



## Living deep-water *Lophelia* and *Madrepora* corals in Maltese waters (Strait of Sicily, Mediterranean Sea)

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**Abstract:** The occurrence of living deep-water corals, *Lophelia pertusa* and *Madrepora oculata*, from stations 21-42 km off the southern and south-western coast of Malta is reported. Fragments of living colonies of both species, as well as some large pieces of *Lophelia* frameworks were recovered from depths of 390-617 m together with the solitary coral *Desmophyllum dianthus* (= *cristagalli*). The accompanying biota included the barnacle *Pachylasma giganteum*, the gastropod *Coralliophila richardi*, the bivalves *Asperarca nodulosa* and *Spondylus gussonii*, and the polychaete *Eunice norvegicus*, all of which are frequently associated with deep-water corals. The occurrence of the *Lophelia-Madrepora-Desmophyllum* triad, the large pieces of coral frameworks consisting predominantly of live, healthy polyps, and the associated biota, suggest that coral patches may be present in at least some of the investigated localities, rather than just fragmented remains or isolated colonies.

**Résumé :** Coraux vivants en eau profonde (*Lophelia* et *Madrepora*) dans les eaux maltaises (Détroit de Sicile, Mer Méditerranée). La présence de coraux vivants en eau profonde, *Lophelia pertusa* et *Madrepora oculata*, dans des stations à 21-42 kilomètres loin de la côte au sud et au sud-ouest de Malte est signalée. Des fragments de grandes colonies vivantes des deux espèces ainsi que de grandes parties du squelette de *Lophelia* ont été récoltées à une profondeur de 390-617 mètres, associées au corail solitaire *Desmophyllum dianthus* (= *cristagalli*). La faune environnante comprend la balane *Pachylasma giganteum*, le gastéropode *Coralliophila richardi*, les bivalves *Asperarca nodulosa* et *Spondylus gussonii* et le polychète *Eunice norvegicus*, tous généralement associés aux coraux vivants en eau profonde. La présence de la triade *Lophelia-Madrepora-Desmophyllum* et de grandes parties de coraux constitués principalement de polypes vivants ainsi que la faune associée suggèrent que des assemblages de coraux sont présents dans au moins quelques-unes des localités étudiées plutôt que des restes fragmentés ou des colonies isolées.

**Keywords:** Cold-water corals • *Lophelia pertusa* • *Madrepora oculata* • *Desmophyllum dianthus* • Malta • Central Mediterranean

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## Introduction

The existence of cold-water coral banks has been known since at least the 1800s but it is only recently that these habitats have been systematically studied, mainly as a result of modern advances in deep sea exploration technology (Freiwald et al., 2004). Cold-water corals generally occur along the edges of continental shelves, in fjords and around offshore submarine banks, vents and seamounts in waters at a temperature of ca 4-13°C, and usually at depths of 200-1000 m, although they have also been recorded from water as shallow as 7-39 m (fjords in Chile; Trondheimsfjord in Norway) to as deep as 3,383 m (the North Atlantic New England Seamount Chain) (Freiwald et al., 2004).

Of the many species of deep-water corals, only about six are considered to form true reefs, in the sense of constructing submarine biogenic calcareous three-dimensional frameworks, rising from the seabed (Freiwald & Roberts, 2005). The two principal reef-building cold-water corals in the NE Atlantic are the scleractinians *Lophelia pertusa* and *Madrepora oculata*, commonly referred to as ‘white corals’ (Pérès & Picard, 1964); the other species are all tropical or southern ocean ones (Cairns, 1995; Freiwald et al., 2004). In the eastern Atlantic, deep-water corals form a dense belt of reefs from the Barents Sea along the eastern Atlantic down to Mauritania in West Africa with scattered occurrences elsewhere, including in the Mediterranean (Freiwald et al., 2004; Cartes et al., 2004; Taviani et al. 2005a).

NE Atlantic deep-water reefs may rise several metres above the sea floor and cover extensive areas of seabed (Freiwald & Roberts, 2005); the largest NE Atlantic cold water reef complex known to date is formed by *Lophelia pertusa* southwest of the Lofoten Islands on the Norwegian shelf, and covers approximately 100 km<sup>2</sup> (Fosså et al., 2002). These NE Atlantic reefs support a high species richness and are considered ‘biodiversity hotspots’ (Freiwald et al., 2004).

