabeled in Neo et al. (2017)
[3] Maragos (1994); Beger et al. (2008)
[4] Purcell et al. (2020)
[5] Rehm et al. (2022)
[6] Ramohia (2006)

Of the 26 locations where *H. hippopus* has been recorded, the best available data suggest that the species is frequent in 5 locations, rare in 11 locations, locally extinct or reintroduced after local extinction in 8 locations, and data deficient (likely exceptionally rare or extinct) in 2 locations. While several countries are known to have imported *H. hippopus* broodstock for the purposes of reintroduction or stock replenishment, there is very little information regarding the success of these efforts in establishing sustainable populations of *H. hippopus* in the wild. An unpublished report by Braley (*n.d.*) describes the outcome of translocating a single cohort of *H. hippopus* (~70,000 specimens) from Australia to Fiji, Tonga, and the Cook Islands in 1991. According to the report, survival to mid-1997 averaged 1.79% across all the countries, but was considerably higher in Tonga (5.2%) compared to Fiji (0.04%) and the Cook Islands (0.13%). In

Fiji and the Cook Islands, only 9 and 27 clams, respectively, remained in 1997 from the original 25,000 and 20,000 clams delivered to the countries in 1991. In Tonga, 1,300 of the 25,000 original clams survived to 1997, but many of these were still being actively managed in protective cages on the sand flat.

There is extensive literature addressing the challenges of giant clam mariculture generally, and particularly for the purpose of stock replenishment (Munro, 1993a; Gomez & Mingoa-Licuanan, 2006; Teitelbaum & Friedman, 2008; Mies, Scozzafave, et al., 2017; Lindsay et al., 2022). The primary barrier to these efforts is the exceptionally low survival rate of giant clam larvae post-fertilization compounded by the time and resources required to protect juveniles once they have been outplanted and before they reach a size at which they are sufficiently protected from predation. Despite the numerous restocking and translocation programs known to exist throughout the Indo-Pacific, most are reported to still be operating on a small or pilot scale with only partial success, and further intensification of giant clam mariculture is in most cases considered economically unviable (Teitelbaum & Friedman, 2008; UNEP-WCMC, 2012; Lindsay et al., 2022). Thus, given these challenges and the poor outcome of a documented *H. hippopus* translocation from Australia to several Pacific island nations, we consider the species to be extirpated (or exceptionally rare) even in locations where it has been reintroduced.

One possible exception is in Palau, where the PMDC successfully produced large numbers of *H. hippopus*, and where there are reports that a portion of seedstock is being used to enhance giant clam populations in 23 conservation areas (Kinch & Teitelbaum, 2010; L. Rehm, pers. comm., May 26, 2022). We could not find any follow-up surveys specifically documenting the success of these efforts (or lack thereof). Moreover, according to L. Rehm (pers. comm.), authorities in Palau struggle to enforce the regulations of conservation areas, particularly those on offshore reefs, because they lack sufficient personnel and equipment, potentially negating any benefit of reseeding. The reseeding efforts may have contributed to *H. hippopus* populations in these areas, but more data is needed to confirm that this is the case.

### 4.1.3 Threats to *Hippopus hippopus*

#### 4.1.3.1 Destruction, Modification, or Curtailment of Habitat or Range

Beyond the information provided in **Section 3.1** related to the threat of habitat destruction or modification to giant clams generally, we could not find any information addressing the threat to *H. hippopus* specifically. However, the species is known to reside preferentially in nearshore sand flats, seagrass beds, and atoll lagoons and is therefore especially vulnerable to threats impacting these habitats. This includes sedimentation, for example, which is likely to be most severe in nearshore environments adjacent to river discharge zones and near areas of intense urban development. As discussed in **Section 3.1.2**, Burke et al. (2012) identified major proportions of coral reefs in Indonesia (20%), Malaysia (35%), Papua New Guinea (25%), and the Philippines (60%) that are currently threatened by the impacts of coastal development. These impacts include runoff from construction and waste from coastal communities, and it is likely that nearshore populations of *H. hippopus* in these areas are also affected to a similar extent. Populations of *H. hippopus* in Pacific island nations, where urban development is less intense, likely do not experience high rates of sedimentation, and the threat of habitat destruction or modification is likely less severe in these locations.

We note in **Section 3.1.2** that we could not find any studies directly investigating the effect of sedimentation on giant clam survival; however, similarities in the biology and behavior of giant clam larvae to that of coral larvae would suggest that comparable results between the taxa can reasonably be expected. In this respect, there is extensive evidence that heavy sedimentation can significantly reduce reproductive success by inhibiting larval settlement, interfering with settlement cues, and physically smothering newly-settled recruits. Accordingly, it is possible that heavy sedimentation may significantly inhibit the recovery of populations that have been reduced by overexploitation or by other means.

Because *H. hippopus* is often found in sandy environments outside of the coral reef framework, the anticipated impacts of climate change (i.e., ocean warming and acidification) on coral reefs will not likely pose a severe threat to this species.

Overall, the threat of habitat destruction or modification due to sedimentation is heterogeneous throughout the range of *H. hippopus* and is likely most severe adjacent to highly populated areas of the central Indo-Pacific (e.g., Indonesia, Malaysia, Papua New Guinea, Philippines). The threat is likely less severe throughout the Pacific Island nations, where human development has been less intense, and in Australia, where water quality management has historically been more effective. Given this geographic heterogeneity, we conclude that this threat is unlikely to contribute significantly to the long-term or near future risk of extinction by itself, but there is some concern that it may, in combination with other VP descriptors or threats (**Low** risk). However, without specific examples of the impact of sedimentation on *H. hippopus* populations in these areas or any experimental evidence validating inferences based on comparison to coral larvae, we have **Low** confidence in this conclusion.

#### 4.1.3.2 Overutilization

Because *H. hippopus* is a free-living species (i.e., unattached to the substrate) and occupies nearshore habitats that are relatively accessible to humans, it is an easy target for reef gleaners (i.e., fishers that collect organisms by hand from nearshore sand and reef flats). Consequently, it has been a popular species for local harvest and consumption throughout its range. Many years of subsistence harvest have driven widespread population declines and local extirpations from many Pacific island nations. In Fiji, for example, Seeto et al. (2012) discovered *H. hippopus* fossils in shell middens from two Lapita-era settlements (1100-550 B.C.), and found that shell size increased with midden depth, suggesting that human consumption contributed to population reductions and its eventual extirpation. Surveys from Palau in the 1970s indicated that *H. hippopus* populations declined drastically as a direct result of overharvest (Bryan & McConnell, 1975). In Singapore, *H. hippopus* was considered rare historically (S. K. Lee, 1966; Dawson & Philipson, 1989), but consistent harvest pressure is thought to have prevented the species from establishing a sustainable population in the area and ultimately led to its extirpation (Neo & Todd, 2012). Additionally, *H. hippopus* continues to be exploited for consumption by coastal communities in Indonesia (Naguit et al., 2012), Malaysia (Neo & Todd, 2012a), New Caledonia (Purcell et al., 2020), the Andaman and Nicobar Islands (Nandan et al., 2016), Papua New Guinea (Kinch, 2003), and virtually every other country where it occurs, except for Australia (S. Wells, 1997).

In addition to the consumption of its meat, *H. hippopus* has been one of the most popular giant clam species in the shell trade because of its size and physical characteristics (e.g., attractive colors, bowl-like shape, etc.) (Shang et al., 1994). As described in **Section 3.2.2**, the

Philippines operated as the largest exporter of giant clam shells in the 1970s and 1980s, with *H. hippopus* being the most frequently traded species during this time. According to CITES annual report data, over 277,000 kg, 341,000 shell pairs, 2 million "shells" (without associated units), and 1.7 million shell carvings of *H. hippopus* were exported from the Philippines from 1985 to 1993. This period of intense harvest left *H. hippopus* severely depleted throughout the Philippines, where it remains at very low abundance except in a few isolated areas.

Presently, CITES trade reports indicate that international trade of *H. hippopus* shells and shell craft is minimal. Since 2010, only the Solomon Islands has exported a significant number of *H. hippopus* shells, with 1,381 shells exported in 2014 to China, Hong Kong, and Thailand. International trade of live *H. hippopus* for the aquarium and mariculture industry is ongoing, but is primarily composed of cultured specimens. Since 2010, a total of 7,028 culture-raised and 190 wild-harvested individuals have been exported, primarily from FSM, Palau, and Indonesia. The main importers of live *H. hippopus* during this period have been the United States (45.4%), Germany (16.2%), United Kingdom (10.8%), and Canada (9.7%).

A long history of subsistence harvest punctuated by two decades of intense commercial exploitation for the shell and shell-craft industry has led to severe declines of *H. hippopus* populations throughout its range. While most countries have imposed prohibitions on the commercial exploitation of giant clams and CITES records indicate that recent international trade of *H. hippopus* is minimal, subsistence harvest continues to pose a threat to the species in most populated areas where it occurs. Without more thorough monitoring from many of these locations, it is difficult to determine if this ongoing harvest is causing further population declines, but at the very least, it is likely preventing any substantial recovery of depleted populations throughout its range. One important exception is Australia, where anecdotal reports suggest that strictly enforced harvest bans have been largely successful in preventing overexploitation and protecting reportedly healthy stocks of this species. For these reasons, and considering the documented effects of past harvest on species abundance, we conclude with **Medium** confidence that overexploitation of *H. hippopus* contributes significantly to the species' long-term risk of extinction, but does not in itself constitute a danger of extinction in the near future (**Moderate** risk).

#### 4.1.3.3 Disease or Predation

Aside from the information discussed above for giant clams in **Section 3.3**, information regarding the prevalence of disease or predation for *H. hippopus* is limited. We could only find one study regarding disease in *H. hippopus*. Norton et al. (1993) reported two incidences of mortality in *H. hippopus* from Rickettsiales-like organisms in cultured clams in the western Pacific, one in the Philippines and one in Kosrae. However, it is not uncommon among individuals cultured in close proximity to be afflicted with parasites or diseases that spread quickly (Norton et al., 1993). Given the limited information available, we find it unlikely that disease and predation contributes significantly to the risk of extinction, either by themselves or in combination with other threats (**Very Low** risk, **Low** confidence).

#### 4.1.3.4 Inadequacy of Existing Regulatory Mechanisms

There are various regulatory mechanisms and management measures in place throughout the range of *H. hippopus* (see Appendix 1). Many implement protections for giant clams broadly (including *H. hippopus*) and generally fall into four categories: a complete ban on harvest, a ban on harvest for commercial sale or export, bag limits, and minimum size restrictions. Below, we summarize the existing regulatory mechanisms in locations where *H. hippopus* is known to occur or once occurred.

Five countries and territories within the range of *H. hippopus* have instituted a total ban on the harvest of giant clams for any purpose—these include Australia, India, Taiwan, Indonesia, and the Philippines. The state of Kosrae in FSM has also established a marine sanctuary for the explicit purpose of protecting giant clams, but it is unclear if there are protections in place outside of the sanctuary. Twelve countries and territories within the range of *H. hippopus* have instituted a ban on the commercial export of giant clams—these include Fiji, Papua New Guinea, Solomon Islands, Vanuatu, Yap state in FSM, Kiribati, Marshall Islands, Palau, Cook Islands, Guam, Samoa, and Tonga. The sale of giant clams in local markets is still permitted in Papua New Guinea, Vanuatu, Palau, Cook Islands, American Samoa, and Tonga, although a license is required for commercial harvest in American Samoa. In the Northern Province of New Caledonia, professional fishers are restricted to harvesting five giant clams per day, and all others are restricted to two per day. In the Southern Province, there is a maximum bag limit of 40 kg and for tourists there is a limit of 3 shells weighing up to 3 kg. Lastly, in Guam, harvesting for subsistence use is limited to no more than three clams per day with minimum size restriction of 18 cm. There are no known local or regional regulations in place for the protection of *H. hippopus* in Malaysia, Singapore, Chuuk and Pohnpei states in FSM, CNMI, or within the South China Sea.

As discussed in **Section 3.4**, in many Pacific islands, national legislation is also supplemented or enforced by way of customary fishing rights and marine tenure systems. This is the case in parts of Fiji, Samoa, Solomon Islands, Cook Islands, Papua New Guinea, and Vanuatu, where indigenous village groups hold fishing rights and regulate access to adjacent reef and lagoon areas. It is unclear whether these small-scale regulatory dynamics typically apply to giant clams broadly, or if certain species may be protected or managed differently than others. Thus, without more information, there is no way to assess the effectiveness of these community-based management systems on the preservation of *H. hippopus*, specifically. Likewise, the paucity of long-term monitoring data in many of the countries and territories where *H. hippopus* occurs makes it difficult to evaluate the effectiveness of local regulatory mechanisms more generally. In many areas, for example, harvest prohibitions have been instituted within the last decade or two, but there have been few, if any, follow-up surveys conducted in the time since.

Using what survey data are available, which consistently indicate population declines and low abundance of *H. hippopus* throughout most of its range, we can infer that existing regulations have not sufficiently protected this species from exploitation. In **Section 3.4**, we discuss specific reports of recent illegal harvest of giant clams in the Philippines, Papua New Guinea, and Malaysia, along with a number of challenges that many countries face related to the management of giant clams. According to Kinch and Teitelbaum (2010), such challenges include a lack of capacity for conducting stock assessments and enforcing harvesting regulations, a lack of education and awareness among community members about sustainable giant clam harvest, an uncoordinated legislative structure, and a lack of international collaboration to promote a sustainable and scalable market for captive-bred giant clams. Each of the countries may experience these challenges to a different degree, but overall it highlights the difficulties in effectively managing giant clam populations, particularly for smaller island nations that may lack enforcement resources or expertise. This is compounded, in many cases, by the traditional importance of giant clams as a coastal resource, which may limit the willingness among indigenous communities to adopt the recommended practices. While these challenges are discussed with respect to giant clams broadly, they also apply specifically to the management of *H. hippopus* throughout its range. Thus, despite widespread commercial export bans, the capacity for enforcing existing regulations is often limited, existing regulations do not restrict continued subsistence harvest in many locations, and illegal harvest and trade of giant clams (particularly for the shell trade) continues to occur. For these reasons, we conclude with **Medium** confidence that the inadequacy of existing local/regional regulations, in combination with past and present rates of exploitation, poses a **Moderate** risk to the extinction of *H. hippopus* (i.e., the factor contributes significantly to long-term risk of extinction, but does not in itself constitute a danger of extinction in the near future).

In terms of international regulations, *H. hippopus* was listed under Appendix II of CITES in 1985 to regulate international trade in any of its parts (shells, tissues, alive or dead). Of the 25 countries and territories throughout its range, only FSM, the Marshall Islands, and the Cook Islands are not Parties to the treaty, and Palau has claimed reservations on all species of giant clams. Any CITES Party permitting the export of *H. hippopus* must provide documentation from their designated Scientific Authority demonstrating that trade is not detrimental to the survival of the species, and any trade from non-Parties to a CITES Party is still required to have documentation comparable to a CITES permit. As discussed in **Section 4.1.3.2**, CITES annual report data indicated that the recent trade of *H. hippopus* internationally is quite low. Since 2010, only 2,756 *H. hippopus* shells and 7,302 live *H. hippopus* specimens have been recorded in trade. Approximately 51.2% of traded shells during this period were of wild-caught origin, primarily from the Solomon Islands in 2014, while 34.1% were reportedly culture-raised. Of the live specimens, only 2.6% were wild-caught, while 96.2% were reportedly culture-raised. Based on this data, CITES regulations have been effective at transitioning much of the international supply of *H. hippopus* products away from wild harvest and towards mariculture operations. It is important to reiterate, however, that CITES trade data must be interpreted cautiously due to various limitations, including frequent discrepancies in recorded import and export quantities, inconsistencies in the terms or units used to describe the trade, occasional omissions of seized or confiscated specimens, erroneous data entry (e.g., wrong source code, submission of the number of permits issued instead of actual numbers of clams traded), and delays or failure to submit trade statistics to the Secretariat. Additionally, CITES only applies to international legal trade and does not regulate domestic trade nor for obvious reasons include any data on illegal trade. Therefore, while it appears that international trade regulations are adequately minimizing the trade of wild-caught *H. hippopus* (**Very Low** risk), our confidence in this assessment is **Low**.

Lastly, with respect to international climate change regulations, we conclude in **Section 3.4.2** that the current implementation of domestic and international climate regulations is insufficient to mitigate the cumulative threat of climate change to giant clam habitat and physiology generally. However, as mentioned in **Section 4.1.3.1**, because *H. hippopus* is often found in sandy environments outside of the coral reef framework, the anticipated impacts of climate change on coral reefs will not likely pose a severe threat to this species. Thus, international climate change regulations are likely most relevant to *H. hippopus* in terms of the impacts of ocean warming and acidification on the species' physiology. As addressed in **Section**

**4.1.3.5** below, there is limited information on the effects of climate change on *H. hippopus* specifically, but the few studies available, as well as inferences based on findings from other species, suggest that *H. hippopus* is likely to experience significant physiological changes under projected ocean warming scenarios. The precise magnitude of these impacts is unknown, but any significant changes in metabolic demand, reproductive success, and the possibility of bleaching due to warming summer temperatures will likely increase the risk of extinction. For this reason, we find that the inadequacy of international climate change regulations may, in combination with the aforementioned impacts, contribute significantly to the long-term or near future risk of extinction (**Low** risk, **Medium** confidence).

#### 4.1.3.5 Other Natural or Manmade Factors

***Climate Change***

Beyond the information presented in **Section 3.5**, we could find very little research addressing the potential effects of climate change on *H. hippopus* specifically. In a laboratory experiment in the Philippines, *H. hippopus* was found to experience a significant increase in respiration under elevated temperatures and was more sensitive to warming than the two other species tested (*T. gigas* and *T. derasa*). After 24 hours of exposure to elevated temperatures (3°C above ambient), no bleaching was observed (Blidberg et al., 2000). Additionally, Schwartzmann et al. (2011) documented the *in situ* response of *H. hippopus* to elevated temperatures in New Caledonia. At the end of the summer, the combination of high temperatures and high irradiance altered the growth and gaping behavior of *H. hippopus*. At the solar maximum, daily growth increments and gaping behavior became erratic, indicating some degree of physiological distress. The effect was pronounced when temperatures stayed above 27°C, which is near the current summer maximum in this region.

We could not find any studies investigating the effect of ocean warming on early life stages nor could we find any reports of bleaching in *H. hippopus*. While there is substantial research on these effects in other giant clam species, we are hesitant to make extrapolations from these studies, as it is possible that susceptibility may vary among species. For example, a species like *H. hippopus* that tends to occur in shallow habitats where temperature fluctuations can be quite extreme may have adapted a higher tolerance to such conditions. On the other hand, given the degree to which warming altered the respiration rate of *H. hippopus* relative to *T. gigas* and *T. derasa*, it is possible that this species may be more sensitive to the impacts of ocean warming on early life stages than other species. Thus, considering the best available information for giant clams in general, and the species-specific information available for *H. hippopus*, we conclude with **Low** confidence that ocean warming may, in combination with other VP descriptors or threats, contribute to the long-term extinction risk of *H. hippopus*, but without more evidence, we cannot conclude that it is a significant threat on its own (**Low** risk).

We were not able to find any additional information regarding the potential impacts of ocean acidification on *H. hippopus* beyond what is provided in **Section 3.5.2**. As discussed in **Section 3.5.2**, the available information regarding the effects of ocean acidification on giant clams more broadly is limited and inconclusive.

***Land-Based Sources of Pollution***

As discussed in **Section 3.5.3**, sedimentation, salinity fluctuations, nutrient enrichment, and elevated heavy metal concentrations represent environmental conditions that giant clams may experience following heavy rains, particularly near coastlines that have been altered by human development. Given its common occurrence in shallow nearshore habitats, *H. hippopus* is likely highly exposed to these threats. However, beyond what is provided in **Section 3.5.3** related to giant clams generally, there is limited information regarding the impacts of these factors on *H. hippopus* specifically. Short-term, sub-lethal exposure to copper ($5\ \mu g\ l^{-1}$) was found to cause a significant decline in gross primary production in adults (Elfwing et al., 2002). Additionally, *H. hippopus* juveniles exhibited a 110% increase in growth per month when exposed to elevated dissolved nitrogen (Solis et al., 1988).

**Section 3.5.3** addresses many other impacts of sedimentation, salinity, nutrient enrichment, and elevated heavy metal concentrations that have been observed for other species of giant clams. Overall, the results provide some indication that these factors may reduce fitness in certain respects; however, in many cases, the effects are not consistent across species or the experimental treatments do not reflect conditions that giant clams may realistically experience in the natural environment. For these reasons, we are reluctant to extrapolate these results to our assessment of *H. hippopus*, and we conclude with **Low** confidence that sedimentation, salinity fluctuations, nutrient enrichment, and heavy metal contamination are unlikely to contribute to the risk of extinction for *H. hippopus*, either by themselves or in combination with other VP descriptors or threats (**Very Low** risk).

***Stochastic Events***

While stochastic events such as extreme weather and mass mortalities of unknown cause may result in severe population loss in localized areas, these threats inherently cannot be predicted with any precision (**Low** confidence). However, because a mass mortality of *H. hippopus* has previously been observed in the Solomon Islands (A. H. Richards et al., 1994), we conclude that the threat of stochastic mortality events may, in combination with other VP factors or threats, contribute significantly to the species' long-term risk of extinction (**Low** risk).

**Table 8.** Summary of the threats analysis for *H. hippopus* and associated confidence ratings.

| 4(a)(1) Factor | Threat | Contribution to Species' Risk of Extinction | Confidence Rating |
|---|---|---|---|
| **Habitat destruction, modification, or curtailment** | *Coastal development* | Low | Low |
| | *Climate change impacts to coral reefs* | Very Low | Low |
| **Overutilization** | | Moderate | Medium |
| **Disease or Predation** | | Very Low | Low |

| **4(a)(1) Factor** | **Threat** | **Contribution to Species' Risk of Extinction** | **Confidence Rating** |
|---|---|---|---|
| **Inadequacy of existing regulatory mechanisms** | *National and local regulations on harvest* | Moderate | Medium |
| | *Regulations on international trade* | Very Low | Low |
| | *Regulations on climate change* | Low | High |
| **Other natural or manmade factors affecting the species' continued existence** | *Physiological impacts of climate change* | Low | Low |
| | *Land-based sources of pollution* | Very Low | Low |
| | *Stochastic events* | Low | Low |

### 4.1.4 Demographic Risk Assessment

***Abundance***

Because there are no global abundance estimates for *H. hippopus*, we rely on the qualitative estimates of population status provided in Table 7, which are based on the best available survey data from all countries or territories where *H. hippopus* has been recorded. These data indicate that *H. hippopus* has suffered significant population declines to the extent that the species is considered "rare," locally extinct, or has been reintroduced after local extinction in 21 of 26 locations throughout its range. In locations where it is considered "rare," this means that available survey data indicate a population density that is less than 10 ind $ha^{-1}$, or one individual spaced approximately every 30 m on average. For broadcast spawning organisms like *H. hippopus*, which rely on the external fertilization of gametes, the implications of such sparse distribution on reproduction can be significant. As discussed in **Section 4.1.2**, Braley (1984) observed that 70% of nearest spawning giant clams (*T. gigas*) were found within 9 m of one another, while only 13% were between 20-30 m of one another. These findings suggest that individuals in "rare" populations are less likely to spawn in synchrony and as a result are likely to experience infrequent, sporadic reproductive success. This negative relationship between population density and productivity, known as the Allee effect, can cause further reductions in population abundance and put "rare" populations of *H. hippopus* at greater risk of extinction.

These "rare" populations are also susceptible to the ongoing threats described in **Section 4.1.3**, including coastal development, ongoing subsistence harvest, the inadequacy of existing regulations, potential physiological impacts of ocean warming, and stochastic mortality events. These factors threaten the persistence of "rare" populations, and in effect, elevate the extinction risk of *H. hippopus*.

In 5 of the 26 locations where *H. hippopus* has been recorded, the species is considered "frequent," indicating population density estimates that are between 10 and 100 ind ha$^{-1}$. This includes the Great Barrier Reef, the outlying islands of NW Australia, the Marshall Islands, Vanuatu, and Palau. Of these locations, only Australia has in place a total ban on the harvest of *H. hippopus*. The other countries have instituted a ban on the commercial export of giant clams, but subsistence harvest is still ongoing. In Vanuatu, *H. hippopus* is considered a prized subsistence food and is harvested regularly for household consumption and special occasions. Zann and Ayling (1988) reported that *H. hippopus* was overharvested on inhabited islands in Vanuatu and secure on only two reefs; it is unknown if these remote populations have been subjected to harvest in the three decades since the observations were published. Similarly, in the Marshall Islands, available reports suggest that giant clams are heavily exploited near population centers, and *H. hippopus* was reported to be abundant only on three remote atolls. Thus, in Vanuatu and the Marshall Islands, overexploitation remains a significant threat to *H. hippopus* populations. In Palau, the most recent survey from Helen Reef, a remote uninhabited atoll in the Western Caroline Islands was conducted in 1976, when the standing stock of *H. hippopus* was estimated to be over 70,500 (or 40.1 ind ha$^{-1}$). However, due to its remoteness from the inhabited islands of Palau and the difficulty of surveilling the area, Helen Reef was historically targeted by giant clam poachers in the 1970s. While we are not aware of any more recent poaching in the area, it is possible that such activities have gone undetected. Thus, the current status of *H. hippopus* at Helen Reef is unknown. A recent survey from the main island group in Palau (Rehm et al., 2022) recorded an average population density of 51.5 ind ha$^{-1}$, but the authors note that harvest of *H. hippopus* in this area is still "very common." In Australia, there are very limited survey data on the abundance of *H. hippopus* on the Great Barrier Reef; however, anecdotal reports commonly suggest that populations of giant clams, in general, are healthy relative to other areas of the Indo-Pacific. Additionally, there is evidence that existing regulations have been effective at preventing illegal harvest and minimizing the risk of overexploitation of giant clams in Australian waters. Several reports have suggested significant population declines from 1999 to 2009 at Ashmore and Cartier Reefs, two islands in NW Australia that have historically had abundant *H. hippopus* populations. The cause of the decline and current status of these populations is unknown.

Thus, while we consider *H. hippopus* to be "frequent" in 5 of the 26 locations where it naturally occurs, in 2 of these locations (i.e., Vanuatu and the Marshall Islands), this assessment is based on only a few remote sites that reportedly have relatively abundant populations. The abundance of *H. hippopus* outside of these areas, particularly near human population centers, is considerably lower and is subject to the ongoing threat of unregulated domestic harvest. Populations of *H. hippopus* in Palau, NW Australia, and on the Great Barrier Reef appear to be healthy, despite ongoing harvest in Palau. Considering these locations alongside the 21 other locations in the species' range where overexploitation has driven *H. hippopus* to low abundance, we find that this factor likely contributes significantly to the species' long-term risk of extinction, but does not in itself constitute a danger of extinction in the near future (**Moderate** risk, **Medium** confidence).

### ***Productivity***

Despite exceptionally high fecundity, there is substantial evidence that low recruitment success and high mortality rates during early development lead to low productivity in most species of giant clams. This is likely true of *H. hippopus* as well; although, observations of this species are limited. Early estimates of fecundity from mariculture operations suggest that *H. hippopus* can produce approximately 25-60 million eggs during a spawning event (Alcala et al., 1986; Jameson, 1976). However, evidence from other species suggests that survival rates through larval and juvenile development can often be less than 1% (Crawford & Lucas, 1986; Fitt et al., 1984; Jameson, 1976). Given the low abundance of *H. hippopus* throughout much of its range and the ongoing threats outlined in **Section 4.1.3**, which are likely leading to continued population declines, such low productivity can significantly limit the capacity for this species to achieve positive population growth rates and recover from low abundance.

Furthermore, as discussed in relation to the Abundance risk factor above, it is likely that *H. hippopus* is experiencing an Allee effect in locations where the species is considered "rare," such that productivity is negatively correlated with population abundance. As a broadcast spawning organism, *H. hippopus* relies on sufficient population density in order to respond to spawning cues of nearby individuals and to facilitate successful external fertilization of their gametes. The best available evidence suggests that spawning synchrony in *T. gigas* drops significantly at population densities lower than 10 ind $ha^{-1}$ (Braley, 1984), and while gametes can remain viable for up to 8 hours in *T. squamosa*, viability decreases significantly with time (Neo, Vicentuan, et al., 2015). While the distance and duration may vary among species, it is likely that the overall effect of low abundance in reducing productivity is applicable to *H. hippopus* as well.

For these reasons, we conclude that the low natural productivity of giant clams as well as decreased productivity due to low abundance contribute significantly to the long-term risk of extinction, but likely does not in itself constitute a danger of extinction in the near future (**Moderate** risk, **Medium** confidence).

### *Spatial Distribution/Connectivity*

We could not find any population genetic information indicating the spatial structure or connectivity of *H. hippopus* across its range. The relatively short duration of the pelagic larval phase (~6-14 days) of giant clams likely limits long-range dispersal between distant locations of the species' range. Available population genetic information for other species that occupy a similar geographic area (*T. squamosa*, *T. maxima*, and *T. crocea*) suggest that there is likely little genetic differentiation among populations in the majority of the Indo-Malay Archipelago, but that there may be a genetic break between this region and the populations in the central and western Pacific. However, without more information regarding *H. hippopus* specifically, we are unable to conclude whether spatial distribution and connectivity are a threat contributing to the species' risk of extinction.

### *Genetic Diversity*

We could not find any information regarding the genetic diversity of *H. hippopus*. However, given the species' significant historical decline in abundance, it is possible that such a decline may have reduced the species' genetic diversity via genetic drift as a result of a population bottleneck. However, without any genetic testing on this species to determine diversity or effective population size, we are unable to conclude whether genetic diversity is a threat contributing to the species' risk of extinction.

**Table 9.** Summary of the demographic risk analysis for *H. hippopus* and associated confidence ratings.

| Demographic Risk Factor | Contribution to Species' Risk of Extinction | Confidence Rating |
|---|---|---|
| **Abundance** | Moderate | Medium |
| **Productivity** | Moderate | Medium |
| **Spatial Distribution/Connectivity** | *Unknown* | *Not applicable* |
| **Genetic Diversity** | *Unknown* | *Not applicable* |

### 4.1.5 Overall Extinction Risk Assessment

Guided by the results of the demographic risk analysis and threats assessment above, we analyzed the overall risk of extinction of *H. hippopus* throughout its range. In this process, we considered the best available scientific and commercial information regarding *H. hippopus* from all locations of the species' range, and analyzed the collective condition of these populations to assess the species' overall extinction risk. We determined that the most critical demographic risks to the species include the low abundance and negative trajectory of populations throughout the majority of its range, compounded by low natural productivity. Additionally, our threats assessment revealed that the past and present overutilization and associated inadequacy of existing regulatory mechanisms at the local level contribute most significantly to the extinction risk of this species. Continued harvest of *H. hippopus* primarily for subsistence purposes, combined with the species' low productivity will likely drive further population declines and prevent any substantial population recovery.

The best available scientific and commercial information indicates that very few abundant populations of *H. hippopus* remain, and that in almost every location outside of Australia, domestic harvest of *H. hippopus* is ongoing. In Palau, Vanuatu, and the Marshall Islands, which are three of the five locations where we consider *H. hippopus* to be "frequent," anecdotal reports indicate that harvest for subsistence and for sale in domestic markets is still very common. In Vanuatu and the Marshall Islands, there is evidence that this has significantly reduced *H. hippopus* abundance in the areas around human population centers, leaving very few remote areas with relatively healthy *H. hippopus* populations. There is very little quantitative information regarding the abundance of *H. hippopus* on the Great Barrier Reef, but anecdotal reports commonly suggest that populations of giant clams in general are healthy. There is also quantitative evidence that *H. hippopus* occurs in significant numbers in the outlying islands of NW Australia (Richards et al., 2009; Skewes et al., 1999), likely benefitting from the strong regulatory protections within Australian waters. Additionally, in Palau, although subsistence harvest of giant clams is permitted and is reported to occur commonly, a recent survey indicated relatively large populations of *H. hippopus* (Rehm et al., 2022). As discussed in **Section 4.1.2**, it is possible that the significant output from the PMDC mariculture facility and reported efforts to use a portion of *H. hippopus* seedstock to enhance depleted populations in certain conservation areas may be offsetting the harvest pressure in Palau. Although, without further information, we are not able to assess with confidence whether populations in Palau are stable, or whether they may be increasing or decreasing significantly due to one factor outweighing the other.

In contrast to these 5 locations where *H. hippopus* populations are relatively healthy (i.e., the Great Barrier Reef, NW Australia, Palau, and remote areas of Vanuatu and the Marshall Islands), the best available data indicate that, at the 21 other locations across the range with documented occurrences of this species, extensive exploitation for past commercial trade, ongoing subsistence use, and illegal harvest have driven *H. hippopus* to low abundance, and in some cases, local extinction. The continued threat of overexploitation and the demographic risks outlined in **Section 4.1.4** likely put the species at a high level of extinction risk in these locations in the foreseeable future (i.e., **Moderate** extinction risk, as defined in Box 2 above). However, because *H. hippopus* populations in Australia and Palau, and certain areas of Vanuatu and the Marshall Islands are relatively abundant, and the enforcement of strict harvest bans has effectively minimized the threat of overexploitation in Australian waters, we cannot conclude that the species is at moderate risk of extinction throughout its *entire* range.

### *Significant Portion of its Range Analysis*

Under the ESA, a species warrants listing if it is in danger of extinction or likely to become so within the foreseeable future throughout all or a significant portion of its range. Thus, a species may be endangered or threatened throughout all of its range, or a species may be endangered or threatened throughout only a significant portion of its range. Having determined that *H. hippopus* is not at moderate risk of extinction throughout all of its range, in order to inform the listing determination, we conducted an additional analysis to assess whether the species is at higher risk of extinction in a “significant portion of its range” —that is, we assessed whether there is any portion of the species' range for which we can conclude that both (1) the portion is significant and (2) the species, in that portion, is at moderate or high risk of extinction. A joint USFWS-NMFS policy, finalized in 2014, provided the agencies’ interpretation of this phrase (“SPR Policy,” 79 FR 37578, July 1, 2014) and explains that, depending on the case, it might be more efficient for us to address the “significance” question or the “status” question first. Regardless of which question we choose to address first, if we reach a negative answer with respect to the first question, we do not need to evaluate the other question for that portion of the species' range.

Because there are infinite ways in which a range could be theoretically divided for purposes of this analysis, the only portions considered are those that have a reasonable likelihood of being at high risk of extinction and have a reasonable likelihood of being biologically significant to the species. In other words, unless portions meet both of these conditions, they are not further considered in this analysis. As discussed in the SPR Policy, as a practical matter, a key part of this analysis is considering whether threats are geographically concentrated in some way. In this case, because we determined that the most significant threats to the species are overexploitation and inadequacy of regulatory mechanisms, we base our analysis here on the portion of the range where these threats are most severe.

As has been discussed previously, several sources indicate that the early adoption of strict harvest prohibitions in Australia has been largely effective at preventing illegal harvest and minimizing the risk of overexploitation of giant clams in Australian waters. This differs considerably from reports from every other location throughout the species' range, which consistently indicate that the threat of overexploitation in combination with inadequate regulation and enforcement poses a significant extinction risk to *H. hippopus*. Thus, for the purpose of this SPR analysis, we distinguish locations in Australia (i.e., the Great Barrier Reef and NW Australia) from all other locations where *H. hippopus* occurs and consider them as two separate portions of the species' range.

The portion under consideration includes 24 countries and territories where the primary threat to the species is overexploitation. In 21 of these locations, the best available survey data, as well as qualitative descriptions of abundance, suggest that extensive commercial, subsistence, and illegal harvest has driven *H. hippopus* to exceptionally low abundance, and in several cases, local extinction. There are three exceptions to this trend—Vanuatu, the Marshall Islands, and Palau. In Vanuatu, a single survey in 1988 spanning 13 islands reported that *H. hippopus* was "overfished on inhabited islands but secure on two remote reefs" (Zann & Ayling, 1988). We are not aware of any follow-up surveys, and the current status of these remote populations is unknown. Available reports from the Marshall Islands suggest that *H. hippopus* is relatively abundant at three less-populated atolls, but do not provide any quantitative data. Lastly, in Palau, a recent survey of the main island group and past surveys of a remote uninhabited atoll indicate that the abundance of *H. hippopus* is relatively high.

Additionally, it is important to note that, while we consider the overall abundance of *H. hippopus* in the Philippines and Indonesia to be "rare," there are a number of studies reporting small areas within each country where *H. hippopus* still occurs at relatively high frequency. This includes, for example, Carbin Reef and Tubbataha Reefs Natural Park in the Philippines, and Raja Ampat and Kei Islands in Indonesia, where recently estimated densities are over 20 ind $ha^{-1}$.

However, in each of these locations, existing regulations do not prohibit the domestic harvest of giant clams for subsistence purposes or for sale in local markets. According to Neo et al. (2017), giant clams, and especially *H. hippopus*, are still a prized subsistence food on most islands in Vanuatu. The same is true in Palau, where the harvest of *H. hippopus* is still very common near populated areas (L. Rehm, pers. comm., May 26, 2022), and in the Marshall Islands, where available information indicates that *H. hippopus* has historically been sold in local markets (S. Wells, 1997). Thus, while the current status of *H. hippopus* in these locations may be healthier than other locations throughout the species' range, the threat of domestic harvest and inadequate regulatory mechanisms continues to expose the species to an elevated extinction risk in the foreseeable future. It seems that the main factor protecting *H. hippopus* in Vanuatu and the Marshall Islands is simply the remoteness of the populations rather than any formal regulatory mechanism.

It is possible that the success of mariculture operations in Palau could potentially prevent the species from going extinct in the foreseeable future. It is also possible that the threat of overexploitation in Palau has been somewhat offset by documented efforts to reseed depleted populations (see **Section 4.1.2**). However, we did not base our assessment on the past success of mariculture operations, because of its reliance on a number of unpredictable factors (e.g., funding, management priorities, natural disasters, etc.). Thus, it is difficult to extrapolate the effect of mariculture beyond the next few years. Basing our assessment on the demographic risks of low abundance and low productivity in 21 of 24 locations where the species naturally occurs, and the ongoing threats overexploitation and inadequate regulatory mechanisms in all 24 locations, we conclude that in the portion of the species' range defined as all locations outside of Australia, *H. hippopus* is at **Moderate** risk of extinction. Because the species still occurs in 24 locations within this portion of its range, which encompass a broad geographic area and variety of environmental conditions, and relatively healthy populations can still be found in the Marshall Islands, Palau, Vanuatu, and a number of small areas within the Philippines and Indonesia, we do not find that *H. hippopus* is at or near a level of abundance that places its continued persistence in question. However, given the ongoing threats of overexploitation and inadequate regulatory mechanisms, as well as documented populations declines that have been attributed to these threats, we find that the species is on a trajectory that puts it at a high level of extinction risk within the foreseeable future.

Having reached a positive answer with respect to the "status" question, we move on to determine whether this portion of the range is "significant." As indicated in the 2014 SPR Policy, the term "significant" in the "significant portion of its range" phrase should be defined generally as biological significance - i.e., biological importance to the conservation and viability of the overall species. Although the specific threshold for determining "significant" set forth in the SPR Policy has since been invalidated (see *Desert Survivors v. DOI,* 336 F. Supp. 3d 1131 (N.D. Cal. 2018)), the general premise that a "significant portion" be defined in a biological sense has not. Therefore, in assessing whether a portion of a species' range is "significant," we consider relevant biological information, such as whether the portion was historically highly abundant, potentially functioning as a source population for other areas of the range, whether there is evidence that it was historically highly productive with potential to contribute to the population growth of this species as a whole, whether the portion encompasses a substantial area relative to the species' current range, whether the portion historically facilitated gene flow between populations, and whether the portion contains genetic or phenotypic diversity that is important to species viability. The contribution or role of that portion to the viability of the species as a whole is also considered from a historical, current, and future perspective to the extent possible.

With respect to *H. hippopus*, there is strong evidence that the portion of the species' range defined as all locations outside of Australia qualifies as a "significant portion." Based on historical trade statistics, as well as the countless reports describing major population losses resulting from years of domestic harvest and intense commercial harvest, primarily for the international shell and shell-craft industry (e.g., see Villanoy et al., 1988; Kinch, 2003; Dolorosa & Schoppe, 2005; Harahap et al., 2018; Purcell et al., 2020), it is clear that *H. hippopus* was historically highly abundant in this portion of its range.

Furthermore, prior to these losses, it is likely that populations in this portion, which includes 24 of 26 locations comprising the species' range (i.e., all locations except for the Great Barrier Reef and NW islands in Australia), played a critical role in maintaining genetic connectivity throughout the species' range. For many marine organisms, and particularly sedentary taxa such as giant clams, long-range dispersal (e.g., between islands and other distant locations) is likely highly stochastic and infrequent (see Cowen et al., 2003; Siegel et al., 2008). As is discussed above in *Growth and Reproduction*, it relies on a process known as 'sweepstakes' reproduction, in which spawning and fertilization coincidentally align with oceanographic conditions that facilitate successful long-distance dispersal and recruitment to a suitable habitat. The relatively short pelagic larval duration of giant clams (~6-14 days) further limits the probability of long-distance dispersal. Thus, it is likely that *H. hippopus* was dependent on serial migration between nearby locations (i.e., ‘stepping stones’) to maintain genetic connectivity throughout its range.

Given its geographic size, this portion of the species’ range encompasses a wide variety of habitats and environmental conditions. Therefore, we expect that, to some extent, past populations were likely genetically adapted to their local setting, as has been demonstrated with respect to numerous other marine organisms across similar geographic scales (e.g., see Sanford & Kelly, 2011 for comprehensive review). Such genetic diversity can function as an important foundation to enhance the resilience of the species and facilitate future adaptation to environmental change. Furthermore, given the geographic extent of this portion of this range and the varied habitats it encompasses, the populations of *H. hippopus* within this portion would have provided an important demographic reserve, which could facilitate recovery following stochastic mortality events or other localized population declines.

Based on the rationale described above, we find that the portion of the species’ range defined as all locations outside of Australia is “significant,” and serves a biologically important role in maintaining the long-term viability of *H. hippopus*.

## 4.2 *Hippopus porcellanus*

### 4.2.1 Life History and Ecology

#### 4.2.1.1 Taxonomy and Distinctive Characteristics

*Hippopus porcellanus,* commonly referred to as the China clam, was originally described by Rosewater in 1982. *H. porcellanus* grows to a maximum size of 40 cm, but is most commonly found at shell lengths of around 20 cm (Kinch & Teitelbaum, 2010). The shell exterior is off-white, occasionally with scattered weak reddish blotches. The shell interior is porcelaneous white, often flushed with orange on the ventral margin, and the mantle ranges from a yellowish-brown to a dull green or grey (Kinch & Teitelbaum, 2010; see Figure 19). This species is distinguished from its congener, *H. hippopus*, by its smoother and thinner valves and presence of fringing tentacles at the incurrent siphon (Neo, Eckman, et al., 2015).

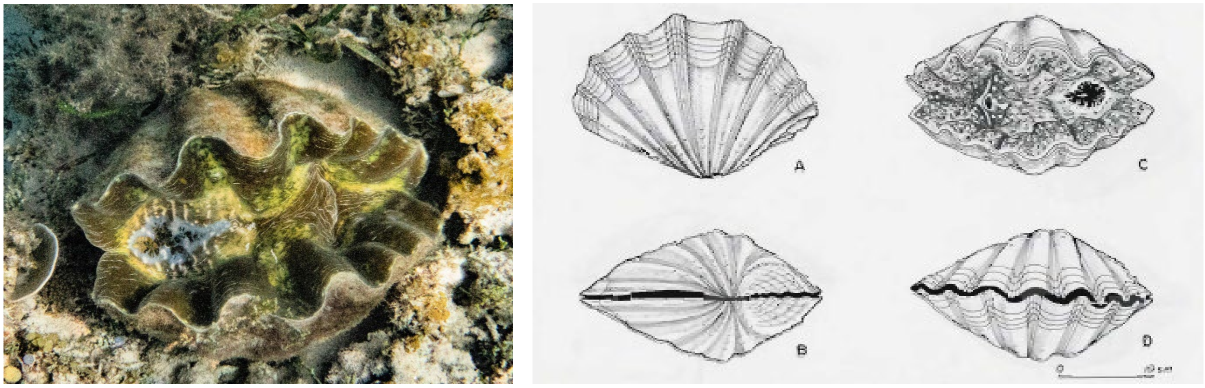

**Figure 19.** *H. porcellanus* morphology. Left: Photograph of *H. porcellanus* taken near Coron, Philippines. Right: Illustrations showing the lateral (A), ventral (B), mantle (C), and dorsal (D) view of a representative specimen. (Photo credit: sykospark/iNaturalist, CC BY-NC 4.0; Diagram source: Calumpong, 1992)

### 4.2.1.2 Range, Distribution, and Habitat Use

*H. porcellanus* has one of the most restricted geographic ranges of the giant clams, centered in the Coral Triangle region (see Figure 20). The species is mostly known from the Sulu Archipelago and Palawan region in the Philippines, but it has also been reported in Palau, the Milne Bay Province (Papua New Guinea), Sabah (Malaysia), and Sulawesi and Raja Ampat (Indonesia) (S. Wells, 1997; Neo et al., 2017).

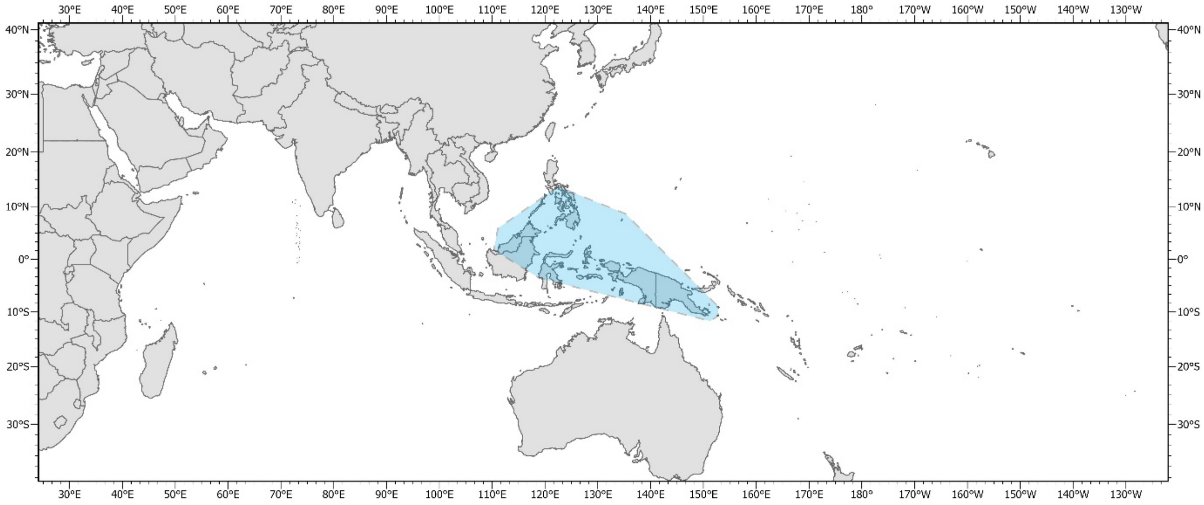

**Figure 20.** Approximate natural range of *H. porcellanus* based on reported occurrences provided by Neo et al. (2017). The range does not include locations where *H. porcellanus* has been introduced.

There is very little information specifying the habitat preferences of *H. porcellanus*, but according to Calumpong (1992), the species is commonly found in shallow, nearshore sandy areas adjoining coral reefs. Juvenile or young *H. porcellanus* are frequently found byssally attached to coral heads, whereas larger mature *H. porcellanus* can be found on sandy bottoms unattached to substrate (Rosewater, 1982; Kinch & Teitelbaum, 2010). Although, Tapilatu et al. (2021) documented the species in areas of coral rubble and live coral.

### 4.2.1.3 Reproduction and Growth

Aside from the information available for giant clams in general, there is very limited information on *H. porcellanus* regarding age at maturity or growth rate. A study conducted by Dolorosa et al. (2014) from 2009 to 2012 evaluated growth rates of *H. porcellanus* at Tubbataha Reefs Natural Park in the Philippines. The results showed that the shell length of *H. porcellanus* increased by approximately 3 cm on average during the 2.5 years of observation. Initial size of these clams ranged between 8.2 and 31.3 cm. The results of this study suggest a rapid growth in the first five years and then a subsequent decline (Dolorosa et al., 2014), a pattern of growth that is observed in other species of giant clam as well.

We could find only two studies addressing the reproduction of *H. porcellanus* (Alcázar et al., 1987; Calumpong et al., 1993). Size at sexual maturity is unknown (Mies, Scozzafave, et al. 2017); although, information from Alcázar et al. (1987) demonstrates the ability to induce the release of sperm in a 16 cm clam and the release of eggs in a 31 cm clam. It is thought that individuals larger than 20 cm may have the ability to spawn (Alcázar et al., 1987; Mies, Scozzafave, et al., 2017). During spawning events, *H. porcellanus* can release five million eggs in a single spawning event (Alcázar et al. 1987). However, despite their high fecundity, high rates of early mortality result in very low levels of natural recruitment (Munro, 1993). For *H. porcellanu*s, survival has been examined at different life stages, with 25% survival for trochophore stage, 10% for veliger stage, and 0.76% for juveniles (Alcázar et al. 1987; Mies, Scozzafave, et al. 2017). An overall survival rate of less than 1% of fertilized eggs surviving larval development (Fitt et al., 1984; Jameson, 1976; Mies, Scozzafave, et al. 2017) can result in low densities of mature individuals and reduce successful recruitment.

#### 4.2.1.4 Feeding and Nutrition

Aside from the general information provided in **Section 2.4** regarding giant clam feeding strategies and diet, we could not find any species-specific information for *H. porcellanu*s.

#### 4.2.1.5 Genetics and Population Structure

We were unable to find any information on the population structure or genetics of *H. porcellanus*.

### 4.2.2 Abundance, Density, and Population Status

The global population status and abundance trends for *H. porcellanus* are summarized in Table 10 and displayed in Figure 21 below. Quantitative estimates of *H. porcellanus* abundance are limited, but several reports indicate that natural stocks have experienced drastic declines since 1980. There are only 5 locations in which *H. porcellanus* has been recorded, and the species is “rare” (<10 individuals ha$^{-1}$) in all of these locations (Table 10). Only two sites, Tubbataha Reefs in the Philippines and Raja Ampat in Indonesia, are thought to have relatively abundant populations of *H. porcellanus*, but the species is considered extremely rare, if not locally extinct in nearly every other region of the two countries (Gomez & Alcala, 1988).

In the Philippines, which was historically the center of *H. porcellanus* distribution, only one individual was recorded in a broad survey encompassing 247 sites and over 31 ha throughout the Luzon, Visayas, Palawan, and Mindanao regions (Gomez & Alcala, 1988). Juinio et al. (1989) noted that abundance was so low in this region that broodstock could not be collected to initiate a restocking program for the species. Likewise, in Tubbataha Reefs, Estacion et al. (1993) encountered only empty shells of *H. porcellanus*, and in the same year, Calumpong and Cadiz (1993) reported finding only “a few individuals.” Together, these studies suggest that *H. porcellanus* was extremely rare and likely overharvested in the Tubbataha Reefs in the early 1990s. More recently, however, Dolorosa and Jontila (2012) encountered 41 individuals within a 0.42 ha survey area in Tubbataha Reefs, equating to a population density of 97.6 individuals ha$^{-1}$. The authors interpret these results as evidence that the population has recovered to some extent following nearly 20 years of protection in the reserve.

In Indonesia, *H. porcellanus* is reportedly “no longer found at many sites” in the Sulawesi region (S. Yusuf & Moore, 2020), and was the only giant clam species native to Indonesia that was not encountered within a 0.25 ha survey area in the Kei Islands (Triandiza et al., 2019). In 2014, Wakum et al. (2017) recorded 14 individuals within a survey area of 0.15 ha in Raja Ampat, West Papua, equating to an estimated population density of 93.3 individuals per ha. Only 6 *H. porcellanus* were observed within a 1 ha survey area near Cenderwasih Bay, Papua (Tapilatu et al., 2021). According to Firdausy and Tisdell (1992), *H. porcellanus* is "extremely rare if not extinct" throughout the rest of Indonesian waters.

*H. porcellanus* has also been recorded in the waters of Milne Bay Province, Papua New Guinea, but abundance is likely very low. One giant clam stock assessment conducted in the Engineer and Conflict Islands in 1996 estimated a population density of 0.3 ind $ha^{-1}$ (Kinch, 2002). However, the author notes that the species may have been misidentified in this survey (J. Kinch, pers. comm., March 18, 2023). *H. porcellanus* was not observed during two subsequent biodiversity surveys in this region in 1997 and 2001 (Allen et al., 2003; Hamilton et al., 2009). Several sources also note the occurrence of *H. porcellanus* in Malaysia and Palau (Newman & Gomez, 2000), but we were not able to find any estimates of population abundance. Shau-Hwai and Yasin (2003) note that *H. porcellanus* is restricted to Sabah, Eastern Malaysia, while in Palau, a recent survey throughout the main islands did not record a single individual (Rehm et al., 2022). It is likely that *H. porcellanus* is extremely rare or extirpated from these locations.

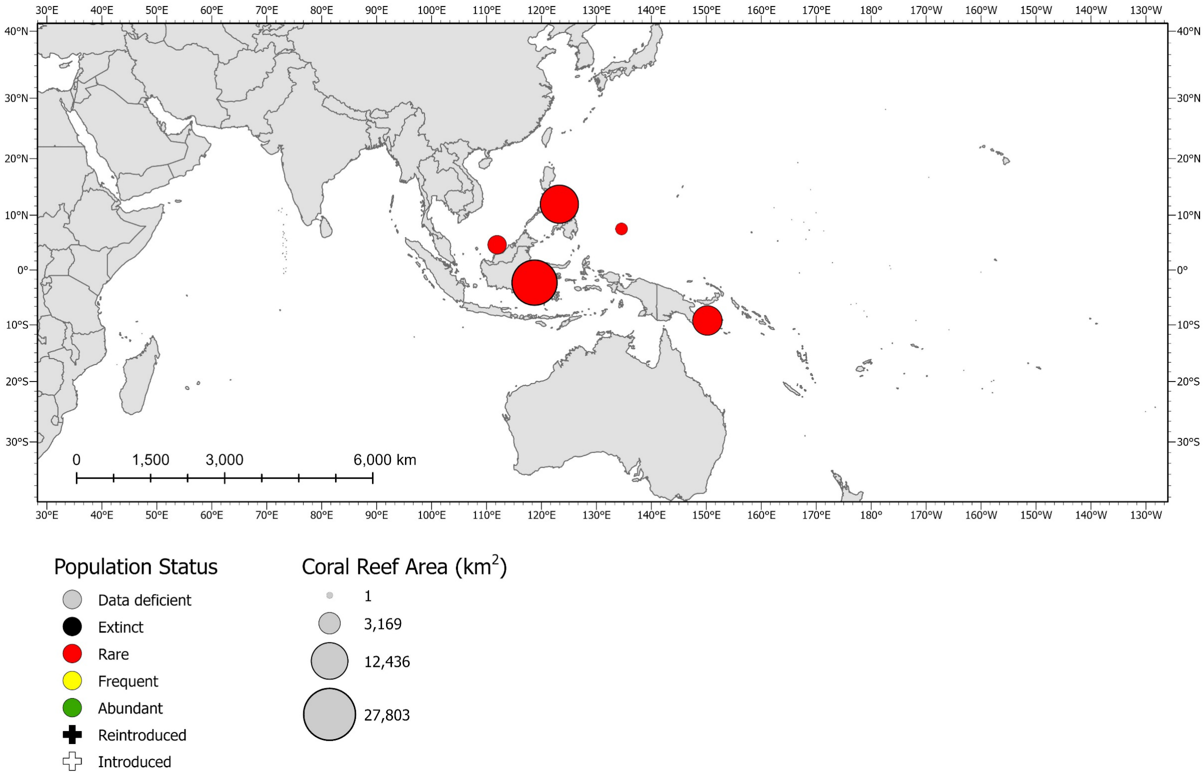

**Figure 21.** Qualitative abundance estimates for *H. porcellanus* based on reported occurrence and survey data. Points are located at the approximate centroid of survey sites within each country, territory, or region from which data has been included in the abundance assessment. Abundance categories are based on those used by Neo et al. (2017), but have been revised as follows: Abundant (>100 ind ha$^{-1}$), Frequent (10-100 ind ha$^{-1}$), Rare (<10 ind ha$^{-1}$), Extinct, Introduced, Reintroduced (i.e., locations where the species was reportedly extirpated in the past but there have since been efforts to restore populations using cultured specimens; current presence/abundance may not be known), and Data Deficient (i.e., locations where reports of species occurrence have not been confirmed). The size of the points reflects the total estimated area of coral reefs within each location based on data compiled by the UN Environment World Conservation Monitoring Centre and the WorldFish Centre (UNEP-WCMC et al., 2021), increasing on a square-root scale. It is used here to roughly approximate the relative amount of giant clam habitat. However, the accuracy of this approximation likely varies between species based on their habitat preferences.

**Table 10.** Summary of *H. porcellanus* population status across its geographic range (adapted from Table 4 in Neo et al. 2017 and supplemented with more recent information where available). Species abundance categories are as follows: Abundant (>100 ind ha$^{-1}$); Frequent (10-100 ind ha$^{-1}$); Rare (<10 ind ha$^{-1}$).

| **Location** | **Status** | **Notes** |
|---|---|---|
| ***South Asia*** | | |
| Indonesia | Rare | A survey in 2014 recorded 14 individuals in a 0.15 ha survey area of Raja Ampat, but the species has otherwise been described as “extremely rare if not extinct” throughout most of Indonesia. Giant clams are exploited for their meat (domestic consumption) and shells, and some for live aquarium trade. |

| | | |
|---|---|---|
| Malaysia | Rare | Restricted to Sabah and Pulau Bidong (Eastern Malaysia). Populations are in a state of decline due to the combined effects of pollution, environmental degradation and harvesting for meat and shells. |
| Philippines | Rare | Widespread subsistence harvesting and commercial exploitation (mainly for international shell trade) severely reduced *H. porcellanus* abundance. An expansive survey in 1989 recorded only one individual across 247 sites (31 ha) in the Luzon, Visayas, Palawan, and Mindanao regions. A 2008 survey indicates some population recovery in Tubbataha Reefs Natural Park. |
| ***Pacific Ocean*** | | |
| Palau | Rare | *H. porcellanus* has been reported to occur in Palau, but Rehm et al. (2021) did not observe any in a survey of the main island group. |
| Papua New Guinea | Rare | Low abundance in Milne Bay Province attributed to unsustainable commercial fishing practices from unsustainable harvest, poaching, and longstanding exploitation. |

### 4.2.3 Threats to *Hippopus porcellanus*

#### 4.2.3.1 Destruction, Modification or Curtailment of Habitat or Range

Beyond the information provided in **Section 3.1.2** related to the threat of habitat destruction or modification to giant clams generally, there is limited information addressing the threat to *H. porcellanus* specifically. Like its congener *H. hippopus*, *H. porcellanus* is known to reside preferentially in nearshore sand flats and areas of coral rubble and is therefore especially vulnerable to threats impacting these habitats. This includes sedimentation, for example, which is likely to be most severe in nearshore environments adjacent to river discharge zones and near areas of intense urban development. As discussed in **Section 3.1.2**, Burke et al. (2012) identified major proportions of coral reefs in Indonesia (20%), Malaysia (35%), Papua New Guinea (25%), and the Philippines (60%) that are currently threatened by the impacts of coastal development. These impacts include runoff from construction and waste from coastal communities, and it is likely that nearshore populations of *H. porcellanus* in these areas, which comprise the majority of the species' range, are also affected to a similar extent.

We note in **Section 3.1.2** that we could not find any studies directly investigating the effect of sedimentation on giant clam survival; however, similarities in the biology and behavior of giant clam larvae to that of coral larvae would suggest that comparable results between the taxa can reasonably be expected. In this respect, there is extensive evidence that heavy sedimentation can significantly reduce reproductive success by inhibiting larval settlement, interfering with settlement cues, and physically smothering newly-settled recruits. Accordingly, it is possible that heavy sedimentation may significantly inhibit the recovery of *H. porcellanus* populations that have been reduced by overexploitation or by other means.

*H. porcellanus* is also faced with an acute threat of habitat destruction in the northern portion of its range, where fishermen primarily from Tanmen, China have been razing shallow reef areas of the South China Sea in a search for giant clam shells (see **Section 3.1.3**). The damage from these operations is extensive and has likely eliminated any *H. porcellanus* that may have previously occurred in the islands of the South China Sea.

Considering this threat, and because the restricted range of *H. porcellanus* is centered in a region of intense urban development, we conclude that habitat destruction and modification contributes significantly to the long-term extinction risk of *H. porcellanus*. However, given the localized nature of these impacts, habitat destruction likely does not in itself constitute a danger of extinction in the near future (**Moderate** risk). Due to the uncertainty and lack of experimental evidence elucidating the impacts of sedimentation on giant clams, and *H. porcellanus* specifically, our confidence in this assessment is **Low**.

Because *H. porcellanus* is often found in sandy environments outside of the coral reef framework, the anticipated impacts of climate change (i.e., ocean warming and acidification) on coral reefs will not likely pose a severe threat to this species.

#### 4.2.3.2 Overutilization

As with its congener, *H. hippopus*, the tendency of *H. porcellanus* to occupy shallow nearshore areas make the species highly vulnerable to harvesting (Dolorosa et al., 2014). Heavy exploitation from both subsistence and commercial harvest has led to severe population declines throughout its range (Dolorosa et al., 2014; Neo et al., 2017). Villanoy et al. (1988) determined that *H. porcellanus* was overexploited in the Philippines as early as the 1980s, and more recently, Rubec et al. (2001) reported that *H. porcellanus* has been depleted to such an extent that it is no longer commercially viable for harvest in the Philippines. Ultimately, while subsistence harvest was widespread, heavy fishing pressure on giant clam stocks in the Philippines for the commercial shell trade has been the primary cause of population decline, and has led to local extinctions throughout the region (Juinio et al., 1987).

Villanoy et al. (1988) documented the export volume of giant clam shells from one major shell dealer in the Zamboanga region of the Philippines, San Luis Shell Industries. From 1978 to 1985, approximately 413,230 pairs of shells were exported by this company, of which about 37% (or nearly 153,000) were *H. porcellanus*. Based on comparisons to data provided by Juinio et al. (1987), the authors estimate that this shell dealer accounted for approximately 18.5% of the estimated total export volume of giant clam shells from the Zamboanga region during this period, suggesting that the total harvest of *H. porcellanus* during this period was likely much higher. According to CITES annual reports, from 1985 to 1992, the Philippines exported an additional 576,298 *H. porcellanus* shells, 145,926 shell pairs, 179,043.5 kg of shell material, 293,110 shell carvings, and 38,138 kg of shell carvings. All were either reported to be wild-caught or did not include the source of harvest. No other nation reported export volumes close to this magnitude during this time. Malaysia reported the export of 500 kg of shell material in 1985, and Indonesia reported the export of 100 kg of shell material in 1986, but there are no other CITES reports relating to *H. porcellanus* from these two countries. CITES reports also indicate that 16 *H. porcellanus* were exported as live specimens from the Philippines to Norway and Germany in 1992 and 1997, respectively; there have been no exports of live *H. porcellanus* specimens since. Additionally, export of 35 live specimens from the Solomon Islands to Germany and the United States was reported in 1997, but this is likely a reporting error, as this species has not been observed in the Solomon Islands.

In Indonesia, *H. porcellanus* is extremely rare. It was historically and still is reportedly exploited for its meat and shells when it is found (Pasaribu, 1988; Neo et al., 2017). Consequently, the species is now thought to occur in only a few locations in Indonesia (Hernawan, 2010; Wakum et al., 2017). Likewise, *H. porcellanus* abundance is also declining in Malaysia, in part due to ongoing harvest of meat and shells (Neo et al., 2017). As they are considered rare and are restricted to Sabah and Pulau Bidong on the east coast of Peninsular Malaysia, continued harvest likely threatens the persistence of these populations. Additionally, international poaching continues to pose a threat, as authorities from both Malaysia and the Philippines reported an increase in the number of fishing boats illegally harvesting giant clams as recently as 2010-2015 (Neo et al., 2017). Although not specific to *H. porcellanus*, Taiwanese boats historically traveled throughout the Indo-Pacific, including the waters and reefs of the Philippines, Indonesia, and Papua New Guinea (Dawson & Philipson, 1989). Poaching by these long-range Taiwanese vessels peaked in the mid-1970s and gradually declined during the 1980s (see **Section 3.2.2** for more information).

Overall, it is clear that *H. porcellanus* has been subject to heavy historical and ongoing harvest pressure across much of its range. This has contributed to documented local extirpations of the species and its current rare abundance. Accordingly, we conclude that overutilization is contributing significantly to the long-term extinction risk of *H. porcellanus* and is likely to contribute to short-term extinction risk in the near future (**High** risk, **High** confidence).

#### 4.2.3.3 Disease or Predation

We could not find any species-specific information regarding disease or predation for *H. porcellanus* beyond what is provided for giant clams generally in **Section 3.3**. Based on information available for other giant clam species, disease and predation likely pose a **Very Low** risk to *H. porcellanus*, but without more species-specific information, we have **Low** confidence in this assessment.

#### 4.2.3.4 Inadequacy of Existing Regulatory Mechanisms

In Malaysia and Indonesia, all species of giant clams are listed as nationally-protected species. However, according to Nijman et al. (2015) trade in protected species does not differ from trade in non-protected species in Indonesia. The authors witnessed open illegal sale and common occurrence of *H. porcellanus* and other protected clam species in Indonesian markets (Nijman et al., 2015). Commercial harvest and export is prohibited in the Philippines, Papua New Guinea, and Palau. However, numerous surveys and observations throughout the region indicate that giant clam populations, including *H. porcellanus,* continue to experience significant fishing pressure and declines throughout their collective ranges (Neo et al., 2017). For this reason, we find that the inadequate enforcement of local regulations, in combination with the species' low abundance and ongoing threat of overexploitation, likely contributes significantly to the species' extinction risk in the near future (**High** risk, **High** confidence).

In terms of international regulations, *H. porcellanus* was listed under Appendix II of CITES in 1985 to regulate international trade in any of its parts (shells, tissues, alive or dead). All five of the countries throughout the species' range are Parties to the treaty; although, Palau has claimed reservations on all species of giant clams. Any CITES Party permitting the export of *H. porcellanus* must provide documentation from their designated Scientific Authority demonstrating that trade is not detrimental to the survival of the species, and any trade from non-Parties to a CITES Party is still required to have documentation comparable to a CITES permit. Since 2010, only five *H. porcellanus* shells have been recorded in trade—two exported from Malaysia to the Netherlands in 2013, and three exported from the Philippines and seized in the United States in 2011 and 2016. However, it is likely that the low trade levels are as much a reflection of the species' low abundance as they are of the effectiveness of international regulation. Moreover, as has been discussed previously, CITES trade data only applies to international legal trade and does not regulate domestic traders nor for obvious reasons include any data on illegal trade. Thus, while there is little evidence to suggest that international trade regulations are inadequate (**Very Low** risk), our confidence in this assessment is **Low**.

Lastly, with respect to international climate change regulations, we conclude in **Section 3.4.2** that the current implementation of domestic and international climate regulations is insufficient to mitigate the cumulative threat of climate change to giant clam habitat and physiology generally. However, as mentioned in **Section 4.2.3.1**, because *H. porcellanus* is often found in sandy environments outside of the coral reef framework, the anticipated impacts of climate change on coral reefs will not likely pose a severe threat to this species. Thus, international climate change regulations are likely most relevant to *H. porcellanus* in terms of the impacts of ocean warming and acidification on species physiology. We were unable to find any information on the effects of climate change on *H. porcellanus* specifically, but inferences based on findings from other species suggest that *H. porcellanus* is likely to experience significant physiological changes under projected ocean warming scenarios. The precise magnitude of these impacts is unknown, but any significant changes in metabolic demand, reproductive success, and the possibility of bleaching due to warming summer temperatures, will likely increase the risk of extinction. For this reason, we find that the inadequacy of international climate change regulations may, in combination with the aforementioned impacts, contribute significantly to the long-term or near future risk of extinction, but is unlikely a significant threat on its own (**Low** risk). However, because there is no species-specific information regarding the impacts of climate change on *H. porcellanus* specifically, our confidence in this conclusion is **Low**.

