

The WHITE CORAL COMMUNITY

in the Central Mediterranean Sea
Revealed by ROV Surveys

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ABSTRACT. White coral communities consist of scleractinian corals that thrive in the ocean's bathyal depths (~ 200–4000 m). In the Atlantic Ocean, white corals are known to form complex, three-dimensional structures on the seabed that attract vast amounts of other organisms, accumulate suspended detritus, and influence the local hydrodynamic flow field. These attributes coincide with what we generally describe as a coral reef. With time, environmental change causes decline of the framework-constructing corals; this is followed by erosion of the reef sequence or its draping with noncoral-related deposits. After several such sequences, the structures are known as coral carbonate mounds, which can grow as high as 350 m. Both bathyal white coral reefs and mounds are widely distributed in the Atlantic Ocean and adjacent marginal seas, such as the Gulf of Mexico. The Mediterranean Sea, however, known for its richness of fossil white coral communities exposed in land outcrops, harbors very few extant coral communities. The HERMES project extended its study sites deep into the Mediterranean with state-of-the-art mapping and visualization technology. By doing so, many previously unknown coral sites were discovered during inspections of Mediterranean narrow shelves, canyon walls, escarpments, and seamounts by remotely operated vehicles. Such shelf and continental margin settings are characteristic of the dynamic margins of the Mediterranean Sea and contrast significantly with the much broader shelves of the Atlantic Ocean. This paper reports on a HERMES cruise that was dedicated to exploring these rough submarine topographies in search of white coral communities in the central Mediterranean, and re-evaluates the general perception of the assumed paucity of white corals in this sea.

INTRODUCTION

In comparison to the Atlantic Ocean, there is still scarce scientific knowledge of the distribution, environmental requirements, and depth limits of living, habitat-forming, deep-water scleractinian corals in the Mediterranean Sea. Even now, the major source of information on the distribution of Mediterranean deep-water corals is based on scientific and fishing dredge and trawl hauls—a method notorious for its biases in terms of precise positioning, catch selectivity, and destructive effect on benthic communities. However,

knowledge of these communities has steadily grown in recent years due to dedicated, cooperative geological and biological deep-sea projects, including much needed visual inspection of Mediterranean deep-water coral habitats using manned submersibles and remotely operated vehicles (ROVs). Based on several ROV dives performed during the HERMES R/V *Meteor* cruise M70-1 in 2006 (Freiwald et al., in press), we shed light on extant deep-water coral habitats in the bathyal zone of the Sicilian Channel and of the southern Adriatic sub-basin. These surveys were

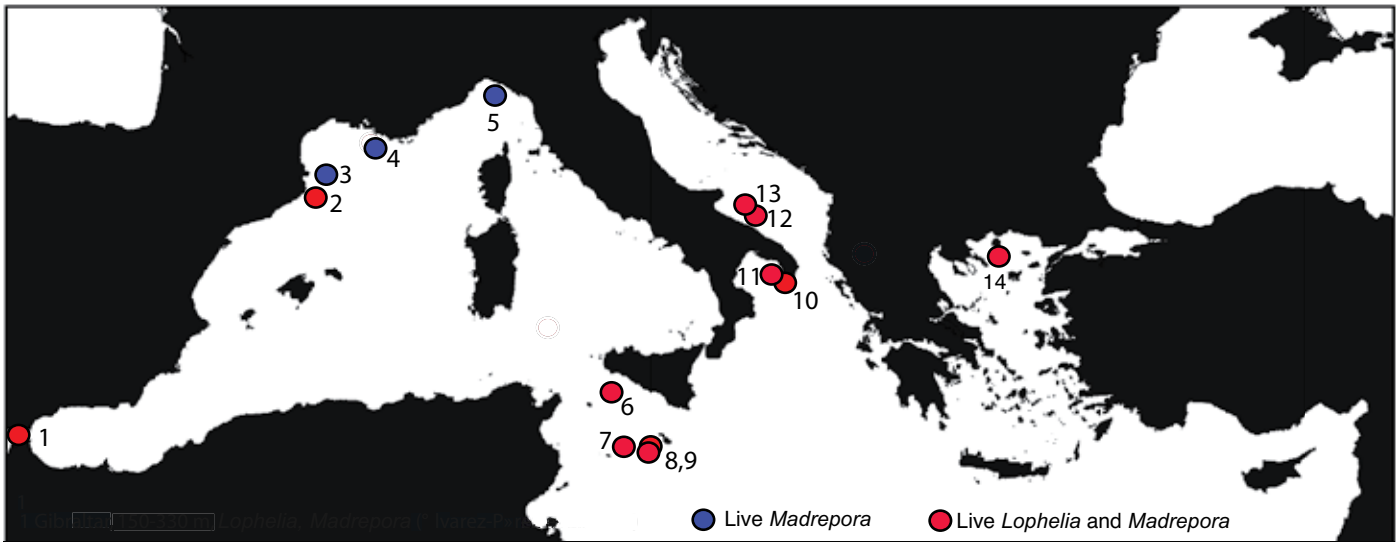
completed by further ROV dives into the better-known Apulian deep-water reefs off Santa Maria di Leuca (Tursi et al., 2004; Taviani et al., 2005a).

THE WHITE CORAL COMMUNITY

The term “white coral” community is local jargon first used by high-seas fishermen to distinguish the “white” *Lophelia pertusa* and *Madrepora oculata* from the “yellow” *Dendrophyllia cornigera* and *D. ramea* in the Atlantic Ocean. This deep-water coral assemblage was frequently encountered in trawl hauls conducted in the canyon-rich Bay of Biscay continental margin (see review by Reveillaud et al., 2008). The soft tissue of *L. pertusa* and *M. oculata* is generally transparent so that the white underlying skeleton is easily differentiated from the yellow soft tissue of *Dendrophyllia* species. Joubin (1922) and Le Danois (1948) introduced the color terminology in scientific papers. In their milestone monograph on the bionomy of Mediterranean benthic communities, Pérès and Picard (1964) adopted this terminology to define a bathyal, hard-bottom community of white corals (*Biocoenose des coraux blancs*), while the yellow coral community created by *Dendrophyllia* was placed in the shallower circa-littoral depth zone (*biocoenose de la roche du large*).

LIVING WHITE CORAL COMMUNITIES IN THE MEDITERRANEAN SEA

The true extent of the white coral community in the Mediterranean Sea is poorly known and the relatively few verified records of live *L. pertusa* and *M. oculata* exhibit a scattered distribution pattern rather than a belt



1. Strait of Gibraltar, *Lophelia, Madrepora*, 150-330 m, grab sampling (Álvarez-Pérez et al., 2005)
2. Cap de Creus Canyon, *Lophelia, Madrepora*, 218 m, ROV, submersible (Orejas et al., 2008)
3. Lacaze-Duthiers Canyon, *Madrepora*, at 300 m, submersible, dredges (Zibrowius, 2003)
4. Cassidaigne Canyon, *Madrepora*, 210-510 m, submersible (Bourcier & Zibrowius, 1973)
5. Portofino, *Madrepora*, 210 m, submersible (Tunesi et al., 2001)
6. Nameless Bank, *Lophelia, Madrepora*, 509-613 m, ROV (this study)
7. Linosa Trough, *Lophelia, Madrepora*, 669-679 m, ROV (this study)
8. Off Malta, *Lophelia, Madrepora*, 453-612 m, ROV (this study)
9. Off Malta, *Lophelia, Madrepora*, 392-617 m, demersal trawl (Schembri et al., 2007)
10. Santa Maria di Leuca, *Lophelia, Madrepora*, 300-1100 m, dredges, ROV (Taviani et al., 2005a; this study)
11. Off Gallipoli, *Lophelia, Madrepora*, 603-744 m, ROV (this study)
12. Bari Canyon, *Lophelia, Madrepora*, 306-640 m, ROV (this study)
13. Gondola Slide, *Lophelia, Madrepora*, 674-714 m, ROV (this study)
14. Off Thassos, *Lophelia, Madrepora*, 300-350 m, dredging (Vafidis et al., 1997)

Figure 1. Known and newly identified occurrences (this study) of live white coral communities in the Mediterranean Sea, with depth ranges.

of occurrences, as is the case in the Northeast Atlantic. The discovery of the largest known live white coral community in the Mediterranean on the Apulian Plateau in the Ionian Sea (Tursi et al., 2004; Taviani et al., 2005a) supports the hypothesis of a disjunctive but flourishing occurrence following a major decline since the postglacial period (Delibrias

and Taviani, 1985). It is clear that the Atlantic flooding of the Mediterranean basin via the Strait of Gibraltar after the Messinian Salinity Crisis about 5.3 Ma (Krijgsman et al., 1999) opened the door for benthic recolonization of the Mediterranean basin from the Atlantic Ocean (Taviani, 2002). From the Pliocene to Early Pleistocene, the white

coral community expanded from the western basins as far east as the southern Aegean Sea, where the corals are exposed in bathyal marls and limestones on Rhodes (Titschack and Freiwald, 2005). The spectacular white coral facies exposed on Sicily and Calabria are latest Pliocene, to Early Pleistocene in age (see review by Taviani et al., 2005b). Dead white coral assemblages of late Pleistocene to Holocene origin have been dredged throughout the entire Mediterranean basin from the Strait of Gibraltar in the west to the Anatolian continental margin near Kastellorizon in the east (see details in Zibrowius, 1980, and Taviani et al., 2005b).