In the Mediterranean, as in the NE Atlantic, deep-water coral reefs are constructed by the scleractinians *Lophelia pertusa* (Linnaeus, 1758) and *Madrepora oculata* Linnaeus, 1758, which form anatomising colonies, and by *Desmophyllum dianthus* (Esper, 1794) (= *D. cristagalli* Milne Edwards & Haime, 1848), which although solitary, also contributes to the reef frameworks. In contrast to the NE Atlantic, however, reefs with live *Lophelia* are very rare in the Mediterranean. In fact, practically the only example is the coral bank discovered off the coast of Santa Maria di Leuca (Apulia, Italy) on the eastern side of the Ionian Sea, north of the Calabrian Arc, on a gently dipping shelf at depths between 425 m and 1110 m (Mastrototaro et al., 2002; Tursi et al., 2004; Taviani et al., 2005b). The

biodiversity associated with these Ionian *Lophelia* banks is lower than their Atlantic counterparts, although still high (Tursi et al., 2004; Taviani et al., 2005b).

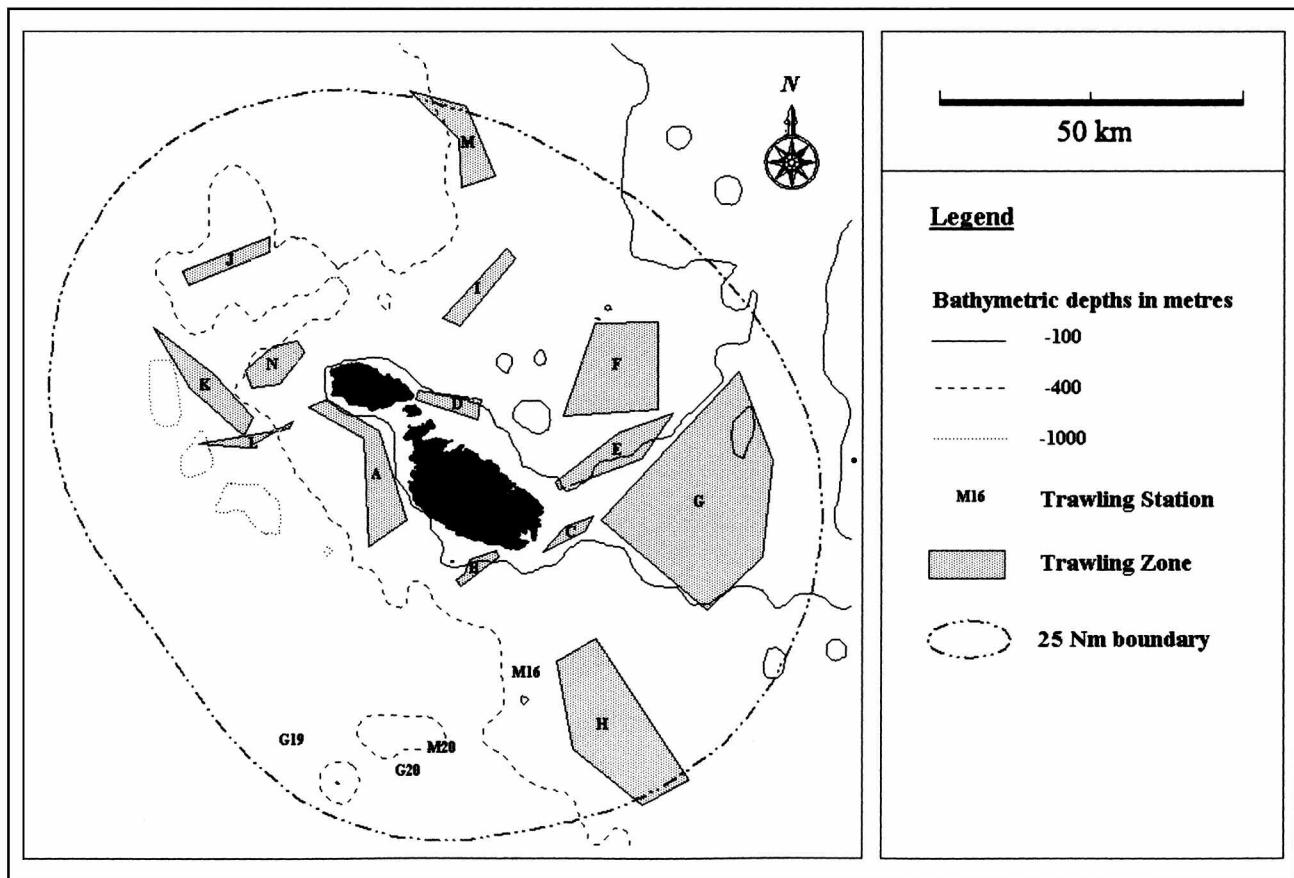
Live *Lophelia* and, to a lesser degree, *Madrepora*, are only known from a very limited number of Mediterranean sites besides Santa Maria di Leuca, including the Alboran Sea and the Gulf of Lions (Zibrowius, 1980; Rogers, 1999; Taviani et al., 2005a). However, these West Mediterranean systems appear to be relicts of much more extensive reefs that populated the Mediterranean in the Pleistocene (Pérès, 1985; Remia & Taviani, 2005; Taviani et al., 2005a) and the colonies consist mainly of dead coral with living polyps only in the terminal portions of the branches (Cartes et al., 2004). It has been suggested that the extensive deep-water coral banks of the Mediterranean Pleistocene underwent cycles of growth and decline correlated with increases and decreases in trophic resources brought about by the temperature changes associated with glacial-interglacial cycles (e.g. Delibrias & Taviani, 1984). The rising water temperatures resulting from the drastic hydrographical changes at the end of the last glacial appears to have affected *Lophelia* more than either *Madrepora* or *Desmophyllum*, which are presently more vigorous and widespread in the Mediterranean than *Lophelia* (Taviani et al., 2005a).

