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Eastern English Channel Fish Community from 1988 to 2003 and its Relation to the Environment

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In the Eastern English Channel, an important area for small fisheries with strong hydrodynamic features, IFREMER (French Research Institute for Exploitation of the Sea) carries out since 1988 an essential ground fish survey enabling ICES to produce annual evaluations of major commercial fish stocks. It is therefore possible to identify and describe the existing communities and to analyse their distribution patterns in disturbed areas supporting important fishery exploitation. During this autumn survey, biological data are collected on all demersal, benthic and pelagic species captured and environmental conditions are also recorded. It was therefore possible to identify and describe the existing communities observed from 1988 to 2003 in the Eastern Channel and to relate them with physical and hydrological features. Multivariate (canonical analyses) and spatial analyses (geostatistical analyses) were used to explore and illustrate the community composition, diversity and spatial structure based on 90 observed species and 1326 haul trawls and revealed their relationships with the environment and their evolution through time. Four sub-communities could be identified with varying diversity levels. The sampling depth, salinity, temperature and the sediment nature were all significantly correlated to the community structure. The study also revealed significant inter-annual community variations but no clear shift in its composition could be distinguished over time with the exception of a few species in particular Striped red mullet (*Mullus surmuletus)*. This species exhibited a significant abundance increase since the late 1990's and this result may confirm recent fishery observations relating marked increases in this species catch. The diversity levels of the community seemed to have increased over the last decade and to be favoured in area with soft sediment type with important temperature and salinity variations, typically, coastal river plumes and estuaries.

Key-words : Eastern English Channel, Fish Community Analyses, Diversity, Spatial Patterns

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Introduction

The English Channel is an international area of multi-specific fisheries and as in many other places, there is growing need for "ecosystem based" assessment and management of fish stocks and assemblages (Jennings and Kaiser 1998; Garrison, 2000, Guitton *et al*. 2003) . This requires an improved understanding of the ecological mechanisms controlling the community composition and the population dynamics of exploited stocks. In continental 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 where co-existent species are likely to interact strongly with one another. These sub-communities may have distinct trophic structure, and may respond differently to human activities, environmental variation, or changes in food resources (Garrison, 2000).

The English Channel constitutes a marine corridor between England and France and is characterised by a contrasted and heterogeneous environment (Fig. 1). The eastern English Channel is limited by the Dover strait to the East and the Cotentin peninsula in the middle of the Channel, which constitutes a physical and hydro-climatic barrier. This part of the continental shelf is shallow (40 to 100m) and its hydrology is marked by a west to east general circulation disrupted by strong tidal currents. Temperature conditions may vary from 7 to 17°C and is identical at all depth due to shallowness and strong seabed currents. The seabed nature is very heterogeneous with a vast pebbly area from the Cotentin to the isle of Wight while sands and gravels are most prominent in the rest of the Eastern Channel. Along the French coast, fresh waters from the Seine and the Somme rivers give rise to the "coastal flow" where low salinity waters are maintained along the coast and pushed eastward toward the strait. On the English coast, fresh water inputs are mostly due to the Solent river to the west and the Thames river to the east.

The whole area is also subjected to continental influence which strongly impacts on the marine ecosystem enabling both temperate Atlantic (such as anglerfish or hake) and boreal North Sea species (cod or whiting) to co-exist. In this area, the species assemblages are therefore strongly structured by environmental variations isolating geological, hydrological and biological units at lesser scale (Pingree & Maddock, 1977, Guitton *et al.*, 2003). Most commercial species of the European waters are represented in the Channel which is characterised by a large specific (flatfish, gadidae, skates and dogfish, crustacean and cephalopods) and functional diversity (benthic, demersal and pelagic). Some species are resident in the Channel, some are seasonal due to their migration or reproduction cycle but most have a larger distribution and may be found in adjacent seas. The diversity and abundance of the fauna makes the Eastern English Channel an important fishery area and is linked to the high benthic animal abundance acting as food source for many fish species (Nival, 1991).

Since 1988, the IFREMER Fisheries laboratory in Boulogne-sur-Mer (France) is carrying out in the Eastern English Channel a yearly bottom trawl survey, named CGFS (Channel Ground Fish Survey). The main aim is to obtain biological data to estimate, directly and by age-groups, the abundance and the recruitment of species of commercial interest. Thus, whiting and plaice abundance indexes are provided to the International Council for the Exploration of the Sea (ICES) stock assessment of round and flatfish. Meanwhile, data on all species (demersal, benthic and pelagic species) encountered during the survey are systematically collected, as well as the associated hydrological parameters being recorded. This survey hence provided the data required for a multivariate study of the structure of the Eastern Channel Fish community in relation to its environment and its evolution over time.

Methods

Survey design

Since 1988, the CGFS survey takes place every year in October on board the N/O Gwen Drez and prospects the Eastern English Channel and the southern North Sea. The area is divided into 15' by 15' rectangles and at least one 30 min trawl haul is carried out in each rectangles at the average speed of 3.5 knots. The systematic sampling schemes aims at the achieving 90 to 120 stations depending on weather conditions.

Fish sampling

A large vertical opening bottom trawl with 10 mm mesh size is used and the haul is preferably performed against the current's direction. This fishing methodology is standardised to obtain a table and comparable specific diversity and species assemblage list as complete as possible. After each haul, all captured species are sorted, identified, weighted, counted, measured and the main exploited species' otolithes and scales are sampled. The abundance indices at each station are standardised into density per km².

Hydrological data

During each fishing operation, the bottom depth is recorded at each station and the shoot and haul are recorded using GPS to compute the haul distance. Since 1997 a Micrel hydrological probe records bottom temperature and salinity every 15 secondes.

Seabed sediments

The sediment type is obtained from the Larsonneur *et al.* (1979) map by re-sampling it at trawl haul locations using the GIS Arcmap software. The original sediment types have been simplified into 5 classes and include by decreasing order of size, pebbles, gravels, biolithoclastic sand, lithoclastic sand and muds.

