

Spatial distribution and inter-annual variations in the size frequency distribution and abundances of *Pleuragramma antarcticum* larvae in the Dumont d'Urville Sea from 2004 to 2010

Philippe Koubbi ^{a,b,*}, Colleen O'Brien ^c, Christophe Loots ^d, Carolina Giraldo ^{a,b},
Martina Smith ^e, Eric Tavernier ^f, Marino Vacchi ^g, Carole Vallet ^{h,i},
Jean Chevallier ^{a,b}, Masato Moteki ^j

^a Université Paris 06, UMR 7093, Laboratoire d'Océanographie de Villefranche, 06230 Villefranche-sur-mer, France

^b CNRS, UMR 7093 Laboratoire d'Océanographie de Villefranche, 06230 Villefranche-sur-mer, France

^c Institute of Antarctic and Southern Ocean Studies, University of Tasmania, Private Bag 49, Hobart TAS 7001, Australia

^d Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER), Laboratoire Ressources Halieutiques, 150 quai Gambetta, BP 699, 62321 Boulogne sur mer, France

^e Spatial Information Science, School of Geography and Environmental Studies, University of Tasmania, Private Bag 76, Hobart TAS 7001, Australia

^f Dpt Génie Biologique, IUT Calais-Boulogne, Bassin Napoléon Quai Masset, BP 120, 62327 Boulogne sur Mer Cedex, France

^g ISPRa, c/o Museo Nazionale dell' Antartide, Università di Genova, Viale Benedetto XV, 5, 16132 Genova, Italy

^h Université du Littoral Côte d'Opale, Laboratoire d'Océanologie et de Géosciences, CNRS, UMR 8187 LOG, 32 Avenue Foch, 62930 Wimereux, France

ⁱ Université d'Artois, Centre IUFM Nord – Pas de Calais, 10 rue Hippolyte Adam, 62230 Outreau, France

^j Faculty of Marine Science, Tokyo University of Marine Sciences and Technology, 4-5-7 Konan, Minato, Tokyo 108-8477, Japan

Received 30 August 2010; revised 25 January 2011; accepted 15 February 2011

Available online 23 February 2011

Abstract

This paper investigates the abundance and distribution of *Pleuragramma antarcticum* larvae by size class in the Dumont d'Urville Sea from 2004 to 2010. Samples were collected between Dumont d'Urville station and the Mertz Glacier Tongue onboard the RV *l'Astrolabe* for studying the inter-annual and spatial distribution of fish larvae and the TRV *Umitaka Maru* for looking at life stages vertical distributions. The seabed depression adjacent to the Mertz Glacier Tongue and in Commonwealth Bay hosted high abundances of small *P. antarcticum* larvae, while larger larvae were found in lower abundance and further offshore. We found that canyons, sea ice, stability of the water column and temperatures are important features for determining suitable areas for young larvae.

© 2011 Elsevier B.V. and NIPR. All rights reserved.

Keywords: *Pleuragramma antarcticum*; East Antarctic shelf; Fish larvae; Life cycle; Inter-annual variations

* Corresponding author. Université Paris 06, UMR 7093, Laboratoire d'Océanographie de Villefranche, 06230 Villefranche-sur-mer, France.
E-mail address: koubbi@obs-vlfr.fr (P. Koubbi).

1. Introduction

Long term synoptic monitoring of polar oceans has always been a challenge and annual mesoscale surveys are rare. In the pelagic zone, while the areas dominated by Antarctic krill (*Euphausia superba*) are quite well studied, monitoring is needed to study the trophic web in the neritic zone. The present study concerns mainly the long term monitoring of *Pleuragramma antarcticum* larvae conducted as part of the multi-annual ICO²TA programme (Integrated Coastal Ocean Observations in Terre Adélie) supported by the French Polar Institute, IPEV (Institut Paul Emile Victor). ICO²TA was a contribution to the Collaborative East Antarctic Marine Census (CEAMARC) part of the Census of Antarctic Marine Life. The ICO²TA programme surveys the Dumont d'Urville Sea between the coast and the margin of the continental shelf, from the vicinity of Dumont d'Urville station (139°E) to the Mertz Glacier Tongue (MGT; 146°E) (Fig. 1). One aim of these surveys was to conduct a regionalisation of this area (Koubbi et al., 2010) which helps to prioritize conservation efforts by determining, for example, Essential Fish Habitat (EFH).

Wasp-waist control was described by Cury et al. (2000) for productive oceanic zones such as upwelling regions. It occurs when there is a large number of species at the lower trophic level (plankton) and large populations of top predators. In between, there is an intermediate trophic level occupied by only few species of small plankton-feeding pelagic species. In the case of the East Antarctic shelf, *P. antarcticum* (Antarctic silverfish) is often considered as a keystone species, much like *E. superba* (Antarctic krill) is for waters beyond the continental shelf (Guglielmo et al., 1998; Fuiman et al., 2002) or *E. crystallophias* (ice

krill) for the neritic zone (Vallet et al., 2009, 2011). It occupies the pelagic niche, as do clupeids in other productive oceans.

P. antarcticum inhabits both open waters and areas of pack ice and can be found from the surface layers to depths of up to 900 m (DeWitt, 1970; Fuiman et al., 2002). This species is the only notothenioid fish in which all stages of development live throughout the water column. Spawning of *P. antarcticum* is thought to occur in late winter-early spring, with eggs hatching in November–December (Vacchi et al., 2004). *P. antarcticum* represents the majority of ichthyoplankton of the neritic zone, sometimes accounting for more than 98% (in abundance) (Guglielmo et al., 1998; Vacchi et al., 1999; Hoddell et al., 2000; Granata et al., 2002; Koubbi et al., 1997, 2009).

Few studies on the distribution of *P. antarcticum* larvae exist in the Dumont d'Urville Sea: one on the coastal zone of the Dumont d'Urville station (140°E) (Koubbi et al., 1997), one including the oceanic zone (Hoddell et al., 2000) and the most recent from Koubbi et al. (2009) describing the spatial distribution of larvae collected in 2004 in the Dumont d'Urville Sea.

The main question is to understand what determines the position of spawning grounds especially for a pelagic species such as *P. antarcticum*. Is it determined geographically or environmentally? How do the larvae disperse from these spawning grounds and what environmental factors influence larval distribution?

2. Materials and methods

2.1. Study area

The Dumont D'Urville Sea is an area of particular interest, because it is very dynamic and is currently

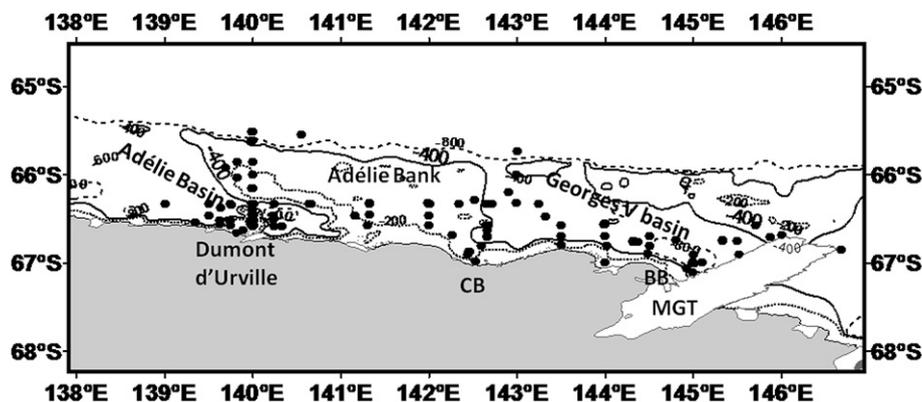


Fig. 1. Location of the stations sampled during the ICO²TA survey since 2004 in the Dumont d'Urville Sea. Along the coastline are marked Dumont d'Urville station, Commonwealth Bay (CB), Buchanan Bay (BB) and the Mertz Glacier Tongue (MGT).

undergoing some significant changes. Two major areas were observed over the shelf during the CEAMARC surveys (Koubbi et al., 2010). The first is to the west of Commonwealth Bay, which has less vertical stratification compared to the second zone to the east of this bay (Fig. 1). Modified Circumpolar Deep Water (MCDW) enters the George V Basin through the sill and follows the eastern side of the basin towards the MGT. The high salinity Shelf Water (HSSW), produced by cooling and sea ice formation in winter, was also found on the eastern side of the basin (deeper than the incoming MCDW) during CEAMARC. Water over the shallow banks was mostly Antarctic surface water (relatively fresh, compared to MCDW and HSSW).

