Seasonal organization patterns of demersal assemblages in the Gulf of Lions (north-western Mediterranean Sea)

J.C. Gaertner*

*IFREMER, Laboratoire Ecologie Halieutique, 1 Rue Jean Vilar, 34200 Sète, France.
Present address: Centre d'Océanologie de Marseille, Station Marine d'Endoume, Rue de la Batterie des Lions,
13007 Marseille Cedex 07, France. E-mail: gaertner@sme.com.univ-mrs.fr

The seasonal organization patterns of demersal assemblages (fish and cephalopods) in the Gulf of Lions were investigated on the basis of a set of bottom trawl surveys. The use of Partial Triadic Analysis (PTA) provided a detailed representation of: (1) the common part of the spatial organization of demersal assemblages at seasonal scale; and (2) the seasonal variability of each species around this common structure. During the course of the study, demersal assemblages exhibited a strong seasonal stability in their organization patterns and only few species showed a strong seasonal variation in their spatial distribution. Demersal assemblages of the Gulf of Lions were structured primarily on the basis of a non depth coast–open sea gradient, which occurred from the coast to the midshelf region. The influence of depth on the structure of fish assemblages appeared to be only of limited importance and mainly restricted to the continental slope area. The PTA combined with contouring technics could be used to improve our knowledge of community structuring factors, and offers a theoretical framework to assess the reproducibility of multispecies structures.

INTRODUCTION

One of the main aims in fishery ecology is the identification and hierarchy of the main processes acting on the dynamics of exploited populations (Christie et al., 1987; Bianchi, 1991; Perry et al., 1994; Miller, 1995; McClatchie et al., 1997). Numerous authors have investigated the patterns of change over time of the spatial organization of fish assemblages (Roel, 1987; Bianchi, 1991; Weinberg, 1994; Gomes et al., 1995; Fujita et al., 1995; Wantiez et al., 1996; Garcia et al., 1998). Rodriguez & Lewis (1994), sought periods of temporal stability in the structuration of fish communities in several Venezuelan lakes, in order to determine whether fish assemblages were mainly structured by stochastic or deterministic factors.

In temperate ecosystems, most of the studies that analyse the structure of demersal fish assemblages are based on the annual monitoring of their spatial distribution (Colvocoresses & Musick, 1984; Biagi et al., 1989; Mahon & Smith, 1989; Gabriel, 1992; Gomes et al., 1992; Gaertner et al., 1998). Nevertheless, numerous authors have showed the necessity to consider several temporal scales to better understand the origin of the observed spatial patterns (Wiens, 1989; Levin, 1992; Langton et al., 1995). In the north-east USA continental shelf and slope, for instance, a survey of several studies (Overholtz & Tyler, 1985; Gabriel, 1992; Murawski, 1993) carried out on seasonal and annual scales was necessary to conclude that nearshore and midshelf species were primarily influenced by variations in temperature, while outer-shelf and slope species appeared more affected by depth (Auster et al., 1995).

In the Gulf of Lions, despite the economic and ecological importance of demersal resources (Taquet et al., 1997), few studies have focused on the determinism of their organization. The study by Maurin (1968) is the only one to deal with the analysis of demersal assemblages at both seasonal and annual scales. This author concluded that demersal species were firstly organized by depth and secondly, in the coastal region, on the basis of water temperature and salinity. However, his conclusions had the disadvantage of being based on qualitative comparisons between non standardized data (i.e. collected with different equipment in several areas of the Gulf). It therefore appeared necessary to develop a quantitative approach based on a set of standardized surveys in order to deal with the variability of demersal assemblages within a reproducible framework. In a recent study it was shown that demersal species were mainly structured along a coast–open sea gradient that is highly persistent on an annual scale (Gaertner et al., 1998). Nevertheless, at this single temporal scale, it was difficult to understand which underlying processes were really responsible for the organization patterns of benthic fish assemblages.

In the present work a multi-table analysis was combined with contouring techniques to analyse the organization patterns of demersal species in the Gulf of Lions on a seasonal scale. The following questions were addressed: (1) how does the spatial organization of demersal assemblages change during the course of the seasons? (2) What are the main common patterns of organization at this seasonal scale? (3) What are the variations over time of each of the species around this common structure?

