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Functional entities in Biscay pelagic ecosystem and their relation with the distribution of fish

by

Pierre Petitgas, Alain Herbland, Daniel Delmas, Paul Bourriau, Jean Pierre Bergeron, Noussithe Koueta, Jean Marie Froidefond, Jacques Massé, Maria Santos, and Pierre Beillois

In spring 2000, IFREMER organised its yearly fisheries acoustic survey on board R/V "Thalassa" over the French shelf of Biscay as a multi-disciplinary platform for estimating and mapping the fish and monitoring the pelagic ecosystem. Acoustics and CUFES (continuous underway fish egg sampler) were coupled allowing combined mapping of the adult fish and its spawned eggs. Four major compartments of the plankton ecosystem were extensively sampled on a grid of stations. More than 50 variables were measured in the plankton relating biomass as well as turn over in four compartments, hydrology, nutrients and particulate matter, bacteria and phytoplankton, meso-zooplankton. First, a joint analysis was performed using Multiple Factorial Analysis (MFA). The method allowed for the estimation of a common factorial space in which to represent the structure in each compartment as well as the common structure to all compartments. The most structuring variables were evidenced. Stations were then grouped based on their positions in the common factorial space. The groups were represented spatially and a strong spatial pattern evidenced. Groups were interpreted as functional pelagic entities as they corresponded to different ecosystems at different state in their seasonal evolution. The distribution of the fish and their eggs was analysed in relation to the hydro-plankton entities using geostatistical variography. Sardine and anchovy distributed in different entities but similar for each fish species and its eggs. Anchovy was shown to be associated with a lesser number of hydro-plankton entities than sardine. Anchovy was more confined to its entities than sardine which crossed the entity borders. Last, the interest in measuring size fractionated chlorophyll during fisheries surveys in Biscay was discussed as the study showed that this parameter enabled to track the river plume hydro-plankton entity in which anchovy spawned.

P. Petitgas, P. Bourriau, J.-P. Bergeron, J. Massé, P. Beillois: IFREMER, Laboratory for Fisheries Ecology, BP 21105, rue de l'ile d'Yeu, 44311 cdx 3, Nantes, France [tel: +33 240 37 40 00, fax: +33 240 37 40 75, e-mail: pierre.petitgas@ifremer.fr]. A. Herbland, D. Delmas: CREMA, BP 5, 17137 L'Houmeau, France [tel: +33 546 50 94 40, fax: +33 546 46 50 06 00, e-mail: Alain.Herbland@ifremer.fr]. N. Koueta: Université de Caen, Esplanade de la paix, Biology et technologie marine, 14032 Caen, France [tel: +33 231 56 55 96, fax: +33 231 56 53 46, e-mail: koueta@criuc.unicaen.fr]. J.-M. Froidefond: Université Bordeaux I, DGO / EPOC, avenue des facultés, 33405 cdx, Talence, France [tel: +33 556 84 88 48, fax: +33 556 84 08 48, e-mail: j.m.froidefo@u-bordeaux.fr]. M. Santos: AZTI, Fisheries department, Herrera Kaia, Portualdea z/g, 20110 Pasajes, España [tel: +34 943 00 48 00, fax: +34 943 00 48 01, e-mail: msantos@pas.azti.es].

Introduction

Fisheries resource monitoring surveys provide a plate-form to monitor the ecosystem at large spatial scale allowing for the characterisation of the link between the fish spatial distribution and its environment. Fish environmental measurements performed during routine pelagic fisheries surveys are usually crude, e.g., temperature and salinity profiles as well as vertically integrated biomass estimates of phytoplankton and zooplankton. In spring 2000, the fisheries acoustic pelagic survey performed by IFREMER on board R/V "Thalassa" was used as a plate-form for an extensive characterisation of the structure of the pelagic ecosystem at large scale over the entire French shelf of the bay of Biscay. Four major compartments were studied: hydrology, nutrients, primary producers and meso-zooplankton. In all, 59 variables were estimated in the four compartments which related to the standing stocks as well as to trophic linkeage between compartments. The study had three objectives. First it was to provide a synthetic and integrated characterisation of the major plankton ecosystem entities based on correlation structure between the many variables from the different compartments. For doing so we used a multi-table factorial analysis. The method allowed for appropriately accounted for correlation structure within and between compartments. Then clustering in the factorial space allowed for grouping stations and mapping. The entities evidenced had integrated characteristics of the different pelagic ecosystem compartments. They were therefore thought of as functional entities. Hydro-plankton functional entities served as integrated descriptors of the plankton dynamical ecosystem the fish trophically depended upon. The second objective of the paper was to characterise the relation between the fish spatial distribution and its trophic environment as characterised by the functional entities. Geostatistical spatial structural tools were used for doing so. Last, because routine fisheries surveys cannot host the sampling of as many variables as was done in 2000, a reduced number of variables were considered to analyse what entities they would detect thus sketching the minimum list of plankton ecosystem variables to be routinely monitored in relation with fish distribution.

Materials

Multi-disciplinary survey. The fisheries survey PEL2000 on board R/V "Thalassa" aimed at assessing anchovy and sardine stocks in ICES areas VIIIa and VIIIb was made a fisheries pelagic ecosystem survey by combining the routine day time fish acoustic survey with an extensive hydro-plankton survey during night time. The following major operations were conducted (Fig. 1): fish echo-integration and mid-water identification trawl hauls were undertaken during day time, a continuous underway fish egg sampler (CUFES, Checkley et al., 1997) was operated during night and day, CTD casts were performed during night time together with the collection of water and plankton at CTD hydro-plankton stations. The survey design was made of parallel transects regularly spaced crossing the entire width of the shelf from 44°N (Gouf de Cap Breton) to 48°N (Pointe du Ratz). Every other transect was sailed also during night time allowing for night CUFES sampling and regularly spaced hydro-plankton CTD stations. The survey lasted 5 weeks, starting in early may in the south and finishing in june in the North. The list of the 19 hydro-plankton variables used in this work is presented in Table 1 and their basic statistics in Table 2.

Hydrology and turbidity. Temperature, salinity, density and fluorescence vertical profiles were obtained using CTD casts at hydro-plankton stations (Fig. 1). Surface temperature and salinity values were those at 5 m depth. Bottom temperature was the last temperature value of the profile. The depth of the maximum density gradient along the density profile estimated the thickness of the mixed layer. Surface water turbidity was estimated by taking a bucket sample of sea water and later analysing its optical properties.

Nutrients and primary producers. After the CTD cast at CTD stations, Niskin bottles were positioned appropriately along the vertical to take water samples at five depths. Sea water samples were taken from the bottles for measurements of nutrients, chlorophyll, and bacteria. For nutrients, seawater samples were filtered on glass fibre filters (Whatman GF/F) with a syringe filtration system. Phosphate was analysed onboard immediately after sampling on a spectrophotometer (Shimadzu UV-

1601) with a 10 cm optical path cell. Samples for nitrate, nitrite and silicate measurements were stored in polyethylene flasks, frozen (-25°C) and analysed later in the laboratory on an autoanalyser apparatus (Skalar). Phosphate, nitrate, nitrite and silicate concentrations were determined according to the classical methods described by Strickland and Parsons (1972) with the respective detection limit of 0.02, 0.05, 0.03, and 0.1 µM and the respective precision of 0.01, 0.05, 0.02 and 0.1 µM. Total chlorophyll a (Chla) and phaeopigments (Phae) were determined by filtration of seawater samples from the Niskin bottles on 25 mm Whatman GFF (generally 100ml). Size fractionation was achieved only at vertical stations and the size fraction limits were respectively 3 µm (Nuclepore polycarbonate filters) and 20 µm (nylon sieve). Filters were frozen and analysed later by the fluorometric acidification procedure in 100% methanol extracts (Holm-Hansen et al. 1965, modified by Holm Hansen and Rieman, 1978). Sea water samples for bacterial counts were preserved with borate-buffered formaldehyde (2% final concentration). Bacteria were enumerated by direct counting after staining with DAPI (Porter and Fieg, 1980). The depth at which 1% of the surface fluorescence was attained determined the euphotic layer. Abundance for each variable was integrated vertically in the euphotic layer.

