

MEDITERRANEAN MARINE DEMERSAL RESOURCES: THE MEDITS INTERNATIONAL TRAWL SURVEY (1994-1999).
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Feeding guilds of western Mediterranean demersal fish and crustaceans: an analysis based on a spring survey*

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SUMMARY: The MEDITS-99 sampling was performed along all the Iberian Peninsula coasts of the western Mediterranean (from the Alborán Sea to Cape Creus) in a space-scale of 1000 Km N-S, at depths ranging between 27-790 m. Fish and decapod crustaceans were dominant in the megafaunal compartment sampled by trawling. Based on both the fish and the decapod crustacean compositions, a comparison of trophic guilds has been attempted, with fish and decapods classified as: 1) migrator macroplankton feeders (mM), 2) non-migrator macroplankton feeders (nmM), 3) nektobenthos-suprabenthos feeders (NS), 4) epibenthos feeders (Epib), 5) large detritus-scavengers (Sca), 6) infaunal feeders (Inf), 7) deposit feeders (Dep) and 8) small detritivorous feeders (Det). Multivariate techniques showed the following differences in the trophodynamics of the megafaunal assemblages along the coasts of the Iberian Peninsula: 1) crustaceans (mainly decapods) have different trophic structures on the shelf and on the slope; 2) on the slope, fish exhibited more clear changes as a function of the geographical gradient than crustaceans; and 3) trophodynamics of bathyal fish showed some geographic variations between the Alborán Sea, the Catalano-Balearic Basin, and the Algerian Basin (Vera Gulf and Alicante sectors), with a progressive north-south increase in planktophagous species.

Key words: feeding guilds, demersal fish, decapod crustaceans, western Mediterranean, trawl survey, Mediterranean.

INTRODUCTION

Demersal fisheries along the Mediterranean coasts have been directed at a variety of resources, including fish, decapod crustaceans and cephalopods (Bertrand and Relini, 2000). Trawling is the main fishing activity below the 50 m isobath, with an important increase in deep-water fisheries (deeper than 150 m) which have been operating for a long time (Bas *et al.*, 1955) on important target

species such as the shrimps *Parapenaeus longirostris* and *Aristeus antennatus*, the Norway lobster *Nephrops norvegicus*, or fish species such as hake *Merluccius merluccius* or *Phycis blennoides*. These fisheries can reach down to 800 m.

During recent years, sustainable use of natural resources has been increasingly enhanced. Deep-water communities have received increasing attention at a global scale because of the interest in new fishing grounds and fisheries at bathyal depths (Hopper, 1994; Merrett and Haedrich, 1997). However, deep-water ecosystems have lower energetical

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turnovers than shallow-water or littoral systems and their carrying capacity is expected to be lower. Since most of the target species are slow growing, overexploitation can be detected in deep-sea fisheries only after some years or decades after the beginning of a fishery (Atkinson, 1994; Bowering and Brodie, 1994; Koslow, 1997).

In addition to indices such as abundance, or harvest-induced mortality (Hutchings and Myers, 1994), to quantify changes and the impact in the carrying capacity of a system, trophodynamic aspects can be studied (Petersen and Curtis, 1980; Robinson and Ware, 1994; Christensen, 1995, among others). Trophodynamic studies constitute the base of mass-balance models (i.e. ECOPATH models), which have increasingly been considered for the study and management of marine ecosystems (Robinson and Ware, 1994; Wolff, 1994; Christensen, 1995; Pauly and Christensen, 1995). In practice, however, great difficulties exist in developing such models in deep-water systems, because only scarce data have been published on important quantitative aspects such as secondary production (Cartes and Sorbe, 1999; Cartes *et al.*, 2000), and daily rations (Maynou and Cartes, 1997; 1998; Cartes and Maynou, 2001), with only some preliminary trophic balances constructed for the mid-slope depths (Cartes and Maynou, 1998). Trophodynamic studies in deep-sea systems have often focused on species of commercial interest (Macpherson, 1985; Bulman and Koslow 1992, Maynou and Cartes 1997), whereas by-catches and studies on the lowest trophic levels, i.e. those compartments that sustain the trophic webs and fisheries, have received, in general, little attention (Christensen, 1995; Cartes and Maynou, 2001).

Even in stable environments such as the deep sea, local changes in the food supply and productivity may affect the trophic structure and dynamics of marine ecosystems, which are reflected for instance in the zonation pattern of species with depth (Haedrich and Merrett, 1990; Maynou and Cartes, 2000). It is, thus, often inappropriate to extrapolate the results obtained in a concrete area to a wider geographic scale. As an alternative to the lack of the integral sampling of trophic webs, comparative studies on trophic guilds composition with depth and geographic gradients can give information on changes in the ecosystem structure and functioning because changes in feeding guilds composition may reflect differences in the structure of trophic webs and in the energy flow. Thus, Koslow (1997) defined a distinct guild of fish species that aggregate around

seamounts in Australian waters where *Hoplostethus atlanticus* is the main target species. This guild is characterized by high levels of pelagic-food consumption and strong swimming performance. Recently, important differences were evidenced between the trophic guilds of bathyal crustaceans inhabiting the Catalan Sea and the SW Balearic Islands, with dominance of non-migrator macroplankton feeders (mainly composed by *Plesionika* spp. shrimps) in the SW Balearic Islands, and higher abundance of infaunal and deposit feeders in the Catalan Sea area (Cartes *et al.*, 2000; Maynou and Cartes, 2000). Plankton and benthos may, thus, support distinctly trophic chains in relatively neighbouring areas. Our objective in this study is to compare and identify zones with different food-web structures (i.e. more or less supported by plankton or benthos productivity), along the wide geographic area covered in MEDITS cruises in a space-scale of 1000 Km. Plankton and benthos are two contrasting food sources in marine environments as evidenced, for instance, from results obtained using $\delta^{13}\text{C}$ stable isotope analysis (Jennings *et al.*, 1997).

