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Habitat modelling of *Electrona antarctica* (Myctophidae, Pisces) in Kerguelen by generalized additive models and geographic information systems

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Abstract *Electrona antarctica* is one of the most abundant mesopelagic fishes in the oceanic zone surrounding the Kerguelen Archipelago in the Indian sector of the Southern Ocean. Generalized additive models (GAM) combined with geographical information systems (GIS) were used to predict and map the abundance of this species according to three environmental variables: sea surface temperature, bathymetry and surface chlorophyll *a*. The model was applied on the Antarctic Polar Front in the eastern part of Kerguelen Archipelago. *E. antarctica* seems to be linked to areas presenting low chlorophyll *a* concentrations, depths greater than 500 m and temperatures lower than 5°C. The model was then applied to the Kerguelen's plateau for three different years: 1998, 1999 and 2000. The position of Antarctic Polar Front and the intensity of an upwelling play an important role in the abundance variability of *E. antarctica*. Furthermore, the model allows the understanding of the habitat of *E. antarctica* and its trophic place in the pelagic ecosystem.

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Introduction

In the Southern Ocean, lanternfishes (Myctophidae) are the second major component after krill in terms of biomass. These mesopelagic fishes represent between 70 and 130 million tonnes (Lubimova et al. 1987). In the trophic web, they are a key component for top predators like seabirds and marine mammals. In the oceanic zone surrounding the Kerguelen Archipelago, some studies focussed on mesopelagic fish community, both larvae (Koubbi et al. 1991, 2003; Koubbi 1993) and adults (Duhamel 1998; Duhamel et al. 2000). From 1998 to 2000, the aim of the ICH-TYOKER programme was devoted to this fish community. This area is influenced by the Polar frontal zone, especially by the Antarctic Polar Front (Park et al. 1993; Park and Gamberoni 1997) which is a highly productive area used for the foraging of King penguins (*Aptenodytes patagonicus*) and fur seals (*Arctocephalus gazella*).

As mesopelagic fishes, Myctophids are highly linked to water mass characteristics, which explains their biogeographic patterns (Hulley 1981). By statistically relating abundances to water masses and topography, we aim at modelling their distribution. Habitat modelling is related to the real ecological niche defined by Hutchinson (1957). It is the combination of environmental factors which explains one species' distribution. Habitat can be mapped by using Geographic Information

Systems (GIS) (Koubbi et al. 2003). We have selected a species with a wide circumantarctic distribution, *Electrona antarctica*, and considered as a key component of the Myctophid assemblage (Kozlov 1993). Its study will evaluate what a pelagic species habitat is and how it changes according to inter-annual variations of the water masses and positions of frontal structures.

Materials and methods

Study site and biological data

The site of study is located on the north-eastern sector of Kerguelen Plateau which include Kerguelen archipelago (49°30′S–69°30′E) and Heard Island both surrounded by a peri-insular plateau (neritic zone) of 200 m depth. Limits of Kergueken Plateau are situated close to depths of 2,000 m. The climatic character of the site is typical of the roaring forties with succession of westerly and heavy depressions. The area lies in the southern part of the Antarctic Circumpolar Current zone close to a meander of a major hydrological front, the Polar Front, where subsurface seawater temperature reaches 2°C. In this area, the Polar Front is closely associated with the sub-Antarctic and sub-Tropical front (Park et al. 1993; Koubbi et al. 1991; Koubbi 1993) located on the northern part of Kerguelen plateau.

Fishes were collected during the ICHTYOKER programme in 1998, 1999 and 2000. Eight hundred and thirty-five pelagic trawlings were achieved by R.V. "La Curieuse", during night and day, for half an hour each at a speed of three knots with an IYGPT (International Young Gadoid Pelagic Trawl). This net is 12 m long, 7 m wide and has an opening of 10.1×5.69 m. The mesh size of its cod end is 10 mm. Trawl locations were based on the position of King Penguins and Antarctic fur seals (Fig. 1), which were tracked by ARGOS systems in their foraging areas (Guinet et al. 2001; Bost et al. 2002). Five vertical strata were sampled (0–20, 20–100, 100–200, 200–300 and 300–450 m) to study the vertical distribution of the pelagic fishes during night and day (Duhamel 1998; Duhamel et al. 2000). The samples were frozen or preserved in 5% formaline. The species identification was done according to the descriptions by Hulley (1990). Data by species were registered in an ® Access database.

