

# Environmental influences on spatio-temporal oceanic distribution of ichthyoplankton around the Kerguelen Islands (Southern Ocean)

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**ABSTRACT:** Ichthyoplankton of the oceanic zone surrounding the Kerguelen Islands (northern part of the Indian sector of the Southern Ocean) was studied. The results concerning both abundance and spatial distribution of fish eggs and larvae are discussed. Samples were collected during joint French-Soviet oceanographic cruises in summer, autumn and winter 1987 and summer 1988. The presence of the Antarctic Polar Front allowed us to show latitudinal distribution of the ichthyoplankton. Topography played an important role in separating mesopelagic and demersal species.

## INTRODUCTION

Topographic factors influence the distribution of antarctic fishes. Indeed, the Southern Ocean ichthyofauna is made up of species belonging to 2 major taxonomic groups (Fischer & Hureau 1987), distinguished from each other according to their bathymetric affinities. One group, the Notothenioidei, is composed of demersal species living on shelves and seamounts. The other, the Myctophidae, contains both mesopelagic and bathypelagic species. The spatial distribution of these species is influenced by the characteristics of water masses (Hulley 1981, Bekker 1985).

The oceanic zone surrounding the Kerguelen Islands (49°21' S, 70°12' E) is strongly influenced by the Antarctic Circumpolar Current. One of the main hydrological characteristics of that zone is that it is limited to the north by a transition zone formed by the joining of 2 fronts, namely the Subantarctic Front and the Subtropical Convergence (Gambéroni et al. 1982; Charriaud & Gambéroni 1987). One must also note the presence of another front, the Antarctic Polar Front, situated by the Kerguelen Island shelf (located in the northern part of the Kerguelen Plateau). This latter front is characterized by the antarctic temperature minimum (Deacon 1934). These hydrological fronts play an essential role in determining the spatial

heterogeneity and dynamics of plankton (Ledenev 1966). The presence of the Antarctic Polar Front will be taken into account in this study.

The topography of the region will also be considered. The study area extends as far as 300 km around the Kerguelen Islands (see Fig. 1) and covers: (1) the wide island shelf (100 495 km<sup>2</sup>) that mainly extends north-westwardly at depths between 0 and 500 m, (2) the 'Skiff seamount', which is separated from the Kerguelen shelf by an area with depths > 1000 m, (3) the 'Kerguelen-Heard seamounts', which are separated from the island shelf by an area with depths of 700 m, and (4) the deep oceanic zone surrounding the area.

In this article, we examine the influence of the above abiotic factors on spatio-temporal distribution of ichthyoplankton in the vicinity of the Kerguelen Islands.

## MATERIALS AND METHODS

**Sampling.** Four oceanographic cruises were carried out from the 82 m Soviet scientific trawler 'Skif' (Table 1). Samples and measurements were taken along 8 radial transects (made up of 52 stations) which formed a star shape centered on the archipelago (Fig. 1). The nearshore zone, a 12 mile (22 km) belt around the archipelago, was not sampled. Three addi-

Table 1. Periods of the 4 joint French-Soviet oceanographic cruises in 1987 and 1988 in the oceanic zone surrounding the Kerguelen Islands, Southern Ocean

Season		Beginning	End
1987	Summer	3 Feb	15 Feb
	Autumn	31 Mar	12 Apr
	Winter	24 Jul	6 Aug
1988	Summer	7 Feb	20 Feb

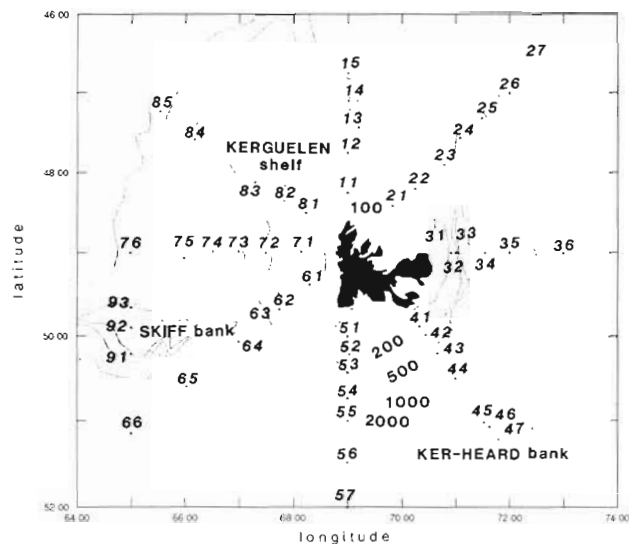


Fig. 1. Geographic location of hydrologic, meteorologic and planktonic stations (designated by numbers) off the Kerguelen Islands, where samples and measurements were taken during 4 cruises in 1987 and 1988

tional stations were located on the Skiff seamount. Meteorological and hydrological measurements, as well as plankton samples, were taken at each station.

**Meteorological observations:** Standard meteorological measurements were taken, including observations of sea state and cloud cover. Only the wind factors, direction and speed, are taken into account in this study, because of their possible influence on ichthyoplankton transport.

**Hydrological measurements:** Nansen type reversing bottles (1.8 l) were lowered down to the international standard depths (between 0 and 1000 m). Temperatures were taken with reversing thermometers; salinity was measured with an inductive salinometer.

**Ichthyoplankton:** A Bongo net was used for sampling as recommended by Smith & Richardson (1977) and Hureau (1982). This sampling device consisted of 2 frames (63 cm diameter) mounted in tandem. Each frame was equipped with a 0.5 mm mesh cylindrical conical net, 3.6 m in length. This mesh is recommended for sampling in the Southern Ocean in order to avoid problems of phytoplankton clogging (Hureau

1982). Flowmeters fixed on the centre of each frame were used to measure the volume of water filtered. Oblique tows were made at a speed of 2 to 3 knots (from the surface down to the fished depth). For shallow tows (depth < 200 m) the Bongo net was lowered close to the bottom. Otherwise, it was lowered to 200 m depth. Net depth was determined during tows by using the wire angle for the first 3 cruises and a bathykimograph for the last cruise. This towing procedure seems to be appropriate for the area, as confirmed by Kellermann (1986), who found that 98.6 % of ichthyoplankton (from the Antarctic Peninsula) occurred in the upper 200 m.

Samples were fixed in seawater formalin (5 %) buffered with sodium borate and kept in darkness at a temperature of between 5 and 10 °C. Afterwards, in the laboratory, zooplankton samples were sorted and fish larvae removed under a stereomicroscope.

