THEME SECTION

Tagging through the stages: ontogeny in biologging

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INTRODUCTION

Tagging through the stages: technical and ecological challenges in observing life histories through biologging

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ABSTRACT: Biologging data have provided important insights into the biology of marine mammals, sea turtles, birds, fish, and some invertebrates. These techniques have primarily targeted adult organisms. As a result, the early life histories of many marine species are still poorly understood. Technological advances have enabled attachment of smaller tags to young animals, although equipment limitations, access to and capture/handling of animals, and equipment and data recovery pose additional challenges to researchers. In this Theme Section, we highlight novel uses of biologging data on juvenile animals, including reviews of tagging efforts on multiple life-history stages and the integration of oceanographic data in tagging efforts.

KEY WORDS: Electronic tags · Tag attachment techniques · GPS tags · Juveniles · Ocean currents · Ontogeny · Hatchling dispersal models · Satellite telemetry · Conservation

Broad-scale anthropogenic impacts, such as climate change, affect all life stages of a species (Brander 2010, Costa et al. 2010, Evans et al. 2010, Fuentes et al. 2011). Advances in understanding the physiology, behavior, and ecology of many marine species have been made through the use of biologging techniques (Mate et al. 2007, Wilson et al. 2008, Ropert-Coudert et al. 2009, Block et al. 2011), which involve attaching electronic tags to animals (Hooker et al. 2007, Rutz & Hays 2009). These techniques have primarily targeted adult organisms, which tend to have higher survival rates than younger life stages. In addition, larger tags can hold more sensors, greater data storage, and larger batteries, resulting in longer deployments (McConnell et al. 2010). Biologging data have provided important insights into the biology of marine mammals, sea turtles, birds, fish, and some invertebrates (Godley et al. 2008, Hays et al.

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2008, Rutz & Hays 2009, Bograd et al. 2010). However, there are few tagging studies on young life stages, and the early life histories of many marine species are still poorly understood (Hazen et al. 2012).

Improvements in biologging technology have resulted in substantial tag miniaturization and enhanced data compression (Fedak et al. 2002). Although it is now possible to attach small tags to young animals (Mansfield et al. 2012), the small size of these tags limits the number of sensors and length of battery life. Thus, it is essential that careful thought goes into what research questions need to be answered and what types of, and how much, data need to be collected to answer these questions (Breed et al. 2011). Attachment mechanisms, durations, and data needs vary greatly across taxa. Young life stages tend to grow rapidly, often requiring attachment methods that are flexible enough to accommodate growth. Assessment in the field or laboratory of suitable attachment methods is necessary to ensure that any tagging effort has minimal impact on the animals and that the benefits of tagging are not outweighed by the costs (Wilson & McMahon 2006, Mansfield et al. 2012).

High mortality during early life history stages makes it difficult to recover tags, may shorten the period of data collection, and may compromise the data set when predation occurs (Hays et al. 2007, Baker 2008, Snoddy & Southwood Williard 2010). Deploying a large number of tags may therefore be necessary to ensure sufficient sample size, particularly if population processes are of interest (Lindberg & Walker 2007). Sample sizes in biologging are generally limited by available funds, so this may require the use of simpler, more inexpensive tags, and careful selection of the type of sensors they contain.

The Editors of this Theme Section convened a workshop entitled 'Tagging through the Stages: Technical and Ecological Challenges in Observing Life Histories through Biologging' on 16 March 2011 in association with the Biologging IV Symposium in Hobart, Tasmania, Australia, with these technical and ecological challenges in mind. Over 40 scientists and tag manufacturers from Australia, North America, Europe, and Japan attended the workshop. The objectives were to (1) establish the current state of knowledge and technologies for studying young life stages, (2) stimulate interdisciplinary discussion regarding ontogeny and biologging, (3) review and discuss tag design and attachment techniques, and (4) integrate a life history perspective within the field of biologging. There were 18 presentations organized in 3 categories: (1) Tag Techniques and Development, (2) Applications, and (3) Models. The studies within this Theme Section represent a selection from the workshop and feature recent advances in our understanding of the life history of marine species and in particular young life stages.

Tag techniques and development

Advances in tagging technology, such as tag miniaturization, increased data storage and transmission capabilities, and improved analytical methodologies, are providing researchers with important tools for understanding the biology of marine species and their environment (Fedak et al. 2002). The development of fast-acquisition GPS tags, such as Fastloc GPS, has provided increasingly accurate location estimates for species that spend little time at the surface. Shimada et al. (2012) propose a new filtering method for these data that will reduce the linear error of Fastloc GPS locations to 47 m while retaining more than 94 % of the data. This increases the accuracy of home range estimates.

Ethical issues of whether the benefits of the scientific research outweigh the costs of disturbance and possible harm to the animals are a key concern when catching and tagging juvenile animals (Godley et al. 2008). In some cases, young animals may be too small or delicate to carry tags and less invasive research techniques are more appropriate. Assessment of the best techniques and practices will help to ensure that any impacts to the animals are kept to a minimum. Mansfield et al. (2012) describe the first satellite tracks of any neonate sea turtle and the first *in situ* data of the movements of neonate loggerheads *Caretta caretta*. They tested several methods for attaching small solar-powered satellite tags, first in the laboratory to determine whether there were any apparent effects on growth or body condition, and then in the field to establish retention durations and to assess the performance of antifoulants (Mansfield et al. 2012). There is increasing evidence that general guidelines and practices may not well reflect species-specific and longer-term harmful tag effects (Sherrill-Mix & James 2008, Vandenabeele et al. 2012).

Assessing effects of drag may also be possible using computer simulations, to determine how an animal's physiology or morphology may assist with creating hydrodynamic tag designs and attachment techniques (Pavlov & Rashed 2012). Abnormal swimming behavior and increased energetic demands can occur if the tag causes high drag (Hammerschlag et al. 2011, Jones et al. 2011). Designing tags and attachments that will reduce drag is therefore of key importance for marine species that rely on swimming to capture prey or escape predators, and during flight for seabirds (Phillips et al. 2003, Wilson & McMahon 2006, Heithaus et al. 2007, Vandenabeele et al. 2012).

Accommodating the rapid rate of growth in young life stages remains a challenge for tag attachment techniques. Implantable tags may be necessary for studying animals over longer time periods and across life history stages (Horning & Hill 2005). Implantable tags have been effectively used in fish (Block et al. 2005). For example, data on depth and temperature have been used to study changes during different stages of the breeding migration in bluefin tuna *Thunnus thynnus* (Teo et al. 2007).

Applications

Biologging has contributed significant insights that inform conservation management and population recovery efforts by identifying important habitats, risks and impacts, and helping to plan effective mitigation measures (Mate et al. 2007, Shillinger et al. 2008, McClellan et al. 2009). This has included the ability to identify life history changes and potential harvest events. Hart et al. (2012) describe the habitat use of juvenile hawksbill turtles *Eretmochelys imbricata* that had core-use areas within a national park. Two of the tagged turtles migrated from the exclusive economic zone of the USA into Cuban waters, where they may have been harvested.

Neonate, juvenile, and subadult animals tend to behave and move differently than do adults, which may be a result of reduced diving and swimming capabilities early in life, and/or may reduce competition for resources (Campagna et al. 2007). Protection by the mother can make it difficult to tag some young animals, and their unpredictable movements can limit tag recovery and thus bias estimates of survival (Bradshaw et al. 2000). Tyson et al. (2012) attached high-resolution digital acoustic recording tags (Dtags) to a mother and calf humpback whale *Megaptera novaeangliae* pair in Wilhelmina Bay (Western Antarctic Peninsula) to examine their concurrent diving and foraging behavior. The pair appeared to dive in synchrony for much of the tag duration while maintaining close proximity (Tyson et al. 2012). These results validate findings that humpback whale calves accompany their mothers following parturition, remaining within several body lengths until they separate permanently (Szabo & Duffus 2008).

Although the number of biologging studies on immature animals has been small relative to studies on adults (Hazen et al. 2012), an increasing number of recent studies, such as those on loggerhead turtles (Mansfield et al. 2009, 2012, Seney et al. 2010), green turtles *Chelonia mydas* (Hart & Fujisaki 2010), and flatback turtles *Natator depressus* (Salmon et al. 2009), have coupled advances in tag miniaturization with innovative deployment techniques to obtain critical information about the dispersal and movements of juvenile animals. Data regarding this early life history phase are essential because it represents a large proportion of the life span for many long-lived species. Moreover, experiences during these periods are often diverse as these animals undergo transition between nursery, foraging, and breeding habitats, which can exert a strong influence upon the population status.

Barbour & Adams (2012) used passive integrated transponders and found that common snook *Centropomus undecimalis* had high site fidelity within specific life history stages, but changed habitat as they transitioned from juvenile to adult. In another example, Melnychuk et al. (2012) utilized acoustic tagging methods to examine the hypothesis that exposure of coho *Oncorhynchus kisutch* and sockeye salmon *O. nerka* to solar UV-B radiation during freshwater rearing of fry and parr increases mortality at the time of smoltification and ocean entry. They found that while exposure to UV-B resulted in stunted growth of juvenile coho salmon, survivorship during the early marine period was unaffected by the UV-B treatment for both populations. These results challenge one of the many hypotheses for declines in marine survival rates of salmon populations.

Models

There are cases, such as for very young animals, where biologging may not currently be the most appropriate technique or the study design could be improved by first gaining some basic knowledge about when and where the animals are going and how they are dispersing. Ocean models provide a valuable resource for investigating potential dispersal patterns and have been of particular use in studying sea turtles (Hays & Marsh 1997, Hamann et al. 2011, Scott et al. 2011). Very little is known about the movements of hatchling turtles after they leave the beach, until they return as adults decades later. As adults, sea turtles show fidelity to their natal nesting areas and then at the end of the breeding season may migrate to distant foraging sites. Hays et al. (2010)

hypothesized a hatchling drift scenario whereby the foraging sites used by individual sea turtles reflect their previous experiences as young juveniles, when they were carried by ocean currents. The pattern of adult dispersion from the breeding area for loggerhead turtles in the Mediterranean reflects the extent of passive drift experienced by hatchlings (Hays et al. 2010). Simulations of leatherback hatchling dispersal in the western Pacific by Gaspar et al. (2012) similarly found that adults targeted favorable foraging areas inside the juveniles' drift area. However, there were drift areas where no adults have been observed (Gaspar et al. 2012). This could occur as a result of high juvenile mortality along drift trajectories towards such areas, or because of a low return rate if the return route to the natal area is difficult to traverse or navigate. Shillinger et al. (2012) investigated leatherback turtle hatchling dispersal in the eastern Pacific Ocean using passive tracer experiments within a Regional Ocean Modeling System. Tracer distribution suggested that hatchling leatherbacks entering the ocean in late winter are rapidly and efficiently transported offshore within eddies, which may provide a productive refuge for them.

These simulations of hatchling dispersal based on ocean models can further be refined through laboratory and field-derived estimates of their swimming behavior (Wyneken et al. 2008, Okuyama et al. 2009, Salmon et al. 2009). Ocean currents may be critical for determining the dispersal of hatchlings and subsequent migrations as adults. Fossette et al. (2012) reviewed various techniques for estimating current velocities, or more directly, passive drift trajectories. All methods have errors that need to be taken into account when inferring about animal behavior, and in particular, swimming activity (e.g. Jonsen et al. 2005).

Conclusions

There are several challenges in biologging-related conservation research efforts, including: (1) equipment limitations (i.e. suitable tag attachment methods, device size, finding funding for sufficient sample sizes), (2) access to and capture/handling of animals, (3) equipment and data recovery, and (4) creating the empirical link between science and policy that encourages support by managers. The first 3 of these challenges are magnified for immature life stages, which impose stronger size, weight, and recovery constraints on tags. Some lessons can be learned from terrestrial efforts, such as those involving butterflies that carried extremely small, lightweight radar transponders to track their flight paths (Cant et al. 2005). Research involving birds who require small, lightweight tags can also provide insights into marine juvenile biologging techniques (Thorup et al. 2007, Egevang et al. 2010). Our knowledge of life histories can greatly benefit from combining biologging data with information from other sources, such as genetics, stable isotope analyses, modeling, and stranding and catch data (Wallace et al. 2006, Dutton et al. 2007, Godley et al. 2010, Taylor et al. 2011). Similarly, burgeoning efforts to develop high seas marine protected areas, define ecologically or biologically significant areas, and establish adaptively-managed marine reserve networks, will draw upon new tracking research that examines animal movements and behaviors across life history stages (Shillinger et al. 2008, 2010, Game et al. 2009, Dunn 2011).

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Contribution to the Theme Section: 'Tagging through the stages: ontogeny in biologging'

Improving data retention and home range estimates by data-driven screening

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ABSTRACT: Fast acquisition GPS technologies such as Fastloc GPS have been commonly used in recent years to study fine scale spatio-temporal ecology of marine vertebrates. While Fastloc GPS gives more accurate locations than earlier methods, it remains important to identify and remove locations with high error because some location fixes are much less accurate than others. Increasing the number of source satellites required for a valid fix is a simple filter method but it comes at the cost of great data loss. Using data sets acquired from loggerhead turtles *Caretta caretta,* we explored an alternative filtering approach, based on speed between successive locations, angles created by 3 consecutive locations, manufacturer's quality index, and number of satellites used for location calculation. The performance of the proposed filter method was evaluated by conducting terrestrial, mobile tests. When our filter method was used, the linear error (mean ± SD) of Fastloc GPS data decreased from 2645.5 ± 29 458.2 m (n = 1328) to 47.1 ± 61.0 m (n = 1246), while retaining more than 94 % of data. Our filter method also led to more accurate home range estimates than the simple filter method. Improvements in data retention and home range estimates will give more reliable information for marine spatial planning and habitat protection.

KEY WORDS: Fastloc GPS · Screening · Accuracy · Data retention · Home range estimation · *Caretta caretta*

INTRODUCTION

Home range analysis can provide fundamental insights into species ecology and has obvious implications for wildlife management (Peckham et al. 2007, Hays 2008, Hamann et al. 2010). Although home range investigations have been carried out for decades on a multitude of taxa, the quantification of home ranges remains challenging. Home range studies have difficulties everywhere, but are more advanced for terrestrial than for marine vertebrates because of the relative ease of animal capture and tracking, especially via GPS tags. Marine studies have progressed more slowly; they tend to be more difficult to execute, and tagging hardware has the additional problem of either transmitting signals through water or relying on short exposure times as animals surface.

Since the 1980s, satellite-linked platform terminal transmitters (PTTs) have been used to study animal movement, and their use in the marine environment has increased rapidly (Stoneburner 1982, Timko & Kolz 1982, Godley et al. 2008). However, the use of PTTs to understand habitat use in marine animals is often limited because signals can only be transmitted when the animal surfaces, and the surface time must be long enough for transmissions to be completed. As a result, sample sizes for marine fauna tend to be lower than those for terrestrial fauna. Moreover, since the accuracy of an acquired location depends on the number of Argos satellites and the number of messages which reach them, accuracy may also be

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low (Goulet et al. 1999, Eckert & Stewart 2001, Godley et al. 2002). Hence, although PTT technology and methods for data analysis have improved over time (Jonsen et al. 2005, Patterson et al. 2010), PTTs are best applied to studies investigating larger scale habitat use, such as long-distance migration.

Standard GPS tags offer better accuracy but still require enough time on the surface to complete a fix, so relatively few attempts to acquire location are successful in the marine environment (Jay & Garner 2002). Some studies increased the frequency of successful location fixes by keeping the power of the tags on so that receivers acquire a GPS fix whenever they happen to surface, but battery life is then greatly reduced (Ryan et al. 2004, Elkaim et al. 2006). More recently, the situation has been improved by the use of fast acquisition GPS technologies such as Fastloc GPS and quick fix pseudoranging (Tomkiewicz et al. 2010). Consequently, in recent years, these alternative GPS tags have been used on several marine species and age classes to investigate fine scale habitat use (Sheppard et al. 2006, Sims et al. 2009, Kuhn et al. 2010), and their results are thus useful for marine spatial planning and habitat protection (Sheppard 2008).

The standard GPS technology is dependent on the number of source satellites for the accuracy of an initial fix but can increase the accuracy of location estimates by correcting the locations from successive GPS fixes. In stationary land-based tests, the accuracy of Fastloc GPS also improved as the number of source satellites increased (Bryant 2007a, Hazel 2009). However, unlike standard GPS, Fastloc GPS records and uses only one set of raw data at each fixing attempt and thus there is no correction from subsequently obtained data. That is, while Fastloc GPS technology has achieved the ability to capture the necessary data in less than 0.1 s, its accuracy does not improve with successive location fixes (Bryant 2007b, Rutz & Hays 2009, Sirtrack 2010). As a consequence of the trade-off, some Fastloc GPS locations are much less accurate than others if fewer satellites have been involved in fix acquisition. The occurrence of location fixes with high error leads to several data analysis challenges with Fastloc GPS data, especially with the analysis of tracking data and estimation of home ranges. Hence, it is important to develop and use methods that can identify and account for locations with high error.

There are many published methods to screen location data when it is obtained with conventional Argos PTT tags (McConnell et al. 1992, Tremblay et al. 2006, Freitas et al. 2008) but fewer exist for data acquired from Fastloc GPS tags, despite the increase in their use. The simplest screening method for Fastloc GPS data involves the use of residual errors. Residual error is a quality index that represents the level of accuracy of a location fix (Sirtrack 2010). This method alone may not remove all locations with high error but it can be supplemented by taking into account the number of satellites used for calculations — e.g. by rejecting locations involving fewer than a given number of satellites. However in some studies, this may result in a majority of the Fastloc GPS data being discarded (Lonergan et al. 2009). An approach which provides a more reliable filter while retaining more of the data is therefore highly desirable.

A screening method often used for PTT locations is the identification of behaviour that is biologically or ecologically unrealistic for the study species. This approach can also be used for Fastloc GPS data. Speed is the popular limiting factor, and recent studies use the maximum speeds that were estimated from the conventional tracking methods, such as acoustic or PTT telemetry, to screen GPS data (Schofield et al. 2007, Preston et al. 2010, Witt et al. 2010). However, because Fastloc GPS data are generally more abundant and more accurate than Argos PTT data, maximum speeds estimated from Fastloc GPS data are likely to be more realistic than those obtained from Argos PTT data. Further, the angle between 3 consecutive locations is also commonly used to filter location data, but the choice of angle is often arbitrary (Costa et al. 2010, Witt et al. 2010). Hence, there is a need for an improved approach to define the limiting speeds and angles for Fastloc GPS data.

Once a data set has been obtained and appropriately filtered, estimation of home range has a choice of possible approaches. Some commonly used methods for home range estimation are minimum convex polygon, kernel density estimation, harmonic mean, linear home range, and grid cell count (Laver & Kelly 2008). Among those methods, kernel density estimator is currently the most frequently used and least biased home range estimator (Kernohan et al. 2001). Although the kernel method measures intensity of use by estimating the probability density along both x and y coordinates (Silverman 1986, Worton 1989), and therefore the influence of locations with high error or over-screening is presumed to be decreased, accuracy and precision of kernel estimates will be affected by the accuracy of location data and sample size.

Given the promising application of GPS satellite telemetry in wildlife studies, it is important to use appropriate filtering methods to increase data accuracy while minimizing unnecessary data loss, and to allow accurate quantification of home range estimates. This paper explores filtering approaches for Fastloc GPS data obtained from loggerhead turtles *Caretta caretta*, and by conducting terrestrial tests, we evaluate the performance of the proposed filtering methods and determine which filter leads to the most accurate home range estimates.

MATERIALS AND METHODS

Turtle tracking

In 2009 and 2010, 4 adult female loggerhead turtles (T93038, T81920, T54430, K22217) were captured while nesting at Mon Repos and 4 adult male loggerhead turtles (K24365, T53800, T74361, QA14215) were captured at the Moreton Bay foraging ground by a rodeo method (Limpus 1978). The sex and maturity of male turtles were identified either using laparoscopy or by determining whether the tail length from the carapace was greater than 19.0 cm (Limpus & Limpus 2003). We mounted a Fastloc GPS unit on the first through third vertebral scutes of the carapace using Sika Anchor fix-3+ epoxy glue with fibreglass for extra strength. The tracking period ranged from 14 to 153 d and the data include the location fixes that were obtained during the foraging, migrating and inter-nesting periods. T54430 was not tracked during the foraging period due to device failure. The location data acquired during unit deployment, nesting and post-release activities were excluded from the data analysis.

Data retrieval and conversion

Data were transmitted via the ARGOS network (K24365, QA14215, T53800, T54430, T81920 and T93038) or via a USB link directly from device to computer (K22217, T74361 and terrestrial tests). We downloaded the data from each unit using manufacturer-supplied software (Sirtrack Fastloc software) and then decoded data into GPS locations. Finally the location data were converted to the Universal Transverse Mercator coordinate system.

Data screening

The first filtering method we used involved the use of the manufacturer's quality index (residual error) and the number of satellites used in each location calculation (hereafter referred to as the generic filter in this paper). Following the manufacturer's instructions, we excluded locations from the analysis when residual error values were greater than 30 or fewer than 4 satellites were used for location calculation (Sirtrack 2010). Data sets after additional filtering according to available satellite number will be referred to as generic>$\#$ where $\#$ represents the number of source satellites (e.g. generic>4). Consequently, the generic>3 data set contains the maximum number of locations and generic>7 limits the data set to locations acquired with 8 satellites (the maximum possible with Fastloc GPS).

The second filtering method, a data-driven filter, extends the generic filter. The data-driven filter screens the data according to the speed between successive locations, and the angle created by 3 consecutive locations, as well as the number of satellites used for location calculation. Speed and turning angles may vary with turtle behaviour (e.g. foraging, migrating, escaping from predators), but there are currently few studies of behavioural effects on swimming speeds and turning patterns of loggerhead turtles. Therefore, we derived the limiting speeds and angles as objectively as possible from the patterns of Fastloc GPS locations obtained from the turtles, informed by the accuracy associated with the number of source satellites. As errors may increase substantially when the number of source satellites is limited to 4 (Bryant 2007a, Hazel 2009), the data-driven filter is designed to remove erroneous locations derived from 4 satellites. The data group that has been screened by a data-driven filter will be referred to as data-driven>3.

To determine the limiting speed for the data-driven filter, and because high error may occur when only 4 satellites were used to estimate locations, we used data acquired from more than 4 satellites (i.e. generic>4) to estimate the maximum linear speed ($V_{\max}$) a loggerhead turtle was observed to swim between 2 consecutive locations. We then extracted the locations that were preceded and followed by unrealistically fast speeds (i.e. $>V_{\max}$) and labelled them over-speed error points (OSEPs). While this identified some erroneous locations (i.e. OSEPs), other obvious errors (e.g. locations on land) remained unscreened (e.g. Fig. 1B). Therefore, we developed additional limiting criteria to identify and screen other locations with high error.

We calculated the angles between the bearings of lines joining successive location points. This represents 180° minus the animal's turning angle; we will call this the inner angle in this paper. We then identi-

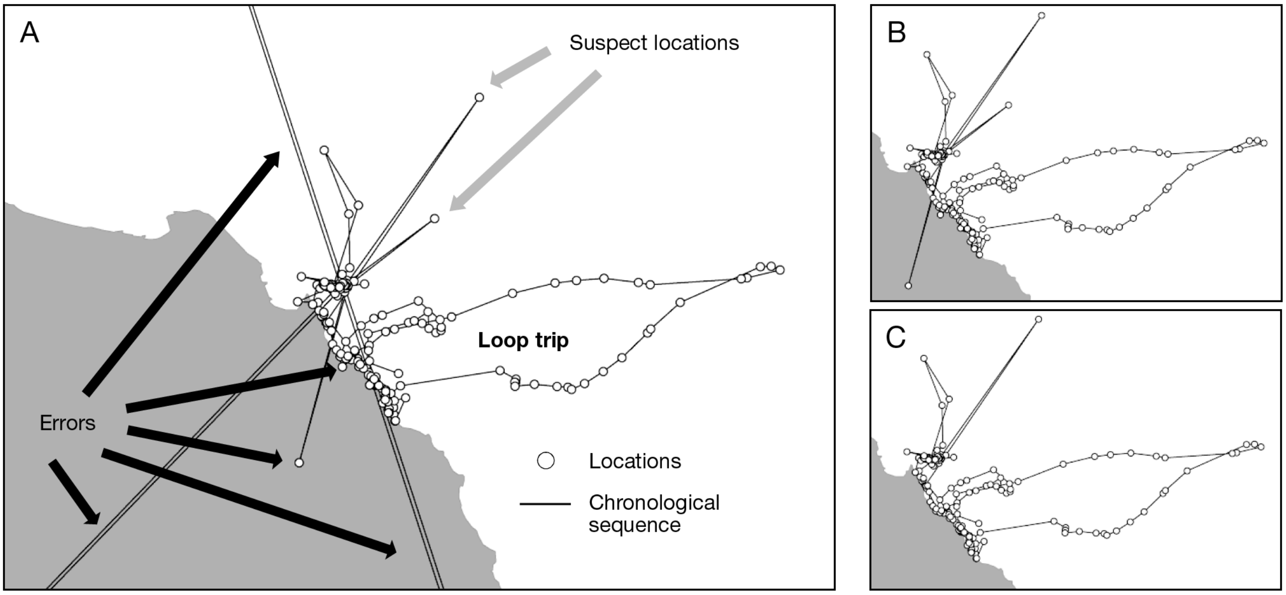

Fig. 1. An example of errors, suspect locations and a loop trip in a data set (A) after screening using the generic>3 filter (i.e. requiring >3 source satellites), (B) after removing locations that were preceded and followed by unrealistically fast speeds, and (C) after screening using the data-driven>3 filter (see 'Materials and methods: Data screening')

fied the inner angles that were associated with OSEPs for comparison with the angles associated with the remainder of the locations (non-OSEPs). Differences between the ranges of angles observed for OSEPs vs. non-OSEPs then guided selection of a limiting angle as described in 'Results: Data-driven filter'. The limiting angle was used to provide a preliminary identification of locations that may be erroneous (suspect locations).

Once suspect locations were extracted by the limiting angle, we calculated the linear speed for the turtle between the suspect location and both its previous location and its following location. The speeds were then compared to the speed of a 'loop trip' for an additional check of the legitimacy of the suspect locations. Loop trip behaviour is represented by spatial departure and return with more than 3 consecutive locations (Fig. 1A). Therefore, a loop trip was considered as an outlier if only one location was obtained during the movement. In our study, we considered continuous straight and fast movement to represent the departure to, and return from, a loop trip. Using the generic>3 data set, we calculated the net (i.e. straight-line) distance between the departure and turning location as well as the turning and return location of the loop trip, and from that calculated the net speed in and out (V_{lp}). We considered the fastest V_{lp} observed in this study as the maximum inward or outward speed of loggerhead turtles during a loop trip. The suspect locations were removed when the speed between the suspect location and either its previous or subsequent location exceeded the maximum V_{lp}.

Kernel estimation

We used a Gaussian kernel density estimator for home range estimation. We chose fixed over adaptive kernel estimators with least squares cross validation (LSCV) as an automated bandwidth selector, because adaptive kernel was not available in the software we used, and because the fixed kernel methods with LSCV to select smoothing parameters appear to produce more accurate and precise estimates of home range areas and are less sensitive to autocorrelation within data sets than adaptive kernel methods (Seaman & Powell 1996, Seaman et al. 1999). While several studies have demonstrated that LSCV can be highly variable (Park & Marron 1990, Gitzen & Millspaugh 2003) and fails to select appropriate bandwidth values when a sample size is too small (e.g. <30 locations; Seaman et al. 1999) or too large (e.g. >100 locations; Hemson et al. 2005), there have been attempts to improve the LSCV method by choosing more appropriate bandwidth values (Duong 2007, 2011). We used the improved LSCV bandwidth selector that is implemented in the R package 'ks' (Duong 2011, R Development Core Team 2011). The 'ks' package was also used to estimate continuous utilization distribution. We used Geospatial Modelling Environment, an extension to ArcGIS, to generate volume contours from the utilization distribution (R Development Core Team 2011, Beyer 2012). A resolution of 50 m was used for the kernel grid because the mean linear error for properly filtered Fastloc GPS data was consistently within 50 m in our terrestrial tests (see Table 1).

Terrestrial mobile test

We recorded walking and biking movements using both a handheld standard GPS receiver and a Fastloc GPS receiver in Townsville, Australia (terrestrial mobile test). The tests were conducted in open areas without overhead cover so as to mirror the environment of the turtles at sea. The tests were commenced after the standard GPS receiver (Garmin GPS60) gained an accuracy of <5 m according to the indication integrated in the unit. Once the standard GPS receiver attains the location estimates with high accuracy, the expected error of the successive locations will remain <15 m, according to the manufacturer (Garmin 2006). The Fastloc GPS unit was set to record a position every 4 min while the standard GPS receiver recorded a position every second. The clocks of the Fastloc GPS receiver and the standard GPS receiver were synchronized before the test began. Following the last test, the time difference between 2 units was recorded. Consequently, using the following equation, the time of each Fastloc GPS fix was adjusted according to the clock difference with the standard GPS so that the time of each standard GPS fix corresponded to the time of each Fastloc GPS fix:

$$\text{Adjusted } Ft_i = Ft_i \frac{\Delta t(Ft_i - t_{\text{sync}})}{t_{\text{end}} - t_{\text{sync}}} \quad (1)$$

where Ft_i is the time when the ith Fastloc GPS fix was acquired, Δt is the final clock difference between the 2 units, t_{sync} is the time at synchronization and t_{end} is the time on the Garmin unit when Δt was recorded. The range of Δt was 1.6 to 4.6 s.

Evaluation of filter performance

We used the terrestrial data to evaluate how data screening improves the accuracy of Fastloc GPS data sets and to determine which screening method leads to the most accurate home range estimates. Unlike for standard GPS, the accuracy of Fastloc GPS locations is not improved by successive fixes, therefore the differences in the interval of location fixing between the turtle tracking and the terrestrial test will not affect the accuracy of Fastloc GPS fixes. Thus, the accuracy of Fastloc GPS locations in the terrestrial test should be comparable to their accuracy in the turtle data.

We screened the data acquired from the terrestrial mobile tests using both the generic and the data-driven filters, following the same procedures used for the turtle data (but with a variation of the loop criterion): the maximum V_{lp} of the terrestrial mobile test was estimated by multiplying the terrestrial V_{max} by the ratio of maximum $V_{\text{lp}}/V_{\text{max}}$ from the turtle data. We then calculated the linear distances between the standard GPS locations and simultaneous Fastloc-derived GPS locations; we interpreted these values as the error distances of Fastloc GPS locations from true locations. After normalizing the data by log-transformation, we compared the means of the linear errors of the generic>3 and data-driven>3 data sets using Welch's 2-sample t-test to assess the performance of the data-driven filter.

We subsampled the Fastloc GPS locations of the terrestrial data using each of the screening methods (i.e. generic>3, data-driven>3, generic>4, generic>5, generic>6 and generic>7). We then calculated the kernel estimates from each of the subsampled Fastloc GPS data and the standard GPS data. We considered the kernel estimates derived from the standard GPS locations to represent the most accurate kernel home range estimates. To measure the differences in the kernel estimates derived from the standard GPS and each of the filtered Fastloc GPS data, we calculated the mean integrated squared error (MISE) as:

$$\text{MISE} = \frac{1}{n}\sum_{i=1}^{n}[f_{\text{Fastloc}}(x_i, y_i) - f_{\text{standard}}(x_i, y_i)]^2 \quad (2)$$

where n is the number of grid points, x and y are the grid coordinates, $f_{\text{Fastloc}}(x_i, y_i)$ is the estimated density derived from Fastloc GPS data at the ith grid point, and $f_{\text{standard}}(x_i, y_i)$ is the accurate density derived from standard GPS data. MISE is widely used as a global measure of differences among different kernel estimates (Seaman & Powell 1996, Horne & Garton 2006, Fieberg 2007b). As a smaller MISE indicates more similarity between estimates, we used MISE as an inverse index of accuracy for kernel estimates.

Home ranges of turtles

We subsampled each turtle data set using each of the alternative screening methods (i.e. generic>3, data-driven>3, generic>4, generic>5, generic>6 and generic>7) and computed home range estimates from the subsampled data sets. We aimed to examine the effect of data screening on the estimates of home range areas of the loggerhead turtles. Since the true home ranges of these animals are not known, the accuracy of the estimates could not be evaluated for the turtle data.

RESULTS

Filter performance in terrestrial tests

The duration of the terrestrial mobile tests ranged from 44 to 136 min and a total of 1583 Fastloc GPS locations were recorded. However, we excluded 255 of them from analysis because the corresponding standard GPS locations were not acquired. The $V_{\max}$ derived from the terrestrial mobile test was 11.9 km h^{-1} (n = 1017). The maximum V_{lp} of the terrestrial data was then calculated as 2.4 km h^{-1} using the ratio of maximum V_{lp} to $V_{\max}$ from the turtle data described in the following subsection (1.8 km h^{-1}:8.9 km h^{-1}). The linear distance between standard GPS and Fastloc GPS locations (Δ_{loc}) decreased as the number of source satellites increased or the data-driven filter was applied (Table 1). In particular, when locations derived from >3 satellites (i.e. generic>3) were used, the linear error was decreased significantly by using the data-driven filter ($t_{(2)\,2239.6} = 2.43$, $p < 0.05$; Table 1). Increasing the number of source satellites required for a valid fix offered further reductions in the linear error but it came at the cost of much greater data loss (Table 1).

We also investigated how data screening influences the accuracy of the home range estimates in the terrestrial test. The kernel estimates derived from data-driven>3 data had the lowest MISE, followed by those derived from generic>4. The remaining generic filters led to higher MISE in the ascending order of generic>5, generic>6, generic>7, and the kernel estimates derived from generic>3 had the highest MISE (Fig. 2).

Table 1. Linear differences between standard GPS locations and screened Fastloc GPS locations (Δ_{loc}, in m). N: no. of locations; numbers in brackets are the percentage of each N when compared to that of the generic>3 data set

No. satellites	Filter	Mean Δ_{loc}	SD	Max. Δ_{loc}	N (%)
>3	Generic	2645.5	29458.2	484640.1	1328 (100)
>3	Data-driven	47.1	61.0	699.5	1246 (94)
>4	Generic	33.1	35.4	328.7	866 (65)
>5	Generic	24.8	22.5	319.5	491 (37)
>6	Generic	19.6	10.8	64.5	228 (17)
>7	Generic	18.8	9.2	40.1	79 (6)

Data-driven filter

We estimated the $V_{\max}$ of the loggerhead turtles as 8.9 km h^{-1} using the location data derived from >4 satellites (n = 3921 fixes). A total of 23 OSEPs was then identified in the data from 8 turtles (n = 6154 fixes) for which the speed both from a previous and to a subsequent location exceeded 8.9 km h^{-1}. We found that all the inner angles at OSEPs were <59° while the inner angles at non-OSEPs were generally higher, ranging up to 180°. The proportion of inner angles ≤59° was significantly different between OSEPs and non-OSEPs (binomial test, $p < 0.0001$). However, using 59° as a limiting angle may be too conservative as a filter since OSEPs are the locations with the most extreme error. Moreover, a previous study using Argos satellite telemetry found that most errors were associated with acute inner angles (i.e. <90°) (Keating 1994). Therefore, we used acute inner angles to make a preliminary identification of suspect locations. We then compared the linear speed immediately prior to and following the suspect location to the maximum V_{lp} to check the legitimacy of each suspect location. The maximum V_{lp} was calculated as 1.8 km h^{-1} from 57 loop trips; each loop trip has 2 V_{lp} (mean ± SD: 0.4 ± 0.3, n = 114).

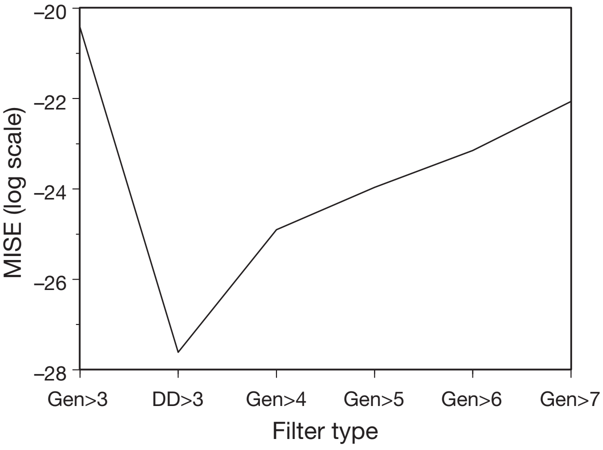

Fig. 2. Mean integrated squared error (MISE) of kernel estimates derived from the Fastloc GPS locations in the terrestrial mobile test. The Fastloc GPS data were screened by the data-driven filter (DD>3) and the generic filters that limited the use of locations by requiring the number of source satellites to be more than 3 (Gen>3), 4 (Gen>4), 5 (Gen>5), 6 (Gen>6), and 7 (Gen>7)

This resulted in a final filtering rule as follows: locations were removed if

- the speed both from a previous and to a subsequent location exceeded 8.9 km h^{-1},

or if all of the following criteria applied:

- the number of source satellites was limited to 4,
- the inner angle was acute and
- the speed either from a previous or to a subsequent location exceeded 1.8 km h^{-1}.

Effect of screening on turtle data

The data-driven filter successfully removed all obvious locations with high error when applied to the generic>3 data sets (e.g. Figs. 1C & 3) while keeping more than 95% of the locations (Table 2). All the locations with high error identified by the data-driven filter were also removed when the generic filters limited the use of locations to those made using >4 satellites (i.e. generic>4) because the obvious errors were all derived from 4 satellites. However, moving from generic>3 to generic>4 (i.e. requiring at least 5 satellites for a valid fix) removed more than a quarter of the location data (Table 2).

The shape and sizes of the home range areas of each turtle varied subject to varying proportions of high-error locations and sample size resulting from the use of different filters (e.g. Fig. 3). The home range boundaries estimated from the generic>3 data were expanded greatly due to the presence of outlying fixes. The data of T53800 did not retain enough locations for home range estimation when it was screened by the generic>7 filter.

DISCUSSION

The results of our terrestrial test and turtle tracking showed that only a small proportion of Fastloc GPS data was highly erroneous but this led to inaccurate quantification of home range estimates (Figs. 2 & 3). We found that a screening method for Fastloc GPS data can be developed by identifying and checking suspect locations characterized by unlikely turning angles and speeds, informed by the location accuracy associated with the number of source GPS satellites.

Loggerhead turtle V_{max} (the preliminary limiting factor used by the data-driven filter) is estimated as 8.9 km h^{-1} in our study. This is similar to the near-sprint linear speed of the same species measured during boat chases (Heithaus et al. 2002), but it is faster than the commonly used limiting speed of 5 km h^{-1}, which was estimated using PTT Argos data obtained from post-nesting green turtles *Chelonia mydas* (Luschi et al. 1998). The swimming speed assessed in our study using Fastloc GPS confirms that the linear speed of the loggerhead turtles is likely to be variable.

The variation in swimming speed is less critical in the filtering process for PTT data because the long interval between consecutive locations would have made short periods at high speed less obvious. Now that more accurate and shorter intervals between locations can be expected using Fastloc GPS, short periods of rapid movement may be mistakenly removed if conventional limiting speeds are used. Through using the faster limiting speed quantified in this study (V_{max}: 8.9 km h^{-1}), we found that the risk of over-screening was minimized, but many locations with high error were not identified because so few data exceeded V_{max}. The locations identified by V_{max} (i.e. OSEPs) can be regarded as the most extreme errors, and additional screening is needed. The combination of acute inner angles and a lower value for limiting speed (i.e. maximum V_{lp}) provided that additional screen.

Our turtle tracking data indicate that OSEPs were associated with inner angles <59°, suggesting that the 20° used by Witt et al. (2010) as a limiting angle may be too conservative when used as a filter for Fastloc GPS data, at least for loggerhead turtles. We used 90° as the limiting angle, which resulted in removing as much as 34% of the original location data in our data set if it was used as a standalone filter. Removing this proportion of data can lead to over-screening: 95% of Fastloc GPS locations had errors ≤219 m in the terrestrial mobile test (this study) or ≤101 m in a stationary test (Hazel 2009), which will be acceptable for many wildlife studies. We overcame the issue of over-screening by supplementing the use of the angle criterion with a maximum loop speed estimate and consequently managed to retain more than 95% of turtle tracking data. Note that the data-driven filter still has the potential to screen real but short sprinting out-and-back movements because animals are capable of short bursts of very fast speed which cannot be maintained for the long periods between most telemetry locations. Although we did not encounter this with our study, researchers should be aware of this possibility when using the data-driven approach.

The generic filters have an advantage in their simplicity, and our terrestrial study found a positive relationship between the number of source satellites and the accuracy of locations for mobile transmitters (Table 1), as found in stationary land-based tests

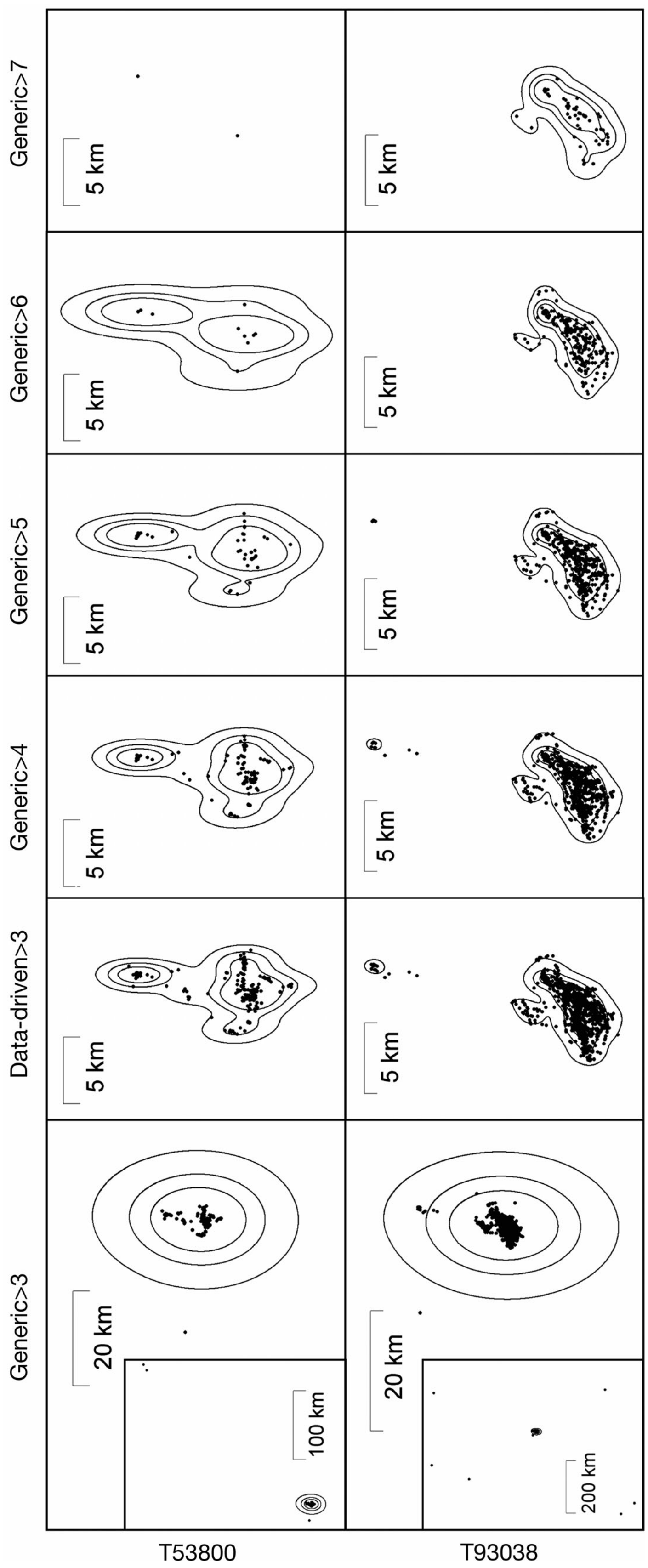

Fig. 3. *Caretta caretta.* Density contours of home range estimates for 2 turtles (T53800 and T93038) during their foraging period. Data were screened by the data-driven filter (data-driven>3) and the generic filters that limited the use of locations by requiring the number of source satellites to be more than 3 (generic>3), 4 (generic>4), 5 (generic>5), 6 (generic>6), and 7 (generic>7). Lines represent 95, 75 and 50% volume contours of the home range estimate. Dots are Fastloc GPS locations

(Bryant 2007a, Hazel 2009). Therefore, using only the location data derived from larger numbers of source satellites can be a straightforward screening method. However, we found that there is a risk of excluding smaller scale but important habitats by the generic filters, even when original sample size is large. For example, the sample size obtained from T93038 was the largest of the 8 turtles, but when the use of locations was limited by requiring the number of source satellites to be more than 6 (i.e. generic>6, generic>7), the northern-most aggregation disappeared because the patch consisted of locations derived from 4, 5 and 6 satellites (Fig. 3). Although the proportion of locations that generated the northern-most patch is small (1.5%), the habitat may be important to the animal during particular times of the year or with variation in availability of food or environmental preferences. In this case, if the use of locations had been limited to those derived from >6 satellites by the generic filters, the habitat distribution would have been underestimated and may not have picked up patches of peripheral habitat that are important to the animal. Moreover, in smaller data sets (e.g. T53800) over-screening may not retain enough locations for a home range analysis (Fig. 3).

For very large data sets (e.g. T93038), requiring locations to be derived from >4 satellites (i.e. generic>4) may be an adequate filtering method because locations with high error were associated with 4 satellites in our data set, and expected errors (mean ± SD) for generic>4 data sets were low 33.1 ± 35.4 m (Table 1). The drawback of the generic>4 filter is that it screens more locations than necessary: moving from generic>3 to generic>4 removed up to 53% of locations in our turtle data set (Table 2). A large reduction in sample size will result in decrease in precision of kernel estimates (Fieberg 2007a), loss of valuable ecological information such as detailed animal movements (Mills et al. 2006) and reduction in the power of statistical comparison (Whitlock & Schluter 2009).

For constructing home range boundaries, removing a large proportion of data by the generic>4 filter may not be so critical since the home range areas derived from the data-driven>3 and generic>4 data sets are very

Table 2. Remaining number of Fastloc GPS locations after each filter was applied to turtle location data sets (turle IDs given above colums). Only the data acquired during the foraging period are shown. The numbers in the brackets are the percentage of each sample size (i.e. number of locations) when compared to that of the generic>3 data set from the same turtle

No. satellites	Filter	Number of locations (percentage against generic>3) K22217	K24365	QA14215	T53800	T74361	T81920	T93038
>3	Generic	475 (100)	504 (100)	226 (100)	219 (100)	964 (100)	1058 (100)	1174 (100)
>3	Data-driven	469 (99)	500 (99)	223 (99)	215 (98)	951 (91)	1009 (96)	1123 (96)
>4	Generic	334 (70)	309 (62)	106 (47)	119 (54)	705 (73)	565 (53)	823 (70)
>5	Generic	242 (51)	167 (33)	40 (18)	45 (21)	459 (48)	299 (28)	490 (42)
>6	Generic	127 (27)	73 (15)	16 (7)	11 (5)	250 (26)	121 (11)	261 (22)
>7	Generic	46 (10)	16 (3)	3 (1)	2 (1)	92 (10)	38 (4)	64 (6)

similar (e.g. Fig. 3). Based on the result of our terrestrial tests, we considered kernel estimates derived from data-driven>3 data sets to represent better home range models than those derived from generic-filtered data. The similarity in the home range areas derived from data-driven>3 and generic>4 data sets indicates that the fixed kernel estimator with the improved LSCV as a bandwidth selector is robust against reduction in sample size as long as high-error locations are properly screened, at least in the volume contours of home ranges.

Although unnecessary data loss with the generic>4 filter did not appear to have a large influence on the construction of home range boundaries, there is little reason to use the generic>4 filter over the data-driven filter when the latter method is available because the data-driven filter (1) will lead to more accurate home range estimates than the generic filters, and (2) will satisfactorily remove locations with high error while retaining more data than the generic filters, as shown in our terrestrial test. Unlike the generic filters, the criteria used in the data-driven filter would need to be determined for each species, and may need to be evaluated separately for different habitats or populations. When the filtering criteria used for a data-driven filter cannot be determined, the generic>4 filter may be an useful alternative screening method.

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Satellite tag attachment methods for tracking neonate sea turtles

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ABSTRACT: Significant gaps exist in our understanding of early sea turtle life stages. Dispersal and habitat use of young oceanic sea turtles are largely inferred. Historically, available tracking technology and tag attachment methods were limited by small body sizes and rapid growth of neonate sea turtles. We tested methods in the laboratory for attaching small solar-powered satellite tags to neonate loggerhead sea turtles *Caretta caretta*, including harnesses, hard epoxy and neoprene-silicone mounts. Non-harness attachments were tested on turtles with clean carapaces and carapaces treated with an acrylic base-coat. Turtle growth and condition were measured among treatment and control groups. We tested surrogate solar cells, coated with clear silicone antifoulant for biofouling and performance, and field tested the performance of 7 solar-powered satellite tags on neonate loggerheads released off southeastern Florida (USA). Attachments with acrylic base-coats remained affixed 4- to 8-fold longer than on untreated carapaces. Harness attachments resulted in long-term tag retention (>60 d). However, harness and hard epoxy attachments did not adjust for turtle growth; we do not recommend these methods for rapidly growing neonate turtles. The method with longest retention was a neoprene-silicone attachment on an acrylic base-coat. Growth and condition were comparable among treated and control turtles using this flexible neoprene-silicone-acrylic attachment. Field-tested tags transmitted for 38 to 172 d. There were significant differences in charge rates of tags treated with an antifoulant and untreated tags; however, all tags charged optimally and transmitted high-quality locations. Our data suggest that small solar-powered tags are viable tools for monitoring the in-water behavior of oceanic sea turtles.

KEY WORDS: *Caretta caretta* · Oceanic stage sea turtles · Lost years · Remote tracking · Solar-powered satellite tags · Telemetry · Transmitter attachment methods

INTRODUCTION

Sea turtles are highly migratory marine species that occur in geographically diverse habitats during different ontogenetic stages. Population recruitment begins when hatchlings enter the ocean; however, significant gaps exist in our understanding of early sea turtle life history, and fine-scale migration and location data are lacking for these youngest life stages. To meet recovery goals for these endangered and threatened species, the status and condition of sea turtle stocks must be understood across all life stages (TEWG 2000, Heppell et al. 2005). While the life history of the loggerhead *Caretta caretta* is the best understood among marine turtles, post-hatching and oceanic stage sea turtle dispersal, in-water habitat use, and survivorship have been largely inferred rather than directly observed (Bolten 2003).

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Empirical data based on opportunistic in-water and stranding observations, phylogeographic studies, and laboratory-based orientation studies indicate that loggerhead hatchlings emerging from nests in the western North Atlantic enter oceanographic current systems that entrain them within the North Atlantic gyre (Brongersma 1968, 1972, 1982, Carr 1986, 1987, Bolten et al. 1992, 1998, Musick & Limpus 1997, Hays & Marsh 1997, Lohmann et al. 2001). These turtles remain offshore for several years, undergoing long trans-oceanic migrations, until they settle in tropical, subtropical, and temperate neritic waters within the Atlantic, Mediterranean, Gulf of Mexico, and Caribbean. As larger neritic juveniles, they move within and among feeding grounds and seasonal habitats, foraging on benthic organisms (Musick & Limpus 1997, Mansfield et al. 2009). Some neritic juveniles return to an oceanic environment for extended periods (McClellan & Read 2007, Mansfield et al. 2009). Mature loggerheads migrate among neritic or oceanic foraging, breeding, and nesting grounds (Hopkins-Murphy et al. 2003).

Historically, hatchling and neonate tracking studies were directly limited by a lack of suitable small-scale tracking technologies capable of remotely recording the animals' positions over a longer term: weeks to months. Existing data are few and based on labor-intensive observations within near-shore habitats. Liew & Chan (1995) radio-tracked leatherback *Dermochelys coriacea* hatchlings off the Malaysian Peninsula, but the tag sizes were large enough to bias behavior. Frick (1976) swam after green turtle *Chelonia mydas* hatchlings a few kilometers from Bermuda's beaches. Ireland et al. (1978) acoustically tracked green turtles up to a few hours as they dispersed from beaches off Tortuguero, Costa Rica. With the exception of a small sample of loggerhead hatchlings followed from shore for up to 3 d (Witherington 1995), most post-hatching loggerhead tracking studies have covered brief periods: a few hours or less (Witherington & Salmon 1992, Stewart & Wyneken 2004, Whelan & Wyneken 2007). Thus, our understanding of early migratory paths and behavior of sea turtles is limited in sample size, and in spatial and temporal scope.

To remotely monitor young oceanic stage turtles, tracking devices must be small, lightweight, have reduced drag profiles, and attachments must not hinder the turtles' growth, movements, or behavior. Sea turtle growth during their first weeks to months at sea can be rapid (Davenport & Scott 1993, Bjorndal et al. 2000, Stokes et al. 2006). Stokes et al. (2006) noted an approximate 3- to 5-fold increase in loggerhead mass under controlled laboratory conditions during the first 3 mo post-hatching. Growth rates for similarly aged turtles in the wild are unknown; however, these rates likely vary in naturally stochastic environments due to variable food availability and intake, and thermal variability (Bjorndal et al. 2003). Developing appropriate tagging technology and attachment methods that accommodate growth for young sea turtles (>20 cm carapace length) would provide insight into the turtles' in-water movements and dispersal routes, and aid in the identification of neonate habitats and developmental areas. Such data would contribute to estimates of the energetic costs incurred by these animals while in their oceanic habitats.

We tested the efficacy of small-scale, solar-powered satellite tags for use on neonate loggerhead sea turtles in a marine environment. Upon entering the ocean, post-hatchling loggerheads tend to remain near the sea surface (Musick & Limpus 1997, Witherington 2002, Bolten 2003). After their first days in the ocean, they associate with flotsam and downwelling lines, exhibiting reduced locomotor activity after the initial frenzy period (Caldwell 1968, Wyneken & Salmon 1992, Witherington 2002, Wyneken et al. 2008). Due to their surface habitat use, neonate loggerheads are excellent candidates for small-scale, solar-powered tags. These tracking devices were designed for terrestrial bird species and have not been tested on marine animals or in a marine environment.

The present study tested satellite tag attachments, tag antifouling methods, and tag performance with the goal of remotely tracking neonate loggerhead sea turtles. Our objectives were to (1) assess whether traditional methods of attaching tracking devices to larger sea turtles are appropriate for smaller, fast-growing neonate sea turtles; (2) develop and test novel alternative attachments for neonate loggerhead sea turtles; (3) test clear, silicone-based coatings on solar cell performance; and (4) field test and assess the performance of small-scale, solar-powered satellite tags attached to neonate loggerhead sea turtles released at sea. Here, we identify a low-impact transmitter attachment method to track small (>13 cm carapace length) loggerhead sea turtles for weeks to months in the wild.

MATERIALS AND METHODS

Study animals

Hatchling loggerhead sea turtles *Caretta caretta* were obtained from nests in Boca Raton, Florida, USA (26.42°N, 80.03°W). Turtles were raised at the

Florida Atlantic University Marine Laboratory following protocols detailed by Stokes et al. (2006). Briefly, turtles were housed in flow-through seawater tanks maintained at 26°C (±2°C), fed 8 to 11% of their bodyweight in food daily, and provided with a fixed 12 h light:12 h dark photocycle. Turtles were reared to minimum weights of ≥300 g (4 to 6 mo old), ensuring that the experimental tags were ≤5% of the turtles' weight, following guidelines designed to minimize the energetic and hydrodynamic costs to tagged animals (Murray & Fuller 2000).

Tag attachment trials

Attachment methods for Microwave Telemetry's PTT-100 9.5 g solar-paneled satellite bird tags and equivalent dummy tags were tested for attachment duration and to assess overall costs to the turtles. The manufacturer pressure-proofed and modified the tags with clear epoxy to protect them in a marine environment. The total weight (in air) of each modified tag was approximately 11 to 13 g (dimensions: 38 mm length × 17 mm width × 12 mm height). We tested 2 tag attachment approaches: 4 *direct* carapace attachments using different adhesives and 2 *indirect* (harness) attachments.

Direct attachment methods

Tags and adhesives were aligned on the carapace, overlapping vertebral scutes I to IV, and slightly overlapping the adjacent costal scutes. The carapace was lightly sanded (Fig. 1a), cleaned using 70% isopropanol, and allowed to air dry. We then treated the carapace with a 2% chlorhexidine diacetate disinfectant solution and air dried again prior to tag attachment. Tag antennae were positioned cranially. Attachments tested included:

(1) Hard epoxy mount: We directly attached dummy tags to turtle carapaces using Sonic Weld™ putty epoxy. This epoxy has been used in other studies to attach satellite tags to larger sea turtles (Mansfield et al. 2009). Approximately 15 to 22 ml of sonic weld epoxy was applied over the vertebral scutes to directly attach tags.

(2) Neoprene-silicone mount: Two strips (approximately 40 mm length × 5 mm width) of 5 mm neoprene wetsuit material were glued on either side of the turtle's vertebral ridge (Fig. 1b) using surgical or cosmetic cyanoacrylate adhesives (e.g. 3M Vet-Bond™ and OnRite™ Perma Rite #9 Plus Hard Bond). Approximately 15 to 22 ml of clear All-Glass™ aquarium silicone was used to affix the dummy tag to the neoprene and shell (Fig. 1c) and to shape a streamlined surface around the attachment site (Fig. 1d).

(3) Hard epoxy mount with acrylic base-coat: We tested PowerFast™ epoxy, another traditional hard epoxy formerly used in telemetry studies of larger turtles (Girard et al. 2009, Mansfield et al. 2009, Seney et al. 2010). This epoxy was placed over scutes that were first treated with a base-coat of manicure acrylic (Kiss® Acrylic Fill Kit, Kiss Products), applied per the manufacturer's instructions. Turtles' shells were sanded and cleaned as described above. The acrylic mixture was 'painted' on the turtles' shells, thinly covering vertebral scutes I to IV and part of the adjacent costal scutes (Fig. 2a). When dry, we attached the dummy tags directly on top of the acrylic, using 15 to 22 ml of PowerFast™ epoxy.

(4) Neoprene-silicone mount with acrylic base-coat: Neoprene-silicone mounts (Attachment Method 2) were attached to turtle carapaces pre-treated with an acrylic base-coat as described above (Fig. 2).