Geostatistics

Geostatistics embodies a suite of methods for analysing spatial data. It is basically a methodology for estimating the values of a property of interest at non sampled locations from more or less sparse sample data points. Geostatistical estimation is known by the general term kriging. It is different from other interpolators because it uses a model of the spatial variation – the variogram. The latter is the central tool of geostatistics and is essential for all of the other geostatistical methods (Webster and Oliver, 2001). Geostatistical analyses were used extensively to produce environmental maps in particular temperature and salinity maps obtained during the surveys. These analyses will not be detailed in this paper but the resulting maps will be used to illustrate the link between the community and its environment and to support the discussion.

Diversity indices

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.

S = number of 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).

$$\text{Shannon Index} = H' = -\Sigma p_i \log_2 p_i$$

where p_i is the percentage cover of the i^{th} species.

$$\text{Shannon Evenness} = E = H' / H_{max}$$

where *Hmax* is the maximum diversity that could possibly occur if all the species were equally abundant, $H_{max} = log_2 S$ and *S* is the number of species.

Community statistical analyses

Data transformation and univariate analyses

Abundance data were transformed to reduce their skewness (> | 1 |) and due to the occurrence of null values in species abundance data the $Log_{10}(X+1)$ transformation was preferred (Legendre and Legendre, 1998). Environmental variable displayed normal distribution and were not transformed. Sediment types were recoded as dummy variables (binary coding). Biplots, boxplots and standard statistical analyses such as ANOVA or linear regression were used to test or illustrate some univariate results.

Multivariate Analyses

Classification and ordination are the two main groups of techniques for the multivariate analysis of community data in ecology. They can describe and recognise patterns in species distribution, define communities and their distribution in relation to environmental factors and gradients.

Classification

The method TWINSPAN (Two-Way INdicator SPecies ANalysis) (Hill *et al.*, 1975) combines ordination and clustering and it is widely used in vegetation science to classify species-by-sample data. It is a hierarchical divisive algorithm based on a correspondence analysis of the original (site x species) data matrix, which attempts to summarise the major trends in the data and is also known as a dichotomised ordination analysis. Sites are divided in two groups based on their signs along the first ordination analysis axis. Each species is then given an 'indicator value' that measures its fit to the group it has been assigned to, and each site is given an indicator score, calculated from the species indicator values. This division is made more distinct by using the sample scores and another 'indicator ordination' is calculated, based on the most distinct taxa to identify the 'indicator species' of each group. Once the data have been divided into two groups, the analysis is repeated and these are further subdivided until the group size reaches a set minimum (Maddy and Brew, 1995). The reciprocal ordination of the species on sites in the TWINSPAN procedure is necessary for the assembly of a species x sample table that is reorganised to provide information about the dichotomies and the indicator species in each class. This final table gives both a classification and an ordination of the data, from which a dendrogram can be constructed (Legendre and Legendre, 1998). The TWNSPAN procedure was used to define different sub-communities based on the species data collected during the CGFS surveys from 1988 to 2003.

Ordination

Principal Components Analysis (PCA)

Principal components analysis (PCA) is an indirect gradient analysis using a linear response model which is a simple approximation of the species response along an environmental gradient (Leps and Smilauer, 1999). The analysis is based on either the covariance or correlation matrix. The covariance matrix is usually used for species data, whereas for environmental data measured on different scales, the correlation matrix is used, because it effectively standardises the data (Maddy and Brew, 1995; ter Braak and Smilauer, 1998). 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,* enabling their passive representation on a biplot (Legendre and Legendre, 1998). This method was used to explore the community structure and the correlation of its main gradients of variation with the potential explanatory variables.

Redundancy Analysis (RDA)

Redundancy Analysis (RDA) is a direct extension of multiple regression to the modelling of multivariate response data (Legendre and Legendre, 1998). This technique considers simultaneously the linear relation between multivariate primary and explanatory (canonical) variables. It is a constrained version of PCA, in that the ordination axes are constrained to be linear combinations of the environmental variables (Maddy and Brew, 1995). This method was used in combination with Monte-Carlo permutation tests to explore the multilinear relationships between fish community and its environment.

Testing the effect of explanatory variables and extracting it

The statistical significance of the relationship between the primary (species) variables and the explanatory (environmental) variables was evaluated using Monte-Carlo permutation tests (ter Braak and Šmilauer, 1998). In the Monte-Carlo permutation test, the reference distribution is simulated by repeatedly permuting the samples. Therefore, the explanatory data are reshuffled and randomly assigned to the primary data set. A statistical test (F-ratio) is computed for the original data and compared to those of each permuted data. Let m, be the number of permutations where the F-test was higher in a random permutation than in the original data, and n, the total number of permutations. The value of the significance test p is the probability that the response is independent from the tested explanatory variable and is calculated as follows:

$$P = \frac{1+m}{1+n}$$

If the variable tested was found significant, it is added to the model and its explained variation is removed from the test of remaining variables. Relevant variables are added successively to the model in order of decreasing contribution (and often significance). Stepwise forward selection is useful for identifying a relevant and sufficient subset of explanatory variables to represent the relation between species and environmental variables (ter Braak and Smilauer, 1998).

There is a need sometimes to extract the variation explained by one set of explanatory variables to analyse the remaining variation. This is done by partial analysis, where the variation explained by the covariable (i.e the variable whose effect should be partialled out) is extracted before a constrained ordination is performed (Leps and Smilauer, 1999). The covariables are often explanatory variables for which the effect is of no interest and this method was used to test whether the detected patterns were independent from inter-annual variation.

Results

Community classification

TWINSPAN classification was computed based on the community abundance data and a dendrogram was produced to represent the results (Fig. 2). The classification process was halted at the second level of division and four sub-communities were defined. The first group included preferentially sharks (dogfish and skates), which were also its indicator species.

Groups 2 and 3 were similar and both included cephalopods, pelagic and demersal species of fish but with different preferential levels. The second group was indicated by mackerel and dragonet species and also included a few preferential pelagic and cephalopods species. Group 3 however was only indicated by squids species and preferentially included pelagic species. The fourth group included flatfish such as sole (*Solea solea*), plaice (*Pleuronectes platessa*) and dab (*Limanda limanda*) but also herring (*Clupea harengus*), whiting (*Merlangius merlangus*) and bib (*Trisopterus luscus*).