#### 4.2.3.5 Other Natural or Manmade Factors

***Climate Change***

Beyond the information presented in **Section 3.5**, we could not find any research addressing the potential effects of climate change on *H. porcellanus* specifically. As discussed in **Section 4.2.3.4** above, there is substantial research on the effect of ocean warming in other giant clam species (i.e., reports of bleaching, impacts on reproduction and early development, alterations to metabolic demand). However, it is possible that susceptibility may vary considerably among species. For example, a species like *H. porcellanus* that resides preferentially in shallow habitats where temperature fluctuations can be quite extreme may have adapted a higher tolerance to such conditions. For these reasons, given the findings from other species that ocean warming will likely negatively impact physiology and reproduction, and may lead to bleaching and possible mortality during high-temperature anomalies, we conclude that ocean warming may, in combination with other VP descriptors or threats, contribute to the long-term extinction risk of *H. porcellanus* (**Low** risk). However, because of the lack of information related to *H. porcellanus* and the possibility that susceptibility may vary from the species on which these conclusions are based, we have **Low** confidence this conclusion.

We were not able to find any additional information regarding the potential impacts of ocean acidification on *H. porcellanus* beyond what is provided in **Section 3.5.2**. As is discussed in **Section 3.5.2**, the available information regarding the effects of ocean acidification on giant clams more broadly is limited and inconclusive.

***Land-based sources of pollution***

As discussed in **Section 3.5.3**, sedimentation, salinity fluctuations, nutrient enrichment, and elevated heavy metal concentrations represent environmental conditions that giant clams may experience following heavy rains, particularly near coastlines that have been altered by human development. Given its common occurrence in shallow nearshore habitats, *H. porcellanus* is likely highly exposed to these threats. However, beyond what is provided in **Section 3.5.3** related to giant clams generally, we could not find any information regarding the impacts of these factors on *H. porcellanus* specifically.

**Section 3.5.3** addresses many impacts of sedimentation, salinity, nutrient enrichment, and elevated heavy metal concentrations that have been observed for other species of giant clams. Overall, the results provide some indication that these factors may reduce fitness in certain respects; although, the effects are often not consistent between species and, in some cases, the experimental treatments do not reflect conditions that giant clams may realistically experience in the natural environment. For these reasons, we are reluctant to extrapolate these results to our assessment of *H. porcellanus*. Given this uncertainty and the likely localized nature of these impacts near areas of high runoff, we conclude with **Low** confidence that sedimentation, salinity fluctuations, nutrient enrichment, and heavy metal contamination are unlikely to contribute to the risk of extinction for *H. porcellanus*, either by itself or in combination with other VP descriptors or threats (**Very Low** risk).

***Stochastic Events***

While stochastic events such as extreme weather and mass mortalities of unknown cause may result in severe population loss in localized areas, these threats inherently cannot be predicted with any precision. However, because *H. porcellanus* has been reduced to such low abundance and remains in only a few locations throughout its range, the possibility of a mass mortality event, similar to what has been observed in other giant clam species, poses a significant threat to the species' persistence. Thus, we conclude that the threat of stochastic mortality events may, in combination with the species' low abundance, contribute significantly to the long-term extinction risk of *H. porcellanus* (**Low** risk. **Low** confidence).

**Table 11.** Summary of the threats analysis for *H. porcellanus* and associated confidence ratings.

| **4(a)(1) Factor** | **Threat** | **Contribution to Species' Risk of Extinction** | **Confidence Rating** |
|---|---|---|---|
| **Habitat destruction, modification, or curtailment** | *Coastal development* | Moderate | Low |
| | *Climate change impacts to coral reefs* | Very Low | Low |
| **Overutilization** | | High | High |
| **Disease or Predation** | | Very Low | Low |
| **Inadequacy of existing regulatory mechanisms** | *National and local regulations on harvest* | High | High |
| | *Regulations on international trade* | Very Low | Low |
| | *Regulations on climate change* | Low | Low |
| **Other natural or manmade factors affecting the species' continued existence** | *Physiological impacts of climate change* | Low | Low |
| | *Land-based sources of pollution* | Very Low | Low |
| | *Stochastic events* | Low | Low |

### 4.2.4 Demographic Risk Assessment

***Abundance***

Although quantitative abundance estimates are limited, the best available information suggests that *H. porcellanus* has suffered significant population declines since the 1970s, leading to low abundance and very few remaining populations throughout its historical range. Only 55 individuals have been observed and recorded in published surveys since 1989, and recent reports suggest that the species has disappeared from most areas of the Philippines and Indonesia, which were once the core of this species' distribution. Only two sites, Tubbataha Reefs Natural Park in the Philippines and Raja Ampat in Indonesia, are thought to have substantial populations of *H. porcellanus*. However, while there is some evidence that *H. porcellanus* may have recovered to an extent in Tubbataha Reefs after two decades of protection from harvest (Dolorosa & Jontila, 2012; see **Section 4.2.2**), the most recent survey data available is from 2008 and covers only 0.42 ha of the 96,828 ha in the park. Given the history of intense exploitation of this species in the Philippines and recent evidence of ongoing giant clam poaching in the region (see **Section 4.2.3.2**), we cannot conclude that this population has recovered to a sustainable level.

With so few remaining populations reduced to such a small fraction of the species' historic range, *H. porcellanus* is highly susceptible to the ongoing and future threats described in **Section 4.2.3**, including coastal development, ongoing harvest, the inadequacy of existing regulations, potential physiological impacts of ocean warming, and stochastic mortality events. Continued population reductions due to these factors threaten the persistence of remaining populations, and in effect, significantly elevate the extinction risk of *H. porcellanus*. For this reason, we find that the species' low abundance puts it in danger of extinction in the near future (**Very High** risk, **High** confidence).

### *Productivity*

Despite exceptionally high fecundity, there is substantial evidence that low recruitment success and high mortality rates during early development lead to low productivity in most species of giant clams. This is likely true of *H. porcellanus* as well; although, observations of this species are limited. Early estimates of fecundity from mariculture operations suggest that *H. porcellanus* can produce approximately five million eggs during a spawning event (Alcázar et al., 1987). However, evidence from other species suggests that survival rates through larval and juvenile development can often be less than 1% (Crawford & Lucas, 1986; Fitt et al., 1984; Jameson, 1976). Given the exceptionally low abundance of *H. porcellanus* and the ongoing threats outlined in **Section 4.2.3**, such low productivity can significantly limit the capacity for this species to achieve positive population growth rates and recover from low abundance.

Furthermore, as with *H. hippopus*, it is likely that *H. porcellanus* is experiencing an Allee effect, such that productivity is negatively correlated with population abundance. As a broadcast spawning organism, *H. porcellanus* relies on sufficient population density in order to respond to the spawning cues of nearby individuals and to facilitate successful external fertilization of their gametes. The best available evidence suggests that spawning synchrony in *T. gigas* drops significantly at population densities lower than 10 ind $ha^{-1}$ (Braley, 1984), and while gametes can remain viable for up to 8 hours in *T. squamosa*, viability decreases significantly with time (Neo, Vicentuan, et al., 2015). While the distance and duration may vary among species, it is likely that the overall effect of low abundance in reducing productivity is applicable to *H. porcellanus* as well.

For these reasons, we conclude that the low natural productivity of giant clams as well as the negative correlation of productivity with low abundance contributes significantly to the long-term extinction risk of *H. porcellanus*, and given the exceptionally low abundance of the species, is likely to contribute to the short-term risk of extinction in the near future (**High** risk, **Medium** confidence).

### *Spatial Distribution/Connectivity*

We could not find any information regarding the spatial structure or connectivity of *H. porcellanus* across its range. Available population genetic information for other species that occupy a similar geographic area (*T. squamosa*, *T. maxima*, and *T. crocea*) suggest that there is likely little genetic differentiation among populations in the majority of the Indo-Malay

Archipelago. With a distribution that is centered in this region, it is possible that there is little genetic differentiation among *H. porcellanus* populations. However, without more information regarding *H. porcellanus* specifically, we are unable to conclude whether spatial distribution and connectivity is a threat contributing to the species' risk of extinction.

***Genetic Diversity***

We could not find any information regarding the genetic diversity of *H. porcellanus*. However, given the species' significant historical decline in abundance, it is possible that such a decline may have significantly reduced the species' genetic diversity. However, without any genetic testing on this species to determine diversity or effective population size, we are unable to conclude whether genetic diversity is a threat contributing to the species' risk of extinction.

**Table 12.** Summary of the demographic risk analysis for *H. porcellanus* and associated confidence ratings.

| Demographic Risk Factor | Contribution to Species' Risk of Extinction | Confidence Rating |
|---|---|---|
| **Abundance** | Very High | High |
| **Productivity** | High | Medium |
| **Spatial Distribution/Connectivity** | *Unknown* | *Not applicable* |
| **Genetic Diversity** | *Unknown* | *Not applicable* |

## 4.2.5 Overall Extinction Risk Assessment

Guided by the results of the demographic risk analysis and threats assessment above, we analyzed the overall risk of extinction of *H. porcellanus* throughout its range. In this process, we considered the best available scientific and commercial information regarding *H. porcellanus* from all locations of the species' range, and analyzed the collective condition of these populations to assess the species' overall extinction risk. Despite a lack of formal, comprehensive abundance estimates, the best available information suggests that *H. porcellanus* has suffered significant population declines since the 1970s, leading to low abundance and very few remaining populations throughout its historical range. The inherent risks of such low abundance are compounded by low natural productivity, which likely prevents any substantial short-term recovery. Additionally, our threats assessment revealed that past and present overutilization and associated inadequacy of existing regulatory mechanisms at the local level contribute most significantly to the extinction risk of this species. *Hippopus porcellanus* has historically been highly desired commercially for the aesthetic of its shell and once comprised a substantial portion of the giant clam shell export volume from the Philippines, reaching a total export of nearly a million *H. porcellanus* shells and shell pairs between 1978 and 1992. While *H. porcellanus* is no longer legally exported from the Philippines, reports of ongoing subsistence harvest throughout its range and illegal poaching to supply a continued demand for giant clam shells and shell-craft throughout East Asia (see **Section 3.1.3**) suggest that the species will likely continue to experience declining trends in its abundance and productivity in the foreseeable future. Based on our assessment of these threats and demographic risk factors, we conclude that *H. porcellanus* is at a **High** risk of extinction throughout its range.

## 4.3 *Tridacna derasa*

### 4.3.1 Life History and Ecology

#### 4.3.1.1 Taxonomy and Distinctive Characteristics

Commonly referred to as the smooth giant clam, *T. derasa* (Röding, 1798) is the second largest giant clam species, with a maximum size of around 60 cm (Neo et al., 2017). The species has a heavy, plain-colored shell and can be distinguished from other species by its low primary and secondary radial sculpture. The primary radial sculpture consists of 7-12 broad, shallow rib-like folds (usually 6-7 main folds), and the shells are often greatly thickened at the umbos (i.e., the oldest, most prominent point of the shell near the ventral margin) (Rosewater, 1965). The mantle is often characterized by elongate patterns of brilliant greens and blues, and the incurrent siphon is equipped with inconspicuous guard tentacles (Figure 22; Neo et al., 2017).

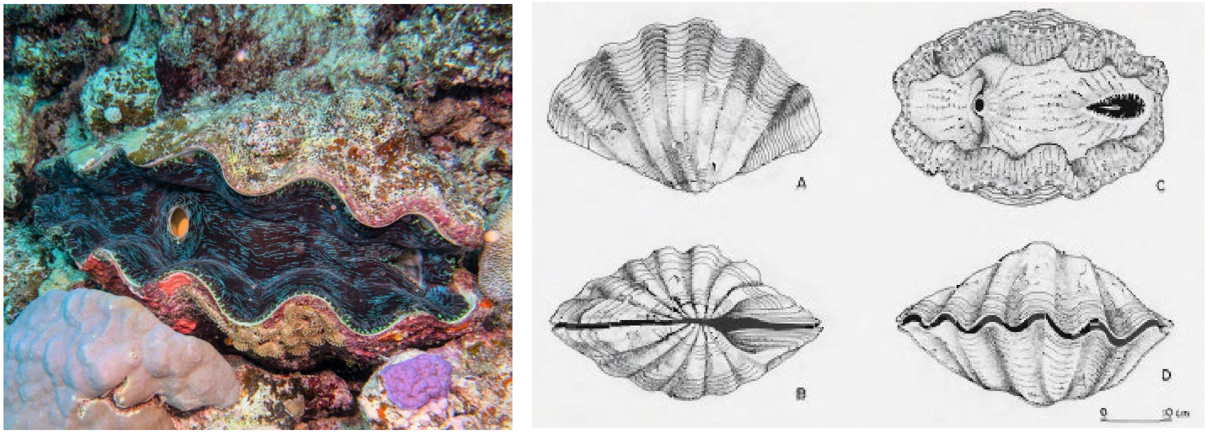

**Figure 22.** *T. derasa* morphology. Left: Photograph of *T. derasa* taken near Isle of Pines, New Caledonia. Right: Illustrations showing the lateral (A), ventral (B), mantle (C), and dorsal (D) views of a representative specimen. (Photo credit: Damien Brouste/iNaturalist, CC BY-NC 4.0; Diagram source: Calumpong, 1992)

#### 4.3.1.2 Range, Distribution, and Habitat Use

The geographic range of *T. derasa* primarily encompasses the Coral Triangle region, although it extends east to Tonga and as far west as the Cocos (Keeling) Islands in the eastern Indian Ocean (Figure 23; Rosewater, 1965). Adams et al. (1988) described *T. derasa* as having a patchy distribution, being rare in many places throughout its range and abundant in others. As discussed in **Section 2.2**, *T. derasa* historically occurred in CNMI and Guam, but is reportedly extirpated in both locations as a result of overutilization. There have been attempts to reintroduce the species to both locations, but in most cases, the primary goal of these efforts is to establish a source of food and income for local communities. Notably, *T. derasa* has been one of the most widely cultured species of giant clam and has been introduced to several countries and territories throughout the central and western Pacific Ocean. This includes American Samoa, FSM, the Marshall Islands, the Cook Islands, Samoa, and Tuvalu.

*T. derasa* preferentially inhabits clear offshore waters distant from areas of significant freshwater run-off (Munro, 1993). According to Calumpong (1992), the species appears to favor oceanic environments (i.e., small islands and atolls) more than fringing reefs adjacent to large island masses. The species is known to occur at depths of 4-25 m (Lewis et al., 1988; Neo et al., 2017), and is usually found weakly attached to the tops and sides of coral outcrops as juveniles, but may become detached upon reaching a larger size (Adams, 1988).

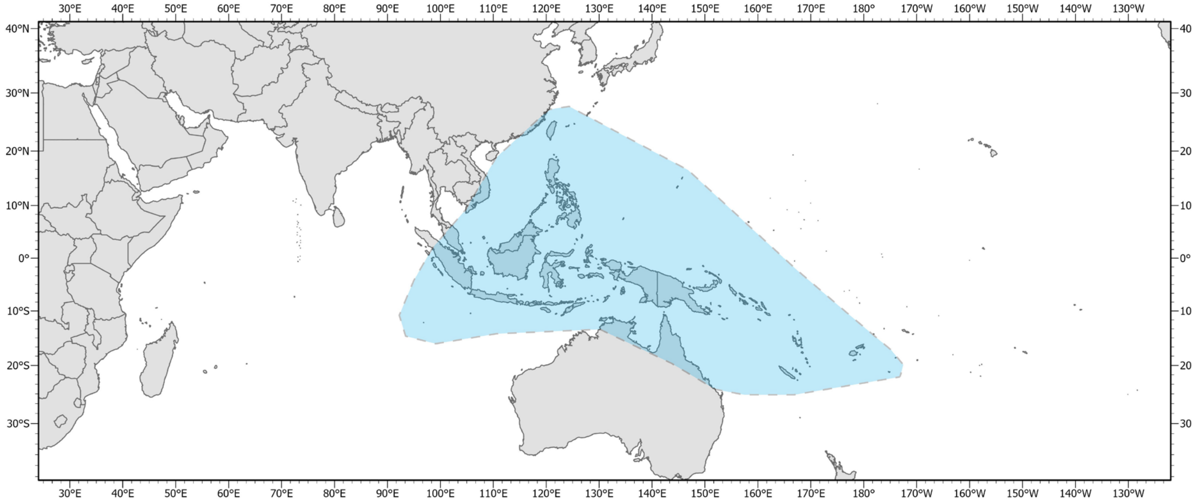

**Figure 23.** Approximate natural range of *T. derasa* based on reported occurrences provided by Neo et al. (2017). The range does not include locations where *T. derasa* has been introduced.

### 4.3.1.3 Reproduction and Growth

*T. derasa* is estimated to reach male-phase sexual maturity at approximately three years of age and female (hermaphrodite-phase) maturity one or two years later (Heslinga et al., 1987). As outlined in Table 1, *T. derasa* tends to spawn annually during early- to mid-summer months; although, there is evidence that the species is able to spawn year-round in Palau, suggesting that seasonality may become more pronounced at higher latitudes. On the Great Barrier Reef (16-19°S), evidence of spawning has been observed between September and February (Braley 1984, 1988), and in Tonga (21-22°S), it has been observed from December to January (McKoy, 1980). In Okinawa, Japan (25-27°N), cultured *T. derasa* specimens spawned between March and May (Iwai et al., 2006). We could not find any estimates of fecundity for *T. derasa*, but based on the average size of the species, it is likely that it falls somewhere between 25 million eggs per spawning event, as was estimated for *H. hippopus*, and 500 million eggs per spawning event, as was estimated for *T. gigas*.

A number of early studies and observations indicate that natural recruitment for *T. derasa* is very low (Hester & Jones, 1974; Yamaguchi, 1977; Pearson, 1977; Gwyther & Munro, 1981;

Heslinga et al., 1984; Braley, 1984). Natural recruitment of *T. derasa* juveniles at four sites on the Great Barrier Reef varied from 1.5% to 25% (Braley, 1988), leading the author to infer that the few reefs with abundant populations of clams may dominate recruit production for extensive areas of the Great Barrier Reef.

An early study on growth, spawning, and rearing of several giant clam species conducted in captivity in Palau predicted an annual growth rate for *T. derasa* of 3-6 cm per year (Beckvar, 1981). Likewise, Adams et al. (1988) found linear growth in *T. derasa* in Fiji to be about 5 cm per year until individuals reached 25 cm (roughly the size at full maturity), at which point growth slowed. These results corroborated similar observations for this species from other locations, including Palau and the Great Barrier Reef. Hart et al. (1998) determined multiple factors that influence the growth of *T. derasa* and other giant clam species, which include water temperature, exposure to wave action, water clarity, and water flow.

#### 4.3.1.4 Feeding and Nutrition

*T. derasa* is able to function as a complete autotroph in its natural habitat down to 20 m depth, relying entirely on the nutrition provided by its symbiotic zooxanthellae (Klumpp & Lucas, 1994). Although, individuals become less photosynthetically efficient as light intensity decreases, likely limiting its depth distribution. According to Klumpp and Lucas (1994), suspension feeding provides relatively little carbon to *T. derasa*, contributing 8-14% of respiratory carbon demands depending on the size of the individual. In another study, cultured *T. derasa* were fed supplemental phytoplankton which resulted in a roughly three-fold increase in growth, but there was no effect on mortality rate (Toonen et al., 2011). Together, these studies indicate that autotrophy is sufficient for *T. derasa* growth and survival, but abundant prey availability may lead to increased suspension feeding and faster growth rates.

#### 4.3.1.5 Genetics and Population Structure

The best available data regarding the population genetics of *T. derasa* is provided by two related studies, which analyzed allozyme variation across nine polymorphic loci (Macaranas et al., 1992; Gomez et al., 1994). Macaranas et al. (1992) analyzed 452 samples from Fiji (n = 40), the Philippines (n = 42), and 12 sites on the Great Barrier Reef (n = 370 total, 23 to 33 per site). Across all loci, they found statistically significant genetic differentiation among the three regions ($F_{ST} = 0.12$), explaining 47% of observed genetic variance. Pairwise estimates of Nei's unbiased genetic distance (D) between Great Barrier Reef sites, Fiji, and the Philippines (D = 0.137-0.341) were considerably greater than estimates from the more widespread giant clam species, *T. maxima*, across similar geographic scales (D = 0.032). This indicates that populations of *T. derasa* are not panmictic and experience some degree of genetic isolation across the range of the species. Pairwise comparisons among Great Barrier Reef sites did not reveal significant differentiation, but a difference in the frequency of rare alleles revealed a more subtle distinction between sites in the South Great Barrier Reef (Swain region) and those in the North-Central Great Barrier Reef. The authors conclude that the species' pelagic larval duration (~10 days) may facilitate genetic exchange among nearby sites; however, large geographic distances have resulted in substantial genetic differences as a result of isolation by distance, genetic drift, and/or local adaptation (Macaranas et al., 1992). Their findings were supported by Gomez et al. (1994), who compared these results to additional samples from Tonga and Palau. Samples from Palau clustered with those from the Philippines, while samples from Tonga clustered with those from Fiji (Gomez et al., 1994). Together, these two studies indicate at least three genetically distinct metapopulations of *T. derasa*: the Great Barrier Reef, western Pacific (Philippines, Palau), and central Pacific (Fiji, Tonga). Based on evidence from other species (e.g., *T. maxima*, *T. squamosa*, and *T. crocea*), it is possible that a fourth population cluster may occur in the Indo-Malay region; however, there are no data to confirm this pattern for *T. derasa*.

*T. derasa* also exhibits regional differences in the degree of genetic variation. Macaranas et al. (1992) found that mean heterozygosity was highest on the Great Barrier Reef ($h$ = 35-46%), intermediate in the Philippines ($h$ = 29%), and lowest in Fiji ($h$ = 14%). Similarly, Gomez et al. (1994) found low mean heterozygosity in both Fiji and Tonga ($h$ = 17-19%). With such limited data, it is difficult to determine the cause of low genetic diversity in the small island populations. Possible explanations include founder effects, the insular and peripheral location of the populations, local adaptation, or an artifact of sampling broodstock from the Makogai Island hatchery, which was the only accessible population in Fiji (Macaranas et al., 1992). Importantly, low genetic diversity may limit adaptive potential, and effectively reduce population resilience to environmental change.

### 4.3.2 Abundance, Density, and Population Status

Below, we synthesize the best available scientific and commercial information to assess the likely status of *T. derasa* in each country, territory, or region where it has been observed or reintroduced. The status and abundance trends in each location are summarized in Table 13 and displayed in Figure 24 below.

***Christmas Island; Cocos (Keeling) Islands – RARE***

According to Hourston (2010), *T. derasa* occurs at Christmas Island and is one of the two most common species, along with *T. maxima*. However, the density estimates provided (30 ind ha$^{-1}$) do not differentiate between the species of giant clams, and it is likely that *T. maxima* makes up the majority of giant clams observed. Hourston (2010) also reported that giant clams were not harvested "in appreciable quantities" by the locals on Christmas Island.

*T. derasa* is also reported to occur on the Cocos (Keeling) Islands, but available population estimates do not differentiate between species. Hender et al. (2001) described the abundance of *T. derasa* and *T. maxima* in the Cocos (Keeling) Island Lagoon as "moderate to low." Hourston (2010) reported that giant clams form a major portion of the diet for Cocos-Malay families and are often collected from the lagoon for their meat. Locals typically collect the clams while walking along shallow reef flats at low tide, leaving deeper, more inaccessible areas of the lagoon relatively untouched. Because of its preference for offshore reef areas, *T. derasa* is likely not the primary species harvested by this method.

***Taiwan – LOCALLY EXTINCT***

*T. derasa* has not been recorded in Taiwan for over three decades and is likely locally extinct (Neo et al., 2017).

### *South China Sea – RARE*

According to Macaranas et al. (1992), "the only reasonably sized extant population of *T. derasa* in the Philippines was discovered in the Scarborough Shoals." However, intense habitat destruction and giant clam shell harvesting in the region by Tanmen fishermen over the past decade (see **Section 3.1.3**) has likely eliminated this population. Zhang et al. (2020) were able to collect *T. derasa* broodstock for a spawning experiment near Huangyan Island. The authors suggested that the sampling site had the "highest densities of *T. derasa*" in the region, but did not provide any estimates of abundance nor any further context for the comparison. Given the proximity of the site to the Hainan Province, where recent demand for giant clams has been very high, as well as the long history of exploitation in the region, it is likely that *T. derasa* is rare throughout the South China Sea.

### *Indonesia – RARE*

Historically, giant clams have been heavily exploited throughout Indonesia for subsistence and commercial purposes (see **Section 3.2**), and several reports indicate that giant clam populations continue to decline due to illegal harvest and habitat destruction (Harahap et al., 2018; Neo et al., 2017; Nijman et al., 2015). An early survey in Karimun Jawa found only one *T. derasa* individual, leading Brown and Muskanofola (1985) to conclude that the species was likely functionally extinct in this region. Hernawan (2010) found small populations and evidence of recruitment failure in six giant clam species during a survey of nine sites in Kei Kecil, southeast Maluku. Only two *T. derasa* were observed within the 2.3 ha survey area. More recently, Triandiza et al. (2020) did not encounter a single *T. derasa* within a 0.25 ha survey area of the same Kei Islands region. In Raja Ampat, which some consider to be one of the few remaining areas of substantial giant clam abundance, Wakum et al. (2017) recorded six individuals within a survey area of 0.15 ha, equating to a population density of approximately 40 ind ha$^{-1}$. Harahap et al. (2018) also observed a similarly high density of *T. derasa* in the Anambas Islands, recording 77 individuals within a survey area of 0.32 ha, equating to a population density of approximately 240 ind ha$^{-1}$. Thus, while *T. derasa* is likely rare throughout most of Indonesia, at least a few areas remain where the species can be considered frequent or abundant.

### *Malaysia – RARE*

According to Shau-Hwai and Yasin (2003), *T. derasa* is restricted to the Sabah region in eastern Malaysia.

### *Philippines – RARE*

According to Villanoy et al. (1988), local extinctions of *T. derasa* are widespread throughout the Philippines, leaving the waters around the Sulu Archipelago and southern Palawan as the species "last stronghold" in the region. In a broad survey encompassing 247 sites and over 31 ha throughout the country, Gomez and Alcala (1988) found 29 individuals in the Luzon region (~1.5 ind ha$^{-1}$), 22 individuals in the Palawan region (~3.4 ind ha$^{-1}$), and did not encounter any *T. derasa* in Mindanao or the Visayas. More recently, Mecha and Dolorosa (2020) reported that *T. derasa* "remained rare" at Tubbataha Reefs Natural Park after nearly 30 years of protection, highlighting the limited recovery potential of this species in this region. Gonzales et al. (2014) reported exceptionally high densities of *T. derasa* at Meara Island (250 ind ha$^{-1}$) and Sabang Reef Fish Sanctuary (100 ind ha$^{-1}$) in Honda Bay, Palawan, but the data used to reach these estimates is not clear and appears to be based on only five belt transects and two quadrats, or a total survey area of less than 0.1 ha. The majority of reports and available survey data suggest that *T. derasa* is extremely rare throughout most of the Philippines, and that there are very few remaining sites where the species occurs in substantial numbers (Gomez & Alcala, 1988; Villanoy et al., 1988; Juinio et al., 1989; Gomez & Mingoa-Licuanan, 2006). Gomez and Alcala (1988) describe *T. derasa* as "virtually extinct from most of the country due to overexploitation."

### *Australia – FREQUENT (Great Barrier Reef); FREQUENT (NW Islands)*

The Great Barrier Reef in Australia is generally considered to have large, healthy stocks of giant clams relative to most other areas in their range (S. Wells, 1997; Neo et al., 2017); although, recent surveys and quantitative estimates of abundance and population density are quite scarce. Pearson and Munro (1991) tracked the survival of *T. derasa* and *T. gigas* at Michaelmas Reef from 1978 to 1985. A total of 46 *T. derasa* individuals were recorded in 1978 and 1980-81, which decreased to 31 individuals by 1985 (17 to 11.5 ind ha$^{-1}$). The authors could not confirm the cause of the mortality, but hypothesized that it may have been a result of disease, illegal harvest, or possibly a change in environmental conditions. Additionally, Braley (1987a, 1987b) recorded *T. derasa* population densities ranging from 2.9 to 92.3 ind ha$^{-1}$ at numerous survey sites spanning 817 km of the Great Barrier Reef. Braley (1987a) noted that population densities were higher farther north (from Cairns to Lizard Island); although, a large number of dead clams were found in the northernmost areas, presumably due to poaching. Pearson (1977) reported considerable variation in the density of *T. derasa* at Swain Reefs, ranging from 12 to 172 ind ha$^{-1}$, and described the species as "common" on the reef flats. More recent surveys have indicated relatively low population density at two offshore reefs, with 8 and 88 *T. derasa* observed at Coringa-Herald Nature Reserve (15.4 ha survey area) and Lihou Reef Nature Reserve (22 ha survey area), respectively (Ceccarelli et al., 2008; Ceccarelli et al., 2009).

Follow-up data for five sites in the far northern Great Barrier (near Lizard Island, Rachel Carson Reef, and Michaelmas Cay) indicate that four of five surveyed populations experienced declines between 1982-84 and 2007-09 (Braley, 2023). Focusing on the three largest sites with the largest populations (22-30 individuals recorded within a 0.55-0.73 ha survey area), population abundance decreased at two sites by 10.3% and 43.3% (Watson's Bay and Rachel Carson Reef West, respectively) and increased by 18.2% at the Palfrey South Channel site. The Watson's Bay and Palfrey South Channel sites were then revisited again in 2017. The Watson's Bay population showed continued decline in 2017, reaching a total decrease of 41.4% compared to 1984. The Palfrey South Channel population showed no change in abundance between 2007 and 2017, yielding a total increase of 18.2% compared to 1984. Despite the negative trend in some areas, population density at all five surveyed sites remained high in 2007-09 relative to other areas of the species' range (25 to 46.9 ind ha$^{-1}$). Analysis of size class distributions revealed "moderate but steady recruitment" on average, although it varied by site (Braley, 2023). The author suggested that this variation may be due to differences in settlement habitat quality (*e.g.*, differences in coral cover), or perhaps differences in water residence time. For example, in areas of greater seawater exchange, spawned larvae may be flushed out of the area before they reach settlement competency, whereas lagoonal habitats with longer residence time may retain larvae long enough for them to settle locally. The virtually undisturbed state of these populations suggests that the trends observed may be characteristic of natural fluctuations in population demographics at these sites, reflecting the sporadic nature of giant clam reproduction and recruitment more generally.

*T. derasa* can also be found in the islands of NW Australia. Skewes et al. (1999) reported population densities ranging from 1.3 ind $ha^{-1}$ at Ashmore Reef to 77.7 ind $ha^{-1}$ at N Scott Reef. More recently, Richards et al. (2009) encountered only three individuals within a 3-ha survey area of Ashmore Reef.

### *Fiji – RARE*

In the 1980s, Lewis et al. (1988) asserted that stocks of *T. derasa* in Fiji were once "probably amongst the most abundant outside the Great Barrier Reef." However, populations on various reefs in the windward (Lau, Lomaiviti) islands were significantly reduced by commercial harvest beginning in 1985 (Lewis et al., 1988). According to Lewis and Ledua (1988), *T. derasa* comprised over 95% of the commercial harvest from the eastern (Lau) islands. Adams et al. (1988) also noted a relative rarity of *T. derasa* juveniles in Fiji, thought to be the result of limited, erratic recruitment and low juvenile survival, which led the authors to question the long-term sustainability of the species in Fiji. More recently, Pinca et al. (2010) recorded only one *T. derasa* individual in a broad survey of finfish and invertebrate communities in Fiji, and estimated an average population density of 0.01 ind $ha^{-1}$ (2.1 ind $ha^{-1}$ at stations where the species was present). Based on this data alongside a long history of commercial and subsistence exploitation, we find it likely that *T. derasa* is rare in Fiji.

### *New Caledonia – RARE*

In a broad survey comprising 50 sites spanning the coastline of La Grande Terre, Purcell et al. (2020) reported an average *T. derasa* population density of approximately 1.4 ind $ha^{-1}$, with significantly higher density in protected marine reserves. The authors note that the species is perhaps slightly more common in New Caledonia than in many other Pacific island nations, but that populations are "still very sparse when considering the necessity for spawning clams to be in relatively close proximity for successful reproduction." Despite its low abundance, *T. derasa* was reportedly one of the giant clam species targeted by subsistence, recreational, and commercial fishermen, leading Purcell et al. (2020) to conclude that the species is at risk of extirpation in New Caledonia.

### *Papua New Guinea – RARE*

Milne Bay Province has historically been the center of giant clam abundance and exploitation in Papua New Guinea. In an early giant clam stock assessment from the area, Chesher (1980) estimated that before commercial harvesting, unfished areas of southern Milne Bay Province contained an overall density of 39 ind $ha^{-1}$ for all giant clam species. However, a large-scale, government-backed fishery for *T. derasa* operated in the Milne Bay Archipelago from 1983 to 1988, which led to severe population declines in this region.

A survey conducted in 1996 by the South Pacific Commission and the Papua New Guinea National Fisheries Authority at the Engineer and Conflict Islands (offshore of Milne Bay Province) found that *T. derasa* occurred at a density of 5.3 ind $ha^{-1}$. Two years later, a stock assessment spanning 1,126 sites throughout the Milne Bay Province revealed that the average population density of *T. derasa* in the region had fallen to 0.3 ind $ha^{-1}$, which the authors estimated was equivalent to a total abundance of 165,966 (±54.6%) in the region (Skewes et al., 2003). F. E. Wells and Kinch (2003) noted that these findings aligned with other reports indicating that giant clam stock levels are very low and heavily depleted in the Milne Bay Province. More recently, Pinca et al. (2010) observed 14 *T. derasa* individuals in a broad survey of finfish and invertebrate communities across Papua New Guinea, and estimated an average population density of 0.54 ind $ha^{-1}$ (13.4 ind $ha^{-1}$ at stations where the species was present). Based on the available survey data and history of exploitation, it is likely that *T. derasa* is rare throughout Papua New Guinea.

### *Solomon Islands – RARE*

According to Hviding (1993), giant clams in the Solomon Islands have been subject to localized depletion from the combination of subsistence harvest and intensive (mostly illegal) harvest by Taiwanese clam boats. Hviding (1993) described the distribution of *T. derasa* as "limited" compared to the other giant clam species present. Ramohia (2006) observed 12 *T. derasa* specimens over nearly 12 ha of survey area, while Pinca et al. (2010) recorded only six individuals in a broad survey of finfish and invertebrate communities in the Solomon Islands, estimating an average population density of 0.36 ind $ha^{-1}$ (14.2 ind $ha^{-1}$ at stations where the species was present). According to Govan et al. (1988), *T. derasa* can only be found in the Marau Sound and Marovo Lagoon.

### *Vanuatu – REINTRODUCED*

According to Teitelbaum and Friedman (2008), *T. derasa* is extirpated in Vanuatu; although, Dumas et al. (2012) reported finding the species at low abundance. Neo et al. (2017) report that it has since been reintroduced in Vanuatu via a restocking program, but we could not find any information as to the success or failure of these initiatives. It is likely that *T. derasa* remains extremely rare in Vanuatu.

### *Palau – FREQUENT*

Early surveys of giant clam abundance in Palau were focused on Helen Reef, a remote atoll in the Western Caroline Islands, and documented the impacts of an intensive illegal harvesting operation by Taiwanese fishing vessels in the early 1970s. In 1972, prior to the poaching, Hester and Jones (1974) recorded 101 *T. derasa* within a survey area of 4.4 ha and estimated the total standing stock at Helen Reef to be approximately 32,800 individuals. Following the poaching, two follow-up studies revealed that *T. gigas* and *T. derasa* had suffered significant population declines. In 1975 and 1976, only six and seven individuals were encountered in surveys of 2.5 and 1.5 ha, respectively (Bryan & McConnell, 1975; Hirschberger, 1980). For comparison, estimates of *T. derasa* population density were 23.1, 2.4, and 4.5 ind $ha^{-1}$ in 1972, 1975, and 1976, respectively. We could not find more recent surveys of Helen Reef, so the current status of this population is unknown. In a broad survey of finfish and invertebrate communities throughout Palau, Pinca et al. (2010) recorded 39 *T. derasa* and estimated an average population density of 1.2 ind $ha^{-1}$ (13.9 ind $ha^{-1}$ at stations where the species was present). Additionally, an opportunistic survey of giant clam populations conducted by Rehm et al. (2022) documented 22 *T. derasa* individuals within a survey area of 0.33 ha, which equates to a population density of 66.7 ind $ha^{-1}$. However, the author has cautioned that the surveys specifically targeted areas where giant clams are known to occur, so the observations likely overestimate the average population density throughout Palau (L. Rehm, pers. comm., May 26, 2022).

As was discussed in relation to *H. hippopus*, Palau is home to the Palau Mariculture Demonstration Center, which is one of the first and most prolific institutions to succeed at mass cultivation of giant clams. Cultured clams, including tens of thousands of *T. derasa*, have been translocated as broodstock to many other countries for the purpose of natural stock enhancement (Kinch & Teitelbaum, 2010). Cultured clams from the PMDC are also often distributed to local clam farmers to be later sold into the commercial meat and aquarium industry (Neo et al., 2017). According to Kinch and Teitelbaum (2010), the PMDC uses some portion of the cultured ‘seedlings’ to restock 23 conservation areas throughout Palau. According to L. Rehm (pers. comm., May 26, 2022), these efforts have primarily focused on *H. hippopus* and *T. derasa*, but we are not aware of any follow-up surveys to measure their success. However, the most recent available survey data from Rehm et al. (2022) and the general success of the PMDC in culturing *T. derasa*, which may provide the capacity to outplant substantial seedstock to these conservation areas, suggest that *T. derasa* is likely frequent in Palau on average.

### *Tonga – RARE*

According to Chesher (1993), *T. derasa* stocks were depleted and largely vanished during the 1960s when modern diving gear became more readily accessible, and McKoy (1980) described *T. derasa* as “relatively uncommon” throughout Tonga, as it was highly sought by fishermen. The species was reported to occur on Minerva Reef, Tongatapu, Vava’u, and on Ha’apai with an average density of 7.3 individuals per ha. Using timed surveys, Chesher (1993) recorded 129 *T. derasa* individuals in the Vava’u island group over the course of 254 hours of diving from 1987 to 1990, equating to approximately one individual encountered every two hours. Using a similar survey method, Tu'avao et al. (1995) found six individuals over two hours of searching in the Tongatapu island group. Pinca et al. (2010) recorded 31 *T. derasa* individuals in a broad survey of finfish and invertebrate communities in Tonga, and estimated an average population density of 0.18 ind ha$^{-1}$ (3.4 ind ha$^{-1}$ at stations where the species was present).

The Ministry of Fisheries estimated that 20-50 fishermen were engaged in the harvest of giant clams in Tonga (Raymakers et al., 2003, cited in UNEP-WCMC, 2011), with *T. derasa* being the most heavily exploited species (Sone & Loto'ahea, 1995). Stocks of *T. derasa* have been described as “overfished especially near population centers” (S. Wells, 1997) and as facing “rapid depletion” throughout the country (Sone & Loto’ahea, 1995). According to Chesher (1993), efforts to restock *T. derasa* populations in Vava’u by aggregating individuals in protected “clam circles” (i.e., ~100 clams spread evenly over 500 m$^2$) were successful at facilitating *in situ* reproduction. The author reported that juveniles began appearing eight months after the clam circles were installed and claimed that by the end of 1989, “survey teams had found more juvenile *T. derasa* in the inner island group of Vava’u than have been recorded from all the surveys on giant clams on the Great Barrier Reef combined.” Additionally, local villagers conveyed to the author that they had never seen so many young clams in surrounding reefs and that the children had collected and eaten “baskets” of them. This report highlights the primary motivation in this case, which was to replenish the natural stocks of *T. derasa* to support sustainable subsistence harvest. More recently, however, Atherton et al. (2014) found that *T. derasa* remained the least common of the giant clam species in Tonga, observing three individuals at only 2 of the 27 sites surveyed in Vava'u, casting doubt on the long-term success of the stock enhancement initiative.

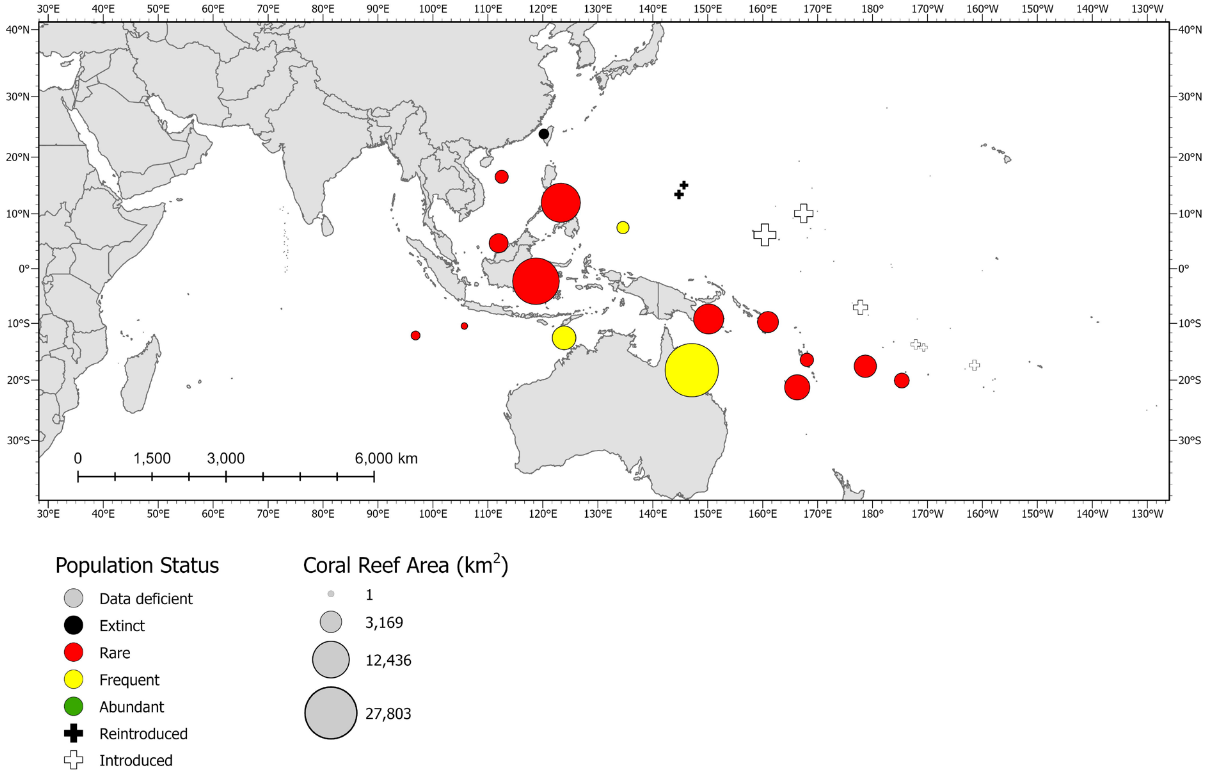

**Figure 24.** Qualitative abundance estimates for *T. derasa* based on reported occurrence and survey data. Points are located at the approximate centroid of survey sites within each country, territory, or region from which data has been included in the abundance assessment. Abundance categories are based on those used by Neo et al. (2017), but have been revised as follows: Abundant (>100 ind ha$^{-1}$), Frequent (10-100 ind ha$^{-1}$), Rare (<10 ind ha$^{-1}$), Extinct, Introduced, Reintroduced (i.e., locations where the species was reportedly extirpated in the past but there have since been efforts to restore populations using cultured specimens; current presence/abundance may not be known), and Data Deficient (i.e., locations where reports of species occurrence have not been confirmed). The size of the points reflects the total estimated area of coral reefs within each location based on data compiled by the UN Environment World Conservation Monitoring Centre and the WorldFish Centre (UNEP-WCMC et al., 2021), increasing on a square-root scale. It is used here to roughly approximate the relative amount of giant clam habitat. However, the accuracy of this approximation likely varies between species based on their habitat preferences.

**Table 13.** Summary of *T. derasa* population status across its geographic range (adapted from Table 4 in Neo et al. 2017 and supplemented with more recent information where available). Species abundance categories are as follows: Abundant (>100 ind ha$^{-1}$); Frequent (10-100 ind ha$^{-1}$); Rare (<10 ind ha$^{-1}$). Where the status has been revised from Neo et al. (2017), footnotes provide the data sources or rationale used to reach the respective status determinations.

| Location | Status | Notes |
|---|---|---|
| ***Indian Ocean*** | | |
| Australia (NW islands) | Frequent | Population densities ranging from 1.3 ind ha$^{-1}$ at Ashmore Reef to 77.7 ind ha$^{-1}$ at N Scott Reef. |
| Christmas Island | Rare | *T. derasa* reportedly occurs at Christmas Island, but abundance is unknown, as available survey data does not differentiate between giant clam species. Harvest of giant clams is not common. |
| Cocos (Keeling) Islands | Rare[1] | A culturally important species, Cocos-Malay fishers harvest *Tridacna* spp. for subsistence consumption. Artisanal harvest appears to be directly responsible for the severe depletion of giant clam stocks. Only one *T. derasa* was found in 2011. Recent surveys in 2014 did not encounter any *T. derasa*. |
| ***East Asia*** | | |
| South China Sea | Rare | Intense habitat destruction and giant clam shell harvesting in the region by Tanmen fishermen over the past decade has likely eliminated the once-substantial population of *T. derasa* at Scarborough Shoals. |
| Taiwan | Locally extinct | *T. derasa* has not been recorded over the last three decades and may be locally extinct. |
| ***South Asia*** | | |
| Indonesia | Rare | Presently extremely rare. Giant clams are exploited for their meat (domestic consumption) and shells, and some for the live aquarium trade. Indonesian Benzi Institute of Science has been culturing *T. derasa* and other species for restocking reefs. |
| Malaysia | Rare | *T. derasa* is restricted to Sabah and Pulau Bidong (east coast of Peninsular Malaysia). |
| Philippines | Rare | Local extinctions of *T. derasa* are widespread throughout the Philippines; waters around Sulu Archipelago and southern Palawan are considered to be the species "last stronghold" in the region. The majority of reports and available survey data suggest that *T. derasa* is extremely rare and that there are very few remaining sites where the species occurs in substantial numbers |
| ***Pacific Ocean*** | | |
| Australia (Great Barrier Reef) | Frequent | Despite early and strict protection in Australian waters, extensive illegal harvesting by foreign vessels occurred in the 1970s to 1980s. Today, populations of giant clams in Australia are considered healthy with some almost pristine examples; although poaching is still occasionally reported on the Great Barrier Reef. |

| Location | Status | Notes |
|---|---|---|
| | | Carried out extensive mariculture of *T. derasa* in late 1980s. |
| CNMI | Reintroduced[2] | *T. derasa* was reintroduced from Palau to Saipan in 1986, 1987, 1988, and 1991. Likely locally extinct from overexploitation (S. Wells, 1997). |
| Fiji | Rare[3] | *T. derasa* was not preferentially targeted for harvest due to a perception of tough meat and coarse flavor. Extensive commercial harvest in the 1980s led to significant population declines, and recent surveys indicate low average abundance. |
| Guam | Reintroduced[4] | *T. derasa* was reintroduced from Palau in 1984 and 1989. Likely locally extinct from overexploitation (S. Wells, 1997). |
| New Caledonia | Rare[5] | An extensive survey of La Grande Terre found an average *T. derasa* population density of approximately 1.4 ind ha$^{-1}$, with significantly higher abundance in protected marine reserves. Due to ongoing harvest, Purcell et al. (2020) concluded that the species is at risk of extirpation. |
| Palau | Frequent[6] | Remote reefs of Palau were subject to intensive illegal harvest in the 1970s, which severely reduced *T. derasa* populations. Harvest of giant clams for subsistence and domestic sale is “very common”—many people target *T. crocea*, but *H. hippopus* and *T. derasa* are highly sought and collected when found (L. Rehm, pers. comm., May 26, 2022). Recent surveys estimate population densities between 1.2 and 66.7 ind ha$^{-1}$. Cultured clams, including tens of thousands of *T. derasa*, from the Palau Mariculture Demonstration Center have been translocated as broodstock to many other countries and are reportedly being used to restock certain conservation areas in Palau (L. Rehm, pers. comm., May 26, 2022). |
| Papua New Guinea | Rare | No monitoring of populations is taking place, and there are no restrictions regarding fishing seasons, fishing gear and size limits. A commercial fishery for giant clams previously operated in the Milne Bay Province until it closed in 2000. A ban on exports was implemented that same year and appears to have been successful in stemming trade of *T. derasa*. |
| Solomon Islands | Rare | *T. derasa* has limited distribution and recent surveys found depleted populations. Harvesting for export, with large-scale commercial harvest, took place in the 1970s to 1980s, and subsistence use was considered a major cause of population declines. Poaching on remote reefs primarily by Taiwanese vessels was not uncommon from the 1960s to 1980s, which exacerbated stock depletion. |

| **Location** | **Status** | **Notes** |
|---|---|---|
| Tonga | Rare | *T. derasa* is heavily exploited, with clams harvested for both subsistence and commercial purposes. Larger species (i.e., *T. gigas* and *T. derasa*) are commercially more valuable. |
| Vanuatu | Reintroduced | *T. derasa* is believed to be locally extinct. It was always very rare in Vanuatu, and a number of individuals were translocated in 1998. |
| ***Non-native locations where T. derasa has been introduced*** | | |
| American Samoa | Introduced | *T. derasa* was previously cultured at a government hatchery "with the main aim of establishing local farms to produce meat for local market." As of September 1995, there were 6 lagoon nursery sites and 25 small-scale farms in operation, but we are not aware of any more recent information to indicate the current status of this initiative. Approximately 650 *T. derasa* specimens were gifted to American Samoa by Samoa at the end of 2023, likely to be used primarily as a sustainable food source for local communities. |
| Cook Islands | Introduced | *T. derasa* introduced from Palau in 1986. |
| FSM | Introduced | *T. derasa* was introduced from Palau; stocks have reproduced and become established only in Yap. FSM has been a significant exporter of live giant clams (including *T. derasa*) for many years, contributing around 10% of global supply; though production has been erratic with recent declines. |
| Marshall Islands | Introduced | *T. derasa* introduced from Palau in 1985 and 1990 as an aquaculture species. Marshall Islands has a longstanding history of aquaculture production with notable technical support from the US and Japan. Numerous giant clam hatcheries are in operation for restocking purposes and mainly for the aquarium trade through engagement with local community farmers. |
| Samoa | Introduced | Broodstock for *T. derasa* and other species have been translocated at various times since 1988 from various Pacific Island countries or territories including Fiji, Tonga, Palau, and American Samoa. |
| Tuvalu | Introduced | In 1988, 1,000 *T. derasa* were introduced for restocking purposes, but due to exploitation only 8 individuals remained in 2011. |

Sources:
[1] Hender et al. (2001)
[2] S. Wells (1997)
[3] Pinca et al. (2010)
[4] S. Wells (1997)
[5] Purcell et al. (2020)
[6] Rehm et al. (2022)

Of the 18 locations where *T. derasa* has been recorded, the best available data suggests that the species is frequent in only 3 locations, rare in 11 locations, and locally extinct or reintroduced after local extinction in 4 locations.

We also note several countries and territories which have cultured or imported *T. derasa* for the purpose of restocking depleted populations or to introduce the species to locations outside of its natural range. Because of its relatively fast growth rate, *T. derasa* has been a priority for mariculture throughout the Indo-Pacific for many years. There are at least 17 countries and territories with hatchery and/or grow-out facilities that have cultured *T. derasa* for the purpose of enhancing depleted populations (Lindsay et al., 2004; Mies, Dor, et al., 2017), and several others that have initiated *T. derasa* restocking programs without domestic hatcheries (Teitelbaum & Friedman, 2008). One facility in particular, the PMDC, has pioneered many of the methods for giant clam mariculture and has focused predominantly on *T. derasa* throughout its operation. Following external funding from the United States in 1982, production of *T. derasa* from the PMDC expanded substantially, and the facility began exporting significant quantities of "seed" clams (i.e., small juveniles) and broodstock to many other Indo-Pacific countries and territories (Shang et al., 1994). It is difficult in most cases to determine the exact purpose of the shipments—some were intended to be used exclusively for conservation-related stock enhancement, while others were used to establish local hatcheries for the purpose of subsistence or commercial harvest. Regardless, because of the pervasiveness of *T. derasa* mariculture initiatives throughout the species' range, it is clear that the potential impact of stock enhancement (and non-native introductions) must be considered as part of an evaluation of the species' status in locations where such initiatives have been explored. Mariculture likely also plays an important role in diverting subsistence and commercial exploitation away from the harvest of wild populations. This topic is discussed in **Section 4.3.3.2** as part of the threats analysis for *T. derasa*.

With respect to stock enhancement, we are aware of two examples that have reported some measure of success in establishing sustainable populations of *T. derasa* in the wild. One is mentioned above in the section on *T. derasa* abundance in Tonga, whereby Chesher (1993) documented successful reproduction and juvenile recruitment of a reintroduced *T. derasa* population, claiming that more juveniles were observed in Vava'u following the reintroduction than had previously been recorded on the entire Great Barrier Reef. A more recent survey, however, found that population density in the Vava'u area was very low, reporting only 3 individuals at 2 of the 27 survey sites in the area. Similarly, with significant financial support from the United States, FSM imported approximately 25,000 *T. derasa* from Palau in 1984-90 with the goal of establishing naturally reproducing populations on Yap and several of its outer atolls (Lindsay, 1995). Because the species is not endemic to FSM, researchers were able to easily monitor whether the introduced populations did indeed reproduce and recruit successfully. However, a number of challenges including theft, neglect, limited aquaculture skills, and storm damage led to large losses of introduced clams (Lindsay, 1995). At the time of the report in 1995, a small percentage (approximately 8%) of introduced *T. derasa* remained, but there was evidence of successful reproduction and recruitment of offspring on surrounding reefs. Surveys conducted by the Secretariat of the Pacific Community (PROC-Fish/C–CoFish programmes) noted the continued presence of *T. derasa* in Yap in low numbers in mid-2006 (Teitelbaum & Friedman, 2008). We were not able to find any more recent monitoring data to indicate the current status of this introduced population, but with subsistence harvest of giant clams prevalent in FSM (Lindsay, 1995), it is unlikely to have grown significantly.

Beyond these examples, we could not find any other records documenting successful *T. derasa* restocking initiatives. In fact, most available research presents these cases as an exception to the rule. As was discussed in relation to *H. hippopus*, there is extensive literature addressing the challenges of giant clam mariculture generally, and particularly for the purpose of stock replenishment (Gomez & Mingoa-Licuanan, 2006; Mies, Scozzafave, et al., 2017; Munro, 1993; Teitelbaum & Friedman, 2008). The primary barrier to these efforts is the exceptionally low survival rate of giant clam larvae post-fertilization compounded by the time and resources required to protect juveniles once they have been outplanted and before they reach a size at which they are sufficiently impervious to predation. Despite the numerous restocking and translocation programs known to exist throughout the Indo-Pacific, most are reported to still be operating on a small or pilot scale with only partial success, and further intensification of giant clam mariculture for the purpose of restocking natural populations is in most cases considered economically unviable (Teitelbaum & Friedman, 2008; UNEP-WCMC, 2012). In fact, Lindsay (1995) contrasts the successful introduction of *T. derasa* in FSM with giant clam reseeding programs throughout the Pacific more broadly, which the author asserts have largely “failed to keep clams alive long enough and in large enough numbers to allow them to mature and reproduce.”

Furthermore, as is explained by Munro (1993b), efforts to restock populations in areas where giant clams are still harvested should more accurately be viewed as “a form of fishery enhancement,” in that outplanted individuals will simply increase harvest volume rather than contribute to the conservation and long-term population growth of the species. To achieve significant conservation success, restocking initiatives must be accompanied by effective enforcement of harvest bans or an otherwise substantial reduction of harvest pressure on giant clams. However, as discussed in the following threats analysis, subsistence fishing for *T. derasa* is ongoing throughout much of the species’ range, and in most locations where harvest bans are in place, regulations are often poorly enforced.

Thus, while many known mariculture facilities throughout the Indo-Pacific have successfully bred and raised *T. derasa* ex situ, there is little evidence that initiatives to replenish natural stocks with culture-raised clams have achieved their goal of enhancing population abundance or productivity. Without further information or survey data demonstrating such success, we consider the impact of these initiatives to be negligible with respect to the status of the species. In other words, where *T. derasa* has been reintroduced or where it has been introduced outside of its native range, we consider the species to be very rare or locally extinct. Likewise, where reseeding has been explored with the purpose of enhancing rare populations (e.g., the Philippines, Indonesia), there is very little evidence to suggest that such initiatives have significantly enhanced population abundance in these locations.

One possible exception is in Palau, where the PMDC has been especially successful in producing large numbers of *T. derasa*, and where there are reports that a portion of seedstock is being used to enhance giant clam populations in 23 conservation areas (Kinch & Teitelbaum, 2010; L. Rehm, pers. comm., May 26, 2022). We could not find any follow-up surveys specifically documenting the success of these efforts (or lack thereof). Additionally, according to L. Rehm (pers. comm., May 26, 2022), authorities in Palau struggle to enforce the regulations of conservation areas, particularly those on offshore reefs, because they lack sufficient personnel and equipment, potentially negating any benefit of reseeding. It is possible that the reseeding efforts have contributed to *T. derasa* populations in these areas, but more data are needed to confirm that this is the case.

## 4.3.3 Threats to *Tridacna derasa*

### 4.3.3.1 Destruction, Modification, or Curtailment of Habitat or Range

Beyond the information provided in **Section 3.1** related to the threat of habitat destruction or modification to giant clams generally, we could not find any studies addressing the threat to *T. derasa* specifically. However, based on its known distribution, we can infer that the most pertinent threats to this species are those that impact offshore coral reef habitats, and particularly those associated with oceanic islands and atolls. As is discussed in **Section 3.1.1**, there is extensive evidence demonstrating that the combined effects of ocean warming and acidification will continue to reduce living coral cover and significantly alter the calcification balance on coral reefs over the foreseeable future. Such impacts have already been observed across most, if not all, of the reef locations within the range of *T. derasa*, including the few locations of greatest abundance, such as the Great Barrier Reef (Hughes, Kerry, et al., 2017) and the atolls in the Coral Sea (Harrison et al., 2019). There is evidence that the negative impacts of warming are most pronounced in the fast-growing branching and tabular coral species, which are the primary contributors to the three-dimensional complexity of reef habitats. Thus, it is likely that ocean warming will significantly reduce the rugosity of future reef ecosystems.

However, as is addressed in **Section 3.1.1**, despite *T. derasa* often occurring on or closely adjacent to coral reefs, there is very little research establishing the degree to which the species relies on living coral cover or on coral reef rugosity and thus might be impacted by any reduction thereof. It is often implied in the literature that substrate rugosity is critical to the recruitment and survival of giant clam larvae by providing adequate grooves and crevices for shelter; however, the empirical support for these suggestions is limited. The few larval choice experiments to date suggest that the larvae of several giant clam species tend to avoid settling on smooth surfaces (e.g., aquarium plexiglass, smooth tiles, etc.). It is possible that *T. derasa* may exhibit a similar settlement preference, particularly given its close association with coral reefs, but it is difficult to extrapolate this finding to the behavior of giant clams *in situ*, and without more information on the direct association between substrate rugosity and juvenile survival, we cannot estimate with any confidence the degree to which reef rugosity must decline to threaten the persistence of the species. Thus, while it is likely that continued ocean warming and acidification will drastically alter coral reef communities and reduce the rugosity of many reef areas, the potential effect on the quality or suitability of habitat for *T. derasa* cannot be confidently assessed.

If *T. derasa* is sensitive to reductions in net ecosystem calcification and reef rugosity, the projected climate change-related impacts on coral reefs would likely pose a **Moderate** extinction risk to the species. We would expect decreased larval recruitment and juvenile survival across broad portions of its range. These early life stages are already known to suffer exceptionally high mortality rates naturally, and any further reduction in productivity would threaten the viability of remaining populations, which would contribute significantly to long-term extinction risk for this species. However, based on the preceding discussion, our confidence in this assessment is **Low**.

Because *T. derasa* is found predominantly in offshore coral reef areas, it is unlikely that habitat degradation of the nearshore environment (e.g., related to coastal development) poses a significant threat to the species.

#### 4.3.3.2 Overutilization

Because of its large size and relatively fast growth rate, *T. derasa* has historically been one of the most widely exploited giant clam species for the consumption of its meat. Reports from throughout the species' range indicate that it is harvested for subsistence consumption in nearly every location where it occurs, except for Australia. It is also one of two species that was heavily targeted by Taiwanese fishermen and traders during the 1970s and 1980s to supply a significant commercial demand for giant clam meat in Southeast Asia, primarily for the Taiwanese restaurant industry. As is discussed in **Section 3.2.2**, Taiwanese vessels traveled across the Indo-Pacific in search of the adductor muscle of *T. gigas* and *T. derasa*, often entering the waters of other nations illegally and concentrating their efforts on remote or uninhabited islands and reefs where giant clam stocks had previously been untouched and where surveillance was limited. First-hand reports of Taiwanese poaching include areas of the Philippines, Indonesia, Papua New Guinea, Australia (the Great Barrier Reef), FSM, the Solomon Islands, Palau, Fiji, Kiribati, and the Marshall Islands.

Data on the landings of giant clam meat in Taiwan, including any differentiation between *T. gigas* and *T. derasa*, are generally unavailable due both to the illegal nature of the harvest and because in the records, landings were combined with the meat of other marine mollusks and collectively referred to as 'ganbei' or 'compoy.' Dawson (1986) estimated that an average giant clamming vessel would have been able to harvest one metric ton of adductor muscle per day and carry a full load of 10 metric tons, or the meat from approximately 11,000 giant clams. Dawson and Philipson (1989) estimated that during the peak of the Taiwanese fishery for giant clams, harvest may have reached 100 tons of adductor muscle per year, though Munro (1989) considered this to be an underestimate. According to Dawson (1986), "it seems certain […] that the total illegal harvest of giant clams over the twenty-odd years that such activities have occurred in the region can safely be measured in the millions." On the Great Barrier Reef alone, 22 Taiwanese fishing vessels were apprehended between 1969 and 1976 while illegally poaching giant clams. According to Pearson (1977), a total of 72 tons of clam meat was confiscated across the 22 ships, which is equivalent to over 500,000 clams. Pearson (1977) estimated that the ships likely represented only 10% of the fleet operating in the Great Barrier Reef at the time. Because the giant clam meat was typically removed from its shell for storage on the vessels, the proportion of *T. gigas* and *T. derasa* in the harvest is difficult to determine, but most accounts suggest that both species were targeted relatively equally.

Poaching by long-range Taiwanese vessels peaked in the mid-1970s and gradually declined during the 1980s as the extension of exclusive economic zones, improved surveillance of reef areas, boat seizures, and depleted stocks made the fishery less profitable. In addition, growing pressure from many Indo-Pacific nations forced the Taiwanese government to take stricter actions against giant clam harvesters, and beginning in 1986, all requests for approval of Taiwanese involvement in any clam fishing activities were rejected by the government. However, even as Taiwanese poaching operations declined, the demand for giant clam meat in Taiwan persisted, incentivizing the development of legal commercial fisheries for export throughout the Indo-Pacific. It was estimated that imports of adductor muscle to Taiwan from these newly formed fisheries totaled approximately 30-40 tons in 1987 and 1988 (Tisdell & Chen, 1994). The fisheries, however, rapidly depleted local stocks and were in most cases short-lived, typically being shut down by local authorities in the span of a few years. In Papua New Guinea, for example, the commercial giant clam fishery reportedly removed at least 85 tons of adductor muscle over a 6 year period from 1983 to 1988, equivalent to over 750 tons of total flesh weight, until it was closed due to depleted stocks (Kinch, 2002; Munro, 1993). The ban was lifted in 1995, at which point another 64-81 tons of adductor muscle were exported over the subsequent 6 years until the ban was reinstated in 2000.

Similarly, *T. derasa* was extensively exploited in Fiji as part of a brief commercial venture in 1985, during which a single ship was permitted to harvest giant clams with minimal restrictions. Teams of divers were reportedly able to collect 50-250 *T. derasa* per day, and at one site, harvesters had taken approximately 80% of the standing stock of *T. derasa*, or nearly 15,000 individuals, from an area of 10 square miles down to a depth of 60 feet. Adams (1988) estimated that harvesting rates averaged 70% of the total living stock at each reef, less for scattered populations and more for denser ones. From 1984 to 1987, *T. derasa* catch rates in Fiji varied between 20 and 40 tons of flesh per year, half of which was exported (Adams, 1988). The Fijian fishery as a whole (including municipal markets, wholesale and retail outlets, and exports) landed nearly 218 tons of giant clam meat (mantle and adductor muscle) from 1979 to 1987, of which approximately 95% was estimated to be from *T. derasa*. The largest annual harvest of 49.5 tons occurred in 1984, the year in which exports began (Lewis et al., 1988).

By the early 1990s, pervasive stock depletions of both *T. gigas* and *T. derasa* across the Indo-Pacific severely limited Taiwanese imports of giant clam meat (Tisdell & Chen, 1994). Many nations also instituted various regulations on the sale and export of giant clam meat (see Appendix 1), further limiting the commercial supply of giant clam meat. While we can rely to some extent on CITES annual reports to provide insight into the recent trends in international trade, many countries have limited their reporting of trade involving giant clam meat to the family or genus level. Based on the documented history of the giant clam meat trade discussed above, it is likely that the majority of trade reported as Tridacninae spp. is from *T. gigas* and *T. derasa*, but the relative contribution of each species is unknown.

Since 2010, the principal exporters of giant clam meat include Tonga (11,712 kg, 107 specimens), Cook Islands (2,205 kg), Marshall Islands (1,161 kg, 6,644 specimens), FSM (954 kg, 2,535 specimens), and Kiribati (950 kg). All trade from these nations was reported to be of wild-caught specimens or to have been seized or confiscated by the importing nation, presumably due to improper or missing CITES export permits. However, the accuracy of this reporting is unknown, as both *T. derasa* and *T. gigas* are either very rare or are not known to occur naturally in the Cook Islands, Marshall Islands, FSM, or Kiribati (see **Sections 4.3.2** and **4.4.2**). It is possible that these exports are of a different species, or perhaps that they were sourced primarily from the established mariculture facilities operating in these nations (Mies, Dor, et al., 2017) and were misreported on permits. We cannot be certain that this is the case; although, Lindsay et al. (2004) report that Tonga and the Marshall Islands in particular "dominate the trade in cultured giant clams" for the aquarium industry, so it is not unreasonable to assume that giant clam meat is sourced from the same or related mariculture operations. CITES reports also indicate that meat from 2,728 culture-raised *T. derasa* has been exported from Palau since 2010, with a relatively consistent annual trade volume averaging 246 specimens per year. This reflects the significant role that mariculture has played in diverting the commercial market for giant clam meat, and likely the subsistence demand to some extent, away from the harvest of wild-caught specimens in Palau.

In some locations, *T. derasa* has also been harvested for the giant clam shell and shell-craft industry. As discussed in **Section 3.2.2**, the Philippines has historically operated as the largest exporter of giant clam shells, accounting for over 95% of the global recorded exports of giant clam shell products since 1983. The two *Hippopus* spp. and *T. squamosa* were the most frequently exploited species for ornamental purposes and handicrafts, and *T. gigas* was most frequently used for basins (Lucas, 1994). *T. derasa* is often absent from trade data, but according to Juinio et al. (1987), this is likely because it was not distinguished by shell dealers as a separate species; rather, it was known as a "heavier variety" of *T. gigas* or *H. porcellanus*. Given the scale of the giant clam shell industry in the Philippines during the 1970s and 1980s, which reached millions of shells exported per year at its peak, even if *T. derasa* only accounted for a small proportion of the trade, it is likely that harvest of *T. derasa* shells contributed in part to the low abundance of the species throughout the Philippines.

According to CITES annual reports, *T. derasa* shells and shell-craft have also been exported in significant quantities from Fiji, New Caledonia, Palau, Solomon Islands, and Tonga. A total of 4,797 and 1,065 shells of wild-caught *T. derasa* were exported from Fiji in 2015 and 2017, respectively. In New Caledonia, an average of 210 *T. derasa* shells were exported annually during the period from 2000-2004, which declined to 23 shells exported annually from 2005 to 2008—all were reportedly of wild-caught origin. There have been no exports of *T. derasa* shells from New Caledonia since 2008. In Palau and the Solomon Islands, the majority of exported shells have been from culture-raised *T. derasa*. This includes 5,036 shells exported from Palau since 1991 and 5,816 shells and shell pairs exported from the Solomon Islands from 1997 to 2006. By comparison, 382 and 632 shells from wild-caught *T. derasa* were exported from Palau and the Solomon Islands, respectively. In Tonga, a total of 1,915 shells and 11,000 kg of shell products of wild-caught *T. derasa* were exported between 2001 and 2012. Maricultured specimens accounted for 355 exported shells during this period.

