



Ecoregionalization of myctophid fish in the Indian sector of the Southern Ocean: Results from generalized dissimilarity models

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ABSTRACT

The Southern Ocean is delimited by major frontal zones which influence pelagic life at the spatial macroscale. There is a sharp ecological segregation of pelagic fish that inhabit this ocean with some families living in the neritic zone and others in the oceanic zone. The neritic zone is dominated by fish of the Notothenioid suborder. In the oceanic zone, mesopelagic species are dominated by myctophids. Their spatial distribution is highly influenced by meso- or sub-mesoscale oceanographic features. Myctophid presence/absence records from historical surveys and from the Census of Antarctic Marine Life were used to model species assemblages in the Indian sector of the Southern Ocean by using generalized dissimilarity modeling. This statistical technique is data-driven and is used in conjunction with Geographic Information Systems for creating models between communities and environmental factors. Application of these models in large unsurveyed areas is possible and helps in delineating regions of potential similar assemblages. This will allow us to move from the bioregionalization of the Southern Ocean based on only abiotic factors and chlorophyll, to its ecoregionalization by adding species assemblages.

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1. Introduction

“Understanding the distributional patterns of individual species, communities and ecosystems is essential to robust conservation management” (Leathwick et al., 2006) and to biogeographic studies in the context of climate change. The Census of Marine Life has adopted the known, unknown, unknowable (KUU) approach. For species and communities spatial distributions: (1) the known is the actual distribution of species estimated from databases (SCAR MarBIN—Marine Biodiversity Information Network) or from the recent surveys of the Census of Antarctic Marine Life programme; (2) the unknown is how we can predict these communities in surveyed areas or after environmental changes and (3) the unknowable seeks to determine

future research, which, in our case, amounts to developing a 4D representation of species habitats or communities.

A mesoscale approach is the first step to the regionalization of the ocean. The definition of mesoscale pelagic regions (large spatial units in terms of 10s or 100s of kilometers) is becoming an important issue for ecology and conservation. Regionalization is “the process and output of identifying and mapping broad spatial patterns based on physical and/or biological attributes through classification methods used for planning and management purposes” (Vierros et al., 2008).

Bioregions are the “assemblages of flora, fauna and the supporting geophysical environment contained within distinct but dynamic spatial boundaries” (Vierros et al., 2008). The result is a set of homogeneous regions with predictable environmental and species assemblages properties that differ from one region to another (Grant et al., 2006; Vierros et al., 2008). There have been few attempts to delineate the Southern Ocean marine bioregions. Longhurst (1998) achieves a global marine biogeographic classification of the epipelagic zone and its productivity, but defines only two provinces (neritic and oceanic) within the Southern

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Ocean. Other initiatives such as the Large Marine Ecosystems (Sherman and Alexander, 1989) and the Marine Ecoregions of the World (Spalding et al., 2007) provide comprehensive regionalization of the oceans' shelves, but they are based more on knowledge of species distribution and geopolitics than solely on physiognomy and fail to consider the open ocean. The methodology chosen by CCAMLR for the Southern Ocean for developing conservation issues such as the definition of Marine Protected Areas uses geophysical characteristics, a physiognomic approach for regionalization that delineates ecosystems boundaries (Grant et al., 2006). This first attempt to establish a pelagic bioregionalization of the Southern Ocean by classification methods was determined by using abiotic variables such as sea surface temperatures (SST), depth, nutrients, sea ice concentration and extent, sea surface height and chlorophyll-*a* as a surrogate for the biotic parameters.

If we want to determine regions based on species occurrences or communities, we need to concentrate on sentinel species or communities. In this paper, we use a mixed approach (combining physiognomic and taxonomic approaches) for determining ecoregions in the Indo-Pacific sector of the Southern Ocean; the procedure we will use is based on the myctophid biocoenoses in relation to pelagic habitats.

In order to achieve such a process, we need coherent databases, dedicated new surveys, and the use or development of methodologies based on statistical predictions associated with Geographic Information Systems. Data used for the present study come from a number of publicly available databases (especially for environmental data), as well as from researchers working on mesopelagic fish. For the Southern Ocean, it was possible to conduct comprehensive biological surveys only during the Census of Antarctic Marine Life programme. From these surveys, we will use data from two of the research vessels that collected pelagic fish in the Southern Ocean: "Umitaka Maru IV" from Japan; and "Tangaroa" from New Zealand. Historic surveys are also needed for achieving the ecoregionalization, so that it is necessary to rely on spatial extrapolations of relationships between biota and the physical environment—i.e. on physiognomic data (*sensu* Vierros et al., 2008) to predict species assemblages in unsurveyed areas. This concept is based on the fact that it is easier to source or predict environmental factors at a large scale (remote sensing, physical or biogeochemical modelisation) than it is to predict species distributions using classical sampling/mapping techniques. The principle is to map species potential habitat by using regression methods such as Generalized Linear Models or Generalized Additive Models (Loots et al., 2007). Here, we used generalized dissimilarity modeling. GDM is a statistical method that can model and predict the community composition across environmental gradients (Ferrier et al., 2007).

In the context of open ocean regionalization, the Southern Ocean is unique as the abiotic forcing is very important latitudinally, with a succession of frontal zones (Orsi et al., 1995) largely associated with the Antarctic Circumpolar Current (ACC). Micronekton and nekton should be some of the best target groups for mesoscale and sub-mesoscale studies because of their multi-year life spans (see Haury et al., 1978). Over the continental or islands shelves or seamounts, Notothenioids dominate. The species of Notothenioids are mainly benthic but some are semipelagic, cryopelagic and pelagic. Among them, and on the Antarctic continental shelf, *Pleuragramma antarctica* highly dominates the pelagic fish fauna but a few other species of Channichthyidae are also pelagic. The cryopelagic *Pagothenia borchgrevinki* is a zooplankton feeder. Around subantarctic islands, species such as *Champscephalus gunnari* are also clearly pelagic. Some of the benthic species forage on plankton in the water column and have pelagic larvae. As few Notothenioid

species are pelagic, there is no need to include them in a macroscale ecoregionalization as they will only allow differentiation of the neritic zone from the oceanic zone. In the oceanic zone, myctophids dominate. Species of this family show a high degree of correlation with oceanographic features. These mesopelagic fish belong to the micronekton together with some of the cephalopods, decapods, mysids and euphausiids. The fish constitute the mid-trophic level between mesozooplankton and top predators (seabirds and marine mammals), and therefore exert a major control on energy flows. The shelf break represents a marked change in assemblages between the oceanic and neritic assemblages (Koubbi et al., 1991; Hulley, 1992).

Our aim is to model the myctophid community at the scale of the Indian part of the Southern Ocean to identify spatial patterns and their relations to the abiotic-chlorophyll environment. This will then allow us to delineate regions that have homogenous myctophid compositions.

2. Materials and methods

The available environmental information and surveys data used herein have been mapped using ARCGIS 9.2 (ESRI), a Geographic Information Systems (GIS). All statistical analyses were done using the R freeware: <http://www.r-project.org/> (R Development Core Team, 2009).