Identification of notothenioid larvae was carried out using descriptions provided by Kellermann (1989) and Koubbi et al. (1990). Myctophid larvae were identified according to Moser & Ahlstrom (1970), Efremenko (1979) and North & White (1982). Pelagic eggs were identified by comparing their mean diameters with those of mature oocytes (Duhamel 1987a, b). We also took into account the season of presence of those eggs in plankton and the spawning periods of the main Kerguelen fishes (Duhamel 1987a, b). Counts of all eggs and larvae were converted into no. of ind. per 10 000 m<sup>3</sup>.

**Numerical methods:** The influence of abiotic factors on ichthyoplankton spatial distribution cannot be determined by means of a correlation analysis between them. In addition to limits imposed by linearity, correlations can only detect a possible link between increasing and monotonous gradients.

We chose to apply the Multiple Correspondence Analysis technique (Volle 1985). Each biological or environmental variable, whether qualitative or quantitative, was divided into a limited number of classes and analyzed for each cruise. Abiotic and biological variable classes were presented in columns, and observations in rows. Contingency boxes corresponded to an observation's characteristic: 0 for all the missing descriptor classes or 1 for all the present classes. Correspondence Analysis performed on that contingency table allowed us to represent the modalities of each descriptor and observation simultaneously in the same analytical framework. We chose a representation of biological and environmental associations in the geographical space from the Correspondence Analysis results. All the classes of descriptor and observation coordinates placed on the first 5 axes of inertia (more than 40 % of the total inertia) were used to calculate their inter-distance and to carry out a classification based on the Lance and

Williams algorithm (Lance & Williams 1967). This consists of a flexible clustering ( $\beta = -0.3$ ). Visualisation of the dendrogram shows the presence of different groups that contain both stations and classes of descriptors. Then we defined geographical zones from the stations which belonged to the same group. These zones are associated with some classes of descriptors that appear mainly in these locations.

This method is linked to 3 arbitrary operations, namely, the choice of descriptor classes, the number of inertia axes to be kept, and the threshold of distance from the dendrograms.

## RESULTS AND DISCUSSION

### Meteorology

Meteorological conditions encountered during the study consisted of permanent, regular, high winds. Average speeds were ca  $4 \text{ m s}^{-1}$ ; it should be stressed that this is an underestimate, since no stations were visited, and therefore no measurements taken, during storms. Azibane et al. (1977) reported an annual average wind speed of  $9.7 \text{ m s}^{-1}$ . The winds all came from the western quadrant.

### Hydrology

Temperature/salinity diagrams for summer and autumn 1987 and summer 1988 (Figs. 2 to 4) show the presence of the Antarctic temperature minimum in subsurface water (Koubbi unpubl. data), indicating the presence of the Antarctic Polar Front. Thus there are 2 regions within the study area – one in the northwest, the other in the southeast – separated by the 5 to  $5.5^\circ\text{C}$  isotherm and the 33.75‰ isohaline. In the northwestern part, waters are warmer, less saline and relatively homogeneous. In the southeast, there are thermal and salinity gradients. In summer 1988, the  $4.5$  to  $6.5^\circ\text{C}$  isotherms were further northward in comparison with summer 1987.

Temperatures in winter 1987 (Fig. 5a) were normally  $2^\circ\text{C}$  less than those of summer. Salinities were almost identical to those of other seasons. The Antarctic Polar Front separated 2 regions, defined by the  $3^\circ\text{C}$  isotherm and the 33.80‰ isohaline. Lower-salinity water was present in the northeastern part of the archipelago; this water mass extended to the northeast shelf/slope break.

### Ichthyoplankton

There were 15 ichthyoplanktonic taxa found. Larvae from mesopelagic species dominated the catches (ca

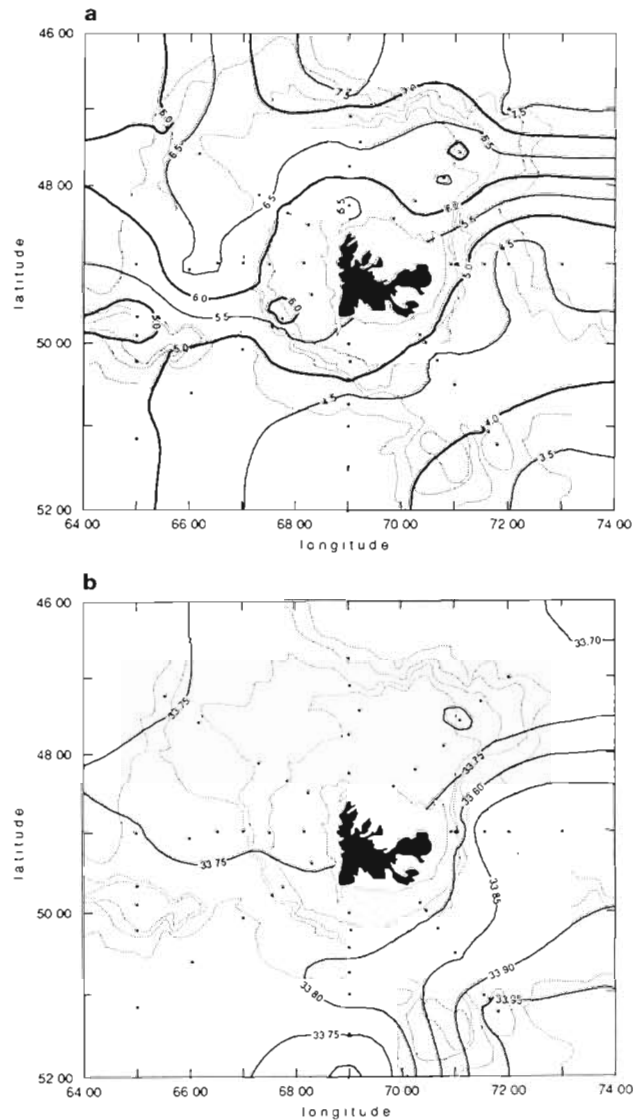


Fig. 2 Hydrologic conditions, summer 1987 (a) Surface temperatures ( $^\circ\text{C}$ ), (b) surface salinities (‰)

95%), followed by notothenioid larvae. Seasonal diversities are low (8 taxa approximately), because of the small number of species found in the area (55) and because demersal species spawn in different seasons and geographic sectors (Duhamel 1987a, b). Lack of sampling in the nearshore zone and in spring may also have influenced the number of taxa collected.

