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Spatial distributions (1989-2004) and preferential habitats of thornback ray and lesser-spotted dogfish in the Eastern English Channel.

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Thornback ray (*Raja clavata*) and lesser-spotted dogfish (*Scyliorhinus canicula*) are two of the most abundant demersal elasmobranchs occurring in the Eastern English Channel. *R. clavata* is commercially exploited, though *S. canicula* is of less commercial importance. As part of the CHARM project (http://charm.canterbury.ac.uk), Catch Per Unit Effort (CPUE) data for the period 1989-2004 were compiled from two annual, fishery-independent trawl surveys that are undertaken in the Eastern English Channel (ICES Division VIId), the English Eastern Channel Beam Trawl Survey (ECBTS) and the French Channel Groundfish Survey (CGFS). Annual patterns in the relative abundance (number of fish per km^2) of *R. clavata* and *S. canicula* were mapped, and seasonal and inter-annual variations examined. Quantile regression modelling was used to relate the relative abundance of both species to significant environmental factors (e.g. depth, seabed sediment type, bed shear stress, water temperature, salinity), and the resulting equation used to map habitat suitability using GIS. Observed patterns in relative abundance and model-derived suitable habitats were discussed in the light of a previous study that investigated the roles of both species as a structuring part of the Eastern English Channel fish community. This works aimed to increase the scientific understanding of the spatial distribution of *R. clavata* and *S. canicula,* so that preferential habitats can be identified in order to facilitate improved management of these stocks. This is particularly relevant since the Eastern English Channel is subject to intense anthropogenic impacts in terms of shipping, aggregate extraction, tourism and both commercial and recreational fishing.

Key-words: Dover Strait, geostatistics, Channel Habitat Atlas for Marine Resource Management, IFREMER, Cefas, classification, Geographical Information Systems

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1. INTRODUCTION

Thornback ray *Raja clavata* Linnaeus, 1758 and lesser-spotted dogfish *Scyliorhinus canicula* (Linnaeus, 1758) are widespread and abundant demersal elasmobranchs in the North-east Atlantic. *R. clavata* (FIGURE 1a) occurs on the continental shelf to depths of about 300 m, and occurs on a variety of sediments (Wheeler, 1978; Stehmann & Bürkel, 1984; Rousset, 1990; Ellis *et al.*, 2005a). Juveniles predate on a variety of small crustaceans (e.g. amphipods and shrimps), with larger individuals consuming larger crustaceans (shrimps and swimming crabs) and demersal fishes (Ellis *et al.*, 1996). *S. canicula* (FIGURE 1b) has a similar distribution to *R. clavata* and also occurs on the continental shelf to depths of 400 m (Wheeler, 1978; Quero, 1984; Ellis *et al.*, 2005a). *S. canicula* predate on a wide variety of invertebrates, especially polychaetes, crustaceans and molluscs, and various demersal fishes (Ellis *et al.*, 1996).

R. clavata and *S. canicula* are two of the most abundant elasmobranchs in the Eastern English Channel (ICES Division VIId). This area is relatively shallow, contains a variety of sediment types, and is bordered by areas of strong hydrodynamics in both the east (Dover Strait) and west (the “narrows”, the region between the Cherbourg Peninsula and Isle of Wight) (Larsonneur *et al.*, 1979; Pawson, 1995). This is a key economic area for numerous human activities, including shipping, sand and gravel extraction, leisure and tourism, and commercial and recreational fisheries. Hence, in this area, natural resources, including *R. clavata* and *S. canicula* and their habitats, may be subject to intense anthropogenic pressure. Phase I of the CHARM project ("Eastern Channel Habitat Atlas for marine Resource Management", 2003-2005, http://charm.canterbury.ac.uk) was funded by the EU under the INTERREG IIIA scheme to assess and map the available physical and biological information for an area centred on the Dover Strait (FIGURE 2). The ultimate aim of the project (over Phases I & II) is to provide decision-makers with the information necessary to deal with the growing pressures and management challenges faced by the region, and raise the awareness of the marine environment of the Eastern English Channel among the wider public. *R. clavata* and *S. canicula* were among the 16 key commercially exploited species selected to be presented in the atlas produced for CHARM Phase I.

Catch Per Unit Effort (CPUE) data for *R. clavata* and *S. canicula* from the Eastern Channel Beam Trawl Survey (ECBTS, taking place annually in July/August) and the Channel Ground Fish Survey (CGFS, taking place annually in October) were provided by Cefas (Centre for Environment, Fisheries and Aquaculture Science) and IFREMER (Institut Français de Recherche pour l'Exploitation de la Mer), respectively. Survey data for *R. clavata* and *S. canicula* were used to map annual patterns in their distribution and relative abundance in July/August and October over the period 1989-2004, thus allowing seasonal and inter-annual variations in spatial distribution to be investigated. Quantile regression was used to model the suitable habitats of these two species using environmental factors. Suitable habitat here refers to geographic areas within which ranges of environmental factors define the presence of a particular species. Observed patterns in relative abundance and model-derived suitable habitats were then discussed in the light of a previous study (Vaz *et al.*, 2004) that investigated the roles of both species as a structuring part of the Eastern English Channel fish community.

2. MATERIALS & METHODS

2.1. Survey data

2.1.1. Eastern Channel Beam Trawl Survey (ECBTS)

The ECBTS has been conducted annually by Cefas in July/August since 1989 using a commercial 4-m beam trawl. The aim of this survey is to provide fishery-independent indices of relative abundance of commercial flatfish, particularly common sole *Solea solea* and plaice *Pleuronectes platessa*, and recruitment indices. This survey samples at approximately 100 fixed stations. Of these, approximately 75 are in ICES division VIId and 25 are in ICES division IVc. At each sampling station, all fish species are sorted, weighed, counted and measured. See Ellis *et al.* (2005a,b) for further details of the elasmobranchs caught during this survey.

2.1.2. Channel Ground Fish Survey (CGFS)

The CGFS has been conducted annually by IFREMER in October since 1988 using a Grande Ouverture Verticale (GOV) trawl. The aim of this survey is to provide fishery-independent survey data for the annual assessment of commercial species. The survey uses a systematic sampling strategy and extends from the Eastern English Channel to the southern North Sea, which corresponds to ICES divisions VIId and IVc. At each sampling station, all the fish species are sorted, weighed, counted and measured.

Survey data for *R. clavata* and *S. canicula* were provided as CPUE, standardised as number of fish per km^2. The data contained both adult and juvenile fish. To reduce skewness ($>|1|$) and due to the large occurrence of null values in species abundance data, data were transformed using $Log_{10}[x+1]$, where x is the species abundance value (Legendre & Legendre, 1998).

2.2. Interpolation of survey abundance data into continuous raster maps

Continuous maps showing survey abundance patterns were created using geostatistics and kriging. Geostatistics embody a suite of methods for analysing spatial data and allow the estimation of the values of a variable of interest at non-sampled locations from more or less sparse sample data points. Kriging uses the parameters of the variogram (the central tool of geostatistics) to predict values at unsampled locations. GENSTAT (version 7) was used to compute experimental variograms, fit these with various authorised mathematical models and use them to calculate kriged estimates on a fine regular grid (of latitudes and longitudes). These grids were then interpolated using ArcMap's Spatial Analyst extension (ArcGIS 8.2, ESRI) to produce continuous rasters. This method was also used to map the environmental factors (water temperature and salinity), which were collected during the ECBTS and CGFS. See Sections I 6.3.1. & I 6.5. in Carpentier *et al.* (2005) for a more detailed description of the method used.

