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Interannual variations in euphausiid life stage distribution in the Dumont d'Urville Sea from 2004 to 2008

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Abstract

Euphausiid larvae were caught by oblique tows of a double-framed bongo net at 118 stations along the coast of Terre Adélie during every summer from 2004–2008. Larvae of *Euphausia crystallorophias* Holt and Tattersall and *Thysanoessa macrura* G.O. Sars were observed in the study area every year in contrast to larvae of *Euphausia superba* which were absent during the entire period of sampling. Highest abundances of both species were observed during the summer of 2005 and the lowest in the summer of 2004. Larvae of *E. crystallorophias* dominated every year and comprised more than 80% of the total abundance of euphausiid larvae. Within species, the calyptopis stages especially calyptopis 1 of *E. crystallorophias* dominated compared to furcilia stages of *T. macrura* which were less abundant. For both species, spatio-temporal variations in abundances of developmental stages were significantly correlated to density and salinity of the deep water layer. In the case of calyptopis 3 of *E. crystallorophias*, spatio-temporal variations were correlated with the number of days between the end of the sea ice retreat and the sampling day and for *T. macrura* inversely correlated to temperature of surface water layer. These variations are discussed and related to the timing of sea ice retreat, the sea ice concentration as well as metabolic conditions of adults of both species during their spawning period. © 2011 Elsevier B.V. and NIPR. All rights reserved.

Keywords: *Euphausia crystallorophias*; *Thysanoessa macrura*; Antarctic; Abundance; Spatial distribution; Environmental factors

1. Introduction

Euphausiids form a significant component of zooplankton biomass in the Antarctic neritic zone (Boysen-Ennen and Piatkowski, 1988; Hosie et al., 2000). Their distribution and abundance vary both within a season and inter-annually (Hewitt et al., 2003) and

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causes for those variations have been ascribed to both biological and physical factors (Mauchline, 1980; Nicol, 2006; Siegel, 2005). The limits of distribution for a particular species appear to be related to hydrographic conditions, with seasonal changes known to occur at the boundaries of their distribution (Brinton, 1976). Such local changes in species often reflect water mass distribution (temperature and currents), but are also linked to the food availability, predation risk, and perhaps physiological conditions. The dominant euphausiids usually found within the seasonal pack ice zone in the Southern ocean are *Euphausia superba* and *Thysanoessa macrura*, whereas *Euphausia crystallorophias* prevails in the permanent pack ice zone (John, 1936; Kaufmann et al., 2003). *E. crystallorophias* and *T. macrura* were the most common euphausiid sampled along the coast of East Antarctica in the Dumont d'Urville Sea (139–145°E) in the summer of 2004 (Vallet et al., 2009). Because of their dominance in inshore waters of the Antarctic continental shelf (Hubold, 1985; Mauchline, 1980; Vallet et al., 2009), *E. crystallorophias* and *T. macrura* are of considerable ecological importance. They form a significant proportion of the food for upper level predators, including fishes (Hubold, 1985, 1990), Adélie and chinstrap penguins (Ainley et al., 1998; Emison, 1968; Thomas and Green, 1988), Crabeater and Weddell seals (Plötz et al., 1991) and whales (Marr, 1962; Mauchline, 1980). However, they also represent the major predators for lower levels of the food web (Mauchline, 1980). *E. crystallorophias* can be classified as a high polar herbivore, adapted to exploit the typical high-latitude bloom situation (Falk-Petersen et al., 2000). This species can supplement its dietary requirements during winter by utilising decaying material of phytoplanktonic origin. It typically spawns in early spring when phytoplankton production is extremely low (Pakhomov and Perissinotto, 1996) and its reproductive processes are fuelled mainly by lipid reserves synthesised during the previous year (Falk-Petersen et al., 2000). This early timing of reproduction has the advantage in that larval stages are able to build up sufficient body mass and energy reserves during their first season (Ju and Harvey, 2004). *T. macrura* is classified as omnivore with dietary input much more diverse than that found in the classical bloom situation. It spawns well before the bloom and its reproduction is independent of the spring-summer phytoplankton bloom as an external food source (Falk-Petersen et al., 2000). Thus, each species must develop a means to cope with periods of very low food supply in winter conditions or interannual changes in the nature of food in summer conditions during the phytoplanktonic bloom. Variability in food abundances ultimately affects survivorship and reproduction.

Vallet et al. (2009) investigated the distribution of euphausiid larvae during summer of 2004 along the coast of East Antarctica, in the Dumont d'Urville Sea, and examined the relationship between the distribution of euphausiid larvae and environmental factors (surface temperature, salinity, nutrients and pigments). From the results obtained in this preliminary study, a French research project ICO²TA (Integrated Coastal Ocean Observations in Terre Adélie) was developed to allow long-term monitoring of the pelagic zone. This project was a contribution to the Census of Antarctic Marine Life and the CEAMARC project (Collaborative East Antarctic Marine Census) that was conducted in 2008.

The objectives of this study were to: (1) document patterns of distribution and abundance in time and space of larval stages of the two euphausiid species *viz* *T. macrura* and *E. crystallorophias* and (2) explore the relationships between distribution and abundance with environmental variables. As a first step in understanding interactions, we present relationships between the long-term distribution of larvae of *T. macrura* and *E. crystallorophias* and annual environmental parameters. These data comprise the first and thus unique long-term series of larval euphausiids in the Dumont d'Urville Sea before the breakout of the Mertz Glacier Tongue (MGT) in February 2010.

2. Material and methods

The survey was conducted from the French RV *l'Astrolabe* in the area 139–145°E each summer from 2004–2008 (Table 1). During each survey, the water was free of sea ice, except in 2008 in the western part of the study area. Each year, sampling locations were defined according to weather and sea conditions or logistics constraints. 118 stations were sampled over the continental shelf (Table 1). A total of 58 stations in the western part of the survey were selected to sample the foraging area of Adélie penguins who were feeding their chicks at the colony near Dumont d'Urville; 30 stations covered the Adélie Bank and 30 covered the Adélie depression near the Mertz Glacier Tongue (MGT, Fig. 1).

At each station, temperature and salinity were measured down to 200 m with a SBE25 (2004, 2007 and 2008) or FSI (2005 and 2006) CTD. From the TS diagrams, thermocline and halocline when present were found at a depth of about 100 m. Therefore, temperature, salinity and density data were pooled from 0 to 100 m (surface layer) and from 100 to 200 m (deep layer) to allow interannual comparisons.

Passive microwave (PMW) systems are the primary source of large scale sea ice concentration data (Massom

Table 1
Sampling details for each summer from 2004–2008.

