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## Diversity and abundance of heterobranchs (Mollusca, Gastropoda) from the mesophotic and bathyal zone of the Mediterranean Sea

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### Abstract

The occurrence, relative abundance and bathymetric distribution of the deep Mediterranean heterobranch fauna were evaluated as a result of an extensive visual census down to 1825 m depth, carried out along the western Italian coasts, covering a latitudinal range of about 600 nautical miles. Observations were conducted using Remotely Operated Vehicles (ROVs) in 551 sites, focusing on the deepest part of the continental shelf, the shelf edge and the upper bathyal zone. The analysis of over 508 hours of video footage and more than 27,000 high-resolution photographs allowed to explore about 594,000 m<sup>2</sup> of rocky outcrops and nearby soft seafloors in four main coastal areas (Ligurian Sea, north-central Tyrrhenian Sea, southern Tyrrhenian Sea, and Sicily Channel) and twelve offshore seamounts. Thirty-six species of heterobranchs, for a total of 559 records, were identified. Sixteen were only sporadically spotted (< 1% of the total observations), while three (*Paraflabellina ischitana*, Tritoniidae and *Peltochlamys atromaculata*) contributed each for more than 10% of the records. An extension of the known Mediterranean bathymetric distribution was reported for 80% of the observed species, with many typically shallow-water taxa being also found in mesophotic environments (40–200 m). The observed marked decrease in diversity and abundance suggested that Mediterranean heterobranchs are mainly a coastal benthic group. From the geographical point of view, the heterobranch fauna present in the Ligurian Sea appeared significantly different from that observed in the Tyrrhenian Sea and the Sicily Channel, and this latitudinal pattern was discussed. Particular attention was given to single out the bathymetric distribution of the food sources of the most frequently observed species, supporting stenophagy as a limiting factor for their colonisation of the deep sea.

**Keywords:** *Nudibranchia*, *deep-sea*, *ROV*, *bathymetric distribution*, *stenophagy*

### Introduction

The Mediterranean malacofauna is considered one of the best-known in the world (Oliverio 2003). In particular, Heterobranchia (Mollusca, Gastropoda) have been significantly studied in the last 50 years, mainly thanks to the advent of scientific SCUBA diving, which has led to a profusion of studies improving our understanding of the species richness,

ecology, phylogeny and geographic distribution (e.g., Vicente 1967; Schmekel & Portmann 1982; Thompson et al. 1990; Templado & Villanueva 2010; Trainito & Doneddu 2014; Furfaro & Mariottini 2016; Zenetos et al. 2016; Betti et al. 2017). Up to date, more than 600 species of heterobranchs have been described from the Mediterranean Sea (Trainito & Doneddu 2014; Parera et al. 2020). Nevertheless, the available

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†This paper is dedicated to the memory of Prof. Riccardo Cattaneo-Vietti, a world-renowned expert in the taxonomy, ecology and biology of Mediterranean heterobranchs. We would like to thank him for the inspiration and passion he put into this paper.

information is skewed towards SCUBA diving depth range (from the surface to around 40 m), while very little is known about the composition and distribution of the heterobranch fauna living in the deepest part of the Mediterranean continental shelf, shelf edge and slope, down to the bathyal habitat.

Most of the available data on deep Mediterranean heterobranchs targets the soft-bottom fauna of the North-West Mediterranean Sea, studied mainly thanks to catches made by destructive gears, such as dredges and trawling nets. Vicente (1967) reported 21 species between 45 and 450 m inside the Gulf of Marseille (France), scattered on detritic, maërl and mud, with only the cephalaspidean *Philine monterosati* Monterosato, 1874 found below 120 m. In an extensive survey off the coasts of Blanes (Spain), Ros (1975) reported 34 heterobranch species from 40 to 250 m, observed on detritic, sand and mud. This faunal census was later updated to 47 species by Domènech et al. (2006), who provided qualitative information on the frequency of occurrence of species found between 50 and 300 m in the same area, indicating the cephalaspideans *Gastroperon rubrum* (Rafinesque, 1814) and *Scaphander lignarius* Linnaeus, 1758 and the nudibranch *Tethys fimbria* Linnaeus, 1767 as the most frequent deep taxa. Bouchet (1977) reported two bathyal nudibranch species (*Baptodoris cinnabarina* Bergh, 1884 and *Doris alboranica* Bouchet, 1977) from the Alboran Sea (500–910 m). Cattaneo-Vietti (1991) recorded 32 species, mostly observed sporadically, from the trawling grounds of the continental shelf and slope of the Ligurian and northern Tyrrhenian seas down to 700 m. Among the most widespread species, there were: *Philine quadripartita* Ascanius, 1772 and *T. fimbria*, mainly linked to the terrigenous mud biocoenosis, *Pleurobranchaea meckeli* (Blainville, 1825) and *Doris pseudoargus* Rapp, 1827 in the coastal detritic one, while *Pleurobranchus membranaceus* (Montagu, 1816) and *Kaloplocamus ramosus* (Cantraine, 1835) frequently appeared in the shelf-edge detritic biocoenosis, characterised by the crinoid *Leptometra phalangium* (Müller, 1841) and by the seapen *Funiculina quadrangularis* (Pallas, 1766). *Scaphander lignarius* was also commonly collected, from coastal detritic to bathyal mud. Finally, *B. cinnabarina* was found in the bathyal mud biocoenosis of the slope, feeding on the sponge *Thenea muricata* (Bowerbank, 1858) (Bouchet 1977; Cattaneo-Vietti 1991). Lastly, a survey conducted in the Cretan Sea (eastern Mediterranean basin) reported nine species living on soft bottoms between 40 and 700 m (Koutsoubas et al. 2000). These included some new findings for this habitat, such as the acteonid

*Crenilabium exile* (Jeffreys, 1870), the cephalaspidean *Roxaniella jeffreysi* (Weinkauff, 1866) and the sacoglossan *Ascobulla fragilis* (Jeffreys, 1856).

On the other hand, information on the Mediterranean heterobranch fauna of mesophotic and bathyal rocky environments is scarce. Recently, *Tritonia callogorgiae* Chimienti, Furfaro and Taviani, 2020, living on the deep alcyonacean *Callogorgia verticillata* (Pallas, 1766), was described on the basis of specimens photographed and collected by Remotely Operated Vehicle (ROV) at 420–430 m depth, off the Montenegro margin (Chimienti et al. 2020). Overall, deep data mainly come from reports of technical divers exploring the upper mesophotic range, but are often based on fortuitous findings, focused on restricted areas, and do not allow for a comprehensive interpretation of the ecology and biogeography of the species.

In the last fifteen years, several ROV surveys were carried out along a large part of the Italian coasts, from the Ligurian Sea to the Sicily Channel, targeting the characterisation of the megabenthic biocoenoses dominated by structuring species thriving between 30 and 1825 m on hardgrounds and nearby soft seafloors (e.g., Bo et al. 2012, 2021; Cau et al. 2015; Angiolillo et al. 2016, 2021; Altobelli et al. 2017; Enrichetti et al. 2019; Moccia et al. 2021). Such habitats constitute Vulnerable Marine Ecosystems (VMEs) (Del Mar Otero & Marin 2019), attracting a rich faunal biodiversity; however, the associated macrofauna was never specifically targeted. These ROV datasets gave a chance, for the first time, to assess the large-scale bathymetric and geographic distribution of a significant number of mesophotic and bathyal Mediterranean heterobranchs and investigate the ecological traits affecting deep-sea colonisation.

## Materials and methods

In total, 551 ROV videos, each corresponding to a different dive and locality, were examined to analyse the large-scale distribution of the heterobranchs present on the rocky bottoms (and soft-bottom surroundings) of the mesophotic and bathyal zone. In total, 502 ROV footages were obtained from explorative campaigns conducted in four Mediterranean coastal areas (Ligurian Sea, north-central Tyrrhenian Sea, southern Tyrrhenian Sea and Sicily Channel), between 30 and 775 m depth (Figure 1). In addition, 12 offshore seamounts, six in the Ligurian basin (namely Penelope, Ulisse, Janua, Spinola, Occhiali and Santa Lucia), four in the central Tyrrhenian Sea (Vercelli, Cialdi, Etruschi and Baronie), and two in the southern

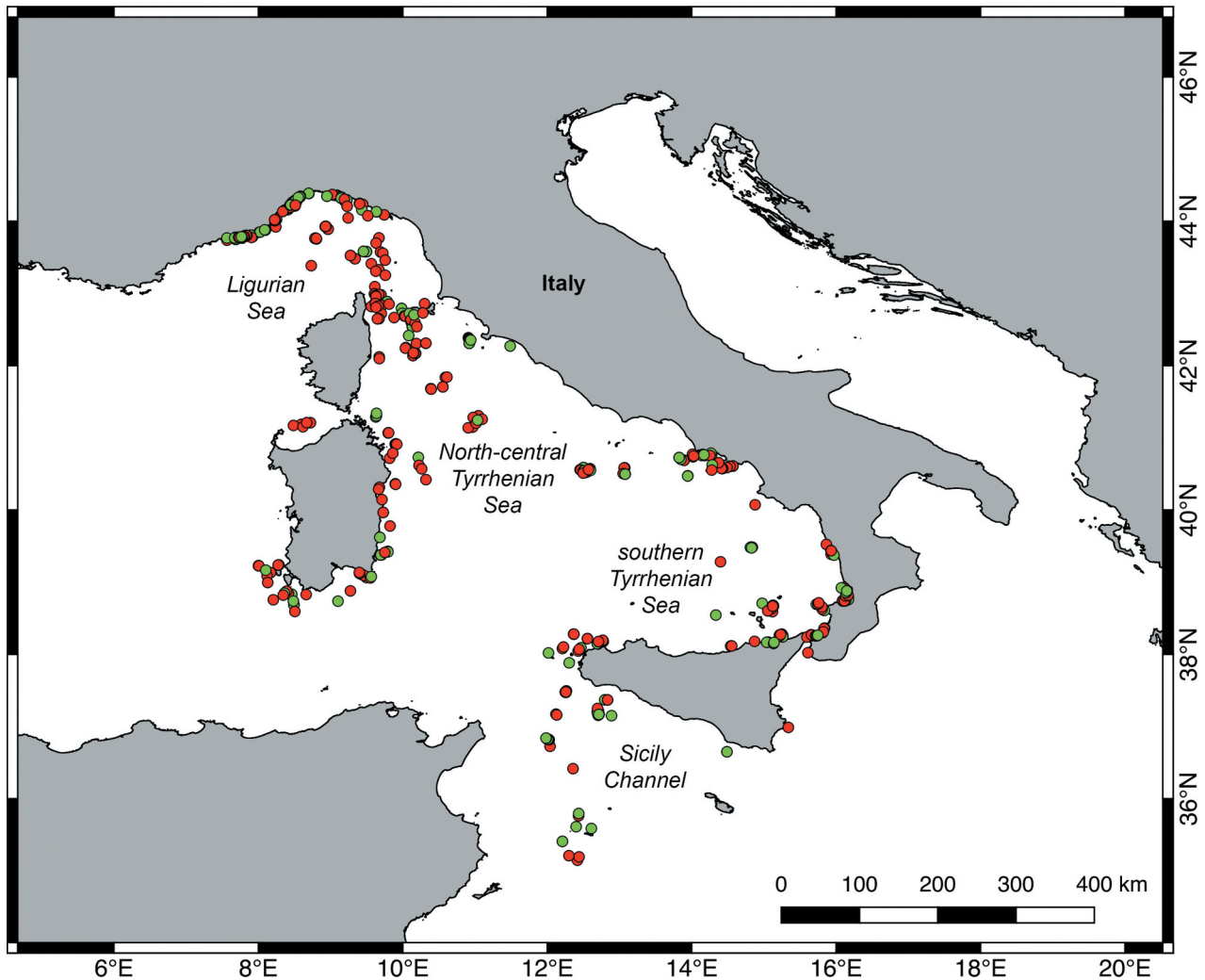


Figure 1. QGIS map of the study area with location of the ROV dives considered in this work. Dives with at least one record of heterobranchs are indicated by green dots, otherwise, they are indicated by red dots.

