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Food preferences of larvae of Antarctic silverfish *Pleuragramma antarcticum* Boulenger, 1902 from Terre Adélie coastal waters during summer 2004

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Abstract

Ichthyoplankton samples were collected from 19 to 31 January 2004 in the Dumont d'Urville Sea (East Antarctic shelf). The Nototheniidae *Pleuragramma antarcticum* comprised more than 90% of the sampled larvae. Gut contents of 95 *P. antarcticum* larvae were examined. Most larvae fed on phytoplankton, especially diatoms, whereas some other specimens had a mixed diet with phyto- and zooplankton prey. A single specimen fed exclusively on copepods. The stomach contents was dominated by three diatoms taxa, such as *Thalassiothrix antarctica*, *Fragilariopsis* spp. and *Chaetoceros* spp. Prey selection was apparently food density dependent, with an inverse relationship between food abundance and selection feeding. Larvae selected positively some diatoms, such as *Coscinodiscus* spp. and *T. antarctica*, presenting a low concentration in the water column compared to *Fragilariopsis* spp., which were strongly negatively selected. During summer, larvae were opportunistic feeders with a broad trophic niche, which allowed them to switch between different food types.

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1. Introduction

The Antarctic silverfish *Pleuragramma antarcticum* belongs to the important nototheniid family and is the most abundant pelagic fish with a circum-antarctic distribution (De Witt and Hopkins, 1977; Hubold and Ekau, 1987; Wöhrmann et al., 1997). This pelagic fish

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is considered to be a possible key species in the food web of continental shelf waters (Fuiman et al., 2002; La Mesa et al., 2004) where adults are eaten by seals (crab-eater, Weddell and fur seals), penguins (emperor, gentoo, Adélie) as well as other species of fish (*Chionodraco hamatus*, *Cryodraco antarcticus*, *Neopagetopsis* spp., *Dissostichus mawsoni*) (Casaux et al., 2003; Cherel and Kooyman, 1998; Daneri, 1996; Daneri and Carlini, 2002; Fuiman et al., 2002; Knox, 1994; Miller, 1993). There is also a high predation pressure on larvae and post-larvae, which are usually eaten by seabirds (snow petrel *Pagodroma nivea*), post-larvae and juveniles of other fish (*Chionodraco myersi*) and even occasionally by adult *P. antarcticum* (Hubold, 1990; Kellermann, 1991; Miller, 1993). In spite of its important trophic role in Antarctic ecosystem and its large distribution in ichthyoplankton at many locations around Antarctica (Koubbi et al., 1997, 2007, 2009; Morales-Nin et al., 1998), their larval survival conditions are poorly understood. Gut analyses of larval and juvenile *P. antarcticum* in different Antarctic areas revealed a mixed diet of several different zooplanktonic taxa, such as eggs and larvae of euphausiids, copepods, amphipods, *Limacina helicina* and tintinnids (De Witt and Hopkins, 1977; Kellermann, 1987; North, 1991; North and Kellermann, 1990). However, observations of diatoms in gut contents of *P. antarcticum* are rare, except during the 1996 ichthyoplankton survey in Terre Adélie, where diatoms were their common food (Koubbi et al., 2007, 2009). Often, gut contents of larval fish are observed by stereomicroscope which is not appropriate to observe phytoplankton (Kellermann, 1987). Consequently, Scanning Electron Microscope

(SEM), already used to perform study on gut microflora (Jolly et al., 1993; Mendez et al., 2003), has also been used to study gut contents of *P. antarcticum* (Koubbi et al., 2007). This method enables determination of the vacuity of larval fish guts and diet composition more precisely. Applying this method, Koubbi et al. (2007) concluded that larvae of *P. antarcticum* are not simply carnivorous, as previously thought (Kellermann, 1987), but omnivorous. Moreover, Kellermann (1987) demonstrated that larvae and juveniles of *P. antarcticum* could select their zooplanktonic prey. Because grazing on phytoplankton has been reported by Koubbi et al. (2007), one of the main question is to know whether larvae of *P. antarcticum* also actively select phytoplankton. To answer to this question, it is necessary to examine the larval diet and the food availability in the natural environment, especially phytoplankton abundance. This study presents data on diet, feeding strategy and food preferences of larvae of *P. antarcticum* in the Dumont d'Urville Sea.

2. Materials and methods

2.1. Field sampling

The survey took place onboard the French RV *l'Astrolabe* from 19 to 31 January 2004 across the area 139°–145°E (Fig. 1), which corresponds with the Collaborative East Antarctic Marine Census (CEA-MARC) survey area of 2007/08. It is a part of the ICO²TA French project (Integrated Coastal Ocean Observations in Terre Adélie). The area was free of sea

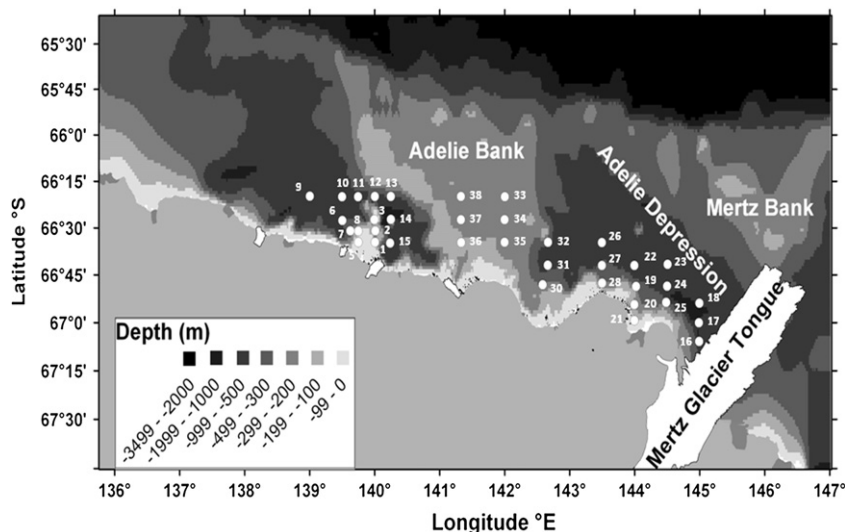


Fig. 1. Locations of sampling stations during the 2004 survey (data source: ETOPO2v2. NOAA. GDC).

ice, while icebergs were only observed around the glaciers. Eleven transects were carried out, generally set northward for a maximum of 20 nautical miles, based on sea ice conditions or navigational safety constraints. Overall 38 stations were sampled (Fig. 1), of which 15 in the Astrolabe basin (zone 1), were selected to sample the foraging area of Adélie penguins, which feed their chicks at the colony near Dumont d'Urville station (from station 1 to 15), nine on the Adélie bank (from 30 to 38, zone 2), and 14 in the Adélie depression (from stations 16 to 29, zone 3). Each zone was defined by Beans et al. (2008) in relation to diatom assemblages.