This Mediterranean-wide white coral

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dispersal in the relatively recent past is in sharp contrast to the few known occurrences of living white coral communities (Figure 1). Near the Gibraltar sill, Álvarez-Pérez et al. (2005) reported the existence of live *L. pertusa* and *M. oculata*. There also appears to be a cluster of live corals in the Northwest Mediterranean canyons between Cap de Creus and the Ligurian Sea (Bourcier and Zibrowius, 1973; Tunesi et al., 2001; Orejas et al., 2008). Prior to the R/V *Meteor* cruise M70-1, only Schembri et al. (2007) and Zibrowius and Taviani (2005) documented living white corals in the Sicilian Channel (Figure 1). A colony of living corals off Apulia, now known as the Santa Maria di Leuca (SML) reef province, was known from dredging done during the famous Adriatic expedition of the Austrian ship *Pola* in 1891 (see review by Taviani et al., 2005a). This area became a coral hotspot in 2000 following the Italian Apulian Plateau Bank Ecosystem Study (APLABES) project (see Tursi et al., 2004; Taviani et al., 2005b). In the Adriatic, only subfossil and fossil white coral communities have been found off Bari and in the Jabuka Trough off Croatia (Zupanovic, 1969; Bombace and Froglija, 1972; Trincardi et al., 2007). Further east, only one isolated spot containing live *L. pertusa* and *M. oculata* was reported from a trough off Thassos, northern Aegean Sea (Vafidis et al., 1997) (Figure 1).

THE OCEANOGRAPHIC ENVIRONMENT

The central Mediterranean Sea, which is the focus here, is the key area for thermohaline water mass exchange between the eastern and western Mediterranean

basins (e.g., Astraldi et al., 2002). From the Strait of Gibraltar, surface inflow of Atlantic water spreads throughout the whole Mediterranean basin, becoming progressively denser while flowing to the east. Part of this inflow comes back to the Atlantic Ocean as intermediate water, while the rest is transformed into deep water, in both the western and eastern Mediterranean (Astraldi et al., 2002).

Modified Atlantic Water (MAW) occupies the surface layer in the central Mediterranean. It flows through the Sicilian Channel into the Ionian Sea but also passes along the western coast of Sicily into the Tyrrhenian Sea (Figure 2). Intermediate- and deep-water circulation within the eastern Mediterranean is complex due to its seasonal variability. Levantine Intermediate Water (LIW),

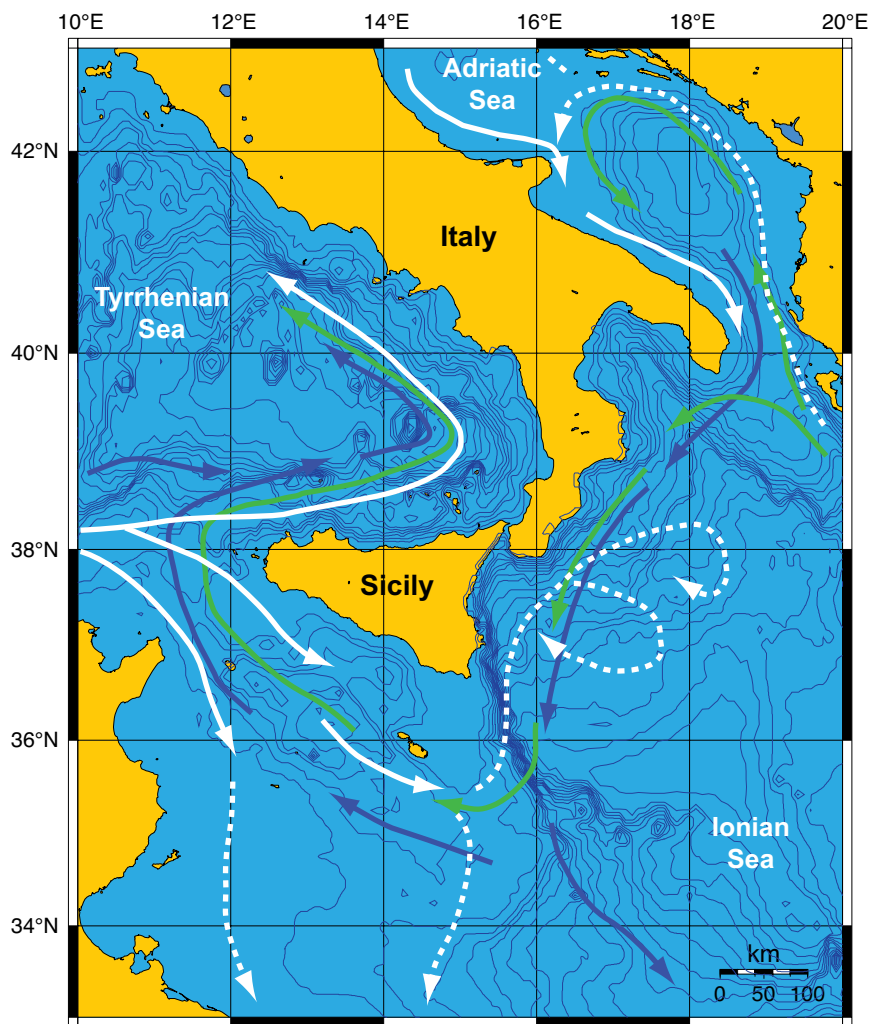


Figure 2. General circulation of surface, intermediate, and deep water masses in the central Mediterranean Sea compiled after Millot (2005), Astraldi et al. (2002), and Millot and Taupier-Letage (2005). White arrows = surface water circulation of Modified Atlantic Water (annual). Dashed white arrows = surface water circulation of Modified Atlantic Water (seasonal, interannual). Green arrows = intermediate water circulation of Levantine Intermediate Water. Blue arrows = deep-water circulation of Eastern Mediterranean Deep Water (and Western Mediterranean Deep Water in the Tyrrhenian Basin).

the Mediterranean's largest water mass, is formed in the northern part of the Levantine Basin and flows, due to the Coriolis force, along the southern continental slope of the Cretan arc islands to the Peloponnesus peninsula (Millot, 2005). Part of the LIW enters the Adriatic Sea, where it mixes with MAW in winter to form Adriatic Deep Water (ADW), which then becomes part of the Eastern Mediterranean Deep Water (EMDW). The remainder of LIW bypasses the southern Adriatic and proceeds south of Italy along the Calabrian-Sicilian margin, passes through the Sicilian Channel, and enters the Tyrrhenian Sea (Figure 2). Because LIW mainly flows along the northern continental slopes, it is involved in the offshore formation of all Mediterranean deep waters, such as the Aegean Dense

Water, the Adriatic Dense Water, and also the Tyrrhenian Dense Water (TDW) in the western Mediterranean basin (Millot, 2005). The deep-water flow of EMDW generally follows the circulation of LIW.

THE HERMES R/V METEOR CRUISE M70-1

R/V *Meteor* carried out a deep-sea mission to explore the status of white coral communities in the Sicilian Channel, the eastern part of the Tyrrhenian Sea, off Apulia, and in the southern Adriatic Sea in late summer 2006. The vessel was equipped with the MARUM ROV *QUEST 4000 m* to visualize the seabed and to collect samples of interest (MARUM is the University of Bremen's Center for Marine Environmental Sciences). Prior to the ROV dives, a

navigation map was generated using hull-mounted Simrad EM120 and an EM710 multibeam echosounder. During the cruise, 16 ROV video surveys were carried out and some of the highlights showing the coral habitats in the Sicilian Channel, off Apulia, and in the southern Adriatic are depicted here (see Table 1 for the positioning of the dives discussed). Conductivity-temperature-depth (CTD) data were obtained with a Sea-Bird Electronics Model 911 plus. Full details of station logging data are provided in Freiwald et al. (in press).

Sicilian Channel Communities and Their Habitats

The Sicilian Channel is a continental rift zone that has been affected by significant tectonic stretching since the Late Miocene; this has resulted in a series

Table 1. Overview of ROV dives encountering live corals with start and end positions on the seabed. Depth ranges (max.–min.) of live, habitat-forming corals are provided. (*) Alive but accumulated as debris fall.

