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Spatial Distribution of *Pleuragramma antarcticum* (Pisces: Nototheniidae) near the Filchner- and Larsen Ice Shelves (Weddell Sea/Antarctica)

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Summary. In the zooplankton collected during three German Antarctic expeditions to the southern Weddell Sea in 1979/80, 1980/81 and 1983, the post-larvae of the nototheniid fish *Pleuragramma antarcticum* were found in 71–94% of the samples and represented 85–98% in numbers of all fish caught. In 1983, the abundance of post-larvae was up to 88 ind./m^2 (corresponding to 3 ind./m^3). Highest concentrations were generally found over the continental slope and innershelf depressions. More than 70% of the post-larvae were caught in the upper 50–100 m water layer, in the well stratified "Summer Water" of −1.3 to −0.5 °C. The Summer Water is shifted towards the outer edge of the shelf by Ekman transport and accumulation of post-larvae in the slope front and eddies can be explained by this drift. Older *Pleuragramma antarcticum* of age 1 resemble in their vertical distribution the juveniles and adults, 40–60% of which were caught on the shallower parts of the shelf in cold "Ice Shelf Water" of −1.8 to −2.1 °C in depths below 200 m. Mean abundances of the yearclasses varied by a factor of 16 in age 0 fish and by factor of 10 in age 1. The size of a yearclass may be related to the varying appearance and persistence of an ice free coastal polynya.

Introduction

In the cold water ecosystems of the high Antarctic shelves, the nototheniid *Pleuragramma antarcticum* is known to be the most abundant fish species. It represented more than 90% in weight and numbers of the midwater fish of the Ross Sea in IKMT hauls (DeWitt 1970). Over 91% of the adult fishes in pelagic RMT (Rectangular Midwater Trawl) catches in the southwest Weddell Sea were *Pleuragramma antarcticum* and in bottom trawls in Gould Bay (77°30 S) this species made up 44% (Hubold, unpublished). Accordingly, the proportion of *Pleuragramma antarcticum* larvae in the total ichthyoplankton in the southern and western Weddell Sea shelf area was 98% (Keller 1983) resp. 85% (Hubold 1984, in press).

The major part of the eastern and southern Weddell Sea coastline is dominated by the vertical ice barriers of the Ekstrøm-, Riiser-Larsen-, Brunt-, and Filchner Ice Shelves (Fig. 1). In water of more than 300 m depth, the ice shields float and the water interacts with the bottom of the ice forming a characteristic water type called Ice Shelf Water (ISW) by Carmack and Foster (1975). The water temperatures are as low as −2.1 °C in the southernmost parts (Vahsel Bay, Gould Bay) and about −1.8 °C near Atka Bay (Wegner, personal communication). A warmer surface layer, usually 50 m thick, is formed during the summer. Surface melting of sea- and shelf ice results in a halocline at corresponding depth.

Towards the open sea, extension of the ISW over the slope of the continental shelf is limited by the westward flowing warmer water of the East Wind Drift (T > 0 °C). A frontal zone was observed at about 100 km north of Atka Bay in 1981 (Wegner, in preparation). Over the wide shelf of the southern Weddell Sea, the ISW extends northward for more than 400 km. The warmer water of the East Wind Drift reaches the shelf edge at depths of more than 500 m, and fills the deep innershelf depressions north of Halley Bay.

The Weddell Sea is covered by sea ice for most of the year. In the summer months (Dec.–March) an ice free polynya[1] forms, in varying extension, parallel to the shelf ice barrier (Strübing 1982).

The distribution of marine life is influenced by the different water masses and the bottom topography. Post-larvae and juveniles of typical oceanic fish species such as myctophids and paralepidids are excluded from the shelf ecosystem and occur only close to the ice barrier where the deep trenches contain warm bottom water (p.e. trench off Camp Norway).