The Mertz Glacier Polynya (MGP), centred on $\sim 67^{\circ}\text{S}$, 145°E , and bays (e.g. Commonwealth Bay) are major sites of the formation of cold, high-density water that contributes to Antarctic Bottom Water (AABW) production, which is globally significant (Massom et al., 2001). The MGP is a seasonally recurrent ice factory, the shape and size of which has been controlled by the Mertz Glacier Tongue (MGT), katabatic winds, weather conditions and the location of very large grounded icebergs and other ice features such as pack ice and sea ice. An important cyclonic gyre transports water within the depression (Williams and Bindoff, 2003).

2.2. Sample collection

Since 2003, the RV *l'Astrolabe* has been adapted for coastal oceanographic surveys with the assistance of IPEV. Data and samples for fish larvae were collected in January from 2004 to 2010 (Fig. 1). Sampling usually started around 9 January except for 2004 and 2007, when surveys started later in January. Time of sampling was linked to the logistics of Dumont d'Urville and Dome C scientific stations. The maximum survey duration was 11 days. Overall, 132 stations were investigated for the study of fish larvae (Table 1), including an area between 139°E – 145°E and $65^{\circ}30'\text{S}$ – 67°S .

The sampling network varied from year to year depending on the weather, sea ice and sea conditions. From 2004 to 2006, location of the westernmost sampling stations was constrained by a study on the foraging of Adélie penguins tracked by Argos.

Other samples collected by the TRV *Umitaka Maru* were used to determine the vertical distribution of life stages and growth rate. Overall, 24 stations were sampled from 29 January to 12 February 2008 from 62°S to 67°S and from 140°E to 145°E .

At each station, a CTD was deployed from the surface to a minimum depth of 200 m (the maximum depth reached by bongo nets for sampling larvae), or close to the seafloor for sites shallower than 200 m, to obtain vertical profiles of temperature and salinity. Temperature and salinity were used to calculate density. Mean values of temperature, salinity and density were calculated for 0–100 m and 100–200 m layers.

An investigation of the inter-annual variability of sea ice concentration (SIC) in the Dumont D'Urville sea area near Terre Adélie for the period 2003–2009 was performed using satellite remotely sensed data. Values for this parameter were determined on a regular spatial grid in the study area for each year of the study from 2003 to 2009. The Aqua Advanced Scanning Radiometer- EOS (AMSR-E) dataset used for this study is derived by Hamburg University (http://ftp-projects.zmaw.de/seaice/AMSR-E_ASI_IceConc/hdf/s6250/). It is the highest resolution (6.25 km) satellite sea ice concentration product available and can be obtained in near real time on a daily basis. For each year, 52 weekly-representative satellite datasets were used. Each of the 52 datasets was processed (using the ArcGIS *Single Output Map Algebra* tool) to produce 52 binary maps for each of three SIC categories; Open Water (0–10% SIC), Transition (10–80% SIC) and Pack Ice (80–100% SIC). The 52 binary maps for each SIC category were then added together (using the ArcGIS *Single Output Map Algebra* tool) to determine the number of weeks at each SIC category for each raster cell. ArcGIS *Zonal Statistics* tool was used to average the raster values for each SIC category within each of the spatial grid squares in the study area. For the present study, only the category corresponding to pack ice was retained.

On the RV *l'Astrolabe*, ichthyoplankton were collected using a double frame 500 μm bongo net (Smith and Richardson, 1977) towed in oblique hauls between 0 and 200 m, at a speed of 2–3 knots. For

Table 1

Dates of the ICO²TA surveys held onboard the RV *l'Astrolabe* in January from 2004 to 2010 in the Dumont d'Urville Sea. The number of stations sampled with a bongo net is also indicated for each year.

Year	Start	End	Number of stations
2004	19/01	28/01	38
2005	10/01	19/01	23
2006	09/01	18/01	24
2007	24/01	01/02	15
2008	10/01	18/01	17
2009	10/01	17/01	15
2010	10/01	21/01	17

each haul, the volume of filtered water was calculated using a flow meter attached to the net. On the TRV *Umitaka Maru*, the different life stages of *P. antarcticum* were collected by an IYGPT (International Young Gadoid Pelagic Trawl) at depths of 50, 200, 500 and 1000 m (Koubbi et al., 2010). Since the mesh size of the net was 100 mm in the front, then tapering progressively from 80 mm to 10 mm mesh size in the cod end, data from young larvae (<30 mm) were not taken into account for this part of the analysis. *P. antarcticum* larvae used in this study were collected using one of the two bongo nets on the RV *Astrolabe*. Samples were preserved in 5% seawater buffered formalin. *P. antarcticum* larvae were identified based on their morphology and pigmentation as described by Kellermann (1990). The total number of larvae identified at each station was recorded to calculate the total abundance of *P. antarcticum* larvae standardized per 100 m³ of filtered water. Standard length (SL) measurements were taken with a calliper under a stereomicroscope for 40–50 larvae, taken randomly from each station, or as many as it was possible to measure for smaller samples. Larvae were allocated to millimetre size classes by rounding SL measurements down to the nearest millimetre. Mean abundance per SL classes was also calculated for each station.

Standard length of juveniles and adults was also measured to the millimetre on a subsample of maximum 50 individuals per each IYGPT catch.

2.3. Data analysis

A Geographic Information System (GIS) (ArcGIS; ESRI) was used to study the spatial pattern of abundances of *P. antarcticum* larvae and environmental conditions. The study area was defined in ArcGIS in a shapefile feature class from Antarctic Digital Database from the Scientific Committee on Antarctic Research (SCAR).

Interpolations using Inverse Distance Weight (with a weight = 2) with the software SURFER were done for studying the yearly variations of temperature, salinity and concentration of pack ice for the study period.

Length–Frequency Distributions (LFD) of the different life stages and their associated growth were studied. The software Statgraphics was used to determine the best linear regression to estimate the daily growth of *P. antarcticum* larvae in January and February. As the maximum duration of surveys was 10 days, measurements from all surveys held on the RV *Astrolabe* from 2004 to 2010 and TRV *Umitaka Maru*

2008 were pooled together for fish larvae analysis. Only samples collected with the TRV *Umitaka Maru* were used for calculating the growth rate of larvae, juveniles and adults.

For each bongo sample, the abundance of larvae per millimetre size class was computed considering LFD and total abundance of larvae. Abundance data was divided amongst 22 size classes. A log ($x + 1$) transformation was applied to the abundance data prior to the analysis. Multivariate analysis of the abundance data was conducted using Correspondence Analysis. Environmental and temporal variables (including sea temperature, salinity, latitude, longitude, day and year) were included as additional variables in the analysis. As both variables (size classes) and observations (stations) had the same weight, they can be represented in the same geometric space due to barycentric projection (Benzéri, 1973). This analysis should allow for detecting any spatial or inter-annual differences in the distribution of the larvae according to their size.

3. Results

3.1. Environmental parameters

The range of temperature and salinity registered in January was narrower in the deep layer (i.e. 100–200 m), with a decreasing trend in temperature until 2009 and a slightly increasing trend in salinity (Fig. 2). The surface layer (0–100 m) also showed major differences between years when considering ranges of temperature and salinity. Ranges of both parameters increased in 2008 and were the highest in 2009. Maximum values of each parameter show that during summer 2005 and 2006, the temperatures were at their lowest maximal values (−0.7 °C). This was also the case for the mean temperatures (−1.06 °C). In 2008, 2009 and 2010, we observed the lowest values of minimum temperature in the surface layer (<−1.28 °C), whereas the maximum temperature attained the highest value. The salinities in the surface layer tended to increase when considering only the maximal and mean values. However, the lowest value was observed in 2009.