Year	Date		Number of samplings with Bongo net by geographic zone			Total
	From	To	Dumont d'Urville zone (DDU)	Adélie Bank (AB)	Adélie depression (MGT)	
2004	19/01	28/01	15	9	13	37
	Station numbers		1–15	30–38	16–28	
2005	10/01	19/01	15	4	4	23
	Station numbers		39–50	132–135	128–131	
2006	09/01	18/01	14	5	6	25
	Station numbers		232–246	209, 225, 229–231	199–204	
2007	24/01	01/02	7	5	3	15
	Station numbers		251–256	257–259, 318	260–262, 317	
2008	10/01	18/01	7	7	4	18
	Station numbers		334, 443–449	341–346	347–351	

et al., 1998). PMW radiometers can collect multifrequency data in darkness and the data is not affected by cloud cover. We used maps of Sea Ice Concentration (SIC) for November sea ice breakout periods in the Dumont d'Urville Sea. Daily resolution of SIC data, obtained via the Advance Microwave Scanning Radiometer – Earth Observing System (AMSR-E) was 6.25 km. The ArcGIS (ESRI) Single Output Map Algebra tool was used to calculate the November SIC averages (Swadling et al., 2011).

Macrozooplankton were collected by oblique tows of a double-framed bongo net with 500 μm mesh and 60 cm mouth diameter (Smith and Richardson, 1977). Tows were carried out at a speed of 2 knots from the surface to 200 m or near the sea bed for depths shallower than 200 m. The volume of water filtered by each net was measured with a flow metre and used to calculate macrozooplankton abundances. Samples were fixed immediately on board with 5% neutral formalin in seawater.

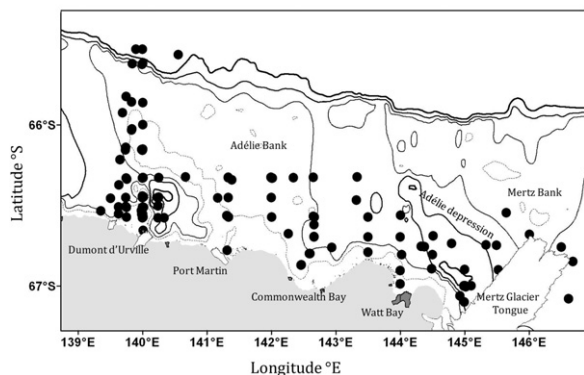


Fig. 1. Locations of sampling stations in the study area from 2004 to 2008.

In the laboratory, euphausiid larvae were sorted, identified and counted. All individuals were separated into the following stages: nauplius 1 and 2, metanauplius, calyptopis 1 to 3, and furcilia 1 to 6, according to Kirkwood (1982).

A Kruskal–Wallis non-parametric test was used to test a possible change in abiotic factors and to compare larval abundance among years. When the difference was significant, a non-parametric multiple comparison test (Bonferroni–Dunn test, XLSTAT 2010.2.03) was used to determine which clusters of samples were significantly different from others.

Multiple Correspondence Analysis (MCA) was used to analyse the variability of the distribution of euphausiid larvae. Correspondence analysis (Benzecri, 1973), an ordination method which has been widely used to analyse ecological data (Gower, 1987), was chosen to describe the total inertia of a multi-dimensional set of data, in a sample of fewer dimensions. In our study, larval stages of both euphausiid species, *E. crystallorophias* (nauplius 2, metanauplius, calyptopis 1, 2, 3 and furcilia 1) and *T. macrura* (calyptopis 1, 2, 3 and furcilia 1, 2, 3 and 4) as well as years and station locations were represented in the same reference system. In order to perform this MCA, the euphausiid abundances for each species were transformed into categorical variables. Three classes of abundances were selected: class 0 with null values; classes 1 (lower values) and 2 (higher values) each containing a similar number of non-null values. Latitude and longitude were coded in modalities of equal size.

Multivariate analyses were performed using CANOCO version 4.53 (Biometrics, Wageningen). Redundancy analysis (RDA) was used to examine the relationships between the euphausiid larvae and the environment variables for the 118 sampling sites. RDA is a direct gradient analysis technique where the ordination

axes are constrained to be linear combinations of environmental factors. RDA was chosen as the appropriate ordination method based on gradient lengths, as determined by detrended canonical correspondence analysis, being less than two (Leps and Simlauer, 2003). The forward selection option of RDA, which is analogous to the technique of stepwise multiple regression, was used to determine the minimum number of explanatory factors that could explain statistically significant ($P < 0.05$) proportions of variation in the euphausiid larvae data. The significance of these variables was assessed using Monte Carlo permutation tests (with 499 unrestricted permutations).

3. Results

3.1. Interannual variability of environmental data

The Kruskal-Wallis test revealed significant differences between years in environmental variables from surface layer data (0–100 m) (Table 2). The surface layer water was significantly warmer in 2004 while it was cooler in 2005, 2006 and 2008. Mean water salinity increased gradually from 2004 to 2008 (Table 2). 2006 was significantly denser over the top 100 m, while 2004 and 2008 were less dense (Table 2). In the deeper layer (100–200 m), temperature, salinity and density were also significantly different from year to year (Table 2). Mean water temperature showed a gradual and significant decrease from 2004 to 2008 whereas mean water salinities showed an inverse gradual trend (Table 2). Only density in 2008 was different from the other years and lower (Table 2). Irrespective of the water layer sampled, the sharp difference in density between 2008 and other years was due to colder and saltier waters of both surface and deep layers in 2008 (Table 2).

The duration of the sea ice retreat varied from 13 days in 2003 to 29 days in 2007 (Fig. 2). The start of

the breakout period ranged from November 2 in 2005 and 2006 to November 15 in 2003, and the end date varied from 19th November, 2006 to 4th December, 2007 (Fig. 2). 2005 and 2006 were the years with the most similar sea ice retreat period. The years 2003 and 2004 showed some similarities because their breakout period began around the middle of November and ended at the end of November. The year 2007 showed the most extended breakout period (29 days), from early November to early December (Fig. 2).

The number of days between the end of sea ice retreat and the beginning of the summer sampling survey can be calculated from the matrix presented in Fig. 2. This number fluctuated from 36 days (December 2007–January 2008) to 65 days (November 2006–January 2007). Similarities existed in 2005 and 2006 with 46 and 49 days respectively, while in 2004, it was a little bit more extended (52 days). The duration of cruises was 9–10 days every year. In 2005, 2006 and 2008, summer sampling cruises were conducted from the early to the middle of January whereas in 2004 and 2007, they occurred in late January.