ROV Dive Station	Site	Start of Dive	Start Depth (m)	End of Dive	End Depth (m)	Live <i>Lophelia</i> (m)	Live <i>Madrepora</i> (m)	Live <i>Dendrophyllia</i> (m)
657	Off Malta	35°30.694' N 14°06.582' E	611	35°30.919' N 14°06.398' E	457	576–453	612–453	none observed
673	Linosa Trough	35°46.010' N 13°02.618' E	803	35°45.924' N 13°02.605' E	536	679–669	679–669	733*
677	Urania Bank	36°50.390' N 13°09.361' E	654	36°50.274' N 13°09.255' E	440	600(604*)–509	600(613*)–509	none observed
708	Gallipoli Escarpment	39°37.283' N 18°04.778' E	823	39°37.511' N 18°05.018' E	574	744–603	744–670	none observed
721	SML	39°33.878' N 18°27.150' E	630	39°33.902' N 18°26.202' E	556	604–556	601–556	567–560
728	SML	39°33.297' N 18°27.385' E	624	39°33.834' N 18°27.037' E	601	624–590	624–590	613–592
735	Bari Canyon	41°17.477' N 17°16.623' E	664	41°16.976' N 17°16.574' E	276	640–374	600–357	494–445
745	Bari Canyon	41°17.825' N 17°10.753' E	557	41°17.532' N 17°09.955' E	315	508–306	517–306	453
752	Gondola Slide	41°43.508' N 17°02.794' E	710	41°43.177' N 17°03.655' E	674	714–674	none observed	none observed

of northwest-southeast trending faults that generate a characteristic horst and graben structure (Civile et al., 2008). Superimposed on this structure are volcanic centers, such as Pantelleria and Linosa, and some submarine edifices. Neogene rifting caused the development of three major depressions, the Pantelleria (1317-m depth), Linosa (1529-m depth), and Malta (1731-m depth) troughs (Figure 3). These troughs are filled with Lower Pliocene to Pleistocene turbidites (Maldonado and Stanley, 1977) and are bounded by subvertical normal faults (Finetti and Del Ben, 2005). These

rifting activities destroyed the former Maghrebidian-Sicilian carbonate platform, whose remnants are exposed on the Maltese islands and as submerged shallow-water banks in the Sicilian Channel, such as the Adventure Bank. Other structural highs are horsts and can be defined as bathyal neritic platforms (Maldonado and Stanley, 1977).

Three escarpments within the Sicilian Channel were inspected with the *QUEST* ROV: an unnamed escarpment off southwest Malta (Dive 657), the southern slope of the Linosa Trough (Dive 673), and the eastern flank of the Urania Bank (Dive 677) (Figure 3 and Table 1).

The unnamed, northwest-southeast trending escarpment is located 30 nm southwest of Malta at 35°30'45"N, 14°06'30"E (see Figure 3), near the area where Schembri et al. (2007) reported live white coral communities from fishery survey trawls. This impressive escarpment forms a near-vertical wall measuring 150–200 m in height. Existing bathymetry of this area shows that this escarpment flanks a larger plateau, located about 400–500-m deep, which separates the Malta Trough from the Linosa Trough (see Figure 3). The escarpment surveyed on ROV dive 657 forms a major topographic obstacle

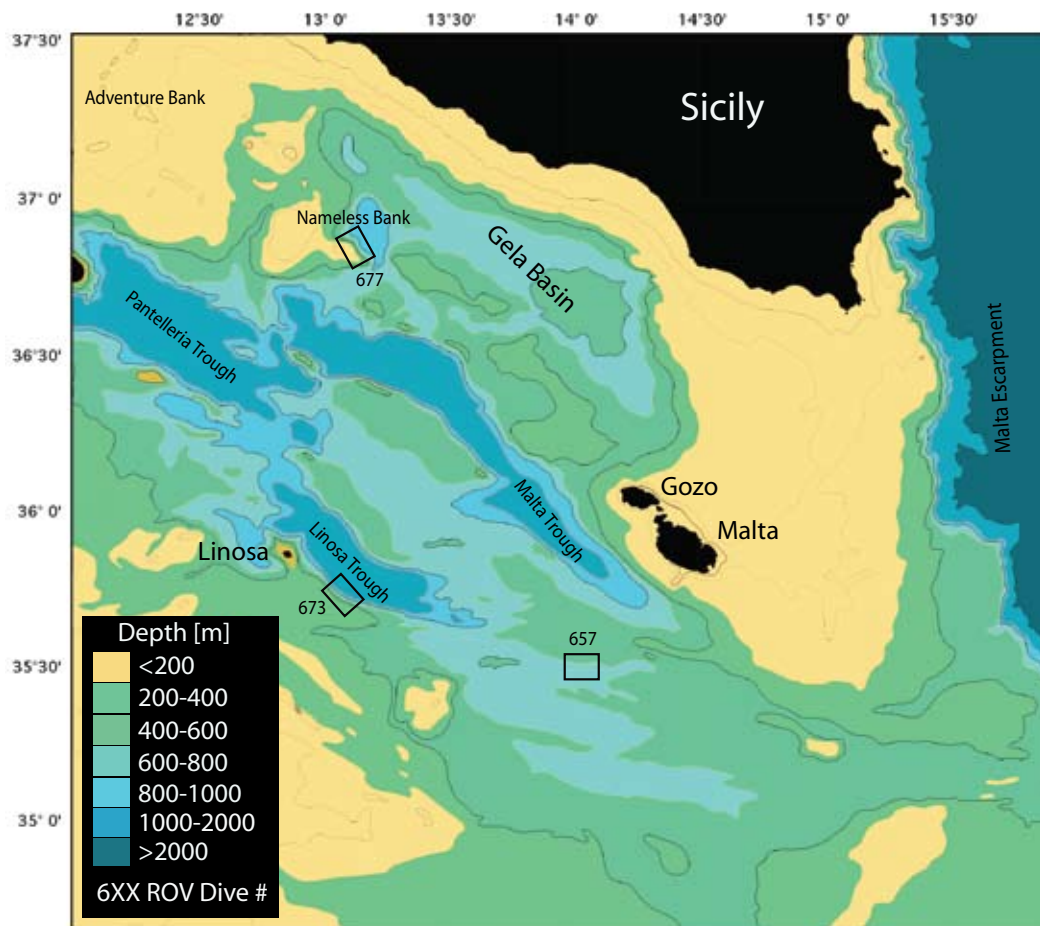


Figure 3. Remotely operated vehicle surveys on R/V *Meteor* cruise M70-1 in the Sicilian Channel with live white coral communities. Bathymetry from the GEBCO International Bathymetric Chart of the Mediterranean.