2.1. Study area and biological data

The study focused on the Indian part of the Southern Ocean, but extended into the Pacific sector, including the northwestern part of the Ross Sea (Fig. 1). The Campbell Plateau extends south of New Zealand to about 54°S, with subantarctic islands on the Plateau including the Auckland group and Campbell Island itself. To the north and west of the Ross Sea are a series of seamounts and ridges, with the Balleny Islands at 67°S. In the Indian part, we find the subantarctic islands of Marion and Prince Edward on the southwest Indian ridge, Crozet Is on the Del-Cano-Crozet plateau and the remaining islands (Kerguelen, Heard and MacDonald) on the Kerguelen Plateau. The latter separate the Enderby Basin and the Australian Antarctic Basin. The Kerguelen Plateau is one of the largest in the Southern Ocean and extends from 46°S to 62°S, but is divided into two by the Fawn Trough (sill depth: 2600 m; 56°S, 78°E). The Kerguelen Plateau is separated from the Antarctic continental shelf by the Princess Elizabeth Trough (sill depth: 3600 m; 64°S, 84°E) (Roquet et al., 2009).

Oceanographic features are characterized by a well-developed horizontal spatial gradient with a succession of frontal zones (Fig. 1) from the north to the south (Orsi et al., 1995). The Southern Ocean is limited to the north by three major fronts: from north to south, the Subtropical Front (STF), which marks the northern boundary limit, the subantarctic front (SAF) and the polar front (PF). The SAF, PF and the southern ACC front (sAACF) are associated with the Antarctic Circumpolar Current (ACC). The southern boundary of the ACC (Bdy) corresponds to the southernmost edge of the Upper Circumpolar Deep Water signal; it is the southern limit of the circumpolar flow. Orsi et al. (1995) have defined the positions of these fronts from oceanographic surveys and Sokolov and Rintoul (2002) from satellites measurements. Between these major fronts there are large, more-or-less uniform oceanographic regions. The subantarctic zone lies between the STF and the SAF. The polar frontal zone (PFZ) is between the PF and the SAF. The Antarctic zone is located between the polar front and the southern boundary of the ACC. It is at its largest extent south of Kerguelen with more than 15° in latitude, while in other sectors it extends only a few degrees. It includes the entire

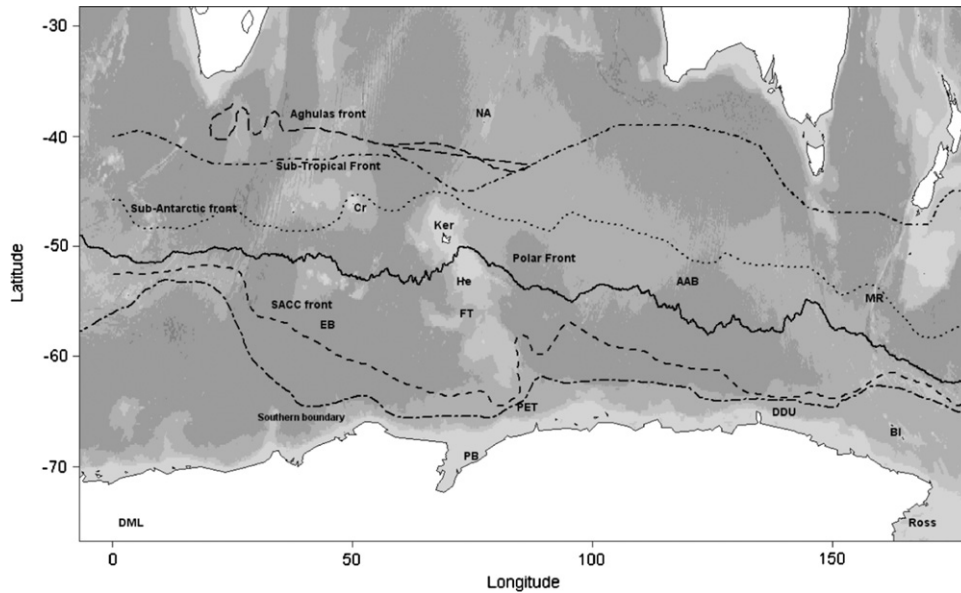


Fig. 1. Positions of the main geographic features of the Indian part of the Southern Ocean (NA: New Amsterdam; Cr: Crozet; Ker: Kerguelen; AAB: Australian Antarctic Basin; MR: Macquarie Island; He: Heard; EB: Enderby Basin; PET: Princess Elisabeth Trough; FT: Fawn Trough; DML: Dronning Maud Land; PB: Prydz Bay; DDU: Dumont d'Urville Sea; BI: Balleny Island) and positions of the major fronts. The Southern boundary (Bdy), the Southern Antarctic Circum-polar Current front (sACCF) and the subantarctic front (SAF) are from Orsi et al. (1995). The south subtropical front (SSTF) is from Belkin and Gordon (1996). The polar front (PF) is from Moore et al. (1999).

Kerguelen Plateau (Roquet et al., 2009). In the Indian sector of the Southern Ocean, the Kerguelen Plateau influences the position of the major frontal zones and acts as a barrier to the ACC, which passes along its northern escarpment and through the Fawn and Princess Elizabeth troughs (McCartney and Donohue, 2007; Roquet et al., 2009). Circulation in the offshore region of the northwestern Pacific sector is dominated by the processes in the wider Southern Ocean. The Antarctic Slope Front (Jacobs, 1991) is bathymetrically locked to the edge of the continental shelf close to the 1000 m depth contour and separates the Ross Sea from waters of the Southern Ocean to the north and east. Circulation on the Ross Sea continental shelf is dominated by a wind-driven gyre that is strongly modulated by three northeast to southwest running submarine ridges. The dominant flow over the Victoria Land coast that forms the western boundary of this gyre is to the north and west (Jacobs and Giulivi, 1999).

Initiatives concerning the archiving of species distributions worldwide started many years ago with projects such as Fishbase (www.fishbase.org) or IOBIS—Ocean Biogeographic Information System (www.iobis.org). SCAR MarBIN—Marine Biodiversity Information Network (www.scarmarbin.be) focuses on the Southern Ocean. These databases compile records of marine species' presence. However, it is possible to refer to the survey (for example, in SCAR MarBIN) and to determine presence–absence data. Some polar institutions such as the Australian Antarctic Division (<http://data.aad.gov.au/>) also make available data with the complete description of the surveys. Within the boundary area of 0–180°W, 40–77°S (Fig. 2), sixty-one species of Myctophidae were obtained from various surveys (Table 1), which deployed a variety of gears (large plankton nets or pelagic trawls) often with different sampling strategies (transects, network or oriented towards penguin or fur seal foraging areas). For each observation, the position, date, time, depth of sampling and gear were collected (if available). As the content of each trawl was fully known, the data were regarded as presence/absence. The database comprised 2366 samples among which 1597 were taken in summer. To prevent seasonal differences in spatial distribution, the analyses were restricted to the summer (December–March) observations.

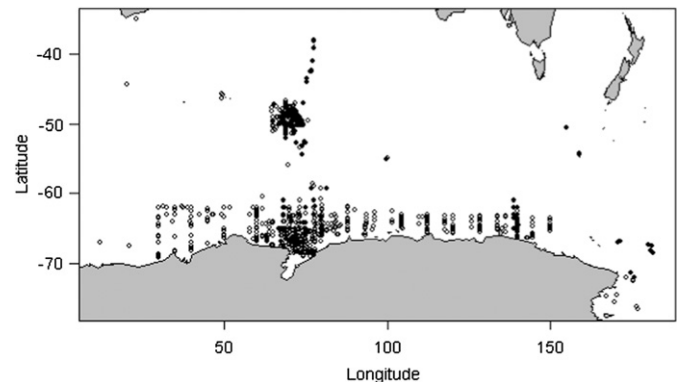


Fig. 2. Position of summer sampling stations available for the Indian part of the Southern Ocean study area: stations kept for the GDM are with solid circles and have at least three different species; open circles stations with less than three species.