For this study, data were standardized in term of number of specimens per volume (individuals 10^5 m^{-3}) according to the calculations of Young et al. (1996).
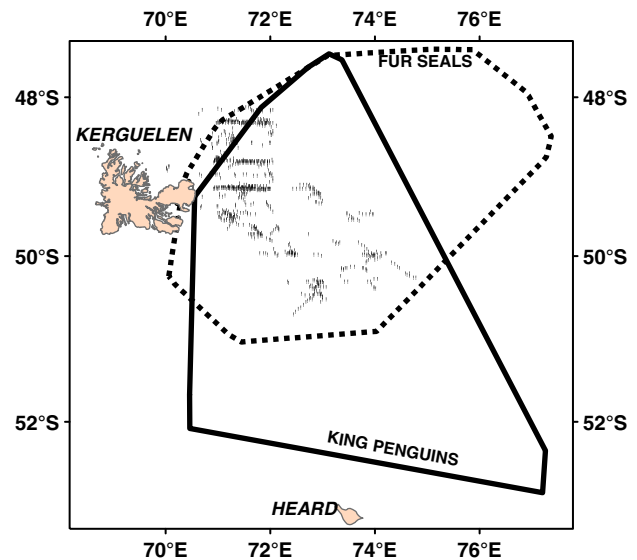
Fig. 1 Location of mesopelagic trawls of ICHTYOKER programme (1998–2000) compared with main foraging areas of satellite-tracked King Penguins (*solid line*) and Antarctic fur seals (*broken line*)

Environmental data

As the main aim is to model *E. antarctica* distribution at a large scale, available satellite data were obtained for each survey. Three major available environmental parameters were used: bathymetry, sea temperatures and chlorophyll *a*. Moreover, these parameters are available worldwide through international databases. The bathymetry data (m) has a resolution of 4 km. They come from the National Geophysical Data Center (http://www.ngdc.noaa.gov). The surface chlorophyll *a* (mg m^{-3}) and the sea surface temperatures (°C) are weekly averaged and have a resolution of 9 km. They come from SeaWifs (http://www.seawifs.gsfc.nasa.gov) and NOAA/NASA AVHRR Ocean Pathfinder (http://www.podaac.jpl.nasa.gov/sst).

Geographical information systems (GIS)

ArcGis 8 was used to map data. Environmental data are punctiform geolocalised data (latitude, longitude and value). The interpolations were calculated to generate raster layers (based on pixels), using the Geostatistical Analyst extension of ArcGis. Variogram calculates spatial correlation (or variance) between each point according to the distance between them by creating a variographic cloud. A variogram model is then fitted to this variographic cloud, to describe the general trend of spatial structure of each parameter. The interpolation was made by kriging, which interpolates between points taking into account spatial

relationship describe by the variogram. Associated to this interpolated map, interpolation error map was automatically calculated using Geostatistical Analyst. As environmental data are remote sensing data, they are available on a large spatial scale with a reasonable good resolution (4–9 km) which avoid high interpolation errors. Consequently, areas presenting high interpolation errors were always situated on the outer border and were withdrawn from maps. As predicted biological data were derived from environmental data, they had the same resolution implicating the same areas of high interpolation errors.

Generalized additive models (GAM)

Generalized additive models (Hastie and Tibshirani 1990; Hastie and Tibshirani 1995) is the non parametric equivalent to generalised linear models (GLM; McCullagh and Nelder 1989). They were introduced in forest ecology by (Yee and Mitchell 1991) to model relations between tree's presence/absence and physical factors (Brown 1994). They were also applied in marine ecology (Daskalov 1999; Bellido et al. 2001; Granadeiro et al. 2004) and essentially used as an explanatory procedure (Guisan and Zimmerman 2000) to describe species-environment relations (Bio et al. 1998). With the development of GIS, GAM and GLM are used to map species' habitat. They are combined with geostatistics (Leathwick 1998; Guinet et al. 2001; Koubbi et al. 2003) in explanatory and predictive studies (Guisan and Zimmerman 2000) to model biogeographic patterns at different scales.

Data of *E. Antarctica* are expressed in term of abundances that can be considered as continuous data. They were log-transformed ($\log(X + 1)$ to take account of zeros) to approach normality and the corresponding "identity" link, for Gaussian distribution, was chosen (McCullagh and Nelder 1989). Response of the species to each predictor was modelled in a smoothing way. Smoothed responses (additive terms) were then added to do an Additive Model with the corresponding identity link and predict the global response:

$$Y = f_1(X_1) + f_2(X_2) + \cdots + f_n(X_n),$$

where "f" are the smoothing functions.

