

## Article

# Brachiopod Fauna from the Deep Mediterranean Sea: Distribution Patterns and Ecological Preferences

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**Abstract:** Compared to their fossil counterparts, living brachiopods are investigated far less often, due to their occurrence in remote environments such as dark caves or deep environments. Due to the scarcity of studies targeting in situ brachiopods' populations, large-scale information on their distribution and ecological preferences is still lacking, especially on hardgrounds. The extensive employment of remotely operated vehicles (ROVs), however, has opened up the chance to better explore this taxon's diversity and ecology in the mesophotic and bathyal zones. The analysis of over 600 h of video footage collected from 624 sites, from 40 m to 1825 m, located along the Ligurian and Tyrrhenian coasts of Italy and the Sicily Channel, allowed for a large-scale investigation. The four identified species, *Novocrania anomala*, *Gryphus vitreus*, *Megerlia truncata* and *Terebratulina retusa*, emerged as common macrofaunal components of the explored habitats, especially between 150 m and 250 m, with high occurrences in the northern areas, especially on offshore seamounts. All species can form dense aggregations of individuals, with *M. truncata* showing the densest populations on steep rocky terraces (up to 773 individuals m<sup>-2</sup>). Except for *G. vitreus*, the only species also recorded on soft bottoms, the others were found exclusively on hardgrounds, with *N. anomala* showing a peculiar ability to exploit anthropogenic substrates such as terracotta amphorae. No stable species-specific associations were noted, even if numerous species were frequently observed together. Although brachiopods do not show the conspicuous tridimensionality of large filter-feeders, their substrate occupancy and their role in pelagic–benthic processes support their importance in deep-sea Mediterranean ecosystems.

**Keywords:** brachiopoda; aggregations; ecology; ROV; Italian coasts



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## 1. Introduction

Brachiopods are exclusively marine, sessile, filter-feeding invertebrates with a soft body enclosed in a shell consisting of two unequal valves [1]. Extremely common throughout the Paleozoic (altogether about 30,000 fossil species have been described), their diversity and abundance suffered a dramatic decline in the Mesozoic, and today they are considered a minor phylum [2]. According to Zezina [3,4], a plausible reason for this drastic decrease could be the change in plankton composition that occurred between the two eras: the new components of the Mesozoic–Cenozoic plankton were thick-walled cells of the so-called “shelly” phytoplankton (diatoms, coccolithophorids, and dinoflagellates), inedible to articulate brachiopods. This hindered the diversification of brachiopods and allowed the survival only of the deeper species, those beyond the photic zone, where they could feed on the products of decomposition of this new plankton [3,4]. For the same reason, various

species found refuge in shallow-water cave environments, where they also escaped grazing and predation [5–13].

The phylum is currently divided into three subphyla, Linguliformea, Craniiformea and Rhynchonelliformea, with the last one being the most diverse and abundant. Only five orders have extant representatives, and, in total, the living brachiopod fauna is comprised of 394 species divided into 116 genera [14].

Recent Brachiopoda are widely distributed geographically, living in all oceans at depths ranging from shallow waters down to more than 5000 m [2]. They are found on different substrates, from muddy bottoms to detritic sediments to rocky outcrops, and their occurrence is controlled by oceanographic factors, especially current strength, nutrient availability, sedimentation rates and oxygen concentration [3,15–19].

It is generally accepted that the brachiopod fauna of the Mediterranean Sea includes 13 species [10,14,20–26]. With the exception of *Tethyrhynchia mediterranea* (Logan, 1994) and *Lacazella mediterranea* (Risso, 1826), which are likely to be endemic, all the others have a North-East Atlantic origin and are widely distributed in the whole Mediterranean basin [14,22,25,26].

Most of the Mediterranean species are distributed at shallow depths, often in cryptic habitats like marine caves [9], while six (namely *Gryphus vitreus* (Born, 1778), *Megathiris detruncata* (Gmelin, 1791), *Megerlia truncata* (Linnaeus, 1767), *Platidia anomioides* (Scacchi and Philippi, 1844), *Terebratulina retusa* (Linnaeus, 1758), and *Novocrania anomala* (Müller, 1776) also live deeper, being either eurybathic or exclusively bathyal [23]. Numerous brachiopod-dominated biocoenoses have been listed in the SPA/RAC classification of benthic marine habitat types of the Mediterranean region [27], from coralligenous outcrops (MC1.529a) to offshore circalittoral and upper bathyal rocks and sediments (MD1.51A, MD3.512, MD6.514, ME1.519, ME4.512, ME5.516, ME6.519), upper bathyal reefs (ME2.516), and thanatocoenoses (MD2.52, ME2.52, MF2.52).

While Mediterranean fossil brachiopods have been investigated extensively ([28–30], among the most recent works), living brachiopods have received far less attention, with only a few studies focused exclusively on them [9,17,20,22]. Furthermore, the most common techniques used to study the deep brachiopod fauna are dredges and grabs, together with the analysis of trawling discard, methods mainly targeting soft bottoms and especially large accumulations of dead individuals (as for *G. vitreus*) [26]. Therefore, information on their distribution and ecological preferences may result as partially biased from a large-scale point of view.

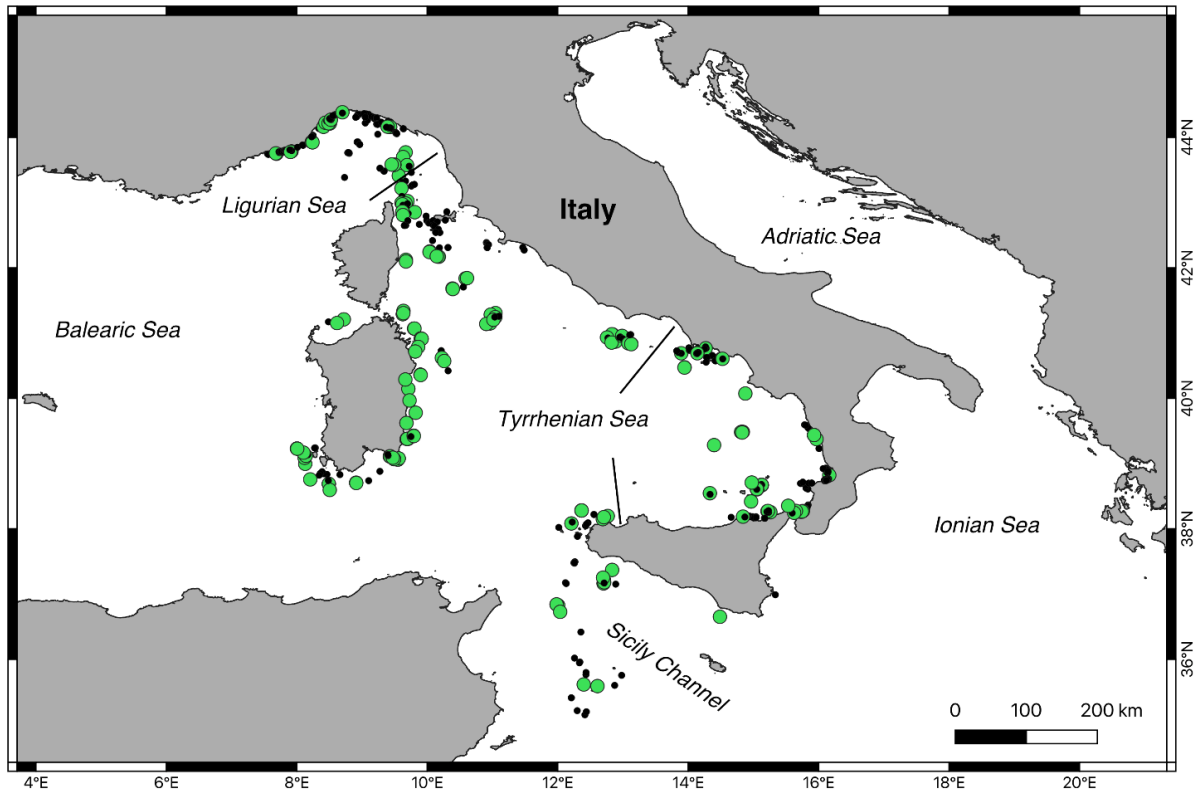
The employment of new technologies, however, such as submersibles and remotely operated vehicles (ROVs), has made the visual exploration of deep-sea environments feasible, greatly enhancing our knowledge of in situ benthic communities, especially in rocky habitats [31–33]. In the last fifteen years, ROVs have been used in several oceanographic surveys along the Italian coasts targeting the characterization of the mesophotic (or circalittoral) and bathyal benthic fauna on hardgrounds and nearby soft bottoms [34–40]. This provided a large amount of data on target megabenthic species (mainly structuring cnidarians forming coral forests), but also on other minor taxa, including brachiopods.