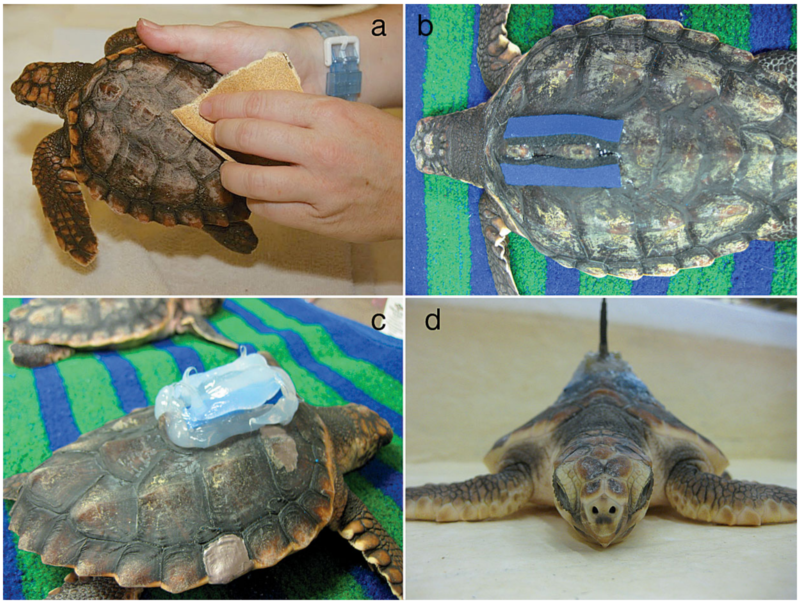

Fig. 1. Procedure for attaching transmitters using a neoprene-silicone mount: (a) sanding carapace at attachment site, (b) attachment of neoprene strips adjacent to vertebral ridge, and (c) addition of aquarium silicone to affix tag. (d) Anterior view of final neoprene-silicone mount

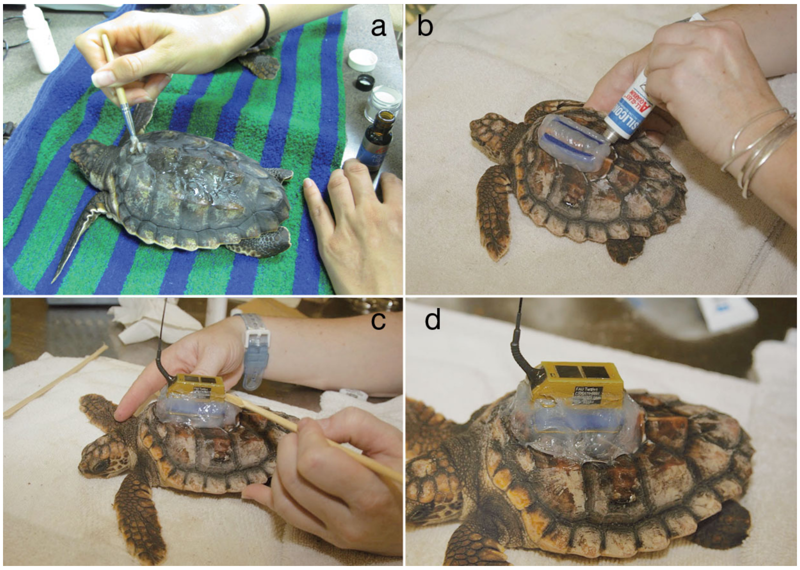

Fig. 2. Attachment process for acrylic base-coat with neoprene-silicone mount: (a) application of acrylic base-coat, (b,c) affixing tag over neoprene strips using aquarium silicone, and (d) final tag attachment

Indirect attachment harness methods

We developed and tested several harness attachments modified from a 'singlet' design (after Salmon & Wyneken 1987) used for tethering turtles for activity and orientation studies. These designs form a 1-piece 'sleeveless/legless' body harness (Fig. 3). Harness materials tested included:

(5) Lycra™ and Velcro™ harness: We tested Lycra™ swimsuit fabric with breakaway Velcro™ hook-and-loop closures. We developed a 'singlet' design with small posterolateral 'straps' that secured the harness posterior to the widest aspect of the carapace and positioned dummy tags dorsomedially, leaving the hind flippers and tail free (Fig. 3a).

(6) Lycra™ and Velcro™ harness with suture material: We tested the above singlet design with additional break-away points sewn into the fabric using dissolvable surgical veterinary suture material. We modified the posterior straps to wrap around the carapace just cranial to the inguinal fossa (the cavity where the hind limb enters the body; Fig. 3b).

Up to 5 replicates of each attachment method were tested initially; we compared turtles fitted with the experimental attachments to control turtles. All turtles were housed under the same laboratory conditions and fed the same diet. Turtles were monitored daily for changes in buoyancy, diving ability, tag stability, and for damage/abrasion caused by attachment materials. Criteria for rejecting any of the experimental attachment methods included (1) inability to feed; (2) lack of in-water stability or buoyancy control (sustained for >30 min), altered swimming, and/or diving ability (sustained for >1 d of observation), and/or abnormal locomotor kinematics; (3) persistent changes in carapace shape due to attachments; (4) short (<3 wk) attachment durations; (5) change in growth or body condition index (CI; measurements described below) relative to the control group. If any of these criteria were met, the tags and associate attachment materials were removed, the turtles' carapaces cleaned, and the attachment method rejected.

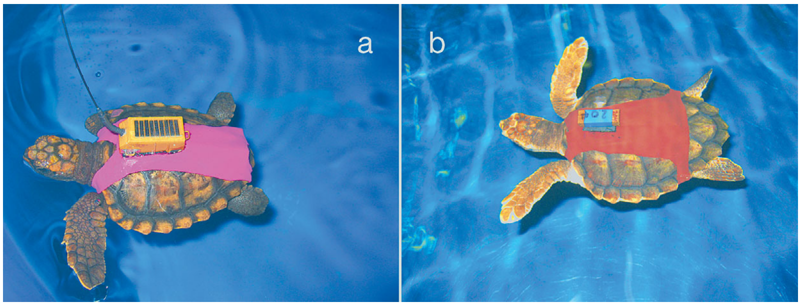

Fig. 3. Examples of indirect harness attachments modified from a 'singlet' design (after Salmon & Wyneken 1987): (a) Lycra™ and Velcro™ harness with post-lateral straps and (b) Lycra™ and Velcro™ harness with suture material and with straps located cranially to the inguinal fossa

Growth study

The tag attachment method(s) which were accepted in the initial trials (described above) were tested again during an expanded study where changes in turtle growth over time among treatment turtles (n = 9) were compared to changes in growth among a treatment-free control group (n = 11). Turtles were measured and weighed within 24 h of nest emergence; measurements were repeated weekly for the duration of the study. Linear measurements of size were made using vernier calipers to the nearest 0.05 mm; standard (notch to tip) straight carapace length (SCL) and width (SCW) were recorded. Mass (g wk^{-1}) and linear measures (mm wk^{-1}; SCL, SCW) were used to quantify absolute growth of turtles in control and experimental groups (body weight was calculated minus the tag and attachment weight). Body condition indices for each turtle were calculated using CI as a function of $M\,L^{-1}$ (where M is mass in g and L is SCL in mm). We used a repeated-measures analysis of variance (RM ANOVA) to determine whether there was a significant change in sea turtle growth rate or condition when satellite tags were attached. All turtles' ages in days were converted to ages in weeks to standardize time to a fixed effect (turtles were measured on the same calendar day but differed in age at the time of measurement).

Tag protection

Silicones are used as anti-corrosive insulators for electrical wires and as antifoulants. Dow Corning T2 Silastic™ (hereafter termed T2) is a transparent silicone coating used experimentally in studies to deter biofouling organisms (Holm et al. 2005, Rittschof et al. 2008). Many silicones, and T2 specifically, release components that interfere with the polymerization of barnacle glue (Rittschof et al. 2008). We tested the effects of T2 coatings on the charging efficiency and for the prevention of corrosion and biofouling of the solar-powered tags, using surrogate solar cells (Plastics Co. WB-15; 20 mm × 20 mm) that were comparable to the cells on the tags.

Testing for energy output

Nine surrogate solar cells were used to test the effects of T2 silicone coating on solar cell performance, tag corrosion, and fouling. Wire ribbons (2 cm long) were soldered to the solar cells using Amtech™ soldering paste (NWS-4100); the wire ribbons were attached to an M2625 Elenco® voltmeter to measure voltage and current output. Prior to treatment, initial voltage and amperage output for all solar cells were recorded to ensure that the cells were capable of conducting and producing energy. We coated the surrogate cells with T2, mixed in accordance with the manufacturer's instructions and placed in a vacuum for de-gassing prior to use. Three control cells were left uncoated, 3 cells were single-coated, and 3 cells were doubled-coated. Coated cells were de-gassed and placed in a 70°C oven until cured. We tested the energy output of cells using a continuously illuminated incandescent lamp with a 52 W bulb (at a distance of 55 cm) as the light source. We recorded the power output (W) generated for each cell.

Power output when submerged

To determine whether the silicone coating interfered with power output of surrogate solar cells while in water, the power output (W) of 2 control cells, 3 single-coated cells, and 3 double-coated cells were tested, both out of water and submerged in seawater. Insulated wires were attached to the cells to suspend them at depth (up to 1 m) and to deliver energy output. Output of cells in air was determined by exposing them to a continuously illuminated 52 W bulb positioned 55 cm from the test cells. For measurements in water, a 52 W bulb was placed 20 cm from the water surface. Cells were submerged at 5 cm intervals (from 5 to 30 cm depth). Energy output was recorded as amps and volts; power is reported as watts with 95% confidence limits (CL).

Corrosion test

To test if T2 prevented solar cell corrosion, each of the 3 treatment groups was isolated in separate glass dishes and completely submerged (with the exception of wires for power measurements) in 30 ml of seawater for 6 d.

Short-term antifouling

To test the antifouling capabilities of T2, solar cells (n = 3 control, 3 single-coated, 3 double-coated) and a Microwave Telemetry 9.5 g dummy tag were attached to a metal screen with a PVC pipe frame. This apparatus was suspended off the research dock at the Duke University Marine Laboratory (DUML) in Beaufort, North Carolina (USA), and observed in the field for 6 d in June 2009. Fouling at this time, though variable, is intense enough that one can assess the antifouling nature of the coatings (Roberts et al. 1991). The control and experimental coatings could not be directly compared because the coating dramatically changes the surface characteristics of the solar cells from hydrophilic to lipophilic, which determines, over short time intervals, the kinds of organisms that will colonize the surface (Roberts et al. 1991). The single- and double-coated surfaces are comparable since they have the same surface characteristics, but differ in the amounts of compounds leaching from the coatings. Treatments were examined under a dissecting microscope every 24 h.

Tag performance

We deployed 7 active satellite tags on laboratory-reared neonate loggerhead turtles. Tags were attached 24 to 36 h in advance of release to allow for a 24 h acclimation period in the laboratory, during which time the turtles were observed to ensure they were capable of diving, foraging, and maintaining buoyancy control. Turtles were released in the Gulf Stream (Table 1) on May 9, 2009 (n = 2 females), June 12, 2009 (n = 3 females), and December 14, 2009 (n = 2; 1 female, 1 male), 10 to 15 km offshore of Riviera Beach, Florida (USA). All tags were configured with a 10 h on, 48 h off duty cycle to allow for full battery charging. Transmitter data (location, battery voltage) were collected by Service ARGOS. Location data were characterized by ARGOS into location class (LC) codes 3, 2, 1, 0, A, and B (listed in order of declining location accuracy; CLS America 2007). ANOVA was used to test for differences in daily battery voltage rates between tags treated with the antifoulant T2 (n = 5; 374 d) and those left untreated (n = 2, May 9 release; 117 d).

RESULTS

Tag attachment trials

Direct attachment methods — no acrylic base-coat

Dummy tags attached with the hard epoxy Sonic Weld™ (n = 5), remained on the turtles for an average (±SD) of 19 ± 12.6 d (range: 3 to 36 d). The tag–carapace 'seal' loosened within an average of 5.4 ± 1.82 d (range: 3 to 8 d). The neoprene-silicone treatment remained on turtles' carapaces for an average of 16.8 ± 4.21 d (range: 11 to 21 d), with the silicone–carapace seal loosening after 8 d (i.e. the tags delaminated from the turtles' shells, forming visually detectable space between the attachment material and carapace). A very thin layer of sloughed keratin was found attached to the base of all attachments at the time the tags detached from the turtles' shells.

Direct attachment methods with acrylic base-coat

Among turtles with carapaces treated with an acrylic base-coat, the PowerFast™ hard epoxy (n = 3) and neoprene-silicone mounts (n = 3) remained attached in the laboratory for a minimum of 50 to 66 d. Turtles quickly adjusted to these attachments and were observed feeding, diving, swimming, and maintaining orientation and buoyancy control with no observable difficulty. Per our permit specifications, we were required to remove attachments and release these turtles (treated with the acrylic base-coat) before all could naturally shed the dummy tags. The hard PowerFast™ epoxy-acrylic attachment temporarily altered the shape of the turtles' carapaces, causing a slight straightening of the carapace along the midline at the site of attachment. This distortion effect was noted only when tags were removed. Shells returned to their natural shape within 24 h of tag removal; the effect was not permanent. Some peeling of the acrylic base-coat occurred after 9 to 12 d, but did not impair the attachment duration. Regardless, non-flexible hard epoxy attachments were rejected due to the potential to alter carapace shape as the turtle grows. No carapace anomalies were noted when the flexible neoprene-silicone attachments were removed. The least consequential and longest lasting direct-attachment method was a neoprene-silicone attachment with acrylic base-coat.

Table 1. *Caretta caretta*. Summary data for field-tested satellite tags and tracked turtles, including turtle identification number (ID), straight carapace length (SCL), total weight, body depth, sex (female/male), whether tags were treated with antifoulant (T2 Silastic^{TM}) prior to release (yes/no), age of turtle, hatch date, release date, and track duration from release location

Turtle ID	SCL (mm)	Weight (g)	Body depth (mm)	Sex	Treatment with antifoulant	Age (d)	Hatch date	Release date	Track duration (d)
92584	149.5	537	71.4	F	N	214	7 Oct 2008	9 May 2009	38
92585	182.8	615	75.9	F	Y	251	4 Oct 2008	12 Jun 2009	59
92586	133.5	364	55.6	M	Y	127	10 Aug 2009	15 Dec 2009	38
92587	163	721	77.8	F	Y	251	4 Oct 2008	12 Jun 2009	55
92588	169	692	78.7	F	Y	281	4 Sep 2008	12 Jun 2009	50
92589	146	475	61.9	F	Y	127	10 Aug 2009	15 Dec 2009	172
92590	150	577	72.5	F	N	247	4 Sep 2008	9 May 2009	79

Indirect attachment methods

Turtles outfitted with harnesses were able to maintain buoyancy control and dive or feed without difficulty. All harness attachments resulted in long-term tag retention; however, they did not adjust for turtle growth, resulting in binding that temporarily altered carapace shape (shape returned to normal in 1 to 3 wk after harness removal). Both break-away designs (Velcro™ and suture thread), failed to release as the turtles outgrew their harnesses. Thus, we rejected all indirect attachment harness designs tested.

Growth study

Here we examined growth rates of turtles treated with the neoprene-silicone tag attachment and acrylic base-coat (n = 9 treatment turtles; n = 11 controls). This was the only method that met Acceptability Criteria (1) to (4), including attachment longevity. The RM ANOVA found no detectable statistically significant effect of satellite tag attachment on any of the growth measures—SCL (RM ANOVA: F = 0.61, p = 0.455), SCW (RM ANOVA: F = 0.3355, p = 0.5784), weight (RM ANOVA: F = 0.0194, p = 0.89600) — or on condition (RM ANOVA: F = 0.3542, p = 0.5936). As expected, the analysis showed a significant increase of all growth variables as a function of time (e.g. SCL: F = 2005.25, $p < 0.001$), with no significant interaction effects (tag attachment by age) except for SCL (RM ANOVA: F = 1.459, $p < 0.05$). The significant interaction between SCL growth and treatment suggests that individual growth in SCL was different through time (different slopes) between control individuals and those that had tags attached (Fig. 4). At the time tags were initially affixed to the turtles for the present study, treatment individuals were slightly larger (mean ± SD SCL = 12.3 ± 0.02 cm; range: 4.3 to 4.9 cm) than control individuals (mean ± SD SCL = 11.6 ± 0.1 cm; range: 4.3 to 4.6 cm), but not significantly larger (t-test: t_{18} = 1.66, p = 0.11). For the first few weeks after tag attachment, treatment turtles appeared to show decreased growth in mean SCL rates compared to the controls; however, they later matched control turtle growth rates for the duration of the study. Tags remained affixed to the turtle carapaces between 59 and 123 d (mean ± SD = 94.8 ± 24.9 d); treatment turtles grew an average of 3.5 ± 1.1 cm (range: 2.2 to 5.1 cm) before shedding the tags.

Tag protection

Energy output in air and at depth

Prior to testing, each solar cell (n = 9) produced between 1.2 and 1.4 mW when placed 55 cm from the light source. Power output in the surrogate cells fluctuated over time from about 30% higher on Day 4 (uncoated) to about 55% of original output by Day 6 (uncoated). Output fluctuation by single-coated cells was variable ranging from 10% higher on Day 2 to about 75% higher on Day 5, as was output by the double-coated cells (10% higher on Day 2 to about 85% of the original on Day 5). Output by Day 6 for single- and double-coated cells was >90% of original and higher than the output of the uncoated cells on the same day.

Current (amps) was comparable among the coated and uncoated solar cells exposed only to air. Power output changed once cells were submerged in seawater, with a large drop with immersions at depth (5 to 10 cm). There was only slight variability (±0.03 mW) among average output for each group (Fig. 5a). The relative difference in output decreased rapidly with depth to 30 cm, at which depth all outputs were roughly comparable and were approximately one-seventh of the output at 5 cm depth (Fig. 5b).

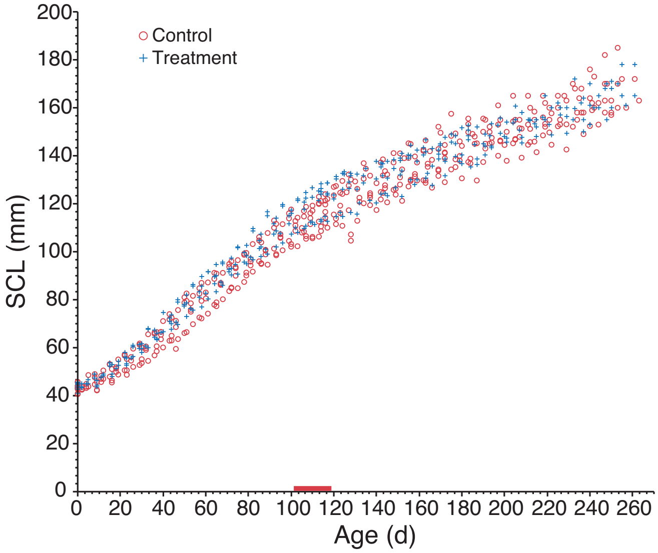

Fig. 4. *Caretta caretta*. Turtle growth (straight carapace length; SCL) over time (d) for control animals and those with neoprene-silicone-acrylic attachments. Start of attachment trial is indicated by red line on the x-axis. Note that the growth study commenced on the same day; however, turtles differed in age at the time of study

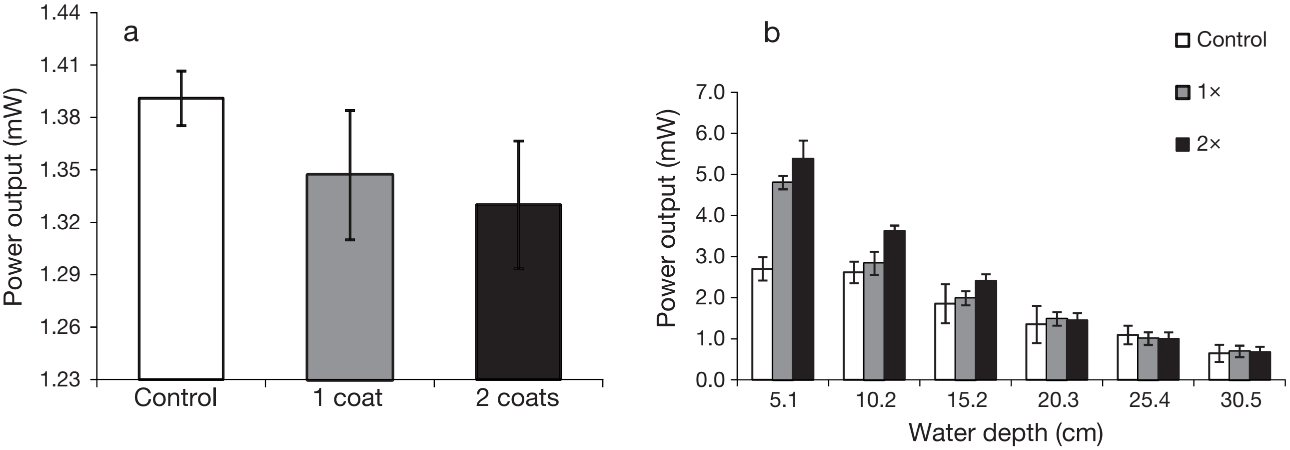

Fig. 5. Solar cell tests. (a) Average power output for treatment groups for control cells and cells treated with 1 (1×) or 2 coats (2×) of T2 Silastic™ and (b) actual power output of surrogate control and treatment (1× and 2×) solar cells at different water depths. Error bars: 1 SD

Corrosion test

Upon continuous exposure to seawater the uncoated cells became visibly corroded, while the coated cells showed no change. In addition, the double-coated Microwave Telemetry tag showed no indication of corrosion after 4 d of submergence.

Antifouling test

Barnacles settled on control and treated cells; all barnacles found on the control cell were alive after 6 d. When soft-bodied organisms were found on the treated cells, they disappeared or died within 1 d. Bryozoans *Bugula neritina*, low surface-energy organisms, settled and grew on single-coated surfaces during Days 1 and 2. Bryozoans were observed on all replicates; however, every bryozoan we observed to settle on the single-coated surfaces died the day after settlement. From Days 3 to 6, five barnacles settled on the single-coated surfaces, 1 of which died. *B. neritina* were not observed growing on the double-coated surfaces — only a single encrusting bryozoan settled and died. No other sessile organisms settled on the double-coated surface until Day 6, when 3 barnacles settled on 1 replicate and 1 barnacle settled on a second. One of the 3 barnacles that settled on the first replicate was dead at the time of observation.

Tag performance in the field

All tags transmitted for at least 38 d. At release, turtles had an average (±SD) SLC of 15.6 ± 1.6 cm (range: 13.4 to 18.3 cm) and weighed 586.6 ± 123.9 g (range: 364 to 721 g) (Table 1). Tags transmitted for an average of 70.1 d ± 47.0 (range: 38 to 172 d) (Table 1). Excluding 1 'outlier' tag that transmitted for 172 d, tags ceased transmitting within 80 d of deployment (n = 6; mean = 53.2 ± 15.3 d; range: 38 to 79 d). The majority of locations received were LC2 (30.1%) and LC1 (27.1%); >77.2% of messages received had associated LCs between 0 and 3 (Fig. 6).

There were significant differences in daily charge voltages (V) among tags treated with T2 and those left untreated (ANOVA: $F = 380.5$; $p < 0.0001$); however, all tags were charging with each duty cycle. Mean (±SD) daily charges for untreated tags was 4.12 ± 0.07 V (range: 3.4 to 4.4 V). Among treated

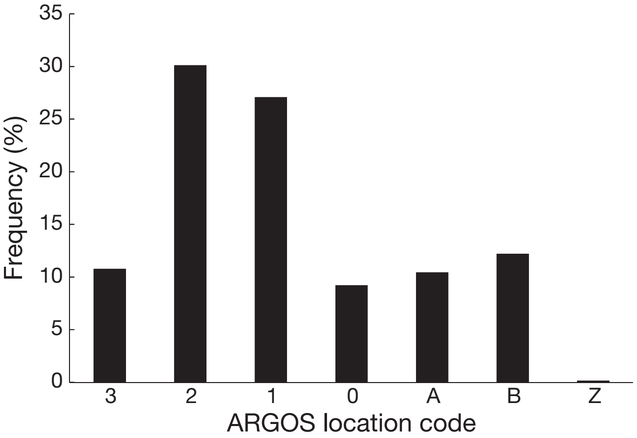

Fig. 6. *Caretta caretta*. Frequency distribution (percent) of ARGOS location codes received during 38 to 172 d field deployment periods (n = 7 tags)

tags, the mean charge was 4.09 ± 0.07 V (range: 3.2 to 4.4 V). All tags maintained adequate operational (approximately >3.2 V; Microwave Telemetry, pers. comm.) and optimal mean (~4.0 V; C. Bykowsky, Microwave Telemetry, pers. comm.) charge rates when transmissions ceased (Fig. 7).

DISCUSSION

Tag attachment

We identified 1 tag attachment method that was superior to all others tested: the neoprene-silicone attachment over an acrylic base-coat. It allowed for neonate turtle growth, showed no detectable effects on swimming or diving behavior in a laboratory setting, shed cleanly from the carapace, performed well in the field, and had attachment durations averaging 2 mo. Due to the rapid growth of neonate sea turtles, tag attachment methods using only hard epoxies are not appropriate. Hard substances or harness attachments should be avoided as they may alter carapace shape if not quickly shed. In the United States, harness methods on larger sea turtles, particularly leatherbacks *Dermochelys coriacea*, are not currently favored due to reports of chafe, abrasion, and the potential for increased hydrodynamic drag (Troëng et al. 2006, Fossette et al. 2008, Sherrill-Mix & James 2008, Jones et al. 2011).

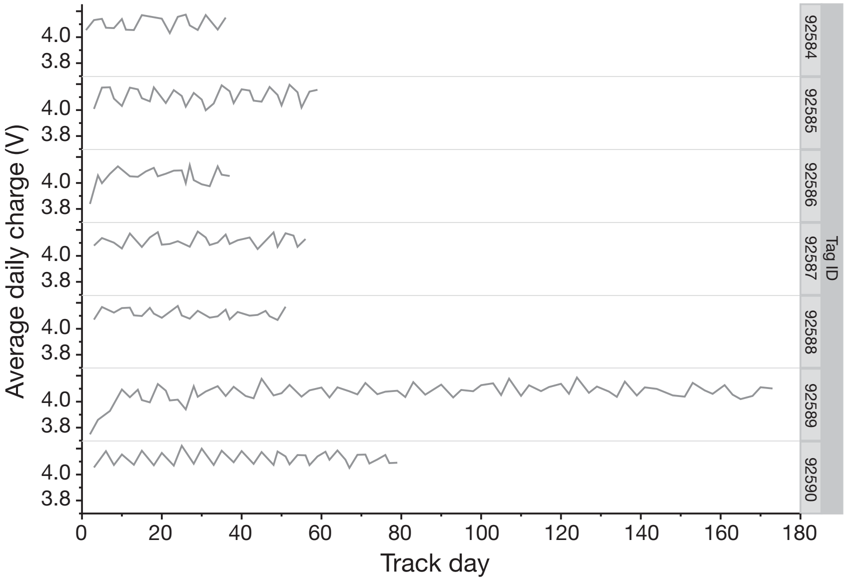

Fig. 7. Average daily charge of solar platform transmitter terminals (n = 7) during 38 to 172 d deployment periods. Lower charges at start of field trials likely reflect lower charge frequency associated with weekly 4 h charge periods pre-deployment (vs. 48 h after 10 h of transmission)

While vertebral ridge profiles make it difficult to attach tags close to the turtle's center of gravity (near the first or second vertebral scutes; Dougherty et al. 2010), we found that gluing small pieces of 5 mm neoprene to either side of the ridge provided an effective cushion, with the additional benefit of the positively buoyant material somewhat offsetting tag weight. The flexibility of the combined neoprene and silicone attachment allowed for growth to occur without altering carapace shape.

Tag placement is critical for minimizing drag effects and potential locomotor costs. We considered and addressed several issues associated with drag. Watson & Granger (1998) tested the hydrodynamic implications of anteriorly placed tags and found the higher the profile, the greater the likely energetic cost. Dougherty et al. (2010) showed that the center of gravity of neonate sea turtles is ventral to the first and second vertebral scutes. Mass added behind the center of gravity could shift the center posteriorly and thus change swimming behavior. By positioning tags towards the front of the carapace and smoothing/tapering the silicone, drag is minimized. While we anticipated small expansion of the drag profile, we saw no substantive changes in drag-related costs. Consequences of drag are realized in energetic costs to the turtle. With neonate turtles, energetic costs are manifested in decreased growth; a decline in growth rate or CI associated with tag attachment would reflect added costs. We retained the treatment turtles for a minimum of 2 wk after the tags were shed. Since sea turtles have the potential to regulate food consumption and energy assimilation, such compensation might minimize any potential impact on condition within 1 or 2 wk (e.g. Roark et al. 2009). During our attachment trials, we found no biologically measureable costs associated with the direct neoprene-silicone-acrylic attachment; however, it is possible that a reduction in growth or body size could have occurred later, and, conceivably, other latent effects not considered by our metrics could also emerge (sensu Wilson 2011), particularly under natural field conditions.

The limiting factor for using any tag attachment method is the necessity of accommodating rapid growth and allowing for subsequent shedding of the tags (minimizing long-term risk to the turtle). In all cases, the neoprene-silicone-acrylic mount sheds cleanly, leaving no residual attachment material on the carapace. While early laboratory trials indicated that rapid integument turnover can result in early tag shedding, adding an acrylic base-coat extended tag attachment durations by 4- to 8-fold, allowing for between 2 and 5 cm in straight carapace growth under laboratory conditions. Thus, the neoprene-silicone-acrylic method provides a smooth, flexible, hydrodynamic surface around the attachment site that allows for normal shell flexion while diving and during subsequent turtle growth.

Tag protection

The variability in energy output of the treated and untreated solar cells in air was so small that it can be concluded that T2 does not decrease the energy output of the solar cells. When tested under water, there was no decrease in efficiency as a result of T2. After 6 d of submersion to test for corrosion, the energy output of the untreated solar cells decreased compared to that of the treated solar cells. More specifically, the solar cells treated with 2 coats of T2 produced more energy than did the single-coated cells or the control cells.

T2 did not prevent all biofouling. Some organisms with base plates, such as barnacles, survived. The calcareous base of barnacles protects their soft tissues from the toxic coating (Rittschof 2000). While a more diverse group of organisms was attracted to T2-treated solar cells, soft fouling organisms died when in contact with T2 and thus did not have long-term fouling effects. While T2 prevents corrosion of solar cells, it is only somewhat effective in reducing biofouling. We expect that the use of T2 as an antifouling agent could be further improved in combination with another substance such as silicone oil (Rittschof et al. 2008). This initial work allows us to conclude that the double-coated system protects the tag from macrofouling for at least 6 d in a near-shore coastal environment. Barnacles are among the most aggressive of macrofoulers, and, although they were colonizing the single-coated surface by Day 3, they did not colonize the double-coated surface until Day 6 — a timeframe that should be sufficient to enable the turtles to reach waters farther offshore where lower concentrations of surface-fouling larval organisms occur.

Tag performance

Solar-powered tags are well suited to tracking neonate loggerheads. These turtles tend to remain near the surface and associate with flotsam (e.g. *Sargassum*), showing little locomotor activity (Caldwell 1968, Witherington 1995, 2002, Smith & Salmon 2009). Thus, the tags are exposed to air, further minimizing the tags' hydrodynamic drag and suitability for some epibionts. This surface-based habitat use is one of the reasons that solar-powered tags are successful for tracking the at-sea movements of these smaller turtles; the tags require direct sun exposure to maintain a charge over time. This prolonged tag exposure also provides longer windows of communication with overhead satellites, a higher degree of location accuracy (LC 3 to 0; Hays et al. 2001, Tougaard et al. 2008), and ample opportunities to recharge solar cells.

Our data indicate that all tags were fully charging when transmissions ceased, likely indicating that (1) turtles were spending most of their time at the surface as is expected, based on the existing scientific understanding of this stage class; (2) tags were likely shed (vs. ceasing transmissions due to lack of charge); and/or (3) the subject animals were preyed upon. It is possible that some other variable caused each of the tags to suddenly cease transmitting and that the tags remained attached to the turtles after the last transmission was received. As such, the length of tag transmission we observed should be considered a minimum estimate for tag attachment duration under field conditions. The tags and attachments are negatively buoyant, and we expect them to sink after falling off the turtles' shells. The tags are only capable of transmitting if the antennae are exposed to air. Thus, abrupt cessation of transmission suggests the antenna was no longer exposed to air.

CONCLUSIONS AND RECOMMENDATIONS

These solar-powered tags are newly adapted for marine use and have considerable potential to revolutionize sea turtle in-water research by identifying nursery areas, preferred habitat characteristics, and quantifying the dispersal patterns, potential growth, and offshore movements of neonate sea turtles (>11 to 12 cm SCL). Under field conditions, tags ceased transmitting after an average of 70 d, less than the average attachment duration (approximately 95 d) under controlled laboratory conditions. Conditions observed in the laboratory are necessarily different in nutrient availability and lack much of nature's stochasticity. The at-sea levels of ultraviolet light exposure, turbulence, amount of flotsam/jetsam encountered, diving behavior, interactions with other species (including cleaner organisms), fouling rates, water temperature, and predation are all factors that may directly or indirectly affect tag performance and attachment duration. While growth rates are likely accelerated in the laboratory, our methods allowed us to successfully track neonate turtles (>13 cm SCL) for at least 2 mo in an open marine environment. Our data also indicate that the neoprene-silicone-acrylic method has a tag attachment duration limited by 2 to 5 cm in turtle growth (SCL). The growth of poikilotherms is influenced by variability in the thermal environmental and available food (Bjorndal et al. 2003). With a larger growth study coupled with environmental analyses, it may be possible to roughly estimate the size of neonate sea turtles tracked in the wild at the time of tag cessation.

With laboratory and field testing, our attachment method may be applicable to other species of sea turtle and other taxa of surface-dwelling marine animals (e.g. crab species, small marine mammals, marine birds). This method will also be applicable for use with other, newer tag technologies as they are developed in the future. The tags we used in the present study were originally designed for terrestrial birds, not marine organisms. Future tag developers should consider reducing the tags' profile, size, and weight — all factors that would further minimize any impacts of drag or turbulent surface conditions on the turtles. Further study is suggested to better assess the long-term impacts of our methods on turtles, including determining drag profiles for the tags under realistic surface conditions and at different attachment sites on the carapace.

Neonate loggerheads spend considerable time at the sea surface; however, other turtle species may not. Shell flexion, a consequence of diving and vigorous swimming, may weaken the attachment site on other species that dive deeper or with more frequency than neonate loggerheads. We therefore recommend further testing (including laboratory and field studies) before applying these methods to other species of sea turtle.

Our methods provide the first successful satellite tracks of any neonate sea turtle. This work will ultimately improve our understanding of their early dispersal paths and rates, providing *in situ* behavioral data that will better inform theoretical dispersal models (e.g. Hays et al. 2010). Satellite tracking data from neonate turtles will also improve our understanding of sea turtle oceanic nursery and developmental habitats, contribute to energetic and life-history models, help identify the threats these young turtles may face, and better delineate areas for targeted species management.

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Contribution to the Theme Section: 'Tagging through the stages: ontogeny in biologging'

Home range, habitat use, and migrations of hawksbill turtles tracked from Dry Tortugas National Park, Florida, USA

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ABSTRACT: To determine habitat-use patterns of sub-adult hawksbills *Eretmochelys imbricata*, we conducted satellite- and acoustic-tracking of 3 turtles captured in August 2008 within Dry Tortugas National Park (DRTO), south Florida, USA, in the Gulf of Mexico; turtles ranged in size from 51.9 to 69.8 cm straight carapace length. After 263, 699, and 655 d of residence in the park, turtles migrated out of the DRTO. Within the park, core-use areas (i.e. 50% kernel density estimates) were 9.2 to 21.5 km^2; all 3 turtle core-use areas overlapped in an area 6.1 km^2 within a zone of the park with multiple human uses (e.g. fishing, anchoring). Two turtles migrated to Cuba and ceased transmitting after 320 and 687 tracking days; the third turtle migrated toward Key West, Florida, and ceased transmitting after 884 tracking days. The present study highlights previously unknown regional connections for hawksbills, possible turtle-harvest incidents, and fine-scale habitat use of sub-adult hawksbills within a United States National Park.

KEY WORDS: Hawksbill · Satellite · Acoustic · Telemetry · Kernel density estimate · Harvest · Dry Tortugas

INTRODUCTION

Understanding home ranges and migration paths for wide-ranging marine species is critical for the design of effective conservation strategies targeting vulnerable life stages of imperiled taxa (Meylan 1999, Bowen et al. 2007, Benson et al. 2011). The hawksbill turtle *Eretmochelys imbricata* is a circumtropically distributed marine species that occupies coral reef habitats throughout most of its range (Carr et al. 1966, Mortimer & Donnelly 2008), except in parts of the eastern Pacific where Gaos et al. (2012) recently discovered hawksbills living in mangrove estuaries. Generally considered spongivores (Meylan 1988, Van Dam & Diez 1997), hawksbills also consume other species such as corallimorphs, hydroids, sea urchins and jellyfish (Carr et al. 1966, Leon & Bjorndal 2002, Blumenthal et al. 2009b). In the Caribbean, hawksbills nest on both insular and mainland sandy beaches (Carr et al. 1966), often in areas with at least some vegetation (Kamel & Mrosovsky 2005).

Like other species of marine turtles, hawksbill hatchlings enter into an initial pelagic phase, where they are likely taken up by strong ocean currents and transported to foraging grounds (Blumenthal et al. 2009a). These foraging grounds can be home to juveniles from many different nesting aggregations, each consisting of genetically distinct subpopulations (Bass et al. 1996, Velez-Zuazo et al. 2008). Long-term

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observations of resident juveniles at foraging grounds (e.g. Puerto Rico; Van Dam & Diez 1997, 1998a) and close proximity of suitable nesting habitat to coral reefs where hawksbills were sighted stimulated debate about whether hawksbills had the need to migrate (see Meylan 1999). However, recaptures of tagged individuals away from original tagging locations (Parmenter 1983), genetic analysis of mixed stocks of hawksbills at foraging grounds (Bowen et al. 1996, 2007, Bass 1999), and satellite tracking studies conducted throughout the Caribbean over the last several decades have demonstrated that hawksbills are indeed migratory (Horrocks et al. 2001, Troëng et al. 2005, Van Dam et al. 2008). Previous records showed travel distances of 110 to 1936 km for adults and 46 to 900 km for juveniles (Meylan 1999). Long-distance migrations have been reported in other areas as well, with 2 tagged juveniles from the Seychelles resighted years later as a sub-adult and adult 1150 and 900 km away, respectively, from their original tagging locations (Mortimer et al. 2012).

The hawksbill was listed as critically endangered on the IUCN Red List of Threatened Species in 1996, based on an overall decline in the species of >80%, and extensive subpopulation declines in all ocean basins. Declines were due to over-harvesting, incidental take and degradation of habitat over the last 3 hawksbill generations (105 yr; Meylan & Donnelly 1999, Mortimer & Donnelly 2008). Wallace et al. (2010) recently defined 13 population segments or regional management units (RMUs) for hawksbills; however, they define 7 population segments as 'putative' RMUs because of a lack of information on distribution and genetics. DRTO hawksbills fall under the 'Atlantic, western Caribbean (USA)' RMU. This new RMU framework provides a strategy for organizing marine turtles into units of protection above the level of nesting populations, but below the level of species, within regional entities that might be on independent evolutionary trajectories.

According to the United States Endangered Species Act, hawksbills are endangered in all parts of their range (NMFS & USFWS 1993, 1998). Because marine turtles undertake extensive migrations, reducing local populations can affect populations throughout the region (Bowen et al. 1996, 2007, Bass 1999, Eckert 2002). Effective implementation of management programs for hawksbills will require a thorough understanding of individual movements throughout the region and the spatial extent of home ranges and core-use areas they establish within foraging grounds.

Many approaches have been taken to understand hawksbill movements, including mark-recapture and flipper-tagging (Bjorndal et al. 1985, Leon & Diez 1999, Richardson et al. 1999, Velez-Zuazo et al. 2008). Acoustic telemetry has also been used to elucidate horizontal movements of hawksbills and sometimes estimate home ranges, either actively with handheld receivers (Van Dam & Diez 1998a, Witt et al. 2010, Scales et al. 2011), passively with fixed receiver arrays (Okuyama et al. 2005), or both (Blumenthal et al. 2009c). While passive acoustic telemetry is inherently limited by the number of receivers in a given array, it is less labor-intensive, provides a larger sample size, and can detect multiple individuals simultaneously and continuously throughout an array (Voegeli et al. 2001, Heupel et al. 2006, Scales et al. 2011). Within an array, acoustic telemetry data are useful for interpreting foraging area habitat use at a scale from 10s to 100s of meters and for discovering diel patterns of movement (Arendt et al. 2001, Heupel et al. 2006). To obtain home-range estimates beyond the scope of receiver arrays, however, satellite telemetry has emerged as the preferred tool and has been utilized to track many marine species in recent years (Hart & Hyrenbach 2009), including sea turtles (Godley et al. 2008). Satellite telemetry can provide the data necessary for accurately estimating home ranges, as well as tracking individuals over large areas. Despite the increasing number of satellite telemetry studies focused on hawksbills, only a few studies have previously assessed home range size or core-use areas.

No home-range estimates for any size-class of hawksbills is available within United States continental waters. Additionally, no hawksbill home-range studies have focused primarily on the sub-adult size-class. Here, we investigate the foraging home range and migrations of 3 sub-adult hawksbills captured and tagged in Dry Tortugas National Park (DRTO), South Florida, USA. Using finer scale location accuracy provided by acoustic tracking in conjunction with satellite-tracking data, we aimed to determine both broad- and fine-scale habitat-use patterns of sub-adult hawksbills at this site. We also aimed to decipher diel movement patterns of 2 of the 3 satellite-tagged hawksbills. Understanding the home-range estimates, core-use areas and movement patterns of hawksbills within the park will help resource managers establish effective local management practices to protect this critically endangered species. Further, protecting this species at 1 foraging ground and furthering the understanding of its migration patterns will contribute to the conservation of hawksbills throughout the greater Caribbean region.

MATERIALS AND METHODS

Study site

The Dry Tortugas consists of 7 small islands ~100 km west of Key West, Florida (near 24° 38′ 00″ N, 82° 55′ 12″ W; Fig. 1). The area resembles an atoll, consisting of a series of carbonate banks and sand shoals in which the banks roughly form a circular pattern (Mallinson et al. 2003). The largest of the islands is Loggerhead Key (~1.5 km long × ~250 m wide). In 1908 the region was designated as a Wildlife Refuge, in 1935 a National Monument and in 1992 a National Park. More recently, in 2007, 120 km^2 of the ~262 km^2 park was designated a research natural area (RNA), creating a no-take preserve within the park to foster ecological self-renewal by minimizing anthropogenic influences (National Park Service 2006). The creation of the DRTO RNA is part of a region-wide effort to strengthen marine protection and complement nearby reserves such as the North and South Tortugas Ecological Reserves (TNER, TSER) of the Florida Keys National Marine Sanctuary (FKNMS), established by the National Oceanic and Atmospheric Administration (NOAA) and the State of Florida. The sandy beaches of DRTO are monitored as part of the State of Florida's marine turtle nest monitoring program (see Witherington et al. 2009).

Turtle capture and standard handling

We captured hawksbill turtles *Eretmochelys imbricata* at DRTO in August 2008 by dip netting during the day (3 m handle with 84 × 102 cm net) while aboard a 4.3 m Livingston skiff equipped with a 25 hp motor. All procedures for turtle handling and sampling followed established protocols (NMFS SEFSC 2008). We tagged each animal with a passive integrated transponder (PIT) tag in the right shoulder region and affixed an individually numbered flipper tag to each of the rear flippers. Immediately after tag-

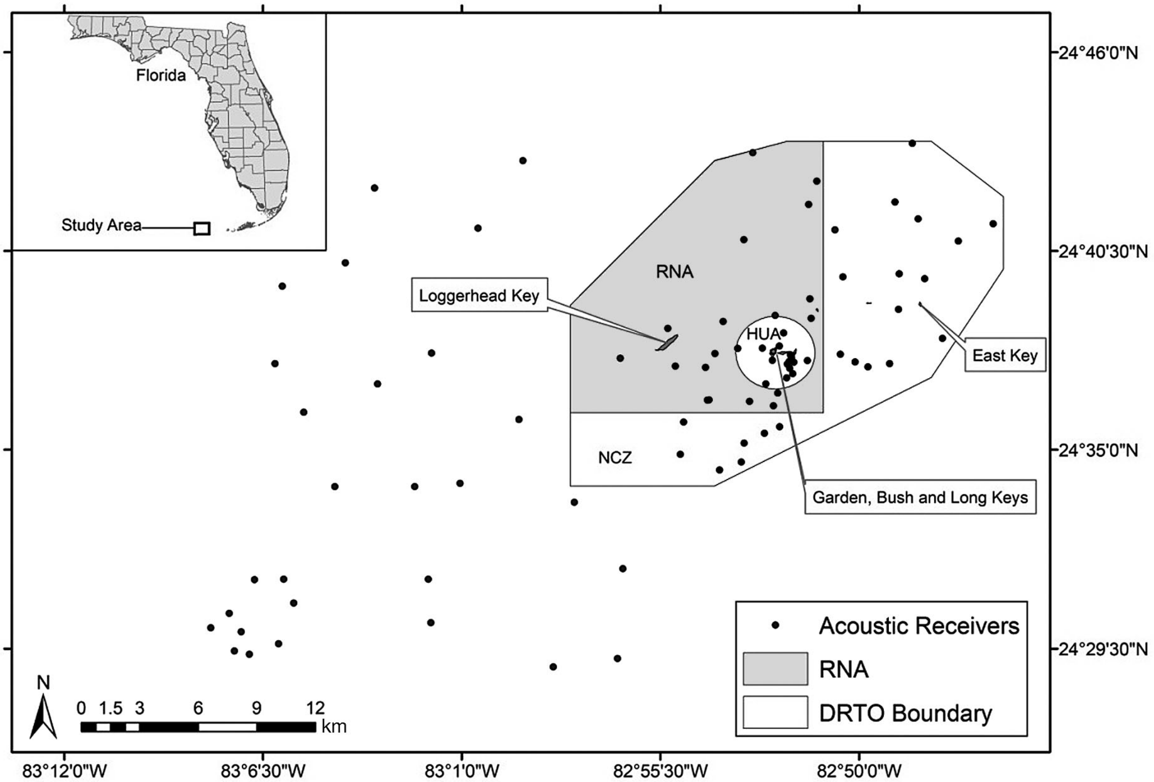

Fig. 1. Study area showing the islands, acoustic receiver array present at time of study, Dry Tortugas National Park (DRTO) boundary and the different management boundaries within. The area outside the research natural area (RNA), but within the park is the natural cultural zone (NCZ), which extends to the east and south of the RNA. There is also a 10.7 km^2 area within the RNA designated as the historic adaptive-use zone (HAU) for a 1 mile radius around Garden Key that allows for human activities such as anchoring and fishing. This area is concentrated around Garden Key and Bush Key where human activities are the most common. There were 55 acoustic receivers in or within detection range (200 m) of the DRTO boundary. Of these, 18 were inside the RNA (with an additional 2 within detection range of the RNA), and another 15 were inside the HAU (with 1 additional receiver within detection range of the HAU)

ging each animal, we took standard carapace measurements, including curved (CCL) and straight (SCL) carapace lengths. We weighed turtles with a spring scale and netting to the nearest 0.1 kg and took photographs to document carapace and skin anomalies.

We fitted a Wildlife Computers SPOT5 platform terminal transmitter (PTT) to each turtle. Each tag (2.5xAA model for Turtles A and C; 2xAA model for Turtle B) had a saltwater switch and output of 0.5 W. The 2xAA model measured 79.7 × 49.5 × 18.1 mm (length × width × height) with a mass of 95 g in air, and the 2.5xAA model measured 71 × 54 × 24 mm with a mass of 115 g in air. Prior to transmitter application with Power-Fast™ 2-part marine epoxy, we removed epibionts (e.g. barnacles, algae) from the carapace of each turtle and sanded and cleaned the carapace with isopropyl alcohol. We streamlined attachment materials and minimized the epoxy footprint. The anticipated battery life of each tag was 1 yr, and each tag was programmed to operate continuously. All tagged turtles were released within 2 h at their capture location.

We outfitted 2 of the 3 turtles with Vemco V16-4L acoustic transmitters (25 g in air, 11 g in water; 16 mm diameter × 68 mm length) on the right rear carapace marginal scute. We prepared the area where the tag was to be affixed as with the satellite transmitters. To affix the acoustic transmitter, we used approximately half of 1 West Marine epoxy putty stick, mixed immediately prior to application. We let the streamlined epoxy dry for approximately 10 min. The anticipated life of each tag was several years.

In DRTO and the surrounding areas of the TSER and TNER, several agencies maintain an array of acoustic receivers (Vemco VR2 and VR2W) spanning approximately 800 km^2. A total of 83 acoustic receivers were active in this array during the study period (Fig. 1).

Satellite-data filtering and analysis

We archived and filtered location data with the satellite-tracking and analysis tool (STAT; Coyne & Godley 2005). Turtle positions were determined with the Argos system, which classified each location message received into 1 of 6 location classes (LCs): 3, 2, 1, 0, A, or B. Argos assigns accuracy estimates of <250 m for LC 3, 250 to <500 m for LC 2, 500 to <1500 m for LC 1, and >1500 m for LC 0; for a satellite pass with 3 messages and 2 messages, the estimated accuracy is unknown and locations are tagged as LC A and LC B, respectively (CLS 2011). Locations failing the Argos plausibility tests are tagged as Class Z (CLS 2011). All location data were filtered by Argos using the traditional least-squares location processing algorithm. Hays et al. (2001) and Vincent et al. (2002) found the accuracy of LC A to be comparable to LC 1 from Argos, so we included LC 3, 2, 1, 0 and A locations and filtered out B and Z locations. We also filtered out locations that required a straight-line travel speed >5 km h^{-1}; we selected this conservative filter based on results by Parker et al. (2009) who reported hawksbill travel speeds of 0.7 to 1.2 km h^{-1} during transit in a Hawaiian study site, as well as previous use of this speed filter in other hawksbill tracking studies (Troëng et al. 2005, Van Dam et al. 2007, Gaos et al. 2012; see also Luschi et al. 1998). Using ArcGIS 9.3 (ESRI 2007), we manually removed obviously erroneous points (e.g. those that 'zig-zagged' land or large areas of open water) and implausible locations remaining after the STAT filtering process. Additionally, for home range and core-use analyses, we removed points received after the turtle's last day within the DRTO boundary (assumed start of migration). From accepted Argos locations, we calculated inferred mean travel speeds during foraging for all turtles using the linear distances between 2 consecutive filtered locations in kilometers per hour.

To minimize autocorrelation in spatial analysis, we generated mean daily locations for each turtle from the accepted locations, following the methods of Seney & Landry (2008). The resulting coordinates provided raw data for individual fixed kernel density estimation (KDE) analysis (e.g. Eckert et al. 2006, Seney & Landry 2008). Kernel density is a non-parametric method used to identify 1 or more areas of disproportionately heavy use (i.e. core areas) within a home range boundary (for review see Worton 1987, 1989, White & Garrott 1990, Laver & Kelly 2008), with appropriate weighting of outlying observations. As Laver & Kelly (2008) suggested, we implemented core-use analysis for each animal following Seaman & Powell (1996) and Powell (2000), and report the 50% contour values at which core areas were delineated. We used the home range tools for ArcGIS extension (Rodgers et al. 2005) and the fixed kernel least-squares cross-validation smoothing factor (h_{cv}) for each KDE (Worton 1995, Seaman & Powell 1996). When the variance of x- and y-coordinates of the points were highly unequal, the data were rescaled before applying the kernel method. We used ArcGIS 9.3 to calculate the in-water area (km^2) within each contour and to plot the data. We used a 50% KDE to represent the core area of activity (Hooge et al. 2001, Laver & Kelly 2008). We combined overlapping areas of each 50% KDE to create a common-use core area for all turtles. We overlaid the DRTO boundary and the RNA boundary on all resulting maps and summed location data with respect to both boundaries.

To test and quantify site fidelity, we used the spatial analyst and animal movement (AMAE) extension for ArcView 3.3. We used Monte Carlo random walk (MCRW) simulations to test for site fidelity (100 replicates), testing tracks for spatial randomness against randomly generated walks (Hooge et al. 2001, Mansfield et al. 2009). We bounded the range for random walks to 0–150 m depth to include only the realistic extent of the in-water habitat for our animals during the study period. Tracks exhibiting site fidelity indicate movements that are more spatially constrained rather than randomly dispersed (Hooge et al. 2001). A very small proportion of accepted turtle locations fell on land (4 points in total for all 3 turtles; 0.7% of filtered locations); this was likely due to a combination of satellite errors and changes in island shape for these highly dynamic small sandy islands at DRTO. We ran the kernel density tests and constrained random walk including these 4 points.

Corresponding water depths for turtle 50% core-use areas were extracted from bathymetry raster data from the NOAA National Geophysical Data Center (GEODAS) US Coastal Relief Model Grids with 2 min resolution (www.ngdc.noaa.gov/mgg/gdas/gd_designagrid.html, accessed 7 November 2011). Using ArcGIS 9.3, we calculated the mean water depth from the raster data for the common-use area.

Acoustic telemetry analysis

The detection distance of acoustic receivers can vary based on transmitter type, salinity and depth of water, ambient noise, presence of pycnoclines and thermoclines, and the behavior of the study animal (see Heupel et al. 2006). Receiver detection distances in our study area could range from 100 to 600 m, depending on weather, terrain and sea state, so we used a conservative detection distance of 200 m for each receiver for all analyses. For each receiver with detections, we summed total detections and calculated the frequency of detections (number of turtle-days). The receivers were deployed at variable times, so we standardized turtle-days at each receiver by dividing them by the total number of days the receiver was deployed.

To determine fine-scale movements and habitat use within the park by time of day, we converted the downloaded acoustic data from UTC to local time and then divided the detections into day and night categories. The average sunrise and sunset times at the study site during the tracking period were 07:06 and 18:43 h, so we calculated movements based on approximate times of 07:00 h for sunrise and 19:00 h for sunset.

We assessed the habitat characteristics at all receivers with turtle detections via snorkel and/or scuba diving in the summer and fall of 2011, collecting digital photographs to create records of habitat type in the immediate vicinity of each receiver. We classified receiver habitat types into 2 categories: sand/coral or seagrass. We then calculated the proportion of days that each receiver detected each tagged turtle during daytime and nighttime hours across all days that a given receiver was deployed. We analyzed the effect of depth, habitat type and time of day on this proportion for each animal separately using a logistic regression analysis with a random effect (e.g. a receiver effect) by implementing a SAS 9.1 GENMOD procedure; an α-level of 0.05 was used to assess significance of these covariates.

We also determined the distance to the nearest coral reef platform for receivers with turtle detections. Using ArcGIS 9.3 and a layer of coral reef habitat for the DRTO area downloaded from the Florida Geographic Data Library (www.fgdl.org, accessed 1 December 2011; published by Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, St. Petersburg, on 28 June 2006), we compared the proportion of daytime and nighttime detections at each receiver to the distance from a coral reef platform with a correlation using the statistical software R (R Development Core Team 2011). Again, we used an α-level of 0.05 to assess significance of these covariates.

RESULTS

Turtles

We captured 3 hawksbills *Eretmochelys imbricata* (Turtles A, B and C) in August 2008 on the relatively shallow flat near Bush Key; individuals ranged in size from 51.9 to 69.8 cm SCL (mean ± SD: 61.53 ± 9.03 cm; Table 1). Based on the minimum SCL reported for adult hawksbills in Panama and Puerto Rico (i.e. 69.1 cm for males and 74.1 for females; Meylan et al. 2011), these turtles would be considered sub-adults at the time of capture. Sexual dimorphism in tail lengths was observed from 68.2 cm SCL

Table 1. *Eretmochelys imbricata*. Body size and satellite-tracking details for 3 sub-adult hawksbill turtles captured during the foraging period in Dry Tortugas National Park (DRTO), South Florida, USA. No. of locations accepted: locations remaining after filtering raw Argos data as described in 'Materials and methods'. Nearest city of last location transmitted is given. SCL-tip: straight carapace length from nuchal scute to tip of carapace; KDE: kernel density estimate

Turtle	SCL-tip (cm)	Mass (kg)	Tracking period (in DRTO)	No. of days tracked	No. of locations received (no. accepted for 50 % KDE)	Last location transmitted
A	51.9	18.1	7 Aug 2008–25 Jun 2010 (7 Aug 2008–24 May 2010)	687	1179 (91)	Playa Jibacoa, Cuba
B	62.9	27.0	10 Aug 2008–11 Jan 2011 (10 Aug 2008–10 Jul 2010)	884	1249 (309)	Key West, FL, USA
C	69.8	42.2	13 Aug 2008–29 Jun 2009 (13 Aug 2008–23 May 2009)	320	743 (114)	Playa Varadero, Cuba

for hawksbills in Puerto Rico (Van Dam & Diez 1998b), and our largest turtle (69.8 cm SCL) had a small tail as usually seen on females. However, it should be noted that growth rates and size at maturity can be variable across sites (Leon & Diez 1999, Diez & Van Dam 2002, Bell & Pike 2012), and these measurements approach mature SCLs. Additionally, these turtles would have experienced continued growth over the tracking periods. We placed satellite transmitters on all 3 hawksbills, and acoustic tags on 2 of the 3 turtles (Turtles A and C).

Satellite tracking and spatial habitat-use patterns

Across all turtles, we obtained a total of 1891 turtle tracking days. During this time we received 3171 satellite-transmitted locations for the 3 tagged turtles from 7 August 2008 to 1 January 2011 (876 d). After the data filtering process, 514 locations remained for analysis of turtle habitat-use in DRTO (i.e. while in foraging mode; Table 1). The turtles were resident in DRTO for a range of 263 to 699 d before leaving the park (Table 1). The spatial extent of both daytime- and nighttime-filtered satellite locations was visually similar throughout DRTO. During this foraging period, mean inferred travel speed from the filtered locations for Turtles A, B, and C were 1.1, 1.2, and 1.3 km h^{-1}, respectively.

The filtered data during the foraging period in DRTO provided 80, 252, and 67 mean daily locations for analysis for Turtles A, B, and C, respectively. The constrained version of a random walk site-fidelity test showed that the observed movements of all 3 turtles were more constrained than random movement paths (i.e. the proportion of the random movement paths with higher mean square distance values than the observed path was >99 % in all cases).

The size of the core-use areas (i.e. 50 % KDEs) for the 3 hawksbills ranged from 9.2 to 21.5 km^2 (mean ± SD: 14.3 ± 6.4 km^2; Table 2). All core-use areas were concentrated around the flat surrounded by Garden Key, Bush Key, and Long Key (Fig. 2a). Notably, a large percentage (Turtles A, B, and C: 98, 60, and 98 %, respectively) of the core-use areas outside the RNA for the 3 turtles fell within a zone of the park called the historic adaptive-use zone (HAU; Fig. 2a); the HAU also comprised a large amount of the turtles' total core-use area (Turtles A, B, and C: 80, 36, and 61 %).

