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Offshore *Neopycnodonte* Oyster Reefs in the Mediterranean Sea

Lorenzo Angeletti [1,*] and Marco Taviani [1,2,3]

1 ISMAR-CNR, U.O.S. Bologna, via Gobetti 101, I-40129 Bologna, Italy; marco.taviani@bo.ismar.cnr.it
2 Biology Department, Woods Hole Oceanographic Institution, 266 Woods Hole Road, Woods Hole, MA 02543, USA
3 Stazione Zoologica Anton Dohrn, Villa Comunale, 80121 Napoli, Italy
* Correspondence: lorenzo.angeletti@bo.ismar.cnr.it

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Abstract: Oysters are important ecosystem engineers best known to produce large bioconstructions at shallow depth, whilst offshore deep-subtidal oyster reefs are less widely known. Oyster reefs engineered by *Neopycnodonte cochlear* (family Gryphaeidae) occur at various sites in the Mediterranean Sea, between 40 and 130 m water depths. Remotely Operated Vehicle surveys provide new insights on this rather neglected reef types with respect to their shape, dimensions and associated biodiversity. We suggest that these little contemplated reefs should be taken in due consideration for protection.

Keywords: oyster reef; mesophotic; Mediterranean Sea

1. Introduction

Oysters are important ecosystem engineers distributed worldwide, with a tendency to aggregate in large numbers creating bioconstructions of considerable lateral and vertical extent such as beds, banks, up to reefs [1,2]. Oyster reefs *sensu lato* play a pivotal ecological role by enhancing biodiversity, fishery and coastal protection, among others [2–12]. Oyster reefs best develop at shallow depths in estuarine, bay or lagoonal settings, as well as in marine shallow subtidal situations [2,13–15]. True oysters (Ostreoidea) may have been arisen at the Permian-Triassic boundary (revised in [16]), with families Ostreidae and Gryphaeidae, and their reefs being positively documented in the Mesozoic and Cenozoic [2,17–24].

At present, the main reef-builders in European waters are members of the family Ostreidae (*Ostrea edulis* Linnaeus, 1758, and *Crassostrea* spp.) constructing reefs at intertidal to very shallow (0–20 m) water depths [25–34]. Analogous bioconstructions engineered by Ostreidae are common in the European Cenozoic record [23,35,36].

Gryphaeidae are also known to produce relevant bioconstructions in European waters, but at deeper depths (> 30 m), and this was the case also in the past, since at least the Middle Miocene (e.g., *Neopycnodonte navicularis*, [36–39] among others). Two extant taxa engineering oyster aggregations in the Mediterranean and Atlantic, which could, at times, be identified as reefs, are *Neopycnodonte cochlear* (Poli, 1795) and *Neopycnodonte zibrowii* Gofas, Salas and Taviani, 2009. The latter settles on hard substrates at bathyal depths (ca. 300–800 m) forming encrustations, rims and occasional small reefs [40–48]. *N. cochlear* is widespread in the Mediterranean at intermediate water depths (ca. 30–150 m), mainly under mesophotic conditions, or even deeper in the NE Atlantic [46,49], and also colonizes dark submarine caves [50]. It forms aggregations in the Mediterranean offshore and its capability to build up or contribute to reefs is recognized [46,51,52]. However, there is a substantial lack of knowledge regarding this intermediate (mesophotic) oyster, and only a few literature records are available on *Neopycnodonte cochlear* occurrences (e.g., [52,53]).

Oyster reefs are of paramount importance worldwide (e.g., [54–58]), and are considered under several protection and management measures (e.g., Habitat Directive: Council Directive 92/43/EEC). According to the EUR28 interpretation manual of the Habitat Directive for the class “1170 Reefs”, it can be defined as reef any biogenic (concretions, encrustations, and bivalve beds originating from dead or living animals) or geogenic (reefs originating on non-biogenic substrate such rocks, boulders, etc.) structure arising from the seafloor [59]. Oyster reefs can raise the height of the seafloor from 0.15 m up to 6 m (e.g., *Crassostrea virginica* reefs in the US coasts and *Ostrea edulis* reefs in the Black Sea, respectively [60,61]).

Here, we describe *N. cochlear* reefs identified by Remotely Operated Vehicle (ROV) surveys in the Adriatic and Ionian seas offshore the Apulian margin of Italy (Figure 1).

