

Fishing effects on diversity, size and community structure of the benthic invertebrate and fish megafauna on the Bay of Biscay coast of France

F. Blanchard^{1,*}, F. LeLoc'h², C. Hily², J. Boucher¹

¹IFREMER, Ressources Halieutiques, BP 70, 29280 Plouzané Cedex, France

²Université Bretagne Occidentale, LEMAR, UMR CNRS 6539, Technopôle Brest-Iroise, Place Nicolas Copernic, 29280 Plouzané, France

ABSTRACT: Within the framework of the 'dynamic equilibrium model', we tested the hypothesis that fishing causes major disturbance to benthic communities on deeper bottoms of the continental shelf. Benthic megafauna on the Bay of Biscay coast of France was sampled on fishing grounds subject to various conditions of exploitation. Samples were taken at around 100 m depth to avoid strong natural disturbances. Species diversity and the largest body mass class of invertebrates were smaller in strongly exploited areas than in moderately exploited ones. Biomass size spectra in strongly exploited areas were characterised by a comparatively large biomass of small invertebrates, hence the K-dominance curve of abundance was either above the biomass curve, or the curves intersected. In moderately exploited areas, the K-dominance biomass curves were above the abundance curves; the dominant species were a commercial species and a benthic species sensitive to the physical effects of the fishing gears. In the heavily exploited areas, the dominant species were opportunistic carnivorous species of minor or no commercial interest. There were no dominant fish species in the most strongly exploited areas, while 2 fish species were found in the moderately exploited areas. No fragile species were found in the most exploited areas, whereas 6 fragile species were found in the moderately exploited ones. It is concluded that the differences between the most strongly exploited and the moderately exploited areas were consistent with the hypothesis.

KEY WORDS: Benthic communities · Community dynamics · Disturbance · Diversity · Size spectrum

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

International concern and systematic research on the physical effects of trawling on the seabed and on benthic communities date from the 1970s, after the rapid expansion of fishing fleets, accompanied by technological innovations. Fishing gear used to catch demersal fish and shellfish often disturb both the seabed and the organisms living within or on it. For the most part the response of benthic communities to fishing disturbance is consistent with the generalised model of disturbance, i.e. increased dominance of small, fast-growing species, and general reductions in species diversity and evenness (Hall 1999).

However, not all communities are equally affected. The findings of empirical studies have not been consistent (Collie et al. 2000), mainly for 3 reasons: (1) non-linearity of the diversity–disturbance relationship, (2) different levels of natural disturbance, (3) different spatial scales of the studies. Diversity is highest at intermediate levels of disturbance (Connell 1978). At low natural disturbance, the additional disturbance of fishing may lead to a diversity increase, whereas diversity may decrease when natural disturbance is intermediate, and it may remain unchanged when natural disturbance is high. Most studies have investigated the effects of fishing on benthic communities on the continental shelf at depths <60 m in shallow seas of northern

*Email: fabian.blanchard@ifremer.fr

Europe and eastern North America (Collie et al. 2000). Benthic communities in these environments experience continuous disturbance at various scales, from a few centimetres in the case of bioturbation by infauna, through metre scales for feeding by predators on the seabed, up to large-scale natural disturbances such as seasonal storms, strong tidal currents, severe winters, or iceberg scouring (see Hall 1994 for a review). The intensity and frequency of natural disturbances therefore vary between the locations analysed. Effects of fishing disturbance on community structure and diversity are then not only likely to depend on the intensity and frequency of fishing, but also on the initial condition of the habitat (Jennings et al. 2002). The effects of trawling on infauna are more noticeable in areas where levels of natural disturbance are low (Brylinsky et al. 1994, Kaiser & Spencer 1996), because in high-disturbance areas the community is already adapted to disturbance (Jennings & Kaiser 1998). Finally, studies have to date been carried out at various spatial scales, but Kaiser (2003) has argued that detecting effects of fishing disturbance is strongly scale-dependent.

The dynamic equilibrium model of Huston (1994) provides a theoretical framework to analyse the effect of fishing disturbance on benthic communities and to reconcile apparently inconsistent findings. At a given productivity level, this model predicts that under conditions of high disturbance frequency and/or intensity, the few species present will be those that are able to complete their life cycles between disturbances and grow rapidly enough for their population size to recover. Under conditions of low disturbance, species whose life history is characterised by slow growth, late reproduction, large size, and efficient resource use will dominate the community. Diversity is then highest at intermediate levels of disturbance.

We conducted surveys on the Bay of Biscay coast of France at around 100 m depth to avoid interference of strong natural disturbances. Benthic megafauna, probably the most vulnerable part of the benthic communities directly impacted by fishing gears, was sampled on fishing grounds subject to different fishery impacts. If the dynamic equilibrium model holds true, then structural differences must be found between heavily fished and moderately fished communities. The following statements were tested: (1) high fishing effort reduces diversity and evenness, (2) reduces the observed maximum body mass, (3) favours a few body mass classes, (4) increases the steepness of the slope of number–size spectra, (5) shifts abundance and biomass distributions among species toward those typical of a disturbed community, (6) changes species composition.

MATERIALS AND METHODS

Sampling strategy. The study zone is located around 47°N and extends between 3 and 4°W off the western Atlantic coast of France (Fig. 1). A bottom trawl survey was carried out with RV 'Côtes de la Manche' during the last week of May and the first week of June 2001. A 2 m beam trawl was used to sample the invertebrate megafauna and demersal fishes (Kaiser et al. 1994, Jennings et al. 1999, Ellis et al. 2000). This proved to be an efficient method for large and rare species and for the integration of small-scale seabed patchiness (Frauenheim et al. 1989). The beam trawl was fitted with a chain mat and a 20 mm mesh liner. During sampling (20 min), warp length was 3 times water depth, the towing speed was 2 knots and the distance trawled was measured by the ship's differential GPS. A Rein-eck corer was used for sediment determinations. We sampled 8 stations within 4 areas around the 100 m isobath (about 2500 m² per haul): 1 station in Area A, 3 in Area B, 2 in Area C, and 2 in Area D. Stratification was based on the spatial variations in the fishing effort of the bottom trawlers in the year of sampling (2001), as determined by ICES statistical rectangle, from data of the Fisheries Monitoring System of IFREMER; the

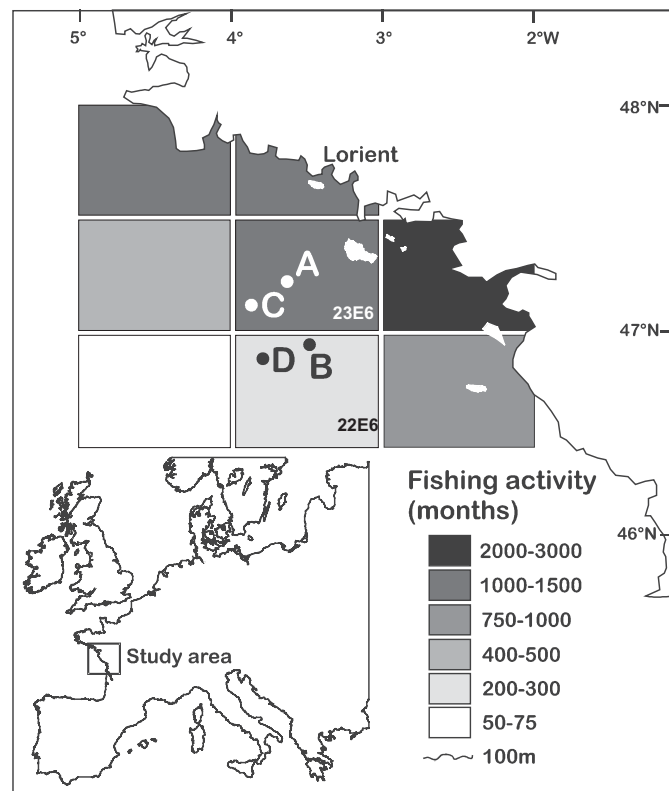


Fig. 1. Location of the 4 areas sampled in the Bay of Biscay and fishing effort of the bottom trawlers (in boat-months) in the ICES statistical rectangles for the year 2001, with $n = 1$ haul for A, $n = 3$ for B, $n = 2$ for C and $n = 2$ for D

entire study zone is used by the fishery, i.e. unfished areas do not exist

Benthic fauna, invertebrates and fishes, were sorted, identified to the lowest possible taxonomic level (usually species), counted and weighed. The species biomass was determined in each sample as wet weight.

