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Atlas of Myctophids from the Southern Indian Ocean and around the subantarctic islands of Crozet and Kerguelen

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Abstract

This paper summarises myctophid distribution from surveys from the Crozet to Kerguelen regions of the Southern Indian Ocean. These fish play a crucial role in the marine ecosystem trophic web as they are important prey for seabirds and marine mammals. This study integrates both the subtropical and Southern Ocean species from surveys from 2017 to 2019. In these surveys, 62 species of myctophids were observed across different oceanographic regions from the subtropical zone to the Subantarctic and the Antarctic zone. These species exhibited high abundances in the Southern Ocean, with concentrated patches in the Subantarctic zone between the Crozet and Kerguelen archipelagos, as well as the eastern part of the Kerguelen Plateau. The fronts at the northern boundary of the Southern Ocean explained the separation of subtropical and Subantarctic faunas.

Résumé

Cet article résume la distribution des myctophidés à partir d'études menées dans les régions de Crozet à Kerguelen dans le sud de l'océan Indien. Ces poissons jouent un rôle crucial dans la chaîne alimentaire marine, car ils constituent une proie importante pour les oiseaux et les mammifères marins. Cette étude intègre à la fois les espèces subtropicales et celles de l'océan Austral issues des campqgnes de 2017 à 2019. Au cours de ces études, 62 espèces de myctophidés ont été observées dans différentes régions océanographiques, de la zone subtropicale à la zone subantarctique et à la zone antarctique. Ces espèces présentaient des abondances élevées dans l'océan Austral, avec des zones de concentration dans la partie subantarctique entre les archipels de Crozet et de Kerguelen, ainsi que dans la partie orientale du plateau de Kerguelen. Les fronts situés à la limite nord de l'océan Austral influençaient la séparation entre les faunes subtropicales et subantarctiques.

Абстракт

В данной работе обобщены данные о распространении миктофовых, полученные в ходе съемок в районах от островов Крозе до островов Кергелен в южной части Индийского океана. Данные виды рыб играют важную роль в трофической сети морской экосистемы, поскольку являются важным источником пищи для морских птиц и морских млекопитающих. В данном исследовании объединены данные о видах, обитающих в субтропических водах и в Южном океане, полученные в ходе съемок, проведенных в период с 2017 по 2019 год. В ходе данных съемок было зарегистрировано 62 вида миктофовых рыб в различных океанографических регионах от субтропической зоны до субантарктической и антарктической зон. Данные виды наблюдались в значительных количествах в Южном океане, с концентрацией в субантарктической зоне между архипелагами Крозе и Кергелен, а также в восточной части плато Кергелен. Линии фронтов на северной границе Южного океана объясняют разделение субтропической и субантарктической фауны.

Resumen

Este artículo reseña la distribución de los mictófidos a partir de prospecciones realizadas en las regiones entre Crozet y Kerguelén, en el Océano Índico Meridional. Esas especies ícticas desempeñan un papel crucial en la red trófica del ecosistema marino, ya que son presas importantes para las aves y los mamíferos marinos. Este estudio integra datos de las especies subtropicales y del océano Austral procedentes de prospecciones realizadas entre 2017 y 2019. En esas prospecciones se observaron 62 especies de mictófidos en diferentes regiones oceanográficas: la subtropical, la subantártica y la antártica. Estas especies mostraron grandes abundancias en el Océano Austral, con focos de concentración en la región subantártica entre los archipiélagos de Crozet y Kerguelén, así como en la parte oriental de la meseta de Kerguelén. Los frentes del límite septentrional del Océano Austral explican la separación de las faunas subtropical y subantártica.

Introduction

The mesopelagic zone is usually considered to be a division of the water column between 200 m (the epipelagic zone) and 1000 m (the upper limit of the bathypelagic zone) (Reygondeau et al., 2017). Abiotic parameters, chlorophyll and species assemblages have been used to define mesopelagic biogeographic provinces (Sutton et al., 2017) and three-dimensional bioregions based on abiotic factors can be modelled (Reygondeau et al., 2017). According to Sutton et al. (2017), the Southern Indian Ocean province has oligotrophic subtropical waters that are well oxygenated. Its planktonic and micronektonic diversity is high. The circum-global Subtropical Front province is associated with strong horizontal hydrological gradients over the upper 400 m. The Subantarctic province is characterised by cold waters with low salinities between the Subtropical Front (STF) and the Polar Front (PF), high primary productivity and a mesopelagic fauna influenced by the Subantarctic Front (SAF) and extending partly into the Southern Ocean (Post et al., 2014). The Antarctic/Southern Ocean province is characterised by cold, dense waters with the SAF as a strong biogeographic barrier and high seasonal primary productivity, but low mesopelagic micronektonic diversity. Koubbi (1993) and Koubbi et al. (2011b) indicated that the area of the Crozet Basin is special because the SAF is the major biogeographic front explaining the biogeography of the myctophids.

Most mesopelagic fishes make regular 24-hour migrations, but some species remain at the same depth (Duhamel et al., 2014). Those migrating, spend the day in deeper waters and move into the epipelagic zone at night. Myctophidae is the dominant mesopelagic fish family in the Southern Ocean in terms of their species richness, abundance and biomass (Hulley, 1981; Duhamel et al., 2014). These micronektonic fish occupy an intermediate trophic level between secondary producers and large predators (Sutton, 2003; Cherel et al., 2020). Myctophids are an important component of the pelagic ecosystem in the Southern Ocean as they are the main prey of several top predators (Caccavo et al., 2021).

A first synthesis of mesopelagic fish distribution between Crozet, Kerguelen, Saint Paul and Amsterdam was provided by Koubbi et al. (2011a). Most surveys in the 1980s and 1990s used bongo nets to collect larval fish (Koubbi et al., 1991, 2009; Koubbi, 1993). In some of these coastal areas, only the dominant myctophid *Krefftichthys anderssoni* larvae were caught in winter (Koubbi et al., 2001). Later surveys used an International Young Gadoid Pelagic Trawl (IYGPT) to sample juveniles and adults at different depths, these surveys were mainly on the eastern part of the Kerguelen shelf where top predators forage, or from Kerguelen to New Amsterdam (Duhamel, 1998; Duhamel et al., 2000; Bost et al., 2002). Hulley and Duhamel (2011) provided additional data from other surveys with less intensive sampling. These data were included in the synthesis on fish in the biogeographic atlas of the Southern Ocean by Duhamel et al. (2014).