Loess and cubic splines (spline with smoothing of degree 3) are the most commonly used smoothing functions. They are respectively based on running means and on polynomial regressions. The idea of smoothing is to replace each value by a weighted value calculated from several values situated in a window called "span". The degree of smoothing also called degree of freedom depends on the size of the span. The bigger is the span, the less precise is the relation, but if the span is too small, there may be have a lot of variations.

Data of *E. antarctica* coming from the summer period (December–March) of 1998, 1999 and 2000 were used to create a model according to the bathymetry, surface chlorophyll *a* and surface temperature. Each environmental mapped raster was resampled, using GIS, to obtain a corresponding environmental value to each biological data. The model fitting quality including choice of the predictors, the smoothing functions and the degree of smoothing was made using deviance (McCullagh and Nelder 1989). Several models with their corresponding deviance were calculated using a forward selection. Significance of decreasing deviance between models was tested by a *F* test (Quinn and Keough 2002) and the model with the significant minimal deviance was kept as the final model. The implementation was done with S-Plus 6.0 (Daskalov 1999; Quinn and Keough 2002).

Combining with GIS

The model was first applied to the frontal zone of Kerguelen on the environmental dataset of the first week of February 1998 (heart of the summer). Predicted data were then imported in the GIS as advised by Lehman (1998) and Koubbi et al. (2003). Data were interpolated throughout the studied zone using geostatistics methods described above.

The main aim of the study was to get a better mapping of *E. antarctica* in the sampled area. Moreover, this method allows the mapping of potential habitats at a broader spatial scale in unsampled areas. The model was then applied to the Kerguelen Plateau in the same environmental range used to create the model. Environmental data for predictions, which were out of the environmental range used to create the model (78–2,400 for bathymetry, 0–2.6 for surface chlorophyll *a* and 2.1–6.15 for surface temperature), were withdrawn in order to not extrapolate.

Validation

The model was developed using data from summer 1998, 1999 and 2000. The model was then applied to environmental data of February 1998 to calculate corresponding predicted abundances. This map was then resampled by locations of observed abundances in February 1998. A Spearman Rank correlation between observed abundances and predictive abundances in

February 1998 was then calculated. The correlations was calculated and tested to be significantly different from zero.

Results

Mapping of environmental data

Raster of bathymetry, surface chlorophyll *a* and surface temperature are presented in Fig. 2a–c. The chlorophyll *a* shows two areas of high concentrations. In the North, high concentrations follow the Kerguelen island shelf which is limited by the 500 m isobaths whereas they are associated on deeper zones in the southern part. The lowest concentrations extend from the North to the South and shape a band that becomes broader in the East, at depths of 2,500–3,000 m. The surface temperature is divided in two areas by the 5°C isotherm which seems to delimitate the two areas of high chlorophyll *a* concentration.

