Polar Biol (1993) 13: 557–564

Polar Biology


# Influence of the frontal zones on ichthyoplankton and mesopelagic fish assemblages in the Crozet Basin (Indian sector of the Southern Ocean)

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**Abstract.** One of the aims of oceanographic campaign MD 68/SUZIL, carried out in austral autumn 1991 in the Indian sector of the Southern Ocean and its adjacent subtropical waters, was to investigate the influence of hydrography on the ichthyoplankton and mesopelagic fish assemblages in the Crozet Basin. It appears that, in contrast to other sectors of the Southern Ocean, the main biogeographical barriers are the Subantarctic Front and the Agulhas Front which appear to be "vertical convergence fronts". The importance of the Antarctic Polar Front and the Subtropical Front as barriers to fish seems to be minimized in this area because of its particular hydrological features, such as the lack of a subantarctic zone, the maximum current intensity of the Subantarctic Front between these fronts, and their structures – they are horizontal convergence fronts.

Biogeographical boundaries in the open ocean are assumed to correspond to hydrological properties, or be indirectly related to these properties through the effects of lower trophic levels on higher ones (Backus 1986). In the Southern Ocean, faunal provinces are considered to be bounded by frontal zones; the Antarctic Polar Front and the Subtropical Front have been considered by Norman (1938), Ekman (1953), Andriashev (1965, 1987) and Dell (1972) as the main oceanic boundaries for austral fishes. However, these authors dealt mainly with demersal and coastal fishes.

One of the aims of the oceanographic campaign MD68/SUZIL was to determine the influence of the different hydrological fronts of the Southern Indian Ocean on the ichthyoplankton and mesopelagic fish assemblages. The studied area is located in the Indian sector of the Southern Ocean and its adjacent subtropical Indian waters (37–51°S, 50–80°E). It covers the Crozet Basin (4500 m depth), the Crozet-Archipelago shelf (located on the west-Indian ridge) and the northern part of the Kerguelen Plateau. Previous ichthyological studies in this sector have been undertaken on mesopelagic fishes – mainly Myctophidae – by Bekker (1985), Duhamel (1987), Hulley (1989), Hulley et al. (1989) and Iwami and Kubodera (1990).

## Materials and methods

The multi-disciplinary oceanographic campaign MD68/SUZIL was carried out from the French vessel "*Marion Dufresne*" between April 12 and May 20, 1991 (Park et al. 1993). Conductivity Temperature Depth (CTD) measurements were taken along 5 transects (a total of 70 stations) which formed a closed "W". At 46 stations of the hydrological network, plankton samples were taken (Fig. 1). Bongo net fitted with 0.5 mm-mesh conical nets was used for sampling; the diameter of each frame was 63 cm. The sampling methodology was standardised for the area as described by Koubbi et al. (1991). The volume of water filtered was measured with a flowmeter placed in the mouth of one of the nets; the average volume of water filtered was 1,354 $m^3$ per tow. Oblique tows were made at a speed of 2 to 3 knots to 200 m depth, or close to the bottom where the water was shallower. The duration of each tow was between 20 and 35 min.

Fish eggs and larvae were removed from the catch under a stereomicroscope. Larval identification was according to Moser et al. (1984) to determine families, North and Kellermann (1989) for antarctic fish, Koubbi et al. (1990) for Kerguelen Island Nototheniodei, and Olivar and Fortuno (1991) for subtropical species.

Because of the high percentage of zero catches for species, the study is qualitative; only presence–absence of a taxon is considered. For each of the stations, a diversity index corresponding to the number of taxa was produced for larvae and juveniles (Patrick 1949; Legendre and Legendre 1979). By means of a non-parametric test, the Kruskal-Wallis analysis of variance (Siegel 1956), the differences in diversity between the major hydrological areas was tested for larvae and juveniles. The 46 stations were divided into 4 groups in relation to hydrological areas: the Subtropical Zone (13 stations), the Transition Frontal Zone (9 stations), the Polar Frontal Zone (19 stations), and the area where the Antarctic Polar Front is observed (5 stations). In the computation of the test, each station's diversity is replaced by ranks. The test determines if the sums of ranks for each

