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RESEARCH ARTICLE

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A critical habitat for Mediterranean fish resources: shelf-break areas with *Leptometra phalangium* (Echinodermata: Crinoidea)

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Abstract This paper considers the potential role of the crinoid *Leptometra phalangium* as an indicator of highly productive areas along the shelf break that can sustain large biomasses of benthopelagic fish and recruits. The structure of fish assemblages in the central Mediterranean Sea (central-western coast of Italy), analysed on the basis of surveys carried out in summer and autumn from 1997 to 2001, revealed the presence of a well-defined group of species on the shelf break. This area, occurring at a depth of between 120 and 170 m, is characterised by detritic organogenic sediments colonised by the crinoid *L. phalangium*, a suspension-feeding macro-epibenthic species confined in the Mediterranean to the shelf-break area. Its abundance in the studied area can reach 12–15 ind. m^{-2}. A total of 121 species belonging to 66 families of demersal organisms (crustacean decapods and stomatopods, cephalopods, selaceens and teleosteens) were caught at shelf-break stations from September to October. The species which typified the assemblage were the fishes *Trisopterus minutus capelanus*, *Merluccius merluccius*, *Glossanodon leioglossus*, *Argentina sphyraena*, *Capros aper*, *Macroramphos scolopax* and *Lepidotrigla cavillone*, the crustacean decapod *Parapenaeus longirostris* and the cephalopods *Illex coindetii* and *Todaropsis eblanae*. Detritic shelf-break stations showed a higher abundance of demersal organisms than stations distributed on muddy bottoms in the same depth range (100–200 m). Such differences appeared to be significant in September–October, when a clear increase in benthopelagic zooplanktivorus species, such as *Glossanodon leioglossus*, *Trachurus trachurus*, *Trachurus picturatus*, was found. The length structure of species occurring on the shelf break showed that for some of them the selection of this area is related to specific phases of their life cycle. Significant highest abundance of recruits and juveniles was observed for *Merluccius merluccius*, *Helicolenus dactylopterus*, *Phycis blennoides*, *Parapenaeus longirostris* and *Capros aper* in at least one of the two seasons. Similarly, an increased abundance of spawners of red mullet *Mullus barbatus* and four-spotted megrim *Lepidorhombus boscii* was observed on the shelf break. Results of this study may have important consequences for management of fish stocks and assemblages in the central Mediterranean. The co-occurrence of high densities of *L. phalangium* and benthopelagic fish, occurring mainly with juveniles and spawners, strongly indicates a potential role of *L. phalangium* as an indicator of highly productive areas around the shelf break. Such areas appear to play a major role in the production of some of the most abundant and commercially important fish species, such as the Mediterranean hake and red mullet.

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Introduction

The shelf break is a high-energy zone as a result of the interplay of tides, storm waves, breaking internal waves and bottom turbulence produced by fronts separating shelf and slope waters (Herman 1972; Vanney and Stanley 1983). Intermittent mixing events may generate increased ammonium and nitrate concentrations in water columns, which, in turn, increase euphotic zone production (Soetaert et al. 2001). An enhanced phytoplankton and zooplankton biomass associated with shelf-break fronts has been observed (see Mann and Lazier 1996). The high production of plankton at the shelf break makes it an important feeding ground for large shoals of fish (Williams et al. 2001), flocks of oceanic birds (Skov and Durinck 1998) and cetaceans (Hain et al. 1985).

Studies of communities in the Mediterranean shelf break have mostly focused on benthic assemblages in relation to sediment characteristics, which are muddy with a component of relict detritic sediments produced during Pleistocenic (20,000–8,000 years ago) fluctuations in sea levels (Pérès and Picard 1964; Reyss 1973). Both eastern Atlantic and Mediterranean benthic communities on the shelf break are characterised by high concentrations of macro-epibenthic filter-feeding and suspension-feeding organisms (Flach et al. 1998; Kallianotis et al. 2000). In the Mediterranean, where a well-defined benthic community on the shelf break has been described (DL, Pérès and Picard 1964), the dominant megabenthic species is generally the crinoid *Leptometra phalangium*. This species is confined to the restricted depth range that corresponds to the shelf-break and canyon-head areas under bottom currents, where it can reach a density of 30–50 ind. m^{-2} (Laborel et al.1961; Vaissière and Carpine 1964; Reyss and Soyer 1965; Bourcier and Zibrowius 1973; Reyss 1973, 1974; Kallianotis et al. 2000). In the Atlantic Ocean, the vicariant species *Leptometra celtica* characterises the shelf break along the northwest Spanish and southwest Irish coasts (Lavaleye et al. 2002).

The impact of towed gear is particularly heavy on these beds, both on *L. phalangium*, a fragile organism that is easily destroyed by trawling, and on other epibenthic organisms that have shown reduced abundance in trawled areas (Smith et al. 2000).

Several studies have shown a relationship between the distribution of macro-epibenthic and of demersal fish assemblages in the Mediterranean (Gaertner et al. 1999; Colloca et al. 2003a), indicating that the negative effects of fishing on the benthic community may be mirrored in the distribution and abundance of fish species.

The role played by the shelf break in the distribution and dynamics of demersal species is very poorly understood in the Mediterranean, even though previous studies have revealed the occurrence of a defined fish assemblage on deeper shelf/shallow slope bottoms (Gaertner et al. 1999; Biagi et al. 2002; Colloca et al. 2003a). It is worth stressing that this assemblage is characterised by high concentrations of juveniles of important commercially exploited species such as European hake (*Merluccius merluccius*).

The main aim of this paper is to evaluate the potential role of *L. phalangium* beds as indicators of highly productive areas along the shelf break, which can sustain large biomasses of benthopelagic fish and recruits. For this purpose, the abundance and population structure of demersal species, including European hake, red mullet (*Mullus barbatus*), John dory (*Zeus faber*), poor cod (*Trisopterus minutus capelanus*), horse mackerel (*Trachurus trachurus*) and deep-water pink shrimp (*Parapenaeus longirostris*) were analysed by comparing data obtained during stratified trawl surveys both on and off the shelf break.

The conservation of shelf-break fish assemblages is also discussed with a view to reducing the fish mortality in the sensitive phases (recruitment, spawning, post-spawning) of the life cycle of demersal fish species.

Materials and methods

Study area

The area investigated covers 15,289 km^2 off the central western coasts of Italy (central Mediterranean Sea) between 10 and 700 m depth (Fig. 1). The continental shelf extends up to 120–150 m depth between 15 and 30 km from the shoreline. The shelf break is characterised by detritic organogenic sediments, with locally high abundances of the crinoid *Leptometra phalangium*. This organism has a patchy distribution with a maximum abundance of 12–15 ind. m^{-2} (Colloca 2003).

Environmental conditions along the continental shelf are heterogeneous due to the presence of both eutrophic areas, like those affected by the Tiber River's waters (central Latium), and oligotrophic areas around the Pontine Islands, lagoons connected to the sea, phanerogam meadows, rocky and sandy shores.

The limit between the upper and middle slopes ranges between 400 and 500 m depth (Carpine 1970; Relini et al. 1986). The temperature down to 120–200 m depth is generally constant at about 13°C (Ifremer 1997). A layer of Levantine intermediate water, characterised by maximal salinity, flows anticlockwise along the slope between 250 and 700 m depth (Serravall and Cristofalo 1999).

