

# Functional changes as indicators of trawling disturbance on a benthic community located in a fishing ground (NW Mediterranean Sea)

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**ABSTRACT:** Trawling disturbs benthic communities, eliminating the most vulnerable organisms and modifying habitat structure. While the cumulative effects of disturbance resulting from commercial trawling activities are poorly understood, several studies suggest that chronically disturbed communities are dominated by opportunistic organisms. This study focuses on changes in functional components of the benthic community occurring in muddy sediments in a NW Mediterranean trawling ground, including an area that has not been fished for 20 yr. In both disturbed and undisturbed areas, the overall benthic community from the fishing ground was dominated by burrowing epifaunal deposit feeders and predators, and deep burrowing infaunal deposit feeders. The fished area had a higher abundance of burrowing epifaunal scavengers and motile burrowing infauna, while the undisturbed area was characterised by higher abundance of surface infauna, epifaunal suspension feeders and predatory fish. This study clearly demonstrates that changes in the functional components of a benthic community can result from fishing in areas dominated by organisms not considered especially vulnerable to trawling activities. Thus, fisheries managers aiming to reduce ecosystem disturbance must consider the implications of trawling on the structure and functioning of all types of benthic communities.

**KEY WORDS:** Functional traits · Commercial fishing · Ecosystem-based management · Rarity

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## INTRODUCTION

Continental shelves have been intensively fished worldwide over the last century, often resulting in the overexploitation of commercial species and the impoverishment of benthic communities (de Groot 1984, Dayton et al. 1995, Pauly et al. 1998). Bottom trawling disturbs benthic communities. However, there is a poor understanding of the degree to which frequency and intensity of fishing disturbance to the seafloor can chronically modify benthic communities (Thrush et al. 1995, Auster et al. 1996, Jennings & Kaiser 1998, Hall 1999, Norse & Watling 1999, Kaiser et al. 2000).

Fisheries management aiming to reduce anthropogenic disturbance on ecosystems should consider the implications of fishing activities for both the struc-

ture and functioning of marine communities. This implies that there is a need to find appropriate indicators of the community response to fishing disturbance (Link et al. 2002, Bustos-Baez & Frid 2003, Frid et al. 2005, Piet & Jennings 2005). Changes in the functional components of the communities represent the organisms' adaptations to the environment and their response to stress; therefore, focusing on how commercial trawling has modified the functional components of the communities can clarify the consequences of this type of fishing for benthic ecosystems. (Bremner et al. 2003, Bremner et al. 2005). Numerous trawling impact studies demonstrate that the organisms' responses to disturbance depend on their biological traits. For example, those organisms possessing traits considered opportunistic and less affected by trawling activities

are likely to respond positively to disturbance events (Kaiser & Spencer 1994, Dayton et al. 1995, Philippart 1998, Thrush et al. 1998, Auster & Langton 1999, Frid 2003, Blanchard et al. 2004).

In this study, several functional traits were selected to represent different components of the organisms' sensitivities to trawling disturbance. These traits were considered important in determining both the responses of benthos to fishing activities and the potential for changes in ecosystem function. Firstly, feeding type reflects the adaptation of the organisms to the habitat, e.g. numerous studies have detected significant increases of motile scavengers in recently trawled areas (Kaiser & Spencer 1994, Collie et al. 1997, Ramsay et al. 1998, Demestre et al. 2000, Rumohr & Kujawski 2000, Bozzano & Sarda 2002). Deposit feeders can also be favoured as trawling increases the availability of organic matter on the sediments (Frid et al. 2000), whereas filter feeders are highly affected by the increase of suspended sediment following trawling (Caddy 1973). Secondly, the motilities of the organisms

and their positions in or on the sediments also influence their vulnerabilities to trawling. Sedentary surface organisms are strongly affected by the trawling gear (Bergman & Hup 1992, Thrush et al. 1995, Auster et al. 1996, Wassenberg et al. 2002). Thirdly, external protecting structures and the body designs of organisms can also affect vulnerabilities. Species protected with a hard shell, or vermiform organisms are considered less vulnerable to trawling impact (Bremner et al. 2003, Blanchard et al. 2004). Finally, other important traits considered in this paper are the body sizes and life spans of organisms. Previous impact studies have observed a shift from large slow growing fauna to less vulnerable smaller and faster growing organisms (Philippart 1998, Roth & Wilson 1998, Kaiser et al. 2000, Rumohr & Kujawski 2000).

The combination of these functional traits allowed estimation of both the vulnerabilities of organisms and the resilience of populations impacted by fishing activities. For example, trawling generally favours less vulnerable motile scavenging fauna over highly vulnerable surface sedentary taxa (McConnaughey et al. 2000, Frid 2003). Population resilience depends on the vulnerabilities of the individuals along with life history traits and reproductive strategies. Small and fast growing organisms are thus more resilient to disturbance. Consequently, highly vulnerable organisms with low population resilience are not expected to be abundant in trawled areas.

The aim of this study was to investigate the functional components of a benthic community subjected to chronic fishing disturbance. The study area was located in a northwestern Mediterranean commercial fishing ground that is exploited by a large trawling fleet operating with well-defined seasonal activity. We compared chronically disturbed and undisturbed benthic communities to obtain the response of functional traits of the faunal assemblages to commercial trawling activities. Our goal was to test predictions and estimate how trawling alters the different functional components of communities, thus improving our knowledge of the ecological implications of fishing.

This study highlights an opportunity to investigate a soft-bottom community from a commercial fishing ground, considering both the large epifaunal and smaller infaunal organisms. Moreover, we emphasise the focus of this study on muddy soft bottoms, one of the most characteristic habitats for species targeted by trawling fisheries worldwide.

## MATERIALS AND METHODS

**Characteristics of the study area.** The study was conducted in the Catalan Sea located in the northwest-

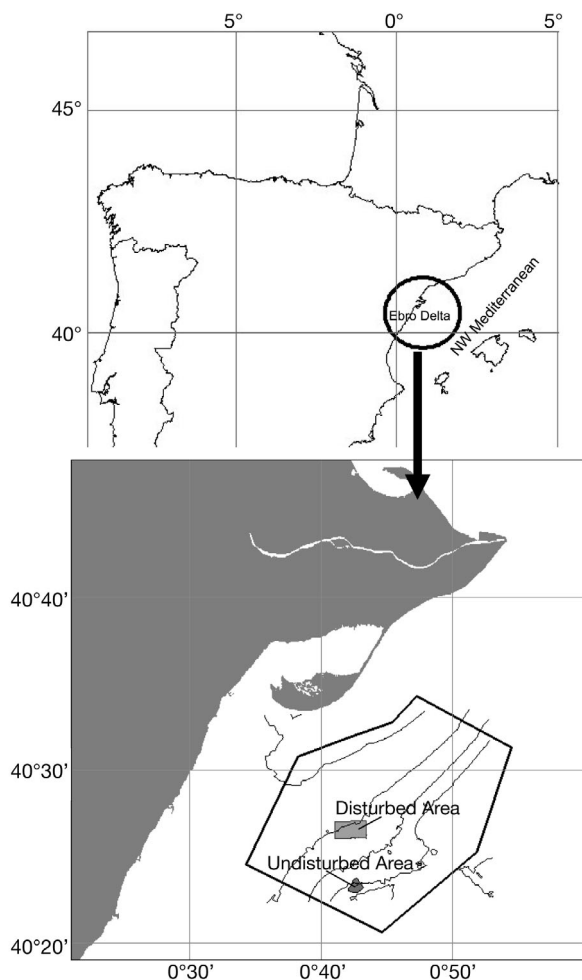


Fig. 1. Location of the study area in the northwestern Mediterranean Sea

ern sector of the Mediterranean Sea (Fig. 1). The fishing ground selected is on the continental shelf off the Ebro Delta. It has a surface area of 400 km<sup>2</sup> and depths between 30 and 80 m. The sediment consists of mud (>95%) and has a median grain size of 2.7 to 4.6 µm. This section of the continental shelf extends for 70 km with a gentle slope, and has highly homogenous sediment and physical parameters (Díaz et al. 1990). The benthic community is considered typical of continental shelf muddy bottoms, with low diversity and high secondary production (Demestre 1986).