The species richness increased from group 1 to 4 (Fig. 3) and a similar pattern was observed when using Shannon index. These patterns were tested using ANOVA and were found to be significant (p>0.001) for both diversity indices. The community evenness however displayed slightly different pattern. The first two groups had similar evenness levels and this may indicate that the diversity differences between groups were due to environmental differences and probably not to inter-species competition. However, they had significantly lower evenness than groups 3 and 4. This indicated that there was a marked increase of dominance of a few or one single species in the first 2 sub-communities.

The sub-community groups were assigned to their corresponding trawl haul positions and showed strong spatial patterns. For illustration purpose, the group levels were treated as continuous variables and spatial interpolation was used to produce a distribution map of the four fish sub-community using GIS (ArcMap) (Fig. 4). The four sub-communities appeared to form a transition from open-sea (group 1) to very coastal and even estuarine locations (group 4) and the community type changed gradually over space.

Community relationship to the environment

A PCA was performed on the community data and environmental variables were projected passively after axes extraction (only the first two axes are represented in Fig. 5). The first axis was associated with a drift in the four subcommunities define by TWINSPAN (thumnail biplot). At each end of this axis, indicator species of group 1 (*Aspitrigla cuculus, Scyliorhinus stellaris, Scyliorhinus caniculus, Spondyliosoma cantharus)* and 4 (*Trisopterus luscus, Pleuronectes platessa, Merlangius merlangus, Limanda limanda, Callionymus lyra)* can be found. Interestingly, sampling depth and sediment particle size (pebbles, gravels, biolithoclastic, lithoclastic sands and muds in decreasing size order) seemed also correlated with this axis. The four types of community seemed strongly structured according to both sediment type and depth. Community drifted from type 1 to 4 with both decreasing depth and sediment particle size. The relationship with temperature and salinity was not clearly identifiable on the first two axes projection plan.

In order to test the significance of all the variable to the community structure, a RDA was performed and Monte-Carlo permutation were computed for all explanatory variables. All the available variables were significantly (p<0.002) correlated to the community structure. The community data and related environmental variables were projected in the plan of the first two axes (Fig. 6). The same pattern observed in the previous PCA was found with the first axis being strongly correlated to depth and sediment types. Here again, the community drift from type 1 to 4 (thumbnail biplot) could be observed with both decreasing depth and sediment particle size. The increasing temperature and salinity gradients were correlated with the second axis over which the community structure also changed from type 1 to 4. The sample position in the plan of the first two axes were stratified along the second axis probably due to inter-annual temperature variation. Cephalopods (*Loligo spp*, *Sepia spp*) and Red Mullet (*Mullus surmuletus*) were strongly correlated to the temperature and salinity gradients.

This would indicate that these species abundances may particularly be affected by variations in these two variables. Geostatistical analyses of the survey temperatures enabled the production of accurate interpolated maps (kriging) and a standard deviation map reflecting the areas with the greatest inter-annual temperature variation (Fig. 7). These were mostly located along the French coast and corresponded with distribution areas of the groups 2, 3 and 4 (Fig. 4).

Inter-annual variation et evolution of three species abundance over time

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 inter-annual variations, although this variable alone explained little of the over all community variation (λ_1 = 2.8 % of species variance).

A close examination of the resulting biplot revealed that although most species experienced inter-annual abundance variation, only few species were correlated with a true time trend. These were red mullet (*Mullus surmuletus*), spider crab (*Maia squinado*) and piper gurnard (*Trigla lyra*) (Fig. 8). Red mullet and spider crab abundance seem to have increased over the last decade but *Trigla lyra* was not observed since 1990. These bivariate trends were tested using ANOVAs and were found to be significant (Table 1).

Removing inter-annual effect

Based on the previous result, it was important to know how much of the community structure was the result of possible change in the environment over time. A partial RDA using year as covariable revealed that the previously tested environmental variables were still significant (p<0.002 for all variables). This tended to show that the community relationship to its environment was independent from inter-annual variation. Although this result was not surprising for variables such as depth and sediment types that are intrinsically independent from time, it was more surprising that the effects of salinity and temperature on community structure are independent from yearly variation. The hydrological effect on community patterns seemed to remain stable over time.

Diversity evolution over time within each community class

The species richness of the Eastern Channel fish community observed in trawl hauls was found to have significantly increased from 1988 to 2003 (Fig. 9). Moreover, this increase was observed in all four sub-communities and was found to be significant by ANOVAs (Table 2). This was although mostly the case for Shannon equitability and Evenness indices with the exception of group 3 and 4 which equitability and evenness values appeared to be independent from time trends. This surprising results revealed the general increase of species diversity in the Eastern English Channel over the last 16 years.

Discussion

Community structure, diversity and environment

The community in the Eastern English Channel was strongly structured spatially and clearly resulted from important community response to the environment. The four sub-communities defined by the TWINSPAN classification seemed to reflect inshore to offshore gradient in its assemblages. The classification first resulted into two distinct and opposed groups. One was characterised by hard sea-bed species (black seabream, red gurnard and selachians), the other by soft sediment species (flatfish, whiting). In the Eastern English Channel, coarse sediments are constituted by gravels and pebbles which can be encountered at greater depth in more oceanic areas (higher salinity and temperature in Autumn). Muddy and sandy sediments, on the contrary are found in coastal shallow waters with lower salinity and winter temperature. Lower temperature and salinity in coastal areas are observed in Autumn and Winter in this area due to water shallowness and colder fresh water inputs from rivers and autumn rainfalls.

The first sub-community (group 1) was characterised by higher abundance of dogfish (*Scyliorhinus stellaris, Scyliorhinus caniculus)*living offshore. These species live at greater depth than other species and prefer gravely and pebbly sea-beds or sometimes bio-lithoclastic sands. This is characteristic of thornback ray and lesser spotted dogfish which have a greater distribution area than other selachians types. However, this pattern may be altered by species like the greater spotted dogfish whose catches are mostly composed of coastal juveniles found on coarse sediment types. Some large individuals may be encountered in the western central area of the Eastern Channel. This species assemblage did not respond strongly to temperature or salinity changes as these remain stable in their area of distribution. Their diversity levels were lower than the rest of the community.