[1] polynya (russ) = stretch of open water in the pack- or fast ice

Krill (*Euphausia superba*) rarely appears on the shelf, where the smaller and less abundant *Euphausia crystallorophias* is the dominant euphausiid (Hempel et al. 1983). *Pleuragramma antarcticum* seems to be the key species in the pelagic system of the Antarctic shelf. The successful occupation of the pelagic niche by *Pleuragramma antarcticum* implies effective mechanisms of larval survival and regular recruitment to the adult stocks. In this paper I will analyze the spatial distribution of different age groups of this species and interprete apparent adaptations to the hydrographic environment.

Material and Methods

During the 1983 German "ANT I" expedition with the newly built research vessel *Polarstern*, zooplankton and nekton was sampled in the summer polynya between Atka Bay (8°W) and Gould Bay (43°W). A RMT 1+8 m (multiple Rectangular Midwater Trawl) closing net was used with 4500/320 μ meshes; net opening 8 m^2 resp. 1 m^2. Standard oblique hauls were made through the depth strata 300 – 200 m, 200 – 50 m and 50 – 0 m (Drescher et al. 1983). Nets were opened during retrieval. The last net pair was hauled open through the surface to continue sampling through the upper meters. Net speed through the water was 1.5 – 2 m/s. For technical reasons, some hauls were made as simple oblique hauls through the upper 200 m or less.

Samples were immediately preserved in 4% borax buffered formaldehyde. Fish were sorted from unsplit samples on ship board or within three months after the catch. Filtered volumes were calculated based on a program of Roe et al. (1980). Quantitative analysis of meso-and macrozooplankton will be published separately (Boysen, personal communication; Piatkowski, personal communication).

A CTD cast preceded each RMT haul. The water temperatures presented in this report were taken with 0.1 °C precision from the TS plots. The final TS analysis of the cruise will be published elsewhere (Koltermann, personal communication).

Of 47 RMT hauls altogether, 36 hauls were made along the coast of the southern and eastern Weddell Sea (Fig. 1).

The age groups were defined according to earlier results of a length frequency analysis (Hubold 1984, in press). *Pleuragramma antarcticum* between 8 and 25 mm SL (Standard Length) were attributed to age 0; those of 30 – 50 mm length belong to age class 1. Age 2+ refers to fish between 50 and 80 mm SL, longer specimens are defined as adults. Age of first maturation has not yet been identified for *Pleuragramma antarcticum*.

Post-larval abundances (age 0) were calculated only from the RMT 1 (320 μ mesh) catches as no/m^2 and no/m^3.

Results

The 36 RMT-hauls in the southern Weddell Sea yielded 5201 specimens of *Pleuragramma antarcticum* (144/haul). The age groups were represented as follows: 5035 post-larvae (140/haul); 70 fish of age 1, 20 juveniles of age 2+; and 76 adults. Near the tip of the Antarctic Peninsula three fish (age 1) and 5 juveniles (age 2+) were caught in two hauls. These specimens were included in the depth distribution analysis.