Vertical distribution of *E. antarctica*

E. antarctica is the second species in abundance (after another lanternfish *Kreffichthys anderssoni*) in the area for the studied period. Trawls data of *E. antarctica* for the 3 years (Fig. 3) show that this species is less abundant during daytime than at night in the strata sampled. During the day, higher abundance (25 individuals
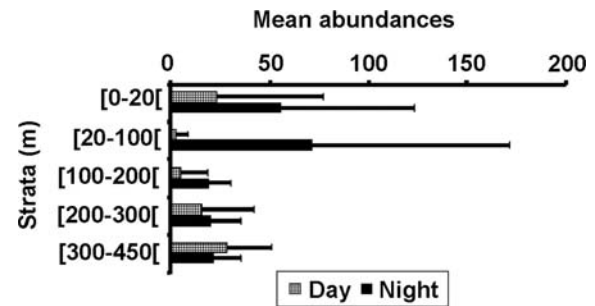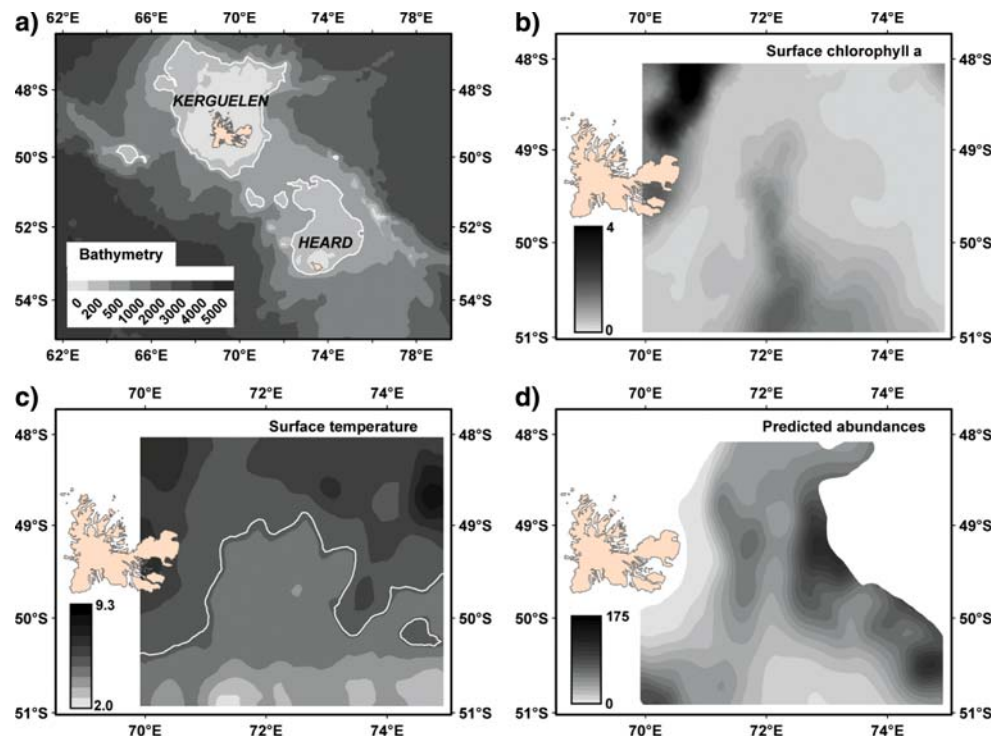

Mean abundances

Fig. 3 Day-night vertical distribution (mean abundances and standard deviation) of *E. Antarctica* for the five strata during summer period (December–March) of ICHTYOKER programme (1998–2000)

10^5 m^{-3}) are observed between 0–20 and 300–450 m whereas it is between 0 and 100 m at night (50–75 individuals 10^5 m^{-3}).

A correlation matrix, calculated between strata, indicate that the 0–20 and 20–100 m have a significant correlation of 0.70 ($P = 0.05$) and can be combined. Log-transformed data of *E. Antarctica* show a quasi normal distribution with a high number of null values (Fig. 4a). According to Charassin et al. (2004), the sea surface temperatures in this area are vertically correlated in the 0–80 m surface layer. From these results, only night abundances from 0 to 80 m were modelled because of the surface distribution of the species, which can be linked to remote sensing data. Several models were compared using their deviance. The

Fig. 2 Mapped rasters of bathymetry (m, **a**), surface chlorophyll *a* (mg/m³, **b**) and surface temperature (°C, **c**), with corresponding mapped raster of predicted data (individuals 10^5 m^{-3}, **d**) of *E. Antarctica*, by night between 0 and 80 m, on the Antarctic Polar front off Kerguelen. *Solid white line* correspond to 500 m isobath (**a**) and 5°C isotherm (**c**)