The Response of the pelagic ecosystem to climate change in the Southern Ocean and Southern Indian Ocean (REPCCOAI) surveys occurred in January and February 2017 to 2019 (Table 1). These cruises crossed several oceanographic and biogeochemical provinces over a small latitudinal range from the tropical waters of the Indian Ocean to the cold waters of the Southern Ocean. The sampling design was based on transects to align with the recurring oceanographic surveys of the Observing the Carbon Cycle and Ocean Acidification in the Indian Ocean (OISO) program. Additionally, the transect captures latitudinal gradients, which are important for understanding changes in species assemblages. The sampling from the different years aimed to collect sufficient information on species presence to be able to model fish habitats in relation to regional oceanography.

Materials and methods

The survey covers a geographical area between 50°E and 85°E and 27°S and 60°S (Figure 1). The transects passed through the Crozet and Kerguelen archipelagos in the Southern Ocean and extended to the vicinity of Saint-Paul and Amsterdam Islands in the Indian Ocean. By spanning several distinct oceanographic and biogeochemical provinces — from the tropical waters of the Indian Ocean to the cold waters of the Southern Ocean — the surveys captured transitions across diverse ecological zones. Conducting these surveys over three consecutive years further allowed for the assessment of interannual variability in ecosystem dynamics, forming a robust dataset for future predictive modeling efforts.

During the REPCCOAI surveys, mesopelagic fish were sampled at 82 stations in January and February 2017, 2018 and 2019 with an Isaacs-Kidd Midwater Trawl net (IKMT). IKMT had a total length of 17 m, a metal wing, an opening area of 7 m^2 and a decreasing mesh size from 3.5 cm at the net entrance to 0.5 cm near the cod-end. The net was towed at a speed of between 2 and 3 knots. It was deployed from the surface to a maximum of 1000–1200 m to integrate species from the epi- and mesopelagic zones. The samples were preserved in a 5% buffered formalin solution.

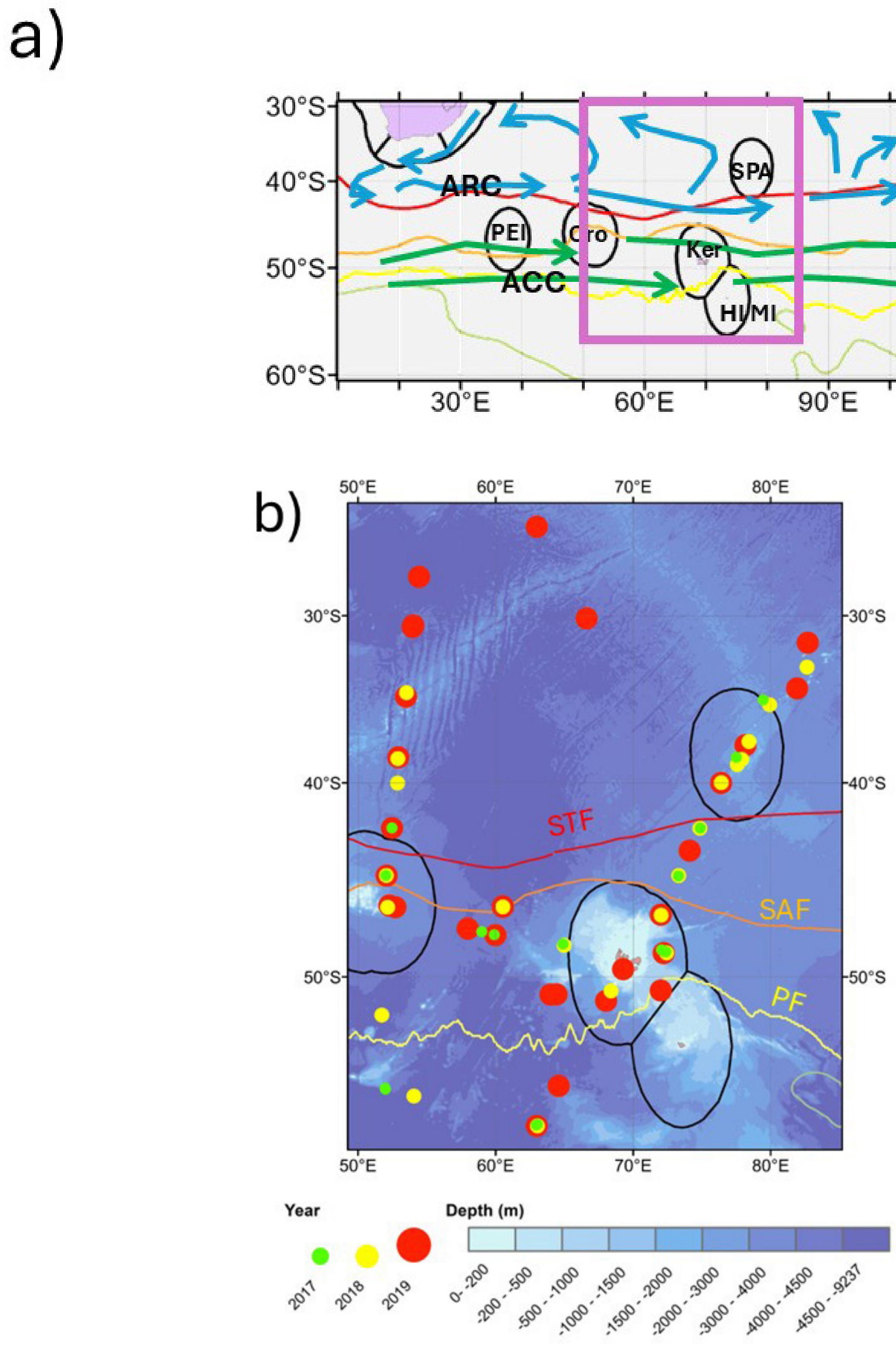


Figure 1: a) location of the study area indicating the main currents and islands (Ker – Kerguelen, Cro – Crozet, SPA – St Paul and Amsterdam, HIMI – Heard Island and McDonald Island, PEI – Prince Edward Islands). ARC is the Agulhas Return Current Front and ACC is the Antarctic Circumpolar Current. The REPCCOAI area is indicated by a purple rectangle. b) IKMT samples positions for the 2017, 2018 and 2019 REPCCOAI surveys. The mean position of oceanographic fronts are shown. Fronts are: STF for Subtropical Front, SAF for Subantarctic Front, PF for Polar Front and SACCF for South Antarctic Circumpolar Front.