Meso-zooplankton. Bottom to surface vertical hauls were performed using a WP2 net with a 200 µm nylon mesh, the boat being stopped at CTD stations (Fig. 1). The sample was concentrated by filtration then diluted in a fixed volume, mixed to destroy the organisms and their cells into a soup which was preserved frozen (-40°C). Protein content and enzyme activity were measured in the laboratory. Specific enzyme activity was estimated by dividing enzyme activity by protein mass. Enzyme activity was an indicator for the whole zooplankton community of the major metabolic processes at work. Three enzymes were considered: trypsine, piruvate kinase (Bergeron, 2001) and adenosine transcarbamylase (ATC, Bergeron, 1992). Trypsine being the specific enzyme for cutting the amino-acid junction, its activity indicated proteolytic activity. Piruvate kinase being also a specific enzyme intervening at the key entrance of carbohydrate catabolism in Krebs cycle, its activity indicated glucid catabolic intensity. The relative importance between trypsine and pyruvate kinase activities indicated the trophic link between meso-zooplankton and its lower trophic level as a developed microzooplankton loop was expected to favour high proteolytic activity and a phytoplankton bloom glucid catabolism. ATC being a specific enzyme in the elaboration of nucleic acids, its activity indicated the (de novo) productivity of meso-zooplankton. Values were integrated vertically.

Fish. The acoustic survey design consisted in cross shelf transect lines from coast (20 m depth) to shelf break (250 m depth) sailed during day time at 10 knots (Fig. 1). Transects were parallel and regularly spaced with an inter-transect distance of 12 nautical miles (12 nm). The acoustic equipment was a hull mounted SIMARD EK500 38 kHz echo-sounder. Expert scrutiny of the echogram together with targeted mid-water trawl hauls were employed to identify echo-traces to species. Fish back-scatter was summed along the vertical dimension and averaged along the horizontal dimension every 1 nm (6 minutes at 10 knots) resulting in echo-integrated energy (mV^2m^2) per elementary sampling distance units (ESDU) of one nautical mile (1 nm) along the survey track. Identification trawl hauls were undertaken conditionally to particular acoustic images (sequence of consecutive ESDUs) which during the survey were considered as representative of communities of echo-traces and thus of species assemblages. The fish caught in the mid-water pelagic trawl hauls allowed for the estimation of the species proportions and the weight-length keys. These biological parameters were used to estimate a species echo-integration factor which allowed for the estimation of the fish species density by multiplying the factor by the total fish back-scatter (for more details about this survey see, e.g., Petitgas et al., 2002). Fish abundance (metric tonnes nm^{-2}) was estimated by species for each 1 nm ESDU.

Fish eggs. The CUFES pump was mounted at the end of a pipe at 3 m depth installed on the starboard side of the R/V "Thalassa". Pumping occurred horizontally at the limit of the turbulence zone surrounding the hull of the vessel. CUFES was operated 'underway' during day acoustic surveying and at night between CTD stations and during CTD stations (Fig. 1). The pumped sea water was filtered on collectors fitted with a 500 µm nylon mesh. The underway CUFES samples were taken every 3 nm

(18 minutes at 10 knots) by removing the collector and placing another one for the next sample. Eggs were preserved in 7% formaldehyde and identified to three species categories (sardine, anchovy, all other species) and counted. The CUFES pump flow was continuously measured allowing together with sample duration for the conversion of egg numbers to egg concentrations. Egg 3 m depth density (egg $10m^{-3}$) was estimated by species for each CUFES sample.

Methods

Multiple Factorial Analysis and hydro-plankton functional entities. Multiple Factorial Analysis (MFA, e.g., Dazy and Labarzic, 1996; Lebart et al., 1995) was specially designed to analyse the multivariate structure of N individuals when the variables characterising them are grouped in T compartments. Here, individuals are the CTD stations (N=43) and groups of variables (T=4) are ecological compartments (hydrology, nutrients, primary producers and zooplankton consumers). The method constructs a factorial space named the compromise in which to represent all variables and the T clouds of N stations. The method proceeds in two steps. First Principal Component Analysis (PCA) is performed for each compartment (partial matrix) and the first eigen value serves for appropriately weighting the variables in that compartment. The weighting thus depends on the internal structure of the compartment the variable belongs to. In the second step, a second PCA is performed on the weighted variables and this allows for the construction of the compromise factorial space. Because of the weighting, no compartment can influence by itself the ensemble structure of the compromise. The weighting by the first eigen value in each compartment provides essential mathematical properties to the compromise factorial space. (i) The compromise is the factorial space which is geometrically closest to each compartment factorial space. (ii) The inter-compartment structure (T points), the intra-compartment structure (T clouds of N points) and the structure between all variables can all be represented and analysed in the one compromise space. (iii) The axes of the compromise factorial space can be interpreted as in PCA by the correlation of active or passive variables with the axes. For each individual station, its trajectory between the compartments can be analysed and its compromise position estimated. Clustering of the compromise stations was performed by using hierarchical clustering (compact method). Computations were undertaken using SPAD software (CISIA inc.). The MFA was applied on the centred and normed CTD hydro-plankton 19 variables (Tables 1 and 2). Resulting Groups of CTD hydro-plankton stations were named functional entities.

Importance of certain variables. Fish environmental variables typically monitored during pelagic fisheries surveys form a reduced set of variables, i.e. temperature, salinity and standing biomass in the phytoplankton (Chlorophyll a) and zooplankton (proteins). A PCA was performed on the matrix made of these variables collected at the CTD stations and its factorial axes were projected in the compromise space of the MFA as passive variables. Their correlation with the MFA compromise factorial axes was estimated. Also, stations were grouped in the factorial space of the reduced list of variables and maps of groups were visually compared between the MFA on the extensive list of variables and the PCA on the reduced list.

Spatial relation between hydro-plankton entities and adult fish and their eggs. Fish spatial distribution and that of their eggs are generally thought of as resulting from trophic and hydrodynamic conditions. Because of fish movements and advection/diffusion processes, direct point to point relation between fish and environmental variables are generally noisy and relations difficult to evidence (Maravelias and Reid, 1997). Hydro-plankton entities provided synthetic descriptions of the structure and productivity of the plankton dynamical ecosystems the fish depended upon. Relation of fish not with individual variables but with synthetic descriptors was thought to lead to a clearer picture. Also, because the relation between fish and its trophic environment was not thought of as a relation between the fish abundance at one point and its environment at the same point we introduced the idea of spatial proximity in the analysis (see, e.g., Schneider and Piatt, 1986) and used the variogram (Matheron, 1971) which is a function giving the variance between pairs of point values as a function of the geographical distance separating them. Each acoustic ESDU and each CUFES sample was attributed the code of the hydro-plankton entity that belonged to its nearest CTD hydro-plankton station.

Average fish and egg abundance in each hydro-plankton entity was estimated. Also in each hydro-plankton entity, the percent of ESDU or CUFES samples which were greater than a given threshold estimated the occupied area by fish or eggs. Threshold chosen was the quantile 0.2. Occupied area and abundance in each hydro-plankton entity allowed for testing whether the fish or their eggs were preferentially distributed in particular plankton entities. A variogram was computed for pairs of points standing in the same hydro-plankton entity (intra-group variogram) and averaged over all entities. Another variogram was computed for pairs of points with one standing in a given entity and the other in another entity (inter-group variogram). Comparison of the two variograms was similar to an analysis of variance but as a function of geographical distance. If the inter-group variogram resulted to be greater than the intra-group variogram, this would mean that when crossing the border of a hydro-plankton entity a significant change in the fish abundance or their eggs was expected thus meaning that the geographical distribution of the hydro-plankton entities followed the spatial distribution of the fish or their spawning. If the inter-group variogram showed a slow increase with distance, spatial variation in the distribution of the fish or their eggs would be gradual across the borders of the hydro-plankton entities meaning that the fish would cross the borders being dispersed across the borders. If the inter-group variogram showed a sharp increase with distance, fish spatial variation would occur quickly at crossing the borders meaning that the fish was confined spatially into particular hydro-plankton entities.