2.2. Environmental variables

Candidate environmental predictors were selected according to their relevance to mesopelagic fish habitat distribution and based on knowledge from previous study (Loots et al., 2007). For each sampling station, chlorophyll concentration (CHL) was acquired using the GES-DISC Interactive Online Visualization AND aNalysis Infrastructure (Giovanni) as part of the NASA's Goddard Earth Sciences (GES) Data and Information Services Center (DISC) from 1998 to 2007 and averaged on a monthly basis (9 km spatial resolution). Sea temperature (TEMP), salinity (SAL) and concentrations in nutrients (phosphate: PHO; silicate: SIL and nitrate: NIT) were extracted from the National Oceanographic Data Center (Locarnini et al., 2006; Antonov et al., 2006; Garcia et al., 2006) for each month at the surface and 200 m depth (1° resolution). For stations with a depth lower than 200 m, the bottom value of the variables was considered. The mixed layer depth (MLD) was obtained monthly from de Boyer Montégut et al. (2004) (2° resolution) and the bathymetry (1 min spatial resolution) (BAT) from the National Geophysical Data Center (<http://www.ngdc.noaa.gov/ngdc.html>). Environmental data were resampled throughout a common grid of 1° of latitude × 1° of longitude.

Table 1
Myctophids data sources for the Indian part of the Southern Ocean used in this study.

Survey	Years	Geographic extent	Number of samples	Institution	Fishing gear
IZIKO	1963–2000	Long: 20.02–81.72 Lat: –66.58 to –35.02	78	IZIKO—South Africa	Various gears
Historical fish database (AAMBER 1 & 2, KROCK, Sibex)	1968–1999	Long: 12.22–159.04 Lat: –88.98 to –40.06	411	AAD—Australia	IYGPT and RMT
Marion Dufresne (MD 03)	1974	Long: 65.72–75.98 Lat: –55.93 to –49.48	4	MNHN—France	Isaac Kid
Marion Dufresne (MD 08)	1976	Long: 50.55 Lat: –46.77	1	MNHN—France	Isaac Kid
Marion Dufresne (MD 25)	1981	Long: 30.1–49.2 Lat: –64.02 to –61.88	13	MNHN—France	RMT and OMORI
Marion Dufresne (MD 42)	1985	Long: 68.17–81.72 Lat: –67 to –33.55	39	MNHN—France	RMT
FIBEX	1985	Long: 61.88–110.75 Lat: –68.59 to –54.97	106	AAD—Australia	RMT
SKALP	1987–1988	Long: 64.65–73 Lat: –52 to –46.6	145	MNHN—France	Bongo nets
IPEKER	1995	Long: 70.78–73.39 Lat: –49.75 to –48.75	65	MNHN—France	IYGPT
Broke East	1996	Long: 79.97–150 Lat: –66.32 to –62.55	156	AAD—Australia	RMT
ICHTYOKER	1998–2000	Long: 70.01–74.47 Lat: –50.43 to –48.08	355	MNHN—France	IYGPT
KERAMS	2000	Long: 74.31–77.54 Lat: –47.07 to –38.06	29	MNHN—France	IYGPT
Broke West	2006	Long: 29.9–80.02 Lat: –69.2 to –61.65	110	AAD—Australia	RMT
CEAMARC—CAML “Umitaka Maru”	2008	Long: 139–143.32 Lat: –66.35 to –61	67	TUMSAT—Japan and LOV—France	IYGPT and RMT
CAML—Ross Sea	2008	Long: 167–181.6 Lat: –76.62 to –66.88	19	NIWA—New Zealand	Midwater Trawl

2.3. Species assemblages modeling

The goal of this study was to model the myctophid community as a function of the environment. The generalized dissimilarity modeling (GDM) routines were developed by Ferrier et al. (2007) for terrestrial ecology. This method is an extension of the matrix regression that can accommodate for two types of non-linearity met in ecological studies: (i) the curvilinear relationship between ecological distance and composition dissimilarity through the use of a Generalized Linear Models (GLM) with the proper link and variance function and (ii) the non-linear response of the community along environmental gradients held with monotonic I-splines functions. The fitting of a GDM first requires the computation of a dissimilarity matrix between each pair of stations (Ferrier et al., 2007). Then, for each environmental predictor, a set of I-splines is fitted to each sampling station. The I-splines coefficients are computed in order to maximize the reduction in deviance achieved by its inclusion (Elith et al., 2006) using the dissimilarity matrix as the response variable. Inclusion of an environmental predictor can be done using selection procedures (for example, backward-elimination).

Many locations had only one recorded species, which would have resulted in a large number of dissimilarity values between sites being equal to one: this cannot be ecologically real. Such a situation would bias the GDM process and therefore create errors in the predicted bioregions. To reduce these potential errors, only sites with three or more recorded species were used in the modeling for each biotic group (Growth, 2009). It should also be noted that sites with only one species would have a dissimilarity value of one, whereas they could have a different species composition. The final data set was then reduced to 435 sample stations. At the final stage, 42 species were included in the analysis.

To identify the environmental variables that contribute most to the change in community composition, GDM were computed by removing one environmental variable at a time. Hence the

explained variance of the model without the considered variable Var_i was compared to the variance of the complete model Var . Since the GDM method is sensitive to collinearity between predictors, highly correlated variables were removed from the analyses (Elith et al., 2006). Variables were considered as highly correlated when showing a pair-wise Spearman correlation coefficient of more than 0.7 as recommended by Leathwick et al. (2006). The selection between two correlated predictors was based on the following procedure: GDM was computed considering one of the two correlated variables, and the environmental predictor having the highest explained variance was retained.

Once the GDM was fitted to the observed data, it was used to predict the dissimilarity for unobserved locations. The output of the GDM was a predicted matrix of pair-wise dissimilarity between sites for the averaged January environmental data. As the predicted dissimilarity matrix was difficult to visualize, a classification was computed on the matrix. In this study, the dissimilarity matrix was processed through a non-hierarchical clustering; it achieved a clustering of the data into k clusters around medoids. The optimal number of groups was chosen according to four indexes: Calinski and Harabasz, Xu, Ratkowski and Lance and Hartigan (see definition in Dimitriadou et al., 2002). This series of tests measured the dispersion of observations within and between clusters.

3. Results

3.1. Species assemblages

The sampling effort used to catch myctophids in the Southern Ocean was not homogenous: the positions of the pelagic trawls were mainly concentrated along the Antarctic coast, in the Ross Sea and mainly on the Kerguelen plateau (Fig. 2). As we restricted analysis to only samples with more than three species (Growth, 2009), some surveys were almost removed from the

analysis (FIBEX and BROKE). The “ICHTYOKER” data set, in the eastern and southeastern part of the Kerguelen oceanic zone, retained the maximum number of samples (281 out of 355), while the “KERAMS” survey (a transect from Kerguelen Is to New Amsterdam Island) was the one for which we kept all the samples (29); these two surveys allowed for the study of myctophid assemblages from the polar frontal zone to the subtropical zone.