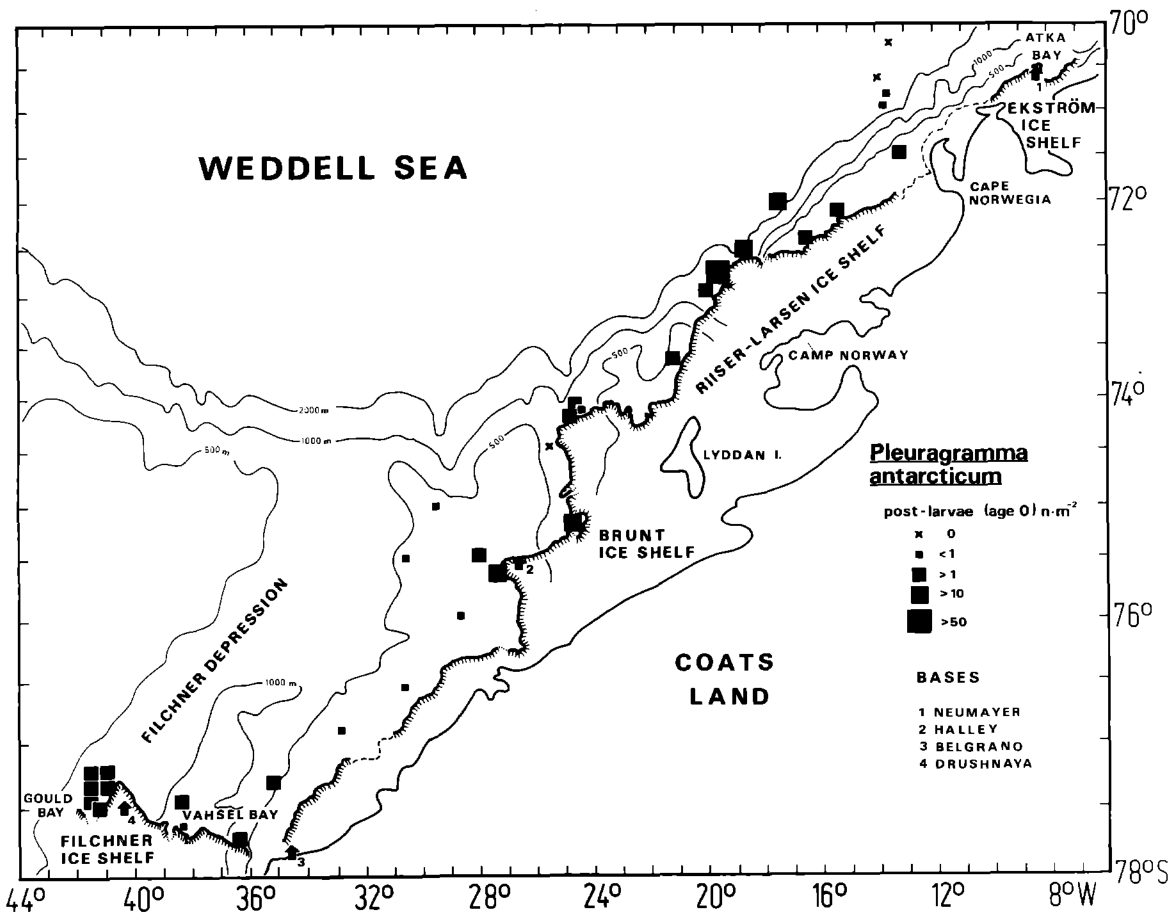

Fig. 1. The investigation area in the southwest Weddell Sea with the geographical locations as used in the text and standarized abundances of *Pleuragramma antarcticum* post-larvae (age 0) from RMT 1 m hauls; nets 1 – 3 combined

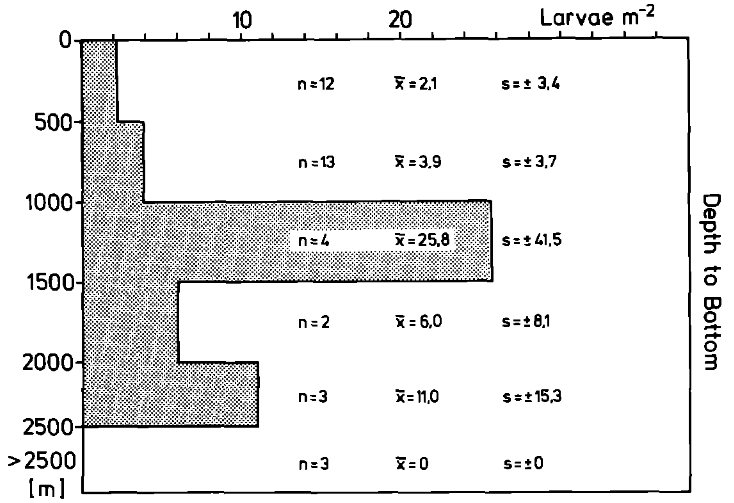

Fig. 2. Standardized abundances of *Pleuragramma antarcticum* post-larvae (age 0) over 500 m bottom depth strata. n = number of hauls per stratum, $\bar{x}$ = mean abundance, s = standard deviation