The following 4 groups can be identified based on seasonal presence or absence: (1) Species whose larvae are found in summer and autumn (*Lepidonotothen squamifrons* and larvae of the genus *Gymnoscopelus*). These species spawn at the end of spring, as verified for *L. squamifrons* by Duhamel & Ozouf-Costaz (1985) and Duhamel (1987a, b). *Zanclus cornutus* juveniles are found in the plankton during summer and autumn and can be included in this group. (2) Species

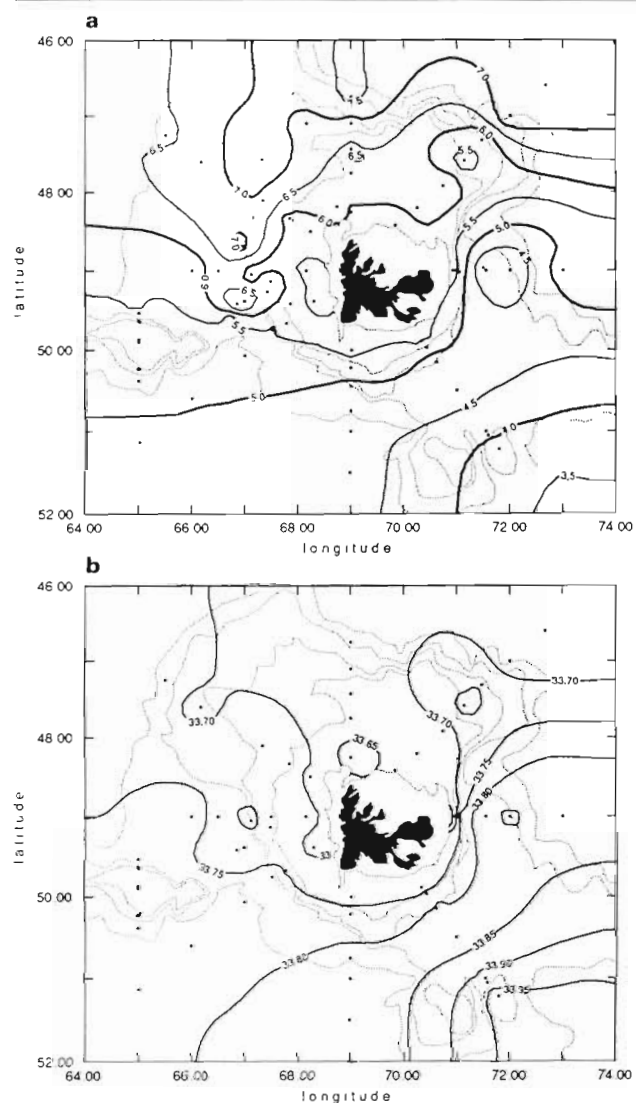


Fig 3 Hydrologic conditions, autumn 1987 (a) Surface temperatures (°C), (b) surface salinities (‰)

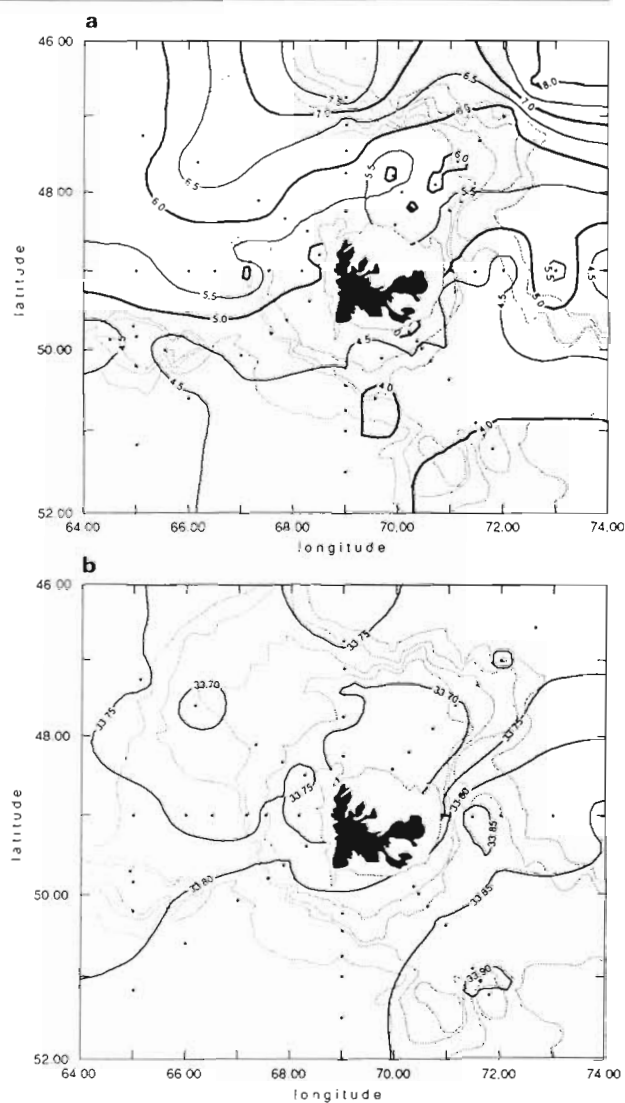


Fig 4 Hydrologic conditions, summer 1988. (a) Surface temperatures (°C), (b) surface salinities (‰)

Table 2 Seasonal median of ichthyoplanktonic abundances (no. of individuals per 10 000 m<sup>3</sup>), (–) Indicates no specimens found

Species	Summer 1987	Autumn 1987	Winter 1987	Summer 1988
<b>Myctophidae</b>				
<i>Protomyctophum</i> sp	12	36	18	16
<i>Krefttichthys anderssoni</i>	37	108	975	44
<i>Gymnoscopelus braueri</i>	80	47	9	51
<i>Gymnoscopelus nicholsi</i>	29	34	–	22
Myctophidae (all species)	156	148	975	169
<b>Nototheniidae</b>				
<i>Lepidonotothen squamifrons</i>	24	37	–	21
<i>Lepidonotothen mizops</i>	–	–	26	39
<b>Other species</b>				
<i>Zanclus cornutus</i>	36	16	–	12
<b>Notothenioid eggs</b>				
<i>Notothenia rossii</i>	–	–	77	–
<i>Champscephalus gunnari</i>	–	–	43	–