The aim of this study is to assess the large-scale geographic and bathymetric distribution of the deep Mediterranean brachiopod fauna identifiable through ROV-imaging, shedding light on its ecological preferences.

## 2. Materials and Methods

An extensive dataset was analysed in order to define the large-scale distribution of the brachiopod populations present along the Italian coasts in the mesophotic and upper bathyal zones. The dataset included 624 ROV videos, each corresponding to a different site, made between 2006 and 2021 (Figure 1). The ROV footages were obtained from explorative campaigns conducted in four coastal macro-areas (Ligurian Sea, North-central Tyrrhenian Sea, southern Tyrrhenian Sea and Sicily Channel), between depths of 40 and 1200 m (inclusive of 55 wrecks), and on twelve offshore seamounts, six in the Ligurian basin,

four in the central Tyrrhenian Sea, and two in the southern Tyrrhenian Sea. Seamounts were explored between depths of 60 and 1825 m and were located from 30 to 70 nautical miles (NM) from the nearest coast; they were grouped under the category of “Offshore reliefs”. Overall, the ROV tracks covered about 680,000 m<sup>2</sup> of the seafloor (hardgrounds and the surrounding soft seafloors) for about 640 h of video footage. Additionally, about 29,000 photos taken by high-resolution cameras were analysed.



**Figure 1.** Distribution map of the investigated sites. Sites including at least one record of brachiopods are indicated with green dots, otherwise with black dots.

Videos were analysed using Apple’s Final Cut Pro X software. The analysis allowed for recording brachiopods larger than approximately 1 cm, identified at the species level.

The number of sites in which brachiopods were present was counted and reported as a percentage of their occurrence in the whole dataset and in the considered macro-areas, also considering species separately. The depth ranges at which the species were recorded in each site and those reported in the available literature regarding Mediterranean brachiopods were used to build a comparative boxplot, with the aim of evaluating the concordance of the present records with the known depth ranges of the species. In addition, the normalised number of sites with brachiopods was obtained for each macro-area at five depth ranges (40–80 m, 80–150 m, 150–250 m, 250–500 m, >500 m), corresponding to the deepest part of the continental shelf, the shelf break, two upper bathyal ranges of the continental slope and seamounts, and the lower bathyal (below 500 m) [41]. In case the occurrence spanned over a wide depth range, the record was split into more depth categories. The resulting bathymetric distribution was presented as a correlation between depth and the percentage of sites with brachiopods, expressed as the average ( $\pm$  SE) of all the macro-areas per each considered depth range (with *n*, the number of macro-areas, varying between 3 and 5).

For each site, the relative abundance of the identified species was reported in terms of (1) rare, scattered specimens; (2) common, aggregated specimens; or (3) abundant, densely aggregated specimens. The percentage of sites hosting populations of different densities was calculated for each species considering both macro-area and depth range. In case the occurrence spanned over a wide depth range, the record was split into more depth

categories. Four distribution maps reporting the relative abundance of the studied species were then created using QGIS (version 3.24). In addition, at least five random pictures were analyzed for each species in order to define the average density values (expressed as  $n^\circ$  of individuals  $m^{-2} \pm SE$ ) used as a reference for the different relative abundance categories. For each picture, the covered surface (evaluated using the laser beams equipped on ROV) and the exact number of specimens present in it was calculated using ImageJ. When pictures were not available, literature data were considered to depict the category density ranges.

The substrate type on which the brachiopods were observed in each site was defined according to six categories: (1) mud, (2) sand to coarse-grained sediment (including biogenic detritus), (3) outcropping rocks, (4) rocks covered by crustose coralline algae (CCA), (5) coral bioconstruction and rubble, and (6) artificial (meaning marine litter, iron wrecks and terracotta manufactures). The percentage of the populations of each species was then calculated for each substrate type.

Moreover, the exact slope of the substrate hosting brachiopods was noted. In case brachiopods were observed in different environmental contexts (substrate and slope) in the same site, a correspondent number of entries was registered. The percentage frequency of populations of each species was then calculated for each considered slope range ( $0-20^\circ$ ,  $20-45^\circ$ ,  $45-70^\circ$ ,  $70-90^\circ$ ), with  $n$ , the number of populations, varying between 34 and 200.

In order to investigate the potential relationship between density (expressed as  $n^\circ$  individuals  $m^{-2}$ ) and slope, a linear correlation was calculated for each species.

Finally, other megabenthic invertebrate taxa present together or in the proximity of the target brachiopods were also reported to evaluate preferential ecological associations. The relation was considered a putative stable association only if the species were co-occurring in at least one-half of the sites with dense aggregations of brachiopods.

### 3. Results

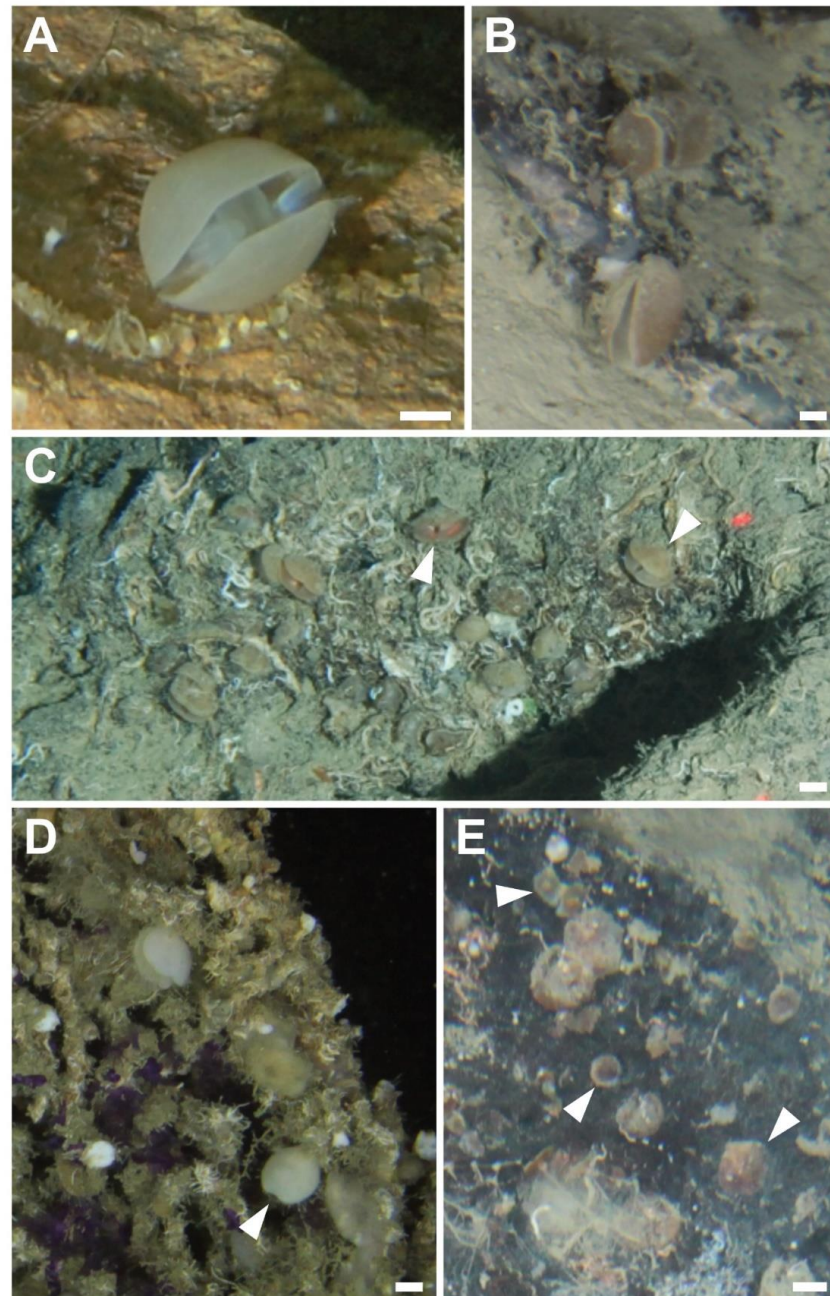
#### 3.1. Morphology of the Target Species

The analysis of the ROV footages revealed the presence of four clearly identifiable brachiopod species in the considered macro-areas, one of whom belonged to the order Craniida (*Novocrania anomala*) and three to the order Terebratulida (namely *Gryphus vitreus*, *Megerlia truncata* and *Terebratulina retusa*) (Table 1). Species identification was based on images, considering various morphological features available in the literature [42–44].

**Table 1.** List of the brachiopod species found in the present study. The number of sites in which each species was recorded per geographic area is given. LIG, Ligurian Sea; NCT, North-central Tyrrhenian Sea; ST, southern Tyrrhenian Sea; SC, Sicily Channel; SEAM, seamounts.