Trawl survey data

Data were collected during eight trawl surveys, as part of the MEDITS and GRUND projects, conducted, respectively, in July and September–October from 1997 to 2001. Both projects used a randomised, stratified sampling design based on depth (five bathymetric strata: 10–50, 51–100, 101–200, 201–500 and 501–700 m) and area. The depth limits were adopted to best cover the distribution areas of the mainly exploited, or potentially exploitable, species. Locations of stations were selected randomly within each stratum at the beginning of the projects (1996). The same stations, 61 for GRUND and 46 for MEDITS, were sampled in the following years (see Relini 1998; Bertrand et al. 2002). Ten stations in all were located on detritic bottoms, with *L. phalangium* along the shelf break (crinoid stations).

There were some differences between the two projects as regards the vessels and equipment used for the surveys. The GRUND project was conducted using a vessel (60 tons and 600 HP) equipped with an Italian otter trawl mounting a 40-m head rope, a 40-mm ground chain and 40- and 30-mm stretched mesh in the wing and cod-end, respectively. MEDITS was carried out from a 88-ton, 800-HP vessel using an otter trawl net with a 40-m head rope, an 8-m wing spread and a 20-mm mesh size

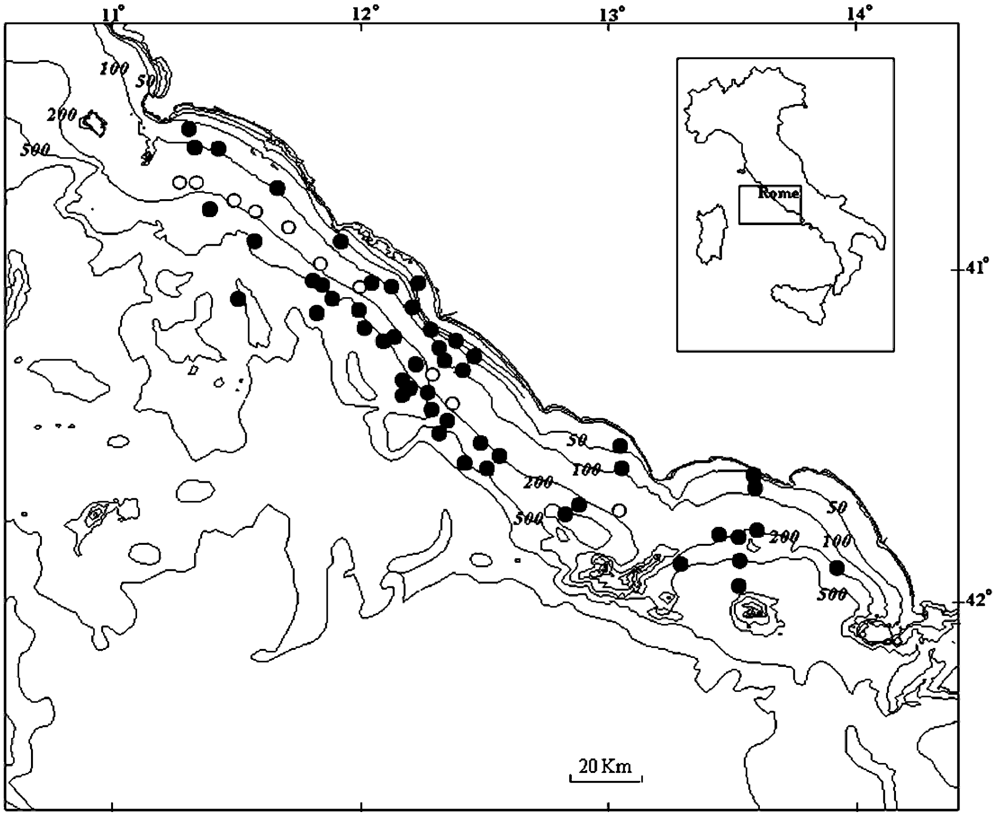


Fig. 1 Trawl stations on the continental shelf and upper slope of the central western coasts of Italy (central Mediterranean Sea) (*open circles Leptometra phalangium* stations on the shelf break)

at the cod-end (Fiorentini et al. 1999). The hauls, conducted during daytime hours (6.00 a.m. to 6.00 p.m.), lasted 60 min during the GRUND project, while the haul duration varied during the MEDITS project according to depth: 30 min up to 200 m depth and 60 min below 200 m depth.

The towing speed of the vessels was about 3.0 knots for both projects. The distance covered by the net on the bottom was calculated using GPS positions when the net reached and left the bottom. The mean opening of the net mouth was directly calculated for most of the hauls by a commercial SCANMAR system. The swept area was then obtained by multiplying the mean mouth opening of the net by the towing distance.

Data analysis

Catches of demersal fauna (teleostean fish, elasmobranchs, cephalopod molluscs and decapod crustaceans) were standardised to numerical abundances (ind. 1 km^{-2} swept by the trawl), making the data from the two projects comparable.

Catch data (ind. km^{-2}) were pooled according to season (July and September–October) and period (1997–1998 and 2000–2001) to obtain four matrixes of species abundance by station: July 1997–1998, July 2000–2001, September–October 1997–1998 and September–October 2000–2001. Four Bray–Curtis dissimilarity matrixes were then constructed to perform non-parametric multidimensional scaling ordinations (MDS) using PRIMER v5 software (Clarke and Warwick 1994).

Pelagic fishes, such as Clupeiformes and mackerel (*Scomber scombrus*), and species whose abundance was < 100 ind. km^{-2} were removed from the original matrixes. Data were root transformed before analysis to reduce high abundance of some species, such as *Merluccius merluccius* or *Macroramphosus scolopax*. The bubble procedure in the PRIMER v5 software was used to graphically better define the position of crinoid stations at the shelf break within ordination plots of continental shelf and slope stations (Clarke and Gorley 2001). The species that contributed most to the within-group similarity of these stations were then identified for each group of surveys using SIMPER (Similarity Percentage Analysis). MDS was also used for ordination of abundance data from crinoid stations to evaluate visually the extent to which the composition of the shelf-break demersal fauna differed between surveys. The *R*-statistic values for pair-wise comparisons provided by a one-way analysis of a similarity randomisation test (ANOSIM) were used to reveal the degree to which the surveys were dissimilar. *R*-statistic values could range from 0, where there was no difference in faunal composition between surveys, to 1, where surveys were very different (Clarke 1993).