Of the 62 species in the data set, 44 were caught during the summer season but only 42 were kept for GDM. Occurrences of species in all summer samples or in samples kept for GDM showed the same rank order (Fig. 3) with four species being highly relevant (> 25% for all summer samples): *Electrona antarctica*, *Protomyctophum bolini*, *Krefflichthys anderssoni* and *Gymnoscopelus braueri*. When looking only at occurrences for samples kept for the analysis, 12 species had occurrences greater than 25%, with *E. antarctica* present in more than 81 of those stations.

3.2. GDM

Two pair-wise correlations between environmental variables were greater than 0.7, which allowed us to withdraw two variables from the analyses. For example, sea surface temperatures were correlated to silicates at 200 m ($\rho = -0.73$). The deviance explained by a GDM without temperatures was superior

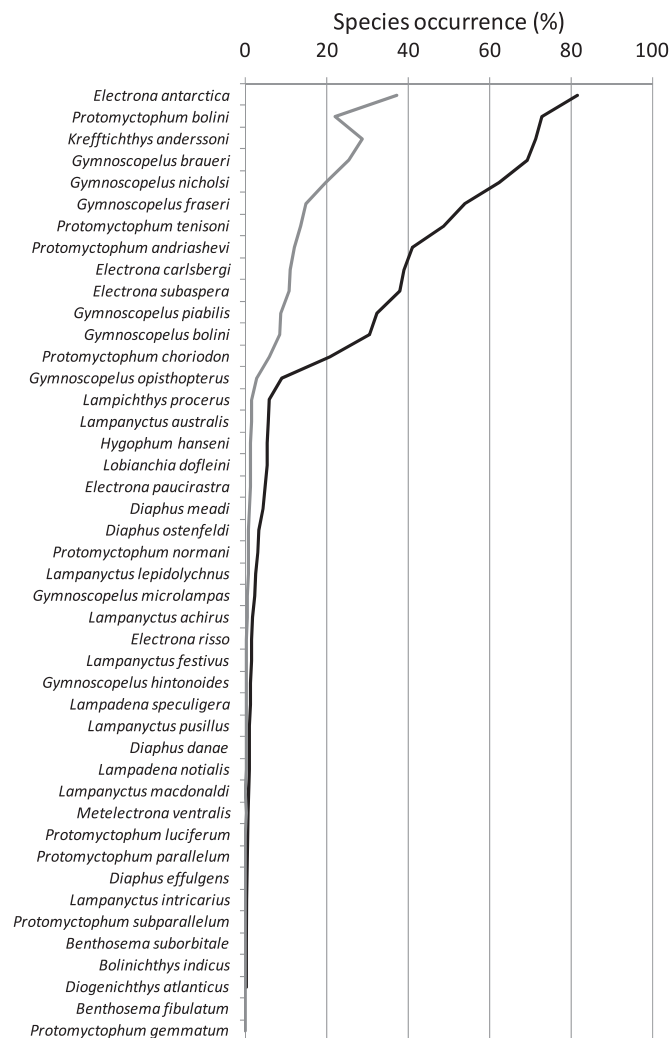


Fig. 3. Percentage occurrence of Myctophid species in all summer samples (gray line) and in samples kept for GDM (black line) for the Indian part of the Southern Ocean.

to one of a GDM without silicates at 200 m. Surface nitrate and phosphate concentrations were also correlated ($\rho = -0.73$), with phosphates being more relevant for the GDM than nitrates. We then decided to discard surface nitrates and silicates at 200 m from the analysis. These variables could be considered as proxy with their corresponding correlated variables.

The percentage of variance in the community composition explained by the GDM was 58.5%. To evaluate the importance of environmental variables on the change of community, GDM were computed by removing one predictor at a time. The variance of the GDM including all predictors was compared to the models minus one predictor. The environmental variables that best explained the change in Myctophid species composition were bathymetry, followed by temperatures at 200 m, the salinity at 200 m, and the chlorophyll-*a* concentration (Table 2). Phosphate concentrations at the surface and 200 m did not change the community composition.

The form of the relationship between community composition and each relevant environmental gradient differed (Fig. 4). Bathymetry impacted the change of community only in the shallow water (< 600 m) whereas the temperature at 200 m depth had a significant effect for temperatures greater than 4 °C. The salinity at 200 m depth and the chlorophyll concentration changed the community composition in their lower range of value. It was interesting to note that the change in myctophid structure was driven by the environmental variables recorded at 200 m depth rather than at the surface.

3.3. Ecoregions

From the dissimilarity matrix, it is possible to construct a non-hierarchical classification of the determined groups (or regions) of species assemblages. Three indexes out of four (Calinski and Harabasz, Xu and Hartigan) gave 12 as an optimal number of groups, and one index (Ratkowski and Lance) the optimal value of 3. Setting the number of groups to 12, they were mapped to delineate regions (Fig. 5). These regions are associated with frontal zones and influence the Southern Kerguelen Plateau. Most of the regions represent the latitudinal environmental gradient, except those of Group 4—which are associated with each basin—and those of Group 2, which are discontinuous. The change of regions is rapid in the northern part of the Southern Ocean between the polar frontal zone and the subtropical front, the discontinuity of these regions being due to the resolution we applied in the analysis; this indicates that steep gradients are observed in most of this area due to the juxtaposition of the frontal zones north of the Kerguelen Plateau.

Table 2

Contributions of the variables for the generalized dissimilarity model (GDM) for myctophid assemblages in the Indian part of the Southern Ocean. Change in the deviance when the variable was removed from the model is shown, as well as the percentage contribution to the model.

Variable	Dev – variable <i>i</i> – Dev	%
Bathymetry	155.10	18.77
Temperature—200 m	148.01	17.92
Salinity—200 m	135.30	16.38
Chlorophyll	125.23	15.16
Mixed layer depth	101.90	12.33
Nitrates—200 m	65.57	7.94
Sea surface temperature	44.61	5.40
Surface silicates	29.15	3.53
Surface salinity	21.24	2.57
Surface phosphates	0	0
Phosphates—200 m	0	0