MATERIAL AND METHODS

The MEDITS-ES99 cruise (May-June 1999) comprised a total of 116 trawls performed between 27 and 790 m depth along the coasts of the Iberian Peninsula (western Mediterranean) from the Straits of Gibraltar to Cape Creus (Fig.1). Fish and crustaceans (mainly megabenthic decapods) were sampled with an especially designed bottom trawl (cf. Bertrand *et al.*, 2000), equipped with two doors, two trawl warps, and a 100 m long bridle, with an horizontal aperture of *ca.* 18 m and a vertical height of *ca.* 2 m. The codend mesh size was 10 mm. In previous studies on MEDITS cruises (Abelló *et al.*, 2000, 2002; Carbonell *et al.*, 2000), this area was divided into eight geographical sectors: (1) Western Alborán Sea (WALB), from Gibraltar to Nerja; (2) Eastern Alborán Sea (EALB), from Nerja to Cape Gata; (3) Vera Gulf (VERA), from Cape Gata to Cape Palos; (4) Alacant region (ALAC), from Cape Gata to Cape La Nao; (5) Valencia (VALE), from Cape La Nao to Castelló; (6) Ebro delta region (DELTA), from Castelló to Tarragona; (7) Northern Catalonia (NCAT), from Tarragona to Cape Creus, and (8) Eivissa island (EIV) (Fig. 1). We adopted this same nomenclature to the *a posteriori* labelling of our sampling stations in the multivariate analysis results.

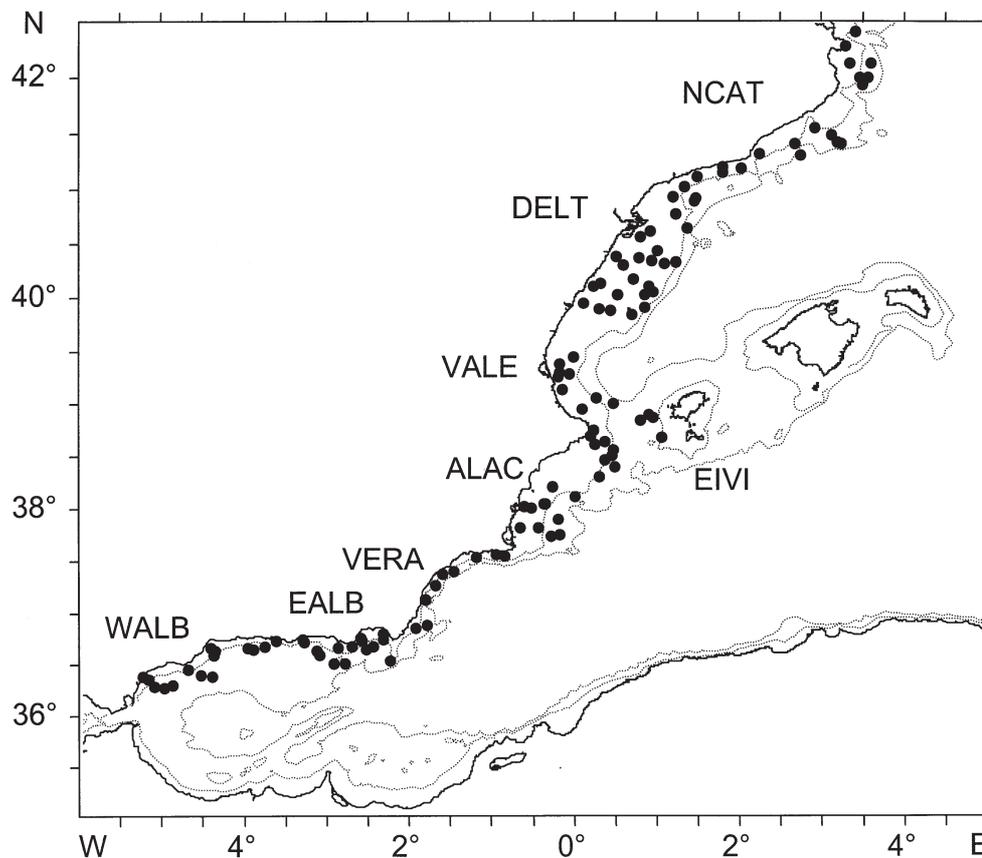


FIG. 1. – Map of the study area off the Mediterranean Iberian Peninsula, showing the trawl location and the sectors in which the coast was divided.

Feeding guilds were established for fish and crustaceans. Both fish and crustacean species were classified within the following feeding groups (or guilds): 1) migrator macroplankton feeders (mM), 2) non-migrator macroplankton feeders (nmM), 3) nektobenthos-suprabenthos (=vagile fauna) feeders (NS), 4) epibenthos (= non vagile fauna) feeders (Epib), 5) large detritivorous-scavengers (Sca), 6) infaunal feeders (Inf), 7) deposit feeders (Dep), and 8) small detritivorous feeders (Det). Guilds 1, 2, 4 and 6 are both common to fish and decapods, guild 3 is described only for fish, while guilds 5, 7 (deposit feeders) and 8 (small detritivorous feeders) only existed among crustaceans (see Table 1).

Trophic guilds have been already defined in previous studies both among fish (e.g. Gartner *et al.*, 1997) and Mediterranean decapod crustaceans (Cartes, 1998; Maynou and Cartes, 2000). In our study, guilds are defined based on detailed information both on crustaceans and on bathyal-fish diets in the western Mediterranean (Cartes, 1991; 1994; 1998; Cartes and Abelló, 1992; Macpherson, 1977, 1979; Carrasson and Matallanas, 1990; Carrasson *et*

al., 1992; Carrasson, 1994; Stefanescu and Cartes, 1992 and references cited therein). In addition, summary diets of a total of seven decapod species, not previously documented, have been included in Table 2. The established guilds show the dependence of the fish/crustacean ratio on the exploitation of benthic or pelagic food resources which may in turn indicate local changes in the trophic structure of trophic webs. It is also well known that, even in a relatively stable environment such as the deep sea, fish have seasonal changes in their diet. The temporal effect is minimized in our study given the practically simultaneous sampling of an extensive area covered in the MEDITS cruise. We also assume that feeding preferences of species did not vary along the geographical gradient covered in the MEDITS cruise (see discussion below).

Crustacean feeding guilds were studied throughout the bathymetric range sampled. Fish, however, were only considered at bathyal depths, due to: (i) the gaps existing for dietary studies in an important proportion of shelf fish in the area; and (ii) we considered it inappropriate to extrapolate the results of

TABLE 1. – Classification of the most abundant species (crustaceans and bathyal fish) in trophic guilds: 1) migrator macroplankton feeders (mM), 2) non-migrator macroplankton feeders (nmM), 3) nektobenthos-suprabenthos feeders (NS), 4) epibenthos feeders (Epib), 5) large detritus-scavengers (Sca), 6) infaunal feeders (Inf), 7) deposit feeders (Dep), 8) small detritivorous feeders (Det). Sources: (1) Dietary information obtained from references included in the reference list or in the present study (see Table 2); (2) from other references not included in the reference list; (3) from general information obtained from the Fishbase dataset (<http://ibs.uel.ac.uk/fishbase/>), and from Wittehead *et al.* (1986); (4) own unpublished data; and (5) diet assumed from neighbouring species.