Species that chose the crinoid stations, reaching higher densities there compared to densities obtained at stations located between 100 and 200 m depth but characterised by muddy sediments (muddy stations),

Table 1 List of all demersal species collected on the central Mediterranean shelf break in the period 1997–2001

Taxon	Species	Taxon	Species
Crustacea		Actinopterygii	
Alpheidae	*Alpheus glaber*	Blenniidae	*Blennius ocellaris*
Calappidae	*Calappa granulata*	Bothidae	*Arnoglossus laterna*
Crangonidae	*Pontocaris lacazei*		*Arnoglossus rueppelli*
	Pontophilus spinosus		*Lepidorhombus boscii*
Galatheidae	*Munida intermedia*		*Lepidorhombus whiffiagonis*
Goneplacidae	*Goneplax rhomboides*	Callionymidae	*Callionymus maculatus*
Homolidae	*Paromola cuvieri*		*Callionymus risso*
Pandalidae	*Chlorotocus crassicornis*		*Synchiropus phaeton*
Calocarididae	*Calocaris macandrae*	Caproidae	*Capros aper*
Parthenopidae	*Partenope macrochelos*	Carangidae	*Trachurus mediterraneus*
Paguridae	*Pagurus alatus*		*Trachurus picturatus*
	Pagurus excavatus		*Trachurus trachurus*
Diogenidae	*Dardanus arrosor*	Centracanthidae	*Centracanthus cirrus*
Majidae	*Macropodia longipes*		*Spicara flexuosa*
Pandalidae	*Plesionika acanthonotus*		*Spicara smaris*
	Plesionika edwardsii	Cepolidae	*Cepola macrophthalma*
Parthenopidae	*Parthenope macrochele*	Chlorophthalmidae	*Chlorophthalmus agassizi*
Pasiphaeidae	*Pasiphaea multidentata*	Citharidae	*Citharus linguatula*
	Pasiphaea sivado	Clupeidae	*Sardina pilchardus*
Penaeidae	*Parapenaeus longirostris*	Engraulidae	*Engraulis encrasicolus*
Portunidae	*Liocarcinus depurator*	Congridae	*Conger conger*
	Macropipus tuberculatus		*Gnathophis mystax*
Processidae	*Processa canaliculata*	Cynoglossidae	*Symphurus nigrescens*
Solenoceridae	*Solenocera membranacea*	Gadidae	*Gaidropsarus mediterraneus*
Xanthidae	*Monodaeus couchii*		*Gadiculus argenteus*
Lysiosquillidae	*Allosquilla africana*		*Merluccius merluccius*
Pseudosquillidae	*Parasquilla ferussaci*		*Micromesistius poutassou*
Squillidae	*Rissoides pallidus*		*Phycis blennoides*
	Squilla mantis		*Trisopterus minutus capelanus*
Mollusca		Gobiidae	*Deltentosteus quadrimaculatus*
Enoploteuthidae	*Abralia veranyi*		*Lesuerigobius friesii*
Loliginidae	*Alloteuthis media*	Labridae	*Acantholabrus palloni*
	Alloteuthis subulata		*Lappanella fasciata*
	Loligo forbesi	Lophiidae	*Lophius budegassa*
	Loligo vulgaris		*Lophius piscatorius*
Octopodidae	*Eledone cirrhosa*	Macroramphosidae	*Macroramphosus scolopax*
	Eledone moschata	Mullidae	*Mullus barbatus*
	Octopus salutii		*Mullus surmuletus*
	Octopus vulgaris	Nettastomatidae	*Nettastoma melanurum*
	Pteroctopus tetracirrhus	Ophichthidae	*Echelus myrus*
	Scaeurgus unicirrhus	Peristediidae	*Peristedion cataphractum*
Ommastrephidae	*Illex coindetii*	Scombridae	*Scomber scombrus*
	Todaropsis eblanae		*Scomber japonicus*
Sepiidae	*Sepia elegans*	Scorpaenidae	*Helicolenus dactylopterus*
	Sepia orbignyana		*Scorpaena elongata*
Sepiolidae	*Neorossia caroli*		*Scorpaena loppei*
	Rondeletiola minor	Serranidae	*Serranus cabrilla*
	Rossia macrosoma		*Serranus hepatus*
	Sepietta oweniana	Sparidae	*Boops boops*
	Sepiola robusta		*Dentex dentex*
	Sepiola rondeleti		*Pagellus acarne*
Chondrichthyes			*Pagellus bogaraveo*
Oxinotidae	*Oxynotus centrina*		*Pagellus erythrinus*
Rajidae	*Raja asterias*	Trachinidae	*Trachinus draco*
	Raja clavata	Synodontidae	*Synodus saurus*
	Raja montagui	Trichiuridae	*Lepidopus caudatus*
	Raja oxyrinchus	Triglidae	*Aspitrigla cuculus*
Scyliorhinidae	*Scyliorhinus canicula*		*Aspitrigla obscura*
Torpedinidae	*Torpedo nobiliana*		*Eutrigla gurnardus*
	Torpedo marmorata		*Lepidotrigla cavillone*
Actinopterygii			*Lepidotrigla dieuzeidei*
Argentinidae	*Argentina sphyraena*		*Trigla lucerna*
	Glossanodon leioglossus		*Trigla lyra*
Aulopidae	*Aulopus filamentosus*		*Trigloporus lastoviza*
		Zeidae	*Zeus faber*

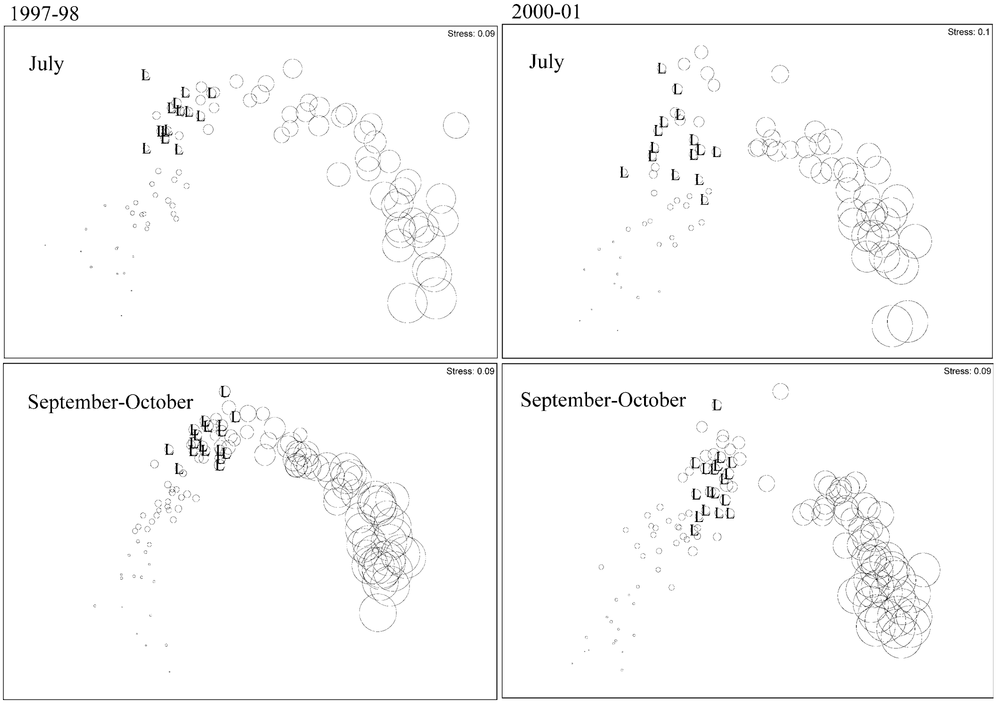


Fig. 2 MDS (multidimensional scaling) ordination plots of abundance data obtained during trawl surveys carried out in July and September–October (1997–1998 and 2000–2001). Depth is superimposed as circles of increasing size with increasing depth. *Leptometra phalangium* stations are indicated (*L*)

were identified by testing the differences in mean abundance with a bootstrap randomisation test (Manly 1997), using 1,000 random samples. Habitat selection in the different life stages of the demersal species was also investigated, by season, by comparing length–frequency distributions (LFDs) obtained at crinoid stations with those obtained by pooling data from all the stations sampled. Data from different surveys were pooled for the two projects, and LFDs for hake (*Merluccius merluccius*), red mullets (*Mullus barbatus*) and pink shrimp (*Parapenaeus longirostris*) were adjusted by means of the selection curve such that:

$$S_{\mathrm{L}} = \frac{1}{1 + \exp(s1 - s2 * L)} \qquad (1)$$

where S_{L} is the number of fish retained, $s1$ and $s2$ are constants (Jones 1976) and L is length. S_{L} was determined by an experiment with a covered cod end conducted in the study area in April 1997.