2.3. Habitat suitability modelling using quantile regression

The method used to construct the habitat models for *R. clavata* and *S. canicula* (juveniles/adults) is termed quantile regression, a method able to estimate environmental imposed upper limits to species-habitat responses (Cade & Noon, 2003). One of the main advantages of this method is that spatial models subsequently constructed in GIS (Geographical Information Systems) tend to describe potential rather than actual patterns of species distributions, the former being less likely to underestimate habitat quality, and therefore have subsequent benefits for precautionary management principles.

Model selection involved assessing the various contributions of five measured environmental factors (depth, seabed sediment type, bed shear stress, surface water temperature and salinity) to estimate the species response (here the catch rate in numbers of fish per km^2). Those environmental factors that offered no appreciable contribution were dropped from the model. Depth, temperature and salinity were measured *in situ* at ECBTS and CGFS trawl stations, while seabed sediments and bed shear stress data were extracted from digital maps. For each species and each survey, the output of the modelling procedure was an equation describing how the maximum abundance for a fish species varied according to changes in each of the environmental factors. The equation was used to recode digital maps of the environmental factors (FIGURE 3) to produce a map of predicted catch rates. The assumption of the modelling procedure is that catch rates are directly related to habitat suitability, so higher catch rates mean higher habitat suitability. See Section I 6.3.3.2. in Carpentier *et al.* (2005) for a more detailed description of the method used.

2.4. Fish community analysis

Vaz *et al.* (2004) identified and described the fish community in the Eastern English Channel and related them to physical and hydrological features. See Vaz *et al.* (2004) and Sections I 6.3.2. & II 4.2. in Carpentier *et al.* (2005) for more detailed descriptions of the methods used.

2.4.1. Classification of the fish community

The classification of the fish community (84 species in total including two cephalopods and three macro-crustacean species) was based on 1988-2004 abundance data from the CGFS (1,448 stations) and was obtained using the TWINSPAN method described in Hill *et al.* (1975). This method combines ordination and dichotomous classification: it is a hierarchical divisive algorithm based on a Detrended Correspondence Analysis (DCA) of the original data matrix (site * species), which attempts to summarise the major trends in the data. The sub-communities are characterised by indicator species (which have a statistical weight in the discrimination of a given sub-community) and preferential species (having a strong affinity for a given sub-community, both in occurrence frequency and abundance). By occurrence frequency, it is meant the number of times a species has been observed in a given sub-community (or "group"). Abundance is given in number of fish per km^2. The results are usually presented using a dendrogram.

2.4.2. Spatial structure of the fish community and relation to the environment

Spatial structure.

The spatial structure of the defined community was investigated using geostatistics through indicator kriging of each sub-community type (Webster & Oliver, 1990). The sub-community groups were assigned to their corresponding station locations and were treated as continuous variables. Spatial interpolation was then used to produce a distribution map of the fish community structure using GIS (ArcGIS).

Relationship to the environment.

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 & Smilauer, 1999). This method was used to explore the fish community structure and the correlation of its main gradients of variation with the potential explanatory (environmental) variables, i.e. depth, temperature, salinity, seabed sediment type.

Redundancy Analysis (RDA) is a direct extension of multiple regression to the modelling of multivariate response data (Legendre & Legendre, 1998). This method was used in combination with Monte-Carlo permutation tests to explore the multilinear relationships between fish sub-communities and the environment, i.e. depth, temperature, salinity, seabed sediment type.

3. RESULTS

3.1. Spatial patterns of abundance in July/August and October (1989-2004)

The spatial patterns of *R. clavata* were rather uneven for the period 1989-2004, though the areas with the highest indices of relative abundance tended to occur in coastal waters, including off the French coast (e.g. near to the Béthune, Somme, Authie and Canche estuaries), the Outer Thames Estuary and off Dungeness and Brighton on the English coast (see FIGURE 2 for location of place names). Such patterns were apparent in both July/August (FIGURE 4a) and October (FIGURE 4b). In July/August 1998, *R.* clavata were relatively abundant from the coast of southern England to the French coast near the Somme, Authie and Canche estuaries. Abundance indices were also relatively high in some offshore areas for some years in October, especially in the south-western part of the study area. Patterns of abundance seemed to be more constrained spatially in October than in July/August. As expected, this species was found on both hard (pebble, gravel) and sandy seabed sediment types in the study area, and was more abundant in coastal areas.

In contrast to *R. clavata*, the spatial patterns of *S. canicula* in the study area were more stable over the period 1989-2004. *S. canicula* was generally found in high abundance in the offshore waters of the south-western part of the study area, and this was observed in both July/August

(FIGURE 5a) and October (FIGURE 5b). *S. canicula* was also abundant in the Dover Strait (FIGURE 5a), though this was less apparent in October (FIGURE 5b). The spatial distributions of abundance were more constrained in July/August than in October, when the south-western area with relatively high indices of abundance extended inshore to both French and English coastal waters. As expected, this species tended to prefer the coarse grounds of the study area, but also occurred on sandy bottoms

3.2. Habitat suitability in July/August and October

The habitat suitability model for *R. clavata* in July/August (N = 587, 90th quantile) only contained parameters for depth and sediment type, whilst the October model (N = 605, 90th quantile) contained four parameters (depth, seabed sediment type, sea surface salinity and bed shear stress). The correspondence between the map of mean survey abundance (FIGURE 6a) and the habitat suitability map (FIGURE 6b) in July/August was relatively high, with both maps indicating that the distribution was mostly inshore, and highest along the French and English coasts, particularly near the mouths of estuaries and in the sandy bays along the southern English coast. The predicted habitat quality of the coarse grounds in the south-western parts of the study area were not supported by survey data (FIGURE 4a) though CGFS data indicated that *R. clavata* could be abundant on these grounds (FIGURE 4b). In October, the map of mean survey abundance (FIGURE 6c) and the habitat suitability map (FIGURE 6d) indicated that the distribution did not follow as clear a pattern as the maps for July/August. Correspondence between the map of mean survey abundance and the habitat suitability map in October were nevertheless relatively high: mean survey abundance and habitat suitability is at their highest close inshore along both French and English coasts, with high habitat suitability and mean survey abundance also located in the south-western part of the study area.

The habitat suitability model for *S. canicula* in July/August (*N* = 587, 85th quantile) contained all parameters (depth, seabed sediment type, bed shear stress, sea surface temperature and salinity), whilst the October model (*N* = 605, 80th quantile) contained all parameters except bed shear stress. The maps of mean survey abundance in July/August (FIGURE 7a) and October (FIGURE 7c) describe a relatively broad distribution across the south-western part of the study area, and these are in close agreement with the predicted habitat suitability maps for the same months (FIGURES 7b & 7d, respectively).