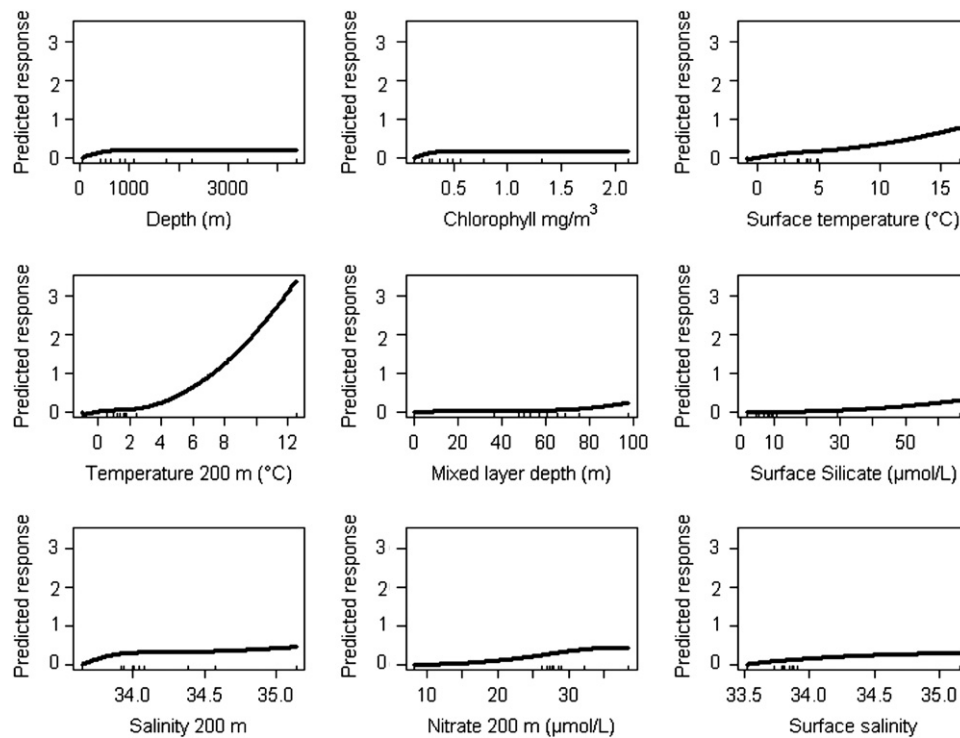


Fig. 4. Fitted splines from the generalized dissimilarity modeling of Myctophid assemblages for each key environmental variables of the Indian part of the Southern Ocean. Variables are ranked according to their relative importance in explaining the deviance.

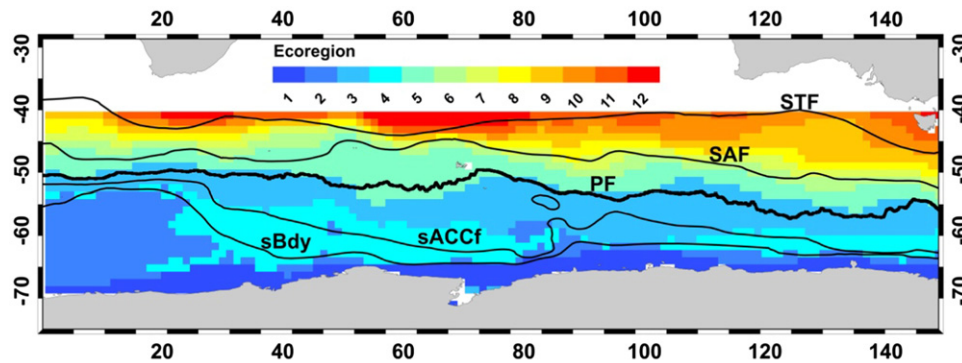


Fig. 5. Ecoregionalization of the Indian part of the Southern Ocean based on Myctophid assemblages. Frontal zones are indicated: STF, Subtropical Front; SAF, subantarctic front; PF, polar front; sACCf, Southern Antarctic Circumpolar Current Front; SBdy, Southern boundary of the Antarctic Circumpolar Current.

The environmental characteristics of the 12 groups (Fig. 6) were interpreted as follows. Group 1 regions have the shallowest bathymetry as it encompasses the Antarctic continental shelf. The interquartile range of bathymetry for Group 8 regions is the greatest because ridges are found in this area. In some areas, outliers linked to the lower values are indicative of island shelves or seamounts. Temperatures and salinity showed a latitudinal gradient from the subtropical zone to the Antarctic continent with sharp gradients in the polar frontal zone North of Kerguelen. The gradient was more spread latitudinally in the other areas. Minimum values for salinities at 200 m were found in Groups 5 and 6 regions, in the polar frontal zone and in the vicinity of the SAF. The mixed layer depth showed its maximum values around in the polar frontal zone and in the northern Kerguelen Plateau. There was a latitudinal gradient of values for nitrates and phosphates, both at the surface and in 200 m, from the subtropical zone to the Antarctic continent. The highest values were observed in the regions of Groups 1–4 from the APF to the Antarctic continent. For silicates, there was no gradient for

the subantarctic and subtropical regions, and there were high concentrations south of the APF. Groups 11 and 12 regions (in the subtropical zone) had high values of chlorophyll, but the highest observed were in regions of Groups 1 and 2 along the Antarctic continent. The concentration of chlorophyll-*a* at the surface was not latitudinally structured, as for the other environmental parameters. The highest concentrations (in summer) were observed along the Antarctic continent with the maximum values in Prydz Bay, the Ross Sea and in the Dumont d’Urville Sea continental shelf. High or intermediate concentrations were observed in the Dronning Maud Land continental shelf in the continuity of the Weddell Gyre, and over the Kerguelen Plateau. There were distinct high concentrations on the eastern part of the Kerguelen Island shelf and over the Southern Kerguelen Plateau. Between these features, there was a “Low chlorophyll zone” in the Fawn Trough. The Australian Antarctic Basin and the Enderby Basin also had low chlorophyll values.

It was not possible to predict species composition for each predicted pixel to derive the species composition of the group

