Marine Biology Research

Seasonal variability of metazooplankton in coastal sub-Antarctic waters (Beagle Channel)

Gastón E. Aguirre [a] , Fabiana L. Capitanio [b c] , Gustavo A. Lovrich [c d] & Graciela B. Esnal [b c]

[a] Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Germany

[b] Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina

[c] Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina

[d] Centro Austral de Investigaciones Científicas, Ushuaia, Tierra del Fuego, Argentina

Available online: 14 Feb 2012

PLEASE SCROLL DOWN FOR ARTICLE

ORIGINAL ARTICLE

Seasonal variability of metazooplankton in coastal sub-Antarctic waters (Beagle Channel)

GASTÓN E. AGUIRRE[1]★, FABIANA L. CAPITANIO[2,3], GUSTAVO A. LOVRICH[3,4] & GRACIELA B. ESNAL[2,3]

[1]*Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Germany,* [2]*Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina,* [3]*Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina, and* [4]*Centro Austral de Investigaciones Científicas, Ushuaia, Tierra del Fuego, Argentina*

Abstract
The aim of this study was to analyse the variability in the species composition and abundance of the metazooplankton community in different coastal areas of the Beagle Channel (southern tip of South America) during a seasonal cycle. Sampling was conducted during November (spring) 2005, March (summer), June (autumn) and September (winter) 2006 at 12 coastal stations. Copepods were the most abundant group throughout the study, and their assemblages were composed of a mixture of species typical of the south-western Atlantic, the south-eastern Pacific and the Southern Ocean. Among them, *Oithona similis*, *Ctenocalanus citer* and *Drepanopus forcipatus* were the dominant species. The copepod *Acartia tonsa* was the only taxon that displayed a spatial pattern of abundance, showing higher densities in areas with lower salinities. The community structure showed a strong temporal pattern. The metazooplankton community in March and June was mainly composed of copepods, while in November and September the community showed a greater diversity. In these two months high densities of meroplanktonic larvae were found, in coincidence with higher chlorophyll-*a* concentration. This temporal pattern seems to be more dependent on primary production than on physical factors such as temperature or salinity. The absence of a clear spatial pattern may suggest that the studied area of the Beagle Channel behaves as a semi-enclosed water body.

Key words: *Zooplankton, community structure, Beagle Channel, sub-Antarctic*

Introduction

The Beagle Channel is situated on the southern tip of South America. It is part of the Fuegian system of fjords and channels of the Magellan region, and its waters belong to the sub-Antarctic neritic domain (Boltovskoy et al. 1999; Hamamé & Antezana 1999). The Fuegian system receives the influence of the Pacific Ocean from the east and of the Atlantic Ocean from the west. It also receives intrusions of Antarctic waters, based on the presence of Antarctic planktonic species in the waters of the Fuegian archipelago (Antezana 1999a).

The zooplankton assemblages of this ecosystem, although part of the sub-Antarctic Magellan region, have been characterized as a distinct and less diverse biota than the open ocean (Hamamé & Antezana

1999; and references therein). Most of the studies on the zooplankton of the Beagle Channel have been performed during the austral spring. During this season, copepods account for more than two-thirds of total zooplankton, followed in density by appendicularians, euphausiids and cladocerans (Defren-Janson et al. 1999). In addition, gelatinous carnivores were reported as an abundant group in the Channel, among which the hydromedusae *Bougainvillia macloviana*, *Clytia simplex* and *Obelia* spp. are the dominant taxa (Pagès & Orejas 1999). The macro-zooplankton (2–20 mm) shows low species richness, being represented almost exclusively by the siphonophore *Muggiaea atlantica*, the chaetognath *Sagitta tasmanica*, and the euphausiid *Euphausia vallentini* (Palma & Silva 2004). Moreover, larvae of benthic

invertebrates reach densities of up to 18% of total zooplankton abundance during spring (Hamamé & Antezana 1999), among which decapod crustacean larvae show a high diversity (Thatje et al. 2003). The coincidence of the spring bloom of phytoplankton with these high abundances of invertebrate larvae has been pointed out as evidence of strong bentho-pelagic coupling in this area (Antezana 1999a).

The zooplankton community of Bahía Ushuaia and Bahía Golondrina, which are located on the northern coast of the Beagle Channel, has been studied in detail during summer (Fernández-Severini & Hoffmeyer 2005) and winter (Biancalana et al. 2007). In both seasons, assemblages of copepods are the main constituent in terms of abundance and are dominated by *Oithona similis* and *Ctenocalanus citer*.

All these previous studies on the metazooplankton community of the Beagle Channel were conducted with 200-μm or coarser mesh size nets. These nets may strongly undersample the smaller copepod species (Galliene & Robbins 2001) and other small metazooplankters such as appendicularians (Jaspers et al. 2009), which are important prey for larval fish (e.g. Purcell et al. 2004) and a trophic link between classical and microbial food webs (e.g. Calbet et al. 2000).

The zooplankton community of this austral area is exposed to a large degree of spatial heterogeneity related to salinity gradients (Palma & Silva 2004). These gradients may be seasonal due to the high-latitude location of this area, and driven by seasonal variations in precipitation and solar radiation. Nevertheless, the work of Lovrich (1999) represents the only study in which the seasonality of a zoo-planktonic group (decapod larvae) has been analysed in the Beagle Channel.

The aim of this study is to investigate the variability in the species composition and abundance of the metazooplankton community in different coastal areas of the Beagle Channel during a seasonal cycle. In particular, we are interested in assessing the quantitative importance in terms of abundance of the smaller metazooplankters, such as appendicularians and small copepods (<1 mm size).

Materials and methods

Study area

The Beagle Channel is 180 km long and has an average width of 5 km (Bujalesky et al. 2004). It has been defined as a shallow (<100 m) marine environment with an estuarine hydrographic regime because the contribution of continental waters originating from nearby rivers, streams and glaciers, causing salinity levels to be generally below 32 psu

(Isla et al. 1999; Palma & Silva 2004). The predominant current runs from west to east along the Channel (Balestrini et al. 1998). Nevertheless, the presence of shallow (<50 m) glacial sills at the eastern and western end of the Beagle Channel may limit water exchange with the surrounding oceans (Antezana 1999b).

The area under study is located on the northern coast of the Beagle Channel (54°48′–54°54′S, 67°30′–68°35′W), mainly in the waters between the Isla Navarino and the Isla Grande de Tierra del Fuego (Figure 1). According to Klöser (1996), these islands act as barriers to give this part of the Channel the character of a semi-enclosed water body. In this area the surface water temperature ranges from 4.2–4.3°C in August to 8.9–9.8°C in January, while salinity ranges from 26.7 psu in November–December to 31.3 psu during July (Balestrini et al. 1998).

Sampling was conducted at 12 coastal stations (25–30 m depth). They were grouped on the basis of their geographical location and their biophysical characteristics into three areas: west (stations 1–4), middle (stations 5–9) and east (stations 10–12). The west area comprised Bahía Lapataia and Bahía Ensenada which are surrounded by the protected areas of the National Park Tierra del Fuego. These bays have marked estuarine characteristics, with a large sediment supply from rivers and meltwater of nearby glaciers (Isla et al. 1999; Bujalesky et al. 2004). The middle area comprised Bahía Golondri-na and Bahía Ushuaia, which are characterized by important rock outcrops (Bujalesky 1998) and high densities of the macroalgae *Macrocystis pyrifera* (Agardh, 1820), which forms extensive submarine forests (Pérez-Barros et al. 2004). Moreover, its shores are influenced by the contribution of organic matter of anthropogenic origin and pollutants such as heavy metals (e.g. Amin et al. 1996) from the city of Ushuaia (>70,000 inhabitants), which has a coastal front of ca. 20 km. Finally, the east area comprised Bahía Brown and Punta Paraná, where the glacier runoff is scarce (Isla et al. 1999). Here, the bottom is mostly sandy with a few rocky out-crops, and several species of bivalves like *Eurhomalea* spp. (Cossmann 1920), *Mytilus edulis chilensis* (Linnaeus 1758) and *Tawera gayi* (Hupé 1854) are present (Diez & Lovrich 2010).