Each fish caught by IKMT was identified to species where possible by using the following keys: Smith and Heemstra (1986); Gon and Heemstra (1990); Duhamel et al. (2005) and Sutton et al. (2020). Abundance was computed as the number of individuals per the volume of filtered seawater which was estimated (1) from the distance travelled by the net and its opening and (2) by flowmeters to calibrate calculations.

The data were mapped using a geographic information system (ArcGIS 10.8), and multivariate analyses were conducted on the log-transformed fish abundances using the PRIMER-e software (Clarke and Gorley, 2015). Log-transformed abundances of the dominant myctophid species collected during the REPCCOAI surveys were classified hierarchically using the Bray-Curtis similarity index. Abundance data were also standardised for the species.

Hydrologic regions based on water mass properties obtained by Djian et al. (2025) were also mapped to describe the myctophid species distributions according to the oceanographic context.

Results

More than 4000 myctophids comprising 62 species were identified (Table 1). The largest abundances were of *K. anderssoni* (Figure 2). In terms of dominance, this species was followed by *Protomyctophum tenisoni, Protomyctophum bolini, Gymnoscopelus braueri* and *Electrona antarctica*, which are all Southern Ocean species. The next four dominant species are from the subtropics: *Lampanyctus alatus, Lampanyctus australis, Lobianchia dofleini* and *Ceratoscopelus warmingii*. There were 38 species with very low abundances for which less than 10 specimens were collected, and most of them were subtropical.

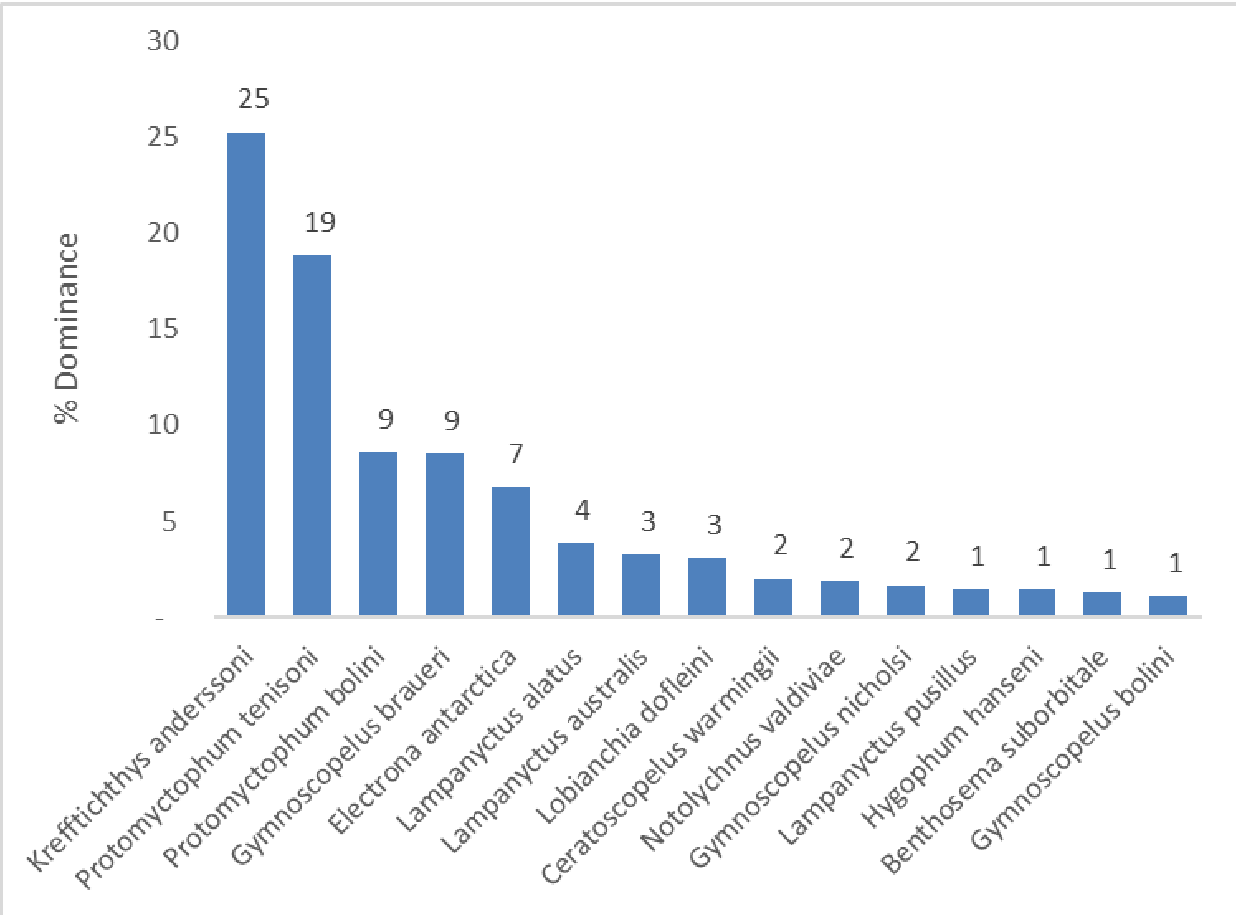


Figure 2: Percentage of dominance of the most abundant species of myctophids during the REPCCOAI surveys.

Table 1: Species of Myctophidae collected during the REPCCOAI surveys and their associated distribution patterns as defined by Duhamel et al. (2014).