Results

Demersal assemblage

A total of 121 species of demersal organisms (25 crustacean decapods, 4 stomatopods, 21 cephalopods, 8 selaceens and 63 teleosteen, see Table 1) were fished at crinoid stations during trawl surveys.

Ordinations of trawl survey data showed that these stations formed a group between shelf and slope stations in both periods, 1997–1998 and 2000–2001, and both seasons, July and September–October (Fig. 2).

An MDS ordination plot of catch data obtained in each survey on crinoid beds showed a high level of

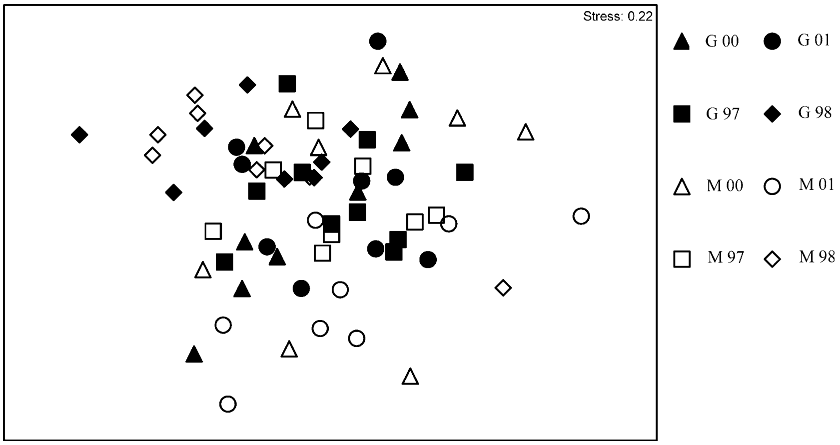


Fig. 3 MDS ordination plot of abundance data of demersal organisms obtained during trawl surveys conducted from 1997 to 2001 (*G* September–October surveys; *M* July surveys)

Table 2 Percentage contribution of typifing species (> 2%) to within-group similarity for the shelf break demersal assemblage according to period (1997–1998, 2000–2001) and season (July, September–October)

Season, period	Species	Percent	Season, period	Species	Percent
July, 1997–1998	*Merluccius merluccius*	25.3	September–October, 1997–1998	*Merluccius merluccius*	17.7
	Macroramphosus scolopax	11.7		*Parapenaeus longirostris*	10.9
	Alloteuthis sp.	8.9		*Trisopterus m.capelanus*	8.9
	Trisopterus m.capelanus	8.5		*Macroramphosus scolopax*	7.0
	Parapenaeus longirostris	8.2		*Argentina sphyraena*	6.4
	Illex coindetii	6.2		*Illex coindetii*	5.2
	Capros aper	5.3		*Alloteuthis sp.*	5.0
	Mullus barbatus	4.4		*Lepidotrigla cavillone*	3.8
	Todaropsis eblanae	2.7		*Capros aper*	2.9
	Argentina sphyraena	2.2		*Todaropsis eblanae*	2.8
July, 2000–2001	*Merluccius merluccius*	14.7	September–October 2000–2001	*Merluccius merluccius*	29.3
	Macroramphosus scolopax	14.4		*Trisopterus m.capelanus*	19.6
	Glossanodon leioglossus	14.3		*Glossanodon leioglossus*	14.6
	Trisopterus m.capelanus	13.4		*Parapenaeus longirostris*	7.5
	Capros aper	9.2		*Macroramphosus scolopax*	6.7
	Mullus barbatus	3.9		*Illex coindetii*	4.2
	Argentina sphyraena	3.6		*Lepidotrigla cavillone*	3.9
	Illex coindetii	2.8		*Argentina sphyraena*	2.6
	Lepidotrigla cavillone	2.3		*Capros aper*	2.2
	Parapenaeus longirostris	2.1			

overlap between surveys (Fig. 3). The ANOSIM test, however, showed significant within-survey differences ($P < 0.01$). This contrasts with the results of pair-wise test comparisons between surveys, which indicated a generally high level of overlap ($0.1 < R < 0.5$). The significance of the differences between surveys could be related to the rather low number of replicates from each survey, which increases the likelihood of making a type I error, more than it could be related to an effective difference in assemblage structure.

The hypothesis of no significant differences between surveys appeared to be reinforced by the similarity analysis (SIMPER). As Table 2 shows, the most typifying species did not change according to either period (1997–1998 and 2000–2001) or season (July and September–October). The main differences were related to the rank order of the species. *Trisopterus m. capelanus* and *Merluccius merluccius* generally ranked higher, followed by the teleosteens *Glossanodon leioglossus*, *Argentina sphyraena*, *Capros aper*, *Macroramphos scolopax* and *Lepidotrigla cavillone*, the crustacean decapods *Parapenaeus longirostris* and the cephalopods *Illex coindetii* and *Todaropsis eblanae*.

The main seasonal changes were the increased importance of *Mullus barbatus* in July and *Lepidotrigla cavillone* in September–October.

Species abundance and length structure

Figures 4 and 5 show the comparison of abundance obtained at crinoid stations versus muddy stations at the same depth range (100–200 m). In both seasons some species, such as *Macroramphos scolopax*, *Capros aper*, *Argentina sphyraena*, *Helicolenus dactylopterus*, *Scaeurgus unicirrhus* and *Lepidorhombus boscii*, showed a significantly higher density at crinoid than at muddy stations.

The general pattern was one of increased density of demersal organisms at crinoid stations (July: crinoid beds 24,136 ind. km^{-2}, muddy stations 19,504 ind. km^{-2}; September–October: crinoid beds 23,447 ind. km^{-2}, muddy stations 11,885 ind. km^{-2}). Such differences appeared to be significant in September–October ($P < 0.001$) when a clear increase in benthopelagic zooplanktivorus species, such as *Glossanodon leioglossus*, *Trachurus trachurus* and *Trachurus picturatus*, was found on crinoid stations (Fig. 4). In July, a greater concentration of some epibenthic (*Trisopterus m. capelanus*, *Mullus barbatus*, *Serranus hepatus*) and ichthyophagous feeders (*Illex coindetii*) was observed on these stations (Fig. 5).

Another group of species (*Cepola macrophthalma*, *Spicara flexuosa*, *Eledone cirrhosa*, *Sepia elegans*, *Macropipus depurator*, *Pagellus erythrinus*, *Citharus linguatula*, *Lesuerigobius friesii*, *Arnoglossus laterna*) seemed to avoid detritic bottoms of the shelf break reaching a significant highest density at muddy stations.