Sampling design

Sampling was conducted between 4–22 November 2005 (spring), 5–20 March (summer), 6–20 June (autumn) and 4–21 September (winter) 2006, during daylight.
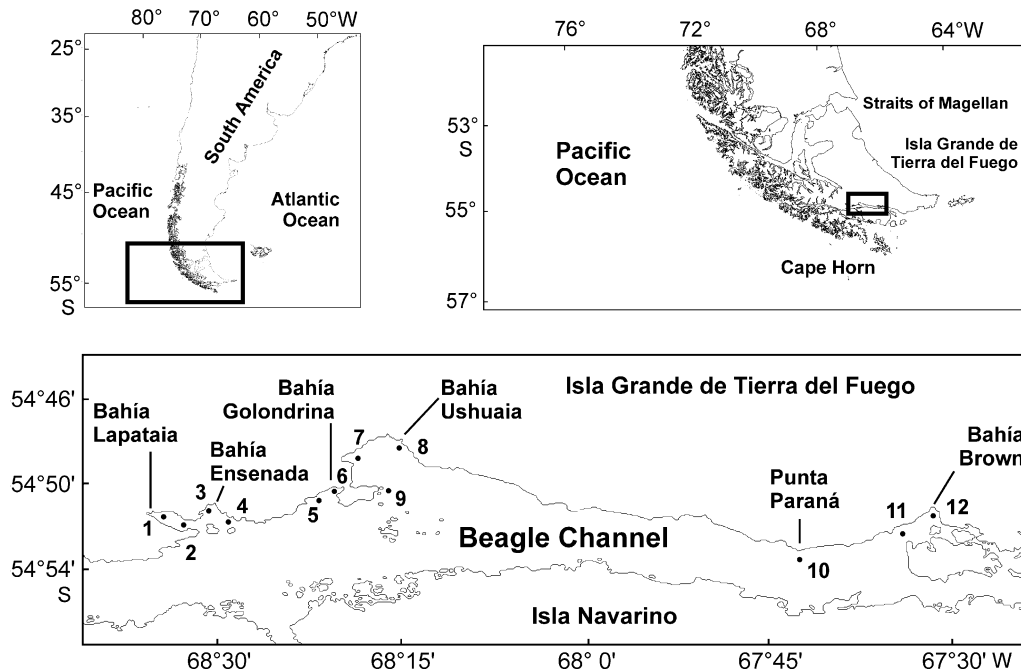
Figure 1. Map including the study area and the sampling stations location.

At each station, surface temperature and salinity were measured at 1 m depth with a Horiba U-10 multiprobe. At this same depth, water was collected with a Niskin bottle for chlorophyll-*a* concentration analysis. Water was kept in dark bottles until arrival at the laboratory, where it was immediately filtered through Whatman GF/F filters. Chlorophyll-*a* extraction was performed with 90% acetone, and its concentration was measured with a spectrophotometer before and after acidification with 0.1 N HCl for a correction for phaeopigments, according to Strickland & Parsons (1972).

Zooplankton samples were collected through the whole water column by obliquely towing from bottom to surface a 100-μm mesh size net, with 0.13 m^2 mouth area, and equipped with a General Oceanics flowmeter to estimate the filtered volume. The filtered volumes (mean $\pm$ SD) were 1.2 ± 0.6 m^3 (November), 27.2 ± 8.9 m^3 (March), 40.8 ± 19.1 m^3 (June) and 11.1 ± 7.2 m^3 (September). The lowest mean volume of water was filtered in November to avoid clogging due to the high amount of chain-forming diatoms in the water. The samples were preserved in 5% seawater formalin, previously buffered with sodium borate. Preserved samples were further divided into varying aliquots in the laboratory employing a Folsom Plankton Splitter, and at least 200 individuals were counted in each taxon. In the case of the least-abundant taxa, the entire sample was analysed. Rotifers, copepod nauplii, copepodids and adult copepods, cladocerans, ostracods, appendicularians, hydromedusae and meroplanktonic larvae were enumerated. The specimens were identified

under stereomicroscope and optical microscope. The abundance values were expressed as individuals per m^{-3}.

The taxonomic identification was carried out to the lowest taxonomic level possible, according to Ruttner-Kolisko (1974), Mazzocchi et al. (1995), Boltovskoy (1999), Lovrich (1999) and Boxshall & Halsey (2004). Copepod nauplii were grouped without specific separation. The copepod *Oncaea curvata* (Giesbrecht 1902) was considered within the order Cyclopoida, according to Boxshall & Halsey (2004). In this study we registered the presence of the copepod *Ctenocalanus citer* (Heron & Bowman 1971). This species is very similar to the tropical and sub-tropical congeneric *Ctenocalanus vanus* (Giesbrecht, 1888), which has also been recorded on the near south-western Atlantic shelf (Fernández-Severini & Hoffmeyer 2005). Here, we followed the criteria of Heron & Bowman (1971) and Mazzocchi et al. (1995) for the identification of *C. citer*.

Data analysis

Pearson correlations were used to study the relationships among the environmental parameters. To study community structure, a similarity matrix was constructed from the abundance data previously $\log(x+1)$ transformed, using the Bray–Curtis similarity coefficient. The similarity between stations was plotted using a non-metric multidimensional scaling (MDS) according to Clarke & Warwick (2001). One-way ANOVA was used to analyse the metazooplankton community structure in the different

months and areas, along the two axes of the MDS. The similarity percentages (SIMPER) analysis was also performed on the $\log(x+1)$ transformed abundance data, allowing the contribution of each species or taxon to the average sample similarity within-groups to be examined. The abundance distribution of the four most abundant species or genus in each of the groups identified by the MDS analysis was plotted.

One-way ANOVA was used to compare the spatial distribution of each zooplankton taxon. Prior to the analysis, data were normalized by logarithmic transformations $\log(x+1)$ to meet the assumptions of normality and homogeneity of variances. When significant differences were found, areas were compared using the Tukey–Kramer test.

Results

Environmental gradients

The minimum and maximum surface temperatures were registered in the west area: $4.5°C$ in September (station 4) and $10.3°C$ in November (station 3), respectively. The temperature showed a clear temporal variability, and was higher in March ($9.0 \pm 0.4°C$) and November ($8.8 \pm 0.8°C$) compared to June ($5.7 \pm 0.6°C$) and September ($5.2 \pm 0.3°C$) (Figure 2A).

Surface salinity exhibited both temporal and spatial variations. The minimum and maximum salinities were registered both in November: 21.7 psu (station 1, west area) and 32.0 psu (station 10, east area), respectively. Hence, November was the month that showed the highest salinity variability among sites. Mean salinity was lower in November (28.2 ± 3.4 psu) and March (29.1 ± 3.3 psu) compared to September (31.0 ± 0.6 psu) and June (31.0 ± 0.3 psu). In the spatial scale, the west area registered the lowest salinity values during November (21.7 psu, station 1), March (23.9 psu, station 3) and September (29.2 psu, station 4) (Figure 2B).

Surface chlorophyll-*a* concentration showed a clear temporal variation. A minimum of chlorophyll-*a* was registered in the west area in June (0.01 mg m^{-3}, station 3), and the maximum was in the middle area in November (3.06 mg m^{-3}, station 8). Mean chlorophyll-*a* was higher in November (1.23 ± 0.74 mg m^{-3}) and September (0.95 ± 0.19 mg m^{-3}) compared to June (0.47 ± 0.37 mg m^{-3}) and March (0.26 ± 0.19 mg m^{-3}) (Figure 2C).