Pleuragramma antarcticum post-larvae were absent or caught only infrequently over the deep Weddell Sea central basin beyond the 2500 m isobath (some stations are beyond the area covered by Fig. 1). Low concentrations of age 0 fish were found over the relative shallow area (depth <500 m) off Brunt Ice Shelf and Coats Land (Fig. 1), where the larval densities ranged from 0.1 to 0.8 ind./m^2 at 5 stations (mean: 0.3, s = ±0.29, only RMT1 catches considered). Uniform distribution of post-larvae was encountered in the southernmost part of Gould Bay and Vahsel Bay over the Filchner Depression. Here (except for 1 station with 0.4 ind./m^2) at 9 stations the densities ranged from 2.4 to 7.8 ind./m^2 (mean: 4.6, s = ±1.9).

Pleuragramma antarcticum abundances varied between 0 and >50 ind./m^2 parallel to the ice barrier near Halley Bay, over the trench off the Brunt Ice Shelf, and over the trench and the continental slope off Riiser-Larsen Ice Shelf. The maximum observed density was 88 ind./m^2 (mean of 16 stations: 10.2, s = ±21.7).

Except for the 2 stations near Halley Bay, higher post-larval concentrations seemed to coincide regionally with the deeper trenches in the shelf. A plot of the larval densities over depth strata of 500 m reveals high concentrations in the 1000–1500 m stratum. The 4 stations sampled yielded a mean density of 26 ind./m^2 (range 0.4–87.9 ind./m^2) (Fig. 2).

In Table 1, numbers of post-larvae, juveniles and adults caught in the RMT nets (RMT 8 and 1 combined) are listed with respect to total water depth at the sampling site. Age 0 post-larvae were present in 31 of 35 shelf- and slope stations (0–2500 m). The older post-larvae (age 1) and juveniles (age 2+) were restricted to stations where the total water depth was less than 1250 m. Adults were caught only over total water depth of less than 1000 m. The maximum catch of age 0 specimens (1965 individuals) was made over 1450 m water depth. The maximum catch of age 1 was over 400 m water depth, of age 2+ over 200 m and of adults over 545 m.

A section parallel to the ice barrier along the ship's route reveals the differences in bottom topography at the "coast" and shows the water temperatures between Kapp Norwegia (72°S) and Gould Bay (77°30S) (Fig. 3).

Ice Shelf Water (ISW) of less than −2.1 °C was found in the Filchner Depression at depths below 450 m, while the maximum surface layer temperature there was −1.7 °C. The −1.8 °C isotherm can be used to trace the ISW in depths between 50 and 400 m throughout the section. Warm Summer Water (WSW) was layered on the top of the ISW. North of 75°S the Summer Water was notably warmer (−1.3 to −0.5 °C) than in the south.

The concentrations of *Pleuragramma antarcticum* post-larvae (age 0, age 1), juveniles (age 2+) and adults combined are given as ind./m^3 (Fig. 3). The values were calculated from the respective net pair (RMT 8 and 1 combined) as total number of individuals per total volume of water filtered. For the age 0 fish this calculation gives an underestimate because the RMT 8 nets do not collect the early postlarvae quantitatively (mesh 4500 μ). An analysis of size distributions of *Pleuragramma antarcticum* in RMT 8 vs RMT 1 net catches is given by Kel-

Table 1. *Pleuragramma antarcticum:* number of positive hauls (n), mean number of fishes per haul ($\bar{x}$), standard deviation (s) for 250 (500) m depth strata. (From RMT 8 + 1 nets combined)