3.3. Fish community analysis

3.3.1. Classification of the fish community

Four sub-community groups could be identified from community analyses of October data (FIGURE 8). *S. canicula* was one of the three indicator species of the offshore fish community (Group 1) and *R. clavata* one of the preferential species of this same group. Group 1 was also characterised by other elasmobranchs, including greater-spotted dogfish *Scyliorhinus stellaris* and starry smoothhound *Mustelus asterias*. Both *S. canicula* and *R. clavata* were also preferential species of the coastal heterogeneous fish community (Group 4), which was characterised by a variety of flatfish, including *S. solea, P. platessa*, and dab *Limanda limanda*. Two gadoids, pout *Trisopterus luscus* and poor cod *Trisopterus minutus*, were also typical of both communities. *S. canicula* occurred at both high abundance and occurrence frequency in Group 1 and at lower occurrence frequency but significant abundance level in Group 4. *R. clavata* had similarly high occurrence frequency and abundance levels in both Groups. For more detailed descriptions of the fish communities, see Section II 4.2. in Carpentier *et al.* (2005) and Vaz *et al.* (2004).

3.3.2. Spatial structure of the fish community and relationship to the environment

Spatial structure. In October, the four sub-community groups showed a clear transition gradient from offshore (Group 1) to very coastal and even estuarine locations (Group 4) (FIGURE 8).

Relationship to the environment. PCA revealed that the four sub-communities were strongly structured according to both sediment type and depth. Sub-communities drifted from Group 1 to Group 4 with both shallower depths and decreasing sediment particle sizes, indicating a transition from offshore waters (deeper and coarser seabed sediment types) to coastal waters (shallower and finer seabed sediment type). The relationship with temperature and salinity was not clearly identifiable.

The RDA in combination with Monte-Carlo permutation tests showed that the tested environmental factors (i.e. depth, seabed sediment type, temperature, salinity) were significantly ($p < 0.002$) correlated to the fish community structure. Consistent with the PCA, the first axis was strongly correlated to depth and seabed sediment type, with sub-communities drifting from Group 1 to Group 4 with both shallower depths and decreasing sediment particle sizes, here again indicating a transition from offshore (Group 1) to coastal waters (Group 4). Temperature and salinity were found to be correlated to the second axis, with sub-communities drifting from Group 1 to Group 4 with both declining temperature and salinity. This also suggested a transition from offshore (Group 1) to coastal waters (Group 4). Indeed, offshore waters in the study area tend to be comparatively warmer and more saline during October than inshore waters. The offshore-inshore salinity gradient is due to the presence of the coastal flow (FIGURE 3e, flowing west to east), which is maintained along the Northern French coast as a result of large inputs of freshwater from French rivers. The temperature gradient is more seasonal, resulting from cold autumn rainfall feeding in the rivers of Northern France, which then feed in the coastal flow.

The RDA analysis suggested that Group 1 was an offshore (deeper water) sub-community, showing a preference for hard sediment types (gravel, pebbles) and oceanic hydrological conditions (higher salinity, warmer temperature; and also high values of bed shear stress as shown in FIGURE 3c). In contrast, Group 4 was a more coastal (shallow water) sub-community, showing a preference for heterogeneous sediment types (mud to coarse sand) and coastal hydrological conditions (lower salinity, colder temperature, lower values of bed shear stress). The results of the RDA analysis were strikingly well matched to the spatial structure of the fish community as obtained by geostatistical interpolation (FIGURE 8), with the exception of the presence of a Group 1 located in the northern part of the Dover Strait. Although not offshore, this area is characterised by hard seabed sediments (gravel and pebbles, FIGURE 3b) and high values of bed shear stress (FIGURE 3c). The fact that *S. canicula* and *R. clavata*, which are benthic feeders, were also preferential species of a more inshore sub-community (Group 4) may be linked to the spatial distribution of their benthic prey in the study area. Indeed, benthic species richness and abundances are relatively high in coastal areas (Section II 2.2. in Carpentier *et al.*, 2005), which may compensate for a habitat less favourable to *S. canicula* and *R. clavata* (i.e. lower salinity and colder waters). Section II

4.2. in Carpentier *et al.* (2005) and Vaz *et al.* (2004) presented more detailed descriptions of the four Groups' spatial structures.

4. DISCUSSION

It is hoped that the present study will help draw a more accurate picture of the spatial distribution of *R. clavata* and *S. canicula* in the Eastern English Channel, as well as increasing the scientific understanding of their relationship with the environment. Depth and seabed sediment types were key factors in defining their suitable habitats, highlighting the strong influence of the physical environment on the distribution of these two species. On a finer scale, the availability of prey and the requirements for females to have suitable egg-laying substrates will also affect the distribution of these species. Indeed, the high abundance of *S. canicula* on the coarse grounds in the Dover Strait and south-west of the study area may be linked to the presence of erect, sessile invertebrates (e.g. *Flustra*) that are important egg-laying substrates (Ellis & Shackley, 1997; Kaiser *et al.*, 1999). It is noteworthy that *S. canicula* are most abundant on such grounds in July, which coincides with the peak spawning season (Ellis & Shackley, 1997), and more widespread in October, when egg-laying is reduced. It is possible that the more widespread distribution in the autumn, apparent from October surveys, reflects an inshore movement onto feeding grounds, as the diet of *S. canicula* is dominated by invertebrates occurring in such habitats (Ellis *et al.,* 1996).

Annual spatial patterns in July/August and October (1989-2004) and suitable habitat modelling have confirmed that, in the Eastern English Channel, *R. clavata* was found mainly in shallow coastal waters, preferentially on sandy seabed sediment types, although it was also found to a lesser extent on harder (pebbles and gravel) seabed sediment types. It is noteworthy that this species tended to be more widely spatially distributed in July/August compared to October, when its coastal distribution was less widespread. In October, this species was also found offshore, consistent with the fact that, in October, this species was a preferential species for two fish sub-communities of seemingly incompatible environmental characteristics (offshore and coastal). One explanation could be that, in October, some of the *R. clavata* stock moved in a south-western direction towards the warmer, high salinity offshore waters. This was supported by the fact that salinity was a significant environmental factor in the delineation of the suitable habitat of this species in October (positive relationship with abundance), and by a less clear habitat map for this month. However, it is more likely that the difference in spatial patterns between July/August and October (at least) partly resulted from differences in sampling gear between the two surveys. Indeed, the British beam trawl is better at catching juvenile rays (which occur on inshore nursery grounds) than mature rays, whilst the French GOV trawl is better to sample larger rays (i.e. mature). Although almost all *R. clavata* caught in October were immature, the French gear may have under-sampled this species, notably in coastal waters.

Annual spatial patterns in July/August and October (1989-2004) and suitable habitat modelling have confirmed that in the Eastern English Channel, *S. canicula* is most abundant on coarse grounds in the Dover Strait and the south-western parts of the study area. This species had a marked preference for hard seabed sediment types (gravel and pebbles), although it is also widely distributed on finer sediments. This species tended to have more constrained spatial distributions in July/August compared to October. The more widespread distributions observed in October were consistent with the fact that during this month, *S. canicula* was an indicator species for a fish sub-community that was characteristic of deep offshore waters (warmer, higher salinity), as well as being a preferential species for a fish sub-community characteristic of shallow coastal waters (colder, lower salinity). The higher abundance of their benthic preys (e.g. *Aphrodita* and *Buccinum)* in coastal waters may have attracted part of this species' stock to more inshore areas in October, despite a relatively less suitable habitat (colder, lower salinity).