Species	Coastal Macro-Areas				Offshore Reliefs SEAM	TOT
	LIG	NCT	ST	SC		
<b>CRANIIDA</b>						
<b>Craniidae</b>						
<i>Novocrania anomala</i> (Müller, 1776)	11	21	1	0	5	38
<b>TEREBRATULIDA</b>						
<b>Terebratulidae</b>						
<i>Gryphus vitreus</i> (Born, 1778)	7	37	3	3	15	65
<b>Kraussinidae</b>						
<i>Megerlia truncata</i> (Linnaeus, 1767)	13	43	32	17	17	122
<b>Cancellothyrididae</b>						
<i>Terebratulina retusa</i> (Linnaeus, 1758)	4	13	2	0	4	23

*Gryphus vitreus* is the largest species, reaching 4 cm in length (Figure 2A). Its valves, rounded and somehow pentagonal, are usually translucent-white in colour, showing the brachidium in transparency. Valves may also be brownish (7.7% of the recorded populations) (Figure 2B).



**Figure 2.** The four brachiopod species identified in the present study. (A) *Gryphus vitreus*, with its typical rounded valves and translucent-white colour (Capri Island, Gulf of Naples, southern Tyrrhenian Sea, 190 m); (B) *G. vitreus* with brownish valves on a rocky substrate (Bordighera Canyon, western Ligurian Sea, 270 m); (C) aggregation of *Megerlia truncata*, with individuals protruding perpendicularly to the rock (Bordighera Canyon, western Ligurian Sea, 170 m); (D) specimens of *Terebratulina retusa* with the typical pear-shaped, white valves (Tavolaria Canyon, North-eastern Sardinia, 185 m); (E) numerous individuals of *Novocrania anomala* with the brown dorsal valves, conical and roughly round shaped, attached to a rocky vertical wall (Bordighera Canyon, western Ligurian Sea, 360 m). Scale bar: 1 cm.

*Megerlia truncata* has a biconvex, slightly flattened shell, light brown in colour, usually around 1.5 cm. The two valves are unequal, with a more pronounced convexity in the ventral valve marked by a rounded carination, and the dorsal valve showing a corresponding narrow sulcus. The outer surface has numerous fine radial ribs and concentric growth-lines. On vertical walls, the ventral valve may become thinner and less rounded in order to adhere to the rock. In the densest aggregations, valves can be protruding perpendicularly to the rock (Figure 2C).

*Terebratulina retusa* is a pedunculated, pear-shaped brachiopod, around 2 cm long (Figure 2D). The valves appear white to light yellow, being darker in female individuals in the breeding season because of the colour of the ripe gonads.

Finally, *Novocrania anomala* is a small (around 0.5–1 cm), inarticulate species with the ventral valve flattened and cemented to the substratum. The dorsal valve, conical with a roughly round shape, is smooth with concentric growth-lines departing from the umbones and is overlaid with a thin brown periostracum, conferring its typical colour (Figure 2E). A taxonomic debate is currently in progress on the validity of the similar-looking cogeneric *Novocrania turbinata* (Poli, 1795), which, however, various authors consider a synonym [26].

### 3.2. Geographic and Bathymetric Distribution

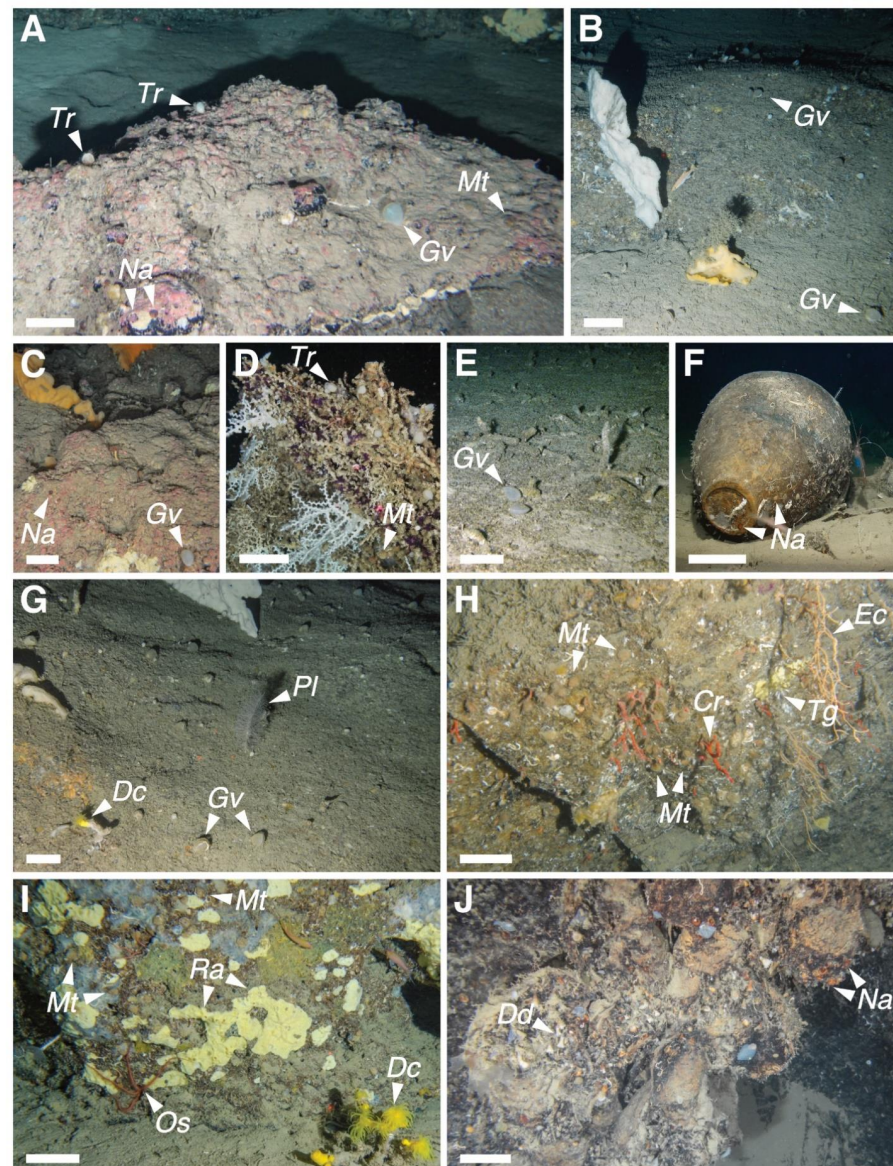
Brachiopods were recorded in 26.3% of the explored sites, corresponding to 164 sites (Figure 1). Considering the four species separately, they were reported in a percentage of sites varying between 3.7% and 19.6% of the total, with *T. retusa* being less frequent and *M. truncata* being the most common. In seven sites (three in the Ligurian Sea, two in the North-central Tyrrhenian Sea and two on Santa Lucia seamount), the four species were observed together, sometimes close to each other (Figure 3A).

Considering the macro-areas separately, *M. truncata* was confirmed as the most common species, being present in all the considered coastal and offshore macro-areas, with a percentage of occurrence ranging from 8.8% in the Ligurian Sea to 34.7% on the explored seamounts (specifically S. Lucia, Cialdi, Etruschi, Baronie, Vercelli and Palinuro) (Figure 4A, Table 1). *Gryphus vitreus*, also present in all the considered macro-areas, showed maximum percentages of occurrence on the seamounts (30.6%) and in the North-central Tyrrhenian Sea (23.1%), while it was scarcely represented in the remaining coastal macro-areas (Figure 4A, Table 1). *Novocrania anomala* and *T. retusa* were less common, being present with occurrences varying between 2.7% and 13.1% in the Ligurian Sea, North-central Tyrrhenian Sea and on seamounts. They were observed at a few sites in the southern Tyrrhenian Sea and were not recorded in the Sicily Channel (Figure 4A, Table 1).