Results

Hydro-plankton entities. Differences in the structure of the compartment matrices (partial matrices) were visualised by the distance between matrix points in the compromise factorial space (Fig. 2). Nutrients and Primary Producers were closer to each other than to any other compartment. The point matrices were distributed at the top of a small isocel triangle meaning that they had a lot in common and that they could be summarised by a compromise structure. The first 3 principal axes of the compromise space represented nearly 50% of total variance and the first 6 represented 75% (Table 3). The variables from the different compartments displayed a coherent structure with 2 major axes (Fig. 3). In the first factorial plane (1,2) of the compromise space, we can see the opposition between Nutrients and salinity. Small phyto (CHL3) and deep upper layer were positively related with salinity. We can also see the opposition between large phyto (CHL20) and dominance of bacteria. Large phyto was positively related with glucids (GLC/PROT), nitrate/phosphate ratio (NOx/PO4) and zooplankton productivity (ATC). Dominance of bacteria was positively related with, phosphates (PO4), zooplankton glucid catabiolism (PK), medium phyto (CHL320), zooplankton abundance (PROTm2). The third principal axis (Fig. 3) was determined by surface temperature (Ts) and ammonium (NH4). 4 groups of variables from different compartments were evidenced by their proximity, i.e. correlation structure (Fig. 3), expressisng the links between ecosystem compartments: (CHL20, GLC/PROT, NOx/PO4); (Cbact/Cphyto, PK, PO4); (Tf, TRYP, ATC); (Ts, NH4). Clustering of hydro-plankton stations was performed after various trials using the coordinates of the stations on the first 4 factorial axes of the compromise space. Six groups (hydro-plankton entities) were retained (Fig. 4) and positioned on the Biscay map (Fig. 5) showing coherent and strong spatial pattern. By estimating for each variable its average value per group (hydro-plankton entity), it was possible to assess whether the group mean was significantly higher or lower than the overall average and therefore interpret functionally the hydro-plankton entity groups (Table 4).

Interpretation of hydro-plankton entities. Entity 6 was characteristic was river plumes and were close to the Loire and Gironde estuaries. Entity 6 was characterised by low salinity, high nutrients and high turbidity. Entity 5 was coastal and south and was characterised by high turbidity, low phosphates, low abundance of small phyto (chl3), high zooplankton productivity and low zooplankton biomass. It seems that the ecosystem in entity 5 was already in a well advanced state in the season evolution: previous phytoplankton blooms have utilised the phosphates, phytoplankton and zooplankton abundance are low but zooplankton shows high productivity. Entity 4 was coastal and north and was characterised by low surface salinity, high surface temperature, important nutrient charge for N, ratio of nitrates over phosphates in favour of nitrates, high abundance of large phytoplankton (chl20) and

low bacteria abundance. It seems that the ecosystem in entity 5 was beginning its seasonal evolution with a phytoplankton bloom of large cells. Entity 3 was characteristic of the mid-shelf in north Biscay. It was characterised by high surface temperature, low bottom temperature (characteristic of the structure known as the "Bourrelet froid" - see, e.g., Koutsikopoulos and Le Cann, 1996), low abundance of large phytoplankton (chl20), high relative abundance of bacteria, more carbon in the non living particular organic matter (Cmicrob/COP), high abundance of zooplankton. A month before the survey at the location of entity 3, an important phytoplankton bloom developed which was traced by ocean colour satellite imagery (F. Gohin, comm.pers.). The ecosystem in entity 3 was in a post bloom situation, with small cell primary producers, important charge of organic matter and high abundance of zooplankton. Higher surface temperature in north Biscay (Entities 3 and 5) in comparison to that in south Biscay was explained by the fact that the survey progressed from south to north together with the seasonal surface warming. Entity 1 was located mid-shelf and at shelf-break in south Biscay. It was characterised by high surface salinity, low surface temperature, high abundance of phytoplankton (both chl20 and chl3), and low relative abundance of bacteria. It is supposed that for the ecosystem in entity 1 phytoplankton blooms were repetitive explaining presence of large and small phytoplankton. Entity 2 was located mainly at the shelf-break in north Biscay and also on the outer shelf in south Biscay. It was characterised by high surface salinity, thick upper mixed layer, high abundance of phosphates, high relative abundance of bacteria, high glucid catabolic activity of zooplankton and high zooplankton abundance. The high abundance of phosphates would come from turbulence mixing at the shelf break due to the interaction between wind and tidal internal waves bringing in the euphotic layer nutrients that were deeper than the pycnocline. The importance of bateria and of zooplankton would attest that the phytoplankton bloom was past.

Fish distribution in relation to hydro-plankton functional entities. Maps of fish abundance and that of the density of their eggs (Fig. 6) evidence a strong spatial pattern for anchovy and sardine. Sardine was distributed along the shelf-break, on the outer shelf and at the coast (off Vendée, 46°-47°N; off Arcachon: 44°30N). Their eggs followed this distribution, being mainly located along the shelf-break, on the outer shelf in north Biscay, and on the shelf off Gironde estuary. Anchovy had a more restricted spatial distribution and was located mainly in south Biscay (south of 46°30N) in the inner shelf north of the Gironde estuary and covering the entire shelf south of the Gironde (shelf of Les Landes, 44°-45°30N). Anchovy eggs were located coastal off Vendée, on the shelf off Gironde and on the outer shelf off Les Landes. Over the range of the fish spatial distributions, the hydro-plankton entities constituted a patch work of pelagic ecosystems with varying structure and productivity characteristics. Anchovy had a greater abundance in hydro-plankton entities 5 and 6 (river plumes and coast south) than in any other entity and geographically full filled these entities (Fig. 7). Sardine abundance was more distributed across the entities and these were occupied by sardine in the range 50-70% of their geographical extension. Eggs displayed a similar pattern although more confined to particular hydro-plankton entities. Sardine eggs were more abundance in entities 1 and 2 (outer shelf and shelf break) with high occupation area of these entities and anchovy eggs were very abundance in entity 6 (river plumes) but also occupied entities 5 and 1 (Fig. 7). From the analysis of the variograms (Fig. 8) the following can be said. For sardine and their eggs, the maximum variogram level (i.e., sill) was approximately equal for the variograms computed within and across meaning that sardine displayed as much variance inside than across the entities. The across variogram was always lower at small scale and reached the sill around 8 n.m. for the fish and 5 n.m. for the eggs. Sardine would therefore cross the borders of the entities and it is only at a greater spatial scale (5-10 nm) that the entities and the fish showed concurrent spatial structuring. In contrast, anchovy was more confined to particular entities with more homogeneous density in these entities as the sill of the across entity variogram was always greater than that of the within entity variogram. For adult anchovy, the across entity variogram crossed the within entity variogram at approximately 5 n.m. meaning that anchovy also crossed the entity borders by a few miles. For anchovy eggs, the across entity variogram did not display any structure meaning that transition in anchovy egg abundance was sharp when crossing the borders thus confirming confinement in the entities occupied.