Niskin bottles were used to sample water at different depths for each station (approximately 5 m, 25 m, 75 m and 150 m) to study concentrations of oxygen, nutrients, total carbon and nitrogen, photosynthetic pigments and abundance in the microplankton community (Beans et al., 2008).

Vertical hauls of a WP2 net of 200 µm mesh size were made at each station down to 200 m depth, to catch zooplanktonic organisms such as copepods, eggs, amphipods and *Limacina helicina*.

Macroplankton samples were collected in 37 stations out of 38 by oblique tows of a double-framed bongo net with 500 µm mesh and 60 cm mouth diameter (Smith and Richardson, 1977). Station 29 was excluded from analyses as we could not sample there due to rough sea conditions. Tows were carried out at a speed of 2 knots from the surface to the sea bed at a maximum depth of 200 m. The volume of water filtered by each net was measured with a Hydro-Bios flowmeter and used to calculate standardized ichthyoplankton abundances. Samples were fixed immediately onboard with 5% neutral formalin in seawater.

2.2. Diet

In the laboratory, fish larvae were sorted, identified according to Kellermann (1990) and counted under a stereomicroscope. For each station, a maximum of five specimens were randomly selected for dissection. Total length of larvae was measured to the nearest 0.1 mm with a digital caliper. The whole digestive tract was removed from the fish larvae under a stereomicroscope and opened. The gut contents of larvae were analysed using a stereomicroscope and also using a Scanning Electron Microscope (SEM) to better identify small microplanktonic individuals when they were present. Large prey were identified when the state of digestion was not too advanced. Food items of each specimen were rinsed in Milli-Q water (Millipore). Each gut content was filtered

on 0.2 µm filter (Millipore polycarbonate) put on a carbon tape attached to a metal stub (25 mm diameter). Stubs were dried under laminar flow hood during 24 h. After drying, stubs were palladium-gold-coated (Polaron SC7620) and observed with a LEO SEM (438VP). Microplankton genus identification was made according to Scott and Marchant (2005). The valve diameter of the centric diatoms, the length of the pennate diatoms and the diameter of the silicoflagellates were measured using an image analyser LEO32, with an accuracy of 0.01 µm. The length of the diatoms of the genus *Thalassiothrix* could not be measured because the cells in the gut were broken. Thus, for this genus, only the width was measured. The individual length of this genus is usually 420–5680 µm (Scott and Marchant, 2005).

Data were pooled and the number of food items (n), the fraction of a food item in the gut (r), and the frequency of occurrence in guts containing food item expressed as percentage (O) were calculated for each taxon. Feeding incidence refers to the percentage of guts that contained at least one food item.

2.3. Feeding strategy

To determine the feeding strategy of larvae, the modified Costello graphical method (Amundsen et al., 1996) was used. In this graphical method, the prey-specific abundance was calculated as follows:

$$P_i = \left(\frac{\sum S_i}{\sum S_r} \right) \times 100 \quad (1)$$

where P_i is the food item-specific abundance of food item i , S_i the number of gut contents composed of food item i , and S_r the total number of food items in all guts.

The food item-specific abundance was plotted against the occurrence in guts containing food items (O), providing a two-dimensional diagram (Amundsen et al., 1996). The interpretation of the diagram (food item importance, feeding strategy and niche breadth) can be obtained by examining the distribution of points along the diagonals and the axes of the graph. The food item importance was represented in the diagonal from lower left (rare food item) to upper right (dominant food item). The vertical axis represents the feeding strategy of the predator in terms of specialisation or generalisation. Predators have specialised on food items if positioned in the upper part of the graph, while food items positioned on the lower part have been eaten only occasionally (generalisation). As for niche breadth, a population with a high between-phenotype component, as different

individuals specialize on different resources types, was characterized by food item points located at the upper left of the diagram, whereas a population with a high within-phenotype component, that is most individuals utilize many resource types simultaneously, was characterized by prey points located at the lower right of the diagram.

2.4. Food selection

A number of indices are available to measure selective feeding. Jacobs (1974) proposed an index to analyse feeding habits and food preference. This selectivity index D derives from the “Electivity” index proposed by Ivlev (Jacobs, 1974):

$$D = \frac{r - p}{r + p - 2r} \quad (2)$$

where p is the fraction of a food item in the gut, r is the fraction of that food item in the water column. The relative difference D varies from -1 to 0 for negative selection and from 0 to $+1$ for positive selection.

2.5. Food diversity

The Shannon diversity index (H') was estimated to characterize the spatial distribution of food diversity in gut contents of *P. antarcticum*.

$$H' = \sum \left(\frac{N_i}{N} \times \log_2 \frac{N_i}{N} \right) \quad (3)$$

where N_i was the individual number of food item i and N was the total number of food items.

3. Results

3.1. Distribution and size of *P. antarcticum* larvae

Larvae of *P. antarcticum* were sampled at 21 stations and were the most abundant over the Adélie Bank (Fig. 2), with a maximum abundance of 111 ind. 100 m^{-3} at station 36. The size of larvae varied from 11.3 mm at station 34 over Adélie Bank to 21.3 mm at station 24 near the Mertz Glacier Tongue (MGT). The most abundant size classes were 16 mm and 17 mm TL, corresponding to 24% and 23% of the total larvae measured, respectively (Fig. 3).