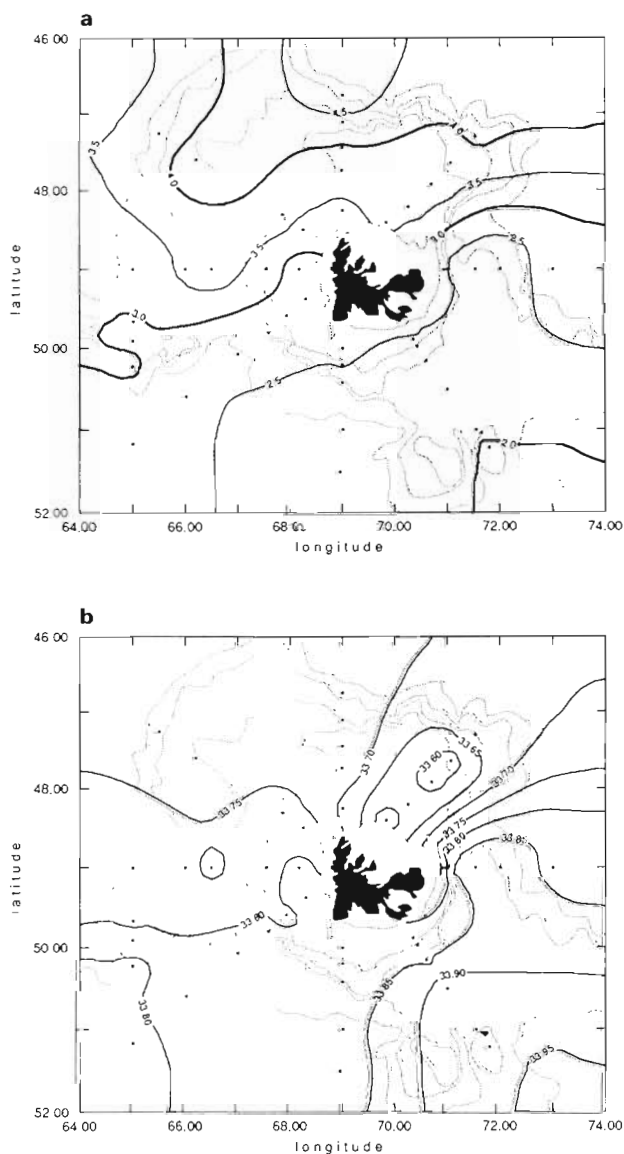


Fig. 5. Hydrologic conditions, winter 1987. (a) Surface temperatures (°C), (b) surface salinities (‰)

whose larvae are found in winter (*Lepidonotothen mizops*), as well as 2 species whose eggs were collected in the plankton only during winter (*Notothenia rossii* and *Champsocephalus gunnari*). These results agree with previous information on spawning of these species (Duhamel 1982, 1987a, b). The presence of eggs in the water column suggests that embryonic development may be pelagic for some species of Notothenioidei. This result, first proposed by Camus & Duhamel (1985) for *N. rossii*, is at variance with the benthic embryonic development hypothesis concerning the Notothenioidei (Marshall 1953). (3) Species whose larvae are found year-round (*Kreftlichthys anderssoni* and *Protomyctophum* sp.). (4) Rare species, including meso- and bathypelagic fishes (*Electrona* sp.

*Notolepis coatsi* and *Macrourus* sp.) and demersal fishes (*Muraenolepis* sp.).

Fish larvae showed low overall abundance (Tables 2 & 3). *Kreftlichthys anderssoni* was the dominant ichthyoplankton in 3 of the 4 seasonal samplings, showing the highest average abundance in all but the summer 1987 series. Myctophids showed the highest average abundances of all recorded taxa (*Gymnoscopelus braueri* for the summers and autumn, and *K. anderssoni* for winter). The high percentage of stations with abundance equal to 0 indicates a spatial distribution linked not to chance but strongly to the influence of external factors or intrinsic factors of each species, such as spawning period and area.

#### Multivariate analysis of larval abundance, environmental factors and stations

##### Summer 1987

The 3 groups (A, B and C) resulting from multivariate analysis (Table 4) each corresponded to a geographically distinct region, characterized by its particular hydrology and topography (Fig. 6).

Group A was clearly distinct from the 2 others. It precisely corresponded to the Kerguelen-Heard seamounts. This region differed from the others by its low temperatures (< 4°C) and high salinities and densities (> 33.90‰ and > 27 respectively). The 2 other groups (B and C) could be distinguished from one another on the basis of 3 factors. Two factors were linked to hydrology: first, the 5°C isotherm, which is the surface manifestation of the Antarctic Polar Front (Ostapoff 1962), and second, the 33.80‰ isohaline. Differences were also observed between the shelf and seamounts and the oceanic zone. Wind factors did not seem to be involved in the observed spatial structure.

Following the classification system, species densities were divided into the last 2 groups. Group B included larvae of deep-living mesopelagic species (*Protomyctophum* sp. and high densities of *Kreftlichthys anderssoni*). The geographic zone (Zones 2 to 4) associated with this group was bounded on the south by the Kerguelen-Heard seamounts and on the north by the Antarctic Polar Front. The deep northern stations were also included despite hydrological differences. This can be explained by the presence of *K. anderssoni* larvae and by the fact that this group included the deepest stations. Group C included the demersal species (*Lepidonotothen squamifrons* and *Zanclus cornutus*), the shelf-living mesopelagic species (*Gymnoscopelus* spp.) and those species the bathymetric distribution of which is limited at a depth of 200 m (weak densities of *K. anderssoni*). From a topographical

Table 3. Ichthyoplanktonic quantitative characteristics for summer 1987, % Zero: percentage of stations for which abundance was 0. Abundances represent no. of individuals per 10 000 m<sup>3</sup> (average, standard deviation, maximum)

Species	Summer 1987 (40 stns)			Autumn 1987 (50 stns)			Winter 1987 (46 stns)			Summer 1988 (47 stns)						
	% Zero	Avg.	SD	% Zero	Avg.	SD	% Zero	Avg.	SD	% Zero	Avg.	SD	Max.			
<b>Myctophidae</b>																
<i>Protomyctophum</i> sp.	78	4.02	9.04	40	23.83	50.42	262	65	10.66	20.17	77	68	11.52	36.05	241	
<i>Electra</i> sp.	90	2.25	8.50	49	0.94	4.03	24	91	1.18	3.84	14	81	2.51	6.27	36	
<i>Krefflichthys anderssoni</i>	43	53.78	9.04	730	32	176.56	50.42	1366	2	1243.30	20.17	3077	13	118.18	241.10	1486
<i>Gymnoscopelus braueri</i>	33	90.49	134.38	601	38	36.60	51.61	175	98	0.20	1.32	9	21	90.81	137.70	584
<i>Gymnoscopelus nicholsi</i>	90	5.24	22.08	137	78	9.98	26.73	151	100	0.00			72	10.48	22.95	100
<i>Gymnoscopelus opisthopterus</i>	95	0.67	3.00	17	100	0.00			100	0.00			89	1.57	4.75	23
<i>Gymnoscopelus</i> (all species)	25	97.94	138.27	618	18	47.29	51.76	175	96	0.44	2.09	11	13	105.43	146.71	619
Myctophidae (all species)	8	193.87	193.00	779	4	252.48	319.23	1452	2	1273.20	961.20	3088	2	239.45	267.26	1529
<b>Nototheniidae</b>																
<i>Gobionotothen acuta</i>	98	0.39	2.41	15	98	0.68	4.76	34	100	0.00			98	0.53	3.61	25
<i>Lepidonotothen squamifrons</i>	78	13.63	43.89	256	90	4.40	14.86	85	100	0.00			77	35.61	139.13	783
<i>Lepidonotothen mizops</i>	100	0.00			100	0.00			76	23.02	79.49	503	96	1.35	6.59	39
Nototheniidae (all species)	78	13.63	43.89	256	86	5.32	15.42	85	76	23.02	79.49	503	74	36.97	139.06	783
<b>Other families</b>																
<i>Zanchlorhynchus spinifer</i>	90	4.44	16.57	95	90	2.79	11.31	74	100	0.00			96	0.51	2.45	12
<i>Macrourus holotrachys</i>	100	0.00			100	0.00			96	0.77	3.78	23	100	0.00		
<i>Notolepis coatsi</i>	100	0.00			100	0.00			100	0.00			96	0.35	1.69	9
<i>Muraenolepis</i> sp.	98	0.30	1.86	12	100	0.00			100	0.00			100	0.00		
<b>Notothenioid eggs</b>																
<i>Notothenia rossi</i>	100	0.00			100	0.00			52	84.89	69.46	2002	100	0.00		
<i>Champsoscephalus gunnari</i>	100	0.00			100	0.00			52	40.56	69.46	265	100	0.00		

