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Eastern English Channel fish assemblages: measuring the structuring effect of habitats on distinct sub-communities

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Abstract:

Multivariate and spatial analyses are used to identify and locate fish, cephalopod, and macrocrustacean species assemblages in the eastern English Channel from 1988 to 2004. Four sub-communities with varying diversity levels were identified in relation to depth, salinity, temperature, seabed shear stress, sediment type, and benthic community nature. From 1997 to 2004, some 25% of overall community structure variance could be related to the available environmental descriptors and 20% to persistent factors such as depth, seabed shear stress, sediment, and macro-invertebrate community type. Although there may be significant interannual shifts in overall community structure and composition, the sub-communities identified persisted over time, reflecting the relative stability of the environmental conditions in this area. The diversity levels of the community appeared to have increased over the past 2 decades and to be higher in areas with soft sediments and wide temperature and salinity variations, typically coastal river plumes and estuaries where bentho-demersal species dominated. The strong spatial structure of the fish communities in the eastern English Channel reflects the different types of habitats shared by differing species assemblages. Such persistence may be useful for spatially explicit planning of human use and resource management.

Keywords: diversity, eastern English Channel, fish community, spatial patterns, structuring environment

Introduction

The English Channel is an international area of mixed fisheries and as elsewhere, there is growing need for ecosystem-based assessment and multispecies management (Jennings and Kaiser, 1998; Valette-Silver and Scavia, 2003; Pikitch *et al.*, 2004; Corkeron, 2006). This requires improved understanding of the ecological mechanisms controlling community composition and the population dynamics of exploited stocks.

A common (but not unique) definition of community is that it is a collection of species found in the same place at the same time (Begon *et al*., 1990, Fauth *et al*., 1996). Ecosystems and communities are viewed as open and naturally changing systems subjected to external driving factors (O'Neill, 2001). However, long-term studies (>10 y) have shown that fish species co-occur persistently and that fish assemblages tend to retain their species composition for periods of time comparable with the lifespan of most of the species present (Gomes *et al.*, 2001). In shelf fish communities, environmental gradients (e.g. temperature and depth) influence patterns of species co-distribution (Murawski and Finn, 1988) and result in regional and subregional geographic assemblages (Overholtz and Tyler, 1985; Gabriel 1992; Gomes *et al*., 1995). Spatial assemblages of species may be important ecological units in which co-existent species likely interact strongly with one another. As such, a sub-community may be defined as a self-contained recognizable subdivision of a community, usually within a distinct location. These sub-communities may have distinct trophic structures, and may respond differently to human activities, environmental variation, or changes in food resources (Garrison, 2000).

Nash (1988) and Gray (1989) highlighted the effect of disturbance and environmental stressors on fish community structure and diversity. In their review of the ecological processes affecting marine communities, Garcia-Charton and Perrez-Ruzafa (1999) described how the effect of fishery management could be confounded with other causal processes that drove the spatial and temporal variability of community structure. They pointed out that both environmental and biological mechanisms could affect the community structure, and that the difficulty rested with determining the relative importance of such processes in influencing community structure. As a result of the complexity, the effects of intense fish exploitation on the marine community are poorly understood, and Gomes *et al.* (2001) suggested the need to monitor community composition and spatial distribution over time in order to evaluate its resistance to perturbation.

There have been some broad-scale studies describing epibenthic species assemblages based on beam trawl surveys around the British Isles (Jennings *et al.*, 1999b, Kaiser *et al.*, 1999, Rees *et al.*, 1999). Although they gave a detailed taxonomic account of the invertebrate fauna, the studies tended to under-represent demersal fish (Ellis *et al.*, 2000). Based on beam trawl surveys from 1990 to 1995, Rogers *et al.* (1998) focused their study on demersal fish of the British continental shelf, but disregarded pelagic species and cephalopods. Since 1988, IFREMER at Boulogne-sur-Mer (France) has been carrying out an annual bottom trawl survey in the eastern English Channel, named CGFS (Channel Ground Fish Survey). The survey provides species data (demersal, benthic, and pelagic) and the associated hydrological parameters required for a multivariate study of the structure of the eastern Channel fish community in relation to its environment and its evolution over time.

Our objective here is first, to identify and describe the composition and spatial structure of the fish, cephalopod, and macro-crustacean assemblages in the eastern English Channel. The relationships between the species composition and the environmental variables are then used to distinguish which part of the community structure may be linked to permanent or slow-changing habitat characteristics and which part may be related to changing environmental variables such as temperature and salinity. The relative importance of each process to community structure is quantified and discussed. Finally, the temporal stability of the structures in the community is explored.

Material and methods

The English Channel is a marine corridor between England and France characterized by a contrasting and heterogeneous environment. The eastern English Channel is here delimited by the Dover Strait to the east and the Cotentin Peninsula to the west, which constitutes something of a physical and hydro-climatic barrier. This part of the continental shelf is shallow (40–100 m), and its hydrology is marked by a west-to-east general circulation disrupted by strong tidal currents (Figure 1a, b). Temperature conditions vary from 7 to 17°C and are homogeneous throughout the water column, because of shallowness, strong currents, and wind and tidal mixing. The seabed is highly heterogeneous, with a vast pebbly area from the Cotentin Peninsula to the Isle of Wight, whereas sands and gravels are most prominent in the rest of the eastern Channel (Figure 1c). Along the French coast, freshwater plumes from the rivers Seine and Somme flow eastwardss along the French coast, generating a coastal flow characterized by low salinity and turbid water (Figure 1d). Along the English coast the salinity is higher because freshwater inputs from the Solent in the west and the Thames in the east are relatively small.

The whole area is subjected to continental influence (with cold winters and large freshwater inputs on the French side), which strongly impacts the marine ecosystem, permitting both temperate Atlantic and boreal North Sea species to co-exist. The species assemblages are therefore strongly structured by environmental variations isolating smaller geological, hydrological and biological units (Pingree and Maddock, 1977, Guitton *et al.*, 2003). There are many commercial European marine species in the Channel, which is characterized by a large species (pelagic, flatfish, gadoids, skates, catsharks, crustaceans, and cephalopods) and functional diversity (benthic, demersal, and pelagic). Some of these species are resident in the Channel, others are seasonal owing to their migration or reproductive behaviour, but most have a broader distribution and are found in adjacent seas. The diversity and abundance of the fauna makes the eastern English Channel an important fishing area that is linked to the high benthic abundance acting as a food source for many fish species (Nival, 1991).

Survey design and sampling

Since 1988, the CGFS survey of the eastern English Channel and the southern North Sea (Figure 2) has taken place every year in October on board the RV “Gwen Drez”. The area is subdivided into 15’ × 15’ rectangles, and at least one 30 min trawl haul is carried out in each rectangle at an average speed of 3.5 knots. A high (about 3 m) vertical opening bottom trawl with 10 mm mesh size in the codend is used, and hauls are towed generally facing into the current. The systematic sampling scheme aims to achieve 90–120 stations, depending on weather conditions. The ship, gear, and sampling protocol remained the same throughout the study period so that the usual biases in community data analysis where patterns can be attributed to changes in sampling intensity (Trenkel *et al.*, 2004) were avoided.

After each haul, all captured species are sorted, identified, and counted. In all, 85 species of fish, cephalopods and macro-crustaceans were consistently recorded over the study period and used for the analysis (Table 1). The abundance indices at each station were standardized to density per km², and average abundance, standard deviation, and frequency of occurrence were computed. For many species, length-at-maturity relevant to the area (Table 1) was available in the literature (including *FishBase*; Froese and Pauly, 2006) and were used to calculate the proportion of mature (adult) and immature (juvenile) fish based on the length distributions.

Environmental data

Since 1997, a Micrel hydrological probe, attached to the headrope of the trawl, has recorded temperature and salinity every 15 s. Average bottom salinity and temperature were computed for each tow and constituted *in situ* observations of the hydrological conditions associated with the catch. These characteristics may vary both spatially and annually, and are descriptors of the dynamic component of the species community. Mean bottom salinity and temperature maps averaged over the whole study period (1988–2004) were created (Figure 1d, e).

Four environmental descriptors were available to explore the static compartment of species community that could be linked to permanent (or very slow changing at a mesoscale) environmental conditions. These were bottom depth, recorded at each station, bed shear stress, seabed sediments, and macrobenthic community.

Bed shear stress (in Newtons per m^2) was estimated using a 2-D hydrodynamic model of the northwest European shelf developed at the Proudman Oceanographic Laboratory (Aldridge and Davies, 1993). Bed shear stress is a function of the maximum predicted tidal current and an appropriate bed friction coefficient, in this case with an assumed value of 0.0025. The parameter was provided as a regular grid of 1/8° of longitude by 1/12° of latitude and used to produce a continuous map (Figure 1b; Carpentier *et al.*, 2005). The bed shear stress data were obtained by re-sampling this map at trawl haul locations using the GIS ArcMap software (ArcGIS Desktop product, v. 8.2, Environmental Systems Research Institute, Inc., ESRI).

Sediment type was obtained from the Larsonneur *et al.* (1979) map of the English Channel, simplified into five main categories of deposit: pebble, gravel, coarse sand, fine sand, and mud, according to granulometric criteria (Figure 1c). These criteria enhanced the importance of smaller particles on one hand, and of coarse particles on the other, both of which determine the physical and chemical properties of the deposits and hence the environmental characteristics.

Macrobenthic communities in the eastern English Channel were investigated by Cabioch *et al.* (1975, 1976, 1977) between 1972 and 1976. Based on these data, benthic community typology and spatial distribution were further studied by Sanvicente Añorve (1995), and five community types were defined and named after their preferential substratum type: fine sand, sand bank, fine homogenous sandy gravel, coarse heterogeneous sandy gravel, pebbles (Figure 1f). These, however, should not confused with the sediment classes described above, because they illustrate a type of habitat rather than an observed substratum.

Seabed sediments and benthic community data corresponding to trawl haul locations were extracted from digital versions of sediment and macrobenthic maps, using the GIS Arcmap software.

Diversity indices

Diversity indices constitute integrated community attributes and seem to be relatively unaffected by changes in species composition attributable to catchability variation (Wantiez, 1996). Species richness, and Shannon diversity and evenness were computed for each sample. Species richness (S or α diversity) relates to the number of species present within a specified area. It is calculated for the whole species composition, and does not account for the relative abundance of each species. Equitability and evenness indices measure the equality of species abundance in a community. The most popular are the Shannon–Weaver entropy index and the evenness index. These two indices are based on the proportional abundances of species, and take both richness and abundance into account (Magurran, 1988):

Shannon index = $H' = -\Sigma\, p_i \log_2 p_i$, where p_i is the percentage cover of the i^{th} species.

Shannon evenness = $E = H' / H_{\max}$, where $H_{\max}$ is the maximum diversity that could be possible if all species were equally abundant, $H_{\max} = \log_2 S$, and S is the number of species.

Community multivariate analyses

Abundance data were transformed to reduce their absolute skewness (<1) and because there were null values in species abundance data, the $\log_{10}(X + 1)$ transformation was preferred (Legendre and Legendre, 1998). Environmental variables displayed normal distribution and were not transformed. Sediment and macrobenthic types were recorded as dummy variables (binary coding).