Faunal diversity. Species diversity is classically assessed with the species richness S , the Shannon-Wiener diversity index H' and the Pielou evenness index J' . S is the number of species. H' was calculated as:

$$H' = -\sum_{i=1}^S p_i \text{Log} p_i \quad (1)$$

where p_i is the abundance ratio of the species i . J' was calculated as follows:

$$J' = \frac{H'}{\text{Log} S} \quad (2)$$

The diversity indices N1 and N2 of Hill (1973) were also assessed, as they are less sensitive to the dominant species and to the sampling effort, respectively, than the previous ones (Lande 1996):

$$N1 = \exp\left(-\sum_{i=1}^S p_i \ln p_i\right) \quad (3)$$

$$N2 = \frac{1}{\sum_{i=1}^S p_i^2} \quad (4)$$

Finally, indices of the taxonomic diversity Δ and distinctness Δ^* (Warwick & Clarke 1995) were assessed. These indices are less influenced by sample size than the other indices.

$$\Delta = \frac{\sum \sum_{i < j} w_{ij} x_i x_j}{\sum \sum_{i < j} x_i x_j + \sum_i x_i (x_i - 1) / 2} \quad (5)$$

$$\Delta^* = \frac{\sum \sum_{i < j} w_{ij} x_i x_j}{\sum \sum_{i < j} x_i x_j} \quad (6)$$

Δ is the average (weighted) path length between every pair of individuals, where w_{ij} is the weight given to the path length linking species i and j in the hierarchical classification and x_i denotes the abundance of the i th species ($i = 1, \dots, S$). Δ^* is the average (weighted) path length, ignoring paths between individuals of the same species. All the indices were calculated separately for each replicate tow, and results were tested for significant differences (ANOVA) between ICES statistical rectangles subject to high and low fishing effort.

Size structure of the macrobenthos. Trawling leads to mortality in benthic invertebrates and fishes, but the rates may be lower for the smallest individuals within and among species, as small organisms may be pushed

aside by the pressure wave in front of the trawl (Gilkinson et al. 1998), or escape from the trawl through the mesh. Larger individuals usually suffer higher mortality when they are in the path of the trawl (Bergman & van Santbrink 2000). Hence, fishing activity may change the community size spectrum structure (Rice & Gislason 1996, Bianchi et al. 2000, Duplisea et al. 2002).

Biomass size spectra were constructed by summing individual biomass in body mass classes arranged on an octave scale, as in Platt & Denman (1978). An increasing octave series means that the nominal weight for each class is double that of the previous one. Biomass size spectra were calculated for each area by pooling data from the respective stations. The normalised number-size spectra were determined by regressing, from the modal class to the largest one, the log of the total number in body mass class against the log of body mass class. The slopes of these regression lines characterise abundance trends across the size spectrum and simplify comparisons between areas (Sheldon et al. 1977, Pope & Knights 1982, Sprules & Munawar 1986, Pope et al. 1988). Differences among slopes were tested by ANCOVA.

Abundance-biomass comparison (ABC method). Combined K-dominance plots for species biomass and numbers may assume 3 possible forms, representing undisturbed, moderately disturbed and strongly disturbed macrobenthic communities (Warwick 1986, Warwick et al. 1987). A relative biomass curve above the relative numbers curve throughout its entire length is expected for undisturbed communities, where biomass is dominated by one or a few large species represented by few individuals. At moderate disturbance, the large competitively dominant species are eliminated, and the inequality in size between the numerically dominant species and the species with high biomass is reduced, so that biomass and number curves (in %) are close and may intersect. As disturbance increases, communities become dominated numerically by one or a few small species. Then the abundance curve is above the biomass curve throughout its length.

Numbers and biomass curves of the most strongly exploited areas (A and C) were compared to the curves of the moderately exploited areas (B and D). The W statistic (Clarke 1990) was calculated for each replicate tow separately and results were tested for significant differences (ANOVA) between ICES statistical rectangles subject to high and low fishing effort.

$$W = \frac{\sum_{j=1}^S [(\sum_{j=1}^i b_j) - (\sum_{j=1}^i a_j)]}{50(S-1)} \quad (7)$$

where W is the standardised sum of the differences between each pair of species cumulative biomass

($\sum_{j=1}^i b_j$) and cumulative abundance ($\sum_{j=1}^i a_j$) value ranked in decreasing order.

Species composition. Biological and ecological characteristics of the species make it possible to group the species according to the potential impact of fishing. Such groups have been defined recently for invertebrates (ICES 2003): scavenger, opportunistic, fragile and sensitive species. Here we have grouped scavengers with opportunistic species and added one more group, the unaffected species. Scavengers have been found more frequently in recent years in the southern North Sea (Lindeboom & de Groot 1998). Apart from possible climate effects, this can be attributed to the fishery impact, as discards and by-catch together with the crushed and broken animals provide large amounts of additional food to scavenging species on the sea floor. Scavengers migrate rapidly into areas of fishing disturbance, where they feed on animals damaged by trawls (Ramsay et al. 1996). Moreover, these species are often not injured by the passage of a trawl. Species with those characteristics sampled here were termed 'opportunistic species', e.g. *Liocarcinus depurator* and *Munida bamffia*. Some species are particularly sensitive to physical injury, as they are characterised by rigid bodies or tubes, and are sessile or slow-moving (MacDonald et al. 1996). Species with those characteristics were termed 'fragile species'; filter feeders were also part of this group, as they are sensitive to particles resuspended by the passage of the trawl, e.g. *Leptometra celtica* and *Virgularia mirabilis*. Species with a hard body that are not scavengers, and species that can escape from the haul after having been caught were termed 'unaffected species', e.g. *Alpheus glaber*. Species not included in these groups may be affected, but less so than the fragile ones. These species were termed 'sensitive', e.g. *Macropodia tenuirostris*. The ratio (in species number) of fragile, sensitive, unaffected and opportunistic species as defined here were computed *a priori* for each sector and compared between ICES rectangles.

RESULTS

Sediment characteristics

According to the classification of the Bay of Biscay by Chassé & Glémarec (1976), the sediments sampled correspond to the muddy sand and sandy mud type with a silt fraction between 10.0% at Stn C3 to 34.9% at Stn B3, and a median particle size between 109 μm at Stn B3 to 201 μm at Stn CC1 (Table 1). Sampling stations were in the depth range from 106 to 129 m.

