

Effect of environmental variations on sharks and other top predators in the deep Mediterranean Sea over the last 60 years

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ABSTRACT: The deep Mediterranean, which is characterized by high thermohaline stability, has suffered important changes in the last century, but these have seldom been analyzed with regard to megafauna. Long-term changes in fish and decapod assemblages in the Balearic Basin (western Mediterranean) were analyzed after compiling (since 1952) the species compositions of hauls taken at depths of ca. 400 to 600 m. Multidimensional scaling analysis (MDS) showed significant segregation between hauls performed in the period 1952–1964 and hauls taken later. MDS segregated hauls taken off Catalonia from those off the Balearic Islands. The most general change recorded was a drop in the occurrence of most of the dominant deep-sea chondrichthyans, especially the shark *Etmopterus spinax*. Environmental analyses (canonical correspondence analysis and BIOENV) suggested a direct relationship between increases in temperature and salinity in intermediate waters and the decline of deep-water sharks. Abundance of *E. spinax* also decreased with decreasing O₂ in the Levantine Intermediate Water (LIW) that may be related to changes in LIW in the western Mediterranean since the 1950s. This is in addition to increased fishery effort as a factor explaining the drop in shark abundance. In other regions of the western Mediterranean subjected to fishery pressure, *E. spinax* is still dominant. We suggest that small changes, both anthropogenic and climatic, occurring in the temperature and salinity of deep-water masses since the 1950s in the Balearic Basin have changed the composition of fish (especially sharks due to their high vulnerability) and crustacean assemblages.

KEY WORDS: Balearic Basin · Megafauna · Environmental change

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1. INTRODUCTION

Marine communities have experienced large changes on different time scales. At a paleoceanographic scale, benthic marine assemblages have often experienced gradual long-term changes (e.g. during several hundred thousand years in marine mollusks: Cintra-Buenrostro et al. 2002; in benthic assemblages in general: Kosnik 2005) related to climate and sea level oscillations. Changes have been recorded not only at various taxonomic levels but also in the composition of ecomorphological (trophic) groups (Kosnik 2005), indicating changes in the habi-

tat and the ecological dynamics of benthic communities. We find examples of such changes in the Mediterranean Sea, including the massive extinction of benthic species during the Messinian salinity crisis (6.5 to 5 million yr ago), during which drying of the Mediterranean Sea occurred (Pérès 1985).

Marine ecosystems also experience changes at decadal time scales related to human impacts, as happened in the Mediterranean during the 20th century. Changes in dominant fish and invertebrates (crustaceans, jellyfish) have been found close to the Suez Canal (Spanier & Galil 1991) after its opening in 1869. 'Lessepsian' fish (e.g. *Saurida undosquamis*

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and *Upeneus moluccensis*) and prawns (*Penaeus japonicus* and *P. monoceros*) have come to constitute up to 30% of the total trawl catches off the Israeli coast (Ben-Tuvia 1973, Galil 2004). Por (1971) predicted that the westward advance of the Lessepsian immigrants would be more pronounced after the damming of the Nile River by construction of the Aswan High Dam. Multiple human activities may simultaneously impact marine ecosystems, generating a multifactor effect in which the impacts of the factors are difficult to separate.

Fishery pressure is also a cause of changes in the composition of marine communities over short time scales, especially in vulnerable habitats (formed by sessile animals like corals: Fosså et al. 2002) and species (e.g. sharks: Ferretti et al. 2008, Maynou et al. 2011) and also in low-productivity habitats such as the deep sea. Deep-water ecosystems have low productivity in comparison with shallow water systems, and bathyal species generally have low turnover rates. As a consequence, decreases in the catch per unit effort (CPUE) and size of exploited deep-sea fish have occurred only a few decades after exploitation began (e.g. rattails *Coryphaenoides* spp.: Hopper 1995), even after the application of total allowable catches per area (e.g. *Hoplostethus atlanticus* off New Zealand: Koslow 1997). Only deep-sea fisheries that are managed by using relatively selective gear (e.g. longlines for *Aphanopus carbo* off Madeira), or by avoiding access to recruitment areas (e.g. the shrimp *Aristeus antennatus*: Cartes et al. 2004) have shown fewer symptoms of overexploitation. All of these induced changes are difficult to distinguish from natural variability (e.g. responses to short-term climatic changes associated with the North Atlantic Oscillation, NAO). Spatial variability must be considered when studying temporal changes in communities, since latitude and depth are important sources of variability in deep-sea systems (Gage & Tyler 1991, Cartes et al. 2009a).

The deep Mediterranean, with its relatively strong thermohaline stability (e.g. near constant conditions of temperature (T) and salinity (S) of ca. 13°C, 38 psu throughout the year below 150 m: Margalef 1985), has suffered important temporal changes. In the last 50 yr, one of the most important environmental changes was the warming and salinization of intermediate and deep waters (below 150 m) in the western Mediterranean (Rixen et al. 2005, Vargas-Yáñez et al. 2009). Temperature changes distinctly accelerated starting about 1955 in the Levantine Intermediate Water (LIW) and Western Mediterranean Deep Water (WMDW), water masses distributed at ca. 150 to 600 m and from 600 m to the bottom, respectively

(Rixen et al. 2005). T and S increased by 0.12°C and 0.03 psu in the deepest layers from 1959–1988/1989 (Béthoux et al. 1990, Rixen et al. 2005, Vargas-Yáñez et al. 2009). These changes may be linked to general climatic change (Williams 1998) and to damming of major rivers (Rohling & Bryden 1992, Béthoux & Gentili 1999) that reduced freshwater discharges into the Mediterranean. The damming effect was particularly important after construction of the Aswan Dam in 1964, which reduced Nile discharge and affected LIW hydrological properties at its formation site in the Eastern Basin (Skirris & Lascaratos 2004). LIW penetrates in the western Basin at T > 13.5°C and S > 38.5 psu (Ghidalia & Bourgois 1961, López Jurado et al. 2008), along with some variability in both T and S (Font 1987, Emelianov et al. 2006).

Analyses of the possible effects of these changes in the ecology of the deep Mediterranean Sea have only been attempted recently, revealing the local extinction/reduction in abundance of some commercial shrimps (*Aristaeomorpha foliacea*: Cartes et al. 2011a,b; *Aristeus antennatus*: Cartes et al. 2011a) in the second half of the 1960s in the Balearic Basin. However, there has been no analysis of deep assemblages at depths occupied by the LIW and WMDW. Our main objectives here were (1) to analyze long-term changes in the composition of deep-water communities of fish and decapod crustaceans in the Balearic Basin since the 1950s; (2) to test possible relationships between these changes and environmental conditions, with special emphasis on changes in T and S of the LIW; and (3) to analyze long-term changes in the frequency of occurrence of some vulnerable species (e.g. sharks and other chondrichthyans) within these communities. We discuss possible influences of environmental changes on deep-sea communities, bearing in mind the fishery effort.