Tyrrhenian Sea (Palinuro and Marsili) were explored thanks to 49 ROV dives between 60 and 1825 m depth (Figure 1). Overall, the ROV tracks covered about 594,000 m<sup>2</sup> of the seafloor for over 508 h of video footage. Besides, more than 27,000 photos taken by high-resolution cameras were analysed, helping identify the smallest and cryptic specimens. Surveys were conducted over several years (2007–2019).

Five depth ranges (30–50 m; 51–100 m; 101–150 m; 151–200 m; >201 m) were defined to depict the bathymetric distribution patterns of the species. Dives extending for a broad depth range (more than 50 m) were divided into parts according to the identified ranges so that the final considered number was 883 (817 for coastal regions and 66 for seamounts).

ROV footage was analysed using Apple's Final Cut Pro X software. The analysis allowed recording

heterobranchs larger than 2 cm, identified by external morphological features at the lowest possible taxonomic level, thanks to field guides and specialist scientific literature. The currently valid scientific species names were checked on the World Register of Marine Species (WORMS). The number of individuals has been counted for each species, and the exact depth at which they were found was reported. Quantitative data about specimens were normalised as the number of individuals per 100 dives for each large geographic area and depth range. Putative food sources (identified based on the literature and the position of the molluscs) were also reported together with any other ecological note (e.g., type of habitat, phenotype, mating events and presence of eggs). The putative associations were explored for four species or groups of species through linear regressions considering the frequency

of occurrence (per 100 dives) of the food sources and their consumers.

Significant differences in the percentage diversity between depth ranges were investigated with a Kruskal–Wallis test (data not normally distributed,  $n = 37$  for each depth range considering 50–100 m, 101–200 m and > 201 m). In order to verify potential differences among the species according to geographic distribution and depth, the whole dataset (expressed as the number of specimens per 100 dives,  $n = 5$  per each species per each depth range) was square-root transformed to underweight abundant taxa and analysed by Principal Component Analysis (PCA) (Bray–Curtis similarity). In order to test for significant differences in the patterns of relative abundance of heterobranchs (total, cladobranchs and dorids, separately) in the four considered macro-areas (LS, Ligurian Sea; NCT, north-central Tyrrhenian Sea; ST, southern Tyrrhenian Sea; SC, Sicily Channel) at the different depth ranges (30–50 m, 51–100 m, 101–150 m, 151–200 m, > 201 m), a two-way PERMANOVA (Bray–Curtis similarity) was performed on the whole dataset (expressed as the number of specimens per dives,  $n = 7$ –114 per depth range).

Analyses were carried out with PAST Statistics Software® (Hammer et al. 2001).

## Results

### *Diversity and occurrence of the heterobranch fauna*

The heterobranch fauna recorded in the analysed ROV footage accounted for 559 specimens identified in 28 genera and 36 species (Tables I, II, Figure 2). The fauna consisted of 21 families divided into seven orders (or lower taxa). The order Nudibranchia showed the highest species richness (78% of the total taxa), with an almost equal contribution for the two represented suborders, Cladobranchia and Doridina (Table I). Altogether, the order Nudibranchia showed also the highest specimen abundance (91% of the total observed individuals, 50.5% and 40.5% in Cladobranchia and Doridina, respectively). These suborders also included the most frequent species, namely, *Paraflabellina ischitana* (Hirano & Thompson, 1990) (17% of the total records), followed by *Peltodoris atromaculata* Bergh, 1880 and Tritoniidae nd (11% and 12%, respectively). The dorids *Felimare tricolor* (Cantraine, 1835), *Felimare orsinii* (Vérany, 1846) and *Felimida purpurea* (Risso, 1831) and the cladobranch *Antiopella cristata* (Della Chiaje, 1841) represented 5–9% of the total records. The sacoglossan *Thuridilla hopei* (Vérany, 1853) and the umbraculid *Umbraculum umbraculum* (Lightfoot,

1786) accounted for 2–3% of the total records and represented the most frequent taxa within non-nudibranchs. Overall, 16 species were observed only sporadically, meaning one to five times, corresponding to less than 1% of the total observations (Tables I and II). A maximum of five species were recorded in the same dive.

All the taxa identified at the species level were previously reported in Mediterranean waters. Following the classification proposed by Bianchi et al. (2012), the biogeographic origin of the studied fauna is as follows: 59% of the taxa are Atlantic-Mediterranean species, 25% are (sub)tropical Atlantic, 13% are Boreo-Atlantic, while one species is cosmopolitan.

### *Bathymetric distribution of the heterobranch fauna*

Heterobranch records were made between 30 and 500 m, with the shallowest finding being *Peltodoris atromaculata* and the deepest Tritoniidae nd.

The highest diversity was observed between 30 and 100 m depth (86.5% of the recorded species). This datum significantly decreased in the depth range 101–200 m (51.4%) and dropped at greater depths (18.9%) (Kruskal–Wallis,  $H = 25.13$ ,  $H_c = 33.57$ ,  $p < 0.001$ ). The species recorded below the mesophotic zone (>200 m) were *G. rubrum* and the cladobranchs *Fjordia lineata* (Lovén, 1846), *Facelina* sp., *P. ischitana*, *Nemesignis banyulensis* (Portmann & Sandmeier, 1960), *T. fimbria* and Tritoniidae nd (Figure 3). Among these taxa, *G. rubrum* and *T. fimbria* were exclusively found in the deepest depth range, even if with a single record each. On the other hand, *P. ischitana* and *N. banyulensis* were mainly observed in the 50–100 m depth range, *F. lineata* in the 100–200 m, while *Facelina* sp. and Tritoniidae nd were consistently present below 200 m. No dorids were observed below 200 m (Figure 3).

The trend of relative abundances of all recorded specimens ( $n^\circ$  specimens/100 dives) showed a marked decrease with depth (Figure 4(a)). This trend was particularly evident for dorids, while cladobranchs showed a mesophotic peak of abundance (Figure 4(b)).

### *Geographic distribution of the heterobranch fauna*

Heterobranchs were reported in 25% of the total dives, with the highest percentage frequency of occurrence in the Ligurian Sea and Sicily Channel (33% of the total dives), followed by the north-

Table I. List of the heterobranch species found in this study. Number of specimens recorded per depth range and geographic area is given. LS, Ligurian Sea; NCT, north-central Tyrrhenian Sea; ST, southern Tyrrhenian Sea; SC, Sicily Channel.

| Species   | Depth ranges (m) |        |         |         |      | Macroareas |     |    |    | TOT |
|---|------------------|--------|---------|---------|------|------------|-----|----|----|-----|
|   | 30-50            | 51-100 | 101-150 | 151-200 | >201 | LS         | NCT | ST | SC |     |
| <b>APLYSIIDA</b>  |                  |        |         |         |      |            |     |    |    |     |
| <b>Aplysiidae</b>   |                  |        |         |         |      |            |     |    |    |     |
| <i>Aplysia depilans</i><br>Gmelin, 1791                       |                  | 3      |         |         |      | 2          | 1   |    |    | 3   |
| <b>CEPHALASPIDEA</b>  |                  |        |         |         |      |            |     |    |    |     |
| <b>Gastropteridae</b>   |                  |        |         |         |      |            |     |    |    |     |
| <i>Gastropteron rubrum</i><br>(Rafinesque, 1814)              |                  |        |         |         | 1    | 1          |     |    |    | 1   |
| <b>PLEUROBRANCHIDA</b>  |                  |        |         |         |      |            |     |    |    |     |
| <b>Pleurobranchaeidae</b>                                     |                  |        |         |         |      |            |     |    |    |     |
| <i>Pleurobranchaea meckeli</i><br>(Blainville, 1825)          |                  | 1      |         |         |      |            |     | 1  |    | 1   |
| <b>Pleurobranchidae</b>                                       |                  |        |         |         |      |            |     |    |    |     |
| <i>Berthella/Berthellina</i> spp.                             |                  | 4      | 1       |         |      |            | 2   |    | 3  | 5   |
| <i>Pleurobranchus testudinarius</i><br>Cantraine, 1835        |                  | 6      | 3       |         |      |            | 2   |    | 7  | 9   |
| <b>SACOGLOSSA</b>   |                  |        |         |         |      |            |     |    |    |     |
| <b>Plakobranchidae</b>  |                  |        |         |         |      |            |     |    |    |     |
| <i>Thuridilla hopei</i><br>(Vérany, 1853)                     | 13               | 3      |         |         |      | 12         | 2   | 1  | 1  | 16  |
| <b>UMBRACULIDA</b>  |                  |        |         |         |      |            |     |    |    |     |
| <b>Umbraculidae</b>   |                  |        |         |         |      |            |     |    |    |     |
| <i>Umbraculum umbraculum</i><br>(Lightfoot, 1786)             | 2                | 9      | 3       |         |      | 3          | 4   | 2  | 5  | 14  |
| <b>NUDIBRANCHIA</b>   |                  |        |         |         |      |            |     |    |    |     |
| <b>(Cladobranchia)</b>  |                  |        |         |         |      |            |     |    |    |     |
| <b>Coryphellidae</b>  |                  |        |         |         |      |            |     |    |    |     |
| <i>Fjordia lineata</i><br>(Lovén, 1846)                       |                  | 2      | 2       |         |      | 1          | 3   |    |    | 4   |
| <b>Dotidae</b>  |                  |        |         |         |      |            |     |    |    |     |
| <i>Doto cf. coronata</i><br>(Gmelin, 1791)                    |                  |        |         | 2       |      |            |     | 2  |    | 2   |
| <b>Facelinidae</b>  |                  |        |         |         |      |            |     |    |    |     |
| <i>Caloria elegans</i><br>(Alder & Hancock, 1845)             |                  | 1      | 5       |         |      |            | 1   | 5  |    | 6   |
| <i>Facelina annulicornis</i><br>(Chamisso & Eysenhardt, 1821) |                  | 1      |         |         |      | 1          |     |    |    | 1   |
| <i>Facelina</i> sp.   | 5                | 7      | 20      |         | 1    | 1          | 6   | 24 | 2  | 33  |
| <i>Pruvotfolia pselliotes</i><br>(Labbé, 1823)                | 1                | 5      | 1       |         |      | 5          |     | 2  |    | 7   |
| <b>Flabellinidae</b>  |                  |        |         |         |      |            |     |    |    |     |
| <i>Edmundsella pedata</i><br>(Montagu, 1816)                  |                  | 3      |         |         |      |            |     | 2  | 1  | 3   |
| <i>Flabellina affinis</i><br>(Gmelin, 1791)                   |                  | 9      | 4       |         |      | 5          | 4   | 3  | 1  | 13  |
| <i>Paraflabellina ischitana</i><br>(Hirano & Thompson, 1990)  | 7                | 49     | 33      | 1       |      | 3          | 17  | 31 | 39 | 90  |
| <b>Janolidae</b>  |                  |        |         |         |      |            |     |    |    |     |
| <i>Antiopella cristata</i><br>(Della Chiaje, 1841)            | 1                | 23     |         |         |      | 4          | 10  | 9  | 1  | 24  |
| <b>Myrrhinidae</b>  |                  |        |         |         |      |            |     |    |    |     |
| <i>Nemesignis banyulensis</i><br>(Portmann & Sandmeier, 1960) |                  | 4      |         |         |      | 4          |     |    |    | 4   |
| <b>Samlidae</b>   |                  |        |         |         |      |            |     |    |    |     |
| <i>Luisella babai</i><br>(Schmekel, 1872)                     |                  | 13     | 2       |         |      | 12         |     | 2  | 1  | 15  |

(Continued)

Table I. (Continued).