Mean values of temperature and salinity for the 0–100 m layer were also plotted according to the longitude (Fig. 3). For temperature, a pattern was observed among years. At longitudes 139°E and 140°E, spatial differences might be due to the latitudinal gradient linked to the sampling design occurring since 2005 from the coast to the shelf break. This problem was limited for the area within 141°E and 146°E as the same

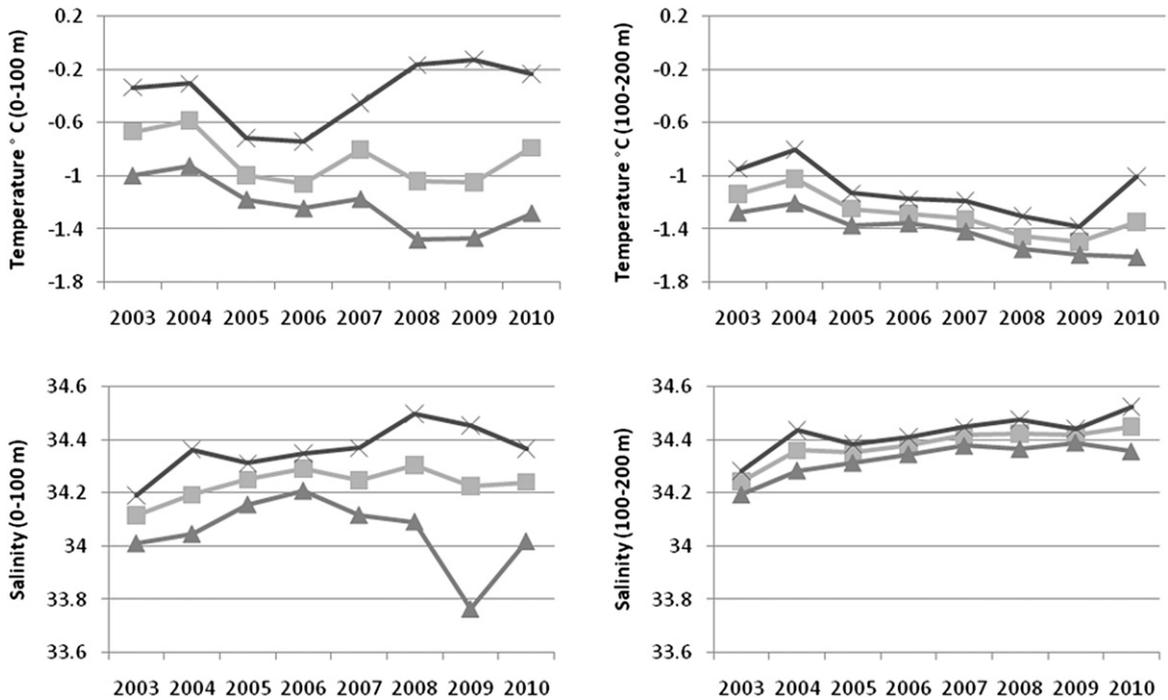


Fig. 2. Mean (squares), minimum (triangles) and maximum (cross) temperatures and salinities measured by CTD in the 0–100 m (left) and 100–200 m layers (right) during the ICO²TA surveys held from 2004 to 2010 onboard the RV *l’Astrolabe* in the Dumont d’Urville Sea.

latitudinal range was sampled every year. The highest values of temperature were observed at the western part of the sampling area and the lowest near the MGT. For all longitudes (except from 143°E–144°E), the trend was towards cooling. Minimum values were observed in 2005, 2006 and 2009. The highest values of temperature and lowest values of salinity were globally observed in 2003 and 2004. Salinities were higher after 2005 for the whole area.

The duration of pack ice cover for years 2003–2009 was expressed as the number of weeks per year with 80–100% of sea ice concentration which corresponds to pack ice (Fig. 4). The pack ice location and coverage varied among years. A global trend towards longer periods of high concentration and shorter periods of low concentration was observed. In 2004, 2006 and 2009, there was less pack ice than in other years. 2008 (the year of the CEAMARC surveys) appeared to be

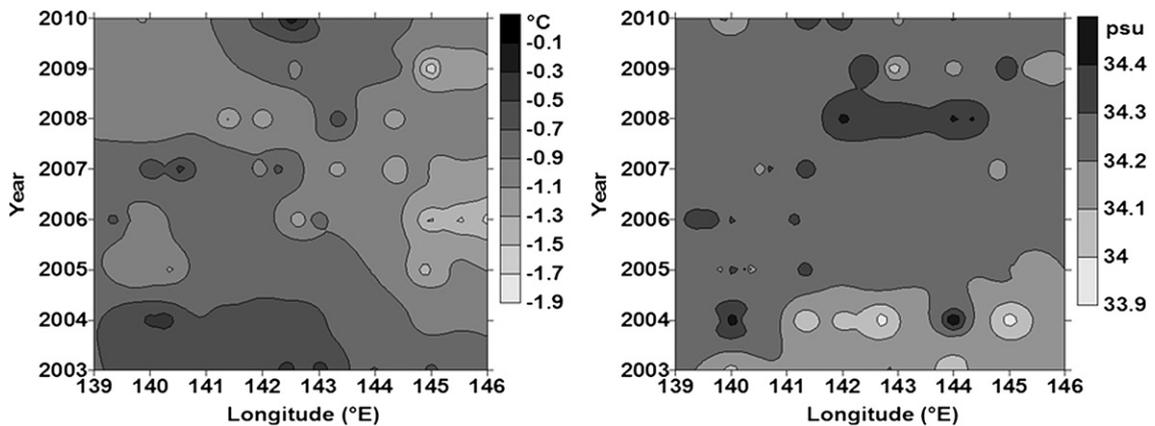


Fig. 3. Time (year) – space (longitude) diagram obtained by interpolation of mean temperature and salinity of the surface 0–100 m layer in January in the Dumont d’Urville Sea.

the year with the longest period of pack ice over the study period. The duration of pack ice cover was lower for MGP (from 144°E to 145°E) than for the rest of the study area. The MGP can be seen as a relatively consistent feature from year to year in terms of its location and extent. However the greatest duration of pack ice for this area was observed in 2008.

Except along 140°E, west of 142°E pack ice duration is highest with at least 30 weeks per year, the maximum observed for this area was in 2005 and 2008.

3.2. Life stages distribution

3.2.1. Larval distribution

Standardized abundances varied from 0 to 3356 larvae per 100 m⁻³, with an average of 63 ± 310 larvae per 100 m⁻³. The map of abundance data from all years of the survey (2004–2010) suggested that the highest larval abundances were found near Commonwealth Bay, alongside the MGT in Buchanan Bay and in the vicinity of the Adélie Basin (Fig. 5). Relatively high abundances were also found close to the coast west of Dumont d'Urville station. Abundances were lower over the shallower waters of the western Adélie Bank.

3.2.2. Length analysis of larvae

A subsample of 2561 larvae was measured to study the size distribution over the years (Table 2). Standard lengths varied from 5 to 27 mm. Plotting size class maximal abundance for all stations sampled between 2004 and 2010 (Fig. 6) revealed that there were some inter-annual variations of abundance. Highest larval abundances were observed in 2005, 2009 and 2010.

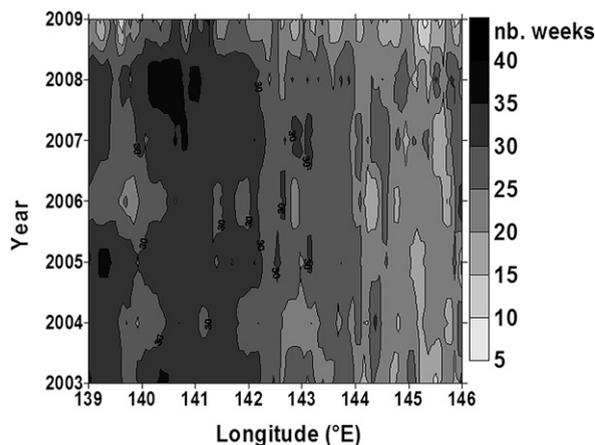


Fig. 4. Time (year) - space (longitude) diagram of number of weeks of pack ice (80–100% sea ice concentration) in the Dumont d'Urville Sea.

While 2005 was the year with the smaller size classes, the years 2004 and 2007 were those with the larger size classes and the lowest larval abundances.

A correspondence analysis was performed to explore size class abundances (20 classes of 1 mm from SL 6 mm–25 mm) for the 125 sampling stations with positive larval catch. The correspondence analysis showed that the first axis accounted for 27.2% of the total variance, with the first two axes accounting together for 41.2%. The correspondence analysis biplot revealed a Gutmann effect, meaning that both axes one and two had a strong influence on the data because of strong environmental gradients influencing them (Figs. 7 and 8).

Plotting the scores of the stations along the first axis according to their longitude revealed three main zones with high scores on this axis (high scores indicate smaller larvae) – one directly offshore from Dumont d'Urville station (140°E), one in Commonwealth Bay (143°E), and another alongside the MGT (145°E) (Fig. 9). Lower scores (i.e. larger larvae) occurred over the Adélie Bank and between Commonwealth Bay and the George V Basin.