As with giant clam meat, it appears that mariculture has played an important role in diverting the commercial industry away from wild populations in Palau and the Solomon Islands, but the recent export of wild-caught *T. derasa* shells from Fiji and Tonga is concerning, as both nations have a ban in place on the commercial harvest and export of giant clams from the wild. The source of exports may have been misreported on CITES permits, as both nations have active mariculture operations for *T. derasa*, but we cannot confirm that this is the case.

Lastly, *T. derasa* is also a popular species in the growing aquarium industry and has been widely cultured for this purpose. Since 2010, CITES records indicate that the primary exporters of live *T. derasa* specimens have been the Marshall Islands (53,374 cultured, 15 wild-caught), Palau (43,484 cultured, 412 wild-caught), and FSM (35,228 cultured, 350 wild-caught). To a lesser extent, other significant contributors include the Solomon Islands (7,548 cultured, 1,692 wild-caught), Tonga (6,961 cultured, 689 wild-caught), Cook Islands (3,155 cultured, 329 wild-caught), and Indonesia (1,750 cultured, 50 of unknown origin). It is clear from the data that the large majority of live *T. derasa* in trade originate from mariculture; although, given the low abundance of wild *T. derasa* populations in these locations, even a relatively limited harvest of wild individuals contributes significantly to the threat of overexploitation.

Overall, the best available information indicates that *T. derasa* has been widely exploited for many years for its meat, shells, and as a popular aquarium specimen. It is highly valued as a subsistence food source in virtually all Pacific island nations where it occurs and, for over two decades, was subject to intense commercial demand for its adductor muscle primarily from consumers in Taiwan. Widespread harvest and poaching of *T. derasa* to supply this commercial market caused severe, documented population losses throughout the majority of its range. The commercial demand for giant clam meat (including *T. derasa*) began to decline by the end of the 1980s due to the low abundance of remaining populations in conjunction with stricter harvest regulations and improved enforcement. However, due to its traditional importance as a food source in many cultures, subsistence harvest of *T. derasa* continues in most locations throughout its range, which may lead to further population decline and likely prevents any substantial recovery of depleted populations. Furthermore, while many Pacific island nations have demonstrated success in culturing *T. derasa*, particularly for the growing aquarium trade, CITES records indicate that significant numbers of wild *T. derasa* have been harvested to supply the international shell-craft and aquarium industry since 2010, despite regulations prohibiting the commercial export of wild-caught giant clams.

The Great Barrier Reef and outlying islands of NW Australia are, for the most part, an exception to the range-wide trends for this species. Northern areas of the Great Barrier Reef were subjected to widespread poaching of *T. derasa* in the 1970s and 1980s, but improved surveillance of Australian fishing grounds and stronger enforcement of harvest bans has reduced the poaching pressure considerably; although, Neo et al. (2017) note that poaching of giant clams on the Great Barrier Reef does still occur. As a result, harvest of *T. derasa* in Australian waters since the 1980s has likely been minimal. Recent quantitative estimates of abundance are scarce, but based on past surveys and the strong protective measures in place, most experts consider the Great Barrier Reef to have relatively large, stable populations of giant clams, including *T. derasa* (Neo et al., 2017; S. Wells, 1997).

Overall, we consider the severe impact of past harvest on species abundance range-wide alongside reports of ongoing subsistence and commercial exploitation in most locations except Australia. Based on this information, we conclude with **Medium** confidence that overexploitation of *T. derasa* contributes significantly to the species' long-term risk of extinction, but because the threat is relatively low in Australia, where *T. derasa* populations are reportedly healthy, this factor likely does not constitute a danger of extinction in the near future (**Moderate** risk).

#### 4.3.3.3 Disease or Predation

Aside from the information discussed in **Section 3.3** with respect to giant clams generally, information regarding the prevalence of disease or predation for *T. derasa* is limited. The most concerning disease in giant clams is caused by the protozoan *Perkinsus* spp., which is ubiquitous across all ocean basins. Perkinsosis, also known as pinched-mantle syndrome, is typically fatal and no treatment has been developed for afflicted clams. However, there are no reports of this condition affecting *T. derasa*. Between July 1985 and January 1987, a mortality event occurred on the fringing reefs of Lizard Island on the Great Barrier Reef in which 42% of *T. derasa* at Watson's Bay and 10% at Palfrey and South Islands died (Alder & Braley, 1989). The authors were not able to identify a cause for the mortality event. They reported the presence of *Perkinsus* sp. and an unidentified unicellular organism found in the tissue of some of the dead specimens; however, dead individuals did not exhibit the common symptoms of Perkinsosis. Based on the best available information, disease does not appear to be a factor contributing significantly to extinction risk for *T. derasa*. Additionally, we found no information indicating predation is a factor influencing the extinction risk for *T. derasa* (**Very Low** risk, **Low** confidence).

#### 4.3.3.4 Inadequacy of Existing Regulatory Mechanisms

As with *H. hippopus*, there are various regulatory mechanisms and management measures in place throughout the range of *T. derasa* (see Appendix 1). Many implement protections for giant clams broadly (including *T. derasa*) and generally fall into four categories: a complete ban on harvest, a ban on harvest for commercial sale or export, bag limits, and minimum size restrictions. Below, we summarize the existing regulatory mechanisms in locations within the natural range of *T. derasa*.

Four countries and territories within the range of *T. derasa* have instituted a total ban on the harvest of giant clams for any purpose—these include Australia, Taiwan, Indonesia, and the Philippines. Eight countries and territories within the range of *T. derasa* have instituted a ban on the commercial export of giant clams—these include Fiji, Papua New Guinea, Solomon Islands, Vanuatu, Kiribati, Palau, Guam, and Tonga. Sale of giant clams in local markets is still permitted in Papua New Guinea, Vanuatu, Palau, and Tonga. In the Northern Province of New Caledonia, professional fishers are restricted to harvesting five giant clams per day, and all others are restricted to two per day. In the Southern Province, there is a maximum bag limit of 40 kg and for tourists there is a limit of 3 shells weighing up to 3 kg. In Guam, harvesting for subsistence use is limited to no more than three clams per day with a minimum size restriction of 18 cm. There are no known local or regional regulations in place for the protection of *T. derasa* in Malaysia, CNMI, or within the South China Sea.

As discussed in **Section 3.4**, in many Pacific islands, national legislation is also supplemented or enforced by way of customary fishing rights and marine tenure systems. This is the case in parts of Fiji, Samoa, Solomon Islands, Papua New Guinea, and Vanuatu, where indigenous village groups hold fishing rights and regulate access to adjacent reef and lagoon areas. It is unclear whether these small-scale regulatory dynamics typically apply to giant clams broadly, or if certain species may be protected or managed differently than others. Thus, without more information, there is no way to assess the effectiveness of these community-based management systems on the preservation of *T. derasa*, specifically. Likewise, the paucity of long-term monitoring data in many of the countries and territories where *T. derasa* occurs makes it difficult to evaluate the effectiveness of local regulatory mechanisms more generally. In many areas, for example, harvest prohibitions have been instituted within the last decade or two, but there have been few, if any, follow-up surveys conducted in the time since.

Using what survey data is available, which consistently indicates population declines and a low abundance of *T. derasa* throughout most of its range, we can infer that existing regulations have not sufficiently protected this species from exploitation. In **Section 3.4**, we discuss specific reports of recent illegal harvest of giant clams in the Philippines, Papua New Guinea, and Malaysia, along with a number of challenges that many countries face related to the management of giant clams. According to Kinch and Teitelbaum (2010), such challenges include a lack of capacity for conducting stock assessments and enforcing harvesting regulations, a lack of education and awareness among community members about sustainable giant clam harvest, uncoordinated legislative structure, and a lack of international collaboration to promote a sustainable and scalable market for captive-bred giant clams. Each of the countries may experience these challenges to a different degree, but overall it highlights the difficulties in effectively managing giant clam populations, particularly for smaller island nations that may lack enforcement resources or expertise. This is compounded, in many cases, by the traditional importance of giant clams as a coastal resource, which may limit the willingness among indigenous communities to adopt the recommended practices. These challenges are discussed with respect to giant clams broadly, but they also apply specifically to the management of *T. derasa* throughout its range. Thus, despite widespread commercial export bans, the capacity for enforcing existing regulations is often limited, existing regulations do not restrict continued subsistence harvest in many locations, and illegal harvest and trade of giant clams (particularly for the shell trade) continues to occur. As with the threat of overexploitation, we also consider the effectiveness of regulation in Australia, which has largely been successful at reducing harvest pressure and protecting some of the few remaining healthy populations of *T. derasa*. For these reasons, we conclude with **Medium** confidence that inadequacy of existing local/regional regulations poses a **Moderate** risk to the extinction of *T. derasa* (i.e., the factor contributes significantly to long-term risk of extinction, but does not in itself constitute a danger of extinction in the near future).

In terms of international regulations, *T. derasa* was listed under Appendix II of CITES in 1985 to regulate international trade in any of its parts (shells, tissues, alive, or dead). All of the 17 countries and territories throughout its natural range are Parties to the treaty, although Palau has claimed reservations on all species of giant clams. As discussed in **Section 4.3.3.2**, CITES annual report data indicated that the recent trade of *T. derasa* internationally is largely restricted to culture-raised specimens. Since 2010, 154,245 of the 158,319 live specimens recorded in trade were culture-raised (97.4%), while only 3,514 were reportedly wild-caught (2.2%). A smaller proportion of shells and shell products recorded in trade since 2010 were of cultured *T. derasa*, but the total trade volume is significantly lower. In total, 3,775 of the 11,100 *T. derasa* shells and shell products were of culture-raised specimens (34%), while 7,312 were wild caught (65.9%). Based on this data, CITES regulations have been effective at transitioning much of the international supply of *T. derasa* products away from wild harvest and towards mariculture operations. It is true that CITES data has a number of limitations, such as reporting errors and inconsistencies; however, the pattern reflected in the data is supported by the widespread success in culturing *T. derasa* across the Indo-Pacific. Therefore, despite the possible errors in CITES reports and missing information on illegal trade, we have **Medium** confidence that international trade regulations adequately minimize the trade of wild-caught *T. derasa* (**Very Low** risk).

With respect to international climate change regulations, we conclude in **Section 3.4.2** that the current implementation of domestic and international climate regulations is insufficient to mitigate the cumulative threat of climate change to giant clam habitat and physiology generally. We find that this conclusion is relevant to *T. derasa* to an extent, based on its documented habitat preference for offshore coral reefs and atolls. The inadequacy of international climate change regulations will likely exacerbate the impacts of ocean warming and acidification on coral reefs, which may affect the quality of *T. derasa* habitat. This leads us to a conclusion of **Low** risk, such that this factor is unlikely to contribute significantly to long-term or near future extinction risk by itself, but may do so in combination with other threats. However, our uncertainty regarding the degree to which *T. derasa* is reliant on coral reefs (see **Section 4.3.3.5**) leaves us with **Low** confidence in this assessment.

#### 4.3.3.5 Other Natural or Manmade Factors

##### *Climate Change*

Beyond the information presented in **Section 3.5**, we could find very little research addressing the potential effects of climate change on *T. derasa* specifically. The few studies available found that *T. derasa* suffered reduced photosynthetic production and respiration when exposed to warming of 3ºC (Blidberg et al., 2000) and experienced faster growth under high-nutrient, low-pH conditions (Toonen et al., 2012). Neither bleaching nor mortality was reported in either study. Neo et al. (2017) also noted significant mortality of *T. derasa* at Lizard Island, Australia following anomalous warming in 2016 that caused widespread coral bleaching. However, the authors did not provide evidence directly tying the mortality to a specific cause and noted that this event occurred after three years of cyclones, which also may have contributed to the observed mortality. While there is considerably more research on possible climate change effects in other giant clam species (see **Section 3.5**), we are hesitant to make extrapolations from these studies, as it is possible that susceptibility may vary among species. Thus, given the limited findings above, we conclude with **Low** confidence that ocean warming may, in combination with other VP descriptors or threats, contribute to the long-term extinction risk of *T. derasa*, but is unlikely a significant threat on its own (**Low** risk).

##### *Land-Based Sources of Pollution*

We could find very little research addressing the potential effects of land-based runoff on *T. derasa* specifically. As mentioned above in relation to climate change effects, Toonen et al. (2012) found that growth rate increased under high-nutrient, low-pH conditions. Likewise, early experimental results from the PMDC showed a similar increase in growth rate under ammonium enrichment (MMDC Bulletin, 1988). Based on these limited results and because *T. derasa* is found predominantly in offshore coral reef areas, it is unlikely that land-based sources of pollution pose a significant threat to the species.

##### *Stochastic Events*

While stochastic events such as extreme weather and mass mortalities of unknown cause may result in severe population loss in localized areas, these threats inherently cannot be predicted with any precision (**Low** confidence). However, as mentioned in **Section 4.3.3.3**, mass mortality of *T. derasa* has previously been observed on the Great Barrier Reef. Alder and Braley (1989) reported that sporadic mortality events between 1985 and 1987 led to a loss of 42% and 10% of *T. derasa* populations at two fringing reefs near Lizard Island. According to the authors, deaths were not restricted to a particular size class, and the distribution of mortality appeared random. Histopathology revealed one unidentified unicellular organism in six of eight specimens that were examined, but the exact cause (or causes) of the mortality was not confirmed. Because the Great Barrier Reef is reported to be one of the few remaining locations with relatively healthy populations of *T. derasa*, we conclude that the threat of stochastic mortality may, in combination with other VP factors or threats, contribute significantly to the species' long-term risk of extinction, but is unlikely a significant threat on its own (**Low** risk).

**Table 14.** Summary of the threats analysis for *T. derasa* and associated confidence ratings.

| 4(a)(1) Factor | Threat | Contribution to Species' Risk of Extinction | Confidence Rating |
|---|---|---|---|
| **Habitat destruction, modification, or curtailment** | *Coastal development* | Very Low | Medium |
| | *Climate change impacts to coral reefs* | Moderate | Low |
| **Overutilization** | | Moderate | Medium |
| **Disease or Predation** | | Very Low | Low |
| **Inadequacy of existing regulatory mechanisms** | *National and local regulations on harvest* | Moderate | Medium |
| | *Regulations on international trade* | Very Low | Medium |
| | *Regulations on climate change* | Low | Low |
| **Other natural or manmade factors affecting the species' continued existence** | *Physiological impacts of climate change* | Low | Low |
| | *Land-based sources of pollution* | Very Low | Medium |
| | *Stochastic events* | Low | Low |

### 4.3.4 Demographic Risk Assessment

***Abundance***

Because there are no global abundance estimates for *T. derasa*, we rely on the qualitative estimates of population status provided in Table 13, which are based on the best available survey data from all countries, territories, and regions where the species has been recorded. These data indicate that *T. derasa* has suffered significant population declines to the extent that the species is considered "rare," extirpated, or has been reintroduced after extirpation in 15 of the 18 locations throughout its range. In locations where it is considered "rare," this means that available survey data indicates an average population density that is likely less than 10 ind $ha^{-1}$ on average, or approximately one individual spaced approximately every 30 m. For broadcast spawning organisms like *T. derasa*, which rely on the external fertilization of gametes, the implications of such sparse distribution on reproduction can be significant. As discussed in **Section 4.1.2**, Braley (1984) observed that 70% of nearest spawning giant clams (*T. gigas*) were found within 9 m of one another, while only 13% were between 20-30 m of one another. These findings suggest that individuals in "rare" populations are less likely to spawn in synchrony and as a result are likely to experience infrequent, sporadic reproductive success. This negative relationship between population density and productivity, known as the Allee effect, can cause further reductions in population abundance and put "rare" populations of *T. derasa* at greater risk of extinction.

Furthermore, the impact of subsistence harvest can be particularly consequential in locations where the abundance of the species is low, because it can reduce the number of reproducing adults and, in effect, constrain the recovery potential of the population. In every location where *T. derasa* is considered rare, subsistence harvest is still permitted or existing harvest bans, such as in Indonesia and the Philippines, have largely been ineffective at eliminating illegal harvest. In these locations, the low abundance of *T. derasa* exacerbates the extinction risk associated with continued harvest pressure.

Of the 18 locations where *T. derasa* has been observed or reintroduced, there are only 3 locations where the species is considered "frequent," indicating population density estimates that are between 10 and 100 ind $ha^{-1}$ on average—these are the Great Barrier Reef, outlying islands of NW Australia, and Palau. Both locations in Australia are subject to a total ban on the harvest of *T. derasa*. While there is very little recent survey data on the abundance of *T. derasa* on the Great Barrier Reef, anecdotal reports commonly suggest that populations of giant clams (including *T. derasa*) in Australia are healthy relative to other areas of the Indo-Pacific. Additionally, regulations have reportedly been effective at preventing illegal harvest and minimizing the risk of overutilization of giant clams in Australian waters. Notably, data from two unpublished surveys indicate that *T. derasa* experienced significant population declines (10.0-83.0%) at four of five sites in the far northern Great Barrier Reef between 1982-85 and 2007-09 (R. D. Braley, reported in Neo et al., 2017), but has since recovered to some extent a decade later (R. D. Braley, *in review*). It is possible that the decline is part of a natural fluctuation in population demographics at these sites, reflecting the sporadic nature of giant clam reproduction and recruitment more generally. Population densities at these sites remain high relative to most other areas of the species' range, and according to R.D. Braley (pers. comm., October 19, 2022) and Neo et al. (2017), giant clams (including *T. derasa*) on the Great Barrier Reef exist in a "natural" and "virtually undisturbed" state.

In NW Australia, population estimates of *T. derasa* are variable, ranging from 1.3 ind $ha^{-1}$ at Ashmore Reef to 77.7 ind $ha^{-1}$ at N Scott Reef. In Palau, there is a ban on the commercial export of giant clams, but harvesting for subsistence and domestic sale is still reportedly very common, and *T. derasa* remains a highly desired food item, leaving these populations at risk of overexploitation.

Overall, the abundance of *T. derasa* is greatly reduced from historic levels throughout its range, leaving only three locations where the species is not considered rare or locally extinct. The species is at continued risk of overexploitation in all locations where it is found, except for Australia, due to ongoing subsistence harvest and inadequate regulation. A long-term population decline has been documented at several sites in the northern Great Barrier Reef, but it is unclear if the decline reflects a natural fluctuation or a more chronic risk of recruitment failure. Based on this information, we find that the abundance of remaining populations contributes significantly to the species' long-term risk of extinction, but does not in itself constitute a danger of extinction in the near future (**Moderate** risk, **Medium** confidence).

### ***Productivity***

Despite exceptionally high fecundity, there is substantial evidence that low recruitment success and high mortality rates during early development lead to low productivity in most species of giant clams. This is likely true of *T. derasa* as well. Braley (1984) described "extremely low" recruitment on the Great Barrier Reef, reporting that juveniles (< 14 cm) comprised 1.5% of the observed *T. derasa* at Escape Reef, while the annual mortality rate of adults was approximately 1.1% from 1981 to 1982. Braley (1988) later measured similar recruitment rates at four sites on the Great Barrier Reef, varying from 1.5% to 25%. This led the author to infer that the few reefs with abundant populations of clams may dominate recruit production for extensive areas of the Great Barrier Reef. An important caveat is that the juveniles of the largest giant clam species (i.e., *T. gigas*, *T. derasa*, *H. hippopus*, and *H. porcellanus*) are cryptic, as their mantles are not as brightly-colored as the smaller species (Munro, 1993a). Hence, Munro (1993a) claimed that "even when experienced divers enumerate the contents of quadrats, relatively large juvenile *T. gigas* and *T. derasa* will be overlooked and only reach full 'findability' at about 20 cm [shell length]."

While we could not find specific fecundity estimates for *T. derasa*, observations of other species suggest that individual giant clams can produce tens to hundreds of millions of eggs during a single spawning event (Lucas, 1988). However, survival rates through larval and juvenile development can often be less than 1% (Crawford & Lucas, 1986; Fitt et al., 1984; Jameson, 1976). Given the low abundance of *T. derasa* throughout much of its range and the ongoing threats outlined in **Section 4.3.3**, which are likely leading to continued population declines, such low productivity can significantly limit the capacity for this species to achieve positive population growth rates and recover from low abundance.

Furthermore, as discussed in relation to the Abundance risk factor above, *T. derasa* is likely experiencing an Allee effect in locations where the species is rare, such that productivity is negatively correlated with population abundance. As a broadcast spawning organism, *T. derasa* relies on sufficient population density to facilitate successful external fertilization of their gametes. The best available evidence suggests that spawning synchrony in *T. gigas* drops significantly at population densities lower than 10 ind ha$^{-1}$ (Braley, 1984), and while gametes can remain viable for up to 8 hours in *T. squamosa*, viability decreases significantly with time (Neo, Vicentuan, et al., 2015). Therefore, while the distance and duration may vary among species, it is likely that the overall effect of low abundance in reducing productivity is applicable to *T. derasa* as well.

For these reasons, we conclude that the low natural productivity of giant clams as well as the negative relationship of productivity with low abundance contributes significantly to the long-term extinction risk for *T. derasa*, but likely does not in itself constitute a danger of extinction in the near future (**Moderate** risk, **Medium** confidence).

### ***Spatial Distribution/Connectivity***

As described in **Section 4.3.1.5**, the best available data suggest that *T. derasa* experiences some degree of genetic isolation (i.e., low connectivity) between populations in the central Pacific (e.g., Fiji and Tonga), western Pacific (e.g., Palau and the Philippines), and the Great Barrier Reef. Without more refined genetic analyses, it is impossible to determine if this spatial structure reflects past or current demographic processes among these regions. However, given the exceptionally low abundance of this species throughout most of its historic range, the low productivity of giant clams generally, and a relatively short pelagic larval duration (~6-14 days), it is likely that larval exchange between distant locations is very low, and perhaps particularly so among these three regions. Importantly, based on the spatial structure suggested by the available genetic data, it is unlikely that populations of *T. derasa* on the Great Barrier Reef provide significant larval subsidy to other locations of the species range. Because the Great Barrier Reef represents one of the few remaining locations supporting relatively healthy populations of *T. derasa*, any barrier to dispersal from this region reduces its capacity as a larval source and limits the species' recovery potential range-wide. Likewise, according to the limited genetic data, populations in Palau may function as a significant larval source only to nearby locations in the western Pacific, such as the Philippines. However, it is important to reiterate that the available population genetic data reflect processes that manifest on an evolutionary time scale (i.e., thousands of years or more). Without more information, it is not possible to determine the extent to which migration between these and other nearby locations occurs currently or how the migration rate may change on an ecological time scale (i.e., tens to hundreds of years), which is more relevant to the recovery of the species.

For this reason, based on the best available population genetic data and considering the abundance distribution of *T. derasa*, we conclude that limited connectivity, particularly between the Great Barrier Reef and other locations within the species' range, likely contributes significantly to the long-term extinction risk for *T. derasa*, but does not in itself constitute a danger of extinction in the near future (**Moderate** risk, **Low** confidence).

### ***Genetic Diversity***

As described in **Section 4.3.1.5**, *T. derasa* exhibits regional differences in the degree of genetic variation. Macaranas et al. (1992) found that mean heterozygosity based on allozyme variation was highest on the Great Barrier Reef ($h$ = 35-46%), intermediate in the Philippines ($h$

= 29%), and lowest in Fiji ($h$ = 14%). Similarly, Gomez et al. (1994) found low mean heterozygosity in both Fiji and Tonga ($h$ = 17-19%). While it is difficult to know the exact cause, the relatively low genetic diversity in the small island populations may be reflective of smaller populations and low rates of immigration due to their geographic remoteness. Macaranas et al. (1992) also note that samples from Fiji were collected from the Makogai Island hatchery, where genetic diversity may be artificially reduced. In general, low genetic diversity may limit adaptive potential, and effectively lower the resilience of populations to environmental change. We find it unlikely that this factor contributes significantly to long-term or near future extinction risk by itself, but have some concern that it may, in combination with other VP factors and threats, particularly in smaller island populations (**Low** risk, **Low** confidence).

**Table 15.** Summary of the demographic risk analysis for *T. derasa* and associated confidence ratings.

| Demographic Risk Factor | Contribution to Species' Risk of Extinction | Confidence Rating |
|---|---|---|
| **Abundance** | Moderate | Medium |
| **Productivity** | Moderate | Medium |
| **Spatial Distribution/Connectivity** | Moderate | Low |
| **Genetic Diversity** | Low | Low |

### 4.3.5 Overall Extinction Risk Assessment

Guided by the results of the demographic risk analysis and threats assessment above, we analyzed the overall risk of extinction of *T. derasa* throughout its range. In this process, we considered the best available scientific and commercial information regarding *T. derasa* from all locations of the species' range, and analyzed the collective condition of these populations to assess the species' overall extinction risk. We determined that the most critical demographic risks to *T. derasa* are the low abundance and negative trajectory of populations throughout the majority of its range, compounded by low natural productivity and the likelihood of the Allee effect. Additionally, our threats assessment revealed that the past and present overutilization and associated inadequacy of existing regulatory mechanisms at the local level contribute most significantly to the extinction risk of this species. Continued harvest of *T. derasa* primarily for subsistence purposes, combined with the species' low productivity will likely drive further population declines and prevent any substantial population recovery. We also consider that the close association of *T. derasa* with coral reefs may make the species more susceptible to the projected impacts of ocean warming and acidification on coral reef habitats.

As with *H. hippopus*, the best available scientific and commercial information indicates that very few healthy populations of *T. derasa* remain and occur primarily in the waters of Australia. Extensive surveys of *T. derasa* on the Great Barrier Reef from the 1980s (Braley, 1987a, 1987b) found that the species' distribution was patchy with several sites of relatively high density (>10 ind ha$^{-1}$) interspersed among many other sites of low density or where the species was completely absent. The Swain Reefs in particular, a group of approximately 350 offshore reefs in the southern region of the Great Barrier Reef, was one area described as having an especially high abundance of *T. derasa*, with densities ranging from 12 to 172 ind ha$^{-1}$ (Pearson, 1977). Based on the species' patchy distribution and the observed pattern of recruitment, Braley (1988) found it likely that the relatively few reefs with abundant populations of clams (mostly in the south) may dominate recruit production for the rest of the Great Barrier Reef.

According to Pearson (1977), during the 1960s and early 1970s, Taiwanese vessels poached giant clams (primarily *T. gigas* and *T. derasa*) from the entire length of the Great Barrier Reef. As surveillance and enforcement efforts by Australian authorities increased in the 1970s, poachers began to concentrate their activities in offshore areas, such as the Swain Reefs. However, this likely only lasted at significant scale for a few years, as Dawson (1986) claimed that during the lead up to the declaration of the Australian Fishing Zone (AFZ) in 1979, Taiwanese authorities were warned that continued illegal poaching of giant clams would jeopardize Taiwan's position in gaining access rights to the AFZ. This forced the Taiwanese government to enhance the inspection of suspected boats upon departure and return to port. According to Dawson (1986), "the combined effect of these two components, almost certain apprehension by the coastal state and effective sanctions by the flag state, combined to result in the virtual cessation of illegal giant clam activities in the AFZ." Based on this assessment and because subsistence demand for giant clams in Australia is minimal, we find it likely that the population density estimates provided by Braley (1987a, 1987b) generally represent the current status of *T. derasa* on the Great Barrier Reef. This is further supported by more recent reviews and reports (bin Othman et al., 2010; Neo et al., 2017; S. Wells, 1997) suggesting that *T. derasa* is still frequent on much of the Great Barrier Reef.

There is also quantitative evidence that *T. derasa* occurs in significant numbers in the outlying islands of NW Australia (Richards et al., 2009; Skewes et al., 1999), likely benefitting from the strong regulatory protections within Australian waters. Additionally, in Palau, although subsistence harvest of giant clams is permitted and is reported to occur commonly, a recent survey indicated relatively large populations of *T. derasa* (Rehm et al., 2022). As discussed in **Section 4.3.2**, it is possible that the significant output from the PMDC mariculture facility and reported efforts to use a portion of *T. derasa* seedstock to enhance depleted populations in certain conservation areas may be balancing the harvest pressure in Palau. Although, without further information, we are not able to assess with confidence whether *T. derasa* abundance in this location is stable, or whether it may be increasing or decreasing significantly due to one factor outweighing the other.

In contrast to these 3 locations where *T. derasa* populations are relatively healthy (i.e., the Great Barrier Reef, NW Australia, Palau), the best available data indicate that at the 15 other locations across the range with documented occurrences of this species, extensive exploitation for past commercial trade, ongoing subsistence use, and illegal harvest have driven *T. derasa* to exceptionally low abundance, and in some cases, extirpation. The continued threat of overexploitation, the possible future threat of habitat degradation due to climate change impacts on coral reefs, and the demographic risks outlined in **Section 4.3.4**, likely place the continued persistence of *T. derasa* in these locations in question. However, because *T. derasa* populations in Australia and Palau are relatively healthy, and the enforcement of strict harvest bans have effectively minimized the threat of overexploitation in Australian waters, we cannot conclude that the species is at moderate or high risk of extinction throughout its *entire* range.

It is important to highlight that, although we refer to the Great Barrier Reef as only one location for the purpose of this analysis, it covers an expansive geographic area that comprises a substantial proportion of the suitable habitat within the species' range (see Figure 24). Additionally, while the future threat of habitat degradation due to climate change impacts on coral reefs may be relevant to these populations, we do not have sufficient information to confidently assess the extent to which the survival or productivity of giant clams (even those species closely associated with coral reefs, such as *T. derasa*) may be impacted by projected changes to coral reef communities in the foreseeable future (see **Section 4.3.3.1**).

### *Significant Portion of its Range Analysis*

Under the ESA, a species warrants listing if it is in danger of extinction or likely to become so within the foreseeable future throughout all or a significant portion of its range. Thus, a species may be endangered or threatened throughout all of its range, or a species may be endangered or threatened throughout only a significant portion of its range. Having determined that *T. derasa* is not at moderate risk of extinction throughout all of its range, in order to inform the listing determination, we conducted an additional analysis to assess whether the species is at higher risk of extinction in a "significant portion of its range" —that is, we assessed whether there is any portion of the species' range for which it is true that both (1) the portion is significant and (2) the species, in that portion, is at moderate or high risk of extinction. A joint USFWS-NMFS policy, finalized in 2014, provided the agencies' interpretation of this phrase ("SPR Policy," 79 FR 37578, July 1, 2014) and explains that, depending on the case, it might be more efficient for us to address the "significance" question or the "status" question first. Regardless of which question we choose to address first, if we reach a negative answer with respect to the first question, we do not need to evaluate the other question for that portion of the species' range.

Because we determined that the most significant threats to *T. derasa* are overexploitation and inadequacy of regulatory mechanisms, we base our analysis here on the portion of the range where these threats are most severe, consistent with the approach used in the SPR analysis for *H. hippopus* (see **Section 4.1.5**). As is discussed above, several sources indicate that the early adoption of strict harvest prohibitions in Australia has been largely effective at preventing illegal harvest and minimizing the risk of overexploitation of giant clams in Australian waters. This differs considerably from reports from every other location throughout the species' range, which consistently indicate that the threat of overexploitation in combination with inadequate regulation and enforcement poses a significant extinction risk to *T. derasa*. Thus, for the purpose of this SPR analysis, we distinguish locations in Australia (i.e., the Great Barrier Reef and NW Australia) from all other locations where *T. derasa* occurs and consider them as two separate portions of the species' range.

In this case, the portion under consideration includes 16 countries and territories where the primary threat to the species is overexploitation. In 15 of these locations, the best available survey data, as well as qualitative descriptions of abundance, suggest that extensive commercial, subsistence, and illegal harvest has driven *T. derasa* to exceptionally low abundance, and in several cases, local extinction. The one exception is Palau, where a recent survey of the main island group and past surveys of a remote uninhabited atoll indicate that abundance of *T. derasa* is likely relatively high. However, while commercial export of wild-caught giant clams is prohibited in Palau, harvest for subsistence purposes and for sale in domestic markets is reportedly very common, and *T. derasa* is one species that is specifically targeted by locals.

As with *H. hippopus*, an argument could be made that the success of mariculture operations in Palau will likely prevent the species from going extinct in the foreseeable future. For example, since 1990, the PMDC alone has cultured over 150,000 *T. derasa* for export internationally, and likely many more that were traded domestically or were otherwise not included in CITES reports. It is possible that the threat of overexploitation in Palau has been somewhat offset by documented efforts to reseed depleted populations (see **Section 4.3.2**). However, as we discussed previously, we are not basing our assessment on the past success of mariculture operations, because of its reliance on a number of unpredictable factors (e.g., funding, management priorities, natural disasters, etc.), and it is difficult to extrapolate the effect of mariculture beyond the next few years. Thus, we based our assessment on the demographic risks of low abundance and low productivity in 15 of 16 locations where the species naturally occurs, and the ongoing threats of overexploitation and inadequate regulatory mechanisms in all 16 locations.

Similar to *H. hippopus*, we considered the geographic range of the remaining populations, noting that the species still occurs in 16 locations within this portion of its range, which encompass a broad geographic area and a variety of environmental conditions within the Indo-Pacific region. However, Palau is the only location in this portion where *T. derasa* is considered frequent (although, we note that two recent surveys have found relatively abundant populations in the Anambas Islands and Raja Ampat region of Indonesia). Because of its large size, *T. derasa* is often the most highly desired species for subsistence consumption and to sell for its meat in local markets. This continued demand at the local level combined with the widespread and lasting impact of the Taiwanese poaching effort has driven the species to exceptionally low abundance on average in this portion of its range. Among the many low estimates of population density, *T. derasa* has been described as "virtually extinct from most of [the Philippines] due to overexploitation" (Gomez & Alcala, 1988), "likely functionally extinct" from Karimun Jawa, Indonesia (Brown & Muskanofola, 1985), and "at risk of extirpation" in New Caledonia (Purcell et al., 2020). For these reasons, despite the geographic scope of the remaining *T. derasa* populations, given the desirability and ongoing demand for *T. derasa* for consumption and sale in local markets, we find that the species is at or near a level of abundance that places its continued persistence in this portion in question (**High** extinction risk).

Having reached a positive answer with respect to the "status" question, we next considered whether this portion of the range is "significant." Similar to the SPR analysis for *H. hippopus* (see **Section 4.1.5**), we considered the historically high abundance of *T. derasa* in this portion of the range, as evidenced by trade statistics and the many reports of major population losses resulting from years of subsistence and commercial harvest. Additionally, as was described with respect to *H. hippopus*, it is likely that populations in this portion played an important role in maintaining genetic connectivity throughout the species' range. Given the relatively short pelagic larval phase of giant clams (~6-14 days), there is a diminishing likelihood of larval dispersal between locations at progressively greater distances. Therefore, genetic exchange between distant populations likely relied on many smaller dispersal events across the network of more closely spaced islands or habitat areas that comprise this portion of the species' range. Lastly, considering the geographic extent of this portion and the diverse habitats that it encompasses, the populations of *T. derasa* within this portion likely served as an important demographic and genetic reserve, which could facilitate recovery following localized population declines. Based on this rationale, we find that the portion of the species' range defined as all locations outside of Australia is "significant," or in other words serves a biologically important role in maintaining the long-term viability of *T. derasa*.

## 4.4 *Tridacna gigas*

### 4.4.1 Life History and Ecology

#### 4.4.1.1 Taxonomy and Distinctive Characteristics

*Tridacna gigas*, commonly referred to as the true giant clam, was originally described by Carl Linnaeus in 1758. It is the largest of all the giant clam species, growing to a maximum shell length of 137 cm and weights in excess of 225 kg (Beckvar, 1981; Rosewater, 1965); although, the species is most commonly found at lengths of about 80 cm (Kinch & Teitelbaum, 2010; Neo, Eckman, et al., 2015). The shells of *T. gigas* are thick and heavy, equivalve (having valves of the same size), and equilateral (symmetrical front-to-back; Hernawan, 2012). The shell exterior is off-white, and is often covered with marine growths (e.g., vermetids, annelid tubes, coral, etc.) (Kinch & Teitelbaum, 2010; Rosewater, 1965). For the most part, the shells lack scales except near the byssal orifice where small scales may be present. The shell interior is porcelaneous white, dull in the area within the pallial line, and shiny above the pallial line to the dorsal end of the shell (Rosewater, 1965). Often, the mantle is yellowish-brown to olive-green and is a darker shade along the mantle's edge and around the clam's siphons (Rosewater, 1965; see Figure 25). Numerous, small, brilliant blue-green rings are dispersed across the mantle, each enclosing one or several hyaline organs. These rings are especially prevalent along the lateral edges of the mantle and around the siphonal openings (Rosewater, 1965). Smaller specimens (i.e., 150-200 mm) may be more uniformly colored, lacking a darker shade along the edge of the mantle and with fewer colored rings (Rosewater, 1965).

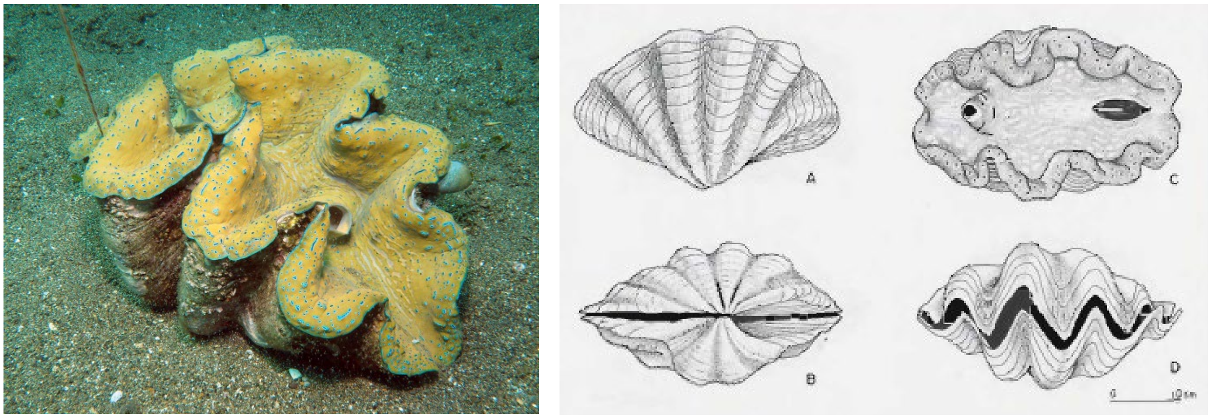

**Figure 25.** *T. gigas* morphology. Photograph of *T. gigas* taken at a giant clam sanctuary near Batangas, Philippines (left), and illustrations showing the lateral (A), ventral (B), mantle (C), and dorsal (D) view of a representative specimen (right). (Photo credit: Scott and Jeanette Johnson/iNaturalist, CC BY-NC 4.0; Diagram source: Calumpong, 1992)

This species is readily identified by many characteristics, most notably its large size. The species can also be identified by four to six deep radial folds that give way to elongate, triangular projections at the upper margins of its shells (Hernawan, 2012; Lucas, 1988), a complete outer demibranch (the V-shaped structure of gills common to bivalves; Rosewater, 1965), the lack of tentacles on the inhalant siphon (Hernawan, 2012), and the lack of byssal attachment (i.e., they are free-living; Rosewater, 1965). Unlike the two *Hippopus* species, *T. gigas* possesses hyaline organs in its mantle, lacks an interdenticulated ventral margin, and when completely open, its mantle may extend beyond the ventral margins of its shells (Hernawan, 2012).

### 4.4.1.2 Range, Distribution, and Habitat Use

The natural range of *T. gigas* spans the shallow (i.e., ≤ 20 m) tropical waters of the Indo-Pacific and the Great Barrier Reef (Figure 26). The clam occurs from Myanmar in the west to the Republic of Kiribati in the east, and from the Ryukyus Islands of southern Japan in the north to Queensland, Australia in the south (bin Othman et al., 2010; Neo et al., 2017). According to fossil records from the Pleistocene (1.6-0.01 million years ago), the historical range of *T. gigas* extended west to the eastern coast of Africa (Braithwaite, 1984; Accordi et al., 2010), and unconfirmed anecdotal accounts also place the species in Madagascar (Hopkins, 2009) and Mauritius (Michel et al., 1985). It is likely that climatic events (e.g., the closure of the Tethyan seaway and sea level changes throughout the Quaternary) pushed the range of *T. gigas* eastward, and combined with the species' short larval period, prevented the species from recolonizing the western Indian Ocean (Harzhauser et al., 2008; Accordi et al., 2010).

As discussed in **Section 2.2**, *T. gigas* historically occurred in CNMI and Guam, but is reportedly extirpated in both locations as a result of overutilization. There have been attempts to reintroduce the species to both locations, but in most cases, the primary goal of these efforts is to establish a source of food and income for local communities. *T. gigas* has also been cultured and introduced in American Samoa for a similar purpose and was introduced to Keahole Point, Hawaii to explore the market potential for culturing ornamental marine invertebrates for the aquarium trade (Heslinga, 1996). Given the primary purpose of these efforts, it is unlikely that wild, reproducing populations of *T. gigas* have been established in any of these locations under U.S. jurisdiction. Additionally, a single *T. gigas* was reportedly observed near Johnston Atoll, and it has been reported that the species historically occurred in Wake Atoll, but both accounts require further corroboration.

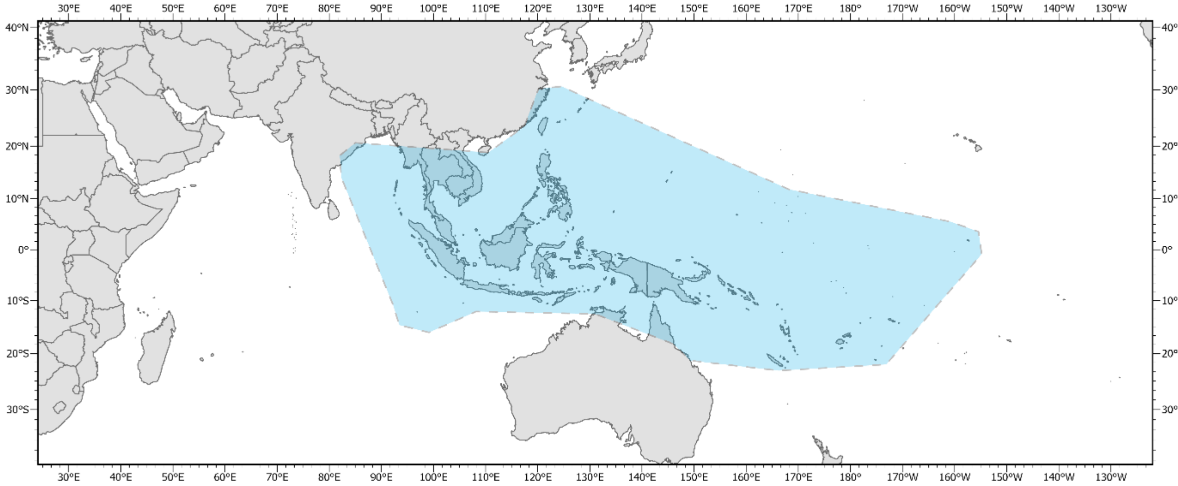

**Figure 26.** Approximate natural range of *T. gigas* based on reported occurrences provided by Neo et al. (2017). The range does not include locations where *T. gigas* has been introduced.

Like most other giant clam species, *T. gigas* is typically associated with coral reefs and can be found in many habitats, including high- and low-islands, atoll lagoons, and fringing reefs (Munro, 1993). In a broad survey of *T. gigas* distribution throughout the Great Barrier Reef, Braley (1987a) found that the species was most common on inshore reefs potentially influenced by seasonal fluctuations in salinity and turbidity and was rare south of 19ºS. The observed distribution was essentially opposite of that for *T. derasa*, which was found primarily on offshore reefs and was common in the Swain Reefs at 21-22ºS. These contrasting distributions led Braley (1987a) to the conclusion that temperature may limit the distribution of *T. gigas*, while *T. derasa* may be more sensitive to salinity and/or turbidity. *T. gigas* is typically found between the depths of 2 to 20 m and is often found among *Acropora* spp. or other hard coral communities, hard reef substrata, or on bare sand (Braley, 1987b; Kinch & Teitelbaum 2010; Rosewater, 1965).

### 4.4.1.3 Reproduction and Growth

*T. gigas* is a long-lived species, with the oldest, reliably aged individual determined to be 63 years old (Lucas, 1994). The average growth rate of *T. gigas* is the fastest of all giant clam species, typically falling in the range of 8-12 cm per year; although, it can vary substantially between individuals (Beckvar, 1981; Crawford et al., 1988; Pearson & Munro, 1991). Growth rate slows with age, a trend which is thought to begin at the onset of female gametogenesis (Beckvar, 1981; Basker, 1991). A comparison of growth rates between wild and cultured *T. gigas* stocks indicated a higher average growth rate in the wild (Pearson & Munro, 1991), which Munro (1993a) posits may indicate selection against slow-growing clams in natural populations.

*T. gigas* has been found to reach male maturity at around 6 years of age and female maturity by 9-10 years of age, later than most other giant clam species (Gomez & Mingoa-Licuanan, 2006). Klumpp and Griffiths (1994) hypothesized that the delayed onset of sexual maturity allows *T. gigas* to allocate energy into growth for an extended period of early development, which may in part explain its large size in comparison to other giant clam species. The reproductive season of *T. gigas* varies with location (see Table 1). In Australia, the optimal reproductive season is restricted to a short summer season (Braley, 1988b), and in Palau, there is evidence that *T. gigas* can reproduce year-round (Heslinga et al., 1984). *T. gigas* may also follow a lunar spawning cycle, as Beckvar (1981) found that many spawning events took place on or near a new moon in the afternoon on a rising tide.

*T. gigas* can release approximately 500 million eggs on average in a single spawning event (Crawford et al., 1986). On one occasion, Lucas (1994) estimated that a single large individual shed nearly a billion eggs in a holding tank. However, as with other species of giant clams, high rates of early mortality result in very low levels of natural recruitment despite such high fecundity (Beckvar, 1981; Braley, 1988a; Pearson & Munro, 1991). According to Lucas (1994), *T. gigas* may have one of the lowest levels of recruit survival in the animal kingdom, with most studies estimating that less than 1% of fertilized eggs survive larval development (Jameson, 1976; Fitt et al., 1984; Mies, Scozzafave, et al., 2017).

#### 4.4.1.4 Feeding and Nutrition

For *T. gigas*, size plays a key role in determining the relative contributions of autotrophic and heterotrophic nutrition. Smaller *T. gigas* (~4 cm) can to utilize rapid rate suspension feeding to provide up to 65% of the total carbon needed for respiration and growth, while larger clams (16-17 cm) may only acquire about a third of carbon from suspension feeding (Klumpp et al., 1992). Similarly, suspension feeding and other non-autotrophic processes decline in significance as a source of nitrogen with increasing clam size (Hawkins & Klumpp, 1995). Even during periods of limited irradiance, the total contribution of nitrogen acquired as ammonium via zooxanthellae exceeds that from ingested particles (Hawkins & Klumpp, 1995). Larger adults are likely able to satisfy all respiratory requirements of carbon and nitrogen via autotrophy, and based on a comparison of four giant clam species, *T. gigas* was found to exhibit the highest photosynthetic efficiency compared to *H. hippopus*, *T. squamosa*, and *T. crocea* (Fisher et al., 1985; Klumpp & Griffiths, 1994).

Interestingly, although the relative nutritional contribution of autotrophy increases with size, photosynthetic productivity decreases in larger clams (Fisher et al., 1985). It is thought that this may be due to a reduction in symbiont density as the size of the host increases, as well as shading caused by the stacking of zooxanthellae in pillar-like microstructures within the tubular system (Rossbach, Subedi, et al., 2020) and thickening of the mantle (Fisher et al., 1985). Estimates of shading of zooxanthellae in *T. gigas* increased from negligible levels in small clams to 80% in large clams (Fisher et al., 1985).

#### 4.4.1.5 Genetics and Population Structure

*T. gigas* exhibits significant spatial structure throughout its range. Analyses of 552 samples at 7 allozyme loci indicated genetic partitioning between two major regional groups: a "central Pacific" group, including Kiribati and the Marshall Islands, and a "west Pacific" group, including the Philippines, Solomon Islands, and the Great Barrier Reef (Benzie & Williams, 1995). Within each of these regions, there is a small but significant genetic differentiation between populations ($F_{ST} = 0.04$; $P < 0.01$). There was no significant genetic difference detected between the Philippines and the Solomon Islands, nor among six reefs of the Great Barrier Reef (Benzie & Williams, 1992, 1995). Although, Evans and Jerry (2006) found small but significant genetic differentiation between two of the more distant reefs within the north-central Great Barrier based on inter-simple sequence repeat (ISSR) nuclear markers and a smaller subset of samples (N = 78). As is mentioned in **Section 2.6**, compared to nuclear and mitochondrial markers, allozyme data are thought to underestimate genetic variation; thus, the pattern of genetic partitioning discussed above likely represents the minimal spatial structure for this species.

Limited westward genetic exchange and the subsequent genetic differentiation between the west Pacific and central Pacific groups have important implications for conserving the genetic diversity of *T. gigas*. Benzie and Williams (1995) showed that the main pathways of gene flow did not follow known major surface currents, which Benzie and Williams (1997) later interpreted as evidence that "other mechanisms dominate present-day dispersal, or that [the observed patterns] reflect past connectivity which present-day dispersal along major surface currents has not altered over thousands of years."

Similar to *T. derasa*, *T. gigas* exhibits regional differences in the degree of genetic variation. Based on the analysis of 8 allozyme loci in 393 samples, Benzie and Williams (1992) reported mean heterozygosity values of 0.221-0.250 across 6 populations of *T. gigas* on the Great Barrier Reef. Likewise, using a smaller subset of 78 individuals from the Great Barrier Reef, Evans and Jerry (2006) reported mean heterozygosity values between 0.28 and 0.34, based on the analysis of 4 ISSR nuclear markers. In a broader geographic comparison using 7 allozyme loci in 552 individuals across the Indo-Pacific, Benzie and Williams (1995) found that genetic diversity (based on the percentage of polymorphic loci and mean number of alleles per locus ($N_a$)) was lowest in the Philippines (57.1%; $N_a = 2$), Marshall Islands (71.4%; $N_a = 2.3$), and Kiribati (57.1%; $N_a = 2.3$), and highest in the Solomon Islands (85.7%; $N_a = 2.4$-$2.7$) and the Great Barrier Reef (100%; $N_a = 2.9$).

### 4.4.2 Abundance, Density, and Population Status

Below, we synthesize the best available scientific and commercial information to assess the likely status of *T. gigas* in each country, territory, or region where it has been observed or reintroduced. The status and abundance trends in each location are summarized in Table 16 and displayed in Figure 27 below.

***Christmas Island; Cocos (Keeling) Islands – LOCALLY EXTINCT***

According to Neo et al. (2017), *T. gigas* was last recorded in Christmas Islands in 1932, but has not been observed since. Similarly, two specimens of *T. gigas* were found in the Cocos (Keeling) Islands in 2001, but recent surveys in 2014 "conclusively identified only [*T. maxima*], with no sightings of [*T. derasa* or *T. gigas*]" (Neo et al., 2017). According to Hourston (2010), one or two *T. gigas* had been present in the lagoon of South Cocos Atoll, but were later harvested for a local celebratory feast. Based on these reports, it is likely that *T. gigas* is locally extinct from these locations.

### ***India – RARE***

There are unconfirmed reports of *T. gigas* in the Andaman and Nicobar Islands (Apte et al., 2010), but in most available reports, *T. gigas* is not listed as a species observed in these areas. It is likely that *T. gigas* is extremely rare or extinct in India.

### ***China – LOCALLY EXTINCT***

*T. gigas* was considered plentiful near the Hainan region in the late 1950s, but extensive harvest for its adductor muscles and shells to supply the intense local demand led to severe population loss. *T. gigas* has not been observed since the late 1990s.

### ***Japan – RARE***

*T. gigas* populations were reportedly threatened in the Ryukyu Archipelago in the early 1980s as a result of over-exploitation, leading S. Wells et al. (1983) to predict that giant clams in the area "could disappear within ten years." According to Neo et al. (2017), there have been no recent records of *T. gigas* in Japan, and no specimens were found by Neo et al. (2019) in their subsequent surveys around Okinawa-jima Island in the Ryukyu Archipelago. It is likely that this species is extremely rare or extinct in Japan.

### ***Taiwan – LOCALLY EXTINCT***

*T. gigas* has not been recorded in Taiwan for over three decades and is likely locally extinct (Neo et al., 2017).

### ***South China Sea – RARE***

According to Zhang et al. (2020), *T. gigas* can be found along the coasts of the South China Sea; however, high demand for their shells to supply the handicraft industry in the Hainan region has led to widespread exploitation. Harvesting of dead *T. gigas* shells remains common in the area, and live clams are harvested whenever found. Because of this over-exploitation, Gomez (2015) noted that *T. gigas* is now "virtually extinct" in the center of the South China Sea, including the Paracels, the Macclesfield Banks, and the Spratlys.

### ***Indonesia – RARE***

Quantitative survey data are sparse, but most available studies report *T. gigas* to be extremely rare throughout much of Indonesia as a result of over-exploitation (Munro, 1993a; S. Wells, 1997; Neo et al., 2017). S. Wells (1997) reported that *T. gigas* was extinct from eastern Sumatra and Java, while Pasaribu (1988, citing Usher (1984)) stated that the species had been eliminated from western Indonesia. Two surveys in the Manado region and the waters of Kei Kecil in southeast Maluku recorded only one individual, respectively, within survey areas of 0.2 and 2.25 ha (C. Yusuf et al., 2009; Hernawan, 2010). More recently, Triandiza et al. (2019) did not observe any *T. gigas* in the Kei Kecil region in a survey area of 0.25 ha. Eliata et al. (2003) also did not record any *T. gigas* in a survey conducted near Pari Island, and only 4 *T. gigas* were observed within a 1 ha survey area near Cenderwasih Bay, Papua (Tapilatu et al., 2021). In Raja

Ampat, a region that is recognized as one of the few remaining bastions of giant clams in Indonesia, Wakum et al. (2017) recorded 14 individuals in a total survey area of 0.15 ha, which equates to 93.3 ind ha$^{-1}$. Thus, while we consider *T. gigas* to be extremely rare throughout most of Indonesia, there may be few remaining sites where the species occurs in somewhat higher abundance.

### *Malaysia – RARE*

According to Neo et al. (2017), over-exploitation has significantly reduced *T. gigas* populations in Malaysia, and the species can now be found only in the Sabah region of eastern Malaysia. However, two reports (Shau-Hwai & Yasin, 2003; Craig et al., 2011) considered *T. gigas* "extinct or virtually extinct" in Malaysia. Similarly, Munro (1993a) described remaining populations in Malaysia as "relic stocks," adding that "in most cases it appears that these stocks are for all practical purposes extinct because of the wide dispersal of the survivors—which renders successful fertilization unlikely." L. K. Lee et al. (2022) did not observe any *T. gigas* across 13 sites (1.12 ha) in Perhentian Marine Park off the eastern coast of peninsular Malaysia. Based on these reports, we consider *T. gigas* to be locally extinct in Malaysia.

### *Philippines – RARE*

According to Villanoy et al. (1988), "local extinctions of *T. gigas* […] are already widespread in the Philippines and the last strongholds of these giant clams are in the waters around the Sulu Archipelago and Southern Palawan." More recently, using a combination of field reports, key informants, and field visits, Mecha and Dolorosa (2020) documented only 29 live *T. gigas* specimens throughout the Palawan region, including Puerto Princesa City, Tubbataha Reefs Natural Park, Cagayancillo, and Coron. As an indication of how rare the species is in this region, some of the clams are promoted as tourist destinations by local resorts. Mecha and Dolorosa (2020) also describe the lack of success of *T. gigas* restocking efforts in the Palawan region, noting that in Silaqui Island and Hundred Islands National Park, two sites with the largest restock population of *T. gigas* (Gomez & Mingoa-Licuanan, 2006), only two recruits had been observed in 2017 (Cabaitan & Conaco, 2017). Lebata-Ramos et al. (2010) also reported that living *T. gigas* were absent from Carbin Reef in the central Philippines, but the presence of dead shells was indicative of its past presence in the area.

Similar to *T. derasa*, Gonzales et al. (2014) reported exceptionally high densities of *T. gigas* at Meara Island (150 ind ha$^{-1}$) in Honda Bay, Palawan, but the data used to reach these estimates are not clear and appear to be based on only five belt transects and two quadrats, or a total survey area of less than 0.1 ha. The majority of reports and available survey data suggest that *T. gigas* is extremely rare throughout most of the Philippines, and that there are very few remaining sites where the species may occur in substantial numbers (Gomez & Alcala, 1988; Gomez & Mingoa-Licuanan, 2006; Juinio et al., 1989; Villanoy et al., 1988).

### *Singapore – LOCALLY EXTINCT*

According to Neo and Todd (2013), *T. gigas* is "presumed nationally extinct" in Singapore, meaning it has not been found alive for more than 50 years.

### *Thailand – LOCALLY EXTINCT*

*T. gigas* has not been recorded within Thai waters for at least a century; although, Neo et al. (2017) report that shells of this species were found at Surin Islands and Racha Yai in 1998. *T. gigas* is likely locally extinct in Thailand.

### *Australia – FREQUENT (Great Barrier Reef); RARE (NW Islands)*

The Great Barrier Reef in Australia is generally considered to have large, healthy stocks of giant clams relative to most other areas in their range (Neo et al., 2017; S. Wells, 1997); although, recent surveys and quantitative estimates of abundance and population density are quite scarce. Pearson and Munro (1991) tracked the survival of *T. derasa* and *T. gigas* at Michaelmas Reef from 1978 to 1985. A total of 1,166 *T. gigas* individuals were recorded in 1978, which decreased to 1,120 in 1980-81 and 764 individuals by 1985 (431.9, 414.8, and 283 ind $ha^{-1}$, respectively). This included 55 recruits observed in 1980-81 and 54 recruits in 1985. The authors could not confirm the cause of the mortality between 1981 and 1985, but hypothesized that it may have been a result of disease, illegal harvest, or possibly a change in environmental conditions. Braley (1987a, 1987b) recorded *T. gigas* population densities as high as 56 ind $ha^{-1}$, with numerous sites across 817 km of the Great Barrier Reef hosting populations of *T. gigas* at densities greater than 10 ind $ha^{-1}$. Braley (1987a) noted that *T. gigas* was present on 36 of 57 randomly chosen survey sites, and 17 of 19 sites chosen specifically because of known giant clam populations. High densities were found in the Cairns, Cooktown, and Escape Reefs transects, while no living *T. gigas* were observed south of 19ºS. Relatively low population density was observed at Coringa-Herald Nature Reserve, an offshore reef in the Coral Sea, with only 15 individuals recorded within a 15.4-ha survey area (Ceccarelli et al., 2009).

Follow-up data for five sites in the far northern Great Barrier (near Lizard Island, Rachel Carson Reef, and Michaelmas Cay) indicate that four of five surveyed populations experienced declines between 1982-84 and 2007-09 (Braley, 2023). Focusing on the three largest sites with the largest populations (28-208 individuals recorded within a 0.55-0.73 ha survey area), population abundance decreased at two sites by 22.8% and 54.1% (Palfrey South Channel and Rachel Carson Reef West, respectively) and increased by 16.2% at the Watson’s Bay site. The Watson’s Bay and Palfrey South Channel sites were then revisited again in 2017. The Watson’s Bay population showed continued growth in 2017, reaching a total increase of 52.9% compared to 1984. The Palfrey South Channel population showed considerable recovery between 2007 and 2017, yielding a total decrease in abundance of only 2.5% compared to 1984. Despite the negative trend in some areas, population density at all five surveyed sites remained very high in 2007-09 relative to other areas of the species’ range (49.9 to 591.7 ind $ha^{-1}$) and at one site showed evidence of natural recovery by 2017. Analysis of size class distributions revealed “moderate but steady recruitment” on average, although it varied by site (Braley, 2023). The author suggested that this variation may be due to differences in settlement habitat quality (*e.g.*, differences in coral cover), or perhaps differences in water residence time. For example, in areas of greater seawater exchange, spawned larvae may be flushed out of the area before they reach settlement competency, whereas lagoonal habitats with longer residence time may retain larvae long enough for them to settle locally. The virtually undisturbed state of these populations suggests that the trends observed may be characteristic of natural fluctuations in population demographics at these sites, reflecting the sporadic nature of giant clam reproduction and recruitment more generally.

*T. gigas* can also be found in the islands of NW Australia. Skewes et al. (1999) reported population densities ranging from 1.2 ind $ha^{-1}$ at Ashmore Reef to 13.5 ind $ha^{-1}$ at N Scott Reef. More recently, Rees et al. (2003) encountered 49 individuals within a 9.7-ha survey area at Ashmore Reef and 79 individuals within a 23.2-ha survey area at Mermaid Reef. No *T. gigas* were observed within an 18-ha survey area at Cartier Reef.

### *New Caledonia – LOCALLY EXTINCT*

*T. gigas* is considered to be extinct in New Caledonia and is only known from fossil records in the country (S. Wells, 1997; Kinch & Teitelbaum, 2010; UNEP-WCMC, 2011; Neo et al., 2017).

### *Papua New Guinea – RARE*

According to S. Wells (1997), *T. gigas* is "locally rare, especially on nearshore reefs or near main towns" due to extensive harvest. Similarly, Ledua et al. (1996) estimated that approximately 98% of *T. gigas* in the Milne Bay Province had been lost since the early 1960s. A survey conducted in 1996 by the South Pacific Commission and the Papua New Guinea National Fisheries Authority at the Engineer and Conflict Islands (offshore of Milne Bay Province) found that *T. gigas* occurred at a density of 0.4 ind $ha^{-1}$ (Kinch, 2003). Two years later, a stock assessment spanning 1,126 sites throughout the Milne Bay Province found that average population density of *T. gigas* in the region was 0.8 ind $ha^{-1}$, which the authors estimated was equivalent to a total abundance of 394,061 (±133.5%) in the region (Skewes et al., 2003). More recently, Pinca et al. (2010) recorded 30 individuals at an average population density of 3.84 ind $ha^{-1}$ in Papua New Guinea; although, the population density specifically at stations where *T. gigas* was present was estimated to be 71.8 ind $ha^{-1}$, suggesting that the distribution of remaining individuals is patchy. We consider *T. gigas* to be extremely rare on average in Papua New Guinea, but based on this data, there may be few remaining sites where abundance is relatively high.

### *Solomon Islands – RARE*

The Solomon Islands were once considered to support abundant populations of *T. gigas*, but longstanding subsistence harvest and illegal exports severely depleted the population numbers (Munro, 1994). According to Govan et al. (1988), *T. gigas* could be found throughout the Solomon Islands, but is generally rare in areas of high human population density and high fishing pressure. *T. gigas* also experienced a mass mortality event in 1992, beginning in the eastern Solomon Islands and subsequently spreading westerly across the archipelago over a period of months (Lucas, 1994). S. Wells (1997) suggested that *T. gigas* may have been abundant in some areas of the Solomon Islands, but we could not find any quantitative data to support this conclusion. For this reason, and given the continuing high subsistence demand for giant clams throughout the Solomon Islands, it is likely that *T. gigas* is rare on average throughout the Solomon Islands.

### *Republic of Kiribati – RARE*

Based on a survey of giant clam stocks in the Abaiang, Abemama, Maiana, and Tarawa Atolls in the central Gilbert Islands group, Munro (1988b) found that the average density of *T. gigas* at Abemama Atoll was 2.16 ind $ha^{-1}$, while the other atolls had significantly lower densities. The greatest densities recorded at two sites in Abemama Atoll averaged only 4.8 ind ha$^{-1}$. Additionally, Taniera (1988) found that *T. gigas* was absent in the Line and Phoenix Island groups. Although we could not find more recent survey data, based on the available data, we find it likely that *T. gigas* is rare in Kiribati.

### *Marshall Islands – RARE*

Some have considered the Marshall Islands to be one of the centers of abundance for *T. gigas* (Munro, 1989); although, S. Wells (1997) reported the species to be depleted in some areas. According to anecdotal reports, *T. gigas* occurs at relatively high abundance in the uninhabited Ailinginae Atoll, but very few individuals were recorded in Namu Atoll, and in Mili and Rongelap Atolls (Beger & Pinca, 2003; Beger et al., 2008). No *T. gigas* were observed in Majuro Atoll (Beger et al., 2008). Pinca et al. (2010) recorded only nine individuals across more than 25 ha of survey area in the Marshall Islands. Thus, despite one report suggesting that the abundance of *T. gigas* is high in Ailinginae Atoll, the lack of supporting quantitative data, as well as several reports indicating that the species' abundance is very low throughout the other atolls, lead us to conclude that *T. gigas* is likely rare on average in the Marshall Islands.

### *Palau – RARE*

Early surveys of giant clam abundance in Palau were focused on Helen Reef, a remote atoll in the Western Caroline Islands, and documented the impacts of an intensive illegal harvesting operation by Taiwanese fishing vessels in the early 1970s. In 1972, prior to the poaching, Hester and Jones (1974) recorded 82 *T. gigas* within a survey area of 4.4 ha and estimated the total standing stock at Helen Reef to be approximately 49,800 individuals. Following the poaching, two follow-up studies revealed that *T. gigas* and *T. derasa* had suffered significant population declines. In 1975 and 1976, only four individuals were encountered in each of two surveys of 2.5 and 1.5 ha, respectively (Bryan & McConnell, 1975; Hirschberger, 1980). For comparison, estimates of *T. gigas* population density were 18.6, 1.6, and 2.7 ind ha$^{-1}$ in 1972, 1975, and 1976, respectively. We could not find more recent surveys of Helen Reef, so the current status of this population is unknown. In a broad survey of finfish and invertebrate communities throughout Palau, Pinca et al. (2010) recorded 28 *T. gigas* and estimated an average population density of 1.1 ind ha$^{-1}$ (18.0 ind ha$^{-1}$ at stations where the species was present). Additionally, an opportunistic survey of giant clam populations conducted by Rehm et al. (2022) documented 11 *T. gigas* individuals within a survey area of 0.33 ha, which equates to a population density of 33.3 ind ha$^{-1}$. However, the author has cautioned that the surveys specifically targeted areas where giant clams are known to occur, so the observations likely overestimate the average population density throughout Palau (L. Rehm, pers. comm., May 26, 2022).

As was discussed in relation to *H. hippopus*, Palau is home to the PMDC, which is one of the first and most prolific institutions to succeed at the mass cultivation of giant clams. Cultured clams have been translocated as broodstock to many other countries for the purpose of natural stock enhancement (Kinch & Teitelbaum, 2010). Cultured clams from the PMDC are also often distributed to local clam farmers to be later sold into the commercial meat and aquarium industry (Neo et al., 2017). According to Kinch and Teitelbaum (2010), the PMDC uses some portion of the cultured 'seedlings' to restock 23 conservation areas throughout Palau; although, according to L. Rehm (pers. comm., May 26, 2022), these efforts have primarily focused on *H. hippopus* and *T. derasa*. Overall, while the available survey data suggest that there may be few areas of relatively high *T. gigas* abundance, we are hesitant to rely too heavily on the estimate of Rehm et al. (2022) given the caveat that the surveys specifically targeted areas where giant clams were known to occur. For this reason, we place more weight on the estimate of Pinca et al. (2010) and conclude that *T. gigas* is likely rare in Palau.

### ***Tuvalu – LOCALLY EXTINCT***

It is unclear if *T. gigas* ever occurred in Tuvalu, but all available reports consider the species to be absent in this location (Munro, 1993a; S. Wells, 1997; CITES, 2004a). In a survey of giant clams in Tuvalu, Pinca et al. (2010) did not encounter any *T. gigas*.

### ***Fiji, FSM, Guam, CNMI, Tonga, and Vanuatu - REINTRODUCED***

Many authors consider *T. gigas* to be locally extinct in Fiji (Kinch, 2009; Ledua, 1993; Munro, 1989; Neo et al., 2017; Raymakers et al., 2003; S. Wells, 1997); although, it is possible that the species was never common in the first place given its location near the southeastern edge of the species' range. Lewis et al. (1988) reported that the last known live specimen was collected in the mid-1970s. In FSM, S. Wells (1997) considered *T. gigas* to be "extinct in known areas, although it could be present in remote atolls." Others have more recently reported the species to be extinct in the whole of FSM (Raymakers et al., 2003; Teitelbaum & Friedman, 2008; Kinch & Teitelbaum, 2010). *T. gigas* is also considered to be extinct in Guam, CNMI, and Tonga (Munro, 1994; Neo et al., 2017; Pinca et al., 2010; UNEP-WCMC, 2011; S. Wells, 1997). In Vanuatu, Zann and Ayling (1988) conducted surveys on 29 sites across 13 islands, and found *T. gigas* to be "either very rare or absent." Likewise, no live *T. gigas* were observed in the Paunangisu and Moso villages, in the Uri and Uripiv Islands, or in the Maskelyne Archipelago (Friedman et al., 2008).