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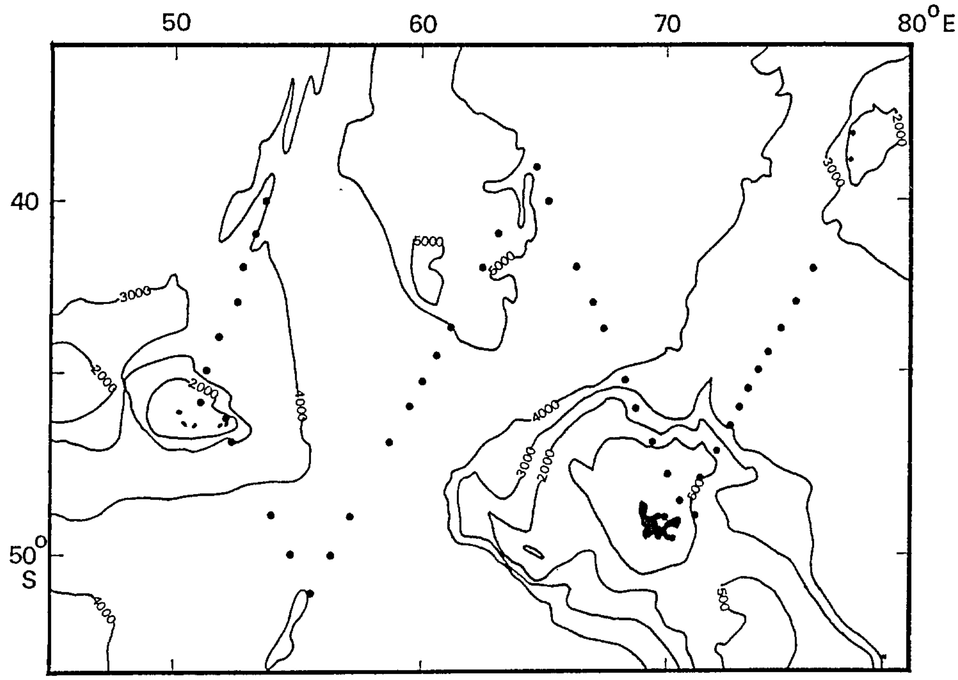



**Fig. 1.** Positions of fishing stations (●)

group are significantly identical. H0, the null hypothesis for this test is: there is no difference among the average diversities of each hydrological area. H1, the alternative hypothesis is: the four hydrological areas are not the same in their average diversities. The region of rejection consists of probability equal to or less than the significance level $\alpha = 0.05$.

To relate fish assemblages to hydrological areas, the percentage of presence in an area of each stage (egg, larvae and juvenile) for each taxon was computed by using presence/absence at each station. Before this could be done, it was determined which area and sub-areas each station belonged to. The sub-areas included were the Kerguelen shelf, the region under the influence of the Agulhas Front and the upwelling zone. A correspondence analysis was then performed which allows the simultaneous representation of variables (taxa) and observations (hydrologic zones).

## Results

### *Hydrology*

Hydrological data for this campaign have been published by Park et al. (1993) who give the positions of the main hydrological fronts. From south to north, considering CTD profiles, these fronts are (Fig. 2) the Antarctic Polar Front, the Subantarctic Front, the Subtropical Front and the Agulhas Front.

During Autumn 1991, in the north-western part of the study area, the highest values of temperature (maximum of 18–19°C) and salinity (maximum of 35.5 psu) were observed (Park et al. 1993). Park et al. (1992) consider that this zone is composed of warm subtropical waters carried by the Agulhas Return Current. Lutjeharms (1985) showed that there is a frontal zone in this part of the Indian Ocean, the Agulhas Front. This front was defined by Nagata et al. (1988) by the occurrence of the 18°C isotherm at 150 m depth and by salinities greater than 35.50 psu. Upwelling of deep water was also observed in this area.

Unlike other sectors of the Southern Ocean, no hydrological subantarctic region is observed. Instead, there is a unique narrow band of 2° latitude caused by the juxtaposition of the Subtropical Front and the Subantarctic Front (Gambéroni et al. 1982; Charriaud and Gamberoni 1987). This unusual hydrological region is named the Transition Frontal Zone.

In the southern part of the study area, the Antarctic temperature minimum (2°C) in subsurface water (200 m depth) was observed. It indicates the presence of the Antarctic Polar Front. It should be noted that the Antarctic Polar Front was closer to the Transition Frontal Zone in the Kerguelen shelf area than it was in the Crozet area. The band between the Antarctic Polar Front and the Transition Frontal Zone is the Polar Frontal Zone.