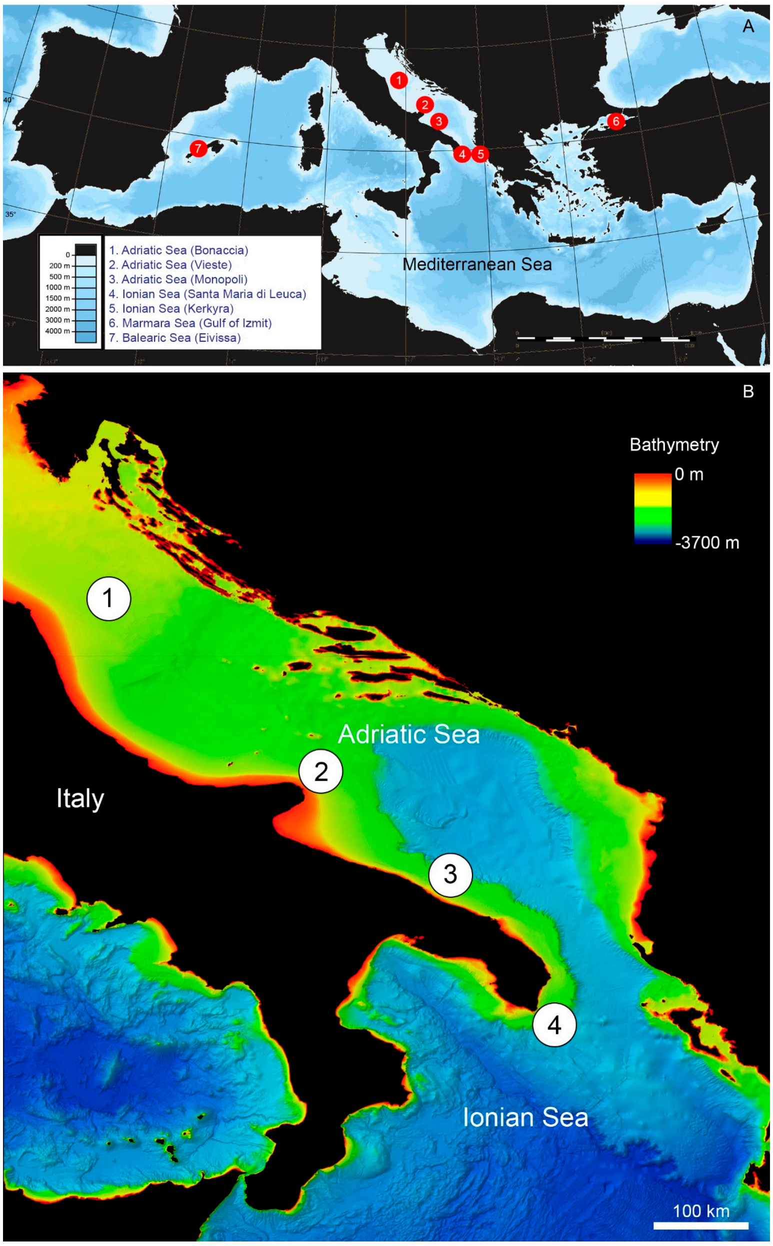

Figure 1. (**A**) Location map of Mediterranean *Neopycnodonte cochlear* reefs (red dots) targeted by ROV surveys and discussed in the text; also shown are sites in the SE Adriatic (Greece, Kerkyra), Marmara Sea (Gulf of Izmit) and Baleares (off Eivissa) which produced compelling evidence of such oyster aggregations through bottom sampling. (**B**) Close-up of the SW Adriatic and N Ionian areas with localisation of main reef sites there. Bathymetry from [62].

2. Materials and Methods

Several cruises have been carried out in the study areas that evidenced the occurrence of *Neopycnodonte cochlear* reefs. Remote Operated Vehicle (ROV) dives surveyed the SW Adriatic and N Ionian oyster sites (Figure 1, Table 1). We used an ROV Pollux III (Global Electric Italiana) equipped with a low-resolution CCD video camera for navigation and a high-resolution (2304 x 1296 pixels) video camera. Three laser beams, each 20 cm apart, provided the scale bar on the videos. The ROV was equipped with an underwater acoustic tracking system that gives position and depth every second. Still-photo footage, one frame every 10 s, was analysed by the VLC freeware software providing taxonomic information. Macro- (>2 cm) and mega-benthic organisms were identified to the lower possible taxonomic rank. Taxa unidentifiable at species level from images alone were categorized as morphological categories (e.g., [63,64]). Taxonomic classification adheres to the World Register of Marine Species database [65]. Species densities were calculated using three photos selected at random, showing live *Neopycnodonte cochlear* reefs, from each transect. ROV exploration was primarily for scientific surveys to monitor the environmental status of marine ecosystems in Italian waters (Marine Strategy Framework Directive).