MATERIALS AND METHODS

Data type and origin

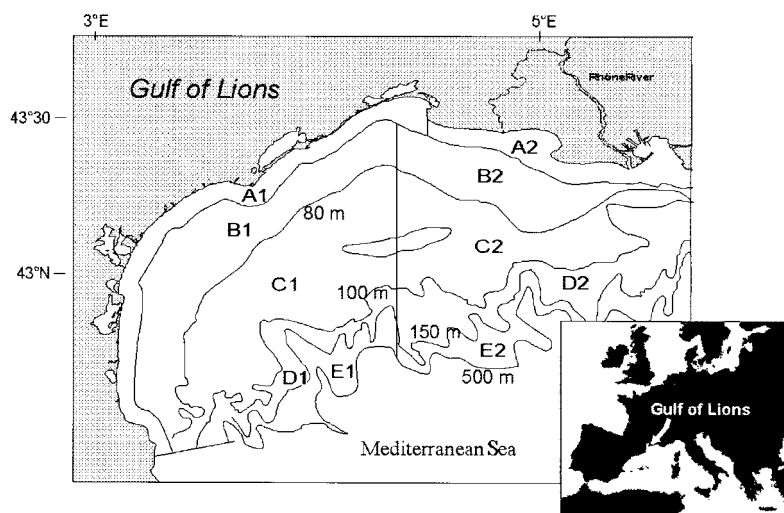The present work is based on a set of abundance indices collected in the Gulf of Lions (Figure 1) during

Figure 1. Gulf of Lions, showing location of strata (A–E) used in sampling design: (A, from coast to 3 nautical miles offshore; B, from 3 nautical miles to 80 m depth; C, 80–100 m depth; D, 100–150 m depth; E, 150–500 m depth; 1, western zone; 2, eastern zone).

three bottom trawl surveys conducted in June 1988, November 1988 and February 1989 by the Resources Halieutiques Laboratory of IFREMER, Sète. A stratified random sampling design was used, based on depth and geographical zones (A1–E1 and A2–E2; Figure 1). Locations of sample units were selected randomly within each stratum before each survey. A bottom ottertrawl (Le Drezen 20 PM) with a vertical opening of less than 1.8 m was used. Tows were about 30 min in duration when the depth was between 10 and 150 m, and 60 min when it was deeper (150–500 m). The catches included 113 species (benthic fish and invertebrates), but only 47 species (benthic fish and cephalopods; see Table 1) were sufficiently abundant to be included in the analysis (i.e. they were present in more than 5% of the tows). For each tow, the densities of individuals were expressed for the same surface unit (hectare). The data were log-transformed before conducting the analysis to minimize the dominant effect of exceptional catches.

Data analysis

The temporal monitoring of species assemblages during the course of the study required the combined analysis of the three different seasonal tables. For this, a method was required to: (1) coordinate the analyses of each survey within a rigorous and reproducible framework; and (2) provide a clear representation of the stable and variable parts of the spatial organization of the species assemblages. Multitable analyses may well meet these requirements, so the Partial Triadic Analysis (PTA; Thioulouse & Chessel, 1987), was used. This is an adaptation of the

STATIS method (Lavit et al., 1994), when tables have the same variables and the same samples.

The general functioning principle of PTA consists in calculating a linear combination of the k initial tables with the aim of constructing a mean table of maximum inertia (compromise table). For that purpose, the first stage of PTA consists in calculating a matrix of scalar product between tables (Robert & Escoufier, 1976). The diagonalization of this matrix provides eigenvectors. The k coefficients of the first eigenvector are then used to weight the k tables in the calculation of the compromise table. In the present work the diagonalization of the compromise table defines axes and components which express the common part of the spatial organization patterns of demersal assemblages during the course of the seasons. Independently, a separate Principal Component Analysis (PCA) (Hotteling, 1933) of each of the three surveys is carried out. This step allows the projection of the first axes of the separate analyses of each survey onto the first axes of the compromise table. This representation indicates how much the main structures of each initial table are taken into account in the compromise (Lavit et al., 1994), (i.e. whether the compromise structure is common to all the surveys or specific to only a few of them). In addition, the projection of the k initial tables onto the compromise allows us to draw the trajectories that represent the temporal variations of each species around the common structure. Technically, this involves projecting the factorial scores that each species obtains in each of the tables onto the axes of the compromise table.

In comparison with the classical version of STATIS, the PTA used in the present work allowed the optimal projection of trajectories (Thioulouse & Chessel, 1987). However, in our study, the stations were not sampled at the same locations during the three surveys. Thus, it was necessary to transform the three initial tables so that each table includes not only the same species, but also the same stations. For that purpose, initial stations in 52 geographical strata were aggregated, where each strata is the same for the three surveys and contained at least one station from each survey.

Table 1. *Matrix of correlations between surveys.*

	June 1988	November 1988	February 1989
June 1988	1		
November 1988	0.59	1	
February 1989	0.51	0.52	1

For further details on the nature of the statistical model underlying PTA, refer to Robert & Escoufier (1976), Thioulouse & Chessel (1987), Lavit et al. (1994) and Gaertner et al. (1998). The ADE-4 software (Thioulouse et al., 1996) was used to perform all the calculations and graphical displays shown in this work. This software is available free of charge at the following address: http://pbil.univ-lyon.fr/ADE-4.html.