Major differences in the abundance size pattern occurred in 2005 and 2006 with the highest scores on axis 1 linked to the smallest larvae (Fig. 10).

Environmental, geographical and temporal variables were projected as supplementary variables onto the first two axes of the analysis (Fig. 11). Larvae sampled later in the month tended to be larger. Inter-annual variations were observed as shown in Fig. 10. Years 2005 and 2006 were on the positive part of axis 1, where higher proportions of small larvae were observed. Years 2004 and 2007 were on the negative part of axis 1, where larvae were larger and this was related to the timing of the sampling. Year 2010 was in the negative part of axis 2 where larvae were of medium size and very abundant.

Geographical location was also a strong indicator of larval size. Smaller larvae tended to be found at higher latitudes and longitudes (i.e. close to the coast and to the east of the study zone) and were more associated with greater depths linked to inner-shelf depressions (positive part of axis 1). Hydrological conditions were represented as the mean values and standard deviations (SD) of temperature, salinity and density at the 0–100 m surface layer and the 100–200 m layer. Mean surface temperature was in the negative part of axis 1 where larger larvae were found. Standard deviation of bottom (linked to axis 1) and surface density (linked to axis 2) was also quite important in this analysis.

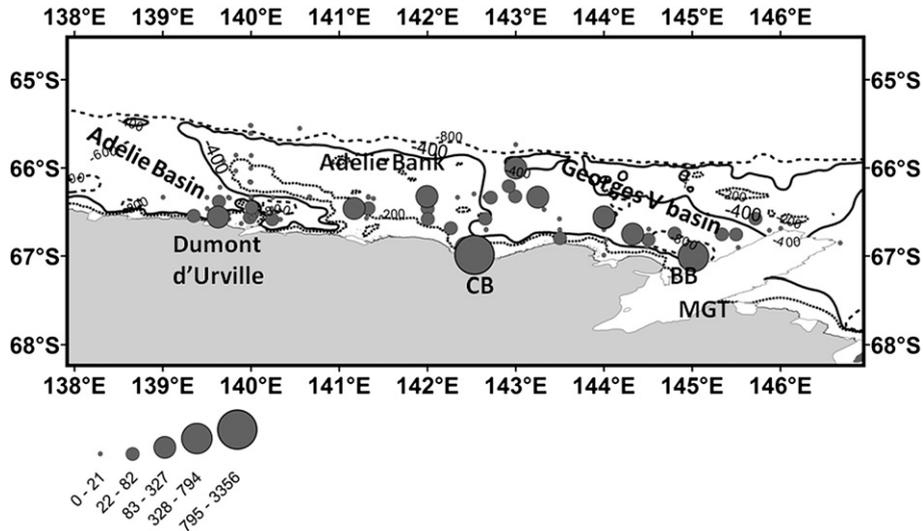


Fig. 5. Spatial distribution of *P. antarcticum* larvae abundance (number of individuals per 100 m³) of all samples from 2004 to 2010 in the Dumont d'Urville Sea.

3.3. Life stages size spectra and growth

Length–frequency distribution of *P. antarcticum* ($n = 1002$) from the Japanese cruise 2007–2008 are presented in Fig. 12. Fish less than 30 mm SL were larvae. Specimens between 30 and 70 mm and 70–110 mm SL were from two size classes of juveniles of age 1 year and those from 70 to 110 mm SL were juveniles of age 2 years. Fish greater than 110 mm SL corresponded to adults.

Size distribution was used to estimate the daily growth of fish larvae. However, because of limited data per year, specimens from the different surveys were pooled together. The growth rate of fish larvae was 0.17 mm SL.d⁻¹ (Fig. 13). Assuming that newly hatched larvae were ~6 mm SL, with a growth rate of 0.17 mm SL.d⁻¹, larvae caught were between 4 and 9

weeks old for the RV *l'Astrolabe* sample and between 8 and 12 weeks old for the TRV *Umitaka Maru* sample. Hatching probably occurred between late-November to mid-December.

The growth rate between 224 larvae (mean size 15.7 mm ± 2.5 mm) caught in 2007 by the RV *l'Astrolabe* and 366 juveniles of the first size mode (mean size 49.2 mm ± 6.0 mm) caught in 2008 by the TRV *Umitaka Maru* was calculated to determine the growth during the first year (Fig. 14). Growth rate was estimated to be 0.08 mm SL.d⁻¹. The linear regression model according to the day of sampling showed a significant relation, with $R^2 = 91.45\%$. Specimens of each size class from the same survey (TRV *Umitaka Maru* 2008) were used to estimate the growth of *P. antarcticum* in this area (Fig. 15). The annual growth rate was estimated to be 39.5 mm SL (0.10 mm SL per day).

Finally, *P. antarcticum* showed a well defined vertical distribution pattern. While small juveniles were present throughout the water column, large juveniles and adults were present only in bottom samples (Fig. 16).

Table 2

Mean size (SL, mm) of *P. antarcticum* larvae collected from 2004 to 2010 in the Dumont d'Urville Sea.

Year	nb. larvae	Mean SL (mm)	Standard dev. SL	Minimum SL (mm)	Maximum SL (mm)
2004	455	15.9	1.7	6	21
2005	209	10.3	2.0	5	21
2006	590	11.9	2.2	6	20
2007	223	15.7	2.5	9	22
2008	391	14.0	1.9	9	20
2009	127	15.5	1.8	11	20
2010	566	14.1	1.7	9	19
Total général	2561	13.8	2.6	5	22

4. Discussion

The size groups identified in this study is comparable to those reported in previous studies and allows determining ages of each of them. In the Weddell Sea, larvae and juveniles between 8 and 25 mm, 30–50 mm and 50–80 mm SL were aged 0, 1 and 2 years old,

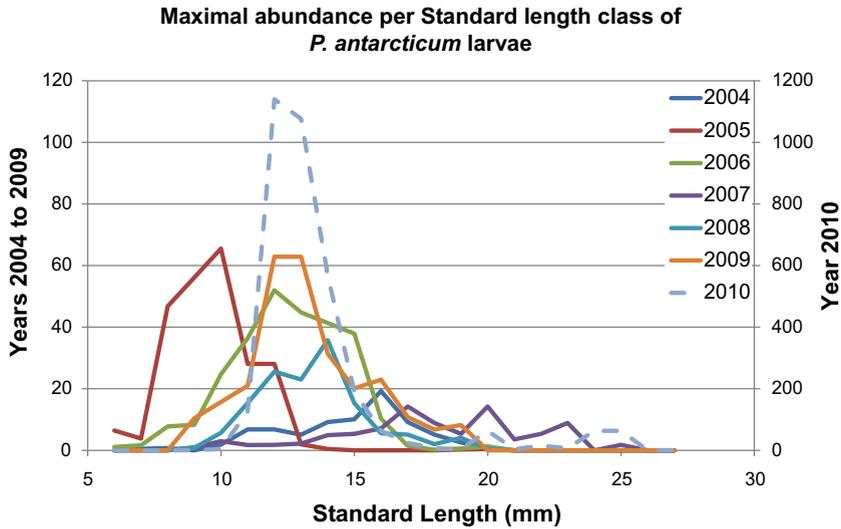


Fig. 6. Maximal abundance (number of individuals per 100 m³) per size class (SL, mm) of *P. antarcticum* larvae in the Dumont d’Urville Sea in the 125 stations with positive catch.

respectively (Hubold, 1985). Larger specimens were defined as adults. Other studies in the Antarctic Peninsula (Liu and Chen, 1995) determined from size frequency distributions that specimens between 26 and 54 mm SL belonged to age group 1 and were 12–13

months old. From the same study individuals between 65 and 82 mm SL were attributed to age group 2. Our results agree with previous studies as fish larvae have lengths <30 mm SL. Juveniles are separated in two groups and the limit between age 1 and age 2 in all

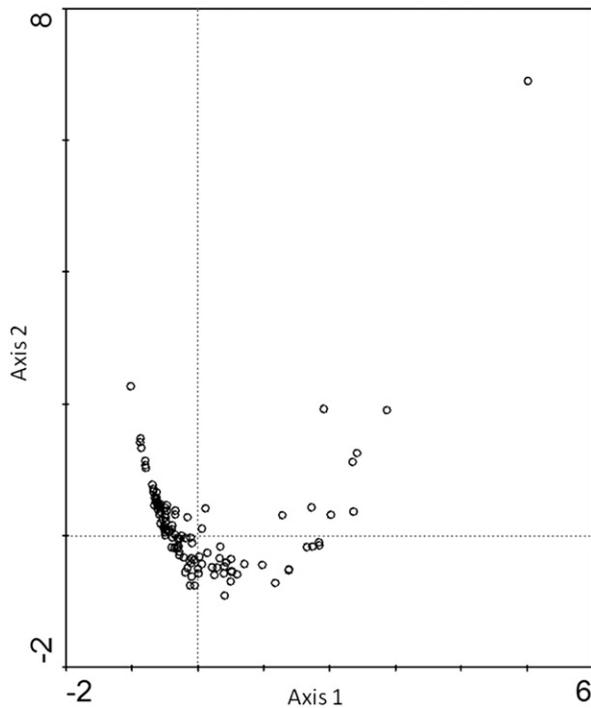


Fig. 7. Correspondence Analysis plot (cloud of observations) including axis 1 and 2.