In the Eastern English Channel, *R. clavata* is a key commercial species for both the French and British fleets. Since 1995, landings in the CHARM study area have nevertheless declined on both sides of the Channel, especially in French harbours (25 tonnes in 2003) (Section II 4.1. in Carpentier *et al.*, 2005). British landings of *S. canicula* in the CHARM study area have remained relatively low during the period 1989-2003 as a result of its low market value, and it is generally discarded. This species is nevertheless abundant: in the CHARM study area, French landings reached 700 tonnes in 1997, but then declined markedly since then (reaching 300 tonnes in 2003) (Section II 4.1. in Carpentier *et al.*, 2005). Neither of these species is managed by TAC (Total Allowable Catch), which raises concern in the light of the observed decline landings from the study area (which could reflect declining stocks). Vaz *et al.* (in preparation) reported that almost all the *R. clavata* in October were juveniles, and the Thames Estuary and Solent are also known to be important nursery grounds for this species (Ellis *et al.,* 2005a). Further studies to examine the preferred habitats of mature female rays and the identification of spawning grounds are also required if effective spatial management for this species are to be considered.

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REFERENCES

Cade, B. S. & Noon, B. R., 2003. A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment*, **1**: 412-420

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. & 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*.

Ellis, J.R., Cruz-Martinez, A., Rackham, B.D. & Rogers, S.I. (2005a). The distribution of chondrichthyan fishes around the British Isles and implications for conservation. *Journal of Northwest Atlantic Fishery Science*, **35**: 195–213. Ellis, J.R., Dulvy, N.K., Jennings, S., Parker-Humphreys, M. and Rogers, S.I. (2005b). Assessing the status of demersal elasmobranchs in UK waters. *Journal of the Marine Biological Association of the United Kingdom*, **85**: In press.

Ellis, J. R., Pawson, M. G., Shackley & S. E., 1996. The comparative feeding ecology of six species of shark and four species of ray (Elasmobranchii) in the North-east Atlantic. *Journal of the Marine Biological Association of the United Kingdom*, **76**: 89-106

Ellis, J. R. & Shackley, S.E. (1997). The reproductive biology of *Scyliorhinus canicula* in the Bristol Channel, U.K. *Journal of Fish Biology*, **51**:361–372.

Hill, M. O., Bunce, R. G. H. & 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

Kaiser, M. J., Rogers, S. I. & Ellis, J. R. (1999). Importance of benthic habitat complexity for demersal fish assemblages. *American Fisheries Society Symposium*, **22**: 212–223.

Larsonneur, C., Vaslet, D. & 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. & Legendre, L., 1998. *Numerical Ecology*. Elsevier, Amsterdam, 853 *pp.*

Leps, J. & Smilauer, P., 1999. *Multivariate Analysis of Ecological Data*. Faculty of Biological Sciences, University of South Bohemia, Ceske Budejovice

Pawson, M.G. (1995). Biogeographical identification of English Channel fish and shellfish stocks. Fisheries Research Technical Report, MAFF Directorate of Fisheries Research, 99: 72pp

Quero, J.-C. (1984). Scyliorhinidae. In: *Fishes of the North-eastern Atlantic and the Mediterranean* (Whitehead, P.J.P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J. and Tortonese, E., eds.). UNESCO, Paris, Volume I, 95–100.

Rousset, J., 1990. Catches and geographical distribution of selachians on the western coast of Brittany. *Journal of the Marine Biological Association of the United Kingdom*, **70**: 255-260

Stehmann, M. & Bürkel, D. L., 1984. Rajidae. In: *Fishes of the north-eastern Atlantic and Mediterranean*. (P. J. P. Whitehead, M. -L. Bauchot, J. -C. Hureau, J. Nielsen and E. Tortonese, eds.) UNESCO, Paris. vol. 1, 163-196.

Vaz, S., Carpentier, A. & Coppin, F., 2004. Eastern English Channel Fish Community from 1988 to 2003 and its Relation to the Environment. In: International Council for the Exploration of the Sea, Annual Science Conference (CM 2004/K:40), Vigo, Spain

Webster, R. & Oliver, M. A., 1990. *Statistical Methods in Soil and Land Resource Survey*. Oxford University Press, New York

Wheeler, A., 1978. *Key to the fishes of Northern Europe: a guide to the identification of more than 350 species*. London: Frederick Warne

FIGURES

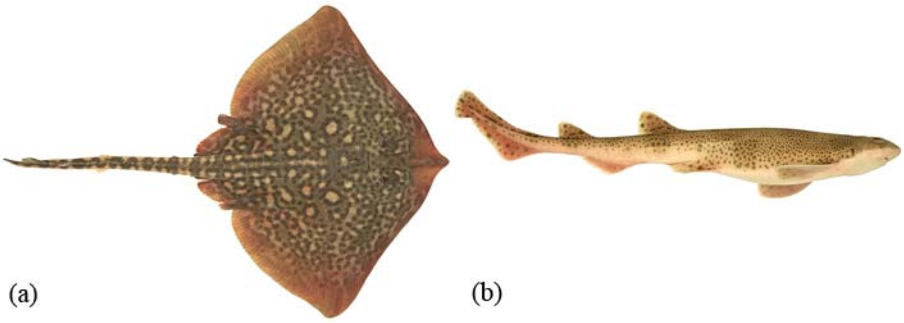


FIGURE 1. (a) Thornback ray *Raja clavata* and (b) lesser-spotted dogfish *Scyliorhinus canicula*, © IFREMER.

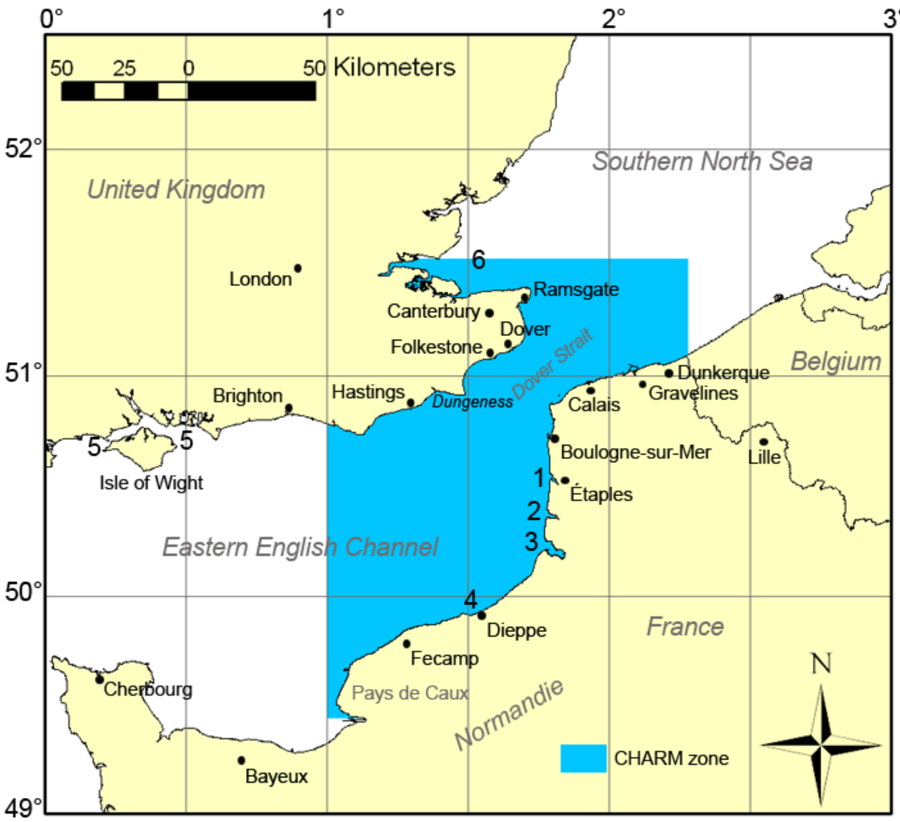


FIGURE 2. The study area of the CHARM project (phase I), showing the Eastern English Channel and the Dover Strait. Estuaries on the French coast: Canche (1), Authie (2), Somme (3), Béthune (4). On the British coast: Solent (5), Thames estuary (6).