Depths to bottom (m)	No. of hauls	Age 0			Age 1			Age 2+			Adults		
		n	$\bar{x}$	s	n	$\bar{x}$	s	n	$\bar{x}$	s	n	$\bar{x}$	s
0–250	4	3	25	11	1	2	–	1	7	–	1	8	–
251–500	10	8	113	175	6	9	15	3	4	2	3	6	5
501–750	12	11	79	104	7	2	1	3	1	0	3	13	9
751–1000	1	1	51	–	1	3	–	1	3	–	1	9	–
1001–1250	3	3	64	58	3	1	0	1	1	–	0	0	–
1251–1500	1	1	1965	–	0	0	–	0	0	–	0	0	–
1501–2000	2	2	76	100	0	0	–	0	0	–	0	0	–
2001–2500	2	2	419	577	0	0	–	0	0	–	0	0	–
>2500	3	0	0	–	0	0	–	0	0	–	0	0	–

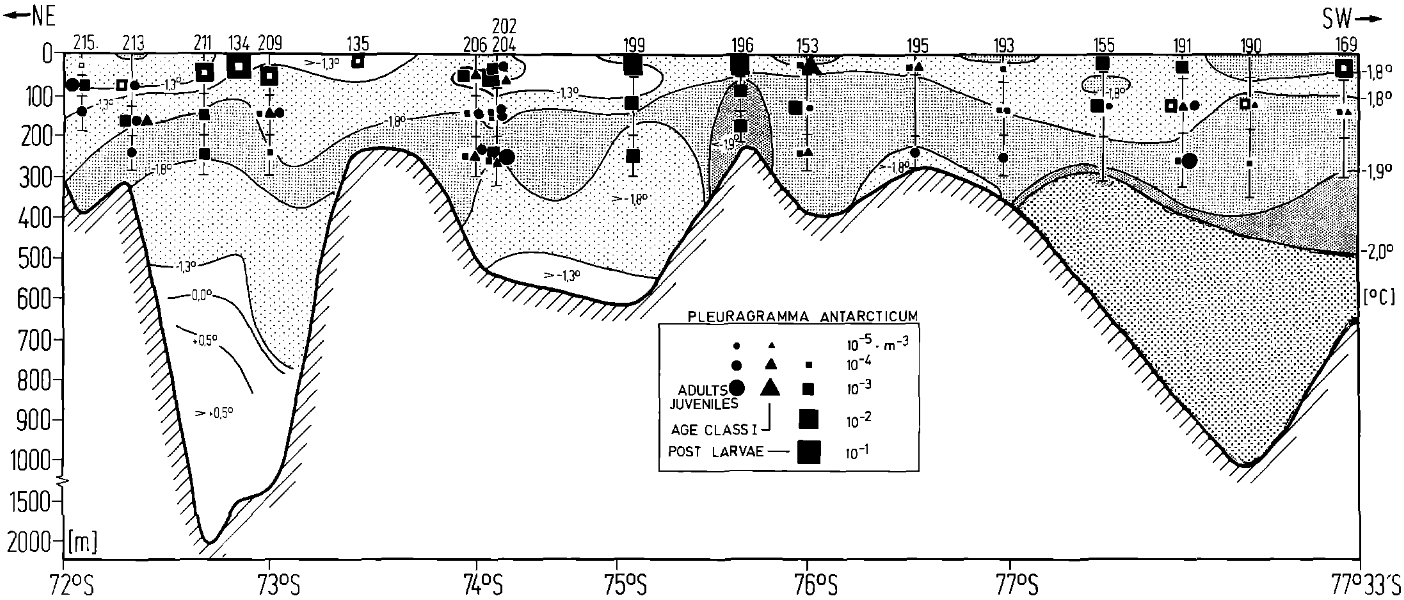

Fig. 3. Coast-parallel section along the main route of the 1983 *Polarstern* expedition, showing bottom depth, temperature, and abundance of *Pleuragramma antarcticum* as number of individuals per m^3 at different sampling depths between Kapp Norwegia and Gould Bay. Open squares indicate the presence of smallest ("age 00") post-larvae. The distances between stations represent travelled distances along the ice front. Bottom topography reveals the innershelf depressions (*from left to right*: Camp Norway trench, Halley Bay trench, Filchner Depression)

lermann (in preparation). Bars indicate the depth ranges sampled by the net pairs.