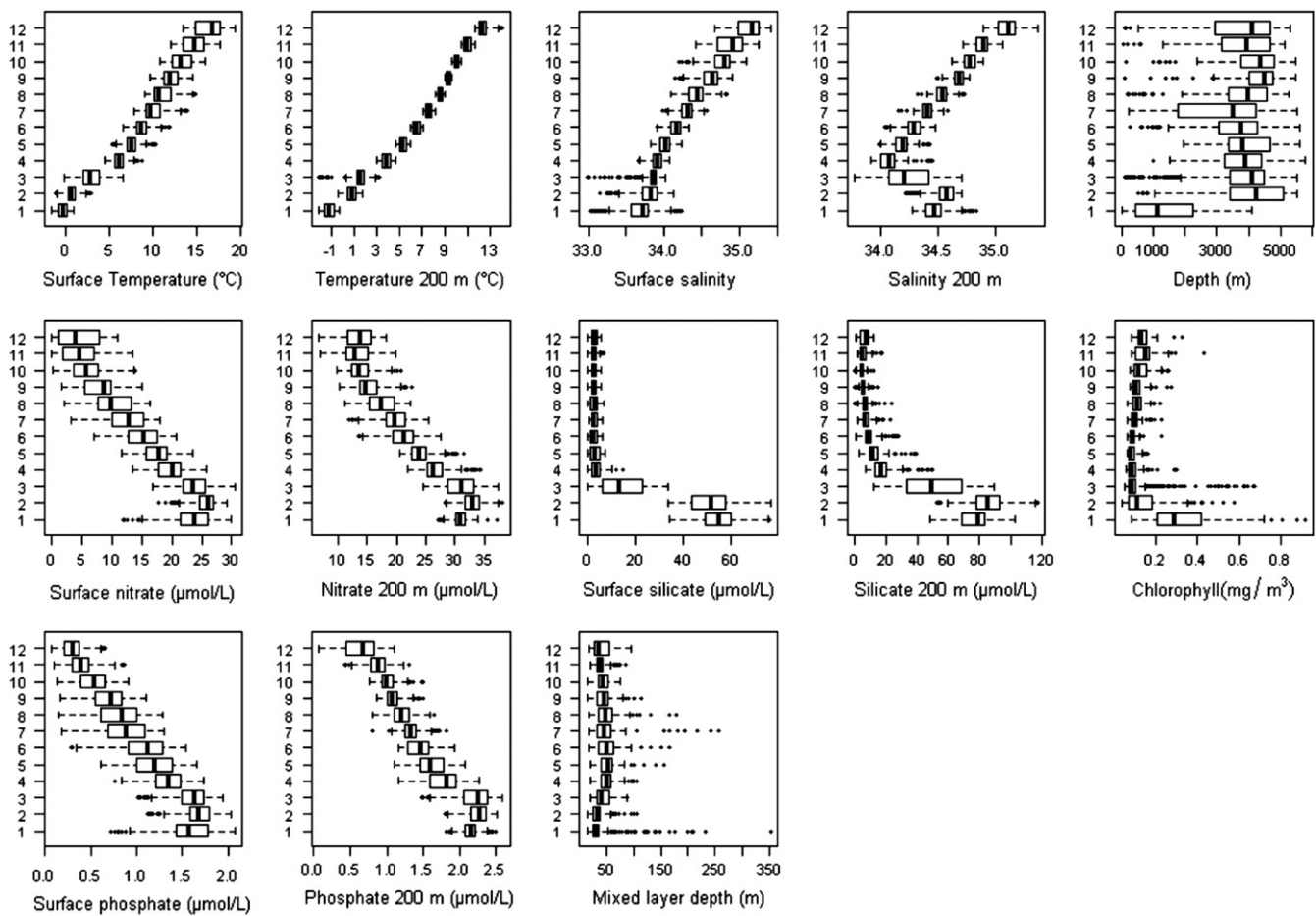


Fig. 6. Physical features associated with Myctophid assemblage groups for the Indian part of the Southern Ocean. The Tukey box has ends at the quartiles, the vertical line in the middle is the median. “Whiskers” are drawn to the farthest points that are not outliers. For every point more than 1.5 times the interquartile range from the end of a box, there is a dot.

(cluster, region). GIS spatial query allowed determination of species composition of each region using geographic joining procedures with the original observations layers (i.e. the observed sampling stations were related to their closest region) facilitating comparisons between regions (Table 3). The maximum number of species was found in Group 12 located in the subtropical zone, north of the STF. With Group 11, these regions were characterized by high values of chlorophyll. No stations were included in regions of Groups 7 and 9 because no samples were inside these areas. The second area with the highest species number was linked to Groups 5 and 6. Group 5 delineates regions of the APF and Group 6 the southern edge of the subantarctic zone. These regions show low value of salinity at 200 m in the polar frontal zone and in vicinity of the SAF. Considering species latitudinal extent (Table 3), we can see that the region of Group 6 was the intermediate area between the more Antarctic species and the subtropical ones. Some species were present in a wide range of regions. They are widely distributed in the Southern Ocean south of the subantarctic front: *Gymnoscopelus bolini*, *Gymnoscopelus microlampas*, *E. Antarctica*, *Electrona carlsbergi*, *G. braueri*, *K. anderssoni*, *P. bolini* and *Gymnoscopelus nicholsi*. Some of them also occurred in the subtropical zone. In contrast, the most subtropical species were limited to the south by the regions of Group 6, which were linked to the SAF. Moving south, the diversity was lower except in areas of Group 2 in the south of the Sby. The lowest diversity was for the more southern region (Group 1) with only four species (*E. antarctica*, *Gymnoscopelus opisthopterus*, *G. braueri* and *G. nicholsi*). The concentration of

chlorophyll-*a* in surface waters was not latitudinally structured as it was for the other environmental parameters. The highest chlorophyll concentrations, in summer, were observed along the Antarctic continent with the highest values in Prydz Bay, the Ross Sea and in other parts of the east continent shelf. Other high or intermediate concentrations were observed in the Western part in the continuity of the Weddell Gyre and over the Kerguelen Plateau. There were clear high concentrations on the Eastern part of the Kerguelen island shelf and in the Southern Kerguelen Plateau. In between, there was a “Low zone” in the Fawn Trough. The Australian Antarctic Basin and the Enderby Basin were low chlorophyll zones, while the highest observed were in regions of Groups 1 and 2 along the Antarctic continent.

4. Discussion

As noted by Vierros et al. (2008), there is no agreed system for developing biogeographic classifications of the high seas. There are three types of methodology: (1) the taxonomic approach, which is based on communities, (2) the physiognomic approach used for the Southern Ocean (Grant et al., 2006), which is theoretically based on habitats/functions/ecological processes, but most often employing only the abiotic characteristics of the habitat and (3) a mixed approach including taxonomic, ecological and physiognomic data. We employ the latter approach in this paper to delineate distinct large areas that are dissimilar in terms of their species composition. This does not mean that the species

Table 3

Latitudinal range of myctophid species used for the analysis and presence in each of the groups found with the generalized dissimilarity model for the Indian part of the Southern Ocean.

Species	Group											Latitudinal range (°S)	
	1	2	3	4	5	6	8	10	11	12	Minimum	Maximum	
Number of species	4	12	8	12	17	20	6	9	14	23			
<i>Gymnoscopelus hintonoides</i>		1				1					68.55	54.31	
<i>Lampanyctus macdonaldi</i>				1							63.00	63.00	
<i>Lampanyctus achirus</i>			1	1							64.99	52.79	
<i>Gymnoscopelus opisthopterus</i>	1	1		1	1						72.07	47.14	
<i>Protomyctophum parallellum</i>					1	1					54.31	49.78	
<i>Electrona antarctica</i>	1	1	1	1	1	1					72.07	47.06	
<i>Gymnoscopelus braueri</i>	1	1	1	1	1	1					71.34	47.05	
<i>Gymnoscopelus microlampas</i>		1		1		1		1	1	1	68.55	41.03	
<i>Krefftichthys anderssoni</i>		1	1	1	1	1	1				65.47	47.05	
<i>Protomyctophum subparallellum</i>							1				50.53	50.53	
<i>Gymnoscopelus nicholsi</i>	1	1		1	1	1					72.07	47.06	
<i>Protomyctophum bolini</i>		1	1	1	1	1	1				65	47.05	
<i>Electrona carlsbergi</i>		1	1	1	1	1			1		68.14	43.59	
<i>Gymnoscopelus piabilis</i>		1			1	1					66.91	48.08	
<i>Protomyctophum andriashevi</i>				1	1	1					63.02	47.05	
<i>Gymnoscopelus bolini</i>		1	1	1	1	1	1	1		1	66.91	42.53	
<i>Protomyctophum choriodon</i>			1		1	1					54.48	47.06	
<i>Gymnoscopelus fraseri</i>		1			1	1					68.55	47.05	
<i>Electrona subaspera</i>					1	1	1				54.50	47.07	
<i>Protomyctophum tenisoni</i>					1	1					50.24	47.05	
<i>Protomyctophum luciferum</i>					1	1					48.77	47.05	
<i>Metelectrona ventralis</i>					1						48.77	41.03	
<i>Lampadena notialis</i>									1	1	43.59	42.40	
<i>Electrona paucirastra</i>						1	1	1	1	1	50.56	38.17	
<i>Protomyctophum normani</i>						1		1	1	1	47.07	38.12	
<i>Benthoosema suborbitale</i>										1	42.53	42.53	
<i>Bolinichthys indicus</i>										1	42.49	42.49	
<i>Lampanyctus intricarius</i>										1	42.4	42.4	
<i>Diaphus danae</i>									1	1	43.56	38.14	
<i>Diaphus meadi</i>								1	1	1	44.08	38.06	
<i>Lampichthys procerus</i>						1		1	1	1	47.06	38.06	
<i>Diogenichthys atlanticus</i>										1	41.03	41.03	
<i>Diaphus effulgens</i>										1	41.02	41.00	
<i>Lampadena speculigera</i>										1	42.44	38.06	
<i>Lampanyctus australis</i>								1	1	1	44.08	38.06	
<i>Hygophum hanseni</i>								1	1	1	44.08	38.06	
<i>Lobianchia dofleini</i>								1	1	1	44.08	38.06	
<i>Electrona risso</i>									1	1	43.56	38.12	
<i>Lampanyctus lepidolichnus</i>									1	1	43.59	38.06	
<i>Diaphus ostenfeldi</i>									1	1	43.59	38.06	
<i>Lampanyctus pusillus</i>										1	41.03	38.06	
<i>Lampanyctus festivus</i>										1	41.03	38.06	

themselves are different in these regions but that the relative mixture of species could be different. The habitat of each region could also be characterized.