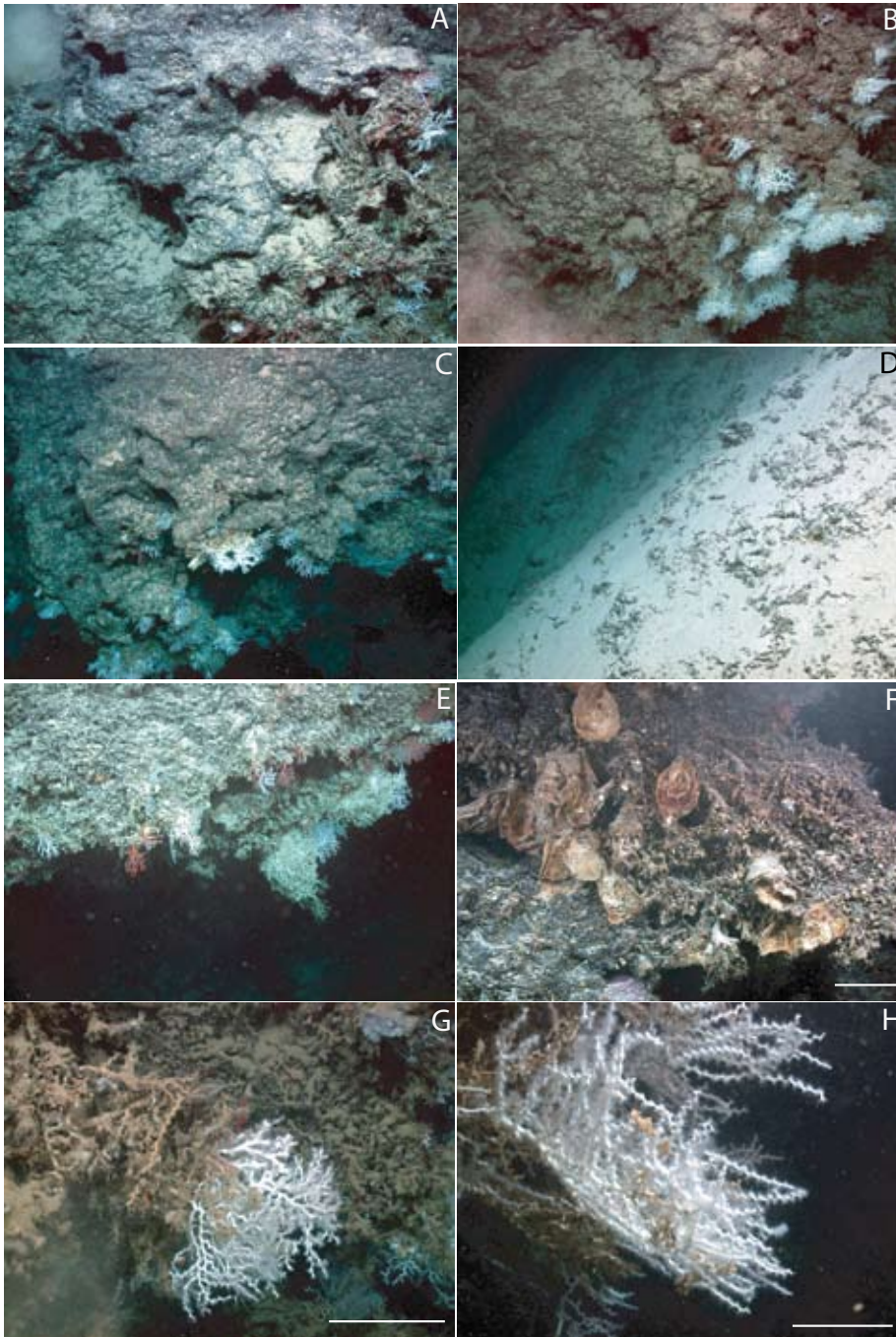


Figure 4. QUEST ROV images of the white coral community in the Sicilian Channel from the unnamed escarpment off Malta (Dive 657, A–C), the Linosa Trough (Dive 673, D–F), and from the Nameless Bank (Dive 677, G–H). (A) Fossil coral debris and framework hardgrounds in an onion-skin-like fabric draping the bedrock; small live coral colonies are visible in the lower right (458-m depth). (B) Fan-shaped *M. oculata* and *C. rubrum* colonies facing downward and against the main current direction (458-m depth). (C) Example of huge cavernous overhangs consisting of fossil coral hardgrounds as the preferred settling ground of the white coral community (453-m depth). (D) Mixture of loose and indurated coral rubble and pelagic mud covering less-inclined portions of the slope (785-m depth). (E) The “Hanging Gardens of Linosa,” a characteristic *M. oculata*, *L. pertusa*, *C. rubrum* community (673-m depth). (F) Deep-sea oyster aggregations attached to fossil coral framework (684-m depth). (G) Small *L. pertusa* colony (thicker white coral branches) next to larger *M. oculata* colony (589-m depth). (H) Large, bowl-shaped colony of *M. oculata* facing against the current (596-m depth). Scale bars = 10 cm. All ROV images courtesy of QUEST ROV MARUM, Universität Bremen

for the westward-flowing LIW. Pelagic muds cover the flat and slightly inclined seabed in front and on top of the near-vertical wall. These muds have been bioturbated by crustacean burrows and by grazing tracks of holothuroids and cidaroid echinoids. The sessile benthos is dominated by the octocorals *Isidella elongata* and *Funiculina quadrangularis*. The outcropping bedrock is hard to identify because of the presence of a near-complete drape of black- and brown-colored lithified carbonate crusts (Figure 4A). The lithified crusts contain fossil *Dendrophyllia cornigera*, *L. pertusa*, *M. oculata*, and—rarely—extremely large growth forms of *Desmophyllum dianthus*. These crusts represent either lithified coral debris flows that became trapped in crevices and fissures of the bedrock or lithified coral framework preserved in situ. In the latter case, the coral framework developed from bedrock overhangs. With time, these corals grew into the water column to form aligned fringes with almost all corallites facing downward to take advantage of the current-advected food supply and to avoid the smothering effects of sedimentation from above. These exposed coral fringes, however, were prone to sedimentation; thus, trapped pelagic ooze subsequently clogged the space between the corallites, and seawater pumping through the framework lithified the corals to generate limestones in the bathyal zone, as described by Noé et al. (2006). Evidently, the fossil coral framework is also the preferred settling site for the present-day coral assemblage consisting of *M. oculata* and (to a much lesser degree) *L. pertusa*, both growing downward like their fossil counterparts, thus resembling hanging gardens with

fan-shaped colonies (Figure 4B, C). The white coral community is associated with *Corallium rubrum* and other gorgonians. *M. oculata* colonies attain heights of 30–40 cm and are relatively fragile and fan-shaped, with zig-zagging individual branches. The colony bases are generally inhabited by the symbiotic polychaete *Eunice norvegica*. Table 1 lists the depth ranges of live *L. pertusa* and *M. oculata* found during ROV dive 657.

ROV dive 673 was conducted at the steepest part of the southern margin of the Linosa Trough, about 8 nm southeast of Linosa Island (see Figure 3) from 803–536-m depth. The bedrock consists of volcanic strata creating a vertical slope and intercalated sedimentary units that are inclined 30° to 60°. The lesser-inclined bedrock is covered by muds and gravity-transported coral branches of *L. pertusa*, *M. oculata*, *C. rubrum*, and *D. cornigera*, mixed with large fossil corallites of *D. dianthus* and fossil shells of *Acesta excavata* (Figure 4D). The transported coral material displays a melange of different preservation stages, from live corals and fresh-looking skeletons to fossil and black-coated material. Both fossil and present-day coral communities thrive under overhangs and in large caves, and developed preferably downward-facing colony growth forms (Figure 4E). The outer rims of the fossil in situ coral framework were further colonized in the recent past by up to 20-cm-large deep-sea oysters, which belong to an undescribed species of *Neopycnodonte* (Figure 4F; Wisshak et al., in press). At this station, the most intense growth of *C. rubrum* was documented among the white coral habitats surveyed in the Sicilian Channel. Table 1 lists the depth ranges of live *L. pertusa*,

“ THE HERMES PROJECT EXTENDED ITS STUDY SITES DEEP INTO THE MEDITERRANEAN WITH STATE-OF-THE-ART MAPPING AND VISUALIZATION TECHNOLOGY. ”

M. oculata, and *D. cornigera* found during ROV dive 673.

ROV dive 677 focused on the eastern deep slope of the Nameless Bank, alternatively referred to as the Urania Bank (see Figure 3) from 654–440-m water depth. The lower 50 m of this slope is subvertical and consists of volcanic material with rough bedrock topography, followed by more gently inclined sedimentary bedrock above. The base of the slope shows a gently inclined apron of pelagic sediments. Close to the foot of the volcanic wall, considerable coral debris flows have accumulated, including more or less intact and partly living *M. oculata*, and to a lesser degree *L. pertusa* and *C. rubrum* colonies. Both the fossil and present-day coral frameworks follow the “hanging garden” principle as described from the previous stations (Figure 4G–H). Up to 70-cm-high and 50-cm-wide *M. oculata* colonies were measured, all with downward-facing frameworks. Colonies of *L. pertusa* are generally smaller, and live portions rarely exceed 10 cm in size. In the gently inclined upper section of this dive, starting at 500-m depth, white corals were found only sporadically. *Dendrophyllia* was not encountered on this survey. Table 1 lists the depth ranges of live *L. pertusa* and *M. oculata* found during ROV dive 677.

Physical water properties were obtained from CTD stations at the coral habitats on R/V *Meteor* cruise M70-1.

In the Sicilian Channel, the water temperature measures between 13.72° and 13.9°C, and salinity ranges from 38.68 to 38.78. The calculated density σ_t of the water is 29.08–29.11. Water is oxic with 3.75–3.84 ml l⁻¹ dissolved oxygen.

Apulian Coral Communities and Their Habitats

The ramplike shelf south of Santa Maria di Leuca, northern Ionian Sea, is part of the Apulian Plateau that rises from about 2400-m to about 200-m water depth and is characterized by westward-dipping faults (Merlini et al., 2000; Figure 5). The large, almost symmetrical depression in front of the Apulian Plateau marks the Taranto trench, which reaches about 2500-m water depth (Figure 5). Ongoing surveys in that area have revealed the existence of hundreds of coral mounds with a mean depth range of 300–1100 m (Taviani et al., 2005a). Fusi et al. (2006) extended the lower limit of probable coral mound occurrences down to about 1600-m water depth by analyzing hydroacoustic data and gravity cores. Side-scan sonographs and chirp profiles yield evidence of a sedimentary environment formed by strong bottom currents. This area is now known as the Santa Maria di Leuca (SML) reef province and represents the largest occurrence of a living white coral community known in the Mediterranean so far. For general aspects of the coral-associated fauna, we refer to papers by Tursi et al. (2004) and Taviani

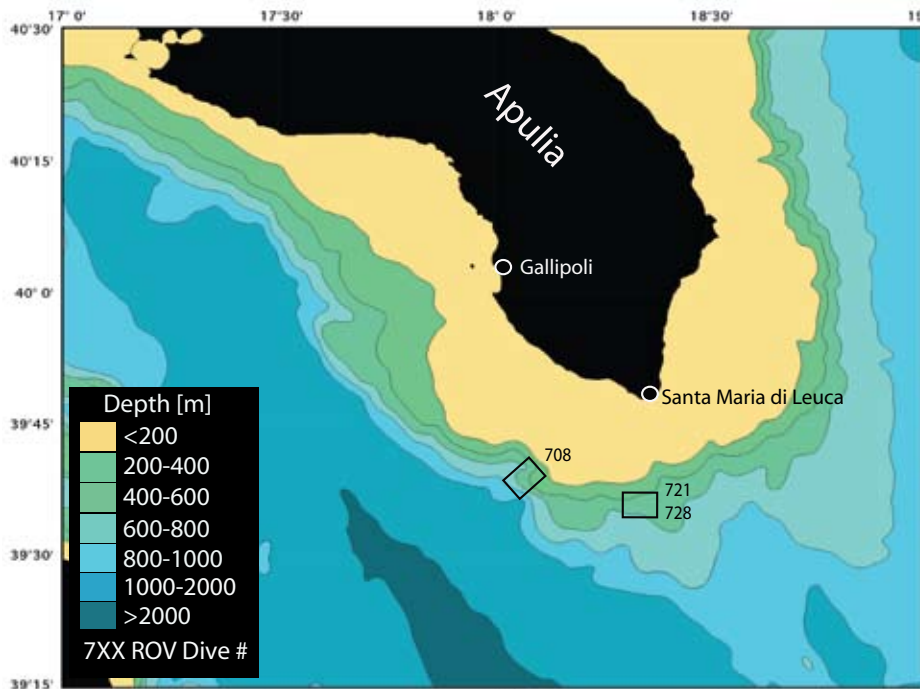


Figure 5. ROV surveys on R/V *Meteor* cruise M70-1 on the Apulian Plateau with live white coral communities indicated. Bathymetry from the GEBCO International Bathymetric Chart of the Mediterranean.

et al. (2005a); the sponges are depicted by Longo et al. (2005) and Schönberg and Beuck (2007), while Yakimov et al. (2006) studied the microbial community of corals and sediment.