Fish		source	Crustaceans		source
<i>Myctophum punctatum</i>	mM	(2)	<i>Gennadas elegans</i>	mM	(1)
<i>Lampanyctus crocodilus</i>	mM	(1)	<i>Pasiphaea multidentata</i>	mM	(1)
<i>Argyroleucus hemigymnus</i>	mM	(2)	<i>Pasiphaea sivado</i>	mM	(1)
<i>Symbolophorus veranyi</i>	mM	(2)	<i>Sergestes arcticus</i>	mM	(2)
<i>Notoscopelus elongatus</i>	mM	(2)	<i>Sergestes arachnipedus</i>	mM	(4)
<i>Benthosema glaciale</i>	mM	(2)	<i>Sergia robusta</i>	mM	(1)
<i>Stomias boa</i>	mM	(2)	<i>Plesionika narval</i>	nmM	(4)
<i>Maurolicus muelleri</i>	mM	(2)	<i>Plesionika acanthonotus</i>	nmM	(1)
<i>Ceratoscopelus maderensis</i>	mM	(3)	<i>Plesionika antigai</i>	nmM	(5)
<i>Mora moro</i>	nmM	(1)	<i>Plesionika edwardsi</i>	nmM	(1)
<i>Etmopterus spinax</i>	nmM	(1)	<i>Plesionika gigliolii</i>	nmM	(1)
<i>Capros aper</i>	nmM	(1)	<i>Plesionika heterocarpus</i>	nmM	(1)
<i>Scyliorhinus canicula</i>	nmM	(1)	<i>Plesionika martia</i>	nmM	(1)
<i>Alepocephalus rostratus</i>	nmM	(1)	<i>Natatolana borealis</i>	Sca	(4)
<i>Micromesistius poutassou</i>	nmM	(1)	<i>Munida intermedia</i>	Sca	(1)
<i>Macroramphosus scolopax</i>	nmM	(1)	<i>Munida rullanti</i>	Sca	(4)
<i>Epigonus denticulatus</i>	nmM	(1)	<i>Munida tenuimana</i>	Sca	(1)
<i>Hoplostethus mediterraneus</i>	nmM	(1)	<i>Pagurus alatus</i>	Sca	(1)
<i>Gadiculus argenteus</i>	nmM	(1)	<i>Pagurus excavatus</i>	Sca	(1)
<i>Galeus melastomus</i>	nmM	(1)	<i>Pagurus prideaux</i>	Sca	(5)
<i>Lepidopus caudatus</i>	nmM	(1)	<i>Dardanus arrosor</i>	Sca	(5)
<i>Trisopterus minutus capelanus</i>	NS	(1)	<i>Polycheles typhlops</i>	Epib	(1)
<i>Ophichthus rufus</i>	NS	(3)	<i>Bathynectes maravigna</i>	Epib	(5)
<i>Lophius budegassa</i>	NS	(1)	<i>Ligur ensiferus</i>	Epib	(1)
<i>Molva dipterygia</i>	NS	(1)	<i>Liocarcinus depurator</i>	Epib	(2)
<i>Conger conger</i>	NS	(1)	<i>Macropipus tuberculatus</i>	Epib	(2)
<i>Nezumia aequalis</i>	NS	(1)	<i>Polybius henslowi</i>	Epib	(3)
<i>Serranus hepatus</i>	NS	(3)	<i>Squilla mantis</i>	Epib	(3)
<i>Hymenocephalus italicus</i>	NS	(1)	<i>Rissoides pallidus</i>	Epib	(5)
<i>Merluccius merluccius</i>	NS	(1)	<i>Aristeus antennatus</i>	Inf	(1)
<i>Chorophthalmus agassizi</i>	NS	(3)	<i>Chlorotocus crassicornis</i>	Inf	(1)
<i>Pagellus acarne</i>	NS	(3)	<i>Calappa granulata</i>	Inf	(1)
<i>Notacanthus bonapartei</i>	Epib	(1)	<i>Geryon longipes</i>	Inf	(2)
<i>Helicolenus dactylopterus</i>	Epib	(1)	<i>Goneplax rhomboides</i>	Inf	(4)
<i>Symphurus ligulatus</i>	Inf	(1)	<i>Medorippe lanata</i>	Inf	(5)
<i>Antonogadus megalokinodon</i>	Inf	(1)	<i>Monodaeus couchii</i>	Inf	(2)
<i>Arnoglossus laterna</i>	Inf	(3)	<i>Nephrops norvegicus</i>	Inf	(1)
<i>Arnoglossus rueppelli</i>	Inf	(3)	<i>Parapenaeus longirostris</i>	Inf	(1)
<i>Phycis blennoides</i>	Inf	(1)	<i>Philocheras echinulatus</i>	Inf	(1)
<i>Lepidorhombus boscii</i>	Inf	(1)	<i>Pontocaris cataphracta</i>	Inf	(5)
<i>Coelorhynchus coelorhynchus</i>	Inf	(1)	<i>Pontocaris lacazei</i>	Inf	(1)
<i>Chimaera monstrosa</i>	Inf	(1)	<i>Pontophilus spinosus</i>	Inf	(1)
<i>Trachyrhynchus trachyrhynchus</i>	Inf	(1)	<i>Processa canaliculata</i>	Inf	(1)
<i>Symphurus nigrescens</i>	Inf	(1)	<i>Processa nouveli</i>	Inf	(1)
			<i>Solenocera membranacea</i>	Inf	(1)
			<i>Atelecyclus rotundatus</i>	Inf	(5)
			<i>Calocaris macandreae</i>	Dep	(1)
			<i>Alpheus glaber</i>	Dep	(4)
			<i>Meganyctiphanes norvegica</i>	Det	(4)
			<i>Pandalina profunda</i>	Det	(4)
			<i>Lophogaster typicus</i>	Det	(4)

dietary studies made in other areas, in view of the high habitat and food-source heterogeneity reported for shelf-living fish (see for instance Jennings *et al.*, 1997). Bathyal hauls for the fish-guilds study were selected after a cluster analysis was performed on the matrix of species composition. This matrix was constructed based on 185,383 specimens pertaining to 114 species captured in 116 trawls. Species occurring with < 5 specimens were removed from the data

matrix and the captures were standardized to 1-h of trawling. The Pearson correlation coefficient (1-r) was used as distance and the UPGMA as the algorithm of aggregation (Statistica 4.5), after log transformation of values to linearize data. The cluster analysis (Fig. 2) exhibited a major fish-faunistic discontinuity situated around 325-341 m, separating the group of bathyal trawls (down to 790 m) from the group including the shelf-fish assemblages (27

Table 2.- Diets of different decapod species dominant in the present survey. (n): number of individuals analyzed; TG: trophic guild assigned. (*) from MEDITS-99 cruise.