| Species  | Depth ranges (m) |        |         |         |      | Macroareas |     |    |    |     |
|--|------------------|--------|---------|---------|------|------------|-----|----|----|-----|
|  | 30-50            | 51-100 | 101-150 | 151-200 | >201 | LS         | NCT | ST | SC | TOT |
| <b>Tethydidae</b>  |                  |        |         |         |      |            |     |    |    |     |
| <i>Tethys fimbria</i><br>Linnaeus, 1767                      |                  |        |         |         | 1    | 1          |     |    |    | 1   |
| <b>Tritoniidae</b>   |                  |        |         |         |      |            |     |    |    |     |
| <i>Duvaucelia odhmeri</i><br>Tardy, 1963                     | 1                |        |         |         |      | 1          |     |    |    | 1   |
| Tritoniidae nd   |                  | 3      | 45      | 12      | 2    | 1          | 26  | 23 | 12 | 62  |
| <b>NUDIBRANCHIA (Doridina)</b>                               |                  |        |         |         |      |            |     |    |    |     |
| <b>Cadlinidae</b>  |                  |        |         |         |      |            |     |    |    |     |
| <i>Cadlina laevis</i><br>(Linnaeus, 1767)                    |                  |        | 1       |         |      |            | 1   |    |    | 1   |
| <b>Calycidorididae</b>                                       |                  |        |         |         |      |            |     |    |    |     |
| <i>Diaphorodoris alba</i><br>Portmann & Sandmeier, 1960      |                  | 6      | 1       |         |      | 4          | 2   | 1  |    | 7   |
| <i>Diaphorodoris papillata</i><br>Portmann & Sandmeier, 1960 |                  | 3      |         |         |      | 1          |     | 2  |    | 3   |
| <b>Chromodorididae</b>                                       |                  |        |         |         |      |            |     |    |    |     |
| <i>Felimare fontandraui</i><br>(Pruvot-Fol, 1951)            | 1                |        |         |         |      |            |     | 1  |    | 1   |
| <i>Felimare orsinii</i><br>(Vérany, 1846)                    | 22               | 19     |         |         |      | 41         |     |    |    | 41  |
| <i>Felimare picta</i><br>(Philippi, 1836)                    | 2                | 7      |         |         |      | 9          |     |    |    | 9   |
| <i>Felimare tricolor</i><br>(Cantraine, 1835)                | 14               | 31     | 1       | 2       |      | 36         | 3   | 2  | 7  | 48  |
| <i>Felimare cf. villafranca</i><br>(Risso, 1818)             | 3                | 10     |         |         |      | 1          | 1   | 7  | 4  | 13  |
| <i>Felimida binza</i><br>(Marcus & Marcus, 1963)             |                  | 1      |         |         |      | 1          |     |    |    | 1   |
| <i>Felimida luteorosea</i><br>(Rapp, 1827)                   |                  | 7      | 1       |         |      | 3          | 3   | 2  |    | 8   |
| <i>Felimida purpurea</i><br>(Risso, 1831)                    | 6                | 22     | 1       |         |      | 2          | 9   | 4  | 14 | 29  |
| <b>Discodorididae</b>  |                  |        |         |         |      |            |     |    |    |     |
| <i>Peltodoris atromaculata</i><br>Bergh, 1880                | 18               | 40     | 5       |         |      | 31         | 9   | 6  | 17 | 63  |
| <b>Goniodorididae</b>  |                  |        |         |         |      |            |     |    |    |     |
| <i>Okenia mediterranea</i><br>(Ihering, 1886)                |                  | 1      |         |         |      |            | 1   |    |    | 1   |
| <b>Phyllidiidae</b>  |                  |        |         |         |      |            |     |    |    |     |
| <i>Phyllidia flava</i><br>Aradas, 1847                       |                  | 2      |         |         |      | 2          |     |    |    | 2   |

central Tyrrhenian Sea (22%), southern Tyrrhenian Sea (20%) and seamounts (15%).

The expected species diversity percentage (number of species per 100 dives) decreased according to latitude from the Ligurian basin (14 species), to the southern Tyrrhenian Sea (7 species), with a second peak in the Sicily Channel (13 species) (Figure 5). The ratio between the taxa of the two Nudibranchia suborders was balanced in the Ligurian and Tyrrhenian seas (6:6, 3:3, 3:3, for Cladobranchia and Doridina, respectively). On the other hand, the Cladobranchia were dominant in the Sicily Channel

(6:3). The fauna of seamounts was composed of only six species, all cladobranchs (Table II; Figure 5).

The four coastal assemblages showed differences also in terms of relative abundance. In the PCA analysis, the first two axes explained 54% of the total variability observed in the dataset (expressed as the number of specimens per 100 dives) (C1: 36.2%, C2: 18.7%) (Figure 6). Based on this analysis, depth played a significant role in distinguishing regional groups. The Ligurian area is distinct from the north-central and southern Tyrrhenian and Sicily Channel areas. The biplot

Table II. Sampling location for each recorded species in the twelve explored seamounts. The numbers in parenthesis are the depth (in m) of each record. LS, Ligurian Sea; NCT, north-central Tyrrhenian Sea; ST, southern Tyrrhenian Sea. Seamounts: Ul, Ulisse; Pe, Penelope; Ja, Janua; Oc, Occhiali; Sp, Spinola; St. L, St. Lucia; Ve, Vercelli; Ba, Baronie; Ci, Cialdi; Et, Etruschi; Pa, Palinuro; Ma, Marsili.

| Geographic area<br>Seamount     | LS         |            |          |     |      |                | NCT       |            |     |     | ST             |     |
|---------------------------------|------------|------------|----------|-----|------|----------------|-----------|------------|-----|-----|----------------|-----|
|                                 | Ul         | Pe         | Ja       | Oc  | Sp   | St. L          | Ve        | Ba         | Ci  | Et  | Pa             | Ma  |
| Sampling period                 | May, Aug   | Aug        | May, Aug | Aug | Aug  | Jun, Aug       | Jul       | Jun        | Jul | Jul | May            | Jul |
| Distance from<br>the coast (NM) | 24         | 26         | 30       | 40  | 40   | 32             | 55        | 23         | 45  | 50  | 45             | 70  |
| Dives (n°)                      | 5          | 3          | 5        | 4   | 1    | 6              | 8         | 5          | 4   | 4   | 5              | 1   |
| Explored depth<br>range (m)     | 410        | 445        | 820      | 300 | 1820 | 140            | 60        | 200        | 340 | 365 | 85             | 485 |
| (min-max)                       | 570        | 520        | 940      | 500 | 1825 | 210            | 550       | 500        | 590 | 390 | 220            | 670 |
| <i>Fjordia lineata</i>          |            |            |          |     |      | 2<br>(165-205) |           |            |     |     |                |     |
| <i>Facelina</i> sp.             |            |            |          |     |      | 1<br>(150)     |           |            |     |     |                |     |
| <i>Paraflabellina ischitana</i> |            |            |          |     |      | 1<br>(205)     |           |            |     |     | 4<br>(100-185) |     |
| <i>Antiopella cristata</i>      |            |            |          |     |      |                | 1<br>(70) |            |     |     |                |     |
| <i>Nemesignis banyulensis</i>   |            |            |          |     |      |                |           | 1<br>(210) |     |     |                |     |
| Tritoniidae nd                  | 2<br>(500) | 1<br>(460) |          |     |      | 1<br>(205)     |           |            |     |     | 3<br>(170-185) |     |

showed that a relatively large number of taxa, including most *Felimare* species, *P. ischitana* and *P. atromaculata* drove the mesophotic faunas, while Tritoniidae nd and *Facelina* sp. drove the deeper ones.

The Ligurian heterobranch fauna showed, indeed, some peculiarities. The cladobranchs *Facelina* sp., *P. ischitana* and Tritoniidae nd, elsewhere relatively frequent, were rare in the Ligurian dataset. On the contrary, *Luisella babai* (Schmekel, 1872) and the sacoglossan *T. hopei* were commoner sightings. Regarding dorids, *F. orsinii* and *Felimare picta* (Philippi, 1836) were observed only in the Ligurian Sea, while *F. tricolor* was predominant in this area, and *F. purpurea* was more rarely reported (Table I).

Latitude and depth significantly contributed to the differences observed in the relative abundance patterns of the heterobranch fauna (Table III). In particular, a marked decrease was observed between the shallower depth ranges (30–100 m) and the deeper ones (>100 m) in the Ligurian Sea and the Sicily Channel (Figure 7(a)), explained by significantly higher abundances of dorids above 100 m (Figure 7(b), Table III). Cladobranchs, instead, mainly contributed to the mesophotic and deep faunas of the Tyrrhenian regions and Sicily Channel (Figure 7(c), Table III).

Overall, not many records were made on the seamounts. Heterobranchs were observed in half

of the sites, with a total of 17 specimens (Table II). Six species were identified: *A. cristata* was the solely reported above 100 m depth (Vercelli Seamount, 70 m depth), while other four cladobranchs (*F. lineata*, *Facelina* sp., *P. ischitana* and *N. banyulensis*) were found between 100 and 210 m, and Tritoniidae nd was observed down to 460–500 m (Penelope and Ulisse seamounts), being the deepest records of this taxon (Table II).

#### Ecological remarks on mesophotic and deep-sea heterobranchs

Almost all sightings of heterobranchs were made in environments characterised by coralligenous formations (48% of the total observations) and rocky hardgrounds (46%) (these latter including large boulders and silted outcrops on the outer shelf and upper slope, and dead coral frameworks, especially on bathyal seamounts). The remaining records were made in detritic environments (4%) (including also rhodolith beds) and soft bottoms (2%) (mud and sand), both mainly found in the proximity of the hardgrounds (Figures 2, 8, Table IV). Dorids contributed to 53% of the total records in coralligenous habitats, while cladobranchs were responsible for 67% of the records on rocky outcrops and 68% of the total occurrences