During the M70-1 cruise, three ROV dives were performed in the SML area. Dive 708 surveyed a vertical escarpment from 823–574-m water depth that we informally named the Gallipoli escarpment (Figure 5). It forms the eastern wall of a major canyon system. The other ROV dives (721, 728) were conducted 12 nm further east in the area of the main reef mounds on the gently inclined Apulian Plateau at water depths between 630 m and 556 m (Figure 5 and Table 1).

From 823-m to about 620-m water depth, the near-vertical Gallipoli escarpment consists of sedimentary bedrock, and the different lithologies and degrees of induration provide a

complex relief with alternating ledges and overhangs. Lithified and Fe-Mn-coated coral rubble debris flows are preserved throughout the escarpment. The overhangs beneath rock ledges and crevices are colonized by solitary corals (*Stenocyathus vermiformis*, *Caryophyllia calveri*, *D. dianthus*) and hexactinellid sponges with down-facing growth. At 620-m depth, the escarpment levels out onto the gently inclined Apulian Plateau. Coral growth of *L. pertusa* and *M. oculata* is present but sporadic throughout the surveyed escarpment. Individual colony sizes rarely exceed 25 cm and show a downward-facing growth down to 744-m depth on the escarpment. At the edge of the escarpment, a more upward-oriented growth habit prevails. The upper 10-m portion of the escarpment at 620-m depth also shows a marked change in the attached

benthic communities. Here, where the bedrock levels out to the Apulian Plateau, settling space on the sediment strata surfaces becomes wider and bottom-current effects are assumed to become more pronounced at this morphological edge. The largest coral thickets (*L. pertusa* only) were found at the upper edge of the escarpment. Meter-sized *Lophelia* colonies were attached on the rock ledges growing to the side and upward. Live corals often use fossilized coral framework as settling ground (Figure 6A). At this edge of the escarpment, there is a sudden increase in fossil and live *D. dianthus* aggregations on lithified carbonate crusts and on fossilized coral framework and coral rubble (Figure 6B). Here, almost all corallites grow downward, although some rare *L. pertusa* colonies show a normal, upright growth habit. The level seabed above the escarpment is covered by muddy sands, heavily bioturbated, and colonized by a soft-bottom fauna (foraminifers, hydroids, polychaetes, crustaceans, echinoderms). The most striking features, however, are 1–2-cm-thick, fresh-looking, oxidized carbonate crusts that have precipitated directly on the sediment surface. Some meter-sized mud ridges are protected against current erosion by this crust, which converted the soft bottom into a solid hardground. Consequently, attached sponges and solitary corals with a dominance of *C. calveri* are important elements of the hard, substrate-associated fauna.

ROV dives 721 and 728 were directed into the central part of the SML coral mound area (see Figures 5 and 7) between 630- and 556-m water depth (see Table 1 for details). The largest mounds encountered during

the ROV dives measure 40–50 m in height and up to 800 m across. Most mounds have an elongated shape with the long axis in a north-south to northeast-southwest orientation. Some mounds are ovoid to subcircular, while others are arcuate. The ovoid mounds are the broadest at 200–300-m diameter, whereas the bases of the elongated and arcuate mounds are about 100-m wide (Figure 7). ROV inspection of the mounds clearly shows a preferred coral growth on the eastern, up-current flanks and on the tops of the mounds, forming upright coral thickets (Figure 6C). Toward the mound flanks, coral coverage fades and turns into a soft muddy bottom.

The living white coral community consists of *L. pertusa* and *M. oculata* with alternating dominance patterns. Some mound tops display aggregations of *D. cornigera* colonies with one to two polyp generations alive (Figure 6D). The living coral framework grows upon dead framework or hardground crusts, which act as armor plates to prevent erosion. Upright-growing colonies on the sediment are predominantly fan-shaped, unlike bigger ones, which lie horizontally on the sediment, reaching approximately 90 cm in length; they are of elongated, flattened shape, slightly expanding in diameter and with apical live portions. This observation suggests that fan-shaped colonies tend to capsized when reaching a certain height (Figure 6E), and continue to grow on the water-exposed upper parts of the structure. Live *L. pertusa* occurs in two distinct soft-tissue color varieties, the common transparent-tissue variety and an orange-tissue variety (Figure 6F).

The dead framework serves as

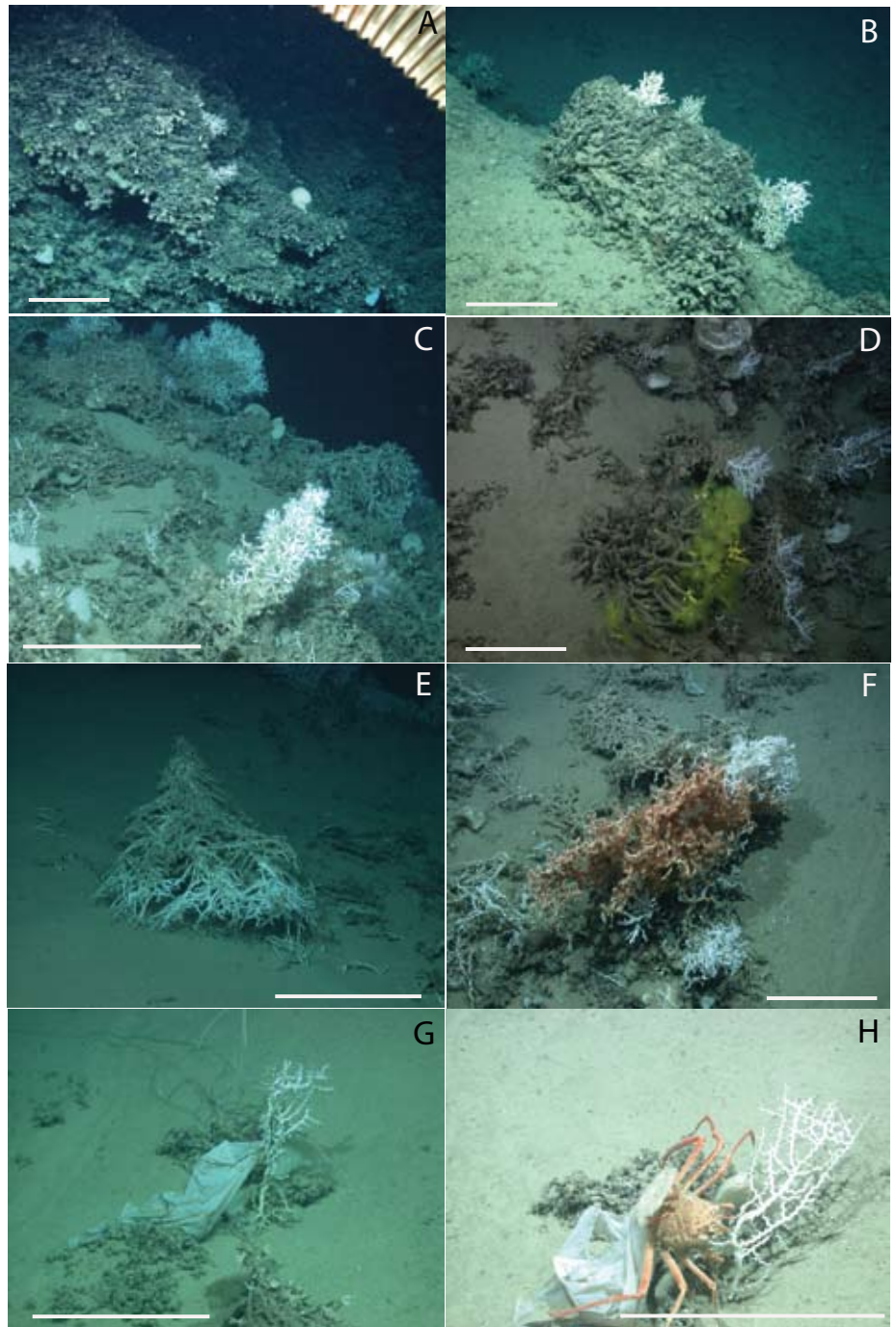


Figure 6. QUEST ROV images of the white coral community on the Apulian Plateau from the Gallipoli escarpment (Dive 708, A–B) and coral mounds from the SML reefs (Dive 721, D, F–H, and Dive 728, C, E). (A) Mass aggregation of *D. dianthus* growing downward (740-m depth). (B) In situ fossil coral framework of thick calcified *L. pertusa* colonized by live *Lophelia* colonies (728-m depth). (C) Coral thicket growing on the up-current flank of a mound (595-m depth). (D) A colony of the yellow *Dendrophyllia cornigera* from the top of a coral mound (566-m depth). (E) Capsized colony of *M. oculata* (606-m depth). (F) The two tissue color varieties of *L. pertusa* growing close to each other (579-m depth). (G) Plastic litter stuck on a *Madrepora* colony, as frequently observed in the SML reefs (582-m depth). (H) Crab *Paromola cuvieri* crawling over entangled garbage (582-m depth). Scale bars = 20 cm. All ROV images courtesy of QUEST ROV MARUM, Universität Bremen