2. MATERIALS AND METHODS

2.1. Dataset

2.1.1. Biological sampling

We compiled the species composition (number) of fish and decapods of 88 hauls performed at depths of 350 to 650 m off the Catalanian coast and around the Balearic Islands, and used literature sources for data from 15 hauls in the period 1950s–1964. Another 73 hauls were from our own datasets, performed between 1972 and 2007. Characteristics of these 73 bottom trawls were 13 hauls performed in 3 fishing grounds

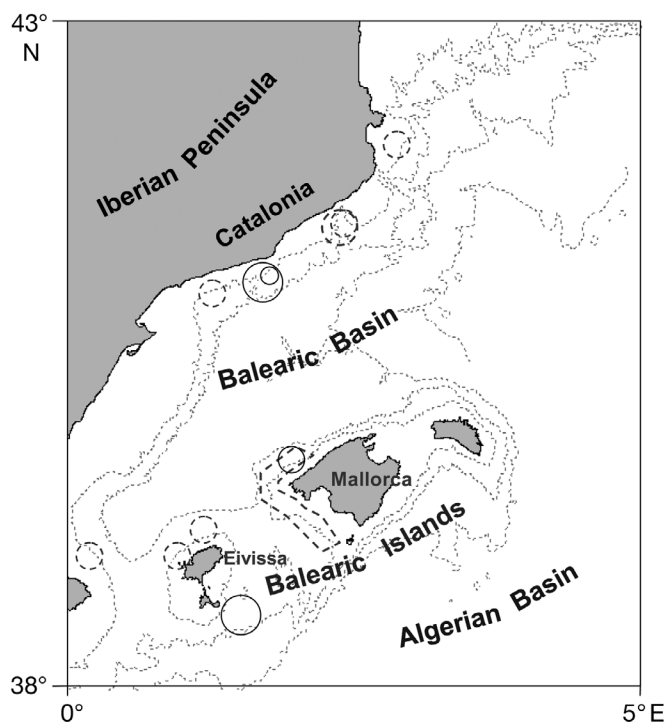


Fig. 1. Study area, showing the sampling sites (circles and polygon) in the periods 1950s–1970s (dashed) and 1980s–2007 (black)

(La Melica, El Sot de La Gamba, and La Barana) off Blanes ($41^{\circ}07'N$, $2^{\circ}03'E$) at depths between 250 and 600 m in 1972, 1973, and 1974 (Matallanas 1975); 13 hauls performed on board RV 'Cornide de Saavedra' in March 1977 from Catalonia (depths: 360–560 m) to Eivissa (Ibiza in Spanish; depths: 320–550 m) (Fig. 1; also see Suau 1981); 26 hauls from 4 fishing grounds (El Buscarró, Serola, Can Pere Negre, Clot de Sant Salvador) off Barcelona (between $40^{\circ}08'$ and $41^{\circ}03'N$, $1^{\circ}56'$ and $2^{\circ}13'E$) in 1988, 1989, 1990, and 2007 (Cartes 1994, Cartes et al. 1993); 13 hauls off the west of Mallorca (between $39^{\circ}45'$ and $38^{\circ}40'N$, $2^{\circ}25'$ and $2^{\circ}30'E$) monthly from October 1996 to December 1997 (Moranta 2007); and 8 hauls taken in May 1996 in the southeast of the Balearic Islands (QUIMERA 1 cruise) on board RV 'Garcia del Cid' (Cartes et al. 2001) at fixed stations between 335 and 601 m.

2.1.2. Limitation of available data

Before the 1970s, information on fish and crustacean assemblages on the continental slope was restricted to the pioneer studies by Oliver (1953) and Massutí (1971) performed around Mallorca (Balearic Islands). The sampling and available data in these studies had some limitations.

The 5 bottom trawls performed in 1952–1953 were on board the commercial trawler 'Maroto' (between 09/10/1952 and 02/06/1953; dd/mm/yyyy) at depths between ca. 300 and 700 m (mainly 400 to 600 m, though with imprecise sounding data taken with lead lines) to the south-SW of Mallorca. The species composition from those trawls was obtained 4 yr after fishery exploitation of bathyal depths around the Balearic Islands had begun. Only 1 vessel operated at bathyal depths in 1948 and 2 in 1949, increasing to 5 vessels in 1952 (Oliver 1953). The list of species provided by Oliver (1953) represented 10% (in biomass) of the total catch, the rest being commercial species, mainly the deep-sea shrimps *Aristaeomorpha foliacea*, *Aristeus antennatus*, and *Parapenaeus longirostris*, and some commercial fish (*Merluccius merluccius*, *Lophius* spp.). The by-catch was classified in the laboratory to species level, counting the numbers and measuring the sizes of specimens (Oliver 1953). In 1964, monthly samplings of megafaunal communities were performed by Massutí (1971) following the same methodology as Oliver (1953). Composition was obtained from similar depths based on the catches of a shrimp trawler. Information is available from 10 bottom trawls with trawl durations of ca. 8 to 10 h, without precise locations of the hauls. However, we can assume they were performed over adjacent (interfluve) slopes, not in submarine canyons because of the technical difficulty of trawling in canyons in 1964.

Data from Matallanas (1975) and Moranta (2007) did not contain quantitative data for crustaceans; only the weights of commercial species (Moranta 2007) and a list of the dominant decapods by fishing ground (Matallanas 1975, Matallanas & Moreno-Amich 1985). Massutí (1971) also provided some data for *Plesionika* spp. without differentiating species. As a consequence, analyses were performed for (1) total megafauna (including fish and mainly commercial decapods) using Spearman distance, a similarity measure based on rank (not abundance); and (2) only fish for canonical correspondence analysis (CCA), after standardization of catches to ind. ha^{-1} . Numbers of decapods were estimated in ca. 30% of hauls by weight/number (mean weight, g ind.^{-1}) conversion factors.

2.1.3. Environmental data

T and S at haul depth and at the LIW core were downloaded from the the MEDATLAS database at www.ifremer.fr/medar/ by Dr. M. Vargas-Yañez (Centro Oceanográfico de Fuengirola, Instituto Español

de Oceanografía, IEO) for the area of the Balearic Basin. We selected for our analyses T and S at the depth nearest to that at which hauls were performed. Rhône flow data ($\text{m}^3 \text{s}^{-1}$) were compiled for the years with biological sampling (from the Global Runoff Data Centre: www.bafg.de/GRDC/EN/Home/homepage_node.html). Annual NAO indices were downloaded from the Climatic Research Unit of East Anglia University (www.cru.uea.ac.uk).