Table 1. Site locations metadata.

Site	Collection Date	Station	Lat N-Long E Start	Lat N-Long E End	Depth Min–Max (m)	Dive Length (m)
Bonaccia	13 August 2017	MS17_III_110	43°35.50′-14°20.11′	43°35.23′-14°20.44′	77–83	1079.93
Vieste	10 November 2015	MS15_47	41°59,62′-16°15,14′	41°59,68′-16°15,13′	55–75	804.72
Vieste	10 November 2015	MS15_48	42°00.81′-16°11.13′	42°00.78′-16°11.13′	48–49	58.70
Vieste	11 November 2015	MS15_62	42°01.94′-16°10.24′	42°01.84′-16°10.25′	60–66	139.52
Vieste	11 November 2015	MS15_63	42°01.02′-16°11.75′	42°00.95′-16°11.79′	50–52	316.75
Vieste	11 November 2015	MS15_67	41°59.60′-16°15.14′	41°59.48′-16°15.23′	52–72	255.95
Monopoli	5 August 2017	MS17_II_180	41°00.19′-17°24.25′	40°59.85′-17°24.89′	95–102	1685.84
Monopoli	15 August 2017	MS17_III_115	41°04.17′-17°18.15′	41°04.38′-17°18.24′	85–87	1039.10
Santa Maria di Leuca	31 July 2017	MS17_II_115	39°44.02′-18°22.26′	39°44.27′-18°22.12′	70–113	1179.90
Santa Maria di Leuca	31 July 2017	MS17_II_117	39°42.31′-18°21.31′	39°42.48′-18°21.68′	90–125	1200.00
Kerkyra Island	3 May 2006	CR83 (Epibenthic haul)	39°46.00′-19°25.52′	39°47.22′-19°25.42′	77–99	n/a
Gulf of Izmit	19 September 2005	GRA02 (Grab)	40°44.00′-29°27.00′	-	56	n/a
Eivissa Island	15 April 2004	COBAS-78 (Epibenthic haul)	38°45.99′-01°18.05′	38°46.74′-01°19.34′	94–96	n/a

Other Mediterranean sites not surveyed using ROVs proved to host abundant *N. cochlear* valves on the sea-bottom, suggesting the existence of related reefs (Figure 1, Table 1). Large volume Van Veen grabs and epibenthic hauls provided samples of oyster specimens from Kerkyra Island (SE Adriatic), Eivissa Island (Balearic Sea), and the Gulf of Izmit (Marmara Sea) [66].

3. Results

3.1. General Features of *Neopycnodonte cochlear* Reefs

The *Neopycnodonte cochlear* reefs surveyed in this research represent various typologies in terms of shape and dimension (Figures 2 and 3). Since based upon ROV observations, their thickness could not be assessed with precision and larger reefs could, in fact, represent encrustations of the underlying substrate by a few generations of grypheid oysters (Figures 2–4).

(i) At Bonaccia in the northern Adriatic Sea (Figure 1), *N. cochlear* bioconstructions (Figure 2a,b) cover 4–5 m in lateral extension (length and width) and reach ca. 2 m in height by likely encrusting over bedrock substrate, reaching maximum (underestimate) oyster densities of 500 ± 158 ind·m^{-2}. The occurrence of substantial oyster growth and related biostromal deposits, including valve embedding into hydrocarbon-imprinted limestone was noticed previously [67].

(ii) Vieste (Figure 1) presents a different situation, with smaller reefs, 1–2 m in length and width, and maximum height of 0.5–1 m; here, oyster density attains ca. 200 ± 158 ind·m^{-2} (Figure 2c,d).

(iii) At Monopoli and Santa Maria di Leuca sites (Figures 1 and 3), the latter in Ionian waters, it is difficult to estimate reef dimensions. In fact, at both sites *N. cochlear* grows on a rocky substrate and covers this primary substrate for several meters, growing thicker than 10–20 cm. However, oyster densities are comparable with the Adriatic sites mentioned above.