Table 1. Sediment characteristics of the sampling stations. Sediment type as defined in Chassé & Glémarec (1976). FV: muddy sand; VS: sandy mud; SHV: heterogeneous muddy sand

Stn	Depth (m)	Silt fraction <63 μm (%)	Median grain size (μm)	Sediment type
AA1	106	12.0	153	FV
BB1	109	15.3	157	FV
B2	109	32.5	115	VS
B3	112	34.9	109	VS
CC1	116	25.1	204	SHV
C3	117	10.0	201	FV
D1	129	11.8	169	FV
DD1	118	12.4	186	FV

Fishing effort

Apart from dredges that are used at depths greater than 50 to 60 m, the only bottom trawl gears used in grounds of 100 m depth in 2001 were otter trawls. Fishing effort of the bottom trawlers was actually lower in Rectangle 22E6, with 299 month-boats, than in Rectangle 23E6, with 1242 month-boats. This is consistent with a previous analysis (Berthou et al. 2000), which showed that fishing effort in 1996 was lower in Rectangle 22E6 (between 130 and 590 month-boats) than in Rectangle 23E6 (between 1900 and 2800 month-boats). In Rectangles 22E6 and 23E6, 4 main 'métiers' (the association of a gear and a species or group of species) accounted for more than 60% of the activity. These were the *Nephrops* twin bottom trawls, the fish twin bottom trawls, the fish bottom otter trawls and the sole twin bottom trawls (Table 2). The reason why fishing effort was lower in Rectangle 22E6 was its greater distance from the main fishing harbour at Lorient, compared to Rectangle 23E6 (Fig. 1); most of the boats are rather small, so that costs increase with distance. The main species landed from Rectangles 22E6 and 23E6 are, in decreasing order: anchovy, horse mackerel, Norway lobster, hake, common sole, and cuttlefish. These 6 species represented 50% of the total landings from these areas in 2001.

Faunal diversity

Of the 58 species sampled in this study, 15 were fishes and 43 were invertebrates (Table 3). Differences between the most strongly exploited areas and the moderately exploited ones are shown in Table 4. Although the species richness was greater in the moderately exploited areas (B and D; between 22 and 33 species) than in the most strongly exploited ones (A and C; between 13 and 23 species), the difference

Table 2. Fishing effort in 2001 for the various 'métiers' (association of a gear, and a species or group of species) in ICES Rectangles 22E6 and 23E6 in number of months (number of boats). BOT: bottom otter trawl; TBT: twin bottom trawl. © IFREMER, Fisheries Monitoring System

Métier	22E6	23E6
Bass BOT	0	3 (2)
Squid BOT	1 (1)	21 (7)
Horse mackerel BOT	0	20 (5)
Bream BOT	0	11 (3)
Fish BOT	16 (4)	192 (31)
Gadoid BOT	0	9 (4)
Pollack BOT	1 (1)	3 (3)
<i>Nephrops</i> BOT	16 (3)	41 (7)
Anglerfish BOT	2 (1)	0
Mackerel BOT	0	23 (7)
Hake BOT	4 (2)	34 (8)
Whiting BOT	0	16 (6)
Skate BOT	2 (1)	0
Gurnard BOT	1 (1)	4 (2)
Cuttlefish BOT	14 (4)	48 (14)
Sole BOT	17 (4)	41 (9)
Bass pair BOT	1 (1)	1 (1)
<i>Nephrops</i> pair BOT	0	2 (2)
Squid TBT	4 (1)	4 (3)
Fish TBT	26 (8)	155 (21)
<i>Nephrops</i> TBT	133 (35)	495 (67)
Anglerfish TBT	11 (3)	23 (5)
Hake TBT	12 (6)	24 (6)
Flatfish TBT	1 (1)	2 (2)
Cuttlefish TBT	13 (4)	27 (12)
Sole TBT	24 (12)	43 (21)
Total	299 (93)	1242 (248)

was not statistically significant (Table 5). There were no significant differences for evenness. On the other hand, diversity H' was significantly greater in the moderately exploited rectangle (0.97 to 1.15), than in the strongly exploited one (0.68 to 0.89). The same holds true with regard to the $N1$ index (2.64 to 3.16 in the moderately exploited rectangle, and 1.97 to 2.43 in the strongly exploited one), and the $N2$ index (5.9 to 9.99 in the moderately exploited rectangle, and 2.44 to 5.56 in the strongly exploited one). No significant differences were found for the indices Δ and Δ^* .

Size structure

Biomass distribution was more similar to a Gaussian one in the moderately exploited areas (B and D) than in the most strongly exploited areas (A and C; Fig. 2). Biomass distributions in Areas A and C were characterised by a large contribution to the total biomass of one body mass class of invertebrates (5 and 2.5 g, respectively). The largest observed body mass class for invertebrates in the moderately exploited areas (B and D) were 10 and 20 g, respectively, while it was smaller in the most exploited areas (A and C; 5 and 10 g, respectively). The largest observed body mass class for fishes in areas (A, B, C and D) were 80, 20, 40 and 40 g, respectively. There were no clear

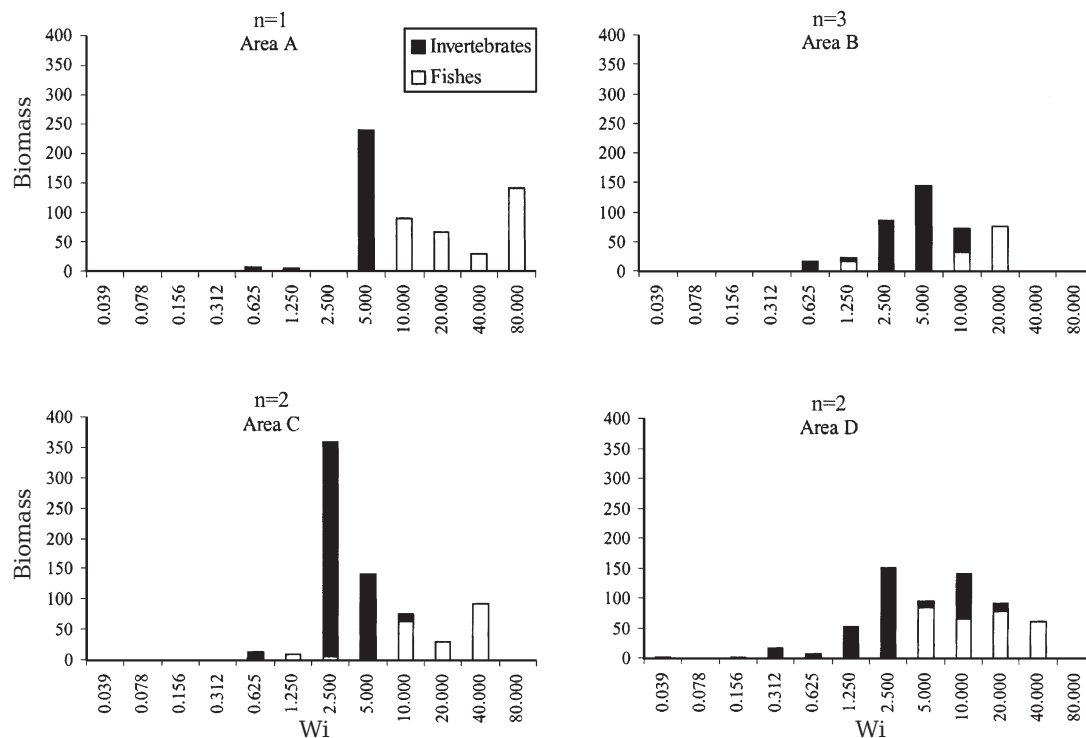


Fig. 2. Mean biomass size spectra for the benthic megafauna of invertebrates and fishes. Biomass and size classes (W_i) are in g wet weight. The number of hauls each panel is indicated above

Table 3. List of species and their abbreviated codes, and taxonomic group (invertebrates [Inv] and fish), abundance (ind.) and biomass (wet weight in g per 1000 m²) in Areas A, B, C and D. SENS: sensitivity of invertebrates (except cephalopods) to physical effects of bottom fishing gears defined *a priori*; f: fragile; s: sensitive; u: unaffected; o: opportunistic