3.2. General food composition

The gut contents of 95 larvae were analysed. Their diet comprised 15 taxa, 12 phytoplankton and three zooplankton taxa (Table 1, Fig. 4). Feeding incidence among the 95 specimens observed was around 99%. Among them, 85 fed exclusively on diatoms, two individuals only fed on copepods, five on diatoms and copepods, and one on diatoms and eggs. A single larvae ate zooplanktonic prey, which could not be identified due to the advanced state of digestion. One gut was empty.

The diatom *Thalassiothrix antarctica* was the most abundant food, representing 25% of the total food items. The small colonial diatoms *Fragilariopsis* spp. were second in abundance, comprising about 24% of the diet. The chain-forming *Chaetoceros* spp. represented more than 21% of the food items (Table 1, Fig. 5a). These three taxa were the most frequently

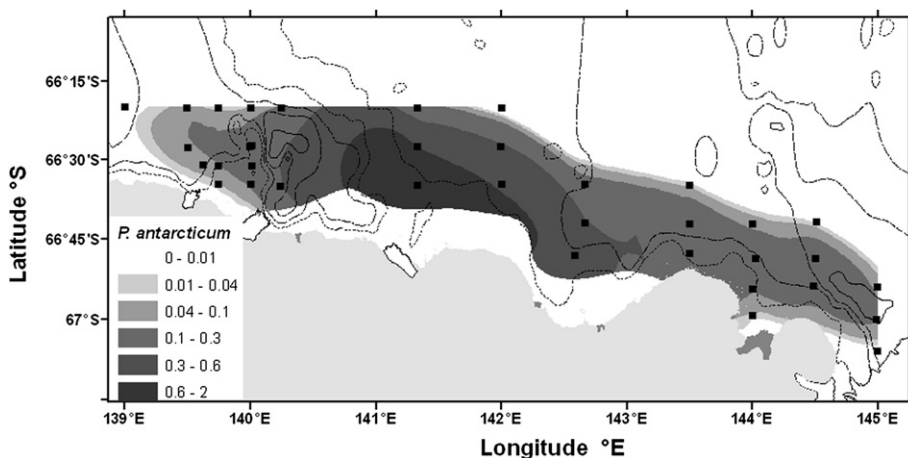


Fig. 2. Spatial distribution of fish larvae in the coastal zone from Terre Adélie to the Mertz glacier in 2004. *P. antarcticum* abundances were mapped by kriging.

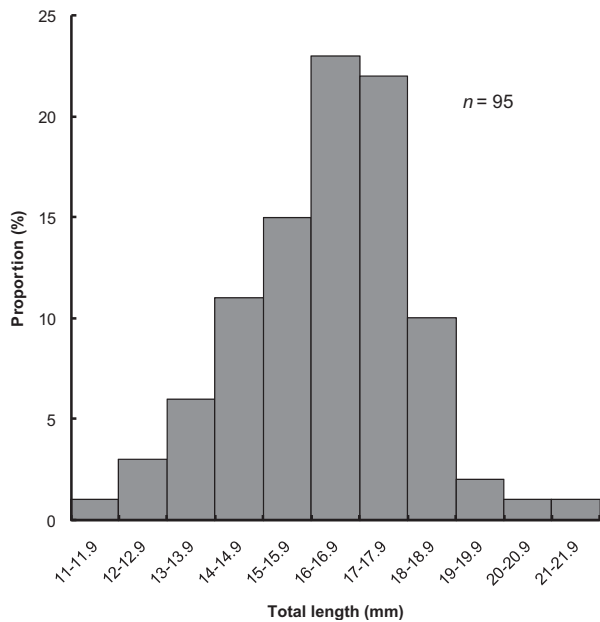


Fig. 3. Length frequency distribution of larval *P. antarcticum* in summer 2004.

ingested food with respectively 84%, 80% and 72% of occurrence (Table 1, Fig. 5a), whereas unidentified eggs and zooplanktonic individuals were of minor importance. Other frequently eaten items were the centric diatoms *Thalassiosira* spp. and the silicoflagellate *Dictyocha speculum*, each of them ingested by 22% of larvae. Large diatoms such as *Corethron pennatum*, *Asteromphalus* spp. or *Coscinodiscus* spp.,

contributed substantially to the diet and were ingested by 16%, 11% and 9% of larvae, respectively.

3.3. Food composition by zone

The diet of larvae varied spatially and significantly as a function of sampling zone (Kruskall–Wallis test, $p = 0.02$). In the Astrolabe Basin to the shelf break (zone 1, Fig. 5b), diet was composed of 14 taxa out of 15, while seven and 11 taxa were present in guts at zones 2 and 3, respectively (Fig. 5c and d). The Shannon index distribution showed that highest diversity in gut contents was located in the Astrolabe basin, with the maximum value at station 4 ($H' = 3.07$), whereas zone 2 (Adélie Bank) presented gut contents with the lowest diversity at station 32 ($H' = 0$, Table 2). The Kruskal–Wallis test showed significant difference between Shannon indexes at each zone ($p = 0.03$). A Bonferroni–Dunn test showed two groups of zones, group 1 including zones 1 and 3 with highest diversity in gut contents and group 2, with zone 2, which is represented by the lowest diversity in gut contents and dominated by a single taxon, i.e. *Chaetoceros* spp.

Feeding incidence was 100% for zones 1 and 3 and 95% for zone 2, because of one empty gut observed at station 32. At this station, other larvae fed only on copepods. Three diatoms taxa, such as *T. antarctica*, *Fragilariopsis* sp. and *Chaetoceros* spp. were the most abundant and the most frequently ingested food in the

Table 1

Food composition of larval *Pleuragramma antarcticum* in summer 2004. Columns are code for each taxa, average size, standard deviation size, number of items (n), food-specific abundance (P_i), and occurrence (O) of each food taxa. Feeding incidence refers to the percentage of guts with at least one food item ($n = 95$).