The group 2 sub-community was characterised mainly by dragonets and mackerels (*Callionymus lyra,* Scomber scomber) but also red mullets, pilchards, squids and cuttlefishes (*Mullus surmuletus, Sardina pilchardus, Loligo spp, Sepia officinalis*) living nearer the coast and at lower depth than the first group. This sub-community which lived on finer sediment types and did not respond greatly to temperature and salinity changes, had higher diversity levels than the first group. In this classification, cuttlefish often occurred in group 2, transitional between coastal and open sea areas. Cuttlefish prefer sandy sediment types to muddy to coarser types and their belonging to this group may be explained by their slow migration flow in October, as they return to their over-wintering deeper areas in the central trench of the western channel after a temporary stay at intermediate depth (20-30m). In spring they leave the deep waters of the Western Channel to reproduce in shallow muddy estuarine areas such as the Mont Saint Michel and the Somme bays (Boismery and Boucaud-Camou, 1991). Their membership to this species assemblage is therefore very seasonal and may not be found at other period of the year.

The third group was yet more diverse than the two first ones and it was distributed even closer to the coast, mostly on sands. The assemblage seemed to respond to temperature and salinity changes which are important in these areas due to shallower waters and river plumes. This sub-community was mostly characterised by squids which can also be found in the preferential species list of the group 2 along with sardine, mackerel and red mullet. In the third group, another pelagic species the horse mackerel was also an indicator species. Therefore groups 2 and 3 are fairly similar, probably revealing an ecological continuum within the community structure. In this assemblage, however, squids were the reference species and regrouped both European (*Loligo vulgaris*) and veined squids (*L. forbesi*) whose distribution are different. The first is distributed in the north-east of the area and the latter in the south-west. Their cumulated area of distribution covers most of the Eastern Channel and were thus classified in both the groups 2 and 3. These semi-pelagic species were probably less likely to be caught at greater depth by a bottom trawl and are very sensitive to variations of water quality and hydrological conditions along the coasts where they appear to be less abundant. This probably explains why they were absent of both groups 1 and 4. The simultaneous presence of red mullet in groups 2 and 3 may be the result of the expending geographical distribution that this species has exhibited since 1997 even in very coastal areas where juveniles can now be found in large quantities.

The fourth group corresponded to flatfish and other demersal fish, mostly juveniles, with a strong affinity with muddy sediments and low depth. These were mostly found on the coast, close to large river estuaries and subjected to important salinity and temperature variations. Possibly resulting from this potentially heterogeneous environment (both in space and time), this sub-community type was the most diversified.

Community evolution over time

The community relationship to its environment was remarkably stable over the 16 years of observation. Still, the community structure changed significantly over time without detectable trend just as did the temperature and salinity. The community is so strongly structured by its environment that it may reflect inter-annual climatic variations although no pattern can be distinguish over this period of time. Only three species displayed a significant abundance evolution over time: red mullet (*Mullus surmuletus*), spider crab (*Maia squinado*) and piper gurnard (*Trigla lyra*). Spider crab and piper gurnard abundance were low and did not accounted for much of the community variation. However, red mullet constituted both a significant member of the community as well as an increasingly important commercial species. Both survey and fishery data confirmed that the Red mullet distribution had increased since 1997 and its abundance seems to peak in the Eastern English Channel in Autumn (Guitton *et al.*, 2003) although it is its northern distribution limits. Guitton *et al.* suggested that this abundance increase could have resulted from sea-water temperature increase in the 1990's but this was not confirmed in this study in which hydrological recording only started in 1997. For this species, both biotic interaction (decreasing competition from other species and recent increase in fishery pressure) and confusion between mature and juvenile fish (for which habitat requirement may be different) could be responsible for the observed pattern. More detailed study is required to fully explore this pattern.

The specific diversity increase is not due to a general diversity level increase in the area. Indeed, a few anecdotic species appeared in the catch since 1998 :

- At least one individual of *Alosa fallax* was caught each year since 1998.
- *Arnoglossus laterna* and Labridae were first found in 1990 then almost every years since 1997
- The occurence of *Pagellus acarné* from 1999 to 2001

In parallel, two species have disappeared from the catches:

- *Squalus acanthias,* since 1999
- *Chelidonicthys lyra*, since 1991

This pattern of diversity increase may be due to an increased presence and larger geographic distribution of some species in the Eastern English Channel. It did not result from the appearance of new species in the area for which the catches are invariably very low nor did it result from a change in the survey design. It may simply reflect the increase co-existence of species at the 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 smaller scale. The impact of fisheries in this area under high exploitation pressure may also be questioned as to its role in the change of species dominance (particularly of predators).

Conclusion

For further community studies it may be useful to dissociate juveniles from mature fish in the analyses. Indeed, red mullet (*Mullus surmuletus*), as a result of important abundance variation between age groups 0 and 1+ living at sensibly different depths and on different sediment types, should be studied in more detailed to investigate in detail the expansion of its geographical distribution since 1997. Similarly black Seabream (*Spondyliosoma cantharus)* juveniles tend to remain on coastal muddy areas until maturity where they move towards their spawning grounds made of pebbly and gravely sea-beds (Soletchnik, 1983).

The strong relation between the environment and the community structure makes it possible to model and predict sub-community distribution from environmental parameters. Habitat Suitability Index approach, linking statistical modelling to GIS mapping 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 the trophic relationships or biotic interaction) an acceptable prediction of the community type (Vaz *et al.*, 2004).

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Tables

Table 1 ANOVA exploring the evolution of *Mullus surmuletus*, *maia squinado* and *Trigla lyra* abundances over time.

n = 1326	Mullus surmuletus	Maia squinado	Trigla lyra
F-value	75.04	62.21	50.09
Significance level	***	***	***
Evolution trend	increase	increase	decrease

*** p<0.001

Table 2 ANOVA exploring inter-annual variation of diversity indices within each sub-communities. F-values and significance levels are shown.