Fish of age 0 (post-larvae) were found in all depth layers. They were, however, more abundant near the surface. Maximum concentration (mean of the net pair) was 0.5 ind./m^3 (age 0) in the warm surface water at st. 134, where only the 50 – 0 m layer was sampled. The calculated density from RMT 1 alone was as high as 3 ind./m^3. The second highest post-larvae concentration was found at st. 133 approximately 30 miles offshore from st. 213 (Fig. 4), where 0.2 ind./m^3 (resp. 0.5 ind./m^3 in RMT 1 net) were collected in warm surface water.

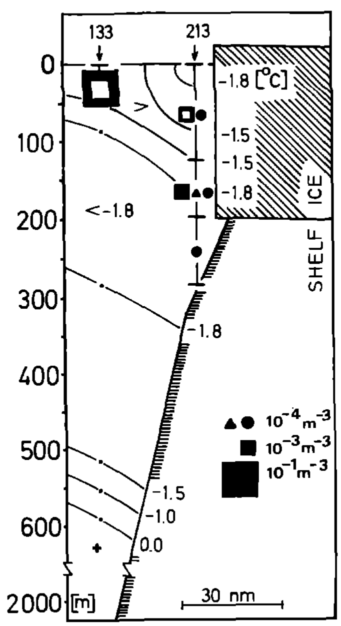

Fig. 4. Cost-normal section off the Larsen Ice Shelf with standardized abundances of *Pleuragramma antarcticum* as numbers of individuals per m^3. The symbols used are the same as in Fig. 3

Throughout the entire sampling period (Jan. – Feb.) the presence of very small larvae of less than 12.5 mm SL was established (named "age 00"). The occurrence of those recently hatched larvae is marked in Figs. 3 and 4 by open squares. Small post-larvae were confined to the surface layers near the two deep shelf depressions.

Age 1 fish were present in low concentrations of 10^{-5} to 10^{-4} ind./m^3 along the section generally in greater depth (Fig. 3). Only at st. 153 was a high concentration of this age class found near the surface (5.3×10^{-3} ind./m^3). Adults and juveniles (age 2+) were abundant in deeper layers over the slopes of the innershelf depressions. Maximum concentration of 2×10^{-3} ind./m^3 was found over the slope of the inner shelf depression off Brunt Ice Shelf (st. 202), off Riiser-Larsen Ice Shelf (st. 215) and over the eastern slope of the Filchner Depression (st. 191).

More than 52% of the age 0 *Pleuragramma antarcticum* in the RMT-m hauls were caught in the upper 50 m layer (Fig. 5). An additional 24% were obtained between 100 and 0 m and 17% between 200 and 50 m. The 300 – 200 and 200 – 100 m hauls yielded only 5 and 2% of the larvae, respectively.

Age 1 fishes were increasingly abundant in deeper layers. The high percentage in the 50 – 0 m stratum is due to one single haul of 34 specimens (= 53%). Excluding this haul, the percentage of age 1 fish caught below 200 m is 40%, which is close to the value for the juveniles 2 + at corresponding depth. The highest numbers of adults were obtained below 200 m.