This study was focused on an otter-trawl fleet from the port of Sant Carles de la Ràpita. With 59 vessels, this is the largest trawling fleet in the region, operating in several well defined fishing grounds (Demestre 2006). Previous studies in the area, as well as historical catch records of the trawlers and daily records from the local auction, permitted selection of a fishing ground characterised by seasonal variation in the activity of the fleet. Fishing fleet activity in this area varies from high effort during autumn and winter (from September to February: 7550 average fishing h mo<sup>-1</sup>), to low effort in spring and the beginning of summer (from March to June: 5520 average fishing h mo<sup>-1</sup>), and a 2 mo fishing closure in summer (July and August). The whole area was surveyed using side scan sonar images that registered the trawl marks on the sea bed. These images confirmed that the fishing ground was evenly trawled. Furthermore, the selected fishing ground includes an area of 2.7 km<sup>2</sup> that has remained undisturbed for 20 yr due to the fragmented remains of an abandoned oil platform. This portion of seafloor was used as a reference area (Demestre 2006).

**Sampling cruises and processing of samples.** Two study sites were selected within the fishing ground: a fished site and the undisturbed area as a reference. A survey carried out in the fishing ground prior to this study characterised the area and identified the benthic community assemblages and environmental characteristics at the 2 study sites. The sites had similar habitat characteristics (Demestre 2006).

Samples of benthic fauna were collected from the fished and reference sites on 7 experimental cruises timed to encompass seasonal variability, as well as the variations in fishing activity (27 to 30 June 2003, with low fishing activity; 14 to 17 July 2003, 28 to 31 July 2003 and 19 to 22 August 2003, during fishing closure; 26 to 29 September 2003 and 14 to 17 November 2003, with high fishing activity; and 18 to 21 June 2004, with low fishing activity).

Epifaunal and infaunal organisms were the focus of this study. The epifaunal fraction comprised the large macrofauna living on the sediment surface or within the first few cm of sediment depth. They were collected with a surface dredge. Infaunal organisms com-

prised smaller macrofauna buried in the sediments. They were collected with a grab. The epifauna was sampled with a surface dredge, similar to a 2 m beam trawl, composed of a 2 m × 40 cm iron-framed aperture, a 40 mm mesh size and a 10 mm cod-end. The minimum sample size to estimate the species richness was determined (based on Sanchez et al. 1998). Accordingly, we made 3 hauls of approximately 15 min duration at 3 knots h<sup>-1</sup> at each site. A total of 3 replicate epifaunal samples was collected randomly on each cruise at both fished and reference sites. Epifaunal samples were standardised to a surface area of 1000 m<sup>2</sup>, thus taking into account variations in haul duration.

To survey the infaunal benthos, sediment samples were obtained with a 0.1 m<sup>2</sup> Van Veen grab. Samples were collected at 5 fixed Stns located in each of the 2 study sites. Five grab samples were collected randomly at each station to determine minimum sample size for species richness estimates (Demestre 2006). Sediment samples were sieved over a 1 mm mesh. Epifaunal and infaunal organisms were identified to the lowest taxonomical level practical, and counted. The data obtained with the epibenthic dredge and the infaunal grab were analysed separately, as they sampled different components of the benthic community.

**Infaunal and epifaunal functional groups.** The analyses were based on groups of organisms with common functional attributes that were predicted to respond in similar ways to fishing disturbance. The data set was reduced to 13 epifaunal species and 25 infaunal taxa to focus the study on the organisms that contributed most to the differences between the fished and reference sites. These species were selected by the SIMPER procedure (PRIMER, Clarke & Warwick 1994) as those that accounted for 90% of the dissimilarity between fished and reference sites. These species were also the most abundant in the community. The epifaunal species selected contributed 90% to total epifaunal abundance, and belonged to Bivalvia, Gastropoda, Crustacea, Echinodermata and Osteichthya. The selected infaunal taxa contributed 80% to overall infaunal abundance, and comprised members of the Polychaeta, Crustacea, Bivalvia, Gastropoda, Echinodermata and the Nemertini. Organisms contributing <1% to overall abundance were aggregated in the analysis into the rare species group.

A set of functional traits was assigned for every selected species (Table 1). The species were classified into different functional categories based on information from a variety of literature sources and from specialist knowledge. Each functional category was predicted to show either a negative, neutral or positive response to trawling activity. The predicted response of each trait to trawling disturbance was formulated on the basis of previous trawling impact studies con-

Table 1. List of functional traits and their corresponding codes used in the multivariate analysis. Codes for epifaunal data include: motility, position, feeding, vulnerability and size. Codes included for infaunal data: motility, position, feeding, vulnerability, body design and protection. -: not coded as trait not in multivariate analysis

| Functional traits | Codes | Functional traits | Codes |
|-------------------|-------|-------------------|-------|
| Motility          |       | Protection        |       |
| Sedentary         | S     | Tube              | t     |
| Low               | L     | None              | n     |
| Medium            | M     | Size              |       |
| High              | H     | <1 cm             | 1     |
| Position          |       | 1–5 cm            | 4     |
| Surface           | S     | 5–10 cm           | 6     |
| Subsurface        | B     | >10 cm            | 9     |
| Feeding type      |       | Life Span         |       |
| Filter feeders    | F     | <1 yr             | –     |
| Deposit feeders   | D     | 1–3 yr            | –     |
| Predators         | P     | >3 yr             | –     |
| Scavengers        | S     | Resilience        |       |
| Vulnerability     |       | Low               | –     |
| Low               | L     | Medium            | –     |
| Medium            | M     | High              | –     |
| High              | H     |                   |       |
| Body design       |       |                   |       |
| Vermiform         | V     |                   |       |
| Shell             | S     |                   |       |
| Scales            | A     |                   |       |

ducted elsewhere, and on the biology of the local organisms.

The functional traits were split up in several categories. Feeding mode comprised 4 categories for epifauna: filter feeders, deposit feeders, predators and scavengers. For infauna, only 3 categories were used, with predators and scavengers included in the same group. Motility was described at the scale of the fishing disturbance, and ranged from sedentary (unable to avoid the disturbance) to highly motile organisms. Categories for position on the sediment were allocated differently for the infaunal and epifaunal organisms. Epifauna were sampled with a surface dredge that also collected organisms burrowing into the sediment. While grabs collected infaunal organisms buried in the sediment, they also included organisms living in the sediment-water interface. External protecting structures and the categories of body design were considered important determinants of infaunal vulnerability to fishing gear. The maximum sizes and life spans were also included as important traits of organisms. However life spans (and consequent resilience against disturbance) were not included in all the analyses, as this information was not available for the entire species list; with few exceptions the infaunal organisms are thought to have a life span of 1–2 yr. Two summary classifications, vulnerability and

resilience, were estimated after combining the different functional traits.

Finally, a category 'rarity' was defined for those organisms that individually contributed <1% to overall abundance. Rare species may provide valuable information for identifying the functional traits highly affected by fishing activities. However, variations in the abundance of this group could not be tested by inferential statistical analysis, due to the high percentage of zero abundance values. Therefore, conclusions drawn from these data must be considered with caution.

**Statistical analyses.** The functional categories (except resilience and life span) were transformed into a list of codes summarising the biological characteristics of each species (Table 1). The abundances of species possessing the same code were summed (Table 2), after which we tested for differences between communities from fished and reference sites (PRIMER statistical package, Clarke & Warwick 1994). Similarity between each pair of samples was calculated using the Bray-Curtis similarity index, after square root transformation of the data to reduce the influence of dominant groups. A non-metric multidimensional scaling ordination (MDS) was developed based on the similarity matrix. An ANOSIM test was used to test the similarity between samples from fished and reference sites. Finally, the data were analysed with the SIMPER procedure to determine which codes accounted for the observed dissimilarities between samples.

Subsequently, epifaunal and infaunal species were combined into groups with common functional attributes. In this way, the list of codes was reduced to 6 epifaunal and 9 infaunal functional groups (Table 3). Abundances of the different functional groups were analysed to compare fished and reference sites at different levels of fishing activity. The densities of the functional groups were expected to either increase or decrease with fishing activities, depending on the functional traits.