Here we report the recent discovery of living *Lophelia* and *Madrepora* frames from the eastern Ionian Sea, off the southern coast of Malta. The Strait of Sicily, where our study area is located, was not known to be a site of significant deep-water coral growth; most records of deep-water corals from here refer to dead Pleistocene assemblages (Taviani & Colantoni 1984; Taviani et al., 2005a), although Zibrowius & Taviani (2005) recorded a small live branch of *Lophelia pertusa* dredged from Nameless Bank.

The deep water corals were accidentally collected during trawl operations within the 25 nautical mile Malta Fisheries Management Zone (FMZ) in the ambit of the MEDITS and GRUND programmes (described by Bertrand et al., 2002 and Relini, 1998, respectively). During the 2003 MEDITS and GRUND cruises, a limited number of exploratory hauls were made on hard grounds in the same general area some 21-42 km (11.3-22.7 nautical miles) off the southern to south-western coast of Malta (Fig. 1).

## Material and methods

The stations (Table 1) were being sampled as part of fishery surveys using two types of bottom trawl gears, GOC 73 (MEDITS; Fiorentini et al., 1999) and the typical commercial ‘tartana di banco Mazarese’ (GRUND). The two gears mainly differ in the vertical opening of the mouth: 2.4-2.9 m (MEDITS) and 0.6-1.3 m (GRUND); both nets have a