Table 4. Groups (A to C) and sub-groups (Zones 1 to 7) of environmental and ichthyoplanktonic characteristics obtained from the summer 1987 cluster Ichthyoplanktonic abundance classes are: Zero density (abundances equal to 0), Class 2 (abundances lower than the seasonal median of abundances; Table 2) and Class 3 (abundances greater than this median). For full genus names see Table 2

Characteristics	A		B		C	
	1	2	3	4	5	7
<b>Hydrology</b>						
Temperature (°C)	3.5–4.0	4.0–4.5	4.5–5.0		> 6.5	5.0–6.5
Salinity (‰)	> 33.90	33.80–33.85			33.70–33.75	33.75–33.80
Density	27.0–27.1	26.8–26.9	26.7–26.8	< 26.4	26.4–26.5	26.5–26.7
<b>Meteorology</b>						
Wind speed (Beaufort scale)		7		2–3	5	6 and 8
Wind direction		NE-E	NW-N		S-SW	SE-S and SW-NW
<b>Topography</b>						
Bathymetry (m)		550–1000		> 1000		< 200
Sites	Ker-Heard bank			Oceanic zone		Island shelf
<b>Ichthyoplankton</b>						
Zero density						All species
Class 2			<i>Protomyctophum</i> sp.		<i>G. nicholsi</i> Myctophidae (all) <i>Z. spinifer</i> <i>L. squamifrons</i>	<i>G. braueri</i> <i>K. anderssoni</i>
Class 3			<i>Protomyctophum</i> sp	<i>K. anderssoni</i>	<i>Z. spinifer</i> <i>L. squamifrons</i>	<i>G. braueri</i> <i>G. nicholsi</i> Myctophidae (all)

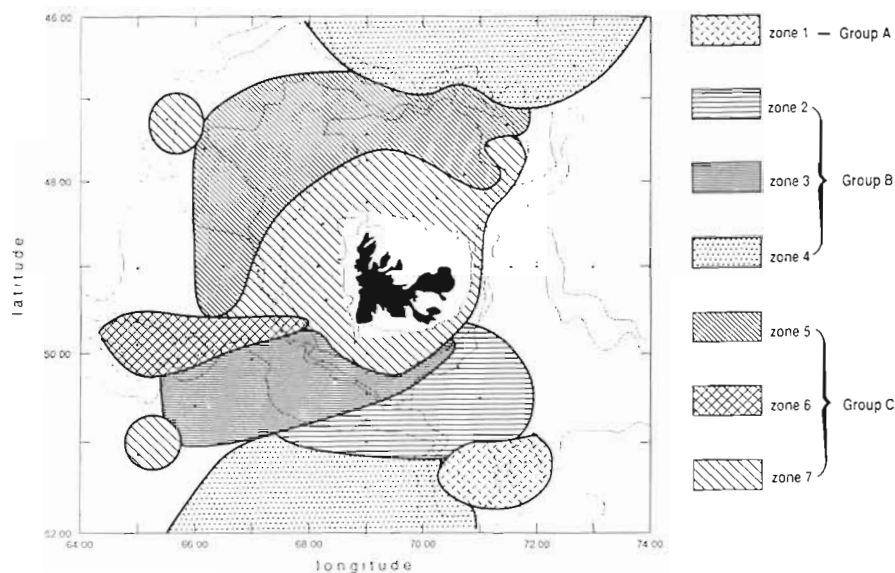


Fig. 6. Summer 1987 Cartogram of zones (sub-group observations; see Table 4) linked to the analysis

perspective, this group included almost the whole island shelf, as well as the Skiff seamount. In a hydrological context, the characteristics corresponded to the Antarctic Polar Front north zone.

#### Autumn 1987

Characteristics of the 5 groups resulting from multivariate analysis are given in Table 5. Each of them defined a geographical zone (Fig. 7) with precise hydrologic and topographic characteristics. Wind factors did not affect spatial structure.

Groups D and E were separated from the other groups. Zone 8, linked to Group E, corresponded to Kerguelen-Heard seamounts, with the same hydrologic characteristics as those in summer. Group D geographically corresponded to the channel situated between the island shelf and the Kerguelen-Heard seamounts. Temperatures were between 4 and 4.5°C. For the other groups, bathymetry and the position of the Antarctic Polar Front (surface temperature ca 5°C), seemed to be the distinctive criteria. Group A, associated with deep oceanic zones, included 2 zones: Zone 1 was limited to the north by the Antarctic Polar Front; Zone 2 corresponded to the deep oceanic zone to the north of the shelf, where densities were < 26.4. Another group, B, included the shelf's slopes and Skiff seamount. Its physical characteristics were similar to those of the region surrounding the Antarctic Polar Front. Finally, Group C included the shelf. Zones 5 and 6 (linked to this group) were limited to the south by the Antarctic Polar Front and to the north by great depth.

Few differences can be seen for ichthyoplankton when compared with summer results. Myctophids were absent

on the Kerguelen-Heard seamounts (Group E). *Protonotophum* sp. larvae were located in autumn to the north of the Antarctic Polar Front, and occurred exclusively outside of the shelf (Zones 2 and 4). *Krefflichthys anderssoni* larvae concentrated on the slopes (Zone 4), but some of them could be observed on the shelf (Zone 6). *Gymnoscopelus* spp. larvae favoured the seamounts and some parts of the island shelf (Groups B and C). Only larvae of *G. braueri* were found outside the shelf (Group A). Demersal species (*Lepidonotothen squamifrons* and *Zanclus cornutus spinifer*) were concentrated on the shelf (Group C), even though some *Z. spinifer* specimens were fished above deep zones (Group A). High densities of *L. squamifrons* were observed on the Skiff seamount (Group B). Hydrologic factors separated these 2 species: *Z. spinifer* were found in the warmer waters north of the Antarctic Polar Front, and *L. squamifrons* in waters surrounding the Antarctic Polar Front.

