

The bathyal benthopelagic fauna in the north-western Ionian Sea: structure, patterns and interactions

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The main knowledge acquired on the structure, patterns and interactions in the bathyal benthopelagic fauna in the north-western Ionian Sea is summarised in this article. Using faunal sampling along a depth range between 200 and 4000 m, a total of 41 cephalopods, 64 crustaceans and 183 fishes have been collected. Some are new findings for the study area and for many of the species the bathymetric distribution has been updated. Distinct faunal assemblages related to the upper slope (400–800 m), middle slope (800–1200 m) and lower slope (> 1200 m) were identified using Abundance Biomass Comparison curves. Species abundance decreases across the bathymetric gradient, whereas the biomass increases to ~1000 m and then decreases again. Beyond this bathymetry, species richness, evenness and diversity index decrease with depth. The distribution pattern 'bigger–deeper' was observed in some species and 'smaller–deeper' in others. Roccella canyon and the Santa Maria di Leuca coral bank were investigated in relation to the distribution of fauna, highlighting migration phenomena in the former and a refuge effect in the latter. The effects of hydrographic conditions and fishing were also examined for the deep-water commercial shrimps *Aristaeomorpha foliacea* and *Aristeus antennatus*.

Keywords: biodiversity; abundance; distribution; fish; crustaceans; cephalopods; sensitive habitat; north-western Ionian Sea

1. Introduction

More than 80% of the Mediterranean floor is deeper than 200 m (bathyal and abyssal zones), with a maximum depth of 5121 m in the eastern Ionian Sea (Matapan Deep) [1]. Because of the logistic/technical difficulties of exploration in the deep-sea environment, little information is available on the deep-water benthopelagic fauna [2,3]. In fact, although early explorations in the deep Mediterranean date back to the end of the 1800s [4], most of the known information on this fauna is limited to the depths from which biological resources are exploited, down to 800–1000 m [5–15]. Beyond these depths, some studies on the biodiversity and assemblages of

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benthopelagic species, represented by cephalopods, crustaceans and fish have been carried out both in the western Mediterranean [6,16–27] and in the eastern part [10,25,26,28–34].

From all these studies, depth was found to be the main factor in structuring assemblages. Considering the stability of the environmental parameters in the deep water of the Mediterranean Sea, the faunal zonation was attributed to the trophic resources available above and below depth boundaries, as well as to the particular stratified hydrological conditions [20,22–26,35]. However, changes in the faunal assemblages and communities also occur over the geographic gradient from the western to eastern Mediterranean. For example, differences in the deep-water ichthyofauna composition and abundance between the eastern and western Mediterranean seem to be due to the different trophic and hydrographic conditions, as well as to anthropogenic impacts, mainly in terms of deep-water fishing, on the two sides of the basin [36].

Usually, the deep Mediterranean biological communities are adapted to general oligotrophic conditions, with a local occurrence of higher productivity and biodiversity hotspots, the latter mainly due to submarine canyons, seamounts and cold-water coral mounds. These communities are very sensitive to human modifications, such as fishing, mostly because of the k-selective character of many constituting species [3,36].

However, considering the wide area covered by the bathyal and abyssal Mediterranean bottoms and the various limitations in sampling deep-water fauna [37], knowledge on the structure and distribution patterns of such fauna, as well as knowledge of interactions with habitats and human activities remains rather poor. Furthermore, considering the expansion of deep-sea fisheries in relation to overexploitation in shelf waters, and the evidence of large-scale human-induced environmental changes in the Mediterranean [38,39] even in deep waters, with effects both on meiofaunal biodiversity [40,41] and megafaunal fluctuations [42,43], the information available on the deep-water species assemblages and diversity can be considered a reference state providing information against which to evaluate changes.

The Ionian is the largest in terms of volume and the deepest sea in the Mediterranean. Biological resources in the Ionian Sea have long been exploited and, between the 1980s and 1990s, the sea experienced a major transition in the water mass structure and properties even at the greatest depths [44,45]. This basin shows a complex geomorphology mainly along the Calabrian–Sicily coasts, which are furrowed by active canyons transporting materials from the shelf break to the bathyal depth. Several slump deposits, which may also extend for many kilometres, have accumulated at the base of the continental slope by gravitational sliding [46]. The central sector of the Ionian Sea is represented by the Taranto Valley, an impressive NW–SE depression, easily recognisable down to depths exceeding 2200 m. The eastern sector is located between the Taranto Valley and Apulia. It is represented by a continental shelf with abrasion terraces and bioclastic calcareous deposits with several coral rocks. Along the Apulia coasts the distribution of living cold water corals has only been documented in the last decade [47,48], thanks to the increasing use of acoustic survey techniques and remotely operated vehicles (ROV). Clustered and isolated mound-like features, tens to a few hundreds of metres in length and no more than 25 m high, are located between 400 and 1000 m in depth within a broad area affected by down slope mass transport deposits. Isolated and patchy distributed colonies of *Lophelia pertusa* and *Madrepora oculata* are widespread on these mounds facing the main bottom current flow mainly coming from the Adriatic Sea.

Recent explorations in the bathyal environment of the Ionian Sea have been conducted within the framework of different projects, aiming to study the bathyal benthopelagic fauna less than 800 m in depth, where fishing activity occurs, and below that depth, where the grounds could be considered ‘virgin’, owing to the absence of fishing activity. These projects have increased knowledge on the deep-water fauna, in terms of structure, distribution patterns and interactions with habitat and human activities. A synthesis of the most important results, integrated with further analyses, is reported in this article.

2. Materials and methods

Data were collected during experimental bottom trawl surveys carried out in the north-western Ionian Sea (Figure 1) as part of a number of study projects financed by the Italian Government and the EU: GRUND [49], RED SHRIMPS [50], MEDITS [51], DESEAS [3], APLABES [52] and GAVIS [53] (Table 1).

The sampling design adopted in each survey was random-stratified. The horizontal and vertical opening of all types of trawl nets was measured using the SCANMAR acoustic system [54,55]. All specimens taken in each haul were identified. For each individual, the following data were taken: length, according to species, to the nearest mm and body weight to the nearest 0.1 g.

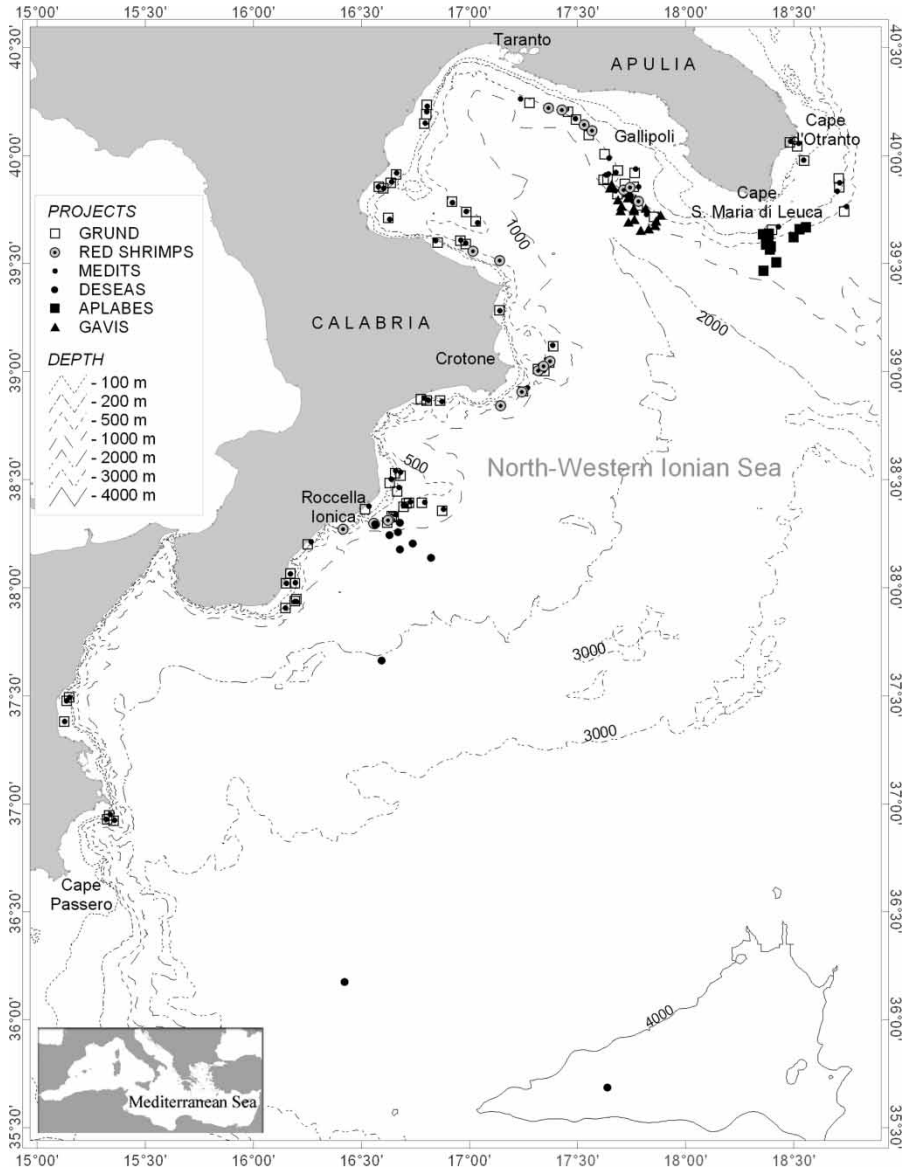


Figure 1. Map of the study area in the north-western Ionian Sea.