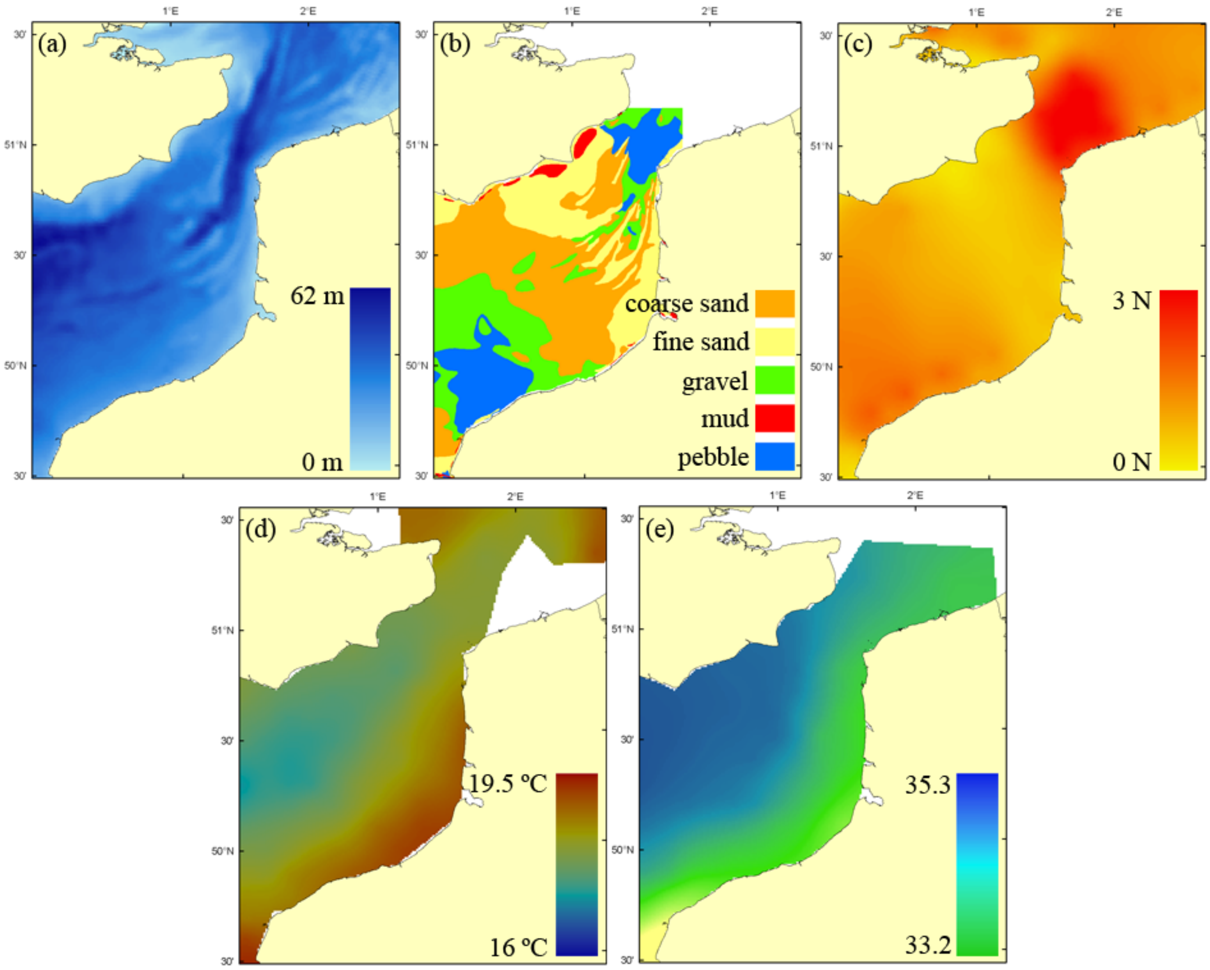
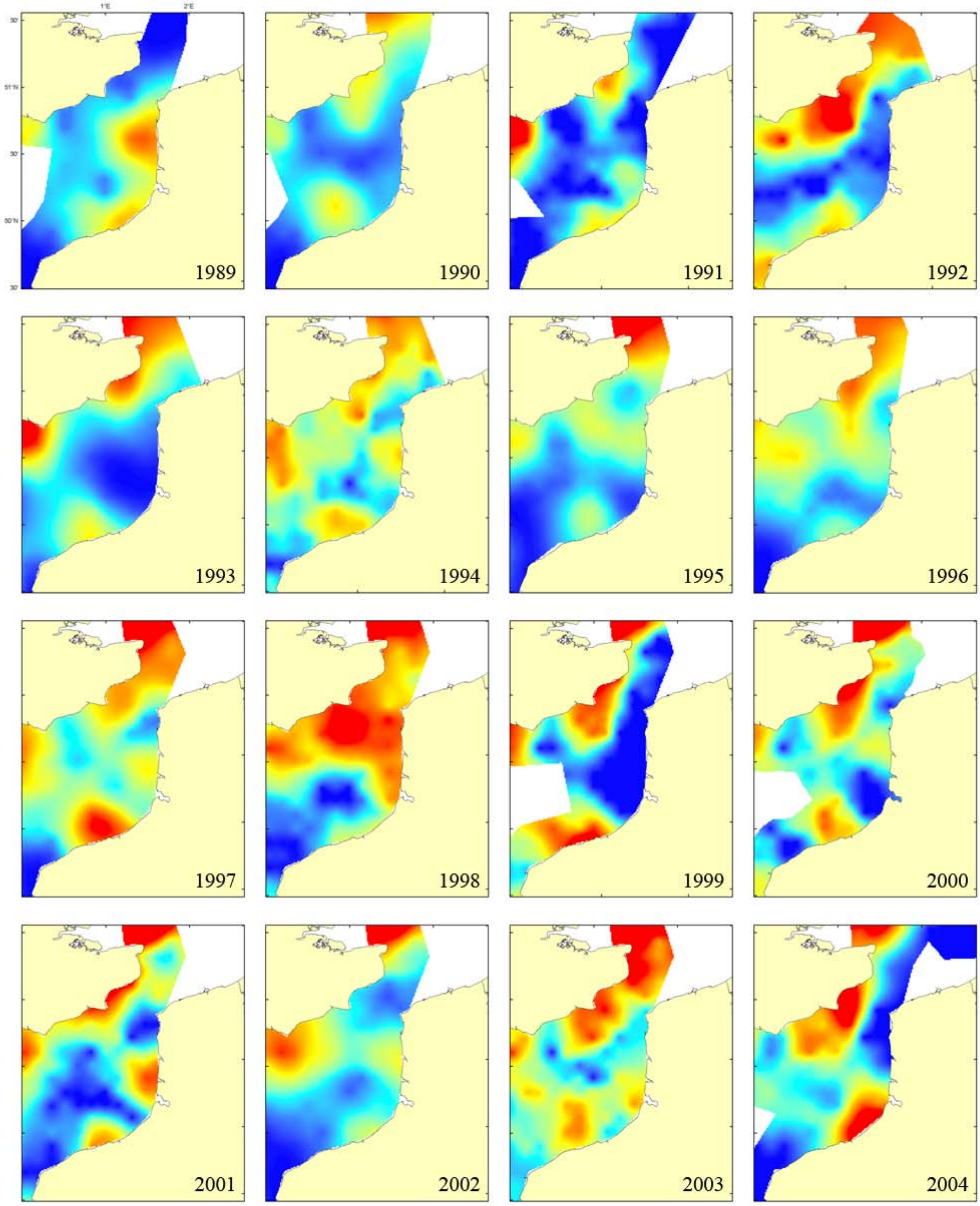