Species	prey items	n	TG	observations
<i>Gemadas elegans</i>	calanoids	7	mM	
<i>Sergia robusta</i>	calanoids, euphausiids, chaetognaths.	18	mM	R1 cruise: April 1990
<i>Plesionika gigliolii</i>	euphausiids, <i>Sergestes</i> sp., siphonophora	16	nmM	R3 cruise: March 1991
<i>Plesionika heterocarpus</i> *	euphausiids	9	nmM	euphausiids: 100% volume
<i>Ligur ensiferus</i>	Gammaridean amphipods, echinoderms	40	Epib	R2 cruise: December 1991
<i>Chlorotocus crassicornis</i> *	euphausiids, molluscs	15	nmM	probably pelagic molluscs
<i>Calappa granulata</i> *	bivalves, foraminiferans	3	Inf	

to 325-341 m). Within this last group, a secondary homogeneous cluster was identified containing trawls between 240 to 341 m. As a consequence, those trawls exceeding 300 m depth were selected in this study for trophic guild analysis, thus avoiding the excess of heterogeneity in the samples. Under this criterion, a total of 18,533 specimens pertaining to 53 bathyal species captured in 42 trawls were selected.

Once feeding groups were established, clustering methods were applied (1-r / UPGMA) to the crustacean and fish matrix feeding groups. For crustaceans, species occurring with < 5 specimens, and trawls where < 8 individuals were captured were removed from the data matrix, resulting in a total of

97 valid trawls. Cluster analysis showed two main assemblages separating the continental shelf and the slope samples (see below). Multidimensional scaling (MDS) techniques were applied to the similarity matrix generated by clustering (1-r measure) to obtain a 2-dimensional representation of the trophic guild composition of: 1) crustaceans from the continental shelf; 2) bathyal fish from those trawls exceeding 300 m depth (see above); and 3) bathyal crustaceans, which were only considered from trawls exceeding 300 m to give a more reliable comparison between fish and crustaceans. The objective was to explore other factors than depth (especially geographical variations) which may contribute to the ordination of trophic guilds along interpretable dimensions.

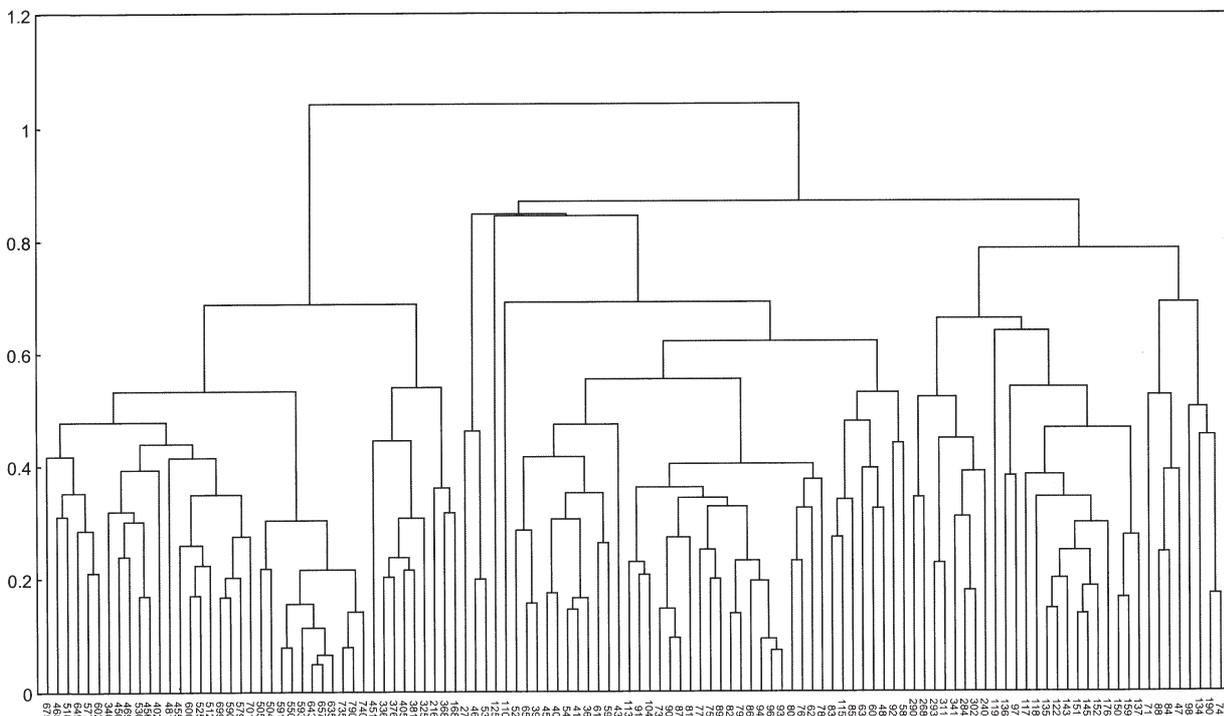


Fig. 2. – Cluster analysis performed on the matrix of fish species composition standardized to 1 h of trawling (1-r; UPGMA). Codes of the samples indicate mean depth of the haul.