Cultured stocks of *T. gigas* from other regions have been reintroduced to each of these locations, primarily as broodstock from Palau and Australia (Munro, 1994; Teitelbaum & Friedman, 2008). However, we could not find any information as to the success or failure of these initiatives, and we find it likely that *T. gigas* remains extremely rare or absent from Fiji, FSM, Guam, CNMI, Tonga, and Vanuatu.

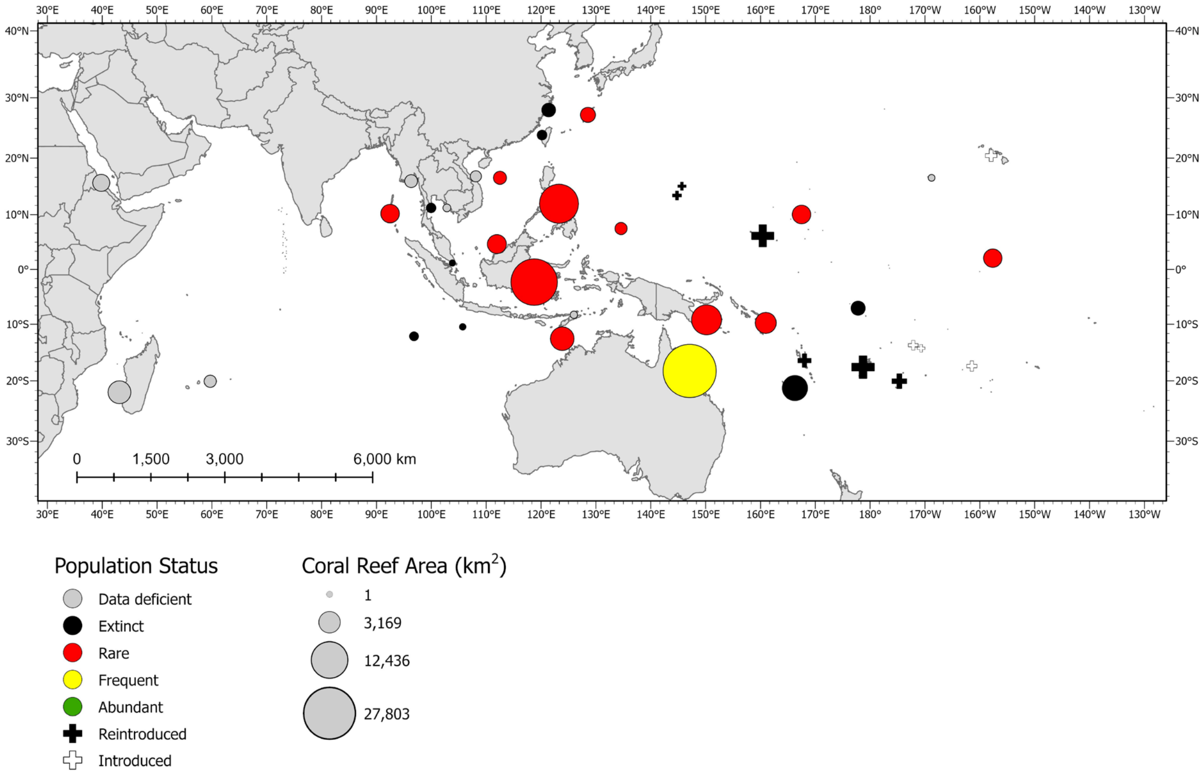

**Figure 27.** Qualitative abundance estimates for *T. gigas* based on reported occurrence and survey data. Points are located at the approximate centroid of survey sites within each country, territory, or region from which data has been included in the abundance assessment. Abundance categories are based on those used by Neo et al. (2017), but have been revised as follows: Abundant (>100 ind ha$^{-1}$), Frequent (10-100 ind ha$^{-1}$), Rare (<10 ind ha$^{-1}$), Extinct, Introduced, Reintroduced (i.e., locations where the species was reportedly extirpated in the past but there have since been efforts to restore populations using cultured specimens; current presence/abundance may not be known), and Data Deficient (i.e., locations where reports of species occurrence have not been confirmed). The size of the points reflects the total estimated area of coral reefs within each location based on data compiled by the UN Environment World Conservation Monitoring Centre and the WorldFish Centre (UNEP-WCMC et al., 2021), increasing on a square-root scale. It is used here to roughly approximate the relative amount of giant clam habitat. However, the accuracy of this approximation likely varies between species based on their habitat preferences.

**Table 16.** Summary of *T. gigas* population status across its geographic range (adapted from Table 4 in Neo et al. 2017 and supplemented with more recent information where available). Species abundance categories are as follows: Abundant (>100 ind ha$^{-1}$); Frequent (10-100 ind ha$^{-1}$); Rare (<10 ind ha$^{-1}$). Where the status has been revised from Neo et al. (2017), footnotes provide the data sources or rationale used to reach the respective status determinations.

| **Location** | **Status** | **Notes** |
|---|---|---|
| ***Indian Ocean*** | | |
| Australia (NW islands) | Rare | Population densities ranging from 1.2 ind ha$^{-1}$ at Ashmore Reef to 13.5 ind ha$^{-1}$ at N Scott Reef. |
| Christmas Island | Locally extinct | *T. gigas* was last recorded in 1932 with no recent sightings. |
| Cocos (Keeling) Islands | Locally extinct | Presence not verified in recent surveys. Artisanal harvest appears to be directly responsible for the severe depletion of giant clam stocks. Only two *T. gigas* were found in 2001 and recent surveys in 2014 did not record any *T. gigas*. The recreational harvest of giant clams is currently unregulated. |
| India | Rare | Recent presence of *T. gigas* is unconfirmed. |
| ***East Asia*** | | |
| China | Locally extinct | Stocks considered plentiful in the late 1950s, but sharply declined by the 1970s due to extensive harvest. *T. gigas* is sought after for its adductor muscles and shells. By the late 1990s, *T. gigas* could no longer be found in coastal waters of China. |
| Japan | Rare | Numbers have declined severely due to heavy exploitation and there have been no recent records of *T. gigas*. |
| Taiwan | Locally extinct | Reduction in population is attributed to overharvesting for shells by tourist divers and locals. *T. gigas* has not been recorded over the last three decades. |
| South China Sea | Rare | Harvesting of dead *T. gigas* shells remains common for shell trade. |
| ***South Asia*** | | |
| Cambodia | Data deficient | Reported subsistence consumption by locals, and harvest for commercial trade has depleted stocks. |
| East Timor | Data deficient | Single photograph reported in Neo et al. (2017), but otherwise presence is unconfirmed. |
| Indonesia | Rare | Presently extremely rare; demand for their meat and shells for subsistence and domestic markets remains high. |
| Malaysia | Rare | Now only found in Sabah (East Malaysia). Populations are in decline due to the combined effects of pollution, environmental degradation and harvesting for meat and shells. |
| Myanmar (Burma) | Data deficient | Relict *T. gigas* populations. |
| Philippines | Rare | Populations are reportedly restricted to the Palawan region in extremely low abundance. Subsistence harvest is widespread and the commercial exploitation for international shell trade has led to severe population loss. Restocking efforts have shown little success to date. |
| Singapore | Locally extinct | Exploited since the mid-19th century, particularly for the curio trade. Subsequently, coastal development |

| Location | Status | Notes |
|---|---|---|
| | | projects led to habitat degradation and pollution, which further impacted the already low stocks. |
| Thailand | Locally extinct | Has not been observed alive within Thai waters for at least a century, but their shells were found washed up on beaches at Surin Islands and at Racha Yai in 1998. |
| Vietnam | Data deficient | A pair of *T. gigas* shells were observed at Ha Long Bay (M.L. Neo, pers. obs.). |
| ***Pacific Ocean*** | | |
| Australia<br>(Great Barrier Reef) | Frequent | Populations are considered healthy with some almost pristine examples. Illegal poaching may still occur in some areas, but strict harvest bans and effective surveillance measures have largely minimized the threat of overutilization in Australian waters. |
| CNMI | Reintroduced | Reintroduced from Palau (1986, 1991). Heavy exploitation resulted in local extinction. No commercial fishery, but subsistence harvesting of clams through reef gleaning. |
| FSM | Reintroduced | Primarily collected as a food source and shells for curios. Previous commercial exploitation of wild stocks was mainly for adductor muscles sold to Southeast Asian markets. As a result, wild stock numbers have severely declined. |
| Fiji | Reintroduced | Thought to be locally extinct, possibly due to previous overexploitation of stocks. Reintroduced in 1986, 1987 and 1990 from Australia. |
| Guam | Reintroduced[1] | Reintroduced from Palau in 1982. Giant clams are highly valued as a local delicacy. |
| Johnston Atoll (U.S. PRIA) | Data deficient[2] | A single *T. gigas* was reportedly observed just outside the lagoon of Johnston Atoll. It is unclear if this is a natural occurrence of *T. gigas*, if it may have been introduced artificially, or if the specimen was misidentified. |
| Marshall Islands | Rare | Populations were severely reduced by illegal fishing, and are still widely harvested for subsistence use. Anecdotal accounts suggest relatively abundant *T. gigas* populations in several areas, but no quantitative estimates; giant clams are generally heavily exploited near population centers. |
| New Caledonia | Locally extinct | Only found as fossils. |
| Papua New Guinea | Rare | Available estimates indicate significant population loss and low abundance in Milne Bay Province. Local extinctions at particular sites and generally low stocks are attributed to unsustainable commercial fishing practices, poaching, and longstanding exploitation. |
| Solomon Islands | Rare | Was formerly widespread and abundant but is now considered depleted. Harvesting for export, with large-scale commercial harvesting, took place in the 1970s to 1980s, and subsistence use was considered a |

| Location | Status | Notes |
|---|---|---|
| | | major cause of population declines. In areas of high population density, there is still high fishing pressure. |
| Republic of Kiribati | Rare | Available surveys from 1988 indicate that abundance is very low. Giant clams are traditionally an important food and shell resource; subsistence fishing is a heavy pressure on clam stocks. |
| Palau | Rare | Populations have been in decline since 1972, but no recent population surveys. |
| Tonga | Reintroduced | Locally extinct since the mid-1970s; reintroduced in 1989–1991. Tongans highly favor giant clam meat, with clams harvested for both subsistence and commercial purposes. |
| Tuvalu | Locally extinct | Shells have been observed but no recent live specimens. |
| Vanuatu | Reintroduced | Reintroduced in 1998 and 2006. |
| ***Non-native locations where T. gigas has been introduced*** | | |
| American Samoa | Introduced | Cultured at a government hatchery with the goal of establishing local farms to produce meat for local market. There were 6 lagoon nursery sites and 25 small-scale farms in operation as of September 1995. However, according to Marra-Biggs et al. (2022), the "stocks were harvested prior to reproduction and appear to be functionally extirpated." |
| Cook Islands | Introduced | Introduced from Australia in 1991. No information on current status. |
| Hawaii (U.S.) | Introduced[3] | *T. gigas* was introduced as part of a commercial venture to explore the potential for culturing marine invertebrates for the aquarium trade. |
| Samoa | Introduced | Samoa Department of Marine and Wildlife Resources (DMWR) has successfully introduced cultured specimens. *T. gigas* has also been translocated at various times since 1988 from various Pacific Island countries or territories. |

Sources:
[1] Heslinga et al. (1984)
[2] Brainard et al. (2019)
[3] Heslinga (1996); mislabeled in Neo et al. (2017)

Of the 32 locations where *T. gigas* has been recorded naturally, the best available data suggest that the species is frequent in only 1 location, rare in 12 locations, locally extinct or reintroduced after local extinction in 14 locations, and data deficient (likely exceptionally rare or extinct) in 5 locations. We also note several countries that are known to have imported *T. gigas* broodstock for the purposes of reintroduction following local extinction or to introduce the species to locations outside its historical range. However, we were not able to find any information regarding the success of these efforts in establishing sustainable populations of *T. gigas* in the wild. As is discussed previously with respect to *H. hippopus*, there is extensive literature addressing the challenges of giant clam mariculture generally, and particularly for the purpose of stock replenishment (Gomez & Mingoa-Licuanan, 2006; Mies, Scozzafave, et al., 2017; Munro, 1993a; Teitelbaum & Friedman, 2008). The primary barrier to these efforts is the exceptionally low survival rate of giant clam larvae post-fertilization compounded by the time and resources required to protect juveniles once they have been outplanted and before they reach a size at which they are sufficiently protected from predation. Despite the numerous restocking and translocation programs known to exist throughout the Indo-Pacific, most are reported to still be operating on a small or pilot scale with only partial success, and further intensification of giant clam mariculture is, in most cases, considered economically unviable (Teitelbaum & Friedman, 2008; UNEP-WCMC, 2012). Thus, without further information regarding the success of efforts specific to *T. gigas*, we consider the species to be locally extinct (or exceptionally rare) even in locations where it has reportedly been reintroduced.

### 4.4.3 Threats to *Tridacna gigas*

#### 4.4.3.1 Destruction, Modification or Curtailment of Habitat or Range

Compared to other giant clam species, *T. gigas* is somewhat of a habitat-generalist and can be found in a variety of habitats, including high- and low-islands, atoll lagoons, and fringing reefs. In determining the habitat characteristics most relevant to the survival and productivity of *T. gigas*, two extensive surveys of *T. gigas* distribution and habitat preference throughout the Great Barrier Reef are especially informative (Braley, 1987a, 1987b). The two studies showed that the species was most common on inshore reefs and could be found among *Acropora* spp. or within other hard coral communities, on hard reef substrata, or on bare sand. Other studies have also reported the versatility of *T. gigas* habitat preference. In Palau, *T. gigas* was observed living both inside shallow lagoons and on outer reefs in areas of turbulent surf action (Hardy & Hardy, 1969). Hester and Jones (1974) reported finding large individuals in an “extensive sand flat with occasional small coral patches” at the remote Helen Reef. In western Indonesia, Hernawan (2010) observed *T. gigas* mostly living in the rubble of dead branching corals, while Tapilatu et al. (2021) found four specimens, all living within the coral reef framework. Additionally, Govan et al. (1988) describe the species’ broad habitat use in the Solomon Islands, suggesting that it can be found “on coral rubble and embedded in living coral, on all types of reefs, between the intertidal and depths to 15 m.” The species was found to be more abundant in outer reef areas than inside the lagoon. Based on these reports, we consider the threat of habitat destruction, modification, or curtailment with respect to both nearshore coastal areas and coral reefs more generally.

Each of these threats has been addressed previously in this review in relation to *H. hippopus* (i.e., impacts of human development on nearshore habitat) and *T. derasa* (i.e., potential impacts of climate change on coral reef habitat). With respect to *H. hippopus*, we found that the threat of nearshore habitat destruction or modification due to coastal development is geographically heterogeneous and is likely most severe adjacent to highly populated areas of the central Indo-Pacific (e.g., Indonesia, Malaysia, Papua New Guinea, the Philippines). The threat is likely less severe throughout the Pacific island nations, where human development has been less intense, and in Australia, where water quality management has historically been more effective. Based on this information, we concluded that this threat is unlikely to contribute significantly to long-term or near future risk of extinction by itself, but there is some concern that it may, in combination with other VP descriptors or threats (**Low** risk). Given the similarity between the geographic range of *H. hippopus* and *T. gigas*, we find this conclusion to be directly applicable to the threat assessment for *T. gigas*. However, without specific examples of the impact of sedimentation on *T. gigas* populations in these areas, we have **Low** confidence in this conclusion. Please refer to **Section 4.1.3.1** for further detail related to this threat.

We previously concluded with respect to *T. derasa* and the potential impact of climate change on the suitability of coral reef habitat that, while there is extensive evidence that the combined effects of ocean warming and acidification will reduce living coral cover and significantly alter the calcification balance on coral reefs over the foreseeable future, there is very little research specifically evaluating the extent to which giant clams rely on these habitat characteristics for their survival and productivity. Without more information on the direct association between substrate rugosity and juvenile survival, we cannot estimate with any confidence the degree to which declines in reef rugosity may threaten the persistence of giant clams. As is discussed previously in relation to *T. derasa*, if *T. gigas* is sensitive to reductions in net ecosystem calcification and reef rugosity, the projected climate change-related impacts to coral reefs would likely pose a **Moderate** extinction risk to the species. We would expect decreased larval recruitment and juvenile survival across broad portions of its range. These early life stages are already known to suffer exceptionally high mortality rates naturally, and any further reduction in productivity would threaten the viability of remaining populations, which would contribute significantly to the long-term extinction risk for this species. However, based on the preceding discussion, our confidence in this assessment is **Low**. Please refer to **Section 4.3.3.1** for further detail related to this threat.

### 4.4.3.2 Overutilization

The threat of overutilization with respect to *T. gigas* is very similar to that of *T. derasa*. Because of the large size of both species, they were often targeted simultaneously and to a similar degree by harvesters and traders of giant clam meat, including the wide-ranging Taiwanese poachers. If anything, *T. gigas* was likely more highly desired simply due to its larger size; certain Pacific island communities attribute unique significance to *T. gigas* as a cultural symbol and place high value on the species as a food item for special occasions (Hviding, 1993). The shell of *T. gigas* is also valued as a traditional resource among many coastal communities for use as basins or as personal or religious decorations (Juinio et al., 1987; Hviding, 1993; Lucas, 1994). It is also highly desired within the Tanmen shell-craft industry, which has led to its likely extirpation from the South China Sea. For these reasons, many consider *T. gigas* to be the most heavily exploited species among all giant clams (Craig et al., 2011; Mies, Scozzafave, et al., 2017; Neo et al., 2017), noting its extensive harvest in nearly every location where it has occurred. Below, we discuss the specific details of its exploitation. Much of the information is drawn from **Section 4.3.3.2** due to the similarity in threat between *T. derasa* and *T. gigas*, but all trade figures and data are specific to *T. gigas* wherever possible.

As with *T. derasa*, the most widespread and significant threat to *T. gigas* until the 1980s was related to the intense demand for giant clam meat in Southeast Asia, and primarily Taiwan. As is discussed in **Section 3.3.2**, Taiwanese vessels traveled across the Indo-Pacific in search of the adductor muscle of *T. gigas* and *T. derasa*, often entering the waters of other nations illegally and concentrating their efforts on remote or uninhabited islands and reefs where giant clam stocks had previously been untouched and where surveillance was limited. First-hand reports of

Taiwanese poaching include areas of the Philippines, Indonesia, Papua New Guinea, Australia (the Great Barrier Reef), FSM, the Solomon Islands, Palau, Fiji, Kiribati, and the Marshall Islands. During the peak of the market, some estimate that harvest likely reached 100 tons of adductor muscle per year, and according to Dawson (1986), "it seems certain […] that the total illegal harvest of giant clams over the twenty-odd years that such activities have occurred in the region can safely be measured in the millions." On the Great Barrier Reef alone, 22 Taiwanese fishing vessels were apprehended between 1969 and 1976 while illegally poaching giant clams. According to Pearson (1977), a total of 72 tons of clam meat was confiscated across the 22 ships, which is equivalent to over 500,000 clams. Pearson (1977) estimated that the ships likely represented only 10% of the fleet operating in the Great Barrier Reef at the time. Because the giant clam meat was typically removed from its shell for storage on the vessels, the proportion of *T. gigas* and *T. derasa* in the harvest is unknown, but most accounts suggest that both species were targeted relatively equally.

Poaching by long-range Taiwanese vessels peaked in the mid-1970s and gradually declined during the 1980s as the extension of exclusive economic zones, improved surveillance of reef areas, boat seizures, and depleted stocks made the fishery less profitable. In addition, growing pressure from many Indo-Pacific nations forced the Taiwanese government to take stricter action against giant clam harvesters, and beginning in 1986, all requests for approval of Taiwanese involvement in any clam fishing activities were rejected by the government. However, the continued demand for giant clam meat in Taiwan incentivized the development of legal commercial fisheries for export of *T. gigas* and *T. derasa* throughout the Indo-Pacific. It was estimated that imports of adductor muscle to Taiwan from these newly formed fisheries totaled approximately 30-40 tons in 1987 and 1988 (Tisdell & Chen, 1994). The fisheries, however, rapidly depleted local stocks and were in most cases short-lived, typically being shut down by local authorities in the span of a few years. Two specific examples are discussed in **Section 4.3.3.2**, including a fishery in Papua New Guinea, which was estimated to harvest 149-166 tons of adductor muscle between 1983 and 2000, and in Fiji, where a single ship was permitted to harvest giant clams in 1985 with minimal restrictions. Although, due to the low abundance of *T. gigas* in Fiji, Lewis et al. (1988) estimated that approximately 95% of the harvest in this case was of *T. derasa*.

By the early 1990s, pervasive stock depletions of both *T. gigas* and *T. derasa* across the Indo-Pacific severely limited Taiwanese imports of giant clam meat (Tisdell & Chen, 1994). Many nations also instituted various regulations on the sale and export of giant clam meat (see Appendix 1), further limiting the commercial supply of giant clam meat. While we can rely to some extent on CITES annual reports to provide insight into the recent trends in international trade, many countries have limited their reporting of trade involving giant clam meat to the family or genus level. Although, based on the history of the giant clam meat trade discussed above, the majority of trade reported as Tridacninae spp. is likely from *T. gigas* and *T. derasa*, but the relative contributions of each species is unknown.

Since 2010, the principal exporters of giant clam meat include Tonga (11,712 kg, 107 specimens), Cook Islands (2,205 kg), Marshall Islands (1,161 kg, 6,644 specimens), FSM (954 kg, 2,535 specimens), and Kiribati (950 kg). All trade from these nations was reported to be of wild-caught specimens or to have been seized or confiscated by the importing nation, presumably due to improper or missing CITES export permits. Assuming that the source of the exports is reported accurately, it is not likely that these numbers represent *T. gigas*, as this species is either rare or not known to occur naturally in these locations (see **Section 4.4.2**). Several additional CITES reports since 2010 specifically indicate smaller export volumes of wild-harvested *T. gigas* meat from Tonga (152 kg), Kiribati (16.4 kg), and the Cook Islands (9.5 kg), but again, it is unclear where this meat is being harvested and our confidence in this reporting is low.

In some locations, *T. gigas* is also highly valued in the giant clam shell and shell-craft industry. As discussed in **Section 3.2.2**, the Philippines has historically operated as the largest exporter of giant clam shells, accounting for over 95% of the global recorded exports of giant clam shell products since 1983. The two *Hippopus* spp. and *T. squamosa* were the most frequently exploited species for ornamental purposes and handicrafts, and *T. gigas* was most frequently used for basins (Lucas, 1994). Given the scale of the giant clam shell industry in the Philippines during the 1970s and 1980s, which reached millions of shells exported per year at its peak, it is likely that harvest of *T. gigas* shells contributed significantly to the extirpation of the species throughout much of the Philippines.

Since 2010, CITES annual reports indicate that *T. gigas* shells and shell-craft have also been exported in significant quantities from Indonesia, Fiji, the Solomon Islands, and Tonga. As recently as 2018, Indonesia exported 59,000 shells of wild-caught *T. gigas* to China. Given the reportedly low abundance of *T. gigas* throughout Indonesia, it is not clear where these shells may have originated. There have been several recent seizures of giant clam shell stockpiles in the Philippines, and in one interview with ABS-CBN News (2021), the executive director of the Palawan Council for Sustainable Development claimed that giant clam shells are being smuggled from the Philippines to other areas of Southeast Asia. We cannot confirm if the reported export from Indonesia is related to this activity, but regardless, it highlights that the market for giant clam shells remains active and threatens the remaining *T. gigas* populations in this region. Unlike *T. derasa*, very little (< 1%) of the reported exports of *T. gigas* shells since 2010 are of maricultured origin.

Lastly, while there is some evidence that *T. gigas* has been a popular species in the growing aquarium industry, Craig et al. (2011) found that international imports of this species for the aquarium trade declined from nearly 4,000 individuals in 2005 to less than 1,000 in 2009. The authors suggested that this is likely related to the low abundance of *T. gigas* in many of the countries most involved in the marine aquarium industry, which has limited the supply. Since 2010, CITES records indicate that the primary exporters of live *T. gigas* specimens have been Fiji (2,218 wild-caught), FSM (1,021 cultured), the Philippines (500 wild-caught), and Kiribati (240 cultured). The accuracy of reporting from Fiji is unclear, as it directly contradicts several reports that *T. gigas* no longer occurs in the wild in Fiji (Kinch, 2009; Ledua, 1993; Munro, 1989; Neo et al., 2017; Raymakers et al., 2003; S. Wells, 1997).

Overall, the best available information indicates that *T. gigas* has been widely exploited for many years for its meat, shells, and as a popular aquarium specimen. It is highly valued as a subsistence food source in virtually all Pacific island nations where it occurs and, for over two decades, was subject to an intense commercial demand for its adductor muscle primarily from consumers in Taiwan. Widespread harvest and poaching of *T. gigas* to supply this commercial market caused severe, documented population losses throughout the majority of its range. The commercial demand for giant clam meat (including *T. gigas*) began to decline by the end of the 1980s due to the low abundance of remaining populations in conjunction with stricter harvest regulations and improved enforcement. However, due to its traditional importance as a food source in many cultures, subsistence harvest of *T. gigas* continues in most locations throughout its range, which may lead to further population decline and likely prevents any substantial recovery of depleted populations.

The Great Barrier Reef and outlying islands of NW Australia are, for the most part, an exception to the range-wide trends for this species. Northern areas of the Great Barrier Reef were subjected to widespread poaching of *T. gigas* in the 1970s and 1980s, but improved surveillance of Australian fishing grounds and stronger enforcement of harvest bans have reduced the poaching pressure considerably (although, Neo et al. (2017) note that poaching of giant clams on the Great Barrier Reef does still occur). As a result, harvest of *T. gigas* in Australian waters since the 1980s has likely been minimal. Recent quantitative estimates of abundance are scarce, but based on past surveys and the strong protective measures in place, most experts consider the Great Barrier Reef to have relatively large, stable populations of giant clams, including *T. gigas* (Neo et al., 2017; S. Wells, 1997).

Therefore, we consider the severe impact of past harvest on species abundance range-wide alongside reports of ongoing subsistence and commercial exploitation in most locations except Australia. Based on this information, we conclude with **Medium** confidence that overexploitation of *T. gigas* contributes significantly to the species' long-term risk of extinction, but because the threat is relatively low in Australia, where *T. gigas* populations are reportedly healthy, this factor likely does not constitute a danger of extinction in the near future (**Moderate** risk).

#### 4.4.3.3 Disease or Predation

Aside from the information discussed in **Section 3.3** with respect to giant clams generally, information regarding the prevalence of disease or predation for *T. gigas* is limited. The most concerning disease in giant clams is caused by the protozoan *Perkinsus* spp., which is ubiquitous across all ocean basins. Perkinsosis, also known as pinched-mantle syndrome, is typically fatal and no treatment has been developed for afflicted clams (Reavill et al., 2009). In a survey of giant clams at Lizard Island on the Great Barrier Reef, 7 of 32 *T. gigas* individuals were infected by *Perkinsus* spp., including all 4 moribund specimens that were sampled (Goggin & Lester, 1987); however, the authors did not provide any information on associated mortality rates. All sampled specimens were visually healthy, suggesting that some level of infection by *Perkinsus* spp. may be a natural condition in giant clams. Between July 1985 and January 1987, a mortality event occurred on the fringing reefs of Lizard Island on the Great Barrier Reef in which 57% of *T. gigas* at Watson's Bay and 63% at Palfrey and South Islands died (Alder & Braley, 1989). The authors were not able to identify a cause for the mortality event. They reported the presence of *Perkinsus* spp. and an unidentified unicellular organism found in the tissue of some of the dead specimens; however, dead individuals did not exhibit the common symptoms of Perkinsosis. Based on the best available information, disease does not appear to be a factor contributing significantly to the extinction risk for *T. gigas*. Additionally, we found no information indicating predation is a factor influencing extinction risk for *T. gigas*.

#### 4.4.3.4 Inadequacy of Existing Regulatory Mechanisms

There are various regulatory mechanisms and management measures in place throughout the range of *T. gigas* (see Appendix 1). Many implement protections for giant clams broadly (including *T. gigas*) and generally fall into four categories: a complete ban on harvest, a ban on harvest for commercial sale or export, bag limits, and minimum size restrictions.

Seven countries and territories within the range of *T. gigas* have instituted a total ban on the harvest of giant clams (or *T. gigas* specifically) for any purpose—these include Australia, Indonesia, the Philippines, Malaysia, India, China, Taiwan, and Japan. Eight countries and territories within the range of *T. gigas* have instituted a ban on the commercial export of giant clams—these include Fiji, Papua New Guinea, Solomon Islands, Vanuatu, Kiribati, Palau, Guam, and Tonga. The sale of giant clams in local markets is still permitted in Papua New Guinea, Vanuatu, Palau, and Tonga. In the Northern Province of New Caledonia, professional fishers are restricted to harvesting five giant clams per day, and all others are restricted to two per day. In the Southern Province, there is a maximum bag limit of 40 kg and for tourists there is a limit of 3 shells weighing up to 3 kg. In Guam, harvesting for subsistence use is limited to no more than three clams per day with minimum size restriction of 18 cm. There are no known local or regional regulations in place for the protection of *T. gigas* in the Marshall Islands, CNMI, Tuvalu, or within the South China Sea.

In general, the threat of inadequate regulatory mechanisms with respect to *T. gigas* is very similar to that of *T. derasa*. Thus, rather than reiterate the details of the threat here, we summarize the conclusions below, and refer the reader to **Section 4.3.3.4** for further details.

Concerning local and regional regulations, despite widespread commercial export bans, the capacity for enforcing existing regulations is often limited, existing regulations in many locations do not restrict continued subsistence harvest, and illegal harvest and trade of giant clams (particularly for the shell trade) continues to occur. As with the threat of overexploitation, we also consider the effectiveness of regulation in Australia, which has largely been successful at reducing harvest pressure and protecting some of the few remaining healthy populations of *T. gigas*. For these reasons, we conclude with **Medium** confidence that inadequacy of existing local/regional regulations poses a **Moderate** risk to the extinction of *T. gigas* (i.e., the factor contributes significantly to long-term risk of extinction, but does not in itself constitute a danger of extinction in the near future).

In terms of international regulations, *T. gigas* was listed under Appendix II of CITES in 1985 to regulate international trade in any of its parts (shells, tissues, alive or dead). Of the 33 locations listed within the range of *T. gigas*, all are Parties to the treaty, except FSM, Kiribati, the Marshall Islands, and Tuvalu; Palau also took reservations on all species of giant clams. However, while most countries and territories within the range of *T. gigas* are regulated under the provisions of CITES, the associated protections to *T. gigas* were clearly not adequate to prevent widespread population loss and local extirpations from many of the same locations. Additionally, as recently as 2018, Indonesia exported 59,000 wild-harvested *T. gigas* shells to China despite the reportedly low abundance of *T. gigas* throughout the region. Unlike *T. derasa*, the majority of the reported trade since 2010 is of wild-caught specimens, suggesting that mariculture has not played a significant role in diverting harvest away from wild populations. For these reasons, we conclude with **Medium** confidence that the inadequacy of international trade regulations poses a **Moderate** risk to the extinction of *T. gigas* (i.e., the factor contributes significantly to the long-term risk of extinction, but does not in itself constitute a danger of extinction in the near future).

With respect to international climate change regulations, we conclude in **Section 3.4.2** that current implementation of domestic and international climate regulations is insufficient to mitigate the cumulative threat of climate change to giant clam habitat and physiology generally. This conclusion is relevant to *T. gigas* based on its documented habitat preference for offshore coral reefs and atolls. The inadequacy of international climate change regulations will likely exacerbate the impacts of ocean warming and acidification on coral reefs, which may affect the quality of *T. gigas* habitat. This leads us to a conclusion of **Low** risk, such that this factor is unlikely to contribute significantly to the long-term or near future extinction risk by itself, but may do so in combination with other threats. However, our uncertainty regarding the degree to which *T. gigas* is reliant on coral reefs (see **Section 4.4.3.5**) leaves us with **Low** confidence in this assessment.

#### 4.4.3.5 Other Natural or Manmade Factors

***Climate Change***

In addition to the information presented in **Section 3.5.1** regarding the effects of climate change on giant clams generally, the best available information suggests that *T. gigas* is sensitive to ocean warming at multiple life stages. Enricuso et al. (2019), for example, found that higher water temperatures (33ºC, compared to 28ºC and 30ºC) promote rapid progression through early development, but result in lower overall survival as a consequence of abnormal development and reduced post-settlement survival. Lucas et al. (1989) found that juvenile growth rate increased during summer months as temperatures rose to 30ºC, but higher temperatures (33-35ºC) can lead to bleaching (Estacion & Braley, 1988). As is discussed in **Section 3.5.1**, widespread bleaching of giant clams was observed in the central Great Barrier Reef, Australia in 1997-1998, when elevated water temperatures in conjunction with low salinity caused 8,000 of 9,000 surveyed *T. gigas* to experience varying levels of bleaching (Leggat, pers. comm., cited in Buck et al., 2002; Leggat et al., 2003). Some individuals suffered a complete loss of symbionts, while others were only affected in the central part or at the margins of the mantle tissue (Grice, 1999). A follow-up experiment designed to replicate the environmental conditions during this event demonstrated that elevated temperatures combined with high solar irradiance induced a consistent bleaching response in *T. gigas* (Buck et al., 2002). However, according to Leggat et al. (2003), of 6,300 *T. gigas* that bleached at Orpheus Island, Australia in 1998, over 95% completely recovered after 8 months, indicating that *T. gigas* can withstand the acute stress of bleaching if anomalous conditions are not prolonged. According to R.D. Braley (pers. comm., September 25, 2019), an increase in temperature on the Great Barrier Reef may actually extend the range of *T. gigas* southward to areas where winter temperatures are currently too low for *T. gigas* to survive.

Based on this information, we conclude with **Medium** confidence that ocean warming may, in combination with other VP descriptors or threats, contribute to the long-term extinction risk of *T. gigas*, but is unlikely a significant threat on its own (**Low** risk).

We were not able to find any additional information regarding the potential impacts of ocean acidification on *T. gigas* beyond what is provided in **Section 3.5.2**. As discussed in **Section 3.5.2**, the available information regarding the effects of ocean acidification on giant clams more broadly is limited and inconclusive.

### *Land-Based Sources of Pollution*

As discussed in **Section 3.5.3**, sedimentation, salinity fluctuations, nutrient enrichment, and elevated heavy metal concentrations represent environmental conditions that giant clams may experience following heavy rains, particularly near coastlines that have been altered by human development. Given its common occurrence in shallow nearshore habitats, *T. gigas* is likely highly exposed to these threats. However, beyond what is provided in **Section 3.5.3** related to giant clams generally, there is limited information regarding the impacts of these factors on *T. gigas* specifically. Blidberg (2004) found that *T. gigas* larvae suffered a significant reduction in survival under low salinity conditions (25‰ and 20‰), an effect that was exacerbated by exposure to a low dose of copper (2.5 µg $Cu^{2+}$ $L^{-1}$). Similarly, Maboloc et al. (2014) reported that lower salinity (18‰ and 25‰ vs. 35‰) reduced the feeding capacity of juvenile *T. gigas* due to alteration of the digestive membrane. Lastly, exposure to a moderate dose of copper independent of salinity changes was found to lower photosynthetic efficiency in *T. gigas* (Elfwing et al., 2002), while nitrogen enrichment has been shown to enhance the shell and tissue growth (Belda, Cuff, et al., 1993; Belda, Lucas, et al., 1993).

Based on this information, it is clear that *T. gigas* is sensitive to salinity fluctuations and elevated heavy metal concentrations, two conditions that giant clams may experience in nearshore areas adjacent to river outflows and coastlines that have been altered by human development. This threat is heterogeneous throughout the range of *T. gigas* and is likely most severe adjacent to highly populated areas of the central Indo-Pacific (e.g., Indonesia, Malaysia, Papua New Guinea, the Philippines). The threat is likely less severe throughout the Pacific island nations, where human development has been less intense, and in Australia, where water quality management has historically been more effective. Given this geographic heterogeneity, we conclude that this threat is unlikely to contribute significantly to the long-term or near future risk of extinction by itself, but there is some concern that it may, in combination with other VP descriptors or threats (**Low** risk, **Medium** confidence).

### *Stochastic Events*

While stochastic events such as extreme weather and mass mortalities of unknown cause may result in severe population loss in localized areas, these threats inherently cannot be predicted with any precision (**Low** confidence). However, as is mentioned in **Section 4.3.3.3**, mass mortality of *T. gigas* has previously been observed on the Great Barrier Reef. Alder and Braley (1989) reported that sporadic mortality events between 1985 and 1987 led to a loss of 57% and 63% of *T. gigas* populations at two fringing reefs near Lizard Island. According to the authors, deaths were not restricted to a particular size class, and the distribution of mortality appeared random. Histopathology revealed one unidentified unicellular organism in six of eight specimens that were examined, but the exact cause (or causes) of the mortality was not confirmed. Because the Great Barrier Reef is reported to be one of the few remaining locations with relatively healthy populations of *T. gigas*, we conclude that the threat of stochastic mortality may, in combination with other VP factors or threats, contribute significantly to the species' long-term risk of extinction, but is unlikely a significant threat on its own (**Low** risk).

**Table 17.** Summary of the threats analysis for *T. gigas* and associated confidence ratings.

| 4(a)(1) Factor | Threat | Contribution to Species' Risk of Extinction | Confidence Rating |
|---|---|---|---|
| **Habitat destruction, modification, or curtailment** | *Coastal development* | Low | Low |
| | *Climate change impacts to coral reefs* | Moderate | Low |
| **Overutilization** | | Moderate | Medium |
| **Disease or Predation** | | Very Low | Low |
| **Inadequacy of existing regulatory mechanisms** | *National and local regulations on harvest* | Moderate | Medium |
| | *Regulations on international trade* | Moderate | Medium |
| | *Regulations on climate change* | Low | Low |
| **Other natural or manmade factors affecting the species' continued existence** | *Physiological impacts of climate change* | Low | Medium |
| | *Land-based sources of pollution* | Low | Medium |
| | *Stochastic events* | Low | Low |

## 4.4.4 Demographic Risk Assessment

### *Abundance*

Because there are no global abundance estimates for *T. gigas*, we rely on the qualitative estimates of population status provided in Table 16, which are based on the best available survey data from all countries, territories, and regions where the species has been recorded. These data indicate that *T. gigas* has suffered significant population declines to the extent that the species is considered "rare," extirpated or has been reintroduced after extirpation, or data deficient (likely exceptionally rare or extinct) in 31 of the 32 locations throughout its range. In locations where it is considered "rare," this means that available survey data indicate an average population density that is likely less than 10 ind $ha^{-1}$ on average, or approximately one individual spaced approximately every 30 m. For broadcast spawning organisms like *T. gigas*, which rely on the external fertilization of gametes, the implications of such sparse distribution on reproduction can be significant. As discussed in **Section 4.1.2**, Braley (1984) observed that 70% of nearest spawning *T. gigas* were found within 9 m of one another, while only 13% were between 20-30 m of one another. These findings suggest that individuals in "rare" populations are less likely to spawn in synchrony and as a result are likely to experience infrequent, sporadic reproductive success. This negative relationship between population density and productivity, known as the Allee effect, can cause further reductions in population abundance and put "rare" populations of *T. gigas* at greater risk of extinction.

Furthermore, the impact of subsistence harvest can be particularly consequential in locations where the abundance of the species is low, because it can reduce the number of reproducing adults and, in effect, constrain the recovery potential of the population. In every location where *T. gigas* is considered rare, except for NW Australia, subsistence harvest is still permitted, or existing harvest bans, such as in Indonesia and the Philippines, have largely been ineffective at eliminating illegal harvest. In these locations, the low abundance of *T. gigas* exacerbates the extinction risk associated with continued harvest pressure.

Of the 32 locations where *T. gigas* has been recorded, the only location where the species is considered "frequent" is the Great Barrier Reef in Australia, indicating population density estimates that are between 10 and 100 ind $ha^{-1}$ on average. Populations on the Great Barrier Reef are protected by a total ban on the harvest of giant clams. While there is very little recent survey data on the abundance of *T. gigas* on the Great Barrier Reef, the data that are available, as well as anecdotal reports, commonly suggest that populations of giant clams (including *T. gigas*) in Australia are healthy relative to other areas of the Indo-Pacific. Additionally, regulations have reportedly been effective at preventing illegal harvest, minimizing the risk of overexploitation of giant clams in Australian waters. Notably, data from two unpublished surveys indicate that *T. gigas* experienced significant population declines (15.7-54.0%) at four of five sites in the far northern Great Barrier Reef between 1982-85 and 2007-09 (R. D. Braley, reported in Neo et al., 2017), but has since recovered to some extent a decade later (R. D. Braley, *in review*). It is possible that the decline is part of a natural fluctuation in population demographics at these sites, reflecting the sporadic nature of giant clam reproduction and recruitment more generally. Population densities at these sites remain high relative to most other areas of the species' range, and according to R.D. Braley (pers. comm., October 19, 2022) and Neo et al. (2017), giant clams on the Great Barrier Reef exist in a "natural" and "virtually undisturbed" state.

Overall, the abundance of *T. gigas* is greatly reduced from historical levels throughout its range, leaving only one location where the species is not considered rare or locally extinct. A long-term population decline has been documented at several sites in the northern Great Barrier Reef, but it is unclear if the decline reflects a natural fluctuation or a more chronic risk of recruitment failure, and populations are still considered healthy on the Great Barrier Reef. Except for in Australia, *T. gigas* is at continued risk of overexploitation in all locations throughout its range due to ongoing subsistence harvest and inadequate regulation. Based on this information, we find that the abundance of remaining populations contributes significantly to the species' long-term risk of extinction, but does not in itself constitute a danger of extinction in the near future (**Moderate** risk, **Medium** confidence).

### *Productivity*

Despite exceptionally high fecundity, there is substantial evidence that low recruitment success and high mortality rates during early development lead to low productivity in most species of giant clams. Pearson and Munro (1991) provided rigorous data on natural recruitment rates for a relatively abundant population of *T. gigas* at Michaelmas Reef, Australia between 1978 and 1985. They showed that recruitment into the population was very low in the decade preceding the survey and remained low over the survey period. They concluded that the majority of the population was likely obtained from a single spawning event in the late 1950s, suggesting that the dense population of *T. gigas* may be the result of a transient phenomenon, rather than the average conditions at that reef. A similar pattern was observed in early 1987 when a major recruitment of *T. gigas* was discovered at Lizard Island—127 juveniles estimated to be 12-18 months old were found in a 1.2 ha survey area, which at the time was considered the largest population of *T. gigas* ever recorded (Braley, 1988a).

As is discussed in **Section 2.3**, these observations align with the concept of 'sweepstakes' reproduction, or the chance matching of reproductive activity with oceanographic conditions conducive to spawning, fertilization, dispersal, and successful recruitment. This can lead to sporadic waves of recruitment depending on the prevailing oceanographic conditions and can be especially sensitive to changes in population density. In particular, low abundance and low population density severely reduce the likelihood of reproductive success by minimizing the chance of fertilization. In effect, this negative relationship between abundance and productivity, known as the Allee effect, can significantly hinder the recovery potential of populations that have been reduced by overexploitation.

Based on this information, we conclude that the low natural productivity of giant clams as well as the negative correlation of productivity with low abundance contributes significantly to the long-term extinction risk for *T. gigas*, but likely does not in itself constitute a danger of extinction in the near future (**Moderate** risk, **Medium** confidence).

### *Spatial Distribution/Connectivity*

As described in **Section 4.4.1.5**, the best available data suggest that *T. gigas* exhibits significant spatial structure between two major regional groups: a "central Pacific" group, including Kiribati and the Marshall Islands, and a "west Pacific" group, including the Philippines, Solomon Islands, and the Great Barrier Reef. Without more refined genetic analyses, it is impossible to determine if this spatial structure reflects past or current demographic processes among these regions. However, given the low abundance of this species throughout most of its historic range and the low productivity of giant clams generally, as well as the short pelagic larval duration (~6-14 days), it is likely that larval dispersal between distant locations is very low, perhaps particularly so between these two regions. The apparent relatedness between *T. gigas* populations on the Great Barrier Reef, the Philippines, and the Solomon Islands indicates that these populations, and perhaps others in the western Pacific region, have been connected to some degree historically. This is relevant, as the Great Barrier Reef represents the only remaining healthy population of *T. gigas*, which could in theory provide larval subsidy to nearby locations that are demographically connected. However, it is important to reiterate that the available genetic data reflect processes that manifest on an evolutionary time scale (i.e., thousands of years or more). Without more information, it is not possible to determine the extent to which migration between these and other nearby locations occurs currently or how the migration rate may change on an ecological time scale (i.e., tens to hundreds of years), which is more relevant to the recovery of the species.

Overall, based on the best available population genetic data and considering the abundance distribution of *T. gigas*, there is some concern that limited connectivity, particularly between the Great Barrier Reef and other locations in the central Pacific, may contribute to the species' long-term extinction risk, but likely does not contribute to the long-term or near future extinction risk by itself (**Low** risk, **Low** confidence).

***Genetic Diversity***

As described in **Section 4.4.1.5**, *T. gigas* exhibits regional differences in the degree of genetic variation. Heterozygosity values on the Great Barrier Reef based on allozymes and ISSR nuclear markers were estimated to be 0.22-0.25 and 0.28-0.34, respectively. Comparing across several locations in the Indo-Pacific, Benzie and Williams (1995) found that genetic diversity (based on the percentage of polymorphic loci and mean number of alleles per locus ($N_a$)) was lowest in the Philippines (57.1%; $N_a = 2$), Marshall Islands (71.4%; $N_a = 2.3$), and Kiribati (57.1%; $N_a = 2.3$), and highest in the Solomon Islands (85.7%; $N_a = 2.4$-$2.7$) and the Great Barrier Reef (100%; $N_a = 2.9$). Based on this information, we find it unlikely that this factor contributes significantly to the extinction risk by itself or in combination with other factors (**Very Low** risk, **Low** confidence).

**Table 18.** Summary of the demographic risk analysis for *T. gigas* and associated confidence ratings.

| **Demographic Risk Factor** | **Contribution to Species' Risk of Extinction** | **Confidence Rating** |
|---|---|---|
| **Abundance** | Moderate | Medium |
| **Productivity** | Moderate | Medium |
| **Spatial Distribution/Connectivity** | Low | Low |
| **Genetic Diversity** | Very Low | Low |

## 4.4.5 Overall Extinction Risk Assessment

Guided by the results of the demographic risk analysis and threats assessment above, we analyzed the overall risk of extinction of *T. gigas* throughout its range. In this process, we considered the best available scientific and commercial information regarding *T. gigas* from all locations of the species' range and analyzed the collective condition of these populations to assess the species' overall extinction risk. We determined that the most critical demographic risks to *T. gigas* are the low abundance and negative trajectory of populations throughout the majority of its range, compounded by low natural productivity and likely the Allee effect.

Additionally, our threats assessment revealed that the past and present overutilization and associated inadequacy of existing regulatory mechanisms at the local level contribute most significantly to the extinction risk of this species. Continued harvest of *T. gigas* primarily for subsistence purposes and illegally by poachers, combined with the species' low productivity will likely drive further population declines and prevent any substantial population recovery in locations where it is rare.

The best available scientific and commercial information indicates that very few abundant populations of *T. gigas* remain and occur exclusively on the Great Barrier Reef in Australia. Extensive surveys of *T. gigas* on the Great Barrier Reef from the 1980s (Braley, 1987a, 1987b) recorded population densities as high as 56 ind $ha^{-1}$, with numerous sites hosting populations of *T. gigas* at densities greater than 10 ind $ha^{-1}$ interspersed among other sites of low density or where the species was completely absent. Braley (1987a) noted that *T. gigas* was present on 36 of 57 (63%) randomly chosen survey sites, and 17 of 19 (89%) sites chosen specifically because of known giant clam populations. High population densities were found in the Cairns, Cooktown, and Escape Reefs transects, while no living *T. gigas* were observed south of 19ºS. Based on the species' patchy distribution and the observed pattern of recruitment, Braley (1988) found it likely that the scattered reefs hosting abundant populations of clams (mostly in the south) may dominate recruit production for the rest of the Great Barrier Reef.

As was discussed in the extinction risk analysis for *T. derasa* (see **Section 4.3.5**), Taiwanese vessels poached giant clams (primarily *T. gigas* and *T. gigas*) from the Great Barrier Reef during the 1960s and 1970s. However, strict enforcement of a harvest ban on giant clams resulted in the virtual cessation of illegal giant clam activities in Australia by the mid-1980s. Based on this information and because giant clams are not harvested for subsistence in Australia, we find it likely that the population density estimates provided by Braley (1987a, 1987b) generally represent the current status of *T. gigas* on the Great Barrier Reef. This is further supported by more recent reviews and reports (bin Othman et al., 2010; Neo et al., 2017; S. Wells, 1997) suggesting that *T. gigas* is still relatively abundant on much of the Great Barrier Reef. According to R.D. Braley (pers. comm., October 19, 2022) and Neo et al. (2017), the distribution of *T. gigas* on the Great Barrier Reef represents a "natural" and "virtually undisturbed" state for the species.

In contrast to the Great Barrier Reef, where *T. gigas* populations are relatively healthy, the best available data indicate that, at the other 31 of 32 locations across the range with documented occurrences of this species, extensive exploitation for past commercial trade, ongoing subsistence use, and illegal harvest have driven *T. gigas* to exceptionally low abundance, and in many cases, local extinction (this applies to all locations except NW Australia, where the low abundance cannot be attributed to harvest). The continued threat of overexploitation, the possible future threat of habitat degradation due to climate change impacts on coral reefs, and the demographic risks outlined in **Section 4.4.4** place the continued persistence of *T. gigas* in these locations in question. However, because *T. gigas* populations on the Great Barrier Reef are relatively abundant, even described as "virtually untouched," and the enforcement of strict harvest bans has effectively minimized the threat of overexploitation in Australian waters, we cannot conclude that the species is at moderate or high risk of extinction throughout its *entire* range.

As with *T. derasa*, it is important to highlight that, although we refer to the Great Barrier Reef as only one location for the purpose of this analysis, it covers an expansive geographic area that comprises a substantial proportion of the suitable habitat within the species' range (see Figure 27). Additionally, while the future threat of habitat degradation due to climate change impacts on coral reefs may be relevant to these populations, we do not have sufficient information to confidently assess the extent to which the survival or productivity of giant clams (even those species closely associated with coral reefs, such as *T. gigas*) may be impacted by projected changes to coral reef communities in the foreseeable future (see **Section 4.4.3.1**).

### ***Significant Portion of its Range Analysis***

Under the ESA, a species warrants listing if it is in danger of extinction or likely to become so within the foreseeable future throughout all or a significant portion of its range. Thus, a species may be endangered or threatened throughout all of its range, or a species may be endangered or threatened throughout only a significant portion of its range. Having determined that *T. gigas* is not at high risk of extinction throughout all of its range, in order to inform the listing determination, we conducted an additional analysis to assess whether the species is at high risk of extinction in a "significant portion of its range"—that is, we assessed whether there is any portion of the species' range for which it is true that both (1) the portion is significant and (2) the species, in that portion, is at moderate or high risk of extinction. A joint USFWS-NMFS policy, finalized in 2014, provided the agencies' interpretation of this phrase ("SPR Policy," 79 FR 37578, July 1, 2014) and explains that, depending on the case, it might be more efficient for us to address the "significance" question or the "status" question first. Regardless of which question we choose to address first, if we reach a negative answer with respect to the first question, we do not need to evaluate the other question for that portion of the species' range.

Because we determined that the most significant threats to *T. gigas* are overexploitation and the inadequacy of existing regulatory mechanisms, we base our analysis here on the portion of the range where these threats are most severe, consistent with the approach used for both *H. hippopus* and *T. derasa* (see **Section 4.1.5** and **4.3.5**). As discussed above, several sources indicate that the early adoption of strict harvest prohibitions in Australia has been largely effective at preventing illegal harvest and minimizing the risk of overexploitation of giant clams in Australian waters. This differs considerably from reports from every other location throughout the species' range, which consistently indicate that the threat of overexploitation in combination with inadequate regulation and enforcement poses a significant extinction risk to *T. gigas*. Thus, for the purpose of this SPR analysis, we distinguish locations in Australia (i.e., the Great Barrier Reef and NW Australia) from all other locations where *T. gigas* occurs and consider them as two separate portions of the species' range.

In this case, the portion under consideration includes 29 countries and territories where the primary threat to the species is overexploitation. In all of these locations, the best available survey data, as well as qualitative descriptions of abundance, suggest that extensive commercial, subsistence, and illegal harvest has driven *T. gigas* to exceptionally low abundance, and in many cases, local extinction (see **Section 4.4.2**). Based on the demographic risks of low abundance and low productivity in this portion (see **Section 4.4.4**), and the ongoing threats overexploitation and inadequate regulatory mechanisms (see **Section 4.4.3.2** and **4.4.3.4**) in all 29 locations, we conclude that in the portion of the species' range defined as all locations outside of Australia, *T. gigas* is at **High** risk of extinction.

To evaluate whether this portion is "significant," we applied similar rationale as was used with respect to the SPR analyses for *H. hippopus* and *T. derasa* (see **Section 4.1.5** and **4.3.5**). We considered the historically high abundance of *T. gigas* in this portion of the range, as evidenced by trade statistics and the many reports of major population losses resulting from years of subsistence and commercial harvest. Additionally, as was described in relation to *H. hippopus* and *T. derasa*, it is likely that populations of *T. gigas* in this portion played an important role in maintaining genetic connectivity throughout the species' range. Given the relatively short pelagic larval phase of giant clams (~6-14 days), there is a diminishing likelihood of larval dispersal between locations at progressively greater distances. Therefore, genetic exchange between distant populations likely relied on many smaller dispersal events across the network of more closely spaced islands or habitat areas that comprise this portion of the species' range. Lastly, considering the geographic extent of this portion and the diverse habitats that it encompasses, the populations of *T. gigas* within this portion likely served as an important demographic and genetic reserve, which could facilitate recovery following localized population declines. Based on this rationale, we find that the portion of the species' range defined as all locations outside of Australia is "significant," or in other words serves a biologically important role in maintaining the long-term viability of *T. gigas*.

# 4.5 *Tridacna mbalavauna*

## 4.5.1 Life History and Ecology

### 4.5.1.1 Taxonomy and Distinctive Characteristics

At the time of Rosewater's seminal report in 1965 on the descriptions and taxonomic characters of giant clam species, *Tridacna mbalavuana* had been only formally described from fossils on Viti Levu, Fiji. However, Fijians had long known of this species occurring in local waters as 'tevoro', or devil clam. Thus, when the species was re-discovered in 1988 (Lewis & Ledua, 1988), it was subsequently described as the new species *T. tevoroa* (Lucas et al., 1991). It was not until 2000 that *T. mbalavuana* and *T. tevoroa* were re-classified as synonymous based on morphological similarities (Newman & Gomez, 2000).

*T. mbalavuana* has been hypothesized to be a transitional species between the *Hippopus* and *Tridacna* genera due to overlapping characteristics (Lucas et al., 1991; Schneider & Foighil, 1999). It has *Hippopus*-like features including the absence of a byssal gape, a mantle that does not extend over the shells, and the absence of hyaline organs (Lucas et al., 1991); however, *T. mbalavuana* looks most like *T. derasa* in appearance. It can be distinguished from *T. derasa* by its rugose mantle, prominent guard tentacles on the incurrent siphon, thinner valves, and colored patches on the shell ribbing (Neo, Eckman, et al., 2015). The shell exterior is off-white, often partly encrusted with marine growths (Figure 28). The shell interior is porcelaneous white, with a yellowish brown mantle (Kinch & Teitelbaum, 2010). It can grow to just over 50 cm long (Lewis & Ledua, 1988; Neo, Eckman, et al., 2015) with the largest specimen recorded at 56 cm (Lucas et al., 1991).

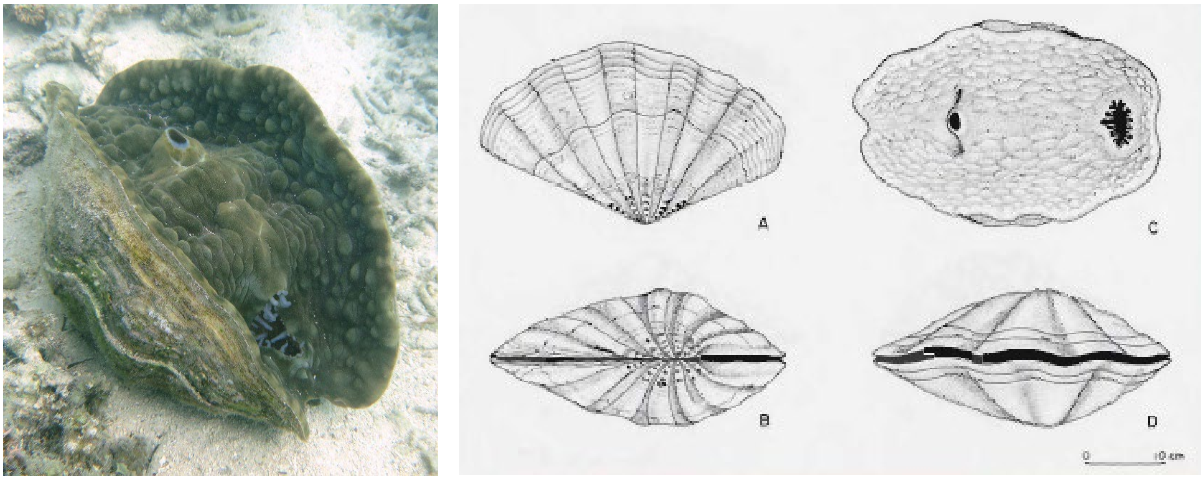

**Figure 28.** *T. mbalavuana* morphology. Photograph of *T. mbalavuana* taken in Tonga (left), and illustrations showing the lateral (A), ventral (B), mantle (C), and dorsal (D) view of a representative specimen (right). (Photo credit: James Fatherree/iNaturalist, CC BY-NC 4.0; Diagram source: Calumpong, 1992).

### 4.5.1.2 Range, Distribution, and Habitat Use

*T. mbalavuana* has one of the most restricted distributions of all the giant clam species (Figure 29). For many years, it had only been observed in Fiji and Tonga, but recent reports indicate that this species may be found in low numbers outside of these two locations. According to Kinch and Teitelbaum (2010), *T. mbalavuana* has been observed in the Loyalty Islands in New Caledonia, a report later supported by Tiavouane and Fauvelot (2016), who encountered two individuals on the northeastern barrier reef of New Caledonia after “exhaustive searches” (Neo et al., 2017). Single individuals were also reportedly observed on Lihou Reef in the Coral Sea (Ceccarelli et al., 2009) and in the Raja Ampat region of West Papua, Indonesia (Wakum et al., 2017), but neither of these reports have been further corroborated.

In Fiji, individuals are most often observed along the outer slopes of leeward reefs in the eastern Lau Islands, in very clear, oceanic water (Ledua et al., 1993). In Tonga, they are found in the northern Vava`u and Ha`apai islands. *T. mbalavuana* has a deeper depth distribution than most other giant clam species. In a study on the spawning and larval culture of *T. mbalavuana*, individuals were collected from the waters of Fiji and Tonga (Ledua et al., 1993). The mean depth of clams collected in Fiji was 27.4 m, with samples collected from depths ranging from 20 to 33 m, and all specimens were found on the leeward side of reefs and islands. Many of the clams found in Tonga were next to the edge of a sand patch and cradled against rocky outcrops, rubble or bare rock with steep slopes (Ledua et al., 1993). During a SCUBA survey in February 1992 in Ha'apai (Tonga), Ledua et al. (1993) found a considerable number of *T. mbalavuana* on live coral. About half of the clams in Tonga were found on the leeward and half on the windward side of reefs.

Overall, the spatial distribution of *T. mbalavuana* is sparse, with single individuals being found at most locations; although, groups of four individuals were seen twice and other smaller groups were seen in Tonga (Ledua et al., 1993). Lewis and Ledua (1988) noted that they observed only 1 *T. mbalavuana* for every 50 *T. derasa* individuals in the Vatoa area of Fiji. The more recent observations of the species at two sites in New Caledonia, one in the Coral Sea, and one in the Raja Ampat Islands each report just one individual per site (Ceccarelli et al., 2009; Tiavouane & Fauvelot, 2016; Wakum et al., 2017). The individual in the Coral Sea was observed at 10 m depth in a sandy bottom of the reef slope and the two in New Caledonia were at 19 m and 20 m depth and also appeared to be on sandy bottom (based on photos provided in Tiavouane & Fauvelot (2016)).

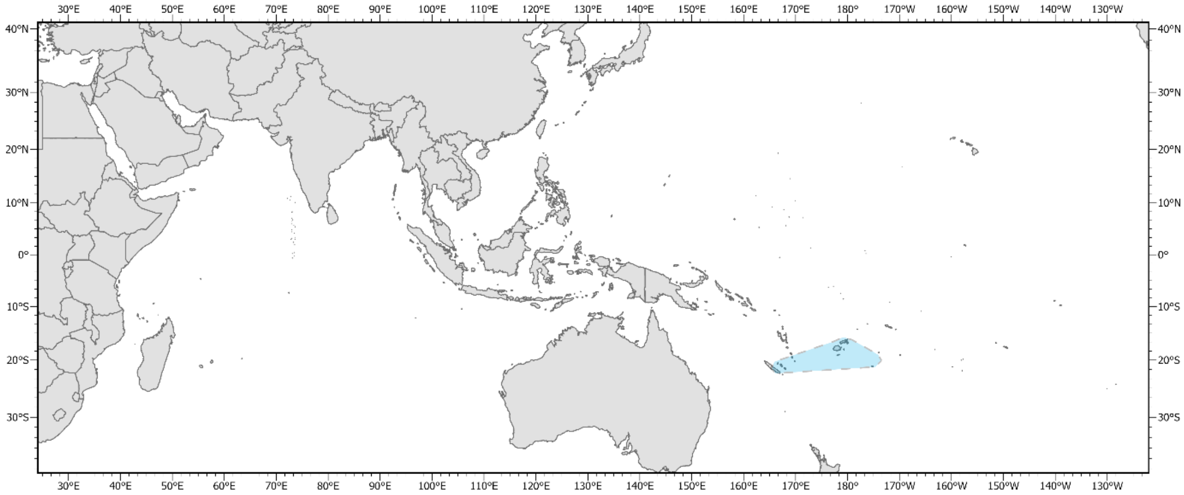

**Figure 29.** Approximate natural range of *T. mbalavuana* based on reported occurrences provided by Neo et al. (2017).

### 4.5.1.3 Reproduction and Growth

We could find only one study describing the reproduction of *T. mbalavuana*, in which Ledua et al. (1993) documented a spawning experiment at the Tonga Fisheries Department in late October 1991. The authors observed 5 of 10 clams released eggs, while 7 released sperm. They recorded 0.3% survival from fertilized eggs to the veliger stage, and 2.2% survival from veligers to juveniles for an overall survival rate of 0.08% survival from fertilized eggs to juveniles at day 90. Subsequent attempts at spawning *T. mbalavuana* in January-February 1992 did not result in any successful sperm or egg release, nor any other spawning behavior, indicating this may have been during the resting period of gametogenesis (i.e., outside of the breeding season). It is difficult to interpret these results as a reflection of natural survival rates, as the authors acknowledged that a lack of equipment for the experiment may have led to polyspermy or self-fertilization and contributed to low survival despite a high fertilization rate. The successful first spawning of *T. mbalavuana* in October indicates that this species has a breeding season that may be similar to that of *T. derasa.* Ledua et al. (1993) describe that the breeding season of *T. derasa* on the Great Barrier Reef in Australia is from late winter-early spring to early summer and virtually all individuals are spent by mid-December.

Klumpp and Lucas (1994) estimated a shell growth rate of 4.2 mm per month based on an 8-month experiment, noting this applies to clams in smaller size categories; larger-sized clams generally grow slower after the onset of sexual maturity. There are no additional reports on size at maturity or growth rate. These parameters are often reported from mariculture operations, but there have been few attempts to culture this species.

#### 4.5.1.4 Feeding and Nutrition

*T. mbalavuana* is able to function as a complete autotroph (capable of self-nourishment using photosynthesis of its symbiotic zooxanthellae) in the shallower parts of its distribution (10 to 20 m) (Klumpp & Lucas, 1994). In order to better understand how *T. mbalavuana* survives in deeper waters with less light attenuation, Klumpp and Lucas (1994) compared the nutrition of *T. mbalavuana* with *T. derasa* in Tonga, measuring rates of suspension feeding, respiration and the photosynthesis-irradiance response in clams of a wide size range (approximately 20 mm to 500 mm). Only *T. mbalavuana* significantly increased its photosynthetic efficiency with increasing depth. As such, it was able to rely on phototrophy (using light as a principle source of energy via symbiotic zooxanthellae) while at greater depths than *T. derasa*. At 28 m, *T. mbalavuana* could satisfy 91-96% of its nutritional requirements from photosynthesis, compared to *T. derasa* which could only obtain 59-62% of its requirements. Suspension feeding provided relatively little carbon to both species contributing 8-14% (depending on size) of respiratory carbon demands.

The species has several unique morphological adaptations that likely increase its photosynthetic efficiency in reduced light intensities (Lucas et al., 1991). These adaptations include a rugose mantle and an unusually wide gape of the valves, both of which increase the surface area available for zooxanthellae to absorb available light. Additionally, a paucity of iridophores (i.e., high-reflectance cells common in the mantle of giant clams) and a relatively shallow distribution of zooxanthellae in the mantle likely maximizes the availability of light to the symbionts. However, despite the increased efficiency of its photosynthetic machinery, Klumpp and Lucas (1994) estimate that, at the deep end of its depth distribution, the combination of suspension feeding and photosynthesis only provide 83% of the nutrition required to maintain growth in *T. mbalavuana*. Thus, the authors hypothesize that the species must have the capacity to access other sources of nutrition, such as dissolved organic matter, to make up the difference.

#### 4.5.1.5 Genetics and Population Structure

We were unable to find information on population structure or genetics for *T. mbalavuana.* DNA has been isolated and sequenced from several samples collected in New Caledonia, as described in Lizano and Santos (2014) and Fauvelot et al. (2022), but these studies primarily address the comparative taxonomy and phylogenetics among giant clams.

### 4.5.2 Abundance, Density, and Population Status

There is very little quantitative information available on the past or current abundance of *T. mbalavuana*. As noted above, the best available information indicates that the species is very rare and sparsely distributed where it has been observed (Ledua et al., 1993; Sone & Loto'ahea, 1995). Lewis and Ledua (1988) described an informal assessment, in which a reward was offered to residents of Vatoa Island, Fiji in 1986 for the collection of any live *T. mbalavuana* from the local waters. Of more than 300 giant clams collected around Vatoa Island, only 6 were identified as *T. mbalavuana*. Five additional specimens were reportedly collected from the area in 1988 (Lewis & Ledua, 1988), followed by another 20 in 1989, 1990, and 1991 (Ledua et al., 1993). An anecdotal account from one diver in Uiha Island, Tonga indicated that the species was significantly more abundant in shallow waters during the 1940s, and could be found in groups on sandy areas adjacent to the reef (Ledua et al., 1993). Others reported similar accounts, suggesting that the abundance of *T. mbalavuana* has declined considerably over the few decades before the study in 1988.

A rapid biological assessment in the Vava`u archipelago in Tonga in 2014 did not observe any *T. mbalavuana* individuals across 27 survey sites (Atherton et al., 2014). Additionally, we received a public comment in response to our 90-day finding detailing a research expedition in the summer of 2017 that included Tongatapu Island in Tonga where, again, no *T. mbalavuana* were observed.