Hydro-plankton characterised with a reduced list of parameters. During routine fisheries acoustic pelagic surveys in Biscay, it is common to record at night hydro-plankton stations, the hydrology and

fluorescence profiles by CTD casts and zooplankton abundance in vertical WP2 net hauls. Thus the reduced set of variables considered was: surface and bottom temperatures, surface salinity, depth of mixed upper layer, total chlorophyll_a, zooplankton abundance (Ts, Ss, Tf, Zmel2, Chl20+Chl320+Chl3, PROTm2). The projection of the principal components c_i ($i=1,...6$) of this reduced set in the factorial space of the MFA showed that they were well correlated with the factorial axes of the MFA (Table 5), in particular with the 4 first axes which were used to make the classification of stations. Thus similar hydro-plankton entities are to be expected if clustering of the stations was performed using the reduced set of variables. Now stations were clustered using the 6 principal axes of the reduced set and choosing 6 groups from the clustering tree (not shown). The hydro-plankton groups of stations obtained (i) by MFA on the extensive list of variables and (ii) by PCA on the reduced set were compared (Fig. 9). With the use of the reduced set of variables, although the general pattern is reproduced (coast-offshore and north-south spatial organisation), one looses to distinguish entities in the coastal areas, i.e., on looses the river plume entity coded 6 as well as the North Biscay coastal entity coded 4.

Conclusion - discussion

In 2000, the French fisheries acoustic survey in Biscay was made an ecosystem pelagic survey and an extensive list of variables were measured to characterise the hydro-plankton compartments. The French shelf in Biscay resulted to be a patchwork of hydro-plankton entities at different states of their seasonal evolution and forced differently in their nutrient inputs (shelf-break and river discharge). In determining the state of the hydro-plankton entity, size fractionated chlorophyll_a abundance were important variables. When entities were defined based on a reduced set of variables containing total chlorophyll_a but not the information on phytoplankton cell size, different coastal hydro-plankton entities were collapsed in one and in particular, the entity characteristic of river plumes was lost. It could therefore be of interest to implement in future routine fisheries surveys automated measurement of size fractionated chlorophyll_a.

During the survey analysed (spring 2000) sardine and anchovy trophic (plankton) environment in Biscay was a patch work of hydro-plankton entities with different ecosystem structure and productivity. Anchovy was related to a lesser number of plankton entities than sardine and its entities were more coastal than those of sardine. Anchovy was more confined in its hydro-plankton entities than sardine which crossed more the entity borders. The scale at which maps of hydro-plankton entities differed with that of fish (fish crossing plankton entity borders) was in the range of 5-10 nm.

More years need be studied to test whether one specie can occupy other hydro-plankton entities than those evidenced here. In the survey analysed, the spatial extension of anchovy distribution was found more restricted than for other years. The methodology used here over a series of years can allow to monitor and characterise the dynamic geography of the fish populations and their spawning in relation with integrated description of plankton ecosystem entities and built the data needed for modelling the spatial dynamics of the fish population across the years. A similar study than the present one across the years would allow for testing with field data the assumption of density-dependent varying habitat occupation. This assumption is the founding assumption underlying the theoretical 'basin' population model (MacCall, 1990) which serves as the basis for spatial dynamic population modelling.

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Table 1: List of variables used in the present work in the different ecological compartments. All variables were measured except Cbact/Cphyto which was estimated by using standard carbon content per cell taken from the litterature.

Ecological compartment	Variables
Hydrology	Ts: surface temperature (°C) Ss: surface salinity (psu) Tf: bottom temperature (°C) Zmel2: depth of upper layer (m) NTU: surface turbitidy (arbitary units)
Nutrients	NOx: nitrates and nitrites abundance (millimole m^{-2}) PO4: phosphate abundance (millimole m^{-2}) NH4: ammonium abundance (millimole m^{-2}) NOx/PO4: ratio of nitrates and nitrites over phosphates
Primary producers	GLC/PROT: ratio of glucids over proteins in particulate organic matter CHL20: chlorophyll a abundance in cells > 20 μm (mg m^{-2}) CHL320: chlorophyll a abundance in cells ranging 3-20 μm (mg m^{-2}) CHL3: chlorophyll a abundance in cells < 3 μm (mg m^{-2}) Cbact/Cphyto: ratio of carbon in bacteria over that in phytoplankton Cmicrob/COP: ratio of carbon in living cells over that in particulate organic matter
Meso-zooplankton	PK: Pyruvate kinase specific activity in water column (mg mn^{-1} g^{-1}) TRYP: trypsine specific activity in water column (mg mn^{-1} g^{-1}) ATC: Adenosine Trans-Carbamylase specific activity in water column (mg mn^{-1} g^{-1}) PROTm2: protein abundance equivalent to referenced bovine serum (mg m^{-2})
Fish	Anchovy abundance (10^3 kg $n.m.^{-2}$) Sardine abundance (10^3 kg $n.m.^{-2}$) Anchovy egg density at 3 m depth (egg 10 m^{-3}) Sardine egg density at 3 m depth (egg 10 m^{-3})

Table 2: Basic statistics of the variables collected at the N=43 CTD hydro-plankton stations. Variable codes and units are in Table 1.

Ecological compartment	Variable	mean	Standard variation	minimum	Maximum
Hydrology	Ts	13.03	0.64	11.98	14.60
	Ss	34.51	1.18	31.10	35.62
	Tf	11.93	0.42	11.06	13.32
	Zmel2	22.51	15.47	6.50	66.50
	NTU	0.35	0.42	0	2.30
Nutrients	NOx	74.40	70.27	11.00	280.00
	PO4	1.66	1.25	0.10	5.40
	NH4	9.13	6.13	0.30	31.00
	NOx/PO4	90.74	152.21	5.00	845.00
Primary Producers	GLC/PROT	1.03	0.33	0.54	1.78
	CHL20	14.41	9.47	0	35.00
	CHL320	8.75	8.69	0	54.30
	CHL3	6.62	4.70	0	18.00
	Cbact/Cphyto	22.26	10.10	7.00	50.00
	Cmicrob/COP	38.49	11.59	20.00	70.00
Meso-zooplankton	PK	0.35	0.29	0.01	1.16
	TRYP	4.16	1.12	2.13	8.46
	ATC	0.37	0.41	0	1.63
	PROTm2	858.29	457.13	120.36	1990.80

Table 3: Cumulative percent explained variance of the 10 first principal axes of the compromise factorial space of the Mulitple Factorial Analysis (eigen values expressed as cumulative percent of their sum).

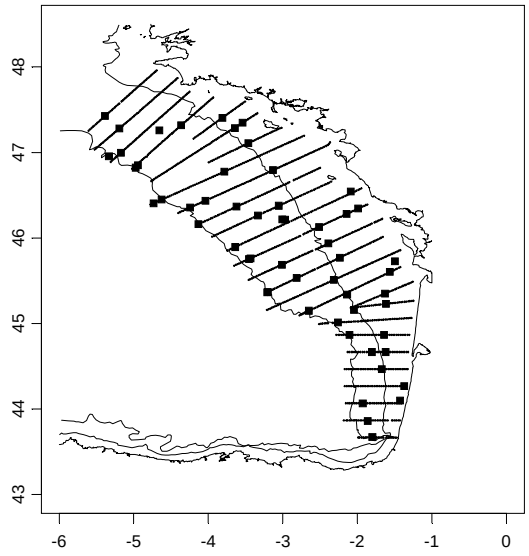
	1	2	3	4	5	6	7	8	9	10
%	22.41	37.75	48.96	59.11	66.86	74.44	79.71	84.47	87.77	90.47

Table 4: Interpretation of each hydro-plankton entity: significant difference (+: positive; -: negative) between overall mean and hydro-plankton entity mean for each variable.