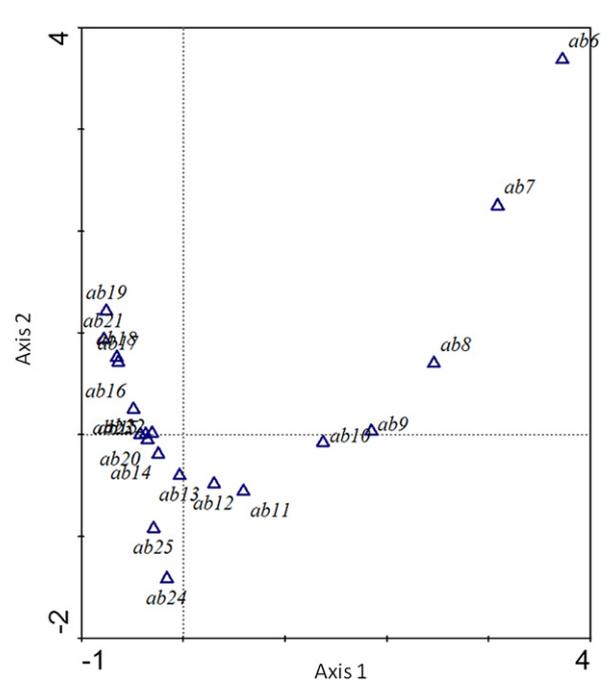


Fig. 8. Plot of size class abundance of *P. antarcticum* larvae in two dimensions, as produced by correspondence analysis. Labels relate to the abundance (ab) of the size class (number) in mm.

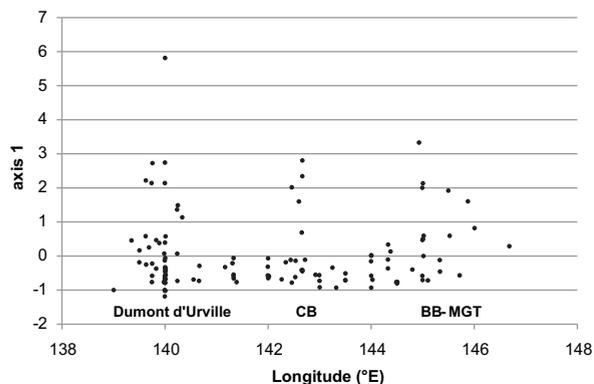


Fig. 9. Plot of the scores of axis 1 with longitudes.

studies is between 50 and 70 mm SL, depending on the study area and period of sampling. The LFD of *P. antarcticum* from TRV *Umitaka Maru* (2008) in relation to sampling depth is in good agreement with results from the Weddell Sea (Hubold, 1984) and the Ross Sea (Granata et al., 2002). Hubold (1985) stated that this strategy of segregation of life stages reduces intra-specific competition.

Combining data from the 2004 to 2010 seasons in the Dumont d'Urville Sea allows us to study the early life history of *P. antarcticum* during the summer period to explore inter-annual variations. *P. antarcticum* has a relatively high fecundity compared to other Antarctic species, with individual absolute fecundity ranging between 4315 and 17,774 eggs (Gerasimchuk, 1987). The larvae experience high rates of mortality as it is reflected by the decreasing abundance of the larger size classes in all years of the study. The high fecundity explains the overwhelming dominance of larvae (>90%) in the samples (Koubbi et al., 1997, 2009), ranging from 0 to 3356 larvae per 100 m⁻³, with an

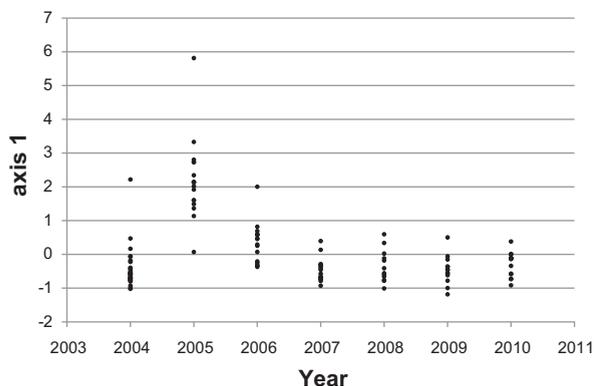


Fig. 10. Plot of the scores of axis 1 with the year of sampling.

average value of 63 ± 310 larvae per 100 m⁻³. The high variability observed among samples would indicate that these larvae live in dense swarms. The other notothenioid fish have generally a different strategy, with fewer offspring per year and, in some cases, parental care (Koubbi et al., 2009).

The geographic and multivariate analysis results support the hypothesis that *P. antarcticum* larvae hatch close to the shore, gradually being carried towards the inner-shelf depression and banks as they increase in size (Hubold, 1984; Koubbi et al., 2009). Larvae caught during these surveys were between 4 and 9 weeks old for those caught in early-mid January and 8–12 weeks old for those caught at the end of January and early February. The hatching date was estimated to take place in late-November and mid-December, in agreement with the results obtained in the Ross Sea (early-mid-December) (Guglielmo et al., 1998).

The size distribution of larvae showed that Buchanan Bay near the Mertz Glacier Tongue and Commonwealth Bay are sites of high larval abundance, and the Adélie Basin seems to be a second site of important larval abundance. This general pattern was observed over the

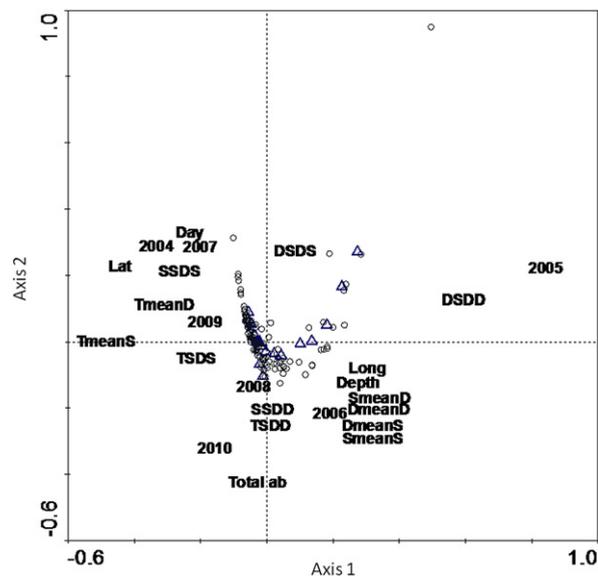


Fig. 11. Supplementary environmental, geographic and time variables used in the analysis represented on the same space as observations and variables. Abundance size class of *P. antarcticum* larvae are shown with triangles and stations in open circles. Years from 2004 to 2010. Day (Julian day), Lat (latitude), Long (longitude), Depth, Total ab (total abundance). Hydrology: T (temperature) or S (salinity) or D (Density) followed by mean or SD (Standard Deviation) and S (0–100 m surface layer) or D (100–200 m deeper layer). TSDD has to be read Standard Deviation of Temperature of the 100–200 m water layer.