2.2. Statistical analyses

2.2.1. Assemblage compositions

Species appearing fewer than 2 times in hauls were removed from all data matrices. Variations in species composition of the 88 hauls were examined by non-parametric multidimensional scaling (nMDS; Clarke & Warwick 1995). To minimize heterogeneity from the use of different trawl types, we used Spearman's rank correlation as a similarity distance. Spearman correlation measures the statistical dependence among pairs of variables based on rank data, not on raw abundances. Spearman's coefficient is therefore useful in assessing the correlation between pairs of variables obtained using heterogeneous samplers (e.g. different trawl types), and it is less sensitive to outliers than Pearson's correlation (Legendre & Legendre 1998).

Factors considered to explain the ordination of hauls were the period of sampling and the area (hauls taken on the continental versus insular slopes). Within the factor Period, 2 groups of hauls were analyzed (1952–1953 and 1964 versus the years from 1972–2007), taking as a criterion the significant drop in deep-sea shrimps in the area between both periods (in 1968–1969: Cartes et al. 2011a,b). We also contrasted hauls taken at the mainland slope of the Balearic Basin (off Catalonia, NE Iberian Peninsula) versus hauls taken around the Balearic Islands. Distance-based permutational multivariate analysis of variance (PERMANOVA, Anderson et al. 2008) was used to test differences among the assemblages (1) between the 2 periods, and (2) between the continental and insular areas. A 2-way model for both factors combined was not possible because no species composition data before the 1970s were available off Catalonia. Separate 1-way univariate factor analyses were performed for Period and Area. A permutational ANOVA was designed for multivariate analyses; however, it can also be used for univariate ANOVA. One-way

analyses for period were also performed separately on data matrices from the Balearic Islands and off Catalonia. In the last case (in the absence of hauls in the 1950–1960s), the 2 periods compared were 1972–1977 versus 1988–2007.

We ranked species by decreasing frequency of occurrence (not abundance) for 2 periods off the Catalanian coast (1972–1977 and 1988–2007) and 2 periods around the Balearic Islands (1952–1953 and 1964 versus 1996–1997). Within each group, the percentage of abundance of dominant species was calculated.

2.2.2. Analyses of possible environmental causes

To identify possible causes of changes in slope assemblages, we examined relationships between species composition (the dependent variables) and the following possible explanatory variables:

(1) T and S at the haul depth and T and S at the LIW core (maximum of T and S in intermediate waters, e.g. between 300 and 600 m);

(2) the (annual) NAO index as a climate oscillation proxy;

(3) the Rhône River discharge (sum of flows from 1 to 3 mo before sampling), in $\text{m}^3 \text{s}^{-1}$. The Rhône has the highest runoff of all rivers in the study area, the northern-central Balearic Basin;

(4) trawling effort as adopted by Cartes et al. (2011a), where effort data derived from raw data (engine power per boat, in horse power, HP) were provided by Fishers' Associations. Total HP of boats per year was adopted as the effort measure.

Trawling effort was analyzed only off Catalonia.

O_2 was not considered as an explanatory variable because complete data series were not available (e.g. off the Balearic Islands in 1996–1997). Therefore, O_2 at the LIW core was tested (Spearman rank) only against the rank of abundance of *Etmopterus spinax* (the species showing the clearest tendency in our analysis) within each haul. In 51 cases, a value of $[\text{O}_2]$ at the LIW was related with *E. spinax* rank abundance. In only 14 cases, $[\text{O}_2]$ at the LIW core was taken simultaneously with hauls (in 1977 and 2007), and in 10 cases, $[\text{O}_2]$ was obtained ± 2 mo from the haul date (in 1989). In the remaining cases, 9 $[\text{O}_2]$ data points were taken in the same year as the haul collection (1990), but 8 mo later, and in 18 cases, data were ± 2 to 3 yr from the haul date (in 1952 and 1972/74). Data were compiled from the MEDATLAS database and from Segura (2007) for 1970–2003 (CSIC cruises).

The BEST (BIO-ENV) procedure was applied to identify those combinations of environmental variables that best matched the distribution of the whole biotic data (Clarke & Ainsworth 1993). BEST is based on Spearman's rank correlation. Relationships were also tested by multivariate CCA (Ter Braak 1986). CCA relates the abundance of each species to each environmental variable, rather than with a combination of variables as BEST performs. For CCAs, we roughly standardized fish abundance considering the basic features of trawls (e.g. approximate horizontal aperture) and characteristics of trawling in each period. Hours of trawling were roughly estimated for operations performed in the 1950s–1970s after interviewing retired fishermen. CCA is useful for extracting environmental gradients from ecological data (Ter Braak & Verdonschot 1995). Arrows in CCA plots represent explanatory variables and are proportional in length to their importance (Ter Braak 1986).

CCAs related abundance (ind. ha^{-1}) of fish in (1) all hauls and (2) separately for hauls performed in the mainland and insular areas. These analyses were performed on 79 hauls (all data were log-transformed), after exclusion of 9 hauls at depths <350 m to minimize the possible effect of depth.

3. RESULTS

MDS showed some degree of separation (Stress = 0.20) among hauls as a function of spatio-temporal factors (Fig. 2). The 2 tested factors, Period (comparing hauls from the 1950s–1960s to those from 1977–2007) and Area (comparing Balearic and Catalan hauls) were significant (1-way PERMANOVAs: for period, pseudo- $F = 2.84$; $p = 0.04$; for area, pseudo- $F = 4.97$; $p = 0.004$). There was a significant trend grouping hauls performed in the periods 1952/53–1964 (B52, B53–B64, upper part of the plot) and those taken in 1988–1990 (grouped at the lower part). These last hauls (CS, CM) were from fishing grounds inside/close to submarine canyons off Catalonia, whilst the 1950s–1960s hauls cited above were from the Balearic Islands. The ordination of hauls as a function of Period occurred both in the Balearic and Catalan areas separately. In the Balearic area, hauls from 1952/53–1964 (B52, B53, B64) were separated in the upper part of the plot from those in 1977 and the 1990s (M2, Q1, and B97; 1-way PERMANOVA, pseudo- $F = 3.48$; $p = 0.001$), grouped in the lowest part. Off Catalonia, the 1970s hauls (CS-72/74, CM1–CM5, M1–M3, M6, M7, and M32) were separated (to the right) of the 1980s–1990s (CS1–