Community classification was accomplished using the TWINSPAN method (Two-Way INdicator SPecies ANalysis) (Hill *et al.*, 1975; Hill, 1979; Gauch and Whittaker, 1981), which combines ordination and clustering and widely used in vegetative science to classify species and samples simultaneously. At its core, TWINSPAN is based on dividing a reciprocal averaging ordination space, as described by Gauch (1982, pp. 201–203) and Kovach (1995). TWINSPAN does not analyse abundance data directly, but is based on presence/absence However, it does approximate quantitative abundance data by creating a variable number of "pseudo-species" to represent abundance classes. The "pseudo-species cut levels" are used to define the ranges of the abundance classes. Here we selected levels that corresponded to natural breaks in overall data distribution of species abundance. In order to aid interpretation of the resulting dichotomies, the TWINSPAN procedure also results in the definition of indicator species. These correspond with the minimal set of species that will reproduce the ordination as closely as possible. A given indicator species associated with a particular group should be interpreted as being usually contained in this group and often lacking in the opposite group. Nevertheless, the affinity of all species investigated for a given group is also measured *post hoc*, depending on their frequency of occurrence within the group. Preferential species are defined as species often in a given group. The TWINSPAN procedure was used to define different sub-communities based on the species data collected during the CGFS surveys from 1988 to 2004 (n = 1448).

The spatial distribution of the defined sub-communities was obtained using indicator kriging of each community type. Indicator kriging is commonly used to separate populations, and may be used to estimate the proportion of different populations within an area (Isaaks and Srivastava, 1989). This interpolation technique is adapted to nominal variables (Webster and Oliver, 2001) and allows production of a map giving the probability of occurrence of community type at any given location. The distribution maps for the defined sub-communities were then combined, selecting at each location the community type displaying the greatest probability of occurrence.

Kendall's Coefficient of Concordance, τ, *a*lso known as Kendall’s correlation, is a measure of association between the rankings of the observations on each variable in turn. The coefficient is constructed from the sum of ranks for each observation over the variables (Gibbons, 1985), and was used to compare community classification for the whole period studied with classifications for single years, in order to verify community stability over time.

Principal components analysis (PCA) is an indirect gradient analysis that employs a linear response model, which is a simple approximation of the species response along an environmental gradient (ter Braak and Smilauer, 2002). Canonical analysis of two data (primary and explanatory) sets is possible in PCA by indirect comparison. The explanatory variables do not intervene in the ordination of the primary data, but their regression vectors are calculated *a posteriori*, allowing their passive representation on a bi-plot (Legendre and Legendre, 1998). This method was used to explore the community structure from 1988 to 2004 (again $n = 1448$) and to verify the TWINSPAN classification. It was also used to study the pattern of interannual variation of community structure and composition.

Redundancy Analysis (RDA) is a direct extension of multiple regression to modelling multivariate response data (Legendre and Legendre, 1998). It is a constrained version of PCA in that the ordination axes are constrained to be linear combinations of the environmental variables (Kovach, 1995). This method was used in combination with Monte-Carlo permutation tests to explore the multilinear relationships between a fish community and its environment. This analysis was performed on a reduced data set, because temperature and salinity data were available for just the period 1997–2004 ($n = 789$).

Testing and extracting the effect of explanatory variables

The statistical significance of the relationship between primary (species) variables and explanatory (environmental) variables was evaluated using Monte-Carlo permutation tests (ter Braak and Šmilauer, 2002). In the Monte-Carlo permutation test, the reference distribution is simulated by repeatedly permuting the samples. A statistical test (F-ratio) is computed for the original data and compared with those of each permuted data. The value of the significance test is the probability that the response is independent from the tested explanatory variable. If the variable tested was significant, it was added to the model and its explained variation was removed from the test of remaining variables. Relevant variables were added successively to the model in order of decreasing contribution (and often significance). Stepwise forward selection was useful to identify a relevant and sufficient subset of explanatory variables to represent the relationship between species and environmental variables (ter Braak and Smilauer, 2002).

There was sometimes a need to extract the variation explained by one set of explanatory variables to analyse the remaining variation. This was done by partial analysis, where the variation explained by the covariable (i.e. the variable whose effect should be partialled out) was extracted before a constrained ordination was performed (ter Braak and Smilauer, 2002). The covariables were often explanatory variables for which the effect was of no interest, so this method was used to test whether the detected patterns were independent from interannual variations. Variance partitioning results may be obtained iteratively by measuring the variation explained by a particular set of variables after partialling out unwanted variable effects. The “Borcard method” was used to determine the proportion of variation attributable to or shared among different variables (Borcard *et al.*, 1992). It first partitioned the variation of explanatory variables into independent components: independent from the environment (pure spatial and pure temporal), environmental, and undetermined. The intrinsic spatial and temporal heterogeneity of a community, as explained by point coordinates and the date of sampling, was distinguished from the environmental relationship, to determine how much of the variation was explained by each and all components. The variance was further partitioned to distinguish the variation attributable to the persistent environment component (sediment, macrobenthic community, seabed shear stress, depth) and changing environmental component (temperature and salinity). Several partial RDAs were required to determine each component. These analyses were also performed on the same reduced data set for the period 1997–2004 ($n = 789$).

Results

Community structure

Sub-communities

TWINSPAN classification was computed on the basis of community abundance data. Pseudo-species cut-off levels numbered 6, and were defined as 0, 1, 1.7, 1.9, 2.4, and 2.8. The first division level separated the eastern English Channel into two large groups represented by *Chelidonichthys cuculus* (red gurnard) and *Spondyliosoma cantharus* (black seabream) on the one hand and *Limanda limanda* (dab), *Pleuronectes platessa* (plaice), and *Merlangius merlangus* (whiting) on the other. The great occurrence and abundance of these species structured the observations along this main first gradient (Table 2). For some of these species the difference in abundance and frequency of occurrence was related to the maturity of the fish (Table 2). For some species (*M. merlangus*, *Clupea harengus*, *Engraulis encrasicolus*, *Trisopterus* sp.), immature specimens were the most abundant and frequent. For others (*L. limanda*, *Microstomus kitt*, *Platichtys flesus*, *P. platessa*, *Solea solea*, *S. cantharus)*, the pattern was reversed and mature fish were more abundant and frequent than immature fish. Many other species abundances or frequencies of occurrence could not be related to the proportion of immature specimens in the catch.

Four sub-communities were defined by the classification process. The first was indicated by catshark (*Scyliorhinus* sp.) and poor cod (*Trisopterus minutus*), and included preferentially elasmobranch species (catshark and skates) and *Trisopterus* spp. Groups 2 and 3 were similar and included both common pelagic and demersal species (*Scomber scombrus*, *Sardina pilchardus*, *Mullus surmuletus*), but with different levels of abundance (Table 2). Group 2 was characterized by mackerel and dragonet. Group 3, however, was only demarcated by squid (*Loligo* spp.), although preferential species included some pelagic species. Group 4 was indicated by *Trisopterus* sp. and *S. solea*, and included many preferential species. Flatfish such as plaice (*P. platessa*), sole (*S. solea*), and lemon sole (*M. kitt*) were well represented, but so too were herring (*C. harengus*), whiting, and gadoids (*Gadus morhua*, *Trisopterus* sp.). Elasmobranchs (*Scyliorhinus canicula*, *Raja clavata*) were also preferential in this group.

Ordination of the community

A PCA was performed on the basis of a covariance matrix of fish community abundance (Figure 3a). The scaling focused on interspecies correlation, and the scores were standardized after axis extraction to produce a correlation bi-plot in which the length of the arrow is a measure of fit to the first factorial plan. Variation explained by the first two axes was respectively 24% and 12.8% of species variance. Species having a poor fit with the projection (<3%) were not represented. Observations were symbolized using the four classes defined by TWINSPAN (Figure 3b), and envelopes delineating each group were created. The community was strongly structured along the first axis, and the TWINSPAN classification patterns with the four sub-communities could be recognized. The first axis was associated with a shift in the community that corresponded to the TWINSPAN first division (Figure 3b), and at each end of this axis, there were indicator species of this division (*C. cuculus* and *S. cantharus* on the negative side, *L. limanda*, *P. platessa*, and *M. merlangus* on the positive side). The second division corresponded to the gradient described by the second PCA axis, with indicator species of groups 1 and 4 in the upper half of the bi-plot, and indicator species of groups 2 and 3 in the lower part. The general pattern along this second axis was that of segregation between demersal species (top of the bi-plot) and some pelagic species (in particular *T. trachurus*, which is one of the most abundant species), red mullet (*M. surmuletus*), and cephalopods (bottom of the bi-plot). Along this axis, the community structure seemed to oscillate between the dominance of these particular species.

Community diversity and spatial patterns

The species richness increased from groups 1 to 4 (Table 3), but Shannon diversity and evenness displayed a slightly different pattern, indicating that group 1 has greater diversity than group 2, with groups 3 and 4 effectively more diverse. These patterns were tested using ANOVA and Least Significant Differences *post hoc* tests, and were significant ($p>0.001$) for all diversity indices. The last two groups had a similar evenness, perhaps indicating that the diversity differences between groups were attributable to differences in environmental preference and probably not to interspecies competition. However, they had significantly greater evenness than groups 1 and 2, indicating a marked increase of dominance of a few or a single species in the first two sub-communities.

The sub-community groups were assigned to their corresponding trawl haul positions and showed strong spatial patterns. Using indicator kriging and after recombining the four sub-communities' maps, the distribution and transition boundaries between sub-communities were revealed, confirming the spatial structure already detected in the classified trawl haul positions (Figure 4). The fish community of the eastern English Channel appeared to change gradually in a spatial context, with its four sub-communities forming a transition from the open sea (group 1) to very coastal and even estuarine locations (group 4). The patterns described by the TWINSPAN classification and confirmed by a PCA were apparently linked to a strong coastal gradient in the area.

Community relationship to the environment

Structuring factors

The relationships between each sub-community type defined by TWINSPAN and the environmental characteristics are summarized in Table 4. Group 1 was characteristic of a benthic community associated with pebbles, hard sediments, oceanic hydrology (high salinity and temperature in October), strong tidal currents, and relatively deep water. Group 2 seemed to be characteristic of a benthic community, associated with pebbly and coarse sand sediments, with hydrology and bathymetry intermediate between offshore and coastal. Group 3, a benthic community, was associated with fine sand sediments, coastal hydrology and bathymetry conditions (low salinity and temperature in October, shallow water, weaker currents). Group 4 was characterized by heterogeneous sediment types (from muds to coarse sands) and the various associated benthic community types, as well as by coastal hydrology and bathymetry.

In order to test the significance of all variables to the community structure, a RDA based on a covariance matrix was performed, and Monte-Carlo permutations were computed for all explanatory variables. Temperature and salinity data were not available for the early years of the study, so the analysis was performed for the period 1997–2004 only (n = 789). All available variables were significantly (p<0.002) correlated to community structure. The available environmental variables explained 22.4% of overall community variation. The relative contribution to the RDA model (Table 5) was illustrated by the importance of depth and sediment in the structuring of the community. There was an important correlation between seabed nature and macrobenthic community type, and this had a significant effect on the fish community structure.

The community data and related environmental variables were projected in the plan of the first two axes (Figure 5). The projection settings were the same as the PCA, and species with a poor fit to the projection (<5%) have been removed. All axes were significant, and the community was highly structured along the first two axes (λ_1 = 15.8% of species variance, and λ_1 = 70.7% of the species/environmental relationship; $\lambda_1 + \lambda_2$ = 17.8% of species variance, and $\lambda_1 + \lambda_2$ = 79.5% of the species/environmental relationship).