### *Fish*

Eggs, larvae and juveniles of 17 families were identified; a total of 4 taxa for the eggs, 28 for larvae and 23 for juveniles was considered. Except for those of the notothenids and channichthyids, all families were represented by meso- and/or bathypelagic species. Myctophidae were the most diverse.

### *Larval diversity*

The results of the Kruskal-Wallis analysis of variance give probabilities of 0.037 for larvae and 0.044 for juveniles. The null hypothesis is then rejected for both tests, indicating that the diversity of larval and juvenile stages between

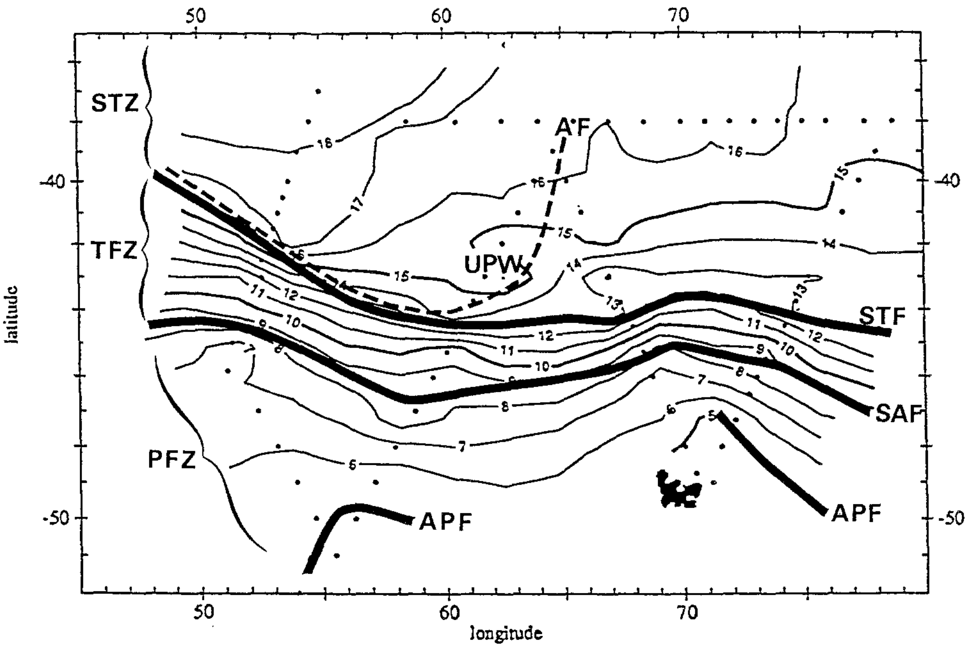



**Fig. 2.** Positions of hydrological stations (●). Surface temperatures (*figures*) and positions of the hydrological zones and fronts in autumn 1991. *APF*, Antarctic Polar Front; *PFZ*, Polar Frontal Zone; *SAF*, Subantarctic Front; *TFZ*, Transition Frontal Zone; *STF*, Subtropical Front; *STZ*, Subtropical Zone; *AF*, Agulhas Front region; *UPW*, upwelling

hydrological zones is not homogeneous in the area and that there are differences between hydrological zones. Cartograms of iso-taxonomic diversities for larvae (Fig. 3a) and juveniles (Fig. 3b) show higher values in the Subtropical Region than south of the Transition Frontal Zone. These observations are in accordance with the hypothesis that species diversity decreases with increasing latitude (Begon et al. 1990).

*Ichthyofaunistic assemblage*

The results of the correspondence analysis are given in Fig. 4a, b. The hydrological area projections show that the first factorial axis separates areas on either side of the Subantarctic Front. The second and third axes split frontal zones (Antarctic Polar Front-APF- and Transition Frontal Zone-TFZ) from the other areas (Fig. 4a, b). The Polar Frontal Zone (PFZ) and the Kerguelen shelf (KER) projections are very close together, as are the Agulhas Front area (AF) and the upwelling (UPW) with the subtropical region (STZ).

The derived variables representing the embryonic, larval and juvenile stages of the taxa are plotted in Fig. 4b. A total of 6 groups of taxa having the same coordinates on the first three axes were formed and coded with a number (Table 1).