	Food taxa	Code	Average size (μm)	Standard deviation size (μm)	n	P_i (%)	O (%)	
Phytoplankton	Centric diatoms	<i>Actinocyclus</i> spp.	1	31.50	9.75	3	0.94	3.16
		<i>Asteromphalus</i> spp.	2	55.33	24.74	10	3.13	10.53
		<i>Chaetoceros</i> spp.	3	22.20	4.94	68	21.25	71.58
		<i>Corethron pennatum</i>	4	32.81	23.67	15	4.69	15.79
		<i>Coscinodiscus</i> spp.	5	67.26	34.92	9	2.81	9.47
		<i>Thalassiosira</i> spp.	6	19.23	9.59	21	6.56	22.11
	Pennate diatoms	<i>Fragilariopsis</i> spp.	7	22.44	9.74	76	23.75	80.00
		<i>Nitzschia</i> spp.	8	71.49	10.43	2	0.63	2.11
		<i>Rhizosolenia</i> spp.	9	23.80	7.94	3	0.94	3.16
		<i>Thalassiothrix antarctica</i>	10	4.04	2.00	80	25.00	84.21
	Unidentified diatoms	11			3	0.94	3.16	
	Silicoflagellates	<i>Dictyocha speculum</i>	12	21.32	6.35	21	6.56	22.11
Zooplankton		Unidentified eggs	13	2.80	–	1	0.31	1.05
		Unidentified Copepods	14	404.50	246.37	7	2.19	7.37
		Unidentified individuals	15	122.72	–	1	0.31	1.05
		Feeding Incidence				94		98.95

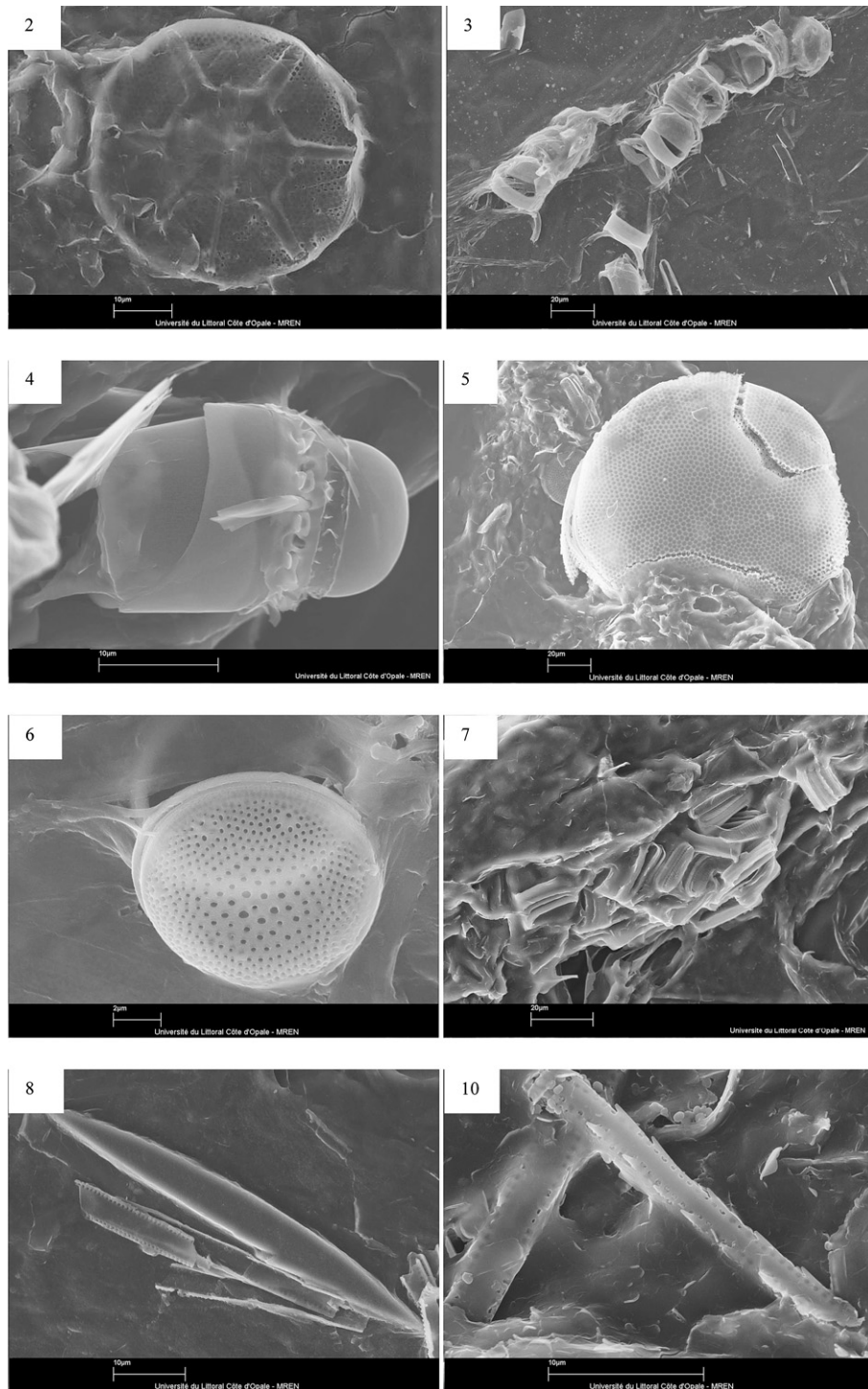


Fig. 4. Scanning Electronic Microscope pictures of the food items found in the gut of larval *P. antarcticum* in summer 2004. Number in the upper left of the picture corresponded to the code of the food taxa reported in Table 1.