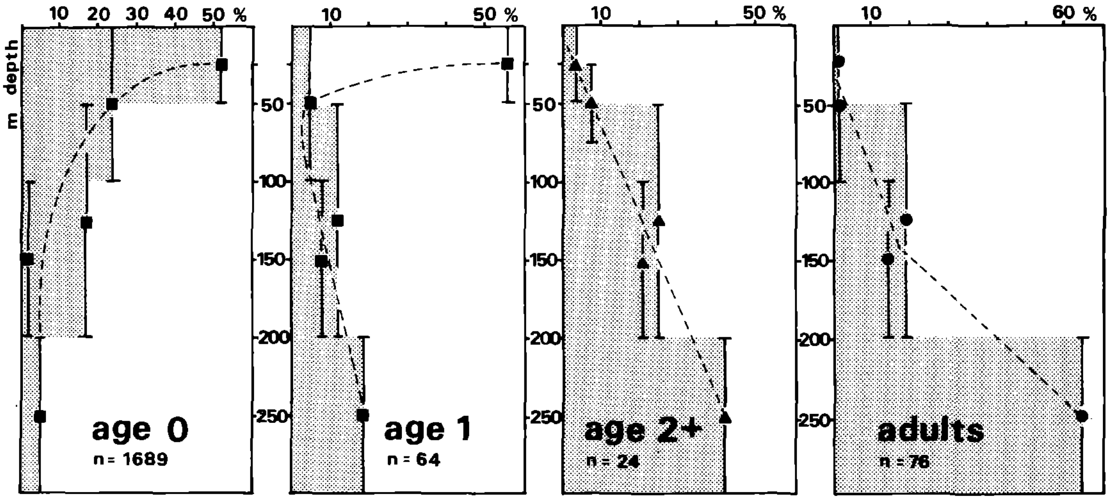

Fig. 5. Percentages of *Pleuragramma antarcticum* caught in the depth strata sampled by RMT 8 + 1 nets

Thus, the smallest post-larvae were found over the greatest total water depth, but were most abundant in the surface layers. With increasing size the fish are found in shallower waters towards the ice shelf "coast", but seem to prefer deeper water layers.

All catches were made between 06.00 and 22.00 h. No trend in the depth distribution of any of the age groups was observed during this period.

Discussion

In 1983, as in preceding years, the post-larvae of *Pleuragramma antarcticum* were widely distributed over the shelf of the southern and eastern Weddell Sea. Due to the increased water volumes strained by the RMT nets, a higher percentage (94%) of the hauls contained the species than in the bongo-net catches of the earlier years (77% resp. 71%).

The general distribution pattern was similar during the three years of study. High or medium abundances prevailed over the Filchner Depression (Vahsel Bay and Gould Bay) and in certain areas off the Brunt- and Riiser-Larsen Ice Shelves. Maximum abundances of *Pleuragramma antarcticum* larvae in the respective years were 3.7 ind./m^3 (= 500 ind./m^2) in 1980 (Keller 1982); 0.3 ind./m^3 (= 59 ind./m^2) in 1981 (Hubold 1984, in press); and 2.9 ind./m^3 (= 88 ind./m^2) in 1983.

From the three years' observations, a series of hypotheses were derived concerning the special adaptations and apparent reproduction strategies of the Weddell Sea *Pleuragramma antarcticum* population.

Nototheniids, in general, have demersal eggs (Andriashev 1965). Recently, pelagic eggs of nototheniids were caught near South Georgia and Elephant Island in late winter (Heywood 1984). Since *Pleuragramma antarcticum* is in many ways adapted to a pelagic life (Eastman and DeVries 1982), it would not be surprising if they also had pelagic eggs. *Pleuragramma antarcticum* eggs have, however, not yet been found. Suitable sites for demersal spawning may be the shallower areas off Coats Land, Lyddan Isl., and west of Kapp Norvegia, where the bottom rises to less than 200 m water depth at certain places (shallow isobaths are not included in Figs. 1 and 3). At these sites, the ice barrier is grounded and there is no water transport under the ice shield which could endanger the early larval stages. Too little is known about the hydrography of the area to permit speculation on the existence of stable gyres which could serve as "retention areas" for pelagic eggs during winter. Due to the assumable long developmental time of the eggs, such hydrographic structures should be of high stability to prevent transportation of floating eggs into the oceanic parts of the Weddell Sea. The eggs are probably spawned in winter and larvae appear from October to December (Andriashev 1965). Hatching may coincide with the stabilization of the water column in local open water areas during spring. The formation of a continuous coastal polynya usually occurs between December in the northern part (Atka Bay) and January near Drushnaya (as estimated from the accessibility for ice breakers; Strübing 1982).