Temperature and salinity were negatively correlated ($r = -0.373$, $p < 0.01$). On the other hand, chlorophyll-*a* was not correlated with temperature or salinity ($p > 0.01$).
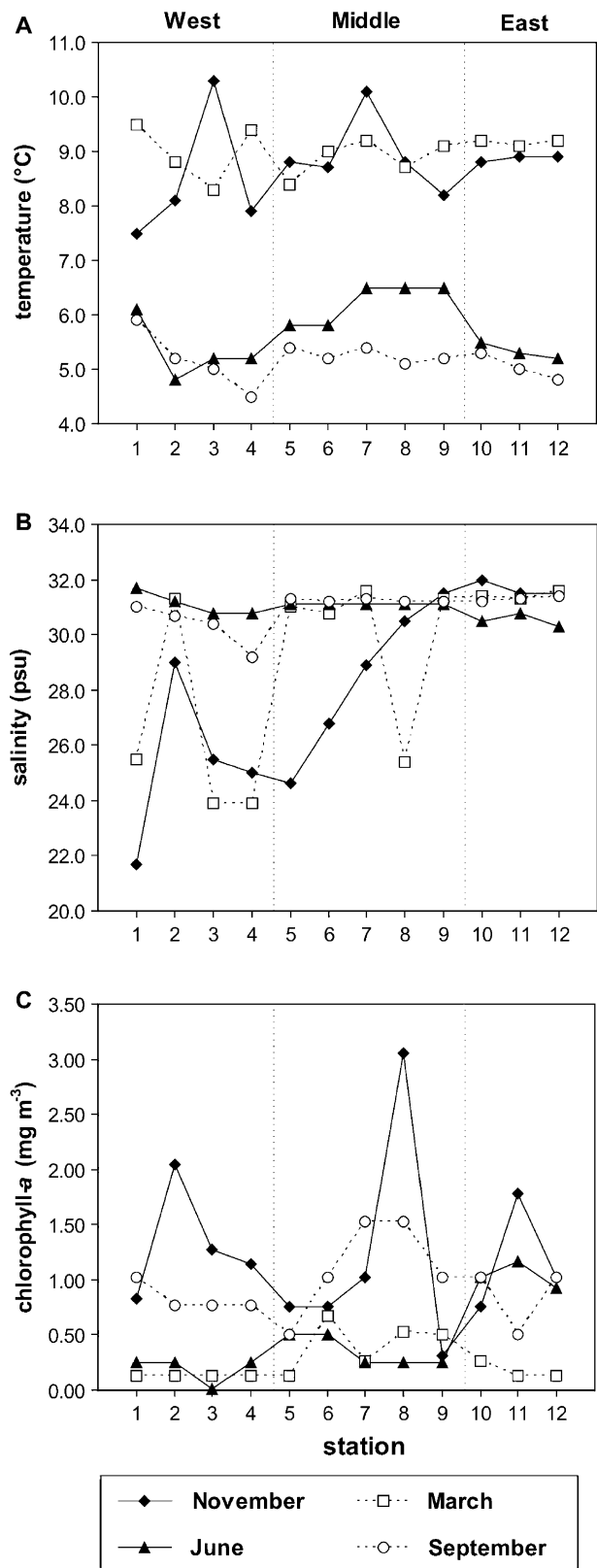

Figure 2. Surface temperature (A), salinity (B) and chlorophyll-*a* concentration (C) values for each sampling station in the Beagle Channel, during November 2005, March, June and September 2006. The areas – west, middle, east – in which the stations were grouped are indicated.

Table I. Mean density (ind m^{-3}) of zooplanktonic taxa in the west, middle and east areas of the Beagle Channel, during November 2005, March, June and September 2006. The standard deviations are indicated between parentheses. W: west, M: middle, E: east. L: larvae.

	NOVEMBER			MARCH			JUNE			SEPTEMBER		
	W	M	E	W	M	E	W	M	E	W	M	E
Total zooplankton	20,236	15,452	59,266	27,439	42,439	16,823	4298	1406	1399	2629	6030	14,201
	(16,126)	(9139)	(21,960)	(12,416)	(29,956)	(4557)	(2060)	(473)	(883)	(1743)	(5909)	(9328)
ROTIFERA												
Synchaeta sp.	4379	5081	22,718	0	0	0	0	0	0	106	3628	6842
(Ehrenberg, 1832)	(3113)	(6175)	(16,666)							(146)	(4873)	(3130)
COPEPODA												
Nauplii	4891	3429	20,553	21,352	35,063	9998	1692	781	862	493	1307	2931
	(3877)	(2424)	(8872)	(11,644)	(28,177)	(3025)	(986)	(282)	(537)	(339)	(1563)	(4514)
Acartia tonsa	3139	53	135	826	171	1046	342	1.5	17	64	0	0
(Dana, 1849)	(4457)	(66)	(234)	(957)	(250)	(1414)	(551)	(3.3)	(15)	(89)		
Calanoides patagoniensis	0	0	0	0	111	45	0	0	0	9.8	0	0
(Brady, 1883)					(249)	(18)				(16.9)		
Calanus australis	0	0	45	4.4	16	0	0	0	0	0	0	0
(Brodskii, 1959)			(78)	(5.1)	(13)							
Centropages brachiatus	150	31	822	115	269	12	0	0	0	5.2	2.0	6.3
(Dana, 1849)	(301)	(69)	(234)	(46)	(319)	(10)				(10.3)	(4.4)	(10.9)
Clausocalanus brevipes	49	54	143	0	26	131	129	13	13	0	12	0
(Frost & Fleminger, 1968)	(98)	(67)	(147)		(57)	(139)	(62)	(23)	(22)		(24)	
Ctenocalanus citer	195	1193	3049	372	582	512	743	135	149	40	46	373
(Heron & Bowman, 1971)	(391)	(1098)	(1381)	(627)	(1178)	(589)	(601)	(81)	(142)	(27)	(80)	(511)
Drepanopus forcipatus	385	310	584	4428	5417	4537	77	0	4.2	0	62	23
(Giesbrecht, 1888)	(475)	(358)	(897)	(2830)	(5419)	(4357)	(32)		(7.3)		(119)	(32)
Microsetella norvegica	0	23	66	16	29	41	4.7	6.2	4.4	0.1	0.5	0.7
(Boeck, 1864)		(28)	(35)	(6)	(22)	(9)	(4.1)	(2.7)	(6.0)	(0.1)	(0.4)	(0.9)
Oithona similis	3029	1340	3858	281	658	427	1294	450	336	321	162	398
(Claus, 1866)	(2302)	(785)	(1234)	(312)	(690)	(481)	(698)	(161)	(207)	(377)	(152)	(483)
Oncaea curvata	999	399	490	0.3	4.0	2.6	0.3	0.7	0.2	19	48	29
(Giesbrecht, 1902)	(1666)	(416)	(274)	(0.3)	(6.1)	(1.0)	(0.4)	(1.0)	(0.2)	(12)	(76)	(25)
Paracalanus parvus	0	0	135	8.8	3.0	1.6	0	0	0	0	0	0
(Claus, 1863)			(234)	(17.5)	(6.8)	(2.7)						
CLADOCERA												
Evadne nordmanni	1.0	0.6	0	0	0	0.8	0	0	0	0	<0.1	0
(Lovén, 1836)	(2.0)	(1.4)				(1.0)						
Podon leuckarti	10(5)	6.1	8.0	0.9	1.0	3.1	0	0	0	0	0.1	0.1
(Sars, 1862)		(3.1)	(7.0)	(0.3)	(1.8)	(4.0)					(0.1)	(0.1)
OSTRACODA	0.4	1.9	1.1	<0.1	0	0.1	0	<0.1	0	0.1	0.2	0.3
	(0.5)	(1.5)	(1.8)			(0.2)				(0.2)	(0.4)	(0.3)
APPENDICULARIA												
Fritillaria borealis	316	2553	5711	0.8	0.5	0.2	9.4	11	2.7	5.1	44	118
(Lohmann, 1896)	(281)	(1960)	(2288)	(0.6)	(0.7)	(0.3)	(13.1)	(8)	(2.8)	(4.6)	(53)	(190)
Oikopleura dioica	0	0	16	0.4	1.3	0	0.7	2.3	0.2	0.1	1.1	0.9
(Fol, 1872)			(13)	(0.3)	(0.9)		(0.4)	(1.8)	(0.2)	(0.1)	(1.6)	(1.3)
Oikopleura fusiformis	19	72	83	<0.1	0.1	0	0	<0.1	0	<0.1	<0.1	0
(Fol, 1872)	(25)	(93)	(31)		(0.2)							
HYDROZOA												
Bougainvillia macloviana	1.0	0.3	0	0	0	0	0	0	0	0	0	0.7
(Lesson, 1836)	(2.0)	(0.6)										(0.8)
Obelia sp.	16	28	81	<0.1	<0.1	0.1	<0.1	<0.1	0.1	0	<0.1	<0.1
(Péron & Lesueur, 1810)	(25)	(38)	(79)			(0.1)			(0.1)			

Table I (Continued)