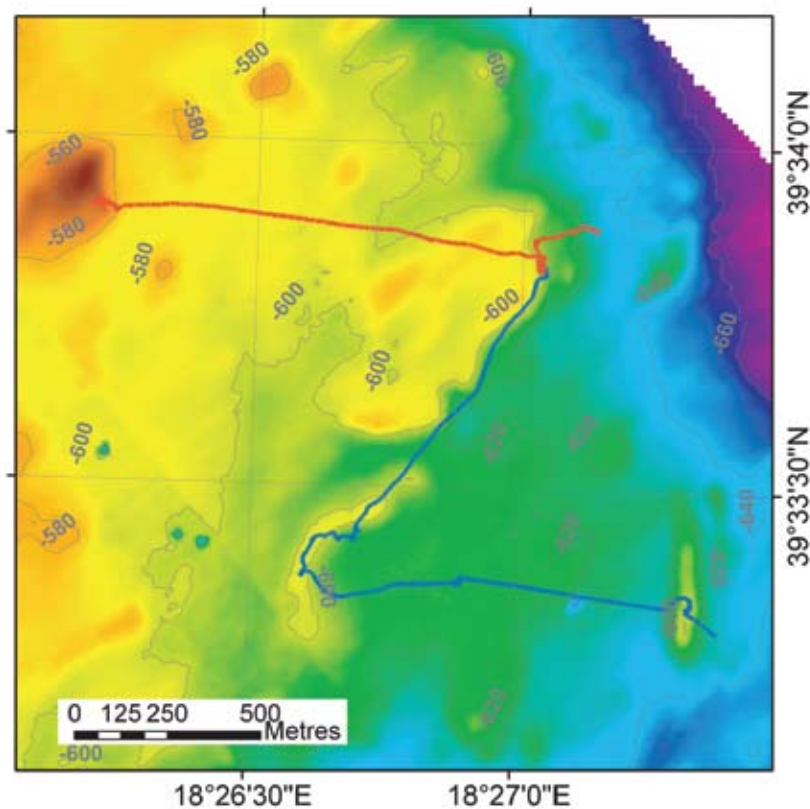


Figure 7. Multibeam map generated on R/V *Meteor* cruise M70-1 from the area of ROV dives 721 (red track line) and 728 (blue track line).

substrate for various organisms, such as several octocoral species, and the antipatharian *Leiopathes glaberrima* (with dimensions of 150 x 70 cm). Sponges, solitary corals (*D. dianthus*, *Caryophyllia* spp., *S. vermiformis*), actinians, bryozoans, sabellids, serpulids, brachiopods, bivalves, and hydroids complete the white coral assemblage. In places, *D. dianthus* pseudo-colonies monopolize dead coral framework. The corals are littered with plastic bags and discarded fishing gear (Figure 6G–H), which are harmful to the corals—in particular the plastic bags, which can rip off portions of the coral as they are dragged away by currents.

CTD stations from the coral habitats reveal water temperatures from

13.5°C to 13.8°C, salinities from 38.65 to 38.67, and a calculated density σ_t of 29.07 to 29.12. The dissolved oxygen is slightly higher than measured in Sicilian Channel coral habitats, with 3.98–4.54 ml l⁻¹, respectively.

Adriatic Coral Communities and Their Habitats

The Adriatic sub-basin is part of the Oligo-Miocene to Early Pleistocene foreland domain of the Apennine belt (Ricci Lucchi, 1986), bordered by the Gargano Promontory in the north and by the Otranto Strait in the south. The sub-basin shows complex deep-water circulation and water-mass stratification. Cold North Adriatic Dense Water (NAdDW), formed in the shallow northern Adriatic

through cold wind forcing and winter heat loss, represents one of the densest water masses in the Mediterranean, up to 29.8 kg m⁻³ (Cushman-Roisin et al., 2001). The NAdDW flows south and cascades into the sub-basin along the southwestern margin of the Adriatic sub-basin, where it mixes with the Adriatic Dense Water (ADW), which is formed through winter deep convection here. This dense water mass flows south through the Otranto Strait and passes along the Apulian Plateau into the Ionian Sea and Levantine Basin (Vilibic and Orlic, 2002). When seasonally present, the NAdDW fills the basin up to 700–400-m water depth and is overlain by the permanent LIW that enters the sub-basin from the south through the deep Otranto Strait and follows the contours of the Adriatic sub-basin in an anticlockwise direction (Vilibic and Orlic, 2002).

Major seabed features that were visually inspected in the search for white coral communities are concentrated along the southwestern Adriatic margin, the Bari Canyon, the Gondola Slide, and the Dauno Seamount (Figure 8). In the bathyal zone of this section of the margin, the circulation brings currents from the north with some force. This area is known for its bottom-current deposits, which document the changing history of deep-water circulation since the Last Glacial Maximum (Trincardi et al., 2007; Verdicchio et al., 2007). Relatively fresh-looking and fossil white corals were dredged in the Bari Canyon (see Figure 8 in Trincardi et al., 2007).

The Bari Canyon is an asymmetric east-west trending incision with two main branches. We inspected the southernmost, steeply inclined slope, which forms a natural obstacle against

the southern flow of the deep-water masses, on two ROV dives (dives 735 and 745, see Table 1 for details). The steep canyon wall has a less-inclined, deeper part that was surveyed from 664-m to 600-m water depth and is characterized by a highly bioturbated, intensely colonized, soft bottom.

Bonellia sp., sabellid worms, and the stalked hadromerid sponge *Rhizaxinella pyrifer* are common. Dispersed hard substrates derived from either in situ hardgrounds or transported crusts from higher up the wall were partly colonized by a sponge-*Madrepora*-serpulid assemblage mixed with bryozoans, ascidians, and brachiopods. *L. pertusa* is less common on these patches and rarely exceeds 15 cm in height. From 600–560-m water depth, the canyon wall becomes near vertical with relatively smooth bedrock surfaces devoid of ledges and overhangs. This cliff face, however, yields the largest colonies of *M. oculata* and, to a lesser degree, of *L. pertusa*. Like candelabras, the coral colonies developed fan-shaped and downward-facing growth forms (Figure 9A). The nearly tissue-free attachment areas of the coral colonies are smothered with pelagic detritus that is piled up against the wall. Individual colonies measure up to 70 cm in size. The fan-shaped colonies themselves form overhangs, providing a microhabitat for sponges, serpulids (*Serpula vermicularis*), and dense aggregations of *D. dianthus*. Above this vertical bedrock, the morphology becomes

more gently inclined, thus allowing fine-grained detritus to settle. In the depth range from 560 to 490 m, a species-rich sponge-white coral-serpulid assemblage colonizes hard substrates within the soft bottom area (Figure 9B). Again, *M. oculata* dominates over *L. pertusa* and solitary corals such as *D. dianthus* and *Stenocyathus vermiformis*. Live *D. cornigera* occur within a narrow depth interval from 494–445 m (see Table 1). Apart from *Dendrophyllia*, this assemblage is similar to the deeper hard substrate patch fauna on this ROV transect, but individual patches are larger and the colonial corals more frequently co-occur with the symbiotic *E. norvegica*. Lobate and fan-shaped sponges grow perpendicular with respect to the prevailing currents, some of them capsized. The hard substrate patches fade off at 357-m water depth, and the soft bottom community persists until the end of the ROV dive, at 276 m.