Table 3 gives the average of sea ice concentrations in the Dumont d’Urville Sea every November prior to sampling campaigns, and the presence or absence of polynya in each zone for the same period. The average sea ice concentration (SIC) was highest in November 2003, decreased in 2004 and remained stable in 2005–2006, to finally increase again in 2007 before the last summer sampling survey in 2008. Every year, a large polynya was clearly identified west of the MGT (Adélie depression zone) up to the Commonwealth Bay, and characterized by low average SIC (0–20%). In 2003, 2006 and 2007, another polynya (SIC = 0–20%) was observed northwest of the Astrolabe Glacier (Dumont d’Urville zone). In 2004, no polynya was observed but the SIC remained low (20–40%) suggesting some areas of thinner ice. The Adélie Bank shows a high average

Table 2
Mean values and standard deviation (SD) for each environmental variable (T, Temperature; S, Salinity; D, Density) for stations sampled each year.

Kruskal-Wallis Test	Surface layer (0–100 m)									Deep layer (100–200 m)								
	T (°C)			S			D			T (°C)			S			D		
	***	*	***	**	*	*												
Year	Mean	SD	BDT	Mean	SD	BDT	Mean	SD	BDT	Mean	SD	BDT	Mean	SD	BDT	Mean	SD	BDT
2004	-0.58	0.20	A	34.19	0.10	A	27.78	0.19	A	-1.02	0.14	A	34.36	0.05	A	28.41	0.17	B
2005	-1.00	0.15	B	34.25	0.05	A-B	27.85	0.17	A-B	-1.25	0.08	A-B	34.35	0.02	A	28.42	0.16	B
2006	-1.06	0.16	B	34.29	0.04	A-B	27.94	0.14	B	-1.28	0.06	A-B	34.38	0.02	A-B	28.41	0.14	B
2007	-0.80	0.23	A-B	34.25	0.07	A-B	27.86	0.18	A-B	-1.32	0.07	A-B	34.42	0.02	B	28.36	0.12	B
2008	-1.04	0.42	B	34.31	0.11	B	27.59	0.10	C	-1.46	0.07	B	34.42	0.02	B	27.73	0.03	A

Significant differences between years (Kruskal-Wallis test) are denoted as follows: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. A, B, C denote which means were similar under the Bonferroni–Dunn test (BDT).

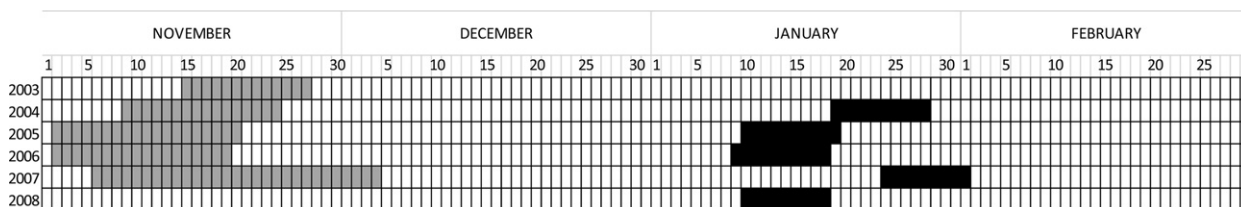


Fig. 2. Timing of sea ice retreat prior to the surveys carried out from 2004 to 2008. Grey indicates the period of sea ice retreat. Black indicates the period of sampling.

SIC (>50%) every year and especially near the coast in 2003 and 2007 (80–100%).

3.2. Spatio-temporal variability of environmental data

The relationship among sampling stations based on the environmental data were assessed using PCA (Fig. 3). PCA axes 1 and 2 accounted for 32 and 22% respectively of the variations in the environmental data (Fig. 3). The third axis explained 18% of the variations. Axis 1 showed a negative trend between year, salinity of the deep layer ($S_{100-200}$) and longitude on the negative part of the axis, and temperature and density of the deep layer ($T_{100-200}$) on the positive part. This axis is representative of stations 348, 350 and 347 sampled near the MGT in 2008 in its negative component and by stations sampled in front of Dumont d'Urville and in Adélie Bank from 2004 to 2007 in its positive component (Fig. 3). The positive component of Axis 2 was characterized by latitude and stations sampled at the shelf break from 2006 to 2008 while its negative component was characterized by longitude, density of surface layer and stations sampled in the Adélie depression near the MGT from 2004 to 2007 (Fig. 3).

3.3. Euphausiid larvae abundance

Abundances of euphausiid larvae were significantly different among years (Kruskal-Wallis test, $P < 0.0001$),

Table 3

Average sea ice concentrations (SIC) for the study region every November from 2003 to 2007 based on AMSR-E data, and presence (+) or absence (–) of polynya by geographic zone.

Date	Average SIC (%)	Polynya		
		DDU	AB	AD
2003	60	+	–	+
2004	40–45	–	–	+
2005	40–45	–	–	+
2006	40–45	+	–	+
2007	52	+	–	+

(DDU: Dumont d'Urville; AB: Adélie Bank; AD: Adélie depression) (Swadling et al. 2011).

varying by nearly an order of magnitude (Fig. 4a). From the Bonferroni–Dunn test, the five years were separated into groups: (1) lowest abundance (2004); (2) average abundance (2006, 2007, 2008); and (3) highest abundance (2005).

Every year for the five summers of sampling, *E. crystallorophias* was the dominant species (Fig. 4b). The larvae of this species represented between 84% (2007) and 96% (2005) of the total abundance of euphausiid larvae. Abundances of larvae of this species were significantly different between years (Kruskal-Wallis test, $P < 0.0001$) especially during the summers 2004 and 2005. The abundance in 2004 was five to seven times lower than that observed from 2006 to 2008 and 70 times lower than that in 2005 (Fig. 4b).

The abundance of *T. macrura* larvae was much lower than that of *E. crystallorophias* (Fig. 4c) and presented a significant year to year difference (Kruskal-Wallis test, $P < 0.0001$). The Bonferroni–Dunn test separated the data from five years into groups ranging from (1) the lowest abundance (2004); (2) average abundance (2006, 2008); and (3) highest abundance (2005 and 2007).

As seen from the results presented above, abundances of both species showed different patterns. Even though 2004 recorded the lowest abundances for both species, abundances of *T. macrura* in 2007 was only two times lower than in 2005, while that of *E. crystallorophias* varied by an order of magnitude between 2005 and 2007 (Fig. 4b and c). Moreover, no significant difference in abundance of *E. crystallorophias* was shown from 2006 to 2008, whereas abundance of *T. macrura* was two to three times higher in 2007 than in 2006 and 2008 (Fig. 4b and c).

3.4. Euphausiid larvae composition

Larvae of *E. crystallorophias* were more abundant and of an earlier developmental stage (calyptopis) than those of *T. macrura* (furcilia, Fig. 4b and c). Thus, calyptopis dominated the larval population as a whole (Fig. 4a). Calyptopis 1 dominated the larvae of *E. crystallorophias* every year (49–77% of its total abundance, Fig. 4b).