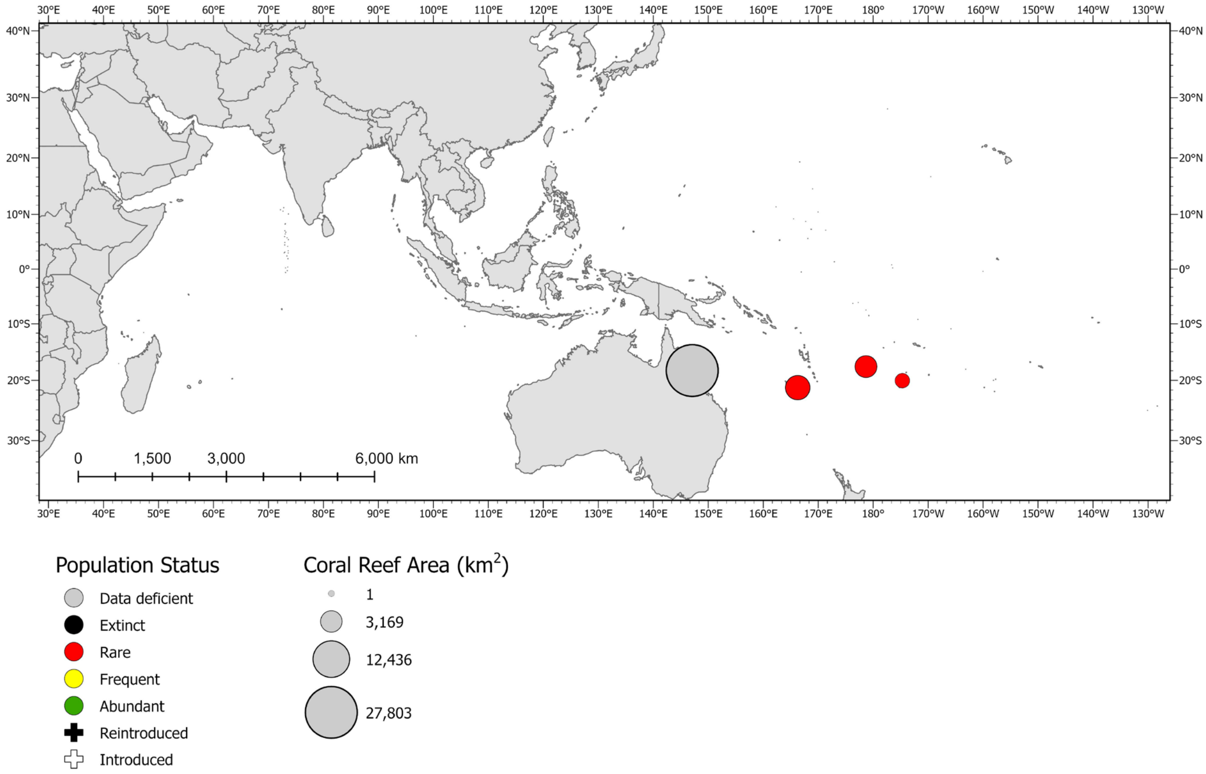

**Figure 30.** Qualitative abundance estimates for *T. mbalavuana* based on reported occurrence and survey data. Points are located at the approximate centroid of survey sites within each country, territory, or region from which data has been included in the abundance assessment. Abundance categories are based on those used by Neo et al. (2017), but have been revised as follows: Abundant (>100 ind ha$^{-1}$), Frequent (10-100 ind ha$^{-1}$), Rare (<10 ind ha$^{-1}$), Extinct, Introduced, Reintroduced (i.e., locations where the species was reportedly extirpated in the past but there have since been efforts to restore populations using cultured specimens; current presence/abundance may not be known), and Data Deficient (i.e., locations where reports of species occurrence have not been confirmed). The size of the points reflects the total estimated area of coral reefs within each location based on data compiled by the UN Environment World Conservation Monitoring Centre and the WorldFish Centre (UNEP-WCMC et al., 2021), increasing on a square-root scale. It is used here to roughly approximate the relative amount of giant clam habitat. However, the accuracy of this approximation likely varies between species based on their habitat preferences.

**Table 19.** Summary of *T. mbalavuana* population status across its geographic range (adapted from Table 4 in Neo et al. 2017 and supplemented with more recent information where available). Species abundance categories are as follows: Abundant (>100 ind $ha^{-1}$); Frequent (10-100 ind $ha^{-1}$); Rare (<10 ind $ha^{-1}$). ** indicates that the status has been revised from Neo et al. (2017) based on updated information.

| Location | Status | Notes |
|---|---|---|
| ***Pacific Ocean*** | | |
| Australia | Data deficient | Only one individual was recorded at Lihou Reef in the Coral Sea. |
| Fiji | Rare | The species is endemic here; all available information indicates that abundance is very low. |
| Indonesia | Data deficient | Unconfirmed report of one individual observed in the Raja Ampat region. |
| New Caledonia | Rare | Only three individuals were observed; one in Loyalty Islands and two on the barrier reef of Grande Terre. |
| Tonga | Rare | The species is endemic here but was not encountered during recent surveys in 2014 and 2017. A photograph of *T. mbalavuana* on iNaturalist indicates that the species was observed in 2018. |

## 4.5.3 Threats to *Tridacna mbalavuana*

### 4.5.3.1 Destruction, Modification, or Curtailment of Habitat or Range

As described above, *T. mbalavuana* occurs primarily in deep coral reef habitats, often on sandy patches adjacent to the reef slope. Thus, the most pertinent threats to this species are likely those that impact offshore coral reef habitats, and particularly those in Fiji and Tonga, where *T. mbalavuana* is most common. Widespread coral bleaching has been observed in Fiji in 2000, 2002, and 2016 following periods of anomalously high temperatures, which led to coral mortality rates exceeding 30% (Cumming et al., 2002; Hughes, Anderson, et al., 2018). Although, in one follow-up report, Sykes and Morris (2009) described the status of coral reefs in Fiji as "generally good," noting that most coral communities had recovered from the first two bleaching events by 2007. Coral reefs in Fiji are also susceptible to tropical cyclones, as was observed in February 2016 when a strong cyclone caused damage to coral reefs as far down as 30 m below the ocean surface (Mangubhai et al., 2019). According to unpublished data from H. Sykes (cited in Mangubhai et al., 2019), many reef areas remained degraded for at least 12 months, indicating the slow pace of recovery from major storm damage. There is less information regarding the status of coral reefs in Tonga; although, a recent baseline study noted that in the past decade, Tonga has experienced five severe tropical cyclones and three coral bleaching events in 2012, 2014 and 2016 (Vava'u Environmental Protection Association (VEPA), pers. comm., cited in Smallhorn-West et al. (2020)).

According to the Sixth Assessment Report from the IPCC, major storms will likely increase in strength and frequency throughout the century. Along with projected ocean warming and acidification, these combined changes will likely reduce coral cover and significantly alter the calcification balance on coral reefs throughout the range of *T. mbalavuana* over the foreseeable future. However, as is addressed in **Section 3.1.1**, despite the species often occurring on or closely adjacent to coral reefs, there is very little research establishing the degree to which *T. mbalavuana* (or giant clams in general) relies on living coral cover or on coral reef rugosity and thus might be impacted by any reduction thereof. If *T. mbalavuana* is sensitive to these factors, the projected climate change-related impacts on coral reefs would likely pose a **Moderate** extinction risk to the species. We would expect decreased larval recruitment and juvenile survival across the species' range. The early life stages of giant clams are already known to suffer exceptionally high mortality rates naturally, and any further reduction in productivity would threaten the viability of remaining populations, which would contribute significantly to long-term extinction risk for this species. However, based on our uncertainty as to the reliance of *T. mbalavuana* on coral reefs, our confidence in this assessment is **Low**.

With respect to habitat degradation in the nearshore environment (e.g., related to coastal development), because *T. mbalavuana* is found predominantly in offshore coral reef areas, it is unlikely that this factor poses a significant threat to the species (**Very Low** risk, **Medium** confidence).

### 4.5.3.2 Overutilization

Based on the best available information, it is likely that past and current subsistence harvest has played a significant role in the low abundance of *T. mbalavuana* throughout its range. S. Lee et al. (2018) attribute its absence from areas outside of the eastern Lau group in Fiji to a combination of ecological factors and "serial overfishing." Additionally, Lewis and Ledua (1988) reported that in Fiji, *T. mbalavuana* is occasionally harvested unintentionally with *T. derasa* due to the similarity in appearance between the two species. In Tonga, *T. mbalavuana* has traditionally been harvested for subsistence consumption and to supply domestic markets (Ledua et al., 1993), and although its occurrence in deeper areas may have offered some protection from harvest historically, the advancement of SCUBA and hookah gear has facilitated greater access to previously inaccessible stocks (Lewis & Ledua, 1988; Lucas et al., 1991; Neo et al., 2017). As discussed in **Section 4.5.2**, interviews with a number of traditional fishermen indicated that the abundance of *T. mbalavuana* in Tonga had declined considerably during their lifetimes (Ledua et al., 1993).

Harvest of giant clams for subsistence consumption and domestic markets is ongoing and largely unregulated in Fiji and Tonga. Thus, the threat of over-exploitation contributes significantly to the long-term extinction risk for *T. mbalavuana* and is likely to contribute to the short-term risk of extinction in the near future (**High** risk). Without more recent reports from Fiji and Tonga indicating the extent to which *T. mbalavuana* has been harvested since the early 1990s, we have only **Medium** confidence in this threat assessment.

### 4.5.3.3 Disease or Predation

We could not find any species-specific information regarding disease or predation for *T. mbalavuana* beyond what is provided for giant clams generally in **Section 3.3**. Thus, we cannot make a confident assessment of the contribution of this factor to the extinction risk of *T. mbalavuana*.

#### 4.5.3.4 Inadequacy of Existing Regulatory Mechanisms

In Fiji and Tonga, the harvest and export of giant clams for commercial purposes have been banned since 1992 and 1993, respectively. However, due to the apparent natural rarity of the species, there has never been a substantial export market for *T. mbalavuana* to our knowledge. Rather, the most significant threat to the species has historically been harvest for subsistence consumption and for domestic sale, which remains largely unregulated in these countries. In Fiji, *T. mbalavuana* is listed under Part 8 of Schedule 1 of the Endangered and Protected Species Act of 2002, which includes species that are indigenous to Fiji and are not listed in CITES Appendix I, but that are "believed to be threatened with extinction." The Act prohibits the import, export, and re-export of any listed species except with a valid permit issued by the CITES Management Authority. However, the Act does not regulate the domestic harvest and consumption of listed species. Tonga has imposed minimum size limits on the collection of *T. derasa*, *T. maxima*, and *T. squamosa*, but does not include *T. mbalavuana* under this regulation. Thus, considering that domestic harvest of *T. mbalavuana* remains common and largely unregulated throughout its range, we find that the inadequacy of existing regulatory mechanisms, in combination with the species' low abundance and the ongoing threat of overexploitation, likely contributes significantly to the species' extinction risk in the near future (**High** risk, **High** confidence).

In terms of international regulations, *T. mbalavuana* was listed under Appendix II of CITES in 1985. Fiji, Tonga, and New Caledonia are Parties to the treaty. However, the species is rare and we did not find any information to indicate there has ever been an international commercial export market for *T. mbalavuana*. Thus, CITES regulations are largely irrelevant to the extinction risk for this species.

With respect to international climate change regulations, we conclude in **Section 3.4.2** that the current implementation of domestic and international climate regulations is insufficient to mitigate the cumulative threat of climate change to giant clam habitat and physiology generally. We find that this conclusion is relevant to *T. mbalavuana* to an extent, based on its distribution primarily in deep offshore coral reef habitats. The inadequacy of international climate change regulations will likely exacerbate the impacts of ocean warming and acidification on coral reefs, which may affect the quality of *T. mbalavuana* habitat. This leads us to a conclusion of **Low** risk, such that this factor is unlikely to contribute significantly to the long-term or near future extinction risk by itself, but may do so in combination with other threats. However, our uncertainty regarding the degree to which *T. mbalavuana* is reliant on coral reefs (see **Section 4.5.3.5**) leaves us with **Low** confidence in this assessment.

#### 4.5.3.5 Other Natural or Manmade Factors

Beyond the information presented in **Section 3.5**, we could not find any research addressing the potential effects of climate change on *T. mbalavuana* specifically. While there is considerably more research on possible climate change effects in other giant clam species (see **Section 3.5**), we are hesitant to make extrapolations from these studies, as susceptibility may vary among species. Thus, given the limited findings above, we conclude with **Low** confidence that ocean warming may, in combination with other VP descriptors or threats, contribute to the long-term extinction risk of *T. mbalavuana*, but is unlikely a significant threat on its own (**Low** risk).

### *Land-Based Sources of Pollution*

We also could not find any research addressing the potential effects of land-based runoff on *T. mbalavuana*. However, because *T. mbalavuana* is found predominantly in deep offshore coral reef habitats, it is unlikely that land-based sources of pollution pose a significant threat to the species (**Very Low** risk, **Low** confidence).

### *Stochastic Events*

While stochastic events such as extreme weather and mass mortalities of unknown cause may result in severe population loss in localized areas, these threats inherently cannot be predicted with any precision. However, because *T. mbalavuana* occurs at such low abundance in very few known locations, the possibility of a mass mortality event, similar to what has been observed in other giant clam species, poses a significant threat the species' persistence. Thus, we conclude that the threat of stochastic mortality events may, in combination with the species' low abundance, contribute significantly to the long-term extinction risk of *T. mbalavuana* (**Low** risk. **Low** confidence).

**Table 20.** Summary of the threats analysis for *T. mbalavuana* and associated confidence ratings.

| 4(a)(1) Factor | Threat | Contribution to Species' Risk of Extinction | Confidence Rating |
|---|---|---|---|
| **Habitat destruction, modification, or curtailment** | *Coastal development* | Very Low | Medium |
| | *Climate change impacts to coral reefs* | Moderate | Low |
| **Overutilization** | | High | Medium |
| **Disease or Predation** | | *Unknown* | *Not applicable* |
| **Inadequacy of existing regulatory mechanisms** | *National and local regulations on harvest* | High | High |
| | *Regulations on international trade* | Very Low | High |
| | *Regulations on climate change* | Low | Low |
| **Other natural or manmade factors affecting the species' continued existence** | *Physiological impacts of climate change* | Low | Low |
| | *Land-based sources of pollution* | Very Low | Low |
| | *Stochastic events* | Low | Low |

### 4.5.4 Demographic Risk Assessment

***Abundance***

Although quantitative abundance estimates are lacking, the best available information suggests that *T. mbalavuana* occurs at exceptionally low abundance and is sparsely distributed "with single individuals being found at most locations" (Ledua et al., 1993). As part of a concentrated effort to collect broodstock specimens of *T. mbalavuana* for attempted spawning and larval culture, Ledua et al. (1993) estimated the number of clams found per man-hour of search on SCUBA. The data showed that an average of about one clam per man-hour was collected in Tonga, while about 0.26 clams per man-hour were collected in Fiji. There were only three sites where more than six clams were found, and all were around Ha'apai, Tonga, which the authors suggested may be the center of distribution for *T. mbalavuana* with the "largest repository of the species." In total, 76 *T. mbalavuana* were observed and collected in Fiji and Tonga between 1986 and 1992 in more than 277 hours of searching by experts with "an eye for clams in the habitat."

Given its exceptionally low abundance, sparse distribution, and highly restricted range, *T. mbalavuana* is highly susceptible to the ongoing and future threats described in **Section 4.5.3**, including continued domestic harvest, the inadequacy of existing regulations, and the possibility of future climate change-related impacts to coral reef habitats. Potential population reductions due to these factors threaten the persistence of remaining populations, and in effect, significantly elevate the extinction risk of *T. mbalavuana*. For this reason, we find that the species' low abundance puts it in danger of extinction in the near future (**Very High** risk, **High** confidence).

***Productivity***

Despite exceptionally high fecundity, there is substantial evidence that low recruitment success and high mortality rates during early development lead to low productivity in most species of giant clams. This is likely true of *T. mbalavuana* as well; although, observations of this species are limited. In the only available report documenting the reproduction and early development of *T. mbalavuana*, Ledua et al. (1993) estimated that four clams released approximately 28 million eggs with a fertilization rate of about 90.6% after 2 hours. However, only 0.3% of fertilized eggs were estimated to survive to the veliger stage, and 2.2% of veligers survived to 90-day-old juveniles for an overall survival rate of 0.08% from fertilized eggs to juveniles at day 90. Given the exceptionally low abundance of *T. mbalavuana* and the ongoing threats outlined in **Section 4.5.3**, such low productivity can significantly limit the capacity for this species to achieve the positive population growth rates that are necessary for its recovery.

Furthermore, *T. mbalavuana* is likely experiencing an Allee effect, such that productivity is negatively correlated with population abundance. As a broadcast spawning organism, *T. mbalavuana* relies on sufficient population density to facilitate successful external fertilization of its gametes with neighboring individuals. It is possible that, at such low abundance and population densities, *T. mbalavuana* may rely to some extent on self-fertilization to produce offspring. However, as is discussed in **Section 2.3**, separation of the timing of sperm and egg release likely limits this possibility in most individuals, and when it does occur, several species of giant clams have been found to experience negative fitness effects, such as reduced larval survival and growth rates. Although, given the morphological similarity (Lucas et al., 1991) and phylogenetic proximity (Moreels, 2018; Tan et al., 2021) of *T. mbalavuana* to *T. derasa*, it is worth noting that *T. derasa* is one species in which offspring of self-fertilization did not show evidence of fitness effects compared to cross-fertilized offspring after one year of development (Zhang et al., 2020). There is no information, however, regarding the possible effects on later-stage development or reproductive fertility. Thus, while self-fertilization may in some cases generate viable offspring for *T. mbalavuana*, the separation in the timing of sperm and egg release, evidence of fitness effects on early life stages in several species of giant clams, and the lack of information as to the possible fitness effects in later-stage development, leads us to conclude that self-fertilization likely does not contribute significantly to the productivity or population growth of *T. mbalavuana*.

For these reasons, we find that the low natural productivity of giant clams, as well as the negative correlation of productivity with low abundance, contributes significantly to the long-term extinction risk of *T. mbalavuana*. Given the exceptionally low abundance of the species, these factors likely also contribute to the short-term risk of extinction in the near future (**High** risk, **Medium** confidence).

### *Spatial Distribution/Connectivity*

We could not find any information regarding the spatial structure or connectivity of *T. mbalavuana* across its range and therefore cannot assess the contribution of this factor to the species' extinction risk.

### *Genetic Diversity*

We could not find any information regarding the genetic diversity of *T. mbalavuana*. Given the species' low abundance, it is likely that genetic diversity is low; however, without any genetic testing on this species to determine diversity or effective population size, we are unable to conclude whether this is a relevant threat contributing to the species' risk of extinction.

**Table 21.** Summary of the demographic risk analysis for *T. mbalavuana* and associated confidence ratings.

| **Demographic Risk Factor** | **Contribution to Species' Risk of Extinction** | **Confidence Rating** |
|---|---|---|
| **Abundance** | Very High | High |
| **Productivity** | High | Medium |
| **Spatial Distribution/Connectivity** | *Unknown* | *Not applicable* |
| **Genetic Diversity** | *Unknown* | *Not applicable* |

### 4.5.5 Overall Extinction Risk Assessment

Guided by the results of the demographic risk analysis and threats assessment above, we analyzed the overall risk of extinction of *T. mbalavuana* throughout its range. In this process, we considered the best available scientific and commercial information regarding *T. mbalavuana* from all locations of the species' range, and analyzed the collective condition of these populations to assess the species' overall extinction risk. Despite a lack of formal, comprehensive abundance estimates, the best available information suggests that *T. mbalavuana* occurs at exceptionally low abundance and is sparsely distributed throughout its highly restricted range. Anecdotal accounts from traditional fishermen in Tonga indicate that the species has experienced significant population declines since the 1940s, which have been attributed at least in part to the longstanding harvest of giant clams in both Fiji and Tonga, where the species primarily occurs. The inherent risks of such low abundance are compounded by low natural productivity and the likelihood of the Allee effect, which likely prevents any substantial short-term recovery. Additionally, our threats assessment revealed that past and present overutilization and associated inadequacy of existing regulatory mechanisms at the local level contribute most significantly to the extinction risk of this species. *T. mbalavuana* has been harvested historically and continues to be harvested for subsistence consumption and for sale in domestic markets, occasionally being mistaken for *T. derasa* by local fishermen. While commercial export of giant clams has been prohibited in both Fiji and Tonga, existing regulations afford little protection to the species from the ongoing domestic harvest. Based on our assessment of these threats and demographic risk factors, we conclude that *T. mbalavuana* is at a **High** risk of extinction throughout its range.

## 4.6 *Tridacna squamosa*

### 4.6.1 Life History and Ecology

#### 4.6.1.1 Taxonomy and Distinctive Characteristics

*Tridacna squamosa* is commonly known as the fluted or scaly giant clam due to the characteristic leaf-like projections on its valves. It was one of the six species described in Rosewater's 1965 seminal paper on giant clam taxonomy and is classified in the sub-genus *Chametrachea*, which also includes *T. maxima*, *T. crocea*, *T. squamosina*, and three recently discovered or resurrected species: *T. noae*, *T. rosewateri*, and *T. elongatissima* (Fauvelot et al., 2020; Tan et al., 2021). Of the species in this group, *T. squamosa* shares the closest phylogenetic relationship with *T. crocea* (Fauvelot et al., 2020; Tan et al., 2021).

The exterior of the shell is grayish white, often with various hues of orange, yellow, or pink/mauve (Rosewater, 1965). The primary radial sculpture consists of 4-12 strongly convex, rib-like folds. The concentric sculpture consists of "undulate lines of growth which produce widely spaced, broadly leaf-like, projecting scales on primary folds" (Rosewater, 1965). The prominent scales on the shell commonly feature different shades or colors (Kinch & Teitelbaum, 2010). The shell interior is porcelaneous white, with an occasional hint of orange (Kinch & Teitelbaum, 2010). Rosewater (1965) describes the mantle as having a main ground color of grayish purple with a row of light blue rhomboidal spots along the outer mantle margin and multicolored irregularly-circular spots toward the center. The outer periphery of the spots is pale yellow, inside of which is a band of dark yellow, and the entire center is nearest to light blue. Generally, *T. squamosa* reaches a maximum shell length of ~40 cm (Neo et al., 2017).

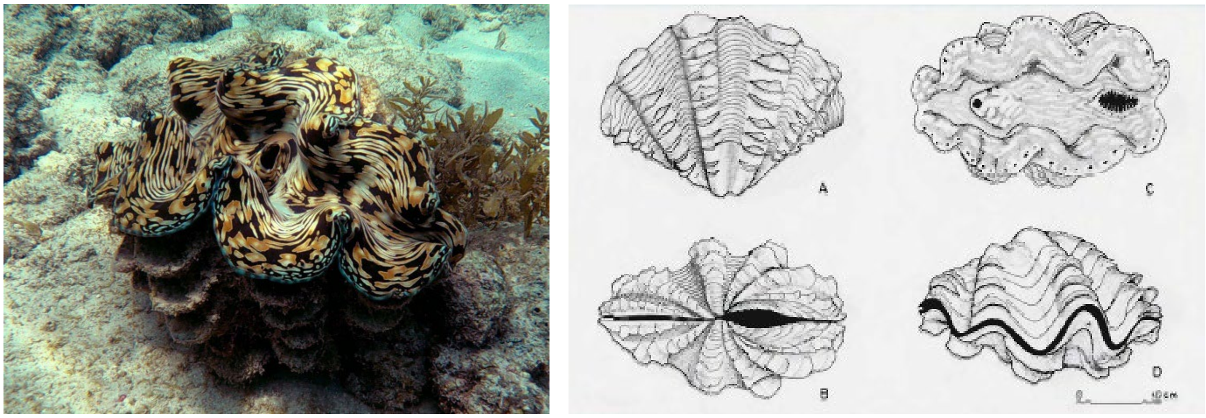

**Figure 31.** *T. squamosa* morphology. Photograph of *T. squamosa* taken near Ko Pha Ngan, Thailand (left), and illustrations showing the lateral (A), ventral (B), mantle (C), and dorsal (D) view of a representative specimen (right). (Photo credit: Warren R. Francis/iNaturalist, CC BY-NC 4.0; Diagram source: Calumpong, 1992)

### 4.6.1.2 Range, Distribution, and Habitat Use

*T. squamosa* is the second-most widely distributed giant clam species, with a broad geographic range that extends from the Red Sea and eastern Africa in the west to the Pitcairn Islands in the east, and from the Great Barrier Reef in the south to southern Japan in the north (bin Othman et al., 2010; Neo et al., 2017; Figure 32). The species has also been introduced in Hawaii and Guam (CITES, 2004b).

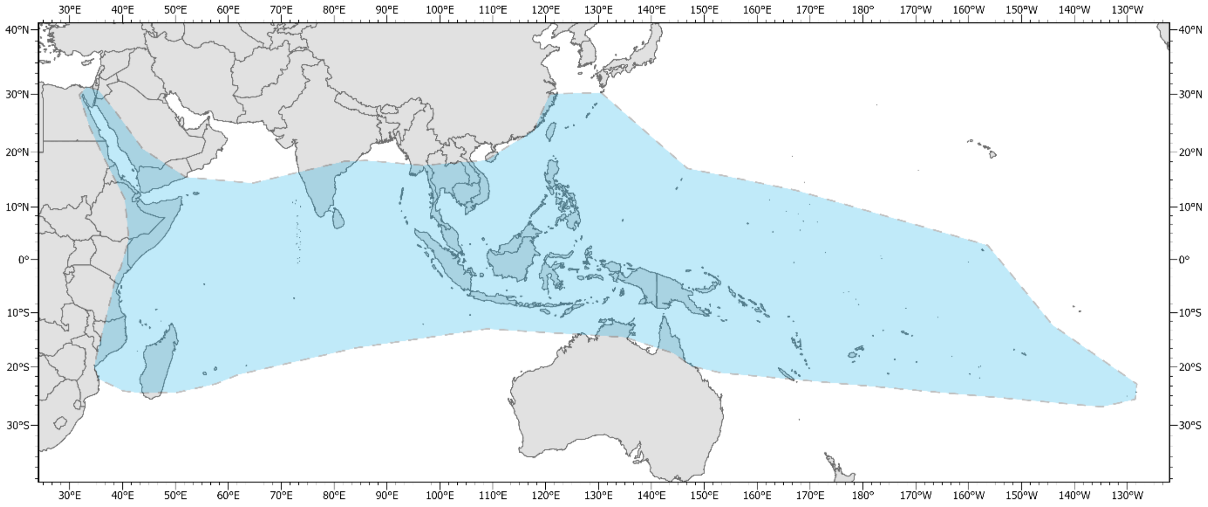

**Figure 32.** Approximate natural range of *T. squamosa* based on reported occurrences provided by Neo et al. (2017). The range does not include locations where *T. squamosa* has been introduced.

As discussed in **Section 2.2**, *T. squamosa* is native to American Samoa, CNMI, and Guam; however, it is reportedly extirpated in CNMI and very rare in American Samoa. According to S. Wells (1997), *T. squamosa* is also extirpated in Guam, although Neo et al. (2017) report that the species may still occur there at very low abundance. *T. squamosa* also occurs within the U.S. Pacific Remote Island Area. The species has been observed at Kingman Reef, although no estimates of abundance were provided (Maragos et al., 2008). Additionally, the 2022 Integrated Natural Resource Management Plan for the Wake Atoll Airfield states that *T. squamosa* historically occurred in the waters around Wake Atoll. However, it is unclear if this assertion is based solely on the species range maps provided by Rosewater (1965). Wake Atoll was included within each species' range boundary, but there were no confirmed observations or archived specimens of either species from Wake Atoll in Rosewater (1965), so whether or not it occurs there is unclear.

There have also been efforts to introduce or reintroduce *T. squamosa* to areas where it no longer occurs. In 1991, *T. squamosa* from the PMDC were reportedly reintroduced to Saipan, CNMI for the purpose of establishing a local market for giant clam meat. However, according to Bearden et al. (2005), the efforts "failed to produce desired economic benefits" and were abandoned due to poaching. The authors indicated that there were plans to initiate another mariculture venture in 2005, which would also include *T. squamosa*, but the status of that initiative is not known. According to Heslinga et al. (1984), the PMDC also shipped 500 *T. squamosa* to the University of Guam Marine Laboratory "to explore the possibility of reintroducing giant clams to areas where they are now extinct or very rare." We could not find any information indicating the outcome of these efforts. In the 1980s, *T. squamosa* was also introduced to Keahole Point, Hawaii as part of a commercial venture to explore the potential for culturing marine invertebrates for the aquarium trade (Heslinga, 1996). However, we are not aware of any efforts to outplant giant clams in Hawaii specifically for the purpose of establishing sustainable populations in the wild.

*T. squamosa* is usually found on coral reefs or adjacent sandy areas (Neo et al., 2017). Juveniles are often attached to the substrate by a "weak but copious byssus," while adults can be found either attached or free-living (Neo et al., 2017; Rosewater, 1965). *T. squamosa* occurs across a broad depth range, which includes shallow reef flats, patch reefs, and reef slopes, both inside and outside of lagoons. Individuals have been observed as deep as 42 m in the Red Sea (Jantzen et al., 2008). *T. squamosa* is typically more common on shelving fringing reefs than reef flats (Govan et al., 1988) and seems to prefer sheltered environments (Kinch & Teitelbaum, 2010; Munro, 1993). Comparing the distribution of *T. squamosa* and *T. maxima* in Mauritius, Ramah et al. (2017) found that *T. squamosa* were most often attached to flat substrata, such as dead plate corals or rubble. Hardy and Hardy (1969) reported that *T. squamosa* and *H. hippopus* occupied much the same habitat in Palau, both being widely distributed in relatively shallow water in the lagoon and on the barrier and fringing reefs; although, *T. squamosa* was reportedly more commonly associated with coral areas of *Acropora* spp. than adjacent sandy areas. In New Caledonia, Purcell et al. (2020) interpreted the relatively high density of *T. squamosa* on barrier reef sites compared to lagoonal reefs as indication that the species may prefer cleaner waters, as opposed to the siltier sediments and more turbid seawater of lagoon reef flats. However, Lewis et al. (1988) note that the species is more tolerant of turbid water than *T. derasa*. Paulay (1987) reported that all observations of *T. squamosa* in the Cook Islands were from the outer reef slope, occasionally to depths of 30 m or more.

*T. squamosa* larvae can move both horizontally and vertically in search of adequate habitat (Huang et al., 2008; Soo & Todd, 2012). Like many reef invertebrates, there is evidence that *T. squamosa* is highly attracted to crustose coralline algae as a settlement cue (Neo et al., 2009; Neo, Vicentuan, et al., 2015). There is also some indication that *T. squamosa* larvae actively avoid settling on live coral, perhaps due to allelopathic compounds or other competitive interactions. Comparing settlement preference on eight different substrate types (black pebbles, cement, coral rubble, dead coral, live coral, rough Mactan stone, smooth Mactan stone, and *Tridacna* shells), Calumpong et al. (2003) observed zero settlement of *T. squamosa* juveniles on live coral but otherwise no significant difference between the other seven substrates.

### 4.6.1.3 Reproduction and Growth

*T. squamosa* is estimated to reach full sexual maturity at 150-200 mm, which is about 3-5 years post-fertilization (LaBarbera, 1975; Isamu, 2008). We were not able to find any information regarding male-phase maturity, but based on what is known about other giant clam species, it likely occurs 1-2 years prior to full maturity. As outlined in Table 1, *T. squamosa* tends to spawn annually, but there is some regional variation in timing. Spawning has been observed in Singapore (1-2ºN) in late August (Neo et al., 2011), at Eniwetok Atoll, Marshall Islands (11-12ºN) in February-March (Rosewater, 1965), and in Palau (6-8ºN) in February (Hardy & Hardy, 1969). Roa-Quiaoit (2005) and Richter et al., (2008) estimated that the spawning season in the Gulf of Aqaba, Red Sea extended from June to November (28-30ºN), while Iwai et al. (2005) reported a spawning season extending from March to August in Okinawa, Japan (25-27ºN). McKoy (1980) recorded two spontaneous spawning events in Tonga (21-22ºS) in December and February. In Fiji (17-18ºS), LaBarbera (1975) found that the gonads of sampled *T. squamosa* were ripe and readily induced to spawn in June and July, which, unlike other reports, falls in the middle of the austral winter. The authors suggested that this discrepancy may be a result of population differences in Fiji, either induced or genetic. We could not find any other reports of winter spawning, so it is unclear how widely it occurs. Based on observations in mariculture, Iwai et al. (2005) estimated that *T. squamosa* produce 10-100 million eggs in a single spawning event.

LaBarbera (1975) summarized the spawning progression of *T. squamosa* based on specimens collected in Fiji. Sperm was released initially, with discharges occurring at approximately 30 second intervals, gradually increasing to 5 minute intervals, and lasting for 1-1.5 hours. This was followed by egg release, which occurred for about the same period of time. All specimens greater than 150-200 mm in size produced both eggs and sperm, while smaller individuals produced only sperm. Neo, Vicentuan, et al. (2015) found that after spawning, *T. squamosa* gametes remain viable for up to 8 hours, although viability decreased gradually with time. According to Fitt and Trench (1981), trochophore larvae develop 12-20 hours post-fertilization followed by the veliger stage 24-30 hours post-fertilization. *T. squamosa* larvae are active swimmers, with swimming speed peaking 6 days post-fertilization (Neo, Vicentuan, et al., 2015). Despite not being particularly strong swimmers, *T. squamosa* larvae can alter their depth distribution, and actively search for and select locations for settlement (Neo, Vicentuan, et al., 2015). Pediveligers developed 10 days post-fertilization and were observed swimming and crawling alternately on the bottom for at least a day prior to metamorphosis (Fitt & Trench, 1981). Notably, there was significant variation in the duration of pediveliger development, as some were observed up to 29 days after fertilization without having undergone metamorphosis.

Such an extended pediveliger stage is likely rare, however, as Neo, Vicentuan, et al. (2015) reported a settlement competency period of 14 days for *T. squamosa* based on experimental trials. According to Fitt and Trench (1981), zooxanthellae are ingested and digested by larvae beginning during the veliger stage, but symbiosis is not established until 2-9 days after metamorphosis, at which point zooxanthellae move into the tubular system (i.e., a diverticular extension of the digestive tract), which houses the symbiotic algal cells in adult clams. Similar observations regarding the onset of symbiosis were also reported by Fitt et al. (1984) and Hirose et al. (2005).

With respect to growth, Calumpong et al. (1992) estimated that the maximum monthly growth rate of *T. squamosa* is approximately 4.5 mm per month, while Beckvar (1981) estimated an annual growth rate of 3.0 cm per year. Standard growth parameters for *T. squamosa* have been documented in Papua New Guinea, Palau, and the Philippines and are presented in Table 22 below. A series of recent studies have used various molecular tools to characterize the mechanisms of light-enhanced calcification in giant clams (Ip et al., 2006; Ip et al., 2015; Hiong et al., 2016; Ip, Hiong, et al., 2017; Ip et al., 2018; Boo et al., 2019). The combined results suggest that exposure to light induces *T. squamosa* to regulate the concentration of $Ca^{2+}$ and $H^{+}$ in the extrapallial fluid (i.e., the region adjacent to the site of calcification) through the activity of several membrane-bound enzymes. Together, the supply of $Ca^{2+}$ and removal of $H^{+}$ from the extrapallial fluid, both of which are induced by light exposure, promotes supersaturation conditions and results in more rapid precipitation of aragonite in the shell.

**Table 22**. Recorded growth parameters for *T. squamosa*. Mean asymptotic size ($L\infty$) and growth coefficient (K) are for shell length and are based on Fabens or Wetberall plot estimates of parameters of the von Bertalanffy equation (adapted from Lucas, 1994).

| Region | L∞ (cm) | K (± SD) | Source |
|---|---|---|---|
| Papua New Guinea | 38.5 | 0.140 (0.021) | Munro & Heslinga, 1983 |
| Palau | 40 | 0.091 | Munro & Heslinga, 1983 |
| Philippines | 30.0 | 0.23 | Villanoy et al., 1988 |

### 4.6.1.4 Feeding and Nutrition

General information regarding the feeding and nutrition of giant clams is described in **Section 2.4**. Klumpp and Griffiths (1994) compared the rates of energy acquisition and expenditure in four species of giant clams from the Great Barrier Reef and found that *T. squamosa* was roughly intermediate with respect to carbon intake and expenditure, between *T. gigas* and *T. crocea* on the high end and *H. hippopus* on the low end. Under optimal light conditions, *T. squamosa* was able to obtain sufficient carbon solely from photosynthesis to satisfy and exceed routine respiratory needs and demand for carbon deposition in tissues and skeletal growth. Similar results were reported by Fitt and Trench (1981), which showed that *T. squamosa* juveniles that had established symbiosis with zooxanthellae were able to survive and grow in filtered seawater with light as the sole energy source for over 10 months. Additionally, as with other giant clam species, the contribution of photosynthesis to the energy requirements of *T. squamosa* was found to increase with body size. The ingestion of particulate organic matter contributed relatively little to the estimated energy requirements for *T. squamosa* at all measured body sizes (0.1-100 g tissue dry weight), accounting for approximately 10-20% of carbon required for respiration and growth (Klumpp & Griffiths, 1994). Although, in a study of photosynthetic performance of *T. squamosa* from the Red Sea, Jantzen et al. (2008) found that despite *T. squamosa*'s depth range (down to 42 m), the species is not a low-light specialist and requires additional nutrition via suspension feeding to satisfy its metabolic needs in low-light conditions.

A number of recent studies have aimed to characterize the symbiont communities that associate with *T. squamosa*. In the Red Sea, for example, Richter et al. (2008) found that *T. squamosa* in the Gulf of Aqaba primarily associated with *Cladocopium* (formerly clade C), although one *T. squamosa* specimen sampled in the central Red Sea reportedly hosted *Symbiodium* (formerly clade A) (Pappas et al., 2017). *T. squamosa* primarily hosted mixed communities of *Symbiodinium*, *Cladocopium*, and *Durusdinium* (formerly clade D) in Okinawa, Japan and eastern Indonesia; although, the relative proportion of each symbiont type was quite different between these two regions (DeBoer et al., 2012; Ikeda et al., 2017). In Indonesia, *T. squamosa* associated more frequently with *Durusdinium* than *Cladocopium*, while *Symbiodinium* was reportedly the least common. In Okinawa, 89.2% of sampled *T. squamosa* hosted *Cladocopium*, while *Durusdinium* was rarely observed, and the relative dominance of *Cladocopium* increased with host body size.

In a recent study examining the effects of five different symbiont genera on the early development of *T. squamosa*, Long et al. (2021) found no significant differences in the size at metamorphosis, mantle color, or survival after one year between clams with different symbiont types. However, individuals hosting *Effrenium* (formerly clade E) exhibited the longest time to metamorphosis and smallest size at 30, 90, and 360 days post-fertilization. There were no significant differences in these parameters between clams hosting the other four symbiont types. Additionally, the proportion of larvae that underwent metamorphosis was highest for clams hosting *Effrenium* and lowest for clams hosting *Breviolum* (formerly clade B).

#### 4.6.1.5 Genetics and Population Structure

There are two main studies that have aimed to characterize the population structure of *T. squamosa* across broad portions of its range. DeBoer et al. (2014) analyzed 413 samples from 32 locations throughout the Indo-Malay Archipelago, the Philippines, and Cenderwasih Bay in northern Papua. Similarly, Hui et al. (2016) analyzed 182 samples from 15 locations throughout the Indo-Malay Archipelago and Cenderwasih Bay, but also included in their analysis 2 additional sites in the Red Sea and western Indian Ocean (Kenya). Based on sequence variation in the mitochondrial cytochrome oxidase I (COI) gene, both investigations yielded similar results indicating relatively little genetic structure among *T. squamosa* populations within the Indo-Malay region, particularly compared to the two other widely distributed species included in these studies, *T. maxima* and *T. crocea*. They both described two "minimally distinct haplogroups" (i.e., separated by one mutational step) that co-occurred throughout the region, which were considered to represent a single genetic clade. The two studies also identified one rare, but more highly divergent haplogroup that occurred predominantly in the northern Philippines and in Cenderwasih Bay (Papua, Indonesia). Additionally, Hui et al. (2016) found that the samples from the Red Sea and western Indian Ocean were highly genetically divergent both from each other

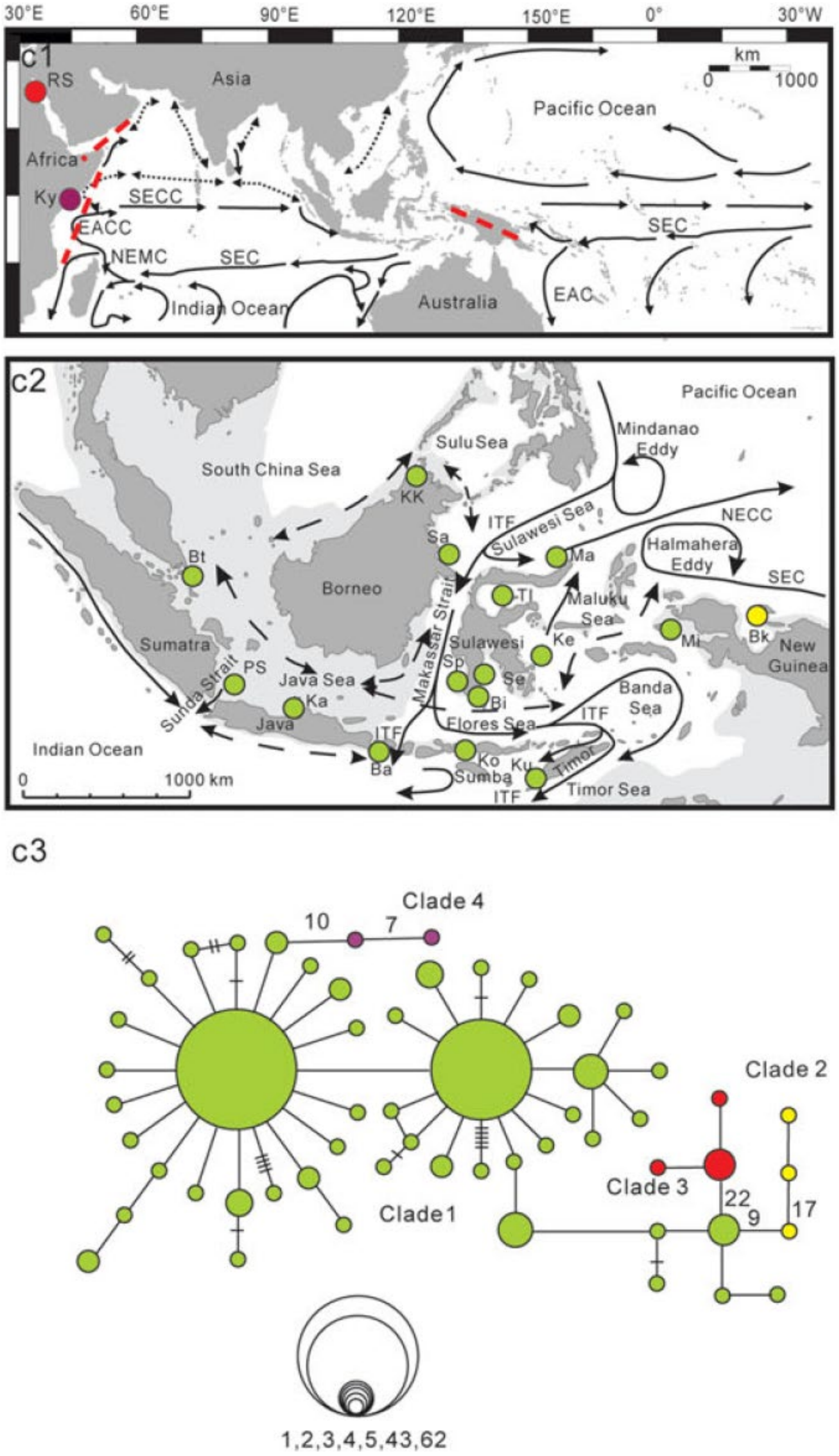

**Figure 33.** *T. squamosa* population genetics throughout the Indo-Pacific region. **C1-C2:** Maps of the Indo-West Pacific (C1) and the Indo-Malay Archipelago (C2) with labeled sampling sites (see Table 1 in Hui et al. (2016) for abbreviations). **C3:** A network of haplotypes based on the mitochondrial COI gene. Each genetic clade is designated with a unique color. Sizes of circles are proportional to haplotype frequencies. Lines between circles represent one mutational step, while the hatches and numbers indicate additional mutational steps. Pie charts on maps represent the relative proportions of clades at each sample site (as defined in haplotype networks). Red dashed lines in C1 indicate major genetic breaks in the Indo-West Pacific. Surface currents with constant (solid arrows) and seasonally changing flows (dashed arrows) are shown: South Equatorial Current (SEC), Northeast Madagascar Current (NEMC), East African Coast Current (EACC), South Equatorial Counter Current (SECC), Indonesian Throughflow (ITF), North Equatorial Counter Current (NECC) and East Australian Current (EAC). Pale grey regions indicate land areas that were emergent during the Pleistocene low sea-level stand (120 m below datum; Voris, 2000), which may play a role in the observed population genetic patterns. (Source: Hui et al. 2016, with permission from Oxford University Press).

and from the populations in the Indo-Pacific. This likely reflects the geographic distance and consequent demographic isolation between these regions (see Figure 33).

Several other studies have investigated the population genetics of *T. squamosa* within smaller portions of the species' range. Kittiwattanawong et al. (2001) found that *T. squamosa* in the Andaman Sea were genetically distinct from those in the Gulf of Thailand. This result aligns with the population genetic patterns observed for *T. maxima* and *T. crocea* (Hui et al., 2016) suggesting that there may be a fifth clade of *T. squamosa* in the Andaman Sea and eastern Indian Ocean that is genetically distinct from the metapopulation occurring throughout the majority of the Indo-Malay region. However, a larger sample size and a more thorough comparison between populations in the eastern Indian Ocean and those throughout the species' range (including the Red Sea and western Indian Ocean) is needed. Two additional studies found no evidence of spatial structure within the waters of Singapore (Neo & Todd, 2012b) and southern Vietnam (Thư et al., 2013), and P. T. Lim et al. (2018) found that *T. squamosa* in the Perhentian Islands, Malaysia were genetically similar to reference samples from throughout the Indo-Malay region.

The best available data suggest that genetic diversity of *T. squamosa* in the Indo-Malay region is low relative to *T. maxima* and *T. crocea*, the two other giant clam species with similarly broad distributions. In southern Vietnam, *T. squamosa* haplotype diversity based on the mitochondrial COI gene was 0.314-0.468 compared to 0.846-0.934 for *T. crocea* (Thư et al., 2013). Likewise, DeBoer et al. (2014) found that global $F_{ST}$ among *T. squamosa* populations in the Indo-Malay region was 0.10, significantly lower than that of *T. crocea* and *T. maxima* populations in the same region, which was 0.56 and 0.49, respectively. In Singapore, Neo and Todd (2012b) found that genetic diversity of *T. squamosa* based the number of haplotypes and polymorphic sites was lower than that of *T. crocea*. The authors recorded 6 haplotypes of the mitochondrial COI gene among 20 *T. squamosa* individuals, 4 of which were distinguished by only 1 mutation. In the Red Sea, Pappas et al. (2017) found that all four of the *T. squamosa* sampled from the central Saudi Arabia coast shared the same 16S haplotype.

### 4.6.2 Abundance, Density, and Population Status

Below, we synthesize the best available scientific and commercial information to assess the likely status of *T. squamosa* in each country, territory, or region where it has been observed. The status and abundance trends in each location are summarized in Table 23 and displayed in Figure 34 below. Given the large number of countries and territories where *T. squamosa* is known to occur, in the following synthesis of species abundance, we have grouped the 61 locations into 6 major regions aligning with the sub-headings in Table 23: the Red Sea, Southeast Africa, Indian Ocean, East Asia, South Asia, and Pacific Ocean.

#### ***Red Sea***

There is limited information regarding the abundance of *T. squamosa* in the Red Sea. The Regional Organization for the Conservation of the Environment of the Red Sea and Gulf of Aden (PERSGA) released a report in 2010 presenting benthic survey data from 36 sites throughout the Red Sea, including 5 sites in Djibouti, 8 in Egypt, 3 in Jordan, 9 in Saudi Arabia, 4 in Sudan, and 7 in Yemen (PERSGA, 2010). The survey was part of a long-term coral reef monitoring program and did not distinguish between giant clam species, as it was focused broadly on fish and invertebrate taxa that were deemed to be indicators of overall reef health. Estimates of mean giant clam density in the six surveyed countries are as follows: Djibouti—104 ± 77 ind ha$^{-1}$, Egypt—293 ± 155 ind ha$^{-1}$, Jordan—75 ± 71 ind ha$^{-1}$, Saudi Arabia—385 ± 292 ind ha$^{-1}$, Sudan—325 ± 88 ind ha$^{-1}$, Yemen—2 ± 3 ind ha$^{-1}$. Hassan et al. (2002) had previously documented a significant decline in giant clam populations in South Sinai, Egypt from 1997-2002 due to major construction activities in the region. However, these more recent estimates indicate that giant clam populations in the Red Sea have mostly remained stable since 2002, or in the case of Saudi Arabia and Sudan, have substantially increased (PERSGA, 2010). According to PERSGA (2010), large size classes of giant clams were "very rare," which the authors implied was due to longstanding harvest in the region. Most giant clams were under 20 cm in length and were embedded in the reef structure, likely because they were more difficult or less worthwhile to collect. Based on what is known about the differences in life history between *T. squamosa* and *T. maxima* (the two predominant species in this region), this observation suggests that the majority of giant clams observed were likely *T. maxima*. This is in line with the observation of Pappas et al. (2017) that *T. maxima* was "far more common" along the central Saudi Arabian coast than *T. squamosa* (although abundance estimates were not provided) and Rossbach et al. (2021), who found that *T. squamosa* accounted for only 11% of giant clams observed at 58 sites along 1300 km of the Saudi Arabian coast. Similarly, Ullman (2013) observed only *T. maxima* within a 491 m$^2$ survey area near El Quseir, Egypt.

We are aware of three studies that provide estimates of population density for *T. squamosa*, specifically, in the Red Sea. El-Sorogy et al. (2003) surveyed 40 stations along approximately 800 km of the Egyptian Red Sea coast from the Gulf of Suez in the north to Berenice in the south. The authors described the collection of "beach sediments or beach rocks or artificial substrates [...] by wandering along the shoreline, mostly from the high tide zone, the intertidal zone, and even below the low tide zone to a maximum of 1.5 m." *T. squamosa* was the only giant clam species recorded in this study and was found at 19 of the 40 stations. The authors reported a maximum "community density" of 2 ind m$^{-2}$ (equivalent to 20,000 ind ha$^{-1}$), but based on the description of survey methods and results, it is not clear if this refers to the density of shells on the shoreline or living individuals in the shallow subtidal habitats. Furthermore, considering that all other available estimates from the Egyptian coast report significantly lower densities of giant clams and suggest that *T. maxima* is more common than *T. squamosa* in this region, we question whether this report accurately reflects the abundance of *T. squamosa* along the Egyptian Red Sea coast.

Along the Jordanian coast in the northern Gulf of Aqaba, Roa-Quiaoit (2005) estimated mean *T. squamosa* population densities of 47 ind ha$^{-1}$ on the deep forereef (9-15 m), 25 ind ha$^{-1}$ on the shallow forereef (3-9 m), and 16 ind ha$^{-1}$ on the reef flats. According to the author, these estimates are an order of magnitude lower than average densities reported in Jordan in the 1970s (Mergner & Schumacher, 1974, cited in Roa-Quiaoit, 2005). The density of giant clams (both *T. maxima* and *T. squamosa*) was found to be significantly higher in protected areas than in open-access areas and was negatively correlated with metrics of human impact, which suggests that the decline in giant clam abundance over the last 50 years is likely in part due to habitat loss and over-exploitation. According to Roa-Quiaoit (2005), 70% of the Jordanian coastline has been developed since the 1970s for ports, coastal industries, and tourism.

Most recently, Rossbach et al. (2021) surveyed 58 sites along 1300 km of Saudi Arabian coastline. Average *T. squamosa* population density was estimated to be approximately 200 ind $ha^{-1}$ but with significant variability between sites (Range: 0-600 ind $ha^{-1}$; SD: 700 ind $ha^{-1}$). The density of giant clams (both *T. maxima* and *T. squamosa*) was significantly greater at northern sites (>25ºN) compared to southern sites (18-20ºN).

According to Neo et al. (2017), giant clam populations are sparse in Somalia, although no information is provided about specific species. Giant clams are also reportedly rare on average in Sudan except in Sanganeb Marine National Park, where they are "very abundant and may represent an unexploited population" (Neo et al., 2017). This is reflected in the population estimates from PERSGA (2010), in which all but one survey site in Sudan appears to be within or directly adjacent to the park.

### *Southeast Africa*

Similar to the Red Sea region, there is very little information regarding the abundance of *T. squamosa* in southeast Africa. In Kenya, Borea et al. (2003) conducted bivalve surveys in the mudflats, seagrass, and shallow lagoon areas of Malindi and Mombasa Marine Parks and the Kanamai region in 1997-98. *T. squamosa* was recorded in all three ecological zones in the marine parks, and in the mudflats and shallow lagoons of Kanamai; although, estimates of abundance were not provided. The authors noted that giant clams were commonly collected as a food source and for their shells. Giant clam harvesting accounted for 26.4% of human activities observed in Kanamai during the survey but was absent in protected areas (Borea et al, 2003).

Ramah et al. (2018) surveyed giant clam populations in 1999, 2010, and 2016 at seven sites in Mauritius, including three inside and four outside marine protected areas. The results indicated a significant decline in *T. squamosa* abundance from 1999 to 2016 at all sites but one, regardless of protection status. Adult and juvenile density were recorded separately, and the highest density of adults in 2016 was 53.2 ind $ha^{-1}$, while the highest density of juveniles was 40.0 ind $ha^{-1}$. Raw survey data were not included in the study, but based on the available figure, the average population density for adults and juveniles in 2016 was approximately 3.7 ind $ha^{-1}$ and 2.9 ind $ha^{-1}$ at the five and six sites where they occurred, respectively (Ramah et al., 2018). In northern Madagascar, Harding and Randriamanantsoa (2008) reported that the average density of giant clams at most surveyed sites was 35-55 ind $ha^{-1}$. The authors did not distinguish between species, but did note that small *T. squamosa* individuals were numerous at Nosy Berafia, Sahamalaza. Additionally, only three specimens were found as part of a broad giant clam sampling effort in Tanzania, which included surveys in Zanzibar, Mikindani, Mafia, Pemba, and Dar es Salaam (Velkeneers et al., 2022).

In a report on the exploitation of mollusks and decapod crustaceans on four islands in the Quirimba Archipelago in northern Mozambique, Barnes et al. (1998) found that *T. squamosa* represented only 0.5% of the total shellfish catch at Quisiva Island, but did not record any catch on the other three islands. Similarly, the best available data on *T. squamosa* abundance in Tanzania are provided in a report describing exploitation of the species in the tourism-based shell trade in Zanzibar. According to Gössling et al. (2004), 1,428 *T. squamosa* shells were on sale in 22 shops and curio stalls, which accounted for approximately 2.5% of the total shell trade at the time of the study. The authors noted that *Tridacna* spp. are known locally as "ashtray shells," indicating their common use in the region.

### *Indian Ocean*

*T. squamosa* has been recorded in the Cargados Carajos Archipelago (Monsecour, 2016, cited in Neo et al., 2017), Sri Lanka (Munro, 1989), and Chagos Archipelago (Neo et al., 2017), but we could not find any estimates of abundance in these locations. At Christmas Island, F. E. Wells and Slack-Smith (2000) observed *T. squamosa* at only 1 of 15 survey stations, suggesting that the species is rare (see also Berry & Wells, 2000, cited in Hourston, 2010). Similarly, Ramadoss (1983) reported that *T. squamosa* was "sparsely distributed in the Andaman and Nicobar Islands" of India. Reports of *T. squamosa* abundance in NW Australia are mixed, as Wilson et al. (2011) described the species as "common" at several sites in Talbot Bay (no quantitative abundance estimates were provided), but only three individuals were observed in a 4-ha survey of the offshore Ashmore and Cartier Reefs (Richards et al., 2009). Based on several observations that have been recorded on iNaturalist (www.inaturalist.org), *T. squamosa* also occurs in the Ningaloo region of Western Australia, but we are not aware of any studies quantifying its abundance in this area.

In the Maldives, Basker (1991) conducted a thorough survey of giant clam abundance at central and northern atolls, including the Raa, Shaviyani, and Khaviyani Atolls. Based on observations of shell middens on R. Ugoofaaru, *T. squamosa* was clearly the main target species of the giant clam fishery in the Maldives, which significantly depleted the species' abundance in the area (Basker, 1991). Reefs that were known to have been fished had low densities of *T. squamosa*, and frequently (on 63% of surveyed reefs), no *T. squamosa* were observed. By comparison, *T. squamosa* occurred on 93% of unfished reefs and, on average, were three times as abundant as on fished reefs; although, the average population density was low relative to other locations within the species' range (10.6 ind ha$^{-1}$ on unfished reefs vs. 3.4 ind ha$^{-1}$ on fished reefs). Several other reefs were surveyed where the fishing status was unknown, and the average density was 3.8 ind ha$^{-1}$. The distribution of the species was described as patchy and restricted to sheltered habitats, from the shallow reef flats down the slope to approximately 15 m depth. Giant clams were especially rare near areas of human activity (e.g., near a large resort and airport). The authors argued that the level of fishing pressure at the time was unsustainable, and described two operations that had collectively harvested over 90,000 clams (mostly *T. squamosa*) in 1990-91 to sell frozen and dried adductor muscle and mantle tissue to Taiwanese buyers. More recently, a 2009 survey found *T. squamosa* to be widespread and particularly abundant in shallow habitats (0-5 m depth) of Baa Atoll (Andréfouët et al., 2012). Together, these two studies suggest that *T. squamosa* is likely rare on average in the Maldives, particularly in areas that are subjected to significant artisanal harvest, but there are also certain sites where the species occurs in greater abundance.

### *East Asia*

We were not able to find any quantitative estimates of *T. squamosa* abundance in China or Taiwan, but based on the few reports available and what is known about exploitation in the region, Neo et al. (2017) considered the species to be rare in both locations. Neo et al. (2019) estimated the density of *T. squamosa* in the Ryukyu Islands, Japan to be approximately 6 ind ha$^{-1}$ and observed the species at only three of seven survey sites. Within the South China Sea, several surveys indicate that the species occurs at relatively high frequency in the Spratly Islands. Based on belt transects, Van Long et al. (2008) and Lasola and Hoang (2008) estimated population densities ranging from 62.5 to 137.5 ind ha$^{-1}$ in the northern Spratly Islands and Trident Shoal.

Additionally, Calumpong and Macansantos (2008) reported densities between 6 and 40 ind $ha^{-1}$ in North Danger Reef and Jackson Atoll. Neo et al. (2018) recorded only two *T. squamosa* individuals in 0.36 ha of survey area of Dongsha Atoll, equivalent to approximately 5.5 ind $ha^{-1}$.

### *South Asia*

*T. squamosa* is considered frequent throughout most of the South Asia region (Neo et al., 2017). In Indonesia, early surveys from the Karimun Java region reported population densities between 5 and 100 ind $ha^{-1}$ (Brown & Muskanofola, 1985). More recently, Wakum et al. (2017) reported a population density of 146.7 ind $ha^{-1}$ in Raja Ampat, while C. Yusuf et al. (2009) estimated 266.7 and 200 ind $ha^{-1}$ in the Seribu waters and Manado region, respectively. Additionally, Harahap et al. (2018) observed 79 *T. squamosa* across 42 transects (0.59 ha) in the Anambas Islands, equivalent to approximately 134.4 ind $ha^{-1}$. *T. squamosa* was less common near Pari Island (0.3-2.3 ind $ha^{-1}$; Eliata et al., 2003) and in the Savu Sea (25.6 ind $ha^{-1}$; Naguit et al., 2012). Two surveys in the Kei Islands in southeastern Maluku yielded significantly different estimates—Triandiza et al. (2019) recorded 122 *T. squamosa* in a survey area of 0.25 ha, equivalent to an average population density of 488 ind $ha^{-1}$, while Hernawan (2010) found only 14 individuals in 2.25 ha survey. Such large variation in these population estimates may be reflective of the species' naturally clumped distribution.

In the Philippines, most available survey data are from two studies conducted in the late 1980s. Alcala (1986) reported population densities between 6.7 and 131.4 ind $ha^{-1}$ at four sites the south-central Philippines. Juinio et al. (1989) later surveyed 247 sites at 21 locations throughout Luzon, Visayas, Palawan, and Mindanao, finding an average population density of 24.4 ind $ha^{-1}$. *T. squamosa* was present at every location surveyed except one. More recently, Dolorosa and Schoppe (2005) recorded only 2 *T. squamosa* in a small survey (0.45 ha) of Tubbataha Reefs Natural Park, while Lebata-Ramos et al. (2010) encountered 12 individuals in a 1 ha survey of Carbin Reef. In addition, Balisco et al. (2022) recorded population densities of 2.2, 15.2, and 10.0 ind $ha^{-1}$ at 3 of 6 survey areas along the eastern coast of Palawan. Accounting for the sites where *T. squamosa* was not observed, the average population density in this region was approximately 4.6 ind $ha^{-1}$. As with *T. derasa* and *T. gigas*, we note that Gonzales et al. (2014) recorded exceptionally high densities of *T. squamosa* at Meara Island (550 ind $ha^{-1}$) and Sabang Reef Fish Sanctuary (150 ind $ha^{-1}$) in Honda Bay, Palawan, but the data used to reach these estimates is not clear and appears to be based on a total survey area of less than 0.1 ha. Based on the other available survey data, these estimates do not appear to be representative of the species' status throughout the Philippines.

There are very limited quantitative data from Malaysia, Singapore, Thailand, and Vietnam. In Malaysia, one survey from the Pulau Tioman region recorded 66 individuals in a survey area of 0.26 ha, which is equivalent to 252 ind $ha^{-1}$ (Yasin & Salleh, 1998, cited in bin Othman et al., 2010). Similarly, L. K. Lee et al. (2022) reported an average population density of 150 ind $ha^{-1}$ across 12 sites in the Perhentian Marine Park, which is off the eastern coast of peninsular Malaysia. Population densities ranged from 30 to 630 ind $ha^{-1}$, with the most abundant populations occurring in the southern region of the park. However, according to bin Othman et al. (2010) and L. K. Lee (2022), the populations of all giant clam species in Malaysia have declined significantly over the past several decades. In Singapore, Neo and Todd (2013) documented a decline in the density of *T. squamosa* from 16 ind $ha^{-1}$ in 2003 (Guest et al., 2008) to 3.2 ind $ha^{-1}$ in 2009-10 (Neo and Todd, 2012). Based on modelled recruitment rates, Neo et al.

(2013) found that “the low density and scattered distribution of the remaining *T. squamosa* in Singapore are likely to significantly inhibit any natural recovery of local stocks,” leading the authors to conclude that the species should be considered “critically endangered” in the country. In Thailand, available reports indicate that *T. squamosa* is “scarce” and “nearing extinction” in Mu Ko Surin Marine National Park (Thamrongnavasawat et al., 2001, cited in Dolorosa & Schoppe, 2005 and bin Othman et al., 2010), and only 1 individual was observed on 11 manta tow surveys around Lee-Pae Island in southwestern Thailand (Chantrapornsyl et al., 1996). The authors noted that “small *T. squamosa* has never been found” in this area, although several larger individuals were observed in deeper water outside the survey area, leading them to infer that the species may have been depleted in shallow areas by locals interested in selling its unique shell. Kittiwattanawong et al. (2001) also reported that *T. squamosa* is “rarely found” along the west coast of Thailand. According to Neo et al. (2017), *T. squamosa* is “widespread across all reefs [in Vietnam], but occur at low to moderate abundances” and is subject to extensive harvest. We were otherwise not able to find any quantitative estimates of abundance in Vietnam.

### *Pacific Ocean*

The Pitcairn Islands represent the eastern edge of the natural range for *T. squamosa*, where the species was once reported to occur “in abundance” on the outer reef slope of Ducie Atoll (Paulay, 1987). We could not find any more recent estimates of population abundance in the Pitcairn Islands; although, according to Neo et al. (2017), present populations of giant clams are under “low threat,” suggesting that *T. squamosa* may still occur at relatively high abundance in this location. In neighboring French Polynesia, it was thought for many years that *T. squamosa* was absent until Gilbert et al. (2007) identified one individual on the outer slope of the barrier reef offshore of Tubuai Island. Subsequent surveys indicated that the species is “rare but present throughout Tuamotu and Gambier,” but has not yet been recorded in Society Islands (Andréfouët et al., 2014). *T. squamosa* is one of four giant clam species that has been observed in Kiribati, but occurs in low abundance. In a series of manta tow surveys of the central Gilbert Islands in 1985, Munro (1988b) provided rough estimates of population density ranging from 0 to 0.9 ind $ha^{-1}$. Similarly, in Tuvalu, Braley (1988c) found that densities of *T. squamosa* were “very low” compared to other islands in the south Pacific and Great Barrier Reef, reporting estimates of 0.7 and 1.4 ind $ha^{-1}$ at Nukufetau and Funafuti, respectively. A more recent survey from the same two islands reported similar densities of 1.2 and 3.0 ind $ha^{-1}$, respectively (Sauni et al., 2008).

Based on available reports, *T. squamosa* is also likely “rare” in the Cook Islands, Tonga, Samoa, American Samoa, Guam, FSM, New Caledonia, and Papua New Guinea. Paulay (1987) described *T. squamosa* as widespread but not common in the Cook Islands, while Sims and Howard (1988) reported that the species was “found only rarely on the outer reef slopes of Rarotonga and Aitutaki.” In Tonga, the only available data on the population density of *T. squamosa* are reported in terms of the number of individuals observed per man-hour of swimming or towed survey. The greatest density was reported in Vava’u in 1990, when Chesher (1990) recorded 266 individuals over approximately 55 hours of survey time, or 4.8 clams per man-hour. All other reports from the same area in 1987-89 (Chesher, 1990) and from Tongatapu in 1993 (Tu'avao et al., 1995) were less than 3 clams per man-hour. More recently, Atherton et al. (2014) recorded only 10 individuals spread across 6 of 27 survey sites in Vava’u. Available reports from the Samoan archipelago (Samoa and American Samoa) indicate that giant clams (*T. squamosa* and *T. maxima*) have been severely depleted throughout the region, and particularly so in areas outside of Rose Atoll—only 88 giant clams in total (*T. squamosa* and *T. maxima*) were observed across 29.3 ha of survey area outside of Rose Atoll (Green & Craig, 1999). Even at Rose Atoll, where the abundance of *T. maxima* is considerably higher, Green and Craig (1999) reported that *T. squamosa* occurred at "low abundance," although they did not differentiate the species in the survey, as small juveniles of the two species (2-3 cm) can be difficult to distinguish visually. Zann and Mulipola (1995) characterized *T. squamosa* as "functionally extinct" in Samoa. We could not find any quantitative estimates of abundance in American Samoa or Guam, but according to available reports, the species is very uncommon or extinct in both locations (Dawson, 1986; S. Wells, 1997). In FSM, *T. squamosa* can reportedly still be found throughout Yap, Chuuk, and Pohnpei states, but in "low to very low numbers" (A. J. Smith, 1992). Houk et al. (2016) recorded only 11 individuals across 75 sites in Chuuk in 2016. There are unconfirmed observations of *T. squamosa* shells in Kosrae, FSM (Smith, 1992), but we could not find any other information on the presence of living individuals there. In New Caledonia, Purcell et al. (2020) recently conducted a thorough survey of giant clams in the waters surrounding Grande Terre and found that *T. squamosa* occurred at an average density of 3.2 (±4.2) ind $ha^{-1}$, with abundance significantly higher at barrier reef sites than lagoon sites, regardless of whether the site was within a protected area. Similarly, Dumas et al. (2013) reported that *T. squamosa* was "found in very low abundance" in New Caledonia, based on a combined survey of giant clam and trochus communities. Available reports indicate that *T. squamosa* is also rare in Papua New Guinea. A survey conducted in 1996 by the South Pacific Commission and the Papua New Guinea National Fisheries Authority at the Engineer and Conflict Islands (offshore of Milne Bay Province) found that *T. squamosa* occurred at a density of 5.8 ind $ha^{-1}$. Two years later, a stock assessment spanning 1,126 sites throughout the Milne Bay Province revealed that the average population density of *T. squamosa* in the region had fallen to 1.4 ind $ha^{-1}$, which the authors estimated was equivalent to a total abundance of 660,983 (±64.3%) in the region (Skewes et al., 2003). Milne Bay Province was once the center of giant clam abundance and exploitation in Papua New Guinea, but intense exploitation during the 1980s and 1990s led to severe population declines (Kinch, 2002).