The first group includes *Krefftichthys anderssoni* juveniles and other Myctophidae juveniles that may be of this species. The plotted points corresponding to these juveniles are very close to the projection of the Antarctic Polar Front (APF; Fig. 4b). *K. anderssoni* is abundant in the region of the Antarctic Polar Front (Koubbi et al. 1991; Koubbi 1992) and its distribution is defined as broadly antarctic by Hulley (1981).

Group 1 includes larval *K. anderssoni*, *Lepidonotothen squamifrons*, *Notothenia cyanobrancha* and *Champsocephalus gunnari* and juvenile *Gobionotothen acuta*. The position of this group on the projected axes is close to that of the Kerguelen shelf (KER) where only the last four species were present. It is the only group with demersal species (except for *K. anderssoni*).

All the following groups are formed only from meso- and/or bathypelagic species, most of them belonging to the Myctophidae.

Group 2 includes juvenile *Protomyctophum tenisoni*, *Loweina interrupta*, *Gymnoscopelus braueri* and *Stomias* sp. and larval *Protomyctophum* sp.. On the first factorial plane, this group is close to the Polar Frontal Zone (PFZ) projection; they were only caught in this area. *L. interrupta* is a bitemperate species (Hulley 1986) whereas *P. tenisoni* and *G. braueri* have a broadly antarctic distribution (Hulley 1981). *P. tenisoni* is circumglobal between the Antarctic Polar Front and the Subtropical Front whereas *G. braueri* occurs between the Antarctic continent and 46°S in the Indian ocean (Hulley 1981). This latitude is roughly where the Subantarctic Front was observed.

Taxa in group 3 were larval *Myctophum* sp., *Hoplostethus* sp., Paralepididae sp2., *Cyclothone* sp2., *Ichthyococcus ovatus*, two unidentified taxa (sp.33 and sp.40) and juvenile *Protomyctophum normani*. The projection of this group on the first factorial plane is close to the Transition Frontal Zone (TFZ) where those taxa were caught. Some of these species are temperate, e.g. *P. normani* (Hulley 1981; Bekker 1985), others are subtropical, e.g. *I. ovatus* (Schaefer et al. 1986), *M. phengodes* (Hulley 1986). The other species are cosmopolitan.

Taxa in group 4 were juvenile *M. phengodes* and larval Photichthyidae sp. and Carangidae sp.. In the first factorial plane, this group is close to the projection of subtropical areas (STZ); all these species are absent from the Southern ocean.

Taxa in group 5 were juvenile *Lampanyctus festivus*, *Diaphus* sp., *Benthosema suborbitale*, *Argyropelecus*