The length structure of species occurring on the shelf break showed that selection of crinoid bottoms could be related to some specific phases of their life cycle. By comparing LFDs obtained on these bottoms with those related to the whole trawling area, three different groups of species were defined on the shelf break:

1. Species only or mainly with recruits or juveniles under length at maturity (Fig. 6A–D). The significantly highest abundance of recruits and juveniles were observed for *Merluccius merluccius*, *Helicolenus dactylopterus*, *Phycis blennoides*, *Parapenaeus longirostris* and *Capros aper* in at least one of the two seasons. The abundance of individuals belonging to the other cohorts is clearly reduced if compared with that of the

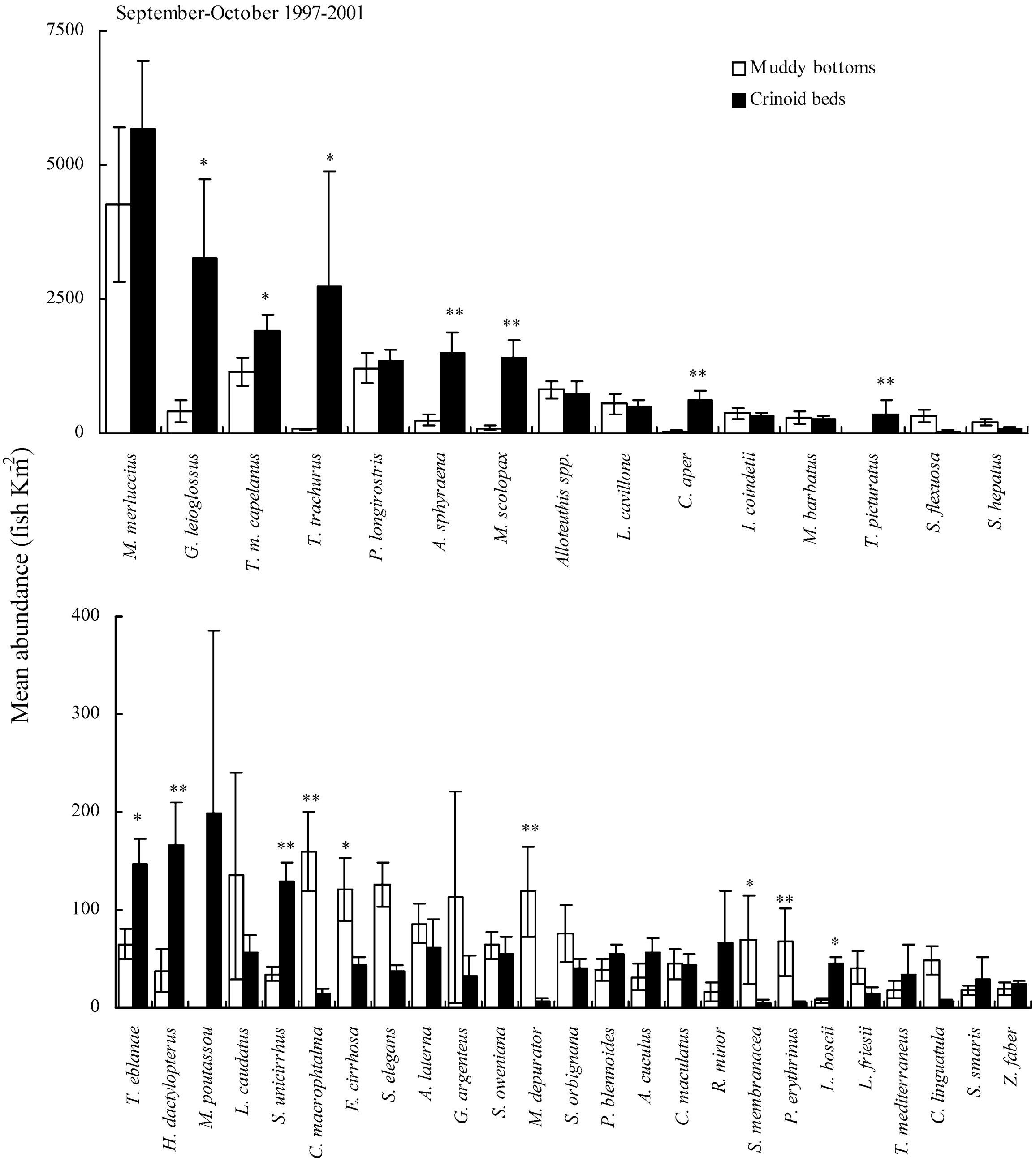


Fig. 4 Comparison of the average abundance of species obtained, respectively, at *Leptometra phalangium* stations (crinoid beds) and muddy stations in the depth range between 100 and 200 m. Data obtained during trawl surveys conducted in September–October from 1997 to 2001 were pooled (full species names, see Table 1)

whole trawling area. Hake, in particular, showed a peak of abundance of newly recruited fish (4–10 cm TL) in September–October.

2. Species with adults over size at maturity (Fig. 6E, F). The red mullet (*Mullus barbatus*) and four-spotted megrim (*Lepidorhombus boscii*) occurred on the shelf break mostly as adults, while the percentage of recruits was strongly reduced or absent if compared with that of the whole area.
3. Species that do not show any significantly greater abundance of some cohorts (Fig. 7) that either actively selected shelf-break bottoms, like *Trisopterus m. capelanus*, *Macroramphosus scolopax*, *Trachurus trachurus*, *Illex coindetii*, or did not show any clear habitat selection (*Aspitrigla cuculus*, *Lepidotrigla cavillone*, *Lophius budegassa*, *Zeus faber*).

Discussion

The results of this study show that the shelf break of the central Mediterranean Sea hosts a well-defined fish assemblage, persistent over years and seasons, charac-