The strong structuring of the community along the first axis appeared to be correlated with decreasing depth, bed shear stress, sediment particle size (from pebbles, gravels, and coarse and fine sand to muds) and their associated benthic community type (from pebbles, fine and coarse sandy gravel to coarse and fine sands). The same indicator and preferential species of open sea sub-community or coastal sub-community were located at each end of the first axis. The second axis was negatively correlated with the almost co-linear temperature and salinity gradients. Cephalopods (*Loligo* spp., *Sepia officinalis*), red mullet (*M. surmuletus*), and horse mackerel (*T. trachurus*) were strongly correlated to the temperature and salinity gradients, indicating that these species abundances may be particularly affected by variations in the two variables. They were also associated with coarse sand sediment and the benthic community associated with sandy gravels. This may describe the characteristic benthic habitat of the species.

Measuring the relative contribution of each environmental component

In order to clarify the relative contribution of the environmental parameters, variance partitioning analyses using the 1997–2004 data set and all available explanatory variables were performed (Table 6). The available explanatory variables included spatial (latitude, longitude), and temporal (year and date) components that were unrelated to the environment, and environmental components that were divided into a changing environment (temperature, salinity) and a persistent environment, the latter also divided into persistent hydrological conditions (depth, bed shear stress), benthic (5 benthic community types), and sediment (5 sediment types) components. Obviously some variability is shared among components, and the variance partitioning procedure described in Borcard *et al.* (1992)

accounts for such an effect. Overall, 30% of the community variation could be explained, 5% of which was purely due to spatial and temporal autocorrelation. In all, 25% of the community variable was related to the environmental variables, 6% of which could be explained by both changing and persistent explanatory variables for which a certain amount of variability is intertwined and almost co-linear. Only 5% of the community variation was correlated with the variation in the changing environmental conditions, temperature and salinity. On the other hand, the remaining 14% of the species community could be linked solely to the persistent environmental conditions. Of the 30% explained, 20% of the species variation was linked to the permanent environment in the area, which itself could be divided into three explanatory compartments: permanent hydrological, benthic, and sediment types.

Synthesis of the community characteristics

The four sub-communities defined by the TWINSPAN classification appeared to reflect inshore-to-offshore gradients in their composition. The classification first resulted in two distinct groups, one characterized by hard seabed species (black seabream, red gurnard, elasmobranchs), and the other by soft sediment species (flatfish, whiting). In the eastern English Channel, coarse sediments comprise gravels and pebbles that can be encountered at greater depths in more oceanic areas. Muddy and sandy sediments in contrast are found in coastal shallow waters with lower salinity and temperature. The second division level of the community further segregated the community into demersal and pelagic subtypes. The pelagic sub-community abundance was related to the temperature and salinity gradient. Pelagic species favoured relatively high temperature and salinity, i.e. an oceanic influence characteristic of the centre of the study area.

The first sub-community (group 1) was an offshore community represented mainly by elasmobranch species (catshark and skates) and poor cod. It co-occurred with benthic communities associated with pebbles, on hard sediment types, in oceanic and stable hydrological conditions, with strong tidal currents and relatively deep water. It did not respond strongly to temperature or salinity change, because these remain stable in the area of distribution. In this sub-community, species diversity levels were relatively lower than in the community classes in more coastal areas.

Group 2 was an intermediate community between coastal and offshore, and was characterized mainly by dragonets and mackerel (*C. lyra*, *S. scombrus*). It was preferred by both pelagic (sardine, mackerel) and bentho-demersal (dragonet, gurnard, red mullet) species living nearer the coast, shallower than that of the first group. Displaying a comparably low diversity to that of the offshore community, this group was characteristic of benthic communities associated with pebbly and coarse sand sediment. It was typical of the hydrology and bathymetry intermediate between offshore and coast, and did not respond greatly to temperature and salinity change.

The third sub-community (group 3) was a coastal homogeneous community represented by squid, and pelagic (sardine, mackerel, anchovy) and demersal (black seabream, sandeel, red mullet) fish species, with greater diversity than the first two groups. It was characteristic of benthic communities associated with fine sand sediments, coastal hydrology and shallow bathymetry, and was close to the coast. It appeared to respond to temperature and salinity changes, which are important in coastal areas because of the shallowness and the freshwater plumes from adjacent rivers.

Group 4 was a coastal heterogeneous community represented by pouting, poor cod, and sole, and was classified as preferential for many flatfish and gadoids. It displayed the greatest diversity and was characterized by heterogeneous sediment type (from muds to coarse sands) and various associated benthic community types, as well as coastal hydrology and bathymetry. It was mostly near the coast, close to large river estuaries, and in areas subject to big salinity and temperature variations. Possibly resulting from this potentially heterogeneous environment (both in space and time), this sub-community type was the most diverse.

Community evolution

Community structure stability

In order to assess the stability of community structure over time and, in particular, that of sub-community definition, TWINSPAN classifications were computed for each year separately. However, the community structure and indicator species observed for each year could be quite different to that of the overall classification, mainly because of fluctuations in the abundance of some dominant species. Notwithstanding, annual classifications resulted in groupings that could be related to those of the original classification for the whole data set (1988–2004), based on the identity of the preferential species in each group. The resulting annual classifications were compared with the original full data set for 1988–2004, and misclassification rates (expressed as a percentage) were computed (Table 7).

Misclassification was highly variable (0–94%) both within classes and annually. Group 2 had the greatest rate of misclassification and group 4 the least. Overall no particular trend in misclassification rate within each group could be found over time. The annual classification results were compared with the original classifications using Kendall's correlation and they were always significantly correlated ($p<0.001$). No significant differences in sub-community structure could be detected over the study period.

Interannual variation and evolution of species abundance over time

Years were projected passively on the PCA performed on the community data after axis extraction (only the first two axes are represented on Figure 3c). No particular shift in community structure could be linked with the passing of time. The years 1988 and 1990 were grouped together in the upper part of the bi-plot, corresponding to offshore communities (group1). This appears to be connected to the abundance of poor cod (*T. minutus*) during those years. The year 1996, however, was isolated at the right side of the bi-plot, corresponding to coastal (groups 3 and 4) communities. This result can be explained by the survey design for that year, which was more coastal and did not extend as far offshore as in other years.

Using year alone as an explanatory variable, a new RDA revealed that the structure of the community was significantly ($F = 37.84$, $p>0.002$) affected by interannual variations, although this variable alone explained little of the overall community variation ($\lambda_1 = 2.8\%$ of species variance). Close examination of the resulting bi-plot revealed that although most species experienced interannual variation in abundance, only one species could be correlated with a true time trend. This was the piper gurnard (*Trigla lyra*), which has not been found during the surveys since 1990.

Extracting the interannual effect

Based on the results above, it was important to know how much of the community structure was the result of changes in the environment over time. Using the 1997–2004 data set including temperature and salinity (which are the only non-persistent environmental variables), another analysis was performed to extract the effect of interannual variation and to test the conditional significance of the environmental parameters. A partial RDA, using year (coded as nominal variables) as covariable, revealed that all available environmental variables were still significant ($p<0.002$ for all variables). All axes were significant, and the community was still highly structured along the first two axes ($\lambda_1 = 15.6\%$ of the species variance and 72% of the species/environmental relationship; $\lambda_1 + \lambda_2 = 17.6\%$ of the species variance and 81.1% of the species/environmental relationship). The sum of all canonical eigenvalues was 0.216, showing that the variance explained by environmental variables was hardly reduced by the use of year as a covariable. This suggests that the community's relationship with its environment from 1997 to 2004 was independent of interannual variations (including both a potential environmental change effect and survey design variability). Although this result was not surprising for variables such as depth, sediment, and benthic community type that are intrinsically independent of time, it was more surprising that the effects of salinity and temperature on community structure were independent of annual variations. The hydrology effect on community patterns seemed to be stable over time.

Diversity evolution over time within each community class

The species richness of the eastern English Channel fish community observed in trawls increased significantly between 1988 and 2004. This increase was observed in all four sub-communities and was significant by ANOVA (Table 8). Overall, species richness increased on average by 1.5% per year during the period studied. Shannon equitability and evenness indices also increased over time, with the exception of group 4 for which equitability and evenness values appeared to be independent of time. These results revealed a general increase in species diversity in the eastern English Channel over the past 17 years.

Discussion

Earlier studies described the distribution of sediment and benthic communities in the eastern English Channel (Larsonneur *et al.*, 1979, Sanvicente-Añorve, 1995), and other studies showed how these two components could structure demersal fish assemblages assessed by beam trawl surveys (Kaiser *et al.*, 1999; Ellis *et al.*, 2000). Similar studies using bottom trawl survey data would be more representative of prevailing fish communities, including the demersal and pelagic assemblages, because bottom trawls sample greater areas and volumes than benthic grabs and beam trawls. Pelagic species, which are often highly reactive to changing hydrology, may indicate community changes taking place as a consequence of climate change. For this reason, they were included in the present study. The bottom trawl used (3 m vertical opening) might not sample efficiently the whole water column, but should catch at least part of the pelagic fauna present. It was therefore considered that the trawl represented accurately the relative patterns of variation in pelagic species abundance, both spatially and temporally. The effect of potentially large catches of pelagic species on the total fish community structure should be limited, because they would occur randomly and act as “white noise” in the analyses. Trawl gear is not suitable, however, for quantitatively sampling smaller flatfish and benthic invertebrates. Our observations had to be compared with the benthic community described from other sources. Here, using various types of multivariate analyses, we attempted to describe the observed community structure and to link it with known patterns of sediment and benthic biota distribution, as well as with other environmental characteristics available for the area, and to quantify the relative importance of the different explanatory components.

Community structure, environment, and diversity

The community in the eastern English Channel was strongly structured spatially, and this clearly resulted from important community responses to the environment. The strong structuring of demersal communities along both depth and sediment gradients had already been reported by Rogers *et al.* (1998), Kaiser *et al.* (1999), and Ellis *et al.* (2000), Temperature and salinity are lower in coastal areas in autumn and winter in the study area because of the shallowness and the extensive input of cold freshwater from rivers and rainfall. These conditions appeared to favour bentho-demersal species and, by contrast, pelagic species were more abundant at the centre of the study area. Such an effect of temperature on benthic and demersal community composition has been reported before (Ellis *et al.*, 2000; Beyst *et al.*, 2001). This coastal community type was the most species-rich and resembled that described by Beyst *et al.* (2001) for surf zones of Belgian sandy beaches. Those authors reported the sensitivity of the Belgian sandy beach community to temperature variation, and important community diversity and structural variations at a seasonal scale.

Groups 2 and 3 shared the preferential species sardine, mackerel, and red mullet, probably revealing an ecological continuum within the community structure. Squid, the indicator species of group 3, included both European (*Loligo vulgaris*) and veined (*L. forbesi*) species, whose respective distributions are different. The first is distributed in the northeast of the area and the latter in the southwest, and their cumulative area of distribution covered most of the eastern English Channel (Carpentier *et al.*, 2005). However, these semi-pelagic species were probably less likely to be caught at depth by a bottom trawl, and they are very sensitive to variations in water quality and hydrology close to the coast, where they appear to be less abundant. This may explain why they were absent from the other groups. Likewise, the simultaneous presence of red mullet in groups 2 and 3 may be the result of the expanding geographical distribution that this species has exhibited since 1997 (Guitton *et al.*, 2003, Beare *et al.*, 2005), even in coastal areas where juveniles are now found in large quantity. Although the species is at its northern distribution limit, red mullet abundance seems to peak in the eastern English Channel in autumn, and Guitton *et al.* (2003) suggested that this abundance increase could have resulted from seawater temperature increases during the 1990s. However, that suggestion was not confirmed during this study because hydrology records only commenced in 1997.