Table 1. Study projects carried out in the north-western Ionian Sea with an indication of geographic area, study period, depth range, gear and mesh size.

Projects	Geographic area	Study period	Depth range (m)	Gear	Stretched mesh (in the codend; mm)
GRUND	Cape Otranto (Apulia) to Cape Passero (Sicily)	1985–2008	10–800	Commercial trawl net	40
RED SHRIMPS	Cape Otranto (Apulia) to Roccella Ionica (Calabria)	1993–1995	250–750	Commercial trawl net	40
MEDITS	Cape Otranto (Apulia) to Cape Passero (Sicily)	1994–2008	10–800	Experimental trawl net	20
DESEAS	Balearic, western Ionian, eastern Ionian Sea	June 2001	600–4000	Otter trawl Maireta net	20
APLABES	Gallipoli, S. Maria di Leuca coral area	September–October 2005	300–800	Commercial trawl net	40
GAVIS	Gallipoli	April, May, June, September 2006	400–1200	Otter trawl Maireta net	20

Abundance data were standardised to km^2 for subsequent numerical processing. In particular, the density ($\text{N}\cdot\text{km}^{-2}$) and biomass ($\text{kg}\cdot\text{km}^{-2}$) indices were computed using the number and weight of the individuals for each haul swept area carried out across the whole bathymetric gradient investigated during DESEAS and GAVIS. The swept area was estimated according to the wing spread of the net (horizontal opening), the speed of the vessel and the haul duration [56].

The structure of faunal assemblages across the bathymetric gradient of 400–4000 m was analysed using Abundance Biomass Comparison (ABC) curves [57,58]. ABC curves were computed considering standardised data of numerical abundance and biomass of fish, crustaceans and cephalopods with respect to three depth ranges, according to the faunal assemblages detected in the upper slope (400–800 m), middle slope (800–1200 m) and lower slope (>1200 m) throughout the Mediterranean [23,24,26].

Univariate ecological indices (Margaleff richness d , Shannon–Wiener diversity index H' , Pielou's evenness J) [59] were also computed across the whole bathymetric gradient investigated during the DESEAS and GAVIS surveys and their changes with depth were evaluated using regression analysis.

All surveys carried out in the north-western Ionian Sea gave the opportunity to record new species for the area and to update the depth range for some others. Depth-size trends for 10 species were also determined by means of regression analysis between the geometric mean of each sample versus depth.

For the two deep-water shrimps, *Aristaeomorpha foliacea* and *Aristeus antennatus*, abundance indices ($\text{N}\cdot\text{km}^{-2}$ and $\text{kg}\cdot\text{km}^{-2}$) were estimated for the period 1995–2005 using data from the GRUND and MEDITS surveys. The temporal trends observed for these indices were correlated (Spearman's rank correlation) with the trend in temperature and salinity detected in the studied area over the same period [60]. In addition, the length/frequency distributions of these two shrimps were calculated from 2001 to 2005 to highlight the fishing effect on these exploited populations.

In the Ionian basin there are two typically bathyal habitats, namely canyons, along the Calabrian coasts, and the Santa Maria di Leuca coral bank. In the first, the shallowest depth findings of *A. antennatus* and *A. foliacea* (144 m) were recorded during hauls carried out only during the night at the head of the Roccella Ionica canyon [61]. Tagging experiments were carried out on *A. antennatus* collected in this habitat [62,63]. These were the first experiments in the Mediterranean Sea on the bathyal fauna and were conducted on May 1998. About the second habitat, abundance in number and weight of the bathyal fauna collected inside and outside the coral bank was estimated. The size structures were computed for the most abundant species which displayed the greatest dissimilarity in abundance between the two study areas [64]. Further differences

between the coral versus non-coral areas are supported in this article using a box-plot of the sizes in some fish species collected inside and outside the S. Maria di Leuca coral habitat.

3. Results

3.1. Structure

Considering depths >200 m, a total of 41 cephalopods, 64 crustaceans and 183 fishes (26 chondrichthyes and 157 teleosts) were collected in the north-western Ionian Sea as part of the above-mentioned studies (Table 2).

ABC plots of this fauna showed a higher curve for abundance than for biomass in the upper slope (400–800 m), a higher curve for biomass than abundance in the middle slope (800–1200 m) and the intersection of the two curves for the species collected in the lower slope (>1200 m) (Figure 2).

Considering the density, the greater number of hauls carried out during GAVIS provided a decreasing trend with depth within the bathymetric gradient of 400–1200 m, whereas the smaller number of hauls conducted during DESEAS showed an increase within 1500 m and then a marked reduction at the greatest depths. For the biomass, both studies showed an increase as far as the middle slope. A marked decrease in the lower slope was shown during the DESEAS project (Figure 3).

With regard to the univariate ecological indices in the depth range of 400–1200 m, the richness index (d) and evenness index (J) decreased and increased significantly with depth, respectively, although the Shannon–Wiener index (H') did not show any trend. Considering depths between 400 and 4000 m, all these indices decreased significantly with depth although the patterns observed within 1200 m were confirmed, that is the decrease in d , the increase in J and the constancy of H' (Figure 4).

3.2. Patterns

The new findings and depth records of the crustaceans and fishes collected in the north-western Ionian Sea are reported in Figure 5. With regard to crustaceans, *Chaceon mediterraneus* and *Nematocarcinus exilis* represent new findings for the study area [25]. For the two most important commercial deep-water shrimps in the Mediterranean, the new maximum depth of finding was 1145 m for *Aristaeomorpha foliacea* and 3300 m for *Aristeus antennatus* [65]. In addition, concerning fishes, *Cataetyx laticeps*, *Coelorinchus mediterraneus*, *Coryphaenoides guentheri*, *Coryphaenoides mediterraneus* and *Lepidion lepidion* represent new findings in the study area [33].

Regarding the depth-size trends, *A. antennatus* and *Polycheles typhlops* exhibited a smaller–deeper trend, whereas a bigger–deeper distribution pattern was shown in *Nephrops norvegicus*, *Plesionika martia*, *Galeus melastomus*, *Mora moro*, *Nezumia sclerorhynchus*, *Phycis blennoides* and *Trachyrincus scabrus*. For *Bathypterois mediterraneus* no significant trend was shown in the broader depth range of 800–3300 m (Figure 6).

3.3. Interactions

The two bathyal shrimps, *A. antennatus* and *A. foliacea*, represent the most important deep-water fisheries resources in the north-western Ionian Sea. The former is generally more abundant than the latter. However, during the period 2000–2004 *A. foliacea* was found to be more abundant than

Table 2. Cephalopods, crustaceans, chondroichthyes and teleosts caught in the north-western Ionian Sea at depths below 200 m.