Species occurring north of the STF		Transitional zone species		Southern Ocean species		
& occasionally recorded South of STF	& not occurring South of STF	Convergence Pattern	Bi-temperate Pattern	Subantarctic Pattern	Broadly Antarctic Pattern	Antarctic Pattern
Mesopelagic species						
Benthosema suborbitale	*Diaphus anderseni*	*Diaphus meadi*	*Lampadena speculigera*	*Diaphus hudsoni*	*Gymnoscopelus braueri*	*Electrona antarctica*
Bolinichthys supralateralis	*Diaphus brachycephalus*	*Diaphus ostenfeldi*	*Lampanyctus intricarius*	*Electrona carlsbergi*	*Gymnoscopelus nicholsi*	
Ceratoscopelus warmingii	*Diaphus fragilis*	*Electrona paucirastra*		*Electrona subaspera*	*Krefftichthys anderssoni*	
Diogenichthys atlanticus	*Diaphus metoclampus*	*Gonichthys barnesi*		*Gymnoscopelus bolini*	*Protomyctophum bolini*	
Electrona risso	*Diaphus mollis*	*Hygophum hanseni*		*Gymnoscopelus fraseri*	*Protomyctophum tenisoni*	
Hygophum hygomii	*Hygophum reinhardtii*	*Lampanyctus australis*		*Gymnoscopelus hintonoides*		
Lampadena chavesi	*Lampadena dea*	*Lampanyctus lepidolychnus*		*Gymnoscopelus microlampas*		
Lampanyctus festivus	*Lampadena luminosa*	*Protomyctophum luciferum*		*Protomyctophum andriashevi*		
Lampanyctus pusillus	*Lampanyctus alatus*	*Protomyctophum normani*		*Protomyctophum choriodon*		
Lampanyctus tenuiformis	*Lampanyctus ater*			*Protomyctophum gemmatum*		
Lepidophanes guentheri	*Lampichthys procerus*			*Protomyctophum parallelum*		
Lobianchia dofleini	*Notoscopelus caudispinosus*					
Myctophum phengodes	*Symbolophorus barnardi*					
Notolychnus valdiviae	*Symbolophorus veranyi*					
Notoscopelus resplendens	*Symbolophorus evermanni*					
Scopelopsis multipunctatus						
Symbolophorus barnardi						
Bathypelagic species						
Taaningichthys bathyphilus				*Lampanyctus achirus*		

Figure 3 shows that the highest abundances of myctophids were found on the northern margin of the Southern Ocean between Crozet and Kerguelen, on the eastern side of the Kerguelen Shelf and in the Southern Ocean as a whole. There were also two sites of high abundances in the northern subtropical region. We observed a latitudinal gradient in species richness (Figure 3). Catches in the Southern Ocean were very low in species richness, often less than four species, while in the sub-tropics they were very rich with up to more than 10 species. The SAF marked a transition in terms of species richness. In the subtropical zone, there was a difference between the west, where the values are higher, and the east.

The map of abundances of each of the most dominant species is shown in Figure 4 with a background representing the hydrologic regions described by Djian et al. (2025). There is a gradient in abundance between the Southern Ocean (Antarctic Zone 7, Polar Frontal Zone 6 and Subantarctic Zone 5), where many individuals were collected, and the subtropics where abundances are lower, with the exception of sampling at the edge of hydrological region 2 (Eastern Subtropical Zone). *P. tenisoni* and *K. anderssoni* dominated Southern Ocean catches with maximum abundances observed annually in the area midway between Crozet and Kerguelen on the boundary between Regions 6 and 5. High dominance of these species plus *E. antarctica* was also observed on the eastern and southern edges of the Kerguelen Plateau. *E. antarctica* occurs mainly in Area 7, the Antarctic Zone. In the subtropical zone, *L. alatus* was most dominant in the northwest, *L. australis* and *C. warmingii* in regions 3 and 4.