Community evolution over time

The community relationship with its environment was remarkably stable over the 17 years of observation. However, community structure changed significantly over time without any detectable trend, as did temperature and salinity. The community is so strongly structured by its environment that it may reflect interannual climate variations, although no patterns could be distinguished over the study period. This result appears to contradict the belief of Genner *et al.* (2004), who observed a marine community shift in relation to climate warming in the English and Bristol Channels. Similarly, Jennings *et al.* (1999) suggested that changes in the North Sea fish community could be linked to the increased fishing effort favouring small species with short life histories. The absence of any trend in the structure of the eastern English Channel fish community suggests that fishing pressure and selectivity have not altered greatly over the study period at least. However, the period considered here (1988–2004) may be insufficient to detect such a trend, and it is often difficult, if not impossible, to separate natural fluctuations from anthropogenic ones such as exploitation (Cushing, 1983). Only one species displayed a significant evolution in abundance over time: piper gurnard (*T. lyra*), which was seldom caught, disappeared from the catches in 1991, and did not account for much of the community variation.

Although in this study no trend could be detected in changes to the structure of the fish community, some irregular shifts towards assemblages dominated by pelagic (*T. trachurus*) and demersal fish (*M. surmuletus*), and cephalopods (*Loligo* spp., *S. officinalis*) have been highlighted. These shifts corresponded to the second division level of the TWINSPAN analysis, and to the second axes of both PCA and RDA. This particular pattern of variation can be related to the changing environmental component (temperature and salinity) and suggests that doimance of these species increased during years when oceanic conditions were warmer in the English Channel during autumn. In cooler years, with more freshwater inputs resulting from precipitation, plus the mixing of coastal and offshore waters by wind action, the bentho-demersal component of the community tended to dominate. Community shifts in the pelagic fish community have been reported in relation to climate shifts (Bailey *et al.*, 1995; Hunter and Alheit, 1995) and can be linked to temperature and salinity changes. Synchronicity of changes in the demersal assemblage and environmental conditions have also been reported for the English Channel (Fromentin *et al.*, 1997) and the North Sea (Austen *et al.*, 1991). In the North Sea, a simultaneous transition in communities of phytoplankton, zooplankton, and macrobenthos took place in the late 1970s, probably as a result of eutrophication (Austen *et al.*, 1991). More controversially, apparent inverse changes in pelagic and demersal stocks have been reported in the North Sea (Cushing, 1983). It seems possible therefore that environmental change may affect trophic relationships within and between all compartments of any fish community, and result in simultaneous changes in species composition of both pelagic and demersal assemblages.

However, bentho-demersal species are often higher trophic level predators, and the complexity of the foodweb and time-lags buffer them from the variability in pelagic secondary production (Bailey *et al.*, 1995). Mueter and Norcross (2000) also suggested predation as a possible mechanism to explain similar changes in demersal fish communities in nearshore waters of Alaska, and the past shift from pelagic to demersal stocks in the North Sea may have been the consequence of overfishing (Cushing, 1983). It is possible that variations in temperature and salinity in the eastern English Channel only affect some part of the fish community. The overall structure would appear to shift towards bentho-demersal species as a result of the loss of ground of particular species. This result may be linked to the size of habitat suitable to each type of community, which would change depending on interannual climate variation and result in shifts in the observed overall structure.

The apparent stability of the fish community structure in the eastern English Channel was also reported by Rochet *et al.* (2005) using community-level indicators for the period 1997–2002. Although no trend was detectable in the community structure, there was an increase in species diversity. The appearance of a few new species in the area since 1998, for which the catches are invariably low, was rare: at least one *Alosa fallax* has been caught each year since 1998. *Arnoglossus* sp. and labrids were first found in 1990, but then inalmost every year since 1997. At the same time, two species disappeared from the catches: *Squalus acanthias* since 1999, and *T. lyra* since 1991.

This trend of increasing diversity might reflect the increased presence and expanded geographic distribution of some species in the eastern English Channel, or it may simply reflect the increasing overlap in species occurrences at a haul scale. Increased co-existence may result from decreasing dominance of a few species (which seems to be the case in the first two sub-community groups) or increased spatial heterogeneity. The important variability of temperature and salinity in coastal areas may reflect an increasingly variable habitat, allowing for more species co-existence at a smaller scale Beyst *et al.* (2001).

The impact of fisheries in this area under high exploitation pressure has likely had a role in changing species dominance (particularly that of predators) through the removal of large fish (Rogers *et al.*, 1998). Bianchi *et al.* (2000) reported increased species diversity resulting from changes in patterns of dominance in response to heavy exploitation. Although the reported impact of fisheries on fish habitat and benthic community is often negative (Auster and Langton, 1999; Dimore *et al.*, 2003; Queiros *et al.*, 2006), fishing activities are seldom homogeneous over an area, and only limited substrata are suitable for the use of some fishing gears. Paradoxically, gap creation on the seabed and the subsequent re-establishment of benthic fauna may result in increased spatial and temporal heterogeneity and contribute to local increases in species co-existence (Johnson, 2000).

The spatially distinct sub-community in the eastern English Channel reflected the importance of the environment effect on fish community structure and composition, and may be considered as distinct ecological units within the larger community. Fishery management typically aggregates single species stocks over large areas, but this study has illustrated that the ecological structure within a community varies at a sub-regional level (smaller than an ICES division). Ecosystem approaches to fisheries assessment and management should account explicitly for such spatial differences in community structure. By applying fishing restrictions to specific areas preferred by species under a protection scheme, both the resources and their habitat would be protected. Such an approach would require knowledge of the seasonal variation in community structure such as described here, and forecasting of the sub-community spatial extent, based on environmental conditions (in particular temperature and salinity).

The importance of both changing and persistent environmental variables for community structure can be tested and measured. The strong relationship between the persistent component of the environment and community structure, reflecting its stability over time, makes it possible to model and predict sub-community distributions from known, stable environmental parameters. The integration of descriptors of climate variation might also allow prediction of the distribution and variability of fish assemblages. Habitat modelling approaches, linking statistical modelling to GIS mapping (Carpentier *et al.*, 2005, Guisan *et al.*, 2006), could be used to model the fish community and to verify whether the environmental descriptors available here can provide on their own (without any information of trophic relationships or biotic interactions) an acceptable prediction of community type. Such an approach may permit management of the shared habitats of fish communities and forecasting of their shifts in term of both composition and location. Sub-community types with contrasting species composition and diversity levels and corresponding to strong habitat affinity may benefit from the establishment of Marine Protected Areas or other spatially explicit management schemes (Garcia-Charton and Perez-Ruzafa, 1999; Frank and Shackell, 2001; Hinz *et al.*, 2003). This type of management may be particularly important in the frame of multiple marine use and increasing human pressure in the eastern English Channel.

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References

Aldridge, J. N., and Davies, A. M., 1993. A high-resolution three-dimensional hydrodynamic tidal model of the eastern Irish Sea. Journal of Physical Oceanography, 23: 207–224.

Austen, M. C., Buchanan, J. B., Hunt, H. G., Josefson, A. B., and Kendall, M. A. 1991. Comparison of long-term trends in benthic and pelagic communities of the North Sea. Journal of the Marine Biological Association of the UK, 71: 179–190.

Auster, P. J., and Langton, R. W. 1999. The effects of fishing on fish habitat. *In* Fish Habitat: Essential Fish Habitat and Rehabilitation, pp. 150–187. Ed. by L. R. Benaka. American Fisheries Society Symposium, 22.

Bailey, K. M., Piatt, J. F., Royer, T. C., Macklin, S. A., Reed, R. K., Shima, M., Francis, R. C., Hollowed, A. B., Somerton, D. A., Brodeur, R. D., Ingraham, W. J., Anderson, P. J., and Wooster, W. S. 1995. ENSO events in the northern Gulf of Alaska, and effects on selected marine fisheries. CalCOFI Report, 36: 78-96

Beare, D., Burns, F., Jones, E., Peach, K., and Reid D. 2005. Red mullet migration into the northern North Sea during late winter. Journal of Sea Research, 53: 205–212.

Begon, M., Harper, J. L., and Townsend, C. R. 1990. Ecology: Individuals, Populations and Communities, 2nd edn. Blackwell Scientific, Oxford.

Beyst, B., Hostens, K., and Mees, J. 2001. Factors influencing fish and macrocrustacean communities in the surf zone of sandy beaches in Belgium: temporal variation. Journal of Sea Research, 46: 281–294.

Bianchi, G., Gislason, H., Graham, K., Hill, L., Jin, X., Koranteng, K., Manickchand-Heileman, S., Paya´, I., Sainsbury, K., Sanchez, F., and Zwanenburg, K. 2000. Impact of fishing on size composition and diversity of demersal fish communities. ICES Journal of Marine Science, 57: 558–571.

Borcard, D., Legendre, P., and Drapeau, P. 1992. Partialling out the spatial component of ecological variation. Ecology, 73: 1045–1055.

Cabioch, L., Gentil, F., Glaçon, R., and Rétière, C. 1976. Le macrobenthos des fonds meubles de la Manche: distribution générale et écologie. *In* Biology of Benthic Organisms. 11th European Symposium on Marine Biology. Galway, October 1976, pp. 115–128. Ed. by B. F. Keegan, P. O. Ceidigh, and P. J. S. Boaden. Pergamon Press, Oxford. 630 pp.

Cabioch, L., and Glaçon, R. 1975. Distribution des peuplements benthiques en Manche orientale, de la baie de Somme au Pas-de-Calais. Comptes Rendus des Séances de l'Académie des Sciences de Paris, Série D, 280: 491–494.

Cabioch, L., and Glaçon, R. 1977. Distribution des peuplements benthiques en Manche orientale. Du cap d'Antifer à la baie de Somme. Comptes Rendus des Séances de l'Académie des Sciences, Paris, Série D, 285: 209–212.

Carpentier, A., Vaz, S., Martin, C. S., Coppin, F., Dauvin, J–C., Desroy, N., Dewarumez, J–M., Eastwood, P. D., Ernande, B., Harrop, S., Kemp, Z., Koubbi, P., Leader-Williams, N., Lefèbvre, A., Lemoine, M., Meaden, G. J., Ryan, N., and Walkey, M. 2005. Eastern Channel Habitat Atlas for Marine Resource Management (CHARM). Atlas des Habitats des Ressources Marines de la Manche Orientale, INTERREG IIIA. 225 pp.

Corkeron, P. J. 2006. Opposing views of the "Ecosystem Approach'' to fisheries management. Conservation Biology, 20: 617–619.

Cushing, D. H., 1983. The decline of the herring stocks and the gadoid outburst. Journal du Conseil International pour l'Exploration de la Mer, 39: 70–81.

Dinmore, T. A., Duplisea, D. E., Rackham, B. D., Maxwell, D. L., and Jennings, S. 2003. Impact of a large-scale area closure on patterns of fishing disturbance and the consequences for benthic communities. ICES Journal of Marine Science, 60: 371–380.