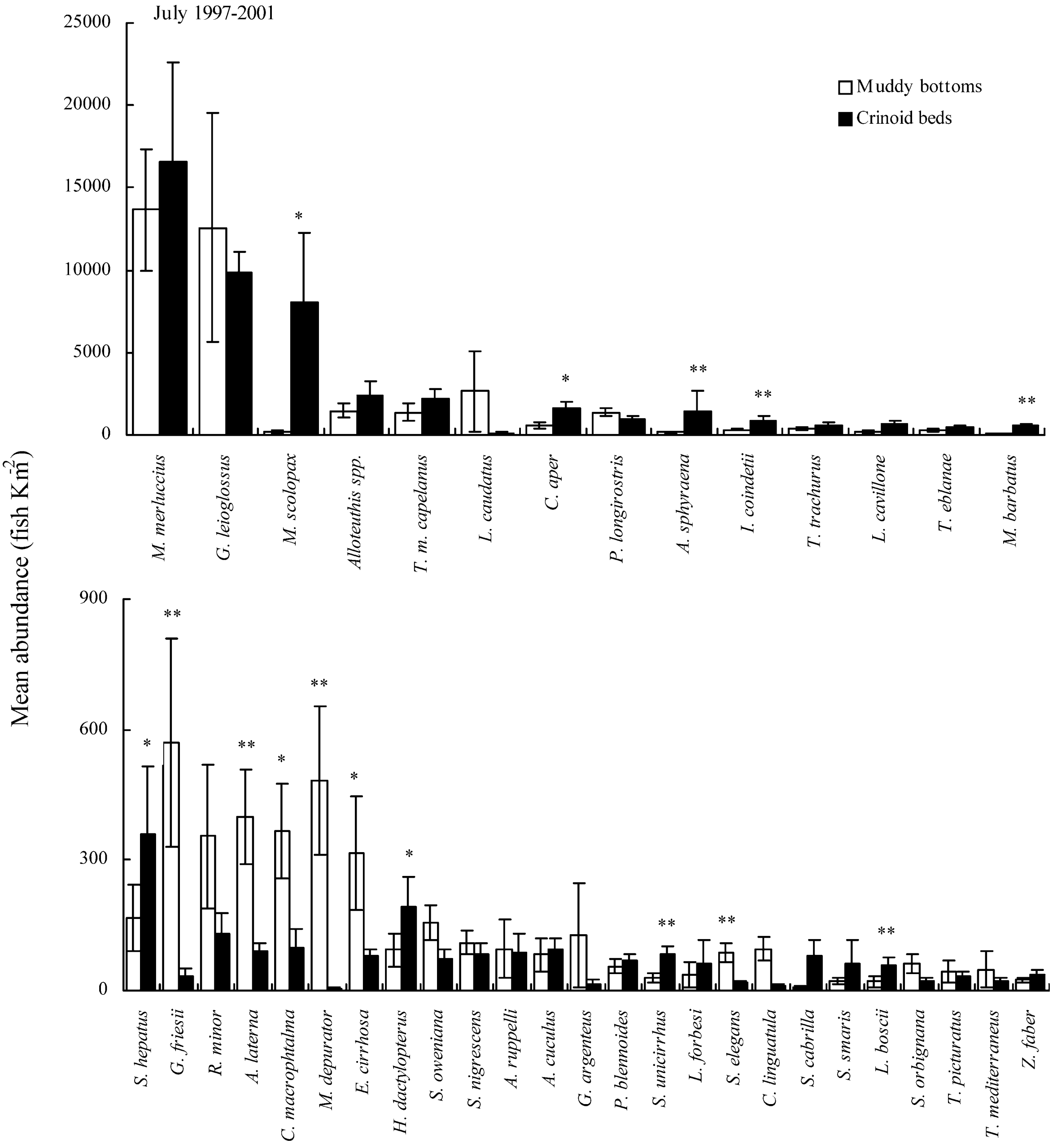


Fig. 5 Comparison of the average abundance of species obtained, respectively, at *Leptometra phalangium* stations (crinoid beds) and muddy stations in the depth range between 100 and 200 m. Data obtained during trawl surveys conducted in July from 1997 to 2001 were pooled (full species names, see Table 1)

terised by a high abundance of juveniles and spawners of commercially exploited species.

The selection of this area by a group of species can be related both to the peculiar oceanographic conditions that characterise the shelf-to-slope sector (Soetaert et al. 2001) and the characteristics of sediments. The shelf-break upwelling (Pinazo et al. 1996) and water turbulence determine both an increase in organic matter transportation and nutrient input into the water column, which could be involved in structuring the benthic and demersal assemblages. High concentrations of epibenthic suspension-feeding organisms, in particular the crinoid *Leptometra phalangium*, occur in this area as a result of bottom currents. Crinoids of the *Leptometra* genus (*L. phalangium* in the Mediterranean, *L. celtica* in the Atlantic) can be considered as indicator species of a shelf break and, more generally, of bottom currents (Lavaleye et al. 2002). Unlike most macro-epibenthic species that are spread over a wide range of depths, these suspension-feeding organisms are generally confined to a restricted depth range (Carpine 1970; Fredj 1974; Stora et al. 1999). Benthic suspension feeders can have a major impact on marine ecosystems, intercepting large amounts of organic particles and regulating production in food chains. Moreover, they enhance habitat heterogeneity by developing three-dimensional communities (Gili and Coma 1998).

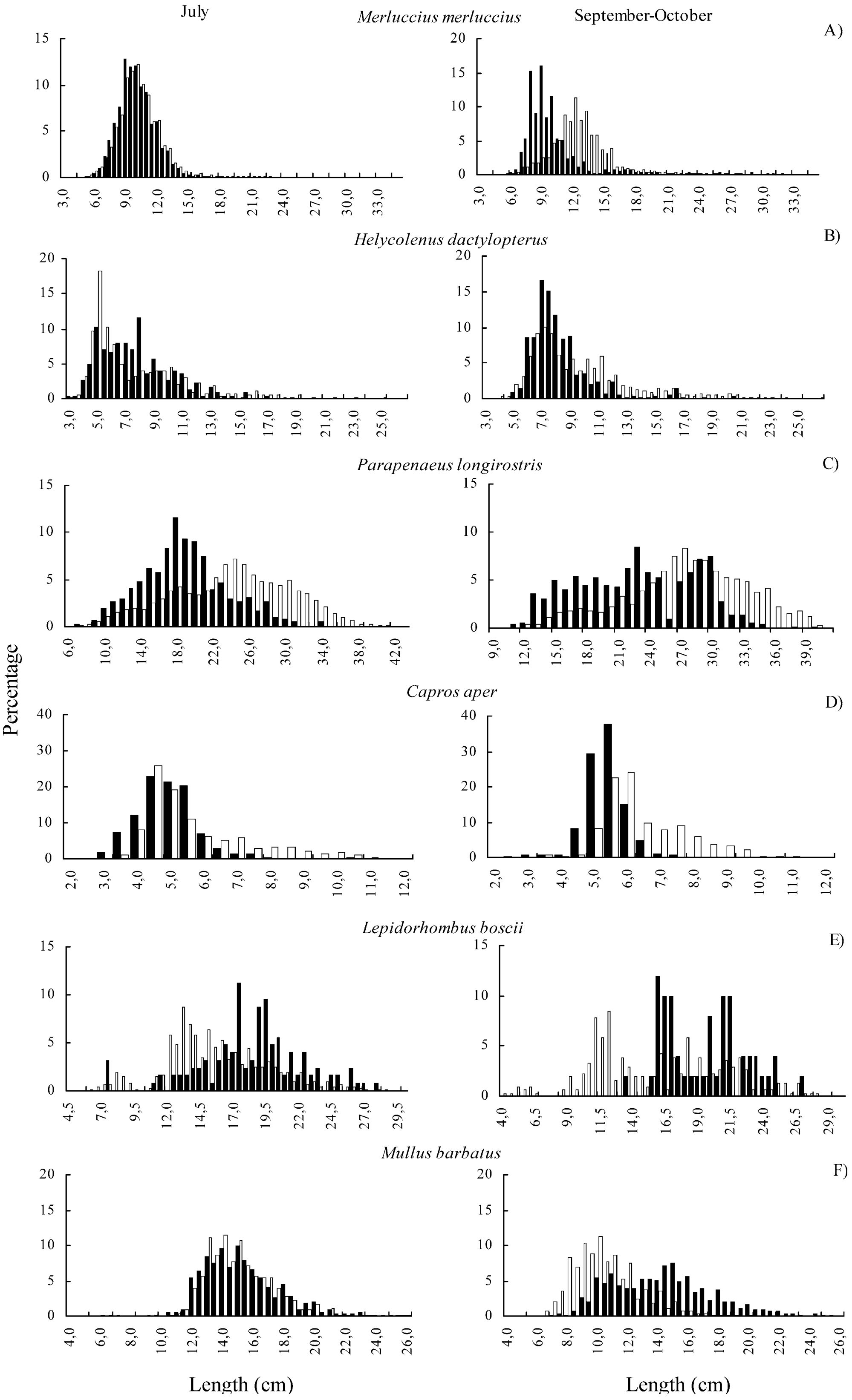


Fig. 6 Comparison of seasonal length-frequency distributions of species showing a higher abundance of recruits (**A**–**E**) or spawners (**F**, **G**) at *Leptometra phalangium* stations (*black bars*) versus the whole trawled area (*white bars*)

Shelf-break crinoid beds can be regarded as equivalent to the well-documented sponge forests, deep-water corals and gorgonids. All these "living bottom structures" form a critical part of the shelf and slope marine ecosystem and are easily damaged by bottom trawling (Rogers 1999; Fosså et al. 2002; Wassemberg et al. 2002).