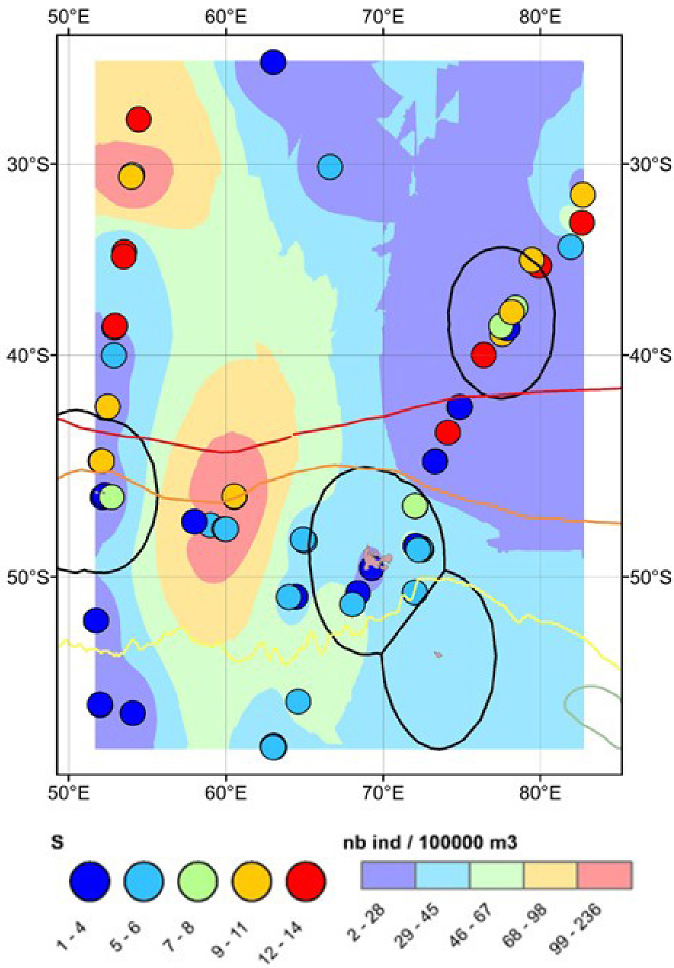
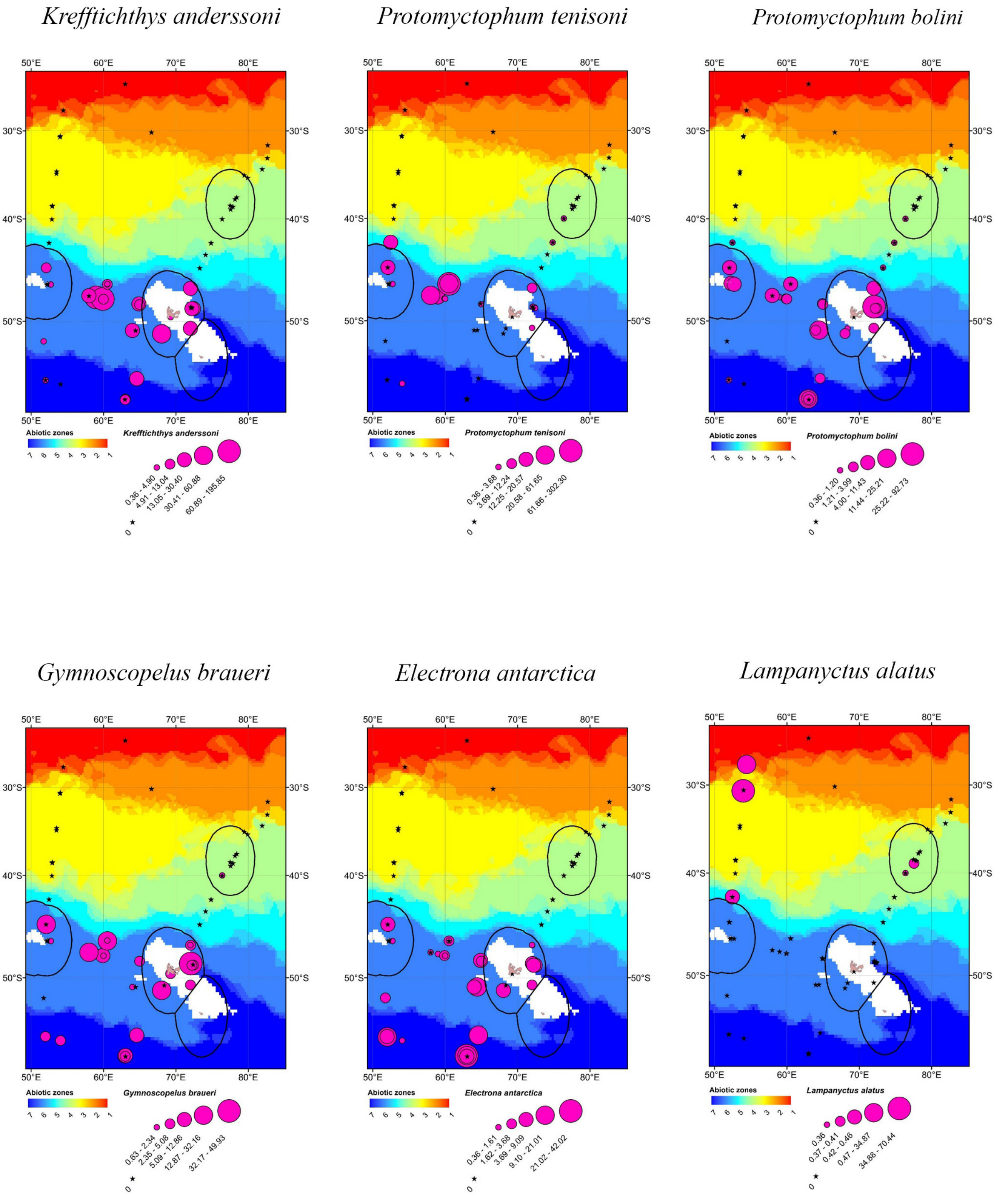
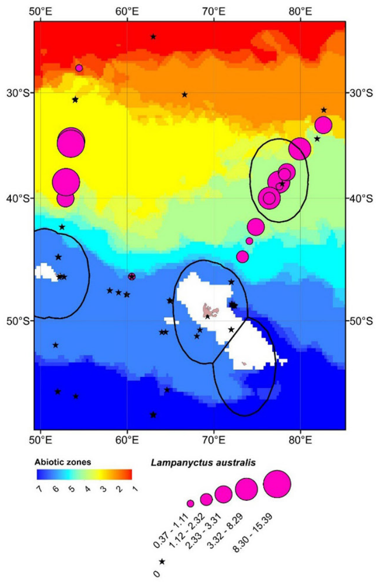


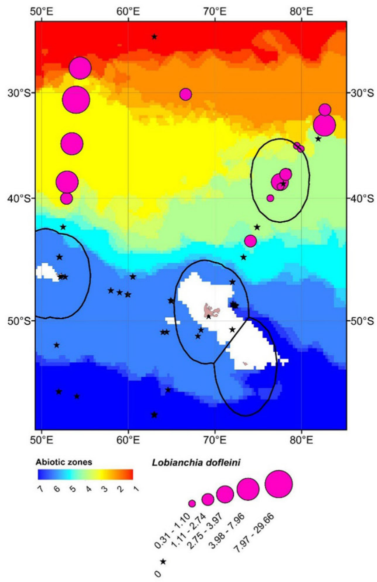
Figure 3: Species richness and interpolated abundance (number of individuals. $10^5 \bullet m^{-3}$) of myctophids captured by an IKMT during REPCCOAI surveys from 2017 to 2019.


Krefftichthys anderssoni
Protomyctophum tenisoni
Protomyctophum bolini
Gymnoscopelus braueri
Electrona antarctica
Lampanyctus alatus
Abiotic zones
7 6 5 4 3 2 1
50°E 60°E 70°E 80°E
30°S 40°S 50°S
0.36 - 4.90
4.91 - 13.04
13.05 - 30.40
30.41 - 60.88
60.89 - 195.85
0.36 - 3.68
3.69 - 12.24
12.25 - 20.57
20.58 - 61.65
61.66 - 302.30
0.36 - 1.20
1.21 - 3.99
4.00 - 11.43
11.44 - 25.21
25.22 - 92.73
0.63 - 2.34
2.35 - 5.08
5.09 - 12.86
12.87 - 32.16
32.17 - 49.93
0.36 - 1.61
1.62 - 3.68
3.69 - 9.09
9.10 - 21.01
21.02 - 42.02
0.36
0.37 - 0.41
0.42 - 0.46
0.47 - 34.87
34.88 - 70.44
0