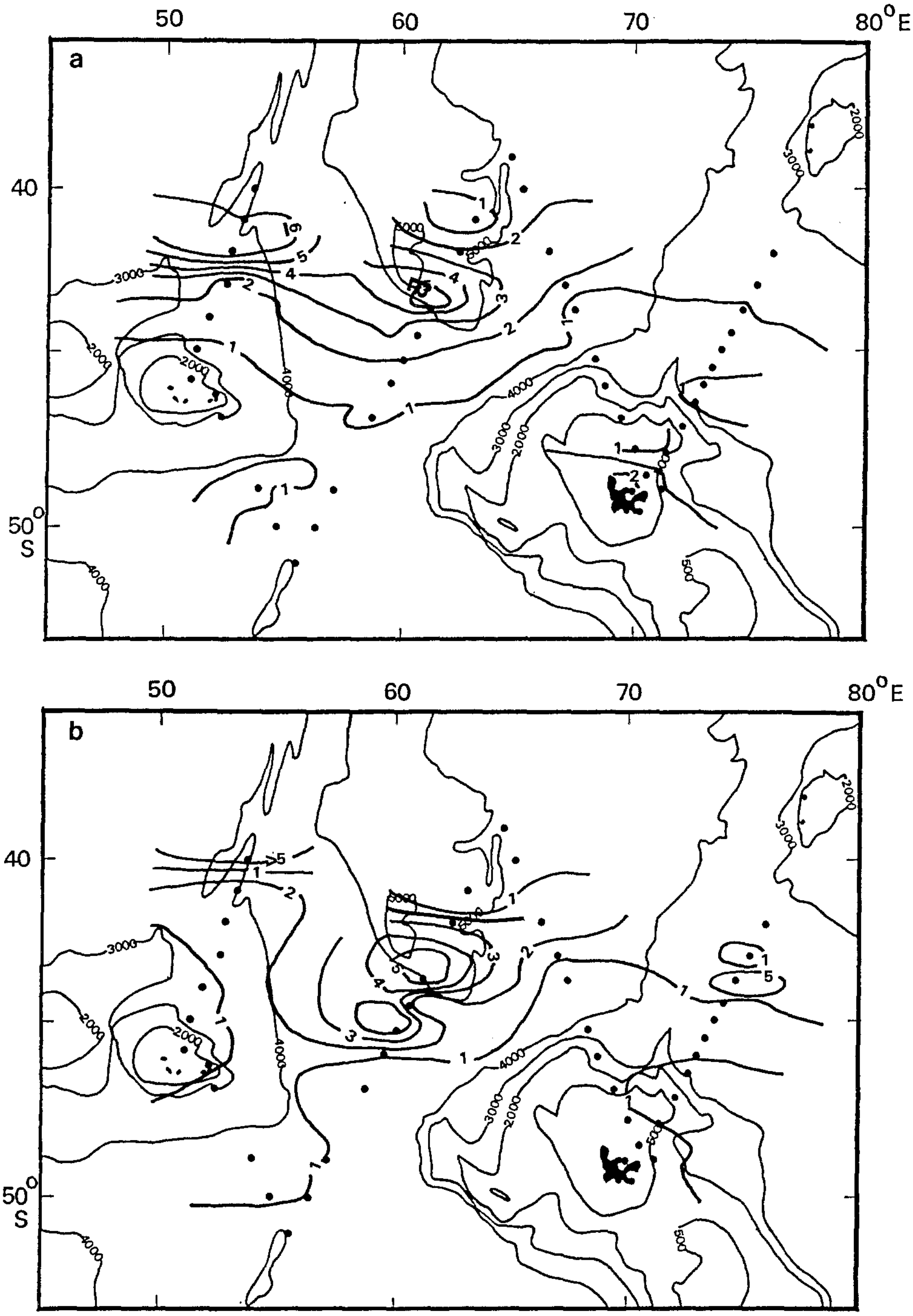



**Fig. 3a, b.** Cartograms of iso-taxonomic diversities: **a** larvae and **b** juveniles

*hemigymnus*, larval Scombridae sp., *Cyclothone* sp.1, Trichiuridae sp., Paralepididae sp.1, one unidentified taxa (sp.22) and two unidentified embryo taxa (WB and WC). This group is very close to the projection of subtropical areas and, in fact, is exclusively linked to the Agulhas Front region (AF). Most of these species have broadly temperate and tropical distributions. Two taxa, *Scopelosaurus* sp. (juvenile-SCJ-) and *Diaphus* sp. (larvae-D?L), are close to this group but individuals were only caught in the subtropical area out of the Agulhas Front.

Taxa in group 6 were juvenile *Cryptosaras couessi*, *Gonostoma* sp., Melamphaidae sp., *Chaudiodus sloani*, Nomeidae sp. and larval *M. phengodes*. On the first factorial plane, this group is close to the projection of subtropical areas. All of them except larval *M. phengodes* were caught exclusively in the upwelling zone. Most of these species are temperate and subtropical.

The last groups of taxa were projected near subtropical zones but they are present in different hydrological areas. They can be divided in two groups depending on whether their southern limit is the Subantarctic Front (group A) or the Antarctic Polar Front (group B). Taxa in group A were juvenile *Lampanyctus pusillus*, *Diaphus meadi*, *Vinciguerria attenuata* and larval *Lampanyctus* sp.,