Sub-community Types	Species Richness (S)	Equitability (H)	Evenness (E)
Group 1 (n = 480)	10.21 **	39.84 ***	30.59 ***
Group 2 (n = 320)	13.57 ***	18.13 ***	12.63 ***
Group 3 (n = 333)	22.60 ***	7.34 **	3.17 NS
Group 4 (n = 190)	103.72 ***	1.65 NS	1.41 NS

*** p<0.001, ** p<0.01, NS: Not Significant (p>0.05)

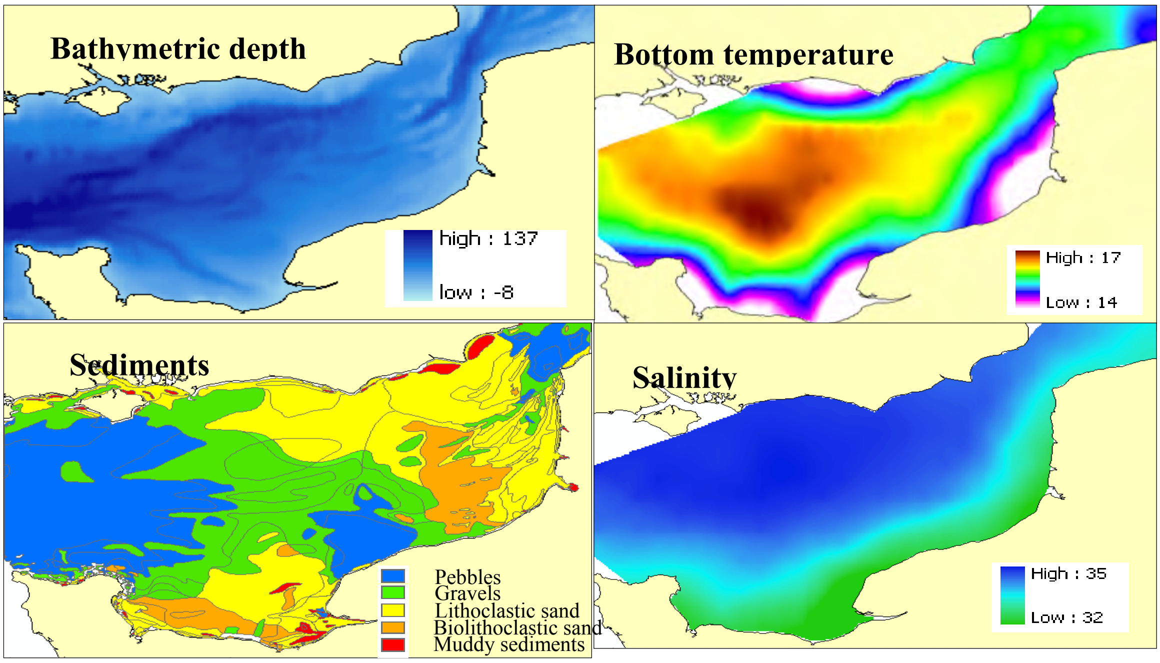

Figure 1 Eastern English Channel physical and hydrological features: Bathymetric depth and simplified sediment types representation. Survey bottom temperature and bottom salinity (averaged for 1997 to 2003) obtained by kriging.

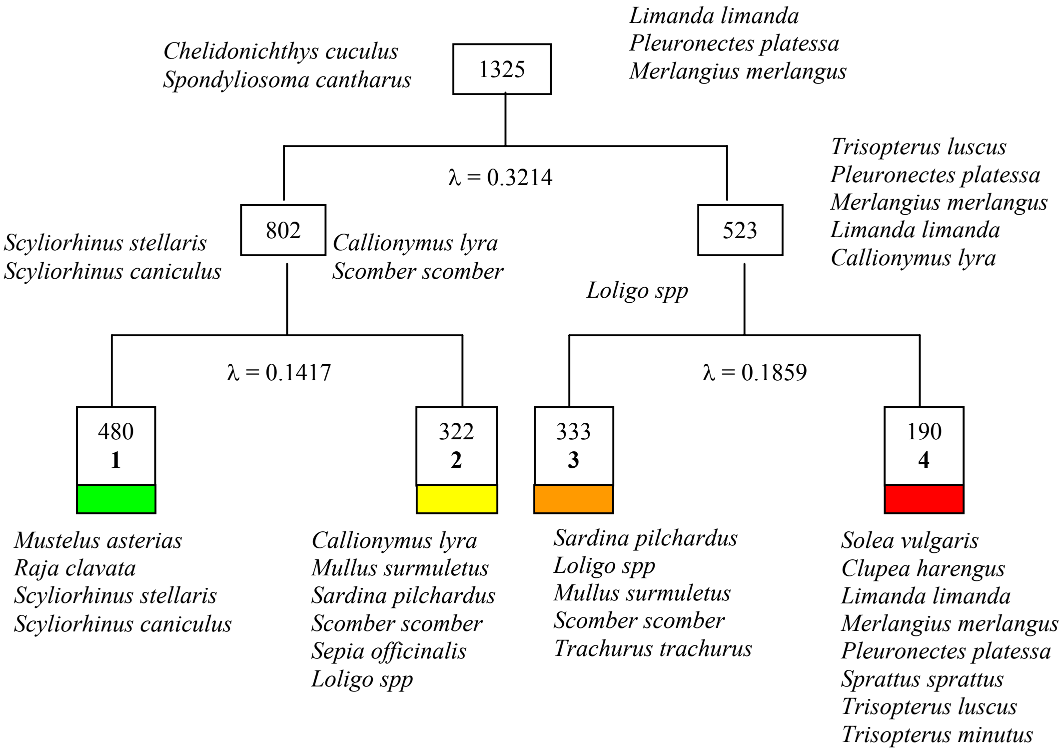

Figure 2 TWINSPAN Classification of Fish Community : the dendrogram represents the first two levels of division. DCA first axis eigen-values are represented for each division and for each group, the corresponding indicator species are given. The number of samples in each sub-group is indicated in the boxes. The preferential species of the four sub-communities are listed at the bottom of the dendrogram.