Cephalopods

Abralia verany (Rüppell, 1844)
Abraliopsis pfefferi Joubin, 1896
Alloteuthis media (Linnaeus, 1758)
Alloteuthis subulata (Lamarck, 1798)
Ancistrocheirus lesueurii (D'Orbigny, 1842)
Ancistroteuthis lichtensteini (Férussac, 1835)
Argonauta argo Linnaeus, 1758
Brachioteuthis nisei (Steenstrup, 1882)
Chiroteuthis veranii (Férussac, 1835)
Ctenopteryx sicula (Verany, 1851)
Eledone cirrhosa (Lamarck, 1798)
Eledone moschata (Lamarck, 1798)
Galiteuthis armata Joubin, 1898
Heteroteuthis dispar (Rüppell, 1844)
Histioteuthis bonnellii (Férussac, 1835)
Histioteuthis reversa (Verrill, 1880)
Illex coindetii (Verany, 1839)
Loligo forbesii Steenstrup, 1856
Loligo vulgaris Lamarck, 1798
Neorossia caroli (Joubin, 1902)
Octopoteuthis sicula Rüppell, 1844
Octopus defilippi Verany, 1851
Octopus macropus Risso, 1826
Octopus salutii Verany, 1839
Octopus vulgaris Cuvier, 1797
Onychoteuthis banksii (Leach, 1817)
Pteroctopus tetracirrus (Celle Chiaje, 1830)
Pyroteuthis margaritifera (Rüppell, 1844)
Rondeletiola minor (Naef, 1912)
Rossia macrosoma (Celle Chiaje, 1830)
Scaevurgus unicirrhus (Celle Chiaje, 1841)
Sepia elegans Blainville, 1827
Sepia officinalis Linnaeus, 1758
Sepia orbignyana Férussac, 1826
Sepietta oweniana (D'Orbigny, 1841)
Sepiola intermedia Naef, 1912
Sepiola ligulata Naef, 1912
Sepiola robusta Naef, 1912
Sepiola rondeletii Leach, 1817
Todarodes sagittatus (Lamarck, 1798)
Todaropsis eblanae (Ball, 1841)

Crustaceans

Acanthephyra eximia S.I. Smith, 1884
Acanthephyra pelagica (Risso, 1816)
Aegeon lacazei (Gourret, 1887)
Alpheus glaber (Olivier, 1792)
Aristaeomorpha foliacea (Risso, 1827)
Aristeus antennatus (Risso, 1816)
Ateleocyclus rotundatus (Olivier, 1792)
Bathynectes maravigna (Prestandrea, 1839)
Calappa granulata (Linnaeus, 1758)
Calappa rissoana Pastore, 1995
Calappa tuerkayana Pastore, 1995
Chaceon mediterraneus Manning & Holthuis, 1989
Chlorotocus crassicornis (A. Costa, 1871)
Ebalia nux A. Milne-Edwards, 1883
Gennadas elegans S.I. Smith, 1882
Geryon longipes A. Milne-Edwards, 1882
Goneplax rhomboides (Linnaeus, 1758)

Homola barbata (J.C. Fabricius, 1793)
Inachus communissimus Rizza, 1839
Inachus dorsettensis (Pennant, 1777)
Latreillia elegans Roux, 1830
Ligur ensiterus (Risso, 1816)
Liocarcinus depurator (Linnaeus, 1758)
Lophogaster typicus M. Sars, 1857
Macropipus tuberculatus (Roux, 1830)
Macropodia longipes (A. Milne-Edwards & Bouvier, 1899)
Macropodia rostrata (Linnaeus, 1761)
Medorippe lanata (Linnaeus, 1767)
Monodaeus couchii (Couch, 1851)
Mumida curvimana A. Milne-Edwards & Bouvier, 1894
Mumida intermedia A. Milne-Edwards & Bouvier, 1899
Mumida rullanti Zariquiey Alvarez, 1952
Mumida tenuimana G.O. Sars, 1872
Nematocarcinus exilis Bate, 1888
Nephrops norvegicus (Linnaeus, 1758)
Parapenaeus longirostris (Lucas, 1846)
Paromola cuvieri (Risso, 1816)
Parthenope macrochelos (Herbst, 1790)
Pasiphaea multidentata Esmark, 1866
Pasiphaea sivado (Risso, 1816)
Penaeus kerathurus (Forsskal, 1775)
Periclimenes granulatus Holthuis, 1950
Philocheirus echinulatus (M. Sars, 1861)
Plesionika acanthonotus (S.I. Smith, 1882)
Plesionika antigai Zariquiey Alvarez, 1955
Plesionika edwardsii (Brandt, 1851)
Plesionika giglioli (Senna, 1903)
Plesionika heterocarpus (A. Costa, 1871)
Plesionika martia (A. Milne Edwards, 1883)
Plesionika narval (J.C. Fabricius, 1787)
Polycheles typhlops Heller, 1862
Pontophilus spinosus (Leach, 1815)
Pontophyllus norvegicus (M. Sars, 1861)
Processa canaliculata Leach, 1815
Pseudosquilla cerisii (Roux, 1828)
Rissoides desmaresti (Risso, 1816)
Rissoides pallidus (Giesbrecht, 1910)
Rochinia rissoana (Roux, 1828)
Scyllarus pygmaeus (Bate, 1888)
Sergestes arachnidopus (Cocco, 1832)
Sergestes arcticus Krayer, 1855
Sergia robusta (S.I. Smith, 1882)
Solenocera membranacea (Risso, 1816)
Squilla mantis (Linnaeus, 1758)

Chondroichthyes

Centrophorus granulosus (Bloch & Schneider, 1801)
Centrophorus uyato (Rafinesque, 1810)
Chimaera monstrosa Linnaeus, 1758
Dalatia licha (Bonnaterre, 1788)
Dipturus batis (Linnaeus, 1758)
Dipturus oxyrinchus (Linnaeus, 1758)
Etmopterus spinax (Linnaeus, 1758)
Galeus melastomus Rafinesque, 1810
Gymnura altavela (Linnaeus, 1758)
Heptanchias perlo (Bonnaterre, 1788)
Hexanchus griseus (Bonnaterre, 1788)
Leucoraja circularis (Couch, 1838)

(Continued)

Table 2. Continued.