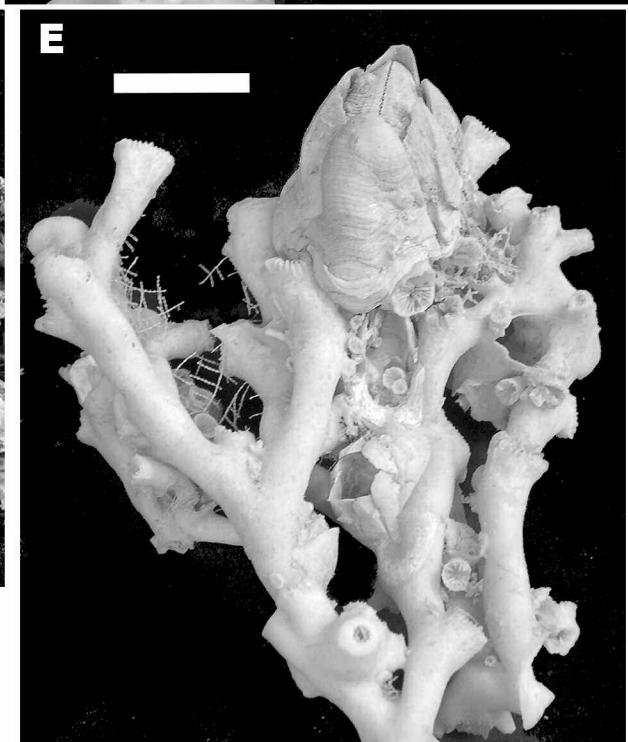
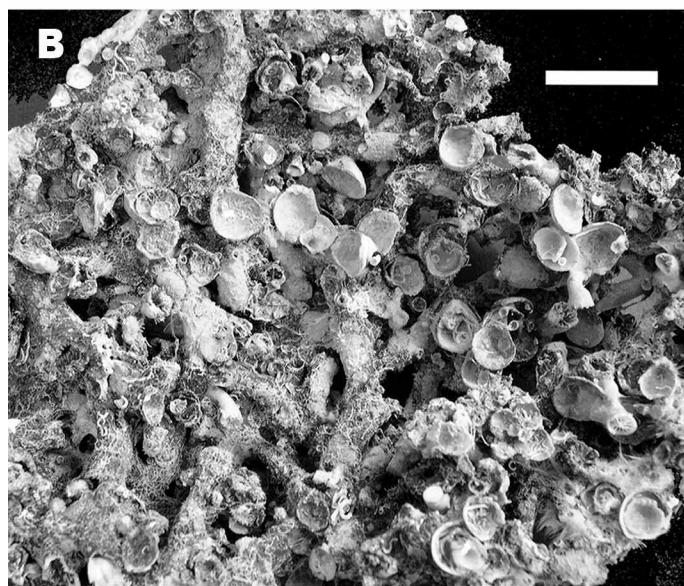
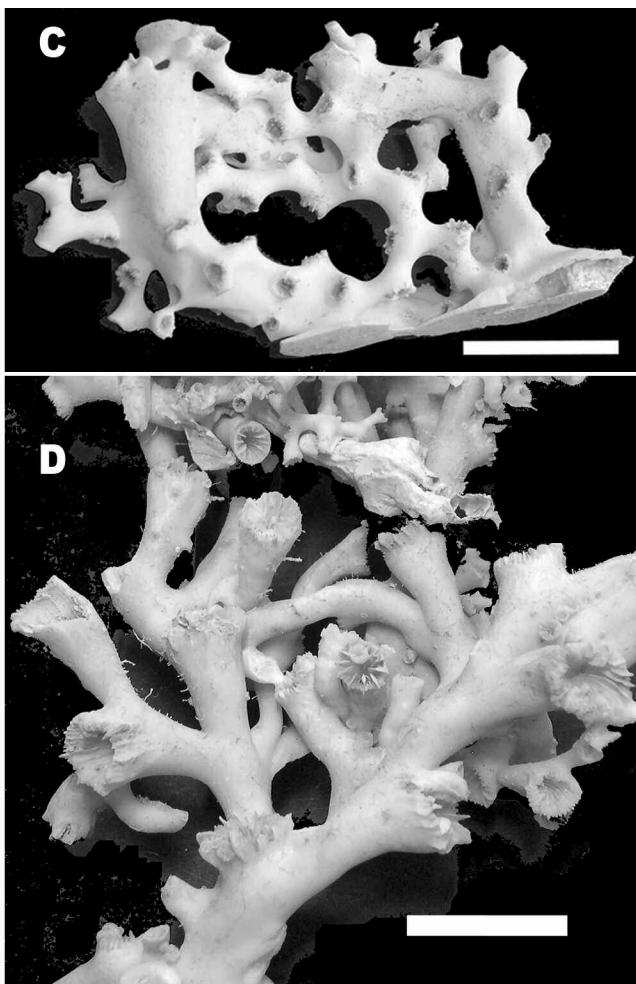
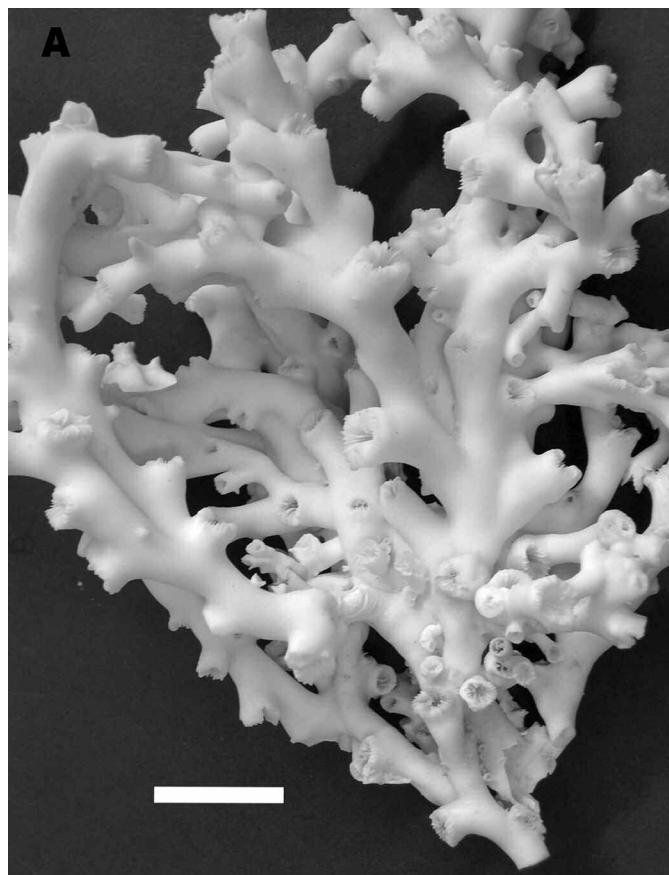
**Figure 1.** Map of the general sea area around the Maltese Islands showing the location of the four stations that provided deep water scleractinian corals during the MEDITIS 2003 (stations M16 and M20) and GRUND 2003 (stations G19 and G20) cruises. The boundary of the 25 nautical mile Fisheries Management Zone and the areas where trawling is allowed within the zone (shaded polygons labelled A – M) are also shown.