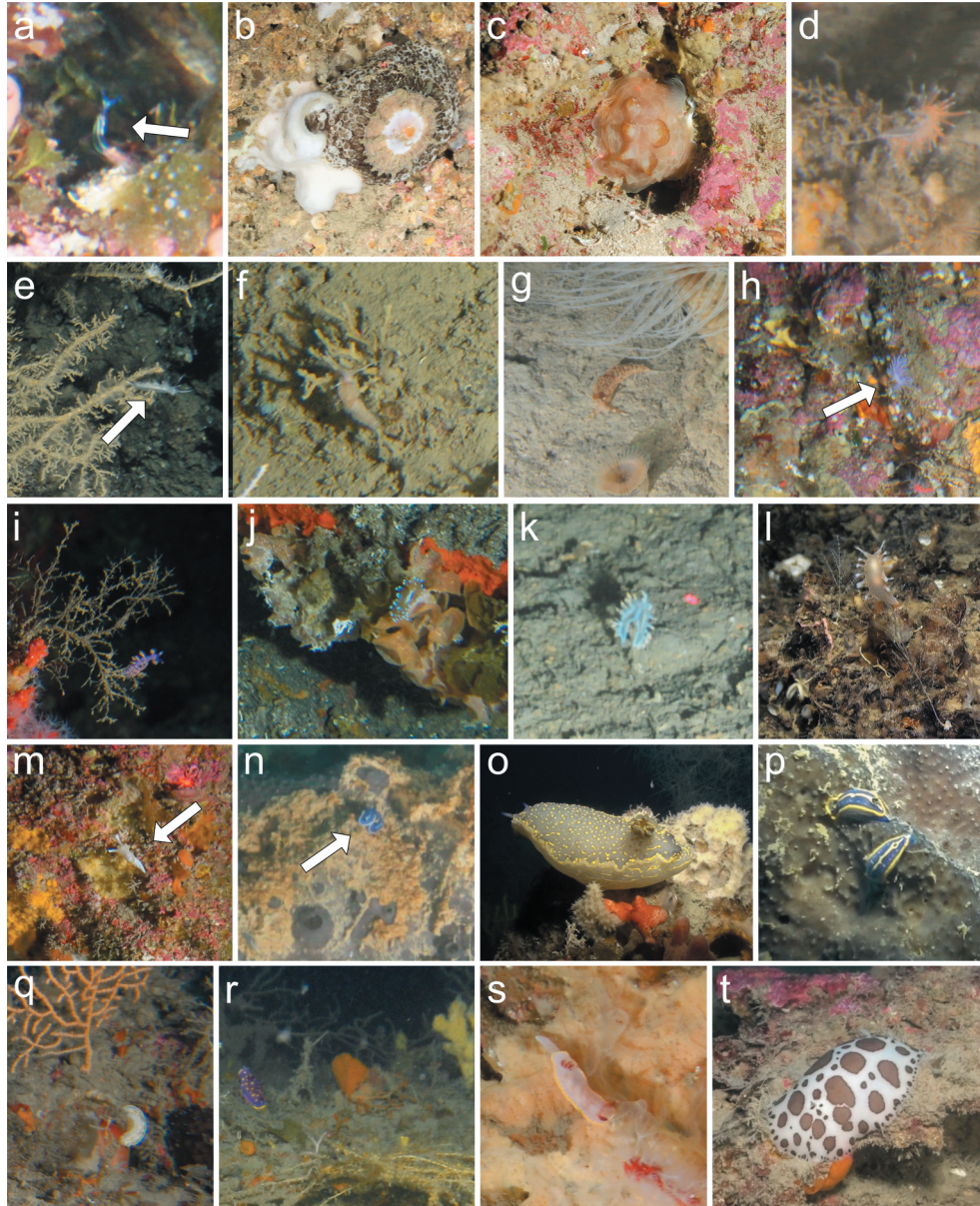


Figure 2. *In situ* ROV images of the 20 most represented species. (a) *Thuridilla hopei* on a bed of green algae in the coralligenous (Ponza, 75 m); (b) *Umbraculum umbraculum* on a silted rocky bank on the shelf edge (Graham Bank, 88 m); (c) *Pleurobranchus testudinarius* in a cavity of a rocky outcrop (Lampedusa, 108 m); (d) *Fjordia lineata* feeding on an hydrozoan growing on a heavily silted rocky outcrop of the shelf edge (Genova Portofino, 100 m); (e) *Caloria elegans* feeding on opportunistic hydrozoans growing on a dead gorgonian on a silted bank (Gulf of Naples, 110 m); (f) *Facelina* sp. on a silted offshore rocky outcrop (St. Eufemia, 122 m); (g) *Pruvotfolia pselliotes* crawling on mud (Bordighera Canyon, 50 m); (h) *Flabellina affinis* moving on a rich coralligenous bed (Ponza, 76 m); (i) *Paraflabellina ischitana* feeding on *Eudendrium* sp. within a red coral forest (SW Sardinia, 85 m); (j) *Antiopella cristata* feeding on the bryozoan *Reteporella* spp. (Tyrrhenian Calabria, 75 m); (k) two specimens of *Luisella babai* mating on detritic mud (Patti Gulf, 82 m); (l) *Tritonia callogorgiae* feeding on the anthozoan *Callogorgia verticillata* in a bathyal environment dominated by fossil hard corals (Ulisse Seamount, 500 m); (m) *Diaphorodoris alba* moving in a coralligenous environment (SW Sardinia, 85 m); (n) two specimens of *Felimare orsinii* mating on a keratose sponge (Savona, 45 m); (o) a large specimen of *Felimare picta* moving on a sponge bed (Imperia, 65 m); (p) two specimens of *Felimare tricolor* feeding on a keratose sponge (Genova Punta Manara, 65 m); (q) *Felimare* cf. *villafranca* crawling on a silted rocky bed on the outer shelf (Tuscan Archipelago, 75 m); (r) *Felimida luteorosea* moving in the understory of a gorgonian forest on a silted offshore rocky outcrop (St. Eufemia, 83 m); (s) *Felimida purpurea* on an encrusting sponge of a rocky outcrop (Gulf of Naples, 80 m); (t) a large specimen of *Peltodoris atromaculata* in a deep coralligenous environment (Egadi Archipelago, 57 m).

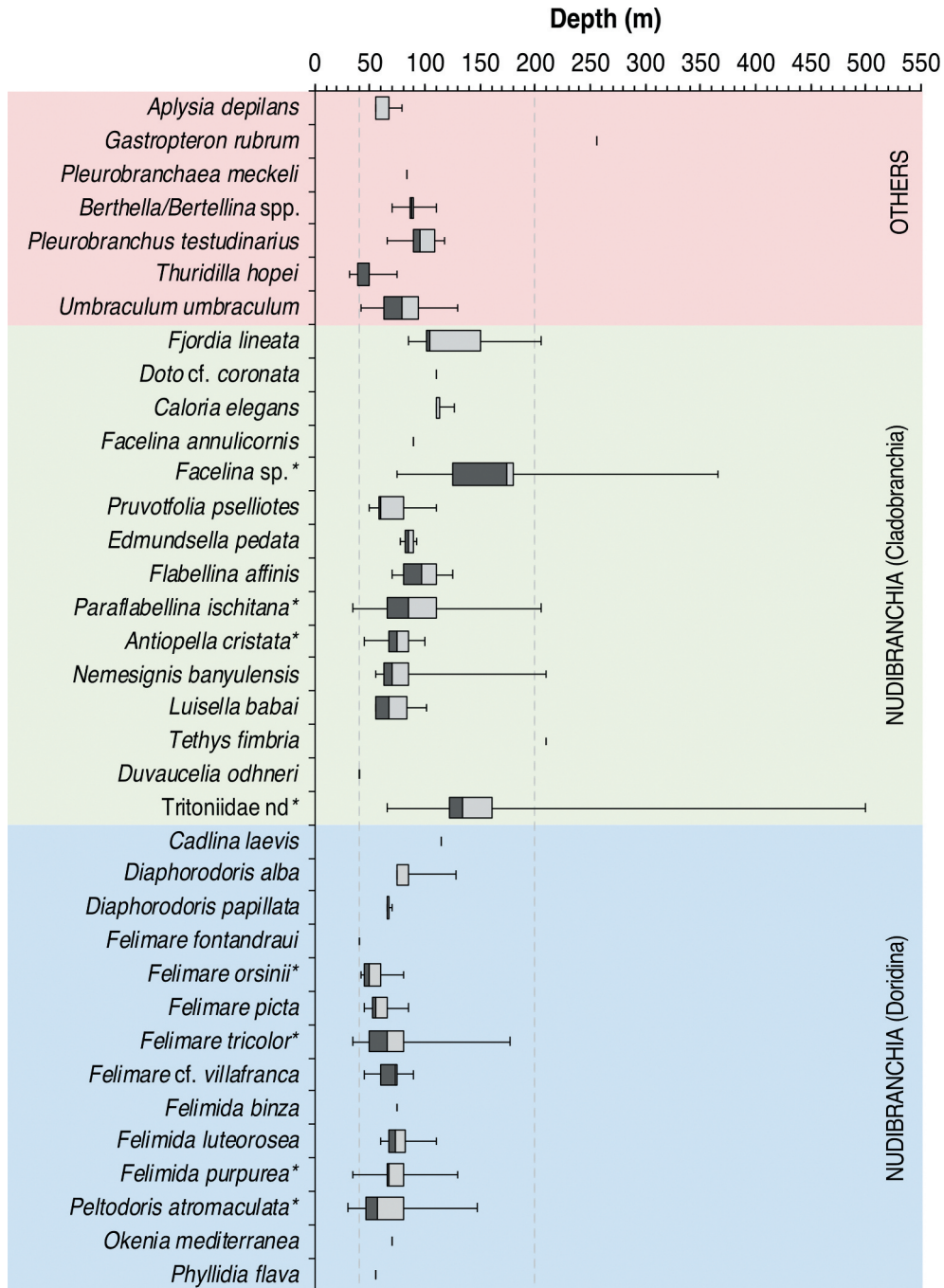


Figure 3. Bathymetric box plots of the 36 heterobranch species observed in this study. Dash lines indicate the limits of the mesophotic zone (40–200 m). \* refers to the most commonly recorded species.

on detritic. Other Heterobranchia, instead, contributed for 54% of the records on soft bottoms.

About 47% of the sightings were represented by the heterobranchs on exclusive or recurrent organisms, which could be identified as possible food sources (Table IV). The sacoglossan *T. hopei* was strictly linked to shallow-water photosynthetic algal communities (Figure 2(a)). *Antiopella cristata* was

observed on the bryozoans *Reteporella* spp. (Figure 2(j)), while *Duvaucelia odhneri* Tardy, 1963 was observed on the gorgonian *Leptogorgia sarmen-tosa* (Esper, 1791), and *U. umbraculum* was three times observed feeding on massive white sponges (Figure 2(b)). However, most of the associations regarded four taxa or closely related groups of species, whose relation to the presence of their putative

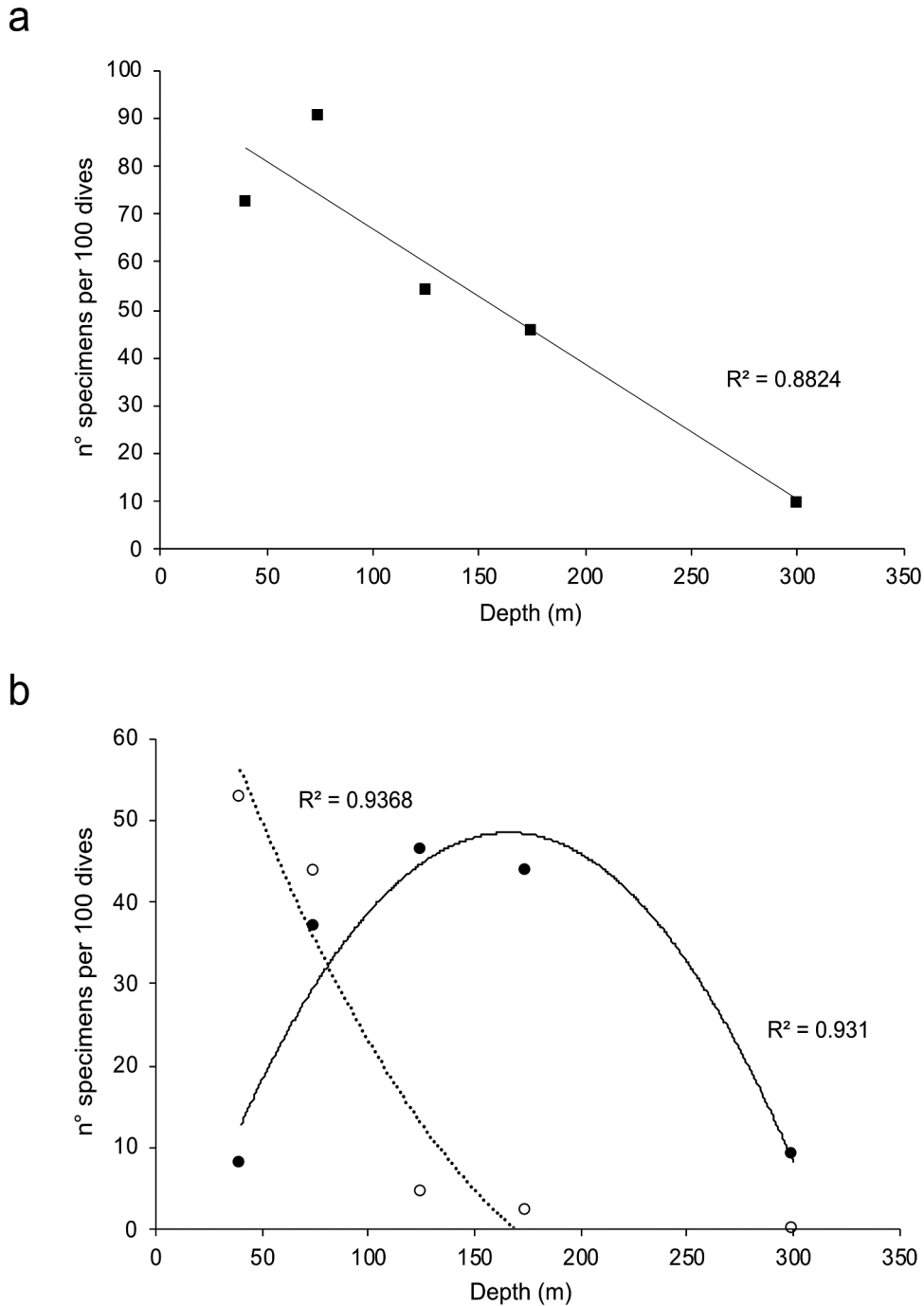


Figure 4. Correlation of (a) the number of heterobranch specimens (normalised on 100 dives) with depth, and (b) the number of specimens (normalised on 100 dives) of Doridina (empty circles) and Cladobranchia (filled circles) with depth.

food sources with depth was explored (Figure 9). The strongest correlation was found between the dorids *Felimare* spp. and keratose sponges, peaking between 30 and 100 m and almost disappearing below 130 m (Figures 8(a), 9(a)). Similarly, the dorid *P. atromaculata* showed an overlap in the occurrence of its food sources, the sponges *Petrosia*

*ficiformis* (Poiret, 1789) and *Haliclona fulva* (Topsent, 1893), both disappearing below the shelf edge (Figures 8(b), 9(b)). The occurrence of the cladobranch Tritoniidae was linked to the presence of deep-sea gorgonians, especially below 100 m (Figures 8 (d)-(g), 9(c)). The specimens were observed feeding on a large variety of