<i>Leucoraja fullonica</i> (Linnaeus, 1758)	<i>Cubiceps gracilis</i> (Lowe, 1843)
<i>Mustelus mustelus</i> (Linnaeus, 1758)	<i>Dalophis imberbis</i> (Celaroché, 1809)
<i>Oxynotus centrina</i> (Linnaeus, 1758)	<i>Deltentosteus quadrimaculatus</i> (Valenciennes, 1837)
<i>Raja asterias</i> Delaroché, 1809	<i>Dentex dentex</i> (Linnaeus, 1758)
<i>Raja clavata</i> Linnaeus, 1758	<i>Diaphus metopoclampus</i> (Cocco, 1829)
<i>Raja miraletus</i> Linnaeus, 1758	<i>Diaphus holti</i> Täning, 1918
<i>Raja montagui</i> Fowler, 1910	<i>Diaphus rafinesquei</i> (Cocco, 1838)
<i>Rostroraja alba</i> (Lacépède, 1803)	<i>Dysomma brevirostre</i> (Facciola, 1887)
<i>Scyliorhinus canicula</i> (Linnaeus, 1758)	<i>Echelus myrus</i> (Linnaeus, 1758)
<i>Somniosus rostratus</i> (Risso, 1827)	<i>Echiodon dentatus</i> (Cuvier, 1829)
<i>Squalus blainvillei</i> (Risso, 1826)	<i>Elates ransonnetii</i> (Steindachner, 1876)
<i>Torpedo marmorata</i> Risso, 1758	<i>Electrona risso</i> (Cocco, 1829)
<i>Torpedo nobiliana</i> Bonaparte, 1835	<i>Engraulis encrasicolus</i> (Linnaeus, 1758)
<i>Torpedo torpedo</i> (Linnaeus, 1758)	<i>Epigonus constanciae</i> (Giglioli, 1880)
<i>Epigonus telescopus</i> (Risso, 1810)	<i>Epigonus denticulatus</i> Deuzeide, 1950
<i>Acantholabrus palloni</i> (Risso, 1810)	<i>Eutrigla gurnardus</i> (Linnaeus, 1758)
<i>Argentina sphyraena</i> Linnaeus, 1758	<i>Evermannella balbo</i> (Risso, 1820)
<i>Argyropelecus hemigymnus</i> Cocco, 1829	<i>Gadella maraldi</i> (Risso, 1810)
<i>Ariosoma balearicum</i> (Celaroché, 1809)	<i>Gadiculus argenteus</i> Guichenot, 1850
<i>Arnoglossus laterna</i> (Walbaum, 1792)	<i>Gaidropsarus biscayensis</i> (Collett, 1890)
<i>Arnoglossus rueppelli</i> (Cocco, 1844)	<i>Gaidropsarus mediterraneus</i> (Linnaeus, 1758)
<i>Arnoglossus thori</i> Kyle, 1913	<i>Glossanodon leioglossus</i> (Valenciennes, 1848)
<i>Aspitrigla cuculus</i> (Linnaeus, 1758)	<i>Gnathophis mystax</i> (Celaroché, 1809)
<i>Aulopus filamentosus</i> (Bloch, 1792)	<i>Gobius niger</i> Linnaeus, 1758
<i>Auxis rochei rochei</i> (Risso, 1810)	<i>Gonichthys cocco</i> (Cocco, 1829)
<i>Bathophilus nigerrimus</i> Giglioli, 1884	<i>Gonostoma denudatum</i> Rafinesque, 1810
<i>Bathypterois mediterraneus</i> Bauchot, 1962	<i>Grammonus ater</i> (Risso, 1810)
<i>Benthocometes robustus</i> (Goode & Bean, 1886)	<i>Helicolenus dactylopterus dactylopterus</i> (Delaroché, 1809)
<i>Benthoosema glaciale</i> (Reinhardt, 1837)	<i>Hoplostethus mediterraneus mediterraneus</i> Cuvier, 1829
<i>Blennius ocellaris</i> Linnaeus, 1758	<i>Hygophum benoiti</i> (Cocco, 1838)
<i>Boops boops</i> (Linnaeus, 1758)	<i>Hygophum hygomii</i> (Lütken, 1892)
<i>Bothus podas</i> (Celaroché, 1809)	<i>Hymenocephalus italicus</i> Giglioli, 1884
<i>Buglossidium luteum</i> (Risso, 1810)	<i>Ichthyococcus ovatus</i> Cocco, 1838
<i>Callanthias ruber</i> (Rafinesque, 1810)	<i>Lampanyctus crocodilus</i> (Risso, 1810)
<i>Callionymus maculatus</i> Rafinesque, 1810	<i>Lepidion lepidion</i> (Risso, 1810)
<i>Callionymus risso</i> Le Sueur, 1814	<i>Lepidopus caudatus</i> (Euphrasen, 1788)
<i>Capros aper</i> (Linnaeus, 1758)	<i>Lepidorhombus boscii</i> (Risso, 1810)
<i>Caranx rhonchus</i> Geoffroy Saint-Hilaire, 1817	<i>Lepidorhombus whiffiagonis</i> (Walbaum, 1792)
<i>Carapus acus</i> (Brünnich, 1768)	<i>Lepidotrigla cavillone</i> (Lacépède, 1801)
	<i>Lesueurigobius friesii</i> (Malm, 1874)
	<i>Lesueurigobius suerii</i> (Risso, 1810)
Teleosts	<i>Lobianchia doffeini</i> (Zugmayer, 1911)
<i>Cataxyx laticeps</i> Koefoed, 1927	<i>Lobianchia gemellarii</i> (Cocco, 1838)
<i>Centracanthus cirrus</i> Rafinesque, 1810	<i>Lophius budegassa</i> Spinola, 1807
<i>Centrolophus niger</i> (Gmelin, 1789)	<i>Lophius piscatorius</i> Linnaeus, 1758
<i>Cepola macrophthalmia</i> Linnaeus, 1758	<i>Macroramphosus scolopax</i> (Linnaeus, 1758)
<i>Ceratospinelus maderensis</i> (Lowe, 1839)	<i>Maurolicus muelleri</i> (Gmelin, 1789)
<i>Chauliodus sloani</i> Schneider, 1801	<i>Merlangius merlangus</i> (Linnaeus, 1758)
<i>Chelidonichthys lastoviza</i> (Bonnaterre, 1788)	<i>Merluccius merluccius</i> (Linnaeus, 1758)
<i>Chelidonichthys lucerna</i> (Linnaeus, 1758)	<i>Micromesistius poutassou</i> (Risso, 1826)
<i>Chelidonichthys obscurus</i> (Bloch & Schneider, 1801)	<i>Molva dipterygia</i> (Pennant, 1784)
<i>Chlopsis bicolor</i> Rafinesque, 1810	<i>Monochirus hispidus</i> Rafinesque, 1814
<i>Chlorophthalmus agassizii</i> Bonaparte, 1840	<i>Mora moro</i> (Risso, 1810)
<i>Cichlasoma bimaculatum</i> (Linnaeus, 1758)	<i>Mullus barbatus barbatus</i> Linnaeus, 1758
<i>Ciclothone braueri</i> Jespersen & Täning, 1926	<i>Mullus surmuletus</i> Linnaeus, 1758
<i>Citharus linguatula</i> (Linnaeus, 1758)	<i>Myctophum punctatum</i> Rafinesque, 1810
<i>Coelorinchus caelorrhynchus</i> (Risso, 1810)	<i>Nansenia oblita</i> (Facciola, 1887)
<i>Coelorinchus mediterraneus</i> Iwamoto & Ungaro, 2002	<i>Nemichthys scolopaceus</i> Richardson, 1848
<i>Conger conger</i> (Linnaeus, 1758)	<i>Nettastoma melanurum</i> Rafinesque, 1810
<i>Coryphaena hippurus</i> Linnaeus, 1758	<i>Nezumia sclerorhynchus</i> (Valenciennes, 1838)
<i>Coryphaenoides guentheri</i> (Vaillant, 1888)	<i>Notacanthus bonaparte</i> Risso, 1840
<i>Coryphaenoides mediterraneus</i> (Giglioli, 1893)	

(Continued)

Table 2. Continued.

<i>Notoscopelus elongatus</i> (Costa, 1844)	<i>Sphoeroides pachygaster</i> (Müller & Troschel, 1848)
<i>Ophichthus rufus</i> (Rafinesque, 1810)	<i>Sphyraena phyaena</i> (Linnaeus, 1758)
<i>Ophidion barbatum</i> Linnaeus, 1758	<i>Spicara maena</i> (Linnaeus, 1758)
<i>Ophidion rochei</i> Müller, 1845	<i>Spicara smaris</i> (Linnaeus, 1758)
<i>Ophisurus serpens</i> (Linnaeus, 1758)	<i>Sprattus sprattus sprattus</i> (Linnaeus, 1758)
<i>Pagellus acarne</i> (Risso, 1826)	<i>Stomias boa boa</i> (Risso, 1810)
<i>Pagellus bogaraveo</i> (Brünnich, 1768)	<i>Sudis hyalina</i> Rafinesque, 1810
<i>Pagellus erythrinus</i> (Linnaeus, 1758)	<i>Symbolophorus veranyi</i> (Moreau, 1888)
<i>Paralepis speciosa</i> Bellotti, 1878	<i>Symphurus ligulatus</i> (Cocco, 1844)
<i>Peristedion cataphractum</i> (Linnaeus, 1758)	<i>Symphurus nigrescens</i> Rafinesque, 1810
<i>Phycis blennoides</i> (Brünnich, 1768)	<i>Synchiropus phaeton</i> Günther, 1861
<i>Phycis phycis</i> (Linnaeus, 1766)	<i>Syngnathus typhle</i> Linnaeus, 1758
<i>Polyprion americanum</i> (Bloch & Schneider, 1801)	<i>Synodus saurus</i> (Linnaeus, 1758)
<i>Sardina pilchardus</i> (Walbaum, 1792)	<i>Tetragonurus cuvieri</i> (Risso, 1810)
<i>Schedophilus ovalis</i> (Cuvier, 1833)	<i>Trachinus draco</i> Linnaeus, 1758
<i>Scomber japonicus</i> Houttuyn, 1782	<i>Trachinus radiatus</i> Cuvier, 1829
<i>Scomber scombrus</i> Linnaeus, 1758	<i>Trachurus mediterraneus</i> (Steindachner, 1868)
<i>Scorpaena elongata</i> Cadenat, 1943	<i>Trachurus picturatus</i> (T.E. Bowdich, 1825)
<i>Scorpaena notata</i> Rafinesque, 1810	<i>Trachurus trachurus</i> (Linnaeus, 1758)
<i>Scorpaena porcus</i> Linnaeus, 1758	<i>Trachyrincus scabrus</i> (Rafinesque, 1810)
<i>Scorpaena scrofa</i> Linnaeus, 1758	<i>Trigla lyra</i> Linnaeus, 1758
<i>Seriola dumerili</i> (Risso, 1810)	<i>Trisopterus minutus</i> (Linnaeus, 1758)
<i>Serranus cabrilla</i> (Linnaeus, 1758)	<i>Uranoscopus scaber</i> Linnaeus, 1758
<i>Serranus hepatus</i> (Linnaeus, 1758)	<i>Vinciguerria attenuata</i> (Cocco, 1838)
<i>Solea solea</i> (Linnaeus, 1758)	<i>Zeus faber</i> Linnaeus, 1758