Taxon	NOVEMBER			MARCH			JUNE		SEPTEMBER		
ASCIDIACEA (L)	0.2 (0.5)	5.9 (5.5)	0	<0.1	0.4 (0.7)	0.2 (0.2)	0.3 (0.3)	0.5 (0.5)	0	0	0
BIVALVIA (L)	944 (1043)	185 (161)	454 (302)	0.2 (0.3)	5.0 (5.1)	2.3 (0.4)	0.3 (0.2)	<0.1	19 (24)	2.9 (5.8)	0.2 (0.2)
BRYOZOA (L)	245 (476)	20 (19)	12 (7)	0.5 (0.4)	79 (79)	60 (25)	2.0 (1.9)	2.4 (0.7)	0.7 (0.6)	1.4 (1.9)	0.4 (0.1)
CIRRIPEDIA (L)	846 (939)	197 (237)	80 (78)	<0.1	<0.1	0	0.8 (1.0)	5.1 (5.7)	3309 (2690)	617 (887)	1542 (1008)
DECAPODA											
Halicarcinus planatus (L) (Fabricius, 1775)	0	0.5 (0.9)	0.7 (0.9)	0	0.1 (0.1)	1.1 (1.4)	0	0	1.6 (2.7)	1.0 (1.8)	0
Munida gregaria (L) (Fabricius, 1793)	0	0	1.0 (1.3)	<0.1	<0.1	0.2 (0.2)	0	0	11 (10)	0.2 (0.2)	<0.1
Pagurus spp. (L) (Fabricius, 1775)	0.1 (0.2)	0.5 (0.9)	0.3 (0.6)	0	<0.1	<0.1	0	0	0.5 (0.2)	0	<0.1
Peltarion spinolosum (L) (White, 1843)	6.1 (4.7)	14 (12)	3.1 (4.1)	0	0	0	0	0	0.8 (0.9)	0.1 (0.1)	<0.1
ECHINODERMATA (L)	5.3 (5.7)	107 (89)	30 (28)	0	<0.1	0	0	0	106 (171)	87 (89)	20 (14)
POLYCHAETA (L)	603 (599)	237 (122)	289 (193)	<0.1	0.6 (0.5)	0	<0.1	0.1 (0.1)	30 (29)	6.1 (5.8)	1.6 (1.1)

Metazooplankton community structure

Mean abundances of total zooplankton and zooplankton taxa varied according to area and season (Table I). In November, the community was composed mainly of copepods (52.2%) and the rotifer *Synchaeta* sp. (33.1%). Other abundant taxa were appendicularians (9.5%) and meroplanktonic larvae (5.1%) (Figure 3A). Among the appendicularians, *Fritillaria borealis* was the most abundant species. The meroplanktonic assemblage was composed mainly of bivalve, bryozoan and cirriped larvae (Table I).

In September, the community was dominated in terms of abundance by the rotifer *Synchaeta* sp. (46.9%), copepods (28.0%) and meroplanktonic larvae (24.3%). The meroplanktonic assemblage was composed mainly of cirriped larvae (Figure 3D).

The metazooplankton community was mainly composed of copepods during March (99.8%) and June (99.4%) (Figure 3B,C). In these months, *Synchaeta* sp. was completely absent from the plankton samples. Moreover, most of the meroplanktonic larvae taxa showed low densities, such as decapod larvae which were almost completely absent. Only bryozoan larvae showed high abundances during March (Table I).

In November, June and September, the copepod assemblages were dominated by the cyclopoid *Oithona similis* and the calanoid *Ctenocalanus citer*. During these three months, other abundant copepod species were *Acartia tonsa*, *Drepanopus forcipatus* and *Clausocalanus brevipes*, while the cyclopoid *Oncaea curvata* was abundant especially in November and September (Figure 4A,C,D). Most of the copepod species, such as *Calanus australis*, *Centropages brachiatus*, *C. brevipes*, *C. citer*, *Microsetella norvegica*, *O. similis* and *Paracalanus parvus*, showed their highest densities during November (Table I). In contrast, during March, *D. forcipatus* was the dominant copepod species, and *A. tonsa* the second most dominant (Figure 4B). The calanoid *Calanoides patagoniensis* was found mainly during this month (Table I).

The two-dimensional MDS plot showed a stress value of 0.11 (Figure 5). According to Clarke & Warwick (2001), stress levels between 0.1 and 0.2 provide a useful representation in two dimensions. Stations were grouped according to a temporal pattern by the MDS analysis. A temporal variation of the zooplankton community structure was observed in both axes of the MDS analysis (axis 1: $F_{3,48} = 402.287$, $p < 0.0001$, axis 2: $F_{3,48} = 58.065$, $p < 0.0001$). The community structure showed no geographical differences in either of the two axes (axis 1: $F_{2,48} = 0.062$, $p > 0.01$, axis 2: $F_{2,48} = 0.107$,

A. November

Meroplanktonic larvae 5.1%
(Bivalvia 38.3%,
Polychaeta 26.5%,
Cirripedia 25.3%,
Bryozoa 6.4%,
others 3.5%)

Copepoda
adults and
copepodites
22.9%

Rotifera
33.1%

Copepoda
nauplii 29.3%

Appendicularia 9.5%
(*Fritillaria borealis* 99.7%,
others 0.3%)

B. March

others 0.2%

Copepoda adults
and copepodites
21.7%

Copepoda
nauplii 78.1%

D. September

Meroplanktonic larvae 24.3%
(Cirripedia 94.6%,
Echinodermata 4.1%,
others 1.3%)

Copepoda adults
and copepodites
7.2%

Copepoda
nauplii 20.8%

Appendicularia
0.7%

Rotifera 46.9%

C. June

Copepoda
nauplii 46.7%

Appendicularia 0.6%

Copepoda
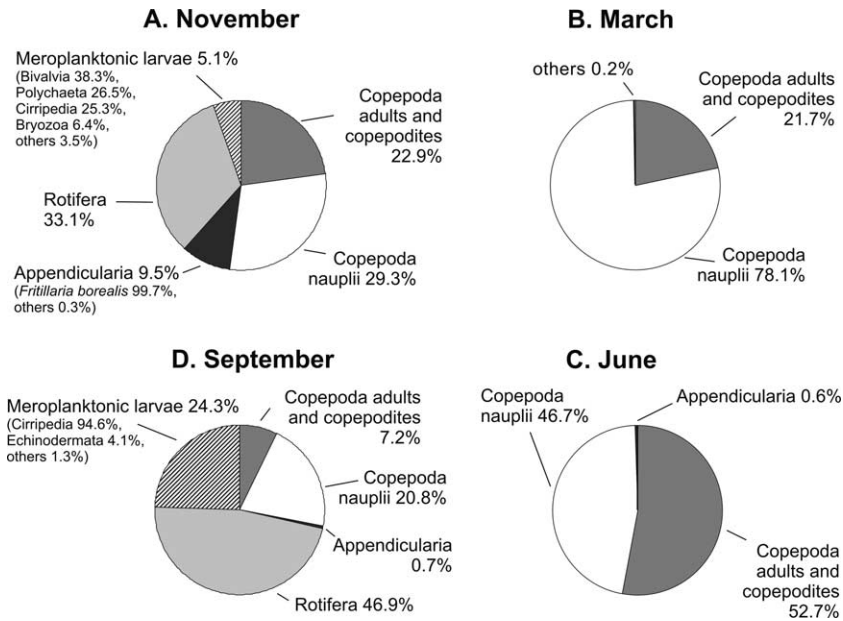adults and
copepodites
52.7%

Figure 3. Percentage taxonomic composition of the zooplankton community in the Beagle Channel, during November 2005 (A), March (B), June (C) and September 2006 (D).

$p > 0.01$). A clear separation is evident along the axis 1 of the MDS, between stations in November and September from those in March and June. Nevertheless, along the axis 2 a separation between stations in November and March, from those in June and September, is observed. This may be due to the higher densities of copepod nauplii during November–March (Table I). The taxa that contributed $\geq 5\%$ to within-group similarity (November–September and March–June) are presented in

Table II. Nine taxa accounted for 85.3% of the November–September within-group similarity, and six taxa for 84.7% of the March–June within-group similarity. The similarity within the March–June group was due to the copepod dominance. The average similarities of the November–September and the March–June groups were comparable: 61.9% and 65.3%, respectively.