FIGURE 3. Digital maps of environmental parameters, used to map habitat suitability of *R. clavata* and *S. canicula*. (a) Depth (bathymetry plus mean sea level), *source:* SHOM & IFREMER; (b) seabed sediment types, *source:* Larsonneur *et al.*, 1979; (c) bed shear stress, a measure of the pressure applied on the sea bed as a result of tidal currents, *source:* POL; (d) mean sea surface temperature (e.g. July/August); (e) mean sea surface salinity (e.g. October). Only FIGURES 3a, 3b, 3d and 3e were used to investigate the relationship between fish communities and the environment.

Raja clavata, ECBTS survey (July/August)



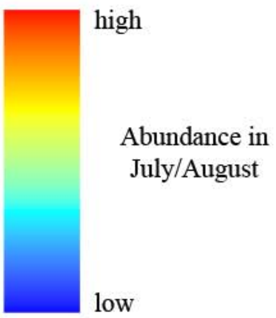


FIGURE 4a. Survey relative abundance patterns (1989-2004) of *R. clavata* in July/August in the study area, mapped using geostatistics.

Raja clavata, CGFS survey (October)

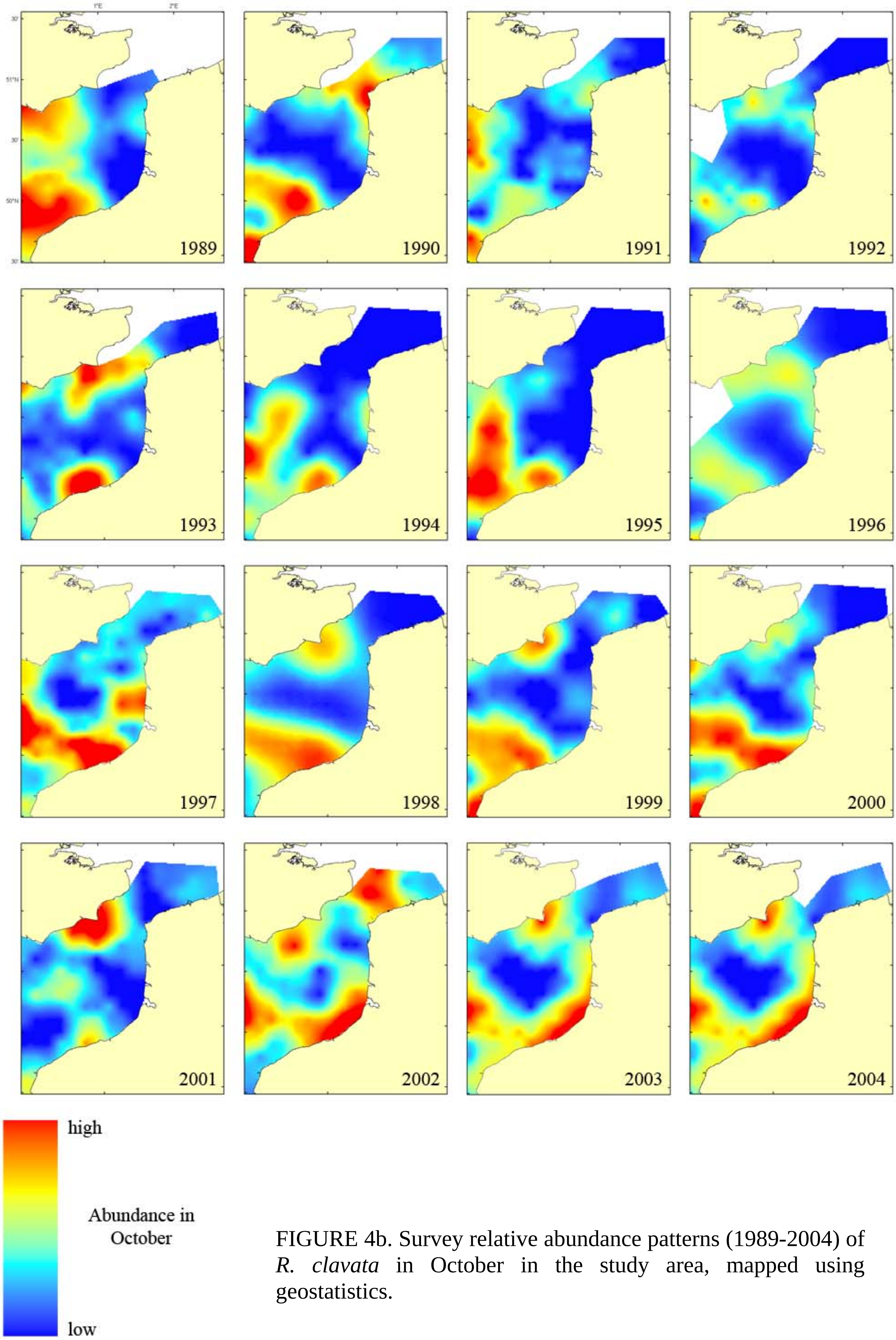
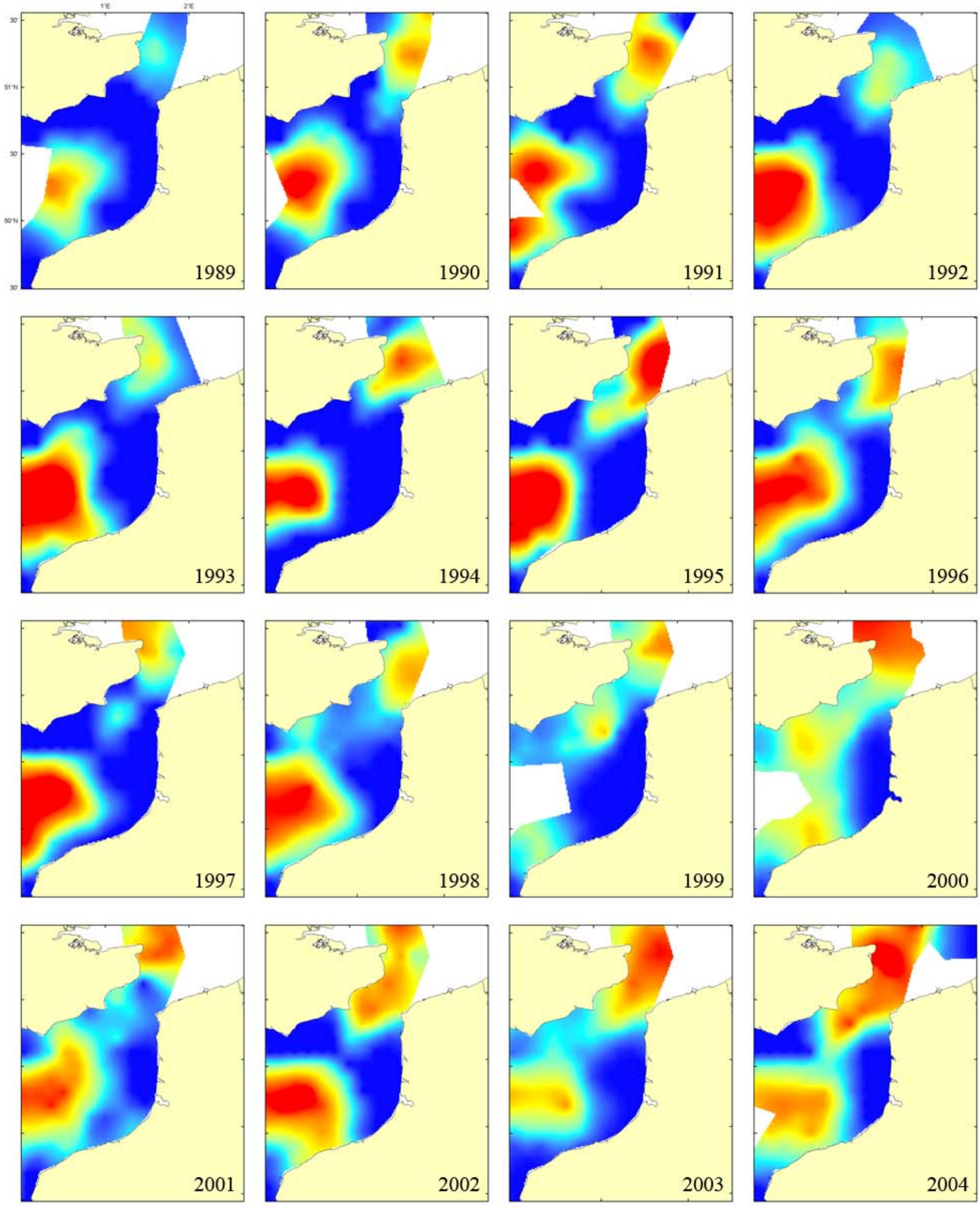