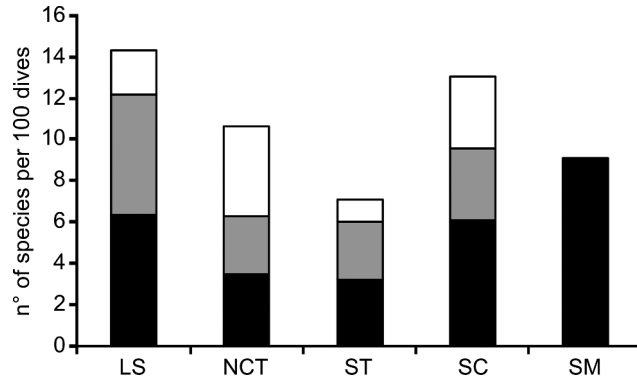


Figure 5. Expected number of species (per 100 dives) of Cladobranchia (black), Doridina (grey) and other Heterobranchia (white) according to the considered macro-areas: LS, Ligurian Sea; NCT, north-central Tyrrhenian Sea; ST, southern Tyrrhenian Sea; SC, Sicily Channel; SM, seamounts.

anthozoans, including *C. verticillata* (46% of the observed associations), *Acanthogorgia hirsuta* Gray, 1857 (25%), *Bebryce mollis* Philippi, 1842 (12%), and, to a lesser extent, *Eunicella cavolini* (Koch, 1887) (7%), *Villogorgia bebrycoides* (Koch, 1887)

(7%), and *Paramuricea clavata* (Risso, 1826) (3%). No strong relationship was observed between the hydrozoan-eater cladobranchs (belonging to the families Facelinidae, Flabellinidae, and, less represented, Coryphellidae, Myrrhinidae and Samlidae)

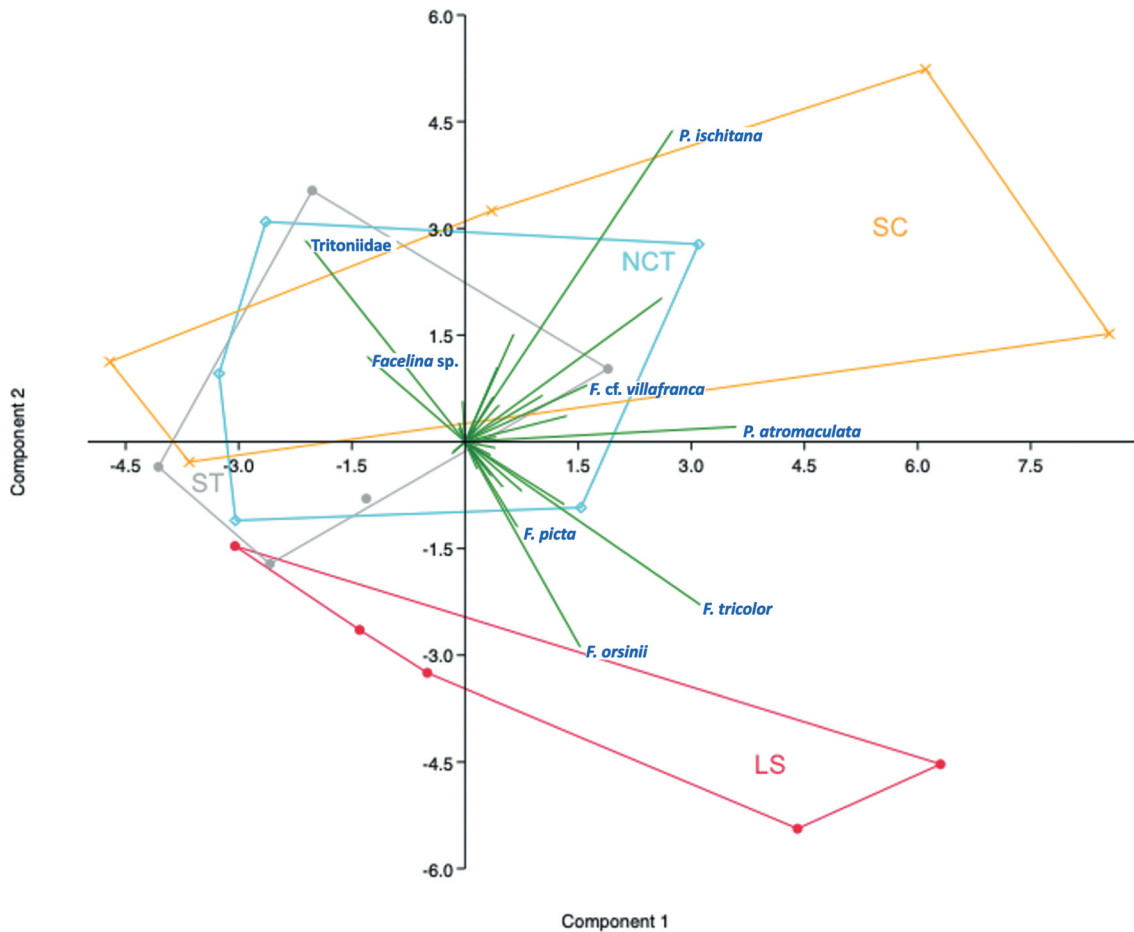


Figure 6. PCA analysis of the species composition and frequency dataset (based on the number of specimens per 100 dives) of the heterobranch assemblages of the four main considered macro-areas (red, Ligurian Sea; blue, north-central Tyrrhenian Sea; grey, southern Tyrrhenian Sea; Orange, Sicily Channel) at all depth ranges (from right to left on C1 axis).

Table III. Results of the statistical analyses.

| Source   | df  | SS      | MS     | F      | p             | Unique perms |
|--|-----|---------|--------|--------|---------------|--------------|
| <b>Figure 7(a)</b> Two-way PERMANOVA – Relative abundance total Heterobranchia |     |         |        |        |               |              |
| Area   | 3   | 2.23    | 0.74   | 0.53   | <b>0.001</b>  | 9999         |
| Depth  | 19  | 11.79   | 0.62   | 0.44   | <b>0.0001</b> |              |
| Interaction  | 57  | -885.09 | -15.52 | -11.09 | ns            |              |
| Residual   | 737 | 1031.7  | 1.39   |        |               |              |
| Total  | 816 | 160.66  |        |        |               |              |

**Figure 7(b)** Two-way PERMANOVA – Relative abundance Doridina

| Source      | df  | SS      | MS    | F      | p             | Unique perms |
|-------------|-----|---------|-------|--------|---------------|--------------|
| Area        | 3   | 3.61    | 1.20  | 1.55   | <b>0.0001</b> | 9999         |
| Depth       | 19  | 10.75   | 0.56  | 0.73   | <b>0.0001</b> |              |
| Interaction | 57  | -492.07 | -8.63 | -11.15 | ns            |              |
| Residual    | 737 | 570.25  | 0.77  |        |               |              |
| Total       | 816 | 92.54   |       |        |               |              |

**Figure 7(c)** Two-way PERMANOVA – Relative abundance Cladobranchia

| Source      | df  | SS      | MS     | F      | p           | Unique perms |
|-------------|-----|---------|--------|--------|-------------|--------------|
| Area        | 3   | 0.38    | 0.12   | 0.12   | ns          | 9999         |
| Depth       | 19  | 4.73    | 0.24   | 0.25   | <b>0.05</b> |              |
| Interaction | 57  | -627.98 | -11.01 | -11.11 | ns          |              |
| Residual    | 737 | 730.85  | 0.99   |        |             |              |
| Total       | 816 | 107.99  |        |        |             |              |

and large colonial hydrozoans (such as Plumularoidea, Sertularioidea, Bougainvillidae, Eudendriidae, Haleciidae, Lafoeidae, Campanulariidae) (Figures 8(c), 9(d)). About 20% of these heterobranchs were found crawling on lost fishing gear, feeding on hydrozoans colonising nets and lines (Figure 8 (h)–(j)). The species most commonly observed in these cases were *Facelina* sp. and *P. ischitana*. This latter, as well as *Flabellina affinis* (Gmelin, 1791) and *Caloria elegans* (Alder & Hancock, 1845), were also observed on hydrozoans colonising dead gorgonians (Figure 2(e)).

Considering soft-bottom species, the scattered records regarding the cephalaspidean *G. rubrum*, the pleurobranchids *P. meckeli* and *Pleurobranchus testudinarius* Cantraine, 1835, and the nudibranch *T. fimbria* provided no evidence of feeding activity (Figure 8 (k)–(l)).

The 883 dives covered all months except for March and December; however, observations were mainly concentrated from June to September, accounting for 79% of the total dives. The summer observations included most of the dives with sightings of heterobranchs (about 87%) (Table IV). Among the species with the highest number of records, *P. atromaculata*, *P. ischitana* and

Tritoniidae nd were also observed during spring (May) and autumn (October), with one winter record (January) for the latter species (370 m). During summer, egg ribbons were observed near specimens of *U. umbraculum*, *C. elegans*, *D. odhneri*, Tritoniidae nd, *Felimare* cf. *villafrenca* (Risso, 1818), and *P. atromaculata* (Figure 8 (m, n), Table IV). Finally, *F. orsinii*, *L. babai* and *P. testudinarius* were observed during mating between June and November (Figures 2(n, k), 8(l)).

## Discussion

Deep-sea heterobranchs have received relatively poor attention compared with their coastal counterpart, particularly those taxa that do not possess a shell remaining in the sediments or that live on hardgrounds unsuitable for traditional destructive sampling gear. These latter species, however, generally present a size compatible with the modern ROV image resolution; therefore, their distribution and ecology could be investigated with targeted studies. So far, only a handful of papers specifically dealt with this group for taxonomic or ecological purposes, in the Atlantic and Pacific oceans down to 2300 m (NRDC, 2014; Valdés et al. 2018; Zhang & Zhang 2021) and in the Mediterranean Sea down to 420 m (Chimienti et al. 2020).

This study enriches the knowledge on deep hard bottom Mediterranean heterobranchs with a novel large-scale approach that includes a bathymetric range embracing the mesophotic and upper bathyal zone and a latitudinal transect of about 600 nautical miles touching all western coasts of Italy and some offshore locations.

ROV technology does not allow for a comprehensive evaluation of the diversity of the subclass Heterobranchia. It misses part of the diversity of this group, especially burrowing taxa with external shells found in sediments (e.g., Acteonoidea, Pyramidelloidea, Valvatoidea) (e.g., Monterosato 1874, 1890; Jeffreys 1882; Smriglio & Mariottini 1996; Bogi & Galil 2004, 2013). In addition, regarding epifaunal species, it is limited in the observation of very small specimens and in the detection of fine external morphological features. Finally, it is not efficient in the collection of a large number of individuals for anatomical studies. Nevertheless, numerous heterobranchs belonging to the taxa considered in this study (Sacoglossa, Umbraculida, Aplysiida, Cephalaspidea, Pleurobranchida, and Nudibranchia) display morphological and ecological traits detectable by ROV and sufficient for a