4.1. Influence of sampling strategies

Summer is the only period when we have sufficient data from the Subtropical Front to the continent. By choosing one season, we avoided problems linked to possible different seasonal spatial patterns of the target community, and better matched them to seasonally variable environmental factors.

We utilized most of the samples from “KERAMS” (transect from Kerguelen Is to New Amsterdam Is) and “ICHTYOKER” (eastern part of Kerguelen Islands oceanic zone) surveys to the exclusion of those from other surveys (e.g. “BROKE”, along the oceanic zone of the Antarctic continent) due to differences in sampling strategy. The most suitable surveys to provide data for this type of analysis were those deploying International Young Gadoid Pelagic Trawls (IYGPTs) or other midwater trawls with sampling depths greater than 200 m. Many other less successful surveys were those that were limited to

the upper 200 m of the water column, where the focus was on the evaluation of abundance of *Euphausia superba* (Hoddell et al., 2000). Collins et al. (2008) caught very few myctophid fish in krill trawls (RMT25) in the upper 200 m of the Scotia Sea, especially during the day. They concluded that this could be due to diurnal migration behavior, net avoidance, or a combination of the two. In considering presence–absence data for GDM, the fishing depth may be more important than the type of sampling gear. Time of day is another important source of bias in our approach. For species undergoing vertical migrations, sampling time is important. There are probably interannual variations that can differ largely with latitude because of changing position of Fronts and also longitudinally because of acyclic differences due to the Southern Ocean wave. By using presence/absence data over the whole water column, we minimize the different sources of these bias. We further believe that abundances cannot be used for large scale studies as they are more linked to sampling strategies and gear type, which make it difficult to compare catches. Ideally, large scale biogeography using abundances should employ one standardized gear such as IYGPT or RMT depending on the species targeted. One good example is the Southern Ocean Continuous Plankton Recorder (SO-CPR) surveys

(Pinkerton et al., 2010), from which large scale habitat modeling was possible because samples were always taken with the same gear, and processed the same way.

For estimating fish diversity, it is not easy to agree on a single gear type and methodology. This means that we underestimate the pelagic diversity of the Southern Ocean if we are not sampling depths greater than 200 m (the standard depth for epipelagic studies); this is obvious for fish (except for fish larvae) as well as for macrozooplankton like jellyfish.

4.2. Ecoregions

As Vierros et al. (2008) stressed, a “biogeographic classification system should emphasise generally recognizable communities of species, and not require presence of either a single diagnostic species or abrupt changes in the whole species composition between regions”. The regionalization of the open ocean based on myctophids is relevant because we are targeting a zoological group with many species and with life spans that are coherent with the spatial and temporal scales we are assessing; there is a high degree of behavioral similarity in this family. The species assemblages that we observed are coherent with the known pelagic habitats of that area with a latitudinal gradient between the subtropical zone to the Antarctic continent (Grant et al., 2006; Longhurst, 1998). There are no major discrepancies with previous biogeographic studies on mesopelagic fish (Bekker, 1985) or on invertebrates. However, these previous studies were made based on expert knowledge and were not able to delineate regions according to spatial features that are better known today. This is especially the case of the positions of frontal zones, but is also true of spatial features that are better known now such as the currents across the Kerguelen shelf. Our methodology represents a more “objective approach” based on up-front techniques, which are repeatable and that can always be corrected using expert knowledge.

This study highlighted the importance of subsurface environmental parameters. It means that to model the distribution of myctophid assemblages, it is necessary to consider not only surface predictors but also deeper ones, which may be more precise in determining transition zones such as fronts. Surface variables have “noise” due to wind-induced turbulence and other physical forcing factors; thus the 2 °C isotherm of the Antarctic Polar Front (Longhurst, 1998; Sokolov and Rintoul, 2002) may be better assessed at 200 m than at the surface. The change in communities is very sharp in the polar frontal zone and the subantarctic zone, such as across a narrow area north of the Kerguelen shelf, because the different frontal zones are close together. Elsewhere transition zones between provinces may be broad (Vierros et al., 2008), such as north of Marion, Prince-Edwards and Crozet Islands, as there is some influence of the Agulhas Front as already underlined by Koubbi (1993) about fish larvae. In contrast to the transition zones, “core areas” represent areas of stability (Vierros et al., 2008). Core areas and transition zones have different spatio-temporal dynamics, but all zones may vary with time.

The STF is the northern limit of the Southern Ocean. The STF lies north of 45°S except south of Tasmania and New Zealand where it has a more southerly position. In the southern Tasman Sea, the Subtropical Frontal Zone is broad and has several branches (Sokolov and Rintoul, 2002) but multiple branches are also found in the rest of our study area. Regions for three groups were identified north of this front (Groups 10–12) in accordance with a latitudinal gradient in community structure in the Australian–New Zealand region, north of Kerguelen and south of South Africa.

The latitudinal position of the SAF and the extent of subantarctic assemblages differ from the west to east in the studied area. Regions are defined by Groups 6–10, with Groups 6 and 10 defining

transition assemblages. The complex regionalization of the myctophid assemblages shows that it is in this SAF region where biogeographic changes mainly occur, as established for mesopelagic fish larvae by Koubbi (1993). The subantarctic front seems to be a more of a barrier for subtropical species but less so for some Antarctic species. This complex regionalization is also consistent with the oceanographic features of the zone as multiple branches of the SAF can be found, especially in the Tasmanian–New Zealand sector with meanders to Macquarie Ridge at 160°E (Sokolov and Rintoul, 2002). Unfortunately, we were not able to give species compositions for the regions of Groups 7 and 9, because no multi-species samples were taken in these areas during summer. In the other part of the study area, the distance between the STF, the SAF and the APF is minimal north of Kerguelen (Park et al., 1991, 1993), where rapid changes in assemblage composition occur. North of Crozet, the frontal zones are even more complex with the juxtaposition of the Agulhas Front (AF), STF and SAF determining the “Crozet Front” (Kostianoy et al., 2004).