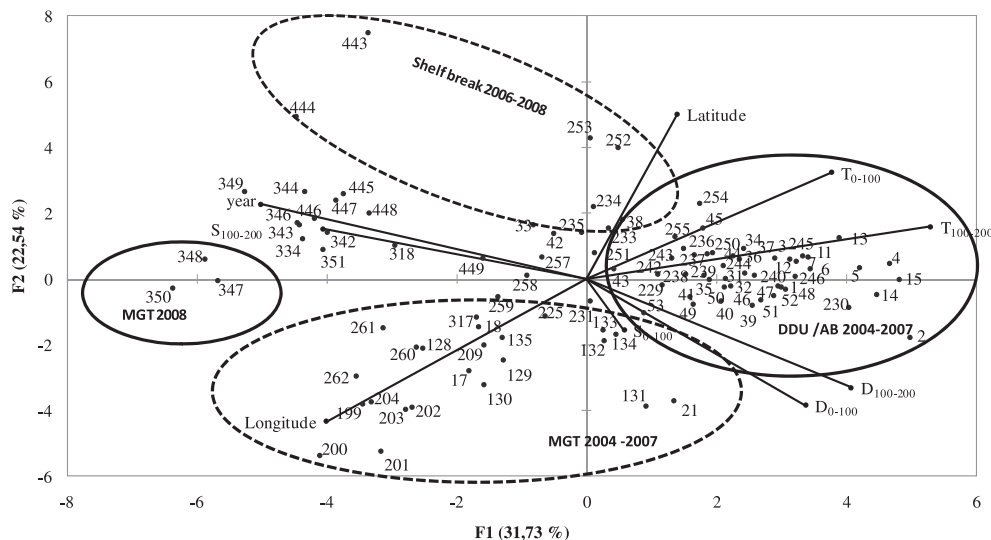


Fig. 3. Ordination diagram showing the position of the sampling stations on a biplot of the first two axes of a Principal Component Analysis (PCA) of environmental data (longitude; latitude; year; mean salinity, temperature and density of surface layer: S_{0-100} , T_{0-100} , D_{0-100} ; mean salinity, temperature, density of deep layer: $S_{100-200}$, $T_{100-200}$, $D_{100-200}$).

Stage composition varied annually: in 2005, metanauplius, the developmental stage younger than calyptopis 1, dominated and represented 20% of the total abundance of *E. crystallorophias*, while in 2007, an older developmental stage (calyptopis 2) dominated and represented 43% of this total abundance. In contrast, larvae of *T. macrura* were dominated by an older developmental stage than *E. crystallorophias* (Fig. 4c). Furchilia 1, 2 and 3 were dominant in 2004 and 2007 (23–34%), whereas in 2006, furchilia 1 and calyptopis 3 dominated (70 and 30% of the total abundance respectively). In 2005 and 2008, three larval stages dominated: calyptopis 3 (18 and 34%), furchilia 1 (43 and 38%) and furchilia 2 (22 and 25%).

One naupliar stage of *E. crystallorophias*, nauplius 1, and four furchilia stages, furchilia 2, 3, 4 and 5, were not observed over the summer (Table 4). When nauplius 2 was present (2005, 2008), its abundance was consistently low (3 and 10 ind. 100 m^{-3} , respectively). Also, low abundances of furchilia 1 and 6 were only observed in 2004 (mean abundance less than 1 ind. 100 m^{-3}). All developmental stages from metanauplius to calyptopis 3 occurred every year. A correlation was shown between frequency of occurrence and abundance for metanauplius ($R = 0.91$, $P < 0.01$) and calyptopis 3 ($R = 0.83$, $P < 0.05$). The year with highest abundance was significantly correlated to that with the highest frequency of occurrence. However, no correlation could be found for calyptopis 1 ($R = 0.51$, $P > 0.05$) and 2 ($R = 0.63$, $P > 0.05$). These results can be explained by the fact that their highest frequencies of occurrence were in 2007 and

2008 while their highest abundances occurred in 2005 (Table 4).

No naupliar and metanauplius stages of *T. macrura* were observed over the years (Table 4). Calyptopis 1 and 2 were rarely present and their abundances were very low (about 3 ind. 100 m^{-3} for calyptopis 1 and from 3 to 7 ind. 100 m^{-3} for calyptopis 2). Older stages, such as furchilia 4, 5 and 6 were occasionally present (Table 4). Their abundances varied from 17 to 36 ind. 100 m^{-3} (furchilia 4), 2.5 to 7 ind. 100 m^{-3} (furchilia 5) and from 0.5 to 17 ind. 100 m^{-3} (furchilia 6). Older stage of calyptopis (calyptopis 3) and younger stages of furchilia (1, 2 and 3) were sampled every year (Table 4). No correlation was observed between the frequency of occurrence and abundance for calyptopis 3 ($R = 0.40$, $P > 0.05$), furchilia 1 ($R = 0.72$, $P > 0.05$) and 2 ($R = 0.78$, $P > 0.05$), because there was no match between these two data. The highest abundances of furchilia 1 and 2 occurred in 2005 whereas their highest frequencies of occurrence were in 2007 while in the case of calyptopis 3 it was in 2008 (Table 4). However, furchilia 3 showed a significant correlation between its frequency of occurrence and its abundance (highest abundance, 150 ind. 100 m^{-3}), both with highest values in 2007 (Table 4).

Multiple Correspondence Analysis (MCA) (Fig. 5) was undertaken on data of euphausiid larval abundances from 2004 to 2008. Axes 1 and 2 represented 18.7 and 10.5% of the inertia, respectively. The first axis was in opposition with the lowest abundances of euphausiid larvae on its positive part in 2004, and the highest