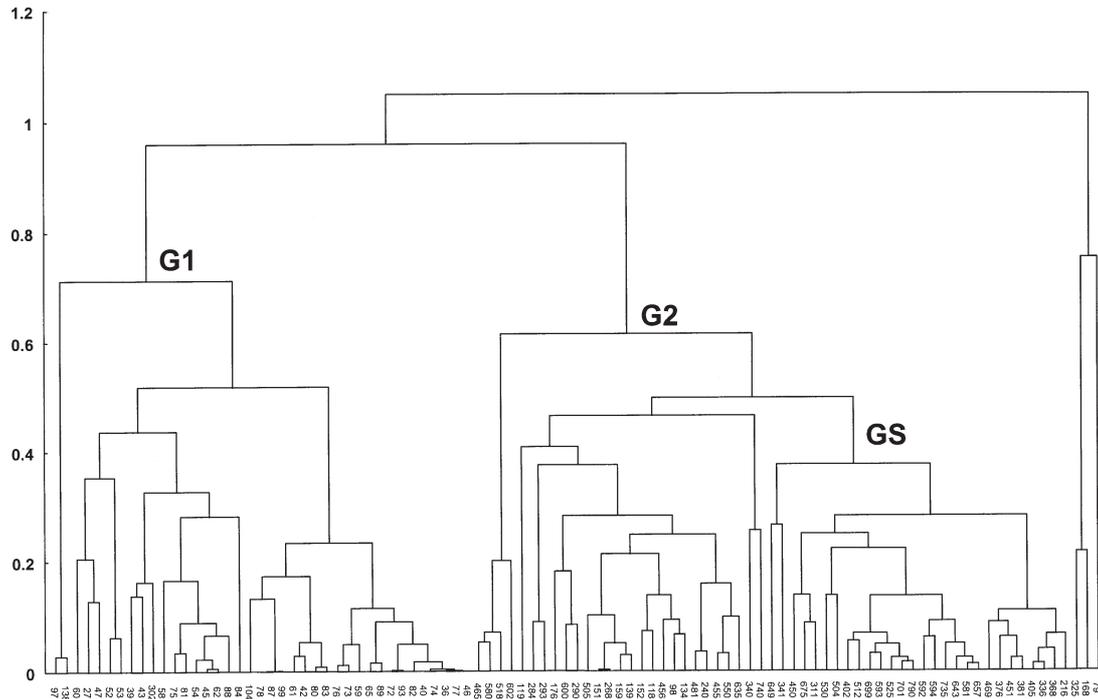


Fig. 3. – Cluster for crustacean trophic guilds showing the shelf (G1) and the slope (G2) groups. 1-r (Pearson correlation) was the distance used and UPGMA was the aggregation algorithm. Codes of the samples indicate mean depth of the haul.

RESULTS

Qualitative data on the diet of seven decapod crustaceans have been obtained based on stomach content analysis. Species were included in their corresponding feeding guild based on this information (Table 2).

Cluster analysis revealed a clear separation in trophic-guild composition among crustaceans (mainly decapods) collected, with low r (of *ca.* 0) separating the two main groups of samples (Fig. 3). These groups were clearly formed as a function of depth, revealing quite different trophic composition and probably trophodynamics on the continental shelf and on the slope: G1 comprised hauls performed between 27 and 138 m (excluding a single haul performed at 302 m); and G2 comprised hauls between 118 and 790 m depth (with the single exception of a haul performed at 98 m). Within G2, further depth separations existed with a deeper homogeneous group which was almost exclusively composed of trawlings performed between 311 and 790 m (Fig. 3; G_s). Similar results, at least concerning the identification of G1 and G2 groups, were attained using the Euclidean distance and Ward algorithm (not included).

We tried to identify some other gradient (e.g. geographical) within the shelf (trawling depths

between 27 and 118 m; 44 samples) and the slope (> 300 m depth; 42 samples) groups: Among crustaceans, MDS based on the 1-r similarity matrix did not reveal any clear subgrouping, neither within the shelf nor the slope groups. The shelf samples were ordered (stress = 0.154) in a 2-dimensional space, as in the case of slope samples (stress = 0.160). The 44 shelf samples were not grouped as a function of any geographical gradient (Fig. 4a). Shelf samples from the area around the Ebro river delta (DELTA sector) and the Alborán Sea occupied the extremes of the gradient in the MDS plot, which suggests that some ordination probably takes place in the continental shelf as a function of small-scale changes in the sediment characteristics (a non-measured parameter in the present study). Among the 42 slope samples, six samples corresponding to the Catalan Sea area (NCAT sector) showed some separation. Also, certain gradient of north-south ordination can be observed along the first axis (factor 1), with some northern (NCAT), and southern (WALB) samples placed in the extremes of the axis (Fig. 4b). However the rest of bathyal samples did not show any ordination.

Among bathyal fish, both the clustering and the MDS, based also on the 1-r similarity matrix, gave some separation of samples. Cluster analysis (Fig. 5) revealed a first homogeneous group of seven trawls

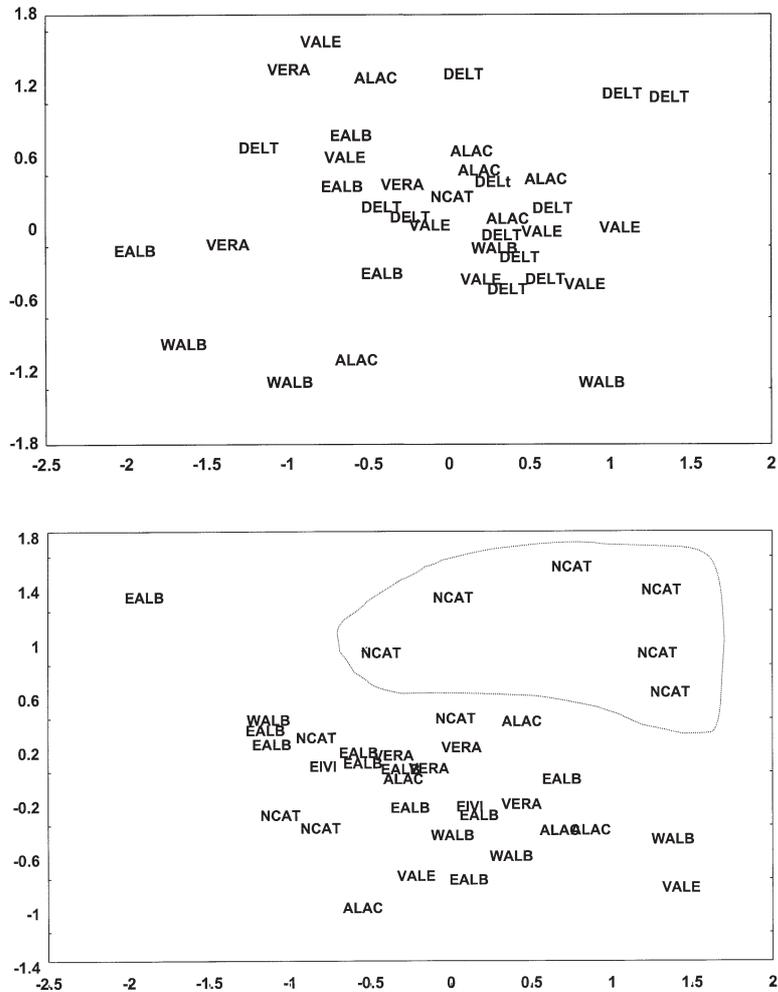


FIG. 4. – MDS for crustacean trophic guilds; (a): shelf species; (b) slope species.