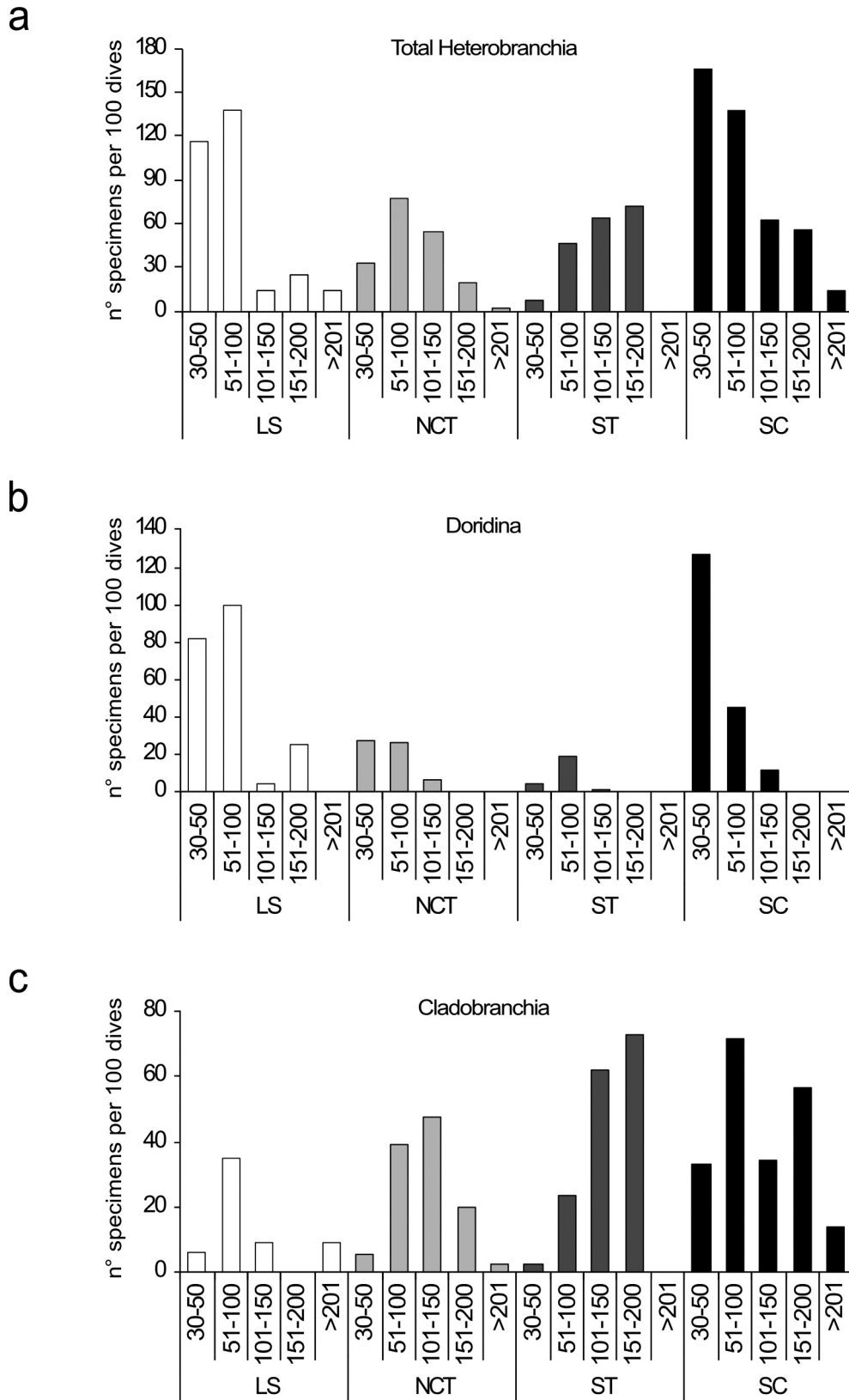


Figure 7. Bathymetric and geographical patterns of relative abundance (expressed as the number of specimens per 100 dives) of (a) total Heterobranchia, (b) Doridina, and (c) Cladobranchia.

Table IV. Ecological observations of the heterobranchs target of this study. Legend to habitats (listed in order of frequency for each species): R, rocky bottom; C, coralligenous; S, soft bottom; D, detritic.

| Species                                 | Observation period | Habitat | Putative prey   | Eggs' presence         |
|---|--------------------|---------|---|------------------------|
| <i>Aplysia depilans</i>                 | Aug                | S, C    |   |                        |
| <i>Gastropteron rubrum</i>              | Aug                | S       |   |                        |
| <i>Pleurobranchaea meckeli</i>          | Jul                | S       |   |                        |
| <i>Berthella/Berthellina</i> spp.       | May, Jul–Aug, Oct  | C, R    |   |                        |
| <i>Pleurobranchus testudinarius</i>     | Jun, Aug           | D, C, S |   |                        |
| <i>Thuridilla hopei</i>                 | Jul, Aug, Sep      | C       | Algal turf  |                        |
| <i>Umbraculum umbraculum</i>            | May–Sep, Nov       | C, R    | Massive sponge  | Sep (102 m)            |
| <i>Fjordia lineata</i>                  | Jun–Aug            | R       | Hydrozoans  |                        |
| <i>Doto</i> cf. <i>coronata</i>         | Sep                | R       | <i>Sertularella gayi</i>  |                        |
| <i>Caloria elegans</i>                  | Jun, Oct           | R       | Bouganvillidae nd   | Jun (115 m)            |
| <i>Facelina annulicornis</i>            | Aug                | D       |   |                        |
| <i>Facelina</i> sp.                     | May–Oct            | R, C, D | Hydrozoans  |                        |
| <i>Pruvotfolia pselliotes</i>           | Aug–Sept           | R, S, C |   |                        |
| <i>Edmundsella pedata</i>               | Jul–Aug, Oct       | C       | Hydrozoans  |                        |
| <i>Flabellina affinis</i>               | May–Oct            | R, C, D | Hydrozoans  |                        |
| <i>Paraflabellina ischitana</i>         | May–Nov            | C, R, D | Hydrozoans  |                        |
| <i>Antiopella cristata</i>              | May–Sep            | C, R    | <i>Reteporella</i> spp.   |                        |
| <i>Nemesignis banyulensis</i>           | Jun, Aug           | R, C, S | Hydrozoans  |                        |
| <i>Luisella babai</i>                   | Jun–Jul, Nov       | D, S, C | Hydrozoans  |                        |
| <i>Tethys fimbria</i>                   | Aug                | S       |   |                        |
| <i>Duvaucelia odhmeri</i>               | Sep                | R       | <i>Leptogorgia sarmentosa</i>   | Sep (40 m)             |
| Tritoniidae nd                          | Jan, May–Oct       | R, C    | <i>Callogorgia verticillata</i> , <i>Acanthogorgia hirsuta</i> ,<br><i>Bebryce mollis</i> , <i>Eunicella cavolini</i> , <i>Villogorgia</i><br><i>bebrycoides</i> , <i>Paramuricea clavata</i> | Sep (130 m)            |
| <i>Cadlina laevis</i>                   | Oct                | R       | Encrusting orange sponges   |                        |
| <i>Diaphorodoris alba</i>               | Jun–Oct            | R, C    |   |                        |
| <i>Diaphorodoris papillata</i>          | Jul–Aug            | C, R    |   |                        |
| <i>Felimare fontandraui</i>             | Aug                | C       |   |                        |
| <i>Felimare orsinii</i>                 | Jun, Aug–Sep       | R, C    | Keratoso sponges  |                        |
| <i>Felimare picta</i>                   | Jun, Aug–Sep       | R, C, D | Demosponges   |                        |
| <i>Felimare tricolor</i>                | May–Sep            | C, R, D | Keratoso sponges  |                        |
| <i>Felimare</i> cf. <i>villafraanca</i> | May, Jul–Aug       | C, R    | Demosponges   | Aug (90 m)             |
| <i>Felimida binza</i>                   | Aug                | R       |   |                        |
| <i>Felimida luteorosea</i>              | Jun–Oct            | C, R    |   |                        |
| <i>Felimida purpurea</i>                | Jun–Sep            | C, R    | Demosponges   |                        |
| <i>Peltodoris atromaculata</i>          | May–Oct            | C, R, D | <i>Petrosia ficiformis</i> , <i>Haliclona fulva</i>   | Jul–Aug (57, 84, 85 m) |
| <i>Okenia mediterranea</i>              | Oct                | C       |   |                        |
| <i>Phyllidia flava</i>                  | Aug                | R       |   |                        |

reasonably good identification. As a result, 36 species were identified in this analysis, of which 13 adds up to the known deep fauna of the basin, previously accounting for 59 taxa found in mesophotic and bathyal environments (40–910 m) (e.g., Vicente 1967; Ros 1975; Bouchet 1977; Cattaneo-Vietti 1991; Koutsoubas et al. 2000; Domènech et al. 2006) (Table V). This result supports the use of ROV, despite its limitations, as an effective tool to characterise deep macrofauna, especially on hard-grounds that are unsuitable for other sampling devices.

Among the most abundant taxa, only two were considered challenging in terms of taxonomic identification. *Facelina* sp. is a 3 cm long cladobranch strongly resembling the recently re-established shallow-water taxon *Facelina vicina* (Bergh, 1882), for long identified

as *Facelina bostoniensis* (Couthouy, 1838) (Carmona 2020). With respect to shallow-water specimens, it is paler, as also reported by Mastrototaro et al. (2017) from bathyal muds (473–552 m) off Ibiza (Balearic Sea). Its collection is mandatory to clarify its identification, possibly as a new species.

Tritoniidae nd represented the second challenging case in terms of identification. Of the 69 records, five could be attributed to *Marionia blainvillea* (Risso, 1818) mainly due to their dark red colouration and common occurrence in coralligenous environments (65–155 m) associated with *E. cavolini* and *P. clavata*, as previously reported in the literature (McDonald & Nybakken 1999; Ponti et al. 2016). Half of the remaining records could be attributed to *T. callogorgiae* due to their generally lighter colouration (from white to yellow, to orange) and the fact

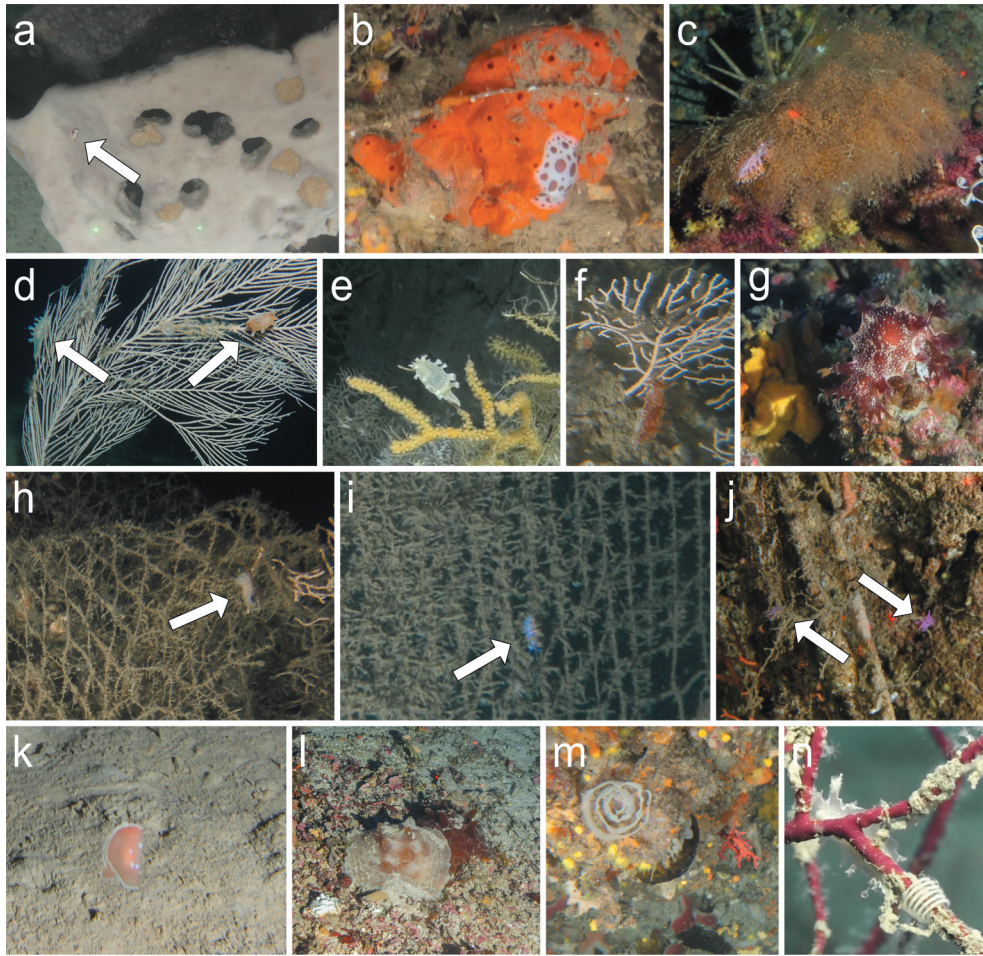


Figure 8. Ecological observations based on ROV footage. (a) *Felimare tricolor* on the keratose sponge *Spongia lamella* (Schultze, 1879) (Savona, 80 m); (b) *Peltodoris atromaculata* feeding on the demosponge *Haliclona fulva* (Spotorno, 57 m); (c) *Paraflabellina ischitana* feeding on the hydrozoan *Eudendrium* cf. *racemosum* (Pantelleria, 102 m); (d-g) various phenotypes of Tritoniidae on the alcyonaceans *Callogorgia verticillata* (d, S. Eufemia, 122 m, probably *Tritonia callogorgiae*), *Acanthogorgia hirsuta* (e), Graham Bank 166 m, probably *T. callogorgiae*), *Eumicella cavolini* (f), Gulf of Naples, 115 m, probably *Marionia blainvillea*), and in the coralligenous environment (g), Cetraro, 65 m, probably *M. blainvillea*); *Facelina* sp. (h), Gulf of Naples, 125 m), *P. ischitana* (i-j), Gulf of Naples, 130 m), and *Flabellina affinis* (j), SW Sardinia, 115 m) crawling on lost fishing gear covered in hydrozoans; (k) a swimming specimen of *Gastropteron rubrum* (Bisagno Canyon, 256 m); (l) two mating *Pleurobranchus testudinarius* on a rhodolith bed (Lampedusa, 95 m); (m) egg ribbon of *P. atromaculata* (Spotorno, 57 m); (n) Egg mass of *Duvaucelia odhmeri* on the alcyonacean *Leptogorgia sarmentosa* (Capo Mortola, 40 m).