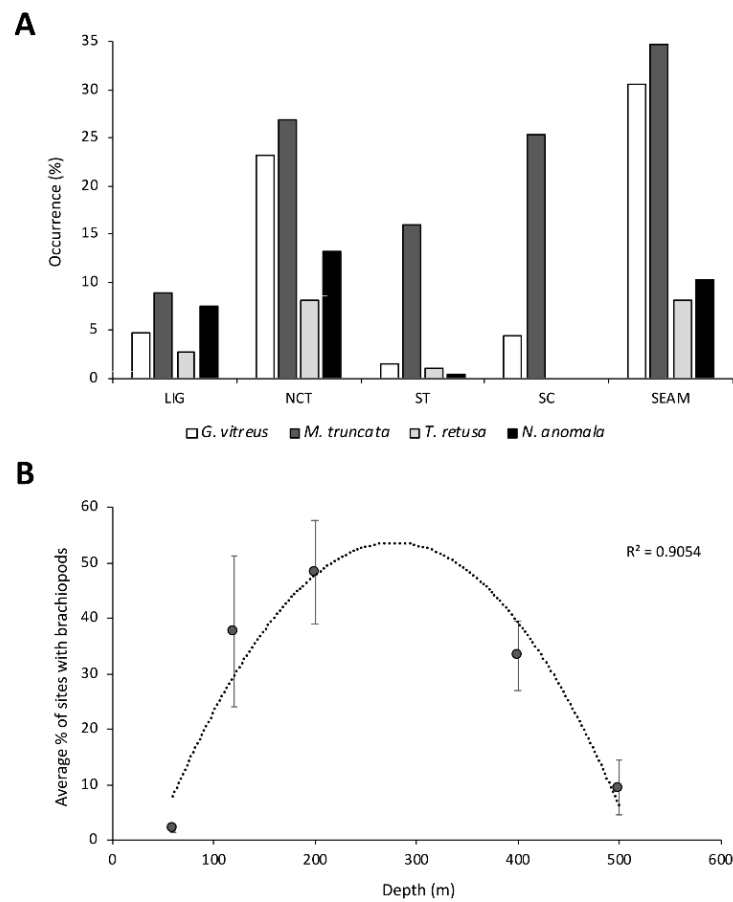
With regard to the overall bathymetric distribution of the target species, the boxplots highlighted wide ranges for all brachiopods, which mainly occurred from the mesophotic zone to the upper bathyal (Figure 5). Brachiopods were observed between 50 m and 659 m, with the shallowest record located in Capo Peloro (Messina Strait, southern Tyrrhenian Sea) and the deepest on Marsili Seamount (South Tyrrhenian Sea). The average percentage occurrence of all brachiopods species is significantly correlated with depth with a peak in the 150–250 m depth range (Figure 4B, Table 2).

*Gryphus vitreus* showed the widest distribution, between 77 m and 659 m, while *T. retusa* had the narrowest, between 110 m and 453 m. The shallowest record belongs to *M. truncata*, at around 50 m. The observed bathymetric distributions, evidenced by the boxplots, all fall within the known literature ranges; however, the main distribution range of *N. anomala* (147–397 m) is far deeper than what is generally reported (7–73 m) (Figure 5).

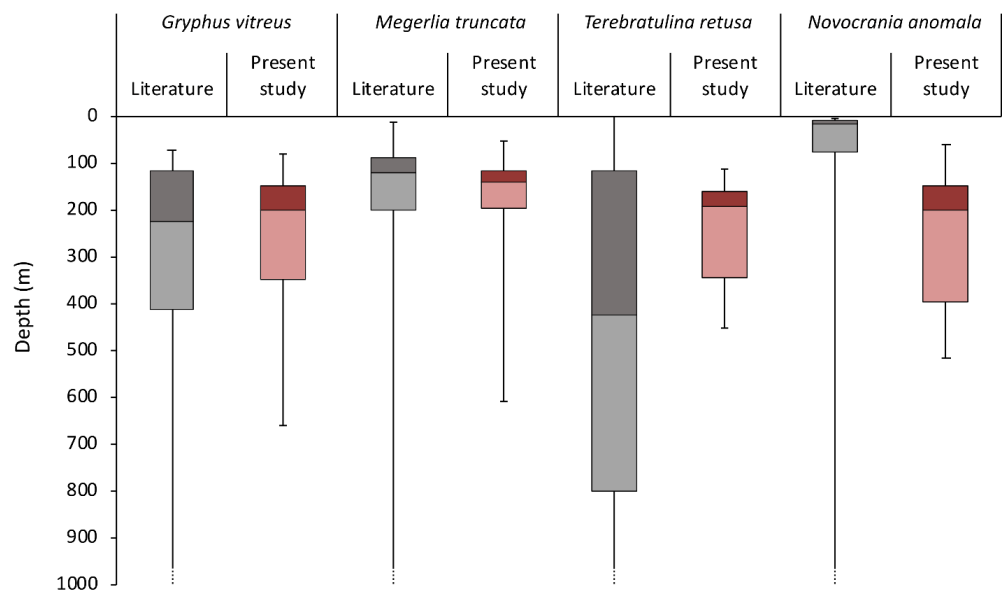
Among the four coastal macro-areas, the Ligurian Sea and the North-central Tyrrhenian Sea were those where all four brachiopod species were found deeper, with the deepest observations always exceeding 400 m. On seamounts, *G. vitreus* and *M. truncata* were the species with the deepest records (659 m and 400 m, respectively), while *N. anomala* and *T. retusa* showed a marked mesophotic distribution, being noted at 202 m and 209 m as a maximum, respectively.



**Figure 3.** Ecology of the target species. (A) The four species together on a CCA-encrusted rock in the Pontine Archipelago (central Tyrrhenian Sea, 160 m); (B) specimens of *G. vitreus* (Gv) on a rocky boulder and on the surrounding soft bottom. Well visible the massive sponges *Pachastrella monilifera* and *Poecillastra compressa* (Vedove Shoal, western Ligurian Sea, 195 m); (C) sloping rock with CCA hosting *G. vitreus* and *N. anomala* (Na), together with *P. compressa* (Pontine Archipelago, central Tyrrhenian Sea, 160 m); (D) *T. retusa* (Tr) and *M. truncata* (Mt) settled on a *Madrepora oculata* bioconstruction, very close to the living portions of the reef (Tavolara Canyon, North-eastern Sardinia, 185 m); (E) individuals of *G. vitreus* on an horizontal plain with skeletons of *Dendrophyllia cornigera* (Dc) on Vercelli seamount (central Tyrrhenian Sea, 160 m); (F) *N. anomala* on the vertical sides of an ancient terracotta amphora. On the right, an individual of *Plesionika narval* walking on the manifold (North Tyrrhenian Sea, 425 m); (G) the sloping rocky terraces of Vedove Shoal host numerous *G. vitreus* specimens and the frequently associated structuring species *D. cornigera* and *Parantipathes larix* (Pl) (western Ligurian Sea, 195 m); (H) aggregation of *M. truncata* and the anthozoans *Thalamophyllia gasti* (Tg), *Corallium rubrum* (Cr), and *Eunicella cavolini* (Ec) on a vertical rocky cliff (Ischia Island, southern Tyrrhenian Sea, 115 m); (I) *Rhabderemia* sp. (Ra), *D. cornigera* and *Ophiacantha setosa* (Os) live in close proximity to a small group of *M. truncata* (Pontine Archipelago, central Tyrrhenian Sea, 140 m); (J) peculiar association between *N. anomala* and the fossil valves of *Neopycnodonte zibrowii* in Sestri Levante (Ligurian Sea, 480 m). Scale bar: 10 cm.



**Figure 4.** Geographic and bathymetric distribution of the target species. **(A)** Percentage of occurrence of the four brachiopod species in the investigated macro-areas. LIG, Ligurian Sea; NCT, North-central Tyrrhenian Sea; ST, southern Tyrrhenian Sea; SC, Sicily Channel; SEAM, seamounts; **(B)** correlation between depth and percentage of sites with brachiopods, expressed as the average ( $\pm$  SE) of all the macro-areas per each considered depth range (with n, the number of macro-areas, varying between 3 and 5).



**Figure 5.** Comparative boxplots depicting the depth distribution of the target brachiopod species, created with data coming from literature (grey plots) and from the present study (red plots).