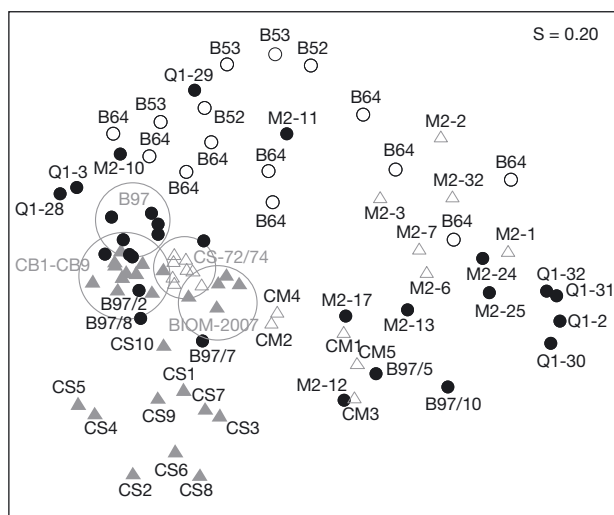


Fig. 2. Multidimensional scaling (MDS) of hauls performed in, and compiled from, the Balearic Basin (and neighboring areas): black symbols: around the Balearic Islands (1950s–1960s: \circ ; and 1990s: \bullet); grey symbols: off Catalonia, in the Iberian Peninsula (1970s: \triangle ; and 1980s–2007: \blacktriangle). B52, B53, and B64 are hauls taken in the 1950s–1960s around Mallorca. M: MEDITERRANEO II cruise (March 1977); CS, CM: hauls performed over the Catalanian slope; Q1: Quimera 1 cruise (May 1996); B97: hauls taken in the Balearic Islands (NW Mallorca) in 1997; BIOM: BIOMARE cruises (2007) off the Catalanian slope; S: MDS stress

CS10; CB1–CB9) and 2007 (BIOM), hauls distributed to the left of plot (1-way PERMANOVA, pseudo- $F = 13.19$; $p = 0.0001$).

The rankings of the most abundant species, comparing the oldest (1950–1960s) and the most recent data obtained since the 1970s are shown in Table 1. In the 1950–1960s, *Aristaeomorpha foliacea* was the most abundant species (31 % of catches). *Plesionika martia*, *Galeus melastomus*, *Aristeus antennatus*, and *Parapenaeus longirostris* represented between 10 and 15 %, while *Lepidorhombus boschii*, *Nephrops norvegicus*, and *Etmopterus spinax* still accounted for >3 % of total individuals caught. After the 1970s, *A. foliacea* disappeared as a dominant species (Table 1), while sharks (*G. melastomus*, *E. spinax*) also fell in the ranking by about an order of magnitude. *A. antennatus* was largely dominant, comprising 53 % of catches.

The most abundant deep sea chondrichthyans generally dropped in their frequency of occurrence (%F) in catches (Fig. 3) after the 1970s. Except for *Galeus melastomus*, whose %F increased in 1997 and 2007, the other species declined, especially *Etmopterus spinax*.

The BEST routine gave the best correlation between fish and decapod composition and a combination of the variables T, S, T and S at LIW (T_{LIW} and

Table 1. Ranking by decreasing order of abundance of fish (OST: teleosts; CHO: chondrichthyans) and decapods (DEC) comparing abundances/occurrences in (1) the 1950–1960s and the 1970s–1990s off the Balearic Islands and (2) the 1970s and the 1980s–2007 off Catalonia. Cum%: abundance within each period; %F: frequency of occurrence

| | Species | Cum% | %F |
|---|--|-------|-------|
| Catalonian coasts | | | |
| Rank 1970s | | | |
| 1 | DEC <i>Aristeus antennatus</i> | 77.4 | 82.0 |
| 2 | OST <i>Micromesistius poutassou</i> | 2.4 | 100.0 |
| 3 | OST <i>Phycis blennoides</i> | 2.3 | 100.0 |
| 4 | DEC <i>Pasiphaea multidentata</i> | 1.4 | 100.0 |
| 5 | OST <i>Merluccius merluccius</i> | 1.1 | 100.0 |
| 6 | OST <i>Lampanyctus crocodilus</i> | 1.1 | 84.6 |
| 7 | DEC <i>Plesionika martia</i> | 1.0 | 100.0 |
| 8 | OST <i>Gadiculus argenteus</i> | 0.9 | 76.9 |
| 9 | CHO <i>Etmopterus spinax</i> | 0.8 | 92.3 |
| 10 | OST <i>Trachyrincus scabrus</i> ^a | 0.7 | 100.0 |
| 11 | DEC <i>Nephrops norvegicus</i> | 0.5 | 76.9 |
| 12 | DEC <i>Parapenaeus longirostris</i> | 0.3 | 53.8 |
| 13 | CHO <i>Galeus melastomus</i> | 0.2 | 92.3 |
| 19 | DEC <i>Aristaeomorpha foliacea</i> | 0.1 | 76.9 |
| 1980s–2007 | | | |
| 1 | DEC <i>Aristeus antennatus</i> | 82.6 | 100.0 |
| 2 | OST <i>Phycis blennoides</i> | 2.4 | 76.9 |
| 3 | OST <i>Trachyrincus scabrus</i> ^a | 2.3 | 61.5 |
| 4 | OST <i>Micromesistius poutassou</i> | 1.6 | 69.2 |
| 5 | DEC <i>Pasiphaea multidentata</i> | 1.4 | 100.0 |
| 6 | DEC <i>Plesionika edwardsii</i> | 1.2 | 38.5 |
| 7 | CHO <i>Galeus melastomus</i> | 1.0 | 69.2 |
| 8 | DEC <i>Plesionika martia</i> | 1.0 | 96.2 |
| 9 | OST <i>Lampanyctus crocodilus</i> | 0.8 | 92.3 |
| 38 | CHO <i>Etmopterus spinax</i> | <0.1 | 38.5 |
| 52 | DEC <i>Aristaeomorpha foliacea</i> | <0.01 | 7.7 |
| Balearic Islands | | | |
| 1950s–1960s | | | |
| 1 | DEC <i>Aristaeomorpha foliacea</i> | 31.2 | 53.3 |
| 2 | DEC <i>Plesionika martia</i> | 15.2 | 86.7 |
| 3 | CHO <i>Galeus melastomus</i> | 12.5 | 100.0 |
| 4 | DEC <i>Aristeus antennatus</i> | 10.9 | 73.3 |
| 5 | DEC <i>Parapenaeus longirostris</i> | 10.3 | 46.7 |
| 6 | OST <i>Lepidorhombus boscii</i> | 7.0 | 80.0 |
| 7 | DEC <i>Nephrops norvegicus</i> | 3.4 | 60.0 |
| 8 | CHO <i>Etmopterus spinax</i> | 3.1 | 100.0 |
| 9 | OST <i>Lampanyctus crocodilus</i> | 2.3 | 60.0 |
| 10 | OST <i>Gadiculus argenteus</i> | 1.8 | 53.3 |
| 11 | OST <i>Phycis blennoides</i> | 1.4 | 93.3 |
| 12 | OST <i>Chlorophthalmus agassizii</i> | 0.9 | 40.0 |
| 1970s–1990s | | | |
| 1 | DEC <i>Aristeus antennatus</i> | 22.7 | 57.7 |
| 2 | DEC <i>Plesionika martia</i> | 11.0 | 69.2 |
| 3 | DEC <i>Pasiphaea multidentata</i> | 9.6 | 50.0 |
| 4 | DEC <i>Nephrops norvegicus</i> | 8.3 | 84.6 |
| 5 | OST <i>Glossanodon leioglossus</i> | 7.0 | 19.0 |
| 6 | OST <i>Phycis blennoides</i> | 6.9 | 100.0 |
| 7 | DEC <i>Parapenaeus longirostris</i> | 3.3 | 28.6 |
| 8 | OST <i>Micromesistius poutassou</i> | 3.2 | 84.6 |
| 9 | CHO <i>Galeus melastomus</i> | 2.7 | 100.0 |
| 10 | OST <i>Lampanyctus crocodilus</i> | 2.2 | 81.0 |
| 26 | OST <i>Lepidorhombus boscii</i> | 0.4 | 61.9 |
| 32 | CHO <i>Etmopterus spinax</i> | 0.3 | 71.4 |
| 41 | DEC <i>Aristaeomorpha foliacea</i> | 0.1 | 14.3 |
| ^a Syn. <i>Trachyrhynchus scabrus</i> | | | |