Code	Species	Taxon group	Abundance				Biomass				SENS
			A	B	C	D	A	B	C	D	
ACD	<i>Actinauges richardi</i>	Inv	0	0	0	0.55	0	0	0	12.47	s
ADP	<i>Adamsia carcinopados</i>	Inv	0	1.28	0	0.25	0	3.75	0	0.11	s
ALD	<i>Alcyonium digitatum</i>	Inv	0	0.12	0	1.78	0	0.48	0	0.49	f
ALGL	<i>Alpheus glaber</i>	Inv	0	8.19	3.32	4.33	0	6.9	2.28	2.75	u
ALV	<i>Anapagurus laevis</i>	Inv	0	0	0	4.31	0	0	0	0.91	s
AMU	<i>Amphicteis gunneri</i>	Inv	0	0.91	1.52	0	0	0.01	0	0	s
APE	<i>Apporhais pespelicani</i>	Inv	0	0.25	0	0	0	0.51	0	0	u
ARLA	<i>Arnoglossus laterna</i>	Fish	2.55	1.61	4.36	12.59	36.5	19.7	47.72	84.41	
ARSP	<i>Argentina sphyraena</i>	Fish	0	0	0.38	0	0	0	1.91	0	
ASL	<i>Astacilla longicornis</i>	Inv	0	0	0	7.73	0	0	0	0.56	s
ASY	<i>Astropecten</i> spp.	Inv	0	0	0	29.53	0	0	0	71.58	s
BRLY	<i>Brissopsis lyrifera</i>	Inv	0	0.41	0	0.55	0	5.27	0	1.38	f
CAAP	<i>Capros aper</i>	Fish	0	0.5	1.32	0.25	0	1.43	4.03	0.97	
CALY	<i>Callionymus lyra</i>	Fish	0.64	0.12	0.38	0	22.84	2.89	10.26	0	
CAMA	<i>Callionymus maculatus</i>	Fish	0	0	0.66	0.76	0	0	2.28	3.18	
CAO	<i>Calliostoma granulatum</i>	Inv	0	0	0	1.85	0	0	0	7.6	u
CERU	<i>Cepola rubescens</i>	Fish	0	0	0.33	0	0	0	7.87	0	
CHCR	<i>Chlorotocus crassicornis</i>	Inv	0	1.82	0.38	1.64	0	3.32	0.79	1.86	s
CRAL	<i>Crangon allmanni</i>	Inv	5.11	6.91	5.35	1.27	5.64	6.3	5.1	0.77	s
CUCU	<i>Cuspidaria cuspidate</i>	Inv	0	0.25	0	0	0	0.22	0	0	s
CUP	<i>Phaxas pellucidus</i>	Inv	0	0	0	0.25	0	0	0	0.03	f
D	<i>Dichelopandalus bonnieri</i>	Inv	0	0	0.38	0	0	0	0.47	0	s
ENCI	<i>Enchylopsus cimbricus</i>	Fish	1.28	2.32	0.33	1.6	43.75	74.5	16.79	46.04	
EUGU	<i>Eutriglia gurnardus</i>	Fish	0.64	0	0	1.02	29.54	0	0	62.51	
GADI	<i>Galathea dispersa</i>	Inv	0	0	0	1.02	0	0	0	0.01	o
GLR	<i>Glycera rouxii</i>	Inv	0	0	0.38	0	0	0	0.01	0	s
GORH	<i>Goneplax rhomboids</i>	Inv	0	6.34	2.94	7.86	0	38.24	15.85	26.07	s
GVU	<i>Gaidropsarus vulgaris</i>	Fish	0	0.16	0	0	0	2.16	0	0	
HEMA	<i>Heterocrypta maltzani</i>	Inv	0	0	0	0.55	0	0	0	0.22	s
IND	<i>Inachus dorsettensis</i>	Inv	0	0	0	0.25	0	0	0	1.2	s
LEFR	<i>Lesueurigobius friesii</i>	Fish	1.28	7.37	3.17	0.25	2.64	18	7.25	0	
LID	<i>Liocarcinus depurator</i>	Inv	14.68	13.04	9.35	2.4	144.84	61.75	94.86	0.67	o
LOPI	<i>Lophius piscatorius</i>	Fish	0	0	0.38	0.51	0	0	5.29	0.61	
LWH	<i>Lepidorhombus whiffiagonis</i>	Fish	0	0.33	0	12.29	0	4.67	0	36.17	
MAN	<i>Macropodia tenuirostris</i>	Inv	0	1.28	0.38	20.24	0	1.29	0.01	10.97	s
MATU	<i>Macropipus tuberculatus</i>	Inv	0	0	0	1.31	0	0	0	5.03	o
MME	<i>Merluccius merluccius</i>	Fish	0.64	0.49	1.8	1.27	87.67	0.68	77.11	43.08	
MUBA	<i>Munida bamffia</i>	Inv	5.11	23.01	76.44	15.18	28.11	79.21	251.37	35.74	o
MVA	<i>Microchirus variegatus</i>	Fish	3.19	1.78	1.09	3.67	52.83	27.57	21.25	56.3	
NEE	<i>Nephtys caeca</i>	Inv	0	0.25	0	9.45	0	0.01	0	86.27	s
NENO	<i>Nephrops norvegicus</i>	Inv	7.02	29.62	23.84	0.55	66.83	196.27	135.65	1.21	o
NUSU	<i>Nucula sulcata</i>	Inv	0.64	7.08	4.36	0.55	0.91	5.92	3.83	3.62	u
PAP	<i>Pagurus pridauxi</i>	Inv	0	0.58	0	0.55	0	8.66	0	0.3	o
PEPH	<i>Pennatula phosphorea</i>	Inv	0	0.25	0	2.28	0	0.13	0	0.56	f
POHE	<i>Polybius henslowi</i>	Inv	0	0.41	0	28.48	0	4.31	0	1.7	o
POPU	<i>Porania pulvillus</i>	Inv	0	0	0	0.25	0	0	0	4.2	u
POSP	<i>Pontophilus spinosus</i>	Inv	0	0	0	0.51	0	0	0	1.07	s
PRNO	<i>Processa novelli</i>	Inv	0	1.49	0	0.55	0	0.36	0	1.58	s
PTH	<i>Pteria hirundo</i>	Inv	0	0	0	2.28	0	0	0	0.56	f
Scal.	<i>Scalpellum</i> spp.	Inv	0	0	0	0.51	0	0	0	1.72	u
Sepiola	<i>Sepiola</i> spp.	Inv	0	0.25	0.38	6.21	0	0.84	0.28	2.96	
SOME	<i>Solenocera membranacea</i>	Inv	0	0	0	5.46	0	0	0	4.56	s
SQDE	<i>Squilla desmaresti</i>	Inv	0	0.66	1.47	0	0	2.19	4.74	0	o
STS	<i>Sternaspis scutata</i>	Inv	0	0.37	0.33	0	0	0.59	0.25	0	s
SVU	<i>Solea vulgaris</i>	Fish	0.64	0	0	0	54.73	0	0	0	
TUC	<i>Turritella communis</i>	Inv	0	0	0.38	0	0	0	0.42	0	u
VEOV	<i>Timoclea ovata</i>	Inv	0	1	0.71	0	0	0.75	0.52	0	u
VIMI	<i>Virgularia mirabilis</i>	Inv	0	0.5	0	0	0	0.96	0	0	f

Table 4. Species richness (S), Evenness index (J'), Shannon diversity index (H'), Hill diversity indices (N1 and N2), and taxonomic diversity and distinctness indices (Δ and Δ^*) in each replicate of Areas A, B, C and D

Stn	S	J'	H'	N1	N2	Δ	Δ^*
Strongly exploited							
AA1	13	0.8	0.89	2.43	5.56	3.77	4.19
CC1	23	0.61	0.83	2.29	3.72	3.03	4.12
C3	18	0.54	0.68	1.97	2.44	2.69	4.51
Moderately exploited							
BB1	23	0.76	1.04	2.83	6.8	3.67	4.26
B2	22	0.72	0.97	2.64	5.9	3.43	3.99
B3	23	0.72	0.98	2.66	6.46	3.99	4.69
D1	26	0.82	1.15	3.16	9.99	4.8	5.31
DD1	33	0.76	1.15	3.16	8.54	4.16	5.02

differences in maximal body mass for fishes between the most exploited areas (A and C) and the moderately exploited areas (B and D) for fishes.