The common-use area was 6.1 km^2 (Fig. 2b). The portion of the common-use area within the HAU accounted for 99.9 % of the area outside the RNA and 95.0 % of the total combined core-use area (Table 2).

Table 2. *Eretmochelys imbricata.* Kernel density estimate (KDE) details for 3 sub-adult turtles satellite-tracked during the foraging period in Dry Tortugas National Park (DRTO) for various lengths of time between August 2008 and July 2010. RNA: research natural area of DRTO; HAU: historic adaptive-use zone; dashes: not applicable; common use: combined overlapping area of each 50 % KDE for all turtles

Turtle	No. of days tracked in DRTO	Total area of 50 % KDE (km^2)	Area of 50 % KDE in RNA (km^2) (percent of total area)	Area of 50 % KDE out of RNA (km^2) (percent of total area)	Area of 50 % KDE inside HAU (km^2) (percent of area out of RNA)	Bandwidth (h_{cv})
A	655	9.24	1.78 (19)	7.46 (81)	7.31 (98)	0.113
B	699	21.45	8.42 (39)	13.03 (61)	7.82 (60)	0.082
C	263	12.20	4.55 (37)	7.65 (63)	7.48 (98)	0.078
Common use	–	6.11	0.33 (5)	5.78 (95)	5.78 (99.9)	–

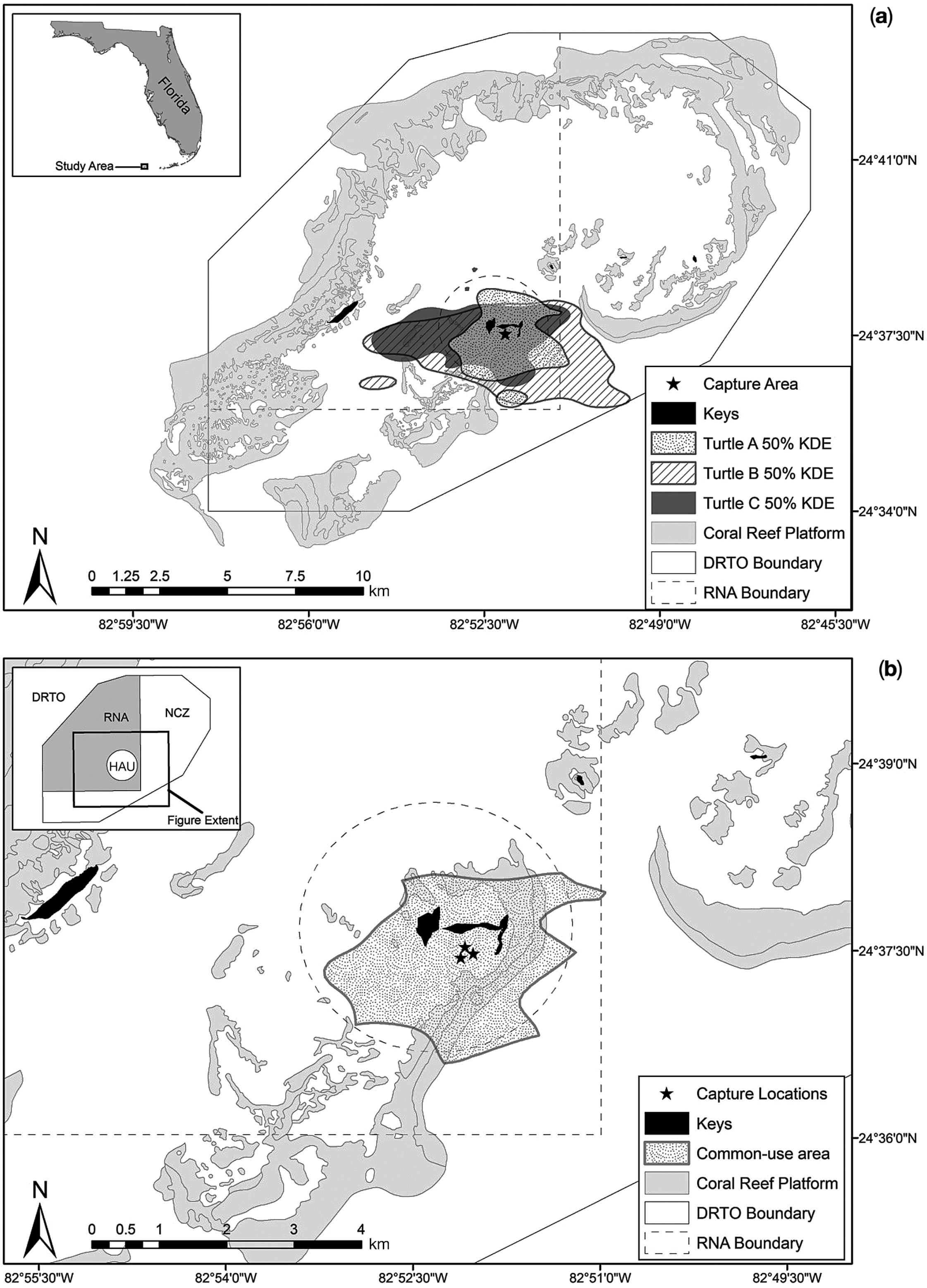

Fig. 2. *Eretmochelys imbricata.* (a) Turtle 50 % kernel density estimates (KDEs) as determined from satellite telemetry within Dry Tortugas National Park (DRTO). (b) Common-use area for 3 hawksbill turtles in DRTO. The coral reef platform was downloaded from the Florida Geographic Data Library (www.fgdl.org, accessed 1 December 2011; published by Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, St. Petersburg, on 28 June 2006). RNA: research natural area; NCZ: natural culture zone; HAU: historic adaptive-use zone

Finally, water depths in the common-use area ranged from 0.1 to 8.0 m (mean ± SD: 3.2 ± 2.1 m).

Acoustic tracking

We received a total of 10 952 detections of 2 tagged turtles at 11 receiver stations in the DRTO area (Table 3, Fig. 3a). Turtle A's detection dates spanned 7 August 2008 to 1 January 2009 (8995 detections over 148 d at 9 receivers), whereas Turtle C's detection dates spanned a shorter time period: 31 August 2008 to 19 October 2008 (1957 detections over 50 d at 6 receivers; Table 3). Within the common-use area and 1000 m around it, there were 9 receivers with no detections.

The 11 receivers with turtle detections ranged in depth from 2.0 to 22.4 m. Three of these receivers were immediately surrounded by seagrass, whereas the remaining 8 were in sand/coral habitat. The majority of Turtle A's detections (60%) occurred at a receiver (R10; Table 3) in the HUA at 2.0 m depth and surrounded by seagrass. Similarly, the highest number of detections for Turtle C (34%) occurred at another receiver (R1) in the HUA at 3.0 m depth and surrounded by seagrass; 25% of the remaining detections for Turtle C were at another receiver (R7) in the HUA at 2.0 m water depth surrounded by sand/coral (Table 3, Fig. 3b).

Logistic regression results indicated that the habitat effect was not significant for either acoustically tagged turtle ($p > 0.05$; Table 4). However, the effect of water depth was significant for 1 turtle (Turtle C, $p = 0.024$); the detection rate for this turtle was higher at receivers deployed in deeper water depths. Next, the effect of time was significant for both turtles ($p < 0.001$); the detection rate for both turtles was higher during daytime than during nighttime hours. For Turtle A, there was moderate inverse correlation between nighttime detection rate and proximity to reef platforms ($r = -0.53$, df = 7, $p = 0.14$), as well as a moderately high correlation between daytime detection rate and proximity to reef platforms ($r = 0.80$, df = 4, $p = 0.05$) for Turtle C.

Table 3. *Eretmochelys imbricata*. Detections of 2 hawksbills (Turtles A and C) at acoustic receivers in Dry Tortugas National Park (DRTO) from 7 August 2008 to 1 January 2009. Location within the DRTO was the historic adaptive-use zone (HAU) in all cases. Habitat type: type of habitat immediately surrounding receiver, classified into 1 of 2 categories — sand/coral or seagrass

Receiver name	Depth (m)	Habitat type	No. of detections Turtle A	No. of detections Turtle C
R1	3.0	Seagrass	0	674
R2	12.8	Sand/coral	0	232
R3	13.7	Sand/coral	507	0
R4	3.0	Sand/coral	602	0
R5	21.0	Sand/coral	126	0
R6	2.0	Sand/coral	187	334
R7	2.0	Sand/coral	16	497
R8	2.0	Sand/coral	242	0
R9	2.0	Seagrass	929	151
R10	2.0	Seagrass	5407	69
R11	22.4	Sand/coral	979	0
Total			8995	1957

Turtle migrations

We tracked Turtle A for 687 d beginning 7 August 2008 (Table 1). Turtle A was resident in DRTO for at least 655 d before migrating south towards Cuba on 27 May 2010 (Day 659 of tracking; Fig. 4). We received 37 locations after the turtle left DRTO. The turtle reached Cuban coastal waters (within 24 km of Cuba) on 4 June 2010 after traveling approximately 212 km for 8 d. Four days later (8 June 2010), this turtle transmitted from the coastline of Cuba. The transmissions remained in a Cuban coastal area (including points onshore) for another 16 d (30 points) until the final transmission on 24 June 2010. Many of these last coastal points (40% versus 8% at foraging grounds) were of the highest location quality (LCs 3, 2, and 1), which is unusual for turtles during foraging and indicates either multiple nesting attempts or that the turtle was onshore for a prolonged period. The last received transmission of high location quality (LC 3) was on land, followed by a lower quality location (LC A) received very close to shore, after which transmissions ceased.

We tracked Turtle B for 884 d beginning 10 August 2008 (Table 1). Turtle B was resident within DRTO for 699 d before migrating away after 10 July 2010. After the turtle left the park, we received only 2 filtered locations on 30 November 2010 (Day 843 of tracking) and 14 December 2010 from east of the DRTO boundary in waters near Key West (Fig. 4); after this date, no further transmissions were received.

We tracked Turtle C for 320 d (13 August 2008 to 18 May 2009; Table 1). Turtle C was resident in DRTO for at least 263 d before migrating south toward Cuba on 4 May 2009 (Day 265 of tracking); we received 37 locations during this migration. The turtle reached Cuban coastal waters on 12 May 2009 (within 35 km of Cuba's northern coast; Fig. 4) after traveling approximately 440 km for 14 d (4 to 18 May 2009). The

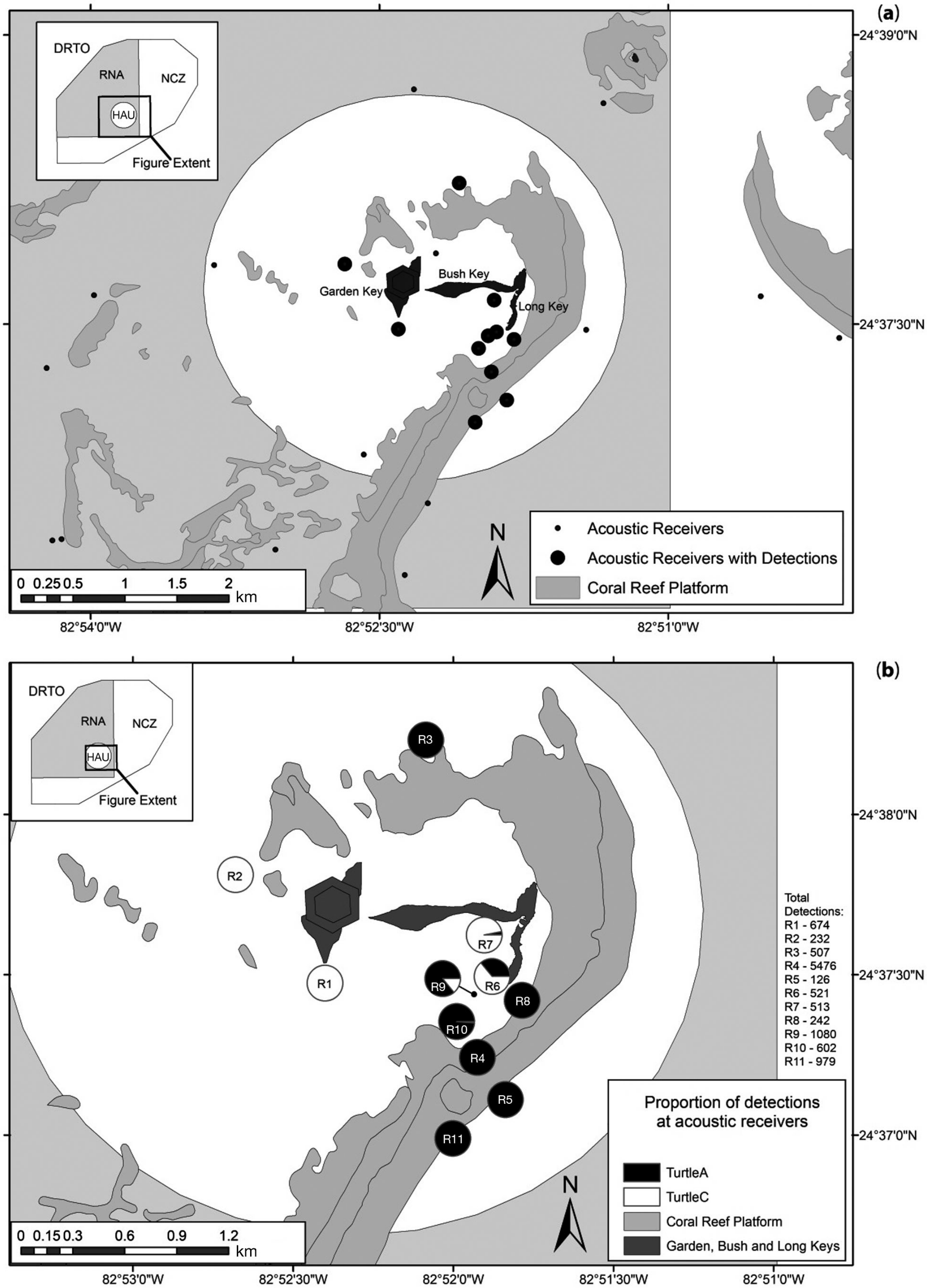

Fig. 3. *Eretmochelys imbricata*. (a) Close-up of area within the park with acoustic receiver detections; receivers with detections are shown larger. (b) Detections for 2 acoustically tagged turtles (Turtles A and C); proportion of detections by turtle is shown with a pie chart at each receiver location, with combined detections totaled to the right of the figure. Receivers are numbered R1 to R11 (see Table 3). All receivers with detections occurred within the historic adaptive-use zone (HAU). The coral reef platform shown was downloaded from the Florida Geographic Data Library (www.fgdl.org, accessed 1 December 2011; published by Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, St. Petersburg, on 28 June 2006), and used in the correlation described in 'Materials and methods'. RNA: research natural area; NCZ: natural cultural zone

Table 4. *Eretmochelys imbricata.* Estimated model parameters of logistic regression to predict detection rate at acoustic receivers (number of detected days per number of days each receiver was deployed) by habitat type (seagrass or sand/coral, seagrass was used as the base category), depth, and time (daytime or nighttime; nighttime was used as the base category). **Bold:** significant at $\alpha = 0.05$

Turtle	Parameter	Estimate	SE	Lower CI	Upper CI	*Z*	p-value
A	Intercept	−2.406	0.445	−3.278	−1.533	−5.40	**<0.001**
	Habitat	−0.776	0.685	−2.118	0.567	−1.13	0.258
	Depth	−0.044	0.030	−0.103	0.015	−1.45	0.146
	Time	1.781	0.397	1.002	2.560	4.48	**<0.001**
C	Intercept	−3.183	0.418	−4.003	−2.363	−7.61	**<0.001**
	Habitat	−0.232	0.241	−0.704	0.240	−0.96	0.336
	Depth	−0.072	0.032	−0.133	−0.010	−2.26	0.024
	Time	1.879	0.346	1.201	2.557	5.43	**<0.001**

day after the turtle's arrival in Cuban waters (13 May 2009), we received locations on land potentially from a nesting event or false crawl (abandoned nesting attempt). A few days later (16 May 2009), we received another location from onshore; however, from that point until 20 June 2009 we received an additional 137 points (unfiltered), all consistently from onshore. Before the final transmission, the locations from Argos suggested extended periods on land, including points along a major road and from within a village near Varadero Beach on the north coast of Cuba.

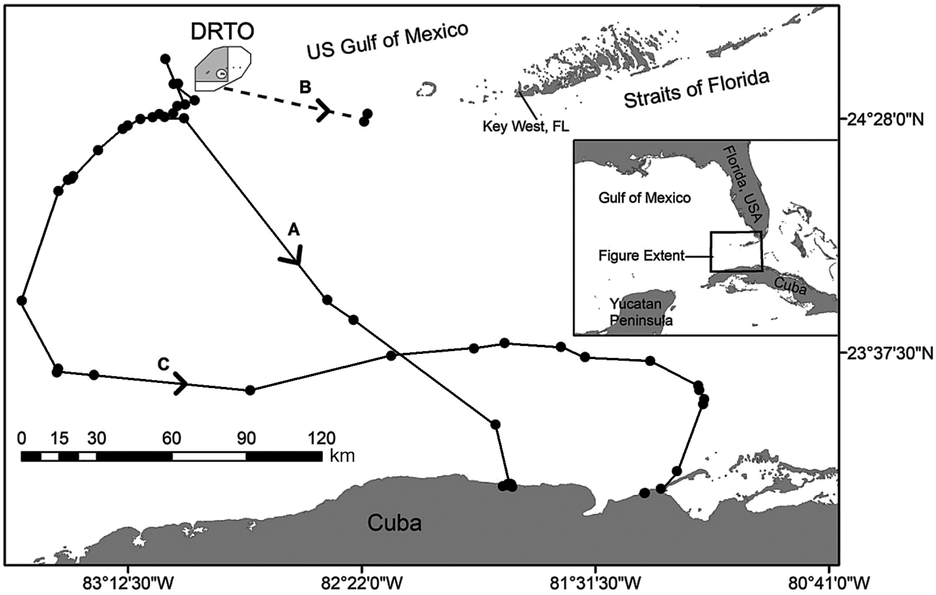

Fig. 4. *Eretmochelys imbricata.* Migrations away from Dry Tortugas National Park (DRTO) for 3 satellite-tracked sub-adult hawksbills. Lines connect filtered satellite locations by date. Turtles A and C ceased transmitting upon arrival in Cuba (many of the last points occurred on land); the migration of Turtle C to Cuba is shown. Turtle B ceased transmission west of Key West, FL (shown by 2 dots with a hatched line to denote inferred tracking path due to gap in transmissions)

DISCUSSION

Turtle core-use areas, habitat use, and daily activity patterns

Using both satellite and acoustic tracking, our results provide the first published summary of hawksbill *Eretmochelys imbricata* core-use areas in the continental United States. Compared to home-range estimates for hawksbills tagged elsewhere and in different size-classes, our results show that the 3 turtles tagged at DRTO had core-use areas ranging from 9.2 to 21.5 km^2. Previously reported home-range estimates for wild adult hawksbills were 2.0 to 49.5 km^2 in Barbados (Horrocks et al. 2001) and 0.5 to 2.0 km^2 in Hawaii (Parker et al. 2009); both of these estimates were determined using a minimum convex polygon (MCP) approach. The few studies estimating home ranges for juvenile hawksbills have generally found areas of 1 km^2 or less (0.07 to 0.14 km^2 in Puerto Rico [Van Dam & Diez 1998a], 1.2 km^2 in Mexico [see Cuevas et al. 2007], 0.15 to 0.56 km^2 in Honduras [Berube 2010], and 545 ± 514 m mean straight-line recapture distance in the Cayman Islands [Blumenthal et al. 2009b]). In a comparison of home range size to turtle size, Scales et al. (2011) used acoustic tracking and MCP analysis to show a positive correlation, with home-range estimates for juveniles (33.0 to 48.6 cm CCL) similar to previous estimates (0.05 to 1.11 km^2), while 2 larger individuals had home ranges of 2.6 km^2 (48.5cm CCL) and 4.04 km^2 (50.8 cm CCL).

Our core-use area estimate was substantially larger than most previously reported (~1 km^2 or less) home-range sizes for immature hawksbills and the 0.5 to 2.0 km^2 adult home-range estimate from Hawaii (Parker et al. 2009). However, this small sample of hawksbill home ranges fell within the adult home-range estimate from Barbados (1.96 to 49.5 km^2; Horrocks et al. 2001). Our measures of home-range size may be larger due to the larger body size of sub-adults compared to juveniles, as the results of Scales et al. (2011) suggest. As well, home-range size at DRTO may be larger than that for hawksbills at other sites simply due to DRTO-specific habitat configurations.

Acoustic tracking allowed for determination of fine-scale patterns of habitat use and movements and were confirmed via Argos satellite tracking. While filtered Argos locations failed to show visually distinct spatial differences in day and night locations, we were able to detect this difference with the fine-scale acoustic data; our tagged hawksbills were more active within their core-use areas during the day. This could indicate more active foraging behavior during the day and possibly resting behavior at night, which would support the findings of Blumenthal et al. (2009b) in the Cayman Islands; through direct visual surveys they found that hawksbills rested on the bottom and under coral reef ledges during the night.

Blumenthal et al. (2009b) found a weak but highly significant positive correlation between turtle size and depth of water at capture. Our study shows some support for this finding as our largest turtle (Turtle C) was detected spending significantly more time near deeper acoustic receivers, exhibiting a possible preference for deeper water. Habitat type at the receiver site was not an important predictor of turtle presence. However, using acoustic detection data, we determined that turtle preference closer to platform reef habitat existed, at least within nighttime hours. Additionally, a high proportion of detections (60%, Turtle A; 34%, Turtle C) for hawksbills occurred at receivers immediately surrounded by seagrass; this result indicates that either the hawksbills were foraging in this habitat or often moving through it. Determining the habitat type within the entire 200 m circumference of each receiver was not within the scope of the present study, and it is possible that the turtles were spending time in mixed or different habitats within range of a given receiver. Blumenthal et al. (2009b) sighted hawksbills in Little Cayman (14%) and Grand Cayman (26%) in habitats in which they did not feed (i.e. uncolonized hardbottom). Additionally, recent studies have shown local adaptation of hawksbills to other habitat types (e.g. mangroves in the eastern Pacific; Gaos et al. 2012), indicating that this species is not strictly an obligate coral reef-dweller. A detailed geo-referenced habitat map in association with acoustic and accelerometer data could help to decipher even finer-scale habitat use by hawksbills in DRTO and whether they rest, forage, or simply move through areas with a high rate of turtle detections.

Turtle size and possible nesting activities

Reported growth rates in the Caribbean region (Cayman Islands, United States Virgin Islands, Bahamas, and Puerto Rico) for hawksbills range from negligible to 15.7 cm yr^{-1} for sizes ranging from 20 to 84.5 cm SCL (Bjorndal & Bolten 1988, Diez & Van Dam 2002). Within this range, 1.0 to 4.5 cm yr^{-1} was reported for turtles of 50 to 60 cm SCL and 1.0 to 4.0 cm yr^{-1} for turtles of 60 to 70 cm SCL (Bjorndal & Bolten 1988, Boulon 1994, Diez & Van Dam 2002, Blumenthal et al. 2009b). Growth rate varied by turtle size (i.e. the rate decreased as turtles grew larger) and location (Diez & Van Dam 2002), indicating either density-dependent or habitat-quality factors may affect growth rates.

Turtle A, the smallest of our 3 hawksbills (51.9 cm SCL upon capture), ceased transmitting in a coastal area of Cuba 687 d (1.8 yr) after tagging. Current estimates for hawksbill growth rates in the Caribbean suggest this turtle may have reached a maximum possible size of 60 cm SCL by the last transmission date. Turtle B measured 62.9 cm SCL upon first capture and may have grown to 72.5 cm SCL over the 884 d (2.4 yr) of tracking; however, the actual size was likely smaller as growth rates begin to slow when a turtle reaches 70 cm SCL. Turtle C, the largest of our hawksbills (69.8 cm SCL), was tracked for 263 d (0.7 yr) and may have grown to 71.7 cm SCL on arrival in Cuba.

While 50% of hawksbill nesters in Cuba were mature at 76 to 80 cm SCL, the smallest known hawksbill nester from the Cuban archipelago measured 58.5 cm SCL (Moncada et al. 1999). Additionally, the smallest recorded successful hawksbill nester in the United States Virgin Islands, one of the largest remaining nesting grounds for hawksbills, was 68.7 cm SCL, 73.6 cm CCL (I. Lundgren, National Park Service, pers. comm.). It is therefore possible that we documented migration from DRTO to possible nesting grounds for the first nesting attempts for Turtles A and C, at projected sizes of 60 and 71.7 cm SCL, respectively. By the time Turtle B ceased transmitting it had not reached an obvious nesting ground, and the reasons for this movement are unclear. This turtle may have made movements towards an as yet unknown breeding ground off Key West, Florida.

Hawksbill harvesting in Cuba

Historically harvested around the world for subsistence, medicine, and oil, hawksbills have been harvested mainly to supply international trade in their thick, keratinized scutes, commonly referred to as 'tortoiseshell' or 'bekko', a highly valued raw material due to the beautiful pattern and plastic-like texture (Carillo et al. 1999). Hawksbills have been harvested in Cuban waters since the 1500s, but during the 20th century harvest was primarily part of a fishery to supply international trade (see Mortimer et al. 2007).

Cuba traded bekko with Japan until 1995 (see Mortimer et. al 2007), despite the listing as an Appendix I species on the Convention on International Trade in Endangered Species (CITES) in 1975, which prohibited all trade. Reports in 1999 and 2000 claimed that the primary purpose for the turtle fishery in Cuba was domestic consumption (Carillo et al. 1999), and the fishery remained open until the end of January, 2008, when the WWF-Canada and the Canadian International Development Agency (CIDA) worked with the Cuban Ministry of Fisheries to ban the harvesting of all marine turtles (http://wwf.ca/about_us/successes/hawksbill; accessed 4 April 2011).

Although Cuba's harvesting history is extensive, there have been many recent moves toward conservation of hawksbills, including implementation of conservation and community outreach programs (e.g. Bretos et al. 2006) and the creation of new marine parks (e.g. Jardines de la Reina created in 2010). WIDECAST (Wider Caribbean Sea Turtle Conservation Network, www.widecast.org) brings together biologists, managers, community leaders, and educators throughout the Caribbean to address sea turtle declines and has programs running in Cuba to both study and conserve sea turtles. Yet, despite these and other steps toward conservation and a sustainable fishery, illegal subsistence fishing may remain a problem for some areas of Cuba, including conservation sites (J. Gerhartz [Director, WWF Cuba Field Office], pers. comm. [15 June 2009], Bretos et al. 2006).

Conservation implications

In addition to revealing patterns of habitat use within DRTO, satellite telemetry enabled us to determine migration paths and potential fates of turtles, possibly indicating where future conservation efforts should be focused. Turtle C's satellite transmitter was found with fishermen in a village near Varadero Beach on the north coast of Cuba (J. Gerhartz [Director, WWF Cuba Field Office] pers. comm., 15 June 2009). Another study satellite-tracked a loggerhead turtle *Caretta caretta* from off the coast of western Florida to northwest Cuba, where the last 2 mo of transmissions came from on land in a coastal town (Girard et al. 2009). Additionally, Sasso et al. (2011) used pop-up archival transmitting tags on 30 loggerheads from the east coast of Florida, and, within 4 mo, 1 of these transmitted from well inland in Cuba. It remains unclear whether Turtle A was harvested or simply stopped transmitting very soon after a nesting event.

Richardson et al. (1999) pointed out that with a reproductive rate of 288 eggs yr^{-1}, adult female hawksbills must be allowed to reproduce for at least 9 yr (4.1 nesting seasons individual^{-1}) to maintain the population. Combined with a generally low hatchling sea turtle survival rate (Heppell 1998), some animals must continue to be reproductively active for several decades or more to balance the early mortality of other individuals. The hawksbill's 'Critically Endangered' status is likely the result of prolonged harvesting of multiple life stages and a resulting lack of long-term reproduction necessary to maintain populations. Further, repopulation of depleted stocks of hawksbills in one foraging ground may not occur if turtles are harvested in other nesting or foraging grounds.

CONCLUSIONS

Even with a low sample size, our results revealed patterns of hawksbill residence in DRTO. We also found previously unknown links between hawksbills in a United States National Park and both Cuba and an area of the Florida Keys (i.e. off Key West). Moreover, we estimated some of the first home ranges and core-use areas for sub-adult hawksbills. Additional tracking of hawksbills from this site will reveal whether the habitat-use and movement patterns documented here are similar to those for a larger number of turtles. Although our acoustic tracking data did not reveal obvious habitat preferences, our analysis indicated that hawksbills were more active during the day within their core-use area. Additionally, the acoustic data revealed that the largest tagged hawksbill spent more time near deeper receivers. Future capture and survey efforts for hawksbills at deeper in-water sites in DRTO may be warranted. Finally, closer examination of hawksbills is needed once they leave the protected area of DRTO. Thus, due to the migratory nature of hawksbills, our results echo Blumenthal et al.'s (2006) findings that effective protection for the species must include international conservation efforts.

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Contribution to the Theme Section: 'Tagging through the stages: ontogeny in biologging'

Synchronous mother and calf foraging behaviour in humpback whales *Megaptera novaeangliae*: insights from multi-sensor suction cup tags

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ABSTRACT: Previously, all inferences regarding fine-scale baleen whale mother–calf relationships have come from surface observations, aerial surveys, or underwater video recordings. On May 19, 2010, we attached high-resolution digital acoustic recording tags (Dtags) to an adult female humpback whale *Megaptera novaeangliae* and her calf in Wilhelmina Bay (Western Antarctic Peninsula) to examine their concurrent diving and foraging behaviour. The Dtags logged ~20 h of concurrent recordings. We used cross-correlation analyses to quantify synchrony between the pair. Dive depth was positively correlated for the duration of the concurrent record and was highest when the calf's track lagged behind the mother's by 4.5 s, suggesting that the calf was 'following' its mother. Pitch and heading were positively correlated but to a lesser degree. Both animals executed feeding lunges; however, the mother foraged more intensively than the calf (792 and 118 lunges over 246 and 30 feeding dives, respectively). Also, the mother fed consistently once she initiated feeding at 16:22:00 h until the tag came off, whereas the calf executed 95.76% of its lunges between 17:00:08 and 19:28:21 h, local time. Correlation coefficients calculated per dive were highest when both animals were feeding and lowest when only the mother was feeding. In addition, 84.26 and 79.63% of the calf's lunges were performed within ±20 s and ±20 m of its mother's lunges, respectively. Our work describes the first record of a long-term continuous underwater relationship and foraging behaviour of a humpback mother–calf pair.

KEY WORDS: Humpback whale · Mother and calf · Foraging · Synchrony · Antarctica

INTRODUCTION

Synchronised behaviours (animals in proximity to one another, performing the same behaviour at the same time), usually in parallel orientation (Fellner et al. 2006), are common in the early stages of cetacean mother–calf relationships (e.g. Bel'Kovich 1991, Gubbins et al. 1999, Fellner et al. 2006). Synchrony serves several functions, such as receiving an aero- or hydrodynamic advantage by slipstreaming (Weihs 2004, Noren et al. 2008, Noren & Edwards 2011), protection from predators (Norris & Schilt 1988), and social learning via imitation during developmental stages that are critical to survival (e.g. independent foraging behaviour; Whiten & Ham 1992, Whiten 2001, Fellner et al. 2006, Bender et al. 2009, Sargeant & Mann 2009). Synchronised behaviours observed in mother–calf southern right whale *Eubalaena australis* and humpback whale *Megaptera novaeangliae* pairs have provided evidence to suggest that mysticetes (baleen whales) and other cetaceans exhibit 'following' behaviour (Taber & Thomas 1982, Thomas

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& Taber 1984, Szabo & Duffus 2008): a strategy for offspring protection in which the offspring accompany their mother soon after parturition and are rarely more than several body lengths from her until they separate permanently (Lent 1974). 'Following' benefits the mother by not requiring her to return to her offspring, and benefits the offspring by gaining maternal vigilance and defence as a means of predator avoidance and protection (Espmark 1971, Lent 1974, Estes 1976, Fisher et al. 2002). Therefore, synchronised behaviours associated with following in cetacean mother–calf pairs may be critical for the success of the calf's behavioural development.

Humpbacks and other baleen whales are constrained in the 'following' strategy in that their young typically suffer from a reduced physiological capacity to dive relative to older conspecifics and therefore do not dive as frequently or as long as their mothers (Würsig et al. 1984, Szabo & Duffus 2008). If the mother–calf pair does not want to lose the benefits of their close proximity when the mother makes long-duration dives (e.g. foraging dives), one individual must actively modify its behaviour in relation to the other individual. On a foraging ground in southeastern Alaska, humpback whale mothers modified their behaviour in the beginning of the foraging season by shortening the duration of their dives whenever their offspring remained at the surface, presumably to minimise the duration of their separation (Szabo & Duffus 2008). Later in the season, however, as the calves grew and gained independence, the mothers became significantly less responsive to their offspring and performed longer dives, thereby forcing their offspring to actively modify their behaviours and increasingly synchronise their dives with their mothers (Szabo & Duffus 2008). This shift has also been documented in southern right whales where calves are primarily responsible for maintaining contact with their mothers at the end of their foraging season (Taber & Thomas 1982). Thus, the mother's foraging efficiency (i.e. amount of energy consumed per unit of energy expended while acquiring food) may be low early in the foraging season because she is primarily responsible for maintaining the pair's proximity and may increase later in the season as the calf takes over this responsibility. In addition, once the calf can begin to forage independently, the energetic burden of lactation for the mother will decrease. Humpback calves may begin to feed independently as early as 6 mo old, although they may nurse for up to a year (Van Lennep & Van Utretcht 1953, Chittleborough 1958, Clapham & Mayo 1987).

Humpback whales belong to a group of baleen whales known as rorquals (Balaenopteridae), which in Antarctica forage primarily on small euphausiid crustaceans (e.g. Antarctic krill *Euphausiia superba*) and other small prey by lunge feeding. Lunge feeding involves accelerating with a burst of energetic fluking towards and engulfing a mass of prey-laden water that may equal up to ⅔ of the animal's body mass (Pivorunas 1979, Brodie 1993). The whales then filter the prey from the ingested water through keratinised plates of baleen and swallow the captured prey. Advancements in bio-logging technologies have enabled a better understanding of the kinematics and energetic costs of lunge feeding in fin whales *Balaenoptera physalus*, blue whales *Balaenoptera musculus*, and humpback whales (e.g. Goldbogen et al. 2006, 2007, 2008, 2011, Simon 2010, Ware et al. 2011); however, to our knowledge, feeding lunges have not been documented in a mother–calf rorqual pair. Mother–calf pairs have additional energetic and behavioural costs associated with foraging compared to non-lactating females and/or adult males, such as the cost of lactation (mother; Lockyer 2007) and the cost of growth (calf). Understanding the foraging behaviour of mother–calf pairs is critical for understanding their energetic demands during the calf's first year.

In the Southern Ocean, humpback calves are born in the winter and early spring in calving grounds found off Australia, Africa, Oceania, and South America (Chittleborough 1965, Mackintosh 1965, Florez-Gonzalez 1991); early August is the peak birth month (Chittleborough 1958, 1965). Several months later, calves migrate with their mothers to their foraging grounds (e.g. Western Antarctic Peninsula [WAP]; Mackintosh 1965, Clapham 1996) where they typically remain and forage on euphausiids from late spring through late autumn (Baker et al. 1986, Clapham & Mayo 1987, Baraff & Weinrich 1993). The majority of mother–calf pairs will separate during, or shortly before, their second winter, although a few pairs remain associated for 2 yr (Clapham & Mayo 1987, Baraff & Weinrich 1993).

To our knowledge, all inferences regarding fine-scale baleen whale mother–calf relationships have come from boat- or land-based surface observations, aerial surveys, or from underwater video recordings (e.g. Taber & Thomas 1982, Baker et al. 1986, Baraff & Weinrich 1993, Szabo & Duffus 2008, Zoidis et al. 2008, Cartwright & Sullivan 2009). Here, we use data collected from high-resolution digital acoustic recording tags (Dtags; Johnson & Tyack 2003) to describe the first record of a long-term (~20 h) continuous underwater relationship and concurrent foraging behaviour of a baleen whale mother–calf pair. We identify feeding lunges executed by both whales and compare the frequency of lunges and related dive parameters, including the number of lunges per dive, maximum dive depth, dive duration, post-dive surface time, and within-dive inter-lunge interval associated with feeding to assess how these parameters may relate to the energetic demands of each animal. We also examine the synchrony of the pair in terms of their feeding events and their underwater behaviour to assess the structure of the pair's relationship. Based on observations made by Szabo & Duffus (2008), we predict that the pair's association was waning as the calf was likely 8 to 12 mo old at the time of tagging (i.e. the austral autumn).

MATERIALS AND METHODS

Dtags (Johnson & Tyack 2003) are small bio-logging tools developed to continuously collect data on the fine-scale behaviour of marine mammals. On May 19, 2010, we attached Dtags to an adult female humpback whale and her calf in Wilhelmina Bay (WAP; Fig. 1). We approached the pair using a rigid-hulled inflatable boat with a 4-stroke outboard engine and placed the Dtags on the dorsal surface of the whales, between the dorsal fin and the blowhole, using an 8 m carbon-fibre pole; Dtags attach to the whales via 4 silicone suction cups. The Dtag incorporates a hydrophone (sampling rate up to 96 kHz), a pressure sensor to measure depth, 3-axis accelerometers, 3-axis magnetometers, and an embedded VHF transmitter. The pressure sensors, magnetometers, and accelerometers measure depth, heading, pitch, and roll, respectively, at 50 Hz and are stored synchronously with audio data on flash memory (16 GB) within the tag. Prior to deployment, the time on the tags was synchronised to the GPS time to ensure the ability to synchronise data parameters (e.g. Friedlaender et al. 2009, Hazen et al. 2009).

The mother was tagged at 11:02:33 h (tag start time: 11:02:58 h local time, GMT −5 h) while the calf was tagged 49 min later at 11:51:56 h (tag start time: 11:52:17 h) (Fig. 1). Whale behaviour was not visibly affected by the tagging (other than immediate startle responses), which is consistent with reports from other studies (e.g. Nowacek et al. 2004, Hazen et al. 2009). The tagged whales were tracked visually during daylight hours (9:11:00 to 14:59:00 h) from a rigid-hulled inflatable that stayed within 500 m of the pair and they were tracked with directional VHF antennas at night. An active release, which corrodes in seawater, was timed to release the tags once data storage was complete (approximately 24 h), causing the tag to float to the surface. Tags released from the animals at 7:46:00 h (mother) and 11:52:07 h (calf) on May 20, 2010. Upon tag retrieval, post-tagging calibration was immediately conducted and the data were downloaded via infrared transmission.

TrackPlot (Ware et al. 2006), a software program designed to interpret data from tags containing accelerometer, magnetometer, and pressure sensors (e.g. Dtags), was used to visualise and analyse the pair's simultaneous 3-dimensional orientations (depth, pitch, roll, and heading). TrackPlot creates a 'pseudotrack' of each whale's movements and behaviours

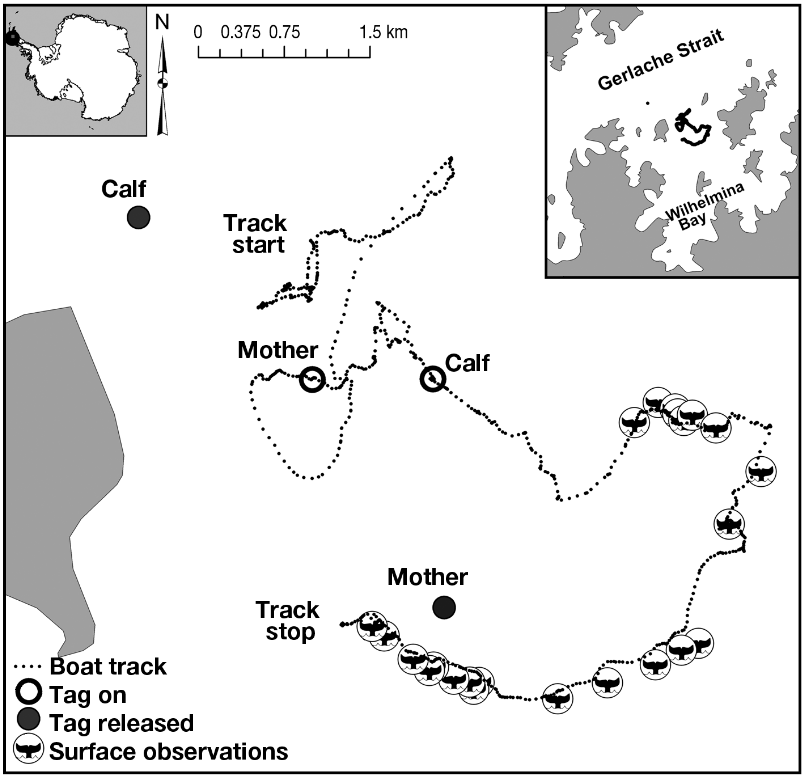

Fig. 1. *Megaptera novaeangliae*. Locations where the mother and calf were tagged, tracked, and observed at the surface, and where their tags released, from May 19 to 20, 2010, Wilhelmina Bay, Antarctica. Note that the mother's tag released 4 h 6 min before the calf's tag; therefore, the separation in tag off locations is not necessarily representative of the pair being separated in space

using dead-reckoning based on the time series of whale orientations and by assuming that the whale moves forward in the rostral direction (Ware et al. 2011). The rate of forward movement at any point on the track is either assumed to be constant (1 m s^{-1}) or is based on the rate of depth change for an ascending or descending individual divided by the sine pitch of the angle (Ware et al. 2011). Dtags do not provide position information (e.g. GPS points), so known fixes need to be integrated into the dead-reckoning process wherever possible to establish horizontal positions. These known fixes were derived from visual observations made by observers in the rigid-hulled inflatable when the animals surfaced during the Dtag deployment. In this study, most of the tag attachment period was at night and there were only 30 and 27 georeferenced locations made for the mother and calf, respectively, during daylight. Therefore, the lack of fixes for the majority of the concurrent records (e.g. night-time) hinders us from confidently interpreting the pair's absolute geographic position. Instead, we could only assess the pair's vertical proximity to each other in the water column (i.e. calculated as the difference in depth of the pair at each specific time). TrackPlot was also used to extract summary data for each dive (defined here as an excursion >10 m; Goldbogen et al. 2006), including dive duration (s), post-dive surface time (s), and the maximum depth (m) of each dive. Extracted track and dive data were synchronised in Microsoft® Excel based on the time parameter.

Feeding lunges executed by each whale were identified from flow noise recorded on the Dtag hydrophone (Goldbogen et al. 2006, 2008, Simon 2010, Ware et al. 2011). When lunging, a rorqual rapidly accelerates, opens its jaws once a sufficient speed (e.g. 3 m s^{-1}) has been obtained, and then rapidly decelerates due to the drag forces related to the opening of its buccal cavity (Goldbogen et al. 2006, Potvin et al. 2009); flow noise will simultaneously increase as the animal accelerates and decrease as the animal is slowed. Ware et al. (2011) used flow noise as an estimate of speed to successfully detect lunges from humpback whales and developed an automatic lunge-detecting filter within TrackPlot. The lunge filter (which detects precipitous drops in the animal's speed) allows the user to examine the putative lunges and the animal's estimated speed alongside a pseudo-track of its behaviour aligned in time. We used this filter to detect feeding lunges executed by the mother and the calf. An experienced analyst in TrackPlot then examined the putative lunges and scanned the entire track for missed lunges. Lunges detected at a depth shallower than 10 m were excluded from analyses due to possible interference from surface interactions (i.e. abrupt changes in flow noise due to surfacing).

The presence of a lunge was confirmed if the following criteria were met: (1) an isolated bout of fluking (identified from angular accelerations about a lateral axis) associated with a distinct speed maximum, followed by a rapid reduction in speed, followed in turn by a period of gliding; and (2) continued swimming and fluking throughout the lunge, particularly during the deceleration (Goldbogen et al. 2006, 2008, Simon 2010, Ware et al. 2011). The experienced analyst removed any false positive lunges. The times of the confirmed lunges were logged and stored in Excel and plotted with the animal's dive profiles. A feeding dive was defined as any dive for which at least 1 lunge was detected. For each feeding dive, the number of lunges per dive, the dive duration, the post-dive surface time, and the maximum depth were recorded to examine and compare feeding effort and behaviour within and between whales. Least-squares linear regressions were performed to determine the relationships between these parameters. Two-sample Student's *t*-tests were computed to assess the probability that these relationships (e.g. dive duration by number of lunges per dive) were significantly different for the mother and the calf. Two-sample Student's *t*-tests were also used to examine the probability that the pair's mean within-dive inter-lunge intervals were significantly different. A significance level of 0.05 was used for all statistical tests. Synchrony in terms of feeding events was examined by comparing the time and depth of the pair's lunges.

The synchrony of underwater behaviours throughout the concurrent dive records was evaluated using a cross-correlation analysis (Pearson product-moment correlation coefficient for angular and non-angular variables) in the software R (R Development Core Team 2008). First, to compare the pair's overall similarity in depth, pitch, roll, and heading, we computed correlation coefficients for both the entire concurrent tag records and at lagged time intervals; correlation coefficients (r) vary from 1.0 (highly positively correlated) to −1.0 (highly negatively correlated), with zero corresponding to no correlation. For the purpose of this paper, r-values greater than 0.5 indicated that the animals were generally behaving synchronously (i.e. their behaviours were positively correlated) and r-values greater than 0.9 indicated that the animals were behaving very synchronously (Cohen 1988). When lagging the tracks for the cross-correlation analyses, we assumed that if the animals exhibited synchronised behaviours, the cross-correlation function would have the greatest correlation at a lag time close to zero. Second, to examine how synchrony changed over the duration of the concurrent tag records and during different behavioural states (e.g. feeding dives versus non-feeding dives), we computed r-values for each dive by comparing the depth, pitch, roll, and heading of each of the mother's dives to the calf's respective depth, pitch, roll, and heading at the same times. The percentage of r-values >0.5 and >0.9 were examined to compare differences in synchronised behaviours between behavioural states (e.g. neither animal feeding during the dive, both animals feeding during the dive, only the mother feeding during the dive, only the calf feeding during the dive). Synchrony of diving and surfacing behaviours was examined by pairing synchronised dives in time and then examining their temporal separation in their descent (when they were submerged <1 m depth) and in their surfacing (when they were >1 m depth). Synchrony in feeding lunges was also examined by comparing the time and depth of the mother's lunges to the time and depth of the calf's lunges.

RESULTS

The tags logged 19 h 54 min of concurrent recordings; data reported hereafter refer only to the time when the 2 animals were simultaneously tagged (11:51:17 h May 19, 2010 to 7:46:00 h May 20, 2010). We recorded 285 dives from the mother's tag (maximum depth = 164.04 m, mean ± SD = 59.24 ± 38.19 m) and 281 dives from the calf's tag (maximum depth = 249.80 m, mean ± SD = 46.20 ± 39.32 m). The pair's vertical proximity was within 20 m (approximately 2 body lengths) for 71.22% of the records.

Feeding lunges were identified for both animals (Fig. 2). The mother executed 792 lunges over 246 foraging dives while the calf executed 118 lunges over 30 foraging dives (note: lunges were not included if they were executed shallower than 10 m). Prior to feeding, the pair generally rested near the surface (as seen from surface observations during daylight hours) and executed a few exploratory dives (defined here as dives >50 m where no lunges were executed). The mother then initiated feeding at 16:22:00 h and fed continuously and regularly until her tag came off (Fig. 2). The calf, however, initiated feeding at 17:00:08 h and executed 95.8% of its lunges by 19:28:21 h. The mother and calf both lunged between one and multiple times per feeding dive (mean ± SD: 3.22 ± 1.88 and 3.93 ± 2.36 lunges per dive, respectively), with the maximum number of lunges executed per dive equalling 8 and 9, respectively (Table 1). The mother's within-dive inter-lunge interval was higher and had a smaller variance than the calf's (mean ± SD = 46.33 ± 8.10 and 33.71 ± 10.32 s, respectively; $t = 13.07$, df = 634, $p < 0.01$); variances between the animals were significantly different ($F = 0.62$, df = 546, $p < 0.01$). Additionally, the mother's inter-lunge interval was consistent throughout the tag record ($y = 0.02x + 45.92$, $p < 0.01$) and the change in inter-lunge interval was not significantly different from zero ($p = 0.82$).

For both animals, an increased number of lunges executed on a foraging dive was associated with longer mean dive durations (mother: $F_{1,252} = 5592$, $R^2 = 0.96$, $p < 0.01$; calf: $F_{1,28} = 33.81$, $R^2 = 0.55$, $p < 0.01$), longer mean post-dive surface times (mother: $F_{1,252} = 180.90$, $R^2 = 0.42$, $p < 0.01$; calf: $F_{1,28} = 32.43$, $R^2 = 0.54$, $p < 0.01$), and deeper mean maximum dive depths (mother: $F_{1,252} = 735.50$, $R^2 = 0.75$, $p < 0.01$; calf: $F_{1,28} = 55.98$, $R^2 = 0.67$, $p < 0.01$). These relationships were more consistent for the mother (always increasing) than for the calf (Table 1, Fig. 3). Additionally, the calf dove shorter and shallower than its mother when comparable numbers of lunges were executed during a given dive (mother versus calf dive duration by number of lunges: $t = -6.79$, df = 282, $p < 0.01$; maximum dive depth by number of lunges: $t = 5.45$, df = 282, $p < 0.01$); However, there was no significant difference in the post-dive surface time between the mother and calf when compared with the number of lunges executed per foraging dive, dive duration, and maximum dive depths (mother versus calf post-dive surface time by number of lunges: $t = -1.71$, df = 282, $p = 0.09$; post-dive surface time by dive duration: $t = 0.63$, df = 282, $p = 0.53$; and post-dive surface time by maximum dive depth: $t = -0.34$, df = 282, $p = 0.71$).

Cross-correlation analyses of the mother and calf's depth, pitch, roll, and heading for the entire concurrent tracks were derived to determine the correlation of the pair's behaviours. Depth was positively correlated ($r = 0.62$, $p < 0.01$) and was greatest when the calf's track lagged behind the mother's track by 4.5 s ($r = 0.62$, $p < 0.01$). Pitch and heading were also positively correlated (pitch: $r = 0.35$, $p < 0.01$; heading: $r = 0.36$, $p < 0.01$); however, this correlation was weaker than the correlation for depth. Pitch and heading were most correlated when the calf's track lagged behind the mother's track by 5 and 11 s, respectively. Rolling was not significantly correlated ($r = 0.02$,

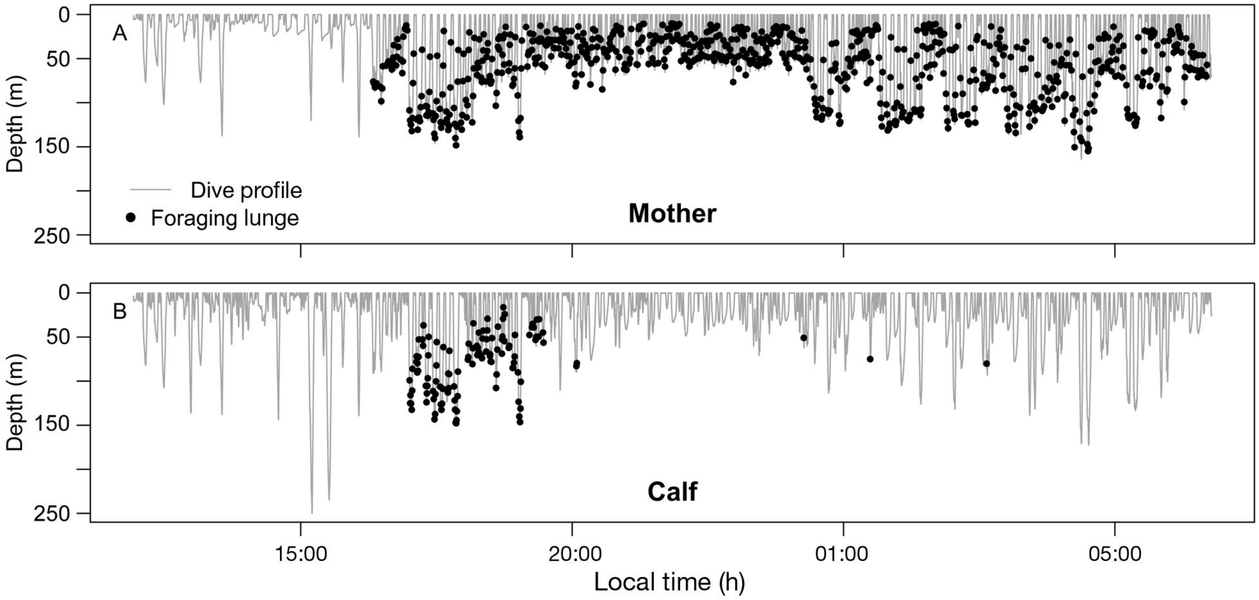

Fig. 2. *Megaptera novaeangliae*. Dive profiles (depth versus time) and foraging lunges executed by (A) the mother and (B) her calf during the duration of the concurrent tag records. Note: simultaneous recordings began at 11:51:17 h on May 19, 2010, occurred overnight, and ceased when the mother's tag came off at 7:42:00 h on the morning of May 20, 2010

$p < 0.01$) and was therefore not considered in further analyses. Correlation coefficients calculated for depth, pitch, and heading for each dive varied during the concurrent tag record and will be discussed in more detail below. In terms of their diving and surfacing behaviours, the pair dove and surfaced within ±20 s of each other for 57.81 and 44.40% of their dives, respectively. Within these ±20 s dives, the mother dove and surfaced before the calf 45.27% and 54.78% of the time, respectively, while the calf dove and surfaced before the mother 20.95 and 33.91% of the time, respectively; the pair dove and surfaced at approximately the same time (within ±1 s) 33.78% and 11.30% of the time, respectively.

Correlation coefficients calculated for the pair's depth, pitch, and heading varied throughout the concurrent tag records and between behavioural states (Figs. 4 & 5). Depth and pitch were highly positively correlated at the beginning of the concurrent record when the animals were resting and gradually weakened when the pair became more active and started making exploratory dives (~15:30:00 h) (Fig. 4A,B); heading showed a similar pattern but with lower r-values overall (Fig. 4C). Correlation coefficients were highly positively correlated again when the mother initiated feeding (16:22:00 h) and strengthened further when the calf joined its mother in feeding (17:00:08 h). After the calf stopped feeding (19:28:21 h), and for the remaining duration of the concurrent records, the correlation coefficients were variable, with lower r-values occurring when the mother was feeding at shallow depths in the middle of the night

Table 1. *Megaptera novaeangliae*. Mean (±SD) values of dive duration, post-dive surface time, and maximum dive depth per number of lunges executed on a dive. (–): not available

Lunges per dive	No. of dives		Dive duration (s)		Post-dive surface time (s)		Max. dive depth (m)	
	Mother	Calf	Mother	Calf	Mother	Calf	Mother	Calf
1	69	5	36.20 ± 9.53	172.64 ± 74.91	21.22 ± 18.83	30.72 ± 30.29	22.21 ± 6.11	64.33 ± 21.21
2	23	6	94.68 ± 15.40	156.93 ± 86.95	25.60 ± 18.58	54.13 ± 43.04	45.38 ± 14.18	60.87 ± 16.05
3	48	4	151.78 ± 20.52	149.80 ± 21.54	34.67 ± 27.27	45.20 ± 28.43	66.06 ± 16.35	71.67 ± 11.20
4	47	3	209.61 ± 27.28	186.93 ± 31.19	62.55 ± 33.69	45.87 ± 32.62	75.80 ± 25.52	84.24 ± 20.72
5	27	4	260.03 ± 36.39	220.40 ± 47.90	67.97 ± 42.07	81.40 ± 52.19	87.24 ± 26.40	78.20 ± 8.13
6	16	2	309.39 ± 23.93	310.40 ± 2.26	97.92 ± 54.19	97.20 ± 14.14	113.53 ± 25.07	140.02 ± 10.25
7	13	4	354.07 ± 21.01	294.60 ± 25.21	89.27 ± 41.90	147.80 ± 45.73	125.99 ± 21.00	118.36 ± 19.08
8	3	1	387.60 ± 32.02	346.4	140.40 ± 16.74	129.6	138.19 ± 11.25	146.79
9	0	1	–	382.4	–	172.0	–	150.36

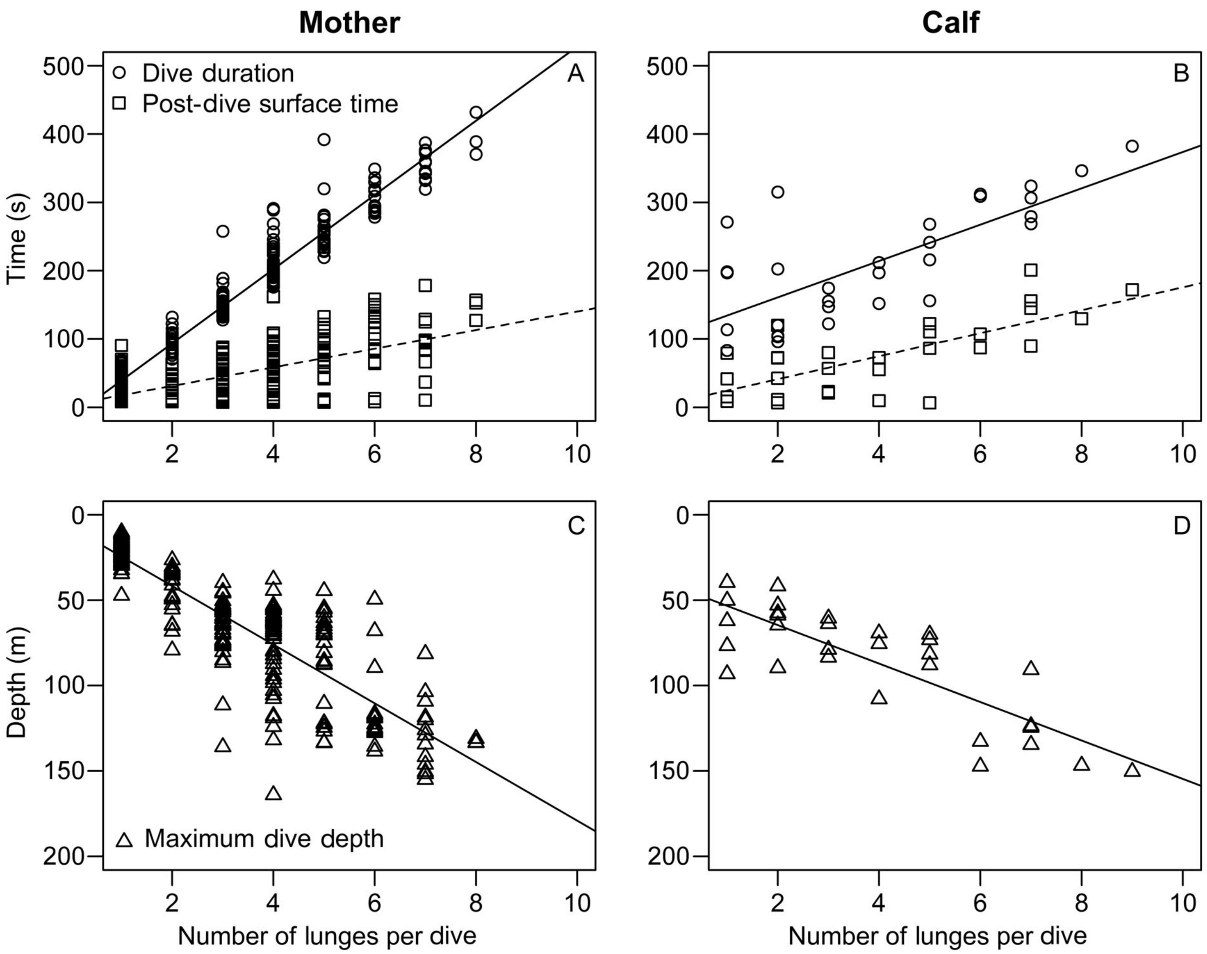

Fig. 3. *Megaptera novaeangliae*. Mean (A,B) dive duration (s) and post-dive surface time (s), and (C,D) maximum depth (m) (and associated best fit lines from least-squared linear regressions) for foraging dives of the mother and her calf

(presumably following the diel vertical migration of krill) and higher r-values when the mother was performing deeper foraging dives later in the morning. The percentage of r-values for depth, pitch, and heading that were >0.5 and >0.9 for the varying behavioural states (Fig. 5) are shown in Table 2 (note: there were no dives during which only the calf was foraging).