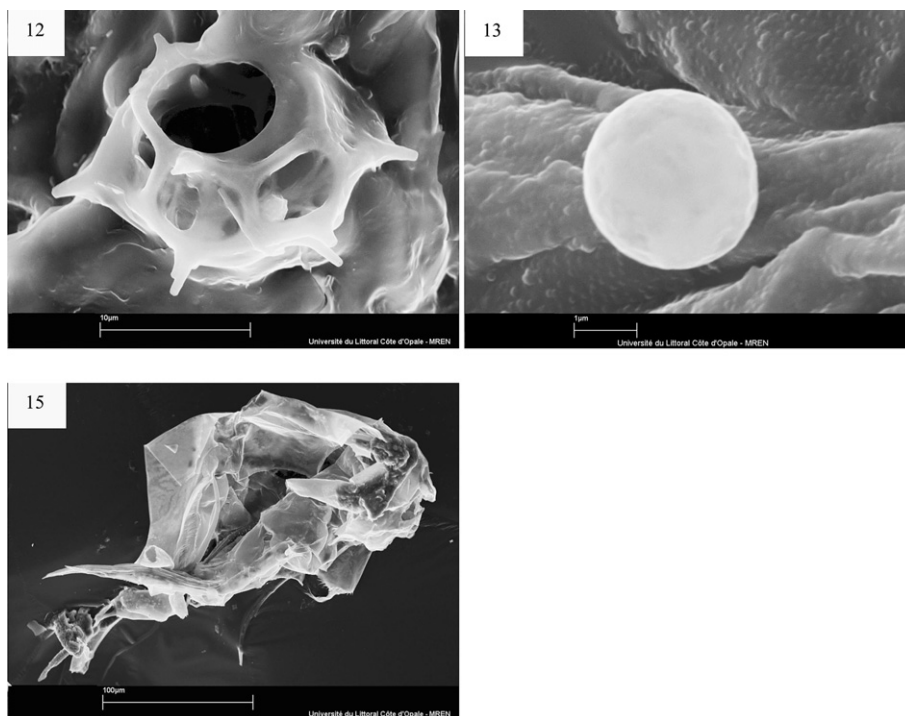


Fig. 4. (continued).

diet. Within zones 1, 2 and 3, prey-specific abundance was respectively 26%, 22% and 26% for *T. antarctica*, 20%, 24% and 26% for *Fragilariopsis* spp. and 15%, 30% and 25% for *Chaetoceros* spp. However their

Table 2
Number of food items (S) and Shannon index (H') at each station in summer 2004.

Zone	Stations	S	H'
1	1	4	1.68
	2	8	2.71
	3	6	2.50
	4	10	3.07
	5	9	2.97
	10	9	2.91
2	15	9	2.74
	31	6	2.35
	32	1	0.00
	34	2	1.00
	35	6	2.35
	37	5	2.08
3	17	7	2.50
	18	4	1.90
	19	6	2.26
	22	5	2.15
	23	5	2.18
	24	8	2.75
	26	4	1.75
	27	6	2.39
	28	5	2.25

occurrence was very different spatially. *T. antarctica* was ingested by 100% of larvae at zone 1, 52% of larvae at zone 2 and 85% at zone 3; *Fragilariopsis* spp. was eaten by more than 80% of larvae at both zones 1 and 3, and by about 58% at zone 2; *Chaetoceros* spp. was fed by 57% of larvae at zone 1, 74% at zone 2 and 83% at zone 3 (Fig. 5).

Others frequently eaten food (>20%) were the centric diatoms *C. pennatum*, *Thalassiosira* spp. and *Coscinodiscus* spp. and the silicoflagellate *D. speculum* at zone 1, unidentifiable copepods at zone 2 and the centric diatom *Thalassiosira* spp. and *D. speculum* at zone 3.

3.4. Feeding strategy

Diet composition of larvae based on the modified Costello method was summarized in Fig. 5. The two-dimensional plot provides information on food item importance, feeding strategy and niche breadth contribution of between and/or within-phenotype components. For food item importance, most items were located in the lower-left corner of the plot, thus representing rare food with low frequency occurrence and low food-specific abundance. The less rare food items were *Chaetoceros* spp., *Fragilariopsis* spp. and *T. antarctica*, owing to their high frequency of