**Figure 1.** Plan de la zone marine des îles maltaises indiquant l'emplacement des quatre stations où les corails d'eau profonde ont été prélevés pendant les croisières de MEDITIS (stations M16 et M20) et de GRUND (stations G19 et G20) en 2003. La limite de la Malta Fisheries Management Zone de 25 milles nautiques et d'autres zones où la pêche au chalut est permise (les polygones hachurés et marqués par les lettres A à M) sont également indiquées.

**Table 1.** The 2003 GRUND and MEDITIS sampling stations within the Malta Fisheries Management Zone that provided the deep-water corals discussed in this paper.

**Table 1.** Les stations d'échantillonnage de GRUND et MEDITIS en 2003 dans la Malta Fisheries Management Zone qui ont fournies les coraux en eau profonde étudiés dans ce document.

Cruise	Station	Date	Start of haul Lat./Long.	End of haul Lat./Long.	Start Depth (m)	End Depth (m)	Scleractinians (L= live; D = dead)
MEDITIS 2003	M16	19.07.2003	N35°35.26/ E14°30.18	N35°37.76/ E14°32.06	444	395	<i>Lophelia pertusa</i> (L) <i>Madrepora oculata</i> (L) <i>Desmophyllum dianthus</i> (L)
MEDITIS 2003	M20	19.07.2003	N35°29.42/ E14°19.60	N35°29.72/ E14°22.98	588	564	<i>Madrepora oculata</i> (L) <i>Desmophyllum dianthus</i> (L)
GRUND 2003	G20	29.09.2003	N35°29.13/1 E14°18.0	N35°29.33/ E14°21.56	540	580	<i>Lophelia pertusa</i> (D)
GRUND 2003	G19	29.09.2003	N35°30.47/ E14°06.27	N35°30.83/ E14°06.02	617	420	<i>Lophelia pertusa</i> (L) <i>Desmophyllum dianthus</i> (L)



cod-end mounting a 20 mm stretched mesh net. Each haul lasted for ca. 30 minutes and the trawl was towed at a speed of about 3 knots; an estimated seabed area of 0.05 km<sup>2</sup> per haul was therefore sampled. These hauls were aimed at sampling demersal fish, and coral was only sampled accidentally. Although the sampling gear was extensively damaged during the hauls, pieces of corals and some of the accompanying biota were entangled in the torn nets. These were removed and stored in 5% formaldehyde in seawater, and were later examined in the laboratory.

## Results

Considerable quantities of live *Madrepora oculata* colonies were recovered from Station M16 (Fig. 2C) but only a few small live colonies from Station M20. *Lophelia pertusa* was retrieved from three stations, but those from Station G20 were all dead, although large colonies (pieces up to 30cm across) were recovered from this station (Fig. 2B). However, small pieces of live *Lophelia pertusa* were hauled from Station M16 and large quantities from Station G19 (Fig. 2A); those from the latter station included some very large pieces of which the biggest was a sheet measuring about 1m x 1m. This station also yielded a few dead colonies.