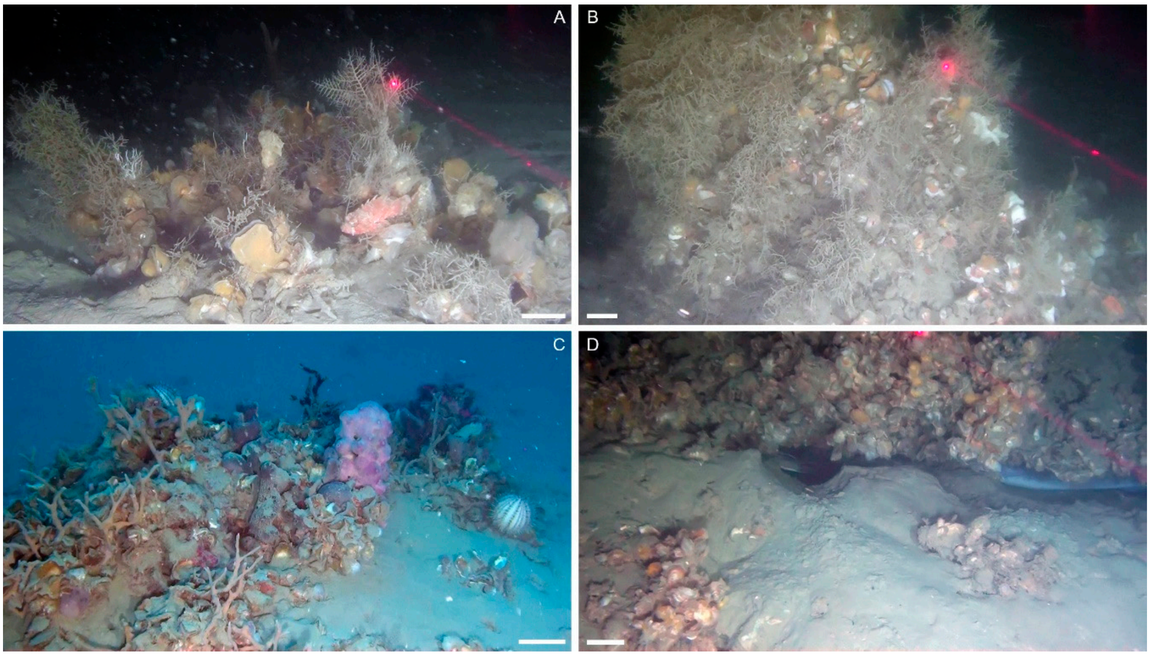

Figure 2. Different typologies of *Neopycnodonte cochlear* reefs on the Adriatic shelf. (**A**) Cluster of *N. cochlear* surrounded by muddy bottom, with hydrozoan turf and a juvenile *Scorpaena scrofa*, at ca. 80 m (Bonaccia); bar = 5 cm. (**B**) Close-up on an oyster-densely-packed *Neopycnodonte cochlear* reef (up to 3 m high) with a dense hydrozoan turf coverage at 80 m (Bonaccia); bar = 5 cm. (**C**) *Neopycnodonte cochlear* reef at 55 m (Vieste) showing intense oyster growth and the presence of the massive-globose cf. *Petrosia* sp. and the erected sponge *Ulosa stuposa*. The echinoid *Echinus melo* is a member of the associated vagrant fauna; bar = 10 cm. (**D**) Base of a *Neopycnodonte cochlear* reef at 75 m (Vieste) providing shelter to a large *Conger conger* individual; bar= 5 cm.

Figure 3. Different typologies of *Neopycnodonte cochlear* reefs in the southern Adriatic and northern Ionian Apulian shelf. (**A**) Dense *Neopycnodonte* growth on a flat sea-bottom at ca. 90 m (Monopoli), offering substrate for the colonial polychaete belonging to *Filograna-Salmacina* complex, undetermined bryozoans and hydrozoans turf; bar = 10 cm. (**B**) Close-up of (**A**) imaging the density of *N. cochlear* at this site; bar = 3 cm. (**C**) Juvenile specimens of *N. cochlear* colonizing a derelict fishing gear at 100 m (Santa Maria di Leuca) document quick oyster colonization of hard substrates here; bar = 3 cm. (**D**) The large *Neopycnodonte cochlear* reef situated at 100 m depth off Santa Maria di Leuca, displays dense oyster aggregation with reduced space for colonization by other epifauna; notice the vagrant echinoid *Cidaris cidaris* as grazing on oyster substrate; bar = 10 cm.