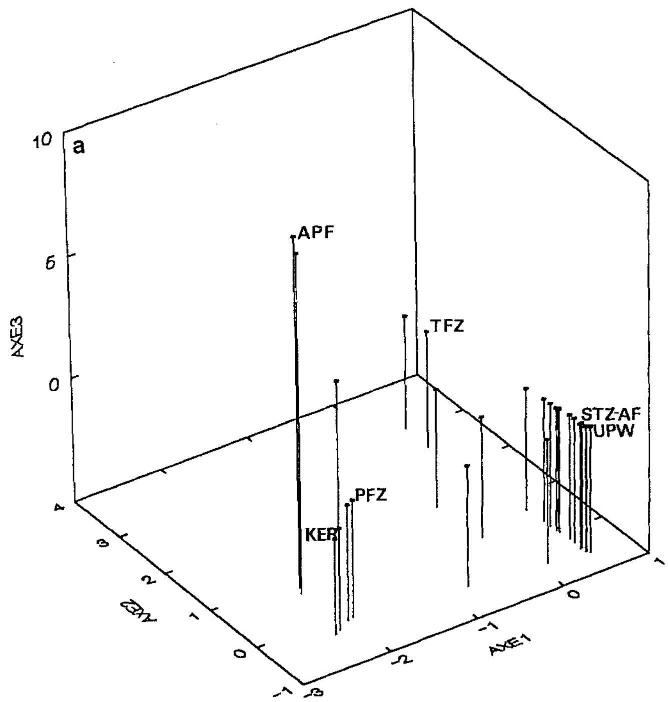
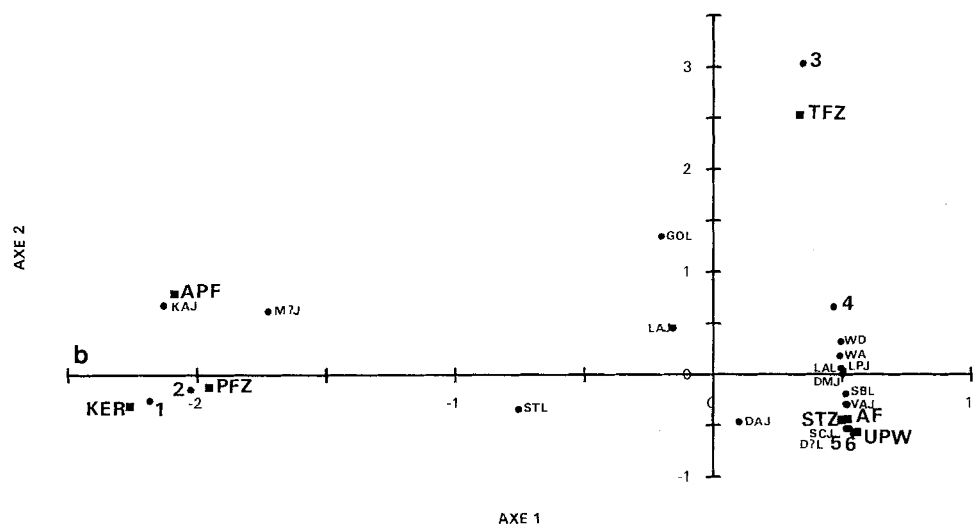



Fig. 4a, b. Correspondence analysis of taxa occurring in the different hydrological sectors. a Hydrological zones and taxa representation in the first three factorial axes (for abbreviations see Fig. 2; *KER*, Kerguelen shelf). b Hydrological zones, eggs, larvae and juveniles and adult stages. ●, Taxa stages (indicated by group number or taxa abbreviation); ■, hydrologic zones; for abbreviations of taxa stage, refer to Table 1




*Symbolophorus boops*. Taxa in group B were larval *Stomias* sp., *Gymnoscopelus opisthopterus* and juvenile *Lampanyctus australis* and *Diogenichthys atlanticus*.

## Discussion

The analyses show that the hydrological fronts in the north of the Southern Indian Ocean can be biological boundaries for meso- and bathypelagic fishes. Species stages were divided according to the groups obtained with correspondence analysis and their presence in one or more hydrological areas. Fish assemblages for each group are listed in Table 1.

Demersal, meso- and bathypelagic taxa can be divided into five categories in relation to their hydrological affinities:

1. Exclusively subtropical taxa (groups 5 and 6). Differences are observed within this category depending on the exclusive presence of taxa in the upwelling zone or in the area under the influence of the Agulhas Front or from taxa having a broadly suptropical distribution.
2. Taxa occurring in the subtropical and Transition Frontal Zone area (group 4 and A). The southern limit of their latitudinal distribution is the Subantarctic Front.
3. Taxa occurring on the border and within the Transition Frontal Zone (group B).
4. Taxa occurring exclusively inside the Transition Frontal Zone (group 3).
5. Antarctic taxa (groups 1 and 2 and *Krefftichthys anderssoni* juveniles) including the demersal species of the Kerguelen shelf.