The copepods *O. similis* and *C. citer* were among the four most abundant species in the groups

A. November

Centropages brachiatus
4.2%

Clausocalanus brevipes
1.2%

others 1.1%

Drepanopus forcipatus
6.3%

Oncaea curvata
9.7%

Oithona similis
39.6%

Acartia tonsa 17.2%

Ctenocalanus citer
20.7%

B. March

Centropages brachiatus
2.3%

others 2.1%

Oithona similis 7.0%

Ctenocalanus citer 7.3%

Acartia tonsa
9.0%

Drepanopus forcipatus
72.2%

D. September

Clausocalanus brevipes
1.0%

Oncaea curvata 6.8%

others 1.6%

Drepanopus forcipatus
6.3%

Acartia tonsa
4.3%

Ctenocalanus citer
25.2%

Oithona similis
54.9%

C. June

Clausocalanus brevipes
4.1%

others 0.5%

Drepanopus forcipatus
2.1%

Acartia tonsa
9.5%

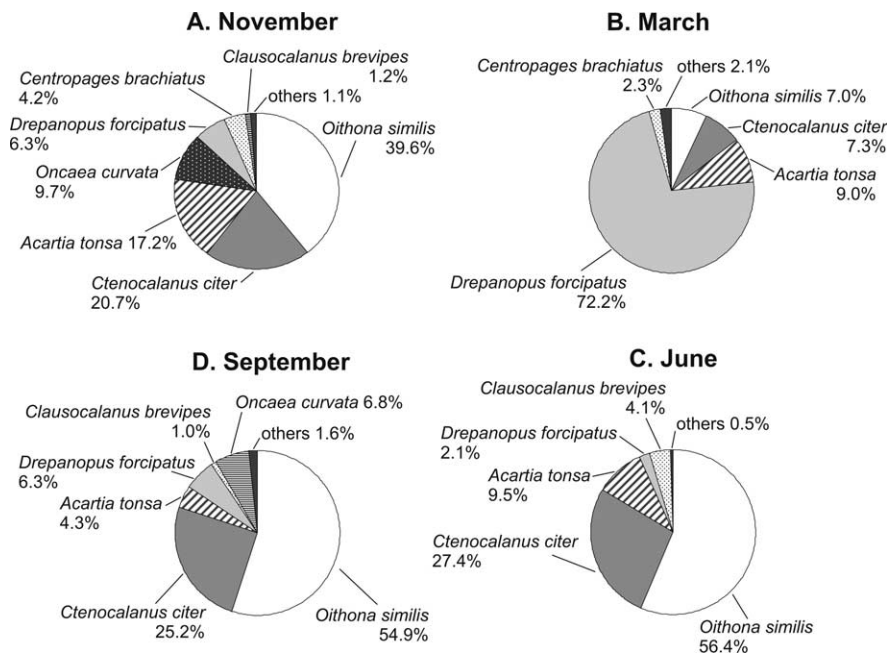*Ctenocalanus citer*
27.4%

Oithona similis
56.4%

Figure 4. Percentage specific composition of copepods assemblages in the Beagle Channel, during November 2005 (A), March (B), June (C) and September 2006 (D).
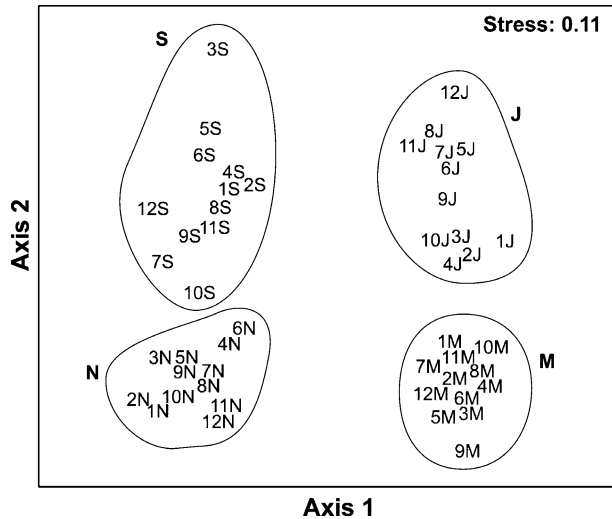
Figure 5. Result of the MDS analysis. Samples are identified according to the sampling station and month. N: November, M: March, J: June, S: September.

March–June and November–September (Table II). During November, *O. similis* showed higher densities in the west and east areas, while the highest density of *C. citer* was found in the east area (Figure 6A,C). During September, both species showed low abundances in the whole studied area (Figure 6B,D). The appendicularian *F. borealis* and the rotifer *Synchaeta* sp. contributed with a high percentage (14.4% and 7.4%, respectively) to the within-group similarity of the November–September group. During November, both taxa showed higher densities in the middle and east areas (Figure 6E,G).

Table II. Zooplankton taxa within the two groups (November–September and March–June) identified by the similarity percentages (SIMPER) analysis as contributing $\geq 5\%$ to the similarity within station groups. Taxa have been ranked in order of decreasing mean abundance (ind m^{-3}) within each group. L: larvae.

Taxa	Mean abundance
November–September	
Synchaeta sp.	6,257
Copepod nauplii	4,820
Oithona similis	1,403
Fritillaria borealis	1,323
Cirripedia (L)	981
Ctenocalanus citer	725
Oncaea curvata	328
Polychaeta (L)	196
Echinodermata (L)	55
March–June	
Copepod nauplii	12,666
Drepanopus forcipatus	2,447
Oithona similis	589
Ctenocalanus citer	418
Acartia tonsa	363
Microsetella norvegica	16

During March, *D. forcipatus* had densities over 5000 ind m^{-3} in the three areas (Figure 7E). During June, *O. similis*, *C. citer* and *D. forcipatus* showed their maximum abundances in the west area (Figure 7B,D,F). *A. tonsa* was especially abundant in Bahía Lapataia (west area) during both March and June (Figure 7G,H), while it was also abundant in Bahía Brown during March (Figure 7G).

Only the copepod *A. tonsa* showed a significant variability associated with location ($F_{2,48} = 10.177$; $p < 0.001$). In the west area, densities of *A. tonsa* were significantly higher than in the middle area (Tukey–Kramer test: $p < 0.001$) and the east area (Tukey–Kramer test: $p < 0.05$).

Discussion

The present study provides information on the metazooplankton abundance and its taxonomic composition in different coastal areas of the Beagle Channel. In particular, the zooplankton community of Bahía Lapataia, Bahía Ensenada and Bahía Brown had not been previously analysed. Also, this work presents for the first time a quantitative temporal comparison of the structure of the metazooplankton community in a coastal area belonging to the sub-Antarctic Fuegian archipelago.