A 2-way analysis of variance (ANOVA) was performed to identify significant differences ( $p < 0.05$ ) in the abundances of the functional groups between fished and reference sites and among the different cruises (each cruise represents a different level of fishing activity). Site and cruise were analysed as fixed factors. A Tukey post-hoc comparison test was applied to detect significant pairwise differences among combinations of Site  $\times$  Cruise. When the factor interaction term was significant, a multiple comparison test based on specific contrasts was used to determine significance of the interaction between different levels of each factor. The Kolmogorov-Smirnov test was used to test the assumption of normality, and Levene's test checked the homogeneity of error variances. When the normality assumptions were not met, a  $\log_{10}$  transfor-

mation was applied. In 2 cases (Group 1e and Group 9i in Table 3) the data were not normally distributed, because the differences in abundance between sites were very large and bimodal; therefore, a Kruskal-Wallis non-parametric test was used to detect significant differences between sites. Univariate analyses were conducted with the statistical package S-plus (Becker et al. 1988).

## RESULTS

Organisms classified as having low vulnerability were the most common within the the epifauna, and were slightly more abundant at the fished site than at the reference site (Fig. 2a). Moderately vulnerable species accounted for most of remaining epifauna at both sites. Highly vulnerable organisms were extremely rare at the fished site and present at low abundances at the reference site (Fig. 2a). Most infaunal species were characterised as medium to low vulnerability with no large differences between sites (Fig. 2b). Highly vulnerable infauna were uncommon at both sites (Fig. 2b).

### Multivariate pattern

Multivariate analysis showed that epifaunal communities from reference and fished sites were 37.5% dissimilar. The MDS ordination of samples (Fig. 3a) and ANOSIM test clearly distinguished fished and reference sites with a stress level of 0.17 and an R value of 0.91 ( $p = 0.001$ ). The SIMPER procedure highlighted the importance of 3 functional codes in discriminating the 2 sites (Table 2a). The fished site was characterised by motile burrowing predators and scavengers (codes HBPM4 and MBSL9), whereas the reference site had higher abundance of highly motile surface predators and burrowing low motility filter feeders (codes HSPM9 and LBFH6).

Multivariate analyses of the infaunal data showed that reference and fished sites were 39.6% dissimilar.

Table 2. Results of SIMPER analysis for (a) epifaunal and (b) infaunal data. Codes and corresponding species; average abundance at fished (Av. N-fished) and reference (Av. N-reference) sites; index of contribution to dissimilarity between sites (Diss/SD); \*indicates indices >1.40

| (a)<br>Codes | Epifaunal species   | Av. N-fished | Av. N-reference | Diss/SD |
|--------------|---|--------------|-----------------|---------|
| LBFH6        | <i>Acanthocardia echinata</i>   | 0.1          | 2.98            | 2.13*   |
| HSPM9        | <i>Citharus linguatula</i><br><i>Lepidotrigla cavillone</i><br><i>Arnoglossus laterna</i> | 4.95         | 22.54           | 1.60*   |
| HBPM4        | <i>Lesuerogobius suerii</i>   | 4.69         | 0.57            | 1.52*   |
| LBDL4        | <i>Nucula nucleus</i>   | 7.46         | 9.81            | 1.32    |
| MBSL9        | <i>Astropecten irregularis</i>  | 73.98        | 57.09           | 1.31    |
| SBDL4        | <i>Trachythone tergestina</i><br><i>Alpheus glaber</i>                                    | 31.61        | 22.28           | 1.24    |
| MBPM4        | <i>Goneplax rhomboides</i>  | 11.29        | 21.98           | 1.24    |
| MSSL6        | <i>Bolinus brandaris</i><br><i>Pagurus excavatus</i><br><i>Liocarcinus depurator</i>      | 9.87         | 6.97            | 1.24    |
| (b)<br>Codes | Infaunal species  | Av. N-fished | Av. N-reference | Diss/SD |
| LBPLVn       | <i>Lumbrineris</i> sp.<br>Nemertini   | 153.18       | 41.17           | 2.84*   |
| LSPMVt       | <i>Marphysa bellii</i>  | 0.76         | 41.66           | 2.18*   |
| SBDLVn       | <i>Aricidea</i> sp.<br><i>Levinsenia gracillis</i><br><i>Labidoplax digitata</i>          | 147.41       | 341.03          | 1.7*    |
| LBDMVn       | <i>Sternaspis scutata</i>   | 98.47        | 31.94           | 1.7*    |
| SSDMVt       | Ampharetidae<br><i>Prionospio</i> sp.<br><i>Scolelepis cantabra</i>                       | 79.94        | 142.8           | 1.44*   |
| SSFHSn       | <i>Thyasira flexuosa</i>  | 22.29        | 18.4            | 1.36    |
| SBDLVt       | Capitellidae<br>Cirratulidae  | 180.82       | 190.17          | 1.33    |
| LSPLVn       | <i>Glycera</i> sp.  | 18.82        | 17.37           | 1.31    |
| SSFHAt       | <i>Ampelisca tenuicornis</i><br><i>Corophium rotundirostre</i>                            | 22.92        | 58.80           | 1.29    |
| SBDMAn       | <i>Apeudes spinosus</i><br><i>Apeudes latreillei</i>                                      | 70.11        | 34.81           | 1.24    |
| SSDMVn       | Flabelligeridae<br><i>Paralacydonia paradoxa</i>  | 36           | 37.26           | 1.16    |
| SBDMSn       | <i>Mysella bidentata</i><br><i>Nucula nucleus</i>   | 19.24        | 14.8            | 1.12    |
| LSPMSn       | <i>Hyala vitrea</i>   | 19.47        | 16.34           | 0.93    |
| MSFMAn       | <i>Leucon mediterraneus</i>   | 29.6         | 17.06           | 0.83    |
| LSDLAn       | <i>Amphiura chiajei</i>   | 0.94         | 3.14            | 0.77    |

The MDS ordination (Fig. 3b) and ANOSIM test divided fished and reference samples into 2 well defined groups with a 0.14 stress level and a 0.98 R value ( $p = 0.001$ ). The SIMPER procedure highlighted 5 functional codes as best discriminators of fished and reference sites (Table 2b). The fished community was



Table 3. Epifaunal (a) and infaunal (b) functional groups. Functional group and species included in each group are indicated in the first 2 columns (left side); the subsequent columns summarise the biological traits. Motility (Motil.): S, sedentary; L, low; M, medium; H, high. Position on the substratum (Posit.): S, surface and SS, subsurface. Feeding mode (Feed.): FF, filter feeders; DF, deposit feeders; P, predators; S, scavengers. Maximum size (Size) for epifauna (a) in cm. Body design (Shape) for infauna (b): Sh, shell; Sc, scales; Verm, vermiform. Maximum age (Age) in yr. Resilience (Resil.) for the epifauna (a), and vulnerability (Vuln.) for epifauna and infauna (a,b): L, low; M, medium; H, high. The last 2 columns (right side) indicate the expected (E) and observed (O) response to trawling disturbance: ↑, increase in abundance; ↓, decrease in abundance; –, no predicted/observed response. d: no data available