RESULTS

The use of PTA showed that the correlations between each of the three surveys were similar (0.51–0.59; Table 1). This result highlighted the fact that the associations between species were stable from one season to another. Furthermore, the contribution of the different surveys to the construction of the compromise table were well-balanced (weighting 0.56–0.59; Table 2). Thus, none of the surveys was either favoured or ignored in the construction of the compromise table.

The fit of each of the tables to the compromise table ($\cos^2$) was homogeneous (0.48 in February to 0.60 in November). In addition, the similarity between the projections of the first two axes of the separate analyses of the three surveys and the first two axes of the compromise table (Figure 2) was very strong. This showed that the two main organizational directions expressed in the compromise table are common to each of the three surveys. The share of the total variability accounted for by each of the first two axes of the compromise was 45 and 16% respectively. So the structure represented by the first axis was by far the most important.

The separate mapping (for each survey) of the samples' factorial scores onto the first two axes of the compromise provided a representation of the stable part of the main spatial structures (Figure 3). The first axis showed that demersal fish species were distributed along a coast–open sea gradient (Figure 3A). The second axis (Figure 3B) was mainly structured (see the area where the isolines are closest) by the opposite positioning of the slope species and those of the continental shelf. The strong stability of this pattern observed for the three surveys was in accordance with our preliminary results (see Tables 1 & 2, Figure 2).

The correspondence with the species (Figure 4A) allowed the identification of the taxa responsible for these gradients. This figure provided a typology of species on the basis of the structure common to the different seasons. On the first axis, the most abundant species caught in the central and deep parts of the shelf (*Scyliorhinus canicula, Argentina sphyraena, Eutrigla gurnardus, Lepidorhombus boscii, Merluccius merluccius*) were opposed to the group of coastal
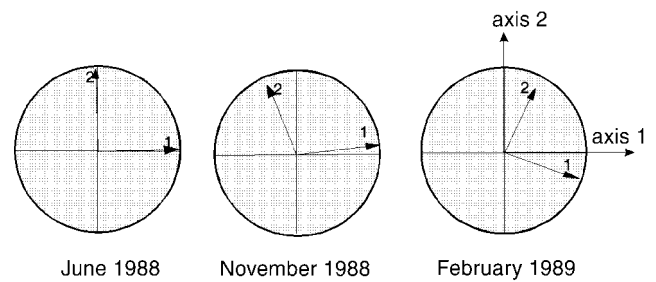

Figure 2. Projection of the first two factorial axes of the separate Principal Component Analysis of each survey (arrows) on the two first factorial axes of the PTA compromise.
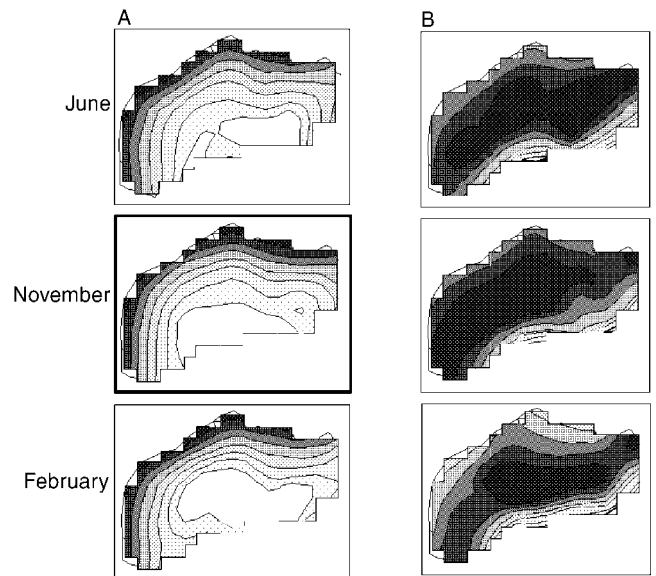

Figure 3. Map of the factorial scores of the stations of each survey on the first (A) and the second (B) factorial axes of the PTA compromise.

species (*Buglossidium luteum, Sepia officinalis, Pagellus erythrinus*). On the second axis, the slope species (*Gadiculus argenteus, Helicolenus dactylopterus, Trigla lyra*) were opposite a group of species found in the central part of the shelf, but absent in the deeper part and in the slope (*Serranus hepatus, Synchiropus phaeton, Deltentosteus quadrimaculatus, Cepola rubescens*, etc.). It is important to note that if a species has high scores on the two first axes of the PTA, it is implied that this species is abundant in two regions of the Gulf of Lions. For instance, the projection of *Arnoglossus laterna* (ARNL) onto the compromise showed that it was very abundant both in the coastal area (high positive score on the axis 1), and in the central part of the shelf (high negative score on the axis 2).