The polar front is characterized by the northernmost position of the subsurface (200 m) temperature colder than 2 °C (Park et al., 1991, 1993; Orsi et al., 1995). The polar frontal zone, between the APF and the SAF, corresponds mainly to Group 5 of GDM. There are some discrepancies between authors concerning the position of this front. Park et al. (1998) showed a different pattern of meandering of this front in the Kerguelen area. According to this author, the APF does not meander to the north of the Kerguelen Shelf but passes to the south of the Shelf, through the Kerguelen–Heard Trough and to the east of the Kerguelen Shelf. This is more in accordance with what we observed from regions based on GDM, as it allows for the clear separation of the Kerguelen and Heard oceanic areas. Roquet et al. (2009) and Park et al. (2008) established that the polar front around the Kerguelen Islands may be the chlorophyll-poor tongue that is observed along the south and east island shelf slope. It cuts the chlorophyll-rich area over the northern Kerguelen Plateau into two parts, which influences the myctophid distribution as shown by Loots et al. (2007) for *E. antarctica*. The high productivity of the waters in the oceanic zone of the Kerguelen Islands is due to an “island mass effect” (Koubbi et al., 2009), which favours productivity by allowing large inputs of iron from the sediment, water runoffs and from the faeces of top predators. Such effects are also observed at a smaller spatial scale at the other subantarctic islands. There are also quite complex meanders of the PF south of South Africa with juxtaposition of this front with the SAF.

The southern regions have a larger spatial extent compared to the northern regions. They are influenced by the SACCF, the SBy, the ice limit and by the topographic features. The SACCF and SBy are adjacent to each other in some areas. They are at their northern position in the Atlantic part of the study area and found around 65°S in the eastern Enderby Basin. They are more to the north through the Princess Elizabeth Trough to reach 62–63°S, and to the south at 150°E than in the rest of the Australian–Antarctic Basin.

The region of Group 3 is clearly between the SACCF and the APF in the Permanent Open Ocean Zone (as defined by Tréguer and Jacques, 1992). It has its greatest latitudinal extent between Kerguelen and the south of Tasmania. In contrast, Group 1 is probably limited by the Antarctic shelf slope front. The remaining regions (Groups 2 and 4) are related to the Southern Frontal zones (SACCF and the SBy). Two regions are clearly determined for Group 4 and they are associated with the deeper part of each basin (Enderby and Australian Antarctic) that surrounds the Southern Kerguelen Plateau, where they are located north of the Antarctic Divergence. Regions of Group 2 are more complex and are probably linked to the northern edge of the sea ice but also to the influence of the Weddell and Ross Sea gyres. It is interesting to note that there is a complex regionalization in the southern Kerguelen

Plateau, especially in the area of the Fawn Trough and Elisabeth Trough, where particular currents have been shown by Roquet et al., (2009). However, the “low zone” of chlorophyll concentration in the Fawn Trough is commonly observed during the summer period (Roquet et al., 2009). The southeast edge of the Kerguelen Plateau as well as the SBy are important areas for top predators such as sperm, minke whales and humpback whales (Tynan, 1998). They are also known as productive regions for Antarctic krill, especially in the rich chlorophyll areas, although not as much as in the Weddell Gyre (Atkinson et al., 2004; Nicol, 2006).

4.3. Perspectives

It is important that ecoregionalization uses a mixed approach, which combines taxa and habitats to delineate homogeneous areas and biogeographic provinces. One of the challenges is to see whether ecoregionalization can combine all species from phytoplankton to fish and top predators, since each group does not react similarly to the spatio-temporal variations of their environment. All the micronektonic species play major roles in the trophic web of the Southern Ocean because they are not only the major prey organisms for top predators (e.g. pinnipeds, penguins, seabirds) but they also control the zooplankton standing stock through their foraging activity. On the other hand, there is advantage to using mesozooplankton for regionalization when high spatial coverage occurs such as through the Continuous Plankton Recorder (Hunt and Hosie, 2005, 2006a,b). An alternative would be to use CPR data in conjunction with abiotic factors when creating the GDM models as we know that the ecological niche of a species is a combination of habitat, foraging activities and biotic interactions.

We do not believe that a single, unique ecoregionalization is able to answer questions at all spatial and temporal scales. As Vierros et al. (2008) have indicated, the use of environmental factors must be considered at the spatial scale where it influences species distributions (local, regional, global). In this study, we were not able to adequately classify some of the areas, whereas it is possible to see differences in habitat of some species at the mesoscale when using appropriate biological and environmental data sets (Loots et al., 2007). The rule is to avoid interpolating at a lower scale than the coarsest environmental parameter used in the analysis. Within ecoregions, we can study interannual variations of species habitats as Loots et al. (2007) have undertaken on *E. Antarctica*. The habitat modeling approach is based on the estimation of potential habitat in relation to environmental factors. As GDM, it is a data-driven approach; once the models are developed, they can be applied to different years and will adjust with the environmental conditions of each year. Habitat modeling based on environmental values was achieved for some species of the Southern Ocean by using the Habitat suitability index (Koubbi et al., 2003), Generalized Additive Models (Loots et al., 2007) or Boosted regression trees (Pinkerton et al., 2010). The difficulty is to determine whether community analysis can be done on potential species habitat, or as we did by GDM. One of the problems with using habitat modeling is that habitat cannot be modeled for all species, as many of them are rare. When using GDM, we can consider all species.

The advantage of the ecoregionalization is that it can always be improved by adding new data; it also shows where future sampling effort should be directed, especially in the transition zones such as frontal zones. We can improve ecoregionalization by having finer spatial resolution environmental data sets in some areas. This is currently under way with the Kerguelen data sets and with the data from Collaborative East Antarctic Marine Census (CEAMARC) in Dumont d'Urville Sea, a project of the

Census of Antarctic Marine Life (Koubbi et al., 2010). In the Indian sector, the importance of the Kerguelen Plateau, and the Fawn and Elisabeth Troughs should be more thoroughly investigated as they appear to play a major role in the oceanic circulation in this area. Additional means of improving the ecoregionalization approach might include the addition of micronektonic species, such as euphausiids, together with a strategy for sampling deeper horizons in the water column, to alleviate the problem of discarding hauls which contain less than three species.

5. Conclusion

This work demonstrates that mesopelagic fish can be used for understanding macroscale oceanic features and their variations. Ecoregionalization, as shown in terrestrial and neritic ecosystems, is an important and immediate issue for the establishment of conservation policy, but it is difficult to achieve for the open ocean because there are limited data. This is the case for the Southern Ocean where the high seas are very important for numerous top predators. In the context of determining Marine Protected Areas for the year 2012, the methodology we have used can contribute to achieving the goal of ecosystem-based management. The regions obtained here are some of the many possibilities that can evolve by adding new information on species distribution. For instance, we have carried out only 2D ecoregionalization but there are possibilities of conducting 3D regionalization. The 4th dimension, time, could also be easily assessed if models are based on seasonally consistent between-year comparison.

Ecoregionalization of the open ocean suffers from a lack of dedicated surveys. In fact, most of the recent data concerning the high seas comes from top predator tracking and CPR surveys. The foraging habitats of these top predators can serve as indicators of the potential habitats of their prey (Bost et al., 2009) to aid and support the ecoregionalization process. More importantly, we need to improve and encourage researchers to share their data, even historical ones, by using a common portal such as SCAR MarBIN. Finally, there is also an important need to generate multidisciplinary efforts between oceanographers, taxonomists and ecologists so as to understand the ocean's biogeographic provinces. We can now explore the meandering of frontal zones and the role of mesoscale gyres, which are now recognized to be far more complex than the traditional latitudinal bands, and link this to planktonic communities. One of the major challenges is to find ways of delineating fuzzy boundaries in a temporally dynamic environment.

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