After hatching, the larvae rise to the surface where they were caught in the upper 50 m layer ("age 00" post-larvae in Figs. 3 and 4). During the first summer, the major portion of the age 0 post-larvae remain near the surface (Fig. 5), where the Warm Summer Water (WSW) with temperatures up to $-0.5\,°C$ and a generally well established stratification provide a stable environment for the plankton. Surface Ekman transport induced by the almost constant katabatic wind field (Mather and Miller 1967) shifts the age 0 post-larvae to the outer edge of the shelf (or to the seaward limit of the polynya).

The slope front probably has a concentrating effect on plankton organisms and the high larval densities over slope depths of 1000 – 1500 m can be explained by this convergence. Increased biomass over the slope front has been observed in the Ross Sea by Ainley and Jacobs (1981). Highest plankton concentrations can be expected in eddies along the frontal zone, which are induced by the bottom topography. Such eddies, although not yet documented for the southeast Weddell Sea, can be expected over the trenches off the Riiser-Larsen- and the Brunt Ice Shelves. The inclination of the deeper isotherms in the trenches (Fig. 3) and a temperature section given by Wegner (1982) indicate the existence of such hydrographic features. The collection of post-larvae in a gyre could account for the high abundance at st. 134 (Fig. 3) and the extremely high density found at 23°30′W/73°S over 1300 m water depth in 1980 (Keller 1982).

A large cyclonic gyre with central upwelling over the Filchner Depression was described by Carmack and Foster (1975) and Gammelsrød and Slotsvik (1981). The gyre may have favored the very intense phytoplankton bloom observed over the trench during the 1983 cruise. The observed homogeneous distribution of *Pleuragramma antarcticum* larvae in Vahsel and Gould Bays may be due to dispersion by the cyclonic water movement. The relative coefficent of variation $V = \frac{s/\bar{x}}{\sqrt{n-1}} 100$ of larval densities was only 15% in this gyre compared to 48% off Coats Land and 55% along the northern ice barrier. The Filchner gyre may represent one large larval retention area in the sense described by Iles and Sinclair (1982), and the front and eddy system off the Riiser-Larsen Ice Shelf another. Both systems are located over deep water and can collect the larvae from neighboring shelves.

The yearly appearance and extension of the coastal polynya is probably the most variable factor in the high Antarctic marine system. Over large potential spawning sites, the fast ice may disappear in some years or remain intact in other years. Variable ice conditions may delay or even prevent local onset of plankton production during the short summer season. At the time of spawning, suitable areas may or may not be available to the fish. Therefore, the occupied spawning sites must match, at least partially, the potential polynya area for the production of a successful yearclass. In 1979/80, a year with an extremely wide open polynya in the southern Weddell Sea, the number of *Pleuragramma antarcticum* postlarvae was 275/bongo haul, i.e. 16 times the value of 1980/81 (17/haul) when ice conditions were severe in Gould Bay (Strübing 1982).

Favorable ice conditions may contribute substantially to the size of the *Pleuragramma antarcticum* population in the Weddell Sea. In regular years, a minimum hatching success can be only achieved by high egg production over all potential spawning sites. A reduction of the spawning stock by commercial fishing may rapidly lead to failure of reproductive success in unfavorable years and endanger the population. High numbers of *Pleuragramma antarcticum* juveniles as by-catch in the krill fishery (Williams, in press) and 1500 t of adults fished in the Pacific sector in 1982 (Anon 1983) are the first reports of human exploitation for this species.

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