There are also several locations in the Pacific Ocean where *T. squamosa* is likely "frequent" or "abundant" based on available reports, although much of this information is dated and may not be representative of the current status of the species. According to Lewis et al. (1988), *T. squamosa* is widespread throughout Fiji, from turbid inshore high island reefs to clear oceanic lagoons. The authors noted that population density was considerably lower near major urban centers. Interviews with Fijian fishermen in 1990 suggested that the species was still common at the time, but less abundant than in the past due to widespread harvest (Vuki et al., 1992). Additionally, *T. squamosa* is one of two giant clam species found in Wallis and Futuna, and while no scientific survey has been conducted to estimate population abundance, local residents suggested that "there were plenty available in the right places" and that numbers had not diminished over the preceding 10-15 years (Pollock, 1992). Giant clams were especially abundant on the southern and western sides of Wallis, as these areas are difficult to access by sea or road and very few people, if any, reportedly live there (Pollock, 1992). We were unable to find any more recent reports or estimates of population abundance from Fiji or Wallis and Futuna. In the Solomon Islands, *T. squamosa* is reportedly "widely distributed" on reef flats, patch reefs, coral drop-offs, both inside and outside of lagoons, and are most abundant on shelving fringing reefs (Govan et al., 1988). Green et al. (2006) found that *T. squamosa* was the most widely distributed bivalve species in the Solomon Islands, occurring at 44 of 66 (66.7%)

shallow survey sites with an average population density of 24 ind ha$^{-1}$ (range: 11-117 ind ha$^{-1}$). Overall, *T. squamosa* accounted for 10.1% of all the bivalve specimens observed during the survey. There are several early reports of *T. squamosa* in the Western Caroline Islands of Palau. Hardy and Hardy (1969) estimated a population density of 63 ind ha$^{-1}$ in the waters south of Koror, while a series of surveys at Helen Reef, a small remote atoll in southern Palau that was subjected to intense poaching operations in the early 1970s, yielded estimates of only 0.2, 0.8, and 1.9 ind ha$^{-1}$ (Hester & Jones, 1974; Bryan & McConnell, 1976; Hirschberger, 1980). Most recently, Rehm et al. (2022) observed 32 *T. squamosa* across 11 sites (0.33 ha) around the main island of Palau, or approximately 97 ind ha$^{-1}$. However, it is important to note that the authors focused their surveys on areas where giant clams were known to occur and therefore the average population density based on randomly selected survey sites may be lower (L. Rehm, pers. comm., May 26, 2022).

There are two locations where the available estimates of *T. squamosa* abundance are mixed. In Vanuatu, Zann and Ayling (1988) described *T. squamosa* as "uncommon" having observed the species at only 4 of 13 surveyed islands. Estimates of population density from two sites in the Malekula Islands were 1.3-2.1 ind ha$^{-1}$. Dumas et al. (2012) also reported that "low populations were found for [*T. squamosa*]" in Vanuatu. However, based on broad-scale manta tow surveys across 17 Pacific Island countries and territories from 2002 to 2009, Pinca et al. (2010) reported that the largest population of *T. squamosa* from the entire survey was observed at Maskelynes in Vanuatu and was estimated to contain 291.7 ind ha$^{-1}$. In the Marshall Islands, two related reports describe the abundance of giant clams anecdotally but provide little quantitative information on *T. squamosa*, specifically (Beger & Pinca, 2003; Beger et al., 2008). According to Beger et al. (2008), "many *T. maxima* and *T. squamosa* were found on the outer coral crest [of Majuro Atoll]," but the authors reported observing only 32 clams in total. Additionally, of the 559 giant clams recorded at 21 sites in Namu Atoll, most were reportedly *T. maxima*. There are two figures provided by Beger and Pinca (2003) summarizing two survey efforts from Mili and Rongelap Atolls. The units of the charts are not clear, but we interpret them to be showing the average number of giant clams that were observed in several habitat categories. Based on this interpretation, it appears that approximately 38 *T. squamosa* were observed across 20 survey sites in Mili Atoll, while 36 were observed across 36 sites in Rongelap Atoll. Given the survey design of four 50 x 5 m transects at each site (i.e., 1,000 m$^2$/site), this would equate to approximately 19 and 10 ind ha$^{-1}$ at Mili and Rongelap Atolls, respectively.

We were able to find only one report documenting *T. squamosa* abundance on the Great Barrier Reef in Australia. Braley (2023) recorded observations of *T. squamosa* at five sites in the far northern region (near Lizard Island, Rachel Carson Reef, and Michaelmas Cay) in 2007-09. *T. squamosa* was observed at only one of the five sites, with a population density of 41.1 ind ha$^{-1}$ (30 individuals in a survey area of 0.73 ha). Braley (2023) revisited the same survey site in 2017 and found that abundance had declined by 23.3%, leaving a population density of 31.5 ind ha$^{-1}$. As has been discussed in previous species sections, anecdotal reports commonly suggest that populations of giant clams in Australia are healthy relative to other areas of the Indo-Pacific. Moreover, regulations have been largely effective at minimizing the risk of overexploitation of giant clams in Australian waters since the 1980s. Thus, according to Neo et al. (2017), *T. squamosa* is likely "frequent" on average throughout the Great Barrier Reef.

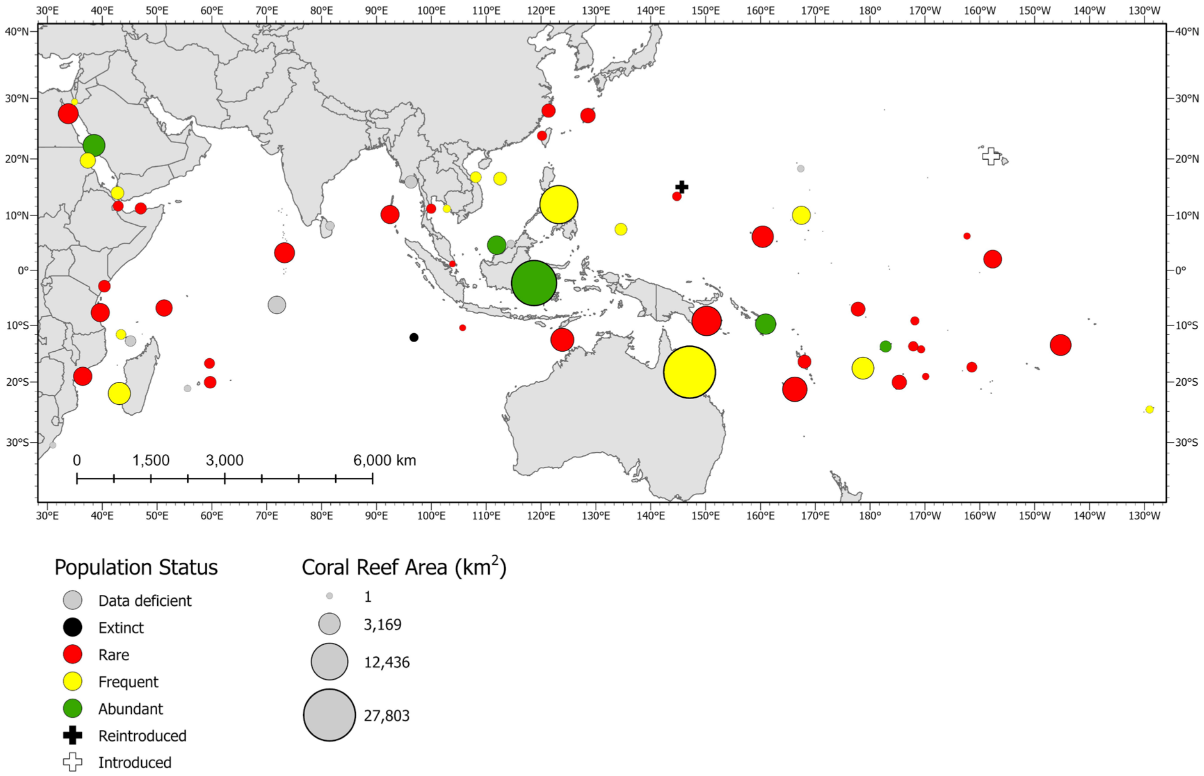

**Figure 34.** Qualitative abundance estimates for *T. squamosa* based on reported occurrence and survey data. Points are located at the approximate centroid of survey sites within each country, territory, or region from which data has been included in the abundance assessment. Abundance categories are based on those used by Neo et al. (2017), but have been revised as follows: Abundant (>100 ind ha$^{-1}$), Frequent (10-100 ind ha$^{-1}$), Rare (<10 ind ha$^{-1}$), Extinct, Introduced, Reintroduced (i.e., locations where the species was reportedly extirpated in the past but there have since been efforts to restore populations using cultured specimens; current presence/abundance may not be known), and Data Deficient (i.e., locations where reports of species occurrence have not been confirmed). The size of the points reflects the total estimated area of coral reefs within each location based on data compiled by the UN Environment World Conservation Monitoring Centre and the WorldFish Centre (UNEP-WCMC et al., 2021), increasing on a square-root scale. It is used here to roughly approximate the relative amount of giant clam habitat. However, the accuracy of this approximation likely varies between species based on their habitat preferences.

**Table 23.** Summary of *T. squamosa* population status across its geographic range (adapted from Table 4 in Neo et al. 2017 and supplemented with more recent information where available). Species abundance categories are as follows: Abundant (>100 ind ha$^{-1}$); Frequent (10-100 ind ha$^{-1}$); Rare (<10 ind ha$^{-1}$). Where the status has been revised from Neo et al. (2017), footnotes provide the data sources or rationale used to reach the respective status determinations.

| **Location** | **Status** | **Notes** |
|---|---|---|
| ***Red Sea*** | | |
| Djibouti | Rare | Surveys indicate generally small stock sizes. |
| Egypt | Rare | Significant declines of giant clams reported from 1997-2002, but later surveys indicated populations were |

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| | | stable through 2008. Generally patchy distribution with some localized declines. |
| Israel | Data deficient | No formal published data on giant clams in Israel. |
| Jordan | Frequent[1] | Available surveys from the northern Gulf of Aqaba indicate population densities of 47 ind $ha^{-1}$, 25 ind $ha^{-1}$, and 16 ind $ha^{-1}$ on the deep forereef, shallow forereef, and reef flats, respectively. Giant clam densities have declined significantly since initial surveys in the 1970s. |
| Saudi Arabia | Abundant[2] | Subjected to widespread exploitation, but no reports of population decline. Based on recent surveys spanning 1,300 km of the Saudi Arabian coastline, average population density was reported to be approximately 200 ind $ha^{-1}$. |
| Somalia | Rare | Populations are sparse. Locally collected for food by fishermen in coral reef areas. |
| Sudan | Frequent | May have an abundant, unexploited population in Sanganeb Marine National Park. |
| Yemen | Frequent | Reported declines in giant clam abundance due to habitat loss and local harvest, but more abundant in protected areas such as Socotra Archipelago. |
| ***Southeast Africa*** | | |
| Cargados Carajos Archipelago | Rare | Local fishermen harvest giant clams for food and later use their shells as ornaments. |
| Comoros | Frequent | Surveys suggest an abundance of clams, but the reefs also face high fishing pressures (e.g. blast fishing). |
| Kenya | Rare | Giant clams are commonly collected as a food source and for their shells. |
| Madagascar | Frequent | Giant clams widely distributed but in small populations. Surveys indicate that offshore reefs (e.g. Nosy Hao, Nosy Fasy) support higher densities of giant clams. *T. squamosa* is commercially fished and considered a high-value food. |
| Mauritius | Rare | Ramah et al. (2018) reports drastic decline of *T. squamosa* from 1999-2016. Giant clams remain a major part of the artisanal fishery, where they are considered a delicacy. Shells are used as birdbaths and holy fonts. |
| Mayotte | Data deficient | *T. squamosa* is considered rare. |
| Mozambique | Rare | Giant clams are subject to subsistence harvest. |
| La Réunion | Data deficient | No status information. |
| Seychelles | Rare | Exploitation of reef species is not a major problem, as locals prefer pelagic fishes. |
| South Africa | Data deficient | No status information. |
| Tanzania | Rare | *T. squamosa* shells are frequently sold as curios (collection and trade). Stocks may be locally depleted. |
| ***Indian Ocean*** | | |
| Australia (NW Islands) | Rare | Only three individuals were recorded within 4 ha survey area at Cartier and Ashmore Reefs (Richards et al., 2009). Records from iNaturalist also indicate that *T. squamosa* occurs in Ningaloo region of W Australia. |

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| Christmas Island | Rare | Naturally small stocks. |
| Cocos (Keeling) Islands | Locally extinct | Presence not verified in recent surveys. Artisanal harvest appears to be directly responsible for the severe depletion of giant clam stocks. |
| Chagos | Data deficient | No status information. |
| India | Rare | Populations are not subjected to extensive commercial exploitation, although subsistence consumption is known to occur on occasion. |
| Maldives | Rare | *T. squamosa* is a major target species of the local giant clam fishery. Concerns of unsustainable harvesting arose when stocks became depleted on numerous atolls. Although, a recent survey in 2009 at Baa Atoll found *T. squamosa* to be widespread and more abundant in shallow areas (0-5 m depth). |
| Sri Lanka | Data deficient | No status information. |
| ***East Asia*** | | |
| China | Rare | Stocks were considered plentiful in the late 1950s, but sharply declined by the 1970s, possibly due to extensive exploitation. Imported and popular in the local aquarium trade. |
| Japan | Rare | Preferred species for domestic market in meat and shells (after *T. crocea* and *H. hippopus*). |
| Taiwan | Rare | Local population reduction is attributed to harvesting of shells by tourists and locals. |
| South China Sea | Frequent | Harvest of giant clams remains common, especially for the Tanmen shellcraft industry, but mostly impacts *T. gigas*. |
| ***South Asia*** | | |
| Brunei | Data deficient | No status information. |
| Cambodia | Frequent | Reported subsistence consumption by locals, and commercial harvest for trade has depleted stocks (e.g., Koh Rong). |
| Indonesia | Abundant[3] | Can be found in relatively healthy numbers but is harvested extensively throughout the region. Available survey data indicates considerable variation in *T. squamosa* abundance throughout Indonesia. |
| Malaysia | Abundant[4] | Still widespread, but populations are reportedly declining due to combined effects of pollution, environmental degradation, and harvesting for meat and shells. Minimal juvenile recruitment observed in surveys at Perhentian Islands in 2017 (Lim et al., 2018). |
| Myanmar (Burma) | Data deficient | No status information. |
| Philippines | Frequent | Subsistence harvest widespread, commercial exploitation for international shell trade decimated populations; cultured for restocking program. |
| Singapore | Rare[5] | Occurs in low abundance; exploited for curio trade. A hatchery has been established with a focus on culturing and restocking *T. squamosa* clams on local reefs. |

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| Thailand | Rare[6] | Mainly harvested for its shell which led to overexploited stocks. A successful breeding program for has been established with the goal of restocking local populations. |
| Vietnam | Frequent | Widespread, but in low to moderate abundance. Giant clam densities declined significantly between 1998 and 2007 likely due to harvest. |
| ***Pacific Ocean*** | | |
| American Samoa | Rare[7] | Anecdotal reports indicate that *T. squamosa* is “very uncommon” in American Samoa (Dawson, 1986). |
| Australia<br>(Great Barrier Reef) | Frequent | Populations considered healthy with some almost pristine examples. Illegal poaching may still occur in some areas, but strict harvest bans and effective surveillance measures have largely minimized the threat of over-exploitation in Australian waters. |
| CNMI | Reintroduced[8] | *T. squamosa* was reintroduced to Saipan in 1991 after it had been reported extirpated for the purpose of establishing a local market for giant clam meat. However, the project was reportedly abandoned due to poaching. It is not clear if plans to restart the initiative in 2005 were realized. |
| Cook Islands | Rare | Reported to be widespread but not common; rare on the outer slopes of Rarotonga and Aitutaki. |
| FSM | Rare[9] | Primarily collected as a food source and shells for curios. Previous commercial exploitation of wild stocks was mainly for adductor muscles sold to Southeast Asian markets. As a result, wild stock numbers have declined. |
| Fiji | Frequent | Heavy artisanal and subsistence fishing in areas close to major population centers. |
| French Polynesia | Rare | Only found on outer reef slopes in Tuamotu-Gambier and Austral Archipelago, but not in any of the Society Islands. |
| Guam | Rare | Giant clams are highly valued as a local delicacy, particularly for their adductor muscles. |
| Kingman Reef (U.S. PRIA) | Rare[10] | *T. squamosa* has been observed at Kingman Reef, but no estimates of abundance were provided. |
| Marshall Islands | Frequent[11] | Rare near population centers, but relatively healthy in Outer Islands. All species widely harvested for subsistence use. |
| New Caledonia | Rare[12] | Preferentially harvested for local consumption; commercial market for meat. |
| Niue | Rare | Absent in surveys since 1998; stocks have declined since the early 1990s. |
| Palau | Frequent[13] | Recent survey by Rehm et al. (2022) recorded a population density of 97 ind ha$^{-1}$ at 11 sites around the main island. Harvest of giant clams for subsistence and domestic sale is “very common” (L. Rehm, pers. comm., May 26, 2022). |

| | | |
|---|---|---|
| Papua New Guinea | Rare | No specific information on *T. squamosa*. Local extinctions at some sites and generally low stocks are attributed to unsustainable harvest and illegal poaching. |
| Pitcairn Islands | Frequent | Population described as fairly common in 1980s, and the present population is reportedly under low threat. |
| Republic of Kiribati | Rare[14] | Giant clams are traditionally important food and shell resource. Subsistence fishing places a heavy pressure on giant clam stocks. |
| Samoa | Rare[15] | Long-term decline in abundance has led some to consider the species functionally extinct. |
| Solomon Islands | Abundant | Relatively healthy stocks remaining, although lower densities than previously reported. |
| Tokelau | Rare | Very scarce as it is preferentially fished. Populations are reportedly in decline. |
| Tonga | Rare[16] | Available survey data suggests relatively low abundance. A maximum of 4.8 clams per hour of survey time reported at Vava'u in 1990 (Chesher, 1990), but a more recent survey recorded only 11 individuals at 27 sites from this region (Atherton et al., 2014). Shallow populations of *T. squamosa* are reportedly heavily fished in the central islands of Vava'u, and large adults are rare in depths shallower than 10 m (Chesher, 1993). |
| Tuvalu | Rare[17] | Stable but low population densities reported from Nukufetau and Funafuti (Braley, 1988c; Sauni et al., 2008). |
| Vanuatu | Rare | Significant numbers traded for the ornamental aquarium industry between the late 1990s and 2007, at which point a ban on harvest and export of wild clams was imposed. There is an ongoing effort to culture *T. squamosa* for restocking and commercial export of live specimens. |
| Wake Atoll (U.S. PRIA) | Data deficient[18] | The Integrated Natural Resource Management Plan for the Wake Atoll Airfield states that *T. squamosa* historically occurred in the waters around Wake Atoll, but the basis for this report is unclear. |
| Wallis and Futuna Islands | Abundant | Locals indicate stocks are abundant around Wallis, particularly in the waters around the southern and western coasts. |
| ***Non-native locations where T. squamosa has been introduced*** | | |
| Hawaii (U.S.) | Introduced[19] | *T. squamosa* was introduced as part of a commercial venture to explore the potential for culturing marine invertebrates for the aquarium trade. |

Sources:

[1] Roa-Quiaoit (2005)

[2] Rossbach et al. (2021)

[3] Various survey data in Eliata et al. (2003); C. Yusuf et al. (2008); Hernwan (2010); Wakum et al. (2017); Harahap et al. (2018); Triandiza et al. (2019)

[4] Yasin & Salleh (1998), cited in bin Othman et al. (2010)

[5] Neo et al. (2013)

[6] Kittiwattanawong et al. (2001); Thamrongnavasawat et al. (2001), cited in Dolorosa & Schoppe (2005) and bin Othman et al. (2010)

[7] Green & Craig (1999)

[8] Reports of extirpation in Dawson (1986); Munro (1989); S. Wells (1983; 1997); reintroduction reported by Bearden et al. (2005)

[9] Smith (1992); Houk et al. (2016)

[10] Maragos et al. (2008)

[11] Beger & Pinca (2003); Beger et al. (2008)

[12] Dumas et al. (2013); Purcell et al. (2020)

[13] Rehm et al. (2022)

[14] Munro (1988b)

[15] Zann & Mulipola (1995); Green & Craig (1999)

[16] Chesher (1990); Tu'avao et al. (1995); Atherton et al. (2014)

[17] Braley (1988c); Sauni et al. (2008)

[18] Integrated Natural Resources Management Plan for Wake Atoll (2022)

[19] Heslinga et al. (1996)

Overall, the population status of *T. squamosa* varies considerably across its geographic range. Of the 63 locations where *T. squamosa* has been recorded naturally, the best available data suggest that the species is abundant in 5 locations, frequent in 14 locations, rare in 33 locations, locally extinct or reintroduced after local extinction in 2 locations, and data deficient (likely exceptionally rare or extinct) in 9 locations. The species is most abundant in South Asia and the Red Sea, and there are certain island nations in the western Pacific where *T. squamosa* still occurs in relatively high abundance. *T. squamosa* is less common in Southeast Africa, East Asia, and much of the Pacific Ocean.

There are also numerous mariculture facilities where *T. squamosa* has been cultured successfully, but most are focused primarily on commercial production for the ornamental aquarium industry. We are aware of facilities in Fiji, Tonga, Cook Islands, Marshall Islands, Palau, Papua New Guinea, American Samoa, Samoa, FSM, Solomon Islands, Tuvalu, Vanuatu, Japan, Philippines, Malaysia, Indonesia, Thailand, Australia, and Hawaii (USA), which produce *T. squamosa* currently or did so in the past (Kittiwattanawong et al., 2001; Lindsay et al., 2004; Gomez & Mingoa-Licuanan, 2006; Teitelbaum & Friedman, 2008; Mies, Dor, et al., 2017; Neo et al., 2019). While many have experimented with outplanting cultured clams with the purpose of restocking natural populations, it seems that the success of these efforts has been limited in most cases for reasons that have been discussed in previous species sections (e.g., difficulties in sustaining funding, monitoring, and protection). For example, the Marine Science Institute at the University of the Philippines produced 23,020 *T. squamosa* juveniles in October 2002 and distributed the clams throughout the Mindanao region to restock natural populations (Gomez & Mingoa-Licuanan, 2006). The fate of this specific restocking effort has not been publicly reported, but other species that had been outplanted during the same period (primarily *T. gigas*) experienced high mortality in part due to a loss of institutional support, which limited the resources and personnel available to maintain and monitor the outplants (Gomez & Mingoa-Licuanan, 2006). Based on this information, the *T. squamosa* outplants likely suffered similarly low survivorship. We are not aware of any other restocking efforts for *T. squamosa* that have been pursued in the Philippines since. In Tonga, village-based nurseries of *T. squamosa* and *T. derasa* led to a notable increase in juvenile recruitment according to local accounts (Chesher, 1993). Villagers of Vava'u conveyed to the author that they had never seen so many young clams in surrounding reefs and that the children had collected and eaten "baskets" of them. This account, however, highlights the primary motivation of this effort, which was to replenish the natural giant clam stocks to support subsistence harvest, not to establish and conserve a sustainable population of the species. The most recent published survey of giant clams in the Vava'u area found that the abundance of *T. squamosa* was very low, reporting only 10 individuals at 6 of the 27 survey sites in the area (Atherton et al., 2014).

These two examples highlight the challenges of culturing giant clams (including *T. squamosa*) with the purpose of stock replenishment. Thus, while many known mariculture facilities throughout the Indo-Pacific have successfully bred and raised *T. squamosa*, there is little evidence that initiatives to replenish natural stocks with culture-raised clams have achieved their goal of enhancing population abundance or productivity. Without further information or survey data demonstrating such success, we consider the impact of these initiatives to be negligible with respect to the status of the species. In other words, where restocking has been explored to enhance rare populations, there is very little evidence to suggest that such initiatives have significantly increased population abundance in these locations.

## 4.6.3 Threats to *Tridacna squamosa*

### 4.6.3.1 Destruction, Modification or Curtailment of Habitat or Range

As discussed in **Section 4.6.1.2**, *T. squamosa* can be found in a variety of habitats and across a broad depth range, including shallow nearshore reef flats, patch reefs, and reef slopes, both inside and outside of lagoons and in every reef type (i.e., fringing reefs, barrier reefs, and oceanic atolls). *T. squamosa* is most often found within or adjacent to the coral reef framework, typically attached to hard substrates via a weak, but copious byssus. Thus, similar to *T. gigas*, we consider the threat of habitat destruction, modification, or curtailment with respect to both the species' distribution in nearshore coastal areas and its association with coral reefs more generally.

Each of these threats has been addressed previously in this review in relation to *H. hippopus* (i.e., impacts of human development on nearshore habitat) and *T. derasa* (i.e., potential impacts of climate change on coral reef habitat). With respect to *H. hippopus*, we found that the threat of nearshore habitat destruction or modification due to coastal development is geographically heterogeneous and is likely most severe adjacent to highly populated areas of the central Indo-Pacific (e.g., Indonesia, Malaysia, Papua New Guinea, Philippines). The threat is likely less severe throughout the Pacific island nations and coastal Africa, where human development has been less intense, and in Australia, where water quality management has historically been more effective.

Specific to *T. squamosa*, there are also several reports detailing the extent of coastal development in the Red Sea and its potential impacts on giant clam distribution and abundance. Gladstone et al. (2013) noted specific areas of the Red Sea coastline that have been targeted for development of tourist activities and infrastructure, including Hurghada and the Gulf of Aqaba coastline from Sharm el-Sheikh to Nuweiba (Egypt), Eilat (Israel), and Aqaba (Jordan). Roa-Quiaoit (2005) estimated that 70% of the Jordanian coastline has been developed into ports, industrial centers, and tourism areas over the past several decades, which the author suggests has likely contributed to a substantial decline in *T. squamosa* populations since the 1970s. In a survey of the area, Roa-Quiaoit (2005) found an inverse relationship between *T. squamosa* population density and several metrics of human impact. Near Hurghada, Egypt, Mekawy and Madkour (2012) observed dredging activities associated with a newly-constructed harbor, as well as offshore trash disposal from boats. The authors also described industrial and tourist activities in several other areas along the coast of mainland Egypt (e.g., oil drilling in El-Esh, dense industrial and tourism-related development near Safaga Harbor, high human activity in Quesir), which they argue has likely been the principal factor driving the declining abundance of giant clams in these areas. Similarly, Hassan et al. (2002) reported "major decreases in giant clam populations [in Egypt] between 1997 and 2002, with many small clams seen in 1997 not surviving through to 2002." The authors attributed this population loss directly to sedimentation from major construction activities in South Sinai.

However, considering that the impacts of coastal development are relatively localized and geographically heterogeneous across the extensive range of *T. squamosa*, we conclude that the threat of habitat destruction, modification, or curtailment related to nearshore impacts of coastal development is unlikely to contribute significantly to long-term or near future risk of extinction either by itself or in combination with other VP descriptors or threats (**Very Low** risk, **Medium** confidence).

With respect to the potential impact of climate change on the suitability of coral reef habitat, we previously concluded for *T. derasa* and *T. gigas* that, while there is extensive evidence that the combined effects of ocean warming and acidification will reduce living coral cover and significantly alter the calcification balance on coral reefs over the foreseeable future, there is very little research specifically evaluating the extent to which giant clams rely on these habitat characteristics for their survival and productivity. The few larval choice experiments to date suggest that *T. squamosa* larvae tend to avoid settling on smooth surfaces (e.g., aquarium plexiglass, smooth tiles, etc.); although, Ramah et al. (2017) reported that *T. squamosa* in Mauritius were most often found attached to flat substrata, such as dead plate corals or rubble. Thus, it is difficult to extrapolate the experimental results to the species' behavior in the wild. Without more information on the direct association between substrate rugosity and *in situ* recruitment rates or juvenile survival, we cannot estimate with any confidence the degree to which reef rugosity must decline to threaten the persistence of the species. Thus, while it is likely that continued ocean warming and acidification will drastically alter coral reef communities and reduce the rugosity of many reef areas, the potential effect on the quality or suitability of habitat for *T. squamosa* cannot be confidently assessed.

As with previous species, if *T. squamosa* is sensitive to reductions in net ecosystem calcification and reef rugosity, the projected climate change-related impacts to coral reefs would likely pose a **Moderate** extinction risk to the species. We would expect decreased larval recruitment and juvenile survival across broad portions of its range. These early life stages are already known to suffer exceptionally high mortality rates naturally, and any further reduction in productivity would threaten the viability of remaining populations, which would contribute significantly to the long-term extinction risk for this species. However, based on the preceding discussion, our confidence in this assessment is **Low**.

#### 4.6.3.2 Overutilization

Compared to the often co-occuring *T. maxima* and *T. crocea*, *T. squamosa* is larger and is easier to physically remove from the reef, which makes it highly susceptible to harvest, particularly in shallow nearshore areas. For this reason, *T. squamosa* is an important resource in subsistence fisheries in nearly every location across its range, and in several locations, it is the preferred giant clam species for meat consumption (Neo et al., 2017). Few exceptions include Australia, where giant clam harvest is strictly prohibited, and in remote areas where the distance from human settlements and infrastructure limits accessibility. However, in most locations where the species occurs, longstanding subsistence harvest has driven widespread population declines (Neo et al., 2017).

The meat of *T. squamosa* has not been traded extensively on the international market. According to CITES annual report data, 13,185 kg of *T. squamosa* meat was exported from the Philippines to Japan in 1985-87, 500 kg was exported from Taiwan to Japan in 1985, and 2,000 kg was exported from Papua New Guinea to Singapore in 1996. There was then no reported trade until 2010, when Palau began to export the meat of culture-raised *T. squamosa* originating from the PMDC. Since 2010, Palau has exported up to 20 kg per year to locations including the United States, Guam, Japan, and Spain.

In many areas, *T. squamosa* is also highly desired for its unique fluted shell and is often collected either for personal use or to be sold in local or international markets (Shang et al., 1994). Domestic sale of shells and shell craft is typically closely associated with the tourism industry. We were not able to find clear statistics indicating the scale of the domestic shell trade, but according to Shang et al. (2014), the shell of *T. squamosa* was typically the second-most frequently sold among the species of giant clams in Australia and Japan, behind only *H. hippopus*. Moreover, several sources note that *T. squamosa* has experienced significant population declines due to overutilization for its shell in Thailand (Chantrapornsyl et al., 1996; Dolorosa & Schoppe, 2005; Neo et al., 2017) and the Philippines (Lucas, 1988; Villanoy et al., 1988; Neo et al., 2017). Historical harvest in Thailand was so intense that *T. squamosa* is reportedly extirpated from the Andaman Sea and is nearing extinction in Mo Ko Surin National Park (Dolorosa & Schoppe, 2005).

As described in **Section 3.2.2**, the Philippines operated as the largest exporter of giant clam shells in the 1970s and 1980s, including significant numbers of *T. squamosa*. According to CITES annual report data, over 82,000 kg, 246,000 shell pairs, 1.2 million “shells” (without associated units), and 350,000 shell carvings of *T. squamosa* were exported from the Philippines from 1985 to 1993. This period of intense harvest drastically depleted *T. squamosa* populations throughout the Philippines; although, unlike the other giant clam species included in this status review, the best available data suggests that *T. squamosa* is still relatively frequent in most areas of the Philippines, possibly due to a larger historical population size. Presently, CITES trade reports indicate that the international trade of *T. squamosa* shells and shell products is minimal. Since 2010, only the Solomon Islands, Tonga, and Fiji have exported a significant number of *T. squamosa* shell products, with the Solomon Islands exporting 1,106 shells to the United States in 2010, Tonga exporting 820 shells to the United States in 2012 and 2,030 shells to China in 2016, and Fiji exporting 834 shells each to the United States, China, and France in 2014.

International trade of live *T. squamosa* for the aquarium and mariculture industry is ongoing and widespread. As described in **Section 3.2.2**, much of the live *T. squamosa* trade originates from countries of Southeast Asia, such as Vietnam, Cambodia and Indonesia, and many of the recent exports from Vietnam and Cambodia are of wild-sourced individuals (Figure 35). Exports from Vietnam peaked in the 2000s and have declined over the last decade, while exports from Cambodia have increased more recently, reaching nearly 10,000 *T. squamosa* specimens in 2019. Neo et al. (2017) note that the decline in exports from Vietnam is related to trade restrictions implemented in response to concerns about the status of wild populations, and it is possible that some giant clams from Vietnam have been re-routed for export through Cambodia. In fact, according to CITES reports, over 99% of the recorded *T. squamosa* exports from Cambodia were imported by Vietnam, implying a close trade connection between the two nations. The total number of live, wild-caught *T. squamosa* specimens recorded as exports from Cambodia and Vietnam since 2010 is 45,358 and 8,727, respectively. Other significant exporters of live *T. squamosa* include Indonesia, Palau, and the Marshall Islands, where the vast majority of exports are of specimens born or bred in captivity (Figure 35).

Since 2010, the United States has been the largest importer of live *T. squamosa*, importing 47,197 specimens and accounting for 34.1% of reported global imports over this period. This includes wild-caught specimens from Cambodia, Vietnam, Australia, Tonga, Vanuatu, Indonesia, Palau, and Hong Kong, in decreasing order of trade volume. Other major importers of live *T. squamosa* specimens include Vietnam (discussed above in relation to Cambodian exports), France, Netherlands, Canada, and Germany, each importing over 5,000 individuals since 2010. Based on the preceding information, it is clear that the demand for *T. squamosa* in the international aquarium trade remains high, and while much of the supply has transitioned to culture-raised specimens in countries such as Indonesia, Palau, and Marshall Islands, there continues to be significant harvest of wild *T. squamosa* in Cambodia and Vietnam, likely putting those populations at increased risk of extinction.

Overall, *T. squamosa* has been harvested extensively for both subsistence and commercial purposes for several decades, which has led to documented population declines in many areas of its range (Neo et al., 2017; see **Section 4.6.2**). While most countries have imposed prohibitions on the commercial exploitation of giant clams, the demand for *T. squamosa* in the ornamental aquarium market continues to pose a threat to wild populations primarily in Cambodia and Vietnam. Additionally, subsistence harvest is ongoing in most populated areas where the species occurs. Without more thorough monitoring from many of these locations, it is difficult to determine if this ongoing harvest is causing further population declines, but at the very least, it is likely preventing any substantial recovery of depleted populations throughout its range. An important exception is Australia, where anecdotal reports suggest that strictly enforced harvest bans have been largely successful in preventing overexploitation and protecting reportedly healthy stocks of giant clams. For these reasons, and considering the documented effects of past harvest on species abundance, we conclude with **Medium** confidence that overexploitation of *T. squamosa* contributes significantly to the species' long-term risk of extinction, but does not in itself constitute a danger of extinction in the near future (**Moderate** risk).

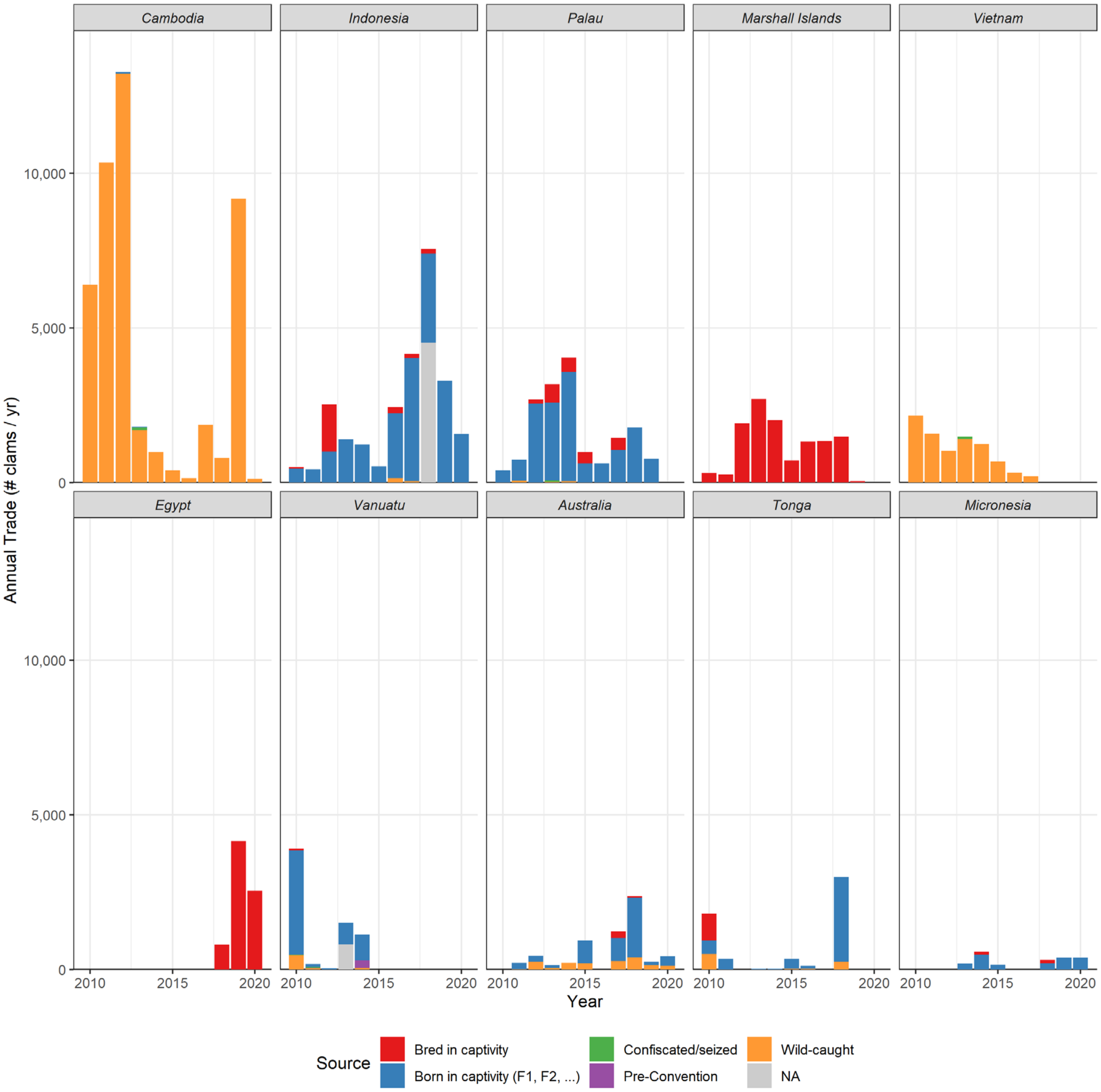

**Figure 35.** Annual exports of live *T. squamosa* (# of specimens) from the top ten exporting countries, based on CITES reports from 1983 to 2020. Values are derived from importers' data. NA indicates trade for which the source of the clams was not specified in CITES reports. (Source: CITES Trade Database, accessed 22 Mar 2022).

### 4.6.3.3 Disease or Predation

Aside from the general information regarding disease in giant clams discussed in **Section 3.3.1**, we could find very little information addressing disease prevalence in *T. squamosa* specifically. In an investigation of *Perkinsus* spp. infection among giant clams from several sites on the Great Barrier Reef, only one *T. squamosa* individual was examined and was found not to be infected (Goggin & Lester, 1987). Additionally, Reavill et al. (2009) reported that

*T. squamosa* was unaffected by an unidentified pathogen that infected and killed numerous *T. crocea* and *T. gigas* specimens in a commercial coral reef tank in California.

Giant clams are most susceptible to predation in early life stages, but as is discussed in **Section 3.3.2**, they employ a number of defense mechanisms, both morphological and behavioral, to resist predatory attacks. *T. squamosa* in particular is equipped with scaly projections on its shell (i.e., scutes) which have been shown to reduce predation from crushing predators like crabs. Han et al. (2008), for example, found that the presence of scutes both increases the overall shell size (excluding crabs with smaller claws) and forces crabs to open their claws wider to grasp the shell, effectively minimizing the crushing force. Positive correlations were also observed between shell length and strength, such that larger clams are less vulnerable to crushing predators (Han et al., 2008). Thus, the scutes of *T. squamosa* juveniles can reduce predation and allow more individuals to reach an escape size at which predation is no longer a significant threat (Han et al., 2008). In addition to the physical structure and strength of its shell, *T. squamosa* also exhibits behavioral responses to the threat of predation. Neo and Todd (2010) found that *T. squamosa* was able to aim its exhalant siphon and expel water in various patterns to successfully hit artificial fish targets.

Based on the limited information available, we find it unlikely that disease and predation contribute significantly to the risk of extinction, either independently or in combination with other threats (**Very Low** risk, **Low** confidence).

#### 4.6.3.4 Inadequacy of Existing Regulatory Mechanisms

As has been discussed with respect to previous species, there are various regulatory mechanisms and management measures in place throughout the range of *T. squamosa* (see Appendix 1). In general, the threat of inadequate regulatory mechanisms with respect to *T. squamosa* is very similar to that of *T. derasa* and *T. gigas*. Thus, rather than reiterate the details of the threat here, we summarize the conclusions below and refer the reader to **Section 4.3.3.4** for further details.

With regard to local and regional regulations, despite widespread commercial export bans, the capacity for enforcing existing regulations is often limited and existing regulations in many locations do not restrict ongoing subsistence harvest. Additionally, the regulatory landscape is further complicated by customary fishing rights, which are honored in many Pacific island nations alongside or in lieu of national legislation. This is the case in parts of Fiji, Samoa, Solomon Islands, Papua New Guinea, and Vanuatu, where indigenous village groups hold fishing rights and regulate access to adjacent reef and lagoon areas. It is unclear whether these small-scale regulatory dynamics typically apply to giant clams broadly, or if certain species may be protected or managed differently than others. Thus, it is difficult to assess the effectiveness of these community-based management systems on the conservation of *T. squamosa* specifically. However, because ongoing subsistence harvest is the most widespread threat to *T. squamosa*, having been implicated in the decline of this species in most areas of its range, it is apparent that the lack of restrictions on subsistence harvest has not adequately protected this species. For this reason, we conclude with **Medium** confidence that the inadequacy of existing local/regional regulations to address overutilization poses a **Moderate** risk to the extinction of *T. squamosa* (i.e., the factor contributes significantly to the long-term risk of extinction, but does not in itself constitute a danger of extinction in the near future).

In terms of regulations on international trade, *T. squamosa* was listed under Appendix II of CITES in 1985. Of the 63 locations listed within its range, all are Parties to the Treaty, except the Cook Islands, FSM, Kiribati, the Marshall Islands, Niue, and Tuvalu; Palau also took reservations on all species of giant clams. The primary market for *T. squamosa* in international trade is of live clams for the ornamental aquarium industry, and it appears that most major exporters have transitioned their supply to cultured specimens. The major exceptions are Cambodia and Vietnam, which together have exported over 50,000 wild-caught *T. squamosa* since 2010. The government of Vietnam instituted a quota system to regulate the commercial harvest of wild giant clams after concerns were raised in the early 2010s about the level of exploitation. However, the subsequent rise in the export of live *T. squamosa* from Cambodia to Vietnam suggests that this regulation simply diverted the harvest to neighboring waters. While this harvest pressure likely threatens the persistence of *T. squamosa* populations in Cambodia in the long term, available reports suggest that the species can still be considered “frequent” in Cambodia and Vietnam (Table 23). Additionally, as mentioned above, CITES annual report data indicates that the large majority of recent recorded trade of *T. squamosa* is of culture-raised specimens and products. For this reason, we conclude with **Medium** confidence that the inadequacy of international trade regulations to address overutilization poses a **Very Low** risk to the extinction of *T. squamosa* (i.e., the factor is unlikely to contribute significantly to the risk of extinction, either by itself or in combination with other VP descriptors or threats).

With respect to climate change, we conclude in **Section 3.4.2** that current implementation of domestic and international climate regulations is insufficient to mitigate the cumulative threat of climate change to giant clam habitat and physiology generally. We find that this conclusion is relevant to *T. squamosa* based on the close association of this species with coral reef habitats and the documented impacts of ocean warming and acidification on the growth and survival of juveniles (see **Section 4.6.3.5** below). The inadequacy of climate change regulations will likely exacerbate the impacts of ocean warming and acidification, which may affect the quality of *T. squamosa* habitat and lower juvenile fitness in some areas; although, as is discussed in **Section 3.5**, the local and regional heterogeneity in projected ocean warming and acidification impacts will likely result in variable impacts across the species’ expansive range. This leads us to a conclusion of **Low** risk, such that the inadequacy of existing regulations to address the potential threat of climate change is unlikely to contribute significantly to the long-term or near future extinction risk by itself, but may do so in combination with other threats. While the degree to which *T. squamosa* is reliant on healthy coral reefs is uncertain (see **Section 4.6.3.1**), the documented impacts of projected ocean warming and acidification conditions on *T. squamosa* fitness gives us **Medium** confidence in this assessment.

### 4.6.3.5 Other Natural or Manmade Factors

#### ***Climate Change***

In addition to the information presented in **Section 3.5.1** regarding the effects of climate change on giant clams generally, the best available information suggests that *T. squamosa* is sensitive to ocean warming and acidification during early life stages. Elfwing et al. (2001) found that experimental warming enhanced the respiration rate in *T. squamosa* juveniles and, in effect, reduced the photosynthesis-respiration ratio. Additionally, three similar studies used a cross-factorial experimental design to examine the synergistic effects of elevated temperature and

$pCO_2$ on the survival and growth rate of juveniles. Watson et al. (2012) found that juvenile survival decreased both with increasing temperature and increasing $pCO_2$, with the lowest survival occurring at the highest acidification treatment (1,019 ppm $pCO_2$, versus 416 and 622 ppm) combined with the moderate and highest seawater temperatures (30.0º and 31.5ºC, versus 28.5ºC). Likewise, Syazili et al. (2020) found that elevated warming and acidification significantly reduced juvenile growth rate, as well as the strength and carbonate content of the shell, based on temperature treatments of 30, 32, and 34ºC and $pCO_2$ treatments of 415, 1,000, and 1,800 ppm. Juvenile survival rate was also drastically reduced in the 34ºC treatment and declined progressively under increasing $pCO_2$ conditions (from 415 ppm to 1,800 ppm) (Syazili et al., 2020). However, a separate study by Armstrong et al. (2022) yielded conflicting results indicating that the growth rate of juvenile *T. squamosa* was unaffected by an increase in temperature and approximately doubled under elevated $pCO_2$. Armstrong et al. (2022) also did not observe any increase in juvenile mortality under elevated temperatures. These findings were based on temperature treatments of 28.5º and 30.5ºC crossed with $pCO_2$ treatments of 450 and 950 ppm, meant to simulate present-day and end-of-century conditions.

The apparent contradiction of the latter two studies may be due to the difference in the severity of the most extreme treatments, as the greatest effects in Syazili et al. (2020) were observed at 34ºC and 1,800 ppm $pCO_2$. The test conditions used by Armstrong et al. (2022) were only 30.5ºC and 950 ppm $pCO_2$, which are more representative of projected end-of-century conditions. This does not explain, however, the conflicting findings by Watson et al. (2012) and Armstrong et al. (2022), which used similar temperature and $pCO_2$ treatments across an equivalent 60-day experimental period. According to Armstrong et al. (2022), low irradiance may have played a role in the reduced juvenile survival observed by Watson et al. (2012), as the average photosynthetically active radiation (PAR) in that study was 65.1 µmol photons $m^{-2}$ $s^{-1}$. By comparison, Armstrong et al. (2022) reported an average PAR of 340 µmol photons $m^{-2}$ $s^{-1}$, which is likely more representative of typical light levels on shallow-water coral reefs (Edmunds et al., 2018).

Elevated temperatures have also been shown to enhance fertilization success but significantly reduce trochophore survival (Neo et al., 2013). Only 3.6-13.9% of trochophores survived 24 hours of exposure to 29.5ºC compared to 32.5-46.8% survival at 22.5ºC. Additionally, Junchompoo et al. (2013) observed bleaching in 12 adult *T. squamosa* near Mannai Island, Thailand following a prolonged period of elevated temperatures (>2 weeks of temperatures between 28.1 and 31.1ºC). Eight of the 12 individuals died following the bleaching event.

Based on this information, it is likely that ocean warming and acidification will negatively impact *T. squamosa* fitness; although, as discussed with respect to the threat of inadequate international climate change regulations above and in **Section 3.5**, the local and regional heterogeneity in projected ocean warming and acidification impacts will likely result in variable impacts across the species' expansive range. For this reason and given the broad distribution of remaining *T. squamosa* populations, we conclude with **Medium** confidence that ocean warming may, in combination with other VP descriptors or threats, contribute to the long-term extinction risk of *T. squamosa*, but is unlikely a significant threat on its own (**Low** risk).

### *Land-Based Sources of Pollution*

As discussed in **Section 3.5.3**, sedimentation, salinity fluctuations, nutrient enrichment, and elevated heavy metal concentrations represent environmental conditions that giant clams may experience following heavy rains, particularly near coastlines that have been altered by human development. Given its distribution which includes shallow nearshore habitats, *T. squamosa* is likely exposed to these threats to some degree. However, beyond what is provided in **Section 3.5.3** related to giant clams generally, there is limited information regarding the impacts of these factors on *T. squamosa* specifically. Two studies found that *T. squamosa* larvae are tolerant to hyposaline conditions and are even able to survive for up to five hours in distilled freshwater (Neo et al., 2013; Eckman et al., 2014).

Several experimental studies have documented the direct impacts of sedimentation on *T. squamosa* physiology and behavior. When placed in sediment-laden waters, *T. squamosa* exhibited partial and full contraction of its mantle, as well as exhalation of the mantle cavity (Elfwing et al., 2001). In another similar experiment, *T. squamosa* was observed ejecting sand from the mantle cavity using sharp muscle contractions, removing most of the material within an hour (Soo & Todd, 2014). In a shading trial, Guest et al. (2008) found that the mean growth rate of *T. squamosa* juveniles declined significantly with decreases in available light, although the authors noted that the species is able to maintain positive growth rates even at the lowest light levels (12% ambient levels). We could not find any studies directly investigating the effect of sedimentation on survival; however, as discussed in **Section 3.1.2**, similarities in the biology and behavior of giant clam larvae to that of coral larvae would suggest that comparable results between the taxa can reasonably be expected. In this respect, there is extensive evidence that heavy sedimentation can significantly reduce reproductive success by inhibiting larval settlement, interfering with settlement cues, and physically smothering newly-settled recruits. Thus, while the available research suggests that adult and juvenile *T. squamosa* can likely tolerate transient sedimentation events, sustained sedimentation may significantly inhibit larval recruitment and the recovery of populations that have been reduced by overexploitation or by other means.

Based on this information, it appears that *T. squamosa* is resilient to salinity fluctuations and elevated turbidity, two conditions that giant clams may experience in nearshore areas adjacent to river outflows and coastlines that have been altered by human development. As is discussed in **Section 4.6.3.1**, the impacts of coastal development are heterogeneous throughout the range of *T. squamosa* and likely most severe adjacent to highly populated areas of the central Indo-Pacific (e.g., Indonesia, Malaysia, Papua New Guinea, Philippines). The threat is likely less severe throughout the Pacific Island nations, where human development has been less intense, and in Australia, where water quality management has historically been more effective. Given this geographic heterogeneity and the apparent resilience of *T. squamosa* to expected impacts, we conclude that this threat is unlikely to contribute significantly to the long-term or near future risk of extinction by itself or in combination with other VP descriptors or threats (**Very Low** risk, **Low** confidence).

### *Stochastic Events*

While stochastic events such as extreme weather and mass mortalities of unknown cause may result in severe population loss in localized areas, these threats inherently cannot be predicted with any precision (**Low** confidence). Considering the expansive range of *T. squamosa*, including several regions of relatively high abundance, we find it unlikely that this threat contributes significantly to the species' long-term or near future risk of extinction by itself or in combination with other VP descriptors or threats (**Very Low** risk).

**Table 24.** Summary of the threats analysis for *T. squamosa* and associated confidence ratings.

| 4(a)(1) Factor | Threat | Contribution to Species' Risk of Extinction | Confidence Rating |
|---|---|---|---|
| **Habitat destruction, modification, or curtailment** | *Coastal development* | Very Low | Medium |
| | *Climate change impacts to coral reefs* | Moderate | Low |
| **Overutilization** | | Moderate | Medium |
| **Disease or Predation** | | Very Low | Low |
| **Inadequacy of existing regulatory mechanisms** | *National and local regulations on harvest* | Moderate | Medium |
| | *Regulations on international trade* | Very Low | Medium |
| | *Regulations on climate change* | Low | Medium |
| **Other natural or manmade factors affecting the species' continued existence** | *Physiological impacts of climate change* | Low | Medium |
| | *Land-based sources of pollution* | Very Low | Low |
| | *Stochastic events* | Very Low | Low |

### 4.6.4 Demographic Risk Assessment

***Abundance***

Based on the best available information, historic demand for *T. squamosa* meat and shells, ongoing demand for live specimens for the ornamental aquarium industry, and longstanding subsistence harvest has depleted *T. squamosa* populations in many areas of its range. Yet, despite the widespread exploitation, the species still occurs in all but 2 locations of its natural range, and 19 locations harbor populations that we consider to be "frequent" or "abundant" based on available survey data and anecdotal accounts. Notably, this includes Australia (Great Barrier Reef), Indonesia, and the Philippines, which are the three locations with the most estimated coral reef area (and likely *T. squamosa* habitat) of all locations within the species' range (see Figure 34). Using the UNEP-WCMC coral reef dataset as a very rough approximation, these three locations alone account for nearly half (~47%) of the coral reef area within the range of *T. squamosa*.

Of the 63 locations where *T. squamosa* has been recorded, it is likely "abundant" in 5 locations, "frequent" in 14, "rare" in 32, and extirpated or reintroduced after extirpation in 2 locations, with the other locations characterized as "data deficient." Available reports suggest that abundance is particularly high in the Red Sea and in the South Asia regions, despite these areas being subject to widespread subsistence harvest and, in the case of South Asia, being at the center of the commercial shell and shell craft industry of the 1980s. Given the significant harvest pressure, this pattern suggests that *T. squamosa* populations in these regions are somewhat resilient to population declines, perhaps due to a large historic population size or due to high demographic connectivity facilitating larval exchange and recovery among connected populations within each region. Such a scenario would align with the genetic connectivity observed throughout the Indo-Malay Archipelago, discussed further in **Section 4.6.1.5** and in regard to the **Spatial Structure/Connectivity** threat below.

It is concerning that *T. squamosa* is "rare" at over half of the locations where it has been observed. This means that the average population density is likely less than 10 ind $ha^{-1}$ on average in these locations, or approximately one individual spaced approximately every 30 m. As has been discussed for the other species in this status review, for broadcast spawning organisms like *T. squamosa*, which rely on the external fertilization of gametes, the implications of such sparse distribution on reproduction can be significant. Individuals in rare populations are less likely to spawn in synchrony and as a result are likely to experience infrequent, sporadic reproductive success. This negative relationship between population density and productivity, known as the Allee effect, can cause further reductions in population abundance and put rare populations of *T. squamosa* at greater risk of extinction. Furthermore, the impact of subsistence harvest can be particularly consequential in locations where the abundance of the species is low, because it can reduce the number of reproducing adults and, in effect, constrain the recovery potential of the population. In every location where *T. squamosa* is considered rare, subsistence harvest is still permitted or existing harvest bans have been largely ineffective at eliminating illegal harvest. In these locations, the low abundance of *T. squamosa* exacerbates the extinction risk associated with continued harvest pressure.

Overall, because the species occurs at relatively high abundance in several major regions of its range, particularly in locations where the total area of coral reefs (and likely *T. squamosa* habitat) is relatively high, we find it unlikely that its abundance contributes significantly to the long-term or near-future risk of extinction by itself. However, its low abundance at many locations in the Pacific islands and southeast Africa, where recovery may be hindered by the relative isolation of these populations from the closest regions of abundance, gives some concern that this factor may, in combination with other VP descriptors or threats, contribute to the species' extinction risk (**Low** risk, **Medium** confidence).

### *Productivity*

Despite exceptionally high fecundity, there is substantial evidence that low recruitment success and high mortality rates during early development lead to low productivity in most species of giant clams. *T. squamosa* is estimated to produce approximately 10-100 million eggs during a spawning event (Iwai et al., 2005). However, evidence from other species suggests that survival rates through larval and juvenile development can often be less than 1% (Crawford & Lucas, 1986; Fitt et al., 1984; Jameson, 1976). Additionally, some observations of *T. squamosa* in mariculture suggest that only 5% of clams release eggs and 15% release sperm during an average spawning event (Jintana Nugranad, pers. comm., cited in Kittiwattanawong, 1997). We could find very few surveys that specifically report on the abundance of *T. squamosa* juveniles, but those that do indicate little to no evidence of recruitment in Singapore (Guest et al., 2008; Neo & Todd, 2012) and in Malaysia, where only 3 juveniles were observed across 13 study sites (P. T. Lim et al., 2018). No *T. squamosa* recruits were observed during a recent survey spanning the main islands of Palau (Rehm et al., 2022). In locations where *T. squamosa* is rare, such low productivity can significantly limit the capacity for this species to achieve positive population growth rates and recover from low abundance.

Furthermore, as discussed for the Abundance risk factor above, *T. squamosa* is likely experiencing an Allee effect, such that productivity is negatively correlated with population abundance. As a broadcast spawning organism, *T. squamosa* relies on sufficient population density to respond to the spawning cues of nearby individuals and to facilitate successful external fertilization of their gametes. The best available evidence suggests that spawning synchrony in *T. gigas* drops significantly at population densities lower than 10 ind $ha^{-1}$ (Braley, 1984), and while gametes can remain viable for up to 8 hours in *T. squamosa*, viability decreases significantly with time (Neo, Vicentuan, et al., 2015). Thus, the species' low abundance in many areas of its range likely exacerbates the risk of low productivity.

For these reasons, we conclude that the naturally low productivity of giant clams as well as decreased productivity due to low abundance in many locations contribute significantly to the long-term risk of extinction, but likely does not in itself constitute a danger of extinction in the near future (**Moderate** risk, **Medium** confidence).

***Spatial Structure/Connectivity***

As discussed in **Section 4.6.1.5**, the best available data indicates four (possibly five) genetically isolated clades of *T. squamosa* in the Indo-Malay Archipelago, the northeastern Indo-Pacific (i.e., northern Philippines and Cenderwasih Bay), Red Sea, and western Indian Ocean (there is some evidence that there may be a fifth clade in the eastern Indian Ocean). We could not find any data pertaining to the genetic signature of populations in the Pacific islands or on the Great Barrier Reef and therefore cannot infer the degree of connectivity to these areas. However, the available data regarding spatial structure suggests that the relatively abundant populations in the Indo-Malay and Red Sea region likely do not provide significant larval subsidy to less abundant populations in the western Pacific and western Indian Oceans. Therefore, it is likely that populations in these regions are primarily dependent on local demographics. Reported declines of many *T. squamosa* populations in these regions due to longstanding harvest for subsistence and commercial purposes suggest that the lack of connectivity may be limiting the species' recovery potential in these regions and exacerbating the species' extinction risk range-wide. For this reason, we have some concern that the observed spatial structure, in combination with other VP descriptors and threats, contributes significantly to the long-term extinction risk of *T. squamosa*. However, because the abundance of *T. squamosa* remains relatively high in major portions of its range (e.g., the Indo-Malay Archipelago, Red Sea, and Great Barrier Reef), we find it unlikely that the observed spatial structure contributes significantly to long-term or near future risk of extinction by itself (**Low** risk, **Medium** confidence).

***Diversity***

As is discussed in **Section 4.6.1.5**, the best available data suggest that the genetic diversity of *T. squamosa* in the Indo-Malay region is low relative to *T. maxima* and *T. crocea*, the two other giant clam species with similarly broad distributions. We could not find any studies documenting the genetic diversity of *T. squamosa* in other areas of its range. In general, low genetic diversity may limit adaptive potential, and effectively lower the resilience of populations to environmental change. However, given the species' extensive geographic distribution and relatively broad habitat usage encompassing a wide range of conditions, we find it unlikely that this factor contributes significantly to the long-term or near future extinction risk either by itself or in combination with other VP factors and threats (**Very Low** risk, **Low** confidence).

**Table 25.** Summary of the demographic risk analysis for *T. squamosa* and associated confidence ratings.

| Demographic Risk Factor | Contribution to Species' Risk of Extinction | Confidence Rating |
|---|---|---|
| **Abundance** | Low | Medium |
| **Productivity** | Moderate | Medium |
| **Spatial Distribution/Connectivity** | Low | Medium |
| **Genetic Diversity** | Very Low | Low |

## 4.6.5 Overall Extinction Risk Assessment

Guided by the results of the demographic risk analysis and threats assessment above, we analyzed the overall risk of extinction of *T. squamosa* throughout its range. In this process, we considered the best available scientific and commercial information regarding *T. squamosa* from all locations of the species' range, and analyzed the collective condition of these populations to assess the species' overall extinction risk. We determined that the most critical demographic risk to the species is the low natural productivity of giant clams generally, corroborated by reports of little to no *T. squamosa* recruitment in several recently published surveys from Malaysia, Singapore, and Palau.

There is also concern regarding the species low abundance in over half of the locations where it occurs (i.e., 32 locations where it is considered rare, 2 locations where it has been extirpated or reintroduced following extirpation, and 9 locations where its presence is unconfirmed) and many reports of population decline throughout its range. The low population density of *T. squamosa* in these locations likely exacerbates the low natural productivity and may be hindering the species' recovery in these locations. However, it is significant that the species still occurs in 61 of the 63 locations where it has been recorded, which span an extensive geographic range and encompass a broad array of environmental conditions. Furthermore, there are several locations where *T. squamosa* still occurs at moderate to high abundance. This includes substantial portions of South Asia and the Red Sea, two regions that notably have been subjected to a long history of subsistence harvest, and in the case of South Asia, intense commercial trade of *T. squamosa* shells throughout the 1980s. We consider *T. squamosa* to be "frequent" (10-100 ind $ha^{-1}$) or "abundant" (>100 ind $ha^{-1}$) in locations such as Indonesia, the Philippines, Malaysia, Australia (Great Barrier Reef), the Solomon Islands, and Saudi Arabia, which together host approximately half of the coral reef habitat within the range of *T. squamosa*, and likely also suitable habitat for *T. squamosa* based on the species' known habitat preferences (see Figure 34). Together, these factors suggest that, despite the many reports of population decline in most locations throughout its range, *T. squamosa* may be somewhat resilient to past and current threats, particularly in the Indo-Malay and Red Sea regions.

Without more information about *T. squamosa* productivity (e.g., natural reproductive and recruitment success) and long-term abundance trends, it is difficult to determine the factors that might explain this apparent resilience. One important factor may be that, although *T. squamosa* was harvested extensively for the commercial shell trade in the 1980s, it was not targeted for its meat by commercial entities and illegal poachers with the same intensity as *T. gigas* and *T. derasa*, which severely depleted these species in the South Asia region. It is also possible that the global abundance of *T. squamosa* was historically larger than other giant clam species, or that high demographic connectivity within the Indo-Pacific and Red Sea regions, as is suggested by the available population genetic data, may facilitate significant larval exchange and recovery of depleted populations. Regardless, given the relatively high abundance of *T. squamosa* in major portions of its range combined with its expansive distribution, we concluded that the species' abundance poses a low demographic risk to the species, or in other words is not likely to contribute significantly to the long-term or near-future risk of extinction by itself.

Our threats assessment revealed that past and present overutilization and the inadequacy of existing regulatory mechanisms to address overutilization contribute most significantly to the extinction risk of this species. In the past, *T. squamosa* was harvested extensively in the South Asia region (predominantly in the Philippines) as part of a commercial shell and shell-craft industry. The industry peaked in the 1980s but was later substantially curbed when the Philippines government instituted a ban on the export of giant clam products (except *T. crocea*) in 1990. In the three decades since, the international trade of *T. squamosa* shells and shell products has been minimal. The most significant current and future threat to *T. squamosa* is the longstanding harvest for subsistence or for sale in local markets, which is ongoing in nearly every location where the species occurs. Based on the best available scientific and commercial data, Australia is the only location within the species' range that effectively prevents the harvest of *T. squamosa*. Most other locations do not regulate subsistence harvest, or those that do typically lack the resources to enforce existing harvest restrictions. As such, continued harvest of *T. squamosa* primarily for subsistence purposes, combined with the species' low productivity may drive further population declines and prevent substantial recovery in locations where the species is already rare, including much of southeast Africa and the Pacific islands. We also considered the acute threat of recent commercial harvest in Cambodia and Vietnam to supply the trade of live specimens internationally. However, outside of these two countries, the vast majority of the live *T. squamosa* in international trade has transitioned to culture-raised specimens, which poses a low overall risk to the species across its range.

Lastly, we considered the future threat of climate change both to the quality of *T. squamosa* habitat and to the fitness and survival of the species. As discussed for other giant clam species, it is clear that ocean warming and acidification will drastically alter the composition and structure of coral reefs in the foreseeable future. However, there is not sufficient information to confidently assess the extent to which the survival or productivity of giant clams (even those species closely associated with coral reefs, such as *T. squamosa*) may be impacted by projected changes to coral reef communities (see **Section 4.6.3.1**). Thus, while the potential impacts of climate change on *T. squamosa* habitat quality may contribute significantly to the long-term extinction risk for this species, our confidence in this conclusion is very low, and therefore this factor did not influence the overall assessment of extinction risk for this species. Additionally, with respect to the species' fitness, there is some evidence that *T. squamosa* is sensitive to ocean warming and acidification. A small bleaching event was observed near Mannai Island, Thailand in which 8 of 12 bleached *T. squamosa* ultimately died. Several studies also document various impacts of experimental warming and acidification on early life stages of *T. squamosa*, including changes in growth and fertilization success, as well as increased mortality rates. However, the findings are not consistent between studies (see **Section 4.6.3.5**), and it is notable that the study that is most representative of projected end-of-century temperature and $pCO_2$ conditions found no effect of warming on juvenile survival and found that elevated $pCO_2$ significantly enhanced juvenile growth rate. Moreover, as discussed in **Section 3.5**, local and regional heterogeneity in projected ocean warming and acidification impacts will likely result in variable impacts across the species' expansive range, not only geographically but also across the broad depth range that *T. squamosa* occupies (often 30 m or more). For these reasons, we concluded that ocean warming and acidification likely poses a low extinction risk to this species across its range.

Overall, considering the aforementioned information, we concluded that *T. squamosa* is at **Low** risk of extinction throughout its range based on the following: (1) the high adaptability of the species based on its use of multiple habitat types and tolerance of environmental conditions across a broad depth range; (2) the species' wide spatial distribution with no evidence of range contractions and few extirpations, even in areas where harvest pressure has historically been high; (3) high estimated abundance in locations, such as Australia (Great Barrier Reef), Indonesia, Malaysia, and the Philippines, which make up the majority of coral reef habitat within the species' range; (4) the persistence of the species at relatively high abundance in several locations that have been subjected to extensive commercial and subsistence harvest; and (5) a lack of consistent evidence indicating that ocean warming and acidification will pose a significant threat to the persistence of the species in the foreseeable future. In other words, based on all of the foregoing information, which represents the best available scientific and commercial data regarding the demographic risks and threats to the species, we find it unlikely that the current and projected threats to the species, mainly ongoing subsistence harvest and inadequate local-scale regulations to address it, place the continued existence of *T. squamosa* in question presently or within the foreseeable future.

### *Significant Portion of its Range Analysis*

Under the ESA, a species warrants listing if it is in danger of extinction or likely to become so within the foreseeable future throughout all or a significant portion of its range. Thus, under the ESA, a species may be endangered or threatened throughout all of its range or a species may be endangered or threatened throughout only a significant portion of its range. Having determined that *T. squamosa* is not at moderate or high risk of extinction throughout all of its range, in order to inform the listing determination, we conducted an additional analysis to assess whether the species is at moderate or high risk of extinction in a "significant portion of its range" —that is, we assessed whether there is any portion of the species' range for which it is true that both (1) the portion is significant and (2) the species, in that portion, is at moderate or high risk of extinction. A joint USFWS-NMFS policy, finalized in 2014, provided the agencies' interpretation of this phrase ("SPR Policy," 79 FR 37578, July 1, 2014) and explains that, depending on the case, it might be more efficient for us to address the "significance" question or the "status" question first. Regardless of which question we choose to address first, if we reach a negative answer with respect to the first question, we do not need to evaluate the other question for that portion of the species' range.

As with the SPR analyses for *H. hippopus*, *T. derasa*, and *T. gigas*, because we determined that the most significant threats to *T. squamosa* are overexploitation and the inadequacy of existing regulatory mechanisms, we base our analysis here on the portion of the range where these threats are most severe. As discussed above, several sources indicate that the early adoption of strict harvest prohibitions in Australia has been largely effective at preventing illegal harvest and minimizing the risk of overexploitation of giant clams in Australian waters. This differs considerably from every other location throughout the species' range, where subsistence harvest is either permitted, in some cases with harvest quotas or gear restrictions (see Appendix 1), or where ongoing illegal harvest highlights the inadequate enforcement of existing harvest bans. Thus, for the purpose of this SPR analysis, we distinguish locations in Australia (i.e., the Great Barrier Reef and NW Australia) from all other locations where *T. squamosa* occurs and consider them as two separate portions of the species' range.