Fishing activity's alteration of seafloor habitat could magnify the effects of overfishing by limiting juvenile survivorship. Fishing activity can have an impact on fish populations in two ways: the first, is the immediate effect on population demographics through the removal of fish and, the second, is the impact on the seafloor (e.g. through bottom trawls and dredges), which can reduce habitat complexity and thus increase the vulnerability of juvenile fish to predation by older conspecifics and other predators (Lidholm et al. 1999).

The impact of otter trawling on *L. phalangium* beds has been documented for the eastern Mediterranean. A strong reduction in *L. phalangium* and other echinoderms was observed in trawled areas, along with a decrease in the richness, abundance and biomass of benthic species (Smith et al. 2000). During trawl surveys, we observed that about 300 kg of crinoids or about 200,000 individuals can easily be collected in 1 h of trawling. Even if the effect of such destruction of the macro-epibenthic fauna on fish assemblage has not been studied, it commonly leads to a decrease in biomass and the recruitment of demersal fish species.

We observed in this study that there was a high abundance of zooplanktivorous species (juveniles of *Merluccius merluccius*, *Trachurus trachurus*, *Glossanodon leioglossus*) on *L. phalangium* detritic bottoms, particularly in September–October. The main prey of these species are euphausiids (*Nyctiphanes couchii* and *Euphausia kronii*, Colloca 2003), which reach highest diurnal abundance on the shelf break (Casanova 1970). The seasonal trend of euphausiids abundance in the western Mediterranean basin generally shows an increase from spring to autumn (Franqueville 1971). The increased abundance of zooplanktivorous predators at the shelf break could be correlated to the concentrations of macrozooplankton in this area. Locally increased primary production, in correspondence to the water column at the shelf-break front, could determine the concentration of benthopelagic resources (both zooplankton and hyperbenthos) in this area, as has been observed in the north-western Mediterranean (Sabatés et al. 1989; Maynou et al. 2003).

An overlap of large shoals of Pacific hake (*Merluccius productus*) and large patches of euphausiids has been observed off the coastline of California at or near the shelf break (Swartzman 1999). Further analysis should be devoted to assess such a hypothesis, which could have important management implications for commercially exploited species such as Mediterranean hake.

By comparing the length structure of hake within and outside the shelf-break area, our study showed that juveniles of hake are recruited to the bottom following metamorphosis exactly on the shelf break. In the Ligurian Sea, hake begins its demersal life close to the bottom at 2–8 cm length (Orsi Relini et al. 1989), as we found in this study. Both in the Mediterranean and the Atlantic, the species' spawning grounds are located around the shelf break (Recasens et al. 1998; Álvarez et al. 2001), where the highest abundance of eggs and larvae are found (Olivar et al. 2003). During the trawl surveys, we obtained the highest catch of mature hake (80%) in the investigated area in the depth range between 100 and 200 m, particularly in correspondence to shelf-break stations (Colloca, personal communication). This overlap between eggs, recruits and adult spawners suggests that hake spawns in highly productive areas represented by the frontal shelf break to ensure resource availability for both larvae and juveniles. A similar pattern was observed for cod (*Gadus morhua*) in the North Sea, which shows concentrations of larvae and small juveniles at the shelf break front (Munk et al. 1995, 1999).

▶

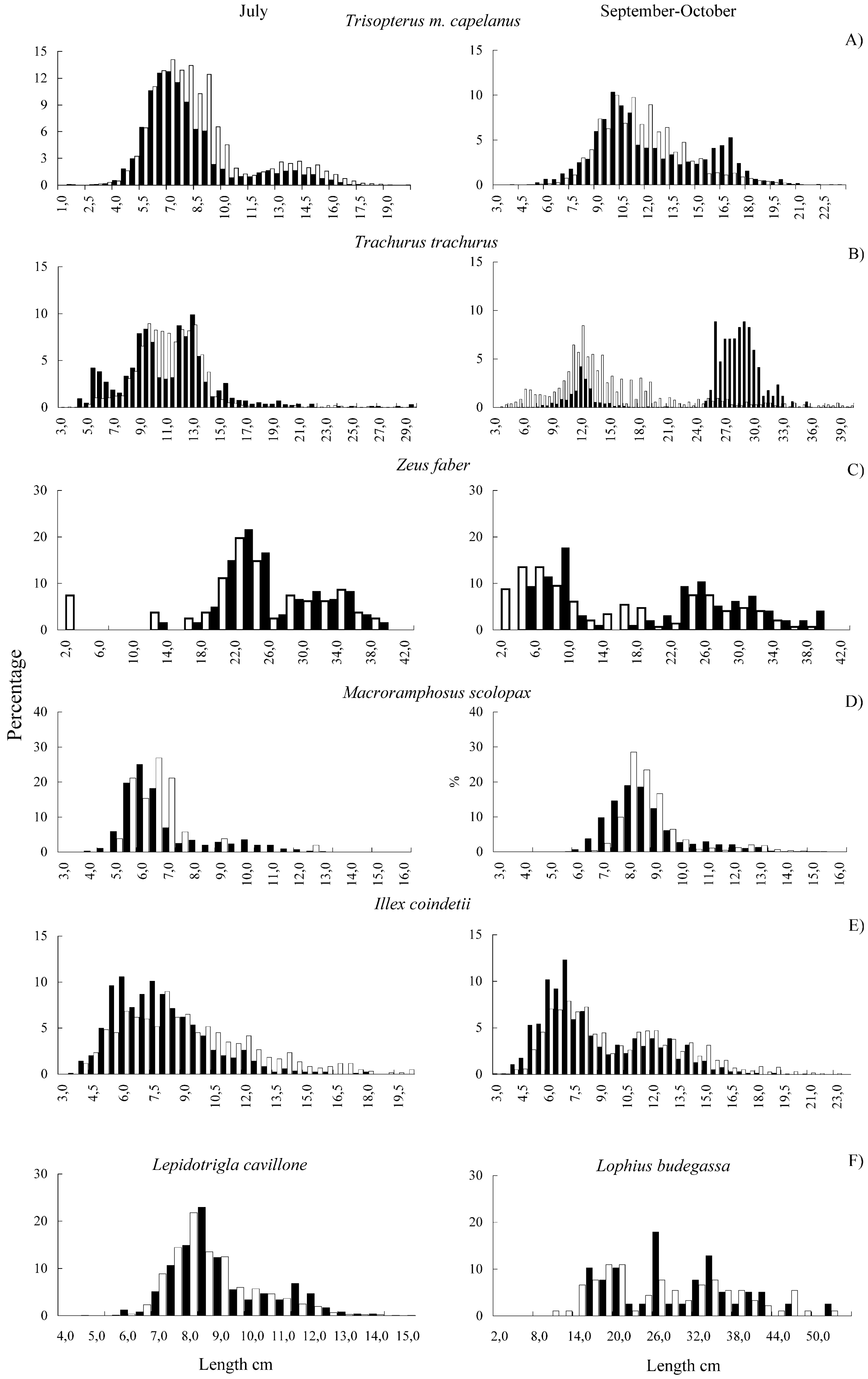
Fig. 7 Comparison of seasonal length frequency distributions of species which did not show any significant increased abundance of some cohorts on *Leptometra phalangium* stations (*black bars*) with respect to the whole trawled area (*white bars*)