#### Winter 1987

Four groups were identified (Table 6). A cartogram of the observation subgroups is shown in Fig. 8.

As in the other seasons, the Kerguelen-Heard seamount region was separated from the other zones (Group C) because of its high salinities (> 33.90‰) and densities (> 27.1). Another zone (linked to Group D) was characterized by its very low salinities and densities (< 33.65‰ and < 26.7 respectively). The Group A region was limited to the southeast by the Kerguelen-Heard seamounts and to the north by the 3°C isotherm. This isotherm is the surface manifestation of the Antarctic Polar Front (Ostapoff 1962), as are the 33.80‰ isohaline and 26.9 isopycnal. The deep



Table 5. Groups (A to E) and sub-groups (Zones 1 to 8) of environmental and ichthyoplanktonic characteristics obtained from the autumn 1987 cluster Ichthyoplanktonic abundance classes as in Table 4. For full genus names see Table 2

Characteristics	A		B		C		D		E	
	1	2	3	4	5	6	7	8		
<b>Hydrology</b>										
Temperature (°C)	4.5–5.0	> 6.5	5.0–5.5		6.0–6.5	5.5–6.0	4.0–4.5	3.5–4.0		
Salinity (‰)	33.80–33.85		33.75–33.80		33.65–33.70	33.70–33.75	33.85–33.90	33.90–33.95		
Density	26.7–26.8	< 26.4	26.6–26.7		26.4–26.5	26.5–26.6	26.8–27.0	27.0–27.1		
<b>Meteorology</b>										
Wind speed (Beaufort scale)	7		1 and 3	6	4	5	2			
Wind direction				NW-NE	SW-W	W-NW				
<b>Topography</b>										
Bathymetry (m)	> 1000			200–550			550–1000			
Sites	Oceanic zone		Skiff bank			Island shelf		Ker-Heard bank		
<b>Ichthyoplankton</b>										
Zero density				<i>G. braueri</i> <i>G. nicholsi</i> <i>L. squamifrons</i> <i>Z. spinifer</i>		<i>K. anderssoni</i> <i>Protomyctophum</i> sp.		Myctophidae (all)		
Class 2	<i>Z. spinifer</i> <i>G. braueri</i>		<i>G. nicholsi</i>	<i>Protomyctophum</i> sp.						
Class 3		<i>Protomyctophum</i> sp.	<i>G. nicholsi</i> <i>L. squamifrons</i>	Myctophidae (all) <i>K. anderssoni</i>						

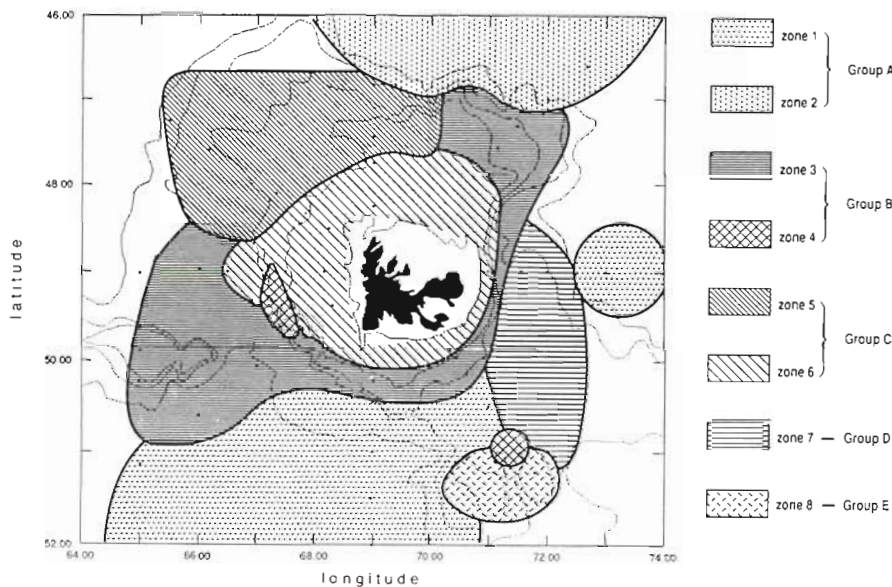


Fig. 7. Autumn 1987. Cartogram of zones (sub-group observations; see Table 5) linked to the analysis

oceanic zone located to the north of the island shelf was also included in this region, since Group B included deep oceanic stations. The area linked to Group B observations corresponded to the north of the Antarctic Polar Front (temperatures  $> 3^{\circ}\text{C}$ ) and was limited to the north by the great depths. This zone mainly covered half the northern part of the island shelf.

With respect to species, there was a noticeable lack of Myctophidae in the 'less-saline' zone (Group D), which was located north-east of the archipelago. Myctophid species (*Krefftichthys anderssoni* and *Protomyctophum* sp.) were found above different depths. *K. anderssoni* larvae, very abundant in winter, were scattered all over the area and were mostly found in the south of the Antarctic Polar Front (Group A). *Protomyctophum* sp. occurred to the north of this front (Group B). The only demersal species for which larvae were found is *Lepidonotothen mizops*, the highest densities of which were observed on the Kerguelen-Heard seamounts (Group C). Otherwise, this species mostly occurred in the north of the Antarctic Polar Front (Group B). Finally, all the collected pelagic eggs were from demersal species. Indeed, high densities were observed on the island shelf (Group B), whereas low densities were seen outside of it (Zone 1). This suggests that high winds – which very often occur there – and currents carry those eggs above the deep oceanic zone. They may also allow colonization of the shelf by mesopelagic larvae.

#### Summer 1988

Four groups were identified (Table 7). A cartogram of the sub-groups is shown in Fig. 9.

The first zone (Group A) covered the Kerguelen-Heard seamounts. Its thermal and salinity characteristics were identical to those of summer 1987, but its densities were little lower. The second zone (Group B) corresponded to the deep part situated to the north of the shelf. It was hydrologically defined by densities  $< 26.4$  and by high temperatures ( $> 7^{\circ}\text{C}$ ). The third zone (Group C) included the island shelf and its slope. It was limited to the south by the  $5.5^{\circ}\text{C}$  isotherm and the 26.6 isopycnal, and was therefore to the north of the Antarctic Polar Front. The last group (D) covered Zones 4 to 6. It was limited to the south-east by the Kerguelen-Heard seamounts and to the north by the Antarctic Polar Front (temperatures  $< 5.5^{\circ}\text{C}$ ), the 33.75‰ isohaline and the 26.6 isopycnal.