ROV dive 745 inspected the southern wall of Bari Canyon further to the west from 557–315-m water depth (see Figure 9C, D and Table 1). Compared to the previous dive, the general morphology is considerably less steep but shows prominent terraced morphological steps that are erosional in origin (Trincardi et al., 2007). The surfaces of the erosional steps are armored by hardgrounds with transitions from continuous crusts to broken and dislodged hardground slabs. Sampled hardgrounds still contain the boring clam *Pholadidea loscombiana* in situ. The white coral community is dominated by *M. oculata* and by rarer *L. pertusa* from 517–306-m water depth, but colonies are small, barely exceeding 15 cm in height, and are widely scattered. If present, they occur on the upper flanks of boulders, and the colonies grow upward. The hard-substrate community is dominated by sponges and serpulids (Figure 9C), and from 307-m water

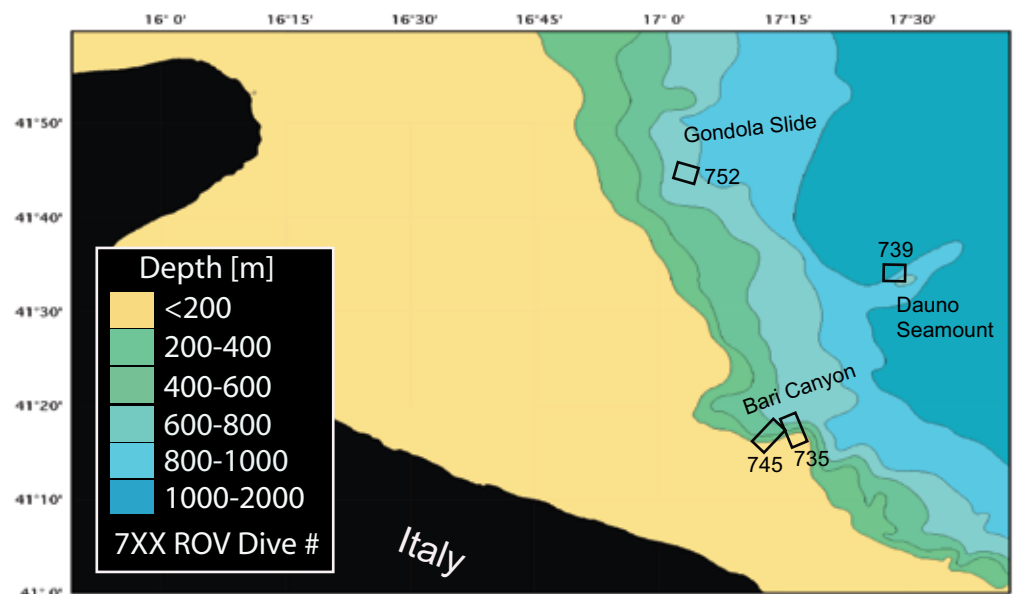


Figure 8. ROV surveys on R/V *Meteor* cruise M70-1 on the southwestern Adriatic margin. Bathymetry from the GEBCO International Bathymetric Chart of the Mediterranean.

depth, colonies of the bryozoan *Myriapora truncata* up to 20-cm-high are associated with sponges, *M. oculata* and *L. pertusa*. In general, the fossil and living white coral community becomes more prominent in the shallower section

of the ROV transect. Coral rubble and fossilized, sediment-smothered coral framework is inhabited by large quantities of ophiuroids (Figure 9D). The species richness of sponges here appeared to be highest compared to all other ROV

transects on this cruise.

ROV dive 752 surveyed a small portion of the Gondola Slide area from 710–674-m water depth (Figure 9E, F and Table 1) that is described in Ridente et al. (2007) and Verdicchio et al. (2007). The dimensions of the slump blocks vary from a few to more than 500-m across and 300-m wide. These giant blocks, or olistoliths, are derived from the upper shelf and still contain the original sedimentary sequences with Late Pleistocene *Pseudamussium peslutrae* beds in situ—but they have slid down into bathyal depths (Verdicchio and Trincardi, 2006). The nearly flat seabed consists of moribund sand waves stabilized by hardgrounds (Figure 9E), which are colonized by both colonial and solitary scleractinians. The largest olistolith in the slide area is 870-m long and 91-m high and is covered by thick hardgrounds that serve as substrate for a large white coral reef rich in sponges (Figure 9F).

ROV dive 739 to the Dauno Seamount yielded no white coral communities (see Figure 8 for location). Some sediment-free outcrops are colonized by solitary scleractinians, like *D. dianthus*.

CTD stations from the coral habitats reveal water temperatures from 13.4°C to 13.7°C, salinities from 38.62 to 38.66, and a calculated density σ_t of 29.07–29.13. Dissolved oxygen values show well-oxygenated conditions, with 4.24–4.54 ml l⁻¹.

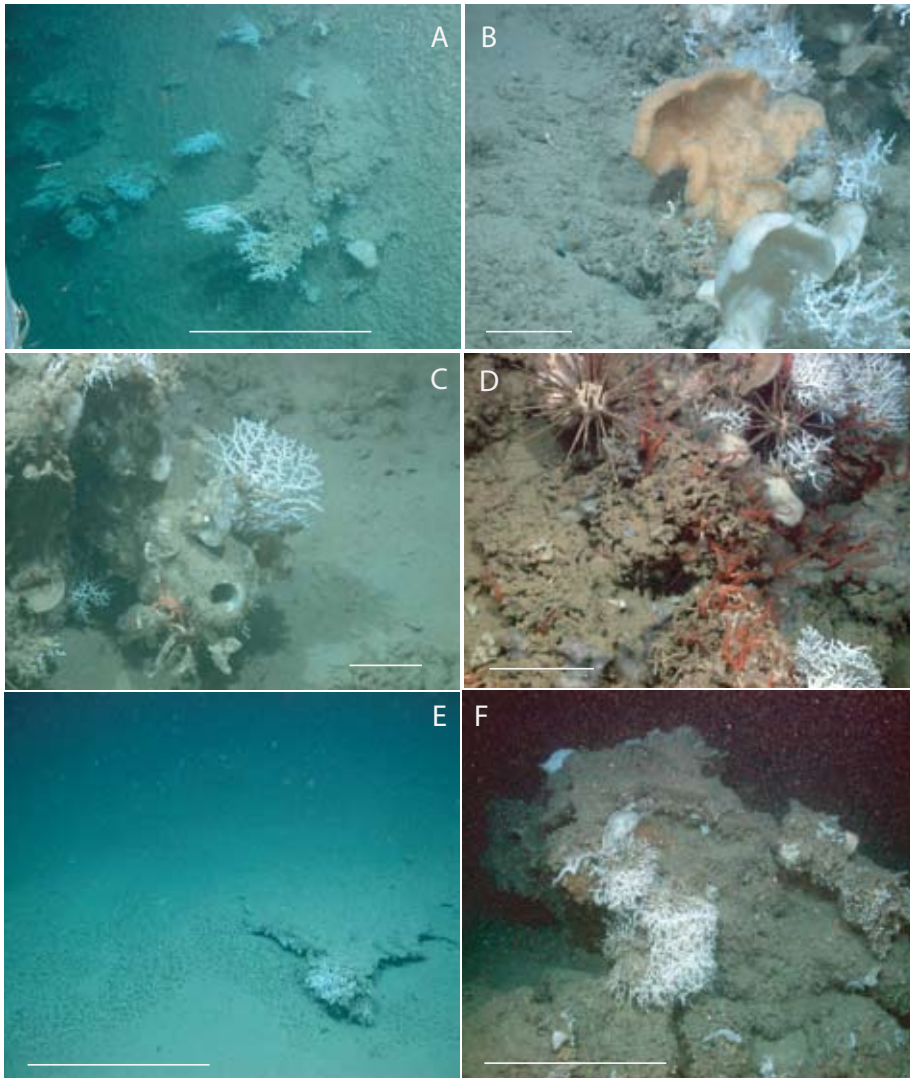


Figure 9. QUEST ROV images of the white coral community from the southwestern Adriatic margin. (A–B) Dive 735 and (C–D) Dive 745 imagery from the southern wall of the Bari Canyon. (E–F) Dive 752 imagery from the Gondola Slide area. (A) *M. oculata* colonies with down-facing, candelabra-like growth habits and effect of sediment trapping on a vertical slope section (571-m depth). (B) Lobate sponges and *M. oculata* attached to coral rubble or hardgrounds on less inclined slopes (536-m depth). (C) *M. oculata* associated with sponges (473-m depth). (D) *M. oculata* thickets and sediment-clogged coral framework inhabited by ophiuroids and grazed by sea urchins (306-m depth). (E) Exhumed hardground crust serving as attachment site for *L. pertusa* (713-m depth). (F) Hardground overgrown by *L. pertusa* and sponges (675-m depth). Scale bars = 1 m in A and E–F and 15 cm in B–D. All ROV images courtesy of QUEST ROV MARUM, Universität Bremen

DISCUSSION

The ROV dives performed during R/V *Meteor* cruise M70-1 yielded evidence of far more living white coral occurrences than previously thought for the central Mediterranean Sea. The findings of Schembri et al. (2007) from

Maltese waters could extend further to the west in the Sicilian Channel. The many records of live corals in the Adriatic sub-basin are also new to science. Their late discovery (compared to those in the Atlantic Ocean) is certainly related to the cryptic microhabitats that the corals prefer to select on steeply inclined walls, which are difficult—if not impossible—to sample with conventional, cable-towed gear.

What are the hydrographic habitat requirements for live coral communities in the central Mediterranean?

Although shallower records are known from the western Mediterranean, at Gibraltar, and in the Gulf of Lion (Figures 1 and 10), *Meteor* cruise scientists found live coral communities at depths ranging from 744 m to 306 m, wherever a colonizable and current-exposed hard substrate was available. Interestingly, this shallowest coral occurrence at 306-m water depth was found in the upper Bari Canyon at the southwestern Adriatic margin. It may be too early for solid conclusions, but canyon systems may better facilitate the spread of the bathyal coral assemblages into shallower depths than open slopes. A plausible explanation might be the seasonal or episodic cascading of water masses loaded with nutrients, food, and organic matter in the northwestern Mediterranean and southern Adriatic Sea (e.g., Canals et al., 2006, this issue). It should be noted, however, that coral depth ranges are still biased by the low numbers of known occurrences, and the deeper boundaries are difficult to measure for methodological reasons.