| (a) Epifaunal taxon Group   | Motil. | Posit. | Feed. | Size    | Age  | Resil. | Vuln. | E  | O  |
|---|--------|--------|-------|---------|------|--------|-------|----|----|
| 1e <i>A. echinata</i>   | L      | SS     | FF    | 5–10    | >3   | L      | H     | ↓↓ | ↓↓ |
| 2e <i>N. nucleus</i> , <i>A. glaber</i> , <i>T. tergestina</i>                                    | S/L    | SS     | DF    | <5      | nd   | nd     | L–M   | ↑  | ↑  |
| 3e <i>C. linguatula</i> , <i>L. cavillone</i> , <i>A. laterna</i>                                 | H      | S      | P     | >10     | >3   | M      | M     | ↓  | ↓  |
| 4e <i>G. rhomboides</i> , <i>L. suerii</i>  | M/H    | SS     | P     | <5      | >2   | nd     | M     | ↓  | –  |
| 5e <i>B. brandaris</i> , <i>L. depurator</i> , <i>P. excavatus</i>                                | M      | S      | S     | >10     | >2   | H      | L     | ↑  | ↑  |
| 6e <i>A. irregularis</i>  | M      | SS     | S     | >10     | >3   | H      | L     | ↑↑ | ↑↑ |
| (b) Infaunal taxon Group  | Motil. | Posit. | Feed. | Shape   | Age  | Vuln.  | E     | O  |    |
| 1i <i>T. flexuosa</i> , <i>A. tenuicornis</i> , <i>C. rotundirostre</i>                           | S      | S      | FF    | Sh/Sc   | nd   | H      | ↓↓    | ↓  |    |
| 2i <i>L. mediterraneus</i>  | M      | S      | FF    | Sc      | nd   | M      | –     | –  |    |
| 3i Ampharetidae, <i>S. cantabra</i> , <i>Prionospio</i> sp., <i>P. paradoxa</i> , Flabillegeridae | S      | S      | DF    | Verm    | nd   | M      | –     | ↓  |    |
| 4i <i>A. chiajei</i>  | M      | S      | DF    | Sc      | >1yr | L      | ↑     | –  |    |
| 5i Capitellidae, <i>L. gracilis</i> , <i>Aricidea</i> sp., Cirratulidae, <i>L. digitata</i>       | S      | SS     | DF    | Verm    | nd   | L      | ↑     | –  |    |
| 6i <i>S. scutata</i>  | M      | SS     | DF    | Verm    | >1yr | M      | ↑     | ↑↑ |    |
| 7i <i>A. spinosus</i> , <i>A. latreillei</i> , <i>M. bidentata</i> , <i>Nucula</i> sp.            | S      | SS     | DF    | Sh/Sce  | >1yr | M      | ↓     | ↑  |    |
| 8i <i>Glycera</i> sp., <i>M. bellii</i>   | M      | S      | P     | Verm    | nd   | L–M    | –     | ↓↓ |    |
| 9i <i>H. vitrea</i> , Nemertini, <i>Lumbrinereis</i> sp.  | M      | SS     | P     | Verm/Sh | nd   | L–M    | ↑↑    | ↑↑ |    |

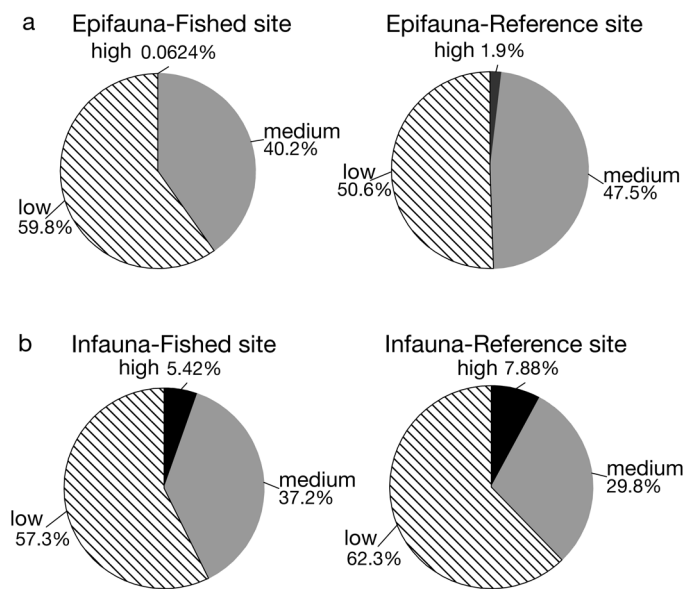


Fig. 2. Vulnerabilities of epifauna (a) and infauna (b) at fished and reference sites

characterised by vermiform motile burrowing predators and deposit feeders, which have low or moderately vulnerabilities to trawling (codes LBPLVn and LBD-MVn). The infauna from the reference site was characterised by sedentary burrowing deposit feeders and sedentary or low motility surface organisms living in tubes (codes SBDLVn, SSDMVt, and LSPMVt).

**Responses of epifaunal functional groups to fishing activity**

The abundances of epifaunal functional groups (Table 3a) were analysed to test for significant differences between fished and reference sites and among the different cruises (Fig. 4). The predicted and observed response of these groups to trawling is included in Table 4a.

The low motility burrowing filter feeders (Group 1e) were characterised by long-life span and low population resilience. As predicted, these organisms were mostly found in low abundance at the reference site

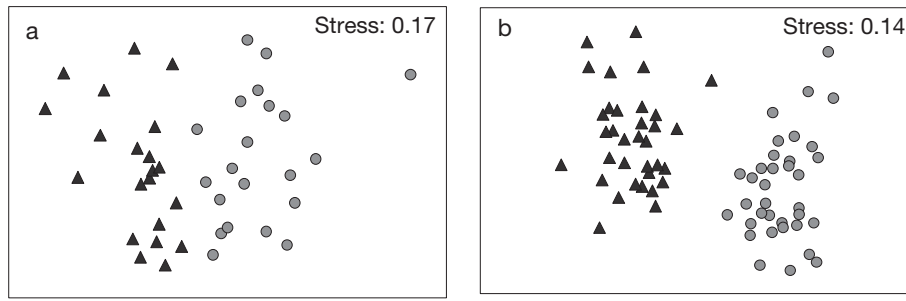


Fig. 3. Multidimensional scaling ordination plot of epifaunal (a) and infaunal (b) functional code abundances.  $\blacktriangle$ : correspond to samples from fished site and  $\bullet$ : from reference site

(i.e. 2–5 ind. 1000 m<sup>-2</sup>;  $p < 0.001$ ). Small burrowing deposit feeders with low motility (Group 2e) comprised the second most dominant group in abundance, with no important differences detected between fished and reference sites (i.e. 15–60 ind. 1000 m<sup>-2</sup> on average at fished and reference sites). The abundance decreased at both sites in September and November, during high fishing activity ( $p < 0.001$ ). Most large surface organisms with long life spans (Group 3e) were highly motile predatory fish. As predicted, these organisms were significantly more abundant at the reference site (i.e. 2–10 and 15–40 ind. 1000 m<sup>-2</sup> at fished site and reference sites, respectively;  $p < 0.001$ ). Fished site abundance remained low throughout the study, except for a transient increase at the beginning of the fishing closure (June to July 2003;  $p < 0.001$ ). The predatory organisms (Group 4e) were characterised by small size, motility and burrowing behaviour. However, these organisms live >2 yr and were classified as moderately vulnerable. The number of individuals from this group was similar at reference and fished sites (i.e. average 5–45 ind. 1000 m<sup>-2</sup>). Abundance decreased in September and November, associated with high fishing activity ( $p < 0.001$ ). Motile scavengers (Group 5e), characterised by surface position, medium size and life spans >2 yr, were highly resilient. These organisms decreased at the fished site in September and November cruises, coinciding with high fishing effort (i.e.

