Offshore Neopycnodonte Oyster Reefs in the Mediterranean Sea

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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 (Ostroidea) 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).

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., [62,63]). Taxonomic classification adheres to the World Register of Marine Species database [64]. 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).

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) [65].

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 [66].

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.
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 Ullosa 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 Smittitina cervicornis is easily recognizable at Monopoli and Santa Maria di Leuca, together with the colonial polychaete belonging to Filagrina-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 Botryloides 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.

3.3. Figures and Tables

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 [67].

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.

**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 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 aug 2017     | MS17_III_110| 43°35.50'-14°20.11'  | 43°35.23'-14°20.44'| 77–83             | 1079.93         |
| Vieste                      | 10 nov 2015     | MS15_47     | 41°59.62'-16°15.14'  | 41°59.68'-16°15.13'| 55–75             | 804.72          |
| Vieste                      | 10 nov 2015     | MS15_48     | 42°00.81'-16°11.13'  | 42°00.78'-16°11.13'| 48–49             | 58.70           |
| Vieste                      | 11 nov 2015     | MS15_62     | 42°01.94'-16°10.24'  | 42°01.84'-16°10.25'| 60–66             | 139.52          |
| Vieste                      | 11 nov 2015     | MS15_63     | 42°01.02'-16°11.75'  | 42°00.95'-16°11.79'| 50–52             | 316.75          |
| Vieste                      | 11 nov 2015     | MS15_67     | 41°59.60'-16°15.14'  | 41°59.48'-16°15.23'| 52–72             | 255.95          |
| Monopoli                    | 5 aug 2017      | MS17_II_180 | 41°00.19'-17°24.25'  | 40°59.85'-17°24.89'| 95–102            | 1685.84         |
| Monopoli                    | 15 aug 2017     | MS17_II_115 | 41°04.17'-17°18.15'  | 41°04.38'-17°18.24'| 85–87             | 1039.10         |
| Santa Maria di Leuca        | 31 jul 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 jul 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 sep 2005     | GGRA02 (Grab) | 40°44.00'-29°27.00'  | -                  | 56               | n/a             |
| Eivissa Island              | 15 apr 2004     | COBAS-78    | 38°45.99'-01°18.05'  | 38°46.74'-01°18.34'| 94–96            | n/a             |

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                               | Autore | Protection |
|----|------------|------------------|-------------------------------------|--------|------------|
| 1  | Porifera   | Demospongiae     | spp.                               |        |            |
| 2  |           |                  | Aplysina aerophoba                  | Nardo, 1833 | 2 (VU)     |
| 3  |           |                  | Axinella cannavina                  | Esper, 1794 | 1, 2 (EN) |
| 4  |           |                  | Axinella polypoides                 | Schmidt, 1862 | 1, 2 (EN) |
| 5  |           |                  | Cliona celata                       | Grant, 1826 |            |
| 6  |           |                  | Haliclona mediterranea              | Griessinger, 1971 |            |
| 7  |           |                  | Hexadella racismizai                | Topsent, 1896 |            |
| 8  |           |                  | Ircinia variabilis                  | Schmidt, 1862 |            |
| 9  |           |                  | Mycale tunicata                     | Schmidt, 1862 |            |
| 10 |           |                  | cf. Petrocia sp.                    |        |            |
| 11 |           |                  | Pocillostra compressa               | Bowerbank, 1866 | 2 (VU)     |
| 12 |           |                  | Spongia spp.                       |        |            |
| 13 |           |                  | cf. Spongia agaricina               | Pallas, 1766 | 1          |
| 14 |           |                  | Spongia lamella                    | Schulze, 1879 | 2 (EN)     |
| 15 |           |                  | Spongia officinalis                 | Linnaeus, 1759 | 1, 2 (EN) |
| 16 |           |                  | Suberites domuncula                 | Olivi, 1792 |            |
| 17 |           |                  | Tethya aurantium                   | Pallas, 1766 |            |
| 18 |           |                  | Tethya cf. citrina                 | Sarà and Melone, 1965 | 1          |
| 19 |           |                  | Ulosa stuposa                      | Espar, 1794 |            |
| 20 | Cnidaria   | Hydrozoa         | cf. Haclecium sp.                   |        |            |
| 21 |           |                  | cf. Haclecium halecium              | Linnaeus, 1758 |            |
| 22 |           |                  | Lytocarpia myriophyllum             | Linnaeus, 1758 |            |
| 23 |           |                  | cf. Sertuariella sp.                |        |            |
| 24 | Anthozoa   | Caryophyllidae    | Aliycyonium palatum                | Pallas, 1766 |            |
| 25 |           |                  | Caryophyllidae spp.                |        |            |
| 26 |           |                  | Caryophylla cf. smithii             | Stokes and Broderip, 1828 | 3 (EN)     |
| 27 |           |                  | Dendrophyllia cornigera             | Lamarck, 1816 |            |
| 28 |           |                  | Paralyconium spinulosum             | Delle Chiave, 1822 |            |
| 29 |           |                  | Phyllogia americana                | Milne Edwards and Haime, 1849 |            |
| 30 | Annelida   | Polychaeta        | Virgularia mirabilis                | Müller, 1776 | 2 (VU),    |
| 31 |           |                  | Bonellia viridis                   | Rolando, 1822 |            |
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

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|------|------------------------|
| 32   | Filograna-Salmacina    |
| 33   | Protula tubularia       |
| 34   | Sabella spallanzani     |
| 35   | Serpula vermicularis    |
| 36   | Terebellides stroemii    |
| 37   | Vermilopsis sp.         |
| 38   | Mollusca Bivalvia       |
| 39   | Neopycnodonte cochlear |
| 40   | Pecten jacobaeus        |
| 41   | cf. Callistoma zizipnum |
| 42   | cf. Fusinus sp.         |
| 43   | Hexaplex trunculus      |
| 44   | cf. Naticidae           |
| 45   | Neopycnodonte cochlear |
| 46   | cf. Caloria elegans     |
| 47   | Flabellina affinis      |
| 48   | Hypselodoris tricolor   |
| 49   | Marginia blainvillea    |
| 50   | cf. Octopus vulgaris    |
| 51   | Teuthida sp.            |
| 52   | Arthropoda Malacostraca |
| 53   | Pagurus cf. excavatus   |
| 54   | Palmarum elephas        |
| 55   | Reteporella grimaldii    |
| 56   | Smittina cervicornis    |
| 57   | Chaetaster longipes     |
| 58   | Echinaster sepositus     |
| 59   | Marthasterias glacialis |
| 60   | Pelaster placenta       |
| 61   | Crinoidea Antedon mediterranea |
| 62   | Echinoidea Centrostephanus longispinus |
| 63   | Cidaris cidaris         |
| 64   | Echinus melo            |
| 65   | Holothuroidea Holothuria forskali |
| 66   | Ophiuroidea cf. Ophiothrix fragilis |
| 67   | Chordata Ascidiacea     |
| 68   | Botylloides sp.         |
| 69   | Didennidiae sp.         |
| 70   | Diplosoma spongiforme   |
| 71   | Halocynthia papillosa   |
| 72   | Callianthias ruber       |
| 73   | Cheilodictyon rubra     |
| 74   | Conger conger           |
| 75   | Muraena helena          |
| 76   | Physyc physis           |
| 77   | Serrasus cabrilla       |
| 78   | Scorpaena scrofa        |
| 79   | Spicara maena           |

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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 *Neopycnodonte cochlear* reefs testifies to dense oyster growth and considerable biodiversity of the associated fauna calling for their protection.

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