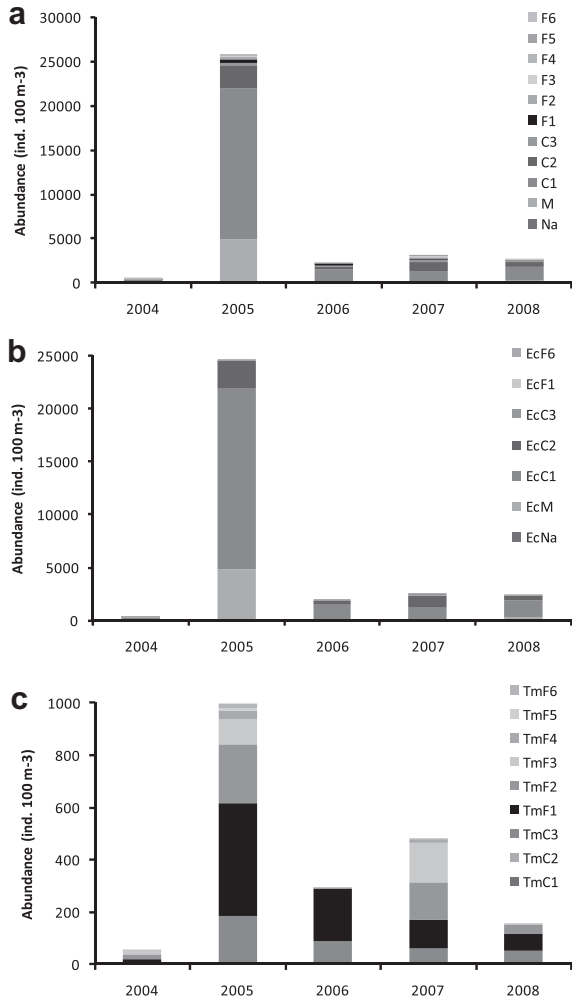


Fig. 4. Total abundances (ind. 100 m⁻³) of (a) the whole euphausiid larvae, (b) *Euphausia crystallorophias* larvae (Ec) and (c) *Thysanoessa macrura* larvae (Tm) of the study area from 2004 to 2008 (Na, Nauplius; M, Metanauplius; C1 to C3, Calyptopis 1 to 3; F1 to F6, Furcilia 1 to 6).

Table 4

Frequency (number of sampling sites where stages are collected × 100/total number of sampling sites) of development stages for *Euphausia crystallorophias* and *Thysanoessa macrura* from 2004 to 2008.

Year	<i>Euphausia crystallorophias</i>						<i>Thysanoessa macrura</i>									
	N2	M	C1	C2	C3	F1	F6	C1	C2	C3	F1	F2	F3	F4	F5	F6
2004	30	86	57	30	19	5	3	14	3	35	41	27				3
2005	4	100	96	87	30					48	83	52	26	17	9	
2006		84	96	96	32					64	88	8	4			
2007		53	100	100	87			13	60	100	100	93	47	13		
2008		6	72	100	100	44				67	89	83	33			

(N2, Nauplius 2; M, Metanauplius; C1 to C3, Calyptopis 1 to 3; F1 to F6, Furcilia 1 to Furcilia 6).

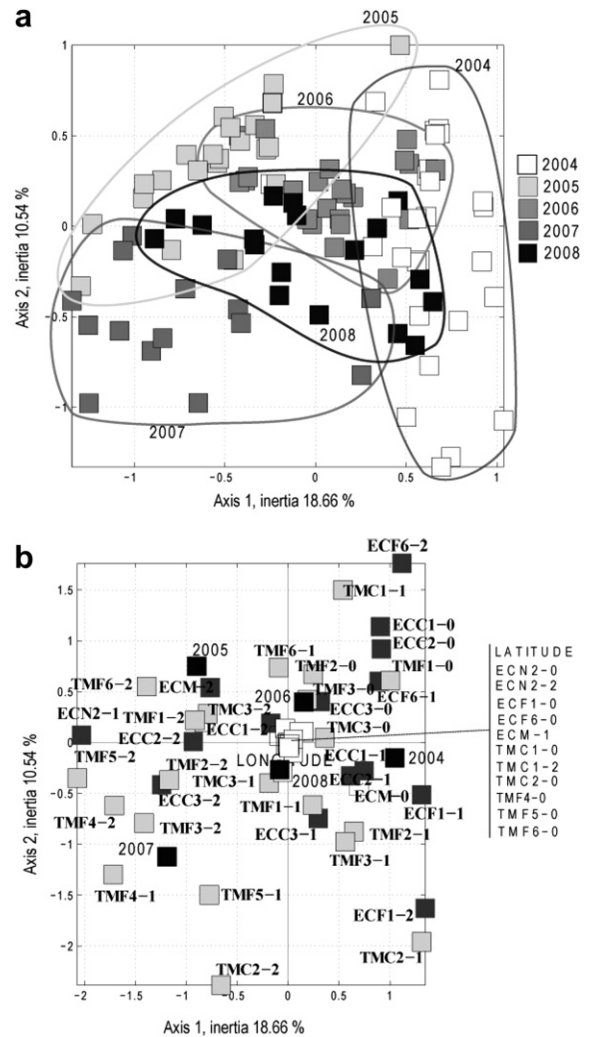


Fig. 5. Plan defined by the 1–2 axes of the Multiple Correspondence Analysis (MCA) of the stations (a) and larval stage classes (b).

abundances recorded in 2005 on its negative part (Fig. 5a). This result is consistent with data presented in section “3.3. Euphausiid larvae abundance”. This means that around 19% of the variability is due to overall larval abundance. Axis 2 was characterised by the highest abundance of stages of *E. crystallorophias* on its positive part in 2005, and, in opposition on its negative part, by the highest abundances of some stages of *T. macrura*, especially furcilia 3 observed in 2007 (Fig. 5b).

3.5. Euphausiid larvae distribution

The spatial distribution of euphausiid larvae fluctuated strongly from year to year (Fig. 6). Maximal abundance was observed on the Adélie bank in 2004, in the Commonwealth Bay in 2005, around the MGT in