S_{LIW}), and NAO (Table 2). The variables depth, Rhône discharge, and fishery effort were not selected as explanatory variables in the most significant BEST models (Table 2). Similar results were obtained when fish compositions of Catalonia and the Balearic Islands were treated separately. Maximum ρ values were 0.327 for Catalan fish assemblages and 0.386 for insular fish. T, T_{LIW} , and S were the most recurring explanatory variables, while depth and Rhône discharge did not contribute to any BEST analyses. NAO only entered as an explanatory variable in some models for Catalonia and never in models of the insular area.

The CCA for the environmental variables T and S at haul depth, T_{LIW} and S_{LIW} , NAO index, and Rhône discharge explained 63.9% of the total variance. Hauls taken in 1952/53 and 1964 (to the south-SW of Mallorca, included within plotted circles: Fig. 4) were located together in the left-upper part of the biplot, linked to the teleost *Lepidorhombus boscii* and to the chondrichthyans *Chimaera monstrosa*, *Etmopterus spinax*, and to a lesser extent to *Galeus melastomus*. These species were negatively correlated with S, both at depth of haul and at the LIW core above; that is, abundance decreased with higher S. In the left-lower part of the biplot are hauls taken in the periods 1972–1974 and 1988–1990 off Catalonia. Some of these hauls (4 hauls from 1973–1974 and 4 from 1988) were positively but weakly (short vector length) correlated with the NAO index and with *Epigonus denticulatus* and the sharks *Dalatias licha* and *Scyliorhynchus canicula*. Most hauls taken off Catalonia were located in submarine canyons (Foix and Blanes canyons), which would also explain the occurrence of *D. licha*. Finally, in the right part of the biplot, we found hauls from the 1970s–1990s taken mainly to the south-SW of the Balearic Islands and associated with the species *Glossanodon leioglossus*, *Chlorophthalmus agassizii*, and *Hoplostethus mediterraneus*. These hauls/species were negatively correlated with T_{LIW} and negative NAO.

The CCA performed separately for Catalonia and Balearic slopes showed similar tendencies (Fig. 5; only species represented). In both areas, S at haul depth and at the LIW core and T_{LIW} were negatively correlated with the abundance of sharks: *Etmopterus spinax* and *Dalatias licha* off Catalonia, and all chondrichthyans (except *D. licha*) off the Balearic Islands. Some species of teleosts, mainly *Merluccius merluccius* and *Gadiculus argenteus*, showed the same tendencies in respect to S_{LIW} and T_{LIW} in both areas. Off Catalonia, the flatfish *Lepidorhombus boscii* was linked to high Rhône discharges. Off Catalonia, trawl-

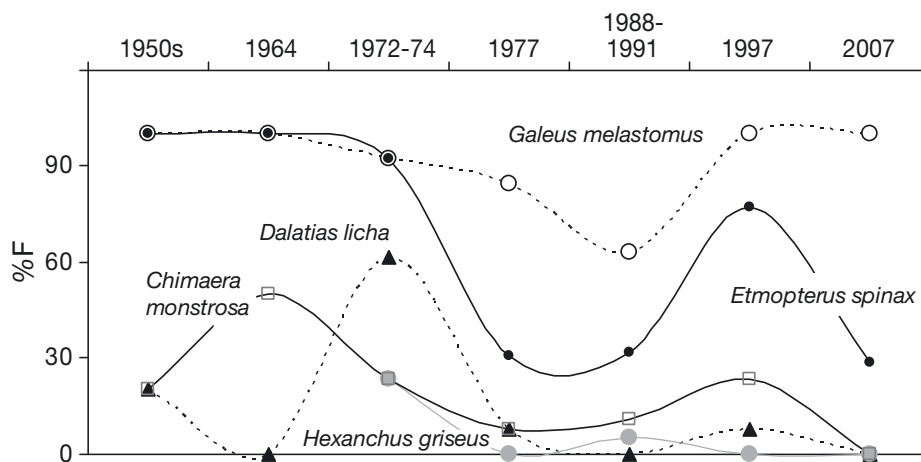


Fig. 3. Temporal trends in the frequency of occurrence (%F) of the most abundant chondrichthyans in the Balearic basin and neighboring areas included in our sampling

ing effort was also negatively correlated with shark abundance in parallel to S (Fig. 5a). When CCA off Catalonia was repeated adding effort, variance was 37.1% at F1 and 30.4% at F2, very similar to results without effort. In general, the main explanatory variables suggested by CCAs coincided with those explaining species composition variability in BEST models.

Table 2. Results of BEST (BIOENV) procedure for the whole megafaunal assemblage, and for fish assemblages over the continental (Catalonia) and insular (Balearic Islands) slopes of the Balearic Basin. Only significant models matching at a maximum of 3 environmental variables with the biotic data (Spearman's ρ) were included. T: temperature; S: salinity; T_{LIW} (S_{LIW}) temperature (salinity) at the Levantine Intermediate Water (LIW) core; NAO: North Atlantic Oscillation

| | No. var. | ρ | Selected variables |
|-------------------------------|----------|-----------|-----------------------------|
| All taxa (both areas) | 3 | 0.272 | T, T_{LIW} , NAO |
| | 2 | 0.272 | T, NAO |
| | 3 | 0.272 | T, S_{LIW} , NAO |
| | 2 | 0.272 | T_{LIW} , NAO |
| | 3 | 0.272 | T_{LIW} , S_{LIW} , NAO |
| | 3 | 0.270 | S, T_{LIW} , NAO |
| Fish (Balearic Islands) | 3 | 0.386 | T, S, S_{LIW} |
| | 2 | 0.383 | T, S |
| | 3 | 0.365 | T, T_{LIW} , S_{LIW} |
| | 2 | 0.364 | T, T_{LIW} |
| | 3 | 0.364 | T, S, T_{LIW} |
| | 2 | 0.360 | T, S_{LIW} |
| | 1 | 0.341 | T |
| | 1 | 0.311 | S |
| 1 | 0.308 | S_{LIW} | |
| Fish (Catalonia) | 3 | 0.327 | T, T_{LIW} , NAO |
| | 3 | 0.324 | T, S, NAO |
| | 2 | 0.323 | T, NAO |
| | 3 | 0.323 | T, S_{LIW} , NAO |
| | 2 | 0.312 | T, S |
| | 1 | 0.311 | T |

With respect to the possible influence of $[O_2]$ at the LIW core on *Etmopterus spinax* abundance, we found significantly negative relationships between the rank occupied by this shark in hauls and $[O_2]$ at LIW, based both on data collected simultaneously (Spearman $\rho = -0.703$; $p = 0.005$) and on all compiled data ($\rho = -0.379$; $p = 0.006$).