Fig. 4 Distribution of log-transformed abundances of *E. Antarctica* (**a**) and additive terms of bathymetry (**b**), surface chlorophyll *a* (**c**) and surface temperature (**d**). *Broken line* give 95% confidence intervals. *s* spline, *lo* loess, with corresponding degree of smoothing
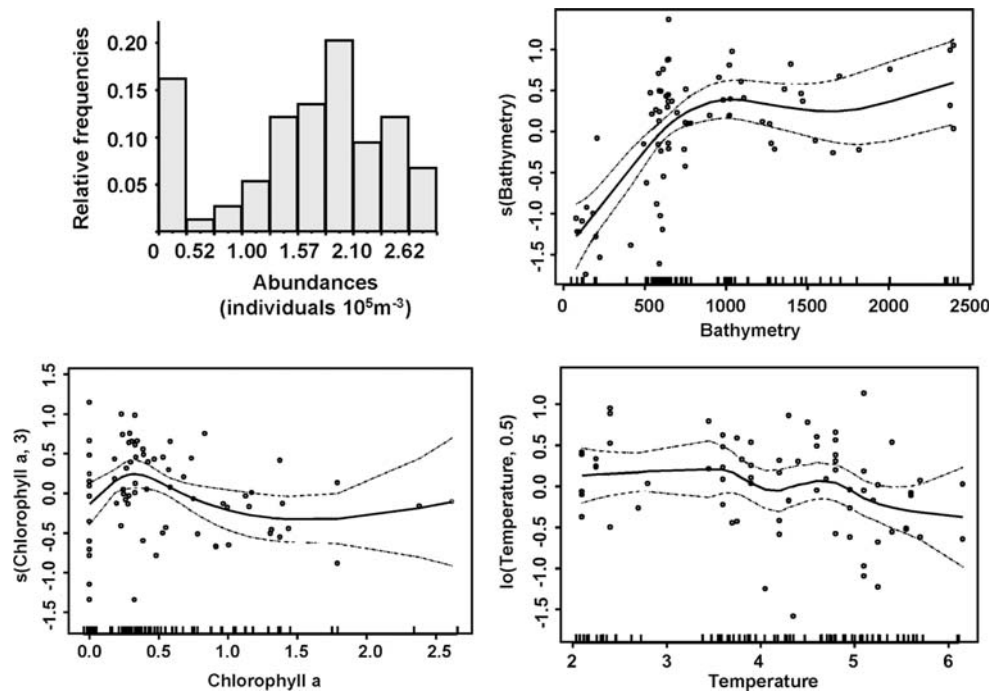
three predictors were kept together and the adjusted smoothed plots of abundances, according to chlorophyll *a*, bathymetry and surface temperatures (Fig. 4b–d) show non-linear relationship between the response and the predictors. The final model was defined as follow:

$$Log(abundances) = s(depth) + s(chlorophyll\ a,\ 3) + lo(temperature, 0.5),$$

where *s s* is the spline (with degree 3 for chlorophyll *a*) and lo the loess (with span of 0.5).

Spatial distribution

From this model, predicted abundances data, for the first week of February 1998 and between 0 and 80 m, are presented as a raster layer in Fig. 2d. Predicted and observed data were found to be positively correlated ($r = 0.6$, $P < 0.05$), whereby validating the model. The areas mapped in blank are the ones where interpolation errors are too high. The predicted data for *E. antarctica*, at night between 0 and 80 m, goes from 0 to 175 individuals $10^5\ m^{-3}$. The repartition is heterogeneous and shows four areas of high abundance. They correspond to the band of low chlorophyll *a* concentration (0.12–0.26 mg/m³) with temperatures below 5°C and depths greater than 500 m. The low abundances are situated over the island shelf and on the areas showing the highest chlorophyll *a* concentrations.

With a positive validation, the model was applied to the Kerguelen plateau and to Heard Island shelf outside the sampling zone according to the environmental factors of the first week of February 1998, 1999 and 2000. At a larger scale, inter-annual potential distributions were studied. The *E. antarctica*'s repartition shows temporal variations in its distribution (Fig. 5a–c). For the three years concerned, the low abundances are situated over the island shelves of Kerguelen and Heard and above the 5°C isotherm. For the oceanic area, the inter-annual variations in abundances correspond to variations in chlorophyll *a* concentrations (Fig. 6a–c). The chlorophyll *a* data are more concentrated around Kerguelen and Heard Islands. This zone can be divided in two areas, one in the Northeast and the second one in the Southeast of Kerguelen, which are influenced by the Antarctic Polar Front recognised as a convergent and trophic front. The high chlorophyll *a* concentrations indicate that it is a high productivity area due to the rise of nutrients in surface probably caused by an upwelling. Each year, spatial repartition and concentrations differ. In 2000, in the South of Kerguelen, the surface temperatures show an area of colder water that is rising more northerly than for the two other years (Fig. 6d–f). This indicates shifts of the Antarctic Polar Front and changes in the intensity of the upwelling. In 1998, the highest abundances are located where chlorophyll *a* concentrations are low, along the Antarctic Polar Front in the eastern part of Kerguelen. The abundances are also high in the South