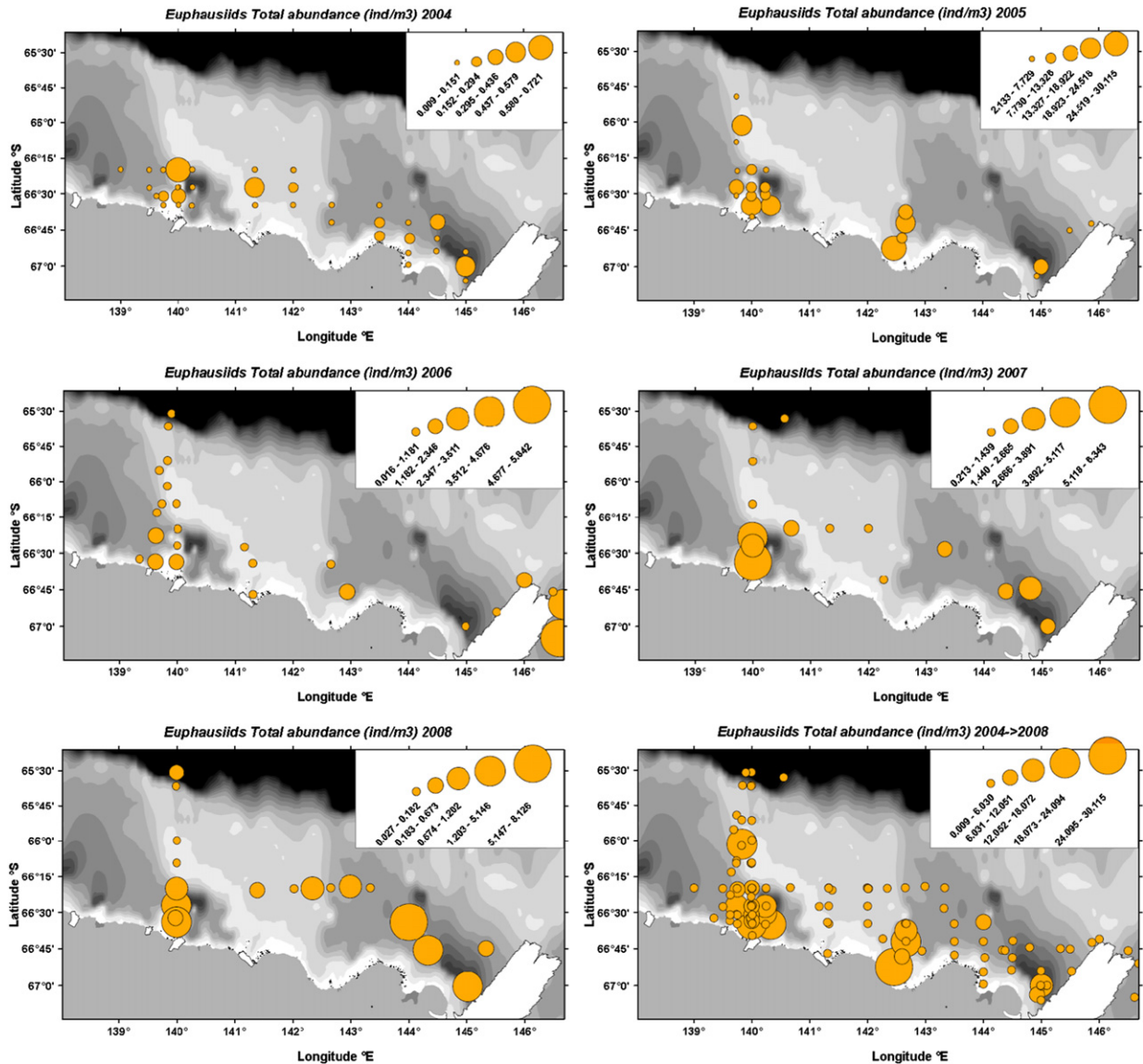


Fig. 6. Spatial distribution and abundance (ind. 100 m^{-3}) of the euphausiid larvae from 2004 to 2008.

2006, in front of Dumont d'Urville in 2007 and in the Adélie depression in 2008 (Fig. 6).

Fig. 6f shows the spatial distribution of euphausiid larvae annually, as well as a panel with the grouped data set from all years sampled. This figure shows that euphausiid larvae were present in high abundance preferentially near the coasts of the Dumont d'Urville and in the Commonwealth Bay.

In order to understand the spatio-temporal distribution, total abundance of *E. crystallorophias* and *T. macrura* larvae was plotted against the mean density of both surface and deep water layers (Fig. 7). Irrespective of the euphausiid species, their maximal abundances were

observed in surface layer around densities between 27.7–27.9 (Fig. 7), corresponding to the mean density of the surface water layer from 2004–2007. Moreover, the abundance of euphausiid larvae of both species were maximal within two limited ranges of deep water densities (Fig. 7): at 27.7 corresponding to mean density of deep water layer in 2008 (Table 2), and between 28.3 and 28.5 which was the range of mean density of deep water layer from 2004 to 2007 (Table 2).

The relationships between the spatio-temporal distributions of larvae and the environmental data were assessed with an RDA (Fig. 8). For *E. crystallorophias*, four environmental variables explained

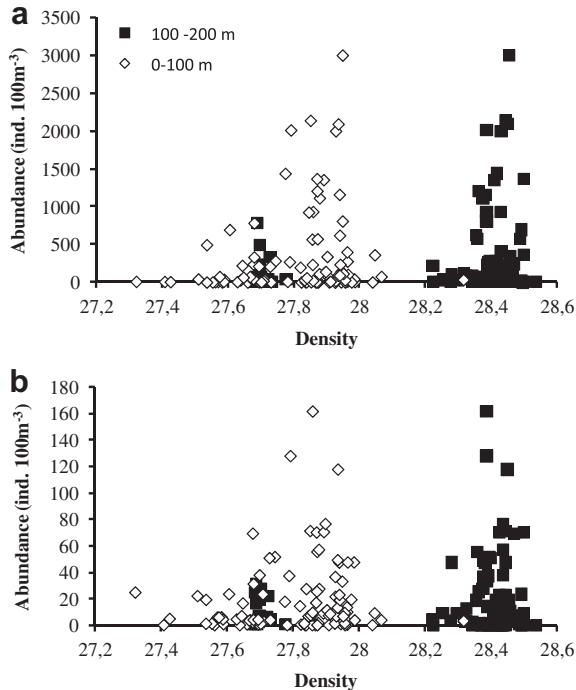


Fig. 7. Abundance (ind. 100 m⁻³) of (a) *E. crystallorophias* and (b) *T. macrura* larvae according to mean densities of surface layer (0–100 m) and deep water layer (100–200 m).

the statistically significant proportions of variation in the developmental stages data: D_{100–200} ($P < 0.01$), S_{100–200} ($P < 0.02$), T_{100–200} and number of days ('Days') between the end of the sea ice retreat and the sampling day at each station ($P < 0.05$). Two canonical axes were necessary for interpretation because the variance percentage of the species-environment relationship explained by the first canonical axis was only 58%. D_{100–200} and S_{100–200} were negatively correlated with the first axis (–0.57) and positively correlated with the second axis (0.26). 'Days' was positively correlated with the first (0.63) and second (0.65) axis. T_{100–200} was positively correlated with the first axis (0.28) and negatively with the second (–0.49). Metanauplius, calyptopis 1 and 2 were positively correlated with density and salinity, and negatively correlated with temperature of the deep water layer, and independent of 'Days' (Fig. 8a). However, calyptopis 3 was positively correlated with 'Days' and independent of density, salinity and temperature (Fig. 8a). From these results, it appears that younger larval stages (metanauplius, calyptopis 1 and 2) tend to be spatially distributed according to deep water density, while calyptopis 3 was more abundant when the interval between the end of the sea ice retreat and the sampling