Lunges performed by the calf appeared to be synchronised with lunges performed by its mother in terms of time and depth. Indeed, 84.26 and 79.63 % of the calf's lunges were performed within ±20 s and within ±20 m, respectively, of its mother's lunges, while 35.19 and 53.70 % were performed within ±5 s and within ±5 m, respectively. Of these, the mother lunged before the calf 60.19 % of the time and shallower than the calf 52.78 % of the time. In addition, 97.46 % of the calf's lunges were executed during a dive in which its mother was also foraging. The mother, however, did not appear to forage based on whether or not her calf was simultaneously foraging or exhibiting synchronised behaviours (based on the continuity and regularity of her within-dive inter-lunge intervals).

DISCUSSION

Here, we describe the first record of a long-term (~20 h) continuous underwater relationship and concurrent foraging behaviour of a baleen whale mother–calf pair. As the calf we tagged was likely between 8 and 12 mo old (assuming it was born in the previous winter or early spring), our findings represent a snapshot of the period of time when the calf was gaining independence and was becoming more responsible for maintaining proximity to its mother. This is supported by the mother's foraging behaviour, which did not appear to change according to changes in the calf's behaviour (e.g. her inter-lunge interval was consistent and stable for the duration of the time she spent foraging, despite changes in the calf's

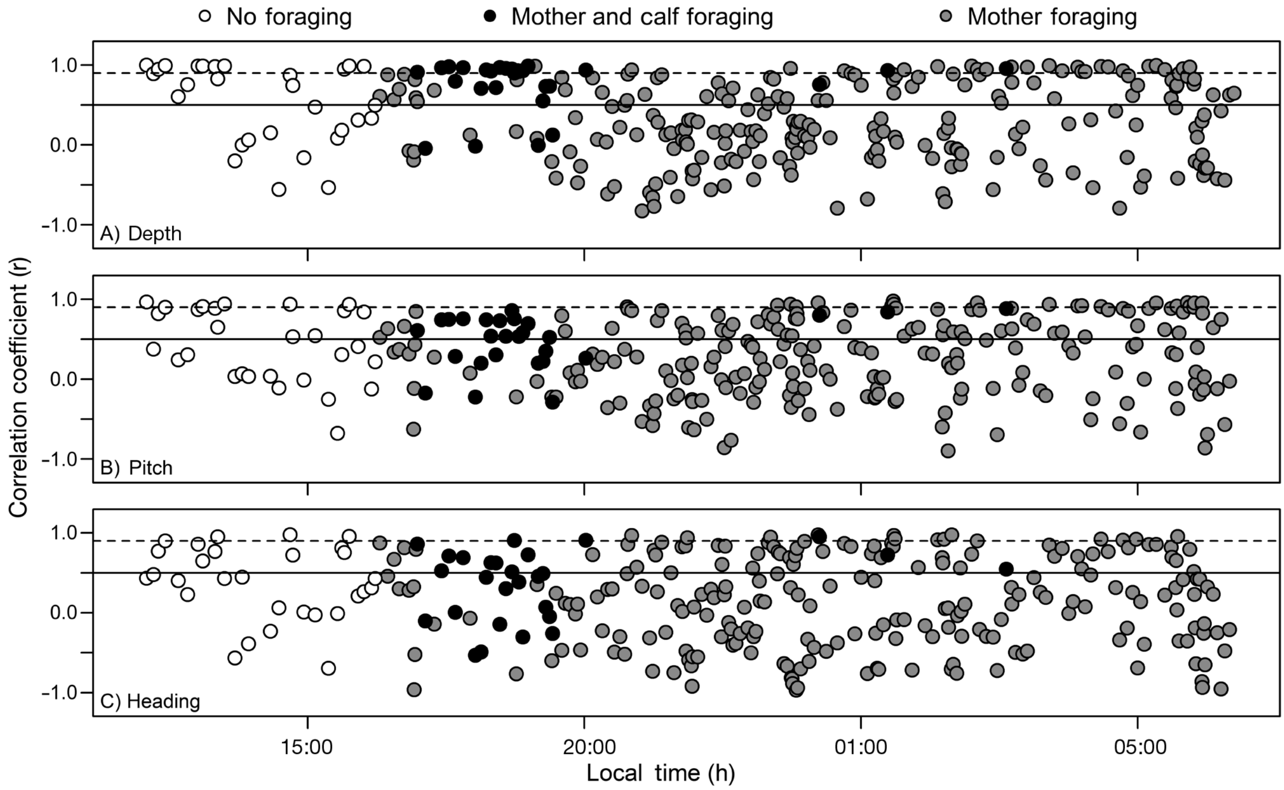

Fig. 4. *Megaptera novaeangliae*. Pearson's product-moment correlation coefficients calculated for each dive for the duration of the concurrent tag records for (A) depth, (B) pitch and (C) heading behaviour. The solid horizontal line represents r = 0.5 (i.e. synchronised behaviour), while the dashed horizontal line represents r = 0.9 (i.e. highly synchronised behaviour)

behaviour), and was instead likely a function of the vertical position of the prey (Croll et al. 2005, Friedlaender et al. 2009, Hazen et al. 2009, Goldbogen et al. 2011). In accordance, the calf appeared to be primarily responsible for altering and synchronising its behaviours to its mother throughout the concurrent tag records. This is similar to other humpback whale calves (Szabo & Duffus 2008, Cartwright & Sullivan 2009), southern right whale calves (Taber & Thomas 1982, Thomas & Taber 1984), and other mammals, such as infant rhesus monkeys *Macaca mulatta* (Berman 1980), during the later stages of the mother–offspring relationship.

While both animals exhibited feeding lunges, there were some striking differences in the frequency and duration of their foraging behaviours that likely correspond to the changes associated with the calf gaining nutritional independence and weaning. For instance, as previously stated, once the mother began feeding, she continued to consistently and regularly feed without resting for any significant period of time. In addition, she executed more lunges (N = 792) than have previously been described for other adult humpback whales (unknown age and/or sex) tagged for similar durations in the WAP (Ware et al. 2011). These findings may be explained by her spending less energy on her calf due to the calf's decreasing vulnerability to being left alone more frequently and for longer periods of time, and spending more energy attending to the increased demands on her personal fitness (e.g. replenishing energy reserves diminished from lactation and the recent migration, and increasing energy reserves for successful future migrations and successful rearing of additional offspring).

While the calf may have still been nursing (although we saw no apparent evidence of its occurrence), it executed 118 feeding lunges over 30 dives. Interestingly, the calf primarily foraged between 17:00:08 and 19:28.21 h. There are several potential reasons for why its foraging behaviour was so discrete in frequency and in duration. First, if the calf was still nursing then its feeding lunges were likely to obtain supplemental energy in addition to nursing. Second, the calf may require proportionally less food than larger animals to support its resting metabolism. Third, when young animals are less active their metabolic rates decline (Arnould et al. 2003) and energy is preferentially allocated to growth (Sibley & Calow

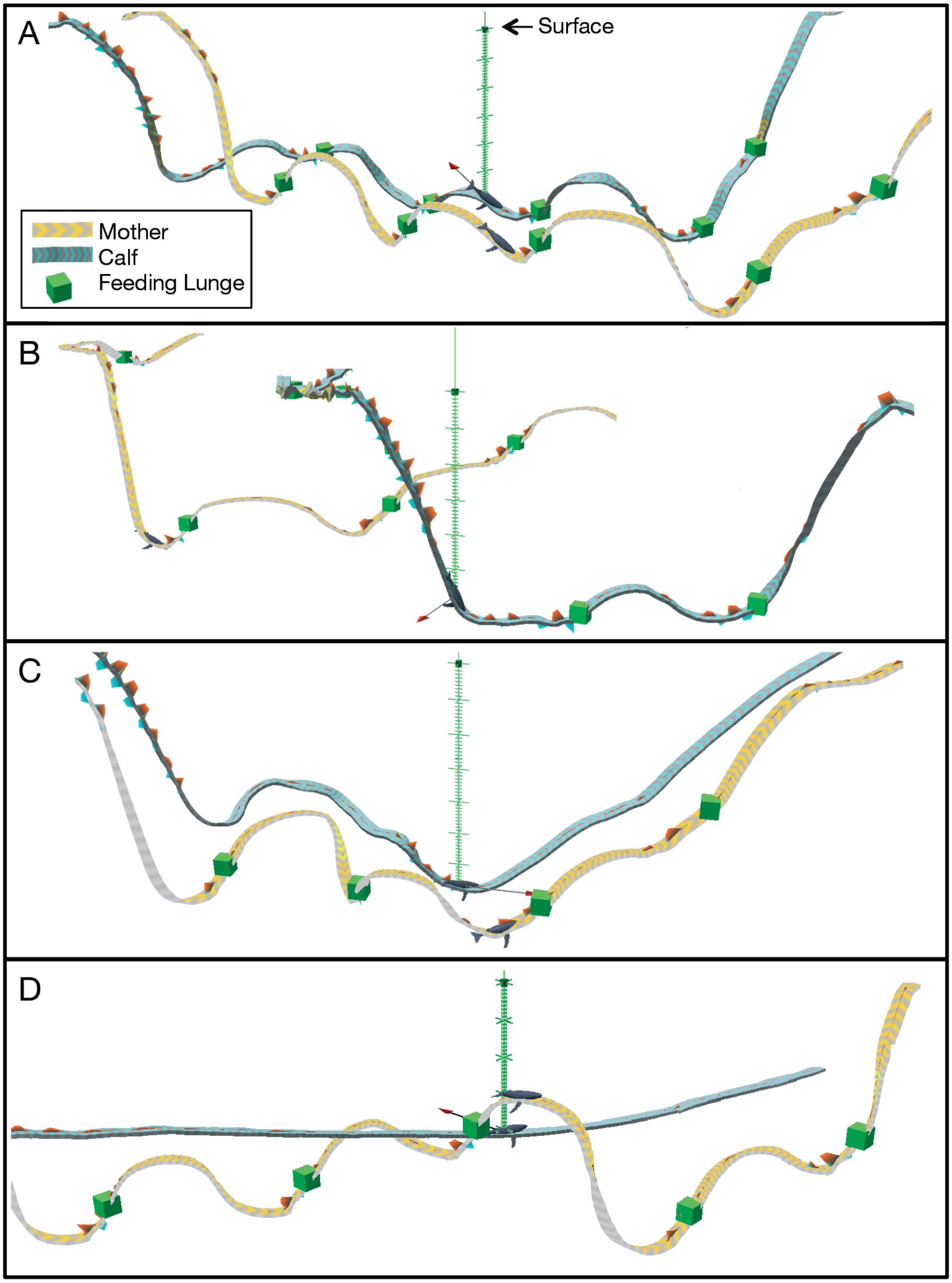

Fig. 5. *Megaptera novaeangliae*. Three-dimensional visualisations of the mother and calf's dive behaviour during varying behavioural states (TrackPlot, Ware et al. 2006). The dashed vertical line represents depth (10 m increments from the surface), the horizontal arrow represents magnetic north, and the blue and red wedges along the track represent the magnitude and frequency of fluke strokes (identified from angular accelerations about a lateral axis). Note: horizontal proximity is approximated based on surface fixes (N = 30 and 27 for the mother and calf, respectively) and dead-reckoning techniques, and may not represent the true horizontal proximity. (A) A synchronised dive during which both animals are foraging; (B) an unsynchronised dive during which both animals are foraging; (C) a synchronised dive during which the mother is foraging and the calf is not foraging but swimming nearby; and (D) an unsynchronised dive during which the mother is foraging and the calf is not foraging and not swimming synchronously

Table 2. *Megaptera novaeangliae*. Percentage of correlation coefficients that were greater than 0.5 (synchronous behaviour; 1st value) and greater than 0.9 (highly synchronous behaviour; 2nd value) for the pair's depth, pitch, and heading

	Depth	Pitch	Heading
Neither foraging	62.07, 34.48	48.28,17.24	37.93, 10.34
Both foraging	85.19, 59.26	62.96, 0.00	48.15, 11.11
Only mother foraging	36.36, 10.45	38.18, 9.09	31.36, 6.36

1986). Thus, it may be beneficial for the calf to spend only a small portion of its time feeding and a larger portion of its time either resting near the surface or swimming in synchrony with its mother gaining the associated hydrodynamic advantage (Noren et al. 2008, Noren & Edwards 2011). This would allow the calf to dedicate more of its energy to growth, which is important for its survival; a large body size reduces the costs associated with travel during migrations (Williams 1999), increases the individual's breath holding and oxygen storage capacity (Schreer & Kovacs 1997), reduces the risk of predation (Chittleborough 1958), and enhances future reproductive success (Spitz et al. 2002).

While adult rorqual dives have been characterised by a gliding descent with a low rate of fluking, a series of lunges at depth, and an ascent to the surface powered by steady fluking (Goldbogen et al. 2006, 2008), preliminary examinations of the calf's dive plot reveal that the calf beats its flukes frequently on the descent, performs a series of lunges at depth, and then ascends to the surface with few, if any, fluke strokes. Positively buoyant whales, such as North Atlantic right whales *Eubalaena glacialis* (Nowacek et al. 2001) and sperm whales *Physeter macrocephalus* (Miller et al. 2004) are known to actively stroke to depth and glide during ascent. Aoki et al. (2011) found that an increase in fat content in a Northern elephant seal *Mirounga angustirostris* resulted in an increased descent stroke rate and decreased ascent stroke rate. This suggests that the calf is more buoyant than its mother and must expend more energy to stay submerged. Further work to characterise buoyancy and fluking effort differences between mother and calf pairs should be conducted to examine this hypothesis more closely.

The frequency of lunges executed per dive has been associated with deeper maximum dive depths, longer dive durations, and longer post-dive surface times in humpback whales (Dolphin 1987a,b, Goldbogen et al. 2008, Ware et al. 2011), fin whales (Croll et al. 2001, Acevedo-Gutiérrez et al. 2002, Goldbogen et al. 2006, 2007), and blue whales (Croll et al. 2001, Acevedo-Gutiérrez et al. 2002, Goldbogen et al. 2011). Our results (Fig. 3, Table 1) are consistent with these findings and thus provide further support for the hypothesis that lunge feeding is energetically costly. Interestingly, the mother and calf had proportionally equivalent post-dive surface times (i.e. recovery times) when considering the number of lunges executed per dive, dive durations, and maximum dive depths. This suggests that foraging dives executed by the mother and calf of comparable foraging effort were equivalently energetically costly. Despite this, the calf dove shallower and had shorter dive durations than its mother for comparable number of lunges executed per dive. These findings are likely related to the calf's limited oxygen capacity and possibly greater buoyancy. The duration for which a diving animal can remain underwater is related to its oxygen storage capacity, the rate at which it uses stored oxygen, and its anaerobic capacity (Schreer & Kovacs 1997); as such, larger animals are better equipped to dive. Thus, a humpback calf should exhibit shorter dives for similar dive depths and durations than its larger mother.

Our results also further support the hypothesis that humpback whales exhibit a following maternal strategy (Lent 1974, Szabo & Duffus 2008). While our pair was not always traveling together, they were within a vertical distance of ±20 m for 71.40% of the concurrent records and exhibited a high percentage of synchronised dives in terms of their depth, pitch, and heading (Fig. 4, Table 2). In addition, the pair's depth was most highly correlated when the calf's track was lagged 4.5 s behind its mother. Also, when the calf was feeding, it lunged after its mother 60.2% of the time. These findings suggest that the pair were generally traveling and feeding in synchrony with each other, with the calf traveling and feeding close behind.

Interestingly, a higher percentage of positively correlated dives were found when both animals were feeding than when neither animal was feeding or when just the mother was feeding. There are several beneficial reasons for the calf to synchronise its feeding behaviour with its mother, including learning how to forage and/or benefiting from the food its mother has found. In addition, synchrony during foraging may ease the energetic costs associated with foraging for the calf by gaining the hydrodynamic advantages associated with synchronised swimming (Noren et al. 2008, Noren & Edwards 2011). This may contribute to the equivalent recovery times we found for the mother and the calf for comparable foraging dive efforts. When the calf was not feeding, it would go in and out of synchrony with its mother (shown by the fluctuation in r-values; Fig. 4), generally behaving independently of its mother when its mother was feeding near the surface and re-synchronising its behaviours when the mother made deeper feeding dives. This suggests that while the mother was feeding near the surface, the calf could behave independently of its mother while maintaining a close proximity. However, when the mother executed deeper dives, the calf had to join and synchronise its behaviour in order to maintain similar levels of proximity.

While our findings only represent ~20 h of a single humpback whale mother–calf pair, they demonstrate how bio-logging tools can enhance our understanding of marine animals during periods that are critical for their behavioural development. It is important to note that the behaviour of mother–calf pairs can vary widely across pairs and over time (Taber & Thomas 1982, Cartwright & Sullivan 2009) and therefore more tags need to be deployed on additional mother–calf pairs at varying times during the first year of their relationship. Such attempts should take the appropriate measures to minimise disturbance during tagging, however, as mother–calf pairs may be more sensitive to boat approaches than groups of adults. These efforts will enable us to gain a better understanding of early baleen whale behavioural ontogeny.

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Contribution to the Theme Section: 'Tagging through the stages: ontogeny in biologging'

Ontogeny in marine tagging and tracking science: technologies and data gaps

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ABSTRACT: The field of marine tagging and tracking has grown rapidly in recent years as tag sizes have decreased and the diversity of sensors has increased. Tag data provide a unique view on individual movement patterns, at different scales than shipboard surveys, and have been used to discover new habitat areas, characterize oceanographic features, and delineate stock structures, among other purposes. Due to the necessity for small tag-to-body size ratio, tags have largely been deployed on adult animals, resulting in a relative paucity of data on earlier life history stages. In this study, we reviewed tagging efforts on multiple life history stages for seabirds, marine mammals, marine turtles, and fish and enumerated studies focusing on each guild that targeted larvae, juveniles or hatchlings. We found that turtles and fish had higher proportion of studies focusing on juveniles (>20%) than seabirds and marine mammals (<10%). On both juveniles and adults, tags were used in a targeted manner with passive and transmitting tags as the main tools for population demography and connectivity studies, while GPS and archival tags were used more frequently for habitat analyses and foraging ecology. These findings identify the need to focus on novel approaches in tagging multiple life history stages both to study marine predator ecology and to effectively manage marine populations.

KEY WORDS: Tagging · Tracking · Biologging · Ontogeny · Juvenile · Top predator

INTRODUCTION

Tagging animals to obtain data on their movements and physiology has resulted in an unprecedented understanding of the distribution and behavior of marine animals (Rutz & Hays 2009, Bograd et al. 2010). However, there are still large gaps in tagging science that need to be addressed (Godley et al. 2007, Hart & Hyrenbach 2009). Though we are rapidly advancing our capacity to close these gaps, important challenges remain; arguably the main limiting factor in furthering our ecological knowledge is the difficulty of advancing tag technology and size concurrently. In this review, we examine gaps in top predator tagging studies by determining the distribution of studies across life history stages, how gaps vary across predator taxonomic groups, and assess which gaps are the most important to fill.

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Tagging of marine animals has developed into an innovative discipline, currently using physical or chemical tracers to mark individuals and technologically advanced data loggers to understand how animals interact with their environment. Early efforts for marine species featured spaghetti tags implanted in fish muscle (e.g. Everhart et al. 1975, Bayliff 1988, Pollock 1991), body markings such as fin/scute clippings or number branding (e.g. L. Gaustella & G. Hughes unpubl.), and metal bands attached to a leg or flipper (Limpus 1992). These simple tags supported the first mark and recapture studies identifying movements and home ranges of many taxonomic groups, and eventually allowed measurements of demographic parameters such as growth rates and age of maturity (e.g. Bjorndal et al. 2000, Sibert & Nielsen 2001, Limpus & Limpus 2003). As electronics became miniaturized, more complex tags were developed and a greater range of species was tagged. The genesis and early history of electronic tagging techniques is summarized in Naito (2004) and Kooyman (2004). Acoustic transmitters, for example, allow for automated resightings of tagged animals to provide a more temporally complete snapshot for mark-recapture analyses (Sibert & Nielsen 2001). More recently, archival and satellite tags often measure light and temperature, and many broadcast an animal's location either upon surfacing, or after tag release and data transmission from the surface. These advances have resulted in a number of broad-reaching findings about animal behavior and distribution (Weimerskirch et al. 2000, Shillinger et al. 2008, Block et al. 2011). However, significant data gaps remain, particularly with respect to smaller organisms and early life history stages (Fedak et al. 2002).

Ship-based survey data, nesting beach, rookery or colony counts, and fisheries catch data are among the traditional methods for measuring marine top predator behavior, distribution, and/or abundance in the field. Survey data provide a Eulerian snapshot of multiple animals sighted at the sea surface (e.g. marine mammals or seabirds), caught by hook or net, or on land (nesting beaches and rookeries). Ship based surveys allow for instantaneous measurements of behavioral state and estimates of abundance, but 'sightability' varies depending on factors such as species, behavior, and weather conditions (e.g. Pollock et al. 2004). Tracking of an individual or group of animals, measuring social and behavioral cues at a fixed interval, can provide more complete behavioral measurements during surveys (e.g. Hodgson & Marsh 2007). Fisheries catch data are similar to survey data in providing a snapshot of distribution, but there is a function of catchability, similar to sightability, as animals have to be both present and unable to avoid hooks or nets. However, for some species, such as the flatback turtle, much of what is known about their non-nesting distribution comes from fisheries catch data (Dryden et al. 2008).

In contrast to the Eulerian approaches, tag data can measure Lagrangian movement of a tagged individual, offering finer scale and longer continuous time series while potentially collecting behavior below the ocean surface. As sighting-based data alone can rarely assess ontogeny, tag data are required to understand how multiple life stages interact with the environment. For juvenile oceanic top predators, some of the key ecological questions that require investigation include (1) population structure and recruit mortality, (2) critical juvenile habitat and overlap with threats, (3) dispersal and population connectivity, and (4) foraging ecology. With numerous deployments, the spatial and temporal resolution of tag data allow scientists to assess abundance using recapture metrics (e.g. Taylor et al. 2011), as well as understand how predators use pelagic environments both behaviorally (e.g. feeding, reproduction, migration corridors) and across temporal scales (daily, seasonally, or annually).

TAGGING TECHNOLOGY

The field of marking and tagging can be classified into 2 broad categories: passive and active. Marking applies or uses an existing visual or otherwise detectable tracer to an organism allowing resighting (e.g coloration, genetics, or chemical patterns). Passive tags can be non-electronic, 'conventional' forms of tagging (e.g. flipper or spaghetti) that have been employed for decades, or can reflect a signal when in contact with an electronic reader. As passive tags are not limited by battery life, they can last across multiple life-history stages if not shed. For example, salmon with passive tags implanted as smolts are measured 3+ yr later as adults when they swim upriver to spawn (e.g. Castro-Santos et al. 1996) and marine turtles tagged with flipper tags as juveniles are recaptured decades later as adults (Limpus & Limpus 2001, Limpus et al. 2003). The simplest and cheapest tags can be deployed on multiple individuals at a fraction of the cost of more complex tags, but collect less information.

Conventional tags are implanted in muscle or attached to the animal with a unique identifier and require recapture to measure growth or to identify a start and end-point of movement patterns (White & Beamish 1972, Balazs 1999). ***Passive integrative transponder* (*PIT*) *tags*** provide automatic identification of tagged individuals either through manual scanning by a researcher or via *in situ* automated receivers deployed at key locations, such that all individuals passing get scanned (e.g. Barbour & Adams 2012, this Theme Section). These approaches do not require power and thus can last until shed by the tagged individual. Results from conventional or PIT tags are traditionally used to inform migration rates, mortality, and ontogenetic shifts in biological parameters.

Active tags include a broad suite of technologies and can be separated into 2 categories: transmitting and archival tags. ***Radio tags*** are commonly used in terrestrial studies as they transmit a radio signal through air for locating a tagged animal, but also have been used on regularly surfacing marine species (e.g. Whiting & Miller 1998) and in combination with archival tags to assist retrieval (Johnson & Tyack 2003, Weber et al. 2011). ***Acoustic tags*** use a specific frequency and transmitting pattern to identify individuals when they pass within detection range of an underwater hydrophone or receiver (Arnold & Dewar 2001). This receiver may be in the form of a listening station such as a hydrophone, or in the form of another animal carrying a receiver. ***'Chat' tags*** record the presence of other animals equipped with transponders, giving data on both the movement of animals in the vicinity of the receivers and inter-individual associations (Voegeli et al. 2001, Holland et al. 2009, Guttridge et al. 2010). Acoustic tags transmit frequently, are detectable up to a few kilometers from a receiver, and allow longer-range detectability than PIT tags. However, acoustic tag duration is limited by battery size, transmission frequency, and detectability.

Satellite tags are particularly useful for flying or air-breathing animals as position information is transmitted when the tag has an uninterrupted path to orbiting satellites upon surfacing. The Advanced Research and Global Observation Satellite (ARGOS) system both allows the positioning of the surfacing animal and can transmit a limited amount of information. As the Global Positioning System (GPS) has a higher accuracy than ARGOS (km for ARGOS, m for GPS; Hazel 2009, Costa et al. 2010a) GPS receivers are often inserted in ARGOS tags. Alternatively, GPS data can be stored on-board for retrieval upon tag recovery for animals with regular surfacing bouts (Phalan et al. 2007, Cordes et al. 2011). ***Fastloc GPS*** receivers have revolutionized the potential for GPS technology use in marine animals, as they gather positioning data in less than a second and therefore allow positioning even during short surfacing events (Sims et al. 2009, Costa et al. 2010a, Witt et al. 2010a).

Archival tags actively record time-series data of multiple sensors, which are stored within the device and can be obtained by researchers upon recovery or, for tags with transmitting capabilities, on detachment (Block et al. 1998, Phillips et al. 2004, Schaefer et al. 2007, Weng et al. 2009). Archival tags originated as depth-loggers that recorded mean dive metrics on a coarse time scale (Arnold & Dewar 2001), but current tags can record behavioral data at high frequency, including detailed dive behavior, energy expenditure, oceanographic data such as subsurface temperature and light levels, and/or location data. Recovery of archival tags occurs either by recapturing the animal and removing the tag with the full dataset, or via pop-up when archival tags detach from the animal at a pre-programmed time, reach the surface, and send summarized archived positions and sensor data to the satellite (Block et al. 1998, Block et al. 2001, Schaefer et al. 2007, Weng et al. 2009). Position data can be calculated from onboard light-sensors based on day lengths and sunrise/sunset times when animals enter the photic zone, also known as geolocation. With such a technique, location errors can exceed 1° latitude and/or longitude (Block et al. 2001). Recent efforts to use additional data sources, such as sea surface temperature (SST) or the Earth's magnetic field, have improved light-based geolocation estimates (Teo et al. 2004, Royer et al. 2005, Nielsen et al. 2006). Archival tag deployments can last from 1 to 3 yr, but longer-term life history transmitters are designed to collect internal vital rates over the life of an animal and transmitting upon mortality and tag release (Horning & Hill 2005).

Short-term archival tags include suction cup tags that can collect high-frequency data over a short duration (e.g. 24 h) and can include multiple sensors when tag size is less limiting (e.g. large baleen whales). This can include 3-axis accelerometers to reconstruct underwater behavior (Johnson & Tyack 2003, Ware et al. 2006, Shepard et al. 2008, Okuyama et al. 2009), stomach temperature sensors, and jaw based accelerometers or magnetic triggers to identify foraging events (e.g. Myers & Hays 2006, Bestley et al. 2008, Hanuise et al. 2010). These have been miniaturized in the example of 'daily-diary' tags, which can be deployed on multiple species providing accelerometer data at extremely high temporal resolution (Wilson et al. 2008). ***Low-light cameras***, which archive still or video images even in low-photic regions, can further improve our understanding of underwater movements, and calibrate behaviors to changes in acceleration data (Heithaus et al. 2001, Gómez Laich et al. 2009). Data visualization of tag data and videos from cameras are important tools for outreach efforts and public education in addition to their scientific merit.

Even though tags are undergoing rapid technological advances (e.g. more sensors, decreased size, and increased battery life), tag makers and researchers must decide on trade-offs across these categories. The choice of tag types has largely been made based on the ecological questions being studied (e.g. fine-scale foraging versus large-scale migration) but often animal size, funding limitations and ethical considerations may dictate the number of tags available, the tagging methodology used, and the ability to re-tag individuals or tag others in the future. As the largest individuals are usually the first to be studied using tagging, one of the biggest data gaps still remaining are the juvenile and subadult life stages, which are often the most critical periods for survival (e.g. Elliott 1989). Tag research and development has progressed to the point that tags are now small and light enough to be used on smaller individuals, and consequently younger life stages, although it is critical that any potential impacts are evaluated (Witt et al. 2011, Vandenabeele et al. 2012).

TOP PREDATOR GROUPS AND TAGGING

Life cycles across top predator taxonomic groups vary widely, and different life stages have contrasting behavioral modes and habitat requirements, resulting in a diversity of challenges in applying tagging techniques (Fig. 1, Tables 1 & 2). Planktonic fish larvae settle in juvenile nursery habitat until they mature into adults, often encompassed by different habitat characteristics and constraints (Balon 1986, Beck et al. 2001). Seabirds and marine mammals have precocial stages during which they are dependent on their parents. For birds and pinnipeds, this stage lasts until they leave the nest or colony and begin their own foraging trips as juveniles, and for cetaceans until they are weaned. Upon maturation, pinnipeds and seabirds undergo yearly or multi-year cycles of molting, breeding, egg-laying or birthing, followed by post-breeding trips that have very different energetic requirements and migration strategies, requiring multi-stage tagging efforts (Kappes et al. 2010). Cetaceans and sirenians have slightly different constraints because they do not have the same ties to land as seabirds and pinnipeds, but some cetaceans breed at low latitudes and undergo long-distance migrations between their foraging

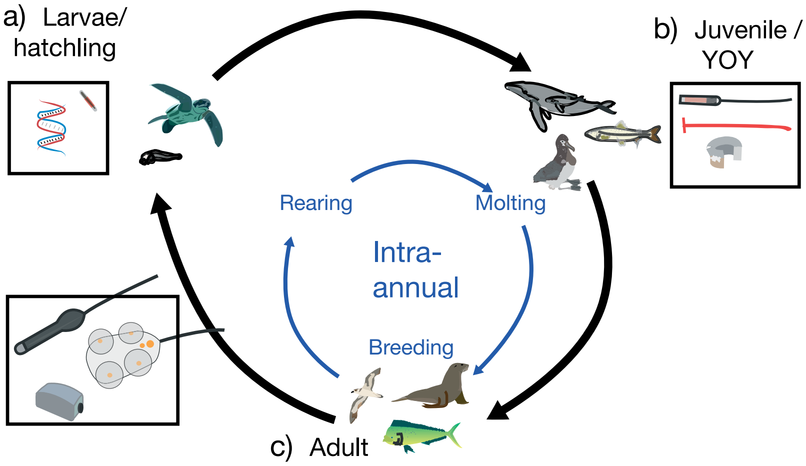

Fig. 1. Simplified representation of life history stages and tags commonly used at that stage for predator taxonomic groups (outer circle). The inner circle (blue) is a reminder of intra-annual stages in adults that can result in different constraints, tag retention rates, and behavioral patterns. (a) Larvae/hatchlings include seabird chicks, sea turtle hatchlings, marine mammal pups and calves, and fish larvae, all of which pose difficulties in tag attachment. Both sea turtles and fish are very small and have very high mortality, making adequate tagging a costly exercise. Three common marking mechanisms include markings (fin clipping), implantable passive integrated transponder (PIT) tags, requiring a reader to get the unique identifier, and isotopic or genetic markers to address habitat and population connectivity questions. Marine mammal and seabird offspring are often tied to their parents (or to land), allowing behavioral inference from their parents or from land. (c) Juveniles and young-of-the-year (YOY) are not yet reproductively active and are focused on minimizing predation risk while maximizing foraging to amass body weight, which may result in different habitat requirements or migration pathways than those of adults. In addition to PIT tags, spaghetti tags in fish, and flipper tags and banding in pinnipeds, turtles, and seabirds can be used for simple mark-recapture data. For larger fish, acoustic tags can be used to identify residence rates and migration behavior across acoustic receivers. (c) Adults can hold the largest tags and have traditionally been the most sampled for this reason. Tags used include GPS positioning tags in birds and mammals, long-term pop-up archival tags for coarse positioning and temperature measurements in fish species, and fine-scale archival suction cup tags to measure underwater behavior of marine mammals

Table 1. Total number of tagging studies and percentage focusing on juvenile life stages by guild from the literature search in Web of Science. The search terms included ('bird*' OR 'mammal*' OR 'fish*' OR 'turtle*' OR 'cetacean*' OR 'dolphin*' OR 'whale*' OR 'otter*' OR 'seal*' OR 'sea lion*') AND ('ocean*' OR 'marine*' OR 'sea*' OR 'pelagic*') AND ('satellite*' OR 'tag*' OR 'track*') AND ('PIT*' OR 'passive integrated transponder*' OR 'ARGOS*' OR 'GPS*' OR 'pop-up*' OR 'radio*' OR 'acoustic*' OR 'archival*') with early life stages including ('juvenile*' OR 'sub-adult*' OR 'subadult*' OR 'fledging*' OR 'hatchling*' OR 'YOY*' OR 'yearling*' OR 'Young of the year*' OR 'fry*' OR 'smolt*' OR 'larvae*')

	Marine mammal	Fish	Turtle	Seabird
All	735	2318	291	603
Juvenile (%)	6.0	23.9	26.5	8.8

and calving grounds (Corkeron & Connor 1999, Rasmussen et al. 2007). Sea turtles arguably have the least understood juvenile stages (Reich et al. 2007). Sea turtle tracking research has focused on nesting females due to accessibility on the nesting beaches (Godley et al. 2007). Hatchling sea turtles have high mortality rates (Santidrián Tomillo et al. 2010), and are not seen again for extended periods (of more than a decade) until they are reproductively active, when only females return to the nesting beaches (Carr 1967, Shillinger et al. 2012).

Fishes

Fishes have had the longest tagging history, given the commercial importance of many species and, in general, less stringent permitting requirements compared to other taxa. Tagging studies have been able to shed light on key ecological processes such as population structure and connectivity (Taylor et al. 2011), movement patterns (Bonfil 2005), and marine hotspots (Block et al. 2011). Of the 4 taxonomic groups considered, relatively greater effort has been devoted to understanding multiple life stages of fish (24.7% of studies were on juveniles), in part because habitat requirements can vary through ontogeny (Table 1). Larval fish are very small (<~5 mm) and have extremely high mortality, due largely to starvation and predation (Houde 1997). This complicates efforts to track juvenile fish in sufficient numbers. The degree of larval dispersal and retention largely determines population connectivity in marine fish populations, and understanding these patterns is critical for management of essential fish habitat, understanding vulnerability to climate variability and threats, and the implementation of space-based management tools (Thorrold et al. 2002, Palumbi et al. 2003). For this reason, many of the studies to date have used modeling approaches to simulate patterns of dispersal (Cowen & Sponaugle 2009), when tag deployments remain untenable due to cost and size

Table 2. Categories of research questions answered using tagging studies, organized by taxonomic group and ontogenetic stage. Each cell indicates the status of tag-based ecological research (many studies: >10; some: >5; few: <3), tag types that were commonly used to answer these questions, and reference to a review, seminal, or novel study where available. Tag types are: (1) visual and molecular techniques (e.g. Photo-ID, branding, genetics, isotope ratios); (2) passive tags (e.g. spaghetti, band, flipper, passive integrated transponder [PIT]); (3) active transmitting tags (e.g. radio, acoustic, chat-tags); (4) satellite tags (e.g. GPS, ARGOS, Fastloc GPS); (5) short-term archival tags (e.g. camera tags, accelerometer-based tags, magnetic sensor tags, internal temperature/heart rate); (6) long-term archival tags (e.g. pop-up archival, internal temperature/heart rate, life history tag, daily diary tag)

	Marine mammal		Fish		Turtle		Seabird	
	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile
Mortality/ population size	Many (1,2) Hammond 2002	Some (1,2) Pistorius et al. 2000	Many (1,2, 3,5) Pine et al. 2003	Many (1,2,3) Pine et al. 2003	Many (1,2,3,4,5) Bradshaw 2005	Some (2) Chaloupka & Limpus 2005	Many (2) Weimerskirch et al. 1998	Few (2)
Connectivity	Many (1,2,4) Witteveen et al. 2009	Some (1,2) Oosthuizen et al. 2011	Many (1,2,3, 5) Thorrold et al. 2002	Many (1,2) Thorrold et al. 2002	Many (1,2,4) Bowen et al. 1994	Some (1,2) Godley et al. 2010	Many (1,2,3, 4,6) Friesen et al. 2007	Some (1,3,4) Votier et al. 2011
Habitat	Many (1,2,4, 5,6) Kenney et al. 2001	Some (4,6) Burns 1999	Many (2,3,6) Block et al. 2011	Many (2,3) Gillanders et al. 2003	Many (1,2,3, 4,6) Bailey et al. 2012	Many (1,3,4) Musick & Limpus 1997	Many (1,4, 5,6) Wakefield et al. 2009	Some (4,6) Kooyman & Ponganis 2007
Foraging ecology	Many (1,5,6) Croll et al. 1998	Some (5,6) Tyson et al. 2012	Many (1,5,6) Cunjak et al. 2005	Some (3,5,6) Bestley et al. 2008	Many (1,2,3, 4,5,6) Eckert et al. 1989	Few (1,3)	Many (1,3,4, 5,6) Wakefield et al. 2009	Some (4,6) Weimerskirch et al. 2006

limitations. As an alternative, developmental tracers such as artificial (e.g. fluorescent or radioactive tracers) and natural isotopic markers have been used to measure connectivity, dispersal, and natal homing in the marine environment (Thorrold 2001, Palumbi et al. 2003). Using a combination of genetic and geochemical techniques, researchers have been able to inform understanding of habitat use and movement, providing critical knowledge for delineating stocks and managing migratory species (Thorrold et al. 2002, Cowen & Sponaugle 2009).

Passive tags have been effective for tracking juvenile fish because of their small size and lower cost, which are important considerations due to the high mortality in this life stage (Kipling & Lecren 1984). Passive markings (e.g. fin clips), spaghetti or coded wire tags, and PIT tags in hatchery fish have been valuable in informing our knowledge of juvenile salmon migration and survival (Castro-Santos et al. 1996). By measuring the proportion of tagged salmon returning to the mouth of a spawning river, scientists can calculate survival rates, which are essential for estimating stock size and setting fisheries catch limits. Unlike fin clippings or coded wire tags, PIT tags can be read by in-water readers without recapture, providing more information on both the onset of migration and the population level timing of migration, independently of sampling effort. These passive techniques are still critical for tagging many smaller fish species, and they have provided insight into the survival, recruitment, and population dynamics of young and adult fish (e.g. Barbour & Adams 2012).

Active tags have been applied to juvenile and adult life history stages to provide measurements of core habitat and improved estimates of survival. Moreover, these tags can also provide information about emigration, when the individual may be lost to re-sampling techniques (Pine et al. 2003, Hammerschlag et al. 2011). Acoustic tags are useful for migration studies of juvenile and adult stages, particularly in areas where a high density of receiver arrays allows the calculation of percent occupancy and migration rates among receivers (Welch et al. 2002). Acoustic tags can also reveal fine-scale responses to estuarine or oceanic processes, e.g. avoidance of hypoxia (Brady et al. 2009) and effects of other environmental variables, e.g. exposure to solar ultraviolet-B radiation (Melnychuk at al. 2012, this Theme Section). Combined with measures of environmental characteristics such as prey distribution, key inferences can be made about foraging behavior and ecology of predatory fish such as tuna, relative to prey distributions (Josse et al. 1998). With the deployment of additional receiver arrays (including mobile tags that serve as arrays; Holland et al. 2009) and greater tagging effort, acoustic tags have potential for monitoring marine populations at multiple spatiotemporal scales, particularly to understand use patterns in critical or protected habitat. Acoustic tags remain a key tool in understanding fine-scale movement and behavior of fish by providing multiple recaptures at a broader scale than PIT tag readers and at lower cost than archival or satellite-based methods.

Larger tags, such as pop-up archival tags, are too large to be applied to most young fish life stages (though see Rowat et al. 2007), but they have provided valuable insights in the study of large predatory fishes and sharks. These fish have been outfitted with pop-up tags to assess movement patterns (Block et al. 2001, Humphries et al. 2010), behavioral ecology (Sims 2010, Hammerschlag et al. 2011), spawning habitat (Block et al. 2001), and more recently to improve stock assessment models (Taylor et al. 2011). One of the broadest syntheses of top predator behavior, habitat use, and migration patterns analyzed 7 fish species (of 23 total top predators) to describe seasonal patterns of migration, identify biodiversity hotspots, and quantify physical characteristics of these hotspots in the North Pacific (Block et al. 2011). Combining pop-up tags with stomach temperature loggers has allowed physiological detection of feeding events through the heat loss of a prey capture event followed by an increase in core body temperature after digestion (Clark et al. 2008). Trawl and longline data, and tag-based mark-recapture studies are the 3 primary tools used to assess fish species biomass, and the integration among data types (e.g. combining passive and active techniques; Cunjak et al. 2005) has improved our understanding of fisheries ecology. Given the large number of species of fish and their varied life-history and behavioral characteristics, smaller and cheaper tags could provide ecological knowledge of pelagic forage species to inform ecosystem studies (Cury et al. 2011), and better estimate fisheries-independent mortality rates for heavily fished species. While spatial management approaches are used to protect adult fish and even spawning aggregations, these efforts may be undermined by high mortality of juvenile life stages outside of protected areas, resulting in poor recruitment to the adult spawning stock (Hooker & Gerber 2004).

Sea turtles

Sea turtle tagging efforts have used technology from flipper tagging and paint-based markers beginning in the 1930s to satellite tracking in the early 1990s (Godley et al. 2007). Despite difficulties, sea turtle researchers have tracked multiple life stages (27.0% of studies explicitly included juvenile life stages; Table 1), though the research questions and methods vary depending on turtle size. For hatchlings, tethered tags have been used to investigate predation rates, dispersal patterns and behavior (e.g. Gyuris 1994, Salmon et al. 2010) and genetic markers have been applied to understand the fidelity displayed by sea turtles to their natal beaches later in life (Bowen et al. 1994). Although there remain logistical and financial challenges in tracking large enough sample sizes of hatchling turtles to answer ecological questions — such as those associated with post-hatching frenzied movements — it is becoming more feasible because acoustic transmitter tags are approaching suitable weights (<1 g).

Passive flipper tags and PIT tags have been used to track the survival, movements and nesting characteristics of turtles large enough to retain tags through time (e.g. Limpus et al. 2003, Chaloupka et al. 2008). While these marking techniques still remain a vital tool for sea turtle monitoring and conservation, the field of sea turtle tagging has grown exponentially as the availability of satellite and archival tags has increased and they have become more affordable. The increase has been particularly evident in the increase in studies using tracking tools to investigate migration pathways, albeit with generally low sample sizes (Godley et al. 2010). Satellite tracking produces data relatively quickly, in comparison to the possibly long waiting time required for recoveries from flipper tags. Moreover the publicly viewable data generated by satellite tracking often has concurrent educational and public awareness benefits for researchers interested in the human aspects of sea turtle conservation.

As many turtle species make ocean-basin scale migrations encompassing multiple years, study of their life history requires a broad-scale (temporal and spatial) approach (Godley et al. 2007). Studies have revealed cross-oceanic migrations by a number of species such as loggerheads and leatherbacks (Hughes et al. 1998, Shillinger et al. 2008, Benson et al. 2011, Witt et al. 2011), as well as fidelity to foraging grounds over the course of years (e.g. Limpus et al. 1992, Limpus & Limpus 2001, Schofield et al. 2010, Shillinger et al. 2011), and fine-scale movements that can span national and international jurisdictions (Eckert 2002, Witt et al. 2008, Shillinger et al. 2010, Maxwell et al. 2011). The technology required to address research questions at a variety of spatial scales is increasingly available. However, the temporal scale is often constrained, particularly as sea turtles are long lived and some of the data gaps in the knowledge of younger life stages span several years (Hazel et al. 2009).

Because many turtles undertake long oceanic migrations, and traditional use of satellite telemetry addressed migration based questions, fine-scale studies using acoustic or radio tags have been less commonly used with sea turtles, although such approaches have been critical for identifying fine-scale foraging habitat and fisheries overlap (Taquet et al. 2006, Brooks et al. 2009, McClellan & Read 2009) and allowing recaptures of individuals for behavioral and physiological studies (e.g. Wibbels et al. 1990, Witt et al. 2010b). Again, advances in automated acoustic telemetry systems and acoustic tags, coupled with larger-scale, multi-species investment in acoustic arrays (e.g. the Australian Animal Tagging and Monitoring System; imos.org.au/aatams.html) address fine-scale habitat use by sub-adult and adult sea turtles.

Although the adult female bias is not as profound as in sea birds and marine mammals. satellite tags are rarely deployed on male or juvenile sea turtles (Godley et al. 2007), despite many juvenile age classes being large enough to carry equipment. This bias is likely due to a variety of reasons. Adult females are the demographic group most encountered as they emerge on land to nest; they are migratory and are highly important for the reproduction of the species. Moreover studies on sub-adult and/or adult male age classes generally require tags with higher accuracy, higher than traditional satellite tags could offer. In addition to the bias towards adult females, most of the studies to date investigate migration, while fewer studies address the behavior of inter-nesting turtles (Tucker et al. 1995, Zbinden et al. 2007, Tucker 2010). Identifying and remedying knowledge deficiencies is necessary in order to adequately protect populations at relevant spatial and temporal scales (Hays et al. 2001, Santidrián Tomillo et al. 2008, Hamann et al. 2010).

Sea turtle researchers have made advances in applying tracking data to understand population level movements and other management-relevant questions. For example, leatherback sea turtle researchers have conducted pan-oceanic syntheses, where multiple tagging datasets have been combined to understand movement patterns across populations in the Pacific Ocean (Bailey et al. 2012) and to investigate the efficacy of the global marine protected areas (MPA) system for green turtles (Scott et al. in press). Tracking data have been combined with genetic analyses and models of juvenile drift trajectories to unravel migratory connectivity in East Atlantic green turtles (Godley et al. 2010). Additionally, passive tags, biologging, and fisheries catch data have been combined to make a novel management tool, *Turtlewatch*, that predicts loggerhead turtle habitat in near real time to reduce interactions with fisheries (Howell et al. 2008). Novel uses and data integrations are critical for the adaptive management of these highly migratory and poorly understood species, and should become more feasible as synthetic data continue to be collected.

Marine mammals

Marine mammal studies are the least focused on multiple life stages, with only 6.0% of studies representing juvenile populations (Table 1). This is largely due to the logistical difficulties of tagging cetaceans and sirenians, obtaining permits, and developing tag designs with low enough drag to minimize its biological effect (Mate et al. 2007, McConnell et al. 2010). Passive tags and marking, however, have proven useful for all life history stages, particularly for pinnipeds. Their regular return to land provides a reliable location for resighting and recovery of tags. Branding and flipper tags have been used extensively (Bradshaw et al. 2000, McMahon et al. 2006) and have allowed estimates of age-specific survival (McMahon et al. 2003). The earliest passive tagging efforts on large cetaceans used numbered 'Discovery' tags deployed via harpoon that were eventually recovered during whaling harvest to reveal migration and population structure (see Mate et al. 2007). Since then, researchers have shifted to using unique markings on flukes, dorsal fins, and saddle coloration in photo-identification based mark-recapture studies (e.g. Wilson et al. 1999, Calambokidis et al. 2001) that identify individuals of multiple age classes (Jefferson et al. 1993). These photographs serve as the largest databases of individuals for many cetacean species. Although these passive tags have provided exceptional knowledge about population biology, including abundance estimates, social structure, reproductive success and long distance migrations, a detailed understanding of the movements of marine mammals cannot be gained from these techniques alone.

Active tagging has been used increasingly frequently for marine mammals since the 1980s and has provided a more detailed understanding of their movements across entire ocean basins (Mate et al. 2007). Ship and land based VHF tracking (Croll et al. 1998, Bjørge et al. 2002), and more recently short-term archival tags (Johnson & Tyack 2003), have been used in fine-scale behavioral studies, while satellite tags have provided broader-scale data on movement, distribution, and behavior of marine mammals (McConnell et al. 1999, Sheppard et al. 2006). At the finest scales, researchers have deduced individual foraging behavior using short-duration suction cup tags (Calambokidis et al. 2007, Hazen et al. 2009). Furthermore, suction cup tags with acoustic recorders have documented novel sound production in feeding whales that had not been previously detected (Stimpert et al. 2007). Due to their size, baleen whales have been outfitted with some of the largest tags and considerable improvements have been made since the earliest satellite tracking techniques (Mate et al. 2007). These approaches have revealed additional migratory routes and foraging habitat that cannot be detected by photo-identification techniques alone because animals often migrate through remote areas where there is little to no survey effort (Mate et al. 2007). Multi-sensor CTD data loggers measure conductivity, temperature and depth alongside a satellite-positioning transmitter (Hooker & Boyd 2003). These sensors have allowed a more complete understanding of the animal's environment at a scale corresponding to the animal's behavior. Furthermore, these individual ocean-observing systems can serve as sentinels for environmental change by measuring physical oceanography and habitat use across multiple years (Boehme et al. 2008, Costa et al. 2010b).

Although there have been many tagging studies of marine mammals, they have mainly targeted adults. The greatest number of tagging studies on juvenile marine mammals has involved pinnipeds. Effort has also been particularly targeted towards northern *Mirounga angustirostris* and southern elephant seals *M. leonina* and Steller sea lions *Eumetopias jubatus*. Elephant seals are among the largest pinnipeds and the current tracking devices do not appear to adversely affect their performance in terms of mass gain or survival probability over short (seasonal) or long (multi-year) temporal scales (McMahon et al. 2008). Studies have tended to focus on survival rates, diving and foraging behavior. For example, time-depth recorders on northern elephant seals have revealed that the level of dive performance increases with age and experience up to 2 yr of age, at which point their modal diving performance reaches that of an adult (Le Boeuf et al. 1996). The average depth, duration and frequency of dives made by Weddell seal *Leptonychotes weddellii* pups also increases rapidly in the period from birth to weaning, but slows soon thereafter, probably as a result of slower changes in mass and body composition (Burns 1999). Young seals tend to forage in shallower waters than adults and this is likely related to their diving ability (Campagna et al. 2007, Jeglinski et al. 2012). The foraging efficiency of younger seals is reduced relative to that of adults, owing to physiological and morphological constraints on aerobic dive duration, suggesting that low juvenile survival might result from behavioral constraints (Burns 1999).

Differences in the movements of juvenile pinnipeds have also been observed. Juvenile elephant seals migrate more slowly and less far than adults (Le Boeuf et al. 1996) — as has also been shown for Australian sea lions *Neophoca cinerea* (Fowler et al. 2007). In southern elephant seals, this results in significant differences in the total amount of the Southern Ocean covered by different age groups of the species (Field et al. 2005). On average younger seals make more trips to sea and do not travel as far on each trip. This leads to temporal and spatial segregation between animals of different ages, which would help to avoid intra-specific competition for resources on land, space on beaches, and at-sea foraging areas (Field et al. 2005). Spatial segregation in foraging areas between adults and juveniles has similarly been found in New Zealand fur seals *Arctocephalus forsteri* (Page et al. 2006). This is in contrast to studies on harbor seal *Phoca vitulina* and grey seal *Halichoerus grypus* movements that indicated that juveniles have larger home ranges and higher foraging effort than adults, which may suggest learning through experience (Lowry et al. 2000, Breed et al. 2011).

Steller sea lions are declining in numbers in most of Alaska and Russia (Loughlin et al. 2003), and reduced juvenile survival is believed to be a major contributing factor (Trites & Donnelly 2003, Raum-Suryan et al. 2004). Understanding the ontogenetic relationship between juvenile Steller sea lions and their foraging habitat is key to understanding their relationship to available prey and ultimately their survival. Loughlin et al. (2003) equipped young-of-the-year (YOY) and yearling Steller sea lions with satellite-linked time-depth recorders. The yearling sea lion movement patterns and dive characteristics suggested that immature Steller sea lions are capable of making the same types of movements as adults. Long-range trips (>15 km and >20 h) start at around 9 mo of age and occur most frequently around the assumed time of weaning. Trip distance and duration increase with age (Loughlin et al. 2003, Raum-Suryan et al. 2004). Horning & Mellish (2012) determined post-weaning juvenile survival and causes of mortality using data received post-mortem via satellite from implanted archival life history transmitters. These showed there is high post-weaning mortality by predation in the eastern Gulf of Alaska region, which may be the largest impediment to recovery in this area (Horning & Mellish 2012).

Very few tagging studies have been performed on juvenile cetaceans or sirenians. The small size of juvenile dolphins and porpoises increases the likelihood of biological impacts from tagging and the issue of hydrodynamic drag is a strong concern as attachment is usually on the dorsal fin. The small amount of work that has been done has mainly involved large whales, and in many cases it is the mother that has been tagged and inferences are then made about the movements of an accompanying calf. Resightings of tagged females with calves demonstrate that there is no apparent effect on the close association between mother and calf (Mate et al. 1997). For example, locations from satellite tagged southern right whale *Eubalaena australis* females with calves were grouped in specific areas along the coastline and corresponded to known concentration areas for mother-calf pairs. Tags on mother–calf pairs have a shorter tag life than in other classes, probably as a result of tag damage arising from the strong thigmotactic behavior shown by neonatal right whales towards their mothers (Best et al. 1993).

Studies on juvenile whales are less common due to permitting and tagging restrictions. Recent tags on both mother and calf humpback whales *Megaptera novaeangliae* have revealed new interactions including frequent synchronous foraging behavior (Tyson et al. 2012, this Theme Section). Belugas *Delphinapterus leucas* tagged as pairs of adults and young also showed correlations of dive behavior (Kingsley et al. 2001). A tagged humpback whale calf exhibited a higher surfacing rate than the adult whales (Lagerquist et al. 2008). It also showed a diel pattern with higher surfacing rates at night than during the day, which indicates it was nursing more at night. Satellite tagged juvenile and subadult (≤13 m) bowhead whales *Balaena mysticetus* in the Canadian Beaufort Sea mainly occurred over shallow water, and although they were tagged within a single week at one site they did not move in unison (Mate et al. 2000).

Tethered VHF and satellite tags have been used to provide knowledge to minimize the impacts of fishing bycatch, boat strikes and habitat loss on sirenians (Marsh et al. 2011). Satellite tracks of dugong *Du-*

gong dugon movements have provided the first evidence that all age-sex classes perform large-scale movements, including mothers with calves. Differences in movement rates of manatees *Trichechus manatus latirostris* were detected between the sexes, with significantly faster rates for males than for females with or without calves (Flamm et al. 2005). Very little is known about the spatial ecology and behavior of sirenians and this is an important area for future research. Tagging techniques can allow information to be obtained in remote areas and higher-resolution location data, such as GPS data, provide fine-scale information for examining risks and interactions with human activities.

Less invasive and short-duration archival tags (e.g. Johnson & Tyack 2003, Andrews et al. 2008) may be preferable to larger, longer-term tags. A recent review on the effects of marking and tagging techniques on marine mammals highlighted that few studies have investigated the effects of markers on reproduction or growth (Walker et al. 2012). This will continue to be an important issue to address if tags are to be applied more frequently to juveniles in the future.

Seabirds

Similar to passive tagging efforts with terrestrial birds, seabird tagging began using leg and flipper bands for mark-recapture studies, followed by radio telemetry studies (Hart & Hyrenbach 2009). These approaches have been used for adults and juveniles and have resulted in extensive understanding regarding population metrics, breeding ecology and to a lesser extent, the movements of birds whose tags have been resighted at sea (Ainley et al. 1994, Weimerskirch et al. 1997, Bonter & Bridge 2011). PIT tags have had limited use in seabirds, though they have been used to answer questions related to breeding ecology (Zangmeister et al. 2009). Advanced tracking techniques such as ARGOS and GPS tracking came later to seabirds than other taxonomic groups, due to small size and low weight requirements in order for tags to be feasible for flight, and consequently these have not been deployed extensively on juveniles (8.9% of studies were on juvenile birds; Table 1). Seabirds sizes range from <30 g to >12 kg and researchers usually restrict tags to 3 to 5% of the animal's body weight (though further consideration of energetic costs are strongly recommended; Vandenabeele et al. 2012). Most tag designs are still too large for a number of species, even their adult stages. Larger seabirds like procellariiforms (albatrosses and petrels) have juvenile stages large enough to be studied; however only a handful of studies exist. This is likely because juveniles experience high tag loss, and also because researchers are concerned about stressing juvenile animals. Still, seabirds can be reliably found on their breeding colonies, making the tracking logistically simpler than with other taxonomic groups, and also allowing tags to be recovered when birds return to the colony (Burger & Shaffer 2008).