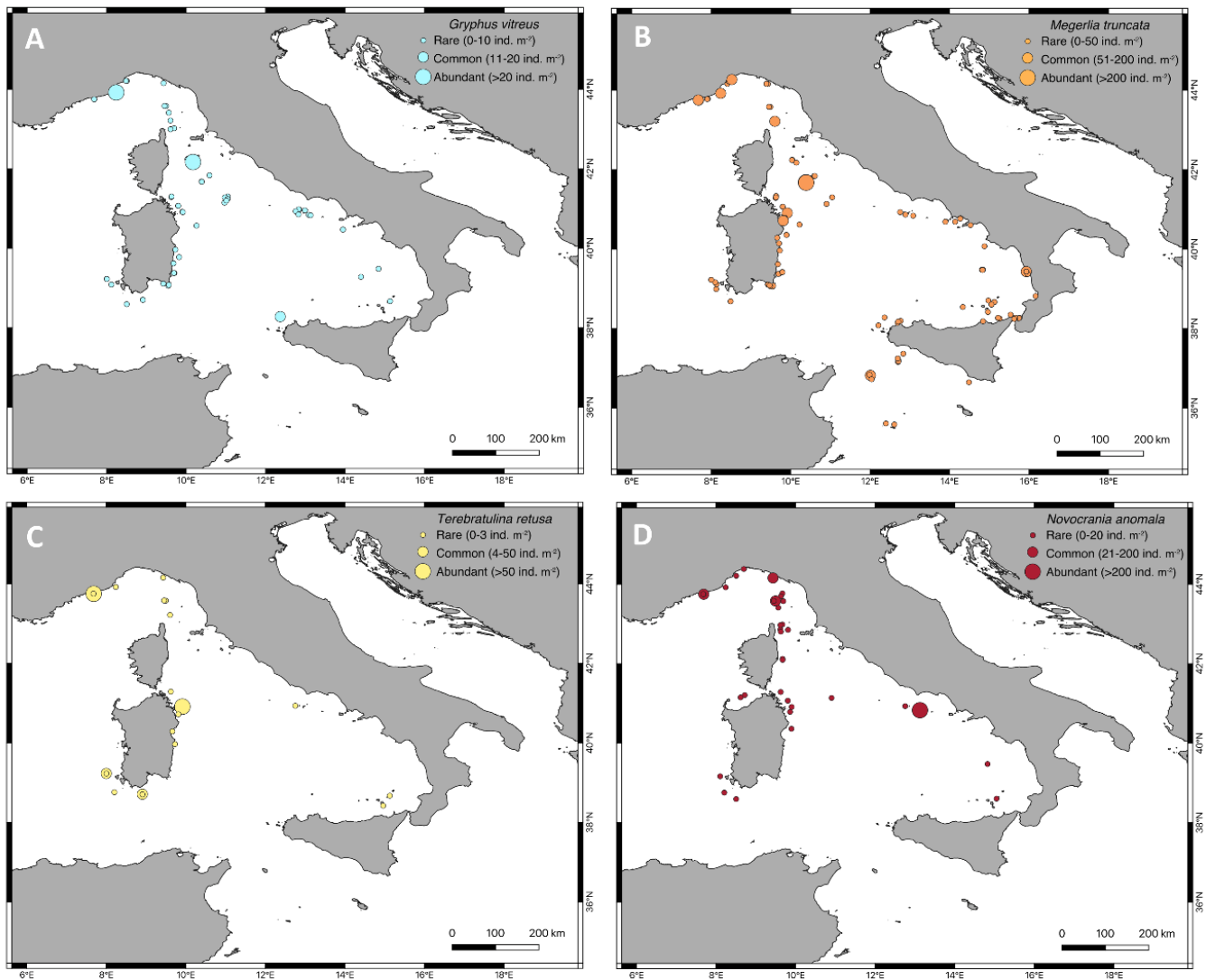


**Table 2.** List of the brachiopod species found in the present study. The number of sites in which each species was recorded per geographic area and depth range is given, together with indications of relative population densities. LIG, Ligurian Sea; NCT, North-central Tyrrhenian Sea; ST, southern Tyrrhenian Sea; SC, Sicily Channel; SEAM, seamounts. Population density: 1, rare; 2, common; 3, abundant.

Macro-Area	Depth Range (m)	<i>N. anomala</i>			<i>G. vitreus</i>			<i>M. truncata</i>			<i>T. retusa</i>		
		1	2	3	1	2	3	1	2	3	1	2	3
LIG	40–80	1											
	80–150	2			1			4	3		1		
	150–250	2			2		1	1	3		1		1
	250–500	4	2		5			3	1		1		
	>500	2	1					1					
NCT	40–80												
	80–150	7			18	1		33	1		4		
	150–250	6	1	1	13	1	1	18	1		4	1	1
	250–500	12			8			1	1		3	1	
	>500												
ST	40–80							3					
	80–150	1						23	1		1		
	150–250	1			3			8					
	250–500							2			1		
	>500												
SC	40–80							1					
	80–150							10	1				
	150–250						1	3					
	250–500				2	1		2					
	>500												
SEAM	40–80												
	80–150	3	1					6			1		
	150–250	1			5			6			4		
	250–500				10			3		4			
	>500				2								

### 3.3. Population Density

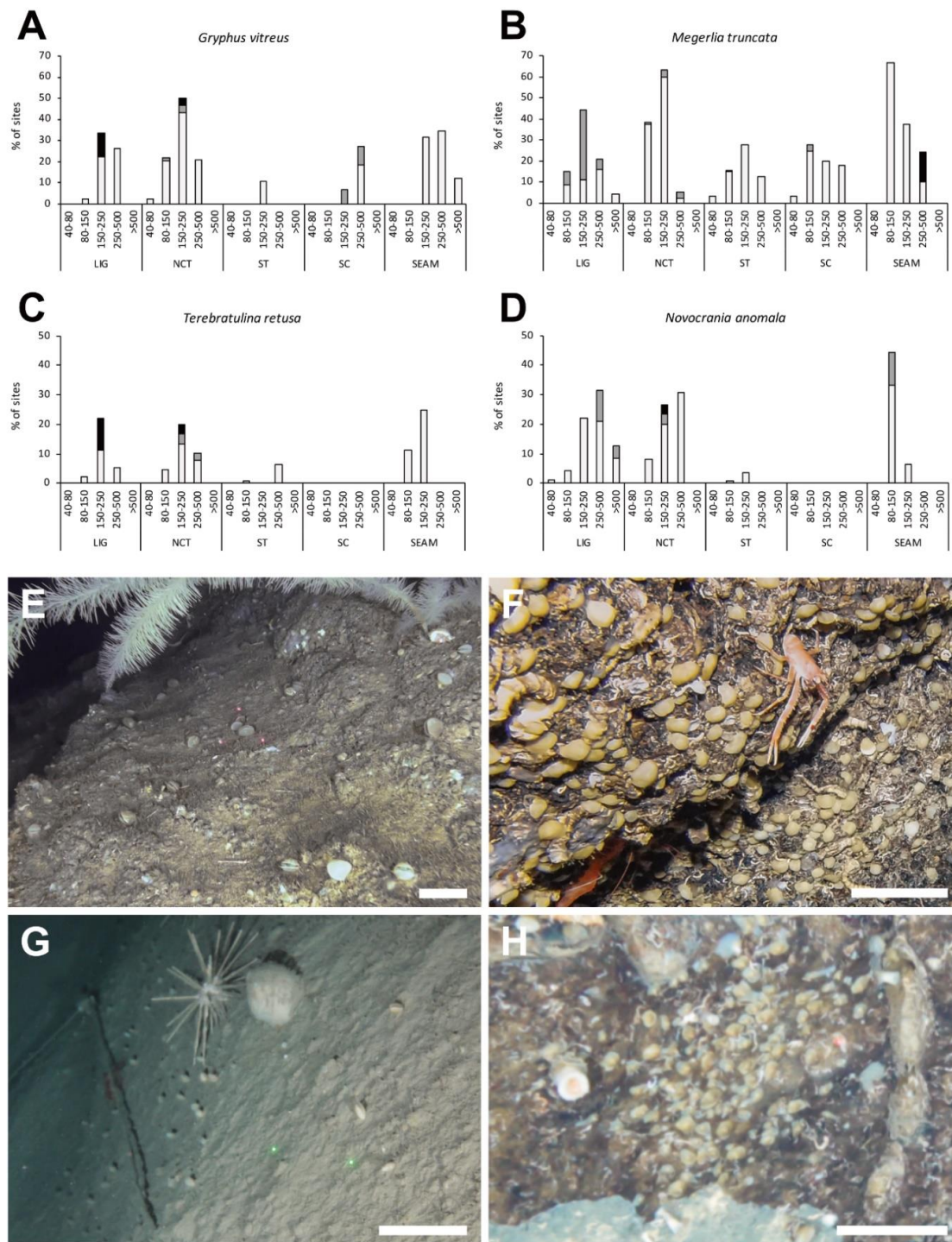
In terms of relative abundance, 89% of the target brachiopod populations were formed by rare, scattered specimens in all the macro-areas and at all depth ranges (Figure 6, Table 2). In the case of *G. vitreus*, between 6.5% and 11% of sites in the 150–250 m depth range hosted common, aggregated or abundant, dense populations in the Ligurian and North-central Tyrrhenian, and similar values were recorded between depths of 150 m and 500 m in the Sicily Channel (Figures 6A and 7A). In the case of *M. truncata*, most aggregated populations (5.3–33.3%) were found between 80 m and 500 m in the Ligurian Sea, while dense populations were observed only on the Etruschi Seamount (13.8%) (Figures 6B and 7B). *Terebratulina retusa* presented aggregated or dense populations especially in the 150–250 m depth range (6.5–11%) in the Ligurian and North-central Tyrrhenian macro-areas (Figures 6C and 7C). Depending on the macro-area, *N. anomala* presented aggregated or dense populations in all depth ranges, from 80 m to over 500 m (Figures 6D and 7D).



**Figure 6.** (A–D) Distribution maps of the four brachiopod species recorded in this study with an indication of the relative abundance of the populations.

Quantitative analysis of the pictures allowed reference average density values for the different relative abundance categories to be obtained for all four of the considered species (Table 3).