As for species, *Protomyctophum* sp. larvae only occurred above deep oceanic zones (Zone 6). *Krefftichthys anderssoni* and *Gymnoscopelus braueri* larvae occurred from the break-point (Group C) to the deep oceanic zone (Zone 6). Yet the highest ichthyoplankton densities were found in the south. *Gymnoscopelus nicholsi* larvae occurred strictly on the shelf (Zones 3 and 5), especially on its northern part, near the Antarctic Polar Front. *Lepidonotothen squamifrons* larvae (demersal species) occurred on both the shelf and the Skiff seamount (Group D). They were found mainly near the Antarctic Polar Front (temperatures between 5 and  $5.5^{\circ}\text{C}$ ). *Zanclus cornutus* juveniles were strictly demersal to the north of the Antarctic Polar Front (Zones 3 and 5). Few significant data are available for *Lepidonotothen mizops* larvae. These are most likely found in the northern part of the archipelago close to the coast.



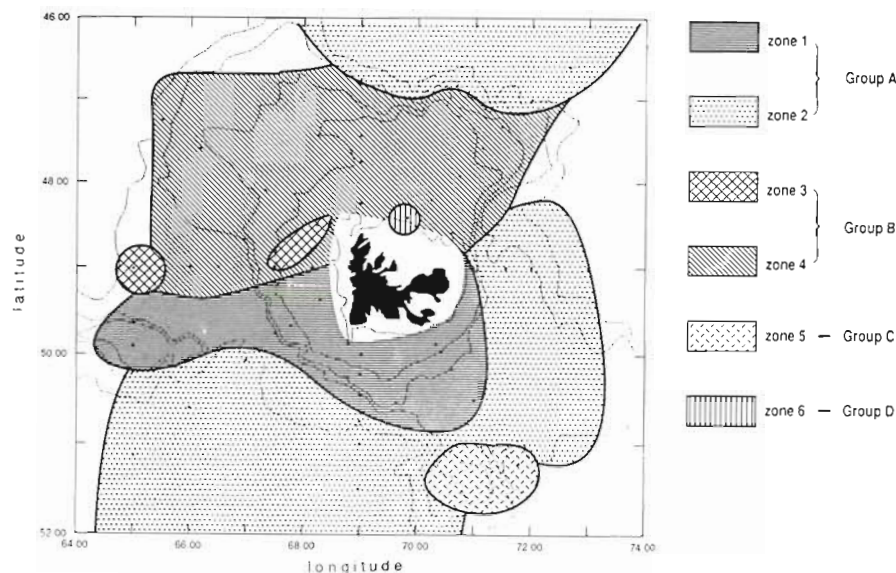


Fig. 8. Winter 1987 Cartogram of zones (sub-group observations; see Table 6) linked to the analysis

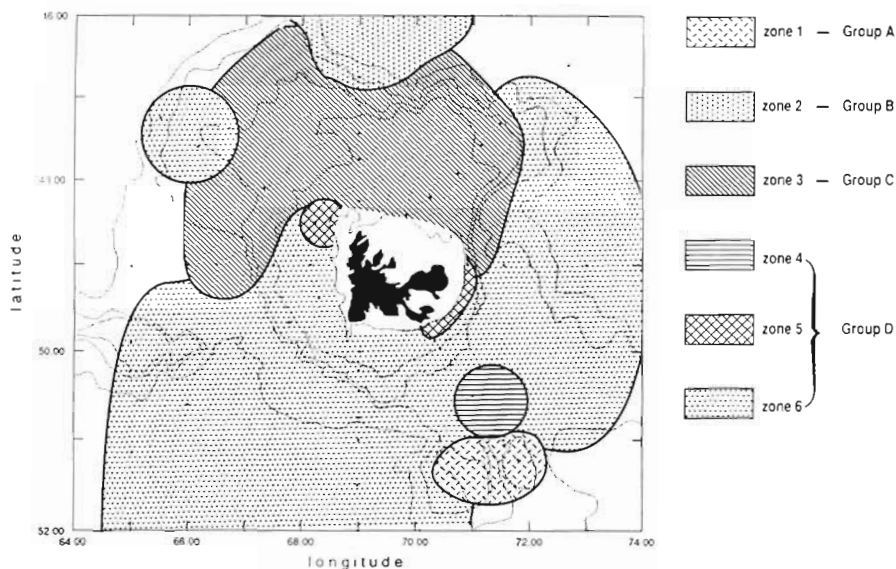


Fig. 9. Summer 1988. Cartogram of zones (sub-group observations; see Table 7) linked to the analysis

## CONCLUSION

By any criterion, differences between summer seasons (autumn included) were minor. On the other hand, their distributions and abundances differed from those of winter.

The study area could be divided into 3 main regions. The first – mainly because of its hydrology – was the Kerguelen-Heard seamount zone (lowest temperatures and highest salinities and densities for the area). The presence of the Antarctic Polar Front and the distinction between the shelf and the deep oceanic zone distinguished the last 2 regions: one was limited to the north by the Antarctic Polar Front and to the southeast by the Kerguelen-Heard seamounts, and included most of the deepest stations, even those

located at the north of the studied area; the other covered most of the island shelf, as well as the Skiff seamount. Some variability existed which isolated individual regions. For example, the northeast of the archipelago was distinct in winter, due to the presence there of low-salinity waters. The latitudinal boundary of the Antarctic Front was further north in summer 1988 than in 1987. Thus, the area south of this front was much wider in 1988.

The spatial distribution of fish larvae was greatly influenced by topographic factors and by hydrology. Wind factors influenced only fish eggs and larvae transport. Two kinds of larvae can be distinguished:

(1) Larvae which occur on the shelf and the surrounding seamounts, such as *Lepidonotothen squamifrons*, *Lepidonotothen mizops* and *Zanclus cornutus*.



Table 7. Groups (A to D) and sub-groups (Zones 1 to 6) of environmental and ichthyoplanktonic characteristics obtained from the summer 1988 cluster. Ichthyoplanktonic abundance classes as in Table 4. For full genus names see Table 2

Characteristics	A		B		C		D	
	1		2		3		5	6
<b>Hydrology</b>								
Temperature (°C)	3.5–4.0		> 6.5		5.5–6.5	4.0–4.5	5.0–5.5	4.5–5.0
Salinity (‰)	33.90–33.95				33.65–33.75	33.85–33.90		33.75–33.80
Density	26.9–27.0		< 26.4		26.4–26.6	26.8–26.9	26.6–26.7	26.7–26.8
<b>Meteorology</b>								
Wind speed (Beaufort scale)	7				5	2–3	0 and 4	6
Wind direction			S-SW, NW-N		SW-NW		N-NE	
<b>Topography</b>								
Bathymetry (m)					200–550	550–1000	< 200	> 1000
Sites	Ker-Heard bank				Island shelf			Oceanic zone and Skiff bank
<b>Ichthyoplankton</b>								
Zero density					All species			
Class 2					Myctophidae (all) <i>L. mizops</i> <i>Z. spinifer</i> <i>G. nicholsi</i> <i>G. braueri</i> <i>K. anderssoni</i>		<i>L. squamifrons</i>	<i>Protomyctophum</i> sp.
Class 3			<i>L. mizops</i>				<i>G. nicholsi</i> <i>Z. spinifer</i>	Myctophidae (all) <i>L. squamifrons</i> <i>Protomyctophum</i> sp. <i>G. braueri</i> <i>K. anderssoni</i>

*Gymnoscopelus nicholsi*, a species defined as bathypelagic (Linkowski 1985), must also be included in this group. These species preferentially occur to the north of the Antarctic Polar Front. The eggs of *Notothenia rossii* and *Champscephalus gunnari* can also be included in this group.