The shelf break also plays a very important role in first recruitment of abundant species like deep-sea pink shrimp (*Parapenaeus longirostris*), rockfish (*Helicolenus dactylopterus*) and boarfish (*Capros aper*). These species spread over a wider depth range during growth (hake: Colloca et al. 2003b), or migrate deeper on upper slope bottoms (deep-sea pink shrimp: Ardizzone et al. 1990; rockfish: Ragonese and Reale 1995; boarfish: Massuti et al. 2001).

On the other hand, the red mullet (*Mullus barbatus*), brown comber (*Serranus cabrilla*) and four-spotted megrim (*Lepidorhombus boscii*) that occurred on the shelf break were mostly adults over the size-at-maturity. The red mullet recruits on shallow sandy bottoms during summer and shows a strong size–depth relationship (Lo Bianco 1909; Ardizzone and Corsi 1997). Largest individuals concentrate on shelf-break bottoms at the end of their reproduction period, so that the trawl catch in this area is mostly made up of fish over the age of first maturity. The brown comber (*Serranus cabrilla*) is a synchronous hermaphrodite species, generally distributed over continental shelf rocky bottoms. According to the growth pattern and length at maturity of this species in the Mediterranean, its occurrence on the shelf break is due to adults over 2 years of age (Siau and Bouain 1994; Tserpes and Tsimenides 2001). *Lepidorhombus boscii* is a shallow slope species, which shows an inverse size–depth relationship: juveniles are distributed deeper than adults, which concentrate close to the shelf break (Mannini et al. 1990; Sartor and De Ranieri 1996).

Another group of species (*Macroramphosus scolopax*, *Trisopterus m. capelanus*, *Trachurus trachurus*, *Zeus faber*, *Illex coindetii*, *Lepidotrigla cavillone*, *Aspitrigla cuculus*, *Lophius budegassa*) select the shelf break in all phases of their life, reaching highest yields in this area.

The spatial overlap of shelf species like *Serranus hepatus*, *Serranus cabrilla* and *Mullus barbatus* with typical slope species like *Phycis blennoides*, *Helicolenus dactylopterus* and *Parapenaeus longirostris* gives this assemblage ecotonal characteristics. As observed by Colloca et al. (2003b), the demersal fauna composition of the continental shelf shows little similarity with upper slope demersal fauna. Most of the species are confined to


July
September-October
Trisopterus m. capelanus
A)
0
3
6
9
12
15
1,0
2,5
4,0
5,5
7,0
8,5
10,0
11,5
13,0
14,5
16,0
17,5
19,0
0
5
10
15
3,0
4,5
6,0
7,5
9,0
10,5
12,0
13,5
15,0
16,5
18,0
19,5
21,0
22,5
Trachurus trachurus
B)
0
5
10
15
3,0
5,0
7,0
9,0
11,0
13,0
15,0
17,0
19,0
21,0
23,0
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27,0
29,0
3,0
6,0
9,0
12,0
15,0
18,0
21,0
24,0
27,0
30,0
33,0
36,0
39,0
Zeus faber
C)
0
10
20
30
2,0
6,0
10,0
14,0
18,0
22,0
26,0
30,0
34,0
38,0
42,0
Percentage
Macroramphosus scolopax
D)
0
10
20
30
40
%
3,0
4,0
5,0
6,0
7,0
8,0
9,0
10,0
11,0
12,0
13,0
14,0
15,0
16,0
Illex coindetii
E)
0
5
10
15
3,0
4,5
6,0
7,5
9,0
10,5
12,0
13,5
15,0
16,5
18,0
19,5
21,0
23,0
Lepidotrigla cavillone
Lophius budegassa
F)
0
10
20
30
4,0
5,0
6,0
7,0
8,0
9,0
10,0
11,0
12,0
13,0
14,0
15,0
2,0
8,0
14,0
20,0
26,0
32,0
38,0
44,0
50,0
Length cm
Length cm

one or the other of the two areas, and only a few eurybathic species (i.e. *Merluccius merluccius* and *Parapenaeus longirostris*) have a depth distribution from shelf to slope. This distribution pattern of species may be related to the oceanographic differences between these two areas: while slope waters show fairly constant temperatures and salinity during the year, the shelf is characterised by marked seasonal variations.

The increased abundance in the above-mentioned species on the shelf break can be related above all to the availability of epibenthic prey, mainly mysids such as *Lophogaster typicus* and *Anchialina* spp. associated with detritic shelf-break bottoms (Pérès and Picard 1964; Elizalde et al. 1991). In a previous study on trophic resources and the partitioning of demersal fish species in the shelf-break area, a correlation was found between abundance of prey resources in the environment and stomach contents (Colloca 2003).

The relationship between fish and benthic assemblage distribution has been documented in the Mediterranean for only a few of the above-mentioned species. A preference of John Dory and triglid species for detritic bottoms of the shelf break has been observed along the western coasts of Italy (Serena et al. 1990; Righini and Voliani 1996; Colloca et al. 1997). Most studies on Mediterranean fish distribution indicate that the main structural force is the depth factor. The other environmental parameters (temperature, salinity, light, sediments) either vary according to depth or play a minor role in species distribution. The benthos appears to play a major structuring role only on the continental shelf (Gaertner et al. 1999; Colloca et al. 2003a).

The occurrence on the Mediterranean shelf break of a defined assemblage of demersal and benthic species over a restricted depth range is of great importance for management and the development of multispecies-based approaches. Mediterranean assemblages are characterised by high diversity (Bianchi and Morri 2000; Colloca et al. 2003a) of either vertebrate (fish) or invertebrate (cephalopods, crustacean decapods, macro-epibenthos) organisms, which is mirrored in the catch composition of trawl fishery.

Management of such fisheries requires the development of technical measures for controlling the fishing effort, especially the establishment of closed areas designed to protect juvenile and spawning fish and fragile benthic communities (Lindeboom 2000; Murawsky et al. 2000).

The results of this study could have important consequences for the management of fish stocks and assemblages in the central Mediterranean. The co-occurrence of high densities of *L. phalangium* (DL-Lept benthic assemblage) and benthopelagic fish, occurring mainly as juveniles and spawners, strongly indicates the potential role of *L. phalangium* as an indicator of highly productive areas around the shelf break. Such areas appear to play a major role in the production of some of the most abundant and commercially important fish species, such as Mediterranean hake and red mullet, and can be viewed as essential fish habitats (e.g. Benaka 1999).

The protection of *L. phalangium* beds could have important consequences for fishery management in the Mediterranean, helping to reduce fish mortality rates in crucial stages of the their life cycle, such as when fish are juveniles or spawners and tend to concentrate in restricted areas. It is at these times that they are particularly vulnerable to towed gear.

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