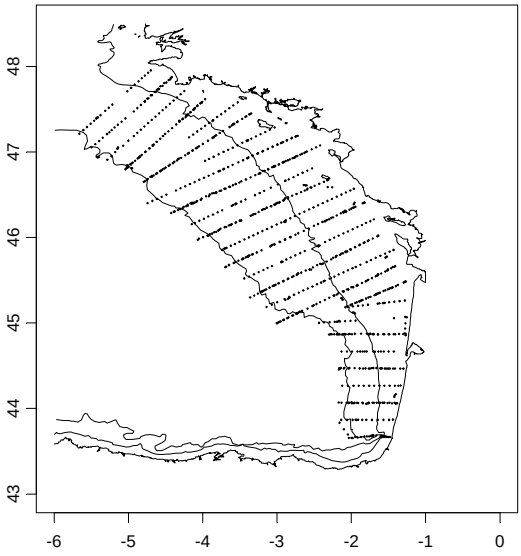
Ecological Compartment	Variables	Entity 1	Entity 2	Entity 3	Entity 4	Entity 5	Entity 6
Hydrology	Ss	+	+		-		-
	Ts	-		+	+		
	Tf			-			
	Zmel2		+				
	NTU					+	+
Nutrients	NOx	-			+		+
	PO4		+			-	+
	NH4				+		
	NOx/PO4				+		
Primary Producers	GLC/PROT		-				
	CHL20	+		-	+		
	CHL320						
	CHL3	+				-	
	Cbact/Cphyto	-	+	+	-		
	Cmicrob/COP			-			
Meso-zooplankton	PK		+				
	TRYP						
	ATC					+	
	PROTm2		+	+		-	

Table 5: Coordinates of the principal components for the reduced set of variables (c) on the principal axes of the Multiple Factorial Analysis for the extensive set of variables (MFA.c). Sum.cos2 is the sum of the square of the coordinates of the components c on the four first MFA.c and it represents the amount of variance in the MFA space that each component c contains.

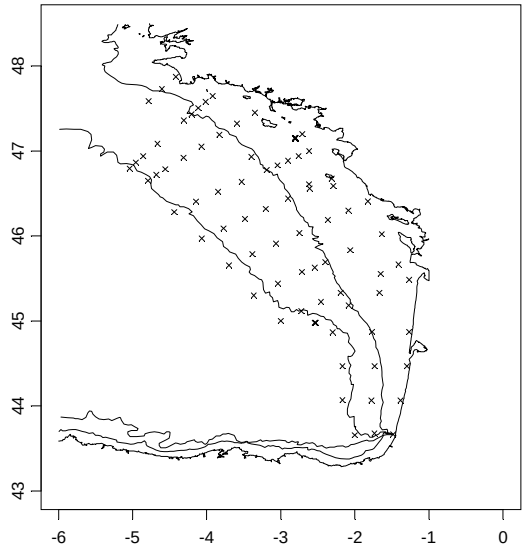
	MFA.c1	MFA.c2	MFA.c3	MFA.c4	Sum.cos2
c1	*-0.849*	0.223	0.213	-0.125	0.83
c2	0.083	*0.438*	-0.078	*0.646*	0.62
c3	-0.213	-0.204	*-0.673*	-0.154	0.56
c4	-0.105	0.211	-0.105	0.366	0.20
c5	0.18	0.007	0.126	-0.08	0.05
c6	-0.004	*0.557*	-0.254	-0.164	0.40



Acoustic records and mid-water trawls



CUFES records



CTD hydro-plankton stations

FIG.1: Sampling designs for adult fish (acoustics), their eggs (CUFES), and CTD hydro-plankton stations during the IFREMER pelagic fisheries and ecosystem survey performed in may 2000 (PEL2000) with R/V “Thalassa”.

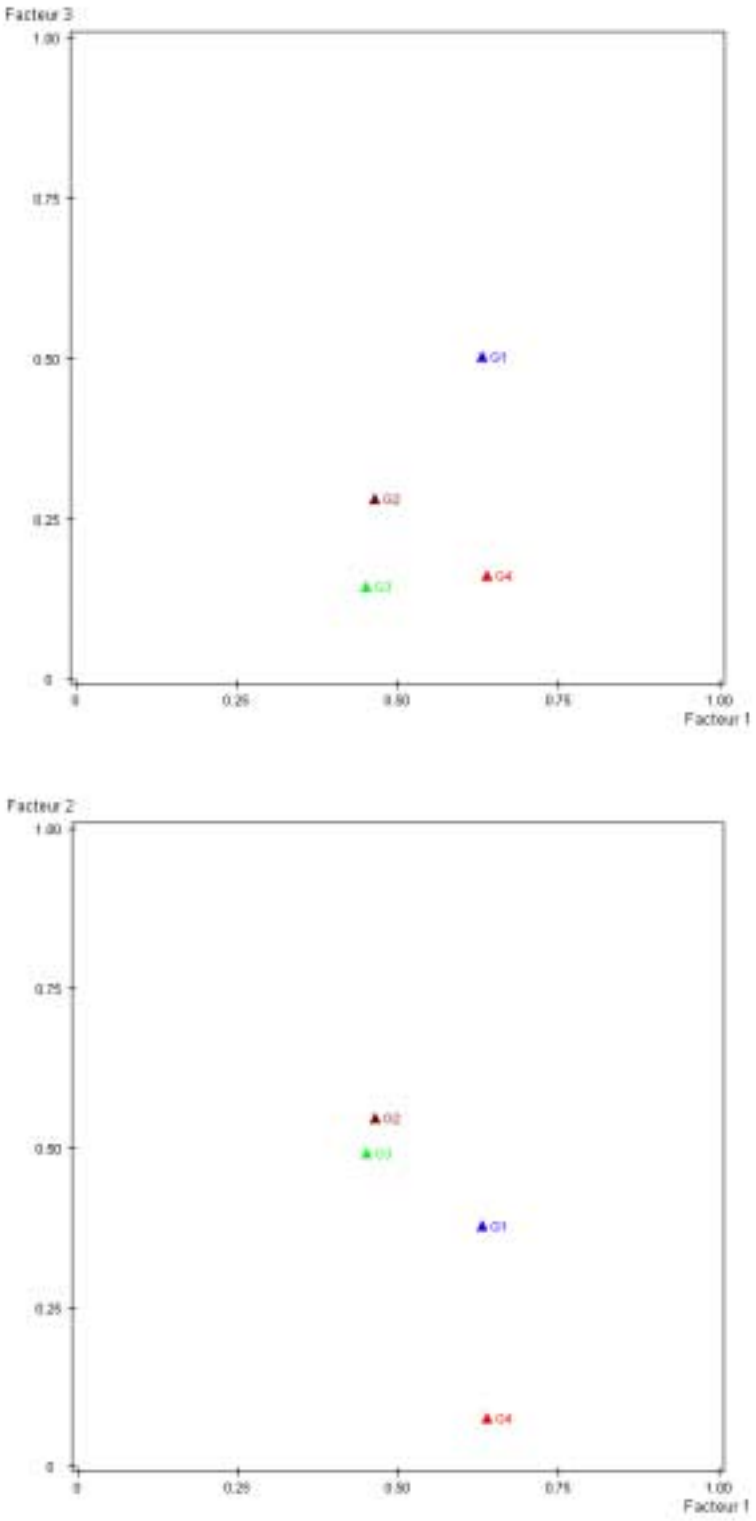


FIG. 2: Inter-structure between ecological compartments: position of the compartments (partial matrices) in the compromise factorial space of the Multiple Factorial Analysis. Above: factorial plane made of axes 1 and 2. Below: factorial plane made of axes 1 and 3. G1 (blue): hydrology compartment; G2 (brown): nutrients compartment; G3 (green): primary producers; G4 (red): meso-zooplankton.