Our results indicate the existence of strong temporal variations in the smaller fractions of the metazooplankton community of the Beagle Channel. In March and June, the community was composed almost exclusively of copepods. Furthermore, in September and November the zooplankton community showed higher diversity, in coincidence with increasing chlorophyll-*a* concentration. In high latitude marine ecosystems – such as the Beagle Channel – there is a phytoplankton bloom in spring, limited primary production in summer and fall, and low production in winter due to reduced daily sunlight. This strong seasonality in primary production leads to shifts in the zooplankton community (Zhou et al. 2009). Although we only measured surface chlorophyll-*a*, our results are in agreement with previous studies. In the Fuegian channels and fjords, as well as in the Straits of Magellan, the maximum chlorophyll-*a* occurs during the austral spring, mainly due to the biomass increase of large diatoms such as *Chaetoceros* sp. (Ehrenberg, 1844) (Hamamé & Antezana 1999; Iriarte et al. 2001). Our results for September indicate that this phytoplankton increase in the Beagle Channel had already started towards the end of the winter, and continues through the spring. During the rest of the year, the values of chlorophyll decrease (Antezana 1999a; this study) and the phytoplankton community is mainly
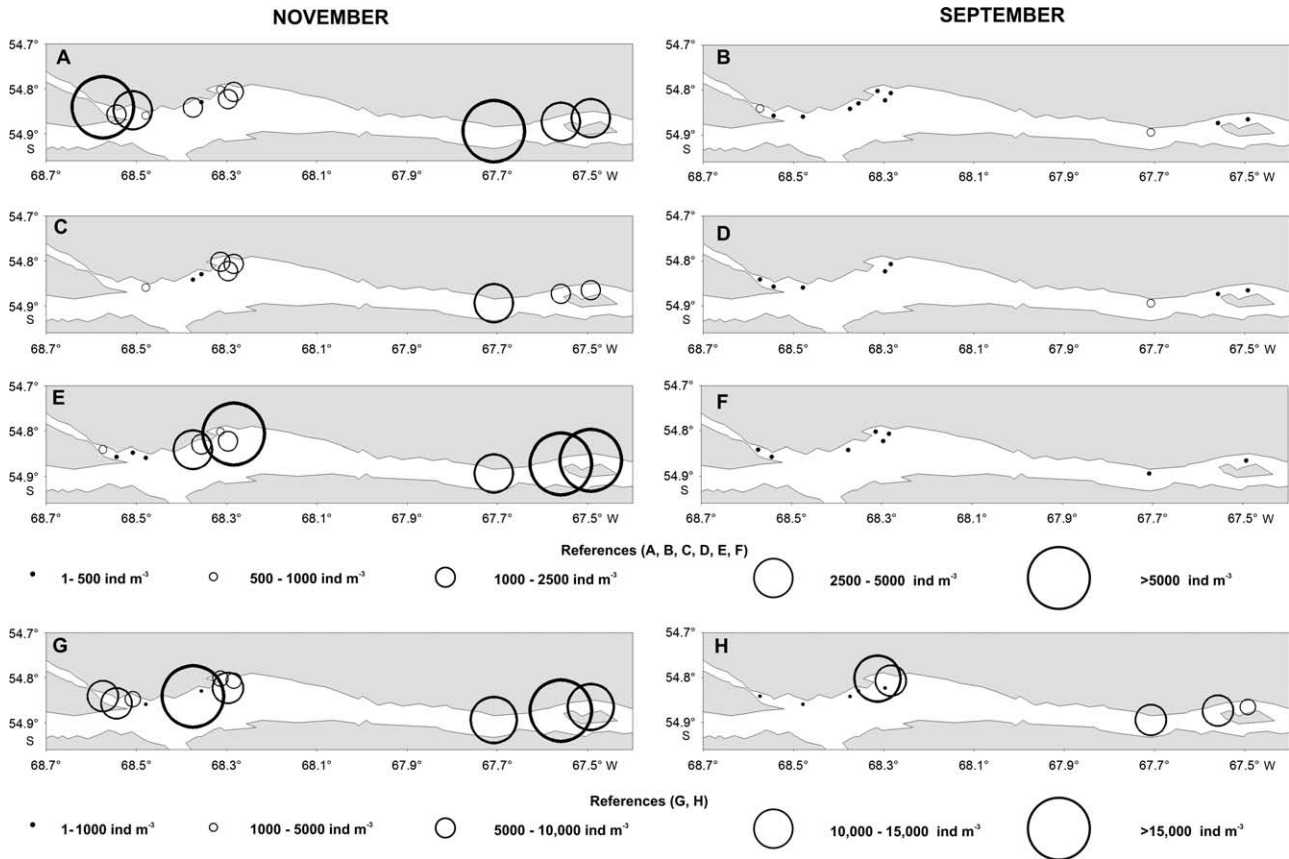
Figure 6. Abundance (ind m^{-3}) distribution of the four most abundant species or genus during November 2005 and September 2006. *Oithona similis* (A, B), *Ctenocalanus citer* (C, D), *Fritillaria borealis* (E, F), and *Synchaeta* sp. (G, H).

dominated by nanoflagellates and picoplanktonic organisms (Antezana 1999a).

During September and November, some groups showed their maximum abundances, such as rotifers and appendicularians. In particular, the rotifer *Synchaeta* sp. was completely absent from the plankton samples during the other two sampling months. This large fluctuation in rotifer density values has been previously observed in coastal waters and estuaries, where *Synchaeta* genus rotifers are abundant (Egloff 1988). Appendicularians had been pointed out as an important component of the metazooplankton community in the archipelago of Tierra del Fuego (Defren-Janson et al. 1999); however, identification to specific level has not been performed previously. In this work, three species of appendicularians were found in the Beagle Channel: *Oikopleura dioica*, *Oikopleura fusiformis* and *Fritillaria borealis*. The latter was especially abundant in November when our values of surface chlorophyll-*a* were maximum. In high latitudes of the northern hemisphere (60–61°N), *F. borealis* exhibits maximum densities when phytoplankton blooms occur (Båmstedt et al. 2005). The populations of both rotifers and appendicularians are characterized by the ability to increase rapidly in response to high concentrations of phytoplankton (Egloff 1988; Båmstedt et al. 2005).

Likewise, in November and September, a large influx of meroplanktonic larvae into the community was observed, which is product of the annual invertebrate reproductive pulse (cf. Diez & Lovrich 2010). In particular, decapod larvae are restricted to occur in the period between September and early March (Lovrich 1999), which is in accordance with our results. Meroplanktonic larvae reached their highest densities in November and September, when surface chlorophyll-*a* concentrations were higher. The importance of the pelagic–benthic coupling in the waters of the Fuegian archipelago has been identified by Antezana (1999a). In high-latitude marine environments, such as the Beagle Channel, a major bloom of phytoplankton occurs in spring, mainly dominated by large diatoms, which sink to the bottom stimulating the release of larvae by benthic invertebrates (Starr et al. 1990). Primary production and photoperiod seem to be the most important factors which influence the timing of marine benthic invertebrate reproduction in high-latitude environments (Pearse 1998; Pearse & Lockhart 2004).
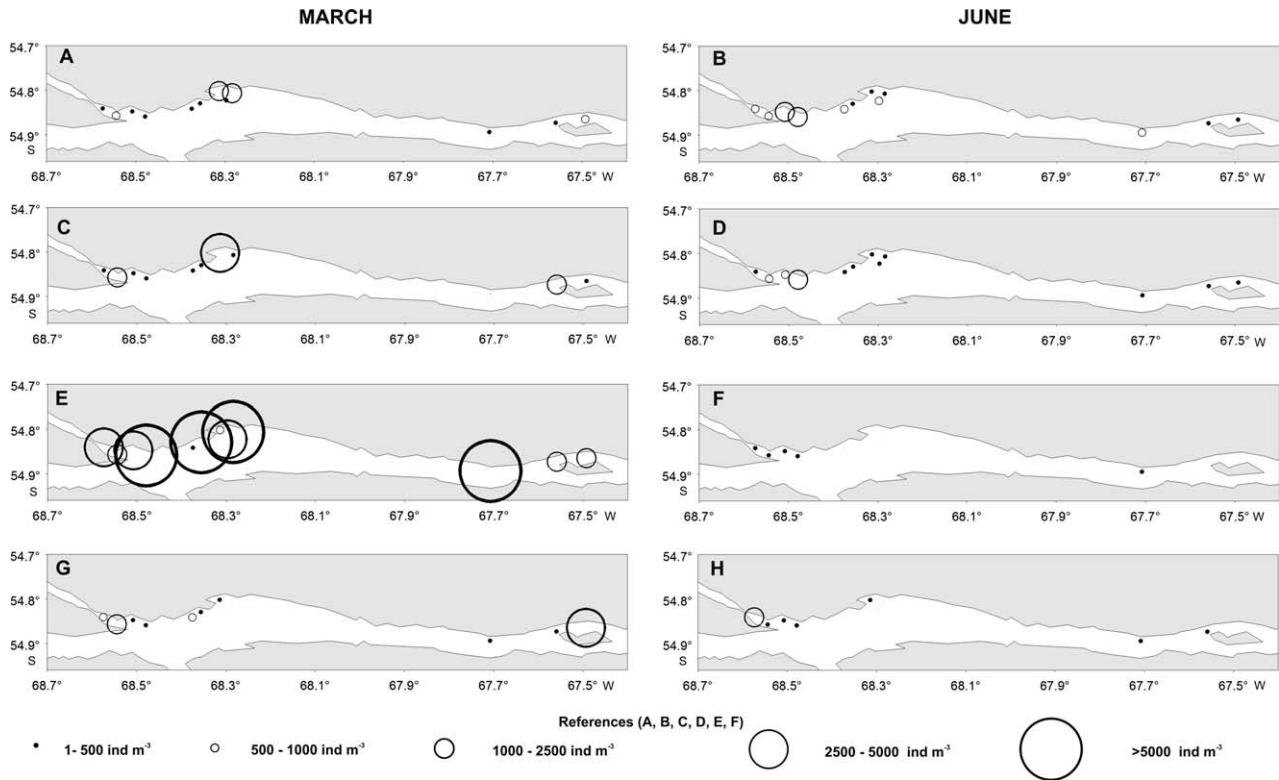
MARCH   **JUNE**

Figure 7. Abundance (ind m^{-3}) distribution of the four most abundant species during March 2006 and June 2006. *Oithona similis* (A, B), *Ctenocalanus citer* (C, D), *Drepanopus forcipatus* (E, F), and *Acartia tonsa* (G, H).