Fig. 5 Spatio-temporal variations of abundances of *E. Antarctica* at Kerguelen's plateau, by night between 0 and 80 m, for the first week of February 1998 (**a**), 1999 (**b**) and 2000 (**c**), as predicted by the model according to bathymetry (m), surface chlorophyll *a* (mg/m³) and surface temperature (°C)
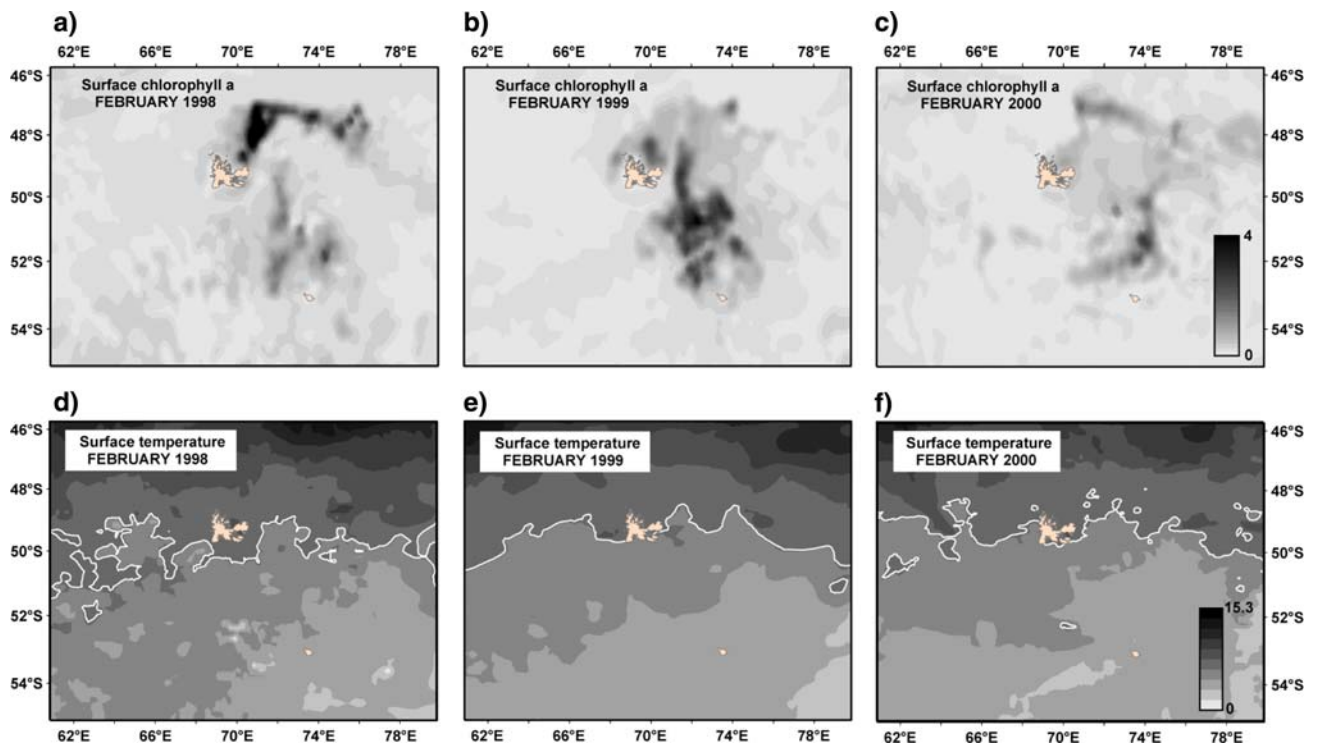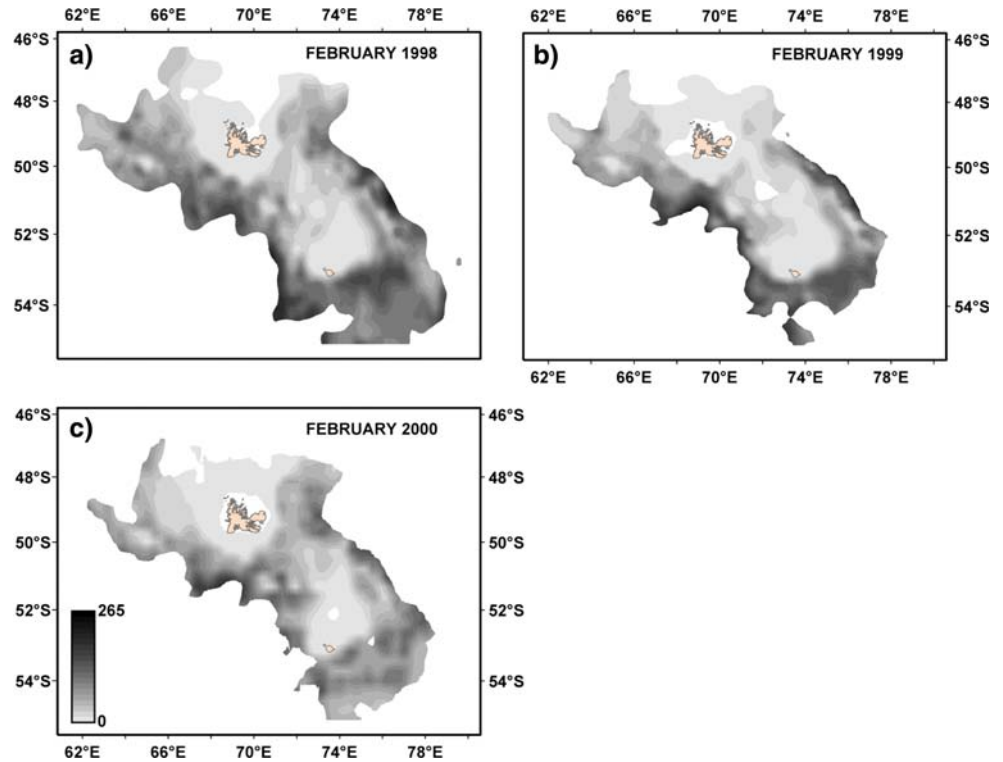
Fig. 6 Spatio-temporal variations of surface chlorophyll *a* (mg/m³, **a–c**) and surface temperature (°C, **d–f**) at Kerguelen plateau for the first week of February 1998, 1999 and 2000. *Solid white line* corresponds to 5°C isotherm