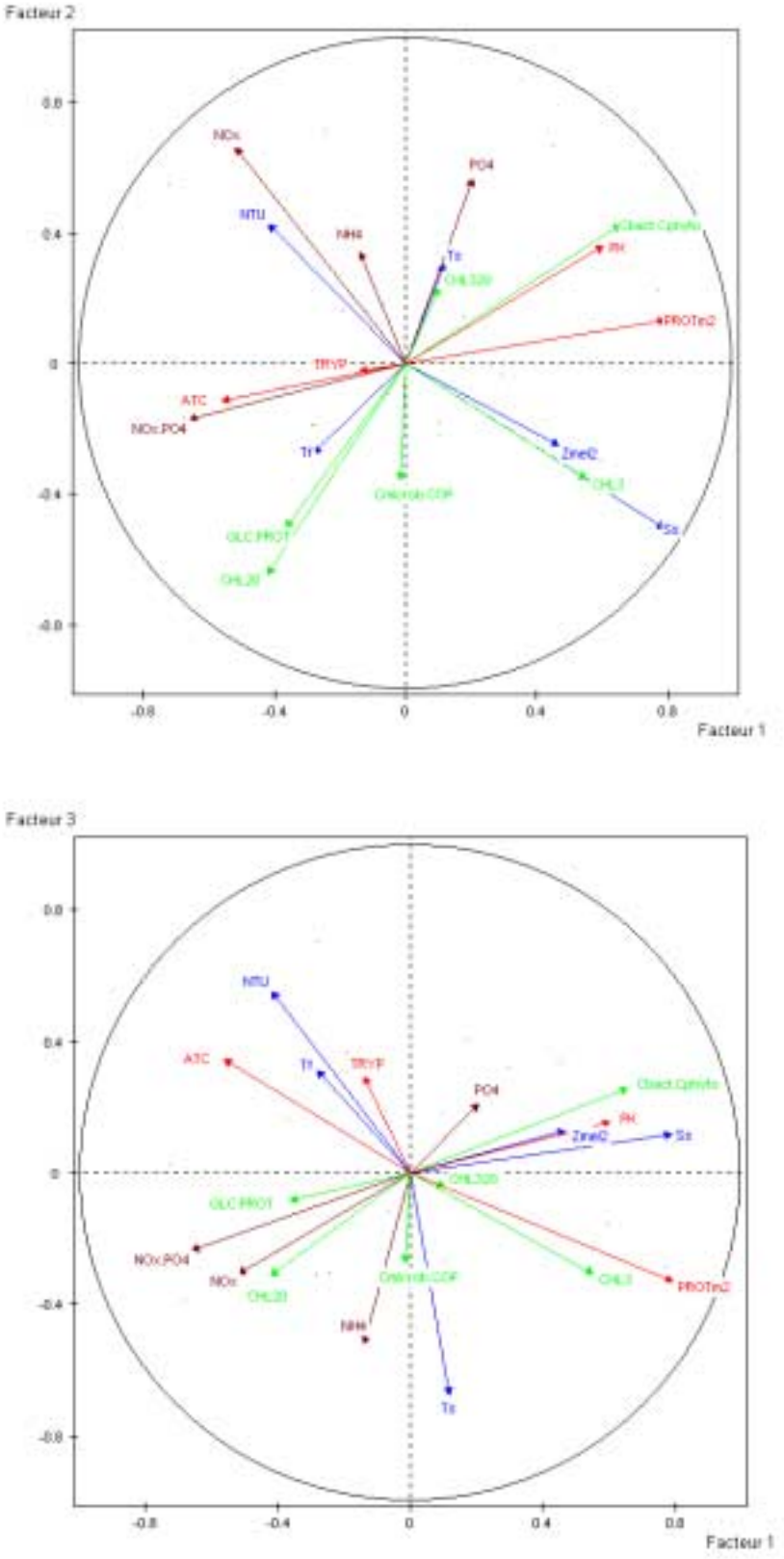


FIG. 3: representation of the variables in the compromise factorial space of the Multiple Factorial Analysis. Names of variables are listed in Table 1. Colours are: blue for hydrology; brown for nutrients; green for primary producers and red for meso-zooplankton.

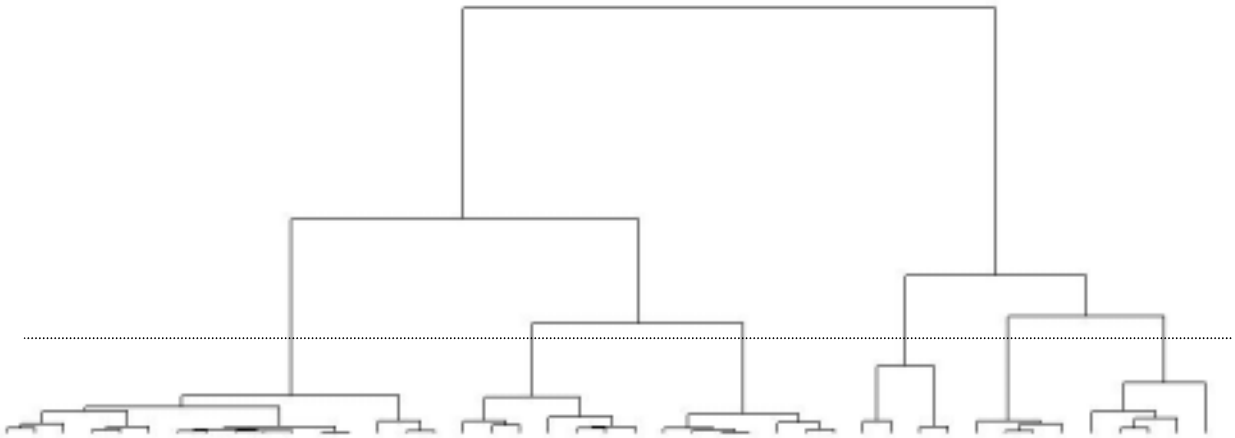


FIG. 4: hierarchical clustering of the compromise point for each CTD hydro-plankton staztion in the compromise factorial space of the Multiple Factorial Analysis. The dashed line represents the cutoff which defined 6 groups of CTD hydro-plankton strations named functional entities.