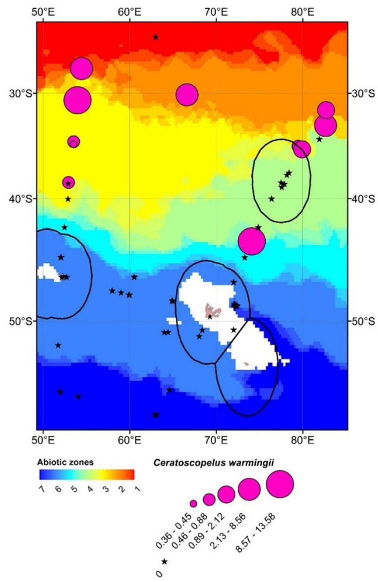
Lampanyctus australis



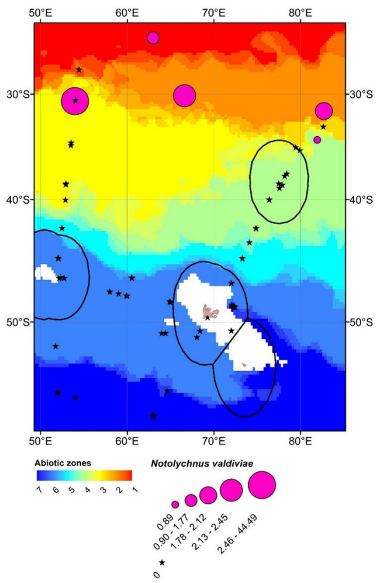
Lobianchia dofleini



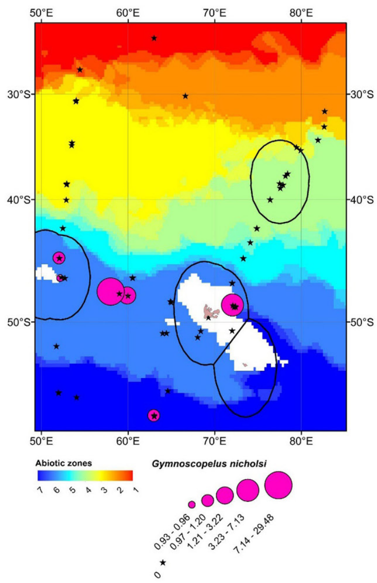
Ceratoscopelus warmingii



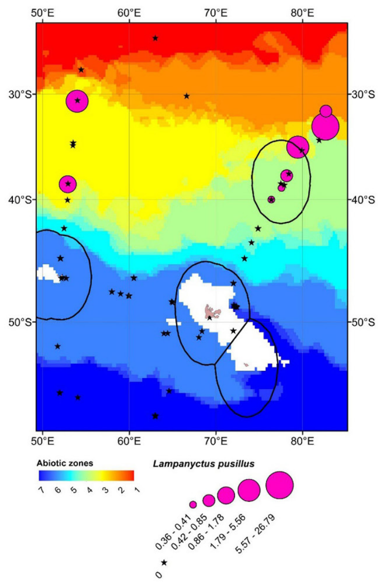
Notolychnus valdiviae



Gymnoscopelus nicholsi



Lampanyctus pusillus



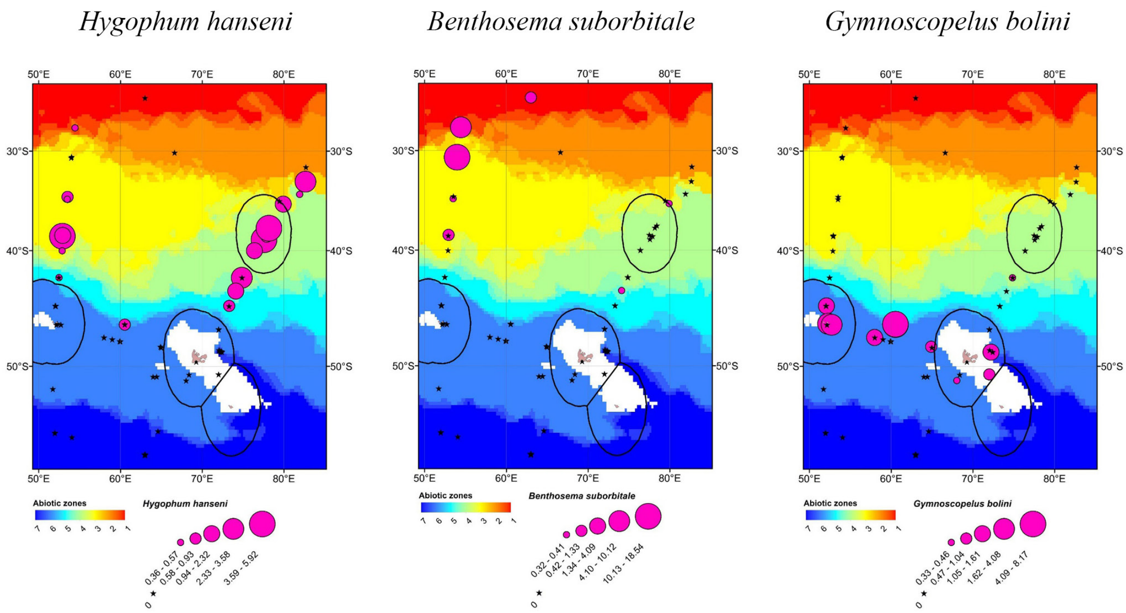


Figure 4: Abundance maps using punctiform symbols (no. Individuals. $10^5 m^{-3}$) of the most dominant Myctophidae during the REPCCOAI surveys. Species are ranked according to their dominance. The abiotic regions defined according to Djian et al.(2025) are shown.