Finally, the representation of the trajectories enables us to identify seasonal variations of the position of species around the common structure (Figure 4B). Trajectories linked the position of each species in each survey to its position in the compromise. Among the species, *Deltentosteus quadrimaculatus* (DELT) exhibited the strongest seasonal variations. By comparison with its position in the compromise, in June DELT appeared less present on the shelf (its factorial score on the negative part of

Table 2. *Description of the structure defined for each survey.*

	Weight	$\cos^2$
June 1988	0.58	0.51
November 1988	0.59	0.60
February 1989	0.56	0.48

Weight, contribution of each table in the construction of the compromise; $\cos^2$, fit of each table to the compromise.
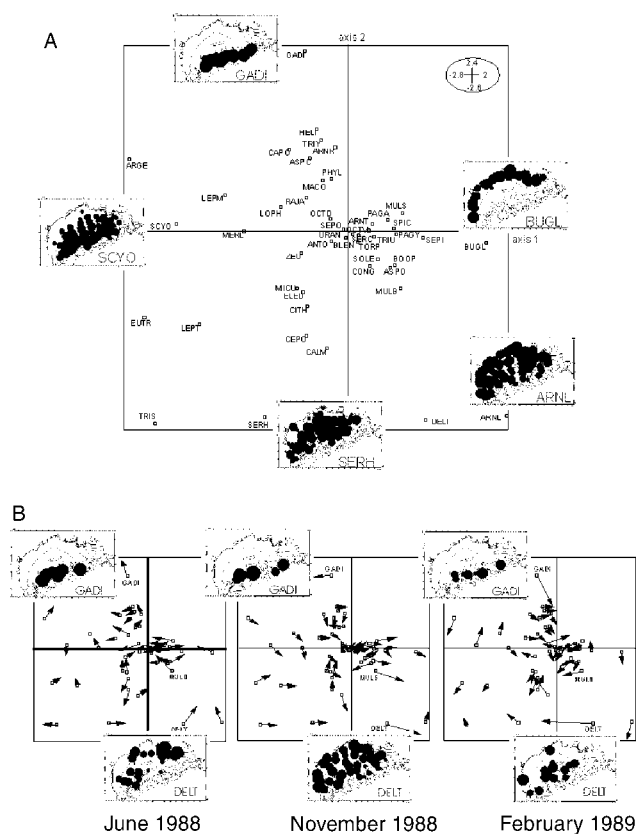
Figure 4. (A) Map of the stable structure. Projection of the species on the first factorial plane of the PTA compromise. Maps of spatial distribution for some characteristic species are given in the small panels (species codes as in Appendix 1). (B) Variability of the species around the stable structure. Projection of the species trajectories, separated by survey, on the first factorial plane of the PTA compromise. The position of a species in each survey (arrow) is related to its position in the compromise (□).

axis 2 was lower than those in the compromise), but more abundant on the coast (its factorial score on axis 1 was higher than those in the compromise). In November, its trajectory showed that it was very abundant in these two regions. Finally, in February, its trajectory on axis 1 evidenced a low abundance on the coast. In addition, *Gadiculus argenteus* showed weak variations during the first two seasons. However in February, its trajectory along the second axis evidenced that this species was caught in the same area (the slope) but at a lower rate than in the two first surveys. With the exception of a few other taxa, such as *Mullus barbatus*, most of the species exhibited a low seasonal variations during the course of the study.

DISCUSSION

This work has shown that the spatial organization patterns of demersal assemblages in the Gulf of Lions were highly persistent during the course of the three seasons considered. At this seasonal scale, the main common features of the organization pattern were firstly a coast–open sea gradient, and secondly an opposite positioning of slope and shelf assemblages. The variations over time of each of the species around the reference

structure was generally low. Only a very limited number of species exhibited a strong variation of their abundance in space at this scale.

The main common organizational patterns described here at a seasonal scale, were similar to those revealed in a previous study conducted in the same area, but on an annual scale (in June) between 1983 and 1992 (Gaertner, 1997). The reproducibility of spatial patterns at different temporal scales is widely attributed to the preponderance of deterministic factors in community structuring (Rahel, 1990; Rodriguez & Lewis, 1994). Consequently, in this study the strong reproducibility of the main structures at two scales highlighted a clear dominance of the deterministic component in the organization of demersal assemblages in the Gulf of Lions. Thus, even if the stochastic processes could not be precisely quantified, their influence on the demersal assemblages of the Gulf of Lions appeared very limited at these two scales.