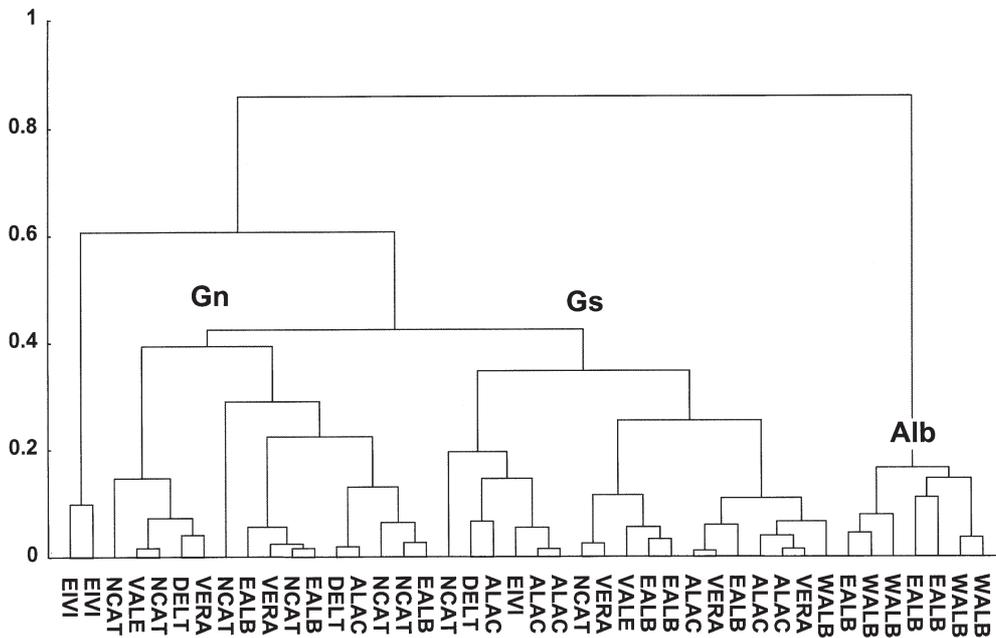


FIG. 5. – Cluster for the trophic guilds of bathyal fish (1-r / UPGMA), showing the formation of groups for the Catalano-Balearic Basin (Gn), the Algerian Basin (Gs), and the Alborán Sea (Alb).

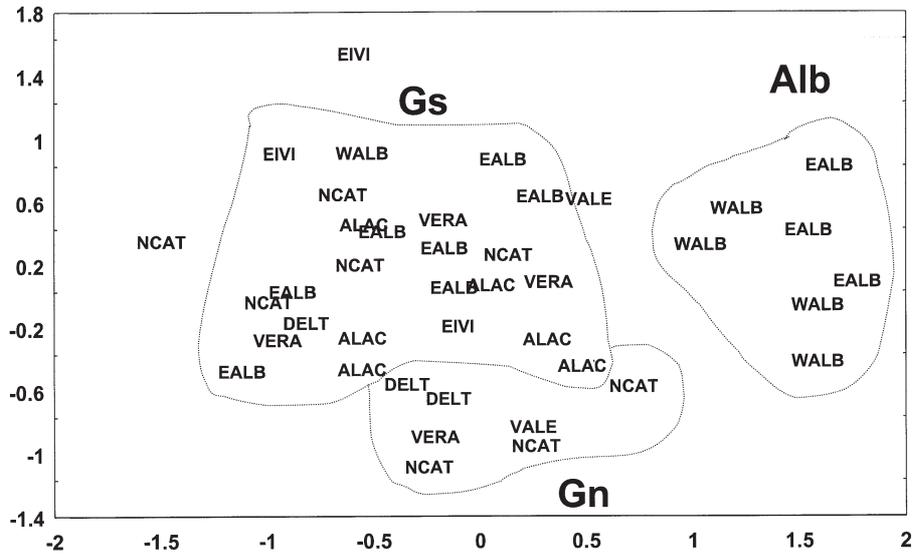


FIG. 6. – MDS analysis showing the distribution of groups of samples for the Catalano-Balearic Basin (Gn), the Algerian Basin (Gs), and the Alborán Sea (Alb).

performed in the Alborán Sea (Alb) which were dissimilar ($1-r = 0.84$) from the rest of samples. Some new groupings were also detected between trawls performed north and south from Cape La Nao (Fig. 5). Gs included 18 trawls, 15 of them performed south from Cape La Nao, whereas Gn included 15 trawls, 10 of them collected in the Catalano-Balearic Basin, north from Cape La Nao. Furthermore, the fact that some samples collected in a same sector (i.e. NCAT, WALB, EIVI....) were further grouped, suggested small-scale or local spatial trends in the changes and distribution of trophic guilds. The MDS (stress = 0.150) separated the Alb group of seven samples (Fig. 6) from the rest. Within this last group, Gs, containing most of the samples from VERA, ALAC sectors, and also samples from EALB not included in the Alb group, can be identified in the top of Axis 2. The Gn group (Axis 2: bottom) is characterized by the dominance of samples

from VALE, DELT, and NCAT sectors and the total absence of EALB-WALB samples. It is interesting to compare the MDS results obtained for bathyal crustaceans and fish (Figs. 4b and 6), with a clearer geographical gradient detected among bathyal fish with some differences in the composition of guilds north and south from Cape La Nao.