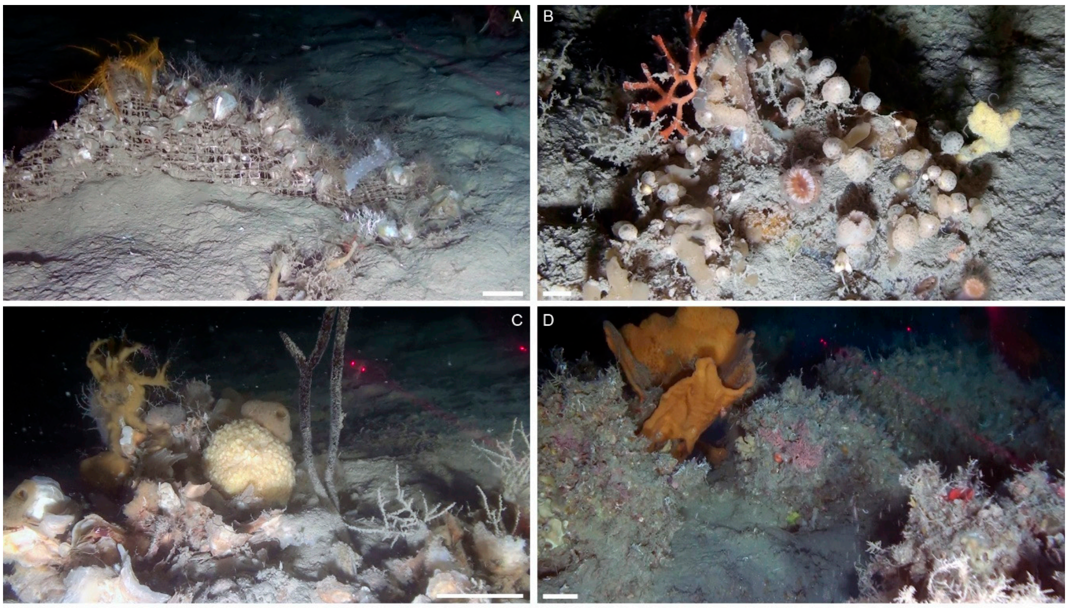

Figure 4. Examples of biodiversity of *Neopycnodonte cochlear* reefs. (**A**) Cluster of *N. cochlear* growing on a lost fishing net with *Antedon mediterranea* (left side) and *Alcyonium palmatum* (Monopoli); bar = 3 cm. (**B**) *Caryophyllia* sp., *Smittina cervicornis* and undetermined lolli-pop and yellow sponges growing on cluster of *N. cochlear* at Monopoli site; bar = 3 cm. (**C**) The golf ball sponge *Tethya aurantium*, protected by the SPAMI directive, is a relatively common record on *N. cochlear* reef (Bonaccia) at 83 m; bar = 5 cm. (**D**) A dense *N. cochlear* reef hosting the large fan-shaped sponge cf. *Pachastrella* sp. at ca. 120 m (Santa Maria di Leuca); bar = 10 cm.

3.2. A Glimpse at Reefs' Associated Biodiversity

The overall biodiversity associated with the *Neopycnodonte cochlear* reef is noticeable (Figures 2–5 and Table 2). Sponges dominate the macro- and mega-benthic associated fauna; *Spongia officinalis*, *S. lamella*, *Axinella polypoides*, *Tethya aurantium* (All listed in Annex II of the Barcelona Convention; if protected, they are so by the regulations of the countries who signed the Convention) and *Ulosa stuposa* are a common occurrence at Bonaccia and Vieste sites. Undetermined encrusting sponges characterize Monopoli and Santa Maria di Leuca, and *A. cannabina* and *T. aurantium* were recorded here. Cnidarians represent another dominant component, with all *Neopycnodonte* reefs surveyed by ROV showing high densities of hydroid turf, mostly cf. *Halecium* sp. and cf. *Sertularella* sp.; the scleractinian cupcoral *Caryophyllia* sp. has been spotted at all such sites, whilst *Alcyonium palmatum* characterizes the Monopoli site. The bryozoan *Smittina cervicornis* is easily recognizable at Monopoli and Santa Maria di Leuca, together with the colonial polychaete belonging to *Filograna-Salmacina* complex, while the solitary *Sabella spallanzanii* seems more abundant at Vieste and Bonaccia sites. A nudibranch in the family Tritoniidae and belonging to *Marionia blainvillea* was observed grazing on muddy sediment around *N. cochlear* reef at Vieste site. Finally, the tunicates *Halocynthia papillosa* and the colonial *Botrylloides* sp. occurs at all *Neopycnodonte* reef sites. The echinoids *Echinus melo* and *Cidaris cidaris* were identified at all sites, while the hatpin urchin *Centrostephanus longispinus*, a protected species (RAC/SPA and SPAMI), was a frequent sight at Vieste site; the crinoid *Antedon mediterranea* was recorded only at Monopoli site. Regarding fish, we have observed the small labrid *Serranus cabrilla*, documented at all sites, whilst *Scorpaena scrofa* and *Conger conger* are relatively common at Bonaccia and Vieste sites, respectively.