The fitted linear relationships between abundances and body mass explained a substantial proportion of the variance (Fig. 3). The r^2 values were 0.8, 0.92, 0.89 and 0.98, respectively, in Areas A, B, C and D. The steepest slope was in one of the most strongly exploited areas (C: -1.62) while the flattest one was in a moderately exploited area (D: -1.26). However, there were no

significant differences among slopes ($F_{\text{observed}} = 0.38$, $v_1 = 3$, $v_2 = 14$, $F_{0.05} = 3.34$) or among intercepts ($F_{\text{observed}} = 0.07$, $v_1 = 3$, $v_2 = 14$, $F_{0.05} = 3.34$).

Abundance–biomass comparison (ABC method)

The communities in the moderately exploited areas (B and D) showed an undisturbed pattern with the biomass curve above the abundance curve (Fig. 4). On the other hand, the communities in the most strongly exploited areas (A and C) showed a disturbed pattern (abundance curve above the biomass curve) and a moderately disturbed pattern with (intersecting curves), respectively. The differences in the abundance/biomass dominance curve between the 2 rectangles were significant (ANOVA, W statistic: Table 5).

Species composition

Relative species abundance (Fig. 5) shows differences in dominance between the rectangles: 7 and 8 species, respectively, represent $>75\%$ of the total abundance in Areas B and D, while only 5 and 4 species attain 75% in Areas A and C. The most dominant species in Area B (moderately exploited) is the Norway

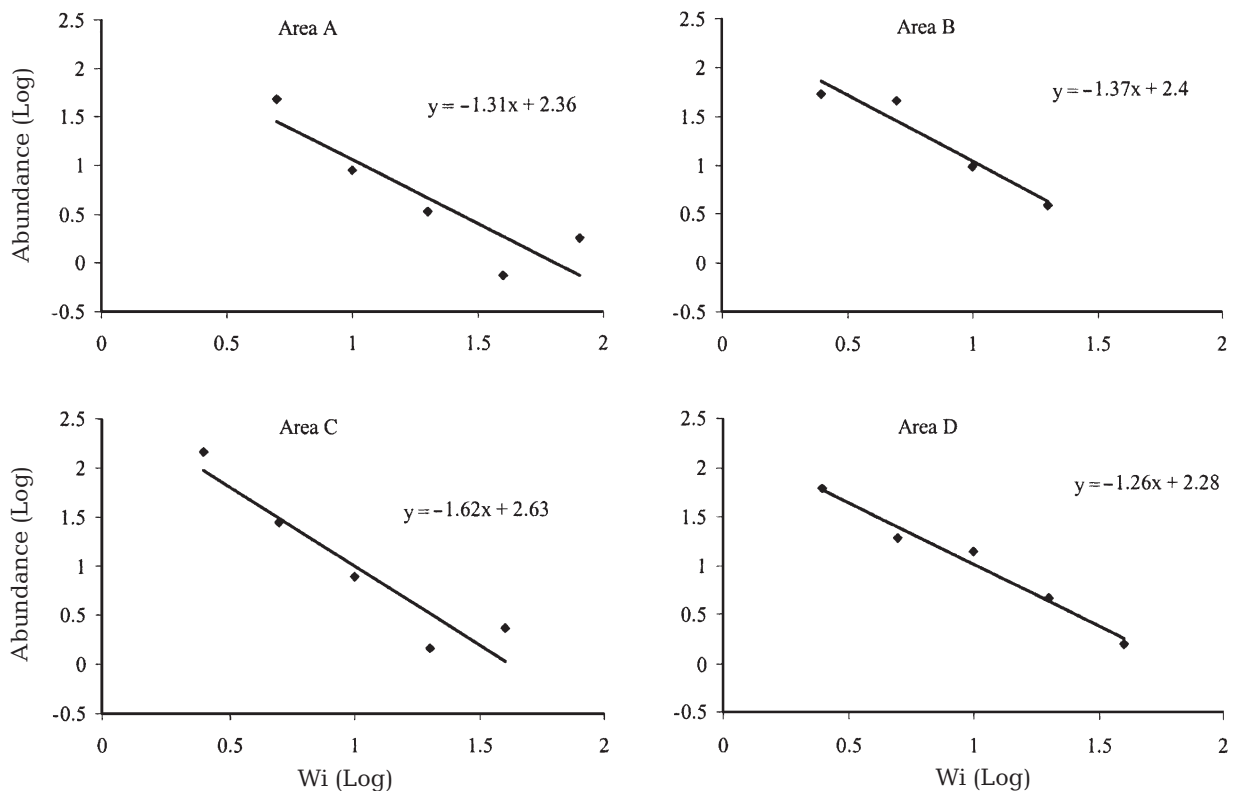


Fig. 3. Normalised size spectra for the benthic megafauna in the 4 areas: abundance vs wet weight (W_i) in g

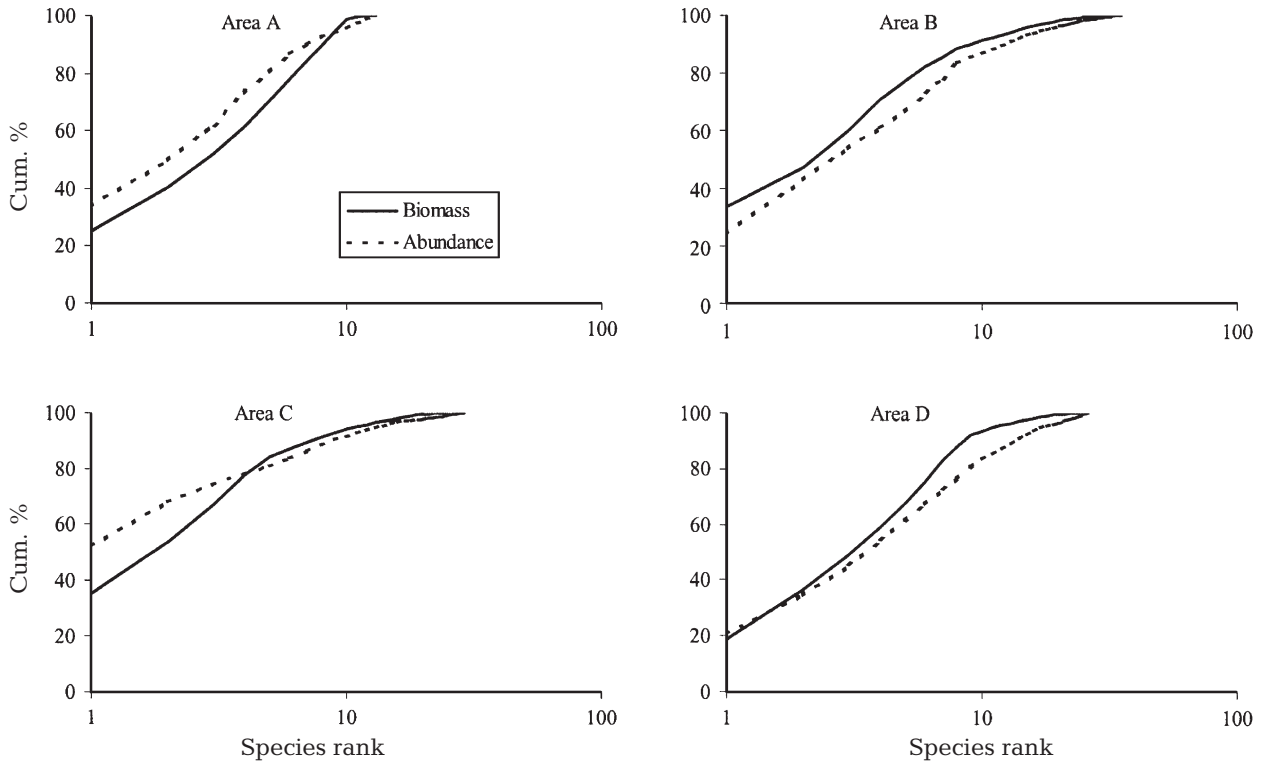


Fig. 4. Cumulative% dominance curves in abundance and biomass of the benthic megafauna communities of fishes and invertebrates from the most exploited areas (A and C) and from the moderately exploited areas (B and D)