(2) Larvae which occur in the oceanic zone. They all belong to the Myctophidae. Some of them can be found on the slope and to a lesser extent on the shelf, such as *Gymnoscopelus braueri* and *Kreftichthys anderssoni* larvae. Hulley (1981) found hydrologic affinities in the adults similar to those that we found for the Kerguelen Islands larvae. According to season, *Protomyctophum* sp. larvae are located either to the north or to the south of the Antarctic Polar Front. *K. anderssoni* and *G. braueri* occur in the Superficial Antarctic Water and the Antarctic Intermediate Water (Hulley 1981). As these 2 water masses are present in the studied area, the larvae are mainly influenced by topography.

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#### LITERATURE CITED

- Azibane, C., Clavier, B., Dujardin, J. L., Le Touze, V., Rigourd, J. F. (1977). Etude sur le climat des îles Kerguelen et de la zone subantarctique de l'océan Indien. Climatologie de Port-aux-Français. Monogr. Météorol. Natl. 99: 1–130
- Bekker, V. E. (1985). Distribution of myctophid fishes and the position of the biogeographical border between the islands of Saint Paul and Kerguelen. J. Ichthyol. 25 (2): 159–162
- Camus, P., Duhamel, G. (1985). Ponte et développement embryonnaire de *Notothenia rossii rossii* (Richardson, 1844), Nototheniidae des îles Kerguelen. Cybium 9 (3): 283–293
- Charriaud, E., Gambéroni, L. (1987). Observations hydrologiques et flux géostrophique entre les îles Kerguelen et Amsterdam – Résultats de la Campagne KERAMS1 (16–20 février 1987). Rapp. Interne Lab. Oceanogr. Phys./Museum Nat. Hist. Nat., Paris
- Deacon, G.E.R. (1934). Die Nordgrenzen antarktischen und subantarktischen Wassers im Weltmeer. Annalen Hydr. Mar. Meteorol. 42: 129–134
- Duhamel, G. (1982). Biology and population dynamics of *Notothenia rossii rossii* from the Kerguelen Islands (Indian sector of Southern Ocean). Polar Biol. 1: 141–151
- Duhamel, G. (1987a). Ichtyofaune des secteurs indien occidental et atlantique oriental de l'océan Austral: biogéographie, cycles biologiques et dynamique des populations. Thèse de Doctorat d'Etat ès Sciences Naturelles, Université Paris VI
- Duhamel, G. (1987b). Reproduction des Nototheniidae et Channichthyidae des îles Kerguelen. In: Colloque sur l'écologie marine des îles subantarctiques et antarctiques (Paris 25 juin 1985). CNFRA 57: 91–107
- Duhamel, G., Ozouf-Costaz, C. (1985). Age, growth and reproductive biology of *Notothenia squamifrons* Günther, 1880 from the Indian Sector of the Southern Ocean. Polar Biol. 4: 143–153
- Etremenko, V. N. (1979). Atlas of fish larvae of the Southern Ocean. Cybium 7 (2): 1–74
- Fischer, W., Hureau, J. C. (1987). Fiches FAO d'identification des espèces pour les besoins de la pêche. Océan Austral (Zones de pêche 48, 58 et 88) (Zones de la Convention CCAMLR). Vols. 1 & 2, FAO, Rome
- Gambéroni, L., Geronimi, P., Jeannin, P. F., Murail, J. F. (1982). Study of frontal zones in the Crozet-Kerguelen region. Oceanol. Acta 5 (3): 289–299
- Hulley, P. A. (1981). Results of the research cruises of FRV 'Walther Herwig' to South America. LVIII Family Myctophidae (Osteichthyes, Myctophiformes). Arch. Fisch.-Wiss. 31 (1): 1–300
- Hureau, J. C. (1982). Methods for studying early life history stages of Antarctic fishes. Cybium 6 (1): 43–51
- Kellermann, A. (1986). Zur Biologie des Jugendstadien der Notothenioidei (Pisces) an der Antarktischen Halbinsel. Ber. Polarforsch. (Bremerhaven) 31: 1–155
- Kellermann, A. (1989). Catalogue of early life stages of Antarctic Notothenioid fishes. In: Identification key and catalogue of larval Antarctic fishes. Biomass scient. Ser. 10: 1–136
- Koubbi, P., Duhamel, G., Camus, P. (1990). Early life stages of Notothenioidei (Pisces) from the Kerguelen Islands. Cybium 14 (3): 225–250
- Lance, G. N., Williams, W. T. (1967). A general theory of classificatory sorting strategies. I. Hierarchical systems. Comput. J. 9: 373–380
- Ledenev, V. G. (1966). Antarctic convergence in the western part of the Indian sector of the Southern Ocean. Sov. Ant. Exp. Inf. Bull. 57/58: 112–116
- Linkowski, T. B. (1985). Population biology of the myctophid fish *Gymnoscopelus nicholsi* (Gillberg, 1911) from the western-south Atlantic. J. Fish. Biol. 27: 683–698
- Marshall, N. B. (1953). Egg size in arctic, antarctic and deep-sea fishes. Evolution 7: 328–341
- Moser, H. G., Ahlstrom, E. H. (1970). Development of lanternfishes (family Myctophidae) in the California current. Part 1: Species with narrow-eyed larvae. Bull. Los Angeles Cty Mus. Sci. 7: 1–145
- North, A. W., White, M. G. (1982). Key to fish postlarvae from the Scotia sea, Antarctica. Cybium 6 (1): 13–32
- Ostapoff, F. (1962). The salinity distribution at 200 metres and the Antarctic frontal zones. Dt. hydrogr. Z. 15: 133–141
- Smith, P. E., Richardson, S. (1977). Standard techniques for pelagic fish egg and larval surveys. FAO Fish. Tech. Pap. 175: 1–100
- Volle, M. (1985). Analyse des données. Economica, Paris

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