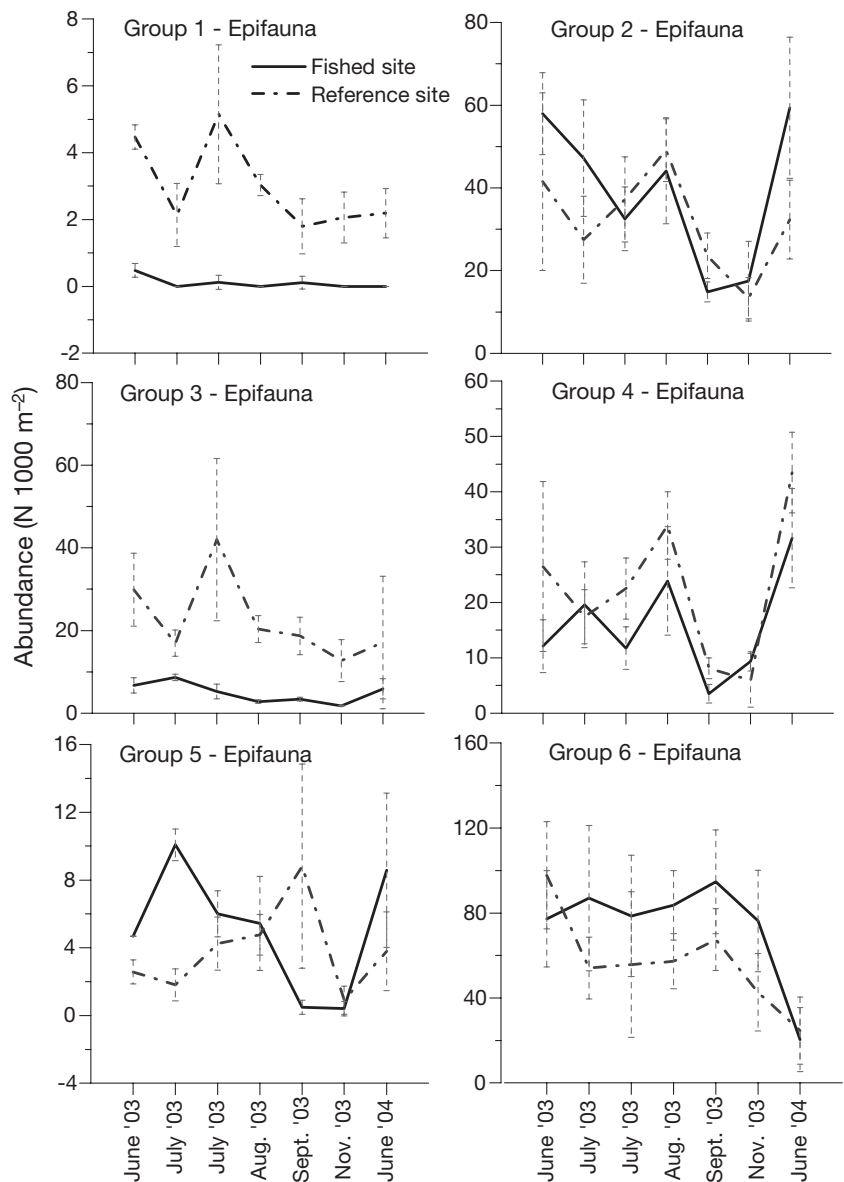


Fig. 4. Mean abundances ( $\pm$ SD) of epifaunal functional groups at fished and reference sites in survey cruises from June 2003 to June 2004. See Table 3 (a) for details of the 6 groups

Table 4. ANOVA test summary. Epifaunal functional groups analysis (a); infaunal functional groups analysis (b); Kruskal-Wallis non-parametric test (c). Groups 2i and 4i were excluded from ANOVA due to low abundance and high variability recorded; see 'Results' for further details. \*indicates significant p-value ( $p < 0.05$ )

| (a) Epifauna       | df | F value  | Pr(F)   |
|--------------------|----|----------|---------|
| Group 2e           |    |          |         |
| Site               | 1  | 3.99     | 0.056   |
| Cruise             | 6  | 8.65     | <0.001* |
| Site × Cruise      | 6  | 2.32     | 0.061   |
| Group 3e           |    |          |         |
| Site               | 1  | 147.56   | <0.001* |
| Cruise             | 6  | 5.96     | <0.001* |
| Site × Cruise      | 6  | 2.94     | 0.023*  |
| Group 4e           |    |          |         |
| Site               | 1  | 3.78     | 0.062   |
| Cruise             | 6  | 3.36     | <0.001* |
| Site × Cruise      | 6  | 2.15     | 0.078   |
| Group 5e           |    |          |         |
| Site               | 1  | 2.91     | 0.099   |
| Cruise             | 6  | 3.75     | 0.007*  |
| Site × Cruise      | 6  | 6.99     | <0.001* |
| Group 6e           |    |          |         |
| Site               | 1  | 5.86     | 0.022*  |
| Cruise             | 6  | 5.21     | 0.001*  |
| Site × Cruise      | 6  | 1.27     | 0.301   |
| (b) Infauna        | df | F value  | Pr(F)   |
| Group 1i           |    |          |         |
| Site               | 1  | 70.05    | <0.001* |
| Cruise             | 6  | 18.78    | <0.001* |
| Site × Cruise      | 6  | 12.25    | <0.001* |
| Group 3i           |    |          |         |
| Site               | 1  | 32.48    | <0.001* |
| Cruise             | 6  | 11.10    | <0.001* |
| Site × Cruise      | 6  | 2.99     | 0.013*  |
| Group 5i           |    |          |         |
| Site               | 1  | 43.81    | <0.001* |
| Cruise             | 6  | 3.49     | 0.005*  |
| Site × Cruise      | 6  | 3.33     | 0.007*  |
| Group 6i           |    |          |         |
| Site               | 1  | 147.02   | <0.001* |
| Cruise             | 6  | 1.86     | 0.104   |
| Site × Cruise      | 6  | 1.76     | 0.125   |
| Group 7i           |    |          |         |
| Site               | 1  | 53.42    | <0.001* |
| Cruise             | 6  | 2.39     | 0.040*  |
| Site × Cruise      | 6  | 4.59     | <0.001* |
| Group 8i           |    |          |         |
| Site               | 1  | 197.43   | <0.001* |
| Cruise             | 6  | 5.02     | <0.001* |
| Site × Cruise      | 6  | 1.47     | 0.207   |
| (c) Kruskal-Wallis | df | $\chi^2$ | p       |
| Group 1e           |    |          |         |
| Site               | 1  | 325.92   | <0.001* |
| Group 9i           |    |          |         |
| Site               | 1  | 44.48    | <0.001* |

5–10 ind. 1000 m<sup>-2</sup> in June–August and 1 ind. 1000 m<sup>-2</sup> in September–November at the fished site;  $p < 0.001$ ). Reference site abundance decreased in November ( $p < 0.001$ ). The low vulnerability burrowing scavengers with large size and long life span (Group 6e) had high population resilience. This was the most abundant group in the community (i.e. 40–100 ind. 1000 m<sup>-2</sup> average at fished and reference sites), with significantly higher number of organisms at the fished site ( $p = 0.022$ ).

Rare epifaunal organisms (1% of the overall abundance) included sedentary or sessile surface filter feeders (the Cnidarians *Alcyonium palmatum* and *Veritillum cynomorium*), and fragile large deposit feeders, represented by the sea urchins *Schizaster canalifera* and *Brissopsis atlantica*.

#### Responses of infaunal functional groups to fishing activity

Abundances of the infaunal functional groups (Table 3b) were analysed to test for significant differences between fished and reference sites and between cruises (Fig. 5). Table 4b includes the predicted and response of infaunal functional groups to trawling disturbance.

The highly vulnerable organisms, represented by sedentary surface filter feeders with shells or scales (Group 1i), were generally less abundant at the fished site (i.e. 15–80 and 50–120 ind. m<sup>-2</sup> at the fished and reference sites, respectively;  $p < 0.001$ ). The abundance followed a seasonal pattern at the reference site, decreasing at the end of summer and autumn ( $p < 0.001$ ). Fished site abundance increased during the fishing closure and during the high fishing activity cruise in September ( $p < 0.001$ ). The low abundance and high variability between cruises hindered detection of significant patterns by analysis of variance of the high motility taxa (Group 2i). Vermiform surface deposit feeders of moderate vulnerability (Group 3i) were significantly more abundant at the reference site in the June and July cruises ( $p < 0.001$ ). The abundance decreased in August and increased again in November (i.e. 100–250 ind. m<sup>-2</sup> at reference site, and 60–180 ind. m<sup>-2</sup> at fished site;  $p < 0.001$ ). The density of low vulnerability motile surface deposit feeders (Group 4i) was low and patchy, which again hindered the detection of significant patterns by the analysis of variance. Sedentary vermiform subsurface deposit feeders (Group 5i) were the most abundant organisms in the community (i.e. 250–750 ind. m<sup>-2</sup> average at fished and reference sites) and exhibited significantly higher densities at the reference site in the June and July cruises ( $p < 0.001$ ); densities decreased at the end