Three recent reviews of seabird ecology discussed the miniaturization of tags and the increase in remotely sensed oceanographic products as 2 major forces driving the field of seabird ecology (Burger & Shaffer 2008, Tremblay et al. 2009, Wakefield et al. 2009). GPS tags have been used more extensively for seabirds than other diving animals because much of their at-sea behavior is above the surface. Moreover these tags are small (<20 g) and can be recovered at breeding colonies (Burger & Shaffer 2008). Innovative biologging technologies are also being applied, such as heartbeat sensors and beak-mounted magnetic sensors, which are being used to further our understanding of locomotion, foraging costs and ingestion events (Weimerskirch et al. 2000, Wilson et al. 2002); and 'daily tags', initially applied to penguins, that record movement, behavior, energy expenditure and environmental characteristics to understand the full suite of what animals encounter (Wilson et al. 2008).

A seminal study using satellite tracking discovered novel patterns in migration and behavior of the wandering albatross *Diomedea exulans*, the largest of the seabirds, giving the first metrics for long-range movements of an animal moving sometimes over 900 km d^{-1} (Jouventin & Weimerskirch 1990). As smaller tags have been developed, more seabird species have been tracked, providing a suite of knowledge about migrations, spatial foraging strategies, diving patterns, and variability across years, breeding status, and sexes, and overall revealing the global use of the oceans by seabirds (see Burger & Shaffer 2008). A number of studies have applied active tags, including GPS, ARGOS and radio-tracking to provide insights into the movements of juvenile penguins, cormorants, albatrosses, boobies, murrelets, and gannets. These studies have shown differences between juvenile and adult movement patterns. A study by Ismar et al. (2010) showed that migratory routes previously unknown for Australasian gannets *Morus serrator* were undertaken by fledglings of this species. Using a combination of GPS, radio-tracking and stable isotopes, Votier et al. (2011) found that northern gannets *M. bassanus* undertake long migrations where they potentially visit non-natal breeding sites. Tracking of pelagic cormorants *Phalacrocorax pelagicus* using ARGOS transmitters in Alaska revealed that while adults return to foraging grounds within approximately 7 mo, juveniles remain on the wintering grounds for over a year, and also tend to remain within localized wintering grounds for longer stretches than adults (Hatch et al. 2011). Several studies on fledgling emperor penguins *Aptenodytes forsteri* have revealed vastly different movements from those found in adults; fledglings move further, and are not associated with sea ice at all, in contrast with adults who forage and breed in close association with the ice edge year round (Kooyman & Ponganis 2007, Wienecke et al. 2010). In contrast, a series of studies on Adélie penguins *Pygoscelis adeliae* showed that fledgling and post-breeding penguins follow similar routes along the ice edge with fledglings having a short 'exploratory' phase at the beginning of their migration (Kooyman et al. 1996, Clarke et al. 2003). One series of studies (Yoda et al. 2004, 2007, Kohno & Yoda 2011) integrated biologging with hand-rearing of brown booby *Sula leucogaster* chicks to understand ontogenetic shifts underlying the long post-fledgling care period in this species.

Seabird biologists have been more prolific in applying tracking to conservation and management questions, particularly fishery bycatch, than other groups. For example, a large-scale, multi-investigator study coordinated by BirdLife International (2004) looked at the distribution of procellariiforms obtained from biologging studies and their overlap with pelagic longline fisheries in the southern hemisphere. This study has been used to increase spatial management and bycatch mitigation techniques throughout the region. A more recent study integrated dynamic habitat models from remotely sensed data and tag-derived tracks for albatrosses, analyzing overlap with fishery effort to assess bycatch risk (Zydelis et al. 2011). Several researchers have also applied study results to management issues relevant to juvenile seabirds, providing new strategies for managing seabird populations. In the Southern Ocean, both fledgling and adult breeding movements of southern and northern giant petrels *Macronectes giganteus* and *M. halli* were examined using ARGOS transmitters, revealing that fledglings move vast distances and overlap more with fisheries than breeding adults, highlighting the need for management strategies that had not been previously considered (Trebilco et al. 2008). Similarly, wandering albatrosses *Diomedea exulans* tracked using ARGOS transmitters in the Indian Ocean forage in areas spatially segregated from breeding adults, but show extensive overlap with longline fishing (Weimerskirch et al. 2006). In a related study, it was shown that juveniles use these areas for several years until reaching breeding age, likely returning to these same areas during non-breeding portions of the year (Akesson & Weimerskirch 2005). These conservation applications of biologging data reap additional benefits over ecological knowledge alone (BirdLife International 2004, Burger & Shaffer 2008).

Despite these studies, some obvious gaps in our understanding of seabird ecology exist. A recent review by Lewison et al. (2012) identified 6 key elements of seabird ecology in need of additional research, particularly across multiple age classes. Many of these can be directly addressed using satellite tracking, particularly gaps in knowledge of at-sea distribution and of environmental drivers determining key foraging grounds. Further study is also required to determine the impacts of fisheries and other anthropogenic stressors in concert with the level of protection provided by marine protected areas. While the studies previously referred to provide a preliminary understanding of changes in the movements of juveniles, there is still insufficient understanding of ecology across age classes to comprehensively manage seabird populations.

DISCUSSION AND CONCLUSIONS

Tagging studies have the unique ability to identify individual-level variability in behavioral data (e.g. Schaefer et al. 2007), previously unidentified habitat (Mate et al. 2007), and ecological linkages at multiple life history stages. To date, tagging efforts have focused on the mature life stages, i.e. on individuals that can carry larger tags and have lower mortality, which has resulted in a gap of studies on less-accessible juvenile and larval life stages. In the literature, we found that marine fish and turtle studies had far greater percentages of tagging studies focused on juvenile life stages (>20%) compared to seabirds and mammals (<10%) (Table 1). Differential life history strategies may in part be responsible for this difference in emphasis. Intra-annual life history stages have different physiological requirements, which may result in different critical habitat and exposure to risks (e.g. breeding versus migration versus foraging; Kenney et al. 2001, Kappes et al. 2010). The literature searches did not examine species-specific patterns in tagging studies, but previous review papers have shown unequal effort across species that is perhaps due to differences in ease of capture for tagging or access to research funding (e.g. Godley et al. 2007).

In order to better understand the biology of marine organisms, one of the next steps will be to increase the diversity of tagging effort, across life history stages, sexes, and species, particularly to inform conservation and management (Maxwell et al. 2011). The majority of large marine taxa are either species of conservation concern, or are critical components of the ecosystem in which they reside. A number of tracking studies have been used to inform management and conservation, particularly to site marine protected areas, reduce bycatch, and to employ other spatial management measures (Grémillet et al. 2000, Chilvers et al. 2005, Boersma et al. 2007, Howell et al. 2008, Shillinger et al. 2008, Zydelis et al. 2011, Hart et al. 2012, Scott et al. in press). It is critical to have a holistic understanding of the distribution of a population in order to effectively protect the entire population, and to not employ management strategies that might have unintended consequences (e.g. shifting of fishing effort to areas of unknown high abundance; Baum et al. 2003).

We identified the following 4 research themes in the introduction, (1) population demography and recruit mortality, (2) critical juvenile habitat and threat overlap, (3) dispersal and population connectivity, and (4) foraging ecology. Table 2 assesses the relative research effort among the themes by taxonomic group. These themes were also identified as research priorities for both seabirds and turtles in recent reviews (Hamann et al. 2010, Lewison et al. 2012). We found that tag-based studies for all 4 groups adequately adressed population structure, mortality, and habitat of juveniles, while questions of dispersal, population connectivity and structure, and foraging ecology were less explored using tag-based methods (Table 2). Furthermore, we found very few tag-based studies that explicitly examined the overlap between juvenile habitat and anthropogenic threats, so we excluded that category from our analyses. Similar to the taxonomic breakdown in Table 1, marine mammals (especially cetaceans and sirenians) and seabirds had the most gaps in juvenile tag-based ecological studies, although sea turtles were not far behind (Table 2). More advanced tags were most useful in answering questions in the categories 'habitat' and 'foraging ecology', although this pattern was not identical across taxonomic groups. Moreover, we found examples of the use of passive tags combined with molecular techniques to answer more complicated ecological questions (e.g. Friesen et al. 2007).

In mark-recapture studies, passive tags are still one of the primary tools used to answer questions about mortality and recruitment, i.e. spaghetti and PIT tags in juvenile fish (Pine et al. 2003), bands for pinnipeds, seabirds, and turtles (Schaub & Pradel 2004, Robinson et al. 2010), and photo-ID catalogs for marine mammals (Hammond 2002). Alternative approaches such as archival tagging paired with genetic techniques have been used to delineate Atlantic bluefin tuna *Thunnus thynnus* stocks, measure migration rates, and estimate mortality (Taylor et al. 2011), building upon the classic mark-recapture technique. Acoustic or archival tags also can be used to measure mortality in a number of these species, but it can be difficult to differentiate between tag failure and mortality (Townsend et al. 2006). Studies of seabirds, turtles and mammals were less likely to use radio or acoustic tags to assess mortality rates compared to fish, perhaps in part due to central place foragers being more easily assessed upon return to land. The effort devoted to assessing dispersal and connectivity was greatest in fish, at least in part due to the longer history of fish tagging studies. Due to the wide-ranging nature of and difficulty in tag attachment for many top predators, molecular and genetic techniques have been more widely used to examine their dispersal and population connectivity (e.g. Thorrold et al. 2002, Amaral et al. 2012). Acoustic and radio tags have been used in concert with portable receiving stations and visual observation to both calculate use metrics for habitat and measure foraging behavior for both turtles and fish species (Cooke et al. 2004, Ropert-Coudert & Wilson 2005, Myers & Hays 2006). Measurements of energetic costs and foraging behavior have been made possible with advanced technologies such as magnetic sensors to identify foraging events in seabirds (Cooke et al. 2004), internal temperature and heart rate loggers in fish and pinnipeds (Andrews 1998, Block 2005), and accelerometer tags in cetaceans (Goldbogen et al. 2011). These advanced techniques have been infrequently applied to juveniles because of tag-size limitations, but bird researchers have been grappling with this issue for some time due to the lower weight of most seabirds, and the other groups could learn from their efforts (e.g. Mansfield et al. 2012, this Theme Section).

Data gaps are common in marine science, as funding opportunities and research topics can be ephemeral. Technological challenges have limited our ability to use tags to study juvenile life stages, but these challenges are being overcome as tags continually become lighter, have increased battery life, and more sensors on-board. Cell phone tags use off-the-shelf products to increase data accessibility and transmission using existing cellular networks (McConnell et al. 2004). Other off-the-shelf products, such as GPS tags originally designed for human recreational activities, are a cost-effective means of tracking seabirds (M. Conners and S. Shaffer, pers. comm.). Oceanographic sensors can turn animals into measurement platforms providing ocean data (Hooker & Boyd 2003, Block 2005). Also, tag miniaturization efforts have allowed novel tagging studies including the tagging of younger life history stages, such as with juvenile loggerhead turtles. Mansfield et al. (2012) have, for the first time, shown novel migration pathways in neonate marine turtles, with some individuals tracking the Gulf Stream and others heading east into the North Atlantic Gyre.

Significant effort has been made to understand the ethical implications of tagging, both in considering the effects on individuals and populations and in defining the goals of tagging studies. There has been much debate in the field of tagging about the negative effects on fitness of specific tag types across taxonomic groups. In seabirds, penguin banding led to decreased breeding success in poor resource years leading to potential spurious interpretations (Saraux et al. 2011). For marine mammals, hot branding for pinnipeds and implantable satellite tags may not cause long-term physiological harm (Merrick et al. 1996, Mate et al. 2007, McMahon et al. 2008), but behavioral effects of such tagging methods have not been well documented (Walker et al. 2010). For turtle species, harness-based satellite tags used largely on leatherback turtles have recently been identified as increasing drag and chafing and alternative attachment methods are now available (Jones et al. 2011, Witt et al. 2011). Mrosovsky (1983) termed the interest in continuing to deploy tags without a clear scientific question or without a given end goal in mind the 'tagging reflex'. Researchers should determine whether enough is known about a species or population before tagging studies begin, otherwise tagging without specific goals may have deleterious population effects that could outweigh the potential knowledge gained. Because scientific questions and ethical considerations drive tag deployments, especially with regard to smaller animals and early life stages, it is important to document and minimize the effect of tagging and to ensure that deployments are only used when necessary to further our knowledge and conservation of the study species.

One of the weaknesses of active tag data is that only a small number of animals tend to be tracked, which generally represents a small proportion of the population. Findings can be scaled up by including complementary forensic methods such as stable isotope tracking (Zbinden et al. 2011). Another approach is represented by interspecific, broad-scale tagging efforts such as the Tagging of Pacific Predators project, which has created a rare and valuable dataset (Block et al. 2011). The Pacific Ocean Salmon Tracking project has adopted a similar broad-scale approach, linking acoustic tagging efforts on the west coast with a series of arrays, thereby allowing nearshore detections of many acoustically tagged individuals as part of the Census of Marine Life (Welch et al. 2002). Synthetic collaboration across multiple datasets can be equally informative, such as BirdLife's Procellariform Database that has aided meta-analyses and informed management objectives on seabirds throughout the world (BirdLife International 2004). Data repositories such as OBIS-SEAMAP (Halpin et al. 2006) or the Satellite Tracking Analysis Tool (Coyne & Godley 2005) serve an equally valuable role in amalgamating data, assessing data gaps and allowing meta-analyses of multiple tagging datasets. These large databases and synthetic research programs provide needed baselines for marine populations that are difficult to study, and cover sufficiently broad scales to allow the examination of long-term processes such as climatic change. With increased collaboration and ongoing diversification of methods and approaches, we can use marking and tagging to continue to answer ecological questions and to adaptively manage marine ecosystems.

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Contribution to the Theme Section: 'Tagging through the stages: ontogeny in biologging'

Biologging to examine multiple life stages of an estuarine-dependent fish

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ABSTRACT: To better understand habitat use through ontogeny, this paper synthesizes 7 yr of biologging research on the adult and juvenile life stages of an estuarine-dependent fish, the common snook *Centropomus undecimalis* in Charlotte Harbor, Florida, USA. During 3 yr of telemetry research in a putative nursery habitat (mangrove creeks), we resighted 85.4% of 1924 juvenile snook marked after, and 13.5% of 2191 juveniles marked prior to, deployment of a telemetry array. During 4 yr of research in spawning habitat (barrier island beaches), we used seine nets and recaptured 5.63% of 3304 marked adult snook. After analyzing these concurrent data sets, we found significant intra- and interannual site fidelity patterns in both life stages, while documenting movement between juvenile and adult spawning habitats. Additionally, this tag-based approach allowed an investigation of the relative effects of a severe cold event, which reduced apparent survival by 22.6 to 38.3% for juveniles and 97.8 to 98.5% for adults. This work presents data within and between life stages that are critical to understanding processes affecting ontogenetic habitat use and connectivity and underscores the importance of incorporating within-stage fidelity and emigration in studies on ontogeny.

KEY WORDS: *Centropomus undecimalis* · Nursery habitat · Spawning habitat · Connectivity · Site fidelity · Emigration · Survival estimation · Disturbance · Metapopulation · Passive integrated transponder · PIT

INTRODUCTION

The life history of many marine fishes is a 3-phase cycle, whereby adults, larvae, and juvenile life stages have different biological requirements and in many cases utilize different habitats. For fishes that use different habitats for each life phase, this 3-phase life cycle decouples reproduction from recruitment of new individuals into the local population. This is especially true for fish taxa with larvae that settle into benthic habitats that are distinct from those of adults (Shulman & Ogden 1987, Eggleston 1995, Peters et al. 1998, Herzka et al. 2002, Shenker et al. 2002), creating 2 stages within the demersal phase of life history. Examination of the processes affecting each of these life stages, and the connections between life stages, is essential to developing a better understanding of ontogenetic habitat requirements of fishes.

The spatial separation between juvenile nursery habitats and adult spawning habitats is well documented for many marine fish (e.g. northern red snapper *Lutjanus campechanus*, Cowan et al. 2010; Nassau grouper *Epinephelus striatus*, Eggleston 1995, Grover et al. 1998, Bolden 2000; common snook *Centropomus undecimalis*, Adams et al. 2006a, 2009). However, despite such documentation of specific habitats used throughout ontogeny, it remains un-

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known to what degree behavioral use differs among these habitats and life stages for most species. Due to recent advances in biologging technology, we are now able to effectively study multiple ontogenetic habitats and life stages to better understand habitat use patterns, which is critical to developing a more complete picture of fish ontogeny. This information allows a better understanding of the processes that structure fish populations.

In this paper, we synthesized 7 yr of biologging research on an estuarine-dependent fish, the common snook, to highlight patterns in habitat use of juveniles in nursery habitat and adults in spawning habitat. We report new information on habitat use of juvenile snook in nursery habitat, summarize and expand upon results of a previous study on fidelity of adult snook to spawning grounds, document habitat overlap between the 2 life stages, and quantify the effects of a severe cold event (disturbance) on both life stages.

MATERIALS AND METHODS

Study area

Charlotte Harbor is a 700 km^2 coastal plain estuarine system in subtropical, southwest Florida, USA (Fig. 1; Hammett 1990). Seagrass flats (262 km^2, Sargent et al. 1995) and mangrove shorelines (143 km^2, L. Kish unpubl. data) are the dominant habitats within the estuary. Three rivers, as well as numerous creeks throughout the drainage, transport large amounts of fresh water into the harbor. The estuary is separated from the Gulf of Mexico by a string of barrier islands, with tidal exchange through 5 inlets that separate these islands (Fig. 1). The gulf-side shorelines of the islands are comprised entirely of sandy beaches. The inlets are a mixture of natural sand and anthropogenically hardened shorelines.

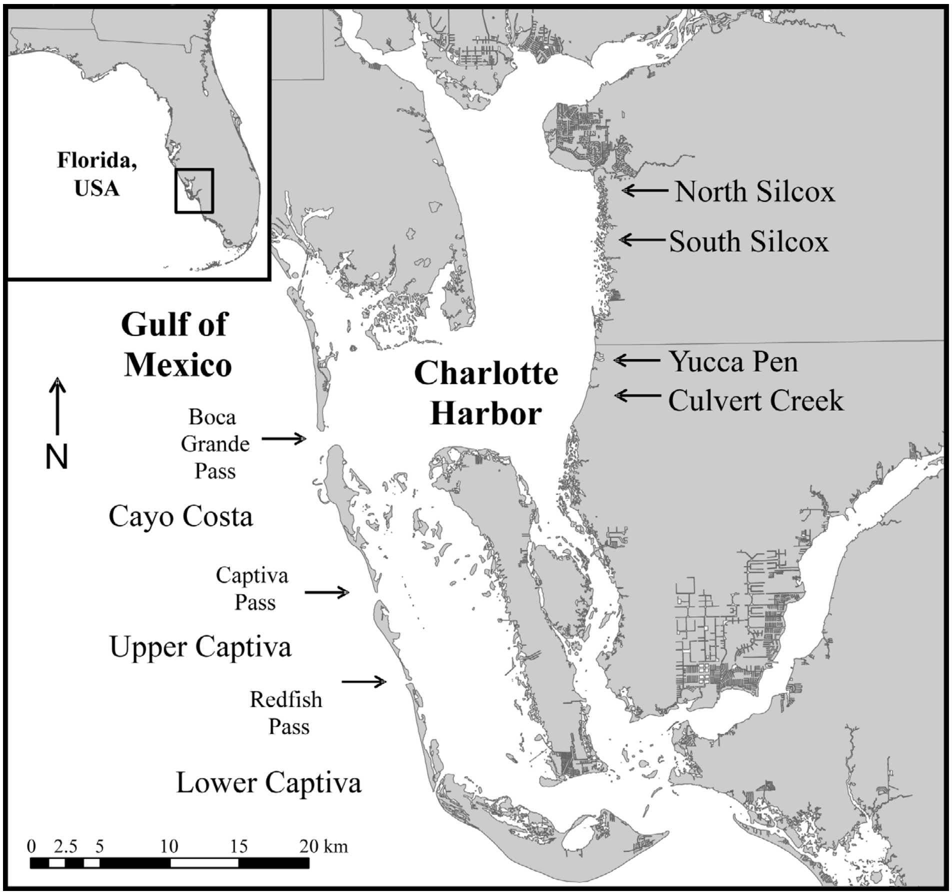

Fig. 1. Southwest Florida, USA. Capture–recapture in spawning adult common snook *Centropomus undecimalis* habitat occurred along barrier island beaches from the northern end of Cayo Costa (Boca Grande Pass) to the southern end of Lower Captiva (Blind Pass). Capture–resighting in juvenile common snook habitat occurred in 4 mangrove creeks (North Silcox to Culvert Creek) on Charlotte Harbor's eastern shoreline

Focal species

The common snook (hereafter referred to as 'snook') is a tropical and subtropical, estuarine-dependent, euryhaline species. Insufficient information exists on life history linkages, but enough is known to allow targeted effort at specific ontogenetic stages. Snook are protandrous hermaphrodites (Muller & Taylor 2006) that congregate in high-salinity environments to broadcast spawn during summer (Chapman et al. 1978, Peters et al. 1998). Typical spawning grounds are passes that connect estuaries and ocean waters, beaches, and perhaps offshore reefs (Taylor et al. 1998, Adams et al. 2011).

Following spawning, the planktonic larval stage lasts ~2 wk (Peters et al. 1998). In Charlotte Harbor, Florida, post-settlement snook (<20 mm standard length, SL) are first captured in tidal mangrove creeks in mid-June (A.J. Adams unpubl. data). Juveniles reach or exceed 150 to 180 mm by age-1, and remain abundant in or near creek habitats year-round until ~300 mm (age-2; Taylor et al. 2000, Stevens et al. 2007), when they enter the adult population. Adults use open estuarine and nearshore habitats from spring through fall, and can overwinter in riverine or creek habitats (Blewett et al. 2009) where they cannibalize juveniles (Adams & Wolfe 2006). Snook in Florida can live for >20 yr, but 1 to 7 yr olds are most common (Taylor et al. 2000).

Juvenile habitat

From June 2004 through April 2011, we studied juvenile snook in 4 red mangrove *Rhizophora mangle*-fringed, tidal, estuarine creeks, each ~1.6 km long, on the eastern shoreline of Charlotte Harbor (Fig. 1). The study creeks varied in width from 2 to 10 m in narrow passes to >60 m in wider bays. Depths were shallow with maximum depth ranging from 0.5 to 2.5 m in narrow passes and from <0.5 to 1.0 m in bays. Approximately 0.75 km of flooded mangroves separated the mouths of the 2 northern creeks (South Silcox and North Silcox) from Charlotte Harbor. The 2 southern creeks (Yucca Pen and Culvert Creek) drained directly into Charlotte Harbor, and the creek mouths were separated by 1.4 km of mangrove shoreline. The northern and southern creeks were separated by 10 to 12 km of mangrove shoreline (Fig. 1).

We primarily captured juveniles (<320 mm SL, McMichael et al. 1989, Stevens et al. 2007) with a center bag seine net (30.5 × 1.8 m, 6.3 mm mesh), but occasionally used a smaller seine (21 × 1.2 m, 3.1 mm mesh) or hook and line. Peak sampling months were October through April following summer spawning (Peters et al. 1998, Taylor et al. 1998). After capture, we scanned all fish with a handheld passive integrated transponder (PIT) tag reader (Allflex® model no. RS601), documented recaptures, and measured SL to the nearest millimeter. We marked juvenile snook >120 mm and <320 mm SL with uniquely coded half-duplex (HDX) PIT tags (23 mm length × 3.4 mm diameter, 0.6 g in air; TIRFID S-2000, Texas Instruments). Snook >120 mm SL showed 100% tag retention with no mortality (Adams et al. 2006a), and snook >320 mm SL were no longer considered juveniles (McMichael et al. 1989, Stevens et al. 2007). We inserted PIT tags into the abdominal cavity of unmarked fish through a 3 mm incision posterior and ventral to the pectoral fin. Since the reading unit powers the tag, the resulting lifespan of the tag exceeds that of the study subject.

Autonomous antennae

We resighted marked snook with autonomous PIT tag antennae. From 2004 through November 2008, we evaluated the efficacy of this approach with 2 antennae (Adams et al. 2006a). From June to November 2008, 9 additional antennae were constructed, resulting in antenna placement in the lower, middle, and upper strata of each of the 4 creeks with the exception of Yucca Pen upper (due to antenna failure and financial constraints; Barbour et al. 2011). Antennae functioned continuously and resighted snook (fish were not physically recaptured) as marked individuals swam past an antenna. We fully described antennae methodology elsewhere (Adams et al. 2006a, Barbour et al. 2011, 2012).

Juvenile habitat use

We marked juvenile snook from June 2004 to January 2011. We defined 'marking years' as starting in or after October, and ending in or before August, due to summer spawning (most marking years began in November and ended in April). We analyzed 3 aspects of juvenile habitat use during the 3 marking years following antennae deployment (November 2008 to April 2011): home range size, intra-annual emigration, and inter-annual site fidelity.

We quantified home range size (Kramer & Chapman 1999) by using resighting by multiple antennae as a proxy for movement. We limited this analysis to movement within an individual's marking year. Since we placed antennae approximately every 0.5 km, resighting an individual snook by 2 antennae represented a minimum movement of 0.5 km.

We quantified intra-annual emigration as occurring any time an individual was detected outside its marking creek during its marking year. We identified all emigrants as either temporary (emigrants that subsequently returned to their original creek) or permanent (emigrants that did not return).

We examined inter-annual site fidelity by quantifying the number of juveniles resighted inside versus outside their marking creek in the year after marking. A chi-squared contingency test was used to test whether emigration rate varied by creek and year. Due to a large juvenile home range size, we next examined fidelity to creek pairs (North and South Silcox versus Yucca Pen and Culvert Creek) with Fisher's Exact test (due to the high incidence of expected values <5).

Adult spawning habitat

We conducted mark–recapture of adult snook on Gulf of Mexico barrier islands during 4 spawning seasons (typically May through September) from May 2007 to August 2010 (Adams et al. 2009, 2011). We sampled adults with 3 seine nets (91.4 × 2.4 m, 19.1 mm mesh; 182.9 × 2.4 m, 15.0 mm mesh; 152.4 × 2.4 m, 19.1 mm mesh) along beaches of 3 islands: Cayo Costa (12.4 km long), Upper Captiva (6.8 km), and Lower Captiva (8.9 km; Fig. 1; see Adams et al. 2009). We scanned all snook for PIT tags after capture and marked adult snook with 23 mm PIT tags (e.g. Boucek & Adams 2011), recording length and position (latitude and longitude) for each fish.

To determine spatial distribution of adult snook on each island, we plotted the locations of all snook (marked and recaptured) per 200 m of linear shoreline with ESRI ArcGIS. We then calculated the shortest shoreline distance between each mark and recapture position to investigate 3 aspects of movement and spawning area site fidelity. (1) To determine whether movement differed by island, distances (m) between mark and recapture were pooled across years by island, square-root transformed, and analyzed with a 1-way analysis of variance supported by a Tukey post hoc test. (2) We determined whether movement differed based on whether fish were recaptured in their marking year or in subsequent years. (3) Distance data for fish recaptured more than once were examined with a paired *t*-test (with Bonferroni adjusted probability of 0.05) to determine whether recapture distance differed during subsequent recaptures.

Habitat linkages

Since we marked juveniles and adults with PIT tags, we were able to examine recapture and resighting data to measure exchange between juvenile and adult habitats. We used PIT tag antennae to resight adults (marked from May 2007 to August 2010) that moved into juvenile habitat, and we used seine nets to recapture juveniles (marked from June 2004 to February 2010) that moved to summer spawning grounds.

Severe cold event

On 2 January 2010, a severe cold front created abnormally cold conditions for 13 d. Charlotte Harbor water temperatures dropped from 18°C on 1 January to 12°C by 6 January, and remained <12°C through 16 January, well below the average winter water temperature of 21°C for the estuary and below the lethal thermal threshold of common snook (12.5°C, Shafland & Foote 1983) for at least 10 d (Adams et al. 2012).

We estimated monthly apparent survival of juveniles (ϕ = 1 − mortality + emigration) from October through April for 3 marking years (2008–09, 2009–10, and 2010–11). For each year, we collapsed antennae resightings into monthly bins, with marked fish classified as '1' if resighted and '0' if not. We allowed ϕ and capture probability to be time-dependent with respect to month and marking year. For adults, we combined marking (seine netting) and recapture (seine netting and recreational angling) information from spawning grounds. Capture histories were constructed on a yearly basis (2007, 2008, 2009, 2010), with fish being assigned a '1' in spawning seasons (May through September) during which they were marked or recaptured, and a '0' in seasons they were not seen. Capture probability was kept constant, as the same sampling methods were used each year, and ϕ was allowed to vary between spawning seasons. We estimated ϕ with the Cormack-Jolly-Seber survival model in Program MARK (White & Burnham 1999, Adams et al. 2006a) for both juveniles and adults.

RESULTS

Juvenile habitat

We marked 2191 juveniles between June 2004 and October 2008 (prior to deployment of the antennae array) and 1924 between November 2008 and January 2011. Snook <320 mm SL dominated catches, and catches consisted of 2 approximated size classes (SC) (Fig. 2, SC1: 120–200 mm SL and SC2: 201–320 mm SL). The 11 autonomous PIT tag antennae logged 536 279 total resightings of 2087 uniquely marked snook (adults and juveniles) from November 2008 to April 2011.

Home range size. Home range size increased with increasing body size (Table 1). Overall, a majority (63.1%) of the 1924 juveniles marked since November 2008 crossed at least 2 antennae, and 28.2% crossed at least 3 within their marking year (Table 1). Thus, a minimum estimate of juvenile snook home range size (distance moved) is 0.5 km. Additionally, 8.7% of juveniles crossed at least 4 antennae, the fourth located in another creek, indicating that a substantial portion of marked juveniles traveled >1.0 km.

Intra-annual site fidelity. Emigration increased with fish size: an equal number of snook in both size classes emigrated from the creek in which they were tagged (177 SC1 and 186 SC2) despite marking 40% more SC1 snook (Fig. 2). In total, 19.8% of 1924 juveniles emigrated, with similar levels of temporary (40%) and permanent (60%) emigration. Similarly to home range size, these are conservative estimates since antennae functioned in a spatially limited region.

Inter-annual site fidelity. When examined by creek, there was no evidence for inter-annual fidelity ($p = 0.1693$; df = 4; $\chi^2 = 3.64$; Table 2a). However, significant evidence existed when using paired creeks to account for home range size (Fisher's Exact test: $p = 0.0036$; Table 2b). Thus, inter-annual site fidelity occurs on a scale similar to that of the juvenile home range, with snook preferentially returning to their juvenile habitats.

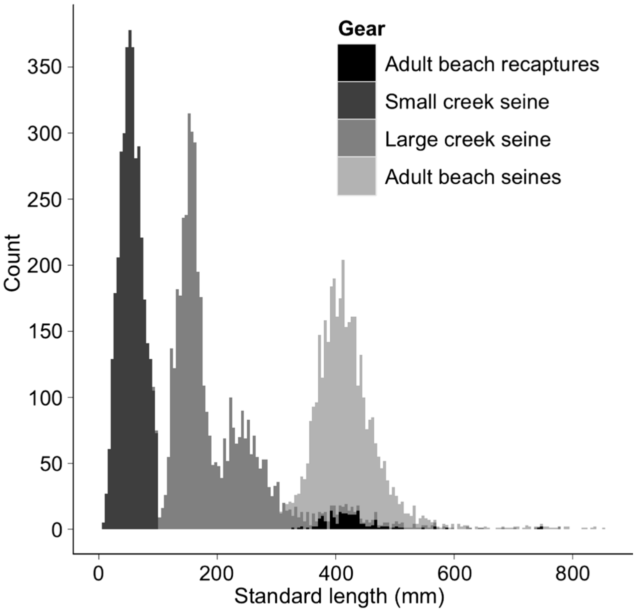

Fig. 2. *Centropomus undecimalis.* Standard lengths (mm) of all common snook captured during this study in Charlotte Harbor, Florida, USA. Snook caught using a small-mesh (n = 3715) and large-mesh (n = 4370) center bag seine in juvenile habitat (mangrove creeks), or 3 large center bag seines in spawning habitat (barrier island beaches: n = 3316). Marked juvenile snook were captured with the large creek seine

Table 1. *Centropomus undecimalis.* Number and percent of juvenile snook marked from November 2008 to January 2011 (1425 size class 1 [SC 1] and 499 SC2) and resighted from November 2008 to April 2011, that were resighted by at least the given number of antennae. For this analysis we limited resightings to instances within an individual's marking year (October through August). Antennae were placed approximately every 0.5 km in each creek, so resighting by 2 antennae represents a minimum movement of 0.5 km

No. of antennae	Number SC1	%	Number SC2	%
2	836	58.7	379	80.0
3	321	22.5	222	44.5
4	83	5.8	84	16.8
5	39	2.7	48	9.6
6	3	0.2	5	1.0
7	0	0.0	2	0.4

Adult habitat

During this study, we marked 3304 adults in spawning habitat (Fig. 2). Although sampling effort was similar on all islands, more snook were marked on Cayo Costa than Upper or Lower Captiva. In total, 186 recaptures were made during the study (5.63%), and sizes of marked and recaptured fish were similar (Fig. 2). Of the 186 total recaptures, 171 were from fish recaptured once and 11 were from fish recaptured multiple times.

Snook capture locations revealed clumped distributions, indicating propensity of snook to aggregate at particular locations (Fig. 4 in Adams et al. 2011). Over the 4 yr study, 166 of the 171 unique recaptures (97.08%) occurred on the same island where they were marked, supporting a pattern of spawning loca-

Table 2. *Centropomus undecimalis.* Quantitative description of inter-annual site fidelity by juvenile snook marked in 4 mangrove creeks. Table shows the marking year (1 = October 2007 to July 2008; 2 = November 2008 to April 2009; 3 = November 2009 to February 2010). Total number of antennae resightings of uniquely marked individuals in the subsequent years were (1) 20 617, (2) 22 632, (3) 11 348. Numbers of resightings of unique individuals were grouped by (a) creek or (b) north vs. south region

Parameter	Marking year		
	1	2	3
(a) By marking creek			
Fish marked	315	851	594
Fish resighted			
Inside creek	32	65	35
Outside of creek	6	14	11
Inside and outside of creek	31	31	28
(b) By marking region (north vs. south)			
Inside region	67	109	65
Outside of region	1	1	7
Inside and outside of region	1	0	2

tion site fidelity. Of the recaptures, 107 occurred in the same year as marking, and 79 occurred 1 or 2 yr after marking. Four of the 5 snook recaptured on a different island were originally marked on Upper Captiva, the shortest barrier island, as well as the middle of the 3 islands (Fig. 1).

Distance between mark and recapture locations differed by island (ANOVA $p < 0.01$, df = 170, F = 6.993): mean ± SE = 1773.7 ± 161.0 m for Cayo Costa; 871.9 ± 75.3 m for Upper Captiva; and 1377.6 ± 334.5 m for Lower Captiva, suggesting that home range size of adults on spawning grounds was <2 km. Distance between mark and recapture locations did not depend upon fish being recaptured in their marking year or in subsequent years (Fig. 2a in Adams et al. 2011). However, fish recaptured twice were recaptured at a greater distance from the marking location at the second recapture ($t = -3.558$, Bonferroni adjusted $p < 0.05$, df = 10).

Habitat linkages

Of 3642 juveniles marked before cessation of spawning habitat sampling, we recaptured 4 (0.1%) on gulf shoreline beaches as adults. Each fish was recaptured once, with a mean of 838 d and a range of 461 to 1207 d between marking and recapture. We recaptured 3 fish on Cayo Costa and 1 fish on Upper Captiva. Two fish were marked in Culvert Creek, 1 in South Silcox, and 1 in North Silcox.

Similarly, of 3304 adult snook marked on Gulf of Mexico beaches, antennae in mangrove creeks detected 5 (0.15%) in the juvenile study creeks. Four were marked on Cayo Costa and 1 on Upper Captiva. Resightings of adults in the juvenile study creeks primarily occurred between October and April, but 1 individual was also resighted during summer. Two adults were detected only in South Silcox, 1 in Culvert Creek, and 1 in Yucca Pen. These 4 fish were resighted for 1 d only. The fifth fish was detected in all 4 creeks, and these resightings occurred over the course of a year.

Severe cold event

Juveniles. The Cormack-Jolly-Seber maximum likelihood estimate for apparent survival (ϕ) during the January 2010 cold event was 0.55, which was 22.6 to 38.3% lower than other monthly maximum likelihood estimates during the 3 yr of survival analysis (minimum = 0.71, maximum = 0.89; Fig. 3). Additionally, when examining 95% confidence intervals, ϕ during the cold event was significantly lower than every other monthly estimate.

Adults. The cold event did not influence patterns of site fidelity by adult snook on spawning grounds. However, ϕ after the cold event was sig-

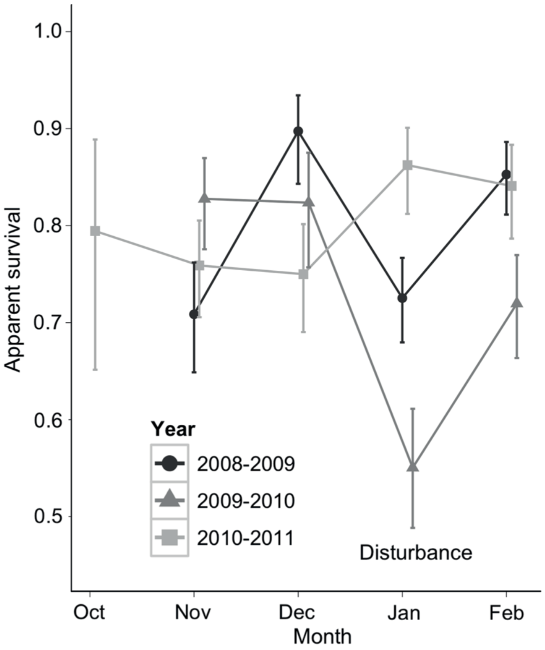

Fig. 3. *Centropomus undecimalis.* Monthly Cormack-Jolly-Seber apparent survival estimates (with 95% CI) from 3 yr of capture–resighting data in juvenile common snook habitat (mangrove creeks)

Table 3. *Centropomus undecimalis.* Total numbers of common snook captured during January through June of each year by the Florida Fish and Wildlife Conservation Commission Fisheries Independent Monitoring program for 4 estuaries

Year	Tampa Bay	Charlotte Harbor	North Indian River Lagoon	South Indian River Lagoon
2008	639	223	190	341
2009	347	123	144	449
2010	90	28	30	154

nificantly lower than before. Apparent survival estimates were 0.45 between the 2007 and 2008 spawning seasons, and 0.65 between 2008 and 2009 (these values aligned with the mortality estimates used in the most recent snook stock assessment: Muller & Taylor 2006, their Fig. 4.3.2.3). After the cold event, ϕ dropped to 0.01 as compared to 0.45 and 0.65 in the 2 yr prior to the cold event. Declines in snook abundance were similar elsewhere in Florida (Table 3).

DISCUSSION

We have developed a better understanding of habitat use in 2 distinct portions of snook life history, which provides a foundation for examining connections between life stages, including spatial dynamics of fish–habitat interactions. For example, prior to this research, the level of site fidelity of adult common snook on spawning grounds was unknown. Such fidelity implies some level of metapopulation structure induced by spawning segregation, and connections between spawning locations and particular juvenile habitats (the latter because, on average, estuary currents will carry larvae to a particular area). Given this new understanding, the focus of future research has changed to address these issues, which had not previously been considered for common snook.

Similarly, we found that the contribution of emigration to declines in apparent survival of juveniles was significant, which requires a reexamination of the general assumption in research on juvenile fishes that declines in abundance at a sample site provide an estimate of mortality. Clearly, emigration is an important factor in local declines that requires revision of juvenile survival estimates for common snook, and likely for other species that exhibit among-habitat mobility (e.g. 'ontogenetic shifters' in Adams et al. 2006b). As with adults, this finding requires a revision of future research focus to address issues such as the effects of habitat contiguity on movement and survival.

Site fidelity

Juveniles

Site fidelity by juvenile snook likely reflects a tradeoff between growth and survival. Because different habitats vary in the quantity and quality of food, as well as refuge and predation potential, there are tradeoffs between achieving a high growth rate and survival. Under the ideal free distribution theory (Fretwell & Lucas 1970), individuals will choose to use a habitat that maximizes resource use of individuals, and will change habitats when per capita resource availability increases in one habitat relative to another. Thus, juvenile snook may use poor-quality habitats when densities are high in high-quality habitats, but such poor-quality habitats may not be used when densities are low in better habitats. Dahlgren & Eggleston (2000), for example, found ontogenetic habitat shifts by juvenile Nassau groupers to be consistent with the predictions that ontogenetic habitat shifts minimize the ratio of mortality risk to growth rate.

The emigration rate for juvenile snook was comparable to other species (Frederick 1997). Emigration may be due to a search for habitat with maximum resource potential and minimal predation risk, or the need for a habitat mosaic that provides multiple resource pools (Sheaves 2009). The expansion of home range with increasing size supports the use of a habitat mosaic, or may be associated with assessment of habitat quality. As juvenile snook grow and their probability of mortality declines, their home range size and movement rates increase as they use alternative habitats to a greater extent, eventually losing their reliance on mangrove creeks.

Although intra-annual juvenile movement was more common than previously assumed, juveniles exhibited inter-annual regional site fidelity. Juveniles likely exhibited inter-annual site fidelity because the habitats had been previously identified as high quality, or due to the risk of movements substantially larger than their home range size. Due to the size of their home range (≥0.5 km), an effective juvenile snook nursery habitat would require relatively large tracts of contiguous suitable habitat.

Adults

Site fidelity for adults poses advantages and disadvantages. There is a benefit to returning to a spawning location if reproductive success at that location is higher than at other locations. For example, mortality from predators may be lower, more or better potential mates may be present, larval survival may be higher, and currents may transport larvae to higher-quality nursery habitats (i.e. high quality nursery habitats = source, low quality nursery habitats = sink; e.g. Lipcius et al. 1997). However, spawning site fidelity may slow the recovery from disturbances. For example, spawning segregation may have led to the slower than expected response of Atlantic cod to overfishing, because site fidelity impedes recolonization of spawning grounds (Robichaud & Rose 2001). Similarly, Colin (1992) determined that Nassau grouper traveled up to 100 km to reach a spawning site, which helps explain the large spatial scale decline of Nassau grouper when spawning sites are targeted by fishing.

Habitat linkages

Connectivity between juvenile and adult marine fish habitats has been difficult to establish through mark–recapture studies (Thorrold et al. 2001). For example, Courtney et al. (2000) recovered only 49 coded wire tags from a marked population of several million salmon. Despite a high number of marks employed, multiple years of recapture, and a highly efficient telemetry array, we were only able to recapture or resight 0.1 % of marked fish as moving between juvenile and adult habitats. Potential causes of low recapture were high mortality in the juvenile life stage, high fishing mortality, and high mortality from the severe cold event described herein. Given the inefficiency of physical recapture (5.63 % beach seine recapture) versus telemetry (Barbour et al. 2012) and the low number of remaining marked individuals after accounting for mortality, this example highlights challenges of quantifying ontogenetic connectivity with a mark–recapture approach.

Despite the difficulty of quantifying habitat linkages through mark–recapture, important information was gained to focus future examination of population segregation. Spawning segregation caused by adult fidelity to spawning grounds suggests a metapopulation structure (Hanski & Gilpin 1997, Smedbol & Stephenson 2001), and the inter-life stage recaptures in this study imply that this metapopulation structure may be extended to the entire population by juvenile-to-adult as well as adult-to-juvenile habitat connections. For example, all of the inter-life stage recaptures/resightings involved movement between the studied juvenile habitats and the 2 closest spawning ground islands. Such connectivity, coupled with site fidelity, may induce a metapopulation structure that requires an estuary-specific rather than regional management approach, has implications for prioritization of habitat conservation and restoration, and may influence the ability of local populations to respond to disturbances.

Severe cold event

Infrequent, severe cold disturbances recur in subtropical southwest Florida, with published reports of cold-related fish kills from as early as the 1800's (e.g. Storey & Gudger 1936, Galloway 1941). Although different life stages may show different responses to disturbances, in part based on characteristics specific to their life stage (e.g. due to physiology, habitat use), we found evidence for major disturbance effects on both adult and juvenile life stages: maximum likelihood estimates of apparent survival decreased by 97.8 to 98.5 % in adults and by 22.6 to 38.3 % in juveniles. This analysis shows independent declines in apparent survival in both habitats (i.e. life stages) that were unprecedented in multiple years.

We suggest 2 possible causes for the decline in adult and juvenile snook apparent survival: lethal and sub-lethal effects. Lethal effects, particularly mortality from a cessation of cellular functioning (Somero 1995) when water temperature dropped below the study subject's lower thermal limit for 10 d, were likely the primary causes of the declines. In the sub-lethal effects scenario, surviving adult snook used available resources to counter stress-related effects (Schreck et al. 2001), leaving fewer resources to allocate to spawning (McCullough et al. 2001), resulting in population-level implications by reducing the population's fecundity.

A sub-lethal response by juvenile snook would occur by emigration from the nursery habitat mosaic in search of thermal refugia. Such movement, however, could increase predation susceptibility (Barbour et al. in press). Although we did document high rates of juvenile emigration throughout the entirety of the study, we did not document an increase in emigration during the cold event. Moreover, juvenile emigrants would have to find alternative suitable nursery habitats following the disturbance since we did not document an increase in temporary emigration.

CONCLUSIONS AND FUTURE RESEARCH

In the constricted juvenile habitat, application of PIT tag telemetry allowed for a high resighting rate and provided new information that traditional physical recapture or more expensive biologging techniques would be unable to yield (Barbour et al. 2012). The demonstration of high levels of site fidelity by both juveniles and adults changes our understanding of habitat use, and implies a metapopulation structure with multi-life stage connectivity and location- and habitat-specific characteristics. Since habitat loss and degradation are among the top causes of fish population declines worldwide, common snook may be especially at risk due to these characteristics. Future research on habitat linkages should incorporate additional methods to augment biologging, such as otolith microchemistry (e.g. Gillanders 2005) and genetic analysis (e.g. Bradbury et al. 2008). Improved knowledge of connectivity would allow a better assessment of the nursery value of the juvenile habitats (Beck et al. 2001, Adams et al. 2006b), and help determine whether a metapopulation structure exists (Hanski & Gilpin 1997, Smedbol & Stephenson 2001), allowing for adaptable regional management plans and proper prioritization of habitat conservation. Overall, the improved understanding of common snook ontogeny will contribute to future management of the western Florida fishery, which has been closed to harvest since the 2010 cold event, and will form a basis by which to evaluate the feasibility of juvenile hatchery enhancement.

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Contribution to the Theme Section: 'Tagging through the stages: ontogeny in biologging'

Effects of solar ultraviolet radiation exposure on early ocean survival and fry-to-smolt growth of juvenile salmon

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ABSTRACT: Marine survival rates of many juvenile salmon populations have declined in recent decades. Although several potential causes have been proposed, there has been little conclusive evidence for which factors are responsible or not responsible for these declines. We experimentally addressed the hypothesis that exposure of coho salmon *Oncorhynchus kisutch* or sockeye salmon *O. nerka* to solar ultraviolet-B radiation (UVB) during freshwater rearing of fry and parr life-history stages increases mortality at the time of smoltification and ocean entry. Juvenile coho and sockeye salmon were reared in outdoor hatchery tanks either exposed to full spectrum sunlight or shielded from UVB radiation by plastic screens for up to 9 mo prior to release. Smolts were tagged with acoustic transmitters and detected with hydrophone receivers during their downriver and early ocean migration. Survival of treatment groups was compared using Cormack-Jolly-Seber and Burnham mark-recapture models. While exposure to UVB resulted in decreased growth of juvenile coho salmon, survivorship during the early marine period was unaffected by the UVB treatment for both populations. This first attempt to experimentally address the hypothesis of impaired survival resulting from solar UVB radiation has shown that other factors are more likely responsible for observed declines in salmon marine survival rates.

KEY WORDS: Mortality · Salmonid · Sunlight exposure · Metabolic impairment · Migratory fish · Capture-recapture · Biotelemetry · Mobile tracking

INTRODUCTION

Many Pacific salmon populations in British Columbia, Canada, and the US Pacific Northwest have declined over the last several decades, largely as a result of lower fisheries-independent marine survival (Coronado & Hilborn 1998, Beamish et al. 2000, Pyper et al. 2005). Large-scale geographic coherence in trends of marine (i.e. smolt-to-adult) survival and abundance suggest that factors at the regional scale are responsible for the declines (Coronado & Hilborn 1998, Peterman et al. 1998, Welch et al. 2000, Malick et al. 2009, Teo et al. 2009; but see Bradford 1999 for exceptions in terms of covariation in smolt abundance at smaller scales). Similar trends have been observed simultaneously in Atlantic salmon *Salmo*

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salar on the east coast of North America (Friedland 1998). Declines occurred in both wild and hatchery-reared fish, tended to occur at southerly latitudes first and progressively move northward, and also tended to occur predominantly in rain shadow areas with resulting high exposure to sunlight (Walters & Ward 1998).

Anadromous salmonids exhibit tremendous diversity in life history strategies. Populations exhibiting declines in marine survival and abundance were typically of species that rear in shallow streams for 1 or more years, like coho (*Oncorhynchus kisutch*), steelhead (*O. mykiss*), and stream-type Chinook (*O. tshawytscha*) salmon (Walters & Ward 1998). Several possible causes of these declines have been suggested, including shifts in ocean climate regimes affecting physiological tolerance limits (Welch et al. 1998), density-dependent survival at sea due to increased hatchery smolt production (Noakes et al. 2000, Levin et al. 2001, Naish et al. 2007), disease (Arkoosh et al. 2004), freshwater habitat loss (Magnusson & Hilborn 2003), fishing mortality (in the case of abundance), and shifts in the abundance and distribution of predators (Ware & McFarlane 1986, Holtby et al. 1990). Food limitation in the first year of ocean life and concentrations of predators that feed on outmigrating salmon smolts at river mouths were leading hypotheses in this debate. The hypothesis of food limitation predicts that mortality should occur whenever post-smolts are faced with food shortage, either in summer (Pearcy 1992) or in winter (Beamish & Mahnken 2001). The hypothesis of predator concentrations predicts that mortality should predominantly occur during the smolt migration, especially at river mouths, estuaries, or soon after ocean entry (Fisher & Pearcy 1988, Greenstreet et al. 1993, Olesiuk et al. 1996, Collis et al. 2002). Most of these hypotheses are difficult if not impossible to test, as salmon usually spend several years and migrate hundreds to thousands of kilometres at sea before returning to freshwater.

One potential cause of elevated marine mortality is ultraviolet-B radiation (UVB) from sunlight during freshwater life, which could result in metabolic damage with physiological and survival consequences once juvenile salmon undergo smoltification and enter saltwater (Walters & Ward 1998). Due to atmospheric ozone depletion at high and mid-northern latitudes (Fig. 1a), levels of incident UVB reaching the ground have gradually increased (Fig. 1b,c) over the same period as marine survival in some salmon populations has declined. These increases in UVB occurred in both summer (average 3.3 to 4.4 % increase per decade) and winter (average 6.2 to 7.9 % increase per decade) months in North America (Tarasick et al. 2003). The increases in UVB have resulted in deleterious effects on several taxa at sub-cellular, cellular, tissue and organismal levels (reviewed by Zagarese & Williamson 2001, Häder et al. 2007), as well as on ecosystem function (Bothwell et al. 1994) and biodiversity (Kelly et al. 2003). The UVB impairment hypothesis of Walters & Ward (1998) is not mutually exclusive with other hypotheses such as shifts in the abundance or distribution of predators, because adverse physiological effects resulting from UVB exposure might make smolts more vulnerable to predation. Ultraviolet radiation exposure has been found to affect the behaviour of juvenile salmonids in the wild (Kelly & Bothwell 2002, Holtby & Bothwell 2008). In the laboratory, UVB exposure effects on survival are typically dose-dependent. Some DNA damage resulting from UVB radiation can be repaired at low doses, but at higher doses, damage is irreparable and mortality ensues (Mitchell et al. 2009). Ultraviolet radiation has also been observed to impair growth (Jokinen et al. 2008) and increase oxygen consumption through increased swimming activity (Alemanni et al. 2003) of salmonids. The timing and intensity of UVB exposure during freshwater rearing may therefore be important determinants of mortality consequences.

To address the possibility that UVB exposure during freshwater rearing might result in reduced survival at the time of smoltification and ocean entry, we conducted a UVB shading experiment with 2 hatchery-reared populations during their outdoor rearing life. We evaluated possible effects on survival of fish under shaded and sunlight-exposed treatments by tagging fish and estimating survival during the smolt migration using the Pacific Ocean Shelf Tracking (POST; www.postprogram.org) telemetry array (Fig. 2). Hatchery-reared Tenderfoot Creek coho salmon exhibited declines in marine survival during the 1990s (Melnychuk 2009), and are a shallow stream-rearing species in the wild. Cultus Lake sockeye salmon *Oncorhynchus nerka* showed pronounced declines in adult returns over time (Melnychuk 2009). Although wild juvenile sockeye are primarily lake-dwelling fish with potential depth refugia from UVB exposure, their hatchery-reared counterparts are likely more susceptible to UVB. For coho, we also evaluated possible effects of sunlight or shading treatments on fry-to-smolt growth and on the concentration of UV-absorbing compounds in the epithelial mucus, as these may impact survival

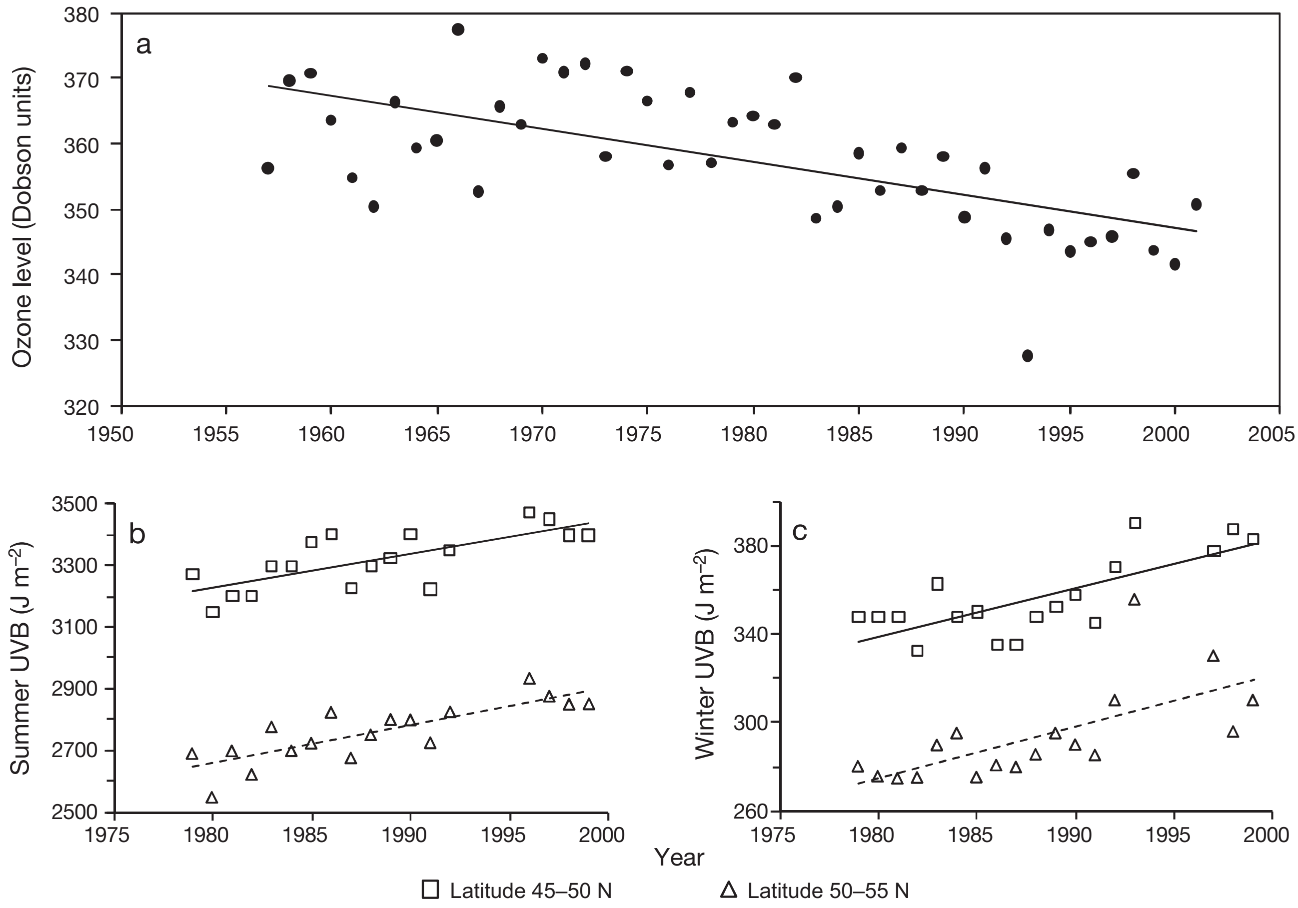

Fig. 1. Environmental data at Canadian latitudes: (a) average annual ozone levels from 1957 to 2001; ultraviolet-B radiation (UVB) during (b) summer (May to August) and (c) winter (November to February) from 1979 to 1999. Ozone data are from the Meteorological Service of Canada, measured over stations at Toronto, Ontario (43° 47′ N), Edmonton, Alberta (53° 33′ N), Resolute, Northwest Territories (74° 43′ N), Churchill, Manitoba (58° 45′ N), and Goose Bay, Labrador (53° 19′ N). Ozone measurements include both tropospheric (ground-level; ~10 % of total column ozone) and stratospheric (~90 %) ozone. UVB data are seasonal averages of monthly mean erythemal-action spectrum-weighted UVB exposure measurements (Tarasick et al. 2003)

indirectly. While a UVB shading experiment is logistically feasible only in a hatchery setting, any effects of UVB radiation found are expected to be similar in wild salmonids that rear in shallow freshwater streams for a year or more.

MATERIALS AND METHODS

Rearing conditions

Coho at Tenderfoot Creek Hatchery. After emergence in April 2006, production stock fry were transferred to a 1 m deep rearing channel. On 20 July 2006, a sample of these fish were netted and randomly distributed into either side of a divided tank (each half ~3 m long × 1 m wide × 0.45 m deep; about 300 fish in each side). One side of the tank contained the control group, where fish were exposed to unfiltered sunlight. The other side contained fish screened from above by a DuPont-Teijin Melinex® 943 plastic film (125 µm thick). This film filtered nearly 100 % of UVB wavelengths but allowed photosynthetically active radiation to penetrate to the water (see Fig. S1 in the supplement at www.int-res.com/articles/suppl/m457p251_supp.pdf). The 2 groups of fish were otherwise treated identically in terms of water flowing through the tanks, feed quantity and type (Skretting Nutra Plus), and tagging procedures. These coho were exposed to, or protected from, UVB for 9 mo prior to tagging and release in May 2007.