Copepods were a main component of the community throughout the whole study, as previously found by other studies in the Beagle Channel (Defren-Janson et al. 1999; Hamamé & Antezana 1999; Fernández-Severini & Hoffmeyer 2005). Larger abundances of copepod nauplii were found during spring (November) and summer (March), suggesting that copepods reproduction is higher in these seasons, when temperatures were also higher. Temperature, and food quantity and quality, are among the most important factors affecting egg production rates of marine copepods (Hirche et al. 1997; Gislason et al. 2008). The two dominant copepod species during June (autumn), September (winter) and November (spring) were *Oithona similis* and *Ctenocalanus citer*, while *Drepanopus forcipatus* was the dominant one during March (summer). This latter species is widely distributed in shelf areas off Argentina and Chile, southern South America (Mazzocchi et al. 1995). During summer, *D. forcipatus* is the most abundant copepod in the Beagle Channel (this study), the Straits of Magellan (Zagami et al. 2011), and some shelf areas of the south-western Atlantic Ocean (Sabatini 2008). The other two dominant species (*O. similis* and *C. citer*) have been previously described as the dominant copepods in some coastal areas of the Beagle Channel (Fernández-Severini & Hoffmeyer 2005;

Biancalana et al. 2007). They are also among the dominant copepod species in the Straits of Magellan (Zagami et al. 2011), some coastal areas of the Antarctic Peninsula (Fuentes et al. 2008), and in the Antarctic Polar Front (Dubischar et al. 2002). Considering that the Beagle Channel is located north of it, our results may confirm that the Antarctic Polar Front is not a biogeographical barrier for the distribution of *O. similis* and *C. citer* (Atkinson & Sinclair 2000). This also seems to be true for *Oncaea curvata*, a species found in all the sampling periods in our study, and which is also present during all year round in coastal Antarctic waters (Metz 1996; Elwers & Dahms 1998).

We report for the first time the presence of the copepods *Microsetella norvegica* and *Calanoides patagoniensis* in the Beagle Channel. The harpacticoid *M. norvegica* is frequently found in coastal waters worldwide (Uye et al. 2002), and it has been previously found in the Aysen Fjord (45°S, 73°W), southern Chile (Hirakawa 1989). Thus, the present study extends its known distribution up to almost 55°S. The calanoid *C. patagoniensis* is one of the dominant copepods in the south-eastern Pacific Ocean (Hidalgo et al. 2010), and has been previously found in the Straits of Magellan and the Fuegian archipelago waters (e.g. Arcos 1976; Mazzocchi et al. 1995). Its presence in the Beagle Channel could be

due to the intrusion of waters from the Pacific Ocean. The Beagle Channel is thought to have a Pacific influence, mainly because the main circulation comes from the West Wind Drift which deflects at the southern tip of South America (Antezana 1999b).

In this study, sampling was performed with a 100 μm mesh size plankton net, allowing a better representation of the smaller size fractions of the metazooplankton community. Nets with mesh size smaller than 200 μm are more efficient in the capture of copepod nauplii and small copepods such as *C. citer*, *Oithona* spp. and *Oncaea* spp. (Galliene & Robins 2001; Dubischar et al. 2002; Antacli et al. 2010), and marine rotifers of the genus *Synchaeta* which have a length of 100–200 μm (Egloff 1988). The abundances of copepod nauplii found in this study during the austral summer ($> 20,000$ ind m^{-3} in March) are comparable to those reported in waters of the Antarctic Polar Front by Dubischar et al. (2002), who also collected their samples with a 100-μm net. Despite these high abundances, we have most probably undersampled a high amount of naupliar stages, which can be as small as 50 μm (Dubischar et al. 2002; and references therein). Also, a net with a 100 μm mesh-size does involve the risk of inaccurate sampling of rare organisms and strong swimmers with a well-developed escape response, such as large copepods (e.g. *Calanus* spp.) and decapod larvae. In order to collect these zooplankters (e.g. large copepods), larger water volumes must be sampled (Calbet et al. 2001).

The structure of the metazooplankton community as a whole shows no geographical variations in this study. Similarly, Defren-Janson et al. (1999) and Hamamé & Antezana (1999) found no differences in the zooplankton community structure of the upper layer between 0 and 50 m when analysing different locations of the Fuegian archipelago, including the Beagle Channel. The measured environmental parameters – temperature, salinity and chlorophyll– showed a temporal pattern, but only salinity exhibited spatial variability. Although we only measured surface salinity, the Beagle Channel may behave as a vertically homogeneous estuary due to its shallow depths (<100 m) (Palma & Silva 2004). Salinity values were lower during spring and summer, especially in the west area. This could be due to the melting ice from glaciers of the Darwin mountains located along the south-western sector of the Tierra del Fuego island, which starts in spring. The low levels of salinity – surface values below 30 psu – coincide with the values reported by other authors in the Beagle Channel (Klöser 1996; Balestrini et al. 1998; Isla et al. 1999). In the west area of this study, *Acartia tonsa* – the only taxon that showed a significant variability in its spatial distribution – showed its

highest densities. This copepod species develops its maximum population density in estuarine regions with low and intermediate salinity (Calliari et al. 2008).

In conclusion, this study shows the existence of strong temporal fluctuations of both holo- and meroplanktonic components of the coastal metazooplanktonic community of the Beagle Channel. These fluctuations seem to be more dependent on the primary production rather than on physical factors such as temperature or salinity. The absence of geographical variability in the metazooplankton community, may confirm that the area of the Beagle Channel comprised in this study behaves as a semi-enclosed water body, as previously stated by Antezana (1999b). Also, our results show that small metazooplankters – such as the copepods *O. similis* and *C. citer*, and the appendicularian *F. borealis* – dominate in terms of abundance in the metazooplankton community. More studies with a better temporal and spatial resolution are required to gain a deeper understanding of the intra- and interannual variability of this community, which in turn will help to interpret the effects of global climate change, particularly intense at high-latitude environments, on planktonic communities.

References

Amin O, Ferrer L, Marcovecchio J. 1996. Heavy metal concentrations in littoral sediments from the Beagle Channel, Tierra del Fuego, Argentina. Environmental Monitoring and Assessment 41:219–31.

Antacli JC, Hernández D, Sabatini M. 2010. Estimating copepods' abundance with paired nets: Implications of mesh size for population studies. Journal of Sea Research 63:71–77.

Antezana T. 1999a. Plankton of Southern Chilean fjords: Trends and linkages. Scientia Marina 63(Suppl 1):69–80.

Antezana T. 1999b. Hydrographic features of Magellan and Fuegian inland passages and adjacent Subantarctic waters. Scientia Marina 63(Suppl 1):23–34.

Arcos RD. 1976. Los copépodos calanoideos de la región Magallánica. Expedición Hero 72-4. Revista de la Comisión Permanente del Pacífico Sur 5:85–100.

Atkinson A, Sinclair JD. 2000. Zonal distribution and seasonal vertical migration of copepod assemblages in the Scotia Sea. Polar Biology 23:46–58.

Balestrini C, Manzella G, Lovrich G. 1998. Simulación de corrientes en el Canal Beagle y Bahía Ushuaia, mediante un modelo bidimensional. Servicio de Hidrografía Naval. Informe Técnico 98:1–58.

Båmstedt U, Fyhn HJ, Martinussen MB., Mjaavatten O, Grahl-Nielsen O. 2005. Seasonal distribution, diversity and biochemical composition of appendicularians in Norwegian fjords. In: Gorsky G, Youngbluth MJ, Deibel D, editors. Response of Marine Ecosystems to Global Change: Ecological Impact of Appendicularians. Paris: Contemporary Publishing International, p 227–54.

Biancalana F, Barría de Cao MS, Hoffmeyer MS. 2007. Micro and mesozooplankton composition during winter in Ushuaia and Golondrina Bays (Beagle Channel, Argentina). Brazilian Journal of Oceanography 55:83–95.

Boltovskoy D. 1999. South Atlantic Zooplankton. Leiden: Backhuys Publishers. 1706 pages.

Boltovskoy D, Gibbons MJ, Hutchings L, Binet D. 1999. General biological features of the South Atlantic. In: Boltovskoy D, editor. South Atlantic Zooplankton. Leiden: Backhuys Publishers, p 1–42.

Boxshall GA, Halsey SH. 2004. An Introduction to Copepod Diversity. London: The Ray Society. 966 pages.

Bujalesky GG. 1998. Holocene coastal evolution of Tierra del Fuego, Argentina. Quaternary of South America and Antarctic Peninsula 11:247–81.