FIGURE 4b. Survey relative abundance patterns (1989-2004) of *R. clavata* in October in the study area, mapped using geostatistics.

Scyliorhinus canicula, ECBTS survey (July/August)



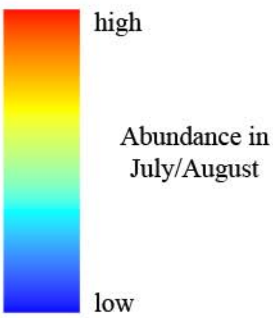
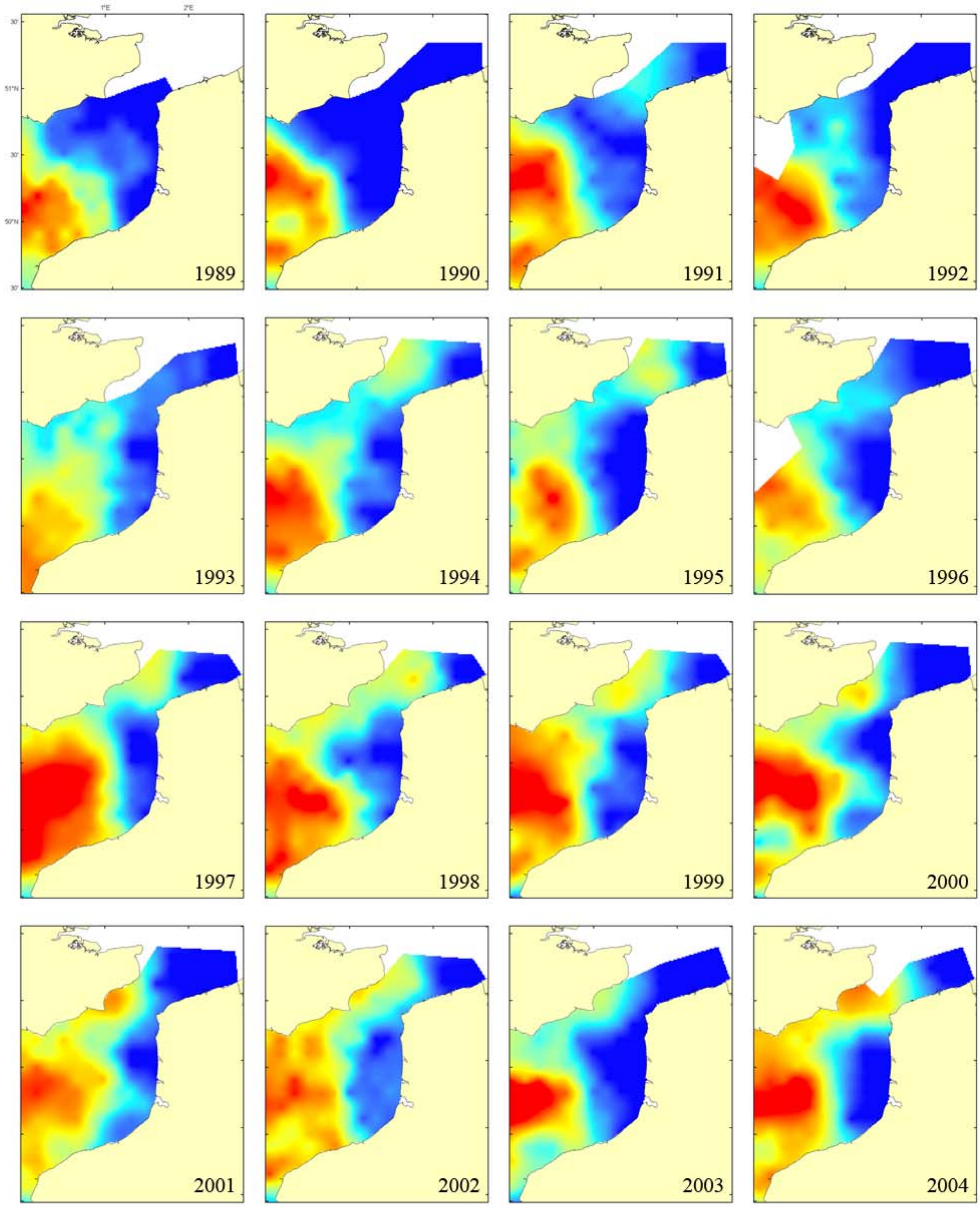


FIGURE 5a. Survey relative abundance patterns (1989-2004) of *S. canicula* in July/August in the study area, mapped using geostatistics.

Scyliorhinus canicula, CGFS survey (October)



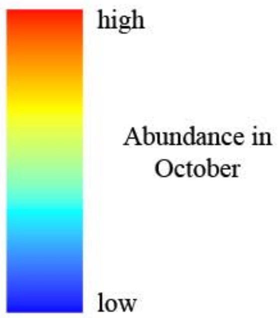


FIGURE 5b. Survey relative abundance patterns (1989-2004) of *S. canicula* in October in the study area, mapped using geostatistics.