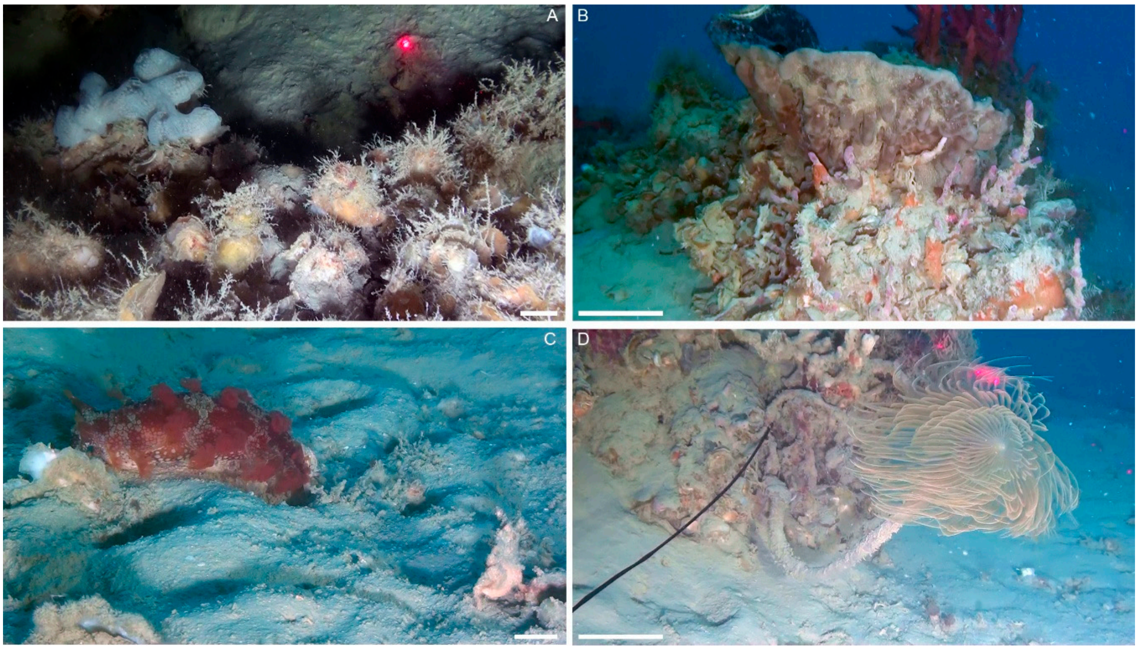

Figure 5. Examples of biodiversity of *Neopycnodonte cochlear* reefs. (**A**) The colonial tunicate cf. *Diplosoma spongiforme* on top of small *N. cochlear* bed, surrounded by a hydrozoan turf at 70 m (Vieste); bar = 3 cm. (**B**) *Spongia lamella*, *Axinella polypoides* and *Ulosa stuposa* are common findings at ca 60 m (Vieste) on *Neopycnodonte* reef; bar = 10 cm. (**C**) *Marionia blainvillea* (family Tritoniidae) grazing on muddy sediment around the *N. cochlear* reef at 50 m (Vieste); bar = 1 cm. (**D**) *Sabella spallanzanii* growing at the base of a m-thick *Neopycnodonte* reef at 60 m (Vieste); bar = 5 cm.