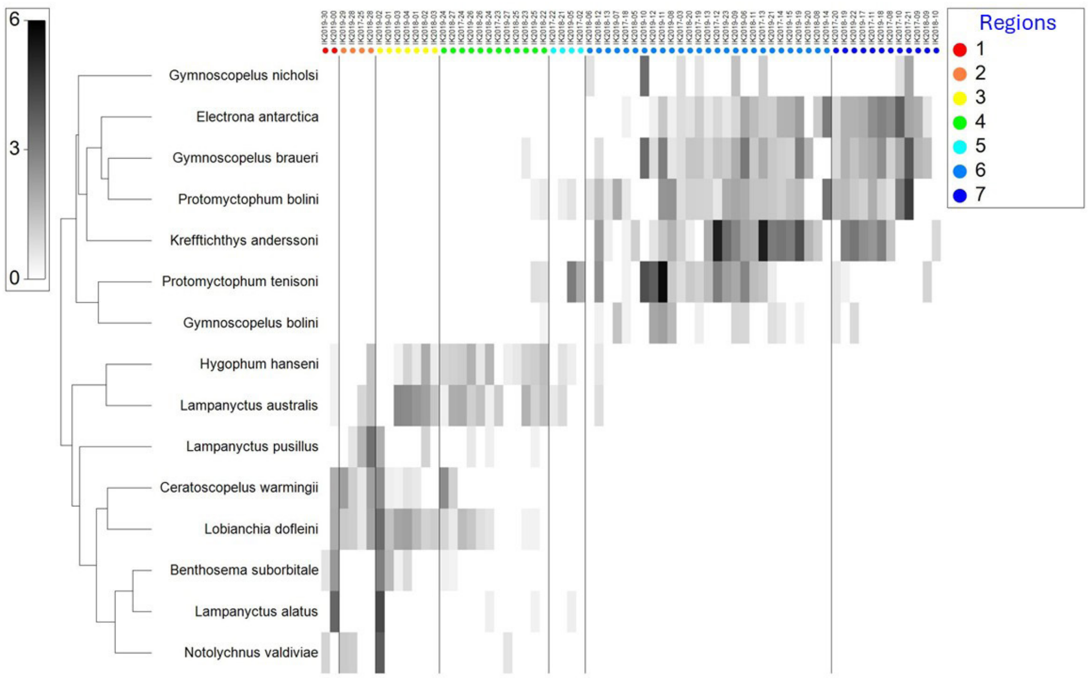


Figure 5: Shade plot of log (abundance+1) species (rows) x samples (columns) matrix of the samplings of Myctophids from the REPCCOAI surveys. Bray-Curtis similarities were performed on the most dominant myctophids. The vertical lines separate groups from the dendrogram of observations (Figure 7). The species dendrogram was made following a standardisation of the data. The grey scale is relative to species abundances with back-transformed abundances. The colour scale applied to the samples is related to the abiotic regions defined Djian et al. (2025).

A shade plot (Figure 5) was obtained using Bray-Curtis similarities on log-transformed abundances to visualise the species groups in relation to the observations. A colour code has been used to link the observations to the hydrological regions from Djian et al. (2025). The dendrogram of the observations shows three main groups of stations at 19% similarity. These can be divided into a total of seven subgroups at the 30% similarity level (Figure 6). These sub-groups have been mapped in Figure 7. The first group of observations is strictly in the Southern Ocean and includes subgroups a, b, c and d. The second group includes subgroups e, f, g and h and is distributed in the Indian Ocean.

The shade plot (Figure 5) shows that the Southern Ocean species are most abundant in the Polar Frontal Zone (hydrologic region 6), especially *K. anderssoni* and *P. tenisoni*. The group of *E. antarctica, G. braueri* and *P. bolini* is mainly abundant in region 7, the Antarctic zone. Very few species are abundant in the Subantarctic zone (hydrologic region 5) where we find Southern Ocean species such as *P. tenisoni* or *P. bolini*, but also subtropical species such as *H. hanseni* and *L. australis*. In the Indian Ocean, there is a clear distinction of assemblages according to latitude.

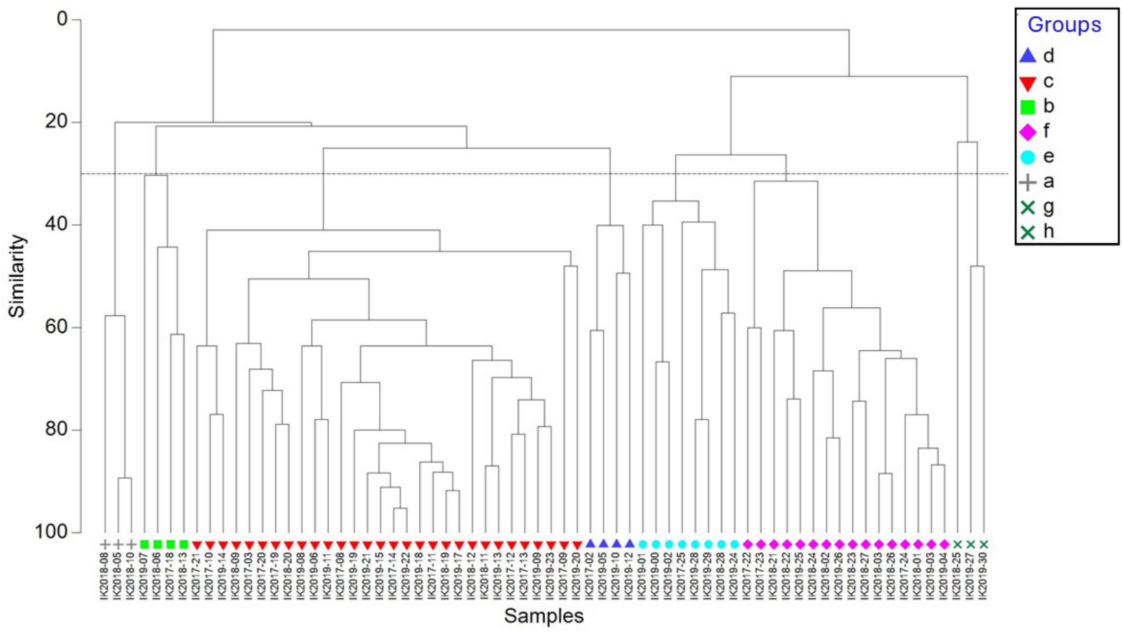


Figure 6: Dendrogram of observations from the collections of the more dominant Myctophidae during the REPCCOAI surveys. A Bray-Curtis similarity and a group average clustering were used. At a similarity level of 30%, 6 groups stand out. The seventh group was created with the samplings from g and h which are grouped together at a similarity level of 20%.

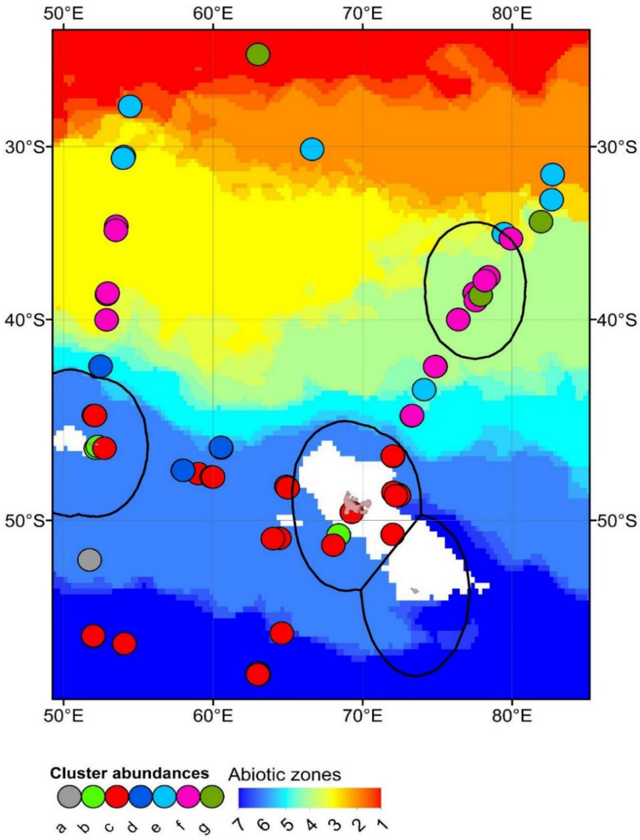


Figure 7: Map of groups from the observation dendrogram (log-transformed abundances, most dominant species, Bray-Curtis similarity, group average).