Ellis, J. R., Rogers, S. I., and Freeman, S. M., 2000. Demersal assemblages in the Irish Sea, St George's Channel and Bristol Channel. Estuarine, Coastal and Shelf Science, 51: 299–315.

Fauth, J. E, Bernardo, J., Camara, M., Resetarits, W. J., Van Buskirk, J. and McCollum, S. A., 1996. Simplifying the jargon of community ecology: a conceptual approach. American Naturalist, 147: 182–186.

Frank, K. T., and Shackell, N. L. 2001. Area-dependent patterns of finfish diversity in a large marine ecosystem. Canadian Journal of Fisheries and Aquatic Sciences, 58: 1703–1707.

Froese R., and Pauly D. 2006. FishBase. World Wide Web electronic publication. www.fishbase.org. Version 06/2006.

Fromentin, J-M., Ibanez, F., Dauvin, J-C., Dewarumez, J. M., and Elkaim, B. 1997. Long-term changes of four macrobenthic assemblages from 1978 to 1992. Journal of the Marine Biological Association of the UK, 77: 287–310.

Gabriel, W. 1992. Persistence of demersal fish assemblages between Cape Hatteras and Nova Scotia, Northwest Atlantic. Journal of Northwest Atlantic Fisheries Science, 14: 29–46.

Garcia-Charton, J. A., and Perez-Ruzafa, A. 1999. Ecological heterogeneity and the evaluation of the effects of marine reserves. Fisheries Research, 42: 1–20.

Garrison, L. P. 2000. Spatial and dietary overlap in the Georges Bank groundfish community. Canadian Journal of Fisheries and Aquatic Sciences, 57: 1679–1691.

Gauch, H. G. 1982. Multivariate Analysis in Community Ecology. Cambridge University Press, New York. 298 pp.

Gauch, H.G., and Whittaker R. H. 1981. Hierarchical classification of community data. Journal of Ecology, 69: 135–152.

Genner, M. J., Sims, D. W., Wearmouth, V. J., Southall, E. J., Southward, A. J., Henderson, P. A., and Hawkins, S. J. 2004. Regional climatic warming drives long-term community changes of British marine fish. Proceedings of the Royal Society, 271: 655–661.

Gibbons, J. D., and Chakraborti, S. 2003. Nonparametric Statistical Inference, 4th edn. Marcel Dekker, New York. 680 pp.

Gomes, M. C., Haedrich, R. L., and Villagarcia, M. G. 1995. Spatial and temporal changes on the north-east Newfoundland/Labrador Shelf, north-west Atlantic, 1978–1991. Fisheries Oceanography, 4: 85–101.

Gomes, M. C., Serrao, E., and Borges, M. F. 2001. Spatial patterns of groundfish assemblages on the continental shelf of Portugal. ICES Journal of Marine Science, 58: 633–647.

Gray, J. S. 1989.Effects of environmental stress on species rich assemblages. Biological Journal of the Linnaean Society, 37: 19–32.

Guisan, A., Lehmann, A., Ferrier, S., Austin, M., Overton, J. M. C., Aspinall, R., and Hastie, T. 2006. Making better biogeographical predictions of species' distributions. Journal of Applied Ecology, 43: 386–392.

Guitton, J., Dintheer, C., Dunn, M. R., Morizur, Y., and Tétard, A. 2003. Atlas des Pêcheries de la Manche. IFREMER. 216 pp.

Hill, M. O., Bunce, R. G. H., and Shaw, M. W. 1975. Indicator species analysis, a divisive polythetic method of classification, and its application to a survey of native pinewoods in Scotland. Journal of Ecology, 63: 597–613.

Hill, M. O. 1979. TWINSPAN: A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Section of Ecology and Systematics, Cornell University Ithaca, New York. 31 pp.

Hinz, H., Kaiser, M. J., Bergmann, M., Rogers S. I., and Armstrong, M. J. 2003. Ecological relevance of temporal stability in regional fish catches. Journal of Fish Biology, 63: 1219–1234.

Hunter, J. R. and Alheit, J. 1995. International GLOBEC small pelagic fishes and climate change program. GLOBEC Report, 8: 72.

Isaaks, E. H., and Srivastava, R. M. 1989. An Introduction to Applied Geostatistics. Oxford University Press, Oxford. 580 pp.

Jennings, S., Greenstreet, S. P. R., and Reynolds, J. D. 1999a. Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. Journal of Animal Ecology, 68: 617–627.

Jennings, S., and Kaiser, M. J. 1998. The effects of fishing on marine ecosystems. Advances in Marine Biology, 34: 203–352.

Jennings, S., Lancaster, J., Woolmer, A., and Cotter, J. 1999b. Distribution, diversity and abundance of epibenthic fauna in the North Sea. Journal of the Marine Biological Association of the UK, 79: 385–399.

Johnson, M.P. 2000. Temporally explicit habitat ecology and the coexistence of species. Proceedings of the Royal Society, 267: 1967–1972.

Kaiser, M. J., Rogers, S. I., and Ellis, J. R. 1999 Importance of benthic habitat complexity for demersal fish assemblages. *In* Fish Habitat: Essential Fish Habitat and Rehabilitation, pp. 212–223. Ed. by L. R. Benaka. American Fisheries Society Symposium, 22.

Kovach, W. L. 1995. Multivariate data analysis. *In* Statistical Modelling of Quaternary Science Data, pp. 1–38. Ed. by D. Maddy and J. S. Brew. Quaternary Research Association, Technical Guide, 5. Cambridge, UK.

Larsonneur, C., Vaslet, D., and Auffret, J–P. 1979. Les Sédiments Superficiels de la Manche. Carte Géologique de la Marge Continentale Française. Bureau des Recherches Géologiques et Minières, Ministère de l'Industrie, Service Géologique National, Orléans, France.

Legendre, P., and Legendre, L. 1998. Numerical Ecology. Elsevier, Amsterdam. 868 pp.

Magurran, A. E. 1988. Ecological Diversity and Its Measurement. Chapman and Hall, London. 192 pp.

Mueter, F. J., and Norcross, B. L. 2000. Changes in species composition of the demersal fish community in nearshore waters of Kodiak Island, Alaska. Canadian Journal of Fisheries and Aquatic Sciences, 57: 1169–1180.

Murawski, S. A., and Finn, J. T. 1988. Biological basis for mixed species fisheries: species co-distribution in relation to environmental and biotic variables. Canadian Journal of Fisheries and Aquatic Sciences, 45: 1720–1735.

Nash, R. D. M. 1988. Effects of disturbance and severe seasonal fluctuations in environmental conditions on north temperate shallow-water fish assemblages. Estuarine, Coastal and Shelf Science, 26: 123–135.

Nival, P. 1991. Manche et mer du Nord: riches et fragiles. Science et Vie. Hors-série. La vie des océans, 176: 106–113.

O’Neill, R. V. 2001. Is it time to bury the ecosystem concept? (with full military honors, of course!). Ecology, 81: 3275–3284.

Overholtz, W. J., and Tyler, A. V. 1985. Long-term responses of the demersal fish assemblages of Georges Bank. Fishery Bulletin US, 83: 507–520.

Pikitch, E. K., Santora, C., Babcock, E. A, Bakun, A., Bonfil, R., Conover, D. O., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E. D., Link, J., Livingston, P. A. Mangel, M., McAllister, M. K., Pope, J., and Sainsbury, K. 2004. Ecosystem-based fishery management. Science, 305: 346–347.

Pingree, R. D., and Maddock, L. 1977. Tide residuals in the English Channel. Journal of the Marine Biological Association of the UK, 57: 339–354.

Queirós, A. M., Hiddink, J. G., Kaiser, M. J., and Hinz, H. 2006. Effects of chronic bottom trawling disturbance on benthic biomass, production and size spectra in different habitats. Journal of Experimental Marine Biology and Ecology, 335: 91–103.

Rees, H. L., Pendle, M. A., Waldock, R., Linpenny, D. S., and Boyd, S. E. 1999 A comparison of benthic biodiversity in the North Sea, English Channel and Celtic Seas. ICES Journal of Marine Science, 56: 228–246.

Rochet, M-J., Trenkel, V. M., Bellail, R., Coppin, F., Le Pape, O., Mahé, J-C., Morin, J., Poulard, J-C., Schlaich, I., Souplet, A., Vérin, Y., and Bertrand, J. 2005. Combining indicator trends to assess ongoing changes in exploited fish communities: diagnostic of communities of the coasts of France. ICES Journal of Marine Science, 62: 1647–1664.

Rogers, S. I., Rijnsdorp, A. D., Damm, U., and Vanhee, W. 1998. Demersal fish populations in the coastal waters of the UK and continental NW Europe from beam trawl survey data collected from 1990 to 1995. Journal of Sea Research, 39: 79–102.

Sanvicente-Añorve, L. E. 1995. Détermination des structures benthiques spatiales en Manche orientale au moyen de méthodes d’analyse multivariable et de techniques d’interpolation (exemple de gestion et de traitement d’une base de données en écologie marine). PhD thesis, Université de Paris VI.

ter Braak, C. J. F., and Smilauer, P. 2002. CANOCO reference manual and CanoDraw for windows User's guide: software for canonical community ordination (version 4.5). Microcomputer Power, Ithaca, New York. 500 pp.

Trenkel, V. M., Pinnegar, J. K., Rochet, M-J., and Rackham, B. D. 2004. Different surveys provide similar pictures of trends in a marine fish community but not of individual fish populations. ICES Journal of Marine Science, 61: 351–362.

Valette-Silver, N. J., and Scavia, D. 2003. Ecological forecasting: new tools for coastal and ecosystem management. NOAA Technical Memorandum, NOS NCCOS 1. 116 pp.

Wantiez, L., 1996. Comparison of fish assemblages sampled by a shrimp trawl and a fish trawl in St Vincent Bay, New Caledonia. Journal of the Marine Biological Association of the UK, 76: 759–775.

Webster, R. and Oliver, M. A. 2001. Geostatistics for Environmental Scientists. Wiley, Chichester. 286 pp.

Table 1. Species list of the studied community including average species abundance and standard deviation, frequency of occurrence (as % of total number of observation; *n* = 1448) and length at maturity.