Table 2. Living macro-organisms observed in the ROV surveyed areas. The numbers indicate the legal instruments under which the species are protected: 1—SPAMI Annex II, III (Specially Protected Areas of Mediterranean Importance); 2—Italian Red List IUCN; 3—Red List IUCN; 4—CITES Appendix II (Convention on International Trade in Endangered Species of Wild Fauna and Flora); 5—Habitat Directive Annex II, IV, V; 6—Bern Convention, Appendix II, III (Convention on the Conservation of European Wildlife and Natural Habitats).

n.	Phylum	Class	Taxon	Auctores	Protection
1	Porifera	Demospongiae	spp.		
2			*Aplysina aerophoba*	(Nardo, 1833)	1
3			*Axinella cannabina*	(Esper, 1794)	1, 2 (EN)
4			*Axinella polypoides*	Schmidt, 1862	1, 2 (EN), 6
5			*Cliona celata*	Grant, 1826	
6			*Haliclona mediterranea*	Griessinger, 1971	
7			*Hexadella racovitzai*	Topsent, 1896	
8			*Ircinia variabilis*	Schmidt, 1862	
9			*Mycale tunicata*	Schmidt, 1862	
10			cf. *Petrosia* sp.		
11			*Poecillastra compressa*	(Bowerbanck, 1866)	2 (VU)
12			*Spongia* spp.		
13			cf. *Spongia agaricina*	Pallas, 1766	1, 6
14			*Spongia lamella*	(Schulze, 1879)	2 (EN)
15			*Spongia officinalis*	Linnaeus, 1759	1, 2 (EN), 6
16			*Suberites domuncula*	(Olivi, 1792)	
17			*Tethya aurantium*	(Pallas, 1766)	
18			*Tethya* cf. *citrina*	Sarà and Melone, 1965	1
19			*Ulosa stuposa*	(Esper, 1794)	
20	Cnidaria	Hydrozoa	cf. *Halecium* sp.		
21			cf. *Halecium halecinum*	(Linnaeus, 1758)	
22			*Lytocarpia myriophyllum*	(Linnaeus, 1758)	
23			cf. *Sertularella* sp.		
24		Anthozoa	*Alcyonium palmatum*	Pallas, 1766	
25			Caryophyllidae spp.		
26			*Caryophyllia* cf. *smithii*	Stokes and Broderip, 1828	4
27			*Dendrophyllia cornigera*	(Lamarck, 1816)	2 (VU), 3 (EN), 4
28			*Paralcyonium spinulosum*	(Delle Chiaje, 1822)	
29			*Phyllangia americana*	Milne Edwards and Haime, 1849	4
30			*Virgularia mirabilis*	(Müller, 1776)	2 (VU),
31	Annelida	Polychaeta	*Bonellia viridis*	Rolando, 1822	
32			*Filograna-Salmacina* complex		
33			*Protula tubularia*	(Montagu, 1803)	
34			*Sabella spallanzanii*	(Gmelin, 1791)	
35			*Serpula vermicularis*	Linnaeus, 1767	
36			*Terebellides stroemii*	Sars, 1835	
37			*Vermiliopsis* sp.		
38	Mollusca	Bivalvia	*Atrina fragilis*	(Pennant, 1777)	
39			*Neopycnodonte cochlear*	(Poli, 1795)	
40			*Pecten jacobaeus*	(Linnaeus, 1758)	
41		Gastropoda	cf. *Calliostoma zizyphinum*	(Linnaeus, 1758)	
42			cf. *Fusinus* sp.		
43			*Hexaplex trunculus*	(Linnaeus, 1758)	
44			cf. Naticidae		
45		Nudibranchia	cf. *Caloria elegans*	(Alder and Hancock, 1845)	