In this study, the coast–open sea gradient accounted for a very important part of the observed organization pattern (axis 1, 45%). The dominance of such a gradient in demersal assemblage organization has been often attributed to the influence of depth (Fager & Longhurst, 1968; Roel, 1987; Mahon & Smith, 1989; Bianchi, 1991; Gomes et al., 1992; Fujita et al., 1995; Garcia et al., 1998). In particular, this has been described for the same benthic fish species, both in the Gulf of Lions (Maurin, 1968) and in the north of the Tyrrhenian Sea (Biagi et al., 1989). Nevertheless, numerous field experiments have demonstrated that several environmental parameters linked to the bathymetric gradient, such as temperature (Mahon, 1985; Mahon & Smith, 1989; Bianchi, 1992; Perry et al., 1994; Gonzalez-Samson et al., 1997), salinity (Quinn, 1980; Mahon, 1985; Loneragan & Potter, 1990; Rakosinski et al., 1992), oxygen concentration (Bianchi, 1991, 1992; Rakosinski et al., 1992), or other habitat features (Jones et al., 1991; Bianchi, 1992; Jackson & Harvey, 1993; Auster et al., 1995) could also strongly influence the organization patterns of benthic fish assemblages. Thus, it is difficult to specify which of the environmental factors was really responsible for faunal changes along the coast–open sea gradient.

However, in this study the map of the results of the PTA (Figure 3) shows that the coast–open sea gradient occurred mainly from the shore to the midshelf area (axis 1, 45%), in a region which is characterized (except for the western area) by weak bathymetric variations (30–60 m). Furthermore, in this region, the observed gradient (see the shape of the isolines) followed the outline of the shore but not the isobaths. Thus, in contrast to Maurin (1968), these results suggested that depth was not responsible for this gradient, and cannot be considered as the most determinant factor in structuring demersal species in the Gulf of Lions. However, the influence of depth could explain the main structure observed on axis 2 of the PTA. This structure did indeed follow the continental slope, which is characterized by the widest bathymetric variations (130–500 m). In short, even if the influence of bathymetry was not negligible (axis 2, 16%), it was not dominant and mainly restricted to the slope area.

Moreover, in the coastal region we found that the spatial structuring of species, which followed the

coast–open sea gradient, showed both a high homogeneity along the shore axis and a strong seasonal reproducibility. This pattern was very different from those exhibited by water temperature and salinity. Indeed, these hydrographic features showed a strong spatial and seasonal variability, linked to the spatio–temporal dynamics of both the Rhône River plume (Demarcq, 1985; Caraux, 1985) and coastal upwellings (Millot & Wald, 1981; Pinazo et al., 1996). This comparison suggested, contrarily to Maurin (1968), that water temperature and salinity did not play a great role in structuring coastal species.

Although our analysis does not permit more detailed predictions about the factors responsible for the coast–open sea gradient in structuring fish assemblages, it indicates some candidates for future study. The strong stability of the coast–open sea gradient, both on seasonal and annual scales, suggested that the environmental factors responsible for this pattern are stable at these two scales. Thus, we can expect the habitat descriptors which showed weak seasonal and annual variability, to be among the causal factors. Numerous studies conducted throughout the world's oceans, have in fact described associations between demersal fish and substrata (Mahon, 1985; Bianchi, 1992; Wantiez, 1993; McCormick, 1995), or benthic macrofauna communities (Jones et al., 1991; Jackson & Harvey, 1993; McCormick, 1995). It was also the case in a previous study led in the Gulf of Lions on an annual scale, in which the influence of benthic macrofauna and substratum type on the spatial organization of demersal assemblages was shown (Gaertner et al., 1999). Nevertheless, to test this hypothesis on a seasonal scale, further experiments based on the simultaneous sampling of both demersal assemblages and habitat components at the four seasons are needed.

In conclusion, these results have demonstrated a strong reproducibility of the seasonal organization patterns of demersal species in the Gulf of Lions. They suggest the dominance of a non depth dependent coastal–open sea gradient. The influence of depth appeared only of limited importance and mainly restricted to the slope region. Otherwise, the reproducibility of the coast–open sea gradient at the seasonal and annual scales allowed us to: (1) test hypotheses suggested by previous authors on the factors controlling the organization of demersal assemblages in the Gulf of Lions; and (2) generate new hypotheses as a basis for future studies. Finally, PTA provided a detailed representation of: (1) the main organizational patterns common to the three seasons; and (2) the variability of each species around this reference structure. Although it is still little used in fishery sciences and ecology, this method combined with contouring techniques, constitutes a useful tool to improve our knowledge of community structuring. It provides a suitable theoretical framework for assessing the reproducibility of multivariate structures and should find numerous applications in several fields of community ecology.

REFERENCES

Auster, P.J., Malatesta, R.J. & La Rosa, S.C., 1995. Patterns of microhabitat utilization by mobile megafauna on the southern New England (USA) continental shelf and slope. *Marine Ecology Progress Series*, **127**, 77–85.