For the Myctophidae, many taxa occurred in a defined hydrological area. However, some species have a wider distribution. Myctophidae dominate the antarctic area, Polar Frontal Zone and Transition Frontal Zone. Our

**Table 1.** Results of the correspondence analysis; occurrence of eggs (*W*), larvae (*L*) and juveniles or adults (*J*) in the different hydrological areas

| Family | Taxa | | UPW | AF | STZ | TFZ | PFZ | APF | KER | AFC Symbol[a] | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Ceratidae | *Cryptosaras* | *couessi* | J | | | | | | | | 6 |
| Chauliodontidae | *Chauliodus* | *sloani* | J | | | | | | | | |
| Gonostomatidae | *Gonostoma* | sp. | J | | | | | | | | |
| Melamphaidae | Melamphaidae | sp. | J | | | | | | | | |
| Myctophidae | *Diogenichthys* | *atlanticus* | L | | | | | | | | |
| Myctophidae | *Myctophum* | *phengodes* | L | L | | | | | | | |
| Nomeidae | Nomeidae | sp. | J | | | | | | | | |
| Notosudidae | *Scopelosaurus* | sp. | | | J | | | | | SCJ | |
| Myctophidae | *Diaphus* | sp. | | J | L | | | | | D?L-D?J | |
| Photichthyidae | *Vinciguerria* | *attenuata* | | L | L | | | | | VAL | |
| Gonostomatidae | *Cyclothone* | sp1. | | L | | | | | | | 5 |
| Myctophidae | *Benthosema* | *suborbitale* | | J | | | | | | | |
| Myctophidae | *Lampanyctus* | *festivus* | | J | | | | | | | |
| unidentified | sp.22 | | | L | | | | | | | |
| unidentified | sp.25 | | | L | | | | | | | |
| unidentified | B | | | W | | | | | | | |
| unidentified | C | | | W | | | | | | | |
| Paralepididae | Paralepididae | sp.1 | | L | | | | | | | |
| Scombridae | Scombridae | sp. | | L | | | | | | | |
| Sternoptychidae | *Argyropelecus* | *hemigymnus* | | J | | | | | | | |
| Trichiuridae | Trichiuridae | sp. | | L | | | | | | | |
| Carangidae | Carangidae | sp. | | L | | L | | | | | 4 |
| Myctophidae | *Myctophum* | *phengodes* | | J | | J | | | | | |
| Photichthyidae | Photichthyidae | sp. | | L | | L | | | | | |
| unidentified | A | | | W | | W | | | | A-WA | |
| unidentified | D | | W | W | | W | | | | WB | |
| Myctophidae | *Diaphus* | *meadi* | J | J | J | J | | | | DMJ | |
| Myctophidae | *Lampanyctus* | *pusillus* | | J | J | J | | | | LPJ | |
| Myctophidae | *Lampanyctus* | *cf. isaacsi* | L | L | | L | | | | LAL | |
| Myctophidae | *Symbolophorus* | *cf. boops* | L | L | | L | | | | SBL | |
| Photichtyidae | *Vincingeria* | *attenuata* | | J | J | J | | | | VAJ | |
| Myctophidae | *Diogenichthys* | *atlanticus* | | J | J | J | | | | B-DAJ | |
| Myctophidae | *Gymnoscopelus* | *cf. opisthopterus* | | L | | L | | | | GOL | |
| Myctophidae | *Lampanyctus* | *australis* | | J | | J | | | | LAJ | |
| Stomiidae | *Stomias* | sp. | | | L | L | | | | STL | |
| Gonostomatidae | *Cyclothone* | sp2. | | | | L | | | | | 3 |
| Myctophidae | *Myctophum* | sp. | | | | L | | | | | |
| Myctophidae | *Protomyctophum* | *normani* | | | | J | | | | | |
| unidentified | sp.33 | | | | | L | | | | | |
| unidentified | sp.40 | | | | | L | | | | | |
| Paralepididae | Paralepididae | sp.2 | | | | L | | | | | |
| Photichthyidae | *Ichthyococcus* | *cf. ovatus* | | | | L | | | | | |
| Trachichtyidae | *Hoplostethus* | sp. | | | | L | | | | | |
| Myctophidae | *Gymnoscopelus* | *braueri* | | | | | J | | | | 2 |
| Myctophidae | *Loweina* | *interrupta* | | | | | J | | | | |
| Myctophidae | *Protomyctophum* | sp. | | | | | L | | | | |
| Myctophidae | *Protomyctophum* | *tenisoni* | | | | | J | | | | |
| Stomiidae | *Stomias* | sp. | | | | | J | | | | |
| Myctophidae | Myctophidae | sp. | | | | | J | J | | M?J | |
| Myctophidae | *Krefftichthys* | *anderssoni* | | | | | J | J | | KAJ | |
| Channicthyidae | *Champsocephalus* | *gunnari* | | | | | | | L | | 1 |
| Myctophidae | *Krefftichthys* | *anderssoni* | | | | | | | L | | |
| Nototheniidae | *Gobionotothen* | *acuta* | | | | | | | J | | |
| Nototheniidae | *Lepidonotothen* | *squamifrons* | | | | | | | L | | |
| Nototheniidae | *Notothenia* | *cyanobrancha* | | | | | | | L | | |