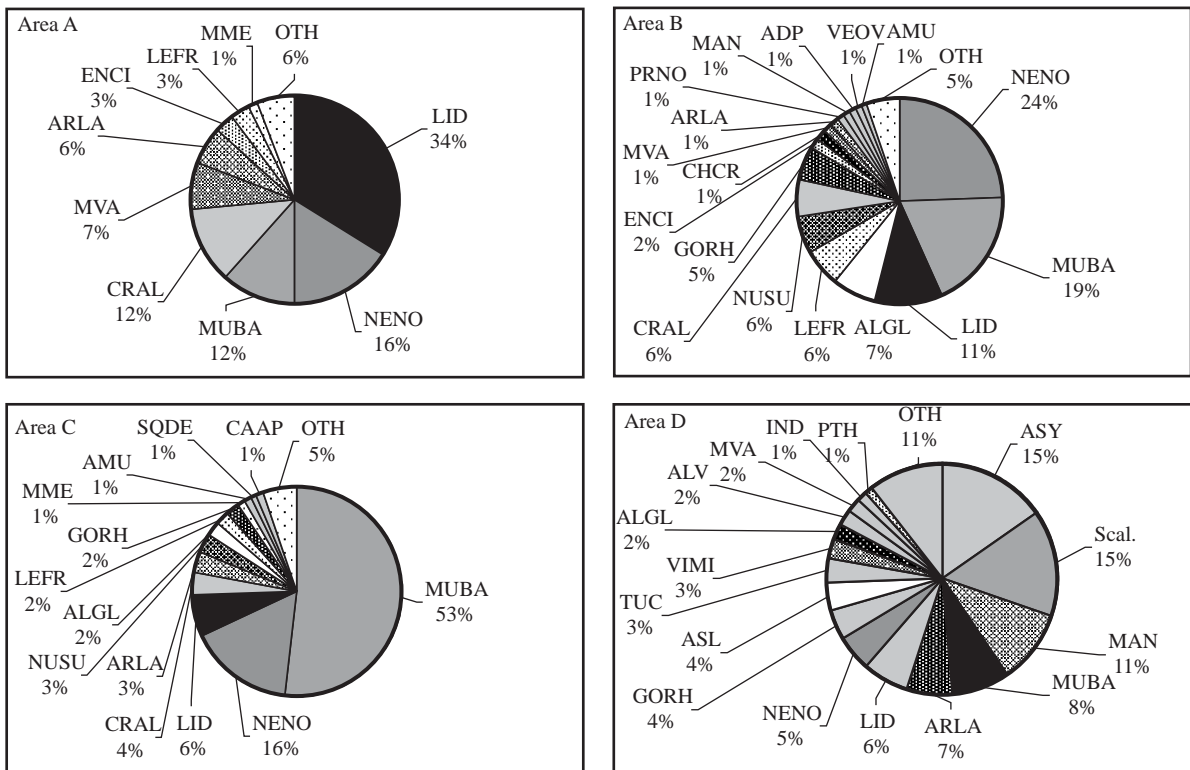


Fig. 5. Relative abundance of species. See Table 3 for the code significance of species (OTH: other species)

Table 5. ANOVA of diversity indices S , J' , H' , $N1$, $N2$, Δ , Δ^* and of the W statistic of the abundance/biomass dominance curves, between rectangles with high and low fishing effort; *significant

	F	p
S	4.096	0.073
J'	2.945	0.137
H'	13.75	0.01*
$N1$	13.03	0.011*
$N2$	9.087	0.024*
Δ	4.47	0.079
Δ^*	0.71	0.43
W	15.009	0.0082*

lobster *Nephrops norvegicus*, an opportunistic commercial species found in all areas of this study. In Area D (moderately exploited), the dominant species is a sensitive echinoderm genus (*Astropecten* spp.); Area D is the only one where this species was found. In the heavily exploited areas, the 2 dominant species are opportunistic carnivores, the blue-leg swimming crab *Liocarcinus depurator* in Area A, and *Munida bamffia*, a crustacean of minor commercial interest, in Area C. These 2 species were found in all areas of this study. There is no fish species within the first 75% of the total abundance in the most strongly exploited areas (A and C), while 2 small non-commercial fish species are found in the first 75% in the moderately exploited area: Fries's goby *Lesueurigobius friesii* and the scadfish *Arnoglossus laterna*.

In the most strongly exploited areas (A and C), the opportunistic species were dominant in species number and fragile species were absent (Fig. 6), while sensitive species were dominant and some fragile species were present in the moderately exploited areas (B and D). However, ANOVA showed significant differences between the most strongly exploited areas (A and C) and the moderately exploited areas (B and D), only for fragile species (Table 6).

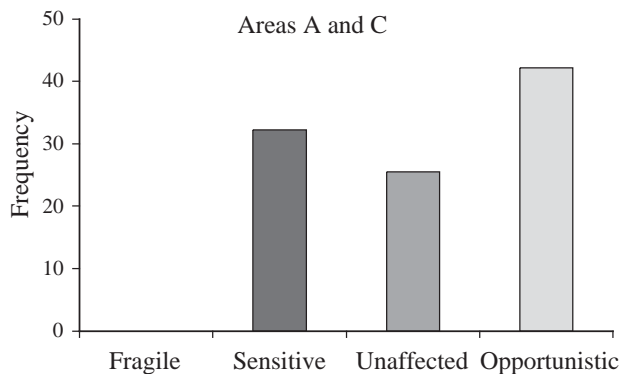


Table 6. Frequency of fragile, sensitive, unaffected and opportunistic species in the samples and ANOVA between the most exploited rectangle (Areas A and C) and the moderately exploited one (Areas B and D). (*Significant difference between rectangles, H_0 rejected)

Stn	Fragile	Sensitive	Unaffected	Opportunistic
AA1	0	20	20	60
CC1	0	46.67	26.67	26.67
C3	0	30	30	40
BB1	6.25	43.75	12.5	37.5
B2	12.5	37.5	18.75	31.25
B3	15.79	47.37	21.05	15.79
D1	13.64	45.45	22.73	18.18
DD1	15	40	20	25
F -value	31.32	2.95	4.26	3.52
p	0.001*	0.137	0.085	0.11

DISCUSSION

Sediment properties are factors influencing the benthic fauna (Basford et al. 1990, Kühne & Rachor 1996, Rees et al. 1999), although the relationship is clearer for infauna than for the epifauna that was the focus in this study (Duineveld et al. 1991). Moreover, the sampling scale of a beam trawl is orders of magnitude larger than that of corers, so that small-scale heterogeneity is integrated (Callaway et al. 2002). To minimise these effects, benthic communities were only sampled on sandy mud and muddy sand. Furthermore, there are no hydrographic features or other environmental factors in this area that could lead to differential settlement of post-larval juveniles, so that fishing effort constitutes the major source of spatial variation.