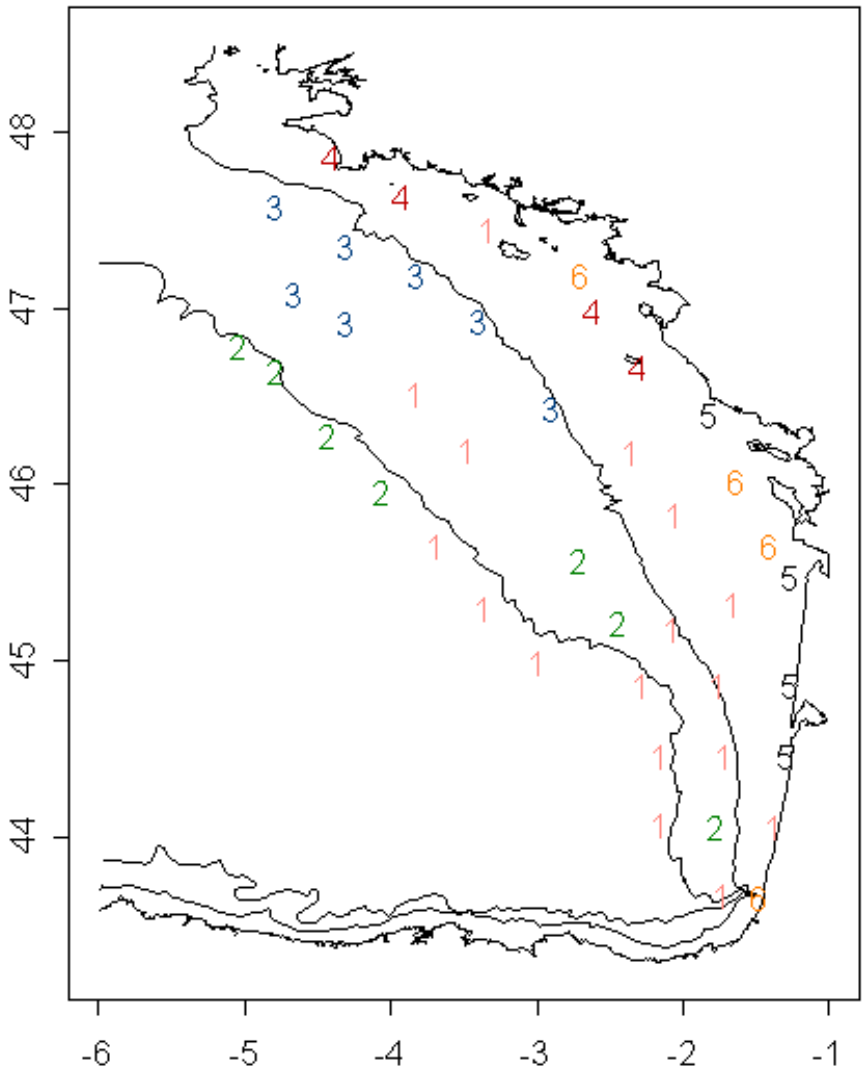


FIG. 5: Map of the hydro-plankton entities resulting from applying Multiple Factorial Analysis to the CTD hydro-plankton stations of the survey PEL2000.

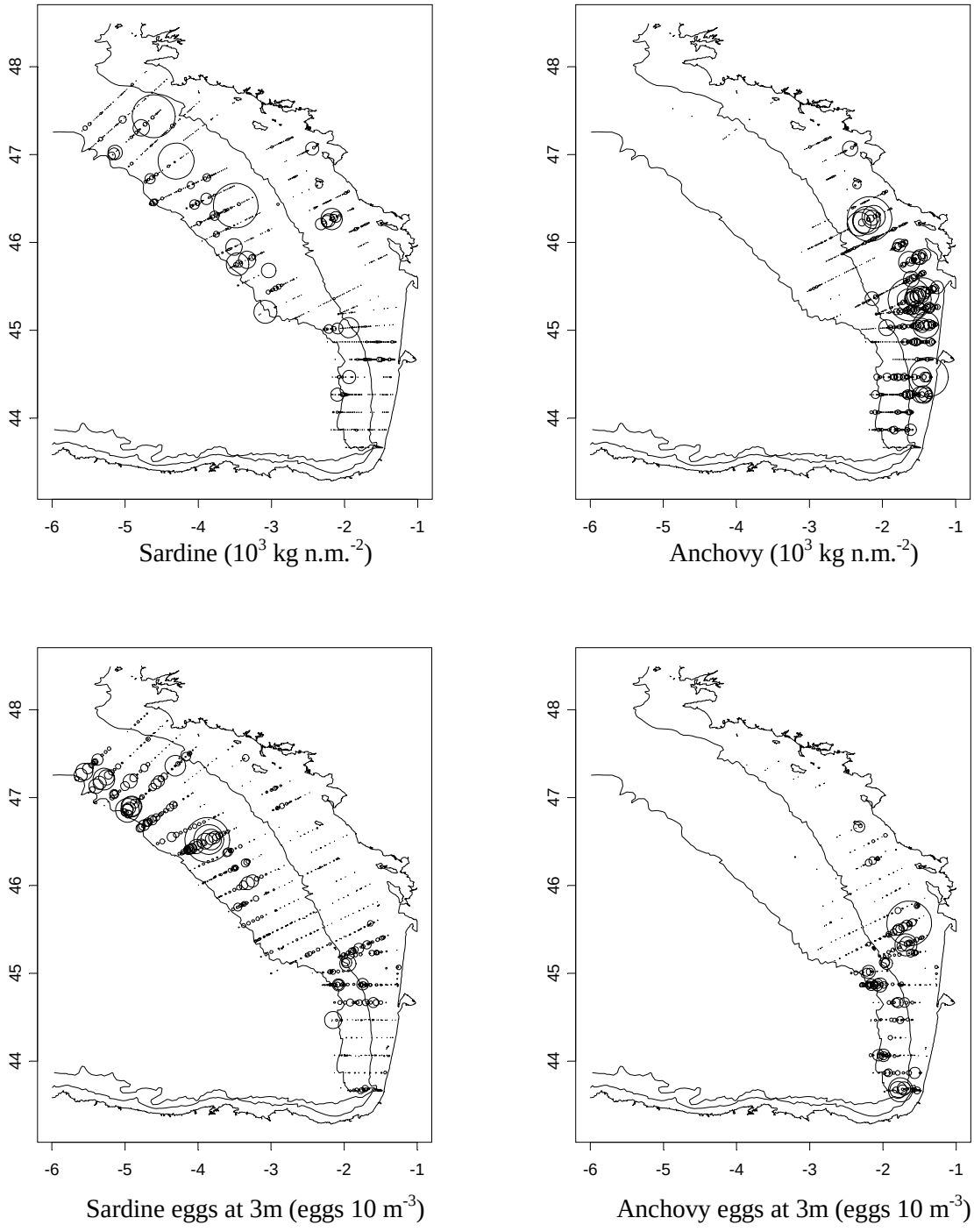
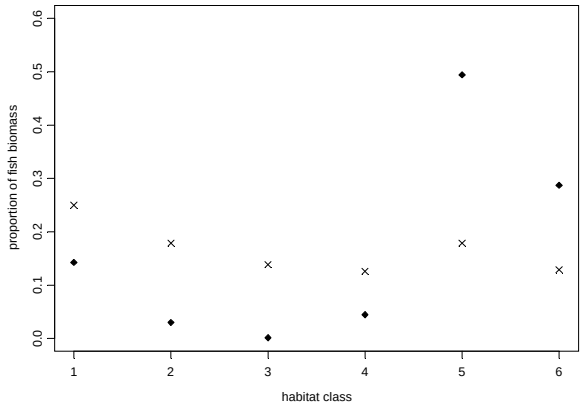
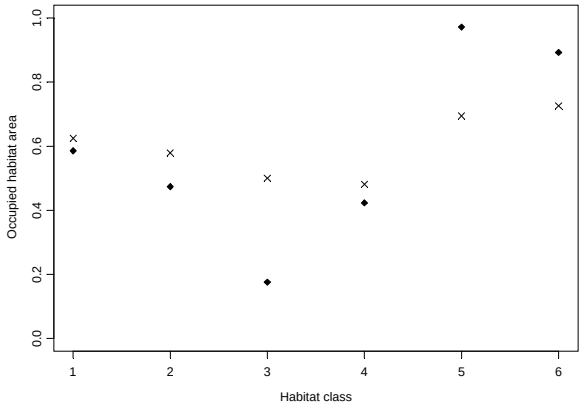


FIG. 6: Maps of sardine and anchovy abundance derived by echo-integration and of their eggs derived by CUFES records. On each map, circle radius is proportional to the sample value and relative to the maximum value.