The portion under consideration includes 61 countries and territories where the primary threat to the species is overexploitation. In this case, however, exclusion of the two locations in Australia (Great Barrier Reef and NW Australia) does not materially change the conclusion of the species' risk of extinction in this portion of its range. Unlike is the case with *H. hippopus*, *T. derasa*, and *T. gigas*, there are a number of locations, including the Philippines, Indonesia, Malaysia, and much of the Red Sea, where the best available information suggests that *T. squamosa* abundance is quite high and where there is substantial coral reef area, and likely suitable habitat for *T. squamosa* based on the species' known habitat preferences. While it is clear that the species has suffered significant population declines throughout much of this portion of its range, available reports suggest that a major fraction of the loss can be attributed to the intense commercial demand for its shell and shell products in the 1980s, particularly in the South Asia region. Since the early 1990s, when the commercial shell industry in the Philippines began to dwindle, harvest of *T. squamosa* has primarily been limited to smaller-scale operations, mostly for subsistence consumption or for sale in local markets. Without the benefit of long-term monitoring data, we are not able to assess population trends over the last few decades to quantitatively evaluate the effect of the ongoing subsistence harvest. However, given the reports of relatively high abundance in locations such as the Philippines, Indonesia, and Malaysia, where *T. squamosa* has been subjected to both commercial harvest and longstanding subsistence harvest, and much of the Red Sea, where subsistence harvest is common, we find that *T. squamosa* is at **Low** risk of extinction in this portion of its range.

Having determined that *T. squamosa* is not at moderate or high risk of extinction in the portion of its range including all locations outside of Australia, we also considered population genetics as a means of delineating alternative portions of the species' range. As discussed in **Section 4.6.1.5**, the best available population genetic information indicates at least four (possibly five) discrete metapopulations, located in the Red Sea, southeast Africa, Indo-Malay Archipelago, and Cenderwasih Bay in northern Papua (and a possible fifth population in the eastern Indian Ocean). Studies of other broadly distributed species (e.g., *T. maxima* and *T. crocea*) suggest that there may also be genetic breaks between the central and western Pacific islands, and also between the western Pacific and Indo-Malay Archipelago (see **Section 2.6**). However, we were not able to find any studies including data from *T. squamosa* populations in the Pacific islands to confirm these patterns in this species, and cannot rely on these inferences for the purposes of this SPR analysis.

Therefore, we consider the populations of *T. squamosa* in the Red Sea, southeast Africa, Indo-Malay Archipelago, and Cenderwasih Bay as four distinct portions of the species' range. As has been addressed above, the relatively high abundance of *T. squamosa* within the Red Sea and Indo-Malay regions leads us to conclude that the species is likely not at moderate or high risk of extinction in these portions of its range. Furthermore, with respect to the portions in southeast Africa and in Cenderwasih Bay, given their genetic and likely demographic isolation from the majority of the species' range, as well as the relatively small geographic area they occupy, we do not find that these two regions can be considered "significant," or in other words that they likely serve a biologically important role in maintaining the long-term viability of this species. Thus, as a result of this SPR analysis, we do not find any portions within the range of *T. squamosa* for which it is true that both the portion is significant and that the species in the portion is at moderate or high risk of extinction.

## 4.7 *Tridacna squamosina*

### 4.7.1 Life History and Ecology

#### 4.7.1.1 Taxonomy and Distinctive Characteristics

*Tridacna squamosina* was first discovered by Rudolf Sturany (1899) during the early Austro-Hungarian expeditions of the Red Sea (Huber & Eschner, 2011). Seven specimens ranging in size from 102 to 190 mm were catalogued: four from the Gulf of Aqaba, two from Sharm el-Sheikh, and one larger specimen from Kamaran Island, off the coast of Yemen (Huber & Eschner, 2011). More recently, Roa-Quiaoit (2005) re-discovered this species, and it was subsequently described as the new species, *T. costata* (Richter et al., 2008), until further morphological comparison revealed that it was indeed synonymous with *T. squamosina* (Huber & Eschner, 2011). Phylogenetic analyses place *T. squamosina* within the *Chametrachea* subgenus, which also includes *T. squamosa*, *T. maxima*, *T. crocea*, and three recently discovered or resurrected species: *T. noae*, *T. rosewateri*, and *T. elongatissima* (Fauvelot et al., 2020; Tan et al., 2021).

*T. squamosina* exhibits a strong resemblance to *T. squamosa*, but can be distinguished by its asymmetrical shells, crowded scutes, wider byssal orifice, and 5-7 deep triangular radial folds (Roa-Quiaoit, 2005; Richter et al., 2008). Additionally, the mantle is most commonly a subdued brown mottled pattern with a green margin that features prominent “wart-like” protrusions and pale markings following the mantle contour (Richter et al., 2008). These are the main diagnostic features separating *T. squamosina* from its sympatric congeners and are conservatively present even in small clams <10 cm shell length (Richter et al., 2008). *T. squamosina* can reach at least 32 cm in shell length (Neo, Eckman, et al., 2015)—the largest specimen recorded was found in the southern Red Sea at Kamaran Island, off the coast of Yemen (Huber & Eschner, 2011).

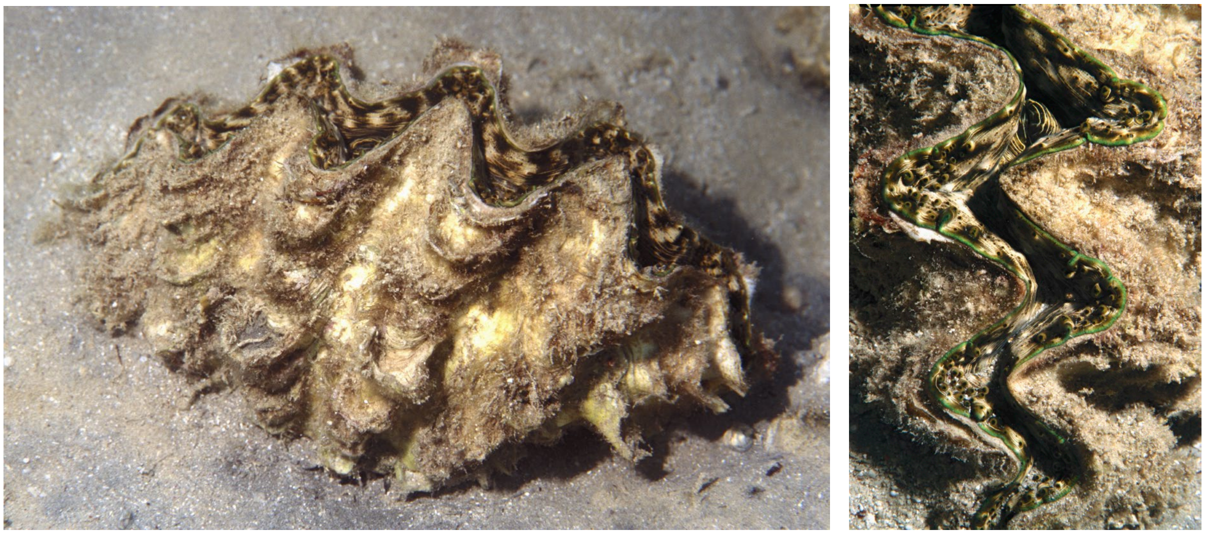

**Figure 36.** *T. squamosina* morphology. Photographs of a *T. squamosina* individual (left) and mantle margin (right). (Photos coutesy of Marc Kochzius).

### 4.7.1.2 Range, Distribution, and Habitat Use

*T. squamosina* is endemic to the Red Sea, with its past and present distribution including the northeastern Gulf of Aqaba, the Sinai coast, and the eastern coast of the Red Sea down to Yemen (Figure 36; Huber & Eschner, 2011; Lim et al., 2021; Richter et al., 2008; Rossbach et al., 2021). There have also been several anecdotal accounts of the species in Mozambique; however, later evidence of genetic divergence between specimens in the Red Sea and Mozambique (Moreels, 2018), as well as the significant geographic distance from its central range, suggests that the reported sightings may be of its recently-resurrected sister species, *T. elongatissima*, with which it shares a close phylogenetic history (Fauvelot et al., 2020; Tan et al., 2021). For this reason, without more information to verify these anecdotal sightings, we do not include the Western Indian Ocean in the natural range of *T. squamosina*. Additionally, in characterizing the close ancestry between *T. squamosina* and *T. elongatissima*, Fauvelot et al. (2020) posited that *T. squamosina* may have originated in the northwestern Indian Ocean and repeatedly colonized the Red Sea during interglacial periods whenever conditions were favorable. The authors base their hypothesis in part on two reports of giant clam valves identified as *T. squamosina* in Pleistocene sediments in the Gwadar region of Pakistan (J.J. ter Poorten, pers. comm., cited in Fauvelot et al., 2020) and in southern Oman (Bosch & Bosch, 1982, cited in Fauvelot et al., 2020). However, with respect to the species' current distribution, we are not aware of any observations of living *T. squamosina* specimens in the Gulf of Aden or Arabian Sea and therefore do not include these regions in the species' natural range.

In a survey of giant clams in the Red Sea, Richter et al. (2008) noted that live specimens of *T. squamosina* were found exclusively in very shallow water habitats (e.g., reef flats, rocky and sandy-rubble flats, seagrass beds, or under branching corals or coral heads shallower than 2 m). Thus, unlike the other two Red Sea species (*T. maxima* and *T. squamosa*), which have broad depth distributions, *T. squamosina* is restricted to the reef top and is usually weakly attached to the substrate (Richter et al., 2008).

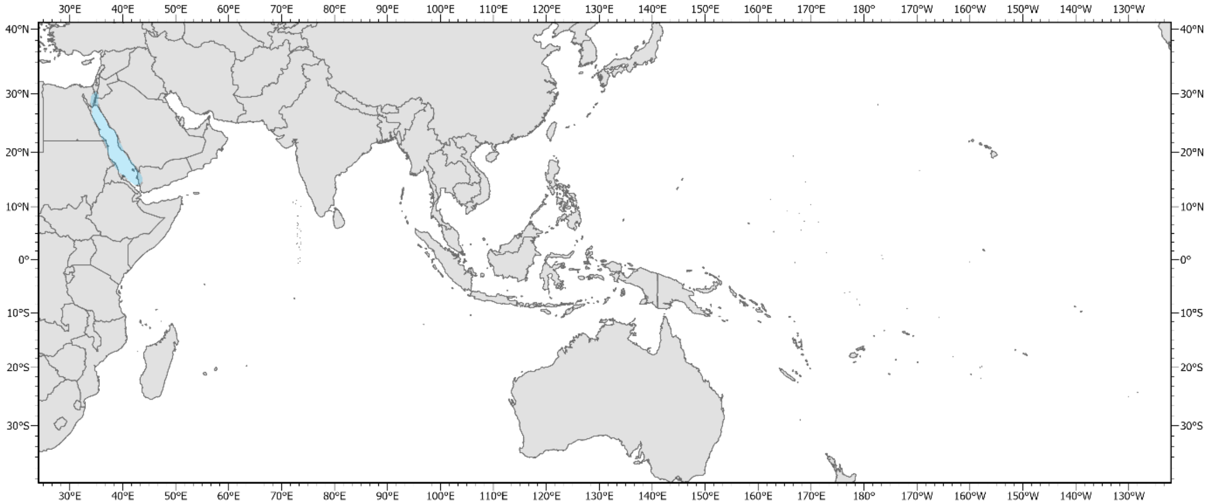

**Figure 37.** Approximate natural range of *T. squamosina* based on reported occurrences provided by Neo et al. (2017).

### 4.7.1.3 Reproduction and Growth

Aside from the life history information available for giant clams in general, there is very limited information regarding the life history of *T. squamosina,* specifically. Information from Richter et al. (2008) suggests a narrow reproductive period for this species, which appears to be a short period in spring that overlaps with the seasonal planktonic bloom. This is markedly different from the seasonal spawning times of the other two Red Sea species, *T. maxima* and *T. squamosa*, which occur later in the summer (Richter et al., 2008). *T. squamosina* also has a smaller ova diameter (75 ± 2 µm) compared to the other two species, which combined with its reproductive timing suggests a planktotrophic development of the larvae (i.e., the larvae feed on plankton) as opposed to the lecithotrophic (i.e., yolk-feeding) larval development in the summer-spawning *T. squamosa* and *T. maxima* (Richter et al., 2008).

#### 4.7.1.4 Feeding and Nutrition

Aside from the general information available on giant clam feeding strategies and diet in general (see **Section 2.4**), we could not find any species-specific information for *T. squamosina*.

#### 4.7.1.5 Genetics and Population Structure

Following the re-discovery of *T. squamosina* in 2005, a number of studies collected genetic data in order to resolve the species' phylogeny within the context of Tridacninae (e.g., Fauvelot et al., 2020; Moreels, 2018; Roa-Quiaoit, 2005). More recently, however, K. K. Lim et al. (2021) used DNA barcoding of two mitochondrial genes (16S and cytochrome oxidase subunit I) to assess the diversity of *T. squamosina* throughout the Red Sea. Only three haplotypes were identified among 24 individuals from the northern and southern Red Sea, and the number of polymorphic loci was very low (n = 5/410, 1%), indicating very low genetic diversity. The authors hypothesized that the low diversity may be the result of a population bottleneck, but cautioned that it may also reflect low natural diversity or a small sample size. Genetic differentiation between the northern and southern samples based on 16S data was very low and statistically non-significant, which the authors note is similar to the pattern observed for *T. maxima* in the same region. This suggests that *T. squamosina* occurs as one panmictic population throughout the Red Sea with very low genetic diversity.

### 4.7.2 Abundance, Density, and Population Status

We are aware of 30 documented observations of *T. squamosina* since its re-discovery. This includes 17 specimens from the Gulf of Aqaba and northern Red Sea (Fauvelot et al., 2020; Huber & Eschner, 2011; Richter et al., 2008; Roa-Quiaoit, 2005), 7 individuals from the Farasan Islands in southern Saudi Arabia (Fauvelot et al., 2020; K.K. Lim et al., 2021), and 6 individuals from an unnamed site in the southern Red Sea (Rossbach et al., 2021). Additionally, Huber and Eschner (2011) described six specimens from the Gulf of Aqaba and southern Sinai and one specimen from Kamaran Island, Yemen that were collected as part of Rudolf Sturany's expedition in 1899. As an indication of its exceptionally low abundance at present, Rossbach et al. (2021) surveyed 58 sites along the entire eastern coast of the Red Sea, from the Gulf of Aqaba down to southern Saudi Arabia, and observed six *T. squamosina* at only one survey site in the southern Red Sea. Similarly, Pappas et al. (2017) did not encounter any *T. squamosina* at nine survey sites in the central Red Sea. Richter et al. (2008) estimated that the average density of the species at sites where it was found was approximately 0.9 (± 0.4) ind ha$^{-1}$.

There are no formal monitoring data to evaluate recent trends in abundance; however, Richter et al. (2008) conducted surveys of well-dated emerged reef terraces in Sinai and Aqaba, historic Bedouin shell middens, and recently discarded shells at presently-used Bedouin boat launch sites to infer the longer-term trends in the composition of Red Sea giant clam communities. Based on this analysis, the authors found that *T. squamosina* constituted greater than 80% of giant clam shell remains prior to the last interglacial (122,000 to 125,000 years ago), but it has since plummeted to less than 5% in freshly discarded shell middens. Although the data do not directly indicate a decline in the absolute abundance of *T. squamosina*, Richter et al. (2008) highlight that Paleolithic artifacts from the region indicate that modern humans have been exploiting Red Sea mollusks for at least 125,000 years. Thus, they find it likely that *T. squamosina*, "by virtue of its dominance, conspicuousness, size, and accessibility," has historically been an important component in the diet of coastal communities during this period, which may have contributed to its current low abundance.

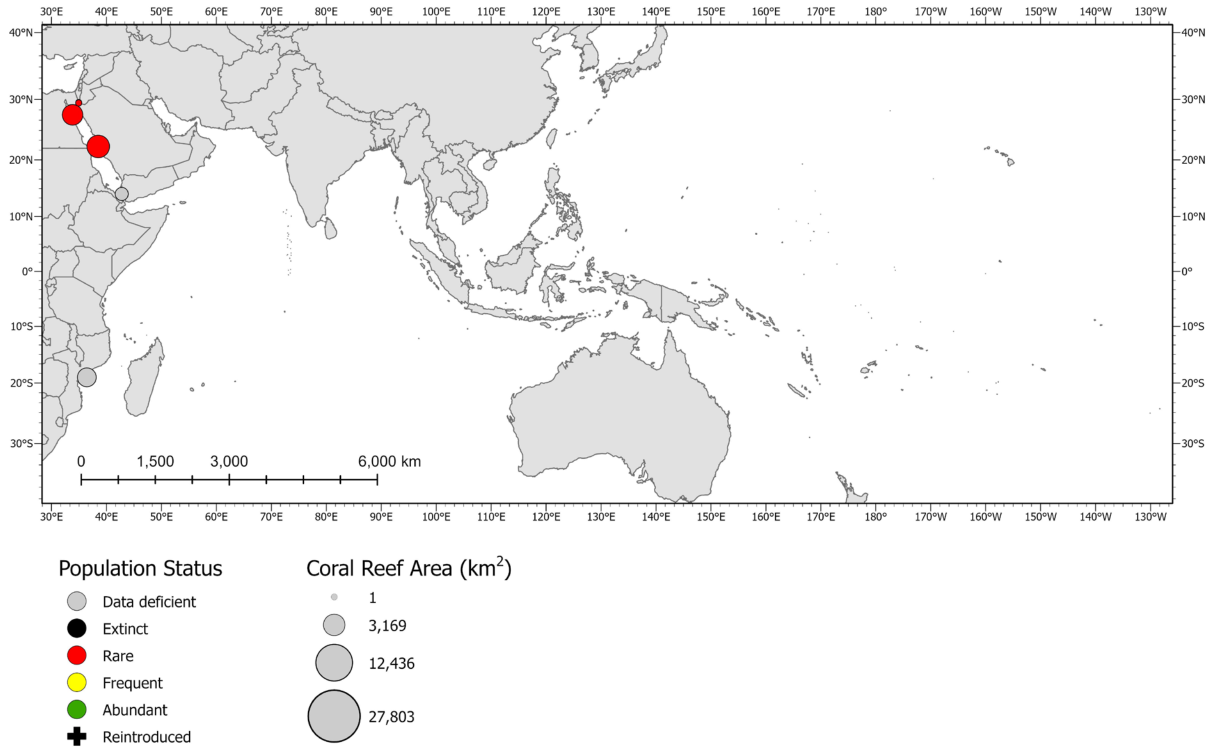

**Figure 38.** Qualitative abundance estimates for *T. squamosina* based on reported occurrence and survey data. Points are located at the approximate centroid of survey sites within each country, territory, or region from which data has been included in the abundance assessment. Abundance categories are based on those used by Neo et al. (2017), but have been revised as follows: Abundant (>100 ind ha$^{-1}$), Frequent (10-100 ind ha$^{-1}$), Rare (<10 ind ha$^{-1}$), Extinct, Introduced, Reintroduced (i.e., locations where the species was reportedly extirpated in the past but there have since been efforts to restore populations using cultured specimens; current presence/abundance may not be known), and Data Deficient (i.e., locations where reports of species occurrence have not been confirmed). The size of the points reflects the total estimated area of coral reefs within each location based on data compiled by the UN Environment World Conservation Monitoring Centre and the WorldFish Centre (UNEP-WCMC et al., 2021), increasing on a square-root scale. It is used here to roughly approximate the relative amount of giant clam habitat. However, the accuracy of this approximation likely varies between species based on their habitat preferences.

## 4.7.3 Threats to *Tridacna squamosina*

### 4.7.3.1 Destruction, Modification, or Curtailment of Habitat or Range

We could not find any information directly linking habitat destruction, modification or curtailment to the low abundance of *T. squamosina*. However, based on its occurrence exclusively in shallow, nearshore habitats (e.g., reef flats, rocky and sandy-rubble flats, seagrass beds, or under branching corals or coral heads shallower than 2 m), it is likely that the species is especially vulnerable to threats impacting these areas. This includes sedimentation and anthropogenic pollution, for example, which is likely to be most severe in nearshore environments adjacent to areas of intense urban development.

Gladstone et al. (2013) noted distinct areas of the Red Sea coastline that have been targeted for development of tourist activities and infrastructure, including Hurghada and the Gulf of Aqaba coastline from Sharm el-Sheikh to Nuweiba (Egypt), Eilat (Israel), and Aqaba (Jordan). These areas are significant, as they directly overlap with the majority of recent *T. squamosina* observations. According to Roa-Quiaoit (2005), an estimated 70% of the Jordanian coastline has been developed into ports, industrial centers, and tourism areas over the past several decades. Additionally, near Hurghada, Mekawy and Madkour (2012) observed dredging activities associated with a newly-constructed harbor and offshore trash disposal from boats. The authors also described industrial and tourist activities in several other areas along the coast of mainland Egypt (e.g., oil drilling in El-Esh, dense industrial and tourism-related development near Safaga Harbor, high human activity in Quesir), which they argue has likely been the principal factor driving the declining *T. maxima* abundance in these areas. Similarly, Hassan et al. (2002) reported "major decreases in giant clam populations between 1997 and 2002, with many small clams seen in 1997 not surviving through to 2002." The authors attributed this population loss directly to sedimentation from major construction activities in South Sinai. While these studies address impacts on giant clams broadly, *T. squamosina* likely experiences a similar threat in these areas. Lastly, Pappas et al. (2017) suggest that coastal development may, in combination with over-exploitation, explain the apparent absence of *T. squamosina* in the central Red Sea, but do not provide any data to support this claim.

Although we do not have any data specifically linking habitat destruction, modification, or curtailment with the abundance of *T. squamosina* (**Low** confidence), based on the species' distribution in nearshore habitats, documented evidence of the impact of coastal development on *T. maxima*, and ongoing regional development goals, we conclude that this threat contributes significantly to the species' long-term extinction risk and is likely to contribute to its short-term extinction risk in the near future (**High** risk).

Because *T. squamosina* is often found in sandy environments outside of the coral reef framework, the anticipated impacts of climate change (i.e., ocean warming and acidification) on coral reefs likely will not pose a severe threat to this species.

#### 4.7.3.2 Overutilization

Specific data on the exploitation rate of *T. squamosina* are not available, as there is no formal fishery for giant clams in the Red Sea. However, several studies provide some insight as to the impact of past and current harvest on the abundance of the species. As discussed in **Section 4.7.2**, Paleolithic artifacts indicate that modern humans have been exploiting mollusks in the Red Sea for at least 125,000 years (Richter et al., 2008). During this time, Richter et al. (2008) found that giant clam communities in the Red Sea have changed dramatically from before the last interglacial period (122,000 to 125,000 years ago), when *T. squamosina* constituted approximately 80% of the shell remains, to *T. squamosina* comprising less than 5% of shells in freshly discarded shell middens. While the authors acknowledge that variable recruitment rates and mortality among the three Red Sea giant clam species may be attributed to natural disturbances, a concurrent decline in the size of giant clam shells strongly suggests that over-exploitation has played a significant role (Richter et al., 2008). In general, giant clam stocks in the Red Sea (including *T. maxima*, *T. squamosa*, and *T. squamosina*) have declined to less than 5% of their historic abundance in the 1980s and 1990s, largely due to artisanal reef-top gathering for meat and shells (Richter et al., 2008).

The distribution of *T. squamosina* in shallow, nearshore habitats makes it particularly accessible to reef-top gatherers and exacerbates the threat of over-exploitation. Bodoy (1984) reported that giant clams had been subject to "heavy exploitation in the vicinity of Jeddah, Saudi Arabia, and they [were] often collected on the reef flat, both for food and for decorative purposes." Additionally, two firsthand accounts from Gladstone (2000, 2002) described the harvest of "a significant number of clams" (primarily *T. maxima*) from the Kharij As Sailah and Kharij Al Qabr areas of the Farasan Islands, noting that "clams were easily harvested in the shallow reef flats." Pappas et al. (2017) hypothesized that such intense harvesting pressure may, in combination with coastal development, partially explain the apparent absence of *T. squamosina* in the central Red Sea; although, no specific data are provided to support this claim. According to Neo et al. (2017), the harvest of giant clams remains prevalent in the Red Sea, but again, no specific data are provided to support this claim.

Overall, the best available information suggests that giant clams have been harvested extensively in the Red Sea for many years. Given their traditional importance in the diets of coastal communities, harvest is likely ongoing in most areas of the Red Sea. In combination with the natural accessibility of *T. squamosina* in shallow nearshore areas, this past and ongoing harvest pressure has likely contributed significantly to the low abundance of this species throughout the region, and with so few *T. squamosina* remaining, we conclude that this factor is likely to contribute to the short-term extinction risk in the near future (**High** risk, **Medium** confidence).

#### 4.7.3.3 Disease or Predation

We could not find any species-specific information regarding disease or predation for *T. squamosina* beyond what is provided for giant clams generally in **Section 3.3**. Thus, we cannot make a confident assessment of the contribution of this factor to the extinction risk of *T. squamosina*.

#### 4.7.3.4 Inadequacy of Existing Regulatory Mechanisms

The principal regulatory mechanism relevant to the protection of giant clams in the Red Sea is the establishment of marine protected areas (MPAs). Based on the known distribution of *T. squamosina*, there are three MPAs that are most relevant to the species: Ras Mohammed National Park in South Sinai, Aqaba Marine Park in Jordan, and the Farasan Islands Protected Area in southern Saudi Arabia. These are three areas where *T. squamosina* has previously been observed, and remaining populations likely benefit from the prohibitions against hunting or collecting wildlife within the boundaries of the MPAs. According to Gladstone (2000), a prohibition on the collection of giant clams in the Farasan Islands appeared to be effective, with harvest-related mortality falling to 1.7%, compared to an estimated 11.1-47.8% mortality rate before the regulation. Ras Mohammed National Park is also regarded as effective in the protection of 345 km$^2$ of marine area, which includes important fringing reef habitats in the southern portion of the Gulf of Aqaba. Based on an assessment of the administration of the park and the quality of marine habitats within its boundaries, the IUCN listed Ras Mohammed National Park on its Green List in recognition of its conservation success.

Collectively, however, these three protected areas encompass only 5,756 km$^2$ of the coastal marine area in the Red Sea. Throughout most of the region, harvest of giant clams remains largely unregulated. Several sources have indicated that the collection of giant clams was banned by the Saudi Arabian National Commission for Wildlife Conservation and Development in the early 2000s (Rossbach et al., 2021; Watson & Neo, 2021), citing the country's First National Report upon signing on to the Convention on Biological Diversity (AbuZinada et al., 2004). However, it appears that this report only identifies *Tridacna* spp. as "Taxa of High Conservation Priority," based on their "critically endangered, endangered, or vulnerable" status and their economic importance, but does not specify any regulations associated with this designation. Rather, the National Strategy for Conservation of Biodiversity in the Kingdom of Saudi Arabia, which was published a year later, states that "restrictions *could* [emphasis added] be imposed to regulate the harvest of mollusks such as giant clams," indicating that such restrictions had not yet been established. We could not find any updated reports or regulations related to the protection of giant clams in Saudi Arabia; thus, we consider harvest to remain unregulated outside of MPAs. This is further supported by a short video that was uploaded to YouTube on September 2, 2021, which shows two recreational divers harvesting giant clam meat off the coast of Al Hassi in central Saudi Arabia ("Hunting Giant Clams in Red Sea at Al Hassi Saudi Arabia," 2021). We could not find regulations related to the harvest of giant clams in any of the other countries bordering the Red Sea.

As described in **Section 4.7.3.2**, historical harvest of giant clams has likely led to the exceptionally low abundance of *T. squamosina* in the Red Sea, and there are reports that harvest is ongoing in most locations. Thus, given the lack of national regulations pertaining to the harvest of giant clams in the Red Sea, we find that the inadequacy of existing regulatory mechanisms contributes significantly to the long-term extinction risk for *T. squamosina*. However, because several MPAs have been established in key areas where the species has been recently observed, we conclude that this factor does not in itself constitute a danger of extinction in the near future (**Moderate** risk, **High** confidence).

In terms of international regulations, *T. squamosina* was listed under Appendix II of CITES in 1985. All of the countries bordering the Red Sea are Parties to the Treaty; however, because of its rarity, there has never been an international commercial export market for *T. squamosina* to our knowledge. Thus, CITES regulations are largely irrelevant to the extinction risk for this species.

Lastly, with respect to international climate change regulations, we conclude in **Section 3.4.2** that the current implementation of domestic and international climate regulations is insufficient to mitigate the cumulative threat of climate change to giant clam habitat and physiology generally. However, because *T. squamosina* is often found in shallow, nearshore habitats (e.g., reef flats, rocky and sandy-rubble flats, seagrass beds, or under branching corals or coral heads shallower than 2m), the anticipated impacts of climate change on coral reefs will not likely pose a severe threat to this species. Thus, international climate change regulations are likely most relevant to *T. squamosina* in terms of the impacts of ocean warming and acidification on species physiology. We were unable to find any information on the effects of climate change to *T. squamosina* specifically, but inferences based on findings from other species suggest that *T. squamosina* may experience significant physiological changes under projected ocean warming scenarios. The precise magnitude of these impacts is unknown, but any significant changes in metabolic demand, reproductive success, and the possibility of bleaching due to warming summer temperatures, will likely increase the risk of extinction. For this reason, we find that the inadequacy of international climate change regulations may, in combination with the aforementioned impacts, contribute significantly to the long-term or near future risk of extinction, but is unlikely a significant threat on its own (**Low** risk, **Medium** confidence).

### 4.7.3.5 Other Natural or Manmade Factors

***Climate Change***

Beyond the information presented in **Section 3.5**, we could not find any research addressing the potential effects of climate change on *T. squamosina* specifically.

As discussed above, there is substantial research on the effect of ocean warming in other giant clam species (i.e., reports of bleaching, impacts on reproduction and early development, alterations to metabolic demand). However, it is possible that susceptibility may vary considerably among species. For example, a species like *T. squamosina* that resides preferentially in shallow habitats where temperature fluctuations can be quite extreme may have adapted a higher tolerance to such conditions. For these reasons, given the findings from other species that ocean warming will likely negatively impact physiology and reproduction, and may lead to bleaching and possible mortality during high-temperature anomalies, we conclude that ocean warming may, in combination with other VP descriptors or threats, contribute to the long-term extinction risk of *T. squamosina* (**Low** risk). However, because of the lack of information related to *T. squamosina* and the possibility that susceptibility may vary from the species on which these conclusions are based, we have very **Low** confidence this conclusion.

We were not able to find any additional information regarding the potential impacts of ocean acidification on *T. squamosina* beyond what is provided in **Section 3.5.2**. As discussed in **Section 3.5.2**, the available information regarding the effects of ocean acidification on giant clams more broadly is limited and inconclusive.

***Land-based sources of pollution***

As discussed in **Section 3.5.3**, sedimentation, salinity fluctuations, nutrient enrichment, and elevated heavy metal concentrations represent environmental conditions that giant clams may experience following heavy rains, particularly near coastlines that have been altered by human development. Given its common occurrence in shallow nearshore habitats and reports of significant development in several areas adjacent to important giant clam habitat, *T. squamosina* is likely highly exposed to these threats. However, beyond what is provided in **Section 3.5.3** related to giant clams generally, we could not find any information regarding the impacts of these factors on *T. squamosina* specifically.

**Section 3.5.3** addresses many impacts of sedimentation, salinity, nutrient enrichment, and elevated heavy metal concentrations that have been observed for other species of giant clams. Overall, the results provide some indication that these factors may reduce fitness in certain respects; although, the effects are often not consistent between species and, in some cases, the experimental treatments do not reflect conditions that giant clams may realistically experience in the natural environment. For these reasons, we are reluctant to extrapolate these results to our assessment of *T. squamosina*. Given this uncertainty and the likely localized nature of these impacts near areas of high runoff, we conclude with **Low** confidence that sedimentation, salinity fluctuations, nutrient enrichment, and heavy metal contamination are unlikely to contribute to the risk of extinction for *T. squamosina*, either by itself or in combination with other VP descriptors or threats (**Very Low** risk).

### *Stochastic Events*

While stochastic events such as extreme weather and mass mortalities of unknown cause may result in severe population loss in localized areas, these threats inherently cannot be predicted with any precision. However, because *T. squamosina* occurs at such low abundance and has been recently observed in only three locations, the possibility of a mass mortality event, similar to what has been observed in other giant clam species, poses a significant threat the species' persistence. Thus, we conclude that the threat of stochastic mortality events may, in combination with the species' low abundance, contribute significantly to the long-term extinction risk of *T. squamosina* (**Low** risk, **Low** confidence).

**Table 26.** Summary of the threats analysis for *T. squamosina* and associated confidence ratings.

| 4(a)(1) Factor | Threat | Contribution to Species' Risk of Extinction | Confidence Rating |
|---|---|---|---|
| **Habitat destruction, modification, or curtailment** | *Coastal development* | High | Low |
| | *Climate change impacts to coral reefs* | Very Low | Medium |
| **Overutilization** | | High | Medium |
| **Disease or Predation** | | *Unknown* | *Not applicable* |
| **Inadequacy of existing regulatory mechanisms** | *National and local regulations on harvest* | Moderate | High |
| | *Regulations on international trade* | Very Low | High |
| | *Regulations on climate change* | Low | Medium |
| **Other natural or manmade factors** | *Physiological impacts of climate change* | Low | Low |

| | | | |
|---|---|---|---|
| **affecting the species' continued existence** | *Land-based sources of pollution* | Very Low | Low |
| | *Stochastic events* | Low | Low |

## 4.7.4 Demographic Risk Assessment

### *Abundance*

As is discussed in **Section 4.7.2**, there have been 30 documented observations of *T. squamosina* since its re-discovery in 2008, including 17 specimens from the Gulf of Aqaba and northern Red Sea, 7 individuals from the Farasan Islands in southern Saudi Arabia, and 6 individuals from an unnamed site in the southern Red Sea. The species was absent from all but one of the 58 survey sites visited by Rossbach et al. (2021) along the eastern Red Sea coast, including all sites in central and northern Saudi Arabia.

Given its exceptionally low abundance, sparse distribution, and highly restricted range, *T. squamosina* is highly susceptible to the ongoing and future threats described in **Section 4.7.3**, including habitat destruction and modification, continued artisanal harvest, and the inadequacy of existing regulations. Potential population reductions due to these factors threaten the persistence of remaining populations, and in effect, significantly elevate the extinction risk of *T. squamosina*. For this reason, we find that the species' low abundance puts it in danger of extinction in the near future (**Very High** risk, **High** confidence).

### *Productivity*

While we are not aware of any estimates of productivity for *T. squamosina*, based on the consistency of observations from other species of giant clams, it is likely that *T. squamosina* is similar to its congeners, in that fecundity is likely high, but recruitment success and juvenile survival are very low. Given the exceptionally low abundance of *T. squamosina* and the ongoing threats outlined in **Section 4.5.3**, such low productivity can significantly limit the capacity of this species to achieve the positive population growth rates that are necessary for its recovery.

Furthermore, it is likely that *T. squamosina* is experiencing an Allee effect, such that productivity is negatively correlated with population abundance. As a broadcast spawning organism, *T. squamosina* relies on sufficient population density to facilitate successful external fertilization of their gametes with neighboring individuals. It is possible that, at such low abundance and population densities, *T. squamosina* may rely to some extent on self-fertilization to produce offspring. However, as is discussed in **Section 2.3**, separation of the timing of sperm and egg release likely limits this possibility in most individuals, and when it does occur, several species of giant clams have been found to experience significant fitness effects, such as reduced larval survival and growth rates. For these reasons, we do not consider self-fertilization to play a significant role in the productivity or population growth of *T. squamosina*.

Overall, we find that the low natural productivity of giant clams as well as the negative correlation of productivity with low abundance contributes significantly to the long-term extinction risk of *T. squamosina*, and given the exceptionally low abundance of the species, is likely to contribute to the short-term risk of extinction in the near future (**High** risk, **Medium** confidence).

***Spatial Distribution/Connectivity***

In the only study to date which investigated the spatial structure or connectivity of *T. squamosina* across its range, K.K. Lim et al. (2021) found that genetic differentiation between the samples collected in the northern and southern Red Sea was very low and statistically non-significant. Therefore, we find it unlikely that this factor contributes significantly to the extinction risk for *T squamosina*, either by itself or in combination with other VP descriptors or threats (**Very Low** risk, **High** confidence).

***Genetic Diversity***

As discussed in **Section 4.7.1.5**, K.K. Lim et al. (2021) measured very low 16S haplotype diversity and very few polymorphic loci, indicating that genetic diversity in *T. squamosina* is very low. The authors hypothesized that the low diversity may be the result of a population bottleneck, but cautioned that it may also reflect low natural diversity or a small sample size. In general, low genetic diversity may limit adaptive potential, and effectively lower the resilience of populations to environmental change. Thus, we have some concern that this factor may, in combination with the low abundance of the species, contribute to the long-term or near future extinction risk for *T. squamosina* (**Low** risk). However, given the uncertainty associated with the one available estimate of genetic diversity for this species, our confidence in this assessment is **Low**.

**Table 27.** Summary of the demographic risk analysis for *T. squamosina* and associated confidence ratings.

| **Demographic Risk Factor** | **Contribution to Species' Risk of Extinction** | **Confidence Rating** |
|---|---|---|
| **Abundance** | Very High | High |
| **Productivity** | High | Medium |
| **Spatial Distribution/Connectivity** | Very Low | High |
| **Genetic Diversity** | Low | Low |

## 4.7.5 Overall Extinction Risk Assessment

Guided by the results of the demographic risk analysis and threats assessment above, we analyzed the overall risk of extinction of *T. squamosina* throughout its range. In this process, we considered the best available scientific and commercial information regarding *T. squamosina* from all locations of the species' range and analyzed the collective condition of these populations to assess the species' overall extinction risk. The best available information suggests that *T. squamosina* occurs at exceptionally low abundance and is sparsely distributed throughout its highly restricted range. Since the re-discovery of the species in 2008, there have been only 30 recorded observations of *T. squamosina*, which are divided between the Gulf of Aqaba in the northern Red Sea and two sites including the Farasan Islands in the south. The inherent risks of such low abundance are compounded by low natural productivity, which likely prevents any substantial recovery of the species in the near future. Additionally, our threats assessment revealed that past and present overutilization and associated inadequacy of existing regulatory mechanisms at the local level contribute most significantly to the extinction risk of this species. *T. squamosina* has historically been and continues to be collected for subsistence consumption and for sale in domestic markets, and the existing regulatory mechanisms are limited to the management of a few protected areas, affording little protection to the species in the remainder of its range. Based on our assessment of these threats and demographic risk factors, we conclude that *T. squamosina* is at a **High** risk of extinction throughout its range.

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# 6.0 Appendices

**Appendix 1.** Local regulations related to the conservation of giant clams throughout their range.

| **Localities** | **CITES** Entry into force | **Regulations** |
|---|---|---|
| **Red Sea** | | |
| Djibouti | 1992 | There are two marine protected areas (Moucha and Maskali) that prohibit the collection of corals and mollusks (with the exception of artisanal fishing of edible species; Neo et al., 2017). |
| Egypt | 1978 | The Nabq Managed Resource Protected Area was established in 1992 by Egyptian Environmental Affairs Agency (Law 102), becoming part of a network of five parks and protected areas in South Sinai Protectorates. It is a 112 sq. km multi-use management are stretching 47 km along the east coast of the Sinai Peninsula in the Gulf of Aqaba (Benzoni et al., 2006). |
| Eritrea | 1995 | We were unable to find regulations specific to giant clams. |
| Israel | 1980 | We were unable to find regulations specific to giant clams. |
| Jordan | 1979 | The Law of Environmental Protection No. 12 passed in 1995, bans the harming of or removal of coral and shellfish from the Gulf of Aqaba (NMFS, 2012). |
| Saudi Arabia | 1996 | Giant clams were listed as "Taxa of High Conservation Priority" in Saudi Arabia's First National Report to the Convention on Biological Diversity in 2004 (AbuZinada et al., 2004), but we could not find any national regulations associated with this designation. |
| Somalia | 1986 | Due to the country's political instability, national conservation legislation is non-existent (Neo et al., 2017). |
| Sudan | 1983 | Sanganeb Marine National Park may contain unexploited populations (Neo et al., 2017) |
| Yemen | 1997 | There are un-fished and protected areas (e.g., the Socotra Archipelago; Neo et al., 2017). |
| **South-East Africa** | | |
| Cargados Carajos Archipelago | Part of the territory of Mauritius 1975 | We were unable to find regulations specific to giant clams. |
| Comoros | 1995 | We were unable to find regulations specific to giant clams. |
| Kenya | 1979 | Kenya has four fully protected marine areas (Marine National Parks) that prohibit any extractive use with the exception of samples for research. Kenya has a total area of 54 km² with full protection as Marine National Parks (NMFS, 2012). Kenya also has seven Marine National Reserves covering an area of 1509 sq. km, which prohibit commercial harvest but allow traditional harvesting of resources as well as tourism and research (Spalding et al., 2001). |
| Madagascar | 1975 | We were unable to find regulations specific to giant clams. |
| Mauritius | 1975 | The Fisheries Regulation 1983 listed Tridacna spp. as 'toxic species' and landing them was prohibited (Wells, 1997). More recently giant clams were protected under the Fisheries and Marine Resources Act 2007 and it is considered illegal to possess them (Ramah et al., 2018). |

| **Localities** | **CITES** Entry into force | **Regulations** |
|---|---|---|
| Mayotte | Dependent territory of France 1978 | We were unable to find regulations specific to giant clams. |
| Mozambique | 1981 | In Quirimbas National Park, fishing by local residents using traditional techniques is permitted. There is no fishing in 30 percent of the national park. In certain zones within the park, it is prohibited to damage coral; take live fish for sale; use gillnets, spearguns, or harpoons; or to kill fish using chemicals, poisons, or explosives. Tourists are not permitted to fish at night. The marine and terrestrial Ramsar site is Marromeu Complex. These areas include lagoon and/or coral reef habitat (NMFS, 2012). |
| La Réunion | Region of France 1978 | Approximately 40 percent of the island of Réunion is part of a France's 9th national park, called La Réunion National Park and was created in 2007. It is one of the protected natural environments in France's Overseas Departments. To combat coral reef degradation, Réunion has also funded a National Natural Marine Reserve with an area of 35 km², encompassing 80% of the island's coral reefs. Under the name of Villages Créoles, there is a network of fifteen communities that are engaged in a quality, responsible approach. Within the reserve, there are three levels of protection: level 1, restricts certain uses; level 2, allows commercial fishing in 20 percent of this area and traditional fishing in certain places; and level 3 prohibits all activities including work, traffic, and moorings, but permits may be obtained for scientific purposes. There are a few fishing restrictions in the reserve, including no night fishing and no recreational fishing, net fishing, or spearfishing in enhanced protection zones. The network's goal is to participate in the development of populations and areas, and to contribute to the preservation of the environment, natural resources, and biodiversity. In 2007, the Réunion National Natural Marine Reserve Won an award in the Culture and Heritage category at the Responsible Tourism Awards (NMFS, 2012). |
| Seychelles | 1977 | The purchase or sale of unworked giant clams is prohibited and the permitted possession of over 20kg or the export of over 2kg requires the permission from the Seychelles Fishing Authority. On the east coast of Mahe, the northern coast of La Digue and the northern coast of Praslin the collection or disturbance of giant clams is prohibited (Seychelles, 2010 - UNEP 2012 status of giant clams). |
| South Africa | 1975 | We were unable to find regulations specific to giant clams. |
| Tanzania | 1980 | A privately owned nature reserve called Chumbe Island Coral Park (CHICOP) has been in existence since 1991 (Neo et al., 2017). |
| **Indian Ocean** | | |
| Christmas Island | Australian external territory 1976 | The Christmas Island National Park protects 63 percent of the Island. The park prohibits commercial fishing or the taking of any organism or object for sale (NMFS, 2012). |
| Cocos (Keeling) Islands | Australian external territory 1976 | The recreational harvest of giant clams is unregulated (Neo et al., 2017). |

| **Localities** | **CITES** Entry into force | **Regulations** |
|---|---|---|
| Chagos | British Indian Ocean Territory | We were unable to find regulations specific to giant clams. |
| India | 1976 | All giant clam species inhabiting Indian waters, except *T. crocea*, are legally protected as Schedule 1 species under the Wildlife Protection Act of India (1972) (Apte et al., 2010 cited in Neo et al., 2020). |
| Maldives | 2013 | The Ministry of Trade and Industries stopped issuing new licenses for the export of giant clam products in 1991. It was also announced that existing licenses would not be renewed once they expired (Basker 1992). Since May 15, 1993 (Notice No. FA-A1/29/93/14 (15-05-1993)) Giant Clams have been listed as a protected species and the killing, catching and collection of these species has been prohibited (http://www.mvlaw.gov.mv/pdf/gavaid/minFisheries/10.pdf). |
| Sri Lanka | 1979 | The Minister declares when fishing season is open or closed, and if a fisheries reserve offers protection to a species in danger of extinction or promotes regeneration of aquatic life. There is no fishing in a reserve except by permit (NMFS, 2012) |
| **East Asia** | | |
| China | 1981 | Giant clams are protected under the Marine Environment Protection Law of the People's Republic of China. *Tridacna gigas* is the only species listed as Category I protection at the national level, which is the highest protection afforded in China under their Wild Animal Protection Act and prohibits trading under any circumstances (Neo et al., 2020). Five additional species were listed as Category II protected species, including *T. derasa, T. squamosa,* and *H. hippopus,* prohibiting trade of these species except with a permit, which can be issued at provincial government level. The law prohibits selling, purchasing, and utilising national protected wildlife and the products made thereof, including on online platforms. Exceptions are given to scientific research, captive breeding, exhibitions, and other special circumstances, in which cases strict permitting rules are established (Wildlife Justice Commission, 2021).<br>Additionally, on January 1, 2017, the Hainan Province People's Congress passed the 'Regulations on the Protection of the Coral Reef and *Tridacna* in Hainan Province', covering all *Tridacna* species listed in the National Key Protected Wildlife List (only *T. gigas* at the time) and CITES (10 *Tridacna* species under Appendix II. The regulations prohibit digging, fishing, selling (including on e-commerce platforms), purchasing, using, and transporting these giant clam species and any products made thereof (Wildlife Justice Commission, 2021). |
| Japan | 1980 | Recreational fishing of giant clams is prohibited under the Okinawa Prefectural Fisheries Regulations. Failing to observe the rules is an infringement of the Japanese Fisheries Law (Neo et al., 2020). |

| **Localities** | **CITES** Entry into force | **Regulations** |
|---|---|---|
| Taiwan | | The Taiwanese government rejects all requests from private, commercial entities for involvement in giant clam fishing activities. Taitung and Penghu counties have banned the harvesting of giant clams and listed them as protected species. There is also an ongoing effort to develop conservation plans to replenish stocks (Neo et al., 2017). |
| South China Sea (SCS) | | Little regional cooperation compounded by territorial disputes in the South China Sea (Neo et al., 2017). |
| **South Asia** | | |
| Brunei | 1990 | The Fisheries Order of 2009 provides for the establishment of marine reserves to afford special protection to the aquatic flora and fauna and to protect, preserve and manage the natural breeding grounds and habitat of aquatic life, with particular regard to the species of rare or endangered flora and fauna. Activities prohibited in marine reserves include fishing (or attempting to fish), taking or removing of any organisms (alive or dead), collection, possession or destruction of coral, sand, and gravel, discharging any pollutant, alteration or destruction of the natural breeding ground of aquatic life or destroying any aquatic life (NMFS, 2012). Approximately .02% of Brunei's waters are designatred as no take reserve (data.worldbank.org). |
| Cambodia | 1997 | The management and conservation of fisheries resources including the establishment of conservation areas is conducted by the community fisheries (Penh, 2005). |
| East Timor | Non-Party | Giant clams are on the Marine Protected Species list which prohibits the take of listed species (https://www.conservation.org/NewsRoom/pressreleases/Pages/Biodiversity-survey-reveals-reefs-in-Timor-Leste-s-Atauro-Island-hold-the-worlds-highest-reef-fish-species-average-.aspx). |
| Indonesia | 1979 | Seven species of giant clams (*H. hippopus, H. porcellanus, T. crocea, T. derasa, T. gigas, T. maxima, T. squamosa*) were listed on Indonesia's list of protected species in 1987 under the Surat Keputusan Menteri Kehutanan No. 12/Kpts/II/1987. This is now consolidated under the Conservation of Living Resources and their Ecosystems Act, 5/1990, specifically the Government Regulation No. 7/1999 on Preserving Flora and Fauna Species that provides the criteria for specifying protected species (Ezekiel, 2018 cited in Neo et al., 2020). It is prohibited to (a) Catch, transport, and trade in a protected animal in a live condition; (b) Keep, possess, transport, and trade in a protected animal in a dead condition; (c) Transfer a protected animal from one place to another, within or outside Indonesia (d) Trade, keep or possess bodies, or other parts of a protected animal or the goods made of parts of the animal, or transfer from one place in Indonesia to another, within or outside Indonesia. If these laws are violated fines of up to IDR 100,000,000 (~USD 10,000) and imprisonment for up to five years can be imposed. Indonesia allows export of maricultured giant clams (Nijman et al., 2015). |

| **Localities** | **CITES**<br>Entry into force | **Regulations** |
|---|---|---|
| Malaysia | 1978 | Protected under the main Fisheries Act No. 317 (1985), specifically defined by the Fisheries (Control of Endangered Species of Fish) Regulation (1999). The latter lists four species (*T. gigas*, *T. squamosa*, *T. crocea*, and *T. maxima*) and states that no person shall fish for, disturb, harass, catch, kill, take, possess, sell, buy, export, or transport any endangered species of fish (including giant clams) specified in the Schedule except with written permission of the Director-General (Gomez, 2015). |
| Myanmar (Burma) | 1997 | The Department of Fisheries Notification for the Control of Endangered Fish Species lists protected species, including giant clams. It is an offense to capture giant clams as specified in this regulation (Ezekiel, 2018 cited in Neo et al., 2020). |
| Philippines | 1981 | Protected under The Philippine Fisheries Code of 1998 (Republic Act No. 8550). Under this law, all species listed on CITES (including giant clams) are considered "endangered" and may not be taken without a special permit from the Bureau of Fisheries and Aquatic Resources (Gomez, 2015 cited in Neo et al., 2020). |
| Singapore | 1987 | There are no specific laws protecting giant clams outside of CITES regulations. The Endangered Species (Import and Export) Act 1989 regulates trade in giant clams through the issuance of CITES permits. Collection and export of wild specimens from Singapore waters is only allowed under special circumstances, e.g. for research (Singapore CITES Management Authority, in litt. To CITES Secretariat, 1995) (Gomez, 2015; Wells, 1997). |
| Thailand | 1983 | Protected under the current Royal Ordinance on Fisheries B.E. 2558 (2015) (previously known as the Fisheries Act 1947) that prohibits fishing of giant clams (Knight et al., 2010 cited in Neo et al., 2020). Giant clams were given "protected" status under ministerial regulations issued under Section 6 of Wild Animal Reservation and Protection Act No. 3 (2003) (Ezekiel, 2018 cited in Neo et al., 2020). |
| Vietnam | 1994 | The Ministry of Agriculture and Rural Development Decision No. 82/2008/QD-BNN listed three species of giant clams, based on IUCN criteria v2.2 and 2007 Red Book for Vietnam (Ezekiel, 2018 cited in Neo et al., 2020). There is a quota system in place that limits the number of clams exported for the aquarium trade (Neo et al., 2017). |
| **Pacific Ocean** | | |
| Australia | 1976 | The harvest and trade of giant clams is managed under the Envrironment Protection and Biodiversity Conservation Act 1999 (Neo et al., 2020). The collection and domestic sale of giant clams is prohibited, except by Aboriginal people (Braley, 1993; Neo et al., 2017). Commercial harvest and export are also prohibited except for aquaculture/mariculture specimens (CITES Management Authority Australia, 2005). Small-scale collection of clams for scientific purposes or to obtain new broodstock for mariculture operations may be allowed with a permit (Wells, 1997). |

| **Localities** | **CITES** Entry into force | **Regulations** |
|---|---|---|
| Fiji | 1997 | Under the Fisheries Act of 1942 (Cap 158), amended in 1992, the export of giant clam meat from Fiji of three species (*T. derasa*, *T. squamosa*, and *T. maxima*) is prohibited (Neo et al., 2020); although, there is a clause allowing the Permanent Secretary responsible for fisheries to make exceptions for meat proven to originate in a mariculture program. More recently, it was reported that management measures for the harvest of giant clams in Fiji consisted of a ban on commercial harvest and export, except for aquacultured specimens and a bag limit of 3 shells per person (weighing no more than 3 kg) for the tourist trade (Kinch & Teitelbaum, 2010; Neo et al., 2017). |
| New Caledonia | Dependent territory of France 1999 | In the Northern Province, there is a bag limit of five giant clams per vessel per trip for professional fishers, and a bag limit of two for others. In the Southern Province, there is a maximum bag limit of 40 kg (Neo et al., 2017). For tourists there is a limit of 3 shells per person, with a maximum weight of 3 kg (Kinch & Teitelbaum, 2010). |
| Papua New Guinea (PNG) | 1976 | Managed by the National Fisheries Authority under the Fisheries Management Act (1998) and Fisheries Management Regulation (2000). A ban on exports of giant clams was implemented in 2000, the same year that the commercial fishery was closed (Neo et al., 2017). It is now forbidden to take all species of giant clams at night using underwater lights (Kinch & Teitelbaum, 2010). |
| Solomon Islands | 2007 | Commercial harvest and export, except for aquaculture species, is banned under the Fisheries Regulation 1998. There is also a marine protected area, Arnavon Marine Conservation Area, where large numbers of clams can be found (Kinch & Teitelbaum, 2010; Neo et al., 2017). |
| Vanuatu (and New Hebrides) | 1989 | Under the Fisheries Act of 2005 (Cap 315), specifically the Fisheries Regulations Order No. 28 (2009), the harvesting of wild giant clams for export is not permitted (Neo et al., 2020). |
| Federated States of Micronesia (FSM) – Kosrae, Pohnpei, Chuuk, Yap States | Non-Party | Only Yap and Kosrae states have laws regarding the exploitation of giant clams. The Yap State Code (Title 18, Section 1008, Protection of clams) prohibits harvest of giant clams for commercial sale, but is reportedly not enforced (Smith, 1992; Neo et al., 2020). Under the Kosrae State Code Section 13.523, a sanctuary area was declared for the purpose of protecting giant clams (Neo et al., 2020). Some States are reportedly developing legislation in their respective jurisdictions to assist in managing subsistence take (e.g., imposing size limits and establishing marine managed areas; Kinch & Teitelbaum, 2010). |
| Guam | Dependent territory of the US 1975 | Commercial harvest and export of giant clams is prohibited, with the exception of cultured clams in a Dept. of Agriculture-approved culture facility. Harvesting for personal use is limited to no more than three clams per person per day, shells included, and is limited to specimens with a shell length not less than 7 inches. Clams must be preserved whole until cooked or frozen to prevent harvesting of only the meat portion. Sale, trade, and bartering of shells is prohibited. Harvesting is not permitted in designated marine preserves (Guam Administrative Rules and Regulations, Title 9, Chapter 12, Article 3, Section 12303-12304). |

| **Localities** | **CITES** Entry into force | **Regulations** |
|---|---|---|
| Republic of Kiribati | Non-Party | Giant clams are protected as endangered species under Fisheries Act, Section 22 and the Environment Act, Section 24. These regulations prohibit the commercial harvest and export of clams, except for aquaculture species. In addition, the removal of clams by visitors is prohibited (Kinch & Teitelbaum, 2010; Neo et al., 2017). |
| Marshall Islands | Non-Party | There appears to be no national legislation regulating the exploitation of giant clams; although, *H. hippopus*, *T. gigas*, *T.derasa*, and *T. squamosa* have all been listed as species "worthy of conservation consideration" based on their IUCN assessments (OEPPC, 2008; http://biormi.org/index.shtml?en/worthy.shtml). Raymakers et al. (2003) report that commercial harvest of giant clams is prohibited. Ordinance No. 1998-74 of Majuro reportedly bans the selling of any Tridacninae species (UNEP-WCMC, 2012). |
| Commonwealth of the Northern Mariana Islands | Dependent territory of the US 1975 | Under the Northern Mariana Islands Administrative Code (Title 85, Chapter 30, Subchapter 30.1, Part 430), harvest of all invertebrates is prohibited in CNMI waters, except as permitted by the Director. It is worth noting, however, that giant clams are not explicitly identified in the regulations, as is the case for hard corals, *Trochus niloctus*, sea cucumbers, and lobsters, so it is not clear the extent to which enforcement of this provision has been extended to giant clams. |
| Palau | 2004 | Under the Domestic Fishing Laws of Palau (Ref. 27 PNCA 1204), it is against the law to export any of the seven giant clam species present in Palau waters, or part thereof, regardless of where the species may have originated, except cultured specimens (Neo et al., 2020). Although a signatory of CITES, Palau has taken reservations on the listing of the giant clams (https://www.cites.org/eng/app/reserve.php). |
| American Samoa | Dependent territory of the US 1975 | Under the American Samoa Administrative Code (Title 24, Chapter 9, Section 24.0953), it is unlawful to take, possess, sell, or import any tridacnid clam from the waters of American Samoa that measure less than seven inches across the longest part of shell. Tridacnid clams imported, sold, or offered for sale must be in whole condition with meat still attached to the shell to facilitate measuring. Tridacnid clams taken for personal consumption must remain in whole condition until they reach the fisherman's home or the place of consumption so that they may be measured. The aforementioned restrictions do not apply to clams raised in captivity, provided that the clam farmer possesses a valid aquaculture permit from the Dept. of Marine and Wildlife Resources and can demonstrate that the clam was raised in captivity.<br>Additionally, it is prohibited for any person to gather, take, break, cut, damage, destroy, or possess any giant clam [*Tridacna* spp.] in all areas of the National Marine Sanctuary of American Samoa (15 CFR §922.104; American Samoa Administrative Code, Title 24, Chapter 9, Section 24.0913). The National Marine Sanctuary of American Samoa replaced the former Fagatele Bay National Marine Sanctuary in 2012 and was expanded to include Fagalua/Fogama'a, Swains Island, Ta'u, Aunu'u, and Muliāva (Rose Atoll) (77 FR 43942). Collection of shellfish (including giant clams) is allowed in all waters of the National Park of American Samoa, subject to Territorial laws and policies (36 CFR §2.3; NPSA Superintendent's Compendium, Mar 2023). |

| **Localities** | **CITES** Entry into force | **Regulations** |
|---|---|---|
| Cook Islands | Non-Party | Gathering of giant clams for export and sale is prohibited under several by-laws, such as the Aitutaki Fisheries Protection By-Laws (1990) and Penrhyn (Prohiition of Exportation of Pasua) By-Laws (2007) (Neo et al., 2020). |
| French Polynesia | Dependent territory of France 1978 | The Délibération n° 2007–98 APF (2007) regulates activities relating to collection, breeding and repopulation of giant clams (Neo et al., 2020). There is a size limit of 120 mm for *T. maxima*. No-take areas, quotas and restocking have been implemented at two atolls of Tuamotu Archipelago (Tatakoto and Reao). Regulations for giant clam farming (spat collection, grow-out, transport and reseeding) were implemented in 2008 (Neo et al. 2017). |
| Pitcairn Islands | British Overseas Territory 1976 | We were unable to find regulations specific to giant clams. |
| Niue | Non-Party | Villages have on occasion put in place temporary harvesting bans to allow stock recovery from extreme weather events. The Niue Domestic Fisheries Regulations of 1996 set a *minimum* size limit of 180 mm and a bag limit of ten clams per person per day for subsistence harvest of giant clams (Neo et al., 2017; Neo et al., 2020). |
| Samoa | 2005 | Commercial harvest and export of wild clams is prohibited. Harvest of clams for subsistence use is allowed as long as minimum size limits are met: 160 mm shell length for *T. maxima*, and 200 mm shell length for *T. squamosa* (Wabnitz & Nahacky, 2015). |
| Tokelau | Territory of New Zealand 1989 | There are no laws in place to regulate traditional harvest of giant clams, but community-based management plans exist (Neo et al., 2017). |
| Tonga | 2016 | The harvesting and export of wild clams for commercial use was banned in December 1993, with the exception of those produced from mariculture (Sant, 1995; Wells, 1997). A provision under the Fisheries Management Regulation (2008) prohibits the selling of giant clams on the local market without its shell to facilitate enforcement of size limits (260 mm for *T. derasa*, 155 mm for *T. maxima*, and 180 mm for *T. squamosa*) (Tisdell, 1992; Kinch & Teitelbaum 2010; Neo et al., 2017). |
| Tuvalu | Non-Party | No regulations in place at this time (Neo et al., 2017). |
| Wallis and Futuna Islands | Dependent territory of France 1978 | We were unable to find regulations specific to giant clams. |

**Appendix 2.** Reported population density estimates for the seven giant clam species addressed in this report, adapted from Neo et al. (2017). Entries highlighted in blue indicate where density estimates were calculated as the average of multiple surveys. Entries highlighted in teal indicate where original figures were erroneous and were corrected here. Entries highlighted in green indicate data that has been added to the original dataset from Neo et al. (2017).