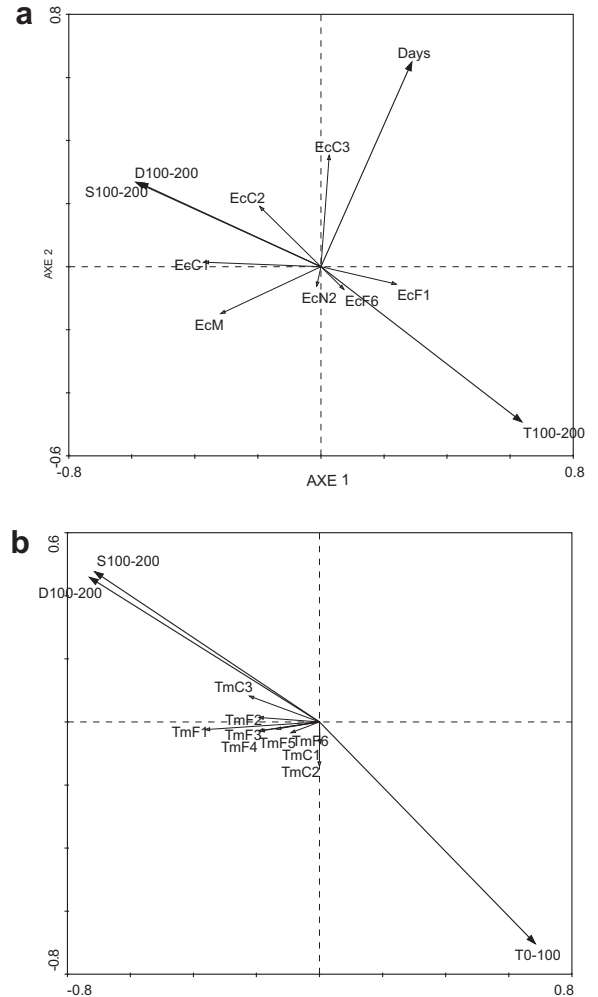


Fig. 8. Redundancy analysis (RDA) of (a) log-transformed abundance of *Euphausia crystallorophias* and environmental parameters (mean salinity, temperature, density of deep layer: S_{100–200}, T_{100–200}, D_{100–200}), and (b) log-transformed abundance of *Thysanoessa macrura* and environmental parameters (mean salinity and density of deep layer: S_{100–200}, D_{100–200}; mean temperature of surface layer: T_{0–100}) from 2004 to 2008.

day was longer. For *T. macrura*, salinity ($P < 0.05$) and density ($P < 0.01$) of the deep water layer and temperature ($P < 0.05$) of surface water layer could explain significant proportions of variation in larval stage distribution (Fig. 8b). The first axis explained approximately 40% of variance of the species-environment. Salinity and density of deep water layer were negatively correlated with axis 1 (–0.72) while temperature of surface layer was correlated with both axis 1 (0.68) and axis 2 (–0.70). Most of developmental stages of this species were positively correlated with salinity and density of deep water layer and independent of surface layer temperature (Fig. 8b).

Our statistical analysis indicates that deep layer density and salinity seem to be the principal environmental factors which govern the spatio-temporal distribution of both species.

4. Discussion

Only two species of euphausiid larvae, *E. crystallorophias* and *T. macrura* were found during the surveys conducted from 2004–2008 (Table 5). No larvae of the Antarctic krill, *E. superba*, were found unlike the study of Falk-Petersen et al. (1999) who observed the larvae of *E. superba* extending off Dronning Maud Land along a transect from the marginal ice zone close to the Antarctic ice shelf to open waters in January 1993.

In our study, we saw older developmental stages of *T. macrura* than those of *E. crystallorophias*. This age difference in developmental stages coincided with the spawning period for each species. Several workers (Harington and Thomas, 1987; Hosie and Kirkwood, 1986; Makarov, 1979; Pakhomov and Perissinotto, 1996) have noted that *T. macrura* spawns well before the phytoplankton bloom from early September to late October, while *E. crystallorophias* spawns in November–December, usually just before the onset of phytoplankton blooms. *E. superba* appears to be the last to start spawning around March in Dumont d'Urville Sea. Like

other southern areas in Antarctic Ocean (Fevolden, 1980; Hempel and Hempel, 1982; Makarov, 1979; Makarov and Menshenina, 1992; Menshenina, 1990), in the Dumont d'Urville Sea euphausiids started spawning in the following order: *T. macrura* - *E. crystallorophias* - *E. superba*.

In this study, the calyptopis 1 was by far the most common stage of *E. crystallorophias* seen annually. When sampling was conducted in early January (2005, 2006 and 2008), the metanauplius stage was present in abundance but when cruises occurred after the mid-January, (2004 and 2007) older stages such as calyptopis 2 and 3 and few furcilia 1 and 6 were observed. Our results are consistent with those of Kirkwood (1996) in Prydz Bay and in the Cooperation Sea (Pakhomov and Perissinotto, 1996) where they observed metanauplius and calyptopis 1 in January and calyptopis 3 and few furcilia 6 in February. As suggested by Menshenina (1990), *E. crystallorophias* larvae developed in summer until the furcilia 2 stage and began overwintering in late summer. Pakhomov and Perissinotto (1996) suggested that stages from furcilia 3 to furcilia 6 would develop under ice during winter and could be found in January–February in the near-coastal water the next summer.

The most commonly observed stage of development of *T. macrura* was furcilia 1. Furcilia 2 and 3 were dominant in 2007, when sampling was conducted in late

Table 5
Comparisons of mean abundance (ind. 100 m⁻³) of euphausiid larvae collected in different site around Antarctica.

Species	Location	Period	Depth (m)	Mean abundance (ind. 100 m ⁻³)	SE	Range (ind. 100 m ⁻³)	Reference
<i>Euphausia crystallorophias</i>	Cooperation Sea	Jan 1980	0–500	25.1	22.6	9.1–41.1	Pakhomov and Perissinotto, 1996
		Jan–Feb 1980	0–500	5.4	5.5	3.9–132.1	
		Jan 1986	0–100	348.7	418.7	80.0–970.0	
		Jan–Feb 1988	0–500	631.1	720.2	3.7–1537.6	
	Cosmonaut Sea	Jan–Feb 1987	0–500	2.2	1.5	0.4–3.4	Hosie and Kirkwood, 1986
		Prydz Bay	Jan–Feb 1984	0–200		0.0 - ≥ 100.0	
	Lazarev Sea	Jan 1995	0–300	50.7	43.6	2.7–169.0	Pakhomov et al., 1998
	Dumont d'Urville Sea	Jan 2004	0–200	10.5	11.7	0.4–52.8	Vallet et al., 2009; this study
		Jan 2005	0–200	1005.1	767.6	131.0–2926.3	This study
		Jan 2006	0–200	40.4	42.2	0.0–566.6	
Jan 2007		0–200	168.0	167.4	9.8–571.5		
Jan 2008		0–200	134.8	210.6	1.6–781.5		
<i>Thysanoessa macrura</i>	Gerlache Strait	Nov 1989	0–290	31.8	40.1	0.0–178.1	Nordhausen, 1994
	Dumont d'Urville Sea	Jan 2004	0–200	1.5	1.9	0.0–5.9	Vallet et al., 2009; this study
		Jan 2005	0–200	43.3	42.6	0.0–161.4	This study
		Jan 2006	0–200	12.0	16.4	0.0–49.1	
		Jan 2007	0–200	32.2	22.6	8.4–76.4	
		Jan 2008	0–200	8.8	9.4	0.7–31.1	

(SE: standard error).