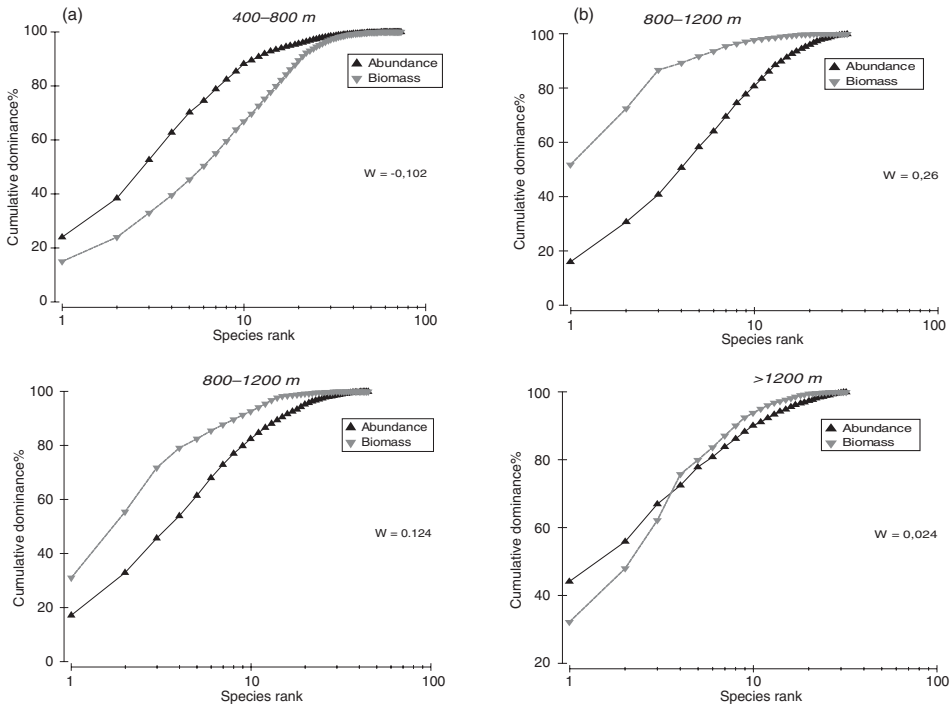


Figure 2. Abundance-Biomass Comparison (ABC) plots for benthopelagic species (fishes, crustaceans and cephalopods) collected from upper to lower slope in the north-western Ionian Sea during DESEAS (a) and GAVIS (b) projects.

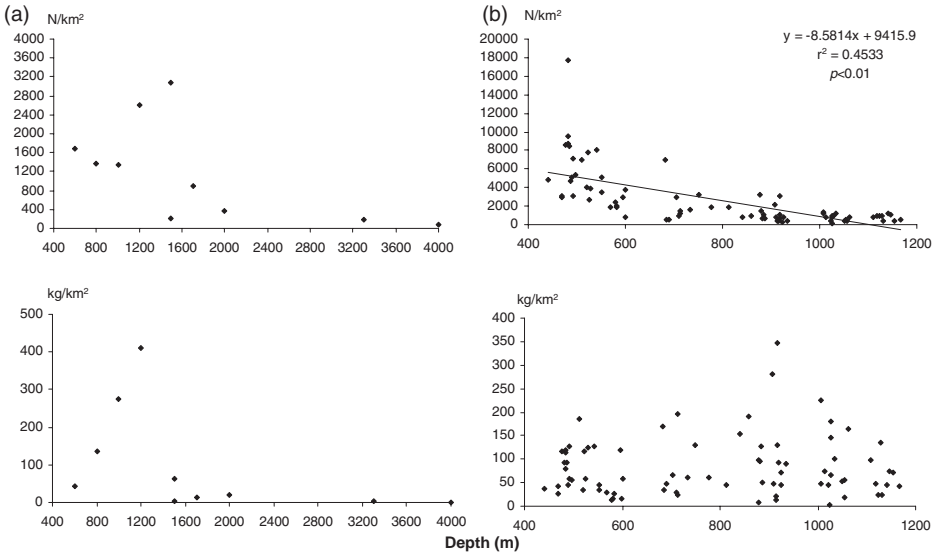


Figure 3. Relationship between density ($N \cdot km^{-2}$), biomass ($kg \cdot km^{-2}$) and depth for the benthopelagic species collected in the north-western Ionian Sea during (a) DESEAS (fish species) and (b) GAVIS (fishes, crustaceans and cephalopods) projects.

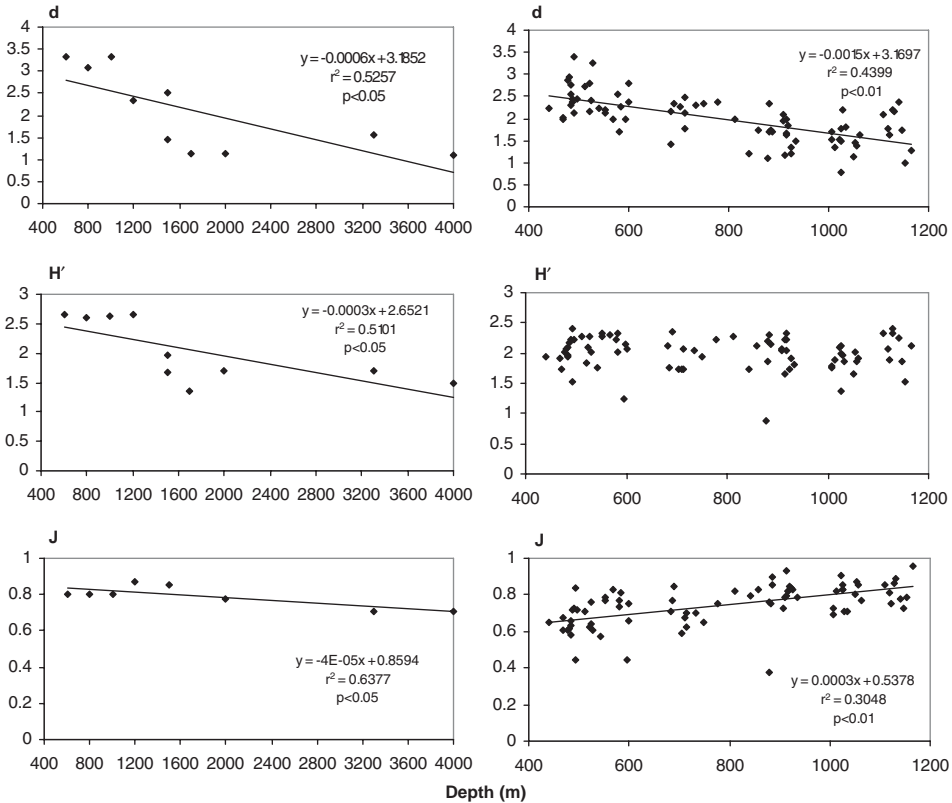


Figure 4. Relationship between species richness (d), diversity (H'), evenness (J') and depth of benthopelagic species collected in the north-western Ionian Sea during (left) DESEAS (fish species) and (right) GAVIS (fishes, crustaceans and cephalopods) projects.