Discussion

Table 1 classifies the species collected during the REPCCOAI surveys according to the distribution patterns defined by Duhamel et al. (2014) which was based on the work of Hulley (1981). Different groups of species can be distinguished, depending on whether they are subtropical species (33 species), transitional zone species (11) or Southern Ocean species (18). Some of the subtropical and transitional zone species also occur mainly in the northern part of Southern Ocean. As noted by Duhamel et al. (2014), it is complicated to estimate the exact number of species of myctophids that occur in the Southern Ocean. If some species occur only in the Southern Ocean (defined here as south of the subtropical front), many others occurring in the subtropical zone are occasionally recorded in the Southern Ocean as well. Some of these species of the subtropical zone have distribution patterns which are widespread, largely tropical, subtropical, convergent or bi-temperate. Five species have a broadly Antarctic distribution pattern and two species (*E. antarctica* and *Gymnoscopelus opisthopterus*) have an Antarctic distribution pattern but as the survey was mainly in the oceanic zone, we did not collect *G. opisthopterus*.

In the study area between Crozet and Kerguelen, there is not a unique biogeographic limit separating the subtropical and the subantarctic/Antarctic faunas, but rather different limits for each of the ichthyofaunal assemblages. The subtropical zone is influenced by the subtropical gyre of the South Indian Ocean and the western inflow of the Agulhas Return Current in the Crozet area. This situation would explain the higher species diversity in the western part of the network than in the eastern part. We also note that the shelf breaks of the subantarctic islands favour higher species richness. This is certainly related to the island mass effect, but also to the northern extension of Antarctic water, as is the case east of Kerguelen. Our results confirm that in the study area with the narrowing of the Subantarctic region north of Crozet because of the triple front and Kerguelen (Djian et al., 2025), the Subantarctic Front is the main barrier to the southward expansion of subtropical species as described by Koubbi (1993) and Duhamel et al. (2014). Conversely, the STF is the front that limits the northward expansion of Subantarctic species. The polar frontal zone north to the SAF is the main northern limit of the Antarctic species such as *E. antarctica,* the dominant species of the Antarctic zone. This species has a broad circumpolar distribution from the Antarctic continental slope to the Polar Front, which is the northern limit of its distribution (Loots et al., 2007; Duhamel et al., 2014). However, there is some evidence of its presence in the subantarctic zone as some juveniles can be observed (Duhamel et al., 2014), or some specimens could be indicators of cold water or deep water intrusions into the Subtropical zone.

Among the main species observed in the area, few are indicators of hydrological regions for the Southern Ocean (e.g. *K. anderssoni, G. braueri, G. nicholsi, P. bolini, P. tenisoni*). *K. anderssoni* has a circumpolar distribution. It is one of the most characteristic species of the polar frontal zone (Hulley, 1981, Koubbi et al., 1991, 1993, 2003). However, individuals can also be found further north in the STF (Duhamel et al., 2005). Koubbi et al. (1991) showed that east of the Kerguelen shelf, there are high concentrations of larvae and, potentially, a spawning ground. While high concentrations of this species were known to the east of the Kerguelen Plateau (Duhamel et al., 2000), we also found significant concentrations of juveniles in the oceanic zone between Crozet and Kerguelen at the boundary between the Polar Frontal Zone and the Subantarctic Zone. This is consistent with the observation and the modelling of potential larval habitats of this species by Koubbi et al. (2003). This is an important result as this species is the main prey of some of the top predators such as King penguins (*Aptenodytes patagonicus*). Its place in the trophic web can be considered as equivalent to that of clupeids in other oceans.

Other species such as *P. tenisoni* were restricted to the Subantarctic area. During the REPCCOAI surveys, we also found important schools of its juveniles between Crozet and Kerguelen in the same location as for *K. anderssoni*. This means that this area has the potential to be a nursery ground for a variety of pelagic species and deserves a particular interest for conservation.

Our results can be compared with the results of modelling of the myctophid assemblages carried out by Koubbi et al. (2011b) or species habitats from the most recent work of Woods et al. (2022). The models on myctophid assemblages were based on presence data in the Indian sector of the Southern Ocean to identify spatial patterns and their relationships with the abiotic/chlorophyll environment. Twelve ecoregions were delineated with many of them in the northern part of the Southern Ocean between the Polar Frontal Zone and the subtropical zone. Increasing species richness with decreasing latitude appears to be the norm for myctophids in this published study and this work on the REPCCOAI surveys. The REPCCOAI surveys will help revisiting habitat and assemblages modelling of myctophid species by adding new results on the influence of latitude. The surveys provided unique samples of this fish to study the importance of the triple front (Agulhas Return Current Front, STF and SAF, see Djian et al., 2025) on species distribution in the Crozet area.

As Koubbi (1993), Koubbi et al. (2011) and Duhamel et al. (2014) have shown, the REPCCOAI surveys also indicate that the SAF appears to be more of a barrier to subtropical species than to Antarctic species whose distribution is limited by the STF. The mesoscale study of this group is important as there are important foraging areas of top predators feeding on these species around the different subantarctic islands but also over seamounts like Ob and Lena nearby the PF (Koubbi et al., 2011b, 2012, 2016a and 2016b). These areas are characterised by the abundance of these fish but also by their easier accessibility to top predators. Modelling the consequences of climate change on the habitats of major myctophid species (Freer et al., 2019) is essential to understanding climate change consequences on their biogeography. What we are uncertain about at the moment is the future replacement of subantarctic species (mainly Myctophids) by subtropical species (like Gonostomatidae) because of climate change. Distribution, size and biomass of the different species should be investigated to understand their relative accessibility to predators.

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