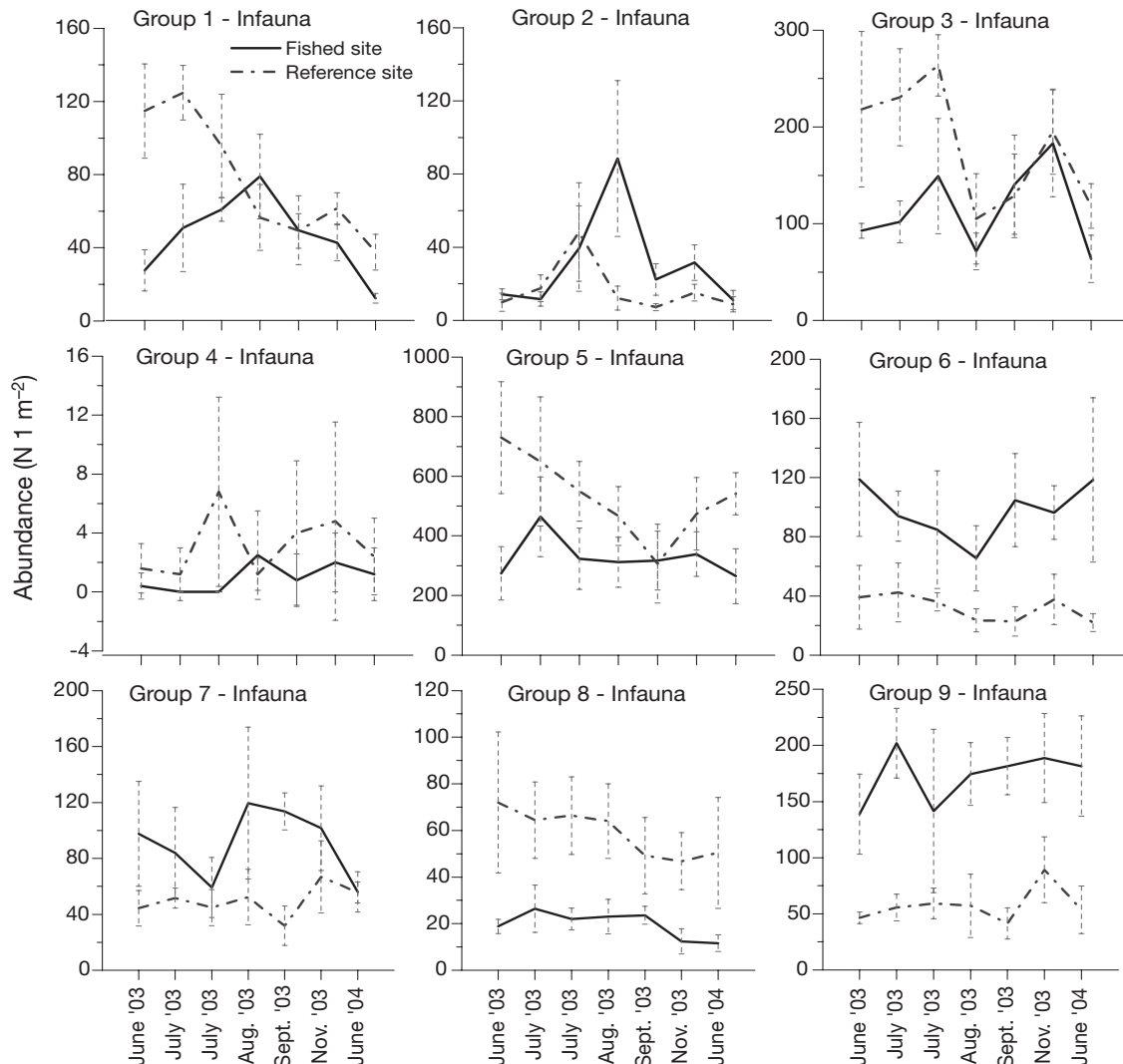


Fig. 5. Mean abundances ( $\pm$ SD) of infaunal functional groups at fished and reference sites in survey cruises from June 2003 to June 2004. See Table 3 (b) for details of the 9 groups

of the fishing closure ( $p = 0.005$ ). At the fished site this variability was not detected. Motile subsurface deposit feeders, with long life span and moderate vulnerability to trawling (Group 6i), were significantly more abundant at the fished site ( $p < 0.001$ ), and the number of individuals was constant during the study period (i.e. 65–120 ind.  $m^{-2}$  at fished site and 20–40 ind.  $m^{-2}$  at the reference site). Sedentary subsurface deposit feeders, with shell or scales body design and life span longer than one year (Group 7i), although predicted to be vulnerable to trawling, were more abundant at the fished site (i.e. 50–120 ind.  $m^{-2}$  at fished site and 30–70 ind.  $m^{-2}$  at reference site;  $p < 0.001$ ). Motile surface carnivores (Group 8i) were significantly more abundant at the reference site (i.e. 50–70 ind.  $m^{-2}$  at reference, and 10–25 ind.  $m^{-2}$  at fished site;  $p < 0.001$ ), decreasing at both sites in

November and June 2004 cruises ( $p < 0.001$ ). As predicted, burrowing carnivores (Group 9i) were significantly more abundant at the fished site (140–200 ind.  $m^{-2}$  at fished and 40–90 ind.  $m^{-2}$  at reference site;  $p < 0.001$ ).

Rare infauna included the tube dwelling polychaetes (Pectinariae, Terebellidae and Serpulidae). These organisms were found mostly at the reference site.

## DISCUSSION

### Responses of functional groups to fishing activity

Trawling disturbance modified the functional components of the benthic community from the Sant Carles de la Ràpita fishing ground. Functional group analyses

differentiated infaunal and epibenthic communities in the fished and reference sites, confirming the sensitivity of the functional traits to trawling disturbance and the potential of benthic communities for functional changes, even when species richness is low. Patterns were apparent in spite of the dominance of organisms with low or medium vulnerability to trawling. The most abundant functional groups occurred at equal densities in the fished and reference sites. The epifaunal community in the fishing ground had a high abundance of small deposit feeders and predators, which avoid direct contact with the fishing gear by burrowing into the sediments. Sedentary deep burrowing deposit feeders dominated the infaunal community in the fishing ground. However it is difficult to ascertain if this assemblage configuration results solely from the trawling disturbance history in the fishing ground, or if it also represents a characteristic community from muddy bottoms.

Muddy bottom communities from continental shelves have been characterised previously by a predominance of subsurface deposit feeders (Roth & Wilson 1998, Pearson 2001, Pranovi et al. 2005). However, the long history of exploitation of Mediterranean benthic communities might have selected those less vulnerable organisms adapted to frequent anthropogenic disturbance (Dayton et al. 1995, Tuck et al. 1998, Thrush & Dayton 2002). The lack of pristine areas with similar characteristics to the fishing ground hampers our ability to conclusively attribute differences in assemblages to chronic trawling impact. Nevertheless, the comparison of fished and reference areas highlighted other functional groups showing a positive response to trawling disturbance. Motile burrowing scavengers dominated the epifaunal community at both sites, but they were significantly more abundant at the fished site. These organisms have low vulnerability to trawling and benefit from the carrion supply in the trawled area (Kaiser & Spencer 1994, Ramsay et al. 1998, Demestre et al. 2000). Importantly, our study demonstrates that the increase in scavenger abundance can be more than a transient response. Among the infaunal organisms, the motile burrowing deposit feeders and carnivores were significantly more abundant at the fished site. Motility and burrowing behaviour proved to be important traits in determining vulnerability, as organisms that burrow deeper than the penetration depth of the trawl gear may avoid trawling disturbance (Philippart 1998, Ramsay et al. 1998, Brown et al. 2005, Frid et al. 2005). These motile deposit feeders and carnivores can therefore benefit from the increase of organic matter available in the sediment column in trawled areas (Frid et al. 2000).

Motile predators and sedentary filter feeders distinguished the undisturbed epifaunal community, while

the infaunal community was differentiated by a higher abundance of surface organisms. This undisturbed area has not been trawled for 20 yr, suggesting that these organisms are sensitive to fishing activities. The highly vulnerable filter feeding epifauna were significantly more abundant in the undisturbed area, with densities in the fished site of  $<2$  ind.  $1000\text{ m}^{-2}$ . This group is represented by large and slow growing sedentary organisms predicted to have little resilience to trawling activities (Hill et al. 1999, Jennings et al. 2001, Blanchard et al. 2004). Filter feeding sedentary infauna living on surface sediments also proved vulnerable to fishing activities, as significantly higher densities of these organisms were recorded in the undisturbed area. These results agree with predictions that filter feeders can be highly affected by trawling, due to increased suspended sediment concentrations (Caddy 1973). The undisturbed infaunal community also had significantly higher abundances of motile carnivores and vermiform sedentary deposit feeders living within surface sediments. When taking into consideration their biological traits, these organisms were expected to be less vulnerable to trawling, however, their surface position increases vulnerability to fishing disturbance (Bergman & Hup 1992). The large motile predators were also significantly more abundant in the undisturbed epifaunal community. These results confirm the suggestion that some fish species are driven out of heavily fished areas, which become dominated by more opportunistic scavengers (Collie et al. 1997, Bozzano & Sarda 2002, Blanchard et al. 2004, Daan et al. 2005). However, it is important to note that the fish driven out of heavily fished area are the target species of the trawling fleet. Regardless of the mechanism that reduces populations of large motile fish predators in the fishing grounds, the higher abundance of these organisms in the undisturbed area suggests closed areas are effective as refuges for commercial species.