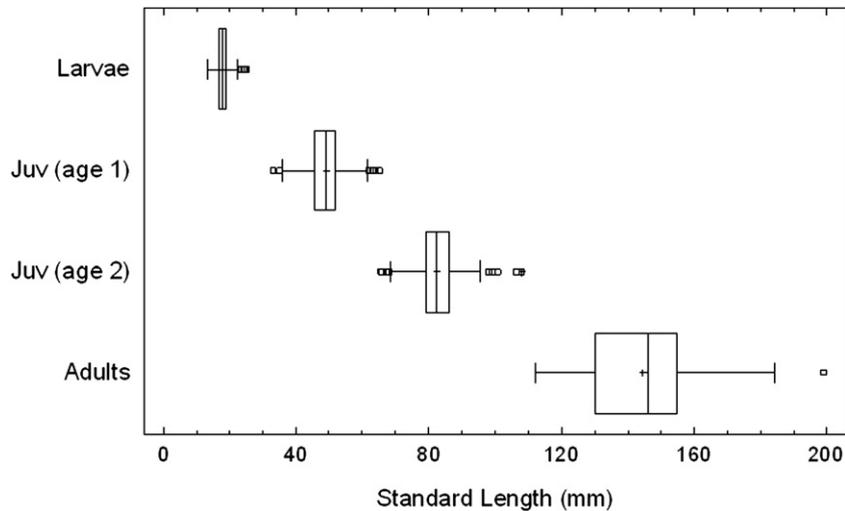


Fig. 12. Box-plot of *P. antarcticum* size classes from the IYGPT samples during the CEAMARC survey onboard the TRV *Umitaka Maru* in the Dumont d'Urville Sea. The left and right bars of the box represent the first and third quartiles, respectively. Therefore, the length of the box equals the interquartile range (IQR). The vertical line inside the box indicates the location of the median. Horizontal lines are drawn from each side of the box and extend to the most extreme observations that are no farther than 1.5 IQRs from the box. Observations farther than 1.5 IQRs from the box are shown as individual points.

years of the study, showing that coastal areas with deep canyons are favourable to the small larvae. This unchanged pattern of larval distribution overtime suggests that homing could be a key mechanism for spawning of *P. antarcticum*. Homing reflects the capacity of fish to return to the same spawning areas from year to year. In geographical homing, i.e. natal homing (Papi, 1992), these areas are determined geographically and fish return to spawn at the same place where they were born. Larval distribution of *P. antarcticum* seems to be geographically determined, as small larvae are preferably found near to the coast whereas larger larvae are located offshore. Recently, environmental homing (Cury, 1994; Baras, 1996) has

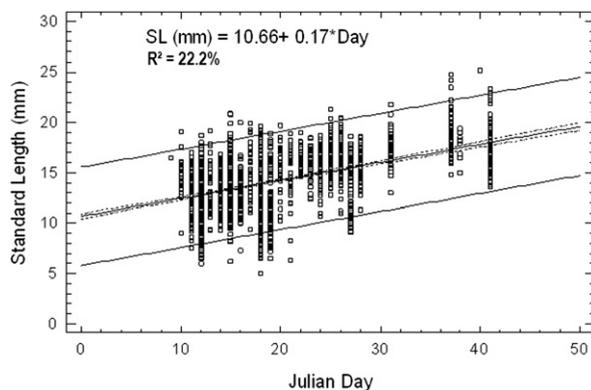


Fig. 13. Daily growth of *P. antarcticum* larvae cumulating all larvae measured from 2004 to 2010 in the Dumont d'Urville Sea. Extremes lines represent the 95% confidence interval with $n = 2748$.

been proposed for anchovy as a generalisation of natal homing, where spawning areas are environmentally determined and fish return to spawn in environmental conditions they experienced at the larval stage (Brochier et al., 2009). Is it the case in sea ice ecosystems dominated by important geographical and oceanographic features like canyons, polynyas and katabatic winds? This strong attachment of adults to their spawning sites may not lead to larvae being released in optimal areas each year, due to inter-annual variations in environmental conditions. However, this might ensure a good larval survival rate over the long term, as it prevents a systematic change in spawning distribution from occurring in response to years of exceptional environmental conditions (Corten, 2002). This conservatism of fish spawning grounds has been demonstrated for North Sea herring, where the knowledge of spawning location is provided by old adults and transmitted across generations by entrainment mechanisms (Petitgas et al., 2006). While this may lead to innovative spawning behaviour in distribution pattern in case of strong year class, this may also create a time lag in the detectable impact of long term environmental change on spawning distribution (Corten, 2002). However, this attachment to spawning grounds for *P. antarcticum* still has to be confirmed by genetic studies.

Coastal canyons are known to be favourable for spawning grounds and young larval development. This is the case for the subantarctic zone, for example the Kerguelen Islands, where fjords and bays are known to

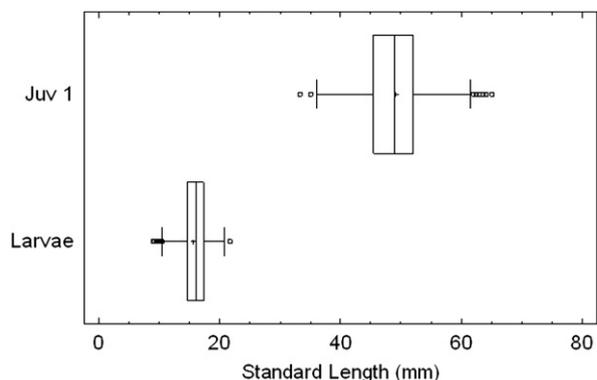


Fig. 14. Box-plot of standard length of larvae (summer 2007) and juveniles of age 1 (summer 2008) of *P. antarcticum* in the Dumont d'Urville Sea.

be very productive because of the presence of coastal gyres in stratified and sheltered areas (Koubbi et al., 2001). Some species, like the icefish *Champsocephalus gunnari*, the dominant pelagic fish of this area, have some of their spawning grounds in such canyons. The topography of a canyon provides many sheltered areas if the larvae are close to the bottom. Near Dumont d'Urville station (Koubbi, unpublished results), we observed large and dense swarms of larvae near the bottom and particularly in or nearby canyons.

Beside geography, are there some common environmental similarities among the potential spawning grounds and will their environmental differences help us

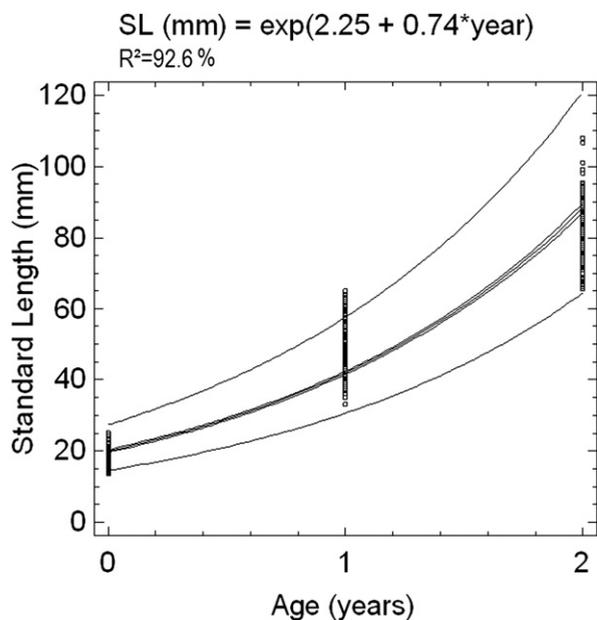


Fig. 15. Growth of *P. antarcticum* considering larvae and juveniles of age 1 and 2 years in the Dumont d'Urville Sea.

to determine the most suitable ones for *P. antarcticum* fish larvae? Several records in the 90 s of early stages of *P. antarcticum* in the Ross and Weddell seas in waters adjacent to the continental ice shelves suggest that *P. antarcticum* larvae are associated with sea ice early in their life history (Kellermann, 1986). More recently *P. antarcticum* eggs have been found within the sea ice in the Ross Sea (Vacchi et al., 2004; Bottaro et al., 2009), and young larvae are often found close to areas of sea ice. Our results show that young larvae are located near polynyas, with the major one being the MGP as shown by the analysis of sea ice. This is a large and permanent polynya observed every year with slight inter-annual differences. The second polynya influencing young larvae is located on the shelf at 140°E, but the intensity of this one varies between years. The MGP accounts for only 0.001% of the total sea ice area in Antarctica, but it is responsible for 1% of total annual sea ice production (Tamura et al., 2008). Antarctic sea ice provides a habitat for a range of organisms such as grazers, and is a site of enhanced primary production during winter that is favourable to the development of young larvae. Indeed, larvae seem to be omnivorous, mainly foraging on phytoplankton and copepods (Koubbi et al., 2007; Vallet et al., 2011; Mayzaud et al., 2011).