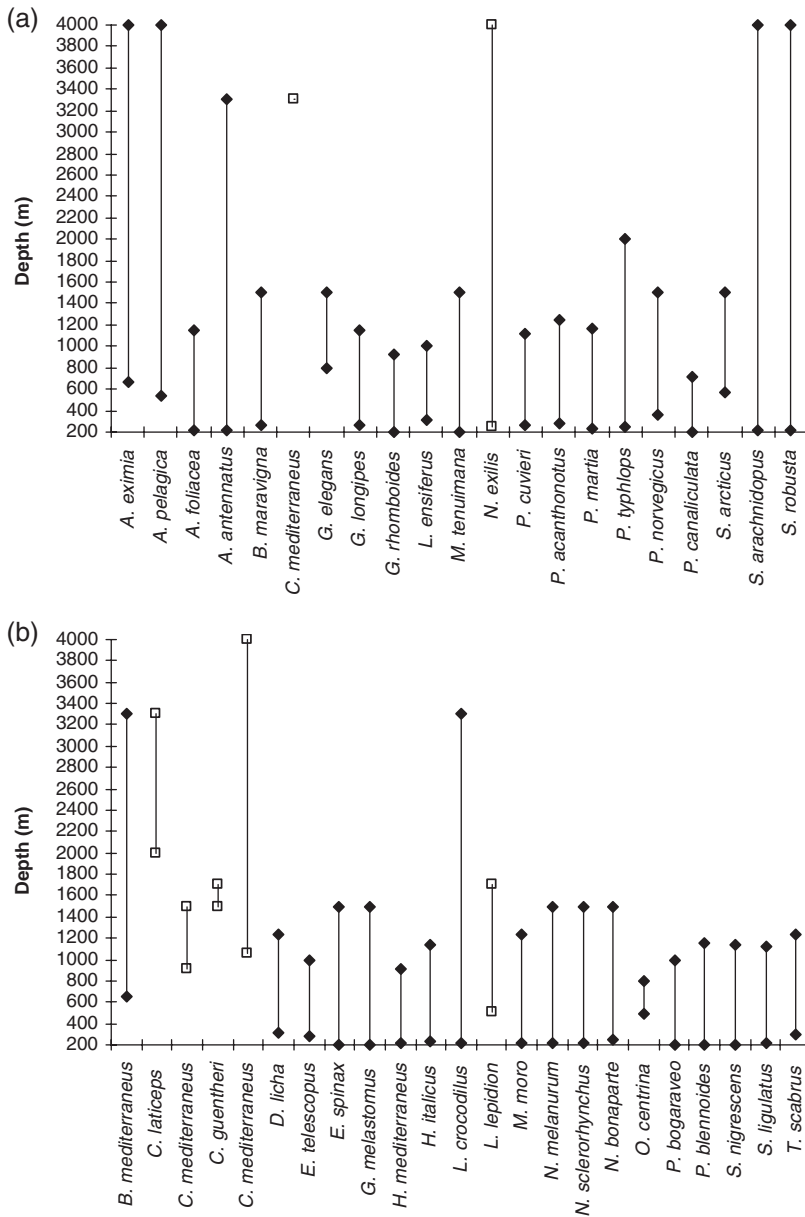


Figure 5. Depth records with indication of new findings (□) of some deep-water crustaceans (a) and fishes (b) collected in the north-western Ionian Sea.

A. antennatus [42]. In particular, although highly variable abundance indices were shown in both shrimps in terms of density and biomass (Figure 7), a significant increase was only detected in *A. foliacea* ($R = 0.521$, $p < 0.05$ for density; $R = 0.606$, $p < 0.01$ for biomass), whereas the abundance changes observed for *A. antennatus* did not show any significant trend. The increase in both biomass and density of *A. foliacea* correlated significantly with the increase in temperature and salinity detected from 1995 to 2005 between 200 and 800 m in the studied area (biomass–salinity: $R = 0.587$, $p < 0.05$; biomass–temperature: $R = 0.627$, $p < 0.01$; density–salinity: $R = 0.503$, $p < 0.05$; density–temperature: $R = 0.558$, $p < 0.05$).

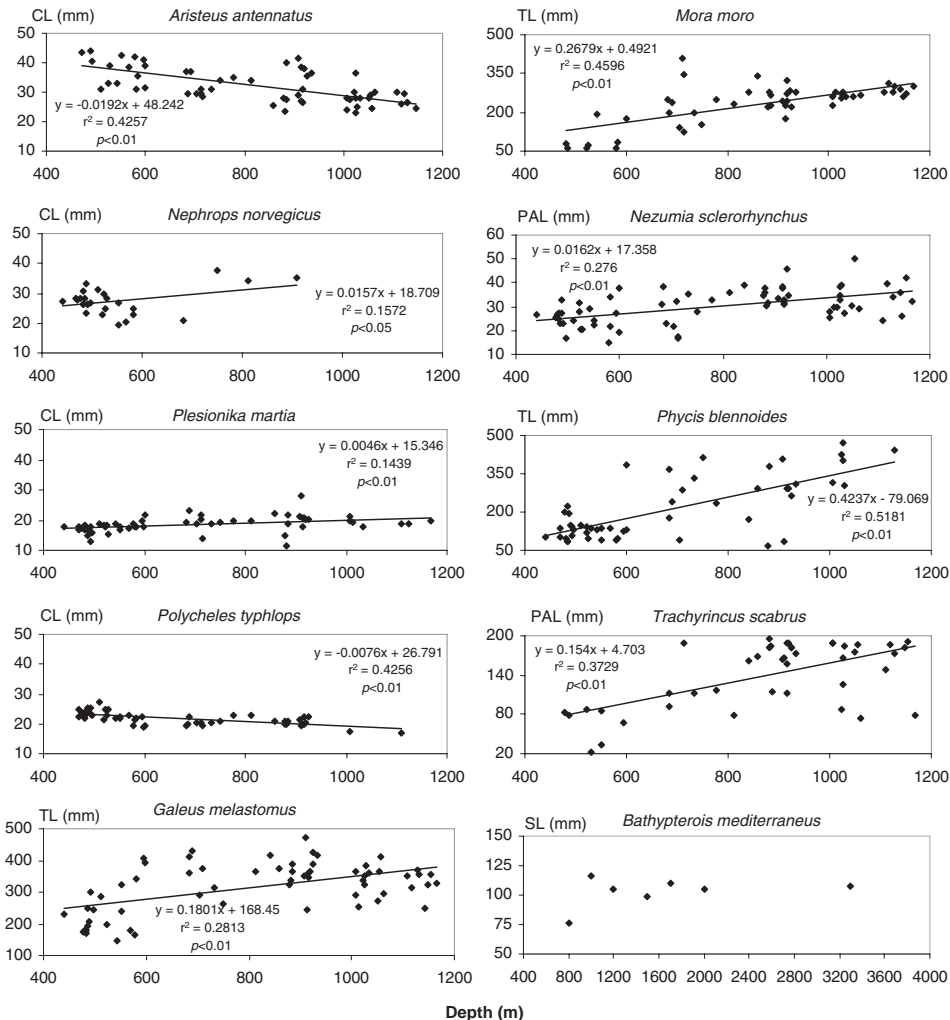


Figure 6. Relationship between size and depth in some deep-water benthopelagic species captured in the north-western Ionian Sea.

The length/frequency distributions of *A. foliacea* and *A. antennatus* also showed a different pattern (Figure 8). In fact, the sampled population mainly consisted of medium–small individuals in *A. foliacea*, whereas all the sizes were well represented in all investigated periods in *A. antennatus* length/frequency distributions.

During tagging experiments carried out in the Roccella Jonica canyon, some individuals of *A. antennatus* were caught at a depth of 198 m and after tagging were released. One month after tagging, one specimen was recaptured at a depth of 506 m. During this month, the tagged specimen covered at least 10 nautical miles, moving north-east and to greater depths. This first recapture gives interesting indications about the displacement of the shrimp both in vertical and horizontal space as well as on its growth rate [62,63].

Concerning the Santa Maria di Leuca coral habitat, density and biomass indices of the benthopelagic fauna showed greater values inside the coral habitat than outside (Figure 9) [64]. The sizes of the species analysed showed of larger individuals inside the coral habitat than outside (Figure 10).