of Kerguelen plateau and outside the eastern part of the Heard Island shelf. In 1999, in the eastern part of Kerguelen, the band of low chlorophyll *a* concentra-tion, is narrower and the abundances are less impor-tant. In the South, the abundances are still high and they surround the shelf of Heard Island. In contrast, in

2000, the abundances in the East of Kerguelen are higher than for the two other years and chlorophyll *a* is less concentrated whereas the abundances around Heard Island are not as high as in 1998 and 1999.

Discussion

Spatio-temporal distribution

Predictive models from night observations between 0 and 80 m clearly show that this species is inversely correlated with the surface chlorophyll *a* as it was observed by Vinogradov (1981). The two areas of high chlorophyll *a* are linked to the Antarctic Polar Front. The Antarctic Polar Front activity is then important to understand the spatial repartition of *E. antartica* because it influences the chlorophyll *a* and the preys of Myctophids. It has been suggested that the Antarctic Polar Front in Kerguelen is more a trophic front than a barrier for pelagic organisms such as larvae (Koubbi et al. 1991, 2003; Koubbi 1993). Though, the model indicates that the abundances are not high in the North of the Front and it is because the front represents the northern extreme limit of *E. Antarctica*, justifying its belonging to the Antarctic pattern (Hulley 1981; Duhamel 1998).

The quasi-absence of *E. antarctica* from island shelves is explained by its pelagic nature and diurnal behaviour. This species has to move to deeper areas during the day, which is not possible over the island shelves for they are not deep enough. So, it can be interesting to compare spatial repartition during night and day in the upper 100 m of water column in order to see if there are horizontal migrations.

Position of *E. antarctica* in the pelagic zone

E. antarctica shows nycthemeral migrations like most Myctophids (Duhamel 1998). During the day, this species is more abundant on the deeper part of the water column than at the surface, even if a peak of abundances is observed at the surface as described by North (1991). At night, it reaches the surface and is very abundant in the upper 100 m water column as already observed by Duhamel et al. (2000). Moreover, the surface's peak of abundances during the night is higher than during the day. Stomach contents and lipids (fatty acids and wax esters) of Myctophids (Duhamel and Hureau 1985; Phleger et al. 1997) and particularly *E. antarctica* indicate that they feed on Euphausiids (*Euphausia superba*, *Thysanoessa macrura*), calanoid copepods (*Calanus propinquus*, *C. similimus*, etc.) and

hyperiid amphipods (*Parathemisto gaudichaudi*) (North 1991; Kozlov 1993). *E. antarctica* simply follows nycthemeral migrations of these zooplankton's species. This positive relationship between secondary and tertiary productions and the spatio-temporal separation between the primary and the secondary ones explain the inverse correlation between chlorophyll *a* and abundances of *E. antarctica*.