that they were associated with the alcyonacean *C. verticillata* in bathyal habitats as described (Chimienti et al. 2020). However, the other records included specimens with overlapping characteristics. Overall, the impossibility of verifying the anatomical characteristics distinguishing the two taxa and the similar morphology in the ROV footage does not allow for a conclusive identification (hence Tritoniidae nd), especially in the putative overlapping depth range. If the records of *T. callogorgiae* are correct, then the known bathymetric distribution of this species should be extended (110–500 m), and its putative diet should also include five other gorgonians, both shallow and deep ones. Species identification and genus-level taxonomic assignments of

Family Tritoniidae are still debated and under investigation (Korshunova & Martynov 2020; Moles et al. 2021); a revision of Mediterranean Tritoniidae, including a study of the type material of *M. blainvillea*, is necessary to disentangle the distinction between these two species.

The heterobranch fauna reported in this study is mainly constituted by Atlantic-Mediterranean species usually found in shallow-water coralligenous biocoenoses (e.g., Ballesteros 2006; Furfaro & Mariottini 2016; Trainito & Doneddu 2016). Although a bias exists due to the lack of precise depth locations of the findings in many literature sources, the observations provided here extend the known bathymetric distribution of 29 of the

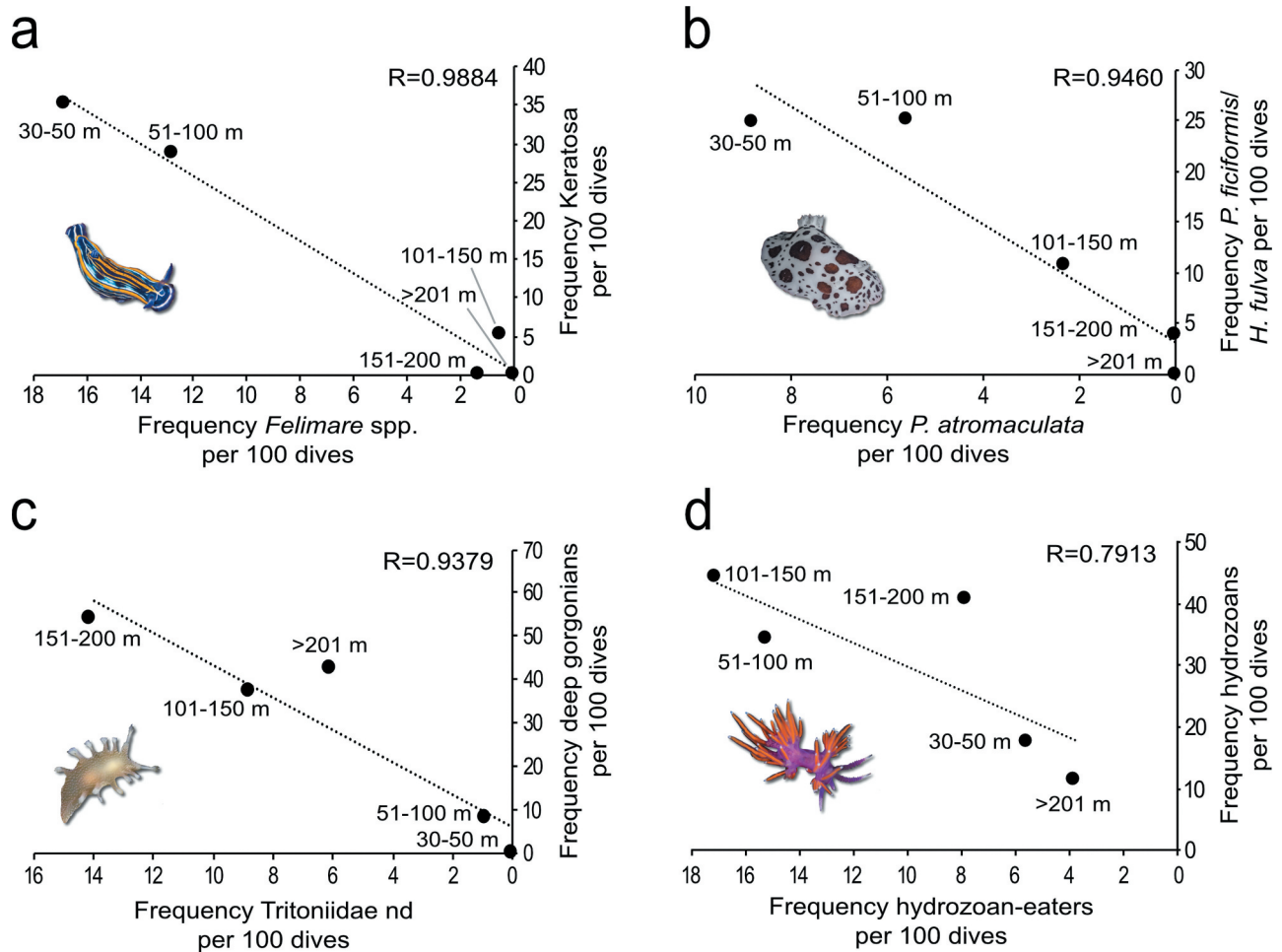


Figure 9. Relationships between heterobranchs and their food sources explored by linear regressions based on the frequency of occurrence per 100 dives of: (a) *Felimare* spp. (including *Felimare fontandraui*, *Felimare orsinii*, *Felimare picta*, *Felimare tricolor*, and *Felimare* cf. *villafraanca*) and keratose sponges (including *Cacospongia mollior* Schmidt, 1862, *Dysidea* spp., *Ircinia* spp., *Sarcotragus* spp., and *Spongia* spp.), (b) *Peltodoris atromaculata* and the sponges *Petrosia ficiformis* and *Haliclona fulva*, (c) Tritoniidae nd and the deep alcyonaceans *Callogorgia verticillata*, *Acanthogorgia hirsuta*, and *Bebryce mollis* and (d) hydrozoan-eaters cladobranchs (including *Caloria elegans*, *Edmundsella pedata*, *Facelina annulicornis*, *Facelina* sp., *Fjordia lineata*, *Flabellina affinis*, *Luisella babai*, *Nemesignis banyulensis*, *Paraflabellina ischitana*, and *Pruvotfolia psellioetes*) and arborescent hydrozoans.

recorded species (Table V). This result supports the ability of some Mediterranean species, traditionally considered of shallow waters (0–40 m), to colonise at least the upper mesophotic depth range (40–80 m), with a conspicuous number also extending in the lower mesophotic (80–200 m). Due to the progressive decrease in the availability of hardgrounds with depth, these species can be found on the scattered *roches du large* (sensu Pérès & Picard 1964; Bo et al. 2012; Montefalcone et al. 2021) of the outer shelf and shelf break, but may also be found in offshore coarse detritic environments, including rhodolith and maërl beds (Vicente 1967). The ability of hard-bottom heterobranchs to colonise unconsolidated, coarse sediments, where they feed on small opportunistic sessile species,

has also been suggested in shallow-water environments (Betti et al. 2017). As a response to the changing habitat, an impoverishment of the diversity and abundance of heterobranchs is observed according to the bathymetric gradient, although with some differences between the two main Nudibranchia suborders. The dorids are driven by a higher abundance of upper mesophotic species such as *Felimare* spp., while the cladobranchs are mainly represented by species with a lower mesophotic peak of occurrence, such as *P. ischitana*, *F. lineata*, *Facelina* sp. and Tritoniidae nd. The most typical bathyal species in the Mediterranean basin (>200 m) occupy detritic or muddy bottoms following a higher availability of these habitats (Vicente 1967; Cattaneo-Vietti 1991).

Table V. Literature (black) and updated (red) bathymetric distribution of the heterobranch species (referring to most taxa of the former “Opisthobranchia” group) known to live in mesophotic and bathyal environments of the Mediterranean Sea (73 total species). Literature data include Vicente (1967), Bouchet (1977), Cattaneo-Vietti (1991), Koutsoubas et al. 2000, Trainito and Doneddu, 2014, OPK website, and present study. Only data reporting depths of living organisms were considered. Legend: H, hardgrounds, S, soft bottoms; \*, species found in the present study; °, species reported here for the first time in the mesophotic/bathyal depth range. The dashed line before the first value indicates that the species is present from near the surface at an unspecified depth. Grey data refer to the wide depth ranges reported in Ros (1975) and Domènech et al. (2006).

| Species                                     | Habitat | Depth range in the Mediterranean Sea |
|---|---------|--------------------------------------|
| <i>Tylodina perversa</i>                    | H       | ----- 55m                            |
| <i>Phyllidia flava</i> <sup>°</sup>         | H       | -- 40m - 55m                         |
| <i>Bulla striata</i>                        | S       | ----- 60m                            |
| <i>Dendrodoris limbata</i>                  | H       | ----- 60m                            |
| <i>Thordisa filix</i>                       | H, S    | ----- 60m                            |
| <i>Diaphorodoris papillata</i> <sup>°</sup> | H       | -- 40m -- 70m                        |
| <i>Okenia mediterranea</i> <sup>°</sup>     | H       | -- 40m -- 70m                        |
| <i>Facelina auriculata</i>                  | H       | -- 50m -- 70m                        |
| <i>Duvaucelia plebeia</i>                   | H       | ? 50m -- 70m                         |
| <i>Discodoris stellifera</i>                | H       | -- 50m -- 70m                        |
| <i>Doris verrucosa</i>                      | H       | -- 50m -- 70m                        |
| <i>Doriopsilla areolata</i>                 | H       | -- 50m -- 70m                        |
| <i>Thuridilla hopei</i> *                   | H       | -- 45m ---- 75m                      |
| <i>Felimida binza</i> <sup>°</sup>          | H       | -- 35m ---- 75m                      |
| <i>Aplysia depilans</i> <sup>°</sup>        | S, H    | - 25m ----- 79m                      |
| <i>Philinopsis depicta</i>                  | S       | ----- 80m                            |
| <i>Felimare orsinii</i> <sup>°</sup>        | H       | -- 40m ---- 80m                      |
| <i>Felimare picta</i> *                     | H       | --- 60m ---- 85m                     |
| <i>Facelina annulicornis</i> <sup>°</sup>   | H       | - 25m ----- 90m                      |
| <i>Felimare villafranca</i> *               | H       | -- 45m ----- 90m                     |
| <i>Edmundsella pedata</i> *                 | H       | -- 45m ----- 93m                     |
| <i>Ascobulla fragilis</i>                   | S       | ----- 100m                           |
| <i>Scaphander punctostriatus</i>            | S       | 40m ----- 100m                       |
| <i>Antiopella cristata</i> *                | H       | -- 50m ----- 100m                    |
| <i>Felimare fontandraui</i> *               | H       | ----- 100m                           |
| <i>Luisella babai</i> *                     | H       | -- 50m ----- 102m                    |
| <i>Okenia elegans</i>                       | H       | ----- 105m                           |
| <i>Doto coronata</i> <sup>°</sup>           | H       | - 30m ----- 110m                     |
| <i>Pruvotfolia pselliotes</i> <sup>°</sup>  | H       | - 25m ----- 110m                     |
| <i>Felimida luteorosea</i> *                | H       | --- 60m ----- 110m                   |
| <i>Cadlina laevis</i> <sup>°</sup>          | H       | - 20m ----- 115m                     |
| <i>Pleurobranchus testudinarius</i> *       | S, H    | -- 50m ----- 117m                    |
| <i>Notarchus punctatus</i>                  | H       | --- 60m ----- 120m                   |
| <i>Flabellina affinis</i> *                 | H       | -- 50m ----- 125m                    |
| <i>Caloria elegans</i> *                    | H       | -- 50m ----- 127m                    |
| <i>Diaphorodoris alba</i> *                 | H       | -- 50m ----- 128m                    |
| <i>Berthella ocellata</i>                   | H       | ----- 130m                           |
| <i>Umbraculum umbraculum</i> *              | H       | ----- 80m ----- 130m                 |
| <i>Felimida purpurea</i> <sup>°</sup>       | H       | -- 40m ----- 130m                    |
| <i>Peltodoris atromaculata</i> *            | H       | ----- 100m --- 148m                  |
| <i>Kaloplocamus ramosus</i>                 | S       | 60m ----- 148m                       |
| <i>Marionia blainvillea</i>                 | H       | ----- 155m?                          |
| <i>Felimare tricolor</i> *                  | H       | --- 60m ----- 177m                   |
| <i>Roxaniella jeffreysi</i>                 | S       | ----- 200m                           |
| <i>Cyllichna cylindracea</i>                | S       | ----- 200m                           |