The multivariate analysis showed that standard deviation of density seemed to be an important factor for explaining young larval abundances. The standard deviation is a way of determining if the water column was stratified or not. In this study, areas of greater differences in density are found in the eastern part of the surveyed area from Commonwealth Bay to the MGT. The MGP and Commonwealth Bay have been

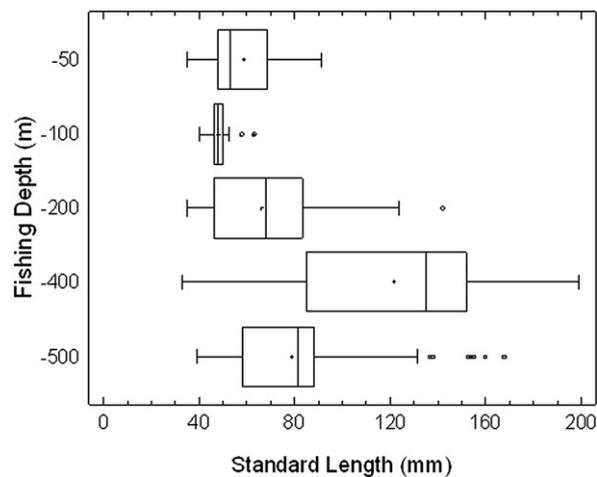


Fig. 16. Box-plot of SL of juveniles and adults of *P. antarcticum* in relation to the fishing depth in the Dumont d'Urville Sea.

separately identified by Massom et al. (2001) as major sites of the formation of cold, high-density water that contribute significantly, on a global scale, to Antarctic Bottom Water (AABW) production. We can estimate that the differences between the eastern and the western part of the study area in terms of stratification is constant but can be changed occasionally according to storms and katabatic winds which are frequent and strong in this area. If water stability is important for young larvae, these differences of water stratification between areas where the young larvae were found can explain why higher abundances were observed in the MGP than in 140°E.

The transport of larvae from the ice edge to the shelf break is probably influenced by the strong katabatic winds in the area, as suggested for *P. antarcticum* larvae in the Weddell Sea (Hubold, 1984). An important gyre transport of waters within the George V Basin allows some retention of larvae in this area. However, this is not sufficient as larvae are also found on the Adélie Bank and in the Adélie Basin. Even older larvae are less abundant north of the Adélie Basin. This shows the importance of having some retention process either linked to the topography (canyons) or to the circulation. Environmental conditions studied in the multivariate analysis show the importance of the surface temperature and its relationship to areas with the most suitable trophic conditions for larger larvae. The shelf break is generally associated with a high concentration of biological activity, and presumably provides a rich food source for developing *P. antarcticum*. The larval growth rate found in this study ($0.17 \text{ mm SL.d}^{-1}$) is comparable to the Western Ross Sea ($0.10\text{--}0.20 \text{ mm SL.d}^{-1}$) (Granata et al., 2009). However, these values are slightly lower than the growth rates of $0.24 \text{ mm SL.d}^{-1}$ found in the Weddell Sea (Keller, 1983; Hubold, 1985) or $0.32 \text{ mm SL.d}^{-1}$ of the Antarctic Peninsula (Kellermann, 1986). These results suggest differences in larval growth between areas of the Southern Ocean, as already postulated by Radtke et al. (1993) or Granata et al. (2009).

Average growth rates between developmental stages show that during the first year of life this rate is about $0.08 \text{ mm SL.d}^{-1}$. The same growth value was determined in the Ross Sea (Guglielmo et al., 1998). Differences between stages are around 30–40 mm SL for the first two years of life, so the average growth rate per day would be between 0.08 and $0.10 \text{ mm SL.d}^{-1}$. Differences between the growth rate estimated for fish larvae during summer ($0.17 \text{ mm SL.d}^{-1}$) and those calculated per year (equivalent of $0.8\text{--}0.10 \text{ mm SL.d}^{-1}$), reflect seasonal and age variations in growth rate. It has been

suggested that the growth increment of Antarctic fishes is linked to the period of the year when their energy intake from food is in excess of their daily energetic requirements. Probably there is a cyclic growth patterns with increased growth rates during the peak of phytoplankton production (White, 1977) leading to a less important growth rate in winter compared with summer.

Antarctic marine ecosystems are strongly linked to the dynamic, seasonal variability of sea ice advance and retreat (Massom and Stammerjohn, 2010). The trend in sea ice concentration (SIC) over the study period 2003 to 2009 was towards longer periods of high sea ice concentration and shorter periods of low sea ice concentration. Not all polynyas in this area respond the same way to inter-annual variations, the MGP is more stable than that on 140°E. As the surveys (except in 2004 and 2007) occurred more or less at the same time of year, we can compare abundance patterns linked to larval size. We showed some important differences between 2005, 2006 and the other years. The size distribution of larvae for these surveys, particularly for 2005, was shifted towards the smaller size, with 4–5 mm less in SL average than the other surveys. The temperatures observed during these two years were colder, which can explain a delay in the larval development. Another explanation is that the pack ice duration was maximum in 2005. Clarke (1980, 1988) has suggested that food availability rather than temperature may usually limit the growth of polar marine ectotherms. Longer pack ice duration could reduce the intensity of light. In these conditions, food quality is believed to be poorer (Clarke, 1988; Hagen, 1988). A combination of these factors probably reduces the food energy intake of fish larvae leading to a slower growth rate.

In light of events occurred in February 2010, when the MGT released a massive ~ 80 by ~ 40 km iceberg, it is very likely that significant changes will occur in the area west of where the former MGT was located, including the changes to the MGP sea ice factory. The implications for marine ecosystems in this region as a result of such regional changes will be significant in terms of sea ice and Antarctic Bottom Water formation, stability of the water mass and circulation pattern. All these parameters were found to be important for the early life stages of *P. antarcticum*, as they provided stability, production of suitable preys and a circulation pattern favourable to the retention of larger larvae over the shelf.

As *P. antarcticum* plays a key role in the wasp-waist control of the pelagic ecosystem of the Dumont d'Urville Sea, this species can be considered as an indicator of the future changes that may occur in this area.

Acknowledgements

This study was conducted onboard the RV *l'Astrolabe* and TRV *Umitaka Maru*. Colleen O'Brien was part of an exchange between the University of Tasmania and Université Pierre et Marie Curie organised through the International Antarctic Institute. This study is funded by Institut Polaire Émile Victor (IPEV), Zone Atelier Antarctique, ANR Glides and ANR Antflocks. This research would not have been possible without the logistic help of Alain Pottier, Alain Pierre and Patrice Godon from IPEV. We want to thank the captains and crew of the RV *l'Astrolabe* and TRV *Umitaka Maru*, the Belgian team linked to PELAGANT and PADI projects, the cadets of TRV *Umitaka Maru* and the volunteers in Dumont d'Urville who participated in the project. We would like to thank Florian Penot and Emmanuelle Sultan for processing the CTD data.