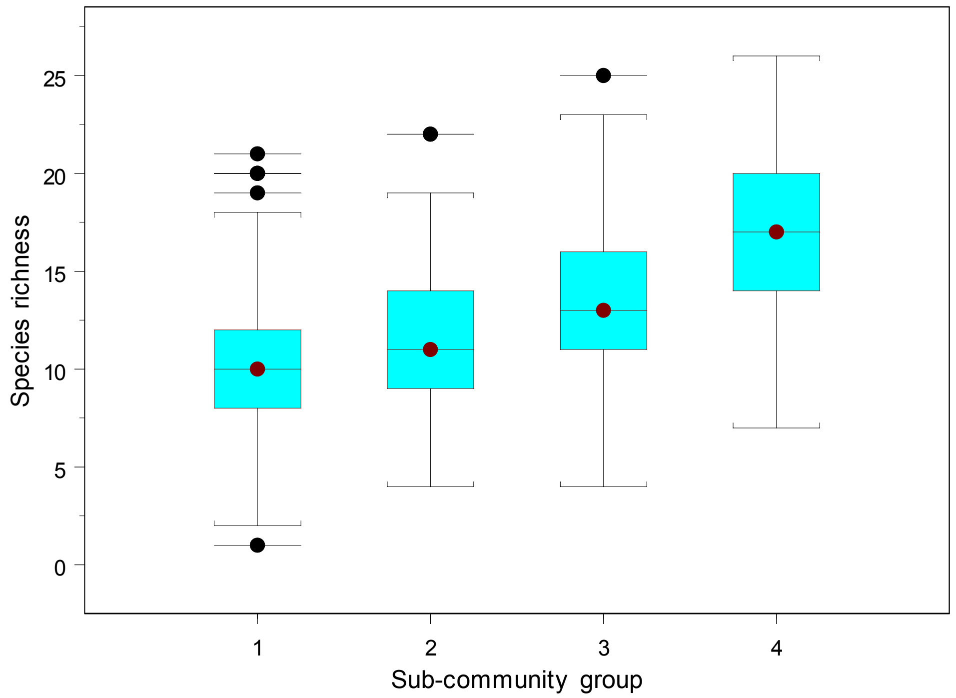

Figure 3 Boxplot representation of species richness levels in the four sub-community groups. The diversity level increased gradually from group 1 (sharks) to 4 (flat fish) (F = 192.0142, p<0.001).

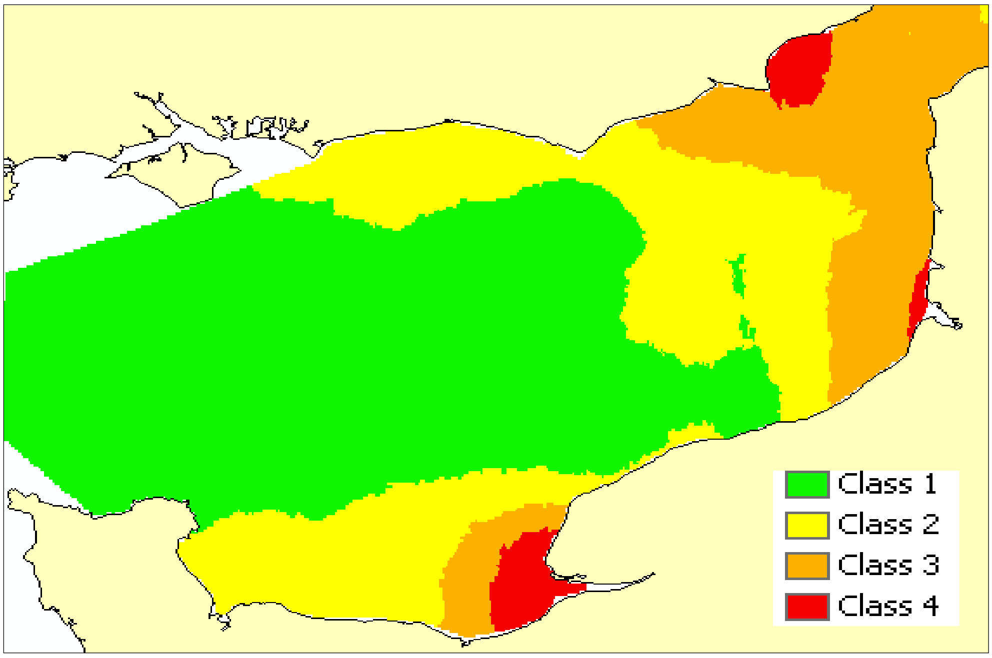

Figure 4 Spatial distribution of Fish Subcommunities in the Eastern Channel from 1988 to 2003. This illustrates the gradation from open sea community to coastal and estuarine communities.