### Seasonality vs. fishing intensity

The seasonality observed in both epifaunal and infaunal communities matches the description by Sardá et al. (1999) of Mediterranean community dynamics, with a decrease in faunal abundance at the end of summer and during autumn. The most abundant epifaunal organisms followed a seasonal pattern marked by a decrease in the numbers of individuals in autumn (September and November). The burrowing scavengers (opportunistic and dominant in the community) did not follow this seasonal trend. Infaunal organisms also showed a seasonal pattern, with higher abundance in spring and early summer, followed by a

decrease in late summer and autumn (August and September). Sometimes, a second peak of abundance occurred in November. In the case of the infaunal community, this seasonal pattern was generally observed only at the undisturbed site.

These results confirm the negative effects of trawling, as the lack of seasonality can be linked to the elimination of natural variation by disturbance events (Hall 1999). The fishing ground surveyed was characterised by variability in the trawling fleet activity regimen: high fishing effort from September to February, low effort from March to June, and a 2 mo fishing closure in July and August. The decrease in the number of epifaunal organisms in September and November coincided with the highest fishing effort in the area. Unfortunately, as the number of individuals decreased equally at both sites, no correlation with the fishing activity can be established.

The reference site corresponds to a small portion of the fishing ground that remains un-trawled, but it is otherwise surrounded by intense trawling activity. Therefore, it is difficult to eliminate indirect influences of trawling activity, operating through effects on the supply of colonists or increases in turbidity (Hill et al. 1999, Palanques et al. 2001). The close correlation between the fishing regimen and biological seasonality imposes a further difficulty in comparing the fished and reference areas. Low fishing activity and the fishing closure occur during spring and summer, whereas high fishing activity is undertaken in autumn months. Mediterranean communities are characterised by an increase of the number of individuals in spring and a sharp decrease at the end of summer and autumn, coinciding with the highest levels of fishing activity. However, some organisms showed specific temporal responses to trawling activities in the study area. The motile surface epifaunal scavengers underwent a sharp decrease of abundance during the period of high fishing effort in the fished area. In contrast, the less vulnerable motile burrowing scavengers were abundant even during the high effort season. No infaunal organisms showed a significant response to the temporal changes in fishing activity regimen. Intense fishing in this portion of the continental shelf might have resulted in adapted communities less sensitive to the activity levels (Thrush et al. 1995, Sanchez et al. 1998, Auster & Langton 1999, McConnaughey et al. 2000).

#### **Functional traits shift: relevance to community function**

Burrowing scavengers dominated the epifaunal community, and responded positively to fishing activities. The infaunal community was dominated by deep

burrowing deposit feeders, and at the fished site, which was characterised by a lack of seasonality, there was a higher abundance of motile burrowing organisms. The undisturbed site contained higher functional diversity, with more epifaunal sedentary suspension feeders and large predatory fish, and a higher number of surface infauna living within tubes. The results support the predictions that opportunistic traits are beneficial in disturbed areas (Dayton et al. 1995, Bremner et al. 2005). In contrast, those traits predicted to be more vulnerable to fishing activities were more abundant in the undisturbed area, presumably because the organisms with these functional characteristics were unable to withstand frequent trawling disturbance. The organisms that respond negatively to trawling disturbance can be considered better indicators than opportunistic species, which tend to adapt easily and respond weakly to disturbance (Frid 2003). The fragile sea urchins *Schizaster canaliferus* and *Brissopsis atlantica*, several sessile surface filter feeders (e.g. the Cnidarian *Alcyonium palmatum*), and surface sessile polychaetes living in tubes were rare organisms in the fishing ground. These organisms are considered highly vulnerable to trawling, and considerably reduced in abundance by fishing activities (de Groot 1984, Kaiser & Spencer 1994, Hill et al. 1999, Kaiser et al. 2000, Wassenberg et al. 2002). Focusing on these organisms, we gain knowledge about the most sensitive functional traits, which may have been eliminated from heavily fished continental shelves. However, despite their low abundance these organisms can play an important role in ecosystem functioning, and increase the functional diversity of the community, which is important for ecosystem resilience.

The dominance of opportunistic traits in the benthic community from the fishing ground might have led to an alternative stable state, with organisms adapted to a frequent disturbance regimen (Auster & Langton 1999). Nevertheless, it is difficult to know the larger implications of the shift in functional traits for ecosystem functioning (Thrush & Dayton 2002). Focusing on the response of those traits that proved to be sensitive to trawling activities might help in understanding changes observed in chronically impacted communities. Functional traits reflect organism–habitat relationship and the ability of species to endure disturbance events or to move (Fauchald & Jumars 1979, Roth & Wilson 1998, Pearson 2001, Frid et al. 2005). In our study, scavengers appeared to replace the less opportunistic predators. This could have important implications for overall benthic community composition and alter predator–prey relationships (Bozzano & Sarda 2002, Thrush & Dayton 2002, Piet & Jennings 2005). Predatory fish are a target for the trawling fleet, and the higher abundance of these organisms in the

undisturbed area may indicate that this area better fulfils the habitat requirements of these organisms. Fragile organisms like sea urchins, or large sedentary filter feeders, although generally at low densities, also appear to have been replaced by burrowing motile epifauna. The elimination of such large organisms leads to reduction of habitat structure, with implications for community diversity. Moreover, these organisms can have important roles in bioturbation and nutrient flux at the sediment–water interface (Dayton et al. 1995, Thrush et al. 1995, Auster et al. 1996, Widdicombe et al. 2000, Wassenberg et al. 2002, Lohrer et al. 2004). The dominance of relatively small organisms is probably an adaptation to frequent trawling disturbance, which implies the elimination of large slow growing organisms (Philippart 1998, Roth & Wilson 1998, Rumohr & Kujawski 2000). The infaunal community from the fished area was characterised by a lack of seasonality, which confirms the organisms' adaptation to disturbance events and environmental variability. The intensively exploited continental shelf holds a highly homogeneous benthic community dominated by opportunistic organisms. Nevertheless, despite the small size of the reference area in the middle of this heavily trawled fishing ground, the functional trait analysis detected important differences amongst the benthic assemblages found in the fished and reference areas.

Community homogenisation and reduction of complexity can result in the loss of ecological function (Thrush & Dayton 2002). Moreover, these changes in benthic communities can have further consequences for benthic invertebrates and commercial species, as habitat structuring fauna can provide refuge and protection from predators for numerous benthic organisms and juveniles of commercial species (Kaiser et al. 2000). We also highlight the importance of considering 'rare organisms' in chronically disturbed communities to provide information about the more sensitive functional components of the community. We propose a different approach focused on functional components analysis, and the necessity of understanding the ecology of disturbed communities. Managers aiming to protect target species must consider these ecosystem function implications.