The hydrographic regime measured in live coral habitats during the cruise

encompass temperatures (T) ranging from 13.4°C to 13.9°C and salinities (S) between 38.4 and 38.9. These data fit well with T and S data for the SML site provided by Taviani et al. (2005b). However, the central Mediterranean T and S values measured in coral habitats are higher compared to those of the Northeast Atlantic (Roberts et al., 2006). Davies et al. (2008) performed an environmental niche factor analysis to define and predict suitable habitat of *L. pertusa* in the Northeast Atlantic. Highest correlation of live *Lophelia* with environmental parameters was at mean temperatures of 6.2–6.7°C and salinities of 35. High ambient water temperatures in the bathyal depths increase the corals' (and

associated organisms') demand for dissolved oxygen. We measured dissolved oxygen values from 3.75 to 4.54 ml l⁻¹ in the coral habitats. Dodds et al. (2007) showed in an ecophysiological study on *L. pertusa* that this species is unable to maintain its oxygen metabolic activity below 3 ml l⁻¹ dissolved oxygen. In the Atlantic, dissolved oxygen levels of 6.0–6.2 ml l⁻¹ are typically encountered in *Lophelia* habitats (Davies et al., 2008). If this result can be translated to natural conditions, then the corals in the central Mediterranean are close to their ecological limit. Again, these hydrographic data represent snapshots and did not cover the annual range of seasonality.

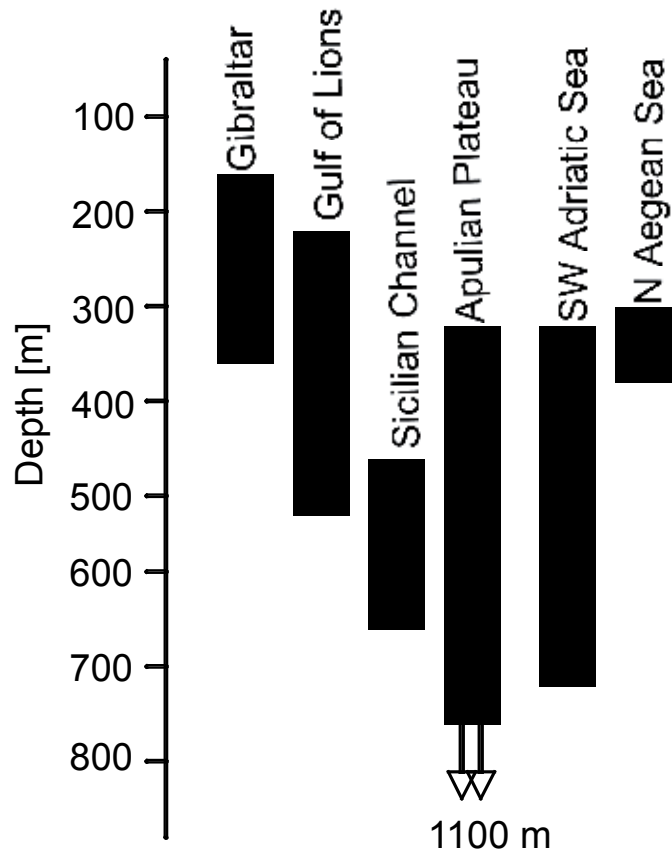


Figure 10. Depth ranges of live *L. pertusa* and *M. oculata* grouped in geographic regions in the Mediterranean Sea. See Figure 1 for cited sources.

“...MANY PREVIOUSLY UNKNOWN CORAL SITES WERE DISCOVERED DURING INSPECTIONS OF MEDITERRANEAN NARROW SHELVES, CANYON WALLS, ESCARPMENTS, AND SEAMOUNTS BY REMOTELY OPERATED VEHICLES.”

What are the types of coral habitats?

Basically, analysis of the ROV dive data allows the recognition of two mesoscale habitats—the steeply inclined walls and the gently sloping shelf. The steeply inclined wall mesohabitat is a common feature in the tectonically active Mediterranean basins. Such walls may represent tectonically derived escarpments or fault lines, belong to canyon systems incised into the continental margin, or be a combination of the two. ROV image data clearly show that the coral colonies are not randomly distributed along a surveyed wall but are concentrated at microtopographic heterogeneities defining the microhabitat. Such microhabitats can be characterized by changes in bedrock lithologies that result in the formation of erosive ledges and overhangs or fissures and crevices that dissect the bedrock. Overhangs underneath outcropping rock ledges are the preferred sites for coral colonization, resulting in a downward growth pattern of the individual polyps and branches. Similar peculiar site selection on steep sloping walls has also been observed in some other cold-water coral settings, such as in the northern Chilean fjords, where *D. dianthus* aggregations were found growing in the same way (Försterra et al., 2005). The corals take advantage of the lateral and/or probably upwelling current regime that also brings the food particles and plankton directly to

the coral polyps. Sediments from shallower slope or shelf areas pass by and do not smother the live corals in their cryptic habitats. This growth pattern from downward- to upward-facing, or “normal” growth habits changes at the upper edges of steeply sloped walls, where the negative effects of sediment burial are limited and current-advected food supply comes from the adjacent shelf. This pattern was observed on the Gallipoli escarpment at the transition from the steep wall to the gently inclined Apulian Plateau within the SML reef province. Obviously, the steep wall coral habitat does not support the formation of huge coral frameworks. Accommodation space is limited and broken corals do not accumulate within the coral habitat because gravitational forces export them further downslope where they accumulate as coral debris flow or related mass-transport sediment types (see Titschack et al., 2005).

The second mesohabitat is the gently inclined shelf, such as the Apulian Plateau and the SML reef province comprising hundreds of elongated mounds covered by a veneer of coral thickets growing in an almost upright position. At a closer look, the most intense coral growth is observed on the up-current, exposed mound summits and eastern flanks that face the intermediate water outflow from the Otranto Strait in the north. In such deep shelf settings, the

interplay between coral growth and subsequent trapping of current-advected detritus eventually results in the formation of a three-dimensional topographic coral mound. Such growth modes have also been found in Northeast Atlantic coral carbonate mounds (Roberts et al., 2006; Rüggeberg et al., 2007; Wheeler et al., 2007). Studies are underway to reveal the Holocene growth dynamics of the SML coral mounds.

Are the live coral populations in the central Mediterranean connected?

Without molecular genetic studies at hand to define the genetic exchange between the coral populations sampled on R/V *Meteor* cruise M70-1, we have to infer possible biogeographic connectivities and causal relationships. The most likely link among the corals in this study is intermediate water circulation in the central Mediterranean. Major elements of our model include the water cascading of the NAdDW into the Adriatic sub-basin in wintertime, where it mixes with the winter-formed ADW to become a compartment water mass of the EMDW. In the Adriatic sub-basin, this deep-water mass is overlain by the less-dense LIW. Both the deep and intermediate water masses flow through the Otranto Strait and pass the Apulian Plateau that hosts the SML coral reef province (Manca et al., 2002). From here, the water masses flow into the Levantine Basin and along the Calabrian-Sicilian margin in the Ionian Sea and enter the Sicilian Channel east of Malta through the deep troughs, thus securing a food supply for the sessile benthic hard-substrate communities (Lascaratos et al., 1999; Astraldi et al., 2002). Seen in this way, the coral provinces might


be connected by deep and intermediate water circulation. The cascading of winter-cooled, dense shelf waters into the deep basin has been recognized as a major driver for the transfer of organic matter and hydrodynamic energy in the Gulf of Lion region, where the canyons act as conduits for the cascading water masses (Canals et al., 2006, this issue). It is not surprising that live coral communities were repeatedly reported to occur at the heads of canyons in this area of the northwestern Mediterranean Sea.

What about other potential regions for live white coral communities in the eastern Mediterranean Sea? A promising area in terms of steep bathymetric gradients and cascading water masses is the Cretan Arc with its two major overflow gateways that control the water exchange between the Cretan Sea and the Aegean Sea—the Antikithira and Kassos straits (Balopoulos et al., 1999; Lascaratos et al., 1999; Lykousis, 2001). So far, only fossil or subfossil white corals have been sampled from these waters (recent work of author Taviani; Zibrowius, 1980) but the relevant depth intervals suitable for white corals have not yet been visually inspected by ROV or submersible. The Cretan Arc is not far from the unusual isolated occurrence of live *L. pertusa* and *M. oculata* in the Aegean Sea (Vafidis et al., 1997).

The HERMES ROV dives on R/V *Meteor* cruise M70-1 demonstrated that the SML coral province is not as geographically isolated as previously believed, and that white coral communities thrive over much wider geographic areas in the central Mediterranean; however, they are difficult to sample with conventional gear—and are therefore generally unrecognized because

they live beneath bedrock overhangs on steeply inclined submarine walls and escarpments.

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