4. DISCUSSION

4.1. Limitations and assumptions of the study

The use of historical data of species composition (fish and decapods) added some degree of uncertainty to our long-term analyses. We minimized this by adopting different criteria in compiling and analyzing the available data. Firstly, we compiled information on species composition exclusively obtained with commercial trawls. Species diversity varies at slope depths for both fish and decapods as a function of the trawl type used (Merrett et al. 1991, Cartes et al. 2009b), particularly as a function of its vertical height and the mesh size at the cod end (Cartes et al. 2009b), which affect species catchability. Our analysis was based on samplings almost exclusively performed with 2-warp trawls and mesh sizes at the cod end that were more homogeneous (between 17 mm in the 1950s and 32–40 mm at present) than in previous comparative studies (Merrett et al. 1991, Gordon & Bergstad 1992, Cartes et al. 2009b). Despite their general similarity, characteristics of trawls used by fishermen changed over time in the Catalan Sea from trawls with vertical heights hardly exceeding 1 m in the 1950s to heights of 3–4 m in the 1990s (Bas et al. 1955, 2003). To minimize sampler heterogeneity, we

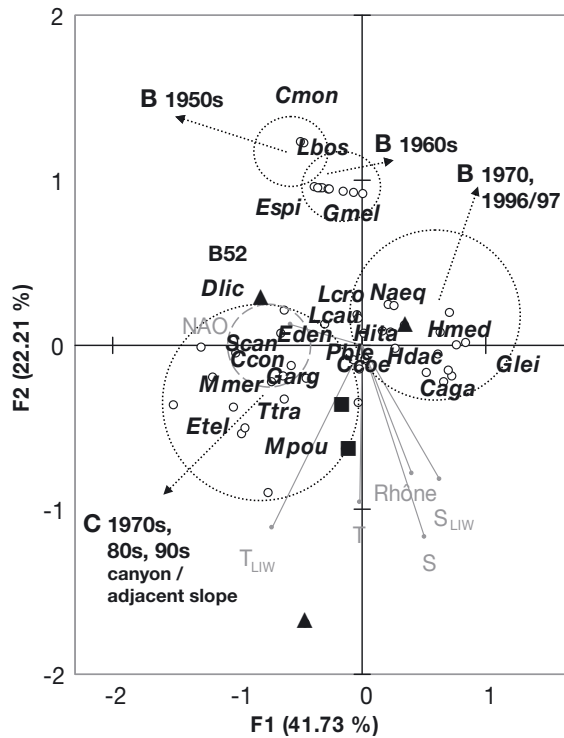


Fig. 4. Canonical correspondence analyses showing hauls and fish species relationships in the Balearic Basin and neighboring areas as a function of environmental (physical/climatic) variables. Variable codes: T: temperature; S: salinity; T_{LIW} (S_{LIW}): temperature (salinity) at the Levantine Intermediate Water (LIW) core; Rhône: river flow; C: hauls taken off the Catalan coasts; B: hauls taken off the Balearic Islands. Dotted circles include all hauls taken at those geographic areas and periods labelled, except some hauls taken at Catalan canyons (▲) and around the Balearic Islands in the 1970s (■). Species codes—Ccoe: *Coelorinchus caelorhinchus* (syn. *C. coelorhynchus*); Ccon: *Conger conger*; Cmon: *Chimaera monstrosa*; Dlic: *Dalatias licha*; Eden: *Epigonus denticulatus*; Espi: *Etmopterus spinax*; Etel: *Epigonus telescopus*; Garg: *Gadiculus argenteus*; Glei: *Glossanodon leioglossus*; Gmel: *Galeus melastomus*; Hdac: *Helicolenus dactylopterus*; Hita: *Hymenocephalus italicus*; Hmed: *Hoplostethus mediterraneus*; Lbos: *Lepidorhombus bosci*; Lcau: *Lepidopus caudatus*; Lcro: *Lampanyctus crocodilus*; Mmer: *Merluccius merluccius*; Mpou: *Micromesistius poutassou*; Naeq: *Nezumia aequalis*; Pble: *Phycis blennoides*; Scan: *Scyliorhinus canicula*; Ttra: *Trachyrhynchus scabrus* (syn. *Trachyrhynchus scabrus*)

analyzed our data comparing the frequency of occurrence of species (not abundance per swept area) among periods using Spearman's rank as a similarity distance (Legendre & Legendre 1998). The only exceptions were the CCAs performed on fish densities. Fish abundances were more homogeneous (comparable) when using different trawl types than those of decapods. Because of their reduced size, some decapods (i.e. crangonids, galatheids) are poorly