Bujalesky G, Aliotta S, Isla F. 2004. Facies del subfondo del canal Beagle, Tierra del Fuego. Revista de la Asociación Geológica Argentina 59:29–37.

Calbet A, Garrido S, Saiz E, Alcaraz M, Duarte CM. 2001. Annual zooplankton succession in coastal NW Mediterranean waters: The importance of the smaller size fractions. Journal of Plankton Research 23:319–31.

Calbet A, Landry MR, Scheinberg RD. 2000. Copepod grazing in a subtropical bay. Species-specific responses to a midsummer increase in nanoplankton standing stock. Marine Ecology Progress Series 193:75–84.

Calliari D, Andersen Borg MC, Thor P, Gorokhova E, Tiselius P. 2008. Instantaneous salinity reductions affect the survival and feeding rates of the co-occurring copepods Acartia tonsa Dana and A. clausi Giesbrecht differently. Journal of Experimental Marine Biology and Ecology 362:18–25.

Clarke KR, Warwick RM. 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. Plymouth: PRIMER-E Ltd. 171 pages.

Defren-Janson K, Schnack-Schiel SB, Richter C. 1999. Mesozooplankton communities in the Magellan region. Scientia Marina 63(Suppl 1):43–50.

Diez MJ, Lovrich GA. 2010. Reproductive biology of the crab Halicarcinus planatus (Brachyura, Hymenosomatidae) in sub-Antarctic waters. Polar Biology 33:389–401.

Dubischar CD, Lopes RM, Bathmann UV. 2002. High summer abundances of small pelagic copepods at the Antarctic Polar Front – Implications for ecosystem dynamics. Deep-Sea Research II 49:3871–87.

Egloff DA. 1988. Food and growth relations of the marine microzooplankter, Synchaeta cecilia (Rotifera). Hydrobiologia 157:129–41.

Elwers K, Dahms HU. 1998. Species composition and seasonal population structure of Oithona similis (Copepoda, Cyclopoida) in the Potter Cove (Jubany, King George Island, Antarctica). Berichte zur Polar- und Meeresforschung 299:150–55.

Fernández-Severini MD, Hoffmeyer MS. 2005. Mesozooplankton assemblages in two bays in the Beagle Channel (Argentina) during January 2001. Scientia Marina 69(Suppl 2):27–37.

Fuentes VL, Schnack-Schiel SB, Schloss IR, Esnal GB. 2008. Mesozooplankton of Potter Cove: Community composition and seasonal distribution in 2002 and 2003. Berichte zur Polar- und Meeresforschung 571:75–84.

Gallienne CP, Robins DB. 2001. Is Oithona the most important copepod in the world's oceans? Journal of Plankton Research 23:1421–32.

Gislason A, Gaard E, Debes H, Falkenhaug T. 2008. Abundance, feeding and reproduction of Calanus finmarchicus in the Irminger Sea and on the northern Mid-Atlantic Ridge in June. Deep-Sea Research II 55:72–82.

Hamamé M, Antezana T. 1999. Chlorophyll and zooplankton in microbasins along the Straits of the Magellan–Beagle Channel passage. Scientia Marina 63(Suppl 1):35–42.

Heron GA, Bowman TE. 1971. Postnaupliar developmental stages of the copepod crustaceans Clausocalanus laticeps, C. brevipes, and Ctenocalanus citer (Calanoida: Pseudocalanidae). Antarctic Research Series 17:141–65.

Hidalgo P, Escribano R, Vergara O, Jorquera E, Donoso K, Mendoza P. 2010. Patterns of copepod diversity in the Chilean coastal upwelling system. Deep-Sea Research II 57:2089–97.

Hirakawa K. 1989. Planktonic copepods from Aysen fjord and adjacent waters, Southern Chile. Proceedings of the NIPR Symposium on Polar Biology 2:46–50.

Hirche HJ, Meyer U, Niehoff B. 1997. Egg production of Calanus finmarchicus: Effect of temperature, food and season. Marine Biology 127:609–20.

Iriarte JL, Kusch A, Osses J, Ruiz M. 2001. Phytoplankton biomass in the sub-Antarctic area of the Straits of Magellan (53°S), Chile during spring–summer 1997/1998. Polar Biology 24:154–62.

Isla F, Bujalesky G, Coronato A. 1999. Procesos estuarinos en el Canal Beagle, Tierra del Fuego. Revista de la Asociación Geológica Argentina 54:307–18.

Jaspers C, Nielsen TG, Carstensen J, Hopcroft RR, Møller EF. 2009. Metazooplankton distribution across the Southern Indian Ocean with emphasis on the role of Larvaceans. Journal of Plankton Research 31:525–40.

Klöser H. 1996. Hydrography of the Beagle Channel. Berichte zur Polar- und Meeresforschung 190:18–19.

Lovrich GA. 1999. Seasonality of larvae of Brachyura and Anomura (Crustacea Decapoda) in the Beagle Channel, Argentina. Scientia Marina 63(Suppl 1):347–54.

Mazzocchi MG, Zagami G, Ianora A, Guglielmo L, Crescenti N, Hure J. 1995. Copepods. In: Guglielmo L Ianora A, editors. Atlas of Marine Zooplankton. Straits of Magellan. Berlin: Springer Verlag, p 1–279.

Metz C. 1996. Life strategies of dominant Antarctic Oithonidae (Cyclopoida, Copepoda) and Oncaeidae (Poecilostomatoida, Copepoda) in the Bellinghausen Sea. Berichte zur Polar- und Meeresforschung 207:1–123.

Pagès F, Orejas C. 1999. Medusae, siphonophores and ctenophores of the Magellan region. Scientia Marina 63 (Suppl 1):51–57.

Palma S, Silva N. 2004. Distribution of siphonophores, chaetognaths, euphausiids and oceanographic conditions in the fjords and channels of southern Chile. Deep-Sea Research II 51: 513–35.

Pearse JS. 1998. Seasonal reproduction, marine invertebrates. In: Knobil E Neill JD, editors. Encyclopedia of Reproduction. San Diego, CA: Academic Press, p 352–55.

Pearse JS, Lockhart SJ. 2004. Reproduction in cold water: paradigm changes in the 20th century and a role for cidaroid sea urchins. Deep-Sea Research II 51:1533–49.

Pérez-Barros P, Tapella F, Romero C, Calcagno JA, Lovrich GA. 2004. Benthic decapod crustaceans associated with captures of *Munida* spp. (Decapoda: Anomura) in the Beagle Channel, Argentina. Scientia Marina 68:237–46.

Purcell JE, Studervant MV, Galt CP. 2004. A review of appendicularians as prey of invertebrates and fish predators. In: Gorsky G, Youngbluth MJ, Deibel D, editors. Response of Marine Ecosystems to Global Change: Ecological Impact of Appendicularians. Paris: Contemporary Publishing International, p 359–435.

Ruttner-Kolisko A. 1974. Plankton rotifers: Biology and Taxonomy. Die Binnengewässer Suppl. 26:1–146.

Sabatini ME. 2008. Life history trends of copepods *Drepanopus forcipatus* (Clausocalanidae) and *Calanus australis* (Calanidae) in the southern Patagonian shelf (SW Atlantic). Journal of Plankton Research 30:981–96.

Starr M, Himmelman JH, Therriault JC. 1990. Direct coupling of marine invertebrate spawning with phytoplankton blooms. Science 247:1071–74.

Strickland JDH, Parsons DR. 1972. A practical handbook of seawater analysis. Journal of Fisheries Research Board Canadian Bulletin 167:1–310.

Thatje S, Schnack-Schiel S, Arntz WE. 2003. Developmental trade-offs in subantarctic meroplankton communities and the enigma of low decapod diversity in high southern latitudes. Marine Ecology Progress Series 260:195–207.

Uye S, Aoto I, Onbé T. 2002. Seasonal population dynamics and production of *Microsetella norvegica*, a widely distributed but little-studied marine planktonic harpacticoid copepod. Journal of Plankton Research 24:143–53.

Zagami G, Antezana T, Ferrari I, Granata A, Sitran R, Minutoli R, et al. 2011. Species diversity, spatial distribution, and assemblages of zooplankton within the Strait of Magellan in austral summer. Polar Biology 34:1319–33.

Zhou M, Tande KS, Zhu Y, Basedow S. 2009. Productivity, trophic levels and size spectra of zooplankton in northern Norwegian shelf regions. Deep-Sea Research II 56:1934–44.

Editorial responsibility: David McKinnon