Biagi, F., De Ranieri, S., Mori, M., Sartor, P. & Sbrana, M., 1989. Preliminary analysis of demersal fish assemblages in the northern Tyrrhenian sea. *Nova Thalassia*, **10**, 391–398.

Bianchi, G., 1991. Demersal assemblages of the continental shelf and slope edge between the gulf of Tehuantepec (Mexico) and the gulf of Papagayo (Costa Rica). *Marine Ecology Progress Series*, **73**, 121–140.

Bianchi, G., 1992. Demersal assemblages of the continental shelf and upper slope of Angola. *Marine Ecology Progress Series*, **81**, 101–120.

Caraux, D., 1985. *Traitement de données satellitaires pour l'étude des structures frontales du golfe du Lion.* Thèse, Université Montpellier, France.

Christie, W.J., Spangler, G.R., Loftus, K.H., Hartman, W.L., Colby, P.J., Ross, M.A. & Talhem, D.R., 1987. A perspective on great lakes fish community rehabilitation. *Canadian Journal of Aquatic and Fisheries Sciences*, **44**, 486–499.

Colvocoresses, J.A. & Musick, J.A., 1984. Species association and community composition of middle Atlantic bight continental shelf demersal fishes. *Fishery Bulletin, National Oceanic and Atmospheric Administration. Washington, DC*, **82**, 295–313.

Demarcq, H., 1985. *Etude de la zone de dilution rhodanienne, observation des zones de production dans le golfe du Lion et estimation de l'éclairement solaire global en Méditerranée occidentale.* Thèse, Université Aix-Marseille II, France.

Fager, E.W. & Longhurst, A.R., 1968. Recurrent group analysis of species assemblages of demersal fish in the Gulf of Guinea. *Journal of the Fisheries Research Board of Canada*, **25**, 1405–1421.

Fujita T., Tadashi, I. & Ishito, Y., 1995. Depth–gradient structure on the demersal fish community on the continental shelf and slope off Sendai Bay, Japan. *Marine Ecology Progress Series*, **118**, 13–23.

Gabriel, W.L., 1992. Persistence of demersal fish assemblages between cape Hatteras and Nova Scotia, northwest Atlantic. *Journal of Northwest Atlantic Fishery Science*, **14**, 29–46.

Gaertner, J.C., 1997. *Organisation des assemblages démersaux dans le golfe du Lion: structures spatiales et stabilité temporelle.* Thèse, Université Aix-Marseille II, France.

Gaertner, J.C., Chessel, D. & Bertrand, J., 1998. Stability of spatial structures of demersal assemblages: a new approach. *Aquatic Living Resources*, **11**, 75–85.

Gaertner, J.C., Mazouni, N., Sabatier, R. & Millet, B., 1999. Spatial structure and habitat associations of demersal assemblages in the Gulf of Lions: a multicompartmental approach. *Marine Biology*, **135**, 199–208.

Garcia, C.B., Duarte, L.O. & Schiller, D. von., 1998. Demersal fish assemblages of the Gulf of Salamanca, Colombia (southern Caribbean Sea). *Marine Ecology Progress Series*, **174**, 13–25.

Gomes, M.C., Haedrich, R.L. & Rice, J.C., 1992. Biogeography of groundfish assemblages on the Grand bank. *Journal of Northwest Atlantic Fishery Science*, **14**, 13–27.

Gomes, M.C., Haedrich, R.L. & Villagarcia, M.G., 1995. Spatial and temporal changes in the groundfish assemblages on the north-east Newfoundland/Labrador shelf, north-west Atlantic, 1978–1991. *Fishery Oceanography*, **4**, 85–101.

Gonzalez-Samson, G. et al., 1997. Variacion espacial de la abundancia de la fauna de fondos blandos en la plataforma continental de Jalisco y Colima. Mexico. *Cienca Marina*, **23**, 93–110.

Hotelling, H., 1933. Analysis of a complex of statistical variables into principal components. *Journal of Educational Psychology*, **24**, 417–441.

Jackson, D.A. & Harvey, H.H., 1993. Fish and benthic invertebrates: community concordance and community environment relationships. *Canadian Journal of Aquatic and Fisheries Science*, **50**, 2641–2651.

Jones, G.P., Ferrell, D.-J. & Sale, P.F., 1991. Fish predation and its impact on the invertebrates of coral reef and adjacent sediments. In *The ecology of fishes on coral reef* (ed. P.F. Sale), pp. 156–179. San Diego: Academic Press.

Langton, R.W., Auster, P.J. & Schneider, D.C., 1995. A spatial and temporal perspective on research and management of groundfish in the northwest Atlantic. *Fisheries Science*, **3**, 201–229.

Lavit, C., Escoufier, Y., Sabatier, R. & Traissac, P., 1994. The ACT (STATIS method). *Computational Statistic and Data Analysis*, **18**, 97–119.