*Gryphus vitreus* showed peaks of abundance of 25 individuals  $m^{-2}$  and 26.7 individuals  $m^{-2}$ , respectively on the hardgrounds of the Vedove Shoal (Imperia, Ligurian Sea) and Montecristo Island (Tuscan Archipelago) (Figure 7A,E). The maximum density value for *M. truncata* was 773 individuals  $m^{-2}$  recorded on the rocky terraces of the Etruschi Seamount (northern Tyrrhenian Sea) (Figure 7B,F). High peaks of abundance for *T. retusa* were recorded in the Tavolara Canyon (North-eastern Sardinia) and Bordighera Canyon (western Ligurian Sea), with 12 and 17 individuals  $m^{-2}$ , respectively (Figure 7C,G). A peak of 333 individuals  $m^{-2}$  of *N. anomala* was registered in the Pontine Archipelago (central Tyrrhenian Sea). At this same site, aggregations of small and large individuals were observed (Figure 7D,H).



**Figure 7.** Populations' relative abundance. (A–D) Percentage of sites with populations of different densities for each species in the five considered macro-areas and depth ranges. The colours of the stacked bars indicate the percentage number of sites with populations characterised by rare, scattered individuals (light grey), common, aggregated (dark grey), and abundant, dense specimens (black). (E–H) Examples of dense patches (relative abundance 3, abundant) of the target brachiopods: (E) *Gryphus vitreus* (Montecristo Island, northern Tyrrhenian Sea, 160 m); (F) *Megerlia truncata* (Etruschi Seamount, northern Tyrrhenian Sea, 385 m); (G) *Terebratulina retusa* (Bordighera Canyon, western Ligurian Sea, 165 m); (H) aggregation of juvenile and adult individuals of *N. anomala* (Pontine Archipelago, central Tyrrhenian Sea, 190 m). Scale bar: 10 cm (E,G), 5 cm (F,H).

**Table 3.** Reference values of average density ( $n^\circ$  individuals  $m^{-2} \pm SE$ ) and density category (min-max) for the four targeted brachiopod species extrapolated from the analysis of the photos for each aggregation category.

Species	Density Value			Density Category		
	1	2	3	1	2	3
<i>Novocrania anomala</i>	10.0 $\pm$ 1.3	52.5 $\pm$ 7.0	271.7 $\pm$ 61.7	0–20	21–200	>200
<i>Gryphus vitreus</i>	4.3 $\pm$ 0.3	13.1 $\pm$ 1.0	23.8 $\pm$ 0.8	0–10	11–20	>20
<i>Megerlia truncata</i>	23.2 $\pm$ 1.9	103.5 $\pm$ 5.2	426.7 $\pm$ 133.0	0–50	51–200	>200
<i>Terebratulina retusa</i>	1.3 $\pm$ 0.3	11.1 $\pm$ 1.8	nd	0–3	4–50	>50

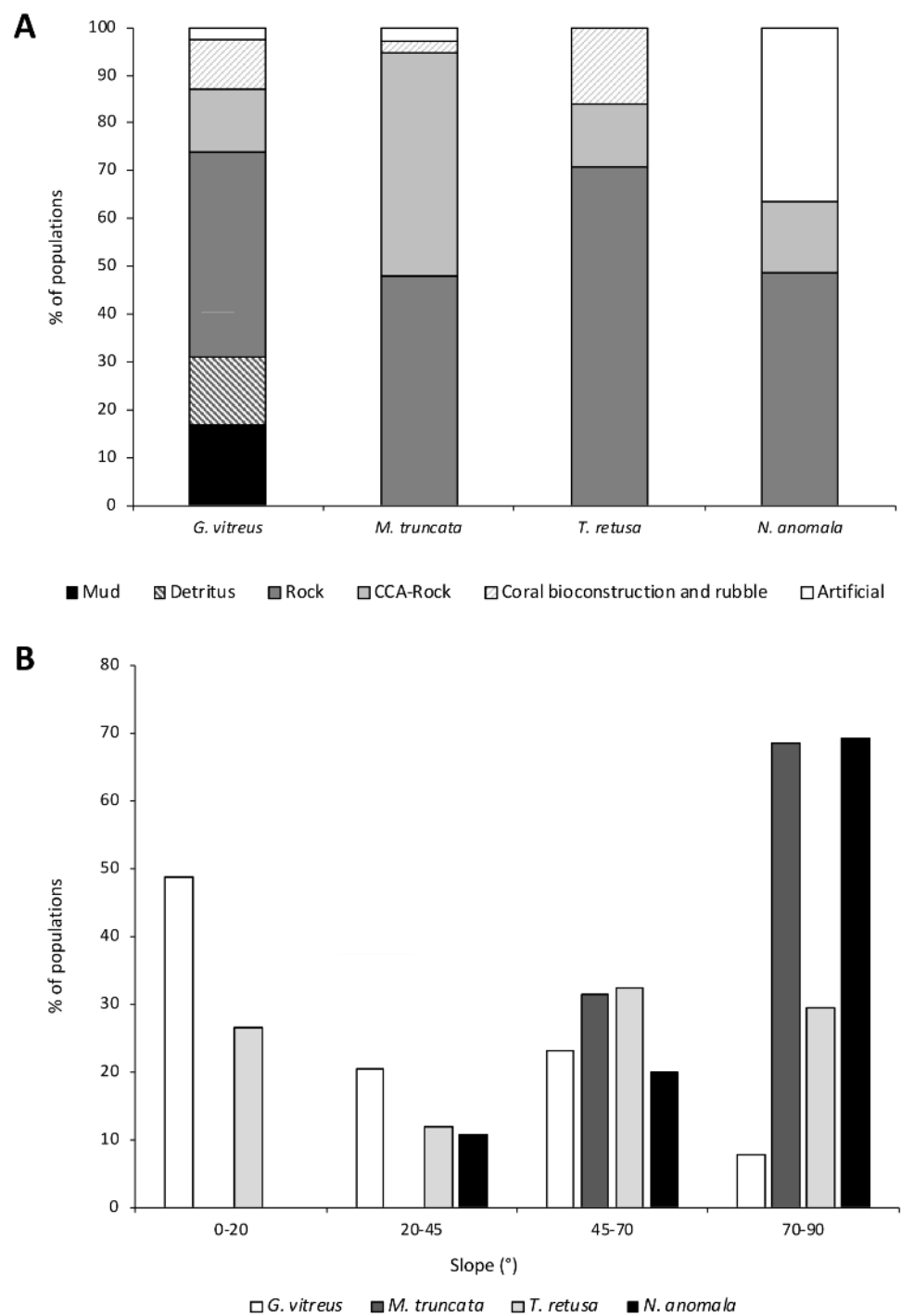
### 3.4. Ecological Preferences and Associated Fauna

Among the four brachiopod species, *G. vitreus* showed the widest substrate preference, being reported on all the six categories, including both hardgrounds and nearby soft bottoms (Figures 3B and 8A). Alternatively, the other three species resulted as more selective and confined only to hard substrates, with *N. anomala* occurring only on a few substrate categories (Figure 8A). The identified brachiopods were primarily observed on rocky outcrops (between 47.4% and 71.0%, respectively, for *M. truncata* and *T. retusa*), followed by rocks with CCA (between 12.9% and 45.9%, respectively, for *T. retusa* and *M. truncata*) (Figure 3C). *Gryphus vitreus*, *M. truncata* and *T. retusa* benefited from the secondary surface offered by dead bioconstructions and coral rubble of numerous cold-water corals scleractinians, including *Madrepora oculata* Linnaeus, 1758, *Desmophyllum pertusum* (Linnaeus, 1758) and *Dendrophyllia cornigera* (Lamarck, 1816) (Figure 3D–E and Figure 8A). In one site in NE Sardinia, namely Tavolara Canyon, the three species were recorded together in this habitat. About 13% of the populations of *T. retusa* were recorded in close proximity to the living portions of the reefs (Figures 3D and 8A). With the exception of *T. retusa*, all of the other three species were observed on a large variety of artificial substrates, including bricks, plastic and jute bags, iron wrecks and terracotta amphorae. A total of 36.6% of the records of *N. anomala* were on ancient terracotta amphorae, to which the species attached on the exposed part (Figure 3F).

In terms of population density, there are no clear patterns; however, the aggregated and dense populations of *G. vitreus* were only found on outcropping rocks and mud, those of *M. truncata* almost exclusively on rocks, those of *T. retusa* on rocks and dead coral bioconstructions, and the densest populations of *N. anomala* were mainly found on rocks.