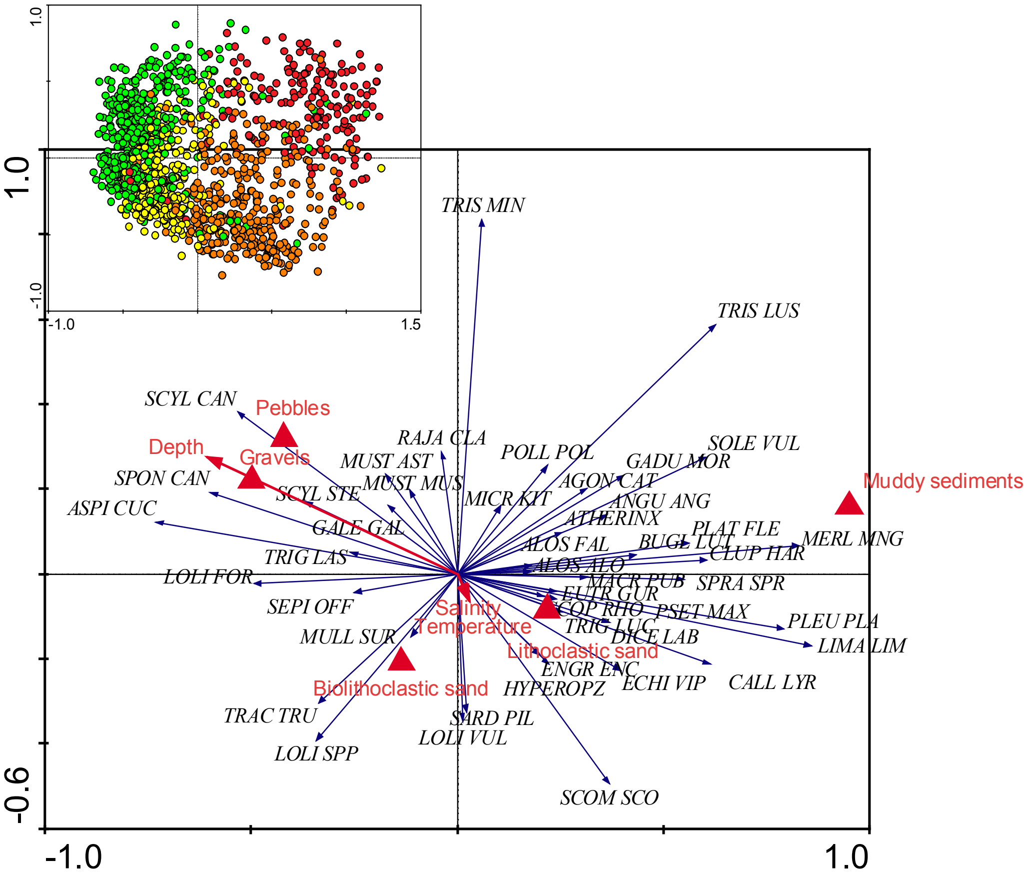

Figure 5 This PCA is based on a covariance matrix. The scaling focus on inter-species correlation and the scores are standardised after axes extraction to produce a correlation biplot where the length of arrow is a measure of fit with the ordination diagram. Species with poor fit with the projection (<3%) have been removed from the figure. Sediments category (nominal variables) are represented as small triangles and other continuous environmental variables are represented by arrows. Samples are represented using the four classes defined by TWINSPAN classification (thumbnail biplot). $\lambda_1 = 22.5\%$ of species variance; $\lambda_1 + \lambda_2 = 34.3$ % of species variance. The community was strongly structured on the first axis and the TWINSPAN classification patterns could be recognised.

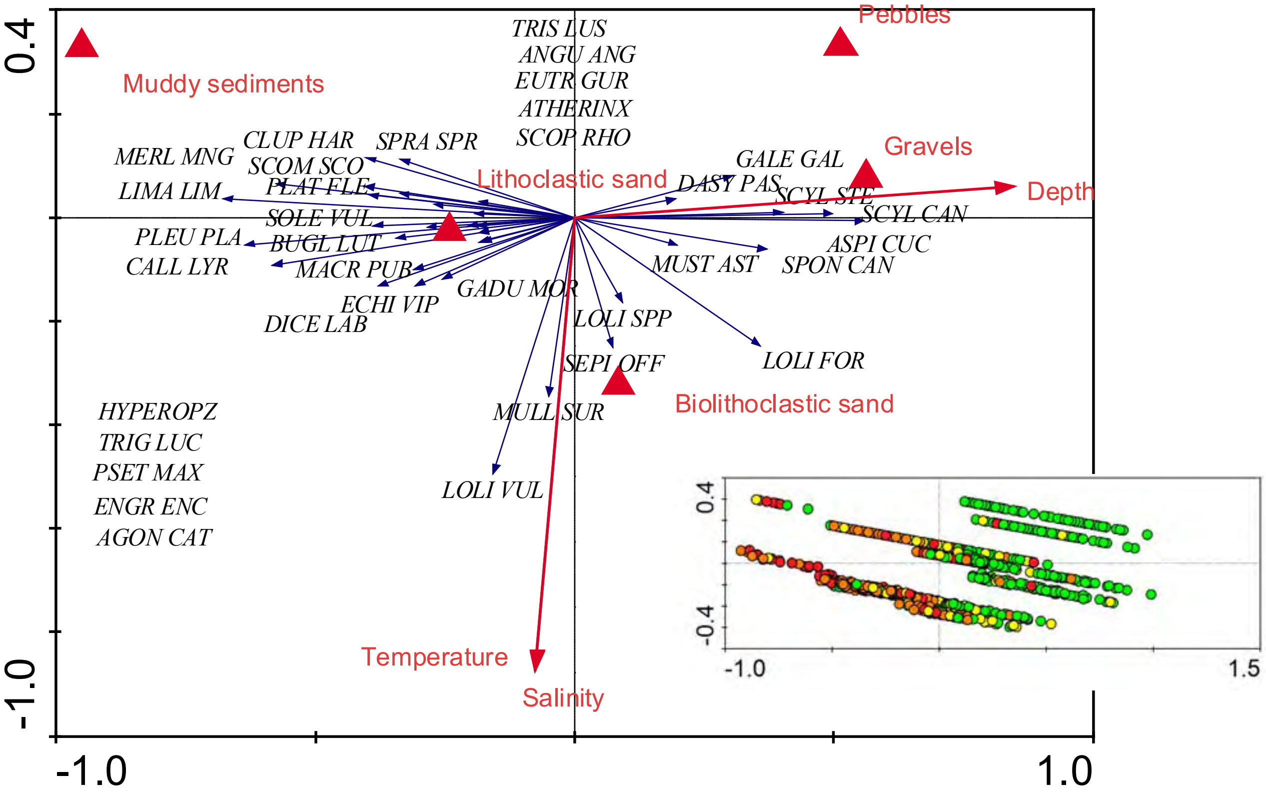

Figure 6 RDA correlation biplot on species data constrained by significant environmental variables

This RDA is based on a covariance matrix. The projection settings are the same as the PCA and species with poor fit with the projection (<3%) have been removed from the figure. Samples are represented using the four classes defined by TWINSPAN classification (thumbnail biplot). λ_1 = 13% of species variance and = 72.2% of species/environment relation, $\lambda_1 + \lambda_2$ = 15.2 % of species variance and = 84.5% of species/ environment. All axes are significant and the sum of all canonical eigenvalues is 0.180. The community is very structured along the first two axes and the TWINSPAN sub-communities can still be recognised. The first axis is strongly constrained by depth and sediment particle size. The second axis follow a temperature and salinity gradient.