Levin, S.A., 1992. The problem of pattern and scale in ecology. *Ecology*, **73**, 1943–1967.

Loneragan, N.R. & Potter, I.C., 1990. Factors influencing community structure and distribution of different life-cycle categories of fishes in shallow waters of a large Australian estuary. *Marine Biology*, **106**, 25–37.

Mahon, R., ed., 1985. Groundfish assemblages on the Scotian shelf. In *Toward the inclusion of fishery interactions in management advice. Canadian Technical Report of Fisheries and Aquatic Sciences*, **1347**, 153–162.

Mahon, R. & Smith, R.W., 1989. Demersal fish assemblages on the Scotian shelf, northwest Atlantic: spatial distribution and persistence. *Canadian Journal of Aquatic and Fisheries Sciences*, **46**, 134–152.

Maurin, C., 1968. Ecologie ichthyologique des fonds chalutables atlantiques (de la baie ibéro-marocaine à la Mauritanie) et de la Méditerranée occidentale. *Revue des Travaux de l'Institut des Pêches Maritimes*, **32**, 5–147.

McClatchie, S., Millar, R.B., Webster, F., Lester, P.J., Hurst, R. & Bagley, N., 1997. Demersal fish community diversity off New Zealand: is it related to depth, latitude and regional surface phytoplankton? *Deep-Sea Research*, **44**, 647–667.

McCormick, M.I., 1995. Fish feeding on mobile benthic invertebrates: influences of spatial variability in habitat associations. *Marine Biology*, **121**, 627–637.

Miller, M.J., 1995. Species assemblages of leptocephali in the Sargasso Sea and Florida current. *Marine Ecology Progress Series*, **121**, 11–26.

Millot, C. & Wald, L., 1981. Upwelling in the gulf of Lions. In *Coastal upwelling*. Vol. 1. *Coastal and estuarine science series* (ed. F.A. Richards), pp. 160–166. Washington DC: American Geophysical Union.

Murawski, S.A., 1993. Climate change and marine fish distribution: forecasting from historical analogy. *Transactions of the American Fisheries Society*, **122**, 647–658.

Overholtz, W.J. & Tyler, A.V., 1985. Long-term responses of the demersal fish assemblages of Georges Bank. *Fishery Bulletin, National Oceanic and Atmospheric Administration, Washington DC*, **83**, 507–520.

Perry, R.I., Stocker, M. & Fargo, J., 1994. Environmental effects on the distribution of groundfish in Hecate Strait, British Columbia. *Canadian Journal of Aquatic and Fisheries Sciences*, **51**, 1401–1409.

Pinazo, C., Marsaleix, P., Millet, B. & Estournel, C., 1996. Spatial and temporal variability of phytoplankton biomass in upwelling areas of the northwestern Mediterranean: a coupled physical and biochemical modelling approach. *Journal of Marine Systems*, **7**, 161–191.

Quinn, N.J., 1980. Analysis of temporal changes in fish assemblages in Serpentine Creek. *Environmental Biology of Fishes*, **5**, 117–133.

Rahel, F.J., 1990. The hierachical nature of community persistence: a problem of scale. *American Naturalist*, **136**, 328–344.

Rakocinski, C.F., Baltz, D.M. & Fleeger, J.W., 1992. Correspondence between environmental gradients and the community structure of marsh-edge fishes in a Louisiana estuary. *Marine Ecology Progress Series*, **80**, 135–148.

Robert, P. & Escoufier, Y., 1976. A unifying tool for linear multivariate statistical methods: the RV coefficient. *Applied Statistics*, **25**, 257–265.

Rodrigez, M.A. & Lewis, W.M. Jr, 1994. Regulation and stability in fish assemblages of neotropical floodplain lakes. *Oecologia*, **99**, 166–180.

Roel, B.A., 1987. Demersal communities off the west coast of South Africa. *South African Journal of Marine Sciences*, **5**, 575–584.

Taquet, M., Gaertner, J.C. & Bertrand, J., 1997. Typologie de la flottille chalutière de Sète: formalisation par une méthode de segmentation. *Aquatic Living Resources*, **10**, 137–148.

Thioulouse, J. & Chessel, D., 1987. Les analyses multi-tableaux en écologie factorielle. I. De la typologie d'état à la typologie de fonctionnement par l'analyse triadique. *Acta Ecologica, Ecologia Generalis*, **8**, 463–480.

Thioulouse, J., Chessel, D., Dolédec, S. & Oliver, J.M., 1996. ADE-4: a multivariate analysis and graphical display software. *Statistics and Computing*, **7**, 75–83.

Wantiez, L., 1993. *Les poissons des fonds meubles du lagon nord et de la baie de Saint Vincent de Nouvelle Calédonie*. Thèse, Université Aix-Marseille II, France.