The slope–frequency distribution analysis highlighted different situations for the investigated brachiopod populations (Figure 8B). *Megerlia truncata* and *N. anomala* showed a marked preference for sloping and vertical walls (up to 70% of the populations were found on substrates with a 70–90° slope), and no sightings were reported in the 10–20° range for both species. In particular, *N. anomala* was commonly recorded on the vertical sides of the terracotta amphorae (Figure 3F). *Terebratulina retusa* showed no clear preference, being observed with similar percentage frequencies (12–32%) in all slope categories. Finally, *G. vitreus* showed a distinctive distribution pattern: two peaks of percentage frequency were observed, one corresponding to populations thriving on horizontal, mainly detritic substrates (48.7% in the 10–20° range) and one corresponding to populations living on sloping hardgrounds (23.1% in the 45–70° range) (Figure 3B,E,G, and Figure 8B). No significant correlation between slope and population density was found for any of the identified brachiopod species (values of  $R^2$  varying between 0.02 and 0.06).

Numerous species were recurrently observed together or nearby the target brachiopods (Figure 3, Table 4).



**Figure 8.** Ecological preferences. (A) Percentage of populations of the target species recorded on different substrate types; (B) percentage frequency distribution of brachiopod populations with slope.

The aggregations of *G. vitreus* found on mesophotic and upper bathyal hardgrounds were usually associated with massive sponges (e.g., *Poecillastra compressa* [Bowerbank, 1866] [Figure 3C]), encrusting sponges (e.g., *Rhabderemia* sp.), as well as numerous structuring anthozoans, especially *D. cornigera* and *Parantipathes larix* (Esper, 1788) (Figures 3G and 7E). Among vagile invertebrates, the crinoid *Leptometra phalangium* (Müller, 1841) and the echinoid *Cidaris cidaris* (Linnaeus, 1758) were frequently observed. The dense aggregations of *M. truncata* on the vertical rocky terraces were usually associated with high densities of caryophyllids and encrusting sponges (Figure 3H,I). Various large structuring sponges and anthozoans (e.g., *Pachastrella monilifera* Schmidt, 1868 and *Corallium rubrum* [Linnaeus,

1758]) often created tridimensionality in these environments, which were frequented by numerous vagile invertebrates, including deep shrimps *Plesionika* spp. and numerous sea urchins (Figure 3H,I). Strictly bathyal populations of *M. truncata* often occurred with the scleractinian *M. oculata* (Figure 3D). The aggregations of *T. retusa* were characterised by the lowest number of closely associated species, including *D. cornigera*, *M. oculata*, crustaceans and cidarids. Finally, the dense aggregations of *N. anomala* on the vertical rocky cliffs were characterised by distinctive assemblages. The mesophotic populations commonly co-occurred with caryophyllids and a few antipatharians, massive demosponges and the echinoderms *Ophiacantha setosa* (Bruzellius, 1805), *C. cidaris* and *Holothuria* (*Roweothuria*) *poli* Delle Chiaje. The strictly bathyal populations were usually more frequented by vagile crustaceans, such as *Plesionika* spp. (Figure 3F) and *Munida tenuimana* (Figure 7F). Two interesting associations were those of *N. anomala* with *Lycopodina hypogea* (Vacelet and Boury-Esnault, 1996) (Pontine Archipelago, central Tyrrhenian Sea) and a fossil aggregation of *Neopycnodonte zibrowii* Gofas, Salas and Taviani, 2009 (Sestri Levante, Ligurian Sea) (Figure 3J).

**Table 4.** List of the megabenthic invertebrate taxa present together or in the proximity of the target brachiopods.

Associated Megabenthic Invertebrates			Brachiopod Species			
Phylum	Class	Taxon	<i>N. anomala</i>	<i>G. vitreus</i>	<i>M. truncata</i>	<i>T. retusa</i>
Porifera	Demospongiae	<i>Hamacantha (Vomerula) falcata</i> (Bowerbank, 1874)	+	+	+	+
		<i>Lycopodina hypogea</i> (Vacelet & Boury-Esnault, 1996)	+			
		<i>Pachastrella monilifera</i> Schmidt, 1868	+	+	+	
		<i>Poecillastra compressa</i> (Bowerbank, 1866)	+	+	+	
		<i>Polymastia polytylota</i> Vacelet, 1969	+			
Cnidaria	Anthozoa	<i>Rhabderemia</i> sp.		+	+	+
		<i>Corallium rubrum</i> (Linnaeus, 1758)	+		+	
		<i>Bebryce mollis</i> Philippi, 1842		+		
		<i>Callogorgia verticillata</i> (Pallas, 1766)		+		
		<i>Eunicella cavolini</i> (Koch, 1887)	+			
		<i>Swiftia dubia</i> (Thomson, 1929)	+			
		<i>Caryophyllia (Caryophyllia) cyathus</i> (Ellis & Solander, 1786)	+		+	
		<i>Caryophyllia (Caryophyllia) smithii</i> Stokes & Broderip, 1828	+		+	
		<i>Dendrophyllia cornigera</i> (Lamarck, 1816)		+	+	+
		<i>Desmophyllum dianthus</i> (Esper, 1794)	+			

Table 4. Cont.

Phylum	Class	Taxon	Brachiopod Species			
			<i>N. anomala</i>	<i>G. vitreus</i>	<i>M. truncata</i>	<i>T. retusa</i>
		<i>Madrepora oculata</i> Linnaeus, 1758			+	+
		<i>Thalamophyllia gasti</i> (Döderlein, 1913)	+		+	
		<i>Antipathes dichotoma</i> Pallas, 1766	+			
		<i>Leiopathes glaberrima</i> (Esper, 1792)	+	+	+	
		<i>Parantipathes larix</i> (Esper, 1788)		+	+	
Annelida	Polychaeta	<i>Apomatus/Protula</i> complex	+		+	
		<i>Bonellia viridis</i> Rolando, 1822			+	
		<i>Filogranula annulata</i> (Costa, 1861)	+		+	
Mollusca	Bivalvia	<i>Neopycnodonte cochlear</i> (Poli, 1795)			+	
		<i>Neopycnodonte zibrowii</i> Gofas, Salas & Taviani, 2009 (fossil)	+			
Crustacea	Malacostraca	<i>Munida tenuimana</i> Sars, 1872	+			
		<i>Munida</i> spp.			+	+
		<i>Paromola cuvieri</i> (Risso, 1816)			+	
		<i>Plesionika giglioli</i> (Senna, 1902)	+		+	
		<i>Plesionika narval</i> (Fabricius, 1787)	+		+	
Echinodermata	Crinoidea	<i>Leptomera phalangiium</i> (Müller, 1841)		+		
	Asteroidea	<i>Hacelia attenuata</i> Gray, 1840	+		+	
	Echinoidea	<i>Cidaris cidaris</i> (Linnaeus, 1758)	+	+	+	+
		<i>Echinus melo</i> Lamarck, 1816	+		+	
		<i>Stylocidaris affinis</i> (Philippi, 1845)			+	
	Ophiuroidea	<i>Ophiacantha setosa</i> (Bruzellius, 1805)	+		+	
	Holothuroidea	<i>Holothuria (Roweothuria) poli</i> Delle Chiaje, 1824	+		+	

#### 4. Discussion

The ROV footage analysis allowed for the identification of about one-third of the known Mediterranean species of brachiopods [10,14,20–26], representing, however, a higher percentage (67%) if we consider the mesophotic and bathyal species known for this basin.

The maximum size of the two missing deep species, *M. detruncata* and *P. anomioides*, is 6 mm, so they were consistently too small to be detected by ROV, and this could be the reason why they were not recorded in the present study. A partial bias in the presence/absence data may exist also for the juvenile specimens (less than 1 cm) of all the recorded species, especially *Novocrania anomala*, which shows sizes borderline with the ROV resolution power.

Overall, however, ROV proved to be an efficient and non-invasive tool to identify and study deep brachiopods. The target species were recognized thanks to some of their morphological features, detectable by ROV and sufficient for reasonably good identification. A similar resolution for macrofauna was recently highlighted also for heterobranchs [45]. The presence of both taxa can be considered partially underestimated due to their small size and rather cryptic colours; however, contrary to heterobranchs, brachiopods often form highly visible aggregations.

Brachiopods emerged as a relatively modest component of the investigated environments, being recorded in about one-fifth of the explored sites, with the highest percentages of occurrence in the northern areas and on seamounts. The high frequency of occurrence in the Ligurian and North-central Tyrrhenian Sea is similar to what was observed for other mesophotic and bathyal Mediterranean species, such as red coral [46]. While the factors potentially involved in explaining this large-scale distribution could be multiple, one may be the water circulation pattern, which has been demonstrated to be one of the main environmental drivers for brachiopods [3,14,47]. In particular, as also suggested for red coral, the Tyrrhenian Gyre may facilitate the dispersal of brachiopod larvae in this region. In addition, the high occurrence of the four target species in the coldest parts of the western basin is in accordance with their boreal biogeographic affinity [4,14,48,49]. This pattern emerged also for numerous other species thriving at bathyal depths in the northwestern Mediterranean Sea [34,50–52].