The composition of trophic guilds for crustaceans has been detailed in Table 3. On the continental shelf, crustacean assemblages were dominated by non-migrator macroplankton feeders (nmM; 54.8%), and by epibenthos feeders (Epi; 25.0%), both accumulating *ca.* 80% of abundance. The pandalid shrimps *Plesionika heterocarpus* and *Chlorotocus crassicornis* were the dominant species among nmM, while portunid crabs (*Liocarcinus depurator* and *Macropipus tuberculatus*) dominated among Epi. On the slope (>300 m depth), migrator macroplankton feeders (mM), and non-migrator macroplankton feeders (nmM), dominated accumulating *ca.* 86% of abundance (Table 3). *Pasiphaea sivado* and *Sergestes arcticus* dominated among the mM, and *Plesionika* spp. among the nmM. Infaunal feeders (Inf; i.e. *Parapenaeus longirostris* and *Aristeus antennatus*) also reached some importance at this level (9.4%).

Bathyal-fish assemblages were dominated by non-migrator macroplankton feeders (nmM) and infaunal feeders (Inf), accumulating *ca.* 70% of abundance (Table 4). The dominant species were the shark *Galeus melastomus*, the bony fish *Gadiculus argenteus* and *Hoplostethus mediterraneus* among

TABLE 3. – Abundance (ind/h) and percentage of the different trophic guilds for crustaceans obtained from cluster analysis. n: number of samples.

	shelf n=44		slope n=42		
	ind./h	(%)	ind./h	(%)	
nmM	56.3	54.8	mM	671.3	55.9
EpB	25.7	25.0	nmM	360.1	30.0
InfB	11.2	10.9	InfB	113.2	9.4
Sca	6.9	6.7	Sca	13.4	1.1
mM	0	0	EpB	9.4	0.8
TOTAL	101.1			1167.4	

TABLE 4. – Abundance (ind/h) and percentage of the different trophic guilds among bathyal fish by geographical area, obtained from cluster and MDS analysis. *Algerian Basin excluding the Alborán Sea area. n: number of samples.

Catalano-Balearic Basin n=12			Algerian Basin* n=15			Alborán Sea n=7		
	ind./h	(%)		ind./h	(%)		ind./h	(%)
infB	106.2	47.5	nmM	184.8	43.8	nmM	309.9	50.0
mM	81.5	36.5	mM	125.7	29.8	vB	188.7	30.4
nmM	20.2	9.0	infB	85.1	20.2	infB	60.4	9.7
vB	9.7	4.3	vB	17.8	4.2	EpB	35.6	5.7
EpB	3.0	1.3	EpB	4.1	1.0	mM	22.7	3.7
TOTAL	220.6			422.5			617.3	

nmM, and *Phycis blennoides* and *Coelorhynchus coelorhynchus* within the Inf group. Geographical changes detected in trophic guilds among fish consisted in a higher percentage of abundance of Inf group in the Catalano-Balearic Basin (47.5%), while nmM were dominant in G2 (Algerian Basin south of La Nao cape; 43.8%) and in the Alborán Sea group (50%) (Table 4). One-way ANOVAs and *post-hoc* Scheffé test indicated higher significant differences in the mean density (ind./h; n=42) of some trophic guilds between the three geographical areas obtained from multivariate analysis of bathyal fish. The density of the mM guild in the Alborán Sea (Alb) was significantly higher than in the Algerian Basin (AB) and in the Catalano-Balearic Basin (CBB) ($p < 0.05$), while the density of nmM feeders was only significant between Alb and CBB ($p < 0.01$). The density of the NS guild in the Alborán Sea (Alb) was also significantly higher than in the Algerian Basin (AB) and in the Catalano-Balearic Basin (CBB) ($p < 0.001$). Between the AB and the CBB significant differences were only recorded comparing the density of the mM guild ($p < 0.05$).

DISCUSSION

Analysis of feeding guilds may show differences in trophic structure and ecosystem dynamics, and therefore may have implications for the management of fisheries (Koslow, 1997). Along the coasts of the Iberian Peninsula, fish and crustacean communities exhibited different trophic structures depending not only on the taxa considered, but also on the depth of occurrence (shelf and slope assemblages), and on a geographical gradient. Shelf crustacean guilds prey more on benthos (42%) than bathyal crustacean guilds (11%), while zooplankton resources were more consumed by bathyal crustaceans (86%) than by shelf species (55%). Crus-

taceans, however, are a secondary taxa in shelf communities (mean density: 100.1 ind/h), where fishes widely dominate (mean density: 1604 ind/h). As in the case of crustaceans, bathyal fish assemblages are also dominated by zooplanktophagous species (61.4%) with some geographical variations (see below). The dominant shelf species were *Capros aper*, *Maurolicus muelleri* or small *Merluccius merluccius* (see Table 5) which also are well-natatory species preying on plankton resources (Macpherson, 1977; Wittehead *et al.*, 1986), attaining similar dominance (> 68.5% of abundance) as that of bathyal fishes. These species are among the dominant fish in previous samplings conducted in the same area (Lloris *et al.*, 2000).

Considering fish and crustaceans together, the plankton/benthos consumer ratio would be situated ~2.3/1 on the continental shelf, increasing to ~4/1 at the slope, which suggests a higher dependence on pelagic trophic resources by bathyal communities. These results are generally consistent with the available data both on the distribution of zooplankton and macrobenthos (available prey) on the shelf and slope in the study area. Thus, Sabatés *et al.* (1989) reported a major density of zooplankton offshore in the

TABLE 5. – Main fish species caught from shelf depths ordered by decreasing order of abundance (ind/h) during the MEDITS-99 survey. %D: percentage of density.

Species	D(ind./h)	%D
<i>Capros aper</i>	296.5	18.5
<i>Maurolicus muelleri</i>	230.2	14.4
<i>Merluccius merluccius</i>	186.1	11.6
<i>Cristallogobius linearis</i>	136.1	8.5
<i>Trachurus trachurus</i>	105.8	6.6
<i>Sardina pilchardus</i>	99.8	6.2
<i>Trisopterus minutus capelanus</i>	67.0	4.2
<i>Macroramphosus scolopax</i>	45.7	2.8
<i>Boops boops</i>	45.1	2.8
<i>Spicara smaris</i>	40.5	2.5
TOTAL	1603.5	78.1

shelf-slope break, associated with the permanent thermohaline front in the Catalan Sea area (Catalano-Balearic Basin). Similar frontal systems are also described in the mainland margins of the Algerian Basin (Millot, 1987). In contrast, benthos resources had higher importance as food-source in shelf communities, which is also consistent with a generally recognised decrease in benthos biomass with depth (Rowe, 1983). In the western Mediterranean, biomass and diversity of megafaunal invertebrates, such as echinoderms, were higher on the shelf (Pérès, 1985), a fact that was also observed in the present sampling (pers. obs.). In the Catalano-Balearic Basin, macrofaunal benthos biomass is 2.04 gAFDW/m² at shelf depths (Guille, 1971), decreasing to 0.37 gDW/m² at bathyal depths (400-600 m) off Barcelona (authors unpubl. data).