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#### LITERATURE CITED

- Auster P, Langton R (1999) The effects of fishing on fish habitat. *Am Fish Soc Symp* 22:150–187
- Auster P, Malatesta R, Langton R, Watling L, and 5 others (1996) The impacts of mobile fishing gear on seafloor habitats in the Gulf of Maine (Northwest Atlantic): implications for conservation of fish populations. *Rev Fish Sci* 4: 185–202
- Becker R, Chambers J, Wilks J (1988) *The new S language. A programming environment for data analysis and graphics.* Wadsworth and Brooks/Cole Advanced Books and Software, Pacific Grove, CA
- Bergman M, Hup M (1992) Direct effects of beamtrawling on macrofauna in a sandy sediment in the southern North Sea. *ICES J Mar Sci* 49:5–11
- Blanchard F, LeLoch F, Hily C, Boucher J (2004) Fishing effects on diversity, size and community structure of the benthic invertebrate and fish megafauna on the Bay of Biscay coast of France. *Mar Ecol Prog Ser* 280:249–260
- Bozzano A, Sarda F (2002) Fishery discard consumption rate and scavenging activity in the northwestern Mediterranean Sea. *ICES J Mar Sci* 59:15–28
- Bremner J, Rogers S, Frid C (2003) Assessing functional diversity in marine benthic ecosystems: a comparison of approaches. *Mar Ecol Prog Ser* 254:11–25
- Bremner J, Frid C, Rogers SI (2005) Biological traits of the North Sea benthos: does fishing affect benthic ecosystem function? In: Barnes PT, Thomas JP (eds) *Benthic habitats and the effects of fishing.* American Fisheries Society, Bethesda, MD, p 477–489
- Brown E, Finney B, Dommissie M, Hills S (2005) Effects of commercial otter trawling on the physical environment of the southeastern Bering Sea. *Cont Shelf Res* 25:1281–1301
- Bustos-Baez S, Frid C (2003) Using indicator species to assess the state of macrobenthic communities. *Hydrobiologia* 496:299–309
- Clarke KR, Warwick RM (1994) *Changes in marine communities: an approach to statistical analysis and interpretation.* Natural Environment Research Council, Plymouth
- Caddy JF (1973) Underwater observations on scallop (*Placopecten magellanicus*) behaviour drag efficiency. *J Fish Res Bd Can* 25:2123–2141
- Collie J, Escanero G, Valentine P (1997) Effects of bottom fishing on the benthic megafauna of Georges Bank. *Mar Ecol Prog Ser* 155:159–172
- Daan N, Gislason H, Pope J, Rice J (2005) Changes in the North Sea fish community: evidence of indirect effects of fishing? *ICES J Mar Sci* 62:177–188
- Dayton PK, Thrush S, Agardy T, Hofman R (1995) Environmental effects of marine fishing. *Aquat Conserv* 5: 205–232
- de Groot SJ (1984) The impact of bottom trawling on benthic fauna on the North Sea. *Ocean Manag* 9:177–190
- Demestre M (1986) Les diferents comunitats naturals de la Mediterrania. In: Diputacio de Barcelona, Lleonart J (eds) *L'Oceanografia II: Recursos pesquers de la mar catalana.* Quaderns d'ecologia aplicada 9:9–41
- Demestre M (2006) Response of benthic communities and sediment to different regimens of fishing disturbance in European coastal waters (EU Project Q5RS-2002–00787). Final Report. ICM-CSIC, Barcelona

- Demestre M, Sanchez P, Kaiser M (2000) The behavioural response of benthic scavengers to otter-trawling disturbance in the Mediterranean. In: Kaiser MJ, de Groot SJ (eds) Effects of fishing on non-target species and habitats. Blackwell Science, Oxford, p 121–129
- Díaz J, Nelson C, Barber J, Giró S (1990) Late Pleistocene and Holocene sedimentary facies on the Ebro continental shelf. *Mar Geol* 95:333–352
- Fauchald K, Jumars P (1979) The diet of worms: a study of Polychaete feeding guilds. *Oceanogr Mar Biol Annu Rev* 17:193–284
- Frid C (2003) Managing the health of the seafloor. *Front Ecol Environ* 1:429–436
- Frid C, Harwood K, Hall S, Hall J (2000) Long-term changes in the benthic communities on North Sea fishing grounds. *ICES J Mar Sci* 57:1303–1309
- Frid C, Robinson L, Bremner J (2005) Muddy thinking: ecosystem-based management of marine benthos. In: Barnes PT, Thomas JP (eds) Benthic habitats and the effects of fishing. American Fisheries Society, Bethesda, MD, p 651–665
- Hall S (1999) The effects of fishing on marine ecosystems and communities. Blackwell, Oxford
- Hill A, Veale L, Pennington D, Whyte S, Brand A, Hartnoll R (1999) Changes in Irish Sea benthos: possible effects of 40 years of dredging. *Estuar Coast Shelf Sci* 48:739–750
- Jennings S, Kaiser M (1998) The effects of fishing on marine ecosystems. *Adv Mar Biol* 34:201–352
- Jennings S, Pinnegar J, Polunin N, Warr K (2001) Impacts of trawling disturbance on the trophic structure of benthic invertebrate communities. *Mar Ecol Prog Ser* 213: 127–142
- Kaiser M, Spencer B (1994) Fish scavenging behaviour in recently trawled areas. *Mar Ecol Prog Ser* 112:41–49
- Kaiser M, Spence F, Hart P (2000) Fishing-gear restrictions and conservation of benthic habitat complexity. *Conserv Biol* 14:1512–1525
- Link J, Brodziak J, Edwards S, Overholtz W, Mountain D, Jossi J, Smith T, Fogarty M (2002) Marine ecosystem assessment in a fisheries management context. *Can J Fish Aquat Sci* 59:1429–1440
- Lohrer AM, Thrush SF, Gibbs M (2004) Bioturbators enhance ecosystem function through complex biogeochemical interactions. *Nature* 431:1092–1095
- McConnaughey R, Mier K, Dew C (2000) An examination of chronic trawling effects on soft-bottom benthos of the eastern Bering Sea. *ICES J Mar Sci* 57:1377–1388
- Norse E, Watling L (1999) Impacts of mobile fishing gear: the biodiversity perspective. In: Benaka L (ed) Fish habitat: essential fish habitat and rehabilitation. American Fisheries Society, Bethesda, MD, p 31–40
- Palanques A, Guillen J, Puig P (2001) Impact of bottom trawling on water turbidity and muddy sediment of an unfished continental shelf. *Limnol Oceanogr* 46:1100–1110
- Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F Jr. (1998) Fishing down marine food webs. *Science* 279: 860–863
- Pearson T (2001) Functional group ecology in soft-sediment marine benthos: the role of bioturbation. *Oceanogr Mar Biol Annu Rev* 39:233–267
- Philippart C (1998) Long-term impact of bottom fisheries on several by-catch species of demersal fish and benthic invertebrates in the south-eastern North Sea. *ICES J Mar Sci* 55:342–352
- Piet G, Jennings S (2005) Response of potential fish community indicators to fishing. *ICES J Mar Sci* 62:214–225
- Pranovi F, Raicevich S, Libralato S, Da Ponte F, Giovanardi O (2005) Trawl fishing disturbance and medium-term macrofaunal recolonization dynamics: a functional approach to the comparison between sand and mud habitats in the Adriatic Sea (Northern Mediterranean Sea). In: Barnes PT, Thomas JP (eds) Benthic habitats and the effects of fishing. American Fisheries Society, Bethesda, MD, p 545–569
- Ramsay K, Kaiser M, Hughes R (1998) Responses of benthic scavengers to fishing disturbance by towed gears in different habitats. *J Exp Mar Biol Ecol* 224:73–89
- Roth S, Wilson J (1998) Functional analysis by trophic guilds of macrobenthic community structure in Dublin Bay, Ireland. *J Exp Mar Biol Ecol* 222:195–217
- Rumohr H, Kujawski T (2000) The impact of trawl fishery on the epifauna of the southern North Sea. *ICES J Mar Sci* 57: 1389–1394
- Sanchez P, Demestre M, Palanques A, Kaiser MJ (1998) Impact of bottom trawling on the sediments and benthic communities in the NW Mediterranean (Project no.: DG XIV, Study 95/52. Final Report. ICM-CSIC, Barcelona
- Sardá R, Pinedo S, Martin D (1999) Seasonal dynamics of macrofaunal key species inhabiting shallow soft-bottoms in the Bay of Blanes (NW Mediterranean). *Acta Oecologica* 20:315–326
- Thrush S, Hewitt J, Cummings V, Dayton P (1995) The impact of habitat disturbance by scallop dredging on marine benthic communities: What can be predicted from the results of experiments? *Mar Ecol Prog Ser* 129:141–150
- Thrush S, Hewitt J, Cummings V, Dayton P, Cryer M, Turner S (1998) Disturbance of the marine benthic habitat by commercial fishing: impacts at the scale of the fishery. *Ecol Appl* 8:866–879
- Thrush SF, Dayton PK (2002) Disturbance to marine benthic habitats by trawling and dredging: implications for marine biodiversity. *Annu Rev Ecol Syst* 33:449–473
- Tuck I, Hall SJ, Robertson M, Armstrong E, Basford D (1998) Effects of physical trawling disturbance in a previously unfished sheltered Scottish sea loch. *Mar Ecol Prog Ser* 162:227–242
- Wassenberg T, Dews G, Cook S (2002) The impact of fish trawls on megabenthos (sponges) on the north-west shelf of Australia. *Fish Res* 58:141–151
- Widdicombe S, Austen M, Kendall M, Warwick RM, Jones M (2000) Bioturbation as a mechanism for setting and maintaining levels of diversity in subtidal macrobenthic communities. *Hydrobiologia* 440:369–377

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