Both live *Madrepora* and live *Lophelia* colonies were white in colour with yellowish polyps. Dead branches varied in colour from yellow to black and were often covered with black films of iron-manganese oxide deposits. Live and dead colonies supported epibionts, predominantly hydroids and dead attached valves of *Spondylus gussonii* (Fig.2B), but also occasional living individuals of this species, and serpulids and sponges.

The solitary coral *Desmophyllum dianthus* was present in Stations M16, M20 and G19 (Fig. 2D) where it grew on both live and dead *Lophelia* and *Madrepora* as well as on other hard substrata, such as stones, nylon fishing lines and other anthropogenic debris. Live adult and juvenile specimens of the barnacle *Pachylasma giganteum* (Fig. 2E) were also quite frequent attached to the living and dead branches of *Lophelia* and *Madrepora* (Stations M16 and M20). Numerous live specimens of the bivalve *Asperarca nodulosa* were collected from between the branches of dead

*Lophelia* from Stations G19 and G20. The polychaete *Eunice norvegicus* was present in large numbers in the interspaces between the branches of live *Lophelia* and the coral formed thin calcareous sheets that enclosed the parchment tubes of the worms as has already been described (Freiwald et al., 1997; Remia & Taviani, 2005). Errant species collected with the *Lophelia* and *Madrepora* included the echinoid *Cidaris cidaris*, the gastropod *Coralliophilia richardi*, and the crab *Anamantha rissoana*, all of which seem to associate with living deep-water coral banks (Tursi et al., 2004).

## Discussion

The present finding of live frame-building deep-water corals south of the Maltese Islands is noteworthy, especially because of the occurrence of large healthy colonies of *Lophelia pertusa*, for which this is the second such record for the Ionian Sea, after that of the Santa Maria di Leuca reef located some 20-25 nautical miles off the coast of Southern Italy (Mastrototaro et al., 2002; Tursi et al., 2004; Taviani et al., 2005a, b). Although we only recovered fragments of *Lophelia* and *Madrepora* frameworks from the by-catch of trawl surveys aimed at the assessment of fishery resources, a number of features suggest that coral patches may be present in at least some of the investigated localities, rather than just fragmented remains or isolated colonies or live terminal branches on otherwise dead frameworks. Such features include: the occurrence of the *Lophelia-Madrepora-Desmophyllum* triad, common to most NE Atlantic and Mediterranean live, subfossil and fossil deep-water coral reefs (Freiwald et al., 2004; Taviani et al., 2005a); the ample quantities of live fragments retrieved, the occasionally large pieces of *Lophelia* frameworks collected (especially that from Station G19), which consisted predominantly of live, apparently vigorously growing polyps; and the biota associated with these corals, especially the bivalves *Asperarca nodulosa* and *Spondylus gussonii*, and the commensal polychaete *Eunice norvegicus* which induces calcification of its tubes by the host corals, that are all known associates of *Lophelia* and *Madrepora* frameworks (Freiwald et al., 1997; Remia & Taviani, 2005; Taviani et al., 2005a, b).

Figure 2. A. Live *Lophelia pertusa* colony from Station G19. B. Dead colony of *Lophelia pertusa* with numerous valves of *Spondylus gussonii* from Station G20. C. Live *Madrepora oculata* colony from Station M16. D. *Desmophyllum dianthus* growing on *Lophelia pertusa* from Station M16. E. *Pachylasma giganteum* growing on *Lophelia pertusa* from Station M16; Station details are given in Table 1. Scale bar 2 cm in all cases.

Figure 2. A. Colonie vivante à *Lophelia pertusa* de la Station G19. B. Colonie morte de *Lophelia pertusa* avec de nombreuses valves à *Spondylus gussonii* de la Station G20. C. Colonie vivante à *Madrepora oculata* de la Station M16. D. *Desmophyllum dianthus* pouvant sur *Lophelia pertusa* de la Station M16. E. *Pachylasma giganteum* pouvant sur *Lophelia pertusa* de la Station M16. Les détails des stations sont indiqués dans le Tableau 1. Echelle de 2 cm dans tous les cas.