January. In Dumont d'Urville Sea, early larval stages may occur from September to December. Makarov (1979) explained that this timing of development took place in spring principally to avoid competition with other euphausiids. Moreover, Makarov and Menshenina (1992) showed a spatial difference in stage composition and abundance of *T. macrura* larvae in a March 1981 study of the Lazarev Sea, a sector of the Southern Ocean along Queen Maud Land. They found that *T. macrura* mainly spawns in the northwest part of the area. Its hatched larvae are then carried in a south-eastern direction during their development, with smaller numbers and more advanced stages in the south-east. It would be interesting to conduct investigations in northern part of Dumont d'Urville Sea in order to see if a similar pattern exists for this species.

The mean abundance of both *E. crystallorophias* and *T. macrura* varied strongly between areas as well as annually, but *E. crystallorophias* was dominant every year (Table 5). The highest mean abundance of *E. crystallorophias* was observed in 2005 at Dumont d'Urville Sea with more than 1000 ind. 100 m⁻³ and in the Cooperation Sea in January–February 1988 with 631 ind. 100 m⁻³ (Table 5). However, very low abundances could be found in the same areas, especially during the summer of 2004 at Dumont d'Urville Sea and at Cooperation Sea during January–February of 1980 (Table 5). Surveys in Dumont d'Urville Sea and in Cooperation Sea occurred at the same latitudes and in near-coastal waters. Consequently, these results confirm previous reports which showed that larvae of *E. crystallorophias* are the dominant species of euphausiids in the near-coastal waters of Antarctica (Hosie and Kirkwood, 1986; Kirkwood, 1996). In the case of *T. macrura*, the highest abundances were observed in January 2005 at Dumont d'Urville Sea and in November 1989 in the Gerlache Strait (Nordhausen, 1994) (Table 5). As suggested by Nicol et al. (2008), it is not surprising that several surveys on euphausiid larvae conducted in different years resulted in measurably different estimates of abundances. Euphausiids, like other zooplanktonic organisms, inhabit a fluid environment which is known to change significantly from year to year both in its structure and in the biological responses to these changes (Nicol et al., 2008). What our study has shown is that some environmental data, such as density, salinity, temperature or 'Days' between the end of the sea ice retreat and sampling, played an important role in the spatio-temporal variability of the abundance of larvae. The spatio-temporal distribution of larvae of *E. crystallorophias* were negatively correlated with temperature of the deep water layers and positively

correlated with density and salinity of the deep water layers. This result was consistent with the findings of Daly and Zimmerman (2004), who showed that *E. crystallorophias* larvae were more closely associated with the pycnocline (ca. 100 m) and increasing sea-water temperatures (0–2 °C) in deeper water. We can hypothesize that because the developmental stages of *T. macrura* larvae were also correlated to density and salinity of deep water layer and temperature of surface water layer, its spatio-temporal distribution could also be dependent on the pycnocline and increasing sea-water temperatures of the surface layer (Fig. 8b).

Pakhomov and Perissinotto (1996) highlighted that the highest abundance of *E. crystallorophias* larvae coincided with earlier ice breakout, suggesting that its spawning success may in general depend on the ice breakout factor. In this study, the highest abundances of *E. crystallorophias* larvae were observed in 2005 and the lowest in 2004. In 2003, the sea ice breakout occurred in late November while in 2004, it started six days earlier and stopped three days earlier (Fig. 2). This difference in the timing of the sea ice retreat between two consecutive years could explain the difference in abundance. However, even though sea ice retreat in 2005 and 2006 occurred much earlier in November than in 2004, abundances of *E. crystallorophias* larvae in 2006 and 2007 varied by nearly an order of magnitude compared to 2005, and were five to seven times higher than in 2004 (Fig. 4b). These results tend to confirm that when the sea ice retreat occurred earlier in November in the Dumont d'Urville sea, the abundance of *E. crystallorophias* was generally higher. Nevertheless, another factor seems to play an important role in the variability of abundance of *E. crystallorophias*. Falk-Petersen et al. (2000) demonstrated that reproductive processes of *E. crystallorophias* depended on the accumulation of large lipid deposits during autumn, which provided enough energy both for survival during the food-limited dark season as well as sexual maturation and early spawning prior to the spring bloom. We can suggest that the best spawning event, and thus the highest abundance of *E. crystallorophias*, will occur when ice breakout is early and immediately prior to the spring bloom and that the accumulation of large lipid deposits are at their maximum. Our study clearly demonstrates that because of the favourable conditions observed, 2005 was a good recruitment year for *E. crystallorophias*.

In contrast, *T. macrura* seems to be less dependent on sea ice retreat than *E. crystallorophias* because it spawns much earlier than *E. crystallorophias*, before the onset of the phytoplankton bloom in late November.

Even if its spawning period was independent of the bloom (Falk-Petersen et al., 2000; Hagen and Kattner, 1998), the abundances of larvae varied strongly from one year to another during summer. Hagen and Kattner (1998) demonstrated that *T. macrura* was able to change its food supply during its life cycle, younger stages being more herbivorous and adults, omnivores or carnivores. Thus, the first feeding stage (calyptopis 1) of *T. macrura* started to accumulate large amounts of lipid from the early phytoplankton bloom. Consequently, SIC and timing of sea ice retreat must influence the survival of the younger developmental stages in late spring and thus, abundances of older stages in summer. As in the case of *E. crystallorophias*, the highest abundance of larvae of *T. macrura* occurred in 2005. During November 2004, SIC was relatively low, allowing greater irradiation at the surface waters (Swadling et al., 2011). These conditions facilitated primary production and younger stages of *T. macrura* found enough food supply to survive and grow. Our results showed a second peak in abundance of *T. macrura* in 2007, which can be explained by similar SIC conditions in November 2006.

In February 2010, a large iceberg collided with the MGT, reducing the length of the tongue by 80% (Young et al., 2010) and presumably inducing a new circulation pattern in the Dumont d'Urville Sea which would influence both sea ice and bottom-water formations in this area. Additional studies are needed to assess the possibly modified distribution of *E. crystallorophias* and *T. macrura* larvae to better understand how these two species could continue to coexist successfully in the same environmental habitats.

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