UPW, Upwelling; AF, Agulhas Front region; STZ, Subtropical Front; TFZ, Transition Frontal Zone; PFZ, Polar Frontal Zone; APF, Antarctic Polar Front; KER, Kerguelen shelf

[a] Group number or taxa abbreviations used in the analysis (Fig. 4b)

results are in accordance with Bekker's (1985) observations between Kerguelen and Saint-Paul Islands. This zonal distribution can be explained by the hydrological characteristics of the fronts in this area. The subantarctic zone is absent in the Crozet Basin and is replaced by the Transitional Frontal Zone, which is the junction between the Subtropical and Subantarctic Fronts. Consequently, subantarctic species are obliged to live within the Transitional Frontal Zone or close to it. This hypothesis was verified by comparing our results with the literature (Hulley 1981, 1986, 1989, 1990).

It has been suggested that the Subtropical Front and the Antarctic Polar Front are barriers to pelagic organisms. It seems that their role is different in the study area because of the presence of the Agulhas Front and the Subantarctic Front. In the Crozet Basin and mainly in the northern part of the Kerguelen plateau, the Subantarctic Front is where the maximum intensity of the Antarctic Circumpolar Current has been recorded (Park et al. 1992). A possible explanation may be that the Subantarctic Front represents a vertical convergence zone, latitudinally narrow, whereas the Subtropical and Antarctic Polar Fronts are horizontal convergence zones marked by a latitudinal difference in their surface and subsurface expression (Lutjeharms et al. 1985). A horizontal convergence zone will allow species derived from either side of a front to coexist latitudinally because at some depth they will always find a convenient water mass. A convergence front is a physico-chemical "wall" that is more difficult for species to cross. This can explain why, in this 200 m-deep surface water, there is so little exchange between either side of the Subantarctic Front. It would be difficult for a larva to cross this front in this area because of the very high current intensity of the Antarctic Circumpolar Current (100 Sverdrup; Park et al. 1992). It corresponds to 80% the intensity of Drake Passage, the highest value for the Southern Ocean (Nowlin and Klinck 1986). For juveniles and adults more able to swim against currents, Hulley (1981) showed that *Krefftichthys anderssoni* juveniles migrate from the Southern Ocean to the subtropical areas by going to deeper zones. Finally, warm water from the Agulhas Front seems to contain high species richness in the western part of the Crozet Basin.

In conclusion, it appears that for meso- and bathypelagic fishes the position and nature of the different hydrological fronts are important for their early stages. Loeb et al. (1993) gave the same conclusion. In the Crozet Basin, in contrast to other sectors of the Southern Ocean, the Subantarctic Front seems to be the main biogeographic barrier, even for young stages. Further attention should be given to the hydrographic structure of frontal zones. This study shows that the distribution of ichthyoplanktonic assemblages can give important information on fish biogeography because, as indicated by Ahlstrom and Moser (1976), in the upper layer one can collect eggs or larvae of all kinds of fishes and obtain information on the whole spectrum of fishes in the area being surveyed.

*Acknowledgements.* The results presented here come from the PhD thesis of the author which was under the direction of Prof. Guy Duhamel of the National Muséum of Natural History in Paris. I thank him for his collaboration and help. My thanks go to the "Mission de Recherche des Terres Australes et Antarctique Françaises" for their support during the oceanographic campaign. This campaign was under the direction of Y.H. Park and his colleagues E. Charriaud and L. Gambéroni; they kindly accepted my program in addition to their hydrological studies. Sampling, fish sorting and identification were in collaboration with S. Weil. Juvenile determinations were checked by Professor P.A. Hulley for Myctophidae and G. Duhamel for the other families. This analysis was possible because of the financial support of "Fondation Maréchal Leclerc".

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