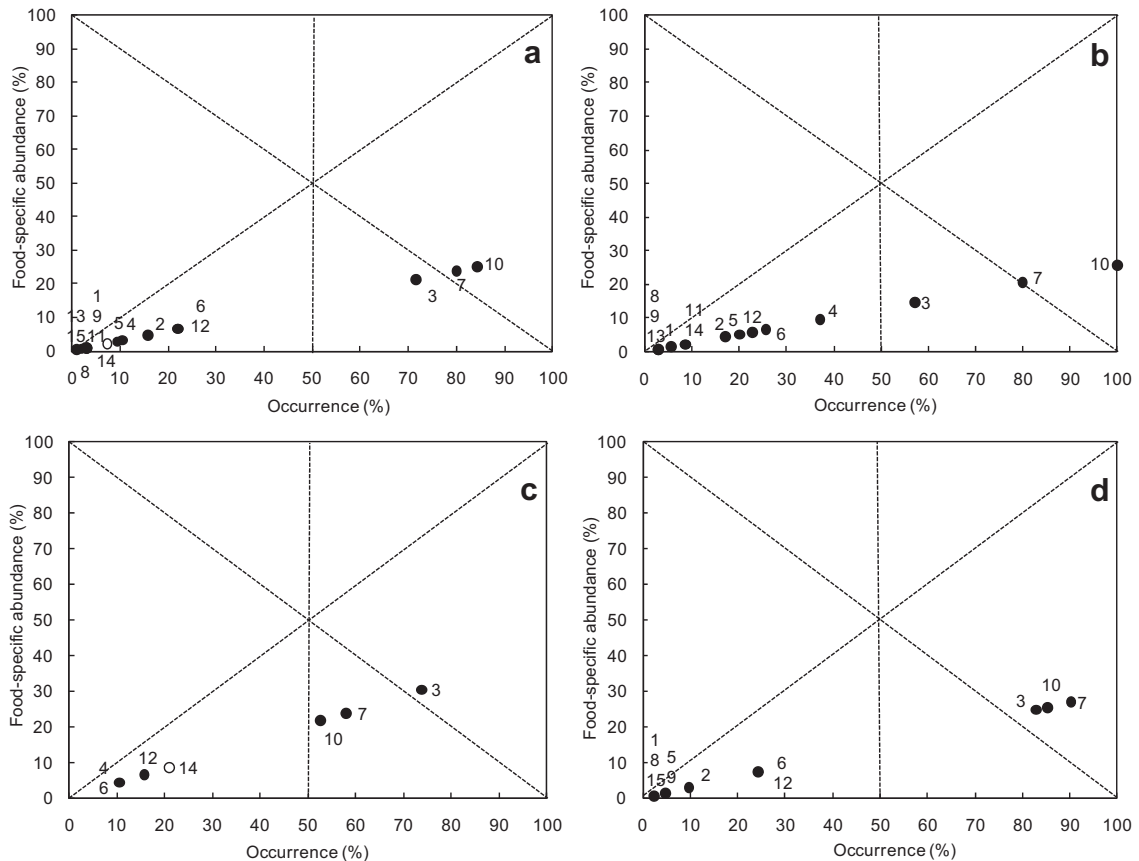


Fig. 5. Feeding strategy diagram for larval *P. antarcticum* (a) from Terre Adélie to Mertz Glacier Tongue (MGT) and in (b) Astrolabe basin (zone 1), (c) Adélie Bank (zone 2) and (d) Adélie depression (zone 3). Numbers in each graph corresponded to the code of each food taxon reported in Table 1 ●: phytoplankton; ○: zooplankton.

occurrence compared to other taxa (Fig. 5). In relation to the feeding strategy axis, larvae of *P. antarcticum* could be considered as generalist feeders, as all food items were located in the lower part of diagram, attaining a low food-specific abundance. As far as the niche width contribution is concerned, the location of main food taxa, *Chaetoceros* spp., *Fragilariopsis* spp. and *T. antarctica*, within the two-dimensional plot indicated a relatively higher within-phenotype component in the utilization of food resources than between-phenotype component. These taxa showed a low specific abundance and a high occurrence (lower right) indicating that they were eaten by most individuals along with other prey.

3.5. Food selection

For the whole study area, the density of suitable food was 251,128 cells per litre for phytoplankton and 9861 individuals per m³ for zooplankton. The pennate diatom *T. antarctica* was the main component of the

diet. However, this species did not occur in the diet at the same proportion than found *in situ* (7488 cells per litre). Positive selection was found for this species ($D = 0.84$), as its abundance in the water column represented around 3% of the total abundance of the phytoplankton and its occurrence in gut contents was 84% (Fig. 6a). Two other phytoplanktonic taxa, *Nitzschia* spp. (80 cells per litre) and *Coscinodiscus* spp. (766 cells per litre), represented less than 1% of the total phytoplankton abundance, but they were positively selected by *P. antarcticum* (Fig. 6a). Positive selection was also observed for *Asteromphalus* spp., *Thalassiosira* spp. and *D. speculum*, as well as for *Chaetoceros* spp. at a lesser extent (Fig. 6a). On the other hand, some phytoplanktonic taxa exhibit a high negative selection, such as *Rhizosolenia* spp., or a low negative selection like the small colonial *Fragilariopsis* spp. and the central diatoms *Actinocyclus* spp. and *C. pennatum* (Fig. 6a). Among zooplanktonic organisms, eggs and copepods were highly positively selected.

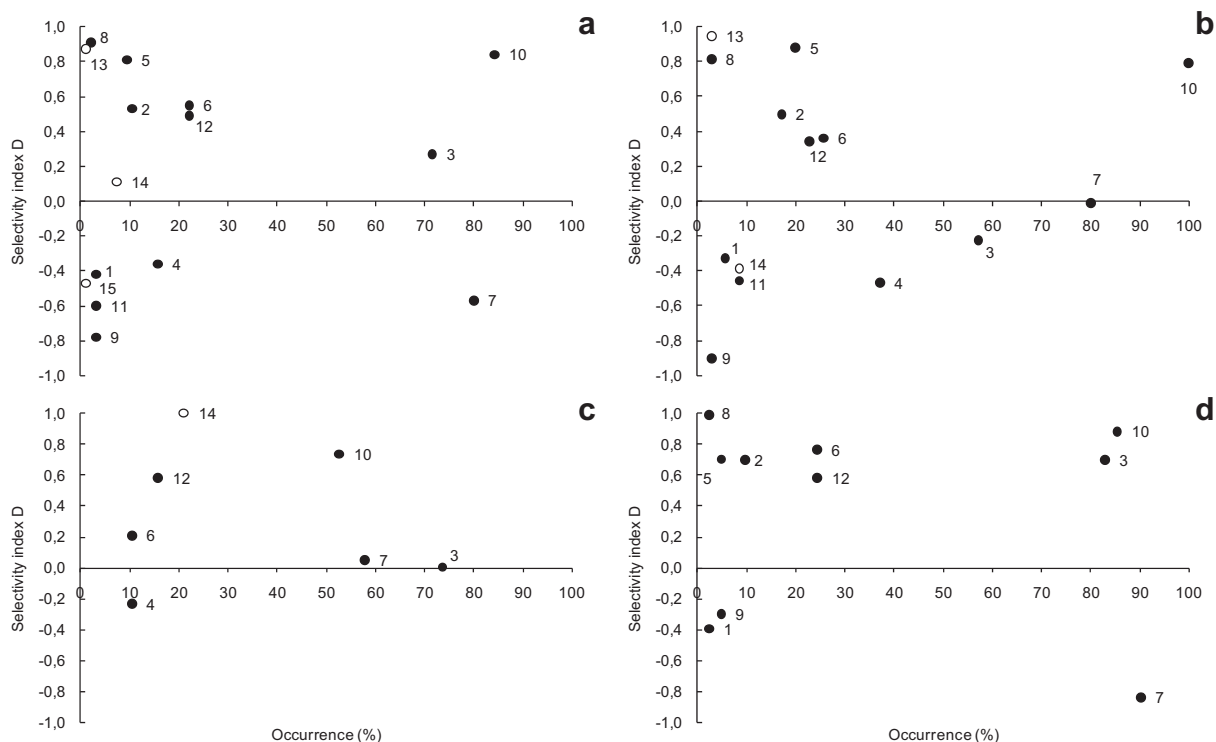


Fig. 6. Selectivity index (D) as a function of occurrence of each food item in summer 2004 in (a) the Dumont d'Urville Sea, (b) Astrolabe basin (Zone 1), (c) Adélie Bank (Zone 2) and (d) Adélie depression (Zone 3). Numbers in each graph corresponded to the code of each food taxon reported in Table 1 ●: phytoplankton; ○: zooplankton.