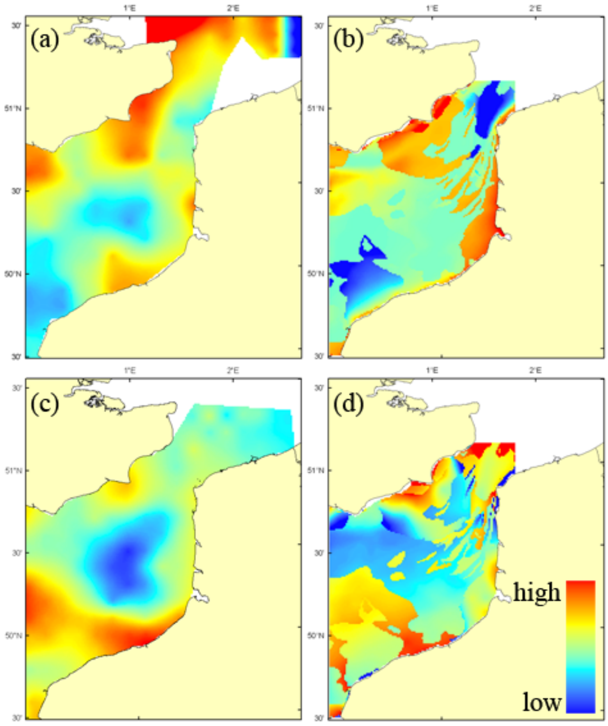


FIGURE 6. Survey mean relative abundance maps in (a) July/August and (c) October, and habitat suitability maps in (b) July/August and (d) October, for *R. clavata*.

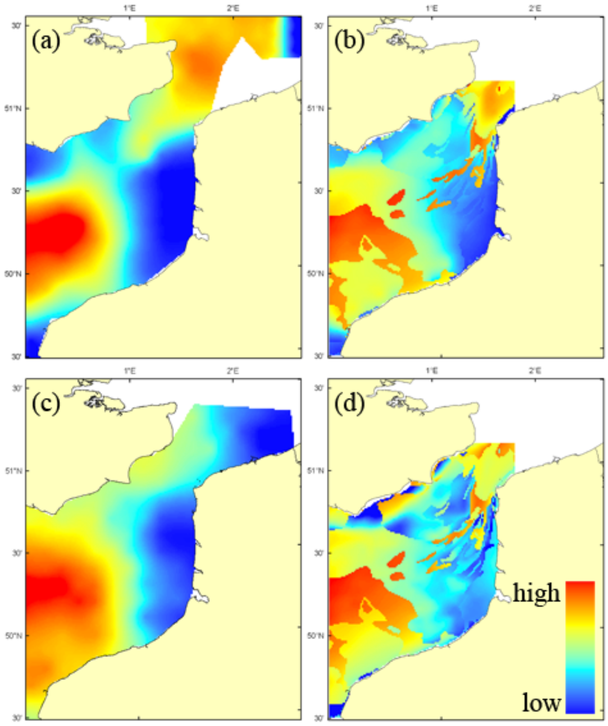


FIGURE 7. Survey mean relative abundance maps in (a) July/August and (c) October, and habitat suitability maps in (b) July/August and (d) October, for *S. canicula*.

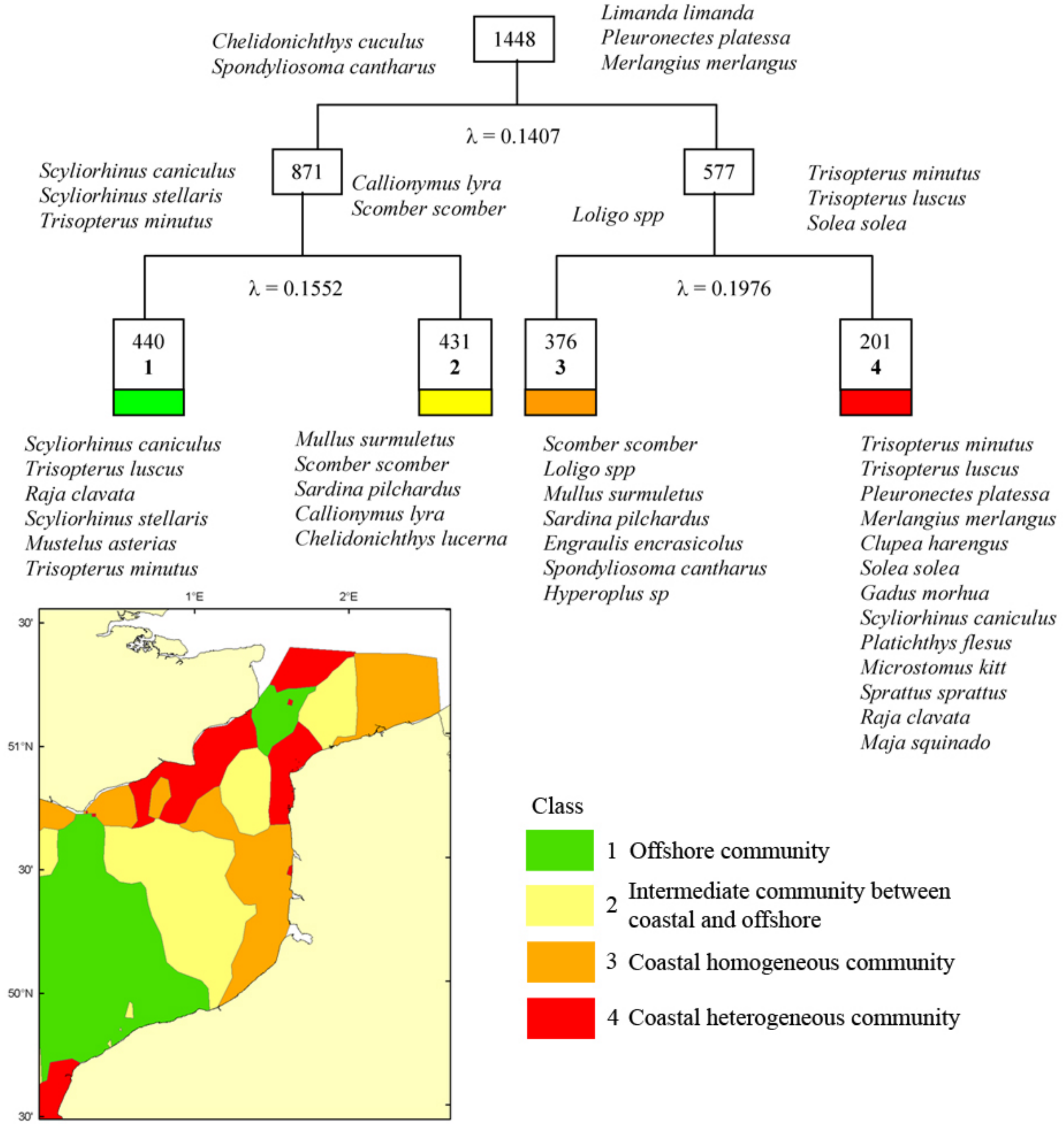


FIGURE 8. TWINSPAN classification of fish communities. The dendrogram represents the first two levels of division. DCA first axis eigen-values are shown for each division. For each group, the corresponding indicator species are listed. The number of samples in each sub-group is indicated in the boxes. The preferential species of the four sub-communities are listed at the bottom of the dendrogram. The map shows the spatial patterns of the four sub-communities in the study area in Autumn (1988-2003).