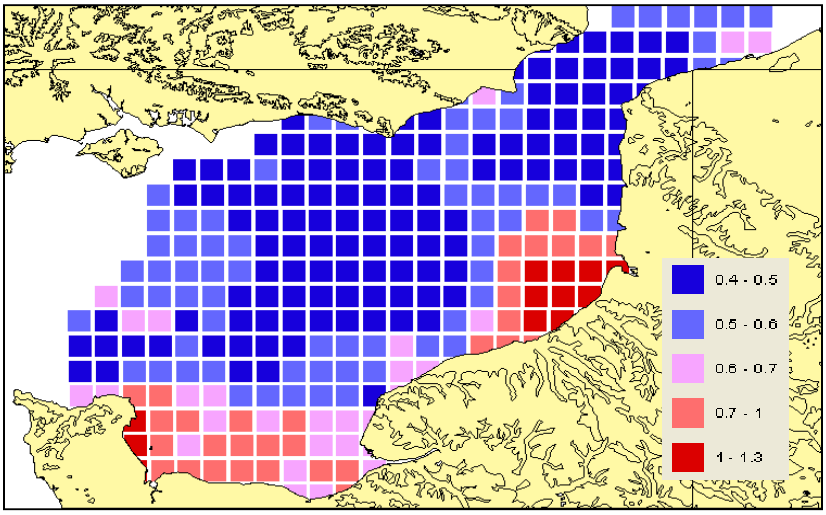

Figure 7 Interannual variation in temperature values (expressed as standard deviation). Areas with the largest interannual variation were observed along the French coast and corresponded to the Seine and Somme river plume extension areas.

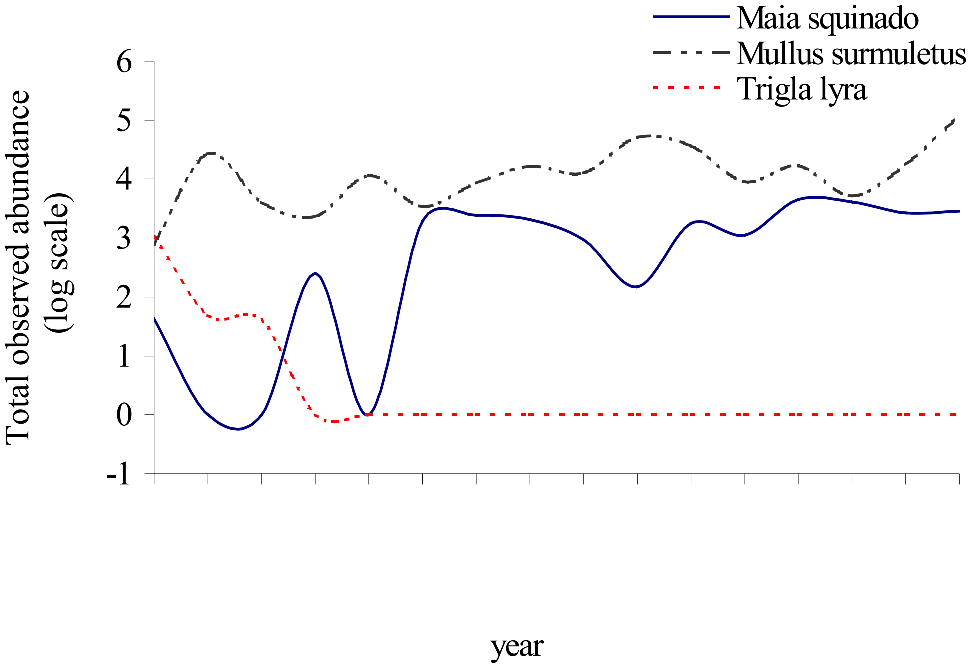

Figure 8 Observed Abundance evolution of three species : *Mullus surmuletus* and *Maia squinado* abundance have increased but *Trigla lyra* have been last observed in 1990.

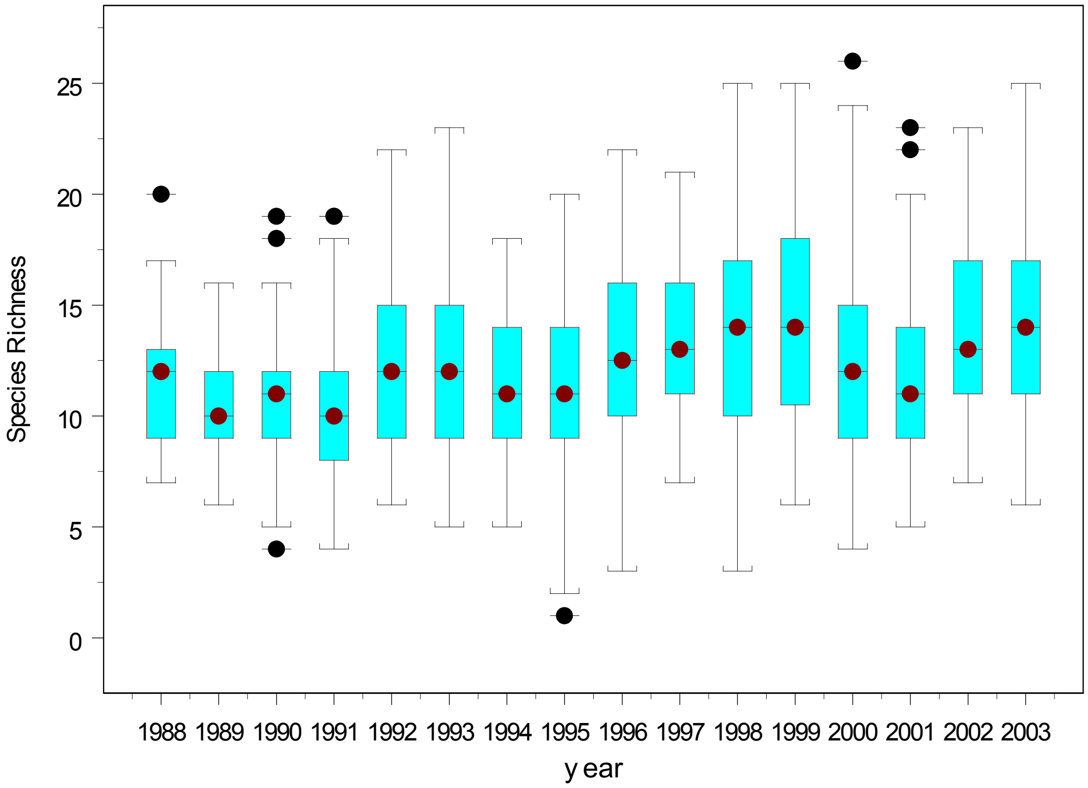

Figure 9 Evolution of species richness from 1988 to 2003. Although this diversity index was very variable, species richness was found to have increased significantly over time (F=79.95; p<0.001).