Table 2. *Cont.*

n.	Phylum	Class	Taxon	Auctores	Protection
46			*Flabellina affinis*	(Gmelin, 1791)	
47			*Hypselodoris tricolor*	(Cantraine, 1835)	
48			*Marionia blainvillea*	(Risso, 1818)	
49		Cephalopoda	cf. *Octopus vulgaris*	Cuvier, 1797	
50			Teuthida sp.		
51	Arthropoda	Malacostraca	*Maja squinado*	(Herbst, 1788)	1, 6
52			*Munida* sp.		
53			*Pagurus* cf. *excavatus*	(Herbst, 1791)	
54			*Palinurus elephas*	(Fabricius, 1787)	1, 3 (VU), 6
55	Bryozoa	Gymnolaemata	*Reteporella grimaldii*	(Jullien, 1903)	
56			*Smittina cervicornis*	(Pallas, 1766)	
57	Echinodermata	Asteroidea	*Chaetaster longipes*	(Bruzelius, 1805)	
58			*Echinaster sepositus*	(Retzius, 1783)	
59			*Marthasterias glacialis*	(Linnaeus, 1758)	
60			*Peltaster placenta*	(Müller and Troschel, 1842)	
61		Crinoidea	*Antedon mediterranea*	(Lamarck, 1816)	
62		Echinoidea	*Centrostephanus longispinus*	(Philippi, 1845)	1, 5, 6
63			*Cidaris cidaris*	(Linnaeus, 1758)	
64			*Echinus melo*	Lamarck, 1816	
65		Holothuroidea	*Holothuria forskali*	Delle Chiaje, 1823	
66		Ophiuroidea	cf. *Ophiothrix fragilis*	(Abildgaard in Müller, 1789)	
67	Chordata	Ascidiacea	sp.		
68			*Botrylloides* sp.		
69			Didemnidae sp.		
70			*Diplosoma spongiforme*	(Giard, 1872)	
71			*Halocynthia papillosa*	(Linnaeus, 1767)	
72		Actinopterygii	*Callanthias ruber*	(Rafinesque, 1810)	
73			*Chelidonichthys lastoviza*	(Bonnaterre, 1788)	
74			*Conger conger*	(Linnaeus, 1758)	
75			*Muraena helena*	Linnaeus, 1758	
76			*Phycis phycis*	(Linnaeus, 1766)	
77			*Serranus cabrilla*	(Linnaeus, 1758)	
78			*Scorpaena scrofa*	Linnaeus, 1758	
79			*Spicara maena*	(Linnaeus, 1758)	

4. Discussion

As exhaustively documented in the literature, oyster reefs serve as habitat refuge for many organisms like decapods and echinoids among invertebrates, and fishes among vertebrates often hosting species of commercial interest (e.g., [3–7,54–57,60,68]).

The *Neopycnodonte cochlear* reefs in the central and eastern Mediterranean represent also a hotspot of biodiversity, as well as are the transitional areas between *Neopycnodonte* reefs and surrounding mobile sediment bottom. Lastly, these reefs are home to protected species such as *Centrostephanus longispinus*, recorded by the ROV surveys.

Despite intense investigation on littoral oyster reefs (e.g., *Ostrea edulis* [54,56,57,60]), information on intermediate *Neopycnodonte cochlear* reefs is still exiguous. The development and improvement of non-invasive technologies (i.e., ROV), coupled with high-definition image acquisition, has paradoxically provided more knowledge on deep *Neopycnodonte zibrowii* oyster occurrences (>200 m) than on *Neopycnodonte cochlear* reefs at intermediate depths (30–150 m). The monitoring program under the Marine Strategy Framework Directive does not consider *Neopycnodonte cochlear* reefs among target habitats. Further research is needed to better understand such reefs, to expand our knowledge about their spatial distribution, associated biodiversity, and goods and services they may provide.

The *Neopycnodonte cochlear* reefs are not considered among the top marine bioconstructions listed by [69]. Their ecosystemic importance, however, strongly advises for the enforcement of adequate management measures to ensure their survival, including fishery restrictions. In fact, the impact by trawling and longlining on oyster reefs cannot be a priori excluded in consideration of the fishery effort in this region (e.g., [70–72]). This approach would be in line with European recommendations for "H1170 Reefs" in the Annex I of the Habitats Directive 92/42/EEC on the conservation of natural habitats and of wild fauna and flora [73]. The inclusion in protected areas of the sites of Bonaccia, Vieste, Monopoli and Santa Maria di Leuca would guarantee the preservation of examples of grypheid reefs growing at different depths and substrates and encompassing slightly different biodiversity content.

5. Conclusions

Albeit relatively neglected thus far, oyster reefs engineered by the grypheid *Neopycnodonte cochlear* are important bioconstructions in the mesophotic zone of the Mediterranean Sea.

Remarkable examples of such reefs occur in the Adriatic and Ionian waters from 40 m down to 130 meters. ROV inspection of these *Neopcynodonte cochlear* reefs testifies to dense oyster growth and considerable biodiversity of the associated fauna calling for their protection.

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