Food selection by larval fish was analysed at each different zone. The total phytoplankton concentration was 1.5 and 7 times higher at zone 3 near the MGT (137,617 cells per litre) than at both zones 1 (93,711 cells per litre) and 2 (19,800 cells per litre), respectively. However the total zooplankton concentration was the same order of magnitude for both zones 2 (3835 ind. m^{-3}) and 3 (3605 ind. m^{-3}), and 1.5 times lower at zone 1 (2421 ind. m^{-3}). At zone 1, *Coscinodiscus* spp., *Nitzschia* spp., *T. antarctica*, copepods and eggs were strongly positively selected, *Fragilariopsis* spp. showed low preference, while highest value of negative indices was observed for *Rhizosolenia* spp. (Fig. 6b). At zone 2, where phytoplankton abundance was the lowest and zooplankton abundance the highest, copepods and *T. antarctica* showed high value of positive indices, whereas values were close to zero for *Fragilariopsis* spp. and *Chaetoceros* spp. (Fig. 6c). Values for *D. speculum* were of moderate preference. Zone 3 was very different compared to both zones 1 and 2 (Fig. 6d). Several taxa (*Asteromphalus* spp., *Chaetoceros* spp., *Coscinodiscus* spp. and *Thalassiosira* spp.) showed value of index D higher than 0.7,

suggesting that all these taxa were ingested preferentially, *D. speculum* was moderately ingested, whereas *Fragilariopsis* spp. was strongly negatively selected (Fig. 6d).

3.6. Food size

The size distribution of the total food ingested by the larvae was polymodal, with the 20 μm size class comprising large portions of their diet (Fig. 7a). At zone 1, *P. antarcticum* larvae fed on the lower size range of prey (from 0 to 10 μm) while at zone 2 they fed mainly on the 10 μm class and ingested larger food items (80–90 μm , Fig. 7a). At zone 3, the 20 μm size class represented the main food items ingested.

The mean food size varied little in relation to the larval length (Fig. 7b). However, extreme values increased with larval length, which suggest that larger larvae of *P. antarcticum* were able to ingest larger food items. Thus, whatever their size, all larvae of *P. antarcticum* were able to ingest prey of size higher than 25 μm (i.e. the mean food size of each length class).

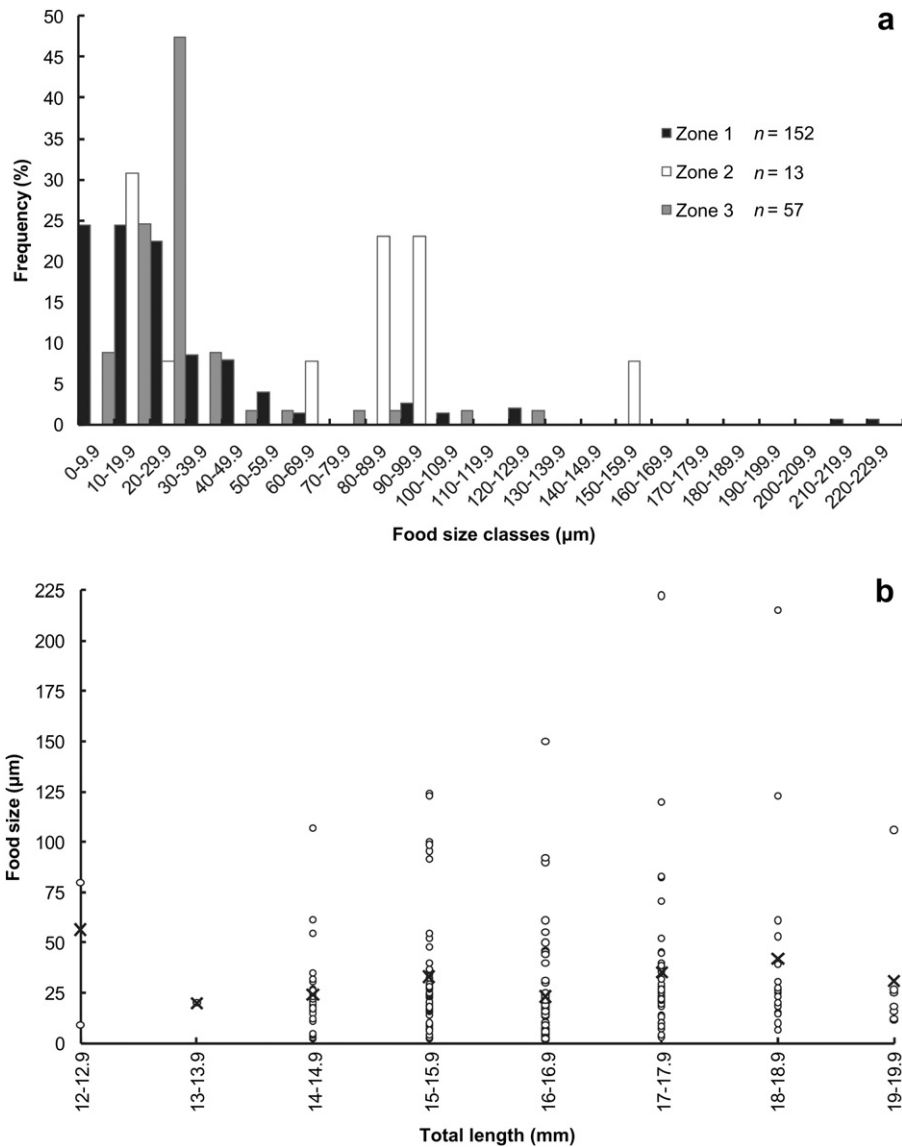


Fig. 7. (a) Prey size frequency for each zone located from Terre Adélie to Mertz Glacier Tongue (MGT) in summer 2004; (b) Food size - larval *P. antarcticum* size relationship observed in summer 2004 (×, mean food size).