On 3 April 2007, a second group of coho from the production channel were transferred to experimental tanks and subjected to the same UVB exposure and shading regime for a 5 wk period immediately prior to tagging and release (hereafter referred to as 1 mo). Thus, the experiment was a 2 × 2 crossed design, with 9 mo UVB-exposed, 9 mo UVB-shaded, 1 mo UVB-exposed and 1 mo UVB-shaded treatment groups. All tagged fish were released into Tenderfoot Lake on 10 May 2007 along with the hatchery production stock.

Sockeye at Inch Creek Hatchery. Newly emerged Cultus Lake sockeye fry were transferred to 6 outdoor, small circular rearing tanks (1 m diameter) during April and May 2006. In mid-June, 3 tanks were shaded by the UVB filters and 3 tanks exposed to full spectrum sunlight (i.e. the experiment was run with the entire production stock). In mid-September, fish were aggregated into larger circular tanks (about 3 m diameter × 1 m deep), maintaining the same light treatments. The groundwater used at both hatcheries had very low dissolved organic carbon concentrations, so little attenuation of UVB would be expected in the shallow tanks (Kirk 1994). The same fish feed (EWOS) was used for all fish. Screening continued until smolts were tagged, shortly before their release and downstream migration in either of 2 release periods. The first group of fish was released along with most of the Cultus Lake production stock on 26 April 2007 into Sweltzer Creek. The second group was released on 16 May into Sweltzer Creek. The experiment was thus a 2 × 2 crossed design with UVB exposure treatments and release groups.

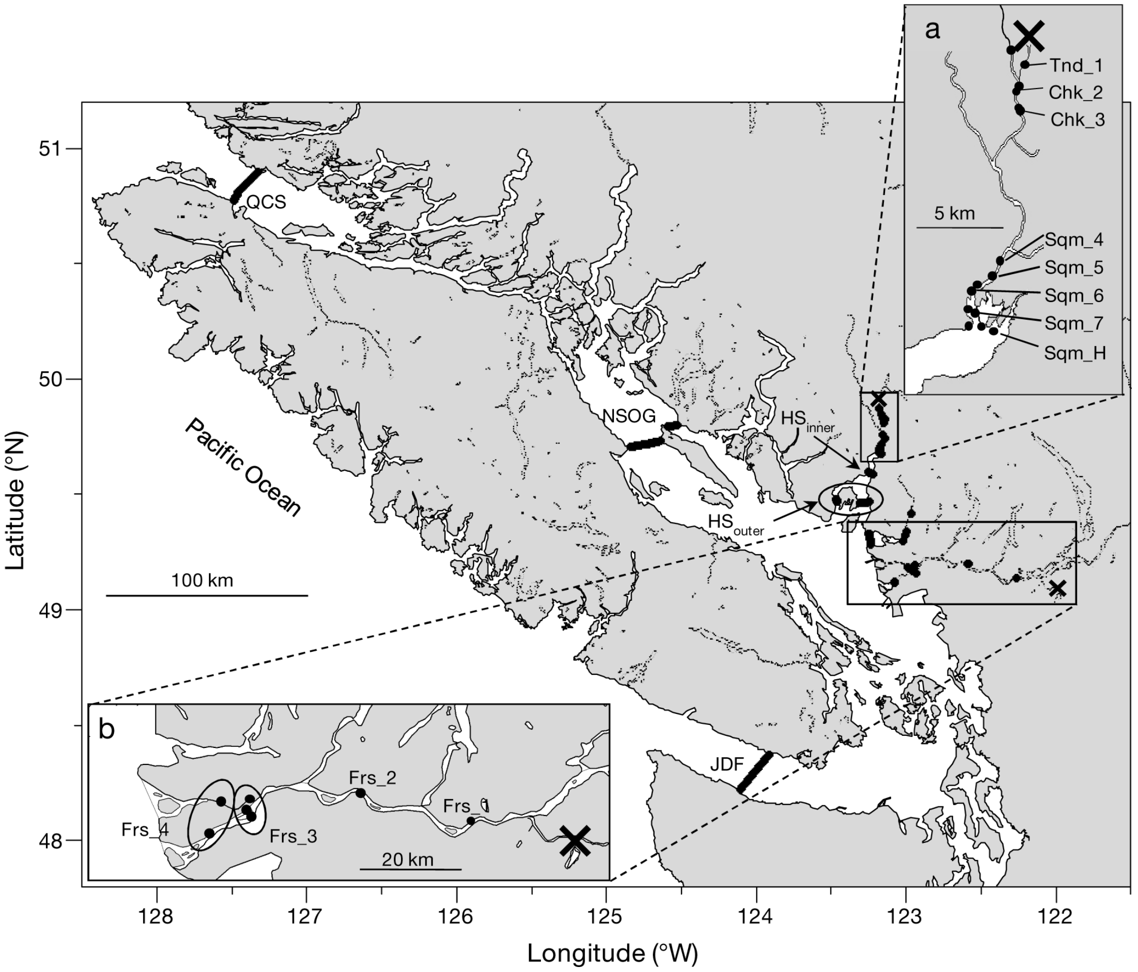

Fig. 2. Map of study area in southern British Columbia, Canada. ● show locations of receiver stations encountered during the 2007 migration of salmon smolts. Ocean stations are labelled in the main map: inner Howe Sound (HS_{inner}), outer Howe Sound (HS_{outer}), northern Strait of Georgia (NSOG), Queen Charlotte Strait (QCS), and the Strait of Juan de Fuca (JDF). River stations are labelled in (a) inset for Tenderfoot Creek coho (Tenderfoot Creek, Tnd; Cheakamus River, Chk; and Squamish River, Sqm stations) and in (b) inset for Cultus Lake sockeye (Fraser River stations, Frs). ✕ = release sites

Smolt tagging

At Tenderfoot Creek Hatchery, 199 coho smolts were tagged, split between UVB-exposed and UVB-shaded treatments and between the 2 exposure durations (Table 1). Average body sizes were smaller in the 9 mo UVB-exposed tagging group than in the other 3 groups (Table 1; ANOVA, $F_{3,195}$ = 5.28, p = 0.002). Tagged fish from all groups represented the upper end of the size distribution of fish in each tank at the end of experimental treatments (Fig. 3a). V7-2L coded acoustic tags (VEMCO) with a 30 to 90 s random delay between transmissions were used for all fish, with tags measuring 7 × 20 mm. Resulting tag length to body length ratios ranged from 13.6 to 16.0 %, adhering to the maximum recommended value of 16 % by Lacroix et al. (2004). Tags were implanted into smolts using standard surgical procedures (Moore et al. 1990, Welch et al. 2007).

At Inch Creek Hatchery, 319 Cultus Lake sockeye smolts were tagged and split between UVB-exposed and UVB-shaded treatments in the first (n = 119) and second (n = 200) release groups. Only tagged fish were measured for length (unlike in Fig. 3a), but all fish sampled were well above the minimum threshold size of 140 mm for V9-6L tags (Fig. 3b; these fish were larger than typical sockeye smolts as they were part of an accelerated-growth rearing program). Lengths of tagged fish were representative of fish in the experimental tanks at the end of the treatment period, as no size-grading was involved prior to tagging. With an extra 3 wk to grow, body sizes were larger in the second release group, but average body length was similar between UVB treatments within each release period (Table 1, Fig. 3b). V9-6L acoustic tags (VEMCO), measuring 9 × 20 mm, were used for smolts in the first release, while V9-1L tags, measuring 9 × 24 mm (with a longer battery lifespan), were used for smolts in the second release. Resulting tag to body length ratios ranged from 10.8 to 12.5 % for the first release and 11.1 to 14.1 % for the second release. All tags had a 30 to 90 s random delay between transmissions.

Study sites and stationary acoustic arrays

Cultus Lake (1.50 m annual precipitation; 179 d yr^{-1} with ≥0.2 mm precipitation) drains into Sweltzer Creek, then the Vedder River, the Sumas River, and finally the Fraser River before reaching the Strait of Georgia (Fig. 2b). Cultus Lake sockeye were released into Sweltzer Creek. They passed up to 4 acoustic receiver stations in the lower Fraser River (14 receivers deployed in 7 sub-stations; Fig. 2b). Tenderfoot Creek (2.37 m annual precipitation; 193 d yr^{-1} with ≥0.2 mm precipitation) drains into the Cheakamus River, then the Squamish River before reaching Howe Sound (Fig. 2a). Howe Sound drains into the Strait of Georgia about 40 km south of the river mouth. Tenderfoot coho were released into Tenderfoot Lake, the acclimation pond upstream of Tenderfoot Creek. They passed up to 8 freshwater or estuarine stations of single or paired receivers: 1 in Tenderfoot Creek, 2 in the Cheakamus River, 4 in the Squamish River, and 1 in Squamish Harbour (Fig. 2a). These lower river and estuary stations permit the partitioning of survival into freshwater and coastal marine components.

Deployment methods for ocean lines of acoustic receivers have been described elsewhere (Melny-

Table 1. *Oncorhynchus kisutch* and *O. nerka.* Release groups of Tenderfoot Creek coho salmon and Cultus Lake sockeye salmon smolts tagged in 2007 under UVB-exposed and UVB-shaded treatments and either different exposure times or different release times

Species	UVB treatment	Release date (2007)	Start of experiment	Fork length (mm) Mean ± SD	Fork length (mm) Range	Number released
Tenderfoot Creek coho						
9 mo exposure duration	Exposed	10 May	20 July 2006	129.1 ± 2.9	125–137	34
	Shaded	10 May	20 July 2006	131.9 ± 5.3	125–146	55
1 mo exposure duration	Exposed	10 May	3 April 2007	133.4 ± 6.1	126–147	56
	Shaded	10 May	3 April 2007	133.2 ± 5.7	125–147	54
Cultus Lake sockeye						
1st release, smaller V9-6L tag	Exposed	26 April	22 June 2006	171.5 ± 6.0	160–184	61
	Shaded	26 April	22 June 2006	171.3 ± 5.9	160–185	58
2nd release, larger V9-1L tag	Exposed	16 May	22 June 2006	189.4 ± 8.2	172–208	100
	Shaded	16 May	22 June 2006	188.1 ± 8.3	170–217	100

chuk et al. 2007, Welch et al. 2009). Receiver lines used for this study included those in Howe Sound (2 lines for Tenderfoot coho, HS_{inner} and HS_{outer}), and for both populations in the northern Strait of Georgia (NSOG), Queen Charlotte Strait (QCS) and Juan de Fuca Strait (JDF) (Fig. 2). Exit routes to the Pacific Ocean from the Strait of Georgia include Johnstone Strait and Queen Charlotte Strait to the north, and

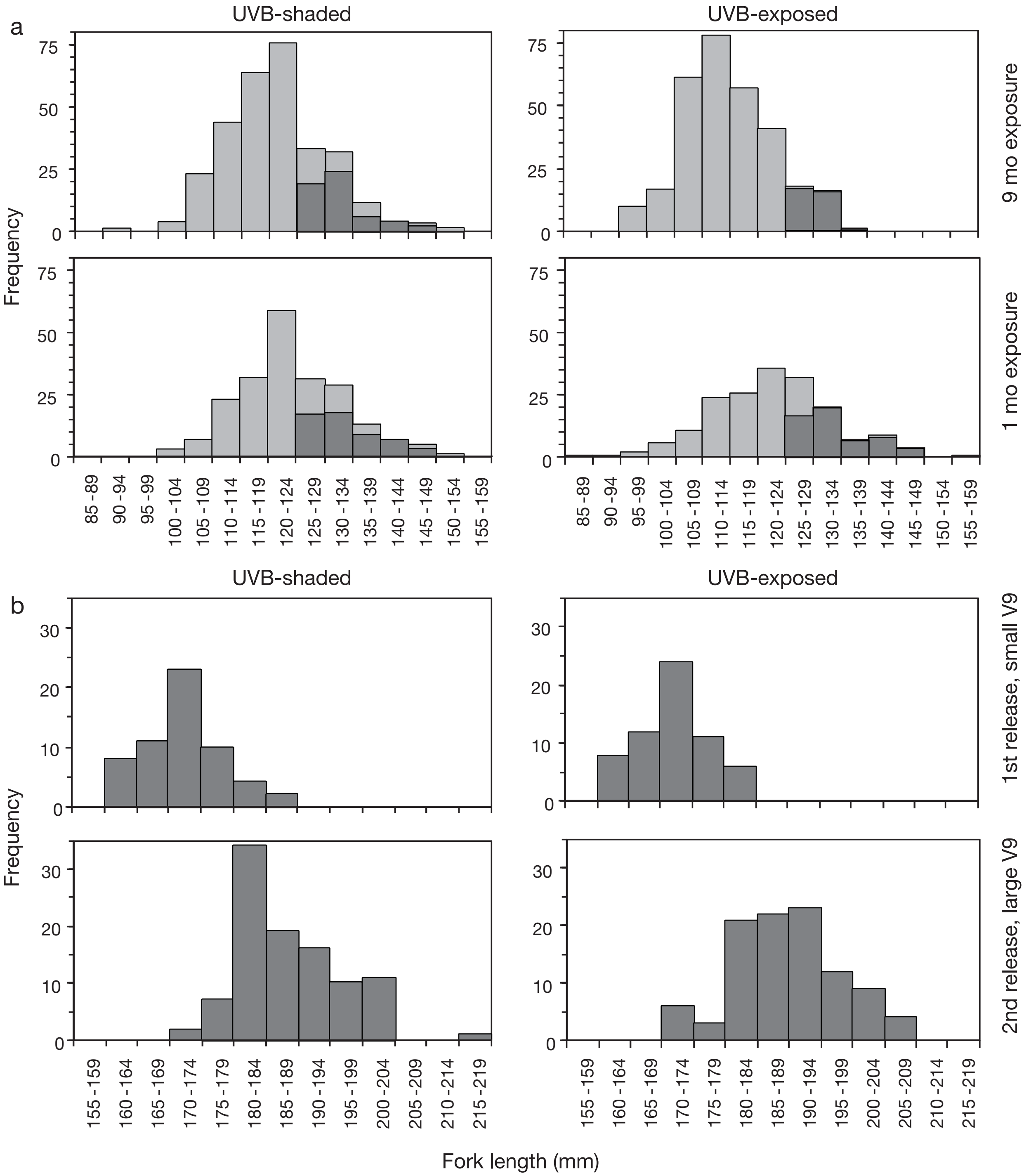

Fig. 3. *Oncorhynchus kisutch* and *O. nerka.* Fork length distributions of 4 treatment groups of (a) Tenderfoot Creek coho and (b) Cultus Lake sockeye. Light grey bars in (a) show the lengths of fish (n = ~300 for 9 mo exposures and 200 for 1 mo exposures) in each tank at the end of the experiment and time of tagging. Dark grey bars show the subset of these fish that were tagged. In (b) only fish that were tagged were measured. Note that *x*-axes differ between (a) and (b)

Juan de Fuca Strait to the south. Ocean receivers and Fraser River receivers were in place throughout the summer, past expected tag battery life. Cheakamus and Squamish River receivers were in place until either mid-June or mid-August, respectively, well beyond the typical migration period of Tenderfoot coho smolts observed in the years 2003 to 2006 (Melnychuk 2009).

Mobile hydrophone operation

Mobile sampling aided in quantifying the potential for differential mortality between UVB-exposed and UVB-shaded Tenderfoot coho during their migration through Howe Sound. Tagged coho smolts were tracked from a boat after they entered Howe Sound, using 2 acoustic receiver systems: a VR-28 receiver with a towed VH-40 directional hydrophone (VEMCO), and a USR-96 receiver with a towed SH-1 omni-directional hydrophone (Sonotronics). Sampling periods occurred towards the end of the migration through Howe Sound (late May to early June, 9 d) and again several weeks after the migration (late July to early August, 9 d), aiming to identify locations where tags had stopped moving and were presumably lying on the seabed. Although the fates of fish carrying these stationary tags are unknown, we assume such locations represent approximate locations of mortality (Melnychuk & Christensen 2009, Melnychuk et al. in press). Assuming a horizontal detection radius of 300 m, about 75 % of the area of Howe Sound in the first trip and 85 % in the second trip was covered by mobile sampling (Fig. 4a,b). Actual detection widths were likely narrower than 300 m, however (Melnychuk & Christensen 2009), so the effective area covered was possibly <50 %. Grid survey methods are described in Melnychuk & Christensen (2009).

UV-absorbing compounds in Tenderfoot Creek coho

Samples for assaying the amount of UV-absorbing compounds in the epithelial mucus of the juvenile coho were collected. Fifteen non-tagged individuals from each of the 4 treatment groups were euthanized with MS-222 and the upper lobe of the caudal fin was clipped, placed on white paper with fin rays fully

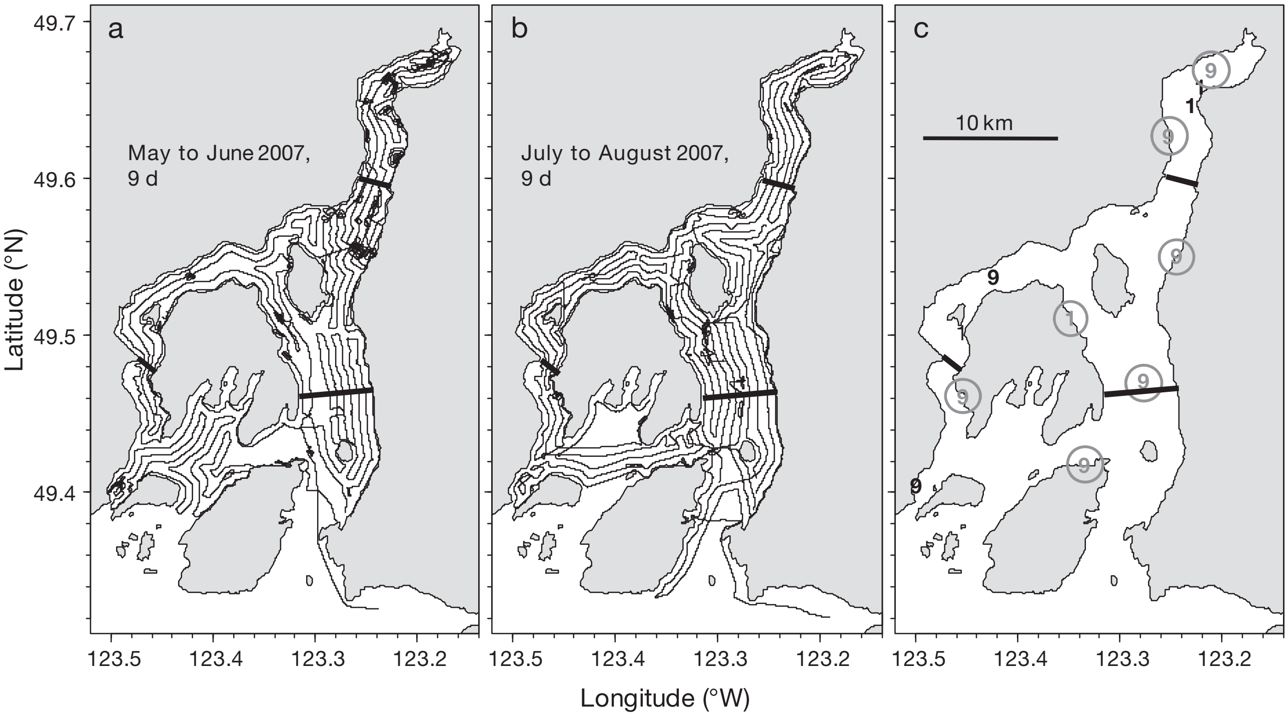

Fig. 4. *Oncorhynchus kisutch.* Sampling tracks in Howe Sound during (a) first and (b) second mobile tracking trips in 2007. (c) Locations in Howe Sound where 2007 coho tags stopped moving. Spacing between parallel tracks (thin lines in a and b) was ~500 m. Approximate mortality locations in (c) are shown by treatment group (9 mo UVB-shaded: **9**; 9 mo UVB-exposed: ⑨; 1 mo UVB-shaded: **1**; 1 mo UVB-exposed: ①). Thick black lines show stationary receiver lines in Howe Sound

extended, and photographed. The area of each fin clip was calculated from photographs using Motic Images Advanced™ image analysis software. Fin clips were frozen for later pigment extraction and assay.

Absorbance of light in the UVB range provides an index of the concentration of UVB-absorbing pigments in the tissue. Pigments in the epithelial mucus of caudal fin samples were extracted overnight in 1.9 ml of 100 % methanol in microcentrifuge tubes in the dark at 4°C (Bothwell & Lynch 2005; based on earlier methods of Fabacher & Little 1995). Absorbance of the extracts was read at 295 nm in a 1 cm cuvette on an Ultraspec 3100 pro UV/Vis spectrophotometer. Absorbance readings were compared among UVB treatment and exposure duration groups in a linear regression model, using computed fin surface area as a covariate to standardize among fish with different fin sizes.

Data analyses

During the migration out of the Strait of Georgia, tagged sockeye smolts passed up to 6 detection stations, while tagged coho smolts passed up to 12 stations. In previous years, however, Tenderfoot coho were rarely detected after entering the Strait of Georgia (Melnychuk 2009). Due to the possibility of summer residency in the Strait, we limited survival inferences to the migration through Howe Sound (including the portion of the lower sound sampled by mobile tracking). We aggregated detections at the Northern Strait of Georgia, Queen Charlotte Strait, and Juan de Fuca Strait stations to represent detection anywhere after entry into the Strait of Georgia.

It was necessary to estimate detection probabilities (p) at each receiver station to estimate the extent of migration of tagged fish. For Cultus Lake sockeye, we concurrently estimated survival probabilities (ϕ) in each segment of the migration using mark-recapture models based on the Cormack-Jolly-Seber (CJS) model (Cormack 1964, Jolly 1965, Seber 1965). For Tenderfoot Creek coho, multiple data sources were used for estimating survival, including mark-recapture data from stationary receiver lines and tag-recovery data from mobile tracking identifications of approximate mortality locations in Howe Sound. The Burnham joint live-recaptures and dead-recoveries model (Burnham 1993) was used, which incorporates both types of data. Typical assumptions of mark-recapture models include independent fates of individuals and homogeneity among individuals with respect to ϕ and p, negligible effect of tags or surgeries on tagged fish, and no tag loss or failure. In spatial applications of tag-detection Cormack-Jolly-Seber models, we also assume that detected tags are in live smolts and not in predator stomachs, and smolts do not permanently reside between successive receiver stations — they either continually migrate past receiver lines or die during the migration. Model details and further assumptions are reported elsewhere (Burnham et al. 1987, Lebreton et al. 1992). The construction of mark-recapture models for our analysis is described in the supplement (www.int-res.com/articles/suppl/m457p251_supp.pdf).

The overall hypothesis of differing survival among UVB treatment groups during the smolt migration was addressed by directly comparing candidate models, some of which included this factor and others that did not. Under this umbrella hypothesis, candidate models were treated as competing hypotheses on a more detailed level, each providing specific predictions about how survival or detection probabilities differ among UVB treatment groups and either release periods (Cultus sockeye) or exposure duration (Tenderfoot coho). Possible effects of body size on survival were explicitly evaluated by including fork length as a covariate in some models. Models were compared using QAICc (Akaike's Information Criterion corrected for overdispersion and small sample sizes; Burnham & Anderson 2002) on the basis of their goodness-of-fit to the data and the number of parameters in the model required to achieve that fit. Detailed descriptions of the candidate models are contained in the supplement. Below, we report results from the most general model for each population and also from QAICc-preferred models.

RESULTS

Migration patterns of both populations were representative of those exhibited by multiple salmon smolt populations in southern British Columbia over 4 yr (Melnychuk et al. 2010). Surviving Cultus Lake sockeye smolts travelled consistently from release to exit from the Strait of Georgia system, with average speeds of treatment groups ranging from 15.9 to 16.6 km d^{-1} for the first release and 19.8 to 21.4 km d^{-1} for the second release (see Fig. S3a in the supplement at www.int-res.com/articles/suppl/m457p251_supp.pdf). Tenderfoot Creek coho smolts travelled consistently from release to the outer Howe Sound line, with average speeds of release groups ranging

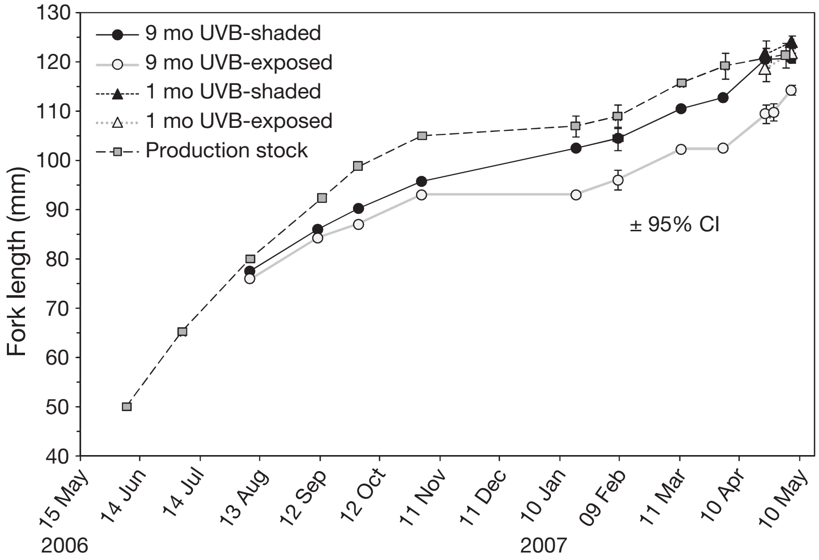

Fig. 5. *Oncorhynchus kisutch.* Average body size of coho treatment groups during rearing at Tenderfoot Creek Hatchery. Average lengths with 95 % confidence limits (CI) were based on measurements of 50 individuals in each group, while those without error bars were based on total mass of several fish weighed together, with average mass then converted to length. UVB-shaded and UVB-exposed groups were reared in small tanks. Also shown is average fork length of the production stock, which were reared in a larger, deeper hatchery channel

from 7.1 to 9.4 km d^{-1} (see Fig. S3b in the supplement). There were no differences in travel speeds among UVB treatment groups within either population (Tenderfoot Creek coho from release to outer Howe Sound line, ANOVA, $F_{3,41} = 0.78$, p = 0.51; Cultus Lake sockeye from release to Queen Charlotte Strait or Juan de Fuca lines, first release group t_{21} = 0.69, p = 0.50, second release group t_{47} = 1.05, p = 0.30). Thus, any differences in estimated survival probabilities among UVB treatment groups are unlikely to be attributed to travel time differences.

UVB exposure effects on coho growth

For 2 mo following the transfer of fish from the rearing channel to experimental tanks in July 2006, fish had similar average weights (and lengths) among UVB treatments (Fig. 5). By mid-January 2007, however, when fish were weighed again, the average body mass of the UVB-shaded group was greater than that of the UVB-exposed group. In February, lengths of individual fish were measured from random samples of each group, and a clear difference was observed between treatments (t_{96} = 5.40, p < 0.001; Fig. 5). This difference was maintained among UVB treatment groups for the remainder of spring 2007 until smolts were tagged and released.

Neither of the UVB treatment groups is a true control group with respect to the Tenderfoot Creek Hatchery production stock. Both treatment groups were reared in smaller, shallower, and lighter coloured tanks than the channel where the production stock are reared. Dorsal pigmentation differences were observed visually, with fish from both treatment groups being lighter in colour than fish from the production stock. Fish from both treatment groups were also smaller on average than fish from the production stock during most of the rearing period (Fig. 5). This margin of difference decreased between the production stock and the 9 mo UVB-shaded group during winter and spring 2007. By the time the 1 mo exposure experiment started and then by the time of tagging, all treatment groups had similar average body lengths to those of the production stock except the 9 mo UVB-exposed group, which had considerably shorter body lengths (Fig. 5).

UV-absorbing compounds in Tenderfoot Creek coho

Concentrations of UV-absorbing pigment in extracts were indirectly proportional to fin area, so analysis of covariance was used with fin area as a covariate, and exposure duration and UV treatment as additive main effects. The linear regression showed an overall effect of fin area, with an increase of 0.366 units of absorbance (± 0.147 SE) for every increase of 1 cm^2 of fin area ($F_{1,55} = 6.19$, p = 0.016). After accounting for the fin area effect, absorbance was greater for the 9 mo exposure duration groups than for the 1 mo groups ($\beta_{duration/9} = 0.224 \pm 0.060$ SE, $F_{1,55} = 18.33$, p < 0.001), but no significant difference was observed between UV treatment groups ($\beta_{UV/sun} = -0.084 \pm 0.059$ SE, $F_{1,55} = 2.92$, p = 0.093, overall intercept of 1.114 ± 0.223 corresponding to the 1 mo, UVB-shaded group; see Fig. S2 in the supplement). If only the 9 mo exposure groups are considered, there was again no difference in absorbance between UV treatment groups ($\beta_{UV/sun} = -0.052 \pm 0.088$ SE, $F_{1,26}$ = 0.500, p = 0.486).

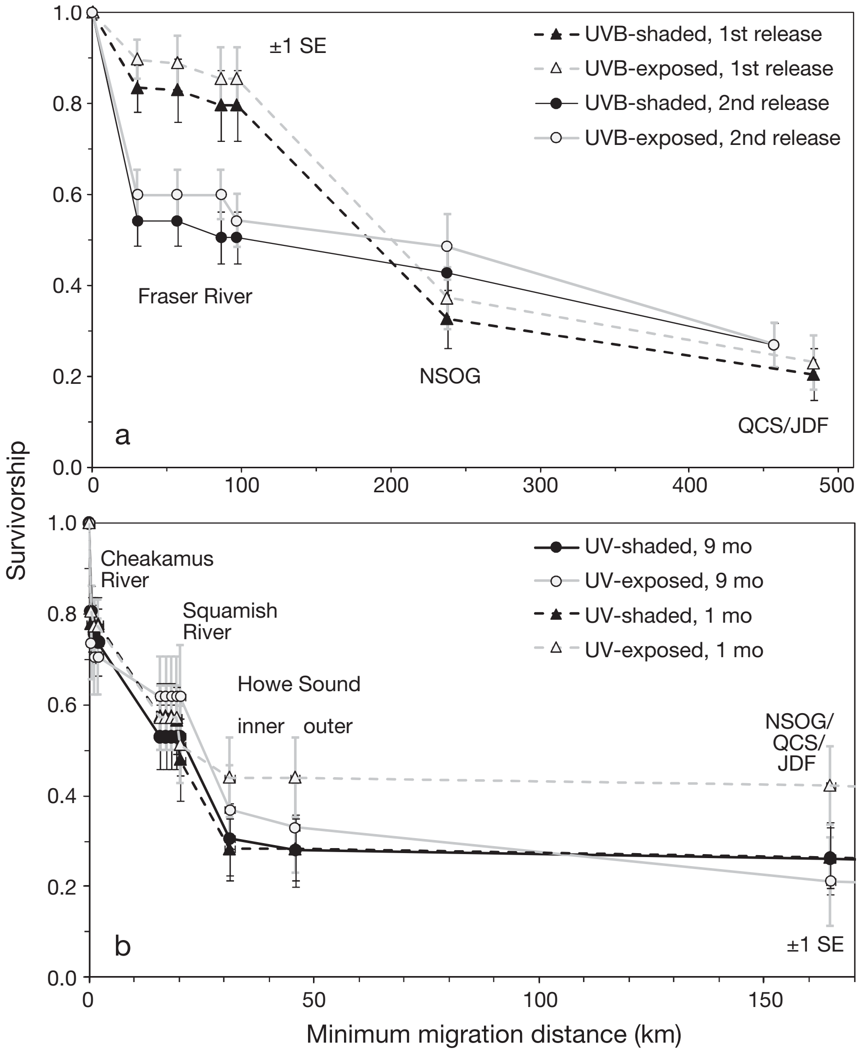

Fig. 6. *Oncorhynchus nerka* and *O. kisutch.* Survivorship curves for (a) Cultus Lake sockeye salmon from release to the Queen Charlotte Strait (QCS) or Juan de Fuca Strait (JDF) line, and (b) Tenderfoot Creek coho salmon from release to the northern Strait of Georgia (NSOG) line. Survivorship estimates are shown for each treatment group, plotted against the cumulative distance from release site to the detection station. (a) The Cormack-Jolly-Seber model for sockeye involves fully independent survival and detection probabilities for each treatment group in each segment or at each station, i.e. model [ϕ(Seg×Rel×Treat), *p*(Station×Rel×Treat)] (see supplement at www.int-res.com/articles/suppl/m457p251_supp.pdf for details). (b) The Burnham model for coho involves fully independent survival and detection probabilities for each treatment group in each segment or at each station, mobile tracking detection efficiencies in each Howe Sound segment that are pooled across treatment groups, and fidelity parameters fixed at 1, i.e. model [*S*(Seg×Treat×Dur), *p*(Station×Treat×Dur), *r*(SegHS), *F*(=1)] (see supplement for details). Error bars show ±1 SE. Note the different *x*-axis scales in (a) and (b)

Howe Sound mobile tracking results

In 2007, 12 motionless coho tags were located in Howe Sound, which we assumed to be approximate locations of mortality (Fig. 4c). The scattered patterns of mortality locations were similar to those observed in previous years (Melnychuk 2009, Melnychuk et al. in press). All 4 treatment groups were represented in these mortality locations, although the proportion of mortalities detected for the 9 mo UVB-exposed group (6 tags out of 34 fish tagged = 17%) was considerably higher than the proportion observed for the other 3 groups (2 to 6%). In the following section, these tag-recovery data are used along with mark-recapture data from stationary receivers in a joint-model analysis of survival.

Survival comparison of UVB-exposed and UVB-shaded groups

Mark-recapture estimates of survival to successive receiver stations along the migration routes of Cultus Lake sockeye and Tenderfoot Creek coho indicate periods of high mortality in both populations, but no difference among UVB treatment groups (Fig. 6). For Cultus Lake sockeye, initial survivorship estimates differed among release periods but not among UVB treatments. Fish from the second release suffered higher mortality between release and the first Fraser River station than fish from the first release (Fig. 6a). Only a small part of this initial decline can be explained by a higher proportion of tagged fish from the second release being detected in Cultus Lake (either residualizing or having been carried into the lake by a predator; see supplement). The first release group had lower survival after ocean entry (from the Fraser River mouth to the Northern Strait of Georgia) compared to the second release. By the end of the coastal inshore migration, estimated survivorship was similar for both release groups, with no difference among UVB treatment groups (Fig. 6a).

For Tenderfoot coho, high mortality (>20%) occurred immediately after release in all 4 treatment groups (Fig. 6b). This is likely attributable to predation in Tenderfoot Lake following the smolt release but before smolts started actively migrating (smolts took 1.6 to 2.2 d on average to travel from the hatchery to the first detection station in Tenderfoot Creek, a distance of <400 m). High mortality continued throughout the downstream migration to the first of the Squamish River stations, Sqm_4 (Fig. 2a), as well as in the first segment after ocean entry from Squamish Harbour to the inner Howe Sound line (Fig. 6b). By the end of the downstream migration there was no difference among groups in survivorship. Similarly, there was no difference among treatment groups by the time fish crossed the outer Howe Sound line (Fig. 6b and especially Fig. S4 in the supplement at www.int-res.com/articles/suppl/m457p251_supp.pdf, which assumes a more parsimonious model). No effects of body size on survival were detected in either population. See the supplement for comparisons of candidate models which serve to evaluate the strength of evidence for an effect of UVB treatment and other factors on salmon smolt survival.

DISCUSSION

Thinning of the atmospheric ozone layer has increased levels of UVB radiation reaching the ground at temperate latitudes over the past several decades. This has resulted in deleterious ecological effects on many taxa and levels of biological organization (reviewed by Zagarese & Williamson 2001, Häder et al. 2007). Recent studies have found behavioural differences in juvenile salmonids as a result of ultraviolet radiation exposure (Kelly & Bothwell 2002, Holtby & Bothwell 2008), but after Walters & Ward (1998) proposed that UVB may be a factor responsible for declines in marine survival of stream-rearing salmon populations, this hypothesis remained untested for nearly 10 yr. While UVB exposure may cause DNA damage during the shallow stream- or hatchery-rearing phase of juvenile salmon, the survival consequences of this exposure may not be realized until ocean entry (Walters & Ward 1998).

Decreased growth was observed in the 9 mo UVB-exposed treatment group of Tenderfoot coho compared with the UVB-shaded group (also compared with the hatchery production stock by the end of the exposure period, at the time of smoltification; Fig. 5). This difference between treatment groups cannot be explained by size-dependent differential mortality in hatchery tanks, as few fish from any treatment died while rearing. Since treatment groups of fish were otherwise treated similarly, UVB radiation from sunlight likely caused reduced growth, although tank effects cannot be completely ruled out. This difference was established by January 2007, and maintained through smoltification. There was little overhead sunlight during autumn 2006 and winter, so the critical exposure period that led to the difference was likely the remainder of summer 2006 after 20 July (The shading experiment was initially set up on 7 June 2006, but in July 2006, the tank partition between treatment groups detached and fish intermixed. This was abandoned, and the experiment was re-started on 20 July 2006 with new fish from the rearing channel.) To note, both shaded and exposed groups initially displayed reduced growth relative to the production stock, but by the time of smoltification, average body length of the UVB-shaded group had caught up with that of the production stock (Fig. 5). The production stock was also exposed to sunlight and hence UVB, but fish were reared at a much higher density than in the experimental tanks, resulting in a higher degree of community self-shading. Fish commonly aggregated in dense formations in the rearing channel, so mean exposure to UVB would be much lower.

Other studies have found effects of UVB exposure on growth of juvenile salmonids. In Atlantic salmon, treatment with sunlight-enhanced UVB levels resulted in decreased growth and reduced immune function (plasma immunoglobulin concentration, IgM) compared with natural sunlight and UVB-shaded treatments (Jokinen et al. 2008). However, they found no difference in growth or IgM in juvenile Atlantic salmon exposed to natural sunlight compared to those in UVB-shaded conditions (Jokinen et al. 2008). This might have resulted from the shorter exposure duration of their experiment (52 d in July and August 2001), a cloudier than average year in which the experiment was conducted (Jokinen et al. 2008), or the shallower angle of incident sunlight at the more northerly latitude (60.9° N, Institute of Marine Research, Norway) compared with our experiment at Tenderfoot Creek Hatchery. Our finding of reduced growth in coho could result from UVB exposure causing increased oxygen consumption and swimming activity (as in a laboratory study with rainbow trout; Alemanni et al. 2003), or increased DNA-repair metabolic activity (specifically, nucleotide excision repair is an energetically expensive process used by rainbow trout *Oncorhynchus mykiss* in response to UVB exposure; Olson & Mitchell 2006).

Coho smolts in the 9 mo exposure groups had a greater concentration of UVB-absorbing mycosporine-like amino acids (MAAs) in the epidermal mucus of fins than smolts in the 1 mo exposure groups that had recently been transferred from the production stock rearing channel. MAAs are taken up from the diet (juvenile salmon at both hatcheries were fed a diet that was largely marine-derived). Provided sufficient intake of MAAs, the concentrations of MAAs in the epithelial mucus of both freshwater and marine fishes have been shown to increase on exposure to UV radiation and are believed to confer protection from UVB (Fabacher & Little 1995, Shick & Dunlap 2002, Zamzow & Losey 2002). The higher concentrations in the 9 mo groups were likely stimulated by greater overall exposure to sunlight as the density of fish and thus opportunity for finding shade was lower in the experimental tanks. Other studies have found that the stimulation of increased MAA concentration is largely in response to the UVA component of sunlight (Bothwell & Lynch 2005), and the UVB-blocking filter we utilized allowed passage of a large portion of the UVA spectrum (see Fig. S1 in the supplement). Therefore, fish in both 9 mo groups were apparently exposed to sufficient UVA to increase the concentration of MAA. The lower levels of MAA in fish in the two 1 mo groups suggest that: (1) for these larger fish at the time of transfer to experimental tanks, this duration was insufficient to increase MAA concentration; and (2) fish in the production channel were sufficiently shielded from UV exposure so as not to develop higher MAA levels, and hence might be potentially more vulnerable to UVB after release.

The effect of UVB exposure on growth of Tenderfoot coho did not later lead to survival differences during the migration downstream and through Howe Sound. With or without accounting for the smaller average body size of the 9 mo UVB-exposed group by using fork length as a covariate (see supplement), no overall difference in survival was observed among treatment groups. Upon arrival at the outer Howe Sound line, all 4 groups had similar survivorship (Fig. 6b or see Fig. S4 in the supplement). It is not possible to make survival inferences beyond Howe Sound since Tenderfoot coho may reside in the Strait of Georgia through the summer months (Healey 1980), where they may go undetected by the more distant receiver lines.

From a conservation viewpoint, it is fortunate that survival differences were not observed in either population between UVB-exposed and UVB-shaded fish because it would be very difficult to ameliorate the consequences of a thinning ozone layer in the wild. Still, there are possible reasons why a true difference could have gone undetected:

(1) Uncertainty in the critical exposure period. The experiment at Tenderfoot Creek was re-started in mid-July 2006. If UVB exposure during late spring to mid-July of the year prior to migration to sea has survival consequences, these would have been missed in the coho experiment.

(2) Uncertainty in latency between exposure and the ensuing period of mortality. Survival was only monitored through Howe Sound for Tenderfoot coho (ca. 5 to 10 d post-release) and through the Strait of Georgia for Cultus Lake sockeye (ca. 25 to 30 d post-release; see Fig. S3 in the supplement). Since the physiological mechanisms are not entirely clear, it is possible that UVB exposure effects may not be realized until several weeks or months after ocean entry.

(3) These experiments were conducted using available tanks at the 2 hatcheries, and such tanks may not be reflective of UVB exposure faced by the production stocks or by wild stocks. On the one hand, tank walls may have provided refugia from UVB during some hours of the day, as salmonids can see in the UVA range and likely at least to some extent in the UVB range of wavelengths (e.g. rainbow trout, Browman et al. 1994), so could have sometimes avoided ultraviolet exposure (Kelly & Bothwell 2002). On the other hand, characteristics of natural streams such as overhead shading and deep pools may provide greater UVB protection for wild fish than that afforded in the experimental tanks or a hatchery environment in general.

Given the unambiguous lack of a survival difference between UVB treatment groups of 2 populations in controlled environments, it seems more likely that other factors are responsible for declines of marine survival rates in coho and sockeye salmon. To hedge our bets, whole life cycle confirmatory experiments could be conducted at hatcheries in sunny areas before finally dismissing the hypothesis of UVB exposure effects on salmon survival (such shading experiments would not be feasible in the wild for freely moving stream-dwelling salmonids). Coded wire tags (CWT) or passive integrative transponders (PIT, in the Columbia River) could be used to monitor the full smolt-to-adult period of hatchery-reared fish. At several hatcheries, CWT or PIT programs are already in use, so the extra marking and recapture costs would be trivial for setting up shading experiments and allocating differently coded CWTs or PIT tags among treatment groups. If any UVB effects were observed under a full approach of egg-to-smolt exposure treatments and smolt-to-adult survival assessment, then subsequent experiments could seek to identify on finer time scales when the critical periods of UVB exposure and ensuing mortality occur. Until that time, attention should turn to other possible causal factors of elevated mortality during the vulnerable period of salmon smolt migrations.

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Oceanic dispersal of juvenile leatherback turtles: going beyond passive drift modeling

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ABSTRACT: The current paper presents the first detailed investigation of open-ocean dispersal of hatchlings and juveniles of the critically endangered western Pacific leatherback turtle *Dermochelys coriacea* populations nesting in New Guinea. Dispersal patterns were simulated by releasing particles drifting passively, or almost passively, into a state-of-the-art World Ocean circulation model. Analysis of the simulation results combined with sighting, genetic, bycatch, and adult satellite tracking information reveals that: (1) Hatchlings emerging from the main New Guinea nesting beaches are likely to be entrained by highly variable oceanic currents into the North Pacific, South Pacific, or Indian Oceans. Those drifting into the Indian Ocean likely suffer very high mortality. This suggests that, as ocean current variability determines the partition of hatchlings into different dispersal areas, it also largely influences juvenile survival rate at the population level. (2) Within 1 to 2 yr, most passively drifting juveniles reach temperate oceanic regions where the water temperature in winter drops well below the minimum temperature likely tolerated by such small individuals. This leads us to hypothesize that, after an initial period of mostly passive drift, juveniles initiate active swimming towards lower (warmer) latitudes before winter and back again towards higher latitudes, where food abounds, during spring. Such seasonal migrations would significantly slow the eastward progression of individuals circulating in the North Pacific current. This slower drift scenario better explains the size distribution of leatherbacks observed, or incidentally caught by pelagic fisheries, in the North Pacific. This dispersal mechanism combining passive drift with active habitat-driven seasonal migrations might well apply to many other sea turtle populations and deserves further study.

KEY WORDS: Leatherback turtle · Juvenile dispersal · Seasonal migrations · Ocean circulation · Western Pacific

INTRODUCTION

The knowledge gaps on the early juvenile life history and spatial ecology of sea turtles continue to impede research and conservation of these threatened species (Hamann et al. 2010). After emerging from their nests, sea turtle hatchlings crawl to the water and swim vigorously towards the open ocean where they become 'lost' to observation for several years. Tracking such small individuals in the open ocean is extremely difficult (e.g. Seney et al. 2010) so that observations of where they disperse, what habitat they occupy and how they exploit it are extremely sparse. A now widely accepted model is that during their first years of life juveniles 'become plankton and drift more or less passively in the open sea' (Carr

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1986a) so that their dispersal follows large-scale oceanic circulation patterns. This hypothesis is corroborated by multiple studies showing that the size and spatial distributions of oceanic juveniles captured at sea or found stranded display patterns that are consistent with transport by major currents downstream of the nesting beaches (Carr 1986b, Collard & Ogren 1990, Bolten et al. 1993). Genetic analyses have also been able to track these juveniles back to their natal rookeries that, indeed, prove to be upstream of the place where they were found (Bowen et al. 1995, 2007, Bolten et al. 1998, Boyle et al. 2009). More recently, studies combining genetic data with surface current analyses have indicated that current patterns also play an important role in determining the genetic structure of juvenile foraging aggregations (Carreras et al. 2006, Bass et al. 2006, Blumenthal et al. 2009, Monzón Argüello et al. 2010, Amorocho et al. 2012), further reinforcing the idea that the juveniles' dispersal is largely driven by oceanic currents. These studies however focus on juvenile sea turtle species that disperse to neritic foraging grounds. The dispersal of leatherbacks *Dermochelys coriacea* has been much less investigated, probably because juveniles remain essentially pelagic and thus more cryptic.

In the present paper we set out to investigate the dispersal of hatchlings and juveniles of the western Pacific leatherback population nesting in New Guinea. This nesting stock is of special conservation concern, because it contains the last remaining sizeable leatherback population in the Pacific (Hitipeuw et al. 2007). Significant efforts have been devoted to characterize its genetic structure (Dutton et al. 1999, 2007) and to identify adults' migration pathways (Benson et al. 2007a,b, 2011), but the juveniles' spatial ecology remains largely unknown. This study is a first attempt to gain insight into dispersal patterns of western Pacific juveniles. It is especially challenging as the western Pacific leatherback population nests in one of the most complex and dynamic areas of the world's oceans, connecting the Pacific to the Indian Ocean. In this area, strong and highly variable currents can push hatchlings in widely different directions depending on when and where they terminate their swimming frenzy. As a result young sea turtles originating from the same nesting beach can rapidly reach different oceanic areas within a few months and thereby experience very different life histories. Variability of oceanic circulation adjacent to the nesting sites thus likely has a profound, but so-far uninvestigated, impact on the dynamics of this sea turtle population.

As in previous juveniles' dispersal studies (Hays & Marsh 1997, Blumenthal et al. 2009, Godley et al. 2010, Hays et al. 2010), we start from the assumption that, after their swimming frenzy, hatchlings behave as drifters passively transported by surface ocean currents. We use a state-of-the-art operational ocean model to simulate the dispersal patterns of such passive drifters released off 2 main nesting beaches and initially perform 1 yr drift simulations to investigate the interannual variability of the dispersal schemes. Passive drift is a reasonable hypothesis for the first year of life during which the swimming activity is probably very limited. Even for older, more powerful, individuals the current-induced drift remains a major component of the movement (e.g. Gaspar et al. 2006) so that passive drift simulations covering periods well exceeding 1 yr have proven to be useful in a number of studies (Hays & Marsh 1997, Putman et al. 2010). We therefore extend our dispersal simulations to 6 yr, first using the strictly passive drift hypothesis, then adding random swimming activity to simulate occasional foraging movements. Both simulations yield quite similar dispersal patterns, showing striking coincidences with some observations and inconsistencies with others. Analysis of inconsistencies suggests that actual juveniles' trajectories must deviate from simulated trajectories after an initial period of several months during which passive drift likely prevails. We finally propose a somewhat more elaborate description of the juveniles' dispersal mechanisms that includes seasonally directed movements and better fits observations.

MATERIALS AND METHODS

Nesting sites

Nesting aggregations of the western Pacific leatherback *Dermochelys coriacea* occur primarily in New Guinea and the Solomon Islands. They comprise a metapopulation composed of a single genetic stock distinct from the eastern Pacific population, and the almost extinct Malaysian population (Dutton et al. 1999, 2007). The 2 largest identified nesting areas of the western Pacific stock are located on the north coast of New Guinea (Fig. 1). Bird's Head Peninsula (Papua-Barat, Indonesia), at the westernmost tip of the island, hosts about 75% of the nesting activity of this regional stock, estimated at 5000 to 9000 nests yr^{-1}. Further east, the Huon Gulf (Papua New Guinea) accounts for another 5% of this activity (Dutton et al. 2007). Drift simulations were performed for hatch-

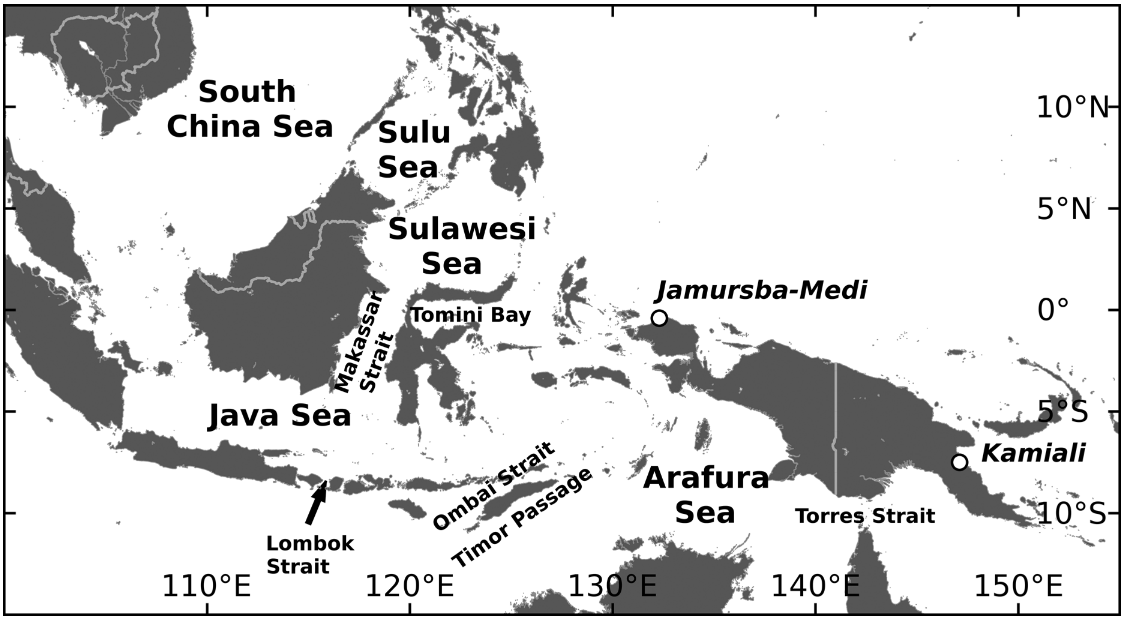

Fig. 1. New Guinea and surrounding area, featuring the 2 studied nesting sites, adjacent seas and main straits

lings emerging from Jamursba-Medi and Kamiali, the 2 main nesting beaches located on Bird's Head Peninsula and in the Huon Gulf, respectively. The migration patterns of adult females nesting on these beaches are known from various satellite-tracking experiments (Benson et al. 2007a,b, 2011).

Surface currents

Trajectories of passively drifting hatchlings and juveniles were computed using the surface current fields produced by the GLORYS-1 (G1) reanalysis of the World Ocean circulation (Ferry et al. 2008). This reanalysis covers the period 1 January 2002 to 31 December 2008 and was performed by the Mercator-Ocean operational oceanography centre (www.mercator-ocean.fr/) with the NEMO numerical ocean model (www.nemo-ocean.eu/). The model version used in G1 has a horizontal resolution of 0.25° and 50 vertical layers. It is forced by daily surface meteorological data from ECMWF (European Centre for Medium-Range Weather Forecasts).

Satellite-derived sea level anomalies, sea-surface temperatures and *in situ* measurements of vertical temperature and salinity profiles are assimilated into G1 so that this state-of-the-art reanalysis provides a close-to-reality, 7 yr long, 3-dimensional simulation of the World Ocean dynamics and thermodynamics (Ferry et al. 2010). The use of such a long reanalysis including data assimilation overcomes important limitations encountered in previous hatchlings' drift simulations: the equatorial area is covered unlike in simulations based on satellite-derived currents (e.g. Godley et al. 2010) and pluriannual trajectory simulations can be performed without concern over excessive error accumulation resulting from possible model drift in the absence of data assimilation.

The G1 surface current field features the main currents and oceanic features that are known to exist in our area of interest (Fig. 2). The complex circulation in the western Equatorial Pacific Ocean (e.g. Arruda & Nof 2003) is faithfully reproduced. The eastward-flowing North Equatorial Countercurrent (NECC) is present around 5° N. It separates the broad westward-flowing North Equatorial Current (NEC) from the more intense, but narrower, South Equatorial Current (SEC). As it reaches the Philippines, the NEC bifurcates into the northward-flowing Kuroshio and the southward-flowing Mindanao Current (MC). The quasi-permanent Halmahera (HE) and Mindanao (ME) Eddies are both correctly simulated in the retroflection area of the SEC and MC.

The New Guinea Coastal Current (NGCC) is also well resolved in the G1 reanalysis. This current proves to be of major importance in the present study as it connects the 2 studied nesting beaches. During the southeast monsoon (May to September), this current flows northwestward along the coast, generally reaching speeds close to or above 0.5 m s^{-1}. During the northwest monsoon (November to March), it weakens and usually reverses direction to flow southeast-

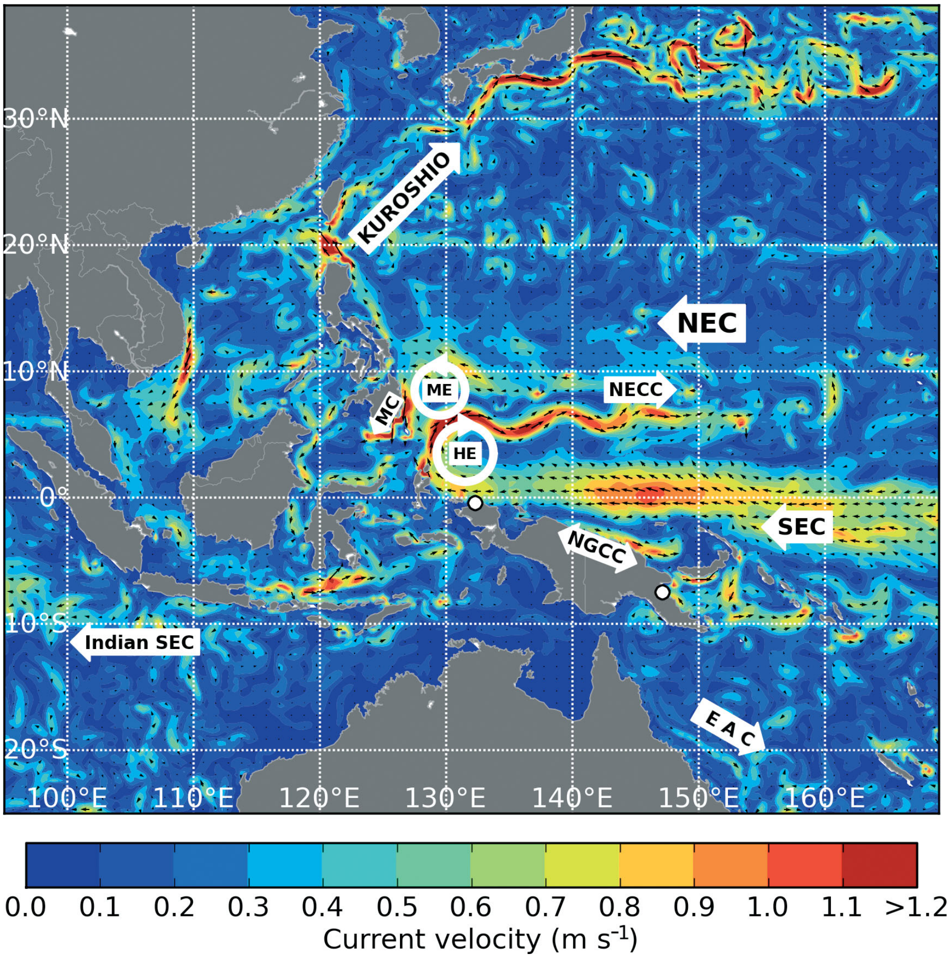

Fig. 2. A surface current field from the G1 simulation (daily mean currents on February 8, 2006). NECC: North Equatorial Countercurrent; NEC: North Equatorial Current; SEC: South Equatorial Current; MC: Mindanao Current; HE: Halmahera Eddy; ME: Mindanao Eddy; NGCC: New Guinea Coastal Current; EAC: East Australian Current

ward at similar speeds (Kuroda 2000). However, this reversal does not always happen. In particular, Ueki et al. (2003) observed that the NGCC did not reverse at all during the 1997–1998 El Niño event. Further south, the model also correctly features the turbulent southward-flowing East Australian Current (EAC), which is part of the western boundary current system of the South Pacific subtropical gyre (Bowen et al. 2005).

The Indonesian Throughflow (ITF), which is the broad flow of Pacific waters into the Indian Ocean through the Indonesian archipelago, is another main circulation feature of the studied area. The volume transport of the simulated ITF is close to 9 Sv, flowing mostly through the Makassar Strait, with secondary pathways to the east, between Sulawesi and New Guinea, consistent with observations (e.g. Gordon 2005). The ITF exits the Indonesian archipelago through 3 main passages: the Lombok Strait, the Ombai Strait and the Timor Passage, as observed (Atmadipoera et al. 2009). The outflowing water mostly augments the Indian Ocean South Equatorial Current (Indian SEC), also in agreement with observations (Wijffels et al. 2008).