| Country | Location descriptions | Species | Year of survey | Method of survey | Approximate survey area (m$^2$) | # of ind. | Density (per m$^2$) | Density (per ha) | Reference (see Neo et al. 2017) |
|---|---|---|---|---|---|---|---|---|---|
| Australia | Escape reefs (west reef, north reef, east bommie, south reef) | Td | 1981 | Census of fixed area | 33,720 | 205 | 0.00608 | 60.8 | Braley (1987b) |
| Australia | Escape reefs (west reef, north reef, east bommie, south reef) | Tg | 1981 | Census of fixed area | 33,720 | 254 | 0.00753 | 75.3 | Braley (1987b) |
| Australia | Escape reefs (west reef, north reef-a, north reef-b, east bommie) | Td | 1982 | Census of fixed area | 10,510 | 97 | 0.00923 | 92.3 | Braley (1987b) |
| Australia | Escape reefs (west reef, north reef-a, north reef-b, east bommie) | Tg | 1982 | Census of fixed area | 10,510 | 141 | 0.01342 | 134.2 | Braley (1987b) |
| Australia | Great Barrier Reef (northern) | Td | 1983 | Quadrat; 50 x 20 m | - | - | 0.00029 | 2.9 | Braley (1987a) |
| Australia | Great Barrier Reef (northern) | Tg | 1983 | Quadrat; 50 x 20 m | - | - | 0.00078 | 7.8 | Braley (1987a) |
| Australia | Great Barrier Reef (southern) | Td | 1983 | Quadrat; 50 x 20 m | - | - | 0.00059 | 5.9 | Braley (1987a) |
| Australia | Great Barrier Reef (southern) | Tg | 1983 | Quadrat; 50 x 20 m | - | - | 0.00006 | 0.6 | Braley (1987a) |
| Australia | Michaelmas Reef, GBR | Tg | 1978 | Quadrat; 180 x 150 m | 27,000 | 1,166 | 0.04319 | 431. 9 | Pearson and Munro (1991) |
| Australia | Michaelmas Reef, GBR | Tg | 1980-1981 | Quadrat; 180 x 150 m | 27,000 | 1,120 | 0.04148 | 414.8 | Pearson and Munro (1991) |
| Australia | Michaelmas Reef, GBR | Tg | 1985 | Quadrat; 180 x 150 m | 27,000 | 764 | 0.02830 | 283.0 | Pearson and Munro (1991) |
| Australia | Michaelmas Reef, GBR | Td | 1978 | Quadrat; 180 x 150 m | 27,000 | 46 | 0.00170 | 17.0 | Pearson and Munro (1991) |
| Australia | Michaelmas Reef, GBR | Td | 1980-1981 | Quadrat; 180 x 150 m | 27,000 | 46 | 0.00170 | 17.0 | Pearson and Munro (1991) |
| Australia | Michaelmas Reef, GBR | Td | 1985 | Quadrat; 180 x 150 m | 27,000 | 31 | 0.00115 | 11.5 | Pearson and Munro (1991) |
| Australia | Ashmore Reef, W Australia (Shallow) | Tg | 1998 | Belt transects; varied lengths (20-100m) x 2 m width | - | - | 0.00026 | 2.6 | Skewes et al. (1999) |
| Australia | Ashmore Reef, W Australia (Shallow) | Td | 1998 | Belt transects; varied lengths (20-100m) x 2 m width | - | - | 0.00013 | 1.3 | Skewes et al. (1999) |
| Australia | Ashmore Reef, W Australia (Shallow) | Hh | 1998 | Belt transects; varied lengths (20-100m) x 2 m width | - | - | 0.01314 | 131.4 | Skewes et al. (1999) |

| Country | Location descriptions | Species | Year of survey | Method of survey | Approximate survey area ($m^2$) | # of ind. | Density (per $m^2$) | Density (per ha) | Reference (see Neo et al. 2017) |
|---|---|---|---|---|---|---|---|---|---|
| Australia | Browse Reef, W Australia | Hh | 1998 | Belt transects; varied lengths (20-100m) x 2 m width | - | - | 0.00063 | 6.3 | Skewes et al. (1999) |
| Australia | Cartier Reef, W Australia | Hh | 1998 | Belt transects; varied lengths (20-100m) x 2 m width | - | - | 0.00750 | 75.0 | Skewes et al. (1999) |
| Australia | Hibernia Reef, W Australia | Hh | 1998 | Belt transects; varied lengths (20-100m) x 2 m width | - | - | 0.00313 | 31.3 | Skewes et al. (1999) |
| Australia | N Scott Reef, W Australia (Shallow) | Hh | 1998 | Belt transects; varied lengths (20-100m) x 2 m width | - | - | 0.00143 | 14.3 | Skewes et al. (1999) |
| Australia | N Scott Reef, W Australia (Shallow Lagoon) | Tg | 1998 | Belt transects; varied lengths (20-100m) x 2 m width | - | - | 0.00135 | 13.5 | Skewes et al. (1999) |
| Australia | N Scott Reef, W Australia (Shallow Lagoon) | Td | 1998 | Belt transects; varied lengths (20-100m) x 2 m width | - | - | 0.00777 | 77.7 | Skewes et al. (1999) |
| Australia | N Scott Reef, W Australia (Shallow Lagoon) | Hh | 1998 | Belt transects; varied lengths (20-100m) x 2 m width | - | - | 0.00034 | 3.4 | Skewes et al. (1999) |
| Australia | S Scott Reef, W Australia (Shallow) | Tg | 1998 | Belt transects; varied lengths (20-100m) x 2 m width | - | - | 0.00012 | 1.2 | Skewes et al. (1999) |
| Australia | S Scott Reef, W Australia (Shallow) | Hh | 1998 | Belt transects; varied lengths (20-100m) x 2 m width | - | - | 0.00176 | 17.6 | Skewes et al. (1999) |
| Australia | S Scott Reef, W Australia (Shallow Lagoon) | Tg | 1998 | Belt transects; varied lengths (20-100m) x 2 m width | - | - | 0.00069 | 6.9 | Skewes et al. (1999) |
| Australia | S Scott Reef, W Australia (Shallow Lagoon) | Td | 1998 | Belt transects; varied lengths (20-100m) x 2 m width | - | - | 0.00042 | 4.2 | Skewes et al. (1999) |
| Australia | S Scott Reef, W Australia (Shallow Lagoon) | Hh | 1998 | Belt transects; varied lengths (20-100m) x 2 m width | - | - | 0.00167 | 16.7 | Skewes et al. (1999) |
| Australia | Seringapatam Reef, W Australia (Shallow) | Tg | 1998 | Belt transects; varied lengths (20-100m) x 2 m width | - | - | 0.00057 | 5.7 | Skewes et al. (1999) |
| Australia | Seringapatam Reef, W Australia (Shallow) | Hh | 1998 | Belt transects; varied lengths (20-100m) x 2 m width | - | - | 0.00227 | 22.7 | Skewes et al. (1999) |
| Australia | Seringapatam Reef, W Australia (Shallow Lagoon) | Td | 1998 | Belt transects; varied lengths (20-100m) x 2 m width | - | - | 0.00069 | 6.9 | Skewes et al. (1999) |
| Australia | Ashmore Reef, W Australia | Tg | 2003 | Distance swim transects; 500 x 5 m | 397,500 | 49 | 0.00012 | 1.2 | Rees et al. (2003) |
| Australia | Ashmore Reef, W Australia | Hh | 2003 | Distance swim transects; 500 x 5 m | 397,500 | 740 | 0.00186 | 18.6 | Rees et al. (2003) |
| Australia | Cartier Reef, W Australia | Tg | 2003 | Distance swim transects; 500 x 5 m | 180,000 | 0 | 0.00000 | 0 | Rees et al. (2003) |
| Australia | Cartier Reef, W Australia | Hh | 2003 | Distance swim transects; 500 x 5 m | 180,000 | 715 | 0.00397 | 39.7 | Rees et al. (2003) |
| Australia | Mermaid Reef, W Australia | Tg | 2003 | Distance swim transects; 500 x 5 m | 232,500 | 79 | 0.00034 | 3.4 | Rees et al. (2003) |

| Country | Location descriptions | Species | Year of survey | Method of survey | Approximate survey area ($m^2$) | # of ind. | Density (per $m^2$) | Density (per ha) | Reference (see Neo et al. 2017) |
|---|---|---|---|---|---|---|---|---|---|
| Australia | Mermaid Reef, W Australia | Hh | 2003 | Distance swim transects; 500 x 5 m | 232,500 | 46 | 0.00020 | 2.0 | Rees et al. (2003) |
| Australia | Coringa-Herald National Nature Reserve | Tg | 2007 | Distance swim transects; 500 x 5 m | 153,500 | 18 | 0.00012 | 1.2 | Ceccarelli et al. (2009) |
| Australia | Coringa-Herald National Nature Reserve | Td | 2007 | Distance swim transects; 500 x 5 m | 153,500 | 8 | 0.00005 | 0.5 | Ceccarelli et al. (2009) |
| Australia | Coringa-Herald National Nature Reserve | Hh | 2007 | Distance swim transects; 500 x 5 m | 153,500 | 150 | 0.00098 | 9.8 | Ceccarelli et al. (2009) |
| Australia | Lihou Reef National Nature Reserve | Tmb | 2008 | Distance swim transects; 500 x 5 m | 220,000 | 1 | 0.00000 | 0.0 | Ceccarelli et al. (2009) |
| Australia | Lihou Reef National Nature Reserve | Td | 2008 | Distance swim transects; 500 x 5 m | 220,000 | 88 | 0.00040 | 4.0 | Ceccarelli et al. (2009) |
| Australia | Lihou Reef National Nature Reserve | Hh | 2008 | Distance swim transects; 500 x 5 m | 220,000 | 33 | 0.00015 | 1.5 | Ceccarelli et al. (2009) |
| Australia | Ashmore Reef, W Australia | Hh | 2009 | Distance swim transects; 100 x 10 m | 30,000 | 8 | 0.00027 | 2.7 | Richards et al. (2009) |
| Australia | Ashmore Reef, W Australia | Ts | 2009 | Distance swim transects; 100 x 10 m | 30,000 | 2 | 0.00007 | 0.7 | Richards et al. (2009) |
| Australia | Ashmore Reef, W Australia | Td | 2009 | Distance swim transects; 100 x 10 m | 30,000 | 3 | 0.00010 | 1.0 | Richards et al. (2009) |
| Australia | Cartier Reef, W Australia | Hh | 2009 | Distance swim transects; 100 x 10 m | 10,000 | 1 | 0.00010 | 1.0 | Richards et al. (2009) |
| Australia | Cartier Reef, W Australia | Ts | 2009 | Distance swim transects; 100 x 10 m | 10,000 | 1 | 0.00010 | 1.0 | Richards et al. (2009) |
| Australia | Watson's Bay, Lizard Island | Tg | 1984 | Quadrats; 50 x 50 m | 5,540 | 136 | 0.02455 | 245.5 | Braley (2023) |
| Australia | Watson's Bay, Lizard Island | Tg | 2009 | Quadrats; 50 x 50 m | 5,540 | 158 | 0.02852 | 285.2 | Braley (2023) |
| Australia | Watson's Bay, Lizard Island | Tg | 2017 | Quadrats; 50 x 50 m | 5,540 | 208 | 0.03755 | 375.5 | Braley (2023) |
| Australia | Watson's Bay, Lizard Island | Td | 1984 | Quadrats; 50 x 50 m | 5,540 | 29 | 0.00523 | 52.3 | Braley (2023) |
| Australia | Watson's Bay, Lizard Island | Td | 2009 | Quadrats; 50 x 50 m | 5,540 | 26 | 0.00469 | 46.9 | Braley (2023) |
| Australia | Watson's Bay, Lizard Island | Td | 2017 | Quadrats; 50 x 50 m | 5,540 | 17 | 0.00307 | 30.7 | Braley (2023) |
| Australia | Watson's Bay, Lizard Island | Hh | 2009 | Quadrats; 50 x 50 m | 5,540 | 14 | 0.00253 | 25.3 | Braley (2023) |
| Australia | Watson's Bay, Lizard Island | Hh | 2017 | Quadrats; 50 x 50 m | 5,540 | 2 | 0.00036 | 3.6 | Braley (2023) |

| Country | Location descriptions | Species | Year of survey | Method of survey | Approximate survey area ($m^2$) | # of ind. | Density (per $m^2$) | Density (per ha) | Reference (see Neo et al. 2017) |
|---|---|---|---|---|---|---|---|---|---|
| Australia | Watson's Bay, Lizard Island | Ts | 2009 | Quadrats; 50 x 50 m | 5,540 | 0 | 0.00000 | 0.0 | Braley (2023) |
| Australia | Watson's Bay, Lizard Island | Ts | 2017 | Quadrats; 50 x 50 m | 5,540 | 1 | 0.00018 | 1.8 | Braley (2023) |
| Australia | Palfrey South Channel, Lizard Island | Tg | 1984 | Quadrats; 50 x 50 m | 7,300 | 79 | 0.01082 | 108.2 | Braley (2023) |
| Australia | Palfrey South Channel, Lizard Island | Tg | 2007 | Quadrats; 50 x 50 m | 7,300 | 61 | 0.00836 | 83.6 | Braley (2023) |
| Australia | Palfrey South Channel, Lizard Island | Tg | 2017 | Quadrats; 50 x 50 m | 7,300 | 77 | 0.01055 | 105.5 | Braley (2023) |
| Australia | Palfrey South Channel, Lizard Island | Td | 1984 | Quadrats; 50 x 50 m | 7,300 | 22 | 0.00301 | 30.1 | Braley (2023) |
| Australia | Palfrey South Channel, Lizard Island | Td | 2007 | Quadrats; 50 x 50 m | 7,300 | 26 | 0.00356 | 35.6 | Braley (2023) |
| Australia | Palfrey South Channel, Lizard Island | Td | 2017 | Quadrats; 50 x 50 m | 7,300 | 26 | 0.00356 | 35.6 | Braley (2023) |
| Australia | Palfrey South Channel, Lizard Island | Hh | 2007 | Quadrats; 50 x 50 m | 7,300 | 38 | 0.00521 | 52.1 | Braley (2023) |
| Australia | Palfrey South Channel, Lizard Island | Hh | 2017 | Quadrats; 50 x 50 m | 7,300 | 23 | 0.00315 | 31.5 | Braley (2023) |
| Australia | Palfrey South Channel, Lizard Island | Ts | 2007 | Quadrats; 50 x 50 m | 7,300 | 30 | 0.00411 | 41.1 | Braley (2023) |
| Australia | Palfrey South Channel, Lizard Island | Ts | 2017 | Quadrats; 50 x 50 m | 7,300 | 23 | 0.00315 | 31.5 | Braley (2023) |
| Australia | Rachel Carson Reef (West) | Tg | 1982 | Quadrats; 50 x 50 m | 5,610 | 61 | 0.01087 | 108.7 | Braley (2023) |
| Australia | Rachel Carson Reef (West) | Tg | 2008 | Quadrats; 50 x 50 m | 5,610 | 28 | 0.00499 | 49.9 | Braley (2023) |
| Australia | Rachel Carson Reef (West) | Td | 1982 | Quadrats; 50 x 50 m | 5,610 | 30 | 0.00535 | 53.5 | Braley (2023) |
| Australia | Rachel Carson Reef (West) | Td | 2008 | Quadrats; 50 x 50 m | 5,610 | 17 | 0.00303 | 30.3 | Braley (2023) |
| Australia | Rachel Carson Reef (West) | Hh | 2008 | Quadrats; 50 x 50 m | 5,610 | 17 | 0.00303 | 30.3 | Braley (2023) |
| Australia | Rachel Carson Reef (West) | Ts | 2008 | Quadrats; 50 x 50 m | 5,610 | 0 | 0.00000 | 0.0 | Braley (2023) |
| Australia | Rachel Carson Reef (East) | Tg | 1982 | Quadrats; 50 x 50 m | 220 | 9 | 0.04091 | 409.1 | Braley (2023) |
| Australia | Rachel Carson Reef (East) | Tg | 2008 | Quadrats; 50 x 50 m | 220 | 5 | 0.02273 | 227.3 | Braley (2023) |

| Country | Location descriptions | Species | Year of survey | Method of survey | Approximate survey area (m$^2$) | # of ind. | Density (per m$^2$) | Density (per ha) | Reference (see Neo et al. 2017) |
|---|---|---|---|---|---|---|---|---|---|
| Australia | Rachel Carson Reef (East) | Td | 1982 | Quadrats; 50 x 50 m | 220 | 6 | 0.02727 | 272.7 | Braley (2023) |
| Australia | Rachel Carson Reef (East) | Td | 2008 | Quadrats; 50 x 50 m | 220 | 1 | 0.00455 | 45.5 | Braley (2023) |
| Australia | Rachel Carson Reef (East) | Hh | 2008 | Quadrats; 50 x 50 m | 220 | 0 | 0.00000 | 0.0 | Braley (2023) |
| Australia | Rachel Carson Reef (East) | Ts | 2008 | Quadrats; 50 x 50 m | 220 | 0 | 0.00000 | 0.0 | Braley (2023) |
| Australia | Michaelmas Reef | Tg | 1984 | Quadrats; 50 x 50 m | 1,200 | 89 | 0.07417 | 741.7 | Braley (2023) |
| Australia | Michaelmas Reef | Tg | 2008 | Quadrats; 50 x 50 m | 1,200 | 71 | 0.05917 | 591.7 | Braley (2023) |
| Australia | Michaelmas Reef | Td | 1984 | Quadrats; 50 x 50 m | 1,200 | 8 | 0.00667 | 66.7 | Braley (2023) |
| Australia | Michaelmas Reef | Td | 2008 | Quadrats; 50 x 50 m | 1,200 | 3 | 0.00250 | 25.0 | Braley (2023) |
| Australia | Michaelmas Reef | Hh | 2008 | Quadrats; 50 x 50 m | 1,200 | 14 | 0.01167 | 116.7 | Braley (2023) |
| Australia | Michaelmas Reef | Ts | 2008 | Quadrats; 50 x 50 m | 1,200 | 0 | 0.00000 | 0.0 | Braley (2023) |
| Egypt | SW of Gulf of Aqaba, between Ras Nosrani and Ras Mohammed | Ts | 1994 | Belt transects; 30 x 2 m | 1,440 | 45 | 0.03125 | 312.5 | Kilada et al. (1998) |
| Egypt | Pharaoh Island/Coral Island, Taba | Ts | ? | Belt transects; 50 x 5 m | 750 | 2 | 0.00320 | 32 | Richter et al. (2008) |
| Egypt | Ras Amira/Taba Heights, Taba | Ts | ? | Belt transects; 50 x 5 m | 750 | 2 | 0.00220 | 22 | Richter et al. (2008) |
| Egypt | Buoy, Nuweiba | Ts | ? | Belt transects; 50 x 5 m | 750 | 1 | 0.00150 | 15 | Richter et al. (2008) |
| Egypt | Fayrouza, Nuweiba | Ts | ? | Belt transects; 50 x 5 m | 500 | 0 | 0.00030 | 3 | Richter et al. (2008) |
| Egypt | Fayrouza, Nuweiba | Tsi | ? | Belt transects; 50 x 5 m | 500 | 0 | 0.00029 | 2.9 | Richter et al. (2008) |
| Egypt | Towers, Nuweiba | Ts | ? | Belt transects; 50 x 5 m | 1,500 | 4 | 0.00248 | 24.8 | Richter et al. (2008) |
| Egypt | Blue Hole, Dahab | Ts | ? | Belt transects; 50 x 5 m | 750 | 6 | 0.00800 | 80 | Richter et al. (2008) |
| Egypt | Blue Hole, Dahab | Tsi | ? | Belt transects; 50 x 5 m | 750 | 0 | 0.00047 | 4.7 | Richter et al. (2008) |
| Egypt | InMo, Dahab | Ts | ? | Belt transects; 50 x 5 m | 750 | 3 | 0.00453 | 45.3 | Richter et al. (2008) |
| Egypt | Lagona, Dahab | Ts | ? | Belt transects; 50 x 5 m | 250 | 1 | 0.00470 | 47 | Richter et al. (2008) |
| Egypt | Lagona, Dahab | Tsi | ? | Belt transects; 50 x 5 m | 250 | 0 | 0.00117 | 11.7 | Richter et al. (2008) |
| Egypt | Shark Point, Ras Mohammed | Ts | ? | Belt transects; 50 x 5 m | 500 | 0 | 0 | 0 | Richter et al. (2008) |

| Country | Location descriptions | Species | Year of survey | Method of survey | Approximate survey area ($m^2$) | # of ind. | Density (per $m^2$) | Density (per ha) | Reference (see Neo et al. 2017) |
|---|---|---|---|---|---|---|---|---|---|
| Egypt | Yolanda Bay, Ras Mohammed | Ts | ? | Belt transects; 50 x 5 m | 250 | 0 | 0 | 0 | Richter et al. (2008) |
| Egypt | Marsa Abu Kalawa, Hurghada | Ts | ? | Belt transects; 50 x 5 m | 250 | 1 | 0.00250 | 25 | Richter et al. (2008) |
| Egypt | Marsa Abu Kalawa, Hurghada | Tsi | ? | Belt transects; 50 x 5 m | 250 | 2 | 0.00622 | 62.2 | Richter et al. (2008) |
| Egypt | Sachwa, Hurghada | Tsi | ? | Belt transects; 50 x 5 m | 500 | 1 | 0.00165 | 16.45 | Richter et al. (2008) |
| Egypt | Shab Abu Nuga, Hurghada | Ts | ? | Belt transects; 50 x 5 m | 250 | 1 | 0.00250 | 25 | Richter et al. (2008) |
| Egypt | Shab El Erg (South), Hurghada | Ts | ? | Belt transects; 50 x 5 m | 750 | 3 | 0.00343 | 34.3 | Richter et al. (2008) |
| Egypt | Stone Beach/Hamda, Hurghada | Tsi | ? | Belt transects; 50 x 5 m | 250 | 1 | 0.00210 | 21 | Richter et al. (2008) |
| Fiji | Cakau Tabu Reef, Lau | Tmb | 1986 | SCUBA search (per man hour effort) | - | 1 | 0.25 clam per man hour | | Ledua et al. (1993) |
| Fiji | Vatoa Island, Lau | Tmb | 1989 | SCUBA search (per man hour effort) | - | 6 | 0.30 clam per man hour | | Ledua et al. (1993) |
| Fiji | Vatoa Island, Lau | Tmb | 1990 | SCUBA search (per man hour effort) | - | 5 | 0.20 clam per man hour | | Ledua et al. (1993) |
| Fiji | Vatoa Island, Lau | Tmb | 1991 | SCUBA search (per man hour effort) | - | 2 | 0.30 clam per man hour | | Ledua et al. (1993) |
| India | Diglipur, Andaman and Nicobar Island (S) | Ts | ? | ? | - | - | 1 | 10000 | Ramadoss (1983) |
| India | Mayabunder, Andaman and Nicobar Island (S) | Ts | ? | ? | - | - | 0.5 | 5000 | Ramadoss (1983) |
| India | Havelock Island, Andaman and Nicobar Island (S) | Ts | ? | ? | - | - | 0.1 | 1000 | Ramadoss (1983) |
| India | Neill Island, Andaman and Nicobar Island (S) | Ts | ? | ? | - | - | 0.5 | 5000 | Ramadoss (1983) |
| India | Long Island, Andaman and Nicobar Island (S) | Ts | ? | ? | - | - | 0.5 | 5000 | Ramadoss (1983) |
| India | Port Blair, Andaman and Nicobar Island (S) | Ts | ? | ? | - | - | 1 | 10000 | Ramadoss (1983) |
| India | Ross Island, Andaman and Nicobar Island (S) | Ts | ? | ? | - | - | 1 | 10000 | Ramadoss (1983) |
| India | Chiriyatapu, Andaman and Nicobar Island (I) | Ts | ? | ? | - | - | 1 | 10000 | Ramadoss (1983) |
| India | Chiriyatapu, Andaman and Nicobar Island (S) | Ts | ? | ? | - | - | 1 | 10000 | Ramadoss (1983) |

| Country | Location descriptions | Species | Year of survey | Method of survey | Approximate survey area ($m^2$) | # of ind. | Density (per $m^2$) | Density (per ha) | Reference (see Neo et al. 2017) |
|---|---|---|---|---|---|---|---|---|---|
| India | Little Andaman, Andaman and Nicobar Island (S) | Ts | ? | ? | - | - | 0.5 | 5000 | Ramadoss (1983) |
| India | Car Nicobar, Andaman and Nicobar Island (S) | Ts | ? | ? | - | - | 0.5 | 5000 | Ramadoss (1983) |
| Indonesia | Gelean, Karimun Java | Ts | 1983 | Belt transects; 100 x 10 m | 2,000 | 1 | 0.00050 | 5 | Brown and Muskanofola (1985) |
| Indonesia | Bengkoang, Karimun Java | Ts | 1983 | Belt transects; 100 x 10 m | 5,000 | 9 | 0.00180 | 18 | Brown and Muskanofola (1985) |
| Indonesia | Menjangan Kecil, Karimun Java | Ts | 1983 | Belt transects; 100 x 10 m | 3,000 | 27 | 0.00900 | 90 | Brown and Muskanofola (1985) |
| Indonesia | Karang Besi, Karimun Java | Td | 1983 | Belt transects; 100 x 10 m | 1,000 | 1 | 0.00100 | 10 | Brown and Muskanofola (1985) |
| Indonesia | Karang Besi, Karimun Java | Ts | 1983 | Belt transects; 100 x 10 m | 1,000 | 10 | 0.01000 | 100 | Brown and Muskanofola (1985) |
| Indonesia | Katang Island, Karimun Java | Ts | 1983 | Belt transects; 50 x 10 m | 500 | 3 | 0.00600 | 60 | Brown and Muskanofola (1985) |
| Indonesia | Cemara Kecil, Karimun Java | Ts | 1983 | Belt transects; 100 x 10 m | 3,000 | 19 | 0.00633 | 63.3 | Brown and Muskanofola (1985) |
| Indonesia | Pari Island | Hh | 1984 | Belt transects; variable lengths x 5 m | 13,036 | 25 | 0.00192 | 19.2 | Eliata et al. (2003) |
| Indonesia | Pari Island | Ts | 1984 | Belt transects; variable lengths x 5 m | 13,036 | 3 | 0.00023 | 2.3 | Eliata et al. (2003) |
| Indonesia | Pari Island | Hh | 2003 | Belt transects; variable lengths x 5 m | 31,692 | 5 | 0.00016 | 1.6 | Eliata et al. (2003) |
| Indonesia | Pari Island | Ts | 2003 | Belt transects; variable lengths x 5 m | 31,692 | 1 | 0.00003 | 0.3 | Eliata et al. (2003) |
| Indonesia | Kepulauan Seribu | Ts | ? | Belt transects; 100 x 5 m | 1,500 | 40 | 0.02667 | 266.7 | Yusuf et al. (2009) |
| Indonesia | Manado | Tg | ? | Belt transects; 100 x 5 m | 2,000 | 1 | 0.00050 | 5 | Yusuf et al. (2009) |
| Indonesia | Manado | Ts | ? | Belt transects; 100 x 5 m | 2,000 | 40 | 0.02000 | 200 | Yusuf et al. (2009) |
| Indonesia | Kei Kecil waters, Southeast Maluku | Hh | 2009 | Quadrat-Transect method; within a 50 x 50 m quadrat | 22,500 | 25 | 0.00111 | 11.1 | Hernawan (2010) |
| Indonesia | Kei Kecil waters, Southeast Maluku | Td | 2009 | Quadrat-Transect method; within a 50 x 50 m quadrat | 22,500 | 2 | 0.00009 | 0.9 | Hernawan (2010) |
| Indonesia | Kei Kecil waters, Southeast Maluku | Tg | 2009 | Quadrat-Transect method; within a 50 x 50 m quadrat | 22,500 | 1 | 0.00004 | 0.4 | Hernawan (2010) |
| Indonesia | Kei Kecil waters, Southeast Maluku | Ts | 2009 | Quadrat-Transect method; within a 50 x 50 m quadrat | 22,500 | 14 | 0.00062 | 6.2 | Hernawan (2010) |
| Indonesia | Savu Sea, East Nusa Tenggara | Hh | 2010 | Belt transects; 50 x 5 m | 6,750 | 11 | 0.00163 | 16.3 | Naguit et al. (2012) |
| Indonesia | Savu Sea, East Nusa Tenggara | Ts | 2010 | Belt transects; 50 x 5 m | 6,750 | 17 | 0.00256 | 25.6 | Naguit et al. (2012) |
| Indonesia | Raja Ampat, West Papua | Hh | 2014 | Belt transects; 100 x 2.5 m | 1,500 | 45 | 0.03000 | 300.0 | Wakum et al. (2017) |

| Country | Location descriptions | Species | Year of survey | Method of survey | Approximate survey area ($m^2$) | # of ind. | Density (per $m^2$) | Density (per ha) | Reference (see Neo et al. 2017) |
|---|---|---|---|---|---|---|---|---|---|
| Indonesia | Raja Ampat, West Papua | Tg | 2014 | Belt transects; 100 x 2.5 m | 1,500 | 14 | 0.00933 | 93.3 | Wakum et al. (2017) |
| Indonesia | Raja Ampat, West Papua | Hp | 2014 | Belt transects; 100 x 2.5 m | 1,500 | 14 | 0.00933 | 93.3 | Wakum et al. (2017) |
| Indonesia | Raja Ampat, West Papua | Ts | 2014 | Belt transects; 100 x 2.5 m | 1,500 | 22 | 0.01467 | 146.7 | Wakum et al. (2017) |
| Indonesia | Raja Ampat, West Papua | Td | 2014 | Belt transects; 100 x 2.5 m | 1,500 | 6 | 0.00400 | 40.0 | Wakum et al. (2017) |
| Indonesia | Raja Ampat, West Papua | Tmb | 2014 | Belt transects; 100 x 2.5 m | 1,500 | 1* | 0.00067* | 6.7 | Wakum et al. (2017) |
| Indonesia | Morela | Hh | 2017 | Quadrat-Transect method; within a 10 x 10 m quadrat | 2,200 | 1 | 0.00045 | 4.5 | Ode (2017) |
| Indonesia | Kei Islands | Ts | 2017 | Quadrat-Transect method; within a 50 x 50 m quadrat | 2,500 | 122 | 0.04880 | 488.0 | Triandiza et al. (2019) |
| Indonesia | Kei Islands | Hh | 2017 | Quadrat-Transect method; within a 50 x 50 m quadrat | 2,500 | 22 | 0.00880 | 88.0 | Triandiza et al. (2019) |
| Indonesia | Kali Lemon, Kwatisore, Cenderwasih Bay, Papua | Hh | 2021 | Cruise method from shoreline; 100 x 100 m survey area | 10,000 | 5 | 0.0005 | 5 | Tapilatu et al. (2021) |
| Indonesia | Kali Lemon, Kwatisore, Cenderwasih Bay, Papua | Tg | 2021 | Cruise method from shoreline; 100 x 100 m survey area | 10,000 | 4 | 0.0004 | 4 | Tapilatu et al. (2021) |
| Indonesia | Kali Lemon, Kwatisore, Cenderwasih Bay, Papua | Hp | 2021 | Cruise method from shoreline; 100 x 100 m survey area | 10,000 | 6 | 0.0006 | 6 | Tapilatu et al. (2021) |
| Indonesia | Kali Lemon, Kwatisore, Cenderwasih Bay, Papua | Ts | 2021 | Cruise method from shoreline; 100 x 100 m survey area | 10,000 | 11 | 0.0011 | 11 | Tapilatu et al. (2021) |
| Jordan | City Beach | Ts | ? | Belt transects; 50 x 5 m | 250 | 1 | 0.00200 | 20 | Roa-Quaoit (2005) |
| Jordan | Clinker | Ts | ? | Belt transects; 50 x 5 m | 750 | 3 | 0.00367 | 36.7 | Roa-Quaoit (2005) |
| Jordan | MSS Reserve | Ts | ? | Belt transects; 50 x 5 m | 750 | 4 | 0.00467 | 46.7 | Roa-Quaoit (2005) |
| Jordan | Tourist Camp | Ts | ? | Belt transects; 50 x 5 m | 750 | 1 | 0.00177 | 17.7 | Roa-Quaoit (2005) |
| Jordan | Japanese Garden | Ts | ? | Belt transects; 50 x 5 m | 750 | 5 | 0.00663 | 66.3 | Roa-Quaoit (2005) |
| Jordan | Gorgon | Ts | ? | Belt transects; 50 x 5 m | 500 | 2 | 0.00395 | 39.5 | Roa-Quaoit (2005) |
| Jordan | Big Bay | Ts | ? | Belt transects; 50 x 5 m | 500 | 2 | 0.00400 | 40 | Roa-Quaoit (2005) |
| Jordan | North Royal Dive | Ts | ? | Belt transects; 50 x 5 m | 750 | 1 | 0.00077 | 7.7 | Roa-Quaoit (2005) |
| Jordan | Intelligence | Ts | ? | Belt transects; 50 x 5 m | 500 | 3 | 0.00515 | 51.5 | Roa-Quaoit (2005) |
| Jordan | Thermal Plant | Ts | ? | Belt transects; 50 x 5 m | 500 | 2 | 0.00300 | 30 | Roa-Quaoit (2005) |
| Jordan | Gas Pipeline | Ts | ? | Belt transects; 50 x 5 m | 500 | 1 | 0.00110 | 11 | Roa-Quaoit (2005) |
| Jordan | Jordan Fertilizer Complex | Ts | ? | Belt transects; 50 x 5 m | 500 | 1 | 0.00230 | 23 | Roa-Quaoit (2005) |
| Jordan | Saudi Arabia Border | Ts | ? | Belt transects; 50 x 5 m | 750 | 2 | 0.00310 | 31 | Roa-Quaoit (2005) |

| Country | Location descriptions | Species | Year of survey | Method of survey | Approximate survey area (m$^2$) | # of ind. | Density (per m$^2$) | Density (per ha) | Reference (see Neo et al. 2017) |
|---|---|---|---|---|---|---|---|---|---|
| Madagascar | Andavadoaka, SW Madagascar | Tg | 2005 | Belt transects; 10 x 2 m | - | - | 0.05000 | 500 | Hopkins (2009) |
| Madagascar | Andavadoaka, SW Madagascar | Tg | 2006 | Belt transects; 10 x 2 m | - | - | 0.04000 | 400 | Hopkins (2009) |
| Madagascar | Andavadoaka, SW Madagascar | Tg | 2007 | Belt transects; 10 x 2 m | - | - | 0.03500 | 350 | Hopkins (2009) |
| Madagascar | Andavadoaka, SW Madagascar | Tg | 2008 | Belt transects; 10 x 2 m | - | - | 0.02000 | 200 | Hopkins (2009) |
| Malaysia | Pulau Tioman | Ts | 1998 | Line intercept transects (density presented is # per 100 m) | 2,620 | 66 | 0.02519 | 251.9 | Tan et al. (1998); no area provided but bin Othman et al. (2010) provided a survey area |
| Malaysia | Perhentian Marine Park | Ts | 2021 | Belt transects; 100 x 4 m or 100 x 8 m, depending on visibility | 11,200 | 186 | 1.5 | 150 | L. K. Lee et al. (2022) |
| Maldives | Fished reefs: Raa Atoll (Beriyanfaru, Hurasfaru, Maadhaffaru, Dhigufaru, Maadhunifaru reefs) and Shaviyani Atoll (Bolissafaru reef) | Ts | 1991 | Manta tows | 38,700 | 15 | 0.00039 | 3.9 | Basker (1991) |
| Maldives | Unfished reefs: Shaviyani Atoll (Hurasfaru, Kilisfaru, Mathikomandoo reefs) and Lhaviyani Atoll (Gaa en faru, Madivaru, Felivaru reefs) | Ts | 1991 | Manta tows | 44,050 | 48 | 0.00109 | 10.9 | Basker (1991) |
| Maldives | Kaafu Atoll | Ts | 1991 | Manta tows | 42,400 | 14 | 0.00033 | 3.3 | Basker (1991) |
| New Caledonia | North Province (Kone, Koumac, Touho, Hienghène) | Hh | 2004 | Belt transects; 40 x 1 m | 8,640 | - | 0.0015 | 15 | Virly (2004) |
| New Caledonia | North Province (Kone, Koumac, Touho, Hienghène) | Hh | 2004 | Manta tows; 300 x 2 m | 83,400 | - | 0.00007 | 0.7 | Virly (2004) |
| New Caledonia | North Province (Kone, Koumac, Touho, Hienghène) | Td | 2004 | Belt transects; 40 x 1 m | 8,640 | - | 0.00034 | 3.4 | Virly (2004) |
| New Caledonia | North Province (Kone, Koumac, Touho, Hienghène) | Td | 2004 | Manta tows; 300 x 2 m | 83,400 | - | 0.00022 | 2.2 | Virly (2004) |
| New Caledonia | North Province (Kone, Koumac, Touho, Hienghène) | Ts | 2004 | Belt transects; 40 x 1 m | 8,640 | - | 0.00081 | 8.1 | Virly (2004) |
| New Caledonia | North Province (Kone, Koumac, Touho, Hienghène) | Ts | 2004 | Manta tows; 300 x 2 m | 83,400 | - | 0.00018 | 1.8 | Virly (2004) |

| Country | Location descriptions | Species | Year of survey | Method of survey | Approximate survey area ($m^2$) | # of ind. | Density (per $m^2$) | Density (per ha) | Reference (see Neo et al. 2017) |
|---|---|---|---|---|---|---|---|---|---|
| New Caledonia | North Eastern Lagoon (Poeubo to Hienghène) | Hh | 2004 | Time swim transects | 165,400 | - | 0.00003 | 0.3 | McKenna et al. (2006) |
| New Caledonia | North Eastern Lagoon (Poeubo to Hienghène) | Td | 2004 | Time swim transects | 165,400 | - | 0.00003 | 0.3 | McKenna et al. (2006) |
| New Caledonia | North Eastern Lagoon (Poeubo to Hienghène) | Ts | 2004 | Time swim transects | 165,400 | - | 0.00077 | 7.7 | McKenna et al. (2006) |
| New Caledonia | Poum | Ts | 2007 | Belt transects; 25 x 5 m | 13,125 | - | 0.00305 | 30.5 | Vieux (2009) |
| New Caledonia | Corne Sud | Td | 2006 | Belt transects; 50 x 10 m | 7,500 | - | 0.00067 | 6.7 | Wantiez et al. (2007a) |
| New Caledonia | Corne Sud | Ts | 2006 | Belt transects; 50 x 10 m | 7,500 | - | 0.00080 | 8 | Wantiez et al. (2007a) |
| New Caledonia | Ile des Pins | Td | 2006 | Belt transects; 50 x 10 m | 11,500 | - | 0.00070 | 7 | Wantiez et al. (2007b) |
| New Caledonia | Ile des Pins | Ts | 2006 | Belt transects; 50 x 10 m | 11,500 | - | 0.00009 | 0.9 | Wantiez et al. (2007b) |
| New Caledonia | Bourail | Hh | 2007 | Belt transects; 50 x 10 m | 3,750 | - | 0.00053 | 5.3 | Wantiez et al. (2007c) |
| New Caledonia | Bourail | Td | 2007 | Belt transects; 50 x 10 m | 3,750 | - | 0.00027 | 2.7 | Wantiez et al. (2007c) |
| New Caledonia | Bourail | Ts | 2007 | Belt transects; 50 x 10 m | 3,750 | - | 0.00080 | 8 | Wantiez et al. (2007c) |
| New Caledonia | Grand Lagon Nord | Hh | 2007 | Belt transects; 50 x 5 m | 7,250 | - | 0.00055 | 5.5 | Wantiez et al. (2008a) |
| New Caledonia | Grand Lagon Nord | Td | 2007 | Belt transects; 50 x 5 m | 7,250 | - | 0.00028 | 2.8 | Wantiez et al. (2008a) |
| New Caledonia | Grand Lagon Nord | Ts | 2007 | Belt transects; 50 x 5 m | 7,250 | - | 0.00069 | 6.9 | Wantiez et al. (2008a) |
| New Caledonia | Merlet | Td | 2008 | Belt transects; 50 x 5 m | 5,250 | - | 0.00076 | 7.6 | Wantiez et al. (2008b) |
| New Caledonia | Merlet | Ts | 2008 | Belt transects; 50 x 5 m | 5,250 | - | 0.00057 | 5.7 | Wantiez et al. (2008b) |
| New Caledonia | New Caledonia (50 sites) | Td | 2006 - 2008 | Manta tows; 100 x 2 m | 227,800 | - | 0.00013 | 1.3 | Purcell et al. (2009) |
| New Caledonia | New Caledonia (50 sites) | Ts | 2006 - 2008 | Manta tows; 100 x 2 m | 227,800 | - | 0.00038 | 3.8 | Purcell et al. (2009) |
| New Caledonia | Noumea | Hh, Ts | 2007 - 2009 | Belt transects; 20 x 1 m | 5,000 | 4 | 0.00078 | 7.84 | Dumas et al. (2013) |
| New Caledonia | New Caledonia (50 sites) | Hh | 2006 - 2008 | Manta tows; 100 x 2 m | 227,800 | 10 | 0.00005 | 0.5 | Purcell et al. (2020) |
| New Caledonia | New Caledonia (50 sites) | Td | 2006 - 2008 | Manta tows; 100 x 2 m | 227,800 | 32 | 0.00014 | 1.4 | Purcell et al. (2020) |
| Niue | Niue | Ts | 1990 | Manta tows | 92,400 | 80 | 0.00087 | 8.7 | Dalzell et al. (1993) |
| Niue | Niue | Ts | ? | Manta tows | 33,840 | 0 | 0 | 0 | Kronen et al. (2008) |

| Country | Location descriptions | Species | Year of survey | Method of survey | Approximate survey area ($m^2$) | # of ind. | Density (per $m^2$) | Density (per ha) | Reference (see Neo et al. 2017) |
|---|---|---|---|---|---|---|---|---|---|
| Palau | South of Koror | Hh | 1968 | Belt transects | 1,100 | 4 | 0.00364 | 36.4 | Hardy and Hardy (1969) |
| Palau | South of Koror | Td | 1968 | Belt transects | 1,100 | 6 | 0.00545 | 54.5 | Hardy and Hardy (1969) |
| Palau | South of Koror | Tg | 1968 | Belt transects | 1,100 | 2 | 0.00182 | 18.2 | Hardy and Hardy (1969) |
| Palau | South of Koror | Ts | 1968 | Belt transects | 1,100 | 7 | 0.00636 | 63.6 | Hardy and Hardy (1969) |
| Palau | Helen Reef, Western Caroline Islands | Hh | 1972 | Line transects, Areal, Drift transects, Towing, Power tows | 43,800 | 58 | 0.00132 | 13.2 | Hester and Jones (1974) |
| Palau | Helen Reef, Western Caroline Islands | Td | 1972 | Line transects, Areal, Drift transects, Towing, Power tows | 43,800 | 101 | 0.00231 | 23.1 | Hester and Jones (1974) |
| Palau | Helen Reef, Western Caroline Islands | Tg | 1972 | Line transects, Areal, Drift transects, Towing, Power tows | 43,800 | 82 | 0.00187 | 18.7 | Hester and Jones (1974) |
| Palau | Helen Reef, Western Caroline Islands | Ts | 1972 | Line transects, Areal, Drift transects, Towing, Power tows | 43,800 | 1 | 0.00002 | 0.2 | Hester and Jones (1974) |
| Palau | Helen Reef, Western Caroline Islands | Hh | 1975 | Line transects, Areal tows | 24,800 | 22 | 0.00089 | 8.9 | Bryan and McConnell (1976) |
| Palau | Helen Reef, Western Caroline Islands | Td | 1975 | Line transects, Areal tows | 24,800 | 6 | 0.00024 | 2.4 | Bryan and McConnell (1976) |
| Palau | Helen Reef, Western Caroline Islands | Tg | 1975 | Line transects, Areal tows | 24,800 | 4 | 0.00016 | 1.6 | Bryan and McConnell (1976) |
| Palau | Helen Reef, Western Caroline Islands | Ts | 1975 | Line transects, Areal tows | 24,800 | 2 | 0.00008 | 0.8 | Bryan and McConnell (1976) |
| Palau | Helen Reef, Western Caroline Islands | Hh | 1976 | Line transects, Areal tows | 15,470 | 63 | 0.00407 | 40.7 | Hirschberger (1980) |
| Palau | Helen Reef, Western Caroline Islands | Td | 1976 | Line transects, Areal tows | 15,470 | 7 | 0.00045 | 4.5 | Hirschberger (1980) |
| Palau | Helen Reef, Western Caroline Islands | Tg | 1976 | Line transects, Areal tows | 15,470 | 4 | 0.00026 | 2.6 | Hirschberger (1980) |
| Palau | Helen Reef, Western Caroline Islands | Ts | 1976 | Line transects, Areal tows | 15,470 | 3 | 0.00019 | 1.9 | Hirschberger (1980) |
| Palau | Palau archipelago | Td | 2015 - 2017 | Non-standardized photographic surveys | 3,300 | 22 | 0.00667 | 66.7 | Rehm et al. (2022) |
| Palau | Palau archipelago | Tg | 2015 - 2017 | Non-standardized photographic surveys | 3,300 | 11 | 0.00333 | 33.3 | Rehm et al. (2022) |
| Palau | Palau archipelago | Ts | 2015 - 2017 | Non-standardized photographic surveys | 3,300 | 32 | 0.00970 | 97.0 | Rehm et al. (2022) |
| Palau | Palau archipelago | Hh | 2015 - 2017 | Non-standardized photographic surveys | 3,300 | 17 | 0.00515 | 51.5 | Rehm et al. (2022) |

| Country | Location descriptions | Species | Year of survey | Method of survey | Approximate survey area ($m^2$) | # of ind. | Density (per $m^2$) | Density (per ha) | Reference (see Neo et al. 2017) |
|---|---|---|---|---|---|---|---|---|---|
| Papua New Guinea | Longman/Kosmann reef | Tg | 1980 | ? | - | - | 0.00090 | 9 | Chesher (1980) |
| Papua New Guinea | Siata reef, Nuakata | Tg | ? | ? | - | - | 0.00100 | 10 | Tarnasky (1980) |
| Papua New Guinea | Engineer and Conflict Group islands | Hh | 1996 | ? | - | - | 0.00201 | 20.1 | Kinch (2001) |
| Papua New Guinea | Engineer and Conflict Group islands | Hp | 1996 | ? | - | - | 0.00003 | 0.3 | Kinch (2001) |
| Papua New Guinea | Engineer and Conflict Group islands | Td | 1996 | ? | - | - | 0.00053 | 5.3 | Kinch (2001) |
| Papua New Guinea | Engineer and Conflict Group islands | Tg | 1996 | ? | - | - | 0.00004 | 0.4 | Kinch (2001) |
| Papua New Guinea | Engineer and Conflict Group islands | Ts | 1998 | ? | - | - | 0.00058 | 5.8 | Kinch (2001) |
| Papua New Guinea | Milne Bay Province | Hh | 2001 | 1126 sites were surveyed | - | - | 0.00004 | 0.41 | Skewes et al. (2003) |
| Papua New Guinea | Milne Bay Province | Td | 2001 | 1126 sites were surveyed | - | - | 0.00003 | 0.34 | Skewes et al. (2003) |
| Papua New Guinea | Milne Bay Province | Tg | 2001 | 1126 sites were surveyed | - | - | 0.00008 | 0.82 | Skewes et al. (2003) |
| Papua New Guinea | Milne Bay Province | Ts | 2001 | 1126 sites were surveyed | - | - | 0.00014 | 1.37 | Skewes et al. (2003) |
| Philippines | Central Visayas, Visayas | Ts | 1984 - 1985 | Quadrat | 30,000 | 20 | 0.00067 | 6.67 | Alcala (1986) |
| Philippines | West Visayas, Visayas | Ts | 1984 - 1985 | Flowmeter method | 7,000 | 92 | 0.01314 | 131.43 | Alcala (1986) |
| Philippines | Cagayan, Sulu Seas | Ts | 1984 - 1985 | Flowmeter method | 5,645 | 7 | 0.00124 | 12.4 | Alcala (1986) |
| Philippines | Palawan | Hh | 1984 - 1985 | Flowmeter method | 21,000 | 29 | 0.00138 | 13.81 | Alcala (1986) |
| Philippines | Palawan | Td | 1984 - 1985 | Flowmeter method | 21,000 | 8 | 0.00038 | 3.81 | Alcala (1986) |
| Philippines | Palawan | Ts | 1984 - 1985 | Flowmeter method | 21,000 | 57 | 0.00271 | 27.14 | Alcala (1986) |
| Philippines | Western Pangasinan, Luzon | Ts | 1984 - 1986 | Belt transects; 100 x 5 m | 53,000 | 17 | 0.00032 | 3.2 | Juinio et al. (1989) |
| Philippines | Polillo, Quezon, Luzon | Hh | 1984 - 1986 | Belt transects; 100 x 5 m | 21,000 | 5 | 0.00024 | 2.4 | Juinio et al. (1989) |
| Philippines | Polillo, Quezon, Luzon | Td | 1984 - 1986 | Belt transects; 100 x 5 m | 21,000 | 6 | 0.00029 | 2.9 | Juinio et al. (1989) |
| Philippines | Polillo, Quezon, Luzon | Tg | 1984 - 1986 | Belt transects; 100 x 5 m | 21,000 | 2 | 0.00010 | 1.0 | Juinio et al. (1989) |
| Philippines | Polillo, Quezon, Luzon | Ts | 1984 - 1986 | Belt transects; 100 x 5 m | 21,000 | 147 | 0.00700 | 70 | Juinio et al. (1989) |
| Philippines | Zambales, Luzon | Ts | 1984 - 1986 | Belt transects; 100 x 5 m | 10,400 | 1 | 0.00010 | 1.0 | Juinio et al. (1989) |

| Country | Location descriptions | Species | Year of survey | Method of survey | Approximate survey area ($m^2$) | # of ind. | Density (per $m^2$) | Density (per ha) | Reference (see Neo et al. 2017) |
|---|---|---|---|---|---|---|---|---|---|
| Philippines | Albay, Luzon | Ts | 1984 - 1986 | Belt transects; 100 x 5 m | 14,500 | 60 | 0.00414 | 41.4 | Juinio et al. (1989) |
| Philippines | Sorsogon, Luzon | Ts | 1984 - 1986 | Belt transects; 100 x 5 m | 14,800 | 4 | 0.00027 | 2.7 | Juinio et al. (1989) |
| Philippines | Calatagan, Luzon | Ts | 1984 - 1986 | Belt transects; 100 x 5 m | 11,100 | 29 | 0.00261 | 26.1 | Juinio et al. (1989) |
| Philippines | Lubang Island, Luzon | Hh | 1984 - 1986 | Belt transects; 100 x 5 m | 14,900 | 1 | 0.00007 | 0.7 | Juinio et al. (1989) |
| Philippines | Lubang Island, Luzon | Ts | 1984 - 1986 | Belt transects; 100 x 5 m | 14,900 | 20 | 0.00134 | 13.4 | Juinio et al. (1989) |
| Philippines | Ambil Island, Luzon | Hh | 1984 - 1986 | Belt transects; 100 x 5 m | 25,000 | 2 | 0.00008 | 0.8 | Juinio et al. (1989) |
| Philippines | Ambil Island, Luzon | Td | 1984 - 1986 | Belt transects; 100 x 5 m | 25,000 | 9 | 0.00036 | 3.6 | Juinio et al. (1989) |
| Philippines | Ambil Island, Luzon | Tg | 1984 - 1986 | Belt transects; 100 x 5 m | 25,000 | 1 | 0.00004 | 0.4 | Juinio et al. (1989) |
| Philippines | Ambil Island, Luzon | Ts | 1984 - 1986 | Belt transects; 100 x 5 m | 25,000 | 82 | 0.00328 | 32.8 | Juinio et al. (1989) |
| Philippines | Apo Reef, Luzon | Td | 1984 - 1986 | Belt transects; 100 x 5 m | 8,800 | 1 | 0.00011 | 1.1 | Juinio et al. (1989) |
| Philippines | Apo Reef, Luzon | Ts | 1984 - 1986 | Belt transects; 100 x 5 m | 8,800 | 1 | 0.00011 | 1.1 | Juinio et al. (1989) |
| Philippines | Puerto Galera, Luzon | Ts | 1984 - 1986 | Belt transects; 100 x 5 m | 14,600 | 14 | 0.00096 | 9.6 | Juinio et al. (1989) |
| Philippines | NE Negros, Visayas | Ts | 1984 - 1986 | Belt transects; 100 x 5 m | 2,900 | 1 | 0.00034 | 3.4 | Juinio et al. (1989) |
| Philippines | El Nido, Palawan | Hh | 1984 - 1986 | Belt transects; 100 x 5 m | 25,500 | 12 | 0.00047 | 4.7 | Juinio et al. (1989) |
| Philippines | El Nido, Palawan | Hp | 1984 - 1986 | Belt transects; 100 x 5 m | 25,500 | 1 | 0.00004 | 0.4 | Juinio et al. (1989) |
| Philippines | El Nido, Palawan | Ts | 1984 - 1986 | Belt transects; 100 x 5 m | 25,500 | 125 | 0.00490 | 49.0 | Juinio et al. (1989) |
| Philippines | Inagauan-Aborlan, Palawan | Td | 1984 - 1986 | Belt transects; 100 x 5 m | 4,500 | 1 | 0.00022 | 2.2 | Juinio et al. (1989) |
| Philippines | Inagauan-Aborlan, Palawan | Ts | 1984 - 1986 | Belt transects; 100 x 5 m | 4,500 | 1 | 0.00022 | 2.2 | Juinio et al. (1989) |
| Philippines | Sombrero Island, Palawan | Hh | 1984 - 1986 | Belt transects; 100 x 5 m | 2,000 | 1 | 0.00050 | 5 | Juinio et al. (1989) |
| Philippines | Sombrero Island, Palawan | Ts | 1984 - 1986 | Belt transects; 100 x 5 m | 2,000 | 2 | 0.00100 | 10 | Juinio et al. (1989) |
| Philippines | Cagayan Island, Palawan | Hh | 1984 - 1986 | Belt transects; 100 x 5 m | 6,400 | 5 | 0.00078 | 7.8 | Juinio et al. (1989) |
| Philippines | Cagayan Island, Palawan | Tg | 1984 - 1986 | Belt transects; 100 x 5 m | 6,400 | 1 | 0.00016 | 1.6 | Juinio et al. (1989) |
| Philippines | Cagayan Island, Palawan | Ts | 1984 - 1986 | Belt transects; 100 x 5 m | 6,400 | 3 | 0.00047 | 4.7 | Juinio et al. (1989) |

| Country | Location descriptions | Species | Year of survey | Method of survey | Approximate survey area ($m^2$) | # of ind. | Density (per $m^2$) | Density (per ha) | Reference (see Neo et al. 2017) |
|---|---|---|---|---|---|---|---|---|---|
| Philippines | Camiguin Island, Mindanao | Ts | 1984 - 1986 | Belt transects; 100 x 5 m | 21,300 | 33 | 0.00155 | 15.5 | Juinio et al. (1989) |
| Philippines | Tubbataha reefs | Hh | 2005 | Belt transects; 150 x 2 m | 4,500 | 10 | 0.00222 | 22.2 | Dolorosa and Schoppe (2005) |
| Philippines | Tubbataha reefs | Ts | 2005 | Belt transects; 150 x 2 m | 4,500 | 2 | 0.00044 | 4.4 | Dolorosa and Schoppe (2005) |
| Philippines | Carbin Reef | Hh | 2006 | Belt transects; 50 x 2 m | 10,000 | 67 | 0.00670 | 67 | Lebata-Ramos et al. (2010) |
| Philippines | Carbin Reef | Ts | 2006 | Belt transects; 50 x 2 m | 10,000 | 12 | 0.00120 | 12 | Lebata-Ramos et al. (2010) |
| Philippines | Tubbataha reefs | Hp | 2008 | Belt transects; 100 x 2 m | 4,200 | 41 | 0.00976 | 97.6 | Dolorosa and Jontila (2012) |
| Philippines | Sabang Reef Fish Sanctuary (inside), Honda Bay, Puerto Princesa City, Palawan | Td | 2004 | Belt transects; 100 x 2 m and two permanent quadrats; 5 x 20 m | - | - | 0.01000 | 100 | Gonzales et al. (2014) |
| Philippines | Sabang Reef Fish Sanctuary (inside), Honda Bay, Puerto Princesa City, Palawan | Ts | 2004 | Belt transects; 100 x 2 m and two permanent quadrats; 5 x 20 m | - | - | 0.01500 | 150 | Gonzales et al. (2014a) |
| Philippines | Meara Island | Td | 2004 | Belt transect; 100 x 2 m | - | - | 0.02500 | 250 | Gonzales et al. (2014) |
| Philippines | Meara Island | Tg | 2004 | Belt transect; 100 x 2 m | - | - | 0.01500 | 150 | Gonzales et al. (2014a) |
| Philippines | Meara Island | Ts | 2004 | Belt transect; 100 x 2 m | - | - | 0.05500 | 550 | Gonzales et al. (2014a) |
| Republic of Kiribati | Abemama Atoll, Central Gilbert Islands group | Hh | 1985 | Manta tows | 28,600,000 | 10,050 | 0.00035 | 3.5 | Munro (1988) |
| Republic of Kiribati | Abemama Atoll, Central Gilbert Islands group | Tg | 1985 | Manta tows | 28,600,000 | 6,592 | 0.00023 | 2.3 | Munro (1988) |
| Republic of Kiribati | Abemama Atoll, Central Gilbert Islands group | Ts | 1985 | Manta tows | 28,600,000 | 137 | 0.000005 | 0.05 | Munro (1988) |
| Republic of Kiribati | Abiang Atoll, Central Gilbert Islands group | Hh | 1985 | Manta tows | 89,900,000 | 19,846 | 0.00022 | 2.2 | Munro (1988) |
| Republic of Kiribati | Abiang Atoll, Central Gilbert Islands group | Tg | 1985 | Manta tows | 89,900,000 | 4,931 | 0.00005 | 0.5 | Munro (1988) |
| Republic of Kiribati | Abiang Atoll, Central Gilbert Islands group | Ts | 1985 | Manta tows | 89,900,000 | 5,319 | 0.00006 | 0.6 | Munro (1988) |
| Republic of Kiribati | Maiana Atoll, Central Gilbert Islands group | Hh | 1985 | Manta tows | 28,000,000 | 1,600 | 0.00006 | 0.6 | Munro (1988) |
| Republic of Kiribati | Maiana Atoll, Central Gilbert Islands group | Tg | 1985 | Manta tows | 28,000,000 | 2,150 | 0.00008 | 0.8 | Munro (1988) |
| Republic of Kiribati | Maiana Atoll, Central Gilbert Islands group | Ts | 1985 | Manta tows | 28,000,000 | 2,580 | 0.00009 | 0.9 | Munro (1988) |
| Republic of Kiribati | Tarawa Atoll, Central Gilbert Islands group | Hh | 1985 | Manta tows | 29,600,000 | 500 | 0.00002 | 0.2 | Munro (1988) |

| Country | Location descriptions | Species | Year of survey | Method of survey | Approximate survey area (m$^2$) | # of ind. | Density (per m$^2$) | Density (per ha) | Reference (see Neo et al. 2017) |
|---|---|---|---|---|---|---|---|---|---|
| Republic of Kiribati | Tarawa Atoll, Central Gilbert Islands group | Tg | 1985 | Manta tows | 29,600,000 | 560 | 0.00002 | 0.2 | Munro (1988) |
| Republic of Kiribati | Tarawa Atoll, Central Gilbert Islands group | Ts | 1985 | Manta tows | 29,600,000 | 780 | 0.00003 | 0.3 | Munro (1988) |
| Seychelles | Aride Island Beach | Ts | 2001-2002 | Daily 30-min walk at low tide | - | - | 4 - Fairly common (21 to 30 specimens) | - | Agombar et al. (2003) |
| Singapore | Southern Islands (7 sites) | Ts | 2003 | Belt transects; 2m wide | 9,670 | 15 | 0.00155 | 15.5 | Guest et al. (2008) |
| Singapore | Southern Islands (29 sites) | Ts | 2009 - 2010 | Belt transects; 6m wide and quadrats; 10 x 10 to 20 x 20 m$^2$ | 87,515 | 28 | 0.00032 | 3.2 | Neo and Todd (2012, 2013) |
| Solomon Islands | Solomon Islands | Hh | 2004 | Belt transects; 300 x 2 m (shallow) and 250 x 50 m (deep) | 118,350 | 4 | 0.00003 | 0.3 | Ramohia (2006) |
| Solomon Islands | Solomon Islands | Td | 2004 | Belt transects; 300 x 2 m (shallow) and 250 x 50 m (deep) | 118,350 | 17 | 0.00014 | 1.4 | Ramohia (2006) |
| Solomon Islands | Solomon Islands | Tg | 2004 | Belt transects; 300 x 2 m (shallow) and 250 x 50 m (deep) | 118,350 | 12 | 0.00010 | 1.0 | Ramohia (2006) |
| Solomon Islands | Solomon Islands | Ts | 2004 | Belt transects; 300 x 2 m (shallow) and 250 x 50 m (deep) | 118,350 | 95 | 0.00080 | 8.0 | Ramohia (2006) |
| South China Sea (Malaysia) | Pulau Layang Layang, Sabah | Hh | 2002 | Timed Roving Diver technique; 1 hour; 9 sampling sites | - | 1 | ? | ? | Sahari et al. (2002) |
| South China Sea (Malaysia) | Pulau Layang Layang, Sabah | Tg | 2002 | Timed Roving Diver technique; 1 hour; 9 sampling sites | - | 6 | ? | ? | Sahari et al. (2002) |
| South China Sea (Malaysia) | Pulau Layang Layang, Sabah | Ts | 2002 | Timed Roving Diver technique; 1 hour; 9 sampling sites | - | 37 | ? | ? | Sahari et al. (2002) |
| South China Sea (North Spratly Islands) | Trident - JOMSRE III | Ts | 2005 | Belt transects; 20 x 10 m | 800 | 10 | 0.01250 | 125 | Van Long et al. (2008) |
| South China Sea (North Spratly Islands) | NE North East Cay | Ts | 2005 | Belt transects; 20 x 10 m | 800 | 8 | 0.01000 | 100 | Van Long et al. (2008) |
| South China Sea (North Spratly Islands) | E North East Cay | Ts | 2005 | Belt transects; 20 x 10 m | 800 | 6 | 0.00750 | 75 | Van Long et al. (2008) |

| Country | Location descriptions | Species | Year of survey | Method of survey | Approximate survey area ($m^2$) | # of ind. | Density (per $m^2$) | Density (per ha) | Reference (see Neo et al. 2017) |
|---|---|---|---|---|---|---|---|---|---|
| South China Sea (North Spratly Islands) | SW North East Cay | Ts | 2005 | Belt transects; 20 x 10 m | 800 | 9 | 0.01125 | 112.5 | Van Long et al. (2008) |
| South China Sea (North Spratly Islands) | NE South West Cay | Ts | 2005 | Belt transects; 20 x 10 m | 800 | 11 | 0.01375 | 137.5 | Van Long et al. (2008) |
| South China Sea (North Spratly Islands) | SW South West Cay | Ts | 2005 | Belt transects; 20 x 10 m | 800 | 6 | 0.00750 | 75 | Van Long et al. (2008) |
| South China Sea (Spratly Islands) | Trident Shoal; Station 1 | Ts | 2005 | Belt transects; 20 x 10 m (10m depth) | 800 | 5 | 0.00625 | 62.5 | Lasola & Hoang (2008) |
| South China Sea (Spratly Islands) | South West Cay; Station 2 | Ts | 2005 | Belt transects; 20 x 10 m (10m depth) | 800 | 6 | 0.00750 | 75 | Lasola & Hoang (2008) |
| South China Sea (Spratly Islands) | North East Cay; Station 3 | Ts | 2005 | Belt transects; 20 x 10 m (10m depth) | 800 | 8 | 0.01000 | 100 | Lasola & Hoang (2008) |
| South China Sea (Spratly Islands) | North East Cay; Station 4 | Ts | 2005 | Belt transects; 20 x 10 m (10m depth) | 800 | 6 | 0.00750 | 75 | Lasola & Hoang (2008) |
| South China Sea (Spratly Islands) | South West Cay; Station 5 | Ts | 2005 | Belt transects; 20 x 10 m (10m depth) | 800 | 11 | 0.01375 | 137.5 | Lasola & Hoang (2008) |
| South China Sea (Spratly Islands) | North East Cay; Station 6 | Ts | 2005 | Belt transects; 20 x 10 m (10m depth) | 800 | 9 | 0.01125 | 112.5 | Lasola & Hoang (2008) |
| South China Sea (Spratly Islands) | NE Cay; North Danger Reef | Hh | 2007 | Belt transects; 500 x 1 m | 1,500 | - | 0.00060 | 6 | Calumpong & Macansantos (2008) |
| South China Sea (Spratly Islands) | NE Cay; North Danger Reef | Ts | 2007 | Belt transects; 500 x 1 m | 1,500 | - | 0.00060 | 6 | Calumpong & Macansantos (2008) |
| South China Sea (Spratly Islands) | S Reef; North Danger Reef | Ts | 2007 | Belt transects; 500 x 1 m | 1,000 | - | 0.00200 | 20 | Calumpong & Macansantos (2008) |
| South China Sea (Spratly Islands) | N Reef; North Danger Reef | Hh | 2007 | Belt transects; 500 x 1 m | 1,000 | - | 0.00100 | 10 | Calumpong & Macansantos (2008) |
| South China Sea (Spratly Islands) | N Reef; North Danger Reef | Ts | 2007 | Belt transects; 500 x 1 m | 1,000 | - | 0.00100 | 10 | Calumpong & Macansantos (2008) |

| Country | Location descriptions | Species | Year of survey | Method of survey | Approximate survey area ($m^2$) | # of ind. | Density (per $m^2$) | Density (per ha) | Reference (see Neo et al. 2017) |
|---|---|---|---|---|---|---|---|---|---|
| South China Sea (Spratly Islands) | Jenkins Reef; North Danger Reef | Ts | 2007 | Belt transects; 500 x 1 m | 500 | 2 | 0.00400 | 40 | Calumpong & Macansantos (2008) |
| South China Sea (Spratly Islands) | Patch Reef; Jackson Atoll | Ts | 2007 | Belt transects; 500 x 1 m | 500 | 1 | 0.00200 | 20 | Calumpong & Macansantos (2008) |
| South China Sea (Dongsha Atoll) | Dongsha Atoll | Hh | 2016 | Belt transects; 6 m (30-500 sq. m) | 3,630 | 1 | 0.00028 | 2.8 | Neo et al. (2018) |
| South China Sea (Dongsha Atoll) | Dongsha Atoll | Ts | 2016 | Belt transects; 6 m (30-500 sq. m) | 3,630 | 2 | 0.00055 | 5.5 | Neo et al. (2018) |
| Thailand | Lee-Pae Island, Andaman Sea | Ts | ? | Belt transects; 100 x 4 m | 6,400 | 1 | 0.00016 | 1.6 | Chantrapornsyl et al. (1996) |
| Thailand | Mannai Island, Rayong Province | Ts | 2010 - 2010 | Belt transect; 100 x 2 m | 200 | 12 | 0.06000 | 600 | Junchompoo et al. (2013) |
| Tokelau | Fakaofo Atoll | Ts | 1989 | Surface tow and reef flat transects | 214,400 | 25 | 0.00012 | 1.2 | Braley (1989) |
| Tokelau | Nukunonu Atoll | Ts | 1989 | Surface tow and reef flat transects | 196,700 | 206 | 0.00105 | 10.5 | Braley (1989) |
| Tokelau | Atafu Atoll | Ts | 1989 | Surface tow and reef flat transects | 111,000 | 0 | 0 | 0 | Braley (1989) |
| Tonga | Vava'u Island Group | Td | 1987 | Timed surveys (64.35 h) | - | 0 | 0 |  | Chesher (1993) |
| Tonga | Vava'u Island Group | Ts | 1987 | Timed surveys (64.35 h) | - | 132 | 2.1 clam per man hour | - | Chesher (1993) |
| Tonga | Vava'u Island Group | Td | 1988 | Timed surveys (69.92 h) | - | 2 | 0.03 clam per man hour | - | Chesher (1993) |
| Tonga | Vava'u Island Group | Ts | 1988 | Timed surveys (69.92 h) | - | 99 | 1.4 clam per man hour | - | Chesher (1993) |
| Tonga | Vava'u Island Group | Td | 1989 | Timed surveys (64.75 h) | - | 45 | 0.7 clam per man hour | - | Chesher (1993) |
| Tonga | Vava'u Island Group | Ts | 1989 | Timed surveys (64.75 h) | - | 161 | 2.5 clam per man hour | - | Chesher (1993) |
| Tonga | Vava'u Island Group | Td | 1990 | Timed surveys (55.37 h) | - | 82 | 1.5 clam per man hour | - | Chesher (1993) |
| Tonga | Vava'u Island Group | Ts | 1990 | Timed surveys (55.37 h) | - | 266 | 4.8 clam per man hour | - | Chesher (1993) |
| Tonga | Lofanga, Ha'apai | Tmb | 1989 | SCUBA search (per man hour effort) | - | 1 | 1 clam per man hour | - | Ledua et al. (1993) |
| Tonga | Auhangamea channel, Uiha Island, Ha'apai | Tmb | 1989 | SCUBA search (per man hour effort) | - | 12 | 2.5 clam per man hour | - | Ledua et al. (1993) |

| Country | Location descriptions | Species | Year of survey | Method of survey | Approximate survey area ($m^2$) | # of ind. | Density (per $m^2$) | Density (per ha) | Reference (see Neo et al. 2017) |
|---|---|---|---|---|---|---|---|---|---|
| Tonga | Kahefahefa Island, Vava'u | Tmb | 1990 | SCUBA search (per man hour effort) | - | 5 | 0.35 clam per man hour | - | Ledua et al. (1993) |
| Tonga | Kahefahefa Island, Vava'u | Tmb | 1991 | SCUBA search (per man hour effort) | - | 6 | 0.04 clam per man hour | - | Ledua et al. (1993) |
| Tonga | Kahefahefa Island, Vava'u | Tmb | 1991 | SCUBA search (per man hour effort) | - | 1 | 2 clam per man hour | - | Ledua et al. (1993) |
| Tonga | Faka'osi Reef, Pangai, Ha'apai | Tmb | 1992 | SCUBA search (per man hour effort) | - | 16 | 0.33 clam per man hour | - | Ledua et al. (1993) |
| Tonga | Luahoko Island, Ha'apai | Tmb | 1992 | SCUBA search (per man hour effort) | - | 21 | 9.1 clam per man hour | - | Ledua et al. (1993) |
| Tonga | Atata Island, Tongatapu Island Group | Ts | 1993 | Free swimming, SCUBA (60 minutes) | - | 4 | 2 clam per man 0.5 hour | - | Tu'avao et al. (1995) |
| Tonga | NW Fafa Island, Tongatapu Island Group | Td | 1993 | Towing (40 minutes) | - | 1 | 0.75 clam per man 0.5 hour | - | Tu'avao et al. (1995) |
| Tonga | NW Fafa Island, Tongatapu Island Group | Ts | 1993 | Towing (40 minutes) | - | 2 | 1.5 clam per man 0.5 hour | - | Tu'avao et al. (1995) |
| Tonga | Hakau Mamao Reef, Tongatapu Island Group | Td | 1993 | Towing (30 minutes) | - | 2 | 2 clam per man 0.5 hour | - | Tu'avao et al. (1995) |
| Tonga | Hakau Mamao Reef, Tongatapu Island Group | Ts | 1993 | Towing (60 minutes) | - | 1 | 0.5 clam per man 0.5 hour | - | Tu'avao et al. (1995) |
| Tonga | Haveluliku, Tongatapu Island Group | Ts | 1993 | Towing (60 minutes) | - | 0.5 | 0.25 clam per man 0.5 hour | - | Tu'avao et al. (1995) |
| Tonga | Monotapu, Tongatapu Island Group | Td | 1993 | Towing (60 minutes) | - | 3 | 1.5 clam per man 0.5 hour | - | Tu'avao et al. (1995) |
| Tonga | Ha'atafu, Tongatapu Island Group | Ts | 1993 | Towing (60 minutes) | - | 1 | 0.5 clam per man 0.5 hour | - | Tu'avao et al. (1995) |
| Tuvalu | Nukufetau Atoll | Ts | ? | ? | - | - | 0.00007 | 0.7 | Braley (1988) |
| Tuvalu | Funafuti Atoll | Ts | ? | ? | - | - | 0.00014 | 1.4 | Braley (1988) |
| Tuvalu | Nukulaelae Atoll | Ts | ? | ? | - | - | 0.00000 | 0 | Braley (1988) |
| Tuvalu | Funafuti Atoll | Ts | 2004 | Belt transects; 300 x 2 m and 40 x 1 m | 54,120 | 16 | 0.00030 | 3.0 | Sauni et al. (2008) |
| Tuvalu | Nukufetau Atoll | Ts | 2004 | Belt transects; 300 x 2 m | 43,200 | 5 | 0.00012 | 1.16 | Sauni et al. (2008) |

| Country | Location descriptions | Species | Year of survey | Method of survey | Approximate survey area ($m^2$) | # of ind. | Density (per $m^2$) | Density (per ha) | Reference (see Neo et al. 2017) |
|---|---|---|---|---|---|---|---|---|---|
| Vanuatu | Inyeug Island, Anatom (Lagoon patch reef) | Hh | 1988 | Spot dives, Manta tows, or Belt transects | - | - | 0.00100 | 10 | Zann and Ayling (1988) |
| Vanuatu | Moso Island, Efate | Hh | 1988 | Spot dives, Manta tows, or Belt transects | - | - | 0.00030 | 3 | Zann and Ayling (1988) |
| Vanuatu | Cook's Reef, Efate (Lagoon) | Hh | 1988 | Spot dives, Manta tows, or Belt transects | - | - | 0.00250 | 25 | Zann and Ayling (1988) |
| Vanuatu | Cook's Reef, Efate (Slope) | Hh | 1988 | Spot dives, Manta tows, or Belt transects | - | - | 0.00010 | 1 | Zann and Ayling (1988) |
| Vanuatu | SE Reef, Pentecost | Hh | 1988 | Spot dives, Manta tows, or Belt transects | - | - | 0.00090 | 9 | Zann and Ayling (1988) |
| Vanuatu | Lesalav Bay, Pentecost | Hh | 1988 | Spot dives, Manta tows, or Belt transects | - | - | 0.00010 | 1 | Zann and Ayling (1988) |
| Vanuatu | Reef Islands, Pentecost | Hh | 1988 | Spot dives, Manta tows, or Belt transects | - | - | 0.00230 | 23 | Zann and Ayling (1988) |
| Vanuatu | Hog Bay, Espiritu Santo | Hh | 1988 | Spot dives, Manta tows, or Belt transects | - | - | 0.00020 | 2 | Zann and Ayling (1988) |
| Vanuatu | Maskelynes, Malekula Group | Ts | 1988 | Belt transects; 50 x 5 m | 18,750 | 4 | 0.00021 | 2.1 | Zann and Ayling (1988) |
| Vanuatu | Malecula, Malekula Group | Ts | 1988 | Belt transects; 50 x 5 m | 7,500 | 1 | 0.00013 | 1.3 | Zann and Ayling (1988) |
| Vietnam | Tho Chau, Con Dao, and Thu Islands (Reef flat) | Ts | 2010 | - | - | - | 0.10000 | 1000 | Latypov and Selin (2011) |
| Vietnam | Tho Chau, Con Dao, and Thu Islands (Reef slope) | Ts | 2010 | - | - | - | 0.2 - 0.5 clams per $m^2$ | - | Latypov and Selin (2011) |
| Vietnam | Giang Bo Reef | Ts | 2004 - 2007 | $1m^2$ Quadrats along 100 - 200 m transect | - | - | 0.10000 | 1000 | Latypov (2013) |
| Vietnam | Mju Island, Nha Trang Bay, Khanh Hoa Province | Ts | 2005 - 2005 | $1m^2$ Quadrats along 100 m transect | 5 | - | 0.10000 | 1000 | Latypov and Selin (2013) |