Species	**Species code**	**Mean abundance (per km^2)**	**Standard deviation (as % of mean)**	**Frequency of occurrence (%)**	**Length at maturity (cm)**	**Species**	**Species code**	**Mean abundance (per km^2)**	**Standard deviation (as % of mean)**	**Frequency of occurrence (%)**	**Length at maturity (cm)**
Agonus cataphractus	AGONCAT	508	159	3.7	6.5	*Mustelus mustelus*	MUSTMUS	82	134	7.9	70
Alosa alosa	ALOSALO	66	124	1.0	40	*Osmerus eperlanus*	OSMEEPE	168	71	0.2	10
Alosa fallax	ALOSFAL	39	32	1.5	25	*Pagellus erythrinus*	PAGEERY	39	38	0.3	15
Amblyraja radiata	AMBLRAD	53	45	0.3	40	*Petromyzonidae*	FMPETRO	31	3	0.2	–
Anguilla anguilla	ANGUANG	105	103	3.5	60	*Phrynorhombus regius*	PHRYREG	32		0.1	–
Argentina sp.	ARGE	29	3	0.1	12	*Platichthys flesus*	PLATFLE	565	407	11.8	20
Arnoglossus sp.	ARNO	57	30	0.6	11	*Pleuronectes platessa*	PLEUPLA	1 060	317	43.4	25
Atherinidae	FMATHER	470	258	2.1	–	*Pollachius pollachius*	POLLPOL	338	185	4.6	–
Balistes sp.	BALI	31	0	0.1	–	*Raja brachyura*	RAJABRA	68	73	2.2	100
Belone bellone	BELOBEL	48	70	1.1	45	*Raja clavata*	RAJACLA	101	113	32.0	85
Callionymus lyra	CALMLYR	1 017	196	63.0	17	*Raja microocellata*	RAJAMIC	55	56	0.7	70
Chelidonichthys cuculus	CHELCUC	384	113	53.0	25	*Raja montagui*	RAJAMON	72	110	5.2	60
Chelidonichthys gurnardus	CHELGUR	249	394	8.7	21	*Raja undulata*	RAJAUND	49	47	3.9	–
Chelidonichthys lastoviza	CHELLAS	52	71	9.2	20	*Salmo trutta*	SALOTRU	33		0.1	24
Chelidonichthys lucerna	CHELLUC	89	118	32.4	–	*Sardina pilchardus*	SARDPIL	4 274	325	23.6	15
Chelon labrosus	CHEOLAB	28		0.1	25	*Scomber scombrus*	SCOMSCO	2 630	414	42.7	30
Ciliata mustela	CILIMUS	65	82	0.4	–	*Scophthalmus maximus*	SCOPMAX	49	67	4.6	38
Clupea harengus	CLUPHAR	8 230	275	14.0	26	*Scophthalmus rhombus*	SCOPRHO	44	53	5.2	25
Conger conger	CONGCON	42	31	0.8	75	*Scyliorhinus canicula*	SCYOCAN	683	199	56.4	55
Ctenolabrus rupestris	CTELRUP	189	99	0.3	–	*Scyliorhinus stellaris*	SCYOSTE	96	136	12.8	–
Dasyatis pastinacus	DASYPAS	44	51	2.1	–	*Solea lascaris*	SOLELAS	62	148	0.9	22
Dicentrarchus labrax	DICELAB	313	255	35.0	35	*Solea solea*	SOLESOL	376	295	16.7	25
Enchelyopus cimbrius	ENCHCIM	33		0.1	25	*Sparus aurata*	SPARAUR	30	3	0.2	–
Engraulis encrasicolus	ENGRENC	1 904	363	18.1	12	*Spondyliosoma cantharus*	SPONCAN	1 211	278	57.3	22
Gadus morhua	GADUMOR	309	325	31.3	55	*Sprattus sprattus*	SPRASPR	48 053	259	12.9	10
Galeorhinus galeus	GALOGAL	106	125	6.4	125	*Squalus acanthias*	SQUAACA	57	60	0.9	70
Hyperoplus sp.	HYPE	878	511	12.9	15	*Syngnathidae*	FMSYNGN	33	10	0.4	–
Labridae	FMLABRI	31	4	0.3	28	*Taurulus bubalis*	TAURBUB	96	95	0.5	–
Leucoraja circularis	LEUCCIR	32	1	0.1	–	*Trachinus draco*	TRAHDRA	44	63	2.5	–
Leucoraja fullonica	LEUCFUL	31		0.1	–	*Trachinus vipera*	ECITVIP	602	179	19.1	–
Leucoraja naevus	LEUCNAE	39	37	1.3	60	*Trachurus trachurus*	TRACTRA	22 544	246	96.3	25
Limanda limanda	LIMDLIM	1 932	276	42.7	19	*Trigla lyra*	TRIGLYR	71	74	1.1	30
Liza aurata	LIZAAUR	195	160	5.9	30	*Trisopterus luscus*	TRISLUS	19 230	292	34.3	20
Liza ramada	LIZARAM	56	76	0.3	25	*Trisopterus minutus*	TRISMIN	22 314	274	56.0	12
Lophius piscatorius	LOPHPIS	41	29	0.3	45	*Zeugopterus punctatus*	ZEUGPUN	30	7	0.1	–
Melanogrammus aeglefinus	MELAAEG	37		0.1	26	*Zeus faber*	ZEUSFAB	58	103	22.9	30
Merlangius merlangus	MERNMER	3 401	307	37.9	25	**Crustaceans**					
Microchirus variegatus	MICUVAR	90	127	3.5	14	*Cancer pagurus*	CANCPAG	46	54	6.1	–
Micromesistius poutassou	MICMPOU	34	0	0.1	22	*Homarus gammarus*	HOMAGAM	40	32	1.0	–
Microstomus kitt	MICTKIT	422	295	18.2	27	*Maja squinado*	MAJASQU	128	160	14.6	–
Molva molva	MOLVMOL	45	45	0.5	85	**Cephalopods**					
Mullus surmuletus	MULLSUR	538	366	47.7	15	*Loligo* spp.	LOLI	1 353	165	88.6	–
Mustelus asterias	MUSTAST	132	173	18.7	78	*Sepia officinalis*	SEPIOFF	198	205	51.7	–

Table 2. Community indicator species composition.

	Group 1				Group 2				Group 3				Group 4			
Species code	**Species level**	**Frequency of occurrence**	**Average abundance**	**Proportion immature**	**Species level**	**Frequency of occurrence**	**Average abundance**	**Proportion immature**	**species level**	**Frequency of occurrence**	**Average abundance**	**Proportion immature**	**Species level**	**Frequency of occurrence**	**Average abundance**	**Proportion immature**
CALMLYR		25%	163	70%	D2, P	68%	337	42%		89%	1 763	50%		87%	1 286	61%
CHELCUC	D1	83%	417	42%	D1	78%	399	46%		13%	127	70%		8%	117	79%
CHELLUC		15%	52	–	P	35%	70	–		43%	110	–		46%	105	–
CLUPHAR		2%	4 257	100%		2%	90	86%		24%	8 859	91%	P	48%	8 604	91%
ENGRENC		6%	343	86%		19%	2 280	93%	P	31%	2 190	95%		17%	1 233	90%
GADUMOR		19%	103	81%		23%	421	90%		35%	197	91%	P	70%	459	79%
HYPE		2%	330	–		9%	2 667	–	P	30%	465	–		14%	205	–
LIMDLIM		3%	76	75%		19%	134	65%	D1	92%	1 714	48%	D1	90%	3 265	63%
LOLI		95%	742	–		98%	1 174	–	D2, P	93%	2 406	–		47%	977	–
MAJASQU		12%	74	–		16%	127	–		9%	94	–	P	27%	202	–
MERNMER		6%	230	0%		13%	206	51%	D1	73%	2 201	56%	D1, P	94%	6 589	42%
MICTKIT		12%	61	90%		20%	95	78%		15%	297	68%	P	35%	1 188	71%
MULLSUR		41%	189	64%	P	61%	599	62%	P	53%	795	78%		23%	443	84%
MUSTAST	P	36%	120	82%		12%	165	97%		5%	117	91%		20%	143	82%
PLATFLE		1%	48	0%		1%	37	100%		21%	164	36%	P	43%	969	30%
PLEUPLA		10%	161	75%		20%	78	76%	D1	87%	660	45%	D1, P	87%	2 505	38%
RAJACLA	P	48%	107	96%		19%	64	96%		19%	101	100%	P	49%	118	100%
SARDPIL		11%	5 525	97%	P	35%	1 936	90%	P	36%	6 719	87%		4%	96	100%
SCOMSCO		12%	109	75%	D2, P	49%	2 614	57%	P	76%	3 624	50%		34%	426	50%
SCYOCAN	D2, P	93%	1 021	46%		61%	320	38%		15%	279	34%	P	44%	454	41%
SCYOSTE	D2, P	38%	101	–		3%	47	–		0%	0	–		0%	36	–
SOLESOL		3%	53	67%		1%	39	0%		18%	82	93%	D2, P	76%	551	77%
SPONCAN	D1	88%	855	62%	D1	74%	1 791	74%	P	26%	1 008	95%		14%	225	91%
SPRASPR		2%	38 271	93%		2%	1 890	97%		23%	58 239	82%	P	41%	43 084	54%
TRISLUS	P	29%	13 116	68%		9%	32 662	93%		35%	19 178	97%	D2	100%	20 658	85%
TRISMIN	D2, P	74%	24 890	70%		39%	30 982	86%		34%	18 351	88%	D2	93%	12 772	60%

D1, indicator species of 1st division level; D2, indicator species of 2nd division level; P, preferential species.

Table 3. Diversity indices and significance level differences between sub-communities.

	Group 1		Group 2		Group 3		Group 4	
Diversity	**Mean (s.d.)**	**LSD**	**Mean (s.d.)**	**LSD**	**Mean (s.d.)**	**LSD**	**Mean (s.d.)**	**LSD**
S (species richness)	10.7 (3.1)	a	10.8 (3.2)	a	13.3 (3.3)	b	16.4 (3.5)	c
H (Shannon diversity)	1.02 (0.50)	b	0.88 (0.52)	a	1.26 (0.55)	c	1.37 (0.44)	d
Eh (Shannon evenness)	0.44 (0.21)	b	0.38 (0.22)	a	0.49 (0.21)	c	0.49 (0.16)	c

s.d. = standard deviation

LSD = least significant difference; groups with different letters had significantly different levels of diversity.

Table 4. Community relation with explanatory environment variables.

	Group 1	**Group 2**	**Group 3**	**Group 4**
Hydrology	**Mean (s.d.)**			
	n = 440	*n* = 431	*n* = 376	*n* = 201
Depth (m)	44.3 (13.7)	35.0 (11.3)	22.8 (7.7)	24.6 (10.7)
Bed shear stress (N m^{-2})	1.7 (0.7)	1.1 (0.6)	0.8 (0.5)	0.8 (0.8)
	n = 234	*n* = 203	*n* = 221	*n* = 104
Surface temperature (°C)	16.0 (0.7)	15.9 (0.9)	15.7 (1.1)	15.7 (1.1)
Surface salinity	34.6 (0.6)	34.3 (0.5)	33.9 (0.8)	33.6 (1.4)
Sediment type	**% Frequency of occurrence**			
	n = 413	*n* = 403	*n* = 317	*n* = 184
Muds (M)	0	3	7	19
Fine sands (FS)	3	11	66	47
Coarse sands (CS)	22	71	21	24
Gravels (G)	40	9	3	1
Pebbles (P)	34	6	2	9
Benthic community	**% Frequency of occurrence**			
	n = 435	*n* = 427	*n* = 360	*n* = 191
Coarse sandy gravel (BenCSG)	12	34	31	23
Fine sandy gravel (BenFSG)	3	9	1	0
Pebbles (BenP)	83	48	10	23
Fine sands (BenFS)	2	3	30	32
Coarse sands (BenCS)	0	6	28	23

n: number of observations; s.d.: standard deviation.

Table 5. Summary of RDA significant variable selection procedure.