Although our data on the Maltese deep-water coral assemblages is very preliminary, nonetheless there are some tantalising similarities with the Santa Maria di Leuca reef, including the more or less similar depths at which both occur, the dominance of *Lophelia pertusa* at both sites, and the similar associated biota (Tursi et al., 2004; Taviani et al., 2005b).

Although we examined fishery trawl-survey by-catch from a large number of stations within the entire 25 nautical mile Malta Fisheries Management Zone, we only found evidence of deep-water corals at the four stations listed in Table 1. Why this area off southern Malta should support such growths is not known, although it may well have to do with the particular topographic and hydrographic conditions there. For the Santa Maria di Leuca coral bank, Taviani et al. (2005b) speculate that the spectacular coral growth there is due to the strong bottom currents coupled with the particular seabed topography at this location. We have no data on the deep currents or bottom topography of the sites where the Maltese coral assemblages were found, and this is certainly one aspect that needs to be investigated further, however, this general locality has an inordinately high demersal secondary production compared to surrounding areas (unpublished data), which is suggestive.

During a later cruise (MEDITS 2005) we recovered three small colonies of *Lophelia* from the same piece of nylon rope dredged from a depth of 622-667 m from a station located at 35°43.47'N/13°38.58'E to 35°41.75'N/13°41.31'E sampled on 17.07.2005. Although no other large *Lophelia* or *Madrepora* colonies were recovered, but only individuals of *Desmophyllum dianthus* growing on anthropogenic debris, the presence of young *Lophelia pertusa* colonies on a modern fishing line suggests active recruitment of *Lophelia* in the area south of Malta.

NE Atlantic deep-water coral systems are under threat (Gubbay, 2003), however, in January 2006, the General Fisheries Commission for the Mediterranean (GFCM) declared a restricted area for deep sea fisheries off Cape Santa Maria di Leuca and has prohibited fishing with towed dredges and bottom trawl nets specifically to protect the coral banks there (GFCM, 2006). The coral sites off southern Malta are located within the Maltese FMZ. Although this FMZ was primarily set up to protect the fish stocks, especially commercial demersal resources, of the Maltese shelf area, the restriction and regulation of trawling activities within the area serves also to protect benthic habitats, including the coral sites reported here. At present there is only a very limited amount of trawling effort in the Malta FMZ and almost none at all where the deep-water coral occurs (Fig. 1). Trawling is formally illegal at these locations (Council of the European Union, 2004), however unauthorised operations may still take place and we recommend that the area where the coral accumulations

occur be declared off limits to commercial trawling, with more rigorous protection in order to preserve these sites and allow their further scientific study. We emphasise that the present collections were made accidentally during fishery trawl surveys and we did not return to trawl the coral sites once it became apparent that deep-water coral patches may occur there. Studies of deep-water corals should not employ bottom trawls of any kind.

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### References

- Bertrand J.A., Gil de Sola L., Papacostantinou C., Relini G. & Souplet A. 2002.** The general specifications of the MEDITS surveys. *Scientia Marina*, **66** (Supplement 2): 9-17.
- Cairns S.D. 1995.** The marine fauna of New Zealand: Scleractinia (Cnidaria: Anthozoa). *New Zealand Oceanographic Institute Memoir*, **103**, 210 pp.
- Cartes J.E., Maynou F., Sardà F., Company J.B., Lloris D. & Tudela S. 2004.** The Mediterranean deep-sea ecosystems: an overview of their diversity, structure, functioning and anthropogenic impacts. In: *The Mediterranean deep-sea ecosystems: an overview of their diversity, structure, functioning and anthropogenic impacts, with a proposal for conservation*; pp 9-38. IUCN: Málaga & WWF: Rome.
- Council of the European Union 2004.** Council Regulation (EC) No 813 /2004. Corrigendum to Council Regulation (EC) No 813/2004 of 26 April 2004 amending Regulation (EC) No 1626/94 as regards certain conservation measures relating to waters around Malta (OJ L 150, 30.4.2004). *Official Journal* L185 (24/05/2004).
- Delibrias G. & Taviani M. 1984.** Dating the death of Mediterranean deep-sea scleractinian corals. *Marine Geology*, **62**: 175-180.
- Fiorentini L., Dremiere P.Y., Leonori L., Sala A., Palumbo V. 1999.** Efficiency of the bottom trawl used for the