Contrary to other studied large-scale distributions, however, such as those of heterobranchs and red coral [45,46], the target brachiopods of this study are particularly common in seamount environments. For instance, brachiopod lecithotropic larvae, transported by currents, have the potential for long-distance dispersal [14]. In addition, the bathyal vertical rocky terraces of seamounts, surrounded by silt, are less favourable to other habitat-forming filter feeders, such as anthozoans and massive sponges, and brachiopods may exploit lower levels of spatial competition here. Finally, it has to be noted that the occurrence of brachiopods, especially Rhynchonelliformea (including the order Terebratulida studied here), in upwelling systems (such as canyons and seamounts) has been debated. Some authors suggested that turbulent hydrodynamic conditions and high loads of nutrients are unfavourable to those species feeding on dissolved organic matter [3,14]; still, other studies, including this investigation, support the ability of some species to settle and create dense monospecific aggregations in these complex environments [53–55]. Trophic studies on Mediterranean seamounts may help to better evaluate these environmental constraints.

The target species were mainly observed from the deep circalittoral to the upper bathyal zone, with a shared peak of occurrence in the 150–250 m depth range. Nearby the continental shelf edge, relatively rapid currents make the sediments coarser, the scarcity or absence of macroalgae reduces competition for hard substrates, and the production of phytoplankton is reduced, so that suspended material is not very rich in the living cells of planktonic algae but is still rich in slightly transformed organic matter produced by bacterioplankton. All these environmental conditions make the shelf–slope break ideal for the brachiopod fauna [4,22,32]. The high frequency of records of the identified brachiopod species in this bathymetric zone is consistent with their known depth range [16,26,32], except for *N. anomala*. This species is most commonly found colonising shallow-water submarine caves, where it creates dense populations cemented to the dark walls and ceilings [5,6,8–10], even if it is known to be a eurybathic species, with its deepest records around 1480 m [26,56]. In the present study, *N. anomala* occurred from 60 m to 515 m, with the main distribution range between 147 m and 397 m. This adds interesting new



information about the optimal bathymetric distribution of *N. anomala*, which is confirmed to be a typical deep-sea species adapted to colonise submarine caves with similar environmental conditions. This phenomenon was reported for numerous other species [5,10,54–58], including the carnivorous sponge *L. hypogea*, here sharing the habitat with *N. anomala* in at least one mesophotic site [59].

Overall, the observed brachiopod populations were mainly formed by solitary, scattered specimens, especially on hardgrounds, with dense aggregations observed only in the 11% of the cases and in areas with an already high frequency of occurrence. This supports the fact that only a few sites show favourable biotic and abiotic conditions for dense patches. The average density resulting from the analysis of the pictures was generally lower than that reported in the literature, but a few considerations should be pointed out. Most of the available data regarding brachiopod density come from sampling methods targeting soft bottoms, like dredges, grabs and trawls, which mainly collect dead specimens, often those accumulated in dense patches by the bottom currents, and thereby result in very high-density values [8,26,56]. This is particularly true for *G. vitreus*, which has been deeply studied and sampled on incoherent substrates [16,26,31], while information on its populations on hardgrounds is very scarce [26,42,60]. Therefore, the results of this study are rarely comparable with literature data, with a few exceptions. The peak of density of 773 individuals  $m^{-2}$  of *M. truncata*, in fact, recorded on the rocky terraces of the Etruschi Seamount, is significantly higher than that obtained with ROV in a remarkable brachiopod biotope in the central Mediterranean Sea (mean density  $176 \pm 128$  individuals  $m^{-2}$ , maximum density  $>300$  individuals  $m^{-2}$ ) [33].

Little is known about brachiopod reproductive cycles and longevity. Similarly to other benthic taxa, it is likely that brachiopods initially grow quickly, thus helping survival in the most critical phase of their life. Growth subsequently becomes more stable, diminishing in the latest stages. In general, they are known to live between 8 and 12 years, with differences between the species [61,62]. A few observations were made in this study with regard to the life history of the studied species. The aggregations of large and small individuals of *N. anomala* observed on a rocky boulder in the Pontine Archipelago may be explained by assuming the population was impacted by a recent phenomenon of settling, with juveniles coexisting with adult specimens. An analogous assemblage was observed in a marine cave in NW Sicily (South Tyrrhenian Sea), with individuals of different sizes living close to each other to create very dense aggregations on the vault and walls of the cave [5]. Other indications of the reproductive status of the populations (e.g., size and colour sexual dimorphism in *T. retusa*) were not observed, but this could be biased by the lack of measurements of individuals. With regard to mortality, instead, the dense patches of *M. truncata* and *N. anomala* provide evidence of population turn-over, with living specimens co-existing with dead ones, but never on top of each other.

The four brachiopod species showed high environmental adaptability, being observed on a large variety of hard substrates. Given that bare rocks are the most-selected type of substrate, and that these tend to progressively decrease with depth, it is not surprising that in a few sites the four species were observed together, sometimes close to each other, confirming they can occasionally coexist [42]. *Gryphus vitreus* was the only brachiopod also observed on soft bottoms, confirming its multiple ecological preferences [42], even if this study supports its additional role and occurrence on hardgrounds. The three terebratulids were reported also on coral bioconstructions, especially the distal dead portions close to the living coral coenenchyme, as observed in the Nora Canyon (South Sardinia, central Tyrrhenian Sea) [60]. Besides substrate type, all species, except for *T. retusa* characterized, however, by a smaller dataset, also showed marked preferences in terms of substrate inclination, with a significantly higher occurrence on sloping and vertical rocky walls. These preferences are essential for explaining the large-scale distribution of these species (especially on the rocky boulders and terraces of canyons and seamounts), for supporting their filter-feeding activity in relatively low silting environments and may also provide important parameters for habitat prediction models.

Specific consideration could be given to anthropogenic objects. These are known to provide a secondary substrate for the settlement of a wide array of benthic organisms [63]. Brachiopods have been previously reported on marine litter, such as plastic (including nylon fishing lines), iron and clinker [64,65]. In the present study, *G. vitreus*, *M. truncata*, and *N. anomala* were observed attached to objects of different origin, confirming their opportunistic settling ability. One-third of the records of *N. anomala* were on ancient terracotta amphorae, suggesting, for the first time, that this material is indeed suitable for the species' settling. Terracotta manufacts are known to host, high levels of biological encrustations, especially on the most exposed, non-silted portions [66,67], yet their unpredictable stability supports species with a fast growth rate and high turn-over, such as brachiopods [61,62]. Moreover, the manufacts are generally located far from other available hardgrounds, surrounded by vast muddy planes, therefore supporting the wide larval dispersal ability of this species. *Novocrania anomala* has also been observed exploiting the shells of the long-living bivalve *N. zibrowii*, known for hosting a rich associated fauna [68,69], thus again supporting the opportunistic behaviour of this brachiopod.

Brachiopods do not form the complex canopy that most typical erect habitat-forming filter feeders are known for (massive sponges and anthozoans) [70–72]; nonetheless, they may represent a dominant component of the basal layer of such forests (e.g., *P. larix*, *E. cavolini*, *C. rubrum*), competing with scleractinians and encrusting sponges, or they may form a distinct monospecific biotope [33]. This may explain why there are no true species-specific associated taxa, especially among benthic taxa, despite *M. truncata* and *G. vitreus* having been reported participating in peculiar megabenthic communities in the Ligurian Sea [37]. In particular, *M. truncata* was one of the main components of the community characterised by serpulids, sea urchins and holothurians developing on bare rocks, while *G. vitreus* participated to the community dominated by *D. cornigera*, cidarids, the sponge *Pachastrella monilifera* and some solitary scleractinians. Only the dense aggregations of *M. truncata* support a certain degree of tridimensionality to the environment, given the high density of individuals, the wide patches and the often-perpendicular position of the shells. Indeed, this type of patch, with a significant number of small cavities and refuges, attracts numerous vagile invertebrates, such as shrimps and squat lobsters. It is worth mentioning that vagile invertebrates (mainly gastropods, crustaceans, polychaetes, and echinoderms) are reported by numerous authors as predators of brachiopods [26,73–75]. Despite this, neither events nor signs of predation were noticed on any of the identified species, some individuals of *Palinurus mauritanicus* (Gravel, 1911) and other decapods (e.g., *Munida* spp.) and several species of echinoderms (e.g., *Cidarid* *cidaris*), known to be brachiopods' predators, were frequently observed to move on or in close proximity to the target brachiopod populations, especially on seamounts, suggesting that they could occasionally feed on them.

Although brachiopods do not show the conspicuous complexity of large filter-feeders and their filtration rate results as one third of that of bivalves of similar-size [4], their substrate occupancy and their role in pelagic–benthic processes still support their importance in deep-sea Mediterranean ecosystems.

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