	Conditional effects			**Marginal effects**
Variable	**Lambda-A**	***F***	***p***	**Lambda-1**
Depth	0.1	161.48	0.002	0.1
BenP	0.03	49.58	0.002	0.08
BenFS	0.02	27.01	0.002	0.06
BenCS	0.01	29.19	0.002	0.03
M	0.01	17.82	0.002	0.02
FS	0.02	23.04	0.002	0.07
Salinity	>0.01	13.4	0.002	0.01
CS	0.01	14.12	0.002	0.02
G	0.01	10.65	0.002	0.04
P	>0.01	7.4	0.002	0.03
M2	0.01	7.5	0.002	0.06
BenFSG	>0.01	4.74	0.002	0.01
BenCSG	>0.01	5.51	0.002	0.01
Temperature	>0.01	4.1	0.002	0.01

Conditional effects are given in order of their inclusion in the model. lambda-A is the additional variance each variable explains at the time it was included, *F* and *p* values give the significance of the variable at that time. Marginal effects (lambda-1) list the variance that environmental variables explain singly. Bed shear stress (M2); sediment particle size: pebbles (P), gravels (G), coarse and fine sand (CS and FS), muds (M); benthic community types: pebbles (BenP), fine and coarse sandy gravel (BenFSG and BenCSG), coarse and fine sands (BenCS and BenFS).

Table 6. Variance partitioning of the fish community from 1997 to 2004 giving the relative amount of variation explained by the different explanatory compartments.

Type of analyses	**Order of analyses**	**Description of component studied**	**Sum of all canonical eigenvalues**	**Sum of all eigen-values**	**% variation explained**
PCA	a	All species variation	1	1	100.0
RDA	b	All explained variation (environment and spatio-temporal autocorrelation)	0.303	1	30.3
RDA	c	Variation explained by environmental variables	0.253	1	25.3
pRDA	d	Changing environment only, others as covariables	0.033	0.731	4.5
pRDA	e	All environmental variables without persistent environment (covariables)	0.071	0.768	9.2
pRDA	f	Persistent environment only, others as covariables	0.118	0.816	14.5
pRDA	g	Benthic community type only, others as covariables	0.022	0.72	3.1
pRDA	h	Sediment type only, others as covariables	0.032	0.73	4.4
pRDA	i	Depth and seabed stress only, others as covariables	0.014	0.711	2.0
	a–b	Unexplained			69.7
	b–c	Unrelated to pure environment			5.0
	c	All available explanatory environmental variable			25.3
	d	Changing environment			4.5
	c–(d+e)	Shared component			6.3
	f	Persistent environment			14.5
	e– (g+h)	Sediment type + benthic community type			1.8
	g	Benthic community type			3.1
	e–(g+i)	Benthic community type + depth and seabed stress			4.2
	i	Depth and seabed stress			2.0
	e–(h+i)	Depth and seabed stress + sediment type			2.9
	h	Sediment type			4.4
	f–(g+h+i)	Benthic community type + depth and seabed stress + sediment type			5.1

Unrelated to environment: variation explained by spatial (latitude and longitude) and time (year and date) autocorrelation only; changing environment: temperature and salinity; shared component: variation explained by both changing and persistent environmental variables; persistent environment: depth and seabed stress, sediment type, and benthic community type, and their shared components.

Table 7. Misclassification rates between the global classification (1988–2004) and the annual classifications obtained for each original sub-community and the associated Kendall's coefficients of correlation.

Year	**Misclassification rate**					**Kendall's τ**
	Group 1	**Group 2**	**Group 3**	**Group 4**	**All groups**	
1988	0.48	0.00	0.67	0.19	0.32	0.80
1989	0.32	0.79	0.31	0.00	0.44	0.65
1990	0.17	0.19	0.10	0.13	0.16	0.91
1991	0.54	0.17	0.25	0.00	0.30	0.78
1992	0.10	0.20	0.00	0.33	0.15	0.89
1993	0.00	0.55	0.53	0.18	0.40	0.76
1994	0.46	0.08	0.17	0.25	0.22	0.83
1995	0.14	0.94	0.52	0.75	0.61	0.60
1996	0.40	0.37	0.20	0.00	0.22	0.87
1997	0.04	0.52	0.66	0.58	0.47	0.73
1998	0.24	0.76	0.46	0.55	0.48	0.69
1999	0.14	0.16	0.15	0.00	0.13	0.90
2000	0.61	0.03	0.19	0.08	0.26	0.78
2001	0.26	0.42	0.00	0.06	0.22	0.76
2002	0.08	0.16	0.10	0.08	0.11	0.90
2003	0.00	0.48	0.30	0.33	0.25	0.85
2004	0.04	0.15	0.21	0.00	0.13	0.91
All years	0.24	0.35	0.28	0.19	0.28	0.78

Table 8. Interannual variation in diversity indices within each sub-community. Annual rates of increase (%) and *p*-values are shown.

Diversity indices	**Sub-community**				
	1 (*n* = 440)	**2 (*n* = 431)**	**3 (*n* = 376)**	**4 (*n* = 201)**	**Total (*n* = 1 448)**
Species richness (S)	0.8 **	1.1 ***	1.5 ***	2.7 ***	1.5 ***
Shannon equitability (H)	4.2 ***	3.8 ***	2.4 ***	0.3 NS	3.1 ***
Shannon evenness (Eh)	3.0 ***	2.5 ***	2.4 *	-0.6 NS	2.0 ***

p: *** <0.001, ** <0.01, * <0.05, NS: not significant (*p*>0.05).

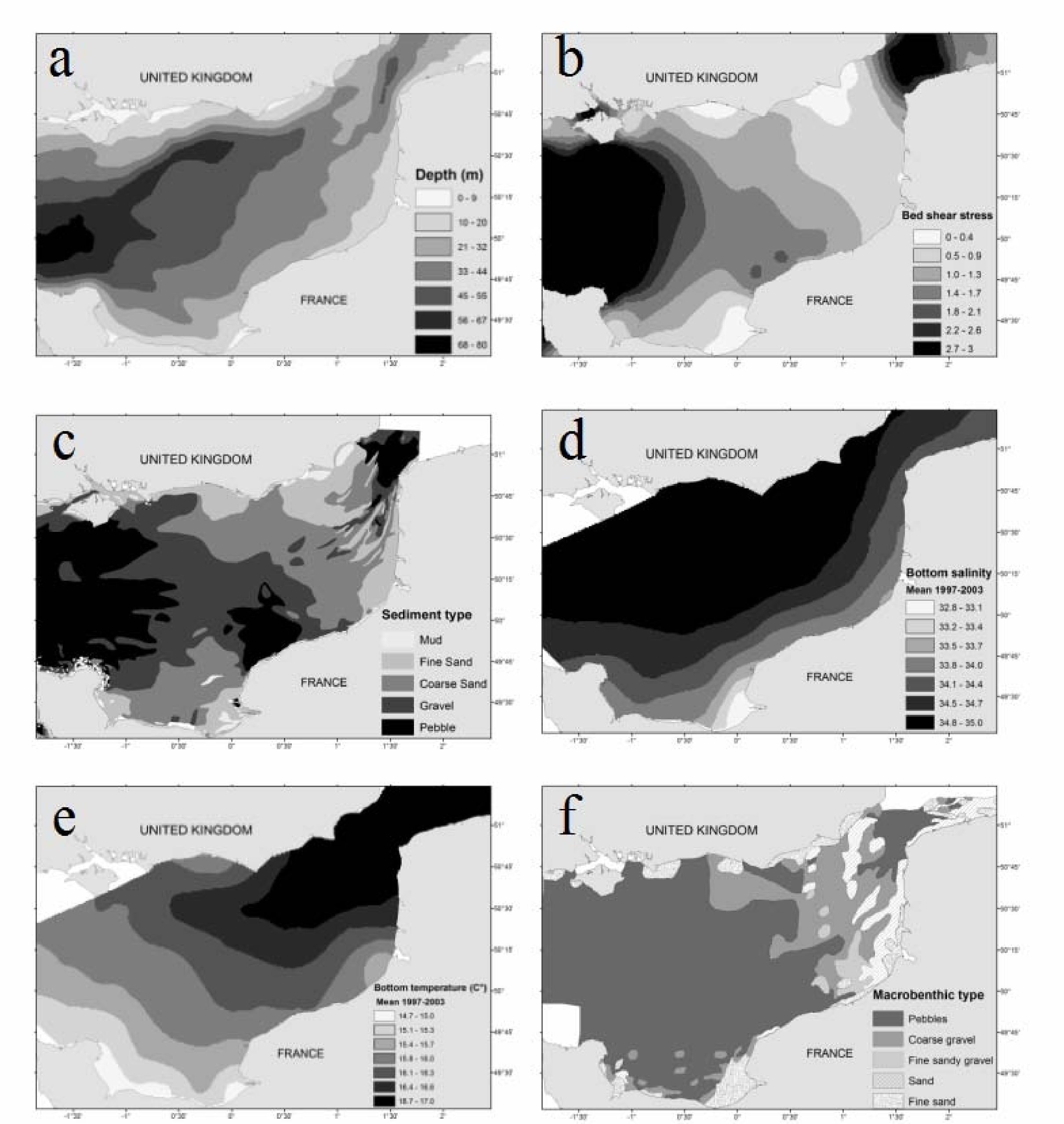

Figure 1 : Environmental maps: (a) depth and mean sea level (m); (b) bed shear stress (N m–2, Aldridge and Davies, 1993); (c) seabed sediment type (Larsonneur et al., 1979); (d) mean bottom salinity; (e) mean bottom temperature (°C); and (f) macrobenthic community distribution (Cabioch and Glaçon, 1975, 1977; Cabioch et al., 1976; Sanvicente Añorve, 1995).

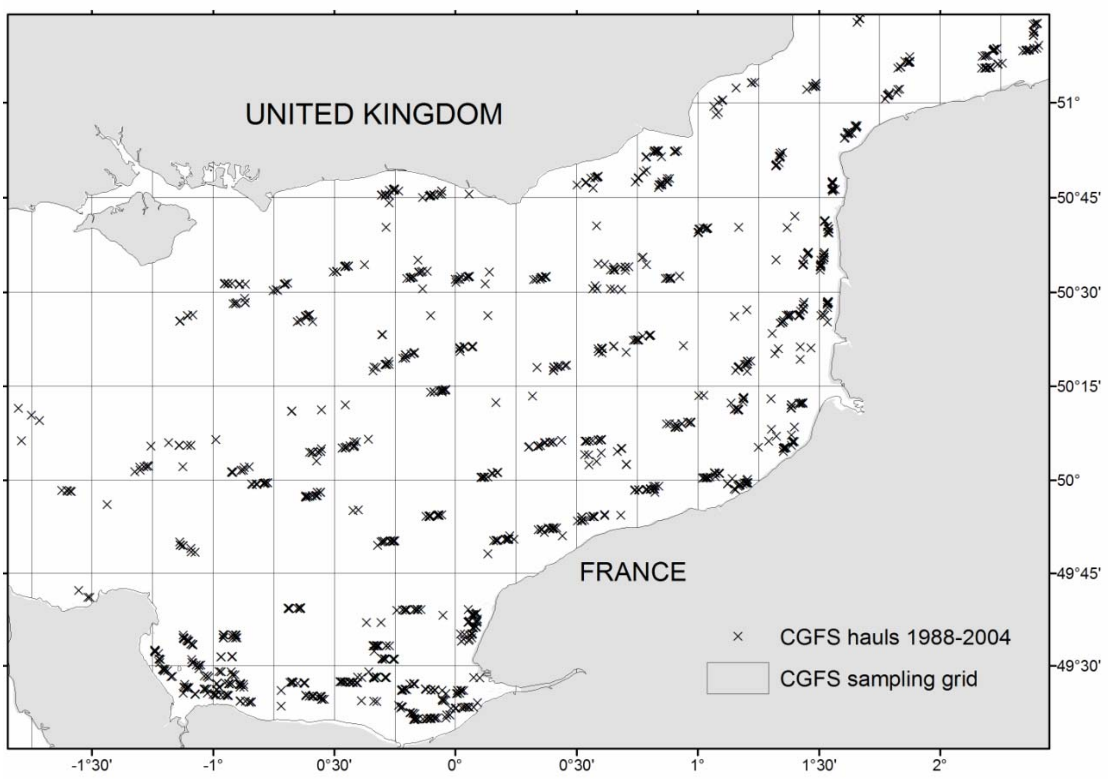

Figure 2 : Station positions for CGFS (1988–2004) surveys.