However, sampling with bottom trawls usually implies high variance, due to a number of factors such as the patchy distribution of various species. Because of the limited sampling carried out in this study, 8 hauls might not have a representative species composition. Long-term surveys would be required to test the relia-

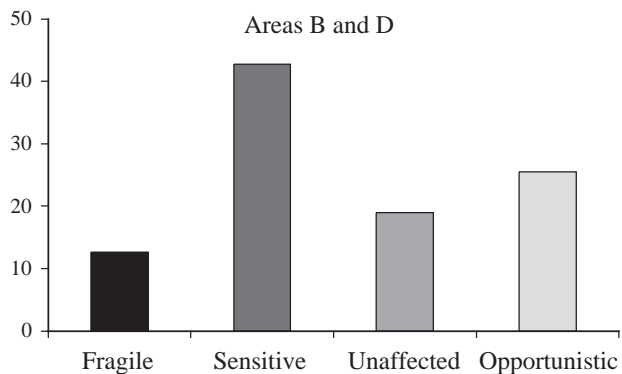


Fig. 6. Averaged frequency (in species number) of fragile, sensitive, unaffected and opportunistic species in the most exploited rectangle (Areas A and C) and in the moderately one (Areas B and D). See the text for the definition of these groups

bility of the data, and caution is in order before generalising or extrapolating the results to the whole region. Our study is probably more useful in detecting patterns of change in community structure according to theoretical ecological guidelines, rather than in really testing an ecological hypothesis.

Species diversity

The diversity indices H' , $N1$ and $N2$ confirmed the disturbance effect of fishing on the community. Results on species richness, evenness, taxonomic diversity and distinctness were less clear. Species diversity was lower where fishing disturbance was high, but it is difficult to conclude whether this is due to a decrease in slow growing sessile fauna and/or to avoidance of the vagile fauna, which is replaced by a few opportunistic species. However, the numbers of both sessile and vagile fragile invertebrate species were lower in the most strongly fished areas (C. Hily pers. obs) so that both processes may apply. No differences were apparent from taxonomic indices; these indices are useful for macrofauna, but our study also included fish megafauna. Taxonomic distances between fishes and invertebrates are huge, compared to distances between invertebrate species, and the values of the taxonomic indices can be so high as to obscure the small spatial differences in taxonomic diversity of invertebrates. These indices should be computed separately for invertebrate and fish species.

Size spectra

Biomass size spectra are widely used to describe the structure of pelagic food chains, demersal fish communities and benthic communities of invertebrates, and sometimes related to the productivity of the ecosystems (Sheldon et al. 1977, Macpherson & Gordo 1996, Saiz-Salinas & Ramos 1999). Normalised number–size spectra have been used to analyse the impact of fishing on demersal fish communities (Pope & Knights 1982, Pope et al. 1988, Murawski & Idoine 1992, Rice & Gislason 1996, Bianchi et al. 2000), showing an increase in the abundance of the smallest body mass classes and a decrease in the largest ones, probably due to: (1) differential mortality, as fishing gears select large individuals; (2) release from predation of small individuals that are prey to the large ones; (3) recovery from continuous fishing mortality by species with early reproduction and fast growth (r -strategists). Although there were no significant differences among slopes of the normalised number–size spectra, different biomass-size structures among areas were found, consis-

tent with the previously quoted fishing effects on demersal fish communities: one small size class was dominant in the most exploited areas compared to the moderately exploited ones.

Abundance–biomass comparison (ABC method)

The ABC method (Warwick 1986) was originally designed to detect pollution effects on macrobenthic invertebrate communities, and then generalised to other physical and biological disturbances (Warwick et al. 1987) and applied to fishery impacts (Lindeboom & de Groot 1998). The method was designed on the basis of the ecological succession theory: after a strong disturbance, (small) opportunistic species are the first to recolonise the habitat, and then (large) conservative species tend to replace them. The ABC method is rarely applied to fishing disturbances in megabenthic communities of invertebrates and fishes, and this study shows that the method can be applied to a wide range of individual sizes, taxa and disturbances. Our results support the hypothesis that fishing acts on communities like a physical disturbance, as well as the underlying theory of ecological succession. Only 3 discrete disturbance levels are defined in this method: highly disturbed, moderately disturbed and undisturbed, whereas in the dynamic equilibrium model, disturbance is a continuous variable. The intercalibration between a discrete variable of disturbance and a continuous one remains to be tackled.

Species composition

Dominant species in the moderately exploited areas were a commercial crustacean species and a sensitive echinoderm, while the dominant species in the most exploited areas were crustacean opportunistic carnivores of minor or no commercial interest. Fishing gear effects may favour scavengers and opportunistic carnivores attracted by crushed organisms, and eliminate fragile species. However, it remains unclear whether increases in scavenger abundance are the result of migration or of population growth. Commercial species such as Norway lobster may be depleted and replaced by a potential competitor such as *Munida bamffia*. Actually, the stock biomass of *Nephrops norvegicus* in the ICES Division VIIIa,b (Bay of Biscay) is at or near the lowest known level and this is attributed to the high exploitation rate and/or fishing patterns that cause high mortality in juveniles (ICES 2002).

We assumed that few differences in grain size of the sediment exist in the study area, so that no natural spatial variation was expected. However, Norway lobster

is the dominant species in Area B, but not in Areas A, C and D (it is second in abundance in Areas A and C, and the 7th in the moderately exploited Area D). Relationships between *Nephrops norvegicus* density and sediment grain size have been shown for several stocks: density increases with particle size up to an optimum particle size value, then decreased for larger particle sizes; the optimum particle size differs between stocks (Afonso-Dias 1997). Moreover, the grain size range may be huge in some cases. The relationship between *N. norvegicus* density and particle size in the Bay of Biscay is unknown. It is therefore difficult to conclude whether the variation in the abundance rank of *N. norvegicus* is really a consequence of fishing or rather of small grain size variations or interactions between both factors. The sensitive species *Astropecten* is only dominant in Area D and is not found anywhere else. This could be due to interactions between small sediment variations and fishing effects. No fragile species were found in the most strongly exploited areas, while 6 species were observed in the moderately exploited ones, and this is more probably due to fishing effects than to sediment grain size. Moreover, there is no fish species among the first 75% of the total abundance in the most strongly exploited area, while 2 fish species are found among the top 75% in the moderately exploited area. Heavy fishing activity in the most exploited areas probably drives fishes out of the area.

Community dynamics

Indices of species diversity, size structure, and abundance–biomass distributions among species proved useful to demonstrate fishing impacts on the benthic communities at low and moderate levels of natural disturbance, when used in the framework of the dynamic equilibrium model.

Management requires quantitative methods that predict changes in communities. Size-based models (Duplisea et al. 2002) have to be designed. However available knowledge of trawling disturbance impacts is based primarily on empirical studies. Then models are only empirical, without strong theoretical underpinnings about the ecological processes involved in community dynamics, or with underpinnings not yet fully acknowledged by the scientific community. More theoretical works on community dynamics supported by empirical analyses are then needed to design convincing and effective management strategies of environmental impacts of fishing.

Community dynamics can theoretically be regulated by competitive interactions or ecological disturbances (including environmental and predation factors). Fishing effects as predation disturbance (removal of indi-

viduals) have been hypothesised (Blanchard 2001). In communities regulated by interspecific interactions a high intensity of predation can alter the strength of competitive interactions and allow for increased coexistence of competitive species (Levine 1976, Vandermeer 1980). Fishing exploitation could have similar effects, i.e. benthic community dynamics under low conditions of exploitation and low or moderate levels of natural disturbance is probably regulated by competitive interactions, and fishing leads to a shift toward community dynamics regulated by fishing disturbance. This underscores the importance of analysing fishing effects as physical disturbances (break and crush effects of gears). Theories on community dynamics that include ecological disturbance, whether physical or predation disturbance, is a promising theoretical framework to analyse the effects of fishing.