Simulating trajectories

Pure drift trajectories induced by the G1-simulated currents were computed using the Lagrangian trajectory code ARIANE. This freely available software (www.univ-brest.fr/lpo/ariane/) uses an accurate, quasi-analytical, solution of the advection equation (Blanke & Raynaud 1997). Daily averaged values of the current in the first model layer (0 to 1 m) were employed in all drift simulations. One position per day was stored for further analysis.

To analyze the initial pathways of hatchlings' dispersal and their interannual variability we first performed a set of six 1 yr long simulations of the passive drift of 1000 hatchlings released off Jamursba-Medi (n = 500) and Kamiali (n = 500). For the 6 nesting seasons from 2002 to 2007, the drift of each hatchling was simulated over 365 d from its date of release.

We then performed a 6 yr long simulation of the purely passive drift of 10 000 hatchlings released, during the 2002 nesting season only, from Jamursba-Medi (n = 5000) and Kamiali (n = 5000). This is the longest possible drift simulation achievable with the G1 current data set.

As mentioned above, the passive drift hypothesis becomes questionable in such a long simulation. In an attempt to obtain a more realistic, albeit incomplete, description of juveniles' movements we performed a second 6 yr long simulation no longer neglecting the juveniles' swimming activity but assuming it is limited to random movements, mimicking motions targeted at randomly encountered drifting prey (Witherington 2002). In practice, such movements are added to passive drift movements (still simulated by ARIANE) by displacing the position of the drifting particles at the end of each (daily) time step by a distance d in a randomly chosen direction D. A similar technique was recently used by Scott et al. (2012) to simulate the impact of a directed swimming activity, governed by magnetic cues (Lohmann et al. 2001), on the drift patterns of North Atlantic loggerhead turtle hatchlings. In our case, simulated swimming movements are random so that the distribution of D is uniform between 0 and 360°. To simulate increased activity with age (a), the distance swum per day (d) is assumed to increase linearly with the straight carapace length (SCL):

$$d = \alpha \mathrm{SCL}(a) \tag{1}$$

where SCL is estimated as a function of age following the von Bertalanffy growth curve fitted for leatherbacks by Jones et al. (2011):

$$\mathrm{SCL}(a) = 1.43[1 - \mathrm{e}^{-0.226(a+0.17)}] \tag{2}$$

In these equations, SCL and d are in meters and a is in years. In practice, we use $\alpha = 3.5 \times 10^4$ so that d = 50 km d^{-1} for adults having reached their maximum size (SCL = 1.43 m) according to Eq. (2). Such large daily movements are more typical of travelling than of foraging activity (Fossette et al. 2010a), but this choice of α was made to obtain an upper bound on the possible effect of random swimming on simulated dispersal patterns. According to Eqs. (1) & (2), 1 yr old simulated individuals have a SCL of 0.33 m and swim 11.5 km d^{-1}, while 6 yr old individuals have a SCL of 1.07 m and swim 37.5 km d^{-1}.

Temperature and foraging habitats along simulated trajectories

To characterize the thermal and foraging habitats encountered by juveniles, we estimated water temperature (T_w) and net primary production (NPP) along all simulated trajectories. Use of the NPP as a proxy for juveniles' food abundance is warranted since sea turtles generally forage at low trophic levels (Polovina et al. 2001, Saba et al. 2008), even if leatherbacks likely have a more specialized diet and essentially feed on gelatinous zooplankton whose abundance is not solely related to NPP (Lilley et al. 2011).

Satellite-derived estimates of NPP can be obtained from the Ocean Productivity web site (www.science.oregonstate.edu/ocean.productivity/). This standard NPP product is based on the vertically generalized production model (VGPM) of Behrenfeld & Falkowski (1997). It is available for the entire 2002 to 2008 period, with a temporal resolution of 8 d and a horizontal resolution of 1/6°. T_w is taken to be the water temperature in the first layer (0 to 1 m) of the G1 model. As G1 assimilates satellite-derived sea-surface temperatures, T_w is within 0.5°C of these temperature observations. Based on these gridded data fields, we used simple linear interpolation in time and bilinear interpolation in space to estimate T_w and NPP values at each simulated (daily) turtle position.

Hatchling release

Given the marked seasonal variability of the regional surface currents, the timing of hatchling releases is important. The nesting season at Jamursba-Medi extends from April to September, peaking in July (Hitipeuw et al. 2007). In Kamiali, the nesting season is from November to March, peaking in December to January (Benson et al. 2007b, Dutton et al. 2007).

Allowing for an incubation period of about 2 mo, our simulated hatchling release period was between June and November, peaking in mid-September for Jamursba-Medi, and between January and May, peaking 1 March for Kamiali. Hatchlings were released daily. We arbitrarily chose the number of hatchlings released in each simulation (see 'Materials and methods: Simulating trajectories') but set the number of releases per day to fit a truncated normal distribution that peaked at the dates mentioned above (Fig. 3).

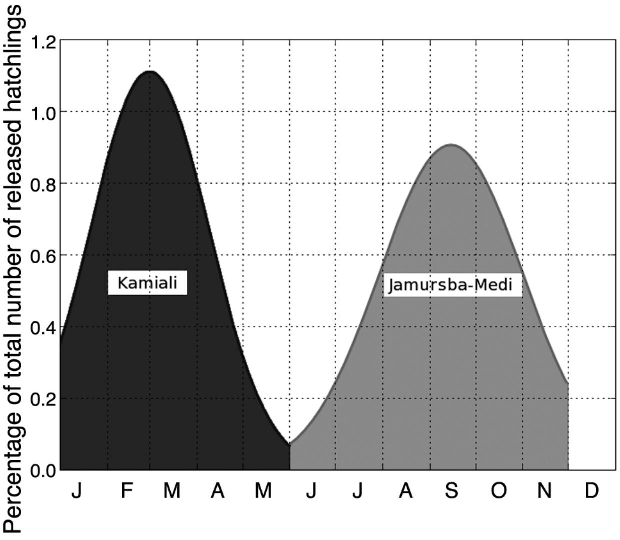

Fig. 3. *Dermochelys coriacea.* Normalized distribution of the number of simulated hatchlings released every day from Kamiali and Jamursba-Medi

To simulate the effect of the swimming frenzy, hatchlings were released in a 0.25° × 0.25° area centered about 40 km off their nesting beach. The release positions were randomly chosen but uniformly distributed inside this area. The observed swimming speed of leatherback hatchlings is close to 1 km h^{-1} during the swimming frenzy (Davenport 1987, Wyneken 1997). Hatchlings should thus be able to reach the release area during their first 24 h of frenzy and then actively disperse in this area within the next few days, when their swimming activity becomes mainly limited to daylight hours (Wyneken & Salmon 1992).

RESULTS

Annual simulations

Results of our 1 yr simulations reveal that oceanic variability off New Guinea generates multiple dispersal patterns (Fig. 4) as hatchlings emerging from the same beach, but on different days, are entrained by currents in different directions. Hatchlings emerging from Jamursba-Medi and Kamiali can, within a few months, reach 4 very different oceanic areas (Fig. 5): the Indonesian Seas and South China Sea (hereafter referred to as IC), the North Pacific (NP), the South Pacific (SP) and the Indian Ocean (IO). In addition, simulations show that complex regional current systems offer multiple pathways between the nesting beaches and these 4 oceanic areas.

Oceanic pathways from Jamursba-Medi

Most simulated hatchlings emerging from Jamursba-Medi initiate their oceanic journey moving westward under the influence of the NGCC and SEC (Fig. 4a). Having reached the western tip of New Guinea they can then follow 2 main pathways. The first follows secondary branches of the ITF and rapidly leads hatchlings into the Indonesian seas through various passages between Sulawesi and New Guinea. The second pathway leads hatchlings northwestward around the anticylonic HE. From there, several drift patterns are possible. Some turtles leave the HE moving east into the narrow NECC, until shear-induced lateral mixing finally entrains them into the NEC, that is back westward into the clockwise circulation of the North Pacific subtropical gyre. Some can drift as far as 170°W before getting entrained into the gyre. A very small number of hatchlings having followed the same route into the NECC get entrained into the SEC and end up in the South Pacific. Other turtles leave the HE to circulate anti-clockwise around the ME. Upon reaching the northwestern flank of this eddy, some are transported further north by the powerful Kuroshio and reach Japan within a year. Others get entrained into the MC that leads them back into the IC area and the Makassar Strait following the main branch of the ITF.

Once in the IC area turtles move through the maze of the Indonesian archipelago before being transported out into the Indian Ocean, mostly through the Lombok Strait, the Ombai Strait, or the Timor Passage. From there they are entrained into the South Indian Ocean subtropical gyre and start flowing westward with the Indian SEC (Fig. 4a).

Oceanic pathways from Kamiali

Kamiali hatchlings also drift into the 4 previously mentioned oceanic areas (Fig. 4b), but their distribution is slightly different and largely controlled by the seasonally variable NGCC. Depending on the NGCC direction at the time of emergence (Table 1), Kamiali hatchlings are transported either southward into the SP or northward along the northern coast of New Guinea and into the NP. All hatchlings sent adrift along the northern coast of the New Guinea coast pass off Jamursba-Medi from where they can follow the oceanic routes described in the previous section and drift into the NP, IC and IO areas. Because of the seasonal current variability, their distribution between these different routes differs from that of the

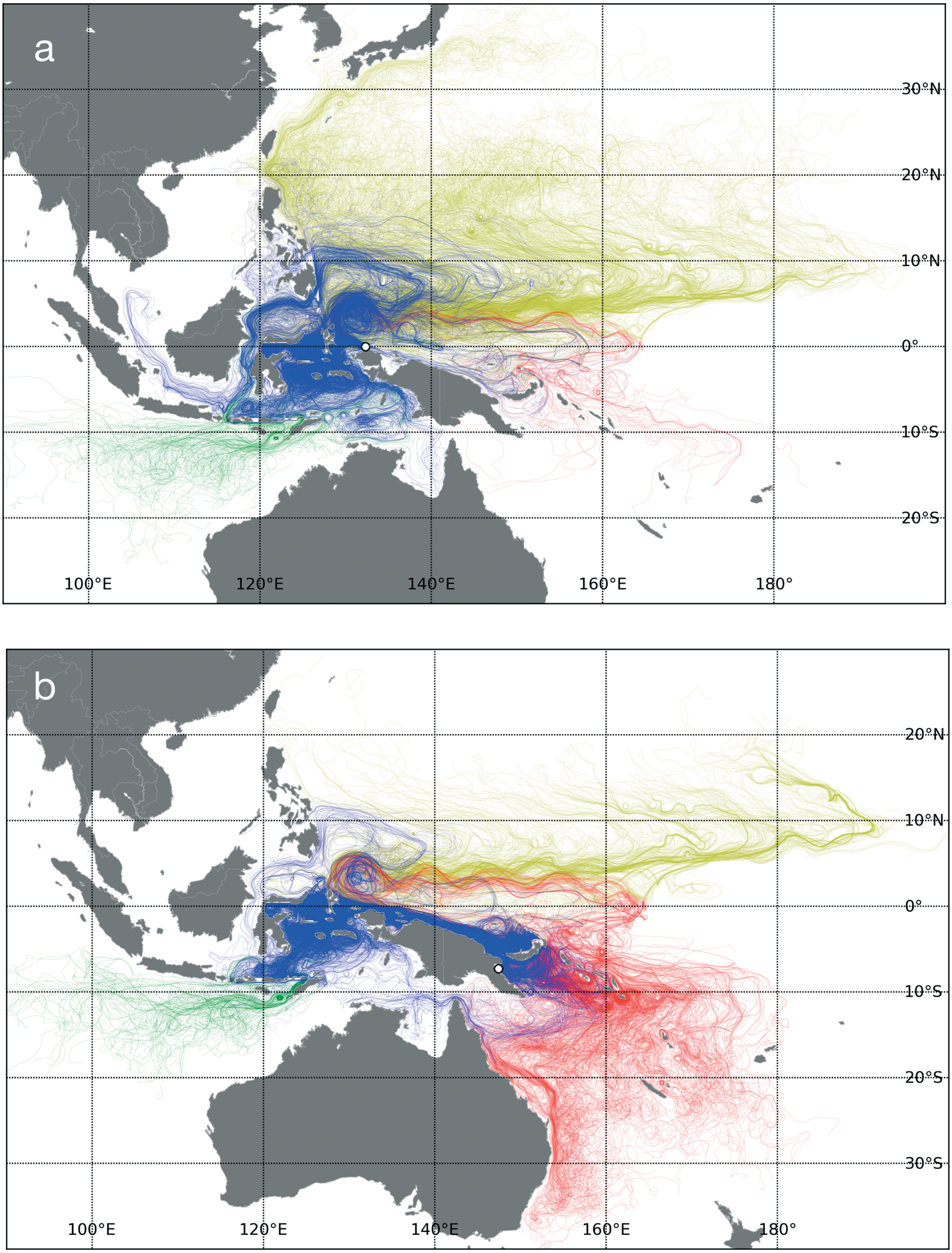

Fig. 4. *Dermochelys coriacea.* One year long trajectories of hatchlings released from (a) Jamursba-Medi and (b) Kamiali beaches. The color of each track depends on the location of its end point (see Fig. 5)

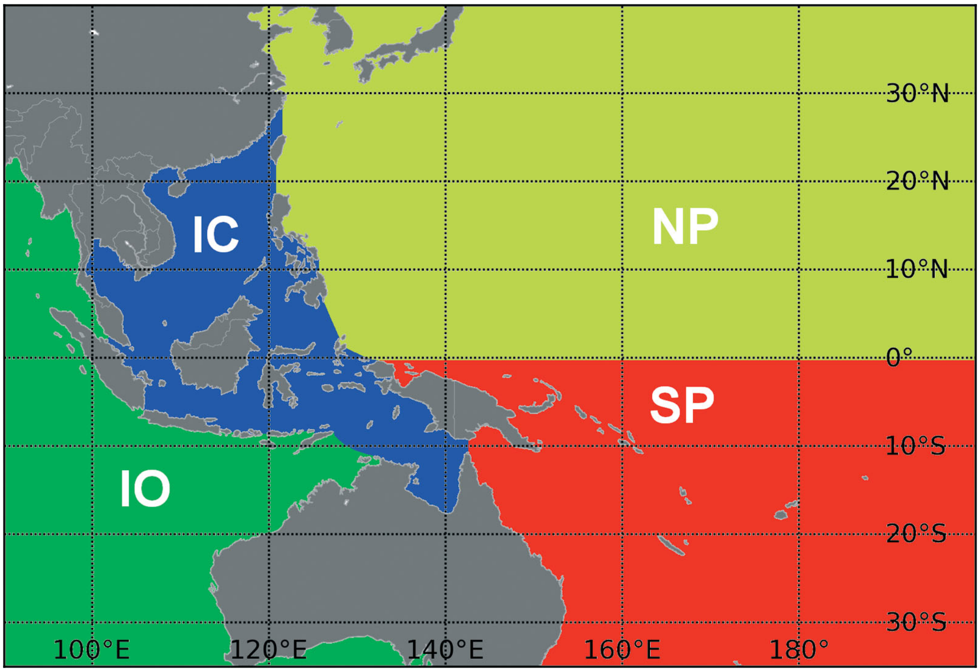

Fig. 5. Geographic extent of the 4 oceanic areas reached by simulated hatchlings. IC: Indonesian seas and China Sea, NP: North Pacific, SP: South Pacific, IO: Indian Ocean

Jamursba-Medi hatchlings. For example, several Kamiali hatchlings circle around the HE, flow into the NECC and then recirculate southward into the SEC. This pathway is used by very few Jamursba-Medi hatchlings (Fig. 4a,b).

Kamiali hatchlings transported south of 10°S are dispersed broadly southward by the complex and highly variable current system of the southwest subtropical Pacific Ocean (e.g. Kessler & Gourdeau 2007). A few (on average 2.5% of all simulated hatchlings) enter the IC area through the Torres Strait, pushed by the weak westward currents that prevail during the southeast trade wind season (Wolanski et al. 1988). Many others get entrained into the EAC as they approach the Great Barrier Reef and then into the South Pacific subtropical gyre.

Table 1. Calendar of New Guinea Coastal Current (NGCC) reversal and monsoonal wind changes together with nesting and emergence periods in Kamiali (K) and Jamursba-Medi (JM). Arrows: direction of NGCC flows. Dotted arrows: current is not always present

	J	F	M	A	M	J	J	A	S	O	N	D
Monsoonal winds	NW	NW	NW		SE	SE	SE	SE	SE		NW	NW
NGCC	↘	↘	↘		↖	↖	↖	↖	↖		↘	↘
Nesting	K	K	K	JM	JM	JM	JM	JM	JM		K	K
Hatchling emergence	K	K	K	K	K	JM	JM	JM	JM	JM	JM	

Main dispersal schemes and variability

Dispersal schemes from the nesting beaches into the different oceanic basins are not only spatially complex, they are also highly variable. We found a large interannual variation in the number of hatchlings present in each oceanic area at the end of each simulated year, with numbers typically varying by factor of 3 to 4 (Table 2).

On average about half of Jamursba-Medi and Kamiali hatchlings end up in the IC area despite the fact that these 2 beaches are not situated there. This highlights the importance of the NGCC current, which entrains hatchlings from both nesting beaches towards the northwestern end of New Guinea from where the ITF then pushes them into the IC area. Since hatchlings in the IC area almost inevitably end up in the Indian Ocean, our results point to 3 main dispersal patterns from Kamiali (into IC-IO, SP and NP) and 2 from Jamursba-Medi (into IC-IO and NP). Dispersal from Jamursba-Medi into SP is not significant.

Year 2002 is of special interest since it is the starting point for the 6 yr simulations and coincidentally is the only departure year for which a significant number of

Table 2. *Dermochelys coriacea.* Number of simulated hatchlings from Jamursba-Medi and Kamiali present in each oceanic area (IC, NP, SP, IO, see Fig. 5) at the end of each simulated year

Area	Year						Minimum (%)	Mean (%)	Maximum (%)
	2002	2003	2004	2005	2006	2007			
Jamursba-Medi									
IC	161	204	211	395	297	391	32.2	55.3	79.0
NP	280	270	264	73	148	67	13.4	36.7	56.0
SP	40	1	0	2	2	1	0.0	1.5	8.0
IO	19	25	25	30	53	41	3.8	6.5	10.6
Kamiali									
IC	235	299	117	343	214	268	23.4	49.2	68.6
NP	134	61	208	49	55	46	9.2	18.4	41.6
SP	111	47	169	100	228	167	9.4	27.4	45.6
IO	20	93	6	8	3	19	0.6	5.0	18.6

Jamursba-Medi hatchlings reach the SP (Table 2). This must be kept in mind and might be related to the fact that 2002 is classified as a moderate El Niño year (www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml). This is, however, difficult to ascertain as the G1 reanalysis does not contain any major El Niño event. In addition, the weak El Niño events of 2004 and 2006 are obviously not associated with an increased number of Jamursba-Medi hatchlings drifting into the SP (Table 2).

Six year simulations

Passive drift simulation

Results of our 6 yr passive drift simulation confirm that the Indonesian seas are only a transit area through which simulated hatchlings released in 2002 from Jamursba-Medi and Kamiali drift into the Indian Ocean (Fig. 6). Very few simulated individuals older than 1 to 2 yr are seen in this area, with the noticeable exception of Tomini Bay (Sulawesi), where a large number of turtles are still found after several years of simulation. In fact, most individuals entering this bay become trapped and circulate there for several months to several years. This is likely an artifact of the G1 model in which horizontal resolution (0.25° × 0.25°) is insufficient to properly simulate the circulation in the narrow semi-enclosed Tomini Bay. The only noteworthy effect of this model shortcoming is to artificially diminish the number of simulated juveniles finally reaching the IO.

Simulated dispersal of juveniles beyond first year appears to be confined to the interior of the 3 subtropical gyres (NP, SP and IO) within which hatch-

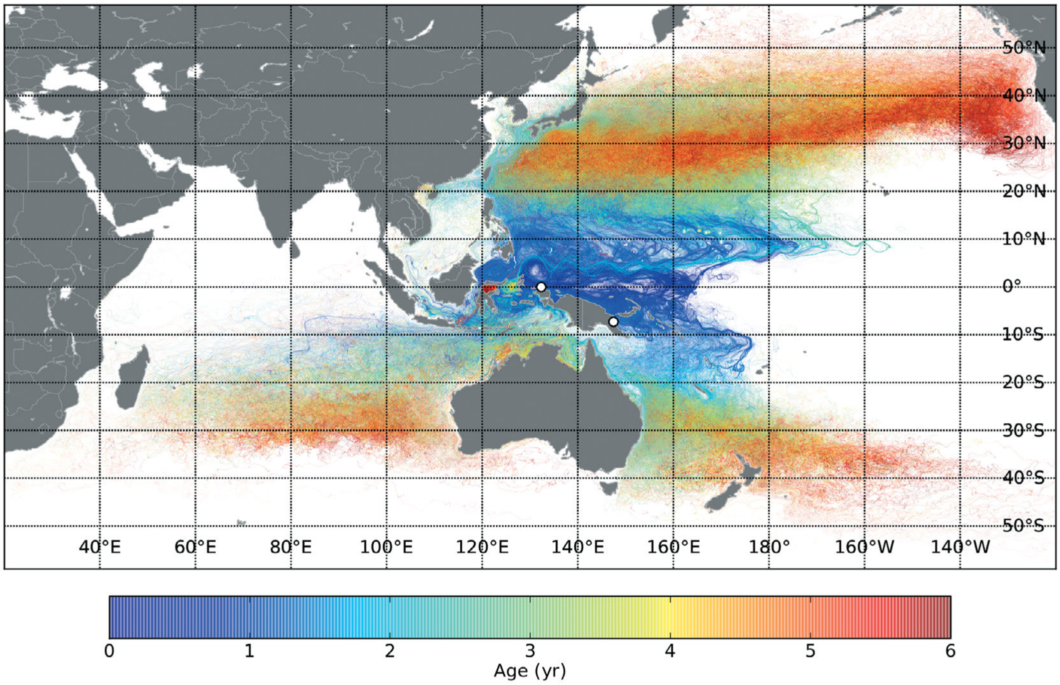

Fig. 6. *Dermochelys coriacea.* Six year long passive drift trajectories of hatchlings released during the 2002 nesting season from both Jamursba-Medi and Kamiali (white dots, see Fig. 1). The color along each track evolves as a function of the age of the simulated turtle

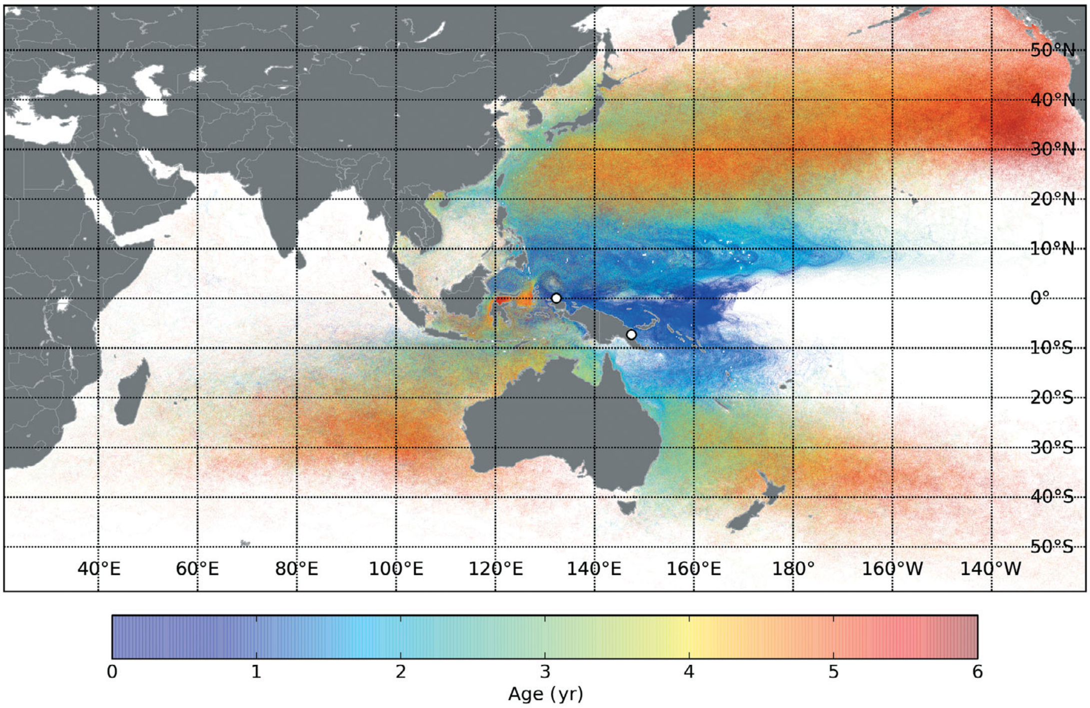

Fig. 7. *Dermochelys coriacea.* As in Fig. 6, but with random movements added to passive drift

lings are injected. Drift movements are markedly different within these 3 gyres. Individuals circulating in the strong NP subtropical gyre move rapidly eastward and reach the United States Pacific coast around 40°N within 5 yr. The fastest ones are found drifting southward in the California current during the last year of simulation (Fig. 6). Hatchlings entrained in the less developed SP gyre do not move as far east as the NP hatchlings. Most recirculate northward (and then westward) before reaching 140°W. Only a dozen (out of 10 000 simulated individuals) drift east of 140°W, pushed by a rather weak South Pacific current (Stramma et al. 1995). The situation is different in the South Indian Ocean as juveniles are injected on the eastern side of the basin from where they are rapidly entrained westward by the broad Indian SEC. This current takes some of them as far as the east coast of Madagascar. However, most individuals leave the SEC and recirculate eastward well before reaching Madagascar. This recirculation keeps them well inside the subtropical gyre so that very few juveniles reach the subtropical front bordering the gyre below 40°S (Stramma & Lutjeharms 1997). During the last simulated year, some individuals end up off Cape Leeuwin and along the southwestern coast of Australia after short loops inside the subtropical gyre.

Simulation with passive drift plus random swimming activity

Fig. 7 shows the simulated juveniles' dispersal patterns when random swimming activity, parameterized following Eq. (1), is added to passive drift. Despite the fact that the added swimming movements likely overestimate the actual juveniles' movements, the simulated dispersal patterns do not differ significantly from those obtained with strictly passive drift (Fig. 6). Dispersal pathways remain essentially the same, and dispersal areas are only broadened by added diffusion, as expected. This clearly indicates that, even in the presence of significant random swimming activity, juveniles' dispersal remains largely shaped by oceanic currents, as commonly observed in various juvenile dispersal studies (e.g. Carreras et al. 2006, Blumenthal et al. 2009).

Primary production along trajectories

NPP sampled along simulated pure-drift trajectories shows that juveniles encounter widely different foraging habitats (Fig. 8). In the NP, juveniles would encounter highly productive areas along the Asiatic continental margin, in the Japan Sea, inside the Northern Pacific Transition Zone (NPTZ, typically

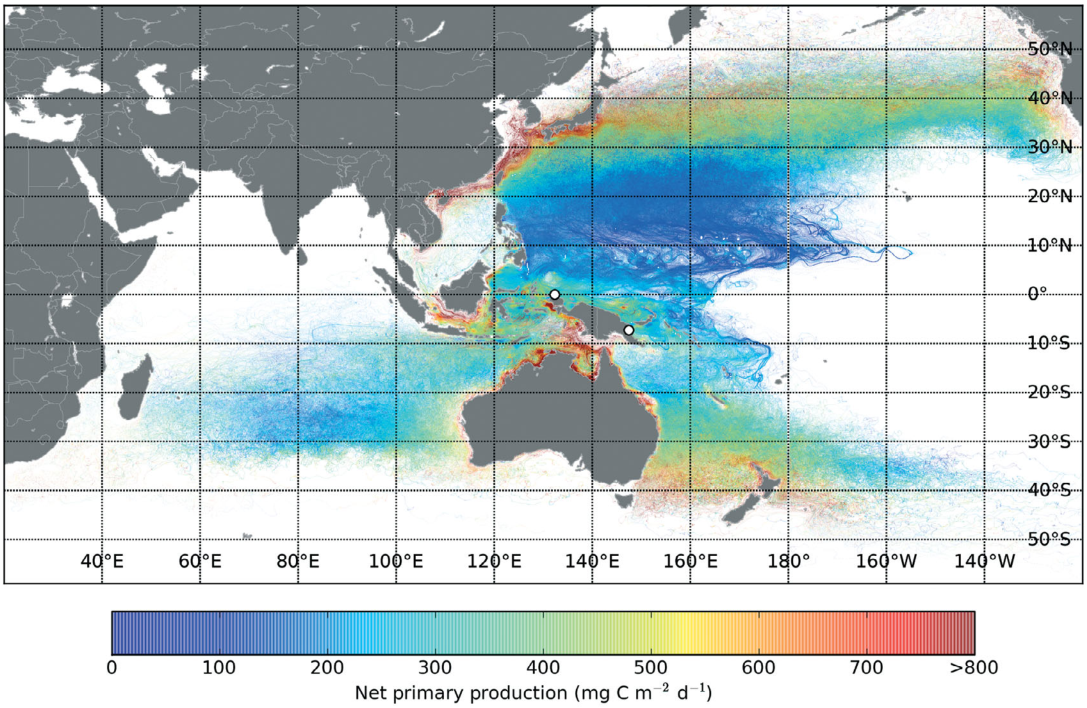

Fig. 8. Net primary production estimated along all 6 yr long passive drift trajectories

found between 30 and 40° N), and finally along the coast of California and Oregon. The NPTZ, in particular, is known to provide very favorable foraging grounds to various marine predators, including sea turtles (Polovina et al. 2001). In the SP, juveniles disperse less widely and would encounter productive areas only in the western part of the basin: along the eastern coast of Australia, the Tasman and the southern subtropical front to about 10° east of New Zealand. Juveniles drifting in the IO are less favored. Some of them can drift into productive waters along the western coast of Australia, but unlike the juveniles circulating in the NP and SP, their drift trajectories maintain most of them in oligotrophic waters inside the gyre without providing the opportunity of encountering the more productive waters of the subtropical front lying south of their dispersal area. The situation is essentially the same when considering trajectories with added random movements.

DISCUSSION

Basis for analyzing model results

While Lagrangian drift simulations have been increasingly used to study juvenile sea turtle dispersal (e.g. Blumenthal et al. 2009, Hays et al. 2010, Scott et al. 2012), the validation of modeling results remains challenging due to the scarcity of direct observations of hatchlings and juveniles at sea, especially for leatherbacks *Dermochelys coriacea*. Fortunately, leatherback bycatch data (provided by the NOAA Fisheries, Pacific Islands Regional Observer Program, Hawaii), including observed interactions with juveniles, were available to ground truth our model results. The results from satellite telemetry and genetic studies also provide useful information to further inform drift simulations (Dutton 2007, Godley et al. 2010). In particular, Hays et al. (2010) first observed a close coincidence between simulated juvenile dispersal patterns and the location of foraging grounds of satellite-tracked adults in a population of loggerhead turtles nesting in the eastern Mediterranean Sea. This led the authors to hypothesize that foraging sites used by sea turtles reflect their previous experiences as hatchlings and young juveniles, a hypothesis also evoked by Fossette et al. (2010b) to explain the observed foraging ground distribution of leatherbacks in the North Atlantic. This idea can actually be traced back to earlier works of Lohmann et al. (1999, 2008) and Freake et al. (2006) who proposed that sea turtles might progressively develop a magnetic map of the oceanic areas visited for use later in life, based on their ability to detect variations in the Earth's magnetic field (Lohmann &

Lohmann 1994, 1996). In particular, hatchlings might imprint on the magnetic characteristics of their natal area to later direct natal homing, and juveniles might record the magnetic positions of randomly discovered foraging areas to return to such sites after reproductive migrations. Natal homing in sea turtles is now generally accepted and supported by a growing body of genetic evidence (Meylan et al. 1990, Bowen & Karl 1996, Dutton et al. 2005). That juveniles record the positions of encountered foraging grounds and re-use them as adults is also a reasonable hypothesis which we term the learned migration goal (LMG) hypothesis. There would certainly be selective pressure to evolve the behavior of targeting previously known foraging areas instead of wandering in search of other unknown feeding grounds as this likely maximizes chances of survival. Note that the targeted migration goal might be a broad pelagic foraging area, at the scale of a large marine ecosystem (LME), as is the case for leatherbacks (Benson et al. 2011), or a more restricted neritic area for species like loggerheads, which recruit as juveniles to such foraging sites. In both cases, the LMG hypothesis is consistent with the observation that adult sea turtles swim fairly direct routes between their distant breeding and feeding areas (e.g. Papi et al. 1995, Luschi et al. 1998, Ferraroli et al. 2004), indicating that they have knowledge of where they are going. It is also consistent with the foraging ground fidelity observed in various sea turtle populations (Limpus et al. 1992, Broderick et al. 2007, Schofield et al. 2010), including leatherbacks (James et al. 2005, Fossette et al. 2010b, Benson et al. 2011).

Juvenile dispersal and adult migration range in the Pacific

Our simulations reveal a rare situation in which hatchlings from the same nesting stock are led by oceanic currents in 3 totally different oceanic basins and disperse quite differently within these basins (Fig. 6): dispersal covers the whole longitudinal extent of the NP, remains limited to the western part of the SP, and is restricted to the tropical band (down to about 30°S) in the South IO. In the Pacific, productive areas visited by simulated juveniles (Fig. 8) appear to coincide with the foraging areas actually used by adults. Multiple observations demonstrate that adult western Pacific leatherbacks indeed exploit the entire North Pacific. They are commonly observed foraging offshore California during summer and fall (Benson et al. 2007c) and are incidentally caught by longline and driftnet fisheries operating in the central and eastern part of the NPTZ. Genetic analyses of individuals caught at sea or found stranded in California confirm that they are almost exclusively from the western Pacific stock (Dutton et al. 2000). Furthermore, satellite tracking of 37 female leatherbacks nesting in Jamursba-Medi (Benson et al. 2011) revealed that they all target foraging grounds situated in the NP basin and adjacent seas, from the Sulu and Japan Seas in the west to the United States Pacific coast in the east. All these adult foraging grounds are commonly visited by simulated, freely drifting, juveniles (Fig. 8), with the only exception being the Sulu Sea and the adjacent southern part of the South China Sea. This area is visited by only 2% of the simulated Jamursba-Medi juveniles, while it was actually exploited by 13 out of 37 adults tracked by Benson et al. (2011). However, the Sulu Sea is separated from much more frequented areas of the North Pacific and Sulawesi Sea by the complex Philippine and Sulu archipelagos, and horizontal resolution of the G1 model only allows a crude and incomplete representation of the many small passages that exist throughout these archipelagos. This likely reduces the simulated exchange of waters, and thus of juveniles, between the Sulu and South China Seas, and the more densely populated adjacent seas. A higher resolution ocean model would be better suited to investigate this further.

Leatherbacks' dispersal is clearly more limited in the South Pacific. Adult leatherbacks are commonly observed along the east coast of Australia (Limpus 2009). Occasional sightings are also reported off New Zealand, mostly during summer around the North Island (Gill 1997). In addition, all 17 females tracked from Kamiali and the neighboring beach of Maus Buang in the Huon Gulf (Benson et al. 2011) migrated exclusively into the southwestern Pacific. All recorded trajectories occur within a narrow angular sector, aiming at the productive waters of the east coast of Australia, the Tasman front, and the western end of the southern subtropical front. This dispersal pattern is remarkably similar to that of the simulated juveniles.

Altogether, these observations clearly support the LMG hypothesis, even if it remains possible that directed swimming towards foraging sites and fidelity to these sites might not be learned but inherited, as is the case in various birds (e.g. Berthold & Helbig 1992). However, this innate migration direction (IMD) hypothesis is less appealing since: (1) assuming inheritance is less parsimonious than assuming learning, particularly given the observed diversity of foraging destinations; (2) it is difficult to conceive why sea turtles, having gained extensive knowledge of an oceanic area as juveniles, would, as adults, choose to migrate in an innate direction instead of in a familiar direction; and (3) the IMD hypothesis provides no explanation for the observation that leatherbacks migrating towards the North Pacific leave their breeding area in a very broad range of directions, while those migrating in the South Pacific migrate in a much narrower angular sector.

The LMG hypothesis implies a strong correlation between juvenile dispersal areas and adult migration goals. Though clearly observed in the Pacific, this correlation must be questioned on (at least) 2 points:

(1) Our model predicts important juvenile dispersal from Kamiali into the NP, and from both Kamiali and Jamursba-Medi into the IC-IO area. However, none of these dispersal patterns is observed in tracked adults. Does this contradict the LMG hypothesis?

(2) Our model simulates juvenile dispersal assuming either pure passive drift or drift plus random movements. While this assumption is likely valid during the first period of life, it might no longer apply to larger juveniles for which swimming activity might induce significant deviations from simple drift trajectories. If so, do the actual juvenile trajectories still lead them towards the same productive areas and thereby maintain the correlation observed in the Pacific between juvenile dispersal areas and adult migration goals?

Missing dispersal patterns

Even if the LMG hypothesis implies that adults target migration goals that they previously visited as juveniles, one would not expect all simulated juvenile drift patterns to be exploited by adults. Indeed, the oceanic circulation can lead hatchlings into unfavorable areas where mortality is so high that few or no individuals survive and later return to their breeding area. Adult migrations may thus represent only a subset of successful juvenile drift scenarios (Hays et al. 2010).

Our simulations show that over half the Jamursba-Medi and Kamiali hatchlings drift into the IC-IO area, while, so far, no adult has been tracked in that direction. Can we thus conclude that this drift pattern comes with little or no chances of survival? The answer is probably yes, for several reasons. Simulated Jamursba-Medi hatchlings cross the Indonesian archipelago in about 8 mo (mean age of the simulated Jamursba-Medi hatchlings when they reach the IO = 240 d, SD = 66 d). During that period, they drift through rich coastal waters where upper predators abound and where fisheries-induced mortality is likely high. Indonesia is, indeed, home to >2.2 million fishermen who exploit a large, mostly artisanal, fishing fleet, including an important shrimping fleet (FAO 2009). Heavily-used surface nets would be most detrimental to post-hatchlings with limited diving abilities. Then, juveniles having survived the crossing of the Indonesian seas will enter the IO close to the equator. They will drift into the South Indian subtropical gyre but without reaching the most productive waters found near its southern boundary (Fig. 8). This developmental habitat might be less favorable than that encountered by juveniles drifting in the NP or SP where currents lead them towards the productive waters of the subtropical fronts. Natural mortality in the IO might thus be higher than in the Pacific. Finally, juveniles having survived until the age of maturity will face the challenge of swimming back to their natal beach through the heavily fished Indonesian Seas. These, now larger, individuals are prone to incidental capture by many types of fishing gear including longlines (Gilman et al. 2009, Jones et al. 2011). Unfortunately, with an estimated effort of >15 million hooks per year and per 5° × 5° area, the broad region between Indonesia and the Philippines is one of the most active longline fishing areas in the world (Lewison et al. 2004). In addition, the journey back to Jamursba-Medi is against the ITF. The different branches of this broad throughflow have velocities of 10s of centimeters per second up to 1 m s^{-1} or more in the main Indonesian straits such as the Makassar, Lombok, or Ombai Straits (e.g. Chong et al. 2000, Sprintall et al. 2009). As adult leatherbacks travel at a typical swimming speed of 0.4 to 0.6 m s^{-1} (Eckert 2006, Fossette et al. 2010a), individuals attempting to return to their natal beach would often be slowed, stopped, or even moved backwards by the currents, making the trip particularly challenging. Adverse currents would also lengthen the time spent in this active longline fishing area, thereby increasing the probability of incidental capture. All together, this makes it unlikely that Jamursba-Medi hatchlings ever return to their natal area once they drift into the IO. Kamiali hatchlings transported into the NGCC before entering the IC area would also meet the same fate as they follow the same trajectory into the IO. In both cases, hatchlings drifting into the IO would have a much smaller probability of survival and return than hatchlings directly drifting into the pelagic waters of the North or South Pacific Ocean. This may explain why adults tracked from Jamursba-Medi or Kamiali have never been observed to migrate into the IO. In addition, any adult migrating in this direction would also incur a higher probability of incidental capture. This would be an additional factor contributing to the final elimination of this dispersal scheme.

Similarly, none of the adults tracked so far from Kamiali migrate into the NP, while our simulations suggest that about 18% of the juveniles are sent adrift in that direction. Is the pathway from Kamiali into the NP also associated with very high mortality? Mortality inside the NP is probably not unusually high as many Jamursba-Medi hatchlings drift into this ocean, survive and are later tracked as adults migrating back into the NP. However, unlike Jamursba-Medi hatchlings, Kamiali hatchlings do not drift directly into the NP but have to undertake a 2000 km long journey drifting northwestward with the NGCC along the north coast of New Guinea before reaching the NP pelagic realm. This journey requires about 4 mo (mean age of passively drifting Kamiali hatchlings when crossing the Jamursba-Medi meridian = 117 d, SD = 52 d) during which hatchlings mostly remain within 10s of kilometers from the coast. They thus travel in rich shelf waters and reef areas where natural predation is expected to be high and where interactions with artisanal fishing fleets are likely to occur. In addition, increased fisheries-induced mortality could impact older juveniles and adults that might be using the coastal NGCC pathway to and from the NP. The coastal leg of this dispersal pathway from Kamiali into the NP might thus be the most perilous part of the journey and reduce the survival rates to levels that preclude production of adults. A similar point was made by Saba et al. (2008) who speculated that coastal migrations are rarely observed in eastern Pacific leatherbacks because of high rates of juvenile and adult mortality induced by gillnet fisheries along the coastline of South and Central America. It is notable that out of the 5 juvenile dispersal patterns simulated here, only the 2 patterns with rapid access to the open ocean (Jamursba-Medi to NP and Kamiali to SP) appear to be re-used by adults. The 3 other juvenile dispersal patterns involve coastal legs and generally do not appear to be used by adults.

We must finally mention an additional possible, but highly hypothetic, explanation for the observation that, so far, no adult leatherback has been tracked from Kamiali into the NP. It is indeed possible that individuals, born in Kamiali and having circulated within the NP during their whole juvenile phase, have adapted to the northern hemisphere phenology where environmental cues would drive them to breed or nest during late boreal spring or summer. If their way back to Kamiali takes them first along the north coast of New Guinea anywhere near Bird's Head Peninsula, they will find themselves in the vicinity of major nesting beaches during the peak nesting season which might induce breeding in this area. The impetus to breed there might even be reinforced by the fact that the NGCC flows northwestward during that period and hence makes the eastward trip towards Kamiali particularly difficult. These individuals might then show fidelity to the site where they first bred or nested and keep foraging in the NP. In this case, they will never be seen again in Kamiali. This possibility is clearly speculative but is consistent with the high degree of genetic connectivity that has been observed between the Huon Gulf and Bird's Head nesting populations (Dutton et al. 2007), as well as the acknowledged flexibility of natal homing in leatherbacks on a broad regional scale (Dutton et al. 1999).

The need to go beyond passive drift modeling

The passive, or nearly passive, drift hypothesis is likely valid during the first months of a sea turtles' life. Differences between simulated and actual movements will thus initially be small but might later increase as individuals grow older and become more powerful swimmers.

Our simulations (Figs. 6 & 7) show that strong regional currents rapidly disperse hatchlings emerging from Jamursba-Medi and Kamiali. Within a few months, up to a year, most of them are injected into the IO, NP, or SP subtropical gyres. Once there, they will progressively drift towards higher latitudes and encounter colder waters. Leatherbacks exhibit the widest thermal tolerance of all sea turtles. Various physiological and behavioral adaptations enable them to maintain a relatively high body temperature (T_b) in cold waters (e.g. Bostrom & Jones 2007). However, the temperature gradient ($T_b - T_w$) that can be achieved increases with size (Bostrom et al. 2010). Therefore, only large adults can exploit the coldest foraging areas, while smaller individuals remain limited to warmer waters. Accordingly, the size of leatherbacks observed at sea exhibits a clear gradient with temperature and latitude (Eckert 2002, Witt et al. 2007). Analysis of a limited set of juvenile leatherback sightings led Eckert (2002) to conclude that individuals with a curved carapace length (CCL)

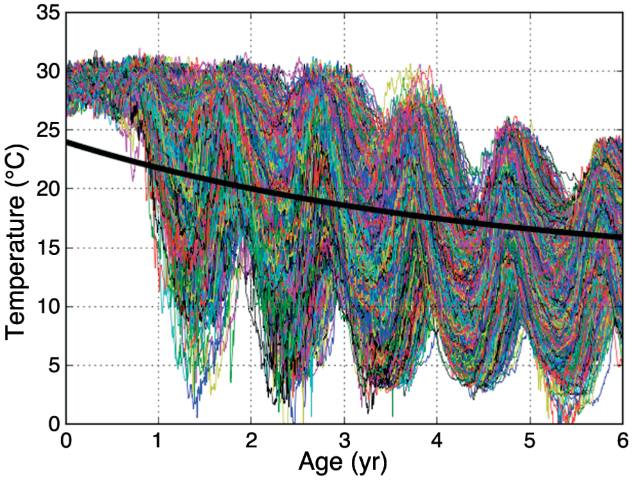

Fig. 9. Water temperature (T_w) encountered by the 1398 simulated Jamursba-Medi juvenile *Dermochelys coriacea* passively drifting towards the United States Pacific coast. The black continuous curve shows their estimated minimum sustainable temperature (T_{min}) as a function of age (Eq. 4)

<1 m occur only in waters warmer than 26°C. If this is the case, none of the 2 to 3 yr old juveniles that we simulate drifting north of 20° N, or south of 20° S, could survive at such latitudes where T_w is generally <26°C. More recently, however, 3 small (63 cm < CCL < 85 cm) leatherbacks were observed off Chile in waters between 18.1 and 21.9°C (Donoso & Dutton 2010). These temperatures are well below 26°C but still above the temperatures that many of our 3 to 4 yr old simulated juveniles encounter during winter poleward of 30°. This suggests that pure passive drift behavior cannot be maintained very long by juveniles which will be prompted to swim towards warmer waters as soon as currents transport them into areas where T_w drops below their preferred temperature and approaches their minimum tolerated temperature (T_{min}). To quantify the occurrence of such events, a precise estimate of T_{min} would be needed. This information is currently unavailable, but a crude estimate can be obtained assuming that: (1) T_{min} decreases linearly with size (SCL); (2) newborn leatherbacks can tolerate T_{min} = 24°C, the mean temperature at which Jones et al. (2011) raised hatchlings; and (3) the immature individual (CCL = 85cm) observed by Donoso & Dutton (2010) in water at a temperature of 18.1°C was close to its T_{min}. It follows that:

$$T_{min}(\mathrm{SCL}) = 24.4 - 7.9 \cdot \mathrm{SCL} \qquad (3)$$

This relation is obtained knowing that the mean SCL of hatchlings (a = 0) is 5.4 cm (based on Eq. 2), and that CCL = 85 cm corresponds to SCL = 79.8 cm, based on the relation SCL = (CCL − 0.0204)/1.04 (Tucker & Frazer 1991). Interestingly, Eq. (3) yields T_{min} = 13.1°C for adults having reached the maximum SCL of 1.43 m given by Eq. (2). McMahon & Hays (2006) situate the lower bound on adult leatherbacks' thermal habitat at around 15°C, while Witt et al. (2007) indicate a smaller value of 10 to 12°C. Our 13.1°C estimate thus appears to be within the reasonable range of values. Using Eq. (2), T_{min} can readily be expressed as a function of age:

$$T_{min}(a) = 13.1 + 11.3e^{-0.226(a+0.17)} \qquad (4)$$

Based on this relation we can easily determine when and where simulated juveniles encounter $T_w \le T_{min}$. The example of the Jamursba-Medi juveniles drifting towards California is especially interesting. The 6 yr long pure drift simulation yields 1398 individuals that move past 140°W in the North Pacific, and are thus headed towards the United States Pacific coast. As shown in Fig. 9, the water temperatures they encounter along their drift trajectories remain well above T_{min} during the first year of simulation, as currents keep them in warm, near-equatorial, areas. During the second year, T_w starts dropping seasonally below T_{min} and nearly 500 simulated juveniles (35%) endure $T_w < T_{min}$, mostly individuals that drifted rapidly northward into the Kuroshio, without circulating first into the NECC. A year later, <250 individuals have not yet encountered $T_w < T_{min}$. At the end of the simulation, essentially all juveniles have endured at least 1 period with $T_w < T_{min}$. Fortunately, this result shows little sensitivity to our, admittedly crude, estimate of T_{min}. Indeed, if T_{min} is lowered by as much as 5°C (for all ages), still 85% of the juveniles drifting towards California encounter water temperatures below their T_{min}.

Seasonal migration towards warmer waters thus appears to be mandatory for the survival of juvenile leatherbacks in the North Pacific. Such migrations towards warmer waters are commonly observed in autumn in both juveniles and adults of other sea turtle populations (e.g. Musick & Limpus 1997, Polovina et al. 2004, Mansfield et al. 2009) and in large juvenile and adult leatherbacks (James et al. 2005, Benson et al. 2011). Similar migrations by small juvenile leatherbacks are thus highly likely. As widely observed in other sea turtle species, and more generally in pelagic predators (Block et al. 2011), this equatorward autumn migration would be followed by a poleward spring migration as water temperatures increase and allow access to more productive, high-latitude foraging grounds. Such north–south migrations governed by thermotaxis and food availability would occur in the predominantly eastward circulation of the central North Pacific so that juvenile leatherbacks would ultimately reach the United States Pacific coast, but probably later than in the passive drift scenario, as juveniles encounter weaker (but still eastward) currents while seasonally retreating towards the center of the subtropical gyre. To evaluate this effect, we performed a simple experiment in which, after 1 yr of pure passive drift, simulated Jamursba-Medi juveniles drifting in the North Pacific initiate seasonal migrations, actively swimming southward during fall and northward during spring. As in the simulation of random swimming activity, a size-dependent displacement of *d* (km d^{-1}) is used, with *d* given by Eq. (1). This displacement is added every day to the current-induced drift, using the following algorithm:

- During spring: a displacement of *d* (km d^{-1}) is applied towards the north; this displacement is not applied if it causes the simulated turtle to enter water with $T_w < T_{min}$
- During summer and winter: no displacement is added (pure drift)
- During fall: a displacement of *d* (km d^{-1}) is applied towards south

With this simple algorithm we ensure that, during spring migration, no turtle moves northward faster than the T_{min} isotherm. Also, with daily meridional movements of around 35 km d^{-1} sustained during the 3 spring or fall months, the oldest simulated individuals (5 to 6 yr old) undertake seasonal migrations spanning nearly 30° in latitude, from about 40° N in summer to 10° N in winter. Such a large migration range is consistent with the amplitude of the seasonal migrations observed in adults tracked from California (Benson et al. 2011).

Results of the simulation with added seasonal migration movements indicate that, at the end of the sixth year of simulation, only 10 % of the simulated turtles heading towards California have reached the longitude of Hawaii (155° W), and <1 % have reached 145° W. This confirms that seasonal migrations effectively slow down the progression of simulated juveniles towards the eastern part of the Pacific basin and suggests that the entire journey to the United States Pacific coast would average 8 to 9 yr versus 5 yr for the passive drift simulation. This slower drift scenario is actually more consistent with the observed size distribution of leatherbacks in the central and eastern North Pacific. Indeed, the recorded sizes of leatherbacks incidentally caught by the Hawaii-based pelagic longline fishery (Fig. 10) show that only large leatherbacks (SCL > 1.3 m), likely much older than 5 yr, are observed east of 150° W. Individuals observed close to the coast of California are also in this size range (Harris et al. 2011). This indicates that 5 yr old leatherbacks are unlikely to be present in the easternmost part of the basin. Medium sized individuals (1 m ≤ SCL ≤ 1.3 m), however, are incidentally caught in the NPTZ at longitudes reaching nearly 150°W, suggesting that 5 to 10 yr old individuals are present in the central Pacific, in agreement with the slower drift scenario. Interestingly, also, bycatch of small leatherbacks is reported south of Hawaii in sizes range between 50 and 87.5 cm, corresponding to 2 to 4 yr old juveniles (Jones et al. 2011). All were captured at locations centered around 10° N, 165° W, which is the area where a number of simulated 2 to 3 yr old juveniles (either purely drifting or drifting and randomly foraging) finish their ride in the NECC before recirculating westward in the NEC. This suggests that passive or nearly passive drift in the warm waters of the NECC might explain how these small individuals reached the area where they were caught.

All together this suggests that juvenile western Pacific leatherback turtles migrating in the North Pacific might act as nearly passive drifters for a period of 1 or 2 yr, until oceanic circulation takes them into areas where T_w approaches T_{min} and induces active swimming towards warmer waters. From this point, displacements will result from a combination of current-induced drift and habitat-driven movement based on temperature and food availability. A similar scenario can be expected in the South Pacific where nearly 75 % of the simulated Kamiali juveniles freely drifting south of 30° S encounter $T_w < T_{min}$. Interestingly, such a scenario would not drastically modify the spatial distribution of juveniles simulated under the passive drift hypothesis. It would essentially add north–south, back and forth, movements to the already simulated drift movements. This would broaden (essentially equatorward) the latitudinal extent of the dispersal areas, but their longitudinal extent (and thus their penetration into the eastern part of the Pacific basin) would be less affected and still controlled by the strength of the circulation in the subtropical gyres. The SP gyre being less developed and weaker than its NP counterpart (e.g. Stramma et al. 1995), our basic finding of a dichotomy between extensive dispersion in the North Pacific and dispersal limited to the western part of the South Pacific remains, and provides support for the LMG hypothesis.

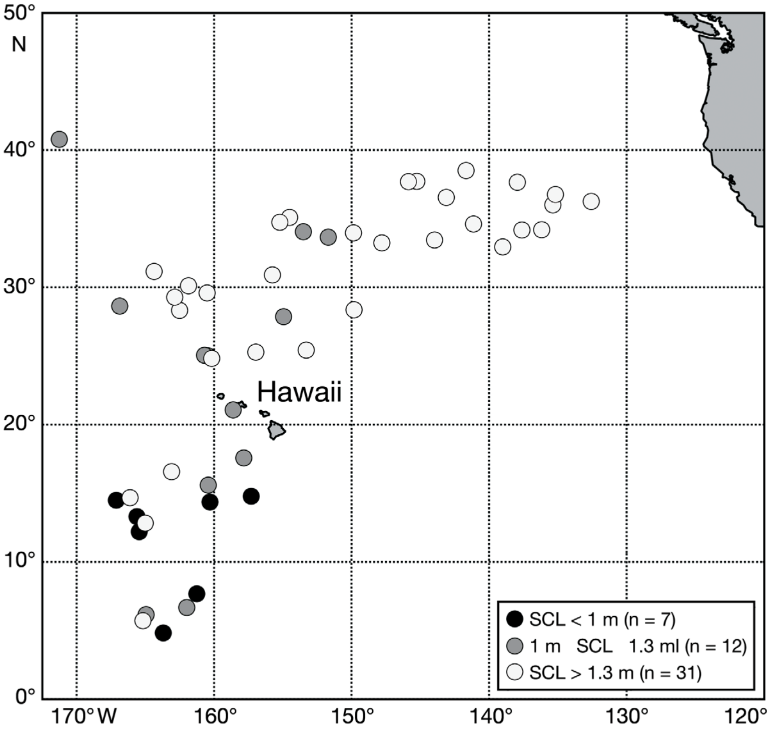

Fig. 10. *Dermochelys coriacea.* Spatial distribution of incidental catches of leatherbacks by the Hawaii-based pelagic longline fishery. These bycatch events were recorded by the NOAA Fisheries, Pacific Islands Regional Observer Program (Hawaii) between April 1994 and March 2011. Only the records including the position, date and size of a captured individual are featured here. All individuals with straight carapace length (SCL) <1 m had their size precisely measured. Only an eyeball estimate of the size was available for larger individuals. This estimate is assumed to be equal to the SCL. Given the limited accuracy of such estimates, only 3 broad classes of sizes are distinguished here. n = sample size

SUMMARY AND CONCLUSIONS

The current paper presents the first model-based investigation of the oceanic dispersal of juvenile western Pacific leatherback turtles *Dermochelys coriacea*. Our passive drift simulations reveal a rare situation in which hatchlings emerging from the same nesting beach are likely to be entrained by highly variable currents into 3 widely different dispersal areas situated in the NP and SP and IO.

The IO dispersal scheme, so far not used by tracked adults, appears to be associated with very high juvenile mortality. Exposure to high predation and fisheries-induced mortality during the crossing of the Indonesian seas, relatively poor foraging habitats in the IO and a strenuous return journey against dominant currents probably all contribute to the low probability of survival by juveniles moving into this area. Our simulations indicate that the percentage of hatchlings drifting into the IC-IO area typically varies between 30 and 80 %, depending on the year of emergence, and suggests that interannual ocean variability may have a major impact on the global juvenile survival rate and thus on the evolution of the western Pacific leatherback population as a whole.

Our simulations also show that, within 1 to 2 yr, currents likely entrain many juveniles towards temperate regions where winter water temperatures drop well below the minimum temperature likely tolerated by such small turtles. This leads us to hypothesize that, after an initial period of mostly passive drift, juveniles must initiate active swimming towards lower latitudes before winter and back again towards higher latitudes, where food abounds, during spring. Such seasonal north–south migrations would significantly slow the eastward progression of individuals circulating in the North Pacific current. This slower drift scenario better explains the size distribution of leatherbacks incidentally caught by pelagic fisheries in the central and eastern North Pacific and the fact that only large individuals are observed off the United States Pacific coast.

The juvenile dispersal mechanism proposed here, combining passive drift movements with seasonal habitat-driven migrations might well apply to many other sea turtle populations. The juvenile dispersal mechanism proposed here, combining passive drift movements with seasonal habitat-driven migrations, might well apply to many other sea turtle populations. It shall serve as a framework for developing more complete models of juvenile sea turtle dispersal, explicitly including the responses of animals to their environment. Such models will be refined as new direct observations of juveniles' movements and more detailed studies of their thermal ecology become available.

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A biologist's guide to assessing ocean currents: a review

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ABSTRACT: We review how ocean currents are measured (in both Eulerian and Lagrangian frameworks), how they are inferred from satellite observations, and how they are simulated in ocean general circulation models (OGCMs). We then consider the value of these 'direct' (*in situ*) and 'indirect' (inferred, simulated) approaches to biologists investigating current-induced drift of strong-swimming vertebrates as well as dispersion of small organisms in the open ocean. We subsequently describe 2 case studies. In the first, OGCM-simulated currents were compared with satellite-derived currents; analyses suggest that the 2 methods yield similar results, but that each has its own limitations and associated uncertainty. In the second analysis, numerical methods were tested using Lagrangian drifter buoys. Results indicated that currents simulated in OGCMs do not capture all details of buoy trajectories, but do successfully resolve most general aspects of current flows. We thus recommend that the errors and uncertainties in ocean current measurements, as well as limitations in spatial and temporal resolution of the surface current data, need to be considered in tracking studies that incorporate oceanographic data. Whenever possible, cross-validation of the different methods (e.g. indirect estimates versus buoy trajectories) should be undertaken before a decision is reached about which technique is best for a specific application.