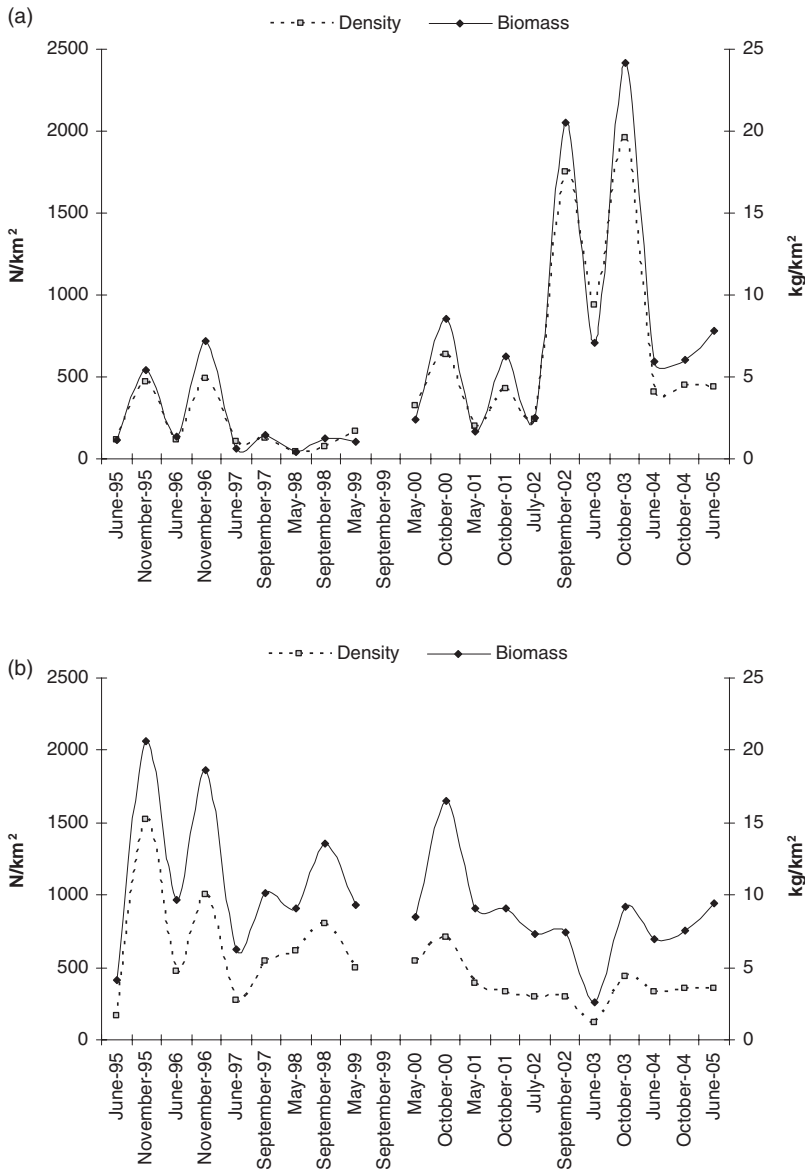


Figure 7. Fluctuations in the density (N·km⁻²) and biomass (kg·km⁻²) indices computed for *Aristaemorpha foliacea* (a) and *Aristeus antennatus* (b) from 1995 to 2005 in the north-western Ionian Sea.

4. Discussion and conclusions

As observed in the North Atlantic [66,67] and in various areas of the Mediterranean Sea [8,23,24], including the Ionian Sea [12,15,26], depth is the main factor influencing the structure of the deep-water demersal assemblages.

The results reported in this study also demonstrate a tight link between the structure of benthopelagic fauna and depth. In fact, abundance and species richness decline with depth, as observed worldwide irrespective of the depth range examined [19,24,25,68,73,77]. Evenness increases making the diversity rather stable within ~1200 m although both evenness and diversity decline with

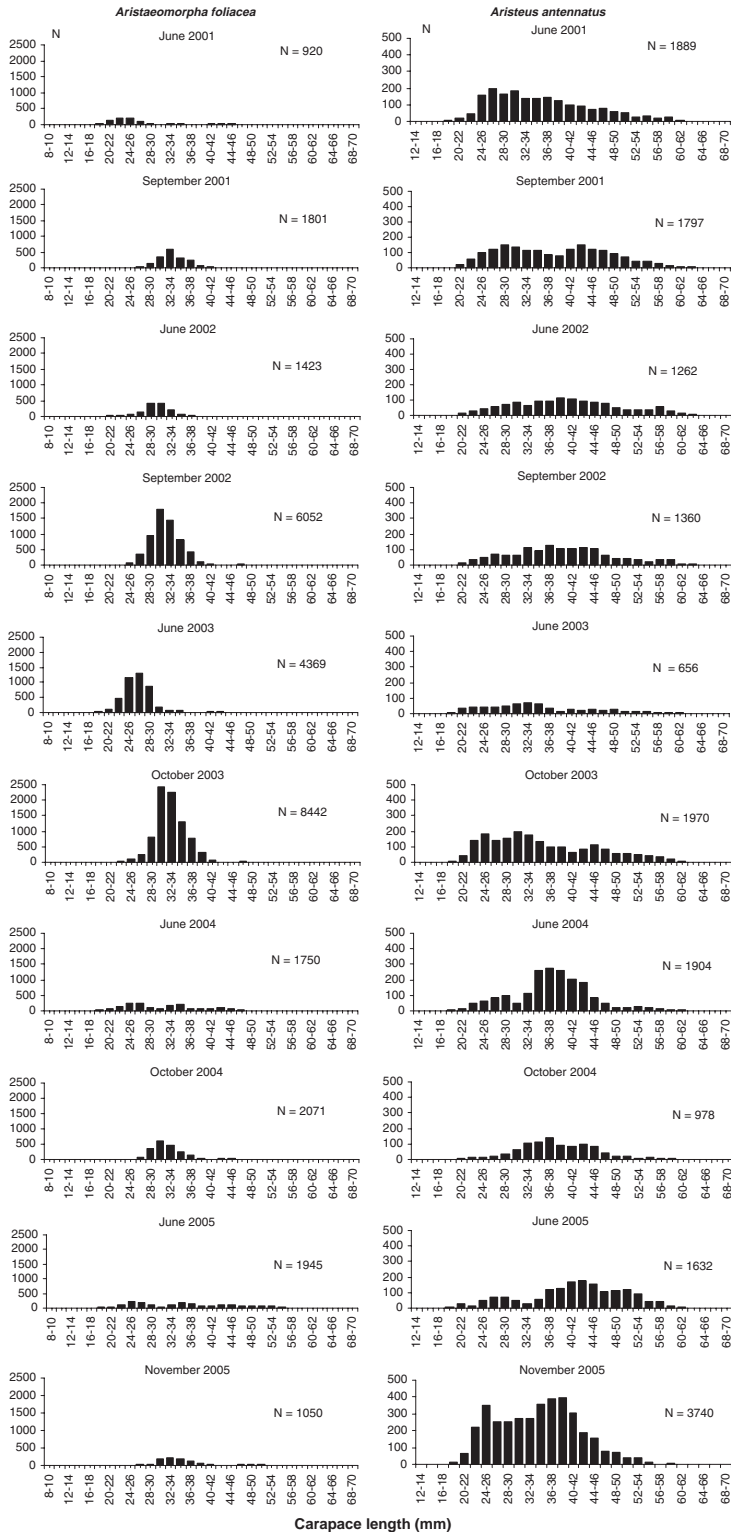


Figure 8. Length–frequency distribution of *Aristaeomorpha foliacea* and *Aristeus antennatus* sampled from 2001 to 2005 in the north-western Ionian Sea.

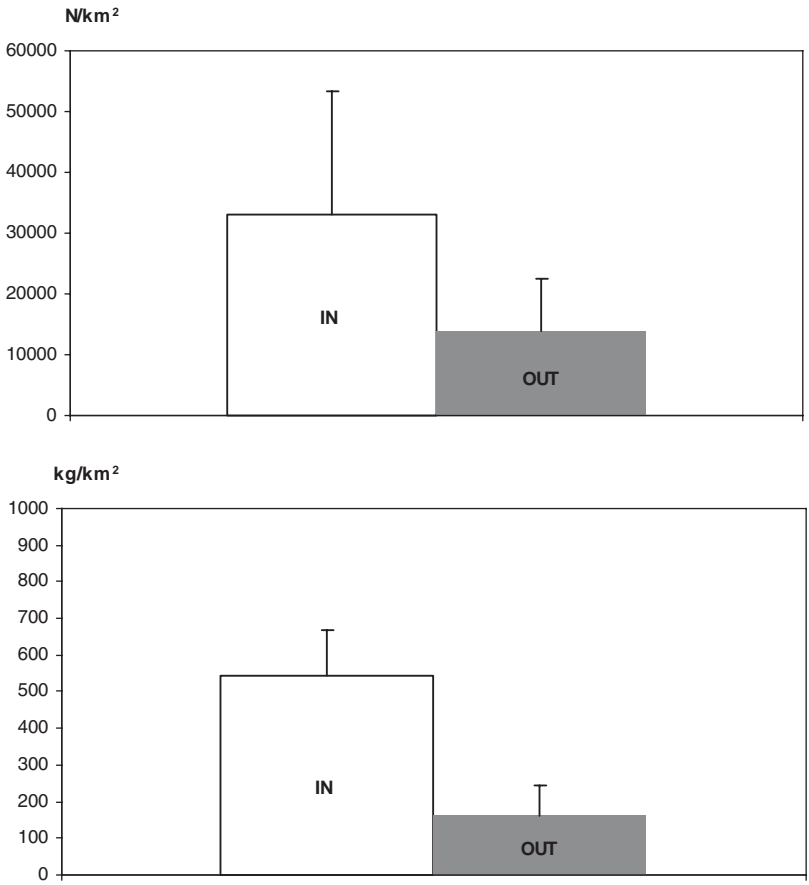


Figure 9. Average density and biomass indices, with standard deviation, computed for the benthopelagic fauna caught by trawl net, inside (IN) and outside (OUT) the Santa Maria di Leuca coral habitat.