4. Discussion

4.1. Distribution of larvae of *P. antarcticum*

Larvae of *P. antarcticum* dominated the neritic assemblage in Terre Adélie coastal waters during summer 2004, as already shown by Koubbi et al. (1997, 2009) or elsewhere reported over the Antarctic continental shelf (Hoddell et al., 2000; Granata et al., 2009). Our results showed that total length of larvae ranged between 11 and 21 mm, suggesting that they could come from coastal reproductive areas, where

hatching takes place in November for larger individuals and at the beginning of January for smaller ones. The same period of hatching was observed in other areas of the Southern Ocean (Hubold, 1984, 1985; Kellermann, 1987; Vacchi et al., 2004). Moreover, Koubbi et al. (1997, 2009) demonstrated that reproduction occurred in deep coastal canyon or in coastal zones near ice-shelves glaciers. Hubold (1984) and La Mesa et al. (2010) stated that larval survival was related to the development of coastal polynya, which could provide favourable conditions for early larval stages growth. Distribution of larvae of *P. antarcticum*

in Terre Adélie coastal waters during summer 2004 coincided with areas of both high primary production and diatom diversity, which provide the necessary nutrients for early stages of *P. antarcticum* (Beans et al., 2008; Koubbi et al., 2009).

4.2. Gut contents

Our results confirmed that larval *P. antarcticum* fed on both phyto- and zooplankton. Compared to present data, feeding incidence was similar in Terre Adélie during summer 1996 (89%) (Koubbi et al., 2007) and lower in the pack ice zone off the Antarctica Peninsula (78%) (Kellermann, 1987). These differences could be explained by the difference of methodology used. Kellermann (1987) observed the digestive tract under a stereomicroscope, while in this study and the previous one (Koubbi et al., 2007), we used a Scanning Electron Microscope, which allowed us to observe smaller food items (from 2 µm, Table 1) and, thus to get a more accurate food identification. However, it was very difficult to determine species among copepods even with a stereomicroscope, because of the state of digestion. No ciliate was observed in guts of *P. antarcticum* larvae, which was different from specimens collected off the Biscoe Islands in the southern continental shelf of Bransfield Strait (Kellermann, 1987). This is also contrary to observations by Beans et al. (2008), who found that ciliates were dominated by tintinnids ($71.6 \pm 32\%$ of all ciliates) during summer 2004 in the Dumont d'Urville Sea. However, ciliate abundance was very low, with an average of 102 ± 126 cells per litre, and several samples had no ciliate (Beans et al., 2008). The low abundance of euphausiids larvae recorded in summer 2004 ($<0.01\%$ of total zooplankton) (Vallet et al., 2009), might explain the absence of this prey in the gut contents of *Pleuragramma* found in the present study.

4.3. Food selection

In aquaculture, marine microalgae are widely used in the first feeding stages of marine fish larvae (Jones et al., 1981; Lubzens, 1987; Naas et al., 1992; Reitan et al., 1993). In our study, diatoms probably stimulate feeding behaviour in larvae of *P. antarcticum* as many compounds, such as betaine or amino-acids, natural constituents of phytoplankton (Dabrowski and Ruseick, 1983), are considered to be the most effective feeding stimulants (Lazo et al., 2000). Our results showed that some diatoms, such as *Coscinodiscus* spp. or *T. antarctica*, were highly positively selected by *P. antarcticum* larvae. Diatoms, especially *Coscinodiscus*

spp., are known to have a high amount of free amino acids (Braven et al., 1995), which could actively contribute to the free amino acid pool in gut contents of larvae, therefore playing an important role in energy production and protein synthesis (Fyhn, 1993). Lazo et al. (2000) demonstrated that the presence of phytoplankton in their culture resulted in increased growth, survival and enzyme activity in fish larvae. It could be possible that in extreme conditions as in the Antarctic waters, *P. antarcticum* larvae need to feed first on phytoplankton for a short period, to get a better digestive system to subsequently assimilate larger zooplanktonic prey, such as copepods or euphausiid larvae.

Moreover, fatty acid composition in *P. antarcticum* larvae from Terre Adélie showed that they are omnivorous, with a marked diatom food source and a slight contribution of small copepods like Oithonidae (Tavernier and Mayzaud, unpublished).

The selectivity index indicated that larvae of *P. antarcticum* were able to select positively some food items, such as *Coscinodiscus* spp., *T. antarctica* and copepods. However, the selective feeding tightly depended on the concentration of food items in the plankton. Furthermore, food sizes were very different between diatoms and copepods. Although *P. antarcticum* larvae were able to ingest large prey, the width of their mouth control the maximum food size (Kellermann, 1987).

4.4. Feeding strategy

In coastal waters of Terre Adélie, larvae of *P. antarcticum* fed on three dominant phytoplanktonic food items, *T. antarctica*, *Chaetoceros* spp. and *Fragilaria* spp. All other food items were consumed occasionally by a few individuals. The feeding strategy of *Pleuragramma* was shifted towards a within-phenotype contribution to the niche breadth, as most food items presented a low food-specific abundance and high occurrence. Larvae of *P. antarcticum* can be considered as generalist feeders, as their diet consisted of a few dominant prey and a relatively high number of other food items, either zooplankton or phytoplankton. As a consequence, larvae of *P. antarcticum* should have a high tolerance of variable environmental conditions, being able to switch between several prey types (Richmond et al., 2005). Other studies already reported that larvae of *P. antarcticum* were well-adapted to feed on a wide spectrum of food, depending on seasonal availability (Hubold and Hagen, 1997). Although many authors hypothesized that physiological plasticity increased energetic costs (e.g. Agrawal, 2000; Coustau

et al., 2000; De Witt et al., 1998; van Kleunen et al., 2000), generalist feeders are favoured in fluctuating environments compared to specialist feeders (Richmond et al., 2005).

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