KEY WORDS: Geostrophic · Ekman drift · Dispersal · Orientation · Turtle · Marine mammal · Plankton · Argos · Satellite-tracking

INTRODUCTION

Currents are a fundamental feature in the oceans and have a number of profound impacts on animal and plant movements (Chapman et al. 2011). Consequently information about currents is often useful to biologists. For example, currents will disperse small animals that cannot swim strongly and thereby influence their distribution and abundance (e.g. Munk et al. 2010, Putman et al. 2010a, Hamann et al. 2011) as well as genetic structuring and connectivity of populations (e.g. Dawson et al. 2005, Godley et al. 2010, White et al. 2010, Casabianca et al. 2012). For decades, marine biologists have therefore needed some knowledge of physical oceanography. Historically, this knowledge was often simply a rudimentary understanding of the main ocean currents (Scheltema 1966, Kleckner & McCleave 1985). For example, almost 30 yr ago, it was inferred that the anticyclonic (clockwise) flow of the North Atlantic gyre would carry hatching turtles from nesting beaches in Florida across the Atlantic to distant sites such as the Azores (Carr 1987). More recently, the easy access to direct measurements of currents has led biologists

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to examine some of the subtleties of current flows (Beaulieu et al. 2009, Landry et al. 2009, Lobel 2011). In some cases, biologists are also interested in knowing the currents at specific locations and at specific times where direct measurements are not always available. For instance, estimating the ocean currents along the paths of satellite-tracked marine species, such as sea turtles, sea birds or marine mammals, may allow inferences of how environmental factors contribute to the animal's movement and behaviour (e.g. Sakamoto et al. 1997, Nichols et al. 2000, Hatase et al. 2002, Luschi et al. 2003a, Gaspar et al. 2006, Cotté et al. 2007, Seminoff et al. 2008, Bailleul et al. 2010).

Three general approaches have been adopted to estimate the effects of currents along the paths of satellite-tracked marine animals. Lagrangian drifter buoys (see Appendix 1) provide 'direct' *in situ* information on surface currents (Campagna et al. 2006, Horton et al. 2011), although there are caveats related to buoy performance. Two additional techniques are well established: (1) satellite observations are used to infer surface current fields at regular intervals (Gaspar et al. 2006, Cotté et al. 2007, Seminoff et al. 2008, Bailleul et al. 2010, Campbell et al. 2010); and (2) particles are tracked in numerical ocean circulation models to mimic Lagrangian drifter buoys (Bonhommeau et al. 2009, Sleeman et al. 2010, Kobayashi & Cheng 2011). While surface currents may be estimated from satellite observations at a spatial resolution of about 25 to 100 km (Rio & Hernandez 2004, Pascual et al. 2006, Rio et al. 2011), the current fields simulated in ocean general circulation model (OGCM) hindcasts (e.g. Chassignet et al. 2007, Lambrechts et al. 2008, Grist et al. 2010, Storkey et al. 2010) may be of finer spatial resolution, higher temporal resolution, and are not compromised by several physical approximations and assumptions, particularly in regions of swift flow. On the other hand, models do not correctly represent all physical processes, and so simulated currents also have limitations that must be considered.

Given the variety of techniques now available for assessing ocean currents, some of which have only recently been used by biologists, it is timely to review the strengths and weaknesses of these different approaches. This paper is organised as follows. We first briefly summarise the physics of ocean currents, paying particular attention to the large-scale circulation. In the subsequent section, we review 3 approaches to surface current estimation. We begin by examining the utility of *in situ* measurements of currents and some of the key resources available to biologists. We then consider various approaches for inferring current fields when *in situ* measurements are not available. We use satellite-tracked leatherback turtles *Dermochelys coriacea* as a case study, and, when possible, we compare the methodologies to each other. Additionally, we highlight some of the potential limitations for inferring animal behaviour from these measures of ocean current data. In this way we identify some general rules to follow when interpreting the paths of satellite tracked marine animals and provide guidance for biologists interested in using ocean current information.

THE PHYSICS OF OCEAN CURRENTS

A number of well known physical processes generate ocean currents. Under a prevailing wind, the balance of surface wind stress and the Coriolis force (see Appendix 1) due to the spin of the Earth result in near-surface 'Ekman' currents (see Appendix 1), with net flow in a surface Ekman layer (the upper few 10s of m) oriented to the right of the wind direction in Northern Hemisphere and to the left of the wind direction in the Southern Hemisphere (Stewart 2008). The resulting 'Ekman transport' further results in variations in the height of the sea surface, which in turn generates horizontal gradients in water pressure. Where the associated pressure gradient force is balanced to first order by just the Coriolis force (where inertial and frictional effects are negligible), the balanced current is termed 'geostrophic' (see Appendix 1) (Stewart 2008).

Geostrophic currents dominate the large-scale ocean circulation. A geostrophic current is a flow moving along contours of equal pressure, often equivalent to sea surface height. The orientation of the flow in relation to the horizontal gradient of pressure, or sea surface height, depends on the hemisphere: viewed from above, geostrophic flow in a subtropical gyre (with central high pressure) is clockwise in the Northern Hemisphere and counterclockwise in the Southern Hemisphere. The strength of a geostrophic current is proportional to the associated pressure (or sea surface height) gradient. The utility of the link between sea surface height and geostrophic currents is emphasised below, where we explain how surface currents are inferred from satellite altimetry.

Weak 'interior' currents across broad expanses of the subtropical ocean basins are essentially in full geostrophic balance. In contrast, narrow, swift currents are found on the western side of the subtropical basins, due to the direction in which the Earth rotates (see Stewart 2008 for a detailed explanation). These 'western boundary currents' include the Gulf Stream (North Atlantic), the Kuroshio (North Pacific) and the Agulhas Current (South Indian), and are only in approximate geostrophic balance. As flow speed increases, geostrophy breaks down to an appreciable extent, the boundary currents become unstable, and meandering develops. Downstream of the meandering a rich 'eddy' field is observed, and the flow may be regarded as rather chaotic, although the weaker flow in individual eddies, drifting away from the boundary current, may return close to geostrophic balance. While some notable currents are also observed on the eastern side of the basins, these are principally linked to surface heat loss and shelf edge topography, and are not intrinsically driven by the wind.

ESTIMATING OCEAN CURRENTS

Measuring surface ocean currents and surface drift

In situ measurements of current flows have traditionally been made in 2 different ways. Eulerian measurements (see Appendix 1) involve recording the currents at one location over time, often with a current meter deployed from a ship or mooring. By contrast, Lagrangian measurements involve releasing an object, often a tracked buoy, to record how a particular 'parcel' of water moves. Current data from these 2 types of measurement are now widely available on the Internet. For example, the PIRATA and TAO moorings in the Atlantic and Pacific provide current meter data at a range of depths from oceanic sites (Table 1). Similarly, Lagrangian data are available for near-surface tracked buoys as well as ARGO floats that travel with deep ocean currents and periodically return to the surface to relay their location (Table 1).

Perhaps the most accessible information on ocean currents for biologists to use is the Atlantic Oceanographic and Meteorological Laboratory (AOML) Lagrangian drifter buoy data set, which extends from 1979 to the present (Table 1). The data consist of numerous trajectories of surface floats attached via a thin tether to a sub-surface drogue (see Appendix 1) centred at 15 m. As the drogue dominates the area of the instrument, the trajectory is determined primarily from the near-surface currents rather than the surface wind (Fig. 1). The buoys are tracked by using the Argos system and then 6 h interpolated locations are provided via a web interface. These Lagrangian drifter trajectories provide a 'direct' *in situ* measurement of near-surface flows. However, it is important to recognise that even Lagrangian drifters do not provide an exact description of the ocean circulation. Drifters are susceptible to slip with respect to the water at 15 m depth, due to the drag on both the tether and the drogue from shear currents, direct wind forcing on the float and impact of surface waves. For instance, at 10 m s^{-1} wind speeds and related wave conditions, the drifter's slip can reach 0.7 m s^{-1} (Niiler & Paduan 1995, Niiler et al. 1995). In addition, the presence of some undrogued drifters in the AOML data set can also result in errors in the measured current velocity (Grodsky et al. 2011). Yet examining groups of drogued drifter trajectories remains a reliable method to reveal the mean flow in a specific area while individual trajectories reveal the complexity underlying these general patterns.

Building on the work of Carr (1987), for example, Lagrangian drifter trajectories have been used to show the variability of the current flows in the North Atlantic gyre. These findings suggest that some hatchling sea turtles passively drifting near the ocean surface could be carried from the coast of Florida on northerly trajectories to the coasts of the UK, Ireland and France. By contrast, others may become entrained in the central part of the North Atlantic gyre (the Sargasso Sea) for long periods, and still others may be carried around the North Atlantic gyre passing the Azores before returning towards the Caribbean (Fig. 1).

More recently, Lagrangian drifters have also been used to test hypotheses of population genetic structuring. For example, for green turtles *Chelonia mydas* in the North Atlantic, haplotypes evident in nesting turtles in Suriname, Ascension Island and Guinea Bissau have also been recorded in juveniles of this species foraging in Cape Verde Islands (Monzón Argüello et al. 2010). Lagrangian drifter trajectories have revealed that passive drift of hatchling turtles is possible between these widely (>1000 km) separated breeding and foraging sites. Hence, the sites that turtles inhabit as juveniles may simply be a consequence of the prevailing surface currents encountered during early life stages rather than some innate tendency to actively swim to particular sites. Lagrangian drifter trajectories can therefore provide information on general current patterns (see also Scott et al. 2012). However, it is difficult to use such drifters to obtain quantitative information about the frequency of different drifting scenarios, for instance.

Table 1. Summary of oceanic physical data-sets and tools to manipulate NetCDF data and for particle tracking

Name	Description	Data access and extraction services	Data format	Website
AVISO	Access to sea surface heights (SSH), dynamic topography (MDT, MADT), sea level anomalies (SLA, MSLA), wind and wave data	AVISO data extraction tool FTP access Live access server	NetCDF GDR	www.aviso.oceanobs.com/
CTOH Legos	Access to global surface currents from 1999–2009: Geostrophic current anomalies from altimetry, Ekman currents at 15 m depth from Quickscat scatterometry and mean geostrophic circulation from a climatological mean sea surface product	Online form FTP access	NetCDF	http://ctoh.legos.obs-mip.fr/products/global-surface-currents
CERSAT	Access to daily wind stresses derived from Quickscat scatterometer measurements	Online form FTP access Data browser		www.ifremer.fr/cersat
HYCOM	Numerical ocean general circulation model with hybrid vertical coordinate (combining vertical levels and isopycnal layers). Access to near real time global HYCOM + NCODA-based ocean prediction system output. Daily global model output available spanning November 2003 to present at a resolution of 0.08°	Live access server FTP access THREDDS access using OPeNDAP	NetCDF	www.hycom.org/
ICHTHYOP	Software tool for offline trajectory calculations with ROMS, MARS and NEMO datasets. Also permits the modelling of certain biological parameters important in characterising the movement of ichthyoplankton	On request (follow website instructions)	JAVA	www.brest.ird.fr/ressources/ichthyop/index.php
NEMO	Numerical ocean general circulation model with constant depth levels as vertical coordinates. Access to 1958–2007 global hindcasts at resolutions of 0.25° and 0.08°	By collaboration with NEMO team	NetCDF	www.noc.soton.ac.uk/nemo/
ARIANE	Software tool for offline trajectory calculations with NEMO datasets	On request (follow website instructions)	Fortran 90 and ancillary files	http://stockage.univ-brest.fr/~grima/Ariane/
Global Lagrangian Drifter Data	Data from satellite-tracked drifting buoys ('drifters') which collect measurements of upper ocean currents and sea surface temperatures (SST) around the world as part of the Global Drifter Program. Observation dates: 1979/02/15 to 2010/12/31	Online form FTP access	Ascii	www.aoml.noaa.gov/envids/gld/
USGODAE Argo Page	The USGODAE server is one of the 2 Argos Global Data Assembly Centers	Live access server	NetCDF	www.usgodae.org/argo/argo.html
	Access to entire set of delayed-mode data from the Argo temperature-salinity profiling floats	USGODAE Argo GDAC data browser FTP access		
TAO: Tropical Atmosphere Ocean project	Access to real-time data from 70 moored ocean buoys in the Tropical Pacific Ocean, telemetering oceanographic and meteorological data to shore in real-time via the Argos satellite system	Live access server Online form FTP site	Ascii NetCDF	www.pmel.noaa.gov/tao/index.shtml
PIRATA: Prediction and Research Moored Array in the Tropical Atlantic	Access to real-time and delayed mode data from moored ocean buoys in the Atlantic Ocean, telemetering oceanographic and meteorological data to shore in real time via the Argos satellite system	Live access server Online form FTP site	Ascii NetCDF	www.brest.ird.fr/pirata/pirata.php
OPeNDAP	Freeware to access and manipulate NetCDF data			www.opendap.org/
Ncdump	Freeware to access and manipulate NetCDF data			www.unidata.ucar.edu/software/netcdf/docs/ncdump-man-1.html
Unidata	List of software packages for manipulating or displaying NetCDFdata			www.unidata.ucar.edu/software/netcdf/software.html

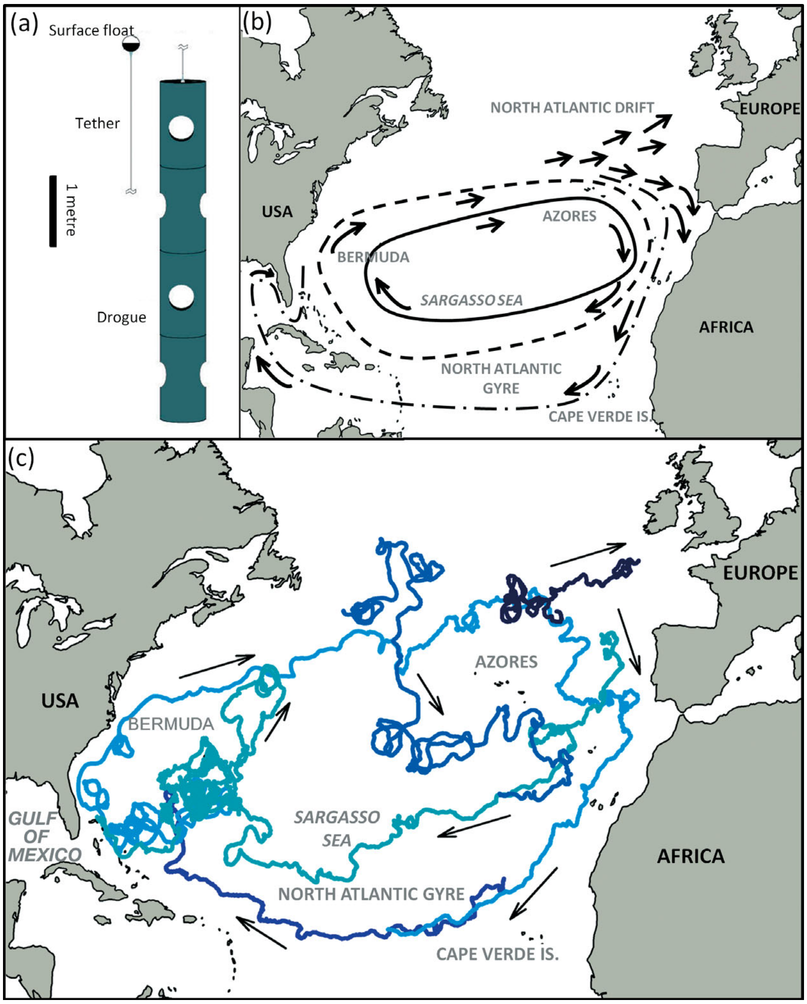

Fig. 1. (a) Schematic diagram of the typical AOML Lagrangian drifter used to determine surface currents (modified from www.aoml.noaa.gov/phod/dac/gdp_drifter.php). The surface float ranges in diameter from 30.5 to 40 cm and contains an Argos transmitter. The drogue is centred at a depth of 15 m. The drogue is cylindrical and each drogue section contains 2 opposing holes, which are rotated 90 degrees from one section to the next. The outer surface of the drogue is made of nylon cloth. The design is thought to be optimum for measuring near-surface currents. Drifters typically function for around 400 d. The AOML Lagrangian drifter data-set contain 1250 individual trajectories. See www.aoml.noaa.gov/envids/gld/. (b) A representation of the general currents in the North Atlantic, modified from Carr (1987). (c) Examples of Lagrangian drift trajectories from the North Atlantic showing the general characteristics of the anticyclonic (clockwise) flow in the North Atlantic as well as the variability in current flows. These trajectories reveal some of the likely variation in the trajectory of animals that are carried passively by the current

The tracks of large marine animals that can swim strongly, such as adult sea turtles or marine mammals, have also been compared to Lagrangian drifter trajectories (e.g. Luschi et al. 2003b, Craig et al. 2004, Campagna et al. 2006, Bentivegna et al. 2007, Horton et al. 2011). The use of drifters in this context can give insights into the general water circulation in an area and how ocean migrants travel long distances with swimming being facilitated or impeded by prevailing currents (Fig. 2). However, due to the dynamic nature of ocean currents, inferences about the movement process of individual animals requires that the drifters (1) occur in close proximity to the location of the tracked animal and (2) that the drifter and animal are transmitting positional data at the same time. For example, comparing movements of southern elephant seals *Mirounga leonina* in the South West Atlantic with those of surface drifters, coinciding in time and space, revealed a strong coupling between the swimming dynamics of seals and the speed and direction of surface currents (Campagna et al. 2006). However Lagrangian drifter buoys often do not cover a sufficient area of ocean to provide estimates of current conditions at the precise location of the marine animal being tracked. Moreover, slight differences in position and timing can greatly affect the path of a buoy. Thus, the path of a single buoy might or might not follow a 'typical' trajectory, and it is also impossible to ascertain whether the velocity field a buoy encounters is representative of that experienced by an animal some distance away. In addition, there may also be inter-annual variability in ocean currents (e.g. Hays et al. 1993), which reiterates the importance of comparing animal tracks and current information from the same time. Therefore, when using Lagrangian drifter buoys to assess ocean currents in a specific area, a conservative approach might be to focus initially on understanding the local circulation patterns by assessing several buoy trajectories before drawing conclusions from any one of them. This approach was used in a study of adult leatherback turtles satellite tracked off the coast of South Africa (Luschi et al. 2003b). Turtles spent weeks or months moving in circles within mesoscale eddies (see Appendix 1) (Fig. 2). This pattern of movement was also observed in Lagrangian drifters tracked over the same period, though leatherbacks displayed more

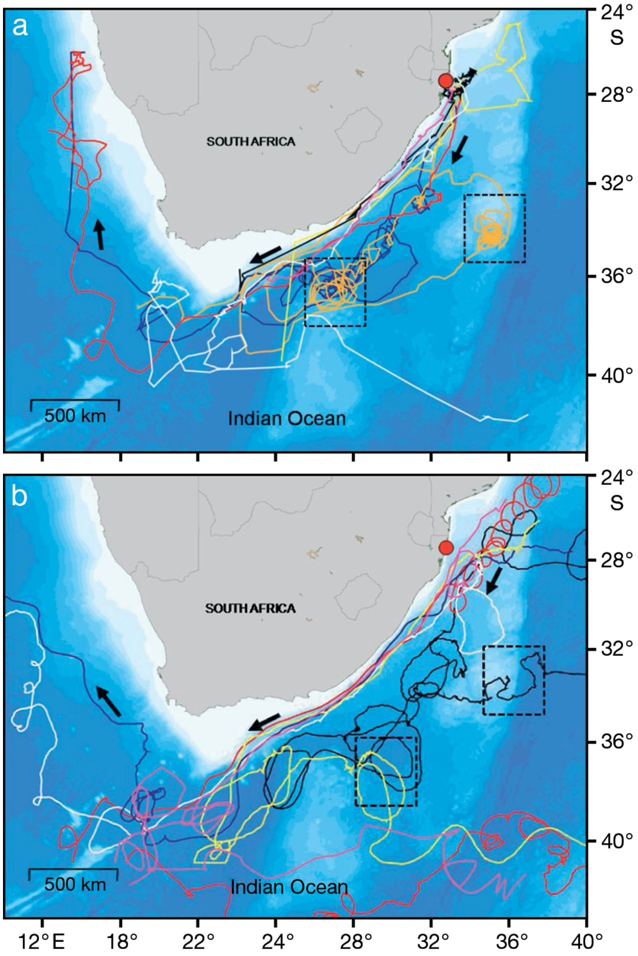

Fig. 2. (a) Routes followed by satellite-tracked leatherback turtles and (b) Lagrangian drift trajectories. Both animal and drifter tracks show prolonged periods of circling in mesoscale eddies (highlighted by dashed black squares; note that eddies are not exactly at the same place on both maps), suggesting the turtles may simply drift passively at these times. The red dot on both maps indicates the deployment location of tags onto turtles. Modified from Luschi et al. (2003b)

tightly constrained circuitous paths (Fig. 2). Data from Lagrangian drifter buoys was insufficient to determine whether the extended time turtles spent within these eddies was the result of passive entrainment or whether turtles actively maintained their position within these areas. A more detailed analysis of the turtle tracks was therefore conducted using sea surface height anomaly (SSHA) maps generated from satellite altimetry measurements. Results suggested that the movement of the turtles was dominated by strong currents within the Agulhas system (Luschi et al. 2003b, Lambardi et al. 2008).

Several other studies have also relied on SSHA maps to get information on the position and dynamics of mesoscale eddies located along the path of a satellite-tracked animal (Polovina et al. 2004, Hays et al. 2006, Sasamal & Panigraphy 2006, Hatase et al. 2007, Revelles et al. 2007, Doyle et al. 2008, Mansfield et al. 2009, Fossette et al. 2010a, Howell et al. 2010, Mencacci et al. 2010). These studies suggest that in order to make inferences about the behaviour of a marine animal, in addition to Lagrangian drifter trajectories, some numerical methods are often needed to estimate the current velocities along its track.

Inferring surface ocean currents with satellite observations

In the absence of direct, *in situ* measurements, and for more complete spatial/temporal coverage, ocean currents may be estimated from satellite observations, based on an informed knowledge of the leading physical balances. Ekman transports and geostrophic currents have been estimated from satellite observations: Ekman transports are computed from winds, inferred in turn from the surface roughness measured by scatterometers; geostrophic currents are estimated from sea surface height fields that are measured by satellite altimeters (Table 1). The effects of geostrophic currents (velocity and direction) on animal movements have been investigated in several marine species (e.g. Polovina et al. 2000, Horrocks et al. 2001, Ream et al. 2005, Seminoff et al. 2008, Godley et al. 2010). However, the state-of-the art approach is now to estimate the effects of total surface currents on animal movements by combining both the mean and anomaly of the surface geostrophic flow and an inferred surface Ekman current (e.g. Gaspar et al. 2006, Shillinger et al. 2008, Fossette et al. 2010b, Robel et al. 2011).

A mean geostrophic current field can be derived from the Mean Dynamic Topography (MDT) (Rio & Hernandez 2004, Rio et al. 2011), while the local anomaly of the surface geostrophic current can be deduced from gridded fields of sea-level anomalies (SLA). Estimation of the surface Ekman current, or drift, involves more assumptions. First, it must be assumed that the winds are changing slowly enough for a quasi-balance between frictional (wind stress) and the Coriolis force, in the Ekman layer. Rapid changes in the winds will give rise to 'inertial oscillations', but this variability can be neglected for currents varying on timescales in excess of around a day. Then, considering the surface Ekman layer for a given constant vertical eddy viscosity (see Stewart 2008), surface Ekman currents may be simply computed from the wind stress. A more sophisticated approach may involve eddy viscosity that can vary in time and space, and the use of an Ekman model (e.g. Rio & Hernandez 2003). In either way, the Ekman component of the current can be deduced using gridded fields of daily wind stresses.

Satellite-derived current products, such as those provided by LEGOS-CTOH (Sudre & Morrow 2008) or OSCAR (Johnson et al. 2007), have been routinely validated with various *in situ* data sets such as the global surface drifter dataset. Consistent agreement has been found between these satellite-derived currents and drifter currents (Pascual et al. 2006, Sudre & Morrow 2008, Dohan et al. 2010). However, it is important to keep in mind that fine-scale features, typically those with a spatio-temporal scale smaller than the resolution of the satellite measurements, may not be well resolved by this technique, which in turn may introduce some uncertainty in the overall current estimates.

Simulating ocean currents and particle drift

Numerical OGCMs are developed with the same equations from which the Ekman and geostrophic currents are estimated. These models mathematically describe current flows by forcing the ocean surface with wind data and buoyancy fluxes (heat and freshwater exchange). OGCMs can be used from a Eulerian perspective or, if combined with particle-tracking software, from a Lagrangian perspective. Particle-tracking calculations are widely used by physical oceanographers for purposes unrelated to biology. Physical oceanographers may be interested in the large-scale circulation, specifically the formation, pathways, and 'destruction' or 'consumption' of water masses — parcels of water with particular properties, most commonly temperature and salinity (e.g. Speich et al. 2002, Koch-Larrouy et al. 2010, Lique et al. 2010). In shelf seas or coastal sites, the interest may be the dispersion of radioactive plumes (e.g. Periáñez & Pascual-Granged 2008) or other pollutants (e.g. oil, Díaz et al. 2008). Other applied uses of these models include helping police forces with hindcast model runs to predict where corpses washed ashore are likely to have entered the water (Ebbesmeyer & Scigliano 2009). Particle tracking has been practised for several decades and the models have greatly improved over time because (1) increased computational power has improved model resolution; (2) the numerical schemes used to solve the model equations have become more sophisticated; and (3) the data used for forcing the models at the surface have become more accurate. In coastal areas, high resolution models may additionally resolve tidal flows that are often the most important component of the current in these areas (e.g. Holt et al. 2005, Cheng & Wang 2009, Hamann et al. 2011). In the open ocean, tidal flows are very weak and can generally be ignored. Regional Ocean Model Systems (ROMS) models have also been used to describe present ocean circulation patterns but also allow projections of future circulation patterns in specific areas used by marine vertebrates (Olsen et al. 2009, Costa et al. 2010).

Particle tracking has also been widely used by biologists to infer the movements of animals as diverse as hatchling turtles (Hays et al. 2010, Putman et al. 2010b, Hamann et al. 2011) and various types of plankton (Speirs et al. 2006, Zhu et al. 2009, Mariani et al. 2010). In some cases, 'behaviour' has been placed within these models. For example, some coastal marine plankton may adjust their depth in the water column depending on the state of the tide, in order to influence their horizontal movement, and this behaviour can be parameterised within particle-tracking models (North et al. 2008, Gilbert et al. 2010, Butler et al. 2011). As a corollary, the same type of approach is used to infer the movement of insects drifting in the atmosphere, with behaviour again added to passive drift scenarios (Reynolds et al. 2009).

In the use of models, perhaps the main limitation is that processes smaller than the horizontal resolution of the models are not explicitly represented. For example, early comparisons of then state-of-the-art ocean particle-tracking models in the 1990s with Lagrangian drifters were undertaken with models that did not resolve mesoscale variability (Hays & Marsh 1997). As the large-scale currents are typically broader and slower at low resolution, such models also tended to underestimate drift times by a factor of ~2. Likewise, many contemporary ocean circulation models take a daily, weekly or even monthly average of current velocities, which are unlikely to be representative of what the animal experiences continuously. Regardless of limitations, the modelling approach has greatly improved over recent decades and has become a powerful tool for assessing the ocean currents encountered by marine animals.

Finally, animal-borne sensors are increasingly providing *in situ* data that is combined with direct or indirect measurements to improve current estimation and resolution, particularly in inhospitable locations (e.g. Boehme et al. 2008, Charrassin et al. 2008, Grist et al. 2011). As the symbiosis of physical and biological data collection increases, so do the opportunities for studies of animal behaviour in the marine environment. Ultimately, the quality of ocean current estimates along the path of a tracked animal will influence our ability to infer the animal's behaviour.

CASE STUDIES

Comparing modelled and satellite-derived currents

The net movement of animals swimming through the ocean can be strongly influenced by the velocity of the fluid through which they are travelling. The speed and direction of their movement is the sum of their own velocity and that of the fluid. For instance, estimates of ocean currents along the animal's path are required to infer what component of these movements is due to active swimming by the animal itself and what component is caused by passive transport in the current (Chapman et al. 2011). Here, we compared current estimates along model trajectories calculated using particle-tracking software with surface currents estimated from combined altimetry and scatterometry satellite observations (following the method of Gaspar et al. 2006) for the path of a satellite-tracked leatherback turtle. To do this, we started with 4 tracks of leatherback turtles travelling through the North Atlantic Ocean (Fossette et al. 2010b). For each track, interpolated locations were calculated every 8 h (see Fossette et al. 2010b). For each 8 h resampled location, we calculated the apparent turtle velocity (i.e. the velocity over the ground) and subtracted from it an estimate of the surface current velocity.

The surface current velocity was estimated through the 2 different approaches. Satellite-derived surface current velocity was estimated as the sum of the mean and anomaly of the surface geostrophic current plus the surface Ekman current, deduced from altimetry and wind-stress data, respectively. The Ekman component of the current was computed from daily wind stress data obtained from CERSAT (Table 1) on a regular 0.5° × 0.5° grid using the Rio & Hernandez (2003) model. The anomaly of the surface geostrophic current was computed from weekly gridded fields of sea-level anomalies obtained from AVISO (Table 1) on a 1/3° × 1/3° Mercator grid. The mean of the surface geostrophic current was provided by Rio & Hernandez (2004) on a regular 1° × 1° grid. Then, at each 8 h re-sampled location, the 3 components of the surface current underwent a time and space linear interpolation from the gridded velocity fields. The accuracy of this method to estimate the overall surface currents has been assessed by Pascual et al. (2006) and Sudre & Morrow (2008).

Modelled surface current velocities were calculated by using the particle-tracking program ICHTHYOP v.2 (Lett et al. 2008) applied to surface currents from the Global Hybrid Coordinate Ocean Model (HYCOM) (Bleck 2002). Global HYCOM output in this configuration has a spatial resolution of 0.08° (~7 km at mid-latitudes) and a daily time step. HYCOM uses data assimilation to produce 'hindcast' model output that better reflects *in situ* and satellite measurements. Global HYCOM thus resolves mesoscale processes such as meandering currents, fronts, filaments and oceanic eddies (Bleck 2002, Chassignet et al. 2007), which are important in realistically characterising oceanic features that affect the movements of individual animals. For advection of particles through HYCOM velocity fields, ICHTHYOP implements a Runge Kutta 4th-order time-stepping method, whereby particle position is updated hourly (Lett et al. 2008). Modelled surface current velocities are calculated by releasing 100 particles in the HYCOM model. These are randomly distributed within a 0.08 × 0.08° box (i.e. the resolution of Global HYCOM) centred on each turtle location. For each release, particles are allowed to drift for 8 h and the mean current vector is then determined by measuring the distance and direction between the start location (0 h) and end location (8 h) of all 100 particles and calculating the arithmetic mean.

We then calculated the turtle swimming velocity as the vector difference between the apparent and the current velocities and reconstructed the turtle's current-corrected tracks using current estimates from both methods. The 2 methods gave similar current-corrected tracks (Fig. 3a). The satellite and HYCOM methods for estimating the direction of currents along the length of these tracks did not significantly differ from each other for Turtle i (1-sample *t*-test on the distribution of oriented angular differences, mean angular difference = 8.2°, 95% CI = –5.8 to 22.3°, p = 0.248) and for Turtle ii (1-sample *t*-test, mean angular difference = 4.3°, 95% CI = –5.0 to 13.7°, p = 0.365). Significant differences were observed between methods in the case of Turtle iii (1-sample *t*-test, mean angular difference = 22.9°, 95% CI = 12.3 to 33.6°, $p < 0.05$) and Turtle iv (1-sample *t*-test, mean angular difference = 17.0°, 95% CI = 8.9 to 25.2°, $p < 0.05$). Currents estimated using the particle-tracking technique in

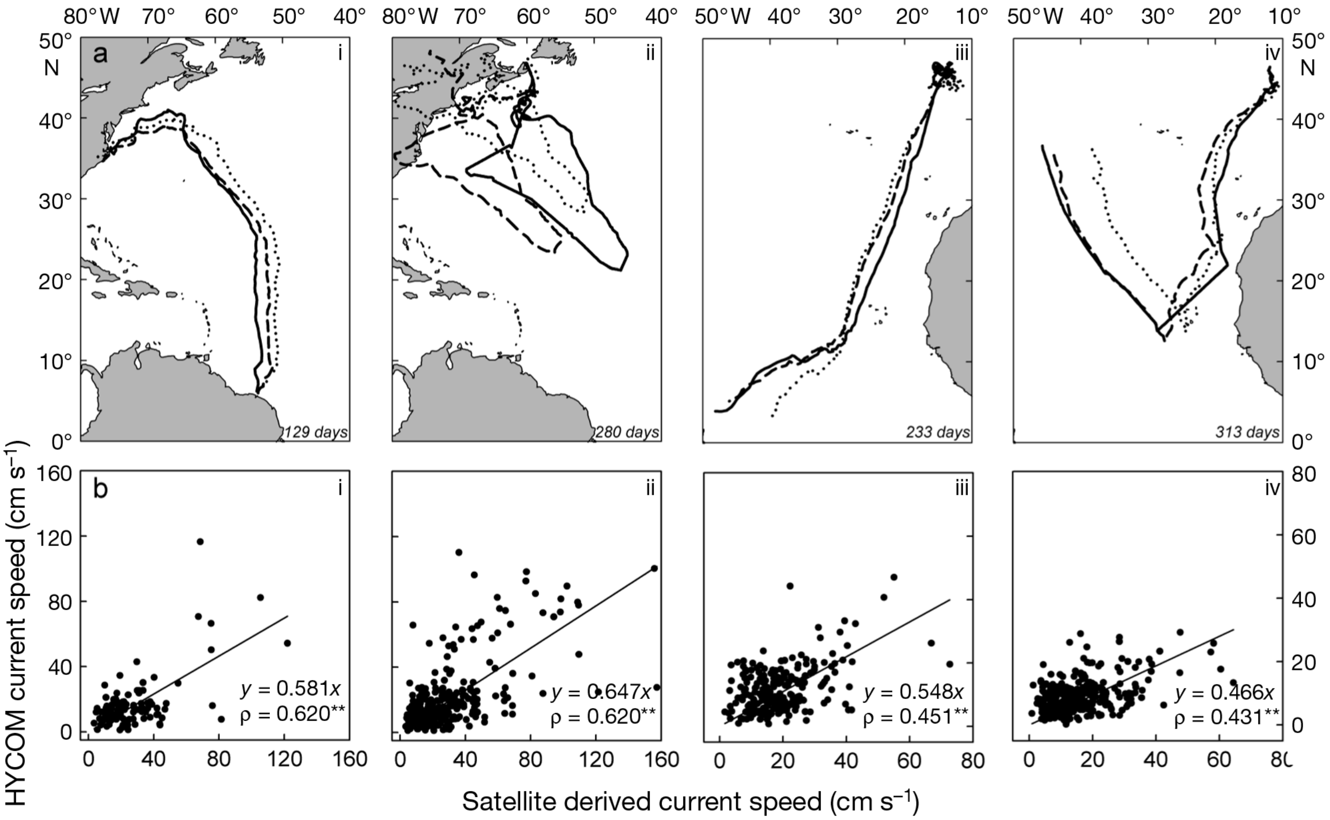

Fig. 3. (a) Observed Argos track (solid line) and current-corrected tracks obtained by using surface currents estimated by the numerical model HYCOM (dotted line) or by satellite observations (dashed line) for 4 leatherback turtles (i, ii, iii, iv) during their post-nesting migration in 2005 to 2006 in the North Atlantic Ocean. (b) Relationships between the speed of the currents estimated by the numerical model HYCOM and the currents derived from satellite observations at each location along the observed turtle tracks. Regression lines, corresponding equations and correlation coefficients are shown in each graph. $^{**}p < 0.01$

HYCOM were systematically slower than satellite-derived estimated currents (about 40% slower, i.e. slope of the relationship ranging from 0.466 to 0.647, Fig. 3b). A possible explanation is that, for Lagrangian particle-tracking techniques, velocity was estimated using the straight-line distance from the start point of particles to their end point in 8 h. Mesoscale processes in HYCOM might tend to reduce the distance travelled by particles (and apparent velocity) compared to the Eulerian satellite-derived current estimates.

In any case, while our analyses suggest that these 2 methods are roughly equivalent, what this comparison does not provide is an indication of how well these methods of current estimates account for the actual current velocities the turtles were exposed to. Such information is clearly of paramount importance in assessing the validity of the conclusions about behaviour derived from current estimates.

Testing numerical methods using Lagrangian drifter buoys

Lagrangian drifter buoys are a valuable tool for validating and parameterising modelled and satellite-derived currents (e.g. Rio & Hernandez 2003, Barron et al. 2007, Dohan et al. 2010). Accordingly, even though the Lagrangian drifter buoy data set has primarily been used by biologists to describe general patterns of ocean circulation, it can also be used to assess how accurately other methods for estimating currents can predict the movement of an object in the ocean. For instance, Lagrangian drifter buoys used as 'null models' could provide an indication of the precision with which biologists can discriminate the passive versus active components of the movement of a satellite-tracked animal.

Robel et al. (2011) reconstructed the current-corrected path of a surface drifter using satellite-derived estimated currents (see previous subsection for details about the method). Despite the drifter being by definition passive, a current-corrected trajectory was obtained, highlighting some uncertainty in the current estimates. A method was then developed by those authors (op. cit.) to allow this uncertainty to be taken into account when investigating the impact of ocean currents on an animal's behaviour. In brief, this method consisted of launching numerical particles in a reconstructed current velocity field along the path of a satellite-tracked animal at regular time intervals. This created an envelope of possible passive trajectories for the actual animal path showing the uncertainties in the velocity field. By juxtaposing the actual track with the cloud of synthetic trajectories, the extent to which the animal displays active or passive movements could then be determined.

As another example, we applied the HYCOM/ICHTHYOP method to several Lagrangian drifter buoy trajectories across the North Atlantic. We selected 6 buoys from the North Atlantic that showed a range of trajectories (Fig. 4a). Each trajectory consisted of locations every 6 h. We used HYCOM hindcast output to provide current estimates for the same times and locations as the buoy data. For the time of each buoy location, we ran HYCOM with 100 particles released randomly within a 0.08 × 0.08° box centred on the buoy location. For each release, particles were allowed to drift for up to 14 d and the particle position was recorded every 6 h. The mean current vector of the first 6 h of each particle release was then determined (hereafter referred to as 'particle vector'). As the displacement of the buoy is entirely driven by ocean currents, we determined the currents experienced by the buoy as the vector between successive buoy locations (hereafter referred as 'buoy vector').

We then compared the currents estimated by HYCOM with those experienced by the drifting buoys by calculating the difference between the buoy vectors

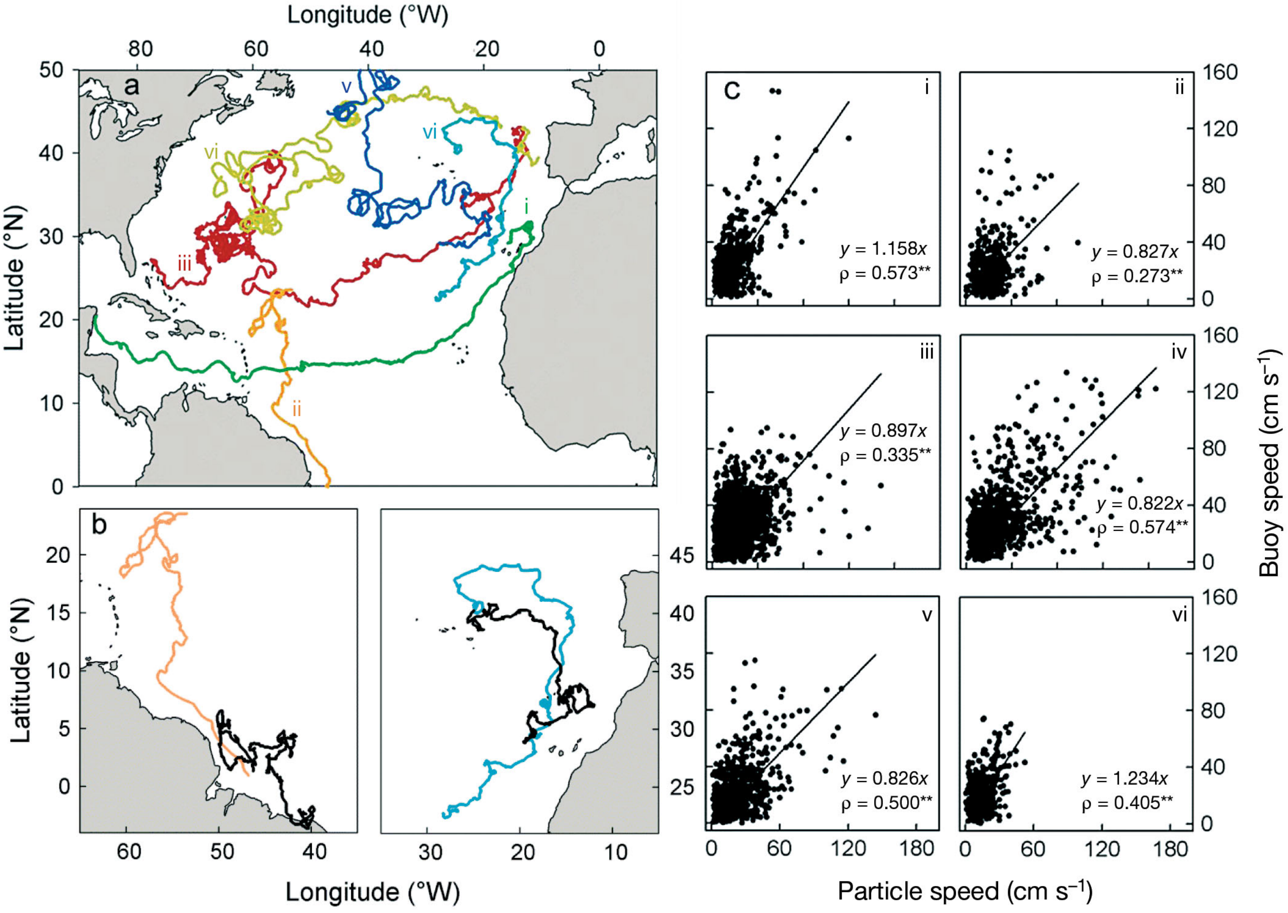

Fig. 4. (a) Trajectories of 6 satellite-tracked drifter buoys in the North Atlantic Ocean (i, ii, iii, iv, v, vi). (b) Observed trajectories (orange and blue lines) and current-corrected tracks (black lines) of drifters (ii) and (vi) (left and right panel respectively). (c) Relationships between the speed of the buoys (i, ii, iii, iv, v, vi) calculated every 6 h and the speed of numerical particles released in the ocean circulation model HYCOM at each drifter location and run for 6 h. Regression lines, corresponding equations and correlation coefficients are shown in each graph. $^{**}p < 0.01$

and the particle vectors along the drifter trajectory. If both methods were equivalent, the difference between the buoy vectors and the particle vectors would be nil and the current-corrected trajectory of the buoy would be static. However, in all 6 cases, the buoys' current-corrected trajectories were not static, suggesting that the currents estimated by both methods were not equivalent (Fig. 4b). Accordingly, the correlation between the speed of the currents experienced by the buoys and the speed of the numerical particles was relatively weak (range = 0.273 to 0.574) but significant (Fig. 4c). In addition, the slope of the relationship was different from 1 in all cases, ranging from 0.8 to 1.2 (Fig. 4c). Four buoys went slower than the numerical particles while the 2 other buoys went faster, suggesting an absence of systematic bias in the model output. Accordingly, the mean angular difference between the particle vectors and the buoy vectors (mean = 14.5°, 95 % CI = –0.99 to 29.9°) was not significantly different from 0 (1-sample *t*-test, $t_5 = 2.406$, n = 6 buoys, p = 0.061). When looking at the impact of ocean currents on animal's movements, such non-biased uncertainties in modelled currents should not affect the overall outcome of the analysis even though they may introduce a larger variation in the data set.

In validation studies of numerical models, the separation distance between both kinds of drifters, i.e. simulated and observed Lagrangian drifters, is typically reported (e.g. Edwards et al. 2006, Barron et al. 2007). Here we found an average distance of 6.7 km between each particle and the next location of the drifter buoy after 6 h. This distance increased to 20.1 km after 1 d and to 77.9 km after 5 d (Fig. 5a,b). These distances are in the same range as values found in previous large scale validation studies of numerical models (Barron et al. 2007). Finally, we assessed the mean 'predictive ability' of HYCOM for

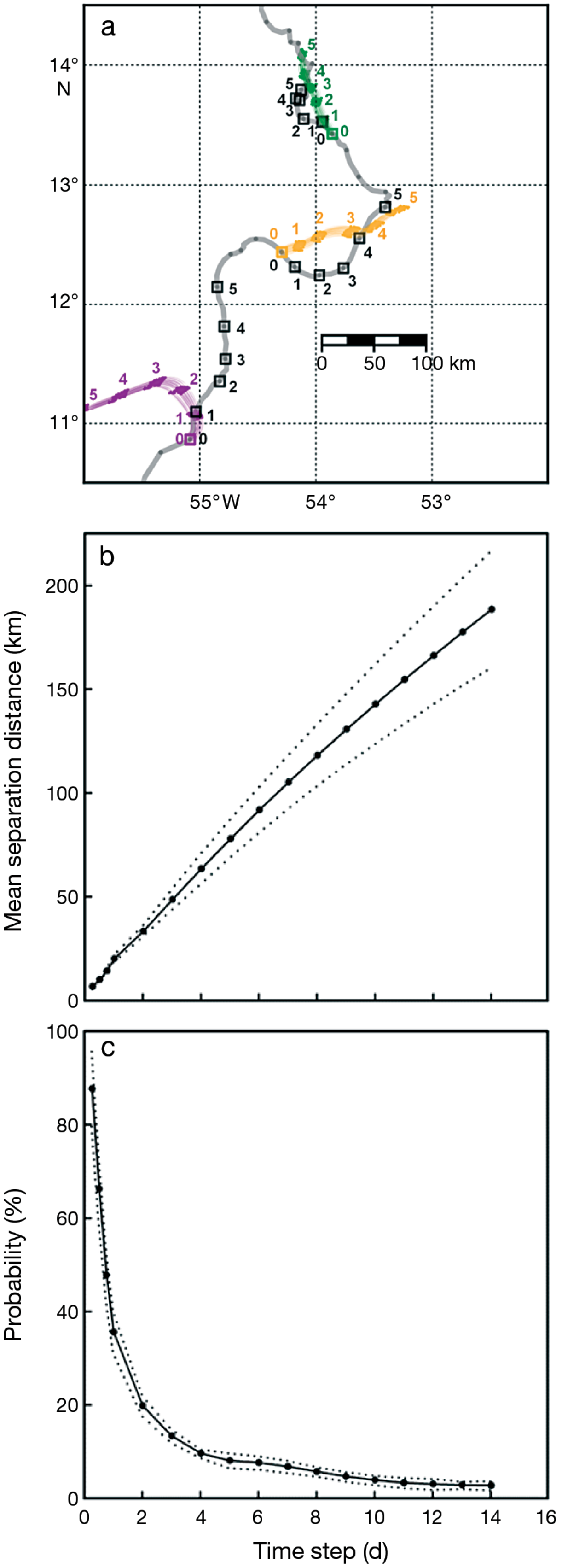

Fig. 5. (a) Drifter track (grey line) with numerical particle trajectories superimposed. For the time of each buoy location the HYCOM model was run with 100 particles released randomly within a 0.08 × 0.08° box centred on the buoy location. Each clump of particles is the particle position after 1 d (for a total of 5 d). Coloured boxes denote the 'start location' on the buoy track. Black boxes indicate the 0.08 × 0.08° box around the buoy location after 1 d. The 5 boxes following the start location are in accordance with the 5 d plotted for particle trajectories. (b) Mean separation distance between each numerical particle and the location of the drifter buoy at each successive time-step (6 h, 12 h, 18 h, 1 d, 2 d, etc.). Dashed lines: 95 % confidence interval. (c) Mean predictive ability for all 6 buoys, defined as the proportion of the track in which at least 1 numerical particle enters a 0.08 × 0.08° box around the buoy location at the appropriate time-step. Dashed lines: 95 % confidence interval

all 6 buoys. For that, we counted the probability along the track that at least 1 numerical particle enters a 0.08 × 0.08° box around the buoy location at the appropriate time-step: 6 h, 12 h, 18 h, 1 d, 2 d, etc. (Fig. 5c). At 6 h, this value was 0.88. It decreased to 0.35 at 1 d, and was 0.08 at 5 d (Fig. 5c).

These results show that, as for satellite-derived estimated currents, there is some uncertainty in OGCM estimated currents as well. This uncertainty needs to be taken into account by biologists when investigating the impact of ocean currents on animal movements and behaviour. Our analysis notably suggests that, overall, a cloud of particles released in HYCOM will provide a good estimate of the main features of the current flow (direction and speed) and, at least initially, accurately represent the path of a buoy. However, individual particle tracks should be treated with caution. Therefore, when using outputs from OGCMs to investigate the impact of currents on the movement of a satellite-tracked animal, we suggest a methodology similar to that of Robel et al. (2011). Numerical particles should be released along the actual path of the animal at regular, relatively short time intervals, i.e. between 6 h and 2 d, as that might give a better estimate of the current speed and direction. The size of the release box can be adjusted according to the quality of the animal location data, i.e. Argos quality or GPS quality. Every segment of the actual path of the satellite-tracked animal should then be juxtaposed with each resulting cloud of numerical trajectories to distinguish between active and passive movements.

RECOMMENDATIONS

Our study shows that the different methods available to measure or estimate ocean currents are not equivalent, notably in terms of spatio-temporal coverage and accuracy. Drifters provide direct measurements of surface current velocities with a very high temporal and spatial resolution, but are limited in spatial coverage. By contrast, numerical methods offer a more consistent and regular spatial and temporal coverage. However, the spatio-temporal resolution of numerical methods may sometimes be too low to capture fine-scale mesoscale oceanographic features. Therefore, each method's limitations should be carefully considered before a decision is reached about the most appropriate technique for a particular application. As each of these methods have already been evaluated and validated, errors and uncertainties in ocean current measurements, as well as limitations in spatial and temporal resolution of the data sets, should always be taken into account or at least discussed in any tracking study.

Best uses of Lagrangian drifter buoys

For studies on the movement of marine animals, Lagrangian drifter buoys are best suited for elucidating the general current patterns individuals might encounter in a specific area (e.g. Landry et al. 2009, Horton et al. 2011), testing the connectivity between spatially separated oceanic sites (e.g. Fossette et al. 2010a, Monzón Argüello et al. 2010) and comparing in a qualitative way passive versus active movement patterns (e.g. Lambardi et al. 2008). In order to use Lagrangian drifter data in a quantitative way, the drifter must occur in close proximity to the tracked animal and transmit positional data at a similar time (Campagna et al. 2006). Moreover, this data set provides a rich resource for assessing how accurately other quantitative techniques for estimating currents can predict the movement of an object in the ocean (see the previous section on testing numerical methods for examples of 'accuracy assessment' techniques).

We also note the reservation that AOML drifters are drogued to 15 m, while small pelagic animals may drift with the 'surface' current; thus, it is important to keep in mind that substantial current shear between the surface and 15 m will inevitably lead to divergence between actual surface currents and drifter trajectories. Finally, although these drifter buoys only capture velocity fields of the near surface (upper ~15 m), it would still be wise to use them for 'accuracy assessment' techniques when examining the movement of pelagic animals at depth.

Best uses of satellite-derived and modelled current data

Satellite-derived estimates of ocean currents and ocean circulation models have been validated in a number of studies and shown to reproduce ocean currents with a high-degree of reliability (e.g. Chassignet et al. 2007, Sudre & Morrow 2008). However, when comparing satellite-derived estimates of currents to Lagrangian drifters, smoothing is often applied to the tracks of drifters to remove short-period signals not detected by altimetric measurements or sampled weekly winds (e.g. Sudre & Morrow 2008). Likewise, studies comparing simulated particle tracks in ocean circulation models to Lagrangian drifters routinely perform additional computations to exclude the influence of wind and surface waves that cause drifter 'slip' (e.g. Edwards et al. 2006). Thus, the reported performance of these tools may tend to overestimate the reliability of such techniques when applied to the tracks of marine animals.

Another important caveat for biologists to keep in mind is that validation studies typically use 1000s of measurements (e.g. 3101 Lagrangian drifters in Sudre & Morrow 2008), whereas biologists are usually only examining 10s of individuals. Thus, while satellite-derived or modelled currents might have a high correlation factor with currents inferred from 1000s of buoy trajectories, any particular handful of trajectories might be quite poorly correlated (e.g. Sudre & Morrow 2008: their Fig. 7 shows a high degree of scatter in the correlation between satellite-derived estimates of currents along the paths of Lagrangian drifters). Thus, it is of paramount importance for biologists, when using estimated currents to infer behaviour of a tracked animal from ocean current data along its path, to perform the same analyses on a comparable number of drifters in close proximity to the study area. In this way the uncertainty and errors in the numerical method used can be parameterised or, at a minimum, acknowledged (Robel et al. 2011).

When used appropriately, these current estimates offer broad flexibility and utility. As illustrated here, these methods can be used to estimate currents along the length of an animal's track and thus infer what component of the path is caused by active movement versus passive drift (e.g. Gaspar et al. 2006, Sleeman et al. 2010). This is critical to discriminate foraging and travelling behaviour (Gaspar et al. 2006, Fossette et al. 2010b, Robel et al. 2011), evaluate orientation and navigation abilities (Girard et al. 2006, 2009, Luschi et al. 2007, Mills Flemming et al. 2010), or understand the influence of the ocean circulation on the spatio-temporal distribution of oceanic migrants (Shillinger et al. 2008, Campbell et al. 2010, Cotté et al. 2011).

Another application is the use of particle-tracking models to infer the general patterns of dispersion for passively drifting organisms (Bonhommeau et al. 2009, Mariani et al. 2010, Hamann et al. 2011). Our results show that groups of trajectories from numerical models do indeed provide a general description of the paths that passively drifting animals will follow. But drift times inferred from the numerical particle trajectories may be different from drift times inferred from drifter buoys (Fig. 4). So this highlights again the importance for biologists to apply their particular particle-tracking models to buoy trajectories so that they understand the strengths and weaknesses of the modelled results. A final important point is that numerical models simulate the 3-dimensional current field. For animals diving to/from different depths, models may thus provide useful additional information on vertical shear in horizontal currents.

CONCLUSIONS

We have a number of recommendations for biologists wanting detailed information on ocean currents. The first is to encourage biologists to make use of the global Lagrangian drifter dataset, which provides readily available 'control data'. However, it is important to recognise that, before drawing conclusions from a specific buoy trajectory, considering several buoy trajectories in the studied area is an essential first step to understand the local circulation patterns. In cases where there is a need for information on the currents at specific locations and times where buoy data is unavailable, satellite observations and/or numerical OGCMs should be used to estimate currents, but data from these methods should be treated with appropriate caution. For analyses that rely on precise measurements of environmental data (such as those designed to examine orientation or navigation behaviour, energetic output, etc.), possible false signals or noise should be parameterised against drifting buoys, for instance. When used appropriately, these approaches can provide useful insights, but they can equally lead to erroneous conclusions. Our findings suggest that people might, for instance, run the risk of reading too much into the 'current-corrected tracks' or could even run into trouble assuming that a deviation from the current is attributable to the animal's own movement (see also Robel et al. 2011). Nevertheless, it is important to keep in mind that these current estimates are the only available ones, and that often, it may be more informative to get an estimate of currents rather than to ignore them entirely.

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Appendix 1. Glossary

Coriolis: The Coriolis force is caused by the rotation of the Earth. In simple terms, when air or water flows from areas of high pressure to low pressure, the rotation of the earth makes the wind or current follow a curved path. Wind and currents tend to turn to the right of their direction of motion in the Northern Hemisphere, and to the left in the Southern Hemisphere. The Coriolis force is zero at the Equator. The Coriolis force is responsible, for example, for the rotation of cyclones.

Ekman flow: Ekman flow is a wind-driven current. Surface waters can be set in motion by the wind blowing across the ocean. Due to the Coriolis effect, this shallow layer of surface water is deflected to the right of the wind direction in the Northern Hemisphere and to the left in the Southern Hemisphere. This surface layer would drag the layer beneath it which in turn would drag the next layer and so on. As each moving layer is deflected slightly to the right (in the Northern Hemisphere) of the overlying layers' movement, the direction of water movement changes with increasing depth, resulting in a so-called 'Ekman spiral'. The total average flow, integrated over depth is called Ekman transport and is oriented 90° to the right (left) of the wind in the Northern (Southern) Hemisphere. The lower limit of the wind's influence on ocean movement is at a depth of about 100 to 150 m. This transport of water due to coupling between wind and surface waters further results in variations in the height of the sea surface which in turn generate horizontal gradients in water pressure. These pressure gradients, in turn, induce geostrophic flow.

Eulerian: measurement of the speed and direction of a current at a fixed point over time, often with a current meter deployed from a ship or mooring.

Geostrophic flow: A geostrophic current is an oceanic flow in which the pressure gradient force (i.e. the force pushing the water from a region of high pressure towards a low pressure region) is balanced by the Coriolis force in the horizontal momentum balance, resulting in the flow moving along the lines of equal pressure (isobars). Viewed from above, geostrophic flow in a subtropical gyre (with central high pressure) is clockwise in the Northern Hemisphere and counter-clockwise in the Southern Hemisphere All the major ocean currents such as the Gulf Stream, the Kuroshio Current and the Agulhas Current are approximately in geostrophic balance and are generally regarded as geostrophic currents (although the geostrophic balance appreciably breaks down with current speed increasing to high values, as non-linear terms become important in the momentum balance).

Lagrangian: measurements of the speed and direction of a current by means of a device, often a tracked buoy, which follows the movement of a particular 'parcel' of water.

Mesoscale: The term mesoscale is used to describe ocean dynamical features having horizontal scales ranging from a few to several hundred kilometres, such as ocean eddies or fronts separating water of different properties (temperature and salinity). In the ocean, mesoscale features are associated with ocean dynamics that are largely controlled by geostrophy

Sub-surface drogue: A drifter consists of a surface buoy and a sub-surface drogue or sea anchor usually attached by a long, thin tether to the buoy (see Fig. 1a). The drogue can be centred at different depths (e.g. 15 m for AOML Lagrangian buoys) beneath the sea surface and measures mixed layer currents in the upper ocean. The buoy can measure sea surface temperature, wind speed or salinity and relay these data via satellites.

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