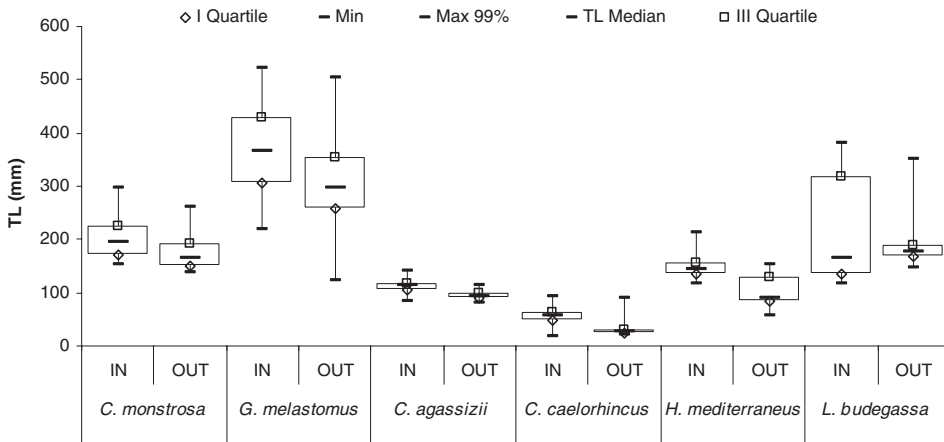


Figure 10. Box-plot of the sizes in *Chimaera monstrosa*, *Galeus melastomus*, *Chlorophthalmus agassizii*, *Coelorhynchus caelorhynchus*, *Hoplostethus mediterraneus* and *Lophius budegassa* collected inside (IN) and outside (OUT) the Santa Maria di Leuca coral habitat.

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depth if a deeper vertical range is examined. Although not significant, the greatest biomass values were recorded on the upper–middle slope as a consequence of an increase in fish size rather than an increase in number.

The 400–800 m assemblage exhibited the greatest mean values of density and species richness with a higher abundance than biomass curve, indicating an assemblage characterised by a greater number of small and more abundant species. In the middle slope, between 800 and 1200 m, the biomass curve is more elevated than that of numerical abundance indicating a greater equitability in the assemblage. In the lower slope, the curve of abundance crosses that of biomass mostly probably because of the occurrence of both smaller and larger species of crustaceans and fishes.

The decrease in species number and the increase in evenness around 1000–1200 m is in agreement with observations carried out in the Cretan Sea on the whole demersal community [10] and in the other Mediterranean areas for deep-water fish assemblages [24,26]. According to deep-water investigations in the Atlantic and Mediterranean [23,24,27,69,70] the peak of biomass recorded on the middle slope is due to the presence of large-sized species, such as *G. melastomus*, *M. moro* and *T. scabrus*, that replace smaller species of both fish and crustaceans which dominate the upper slope species assemblage. This is a common pattern throughout the Mediterranean, although some geographic differences are due to energetic constraints and physical conditions [26,33]. The availability of trophic resources linked to the distribution of mesopelagic organisms has often been considered the main cause of a biomass peak in the middle slope [23,69,70]. Moreover, the biomass peak observed in the suprabenthos organisms between 800 and 1300 m in the western Mediterranean [71] can also explain the abundance of deep-water fishes which feed on these organisms [72–74].

As reported by Moranta et al. [27], the biomass peak is related to the species-specific bathymetric responses of the above-mentioned species distributed with the largest individuals in the middle slope. In fact, the species turnover also seems to reflect the depth-related trend of the dominant species which perform ontogenetic migration along the bathymetric gradient [18,75]. Stefanescu et al. [22] did not reveal any depth–size trend in *M. moro* because they investigated a depth range, between 1000 and 2250 m, deeper than where recruitment of this fish occurs. Also Morales-Nin et al. [76] and Moranta et al. [27] reported positive trends in *G. melastomus*, *P. blennoides* and macrourid fish, but not in *M. moro*. However, they collected this fish at depths >700 m. The positive relationship between size and depth detected in *P. martia* is in agreement with observations by Company and Sardà [77] in the western Mediterranean and Maiorano et al. [78] in the Ionian Sea. The smaller–deeper trend observed in *A. antennatus* and *P. typhlops* is due to the deeper distribution of juveniles and males which are smaller than females in both species [79–81].

Many studies on feeding habits in the lower slope fish species have indicated the presence of active predators such as *C. coelolepis* and *E. spinax* feeding on a wide range of benthic and free-swimming organisms, and species such as *B. mediterraneus* with reduced mobility and a microphagous filtering diet [37,82–84]. In addition, a degree of overlap between these two extreme trophic strategies seems to be due to other species, belonging to the Macrouridae, Moridae and Bythitidae families, which feed on food occurring within the benthic boundary and at the bottom interface [72,82,83,85–87].

It is well known that most deep-water species are slow-growing with a low reproductive capacity and are adapted to live in an ecosystem of low energy turnover. Thus, they are highly vulnerable to exploitation [37]. In relation to the importance of depths below 800–1000 m for the reproduction of many species, as well as for the juveniles of others such as *A. antennatus*, the exploitation of these bottoms would determine negative effects on shallower ecosystems, beyond the quick depletion of the several stocks [36].

Although the effects of fishing have been detected for the deep-water shrimp *A. foliaceus* according to previous observations in the Ionian Sea [88], during the period 2000–2004 an uncommon

increase in the abundance of this shrimp was recorded with both density and biomass found to be far greater than those of *A. antennatus* [42]. The inverted abundance of the two red shrimps during 2000–2004 seems to have been due to a temporary change in hydrographic conditions in the Ionian Sea. According to Ghidalia and Bourgois [89] and Bombace [35], such hydrographic conditions seem to favour *A. foliacea* but not *A. antennatus*, which seems to be more linked to colder and less saline waters. These results point out how the dynamics of the aquatic populations are influenced by the complexity of the ecosystem processes coupled with human activities [43].

In the Mediterranean, deep-water species are adapted to a general oligotrophic environment with local habitats of higher productivity and biodiversity hotspots. These deep-water habitats are also sensitive to human modification related to fishing, waste disposal and chemical pollution. The canyons represent a physical discontinuity over the continental slope which plays a role in the migrating processes of the fauna, favouring a coupling between bathyal and coastal waters due to both upwelling and cascading conditions [36,43]. Interactions between fauna and canyons determine differences in the distribution of the species and biomass between this type of habitat and surrounding areas on the continental slope. In addition, canyons can act as an ‘ecological refuge’ for many bathyal species. In fact, these habitats are unsuitable for trawling and represent a sheltered site for species during sensitive phases of their life cycle or for species well adapted to unstable environments.

The Santa Maria di Leuca coral bank represents a rare example of living *Lophelia–Madrepora*-bearing coral mounds and a biodiversity hotspot in the Mediterranean Sea, because more than 220 species have been recorded to date [90]. Data from trawling has revealed significant differences in the abundance of the fauna between coral and non-coral habitats [64]. The greater sizes shown in different species of fish inside the coral habitat indicate that it acts as a refuge area for these demersal species which are accidentally exploited outside. Considering the evidence of the negative impact of bottom trawling and, to a lesser extent, longlining, the Santa Maria di Leuca coral bank plays a role in the conservation of unique species and habitats as well as in providing benefit to adjacent fisheries through the spill-over effect of eggs, larvae, juveniles and adults [64]. Finally, the results summarised in this article point out the importance of the deep-sea investigations according to multidisciplinary approaches. Indeed, very little is still known about bathyal benthopelagic fauna and biodiversity, as well as on their relevant variations with respect to the different habitats and in relation to human intervention in the deep-sea both directly, through fishing and pollution, and indirectly by climate changes.

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