LITERATURE CITED

- Basford DJ, Eleftheriou A, Raffaelli D (1990) The infauna and epifauna of the northern North Sea. *Neth J Sea Res* 25: 165–173
- Bergman MJN, van Santbrink JW (2000) Mortality in megafaunal benthic populations caused by trawl fisheries on the Dutch continental shelf in the North Sea in 1994. *ICES J Mar Sci* 57:1321–1331
- Berthou P, Jézéquel M, Lespagnol P, Larvor S (2000) Répartition spatiale de la flotte de pêche française de Manche Atlantique en 1996. In: IRD (ed) *Les espaces de l'halieutique*. Actes du Quatrième Forum Halieumétrique, ENSA Rennes (France), 29 juin au 1er juillet 1999, Collection Colloques et Séminaires. IRD, Paris
- Bianchi G, Gislason H, Graham K, Hill L and 7 others (2000) Impact of fishing on size composition and diversity of demersal fish communities. *ICES J Mar Sci* 57:558–571
- Blanchard F (2001) The effect of fishing on demersal fish community dynamics: an hypothesis. *ICES J Mar Sci* 58: 711–718
- Brylinsky M, Gibson J, Gordon DC (1994) Impacts of flounder trawls on the intertidal habitat and community of the Minas Basin, Bay of Fundy. *Can J Fish Aquat Sci* 51: 650–661
- Callaway R, Alsvag J, de Boois I, Cotter J and 8 others (2002) Diversity and community structure of epibenthic invertebrates and fish in the North Sea. *ICES J Mar Sci* 59: 1199–1214
- Chassé C, Glémarec M (1976) Principes généraux de la classification des fonds pour la cartographie sédimentaire. *J Rech Oceanogr* 1:1–11
- Clarke RC (1990) Comparisons of dominance curves. *J Exp Mar Biol Ecol* 138:143–157
- Collie JS, Hall SJ, Kaiser MJ, Poiner IR (2000) A quantitative analysis of fishing impacts on shelf sea benthos. *J Anim Ecol* 69:785–798
- Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310
- Duineveld GCA, Künitzer A, Niermann U, De Wilde PAWJ, Gray JS (1991) The macrobenthos of the North Sea. *Neth J Sea Res* 28:53–65
- Duplisea DE, Jennings S, Warr KJ, Dinmore TA (2002) A size-

- based model of the impacts of bottom trawling on benthic community structure. *Can J Fish Aquat Sci* 59:1785–1795
- Ellis JR, Rogers SI, Freeman SM (2000) Demersal assemblages in the Irish Sea, St George's Channel and Bristol Channel. *Estuar Coast Shelf Sci* 51:299–315
- Frauenheim K, Neumann V, Theil H, Turkay M (1989) The distribution of the larger epifauna during summer and winter in the North Sea and its suitability for environmental monitoring. *Senckenb Marit* 20:101–118
- Gilkinson K, Paulin M, Hurley S, Schwinghamer P (1998) Impacts of trawl door scouring on infaunal bivalves: results of a physical trawl door model/dense sand interaction. *J Exp Mar Biol Ecol* 224:291–312
- Hall SJ (1994) Physical disturbance and marine benthic communities: life in unconsolidated sediments. *Oceanogr Mar Biol Annu Rev* 32:179–239
- Hall SJ (1999) The effects of fishing on marine ecosystems and communities. Blackwell Science, Oxford
- Hill MO (1973) Diversity and evenness: a unifying notation and its consequences. *Ecology* 54:427–432
- Huston MA (1994) Biological diversity. The coexistence of species on changing landscapes. Cambridge University Press, Cambridge
- ICES (2002) Report of the ICES Advisory Committee on Fishery Management. ICES CRR 255:835–838
- ICES (2003) Report of the Working Group on Ecosystem Effects of Fishing Activities. Advisory Committee on Ecosystems. ICES CM 2003/ACE:05
- Jennings S, Kaiser MJ (1998) The effects of fishing on marine ecosystems. *Adv Mar Biol* 34:201–352
- Jennings S, Lancaster J, Woolmer A, Cotter J (1999) Distribution, diversity and abundance of epibenthic fauna in the North Sea. *J Mar Biol Assoc UK* 79:385–399
- Jennings S, Nicholson MD, Dinmore TA, Lancaster JE (2002) Effects of chronic trawling disturbance on the production of infaunal communities. *Mar Ecol Prog Ser* 243:251–260
- Kaiser MJ (2003) detecting the effects of fishing on seabed community diversity: importance of scale and sample size. *Conserv Biol* 17:512–520
- Kaiser MJ, Spencer BE (1996) The effects of beam-trawl disturbance on infaunal communities in different habitats. *J Anim Ecol* 65:348–358
- Kaiser MJ, Rogers SI, MacCandless DT (1994) Improving quantitative surveys of epibenthic communities using a modified 2 m beam trawl. *Mar Ecol Prog Ser* 106:131–138
- Kühne S, Rachor E (1996) The macrofauna of a stony sand area in the German Bight (North Sea). *Helgol Meeresunters* 50:433–452
- Lande R (1996) Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76:5–13
- Levine SH (1976) Competitive interactions in ecosystems. *Am Nat* 110:903–910
- Lindeboom HJ, de Groot SJ (eds) (1998) The effects of different types of fisheries on the North Sea and Irish Sea benthic ecosystems. Netherlands Institute of Sea Research, Texel
- MacDonald DS, Little M, Eno C, Hiscock K (1996) Disturbance of benthic species by fishing activities: a sensitivity index. *Aquat Conserv: Mar Freshw Ecosyst* 6:257–268
- Macpherson E, Gordo A (1996) Biomass spectra in benthic fish assemblages in the Benguela System. *Mar Ecol Prog Ser* 138:27–32
- Murawski SA, Idoine JS (1992) Multispecies size composition: a conservative property of exploited fishery systems? *J Northwest Atl Fish Soc* 14:79–85
- Platt T, Denman K (1978) The structure of pelagic marine ecosystems. *Rapp P-V Reun Cons Int Explor Mer* 173:60–65
- Pope JG, Knights BJ (1982) Comparison of length distributions of combined catches of all demersal fishes in surveys in the North Sea and at Faroe Bank. *Can Spec Publ Fish Aquat Sci* 59:116–118
- Pope JG, Stockes TK, Murawski SA, Idoine SI (1988) A comparison of fish size composition in the North Sea and on Georges Bank. In: Wolff W, Soeder CJ, Drepper FR (eds) *Ecodynamics, contributions to theoretical ecology*. Springer-Verlag, Berlin, p 146–152
- Ramsay K, Kaiser MJ, Hughes RN (1996) Changes in hermit crab feeding patterns in response to trawling disturbance. *Mar Ecol Prog Ser* 144:63–72
- Rees HL, Pendle MA, Waldock R, Limpenny DS, Boyd SE (1999) A comparison of benthic biodiversity in the North Sea, English Channel, and Celtic Seas. *ICES J Mar Sci* 56:228–246
- Rice J, Gislason H (1996) Patterns of change in the size spectra of numbers and diversity of the North Sea fish assemblage, as reflected in surveys and models. *ICES J Mar Sci* 53:1214–1225
- Saiz-Salinas JI, Ramos A (1999) Biomass size-spectra of macrobenthic assemblages along water depth in Antarctica. *Mar Ecol Prog Ser* 178:221–227
- Sheldon RW, Sutcliffe WH, Paranajpe MA (1977) Structure of pelagic food chain and relationship between plankton and fish production. *J Fish Res Board Can* 34:2344–2353
- Sprules WG, Munawar M (1986) Plankton size spectra in relation to system productivity, size and perturbation. *Can J Fish Aquat Sci* 43:1789–1794
- Vandermeer JH (1980) Indirect mutualism: variations on a theme by Stephen Levine. *Am Nat* 116:441–448
- Warwick RM (1986) A new method for detecting pollution effects on marine macrobenthic communities. *Mar Biol* 92:557–562
- Warwick RM, Clarke KR (1995) New biodiversity measures reveal a decrease in taxonomic distinctness with increasing stress. *Mar Ecol Prog Ser* 129:301–305
- Warwick RM, Pearson TH, Ruswahyuni (1987) Detection of pollution effects on marine macrobenthos: further evaluation of the species abundance/biomass method. *Mar Biol* 95:193–200

Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

*Submitted: September 17, 2003; Accepted: June 1, 2004
Proofs received from author(s): September 28, 2004*