Abundance

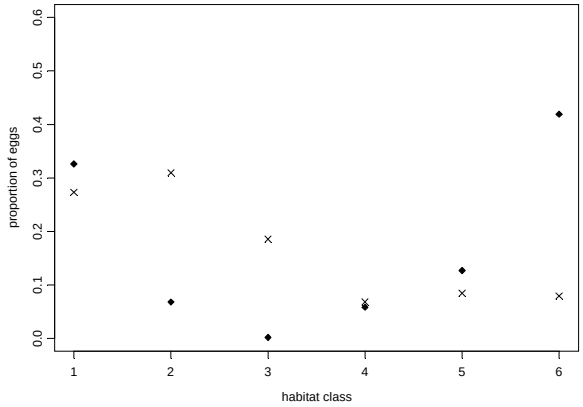
Occupied area

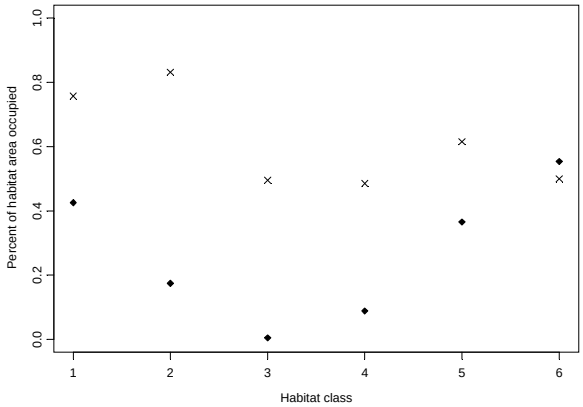




Adult fish

Adult fish

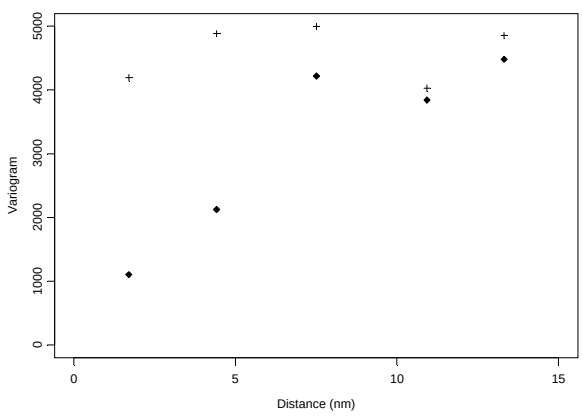




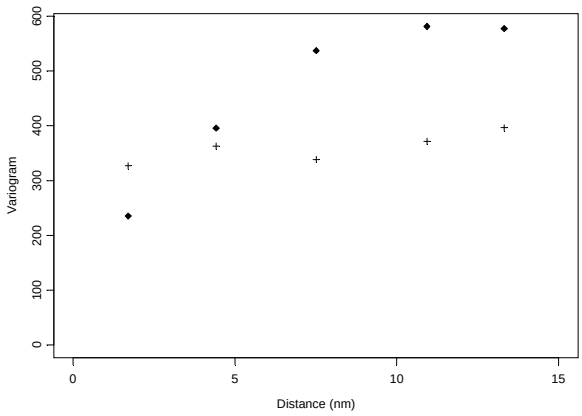
Eggs

Eggs

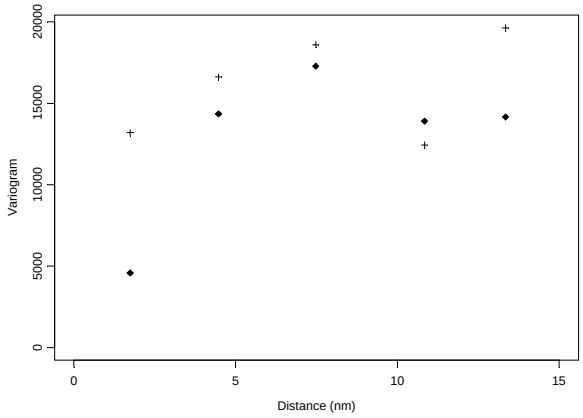
FIG. 7: distribution of sardine and anchovy fish and eggs in the hydro-plankton entities (habitat class). Cross: sardine; diamonds: anchovy. Left: mean abundance per hydro-plankton entity expressed as percent of overall mean; right: area of each hydro-plankton entity occupied by anchovy and sardine expressed in percent of hydro-plankton entity area.



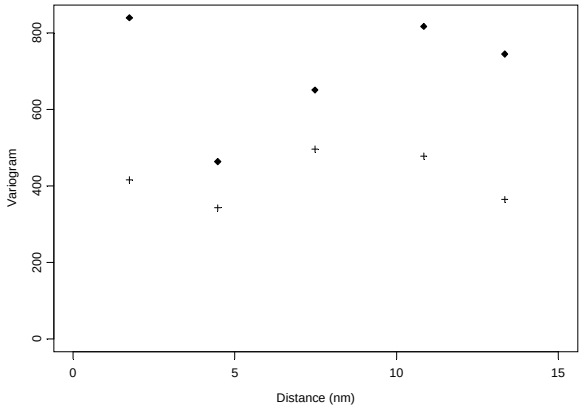
Adult sardine



Adult anchovy

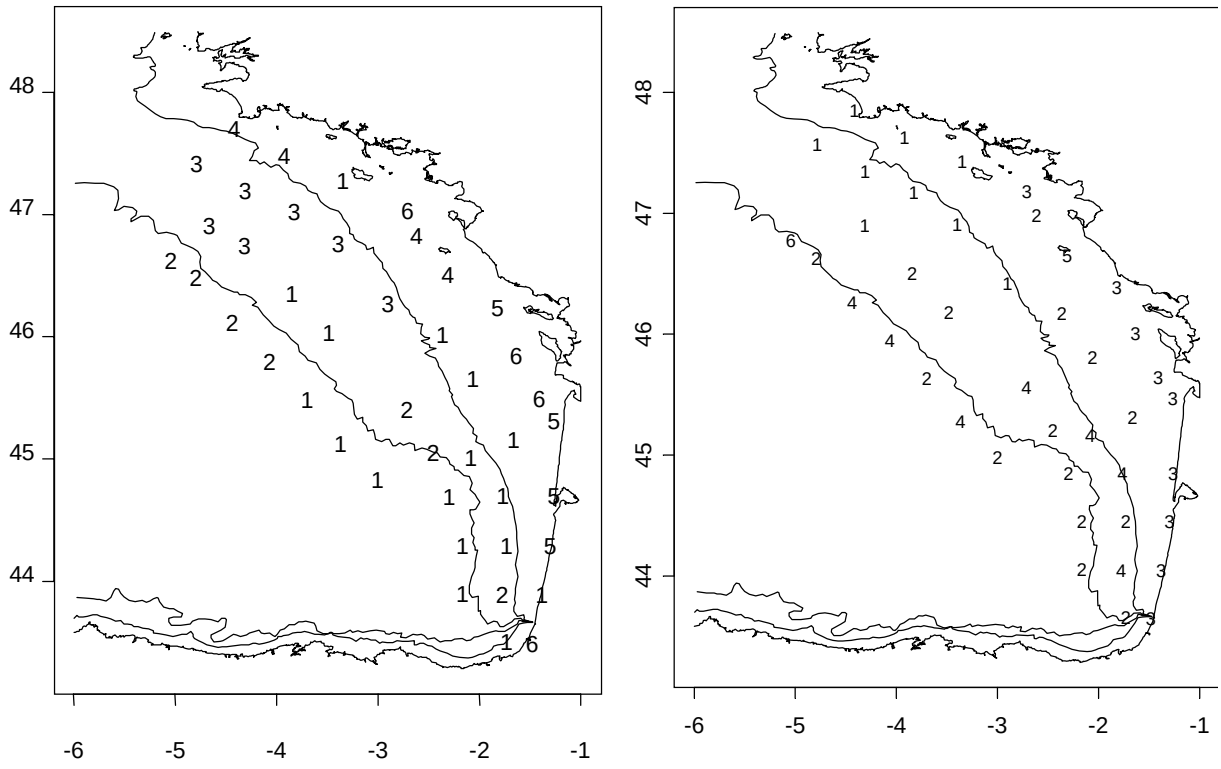


Sardine eggs



Anchovy eggs

FIG. 8: Variograms computed for pairs of points standing in the same hydro-plankton entity (crosses) and in different entities (diamonds) for sardine and anchovy and their eggs.



AFM on extensive list PCA on Reduced list

FIG. 9: Groups of CTD hydro-plankton stations (hydro-plankton entities) obtained by using the extensive list of variables of Table 1, applying Multiple Factorial Analysis and clustering (left) and (right) using the reduced list of variables, applying PCA and clustering. Codes of hydro-plankton entities are not the same in the two figures.