(Continued)

Table V. (Continued).

|  |      |                              |
|--|------|------------------------------|
| <i>Berthella aurantiaca</i>                    | H    | --- 60m ----- 200m           |
| <i>Doris pseudoargus</i>                       | S, H | ----- 200m                   |
| <i>Fjordia lineata</i> *                       | H    | -- 45m ----- 205m            |
| <i>Paraflabellina ischitana</i> * <sup>o</sup> | H    | -- 40m ----- 205m            |
| <i>Nemesignis banyulensis</i> * <sup>o</sup>   | H    | -- 40m ----- 210m            |
| <i>Berthella elongata</i>                      | H    | ----- 100m ----- 250m        |
| <i>Tritonia hombergi</i>                       | H    | ---?--- 70m ----- 250m       |
| <i>Jorunna tomentosa</i>                       | H    | ----- 150m ----- 250m        |
| <i>Pleurobranchus membranaceus</i>             | S    | ----- 260m                   |
| <i>Aglaja tricolorata</i>                      | S    | --- 50m ----- 300m           |
| <i>Gastropterion rubrum</i> *                  | S    | ----- 300m                   |
| <i>Armina maculata</i>                         | S    | 20m ----- 150m ----- 300m    |
| <i>Armina neapolitana</i>                      | S    | 50m ----- 300m               |
| <i>Armina tigrina</i>                          | S    | -- 50m ----- 300m            |
| <i>Lomanotus marmoratus</i>                    | H    | 50m ----- 300m               |
| <i>Doris sticta</i>                            | H    | 50m ----- 300m               |
| <i>Doriopsilla pelseneeri</i>                  | H    | 50m ----- 300m               |
| <i>Geitodoris planata</i>                      | H    | -- 50m ----- 300m            |
| <i>Philine quadripartita</i>                   | S    | ----- 430m                   |
| <i>Philine monterosati</i>                     | S    | 120m ----- 450m              |
| <i>Pleurobranchaea meckeli</i> *               | S    | ----- 470m                   |
| <i>Philine catena</i>                          | S    | ----- 500m                   |
| <i>Tritonia callogorgiae</i> *                 | H    | 110m ----- 400-420m --- 500m |
| <i>Scaphander lignarius</i>                    | S    | ----- 550m                   |
| <i>Baptodoris cinnabarina</i>                  | H    | ----- 550m                   |
| <i>Facelina vicina</i> *                       | H    | ----- 552m                   |
| <i>Tethys fimbria</i> *                        | S    | ----- 600m                   |
| <i>Doris alboranica</i>                        | S    | - 910m                       |

Nonetheless, most of these species are eurybathic (Table V), with only *T. callogorgiae*, among the hard-bottom species, showing a clear specialisation for deep habitats, probably driven by a diet based on anthozoans forming forests on the mesophotic and bathyal hardgrounds (Bo et al. 2012; Angeletti et al. 2014; Chimienti et al. 2020). As observed for numerous other deep marine animal taxa (Bianchi et al. 2012), various heterobranchs extending in the deepest ranges have a Boreo-Atlantic origin (e.g., *F. lineata*, *P. membranaceus*, *S. lignarius*, and the family Tritoniidae), hence are cold-affinity species. Interestingly, numerous species reaching high depths in the Mediterranean basin (e.g., *T. fimbria*, *P. quadripartita*, *P. meckeli*, *D. pseudoargus*, *F. lineata*) are also found in very shallow and cold waters (such as the north and the central Adriatic Sea or canyon areas subjected to upwelling currents), with a marked seasonality (Zenetos et al. 2016; Betti et al. 2017; Betti 2021).

The scenario obtained from the latitudinal analysis of the findings showed that the heterobranch fauna present along the Ligurian continental shelf is significantly different from the Tyrrhenian and Sicilian ones. This situation could be attributed to the distinctive northern distribution of some *Felimare* species and the paucity of *Facelina* sp., *P. ischitana* and Tritoniidae nd, more represented in the southern regions. Cattaneo-Vietti (1991) suggested that the narrow extension of the Ligurian continental shelf and the occurrence of a patchwork of habitats could be listed among the reasons explaining the high species richness of the deep soft-bottom heterobranch fauna in this region and the wider bathymetric ranges of the species. Overall, a marked decrease in biodiversity was observed from North to South, with a secondary high peak of species richness in the Sicily Channel. This latter is indeed an important boundary area, known for its complex geomorphologic and oceanographic

conditions, ultimately leading to a hotspot of biodiversity (Bianchi & Morri 2000; Evans et al. 2016; Altobelli et al. 2017).

The specific richness of the seamounts appears modest: this may be related to the relative paucity of dives carried out in the offshore locations and to the fact that surveys started at 60 m, excluding therefore the possibility to compare the 30–50 m depth range, which, in the coastal areas, hosted a distinctive heterobranch assemblage adapted to coralligenous environments with high biological coverage. Moreover, the investigated seamounts are generally dominated by soft-bottom habitats, limiting the observations of heterobranchs by ROV. The sightings are concentrated on the peaks, which, due to more turbulent conditions, are dominated by lush communities of filter-feeders (Bo et al. 2011, 2021), attracting the most commonly observed tritoniid species. Nevertheless, the low diversity and abundance can also be related to another factor. It is reasonable to think that these offshore structures, located between 23 and 70 nautical miles from the shore (Bo et al. 2021), are not significantly interested by the coastal larval flux. This process seems particularly effective for the investigated dorids, which shows a sort of costaphily (sensu Cornelius 1992). Such pattern would be related to a low dispersal ability, which, in some cases (e.g., *F. cf. villafranca*, *F. orsinii*, *C. laevis*) is supported by direct development (Thompson 1967; Ortea et al. 1996; Coelho & Calado 2010). The different larval dispersal abilities showed by heterobranchs (ranging from <10 km to 10,000 km) (Todd et al. 1998), alongside local hydrodynamic patterns, may affect the species composition of the assemblages, especially in offshore locations (Todd 1981; Fritts-Penniman et al. 2020).

The observed bathymetric and geographic distribution patterns of the heterobranch assemblages are the result of numerous biological and ecological factors, including the physiology of the species and their adaptation to depth, the habitat complexity, the presence of suitable substrates, the larval dispersal ability, but also depends on the availability of food sources. The widespread stenophagy of many heterobranch taxa (e.g., Nudibranchia, Sacoglossa) (McDonald & Nybakken 1997; Megina et al. 2002; Gemballa & Schermutzki 2004), in fact, has a crucial role in influencing their evolutionary processes (e.g., Jensen 1997; Goodheart et al. 2017) and the availability of the food sources may drive the composition and distribution of the assemblages (e.g., Betti et al. 2017; Canessa et al. 2021).

The strongest trophic relationship is found between the species belonging to the genus

*Felimare* and the keratose sponges they exclusively feed on (McDonald & Nybakken 1997), co-occurring down to 130 m and then completely disappearing. These species are particularly abundant in the Ligurian Sea, where keratose-dominated sponge grounds are widely documented at mesophotic depths (Enrichetti et al. 2020). A similar situation involves *P. atromaculata*, whose distribution mirrors that of its favourite food sources, the sponges *P. ficiformis* and *H. fulva* (Gemballa and Schermutzki, 2004), largely present in all the considered areas, but never below 150 m depth.

Another strong relationship occurs between *T. callogorgiae* and deep gorgonians. The species belonging to the family Tritoniidae are known to be specialised anthozoan-feeders (Schmekel & Portmann 1982; McDonald & Nybakken 1999) and have been worldwide reported as typical inhabitants of the deep sea (e.g., Valdés 2006; Valdés et al. 2017, 2018; Chimienti et al. 2020; Penney et al. 2020). The observed ability of *T. callogorgiae* to feed on different alcyonaceans could explain its success in the hardbottom Mediterranean coral communities, which are greatly diffused (Chimienti et al. 2018). The high reproductive potential of tritoniids (Vayssière 1901) may also concur in explaining the wide distribution of this species.

On the contrary, a weak relationship was detected between the hydrozoan-feeder cladobranchs and their food source, partially due to the limited possibility of identifying hydrozoan species exclusively through ROV images. Interestingly, however, the most stenophagous species, *F. affinis* and *P. ischitana*, known to feed exclusively on *Eudendrium* hydrozoans in shallow waters (Schmekel & Portmann 1982; Hirano & Thompson 1990; Furfaro & Mariottini 2016), seem to shift their feeding preferences on other hydrozoans when reaching the outer shelf or offshore seamounts, where *Eudendrium* spp. seem rarer. *Paraflabellina ischitana*, for example, has been observed on a wide range of other hydrozoans (e.g., Plumularioidea, Bougainvilliidae, Haleciidae) between 150 and 200 m. On the other hand, the complete lack of sightings of a very common shallow-water *Eudendrium*-eater, *Cratena peregrina* (Gmelin, 1791) (Di Camillo et al. 2012; Lombardo & Marletta 2020), suggests that not all species are able to adjust their diets. The depth-related food-shifting ability could also be shared by nudibranchs targeting other taxa. For example, *A. cristata*, known to eat various bryozoans (e.g., Bugulidae, Celleporidae) in shallow waters (Schmekel & Portmann 1982; Urgorri &

Besteiro 1984), was observed feeding on *Reteporella* spp. in deep coralligenous environments (50–85 m). The dorid *B. cinnabarina* is known to eat the sponge *T. muricata* (Bouchet, 1977; Cattaneo-Vietti 1991) in deep bathyal muds, necessarily turning to other sponge species in shallow and mesophotic waters (Ballesteros & Valdés 1999). Potentially, a similar situation could also exist for anthozoan-feeders such as tritoniids.

Both hydrozoans and bryozoans include small, fast-growing opportunistic species, which easily colonise the surface of seafloor macro-litter, such as lost fishing gear (Enrichetti et al. 2021). These objects may be locally abundant and indirectly act as poles of attraction for generalist consumers. It is the case of *Facelina* sp. and *P. ischitana* commonly observed crawling on lost nets and lines as well as skeletons of dead gorgonians. Their occurrence on the St. Lucia Seamount may reflect the high fishing impact of the site, including high densities of lost gear and mass mortalities of structuring species (Bo et al. 2014).

Ultimately, the stenophagy of many heterobranch species, representing one of the key factors of their evolutionary success in shallow waters, may represent a limit in their expansion towards the deeper ecosystems. This is also supported by the fact that most of the species known to dwell in the deepest depth ranges (> 300 m) (Table V), besides being adapted to soft-bottom habitats, are also distinctly euribathic and euryphagous (e.g., *Philine* spp., *S. lignarius*, *P. meckeli*, *T. fimbria*) (Thompson 1976; Schmekel & Portmann 1982; Cattaneo-Vietti et al. 1993).

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### Data availability

The authors confirm that the data supporting the findings of this study are available within the article.

### Disclosure statement

No potential conflict of interest was reported by the author(s).

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