Wantiez, L., Harmelin-Vivien, M. & Kulbicki, M., 1996. Spatial and temporal variation in a soft bottom fish assemblage in Saint Vincent Bay, New Caledonia. *Marine Biology*, **125**, 801–812.

Weinberg, K.L., 1994. Rockfish assemblages of the middle shelf and upper slope off Oregon and Washington. *Fishery Bulletin. National Oceanic and Atmospheric Administration, Washington, DC*, **92**, 620–632.

Wiens, J.A., 1989. Spatial scaling in ecology. *Functional Ecology*, **3**, 385–397.

Appendix 1. *List of the species considered with detail on the abbreviated names used.*

Label	Species	Family
ANTO	*Antonogadus megalokynodon* Kolombatovic, 1894	Gadidae
ARGE	*Argentina sphyraena* Linnaeus, 1758	Argentinidae
ARNL	*Arnoglossus laterna* (Walbaum, 1792)	Bothidae
ARNR	*Arnoglossus rueppeli* (Cocco, 1844)	Bothidae
ARNT	*Arnoglossus thori* Kyle, 1913	Bothidae
ASPC	*Aspitrigla cuculus* (Linnaeus, 1758)	Triglidae
ASPO	*Aspitrigla obscura* (Linnaeus, 1764)	Triglidae
BLEN	*Blennius ocellaris* Linnaeus, 1758	Blennidae
BOOP	*Boops boops* (Linnaeus, 1758)	Sparidae
BUGL	*Buglossidium luteum* (Risso, 1810)	Soleidae
CALM	*Synchiropus phaeton* (Günther, 1861)	Callionymidae
CAPO	*Capros aper* (Linnaeus, 1758)	Caproidae
CEPO	*Cepola rubescens* Linnaeus, 1766	Cepolidae
CITH	*Citharus linguatula* (Linnaeus, 1758)	Citharidae
CONG	*Conger conger* (Linnaeus, 1758)	Congridae
DELT	*Deltentosteus quadrimaculatus* Valenciennes, 1837	Gobiidae
EUTR	*Eutrigla gurnardus* (Linnaeus, 1758)	Triglidae
GADI	*Gadiculus argenteus* (Guichenot, 1850)	Gadidae
HELI	*Helicolenus dactylopterus* Delaroche, 1809	Scorpaenidae
LEPM	*Lepidorhombus boscii* (Risso, 1810)	Scophtamidae
LEPT	*Lepidotrigla dieuzeidei* (Lacépède, 1801)	Triglidae
LEPC	*Lepidotrigla cavillone* (Lacepède, 1801)	Triglidae
LOPB	*Lophius budegassa* Spinola, 1807	Lophiidae
MACO	*Macroramphosus scolopax* (Linnaeus, 1758)	Macroramphosidae
MERL	*Merluccius merluccius* (Linnaeus, 1758)	Merluciidae
MICU	*Microchirus variegatus* (Donovan, 1808)	Soleidae
MULB	*Mullus barbatus* Linnaeus, 1758	Mullidae
MULS	*Mullus surmuletus* Linnaeus, 1758	Mullidae
PAGA	*Pagellus acarne* (Risso, 1826)	Sparidae
PAGY	*Pagellus erythrinus* (Linnaeus, 1758)	Sparidae
PHYL	*Phycis blennoides* (Brünnich, 1768)	Gadidae
RAJA	*Raja clavata* Linnaeus, 1758	Rajidae
SCYO	*Scyliorhinus canicula* (Linnaeus, 1758)	Scyliorhinidae
SERC	*Serranus cabrilla* (Linnaeus, 1758)	Serranidae
SERH	*Serranus hepatus* (Linnaeus, 1758)	Serranidae
SOLE	*Solea vulgaris* Quensel, 1806	Soleidae
SPIC	*Spicara maena* (Linnaeus, 1758)	Centracanthidae
TORP	*Torpedo marmorata* Risso, 1810	Topenididae
TRIU	*Trigla lucerna* Linnaeus, 1758	Triglidae
TRIY	*Trigla lyra* Linnaeus, 1758	Triglidae
TRIS	*Trisopterus minutus capelanus* Lacepède, 1800	Gadidae
URAN	*Uranoscopus scaber* Linnaeus, 1758	Uranoscopidae
ZEUS	*Zeus faber* Linnaeus, 1758	Zeidae
ELED	*Eledone moschata* (Lamarck, 1798)	Octopodidae
OCTD	*Octopus deilippi* (Verany, 1851)	Octopodidae
OCTV	*Octopus vulgaris* (Cuvier, 1797)	Octopodidae
SEPI	*Sepia officinalis* (Linnaeus, 1758)	Sepiidae
SEPO	*Sepia orbignyana* de Ferussac, 1826	Sepiidae