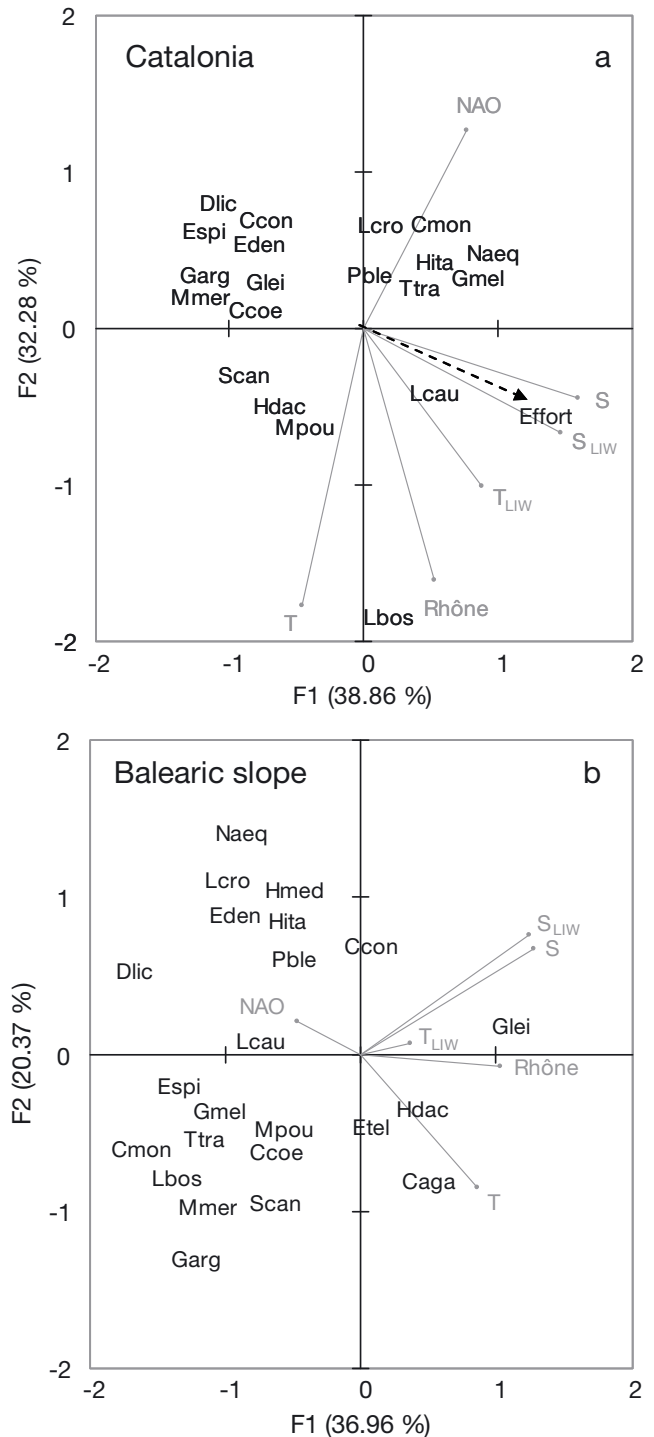


Fig. 5. Canonical correspondence analyses (CCAs) showing fish species relationships in the Balearic Basin and neighboring areas as a function of environmental variables over (a) continental (Catalonia) and (b) insular (Balearic Islands) slopes. Over Catalonia, a parallel CCA was performed adding effort as a variable with results very similar (F1 = 37.1%; F2 = 30.4%) to those when only physical-climatic variables were considered. The arrow vector representing effort was superimposed on the CCA plot based only on physical-climatic variables. Species and variable codes as in Fig. 4

captured by commercial trawls with large mesh sizes at the cod end (Cartes et al. 2009b).

We also found some taxonomic confusion in the studies from the 1950s–1960s, although the only one relevant was the citation of the shark *Centrophorus granulosus* as a dominant species off the Balearic Islands (Oliver 1953, Massuti 1971). This species was in reality *Etmopterus spinax*, a smaller shark. Oliver (1953) cited *C. granulosus* as a very abundant species in the Balearic Sea, represented by small individuals (always with a maximum size of 26.5 cm). *C. granulosus* is a large species (to 150 cm, common size range: 45–90 cm: D. Lloris unpubl. data) with very low fecundity (only 1 embryo female⁻¹; Tortonese 1956) and only occurring in hauls as 1 or 2 specimens. The fetus of *C. granulosus* is 33–35 cm (Capapé 1985), larger than the specimens cited by Oliver (1953). *E. spinax* was also cited on the Balearic slope (Maurin 1968) as a dominant species over *Isidella elongata* grounds (at depths of 500 m), and it has been cited around the Balearic Islands more recently (Moranta 2007, Moranta et al. 2008).

4.2. Changes in deep ecosystems and possible causes

Chondrichthyans (e.g. sharks, rays) play an important role in maintaining the balance of marine ecosystems, because they are often top predators (Dulvy et al. 2008a). The global decline of large sharks (Myers & Worm 2005) has been documented in coastal and pelagic ecosystems (Ferretti et al. 2008, Maynou et al. 2011) in the Mediterranean. Data on deep-sea systems are often insufficient for quantitative analysis (as in the case of *Hexanchus griseus* in Ferretti et al. 2008). Sharks play the same trophic role in the deep sea as in other systems, being at the top of trophic webs as documented by dietary studies (Carrassón et al. 1992, Carrassón & Cartes 2002) and by stable isotope analyses (Polunin et al. 2001, Papiol et al. 2013). This is the case in the deep western Mediterranean for large *Galeus melastomus* and *Etmopterus spinax* that prey on fish and cephalopods (Carrassón et al. 1992), and for *Dalatias licha* preying on other sharks (Matallanas 1982). A high trophic level was deduced for these species based on $\delta^{15}\text{N}$ analyses: between 12.28 and 13.08‰ for large specimens (highest $\delta^{15}\text{N}$ in slope fish community = 14.08‰; Polunin et al. 2001, Papiol et al. 2013).

The decline of top predators in marine ecosystems has been related to the increase in fishery effort (Hutchings & Myers 1994, Ferretti et al. 2008). Factors other than fisheries have rarely been considered

to explain drops in species abundance in open seas. For neritic (coastal) areas, some studies related changes in species composition to climatic (NAO) oscillations (e.g. for copepods: Molinero et al. 2005) and warming water masses (e.g. fish assemblages: Dulvy et al. 2008b). CCA results in the present study show an inverse relationship between positive NAO and low Rhône discharges. This is expected, since high NAO periods are linked to low rainfall episodes (and low river flows) in the western Mediterranean (Mariotti et al. 2002, Cartes et al. 2009a). Our analyses suggest a direct relationship between the increase in T and S at intermediate waters and the decline in deep-water sharks. This is a factor additional to the increases in fishery effort and (probably also) of efficiency in catching swimming species (e.g. sharks) by an increase in the vertical height of commercial trawls. T changed in the LIW at ca. 200 to 600 m (Font 1987), distinctly accelerating since the 1950s (Rixen et al. 2005). LIW arrives in the western Basin, producing intermediate maxima in T and S at ca. 400 m (Emelianov et al. 2006, López-Jurado et al. 2008). In the Balearic Basin, T increased from 12.95°C in 1957 to >13.40°C in the 1990s and 2007 (compiled by Cartes et al. 2011b). S showed a similarly increasing tendency. In a parallel study, we have shown a local extinction of the shrimp *Aristaeomorpha foliacea* in the Balearic Basin (from 4 to 32 ind. ha⁻¹ in 1950–1966 to <0.1 ind. ha⁻¹ more recently, Cartes et al. 2011a). The decrease of *A. foliacea* in the Balearic Basin was linked to an increase of T (and S) in the LIW, which is distributed immediately above the shrimp's preferred habitat depth. This new analysis suggests that the whole assemblage of fish dwelling in intermediate waters could have had a similar response to environmental changes. Such changes in deep communities are independent of cascading events (episodic formation of dense cold waters arriving at great depths: Béthoux et al. 2002). Events of intense cascading of dense water from the shelf in the Gulf of Lions occurred in 1971, 1980, 1988, and 1999, affecting the hydrology of WMDW. Only one of those events (1988) coincided with our samplings. As discussed for the decline of *A. foliacea* and *Aristeus antennatus* in the Balearic Basin (Cartes et al. 2011a), changes found here in slope communities may be related to the observed warming and the reduction of freshwater input by river damming in the Mediterranean (Béthoux & Gentili 1999). This response would be more identifiable among particularly vulnerable taxa (e.g. sharks) due to their slow growth, late age of maturity, and low reproductive rate (Myers & Worm

2005). *Etmopterus spinax*, for instance, is ovoviviparous with low fecundity and considerable longevity (ca. 20 yr: Coelho & Erzini 2008).