References

- Baras, E., 1996. Commentaire à l'hypothèse de l'éternel retour de Cury (1994): proposition d'un mécanisme fonctionnel dynamique. *Can. J. Fish. Aquat. Sci.* 53, 681–684.
- Benzéri, J.P., 1973. *L'analyse des données*. Dunod, Paris.
- Bottaro, M., Oliveri, D., Ghigliotti, L., Pisano, E., Ferrando, S., Vacchi, M., 2009. Born among the ice: first morphological observations on two developmental stages of the Antarctic silverfish *Pleuragramma antarcticum*, a key species of the Southern Ocean. *Rev. Fish. Biol.* 19, 249–259.
- Brochier, T., Colas, F., Lett, C., Echevin, V., Cubillos, L.A., Tam, J., Chlaida, M., et al., 2009. Small pelagic fish reproductive strategies in upwelling systems: a natal homing evolutionary model to study environmental constraints. *Prog. Oceanogr.* 83, 261–269.
- Clarke, A., 1980. A reappraisal of the concept of metabolic cold adaptation in polar marine invertebrates. *Biol. J. Linn. Soc.* 14, 77–92.
- Clarke, A., 1988. Seasonality in the Antarctic marine environment. *Comp. Biochem. Physiol.* 90B, 461–473.
- Corten, A., 2002. The role of "conservatism" in herring migrations. *Rev. Fish Biol. Fish.* 11, 339–361.
- Cury, P., Bakun, A., Crawford, R.J.M., Jarre-Teichmann, A., Quiñones, R.A., Shannon, L.J., Verheye, H.M., 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. *ICES J. Mar. Sci.* 57, 603–618.
- Cury, P., 1994. Obstinate nature: an ecology of individuals. Thoughts on reproductive behaviour and biodiversity. *Can. J. Fish. Aquat. Sci.* 51, 1664–1673.
- DeWitt, H.H., 1970. The character of the midwater fish fauna of the Ross sea, Antarctica. In: Holdgate, M.W. (Ed.), *Antarctic Ecology*, vol. I. Academic Press, London, pp. 305–315.
- Fuiman, L.A., Davis, R.W., Williams, T.M., 2002. Behavior of midwater fishes under the Antarctic ice: observations by a predator. *Mar. Biol.* 140, 815–822.
- Gerasimchuk, V.V., 1987. On the fecundity of the Antarctic silverfish *Pleuragramma antarcticum*. *J. Ichthyol.* 28, 98–100.
- Granata, A., Cubeta, A., Guglielmo, L., Sidoti, O., Greco, S., Vacchi, M., La Mesa, M., 2002. Ichthyoplankton abundance and distribution in the Ross sea during 1987–1996. *Polar Biol.* 25, 187–202.
- Granata, A., Zagami, G., Vacchi, M., Guglielmo, L., 2009. Summer and spring trophic niche of larval and juvenile *Pleuragramma antarcticum* in the Western Ross sea, Antarctica. *Polar Biol.* 32, 369–382.
- Guglielmo, L., Granata, A., Greco, S., 1998. Distribution and abundance of postlarval and juvenile *Pleuragramma antarcticum* (Pisces, Nototheniidae) off Terra Nova bay (Ross sea, Antarctica). *Polar Biol.* 19, 37–51.
- Hagen, W., 1988. On the significance of lipids in Antarctic zooplankton. *Ber. Polarforsch.* 49, 1–129.
- Hoddell, R.J., Crossley, A.C., Williams, R., Hosie, G.W., 2000. The distribution of Antarctic pelagic fish and larvae (CCAMLR Division 58.4.1). *Deep-Sea Res. II* 47, 2519–2542.
- Hubold, G., 1984. Spatial distribution of *Pleuragramma antarcticum* (Pisces: Nototheniidae) near the Filchner and Larsen ice shelves (Weddell sea/Antarctica). *Polar Biol.* 3, 231–236.
- Hubold, G., 1985. The early life-history of the high-Antarctic silverfish *Pleuragramma antarcticum*. In: Siegfried, W.R., Condy, P.R., Laws, R.M. (Eds.), *Antarctic Nutrient Cycles and Food Webs*. Springer, Berlin, pp. 445–451.
- Keller, R., 1983. Contributions to the early life history of *Pleuragramma antarcticum* Boul. 1902 (Pisces, Notothenioidei) in the Weddell sea. *Meersforsch.* 30, 10–24.
- Kellermann, A., 1986. Geographical distribution and abundance of postlarval and juvenile *Pleuragramma antarcticum* (Pisces, Notothenioidei) off the Antarctic Peninsula. *Polar Biol.* 6, 111–119.
- Kellermann, A., 1990. Identification key and catalogue of larval Antarctic fishes. *Ber. Polarforsch.* 67, 1–136.
- Koubbi, P., Duhamel, G., Hebert, C., 2001. Seasonal relative abundance of fish larvae inshore at Iles Kerguelen, Southern ocean. *Antarct. Sci.* 13, 385–392.
- Koubbi, P., Duhamel, G., Hecq, J.-H., Beans, C., Loots, C., Pruvost, P., Tavernier, E., Vacchi, M., Vallet, C., 2009. Ichthyoplankton in the neritic and coastal zone of Antarctica and Subantarctic islands: a review. *J. Mar. Syst.* 78, 547–556.
- Koubbi, P., Hureau, J.-C., Vacchi, M., White, M., 1997. Results of the preliminary survey on the coastal distribution of fish larvae in Adelie land (Southern Ocean) during January–February 1996. *Cybiurn* 21, 381–392.
- Koubbi, P., Ozouf-Costaz, C., Goarant, A., Moteki, M., Hulley, P.A., Causse, R., Dettai, A., Duhamel, G., Pruvost, P., Tavernier, E., Post, A., Beaman, R.J., Rintoul, S., Hirawake, T., Hirano, D., Ishimaru, T., Riddle, M., Hosie, G., 2010. Estimating the biodiversity of the east Antarctic shelf and oceanic zone for ecoregionalisation: example of the ichthyofauna of the CEAMARC (collaborative east Antarctic marine census) CAML surveys. *Polar Sci.* 4, 115–133.
- Koubbi, P., Vallet, C., Razouls, S., Grioche, A., Hilde, D., Courcot, L., Janquin, M.A., Vacchi, M., Hureau, J.-C., 2007. Condition and diet of larval *Pleuragramma antarcticum* from Terre Adélie (Antarctica) during summer. *Cybiurn* 31 (1), 67–76.
- Liu, Q., Chen, D.G., 1995. Length frequency analysis of *Pleuragramma antarcticum*, *Electrona antarctica*, *Protomyctophum bolini*. *Chin. J. Oceanol. Limnol.* 13, 380–384.
- Massom, R.A., Hill, K.L., Lyttle, V.I., Worby, A.P., Allison, I., 2001. Effects of regional fast-ice and iceberg distribution on the behavior of the Mertz Glacier polynya. *East Antarctica. Ann. Glaciol.* 33, 391–398.
- Massom, R.A., Stammerjohn, S.E., 2010. Antarctic Sea ice change and variability- Physical and Ecological implications. *Polar Sci.* 4, 149–186.

- Mayzaud, P., Chevalier, J., Tavernier, E., Moteki, M., Koubbi, P., 2011. Lipid composition of the high Antarctic fish *Pleuragramma antarcticum*. Influence of age class. *Polar Sci.* 5 (2), 264–271.
- Papi, F., 1992. *Animal Homing*. Chapman & Hall, London.
- Petitgas, P., Reid, D., Planque, B., Nogueira, E., O’Hea, B., Cotano, U., 2006. The Entrainment Hypothesis: An Explanation for the Persistence and Innovation in Spawning Migration and Life Cycle Patterns ICES CM 2006/B:07.
- Radtke, R.L., Hubold, G., Folsom, S.D., Lenz, P.H., 1993. Otolith structural and chemical analyses: the key to resolving age and growth of the Antarctic silverfish, *Pleuragramma antarcticum*. *Antarct. Sci.* 5, 51–62.
- Smith, P.E., Richardson, S., 1977. Standard Techniques for Pelagic Fish Eggs and Larval Surveys. FAO Fish. Tech. Pap. 175, 8–16.
- Tamura, T., Ohshima, K.I., Nihashi, S., 2008. Mapping of sea ice production for Antarctic coastal polynyas. *Geophys. Res. Lett.* 35 (L07606), 5. doi:10.1029/2007GL032903.
- Vacchi, M., La Mesa, M., Dalu, M., Macdonald, J., 2004. Early life stages in the life cycle of Antarctic silverfish, *Pleuragramma antarcticum* in Terra Nova bay, Ross sea. *Antarct. Sci.* 16, 299–305.
- Vacchi, M., La Mesa, M., Greco, S., 1999. Summer distribution and abundance of larval and juvenile fishes in the western Ross sea. *Antarct. Sci.* 11, 54–60.
- Vallet, C., Beans, C., Koubbi, P., Courcot, L., Hecq, J.H., Goffart, A., 2011. Food preferences of larvae of Antarctic Silverfish *Pleuragramma antarcticum* Boulenger, 1902 from Terre Adélie coastal waters during summer 2004. *Polar Sci.* 5 (2), 239–251.
- Vallet, C., Koubbi, P., Sultan, E., Goffart, A., Swadling, K.M., Wright, S.W., 2009. Distribution of euphausiid larvae along the coast of east Antarctica in the Dumont d’Urville sea (139–1458E) during summer 2004. *Antarct. Sci.* 21, 197–207.
- Vallet, C., Labat, J.-P., Smith, M., Koubbi, P., 2011. Interannual variations in Euphausiid life stage distribution in the Dumont d’Urville Sea from 2004 to 2008. *Polar Sci.* 5 (2), 166–178.
- White, M.G., 1977. Ecological adaptations by Antarctic poikilotherms to the polar marine environment, in: Llano, G.A. (Eds.), *Adaptations Within Antarctic Ecosystems*. In: *Proceedings of the Third SCAR Symposium on Antarctic Biology*, Washington D.C., U.S.A., pp. 197–208.
- Williams, G.D., Bindoff, N.L., 2003. Wintertime oceanography of the Adélie depression. *Deep-Sea Res. Part II* 50, 1373–1392.