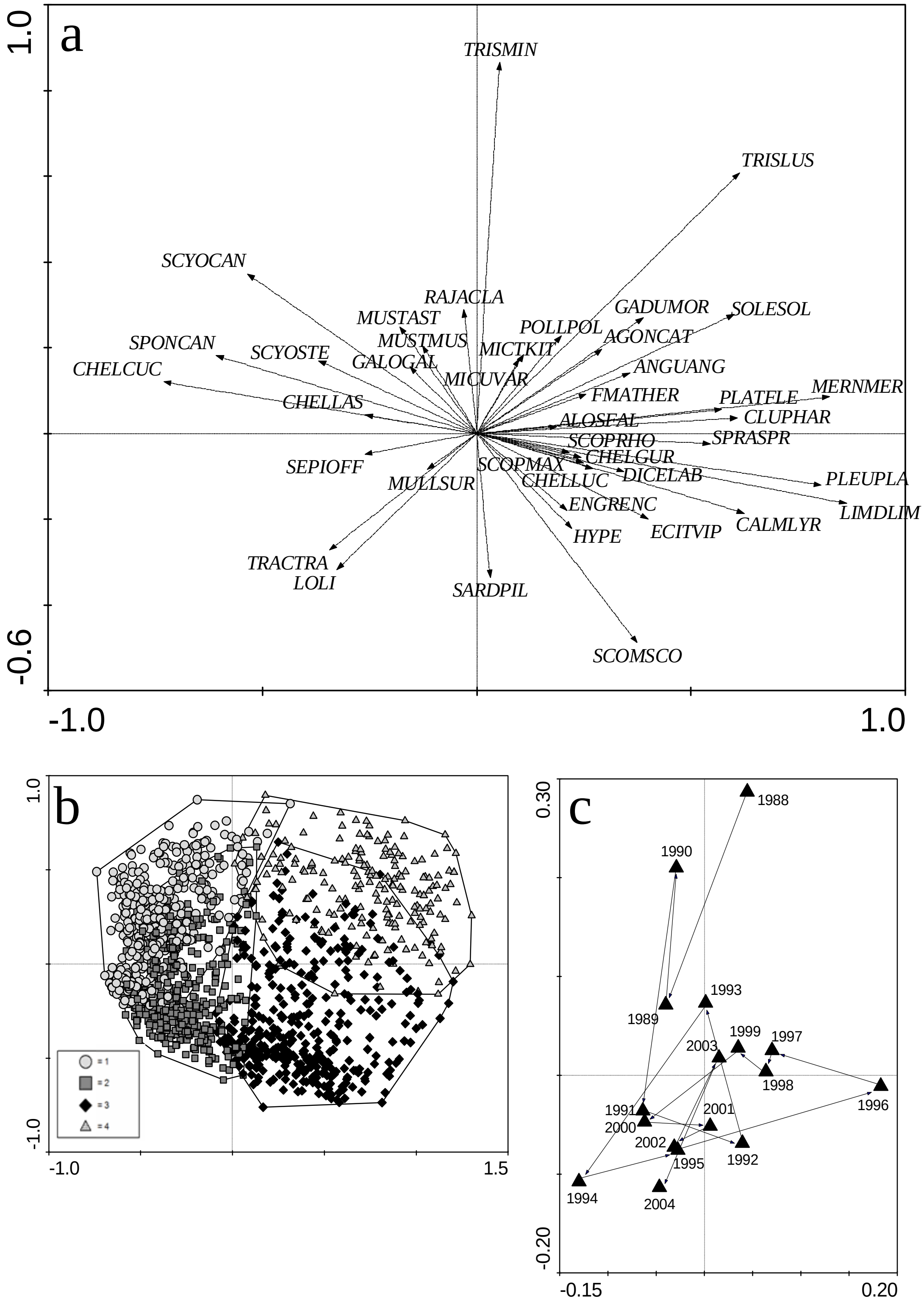

Figure 3 : Principal components analysis based on fish community abundance from 1988 to 2004: (a) Correlation bi-plot of the first two axes of species variance; (b) observations represented using the four groups defined by TWINSPAN, with envelopes delineating each group created; (c) years (nominal variables) represented passively as small triangles, linked chronologically by arrows, and located at the centroid of all observations for each year.

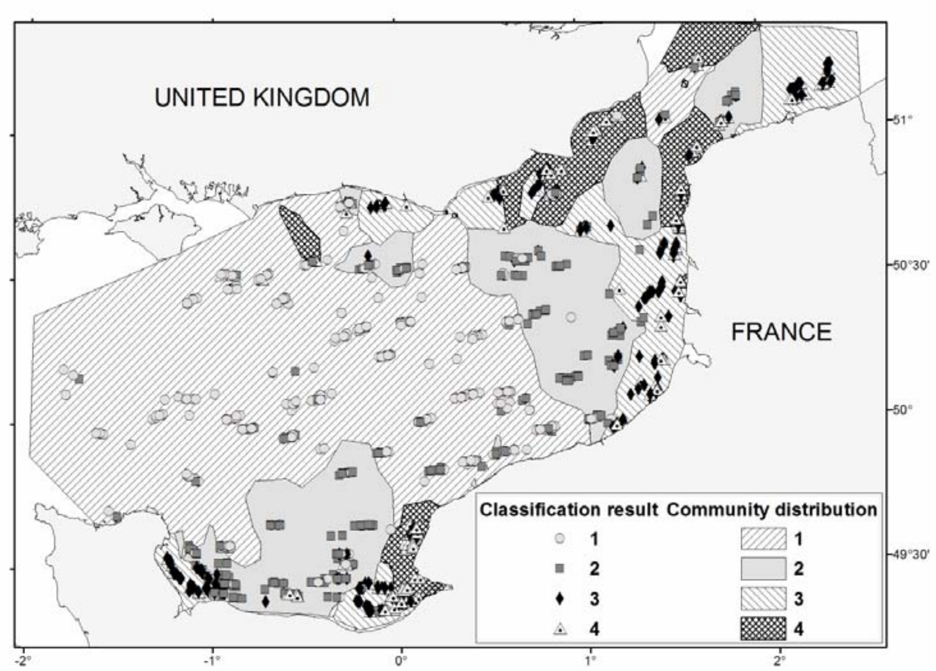

Figure 4 : Spatial distribution of fish sub-communities in the eastern English Channel from 1988 to 2004. The gradation from open sea community to coastal and estuarine communities is shown.

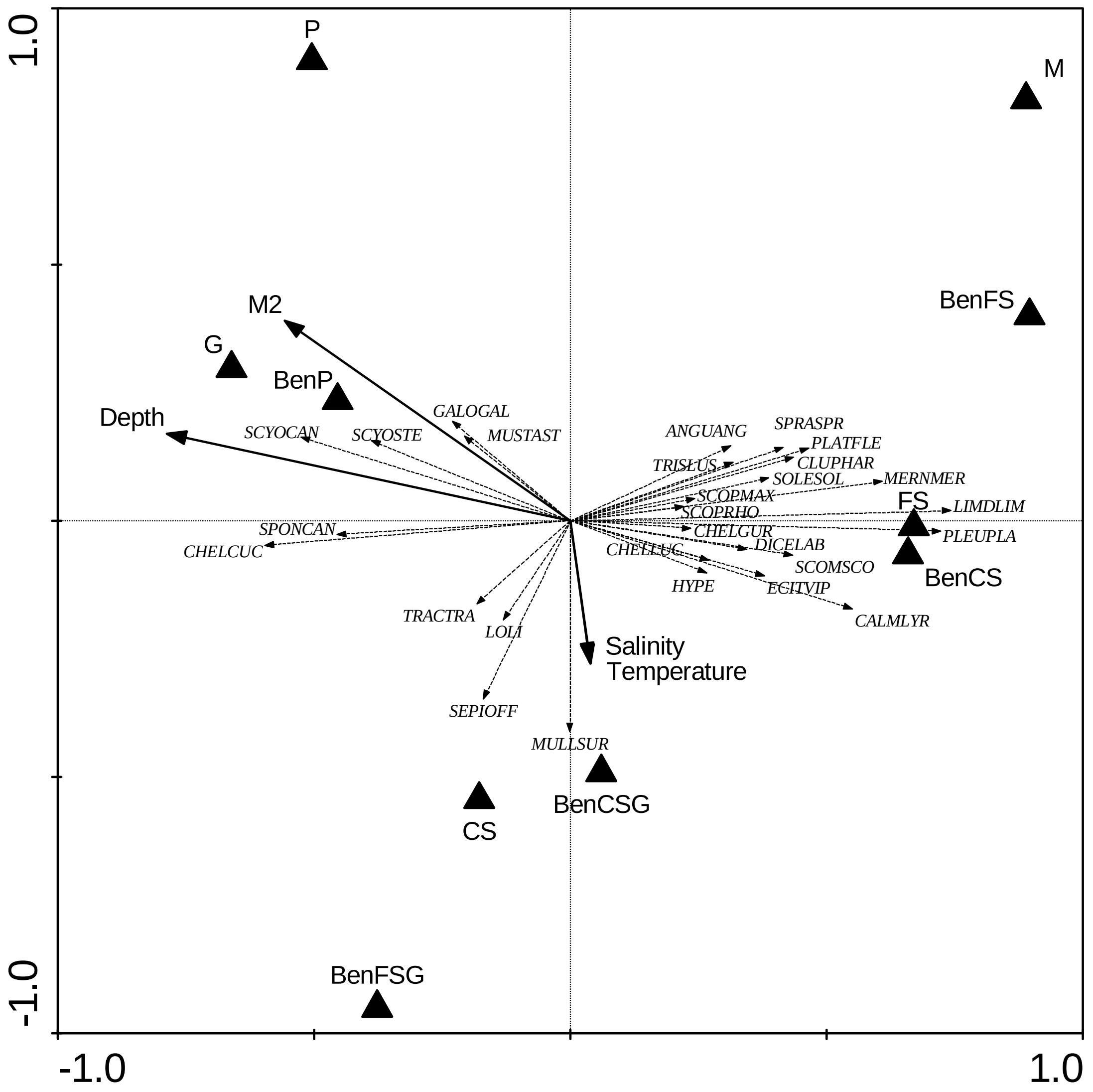

Figure 5 : RDA correlation bi-plot on species data from 1997 to 2004 constrained by significant environmental variables: temperature, salinity, depth, bed shear stress (M2); sediment particle size: pebbles (P), gravels (G), coarse and fine sand (CS and FS), muds (M); benthic community types: pebbles (BenP), fine and coarse sandy gravel (BenFSG and BenCSG), coarse and fine sands (BenCS and BenFS). Sediments and benthic community types (nominal variables) are represented as small triangles, and the other continuous environmental variables are represented by arrows.