Trophic guilds are widely defined and employed in macrobenthos studies (i.e. polychaetes: Fauchald and Jumars, 1979). Although this concept is less used in megafaunal studies, some authors also defined trophic guilds for fish (Gartner *et al.*, 1997) using also equivalent functional feeding terms, such as trophic groups (Cartes, 1998) or feeding associations (Macpherson and Roel, 1987) both for fish and for large decapod crustaceans. The fact of including a species within a concrete feeding group or guild may be submitted to some criticisms since fish (and decapods) are euryphagous with a mixed diet, mainly, but not strictly, based on benthos or plankton prey (Macpherson and Roel, 1987; Mauchline and Gordon, 1991; Cartes, 1998). Furthermore, even in a relatively stable environment such as the deep sea, fish and invertebrates have changes in diet depending on size and season (Macpherson and Roel 1987; Cartes, 1994; 1998).

Our study has basically a comparative value, since the MEDITES-99 cruise was performed in May-June, the period after the peak of primary production when a higher plankton biomass is available, thus probably biasing the diet of fish and crustaceans. We also assume that feeding preferences of species do not vary along the geographic gradient covered, this seeming reasonable when comparing the diet of some representative species from distant geographical areas. Thus, the red shrimp *Aristeus antennatus* preys mainly on polychaetes, bivalves and small peracarid crustaceans in the Catalan Sea (Cartes, 1994), in the Ligurian Sea (Relini Orsi and Würtz, 1977), and on the Atlantic coast of Morocco (Lagardère, 1972). A similar case is that of the shrimp *Aristeomorpha foliacea* which has a similar

diet, based on pandalid shrimps and euphausiids, off the Balearic Islands (Cartes, 1995), off Morocco (Lagardère, 1972) and also probably in Australian waters, where this shrimp preys on midwater crustaceans (Rainer, 1992). The Norway lobster *Nephrops norvegicus* preys on similar resources (polychaetes, decapod crustaceans and fish) at bathyal depths in the Bay of Biscay (Lagardère, 1977) and in the deep-Mediterranean (Cristo and Cartes, 1998; unpubl. data), with small changes only among secondary prey. Among fishes, bathyal species such as *Helicolenus dactylopterus* or vicariant *Merluccius* spp. (among many others) also have similar diets, concerning feeding guilds, in the western Mediterranean and off Namibia (Macpherson, 1977; Macpherson and Roel, 1987). There are numerous similar examples, not only restricted to commercial species (cf. Cartes, 1991, 1995), which generally support the assumption that feeding preferences of species do not vary along their geographical distribution covering similar habitats, particularly at bathyal environments.

Along the geographical gradient covered in this study, fish showed the most clear variations in trophodynamics in contrast to the almost non-existent changes detected for crustaceans. A latitudinal gradient on the trophic structure of marine ecosystems has already been cited, with energy flow being distinctly partitioned between benthos/plankton production from subarctic to tropical waters, thus supporting more demersal or pelagic fisheries (Petersen and Curtis, 1980). At our spatial scale, similar trends seem to occur only within bathyal fish assemblages, with an increase in macroplankton feeders in the Algerian Basin (southern Cape La Nao). Among crustaceans, distinct trophic guild composition has been detected previously comparing bathyal assemblages off the Catalan Sea and the SW Balearic Islands (off Eivissa), with higher dominance of the non-migrator macroplankton feeders (mainly composed by *Plesionika* spp.) off the SW Balearic Islands, and infaunal and deposit feeders in the Catalan Sea (Cartes *et al.*, in press). These changes were probably not observed here because none of the Iberian coast sectors sampled have the characteristics of an open-sea area (i.e. low river discharges, absence of large submarine canyons....) occurring in the SW Balearic Islands.

Changes in the trophic structure detected among fish, may probably be related to their higher trophic level (TL) in comparison to decapods. Further to dietary studies which confirm that large fish (i.e.

sharks, *Mora moro*, *M. merluccius*) prey on decapods, thus occupying a higher TL (i.e. Carrasson *et al.*, 1992), recent data on $\delta^{15}\text{N}$ stable isotopic composition confirm this same trend (Polunin *et al.*, in press). Rex (1977) postulated more rapid changes in marine species substitution with depth with increasing trophic level, a hypothesis that has also been documented among deep-sea decapod crustaceans (Cartes, 1998). An extrapolation of this hypothesis at a "horizontal" spatial scale may explain why only fish, situated in a higher TL than decapods, showed geographical changes in the composition of their trophic guilds. Changes in deep-demersal fish communities at similar spatial scales as ours have been already documented off New Zealand (McClatchie *et al.*, 1997), correlated to regional changes in surface phytoplankton production, while bottom substratum is also important in the distribution of continental shelf and upper slope fish assemblages off the Catalan coasts (Demestre *et al.*, 2000). The Alborán Sea has an unusual high primary production in comparison to other neighbouring Mediterranean areas, as can be observed based on satellite imagery. This feature may support a similar conclusion to that discussed for deep fish communities off New Zealand (McClatchie *et al.*, 1997).

In summary, in the present study we have shown the following trends in the trophodynamics of the megafaunal assemblages along the coasts of the Iberian Peninsula depending on depth, taxa and the geographical gradient: 1) crustaceans (mainly decapods) have different trophic structure on the shelf and on the slope; 2) on the slope, fish exhibited clearer changes as a function of the geographical gradient than crustaceans; and 3) trophodynamics of bathyal fish showed some geographical variations between the Alborán Sea, the Catalano-Balearic Basin, and the Algerian Basin (basically VERA-ALAC sectors), with a progressive north-south increase in planktophagous species. More detailed and smaller spatial-scale studies on these trends (and their possible causes) may confirm whether the future management of these ecosystems should be considered under the depth and geographical strata here suggested.

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