Higher abundances of *E. antarctica* at the surface make it a potential prey for Antarctic fur seals (*A. gazella*) that dive essentially at night in the upper 100 m (Guinet et al. 2001) and for King penguins (*A. patagonicus*) that dive to a maximum depth of 250 m during the day and to 60 m at night (Bost et al. 2002). However, the position of *E. antarctica* in the trophic web needs to be clarified. Bost et al. (1997) found that *E. antarctica* dominated the diet of King penguins during summer at Crozet Islands whereas it was not the case in February 1989 (Cherel and Ridoux 1992). Moreover, *E. antarctica* is poorly present in the diet of King penguins from sub-Antarctic Marion Island (Adams and Brown 1989) and Kerguelen Island (Bost et al. 2002). Raclot et al. (1998) assumed that it was because of its low energetic value due to its lipid composition (Reinhardt and Van Vleet 1984; Phleger et al. 1999). *E. antarctica* is mainly composed of wax esters, which is more an energetic reserve than food that is immediately available (Phleger et al. 1997). This can explain its absence from the diet of King penguins's chicks (Raclot et al. 1998).

E. antarctica's importance in Antarctic fur seals' diet is not clearly defined. Daneri and Coria (1993) observed that *E. antarctica* primarily constitutes the diet of fur seals and was observed in their faeces at King George Island in the Atlantic sector of the Southern Ocean. However, it is not the case in Kerguelen (Cherel et al. 1997). Its small size makes it less interesting for fur-seals in the Kerguelen area which feed on larger myctophid of genera *Gymnoscopelus* and *Electrona* (Lea et al. 2002a). The variability in the diving activity of Antarctic fur seals linked to the Antarctic Polar Front's position and variations in oceanographic conditions can be another explanation as suggested by Guinet et al. (2001) and Lea et al. (2002a, b). It was found that *E. antarctica*'s abundances were varying along the years according to Polar Front and surface chlorophyll *a* at a small scale as well as at a larger scale.

Habitat modelling

Generalised Additive Models have been chosen because they use smoothing functions that model

non-linear relationship, as it was the case for *E. Antarctica*, which often occurs in ecology (Yee and Mitchell 1991). These functions imply several statistical decisions (Guisan and Zimmerman 2000; Lehman 1998). Locations of trawls were only based on the positions of Penguins and Antarctic fur seal and this adaptive procedure may introduce biases to the results. As it has been explained, *E. antarctica* is not an important prey for these two top predators so their foraging positions do not automatically reflect high abundances areas of *E. antarctica*. Trawl samples are assumed to be representative of the population of *E. antarctica* in the sampling area as shown by numerous zero values. Zero values tend to distort smoothing functions making them more linear (Austin and Meyers 1996). Austin and Meyers (1996) and Koubbi et al. (2003) suggest that only non-null values have to be kept. But, as far as pelagic studies are concerned, it must be paid attention to the ecological meaning of null values. Do they reflect a shoal living behaviour or a response to an environmental factor, or both?

Usually, choice of predictors is constrained by limited field data available which is specially the case in this region where climatic conditions do not make field work very easy. That's why, remote sensing data is a good alternative even if they do not automatically reflect a direct or proximal impact on the species. They are also of great utility in a predictive way at a large scale because in situ data are not always available trough a large area.

Conclusion and perspectives

Habitat modelling of *E. antarctica* highlights the mesopelagic nature of this species. It lives outside island shelves, on deep areas, mainly in the south of the Polar frontal zone and is influenced by the physical characteristics of water masses such as surface temperatures and chlorophyll *a*.

This methodological approach can be used to model large scale biogeographic patterns of pelagic species in unsampled areas, provided that the models are not applied outside of the ranges of parameters used to develop the model. Data from several databases could be used and combined to model potential distribution all over the Southern Ocean. However, this work is a first step in better understanding the distribution of *E. Antarctica* and it is clear that the model could be improved. Ideally, sampling has to be systematic or random trough the study area and some trawls would need to be allocated in areas where neither penguins nor fur

seals forage. We choose to use only three environmental variables but more environmental variables could be added such as salinity. In term of biotic predictors, the positive trophic relationship between *E. antarctica* and secondary production suggests that the zooplankton repartition could be a more proximal factor with *E. antarctica* than chlorophyll *a*. At this large spatial scale, data from continuous plankton recorder could be of great interest to answer this question. With this positive relationship, knowledge of *E. antarctica* distribution using statistical modelling could help in understanding and predicting potential areas of krill concentration. Validation could be improved by using an external data set to compare with predicted abundances and predicted abundances at large spatial scale should be compared with observed data (if available) to assess the strength of the model. However, combining GAM and GIS in a statistical model is a useful tool to understand relationships that link a species to its environment.

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