In the deep Mediterranean Sea, only small seasonal oscillations in T and S occur below ca. 150 m (Margalef 1985). There must be, therefore, no adaptive value for deep-sea organisms in evolving wide temperature tolerance or strong osmoregulatory mechanisms. Accordingly, we hypothesize that small environmental variations (occurring, for instance, over decades) may be significant for species living in these habitats, as previously suggested for explaining the local extinction of *Aristaeomorpha foliacea* in the Balearic Basin (Cartes et al. 2011b). The increase of T and S in the LIW has been coupled with lower [O₂] (Kress & Herut 2001, Roether & Well 2001), which could especially influence species with high metabolic (or swimming) activity as hypothesized for *A. foliacea*. In the Catalan Sea, a linear drop in O₂ was recorded at the LIW core ($r = -0,87$; $p < 0.01$, $n = 20$: Segura 2007) between 1970 and 2003, with maximum O₂ concentrations at the LIW core declining from 4.6–4.8 ml l⁻¹ to 4.0–4.2 ml l⁻¹ (Segura 2007). Our CTD data during 2007 confirmed this trend in the O₂ at the LIW core, with a maximum O₂ of 4 ml l⁻¹ (ca. 55 % of O₂ saturation: Cartes et al. 2011b). This is below the O₂ saturation estimated by the 'Thor' expedition (Nielsen 1912) of 76 % (5.8 ml l⁻¹) at depths of maximum S (300–600 m) in the Catalan Sea. We found that the abundance of *Etmopterus spinax* decreased with decreasing O₂ at the LIW core. *E. spinax* has strong swimming capacity compared to other bathyal sharks, having, for example, a more pelagic diet than *Galeus melastomus* (Relini-Orsi & Wurtz 1977), and lower catchability with trawls of low vertical height (Cartes et al. 2009b). In addition, marine elasmobranchs maintain serum osmolarity similar to that of their surrounding seawater (Pang et al. 1977), a different strategy than that found among bony fishes with a blood osmolarity one-third below that of seawater (Pang et al. 1977). Thus, there must be a different pattern of acclimation to changes in environmental S by elasmobranchs and teleosts, with an apparently lesser capacity of the former to regulate the osmolarity of internal fluids. Maintaining an inner osmotic balance after small changes at LIW could imply a high energy cost for some sharks.

The response of sharks (e.g. *Etmopterus spinax*, *Dalatias licha*) to these changes in the LIW was not the same as that of *Aristaeomorpha foliacea*. *E. spinax* was a dominant species on the Balearic slope 40 yr ago (Maurin 1968). Both *E. spinax* and *D. licha* were still (relatively) abundant until the 1970s, while

the extinction of *A. foliacea* occurred at the end of the 1960s (Cartes et al. 2011a). Large *E. spinax* are found in the western Mediterranean to 1400 m, below depths of highest S (and of fishery pressure). This can contribute to explaining why the decline of *E. spinax* occurred later than that of the shrimp. In any case, the influence of the fishery effort seems unlikely to be the only cause of the decline in abundance of sharks over the slope of the Balearic Basin. In other regions of the western Mediterranean submitted to strong fishery pressure (e.g. around 470 vessels operating in the Sicily Channel: Fiorentino 2009), *E. spinax* is still a dominant species (Table 3). The

Table 3. Relative abundance (N) and rank occupied by chondrichthyans in deep-sea fish assemblages in 3 areas of the western Mediterranean at depths between 400 and 800 m (between 200 and 800 m in the Tyrrhenian Sea and Sicily Channel). Data from 1994–2009 (to 2005 in the Alboran Sea). Abundance in ind. h⁻¹ in the Alboran Sea. Rank of *Galeus melastomus* in the Sicily Channel based on F. Fiorentino (pers. comm.)

| Rank | Species | N | % |
|-----------------------|------------------------------|------------------------------------|-------|
| Alboran Sea | | | |
| 1 | <i>Galeus melastomus</i> | 3050.6 | 84.2 |
| 7 | <i>Etmopterus spinax</i> | 376.7 | 10.4 |
| 15 | <i>Chimaera monstrosa</i> | 80.3 | 2.2 |
| 16 | <i>Galeus atlanticus</i> | 83.8 | 2.3 |
| 28 | <i>Scyliorhinus canicula</i> | 18.8 | 0.5 |
| 30 | <i>Dalatias licha</i> | 7.6 | 0.2 |
| 41 | <i>Centrophorus uyato</i> | 2.7 | 0.1 |
| | <i>Oxynotus centrina</i> | 1.6 | 0.04 |
| | <i>Galeorhinus galeus</i> | 0.2 | 0.005 |
| | <i>Heptanchias perlo</i> | 0.2 | 0.005 |
| | <i>Raja circularis</i> | 0.3 | 0.009 |
| | <i>Torpedo nobiliana</i> | 1.3 | 0.034 |
| | <i>Torpedo marmorata</i> | 0.3 | 0.007 |
| Rank | Species | Abundance (n km ⁻²) | % |
| Tyrrhenian Sea | | | |
| 3 | <i>Galeus melastomus</i> | 397.1 | 87.0 |
| 6 | <i>Etmopterus spinax</i> | 56.0 | 12.3 |
| | <i>Chimaera monstrosa</i> | 1.5 | 0.3 |
| | <i>Scyliorhinus canicula</i> | 0.8 | 0.2 |
| | <i>Dalatias licha</i> | 0.8 | 0.2 |
| | <i>Centrophorus uyato</i> | 0.2 | 0.05 |
| Rank | Species | Abundance (n km ⁻²) | % |
| Sicily channel | | | |
| 1 | <i>Galeus melastomus</i> | 2866.9 | 95.8 |
| | <i>Scyliorhinus canicula</i> | 58.9 | 2.0 |
| | <i>Etmopterus spinax</i> | 51.0 | 1.7 |
| | <i>Chimaera monstrosa</i> | 12.9 | 0.4 |
| | <i>Dalatias licha</i> | 1.4 | 0.05 |
| | <i>Centrophorus uyato</i> | 1.2 | 0.04 |
| | <i>Heptanchias perlo</i> | 0.4 | 0.01 |
| | <i>Galeorhinus galeus</i> | 0.5 | 0.02 |

responses of populations of a given species living in different regions (e.g. in the Alboran and Tyrrhenian seas) to similar changes in habitat conditions may vary depending upon the specificity of their regional adaptations.

In conclusion, we suggest that small changes in the hydrological conditions (T, S, and dissolved O₂) of deep-water masses since the 1950s in the generally stable environment of the deep Balearic Basin have contributed to some significant changes in fish and crustacean assemblages. Sharks (especially *Etmopterus spinax*) would be the clearest examples of a negative response to these changes.

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