- Mediterranean international trawl survey (MEDITS). *Aquatic Living Resources*, **12**: 187-205.
- Freiwald A., Fosså J.H., Grehan A., Koslow T. & Roberts J.M. 2004.** *Cold-water Coral Reefs*. UNEP-WCMC: Cambridge, UK. 84 pp.
- Freiwald A., Henrich R. & Pätzold J. 1997.** Anatomy of a deep-water coral reef mound from Stjernsund, West Finnmark, Northern Norway. In: *Cool-water carbonates* (N.P. James & J.A.O. Clarke eds), pp. 141-161. Society for Sedimentary Geology Special Publication, 56. SEPM (Society for Sedimentary Geology): Tulsa, Oklahoma, USA.
- Freiwald A. & Roberts J.M. 2005.** Preface. In: *Cold-water corals and ecosystems* (A. Freiwald & J.M. Roberts eds), pp. vii-xii. Springer-Verlag: Berlin.
- Fosså J.H., Mortensen P.B. & Furevik D.M. 2002.** The deep-water coral *Lophelia pertusa* in Norwegian waters: distribution and fishery impacts. *Hydrobiologia*, **471**: 1-12.
- General Fisheries Commission for the Mediterranean 2006.** Recommendation GFCM/2006/3. *Report of the Thirtieth Session Istanbul, Turkey, 24-27 January 2006*. Food and Agriculture Organization of the United Nations: Rome, Italy. 55 pp.
- Gubbay S. 2003.** *Seamounts of the North-East Atlantic. Project OASIS*. World Wildlife Fund: Frankfurt. 38 pp.
- Mastrototaro F., Matarrese A. & Tursi A. 2002.** Un mare di coralli nel mar Ionio. *Biologia Marina Mediterranea*, **9**: 616-619.
- Pérès J.M. 1985.** History of the Mediterranean biota and the colonisation of the depths. In: *Western Mediterranean* (R. Margalef ed), pp 198-232. Pergamon Press: U.K.
- Pérès J.M. & Picard J. 1964.** Nouveau manuel de bionomie benthique de la mer Méditerranée. *Recueil des Travaux de la Station Marine d'Endoume*, **31**: 5-137.
- Relini G. 1998.** Valutazione delle risorse dimersali. *Biologia Marina Mediterranea*, **5**: 3-19.
- Remia A. & Taviani M. 2005.** Shallow-buried Pleistocene *Madrepora*-dominated coral mounds on a muddy continental slope, Tuscan Archipelago, NE Tyrrhenian Sea. *Facies*, **50**: 419-425.
- Rogers A.D. 1999.** The biology of *Lophelia pertusa* (Linnaeus 1758) and other deep-water reef-forming corals and impacts from human activities. *International Review of Hydrobiology*, **84**: 315-406.
- Taviani M. & Colantoni P. 1984.** Paleobiocoénoses profondes à scléractiniaires sur l'escarpement de Malte-Syracuse (Mer Méditerranée): leur structure, leur âge et leur signification. *Revue de l'Institut Français du Pétrole*, **39**: 547-559.
- Taviani M., Freiwald A. & Zibrowius H. 2005a.** Deep coral growth in the Mediterranean Sea: an overview. In: *Cold-water corals and ecosystems* (A. Freiwald & J.M. Roberts eds), pp 137-156. Springer-Verlag: Berlin.
- Taviani M., Remia A., Corselli C., Freiwald A., Malinverno E., Mastrototaro F., Savini A. & Tursi A. 2005b.** First geo-marine survey of living cold-water *Lophelia* reefs in the Ionian Sea (Mediterranean basin). *Facies*, **50**: 409-417.
- Tursi A., Mastrototaro A., Matarrese A., Maiorana P. & D'Onghia G. 2004.** Biodiversity of the white coral reefs in the Ionian Sea (Central Mediterranean). *Chemistry and Ecology*, **20** (supplement 1): 107-116.
- Zibrowius H. 1980.** Les Scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental. *Mémoires de Institut Océanographique de Monaco*, **11**, 107 pp.
- Zibrowius H. & Taviani M. 2005.** Remarkable sessile fauna associated with deep coral and other calcareous substrates in the Strait of Sicily, Mediterranean Sea. In: *Cold-water corals and ecosystems* (A. Freiwald & J.M. Roberts eds), pp 807-819. Springer-Verlag: Berlin.