Polar Biology (2018) 41:663–678
https://doi.org/10.1007/s00300-017-2227-8

ORIGINAL PAPER

Appendicularians and copepods from Scotia Bay (Laurie island, South Orkney, Antarctica): fluctuations in community structure and diversity in two contrasting, consecutive summers

Mariela L. Spinelli[1,2] · **Claudio Franzosi**[3] · **Héctor Olguin Salinas**[4,5] · **Fabiana L. Capitanio**[1,2] · **Viviana A. Alder**[3,4,5]

Received: 21 February 2017 / Revised: 29 August 2017 / Accepted: 3 December 2017 / Published online: 12 December 2017

Abstract

Coastal Antarctic waters involve habitats of high primary and secondary production with a remarkable sensitivity to environmental changes on different spatio-temporal scales. The current study is the first comprehensive approach to the spatial distribution and the fluctuations in abundance, biomass, community structure, and diversity of the mesozooplankton from different habitats located in Scotia Bay in summers: 2014 and 2015, characterized by a different timing in seasonal sea ice retreat. Mean seawater temperature and abundances of calanoids, cyclopoids, nauplii, and appendicularians were one order of magnitude higher in summer 2014. Despite these environmental differences, biomass values of these groups proved similar for both summers. A total of ten species of copepods and one of appendicularians (*Fritillaria borealis)* were identified. Oithonid copepods—*O. similis*, followed by *O. frigida*—represented the bulk of mesozooplankton abundances in both summers. The highest total mesozooplankton abundance (2111 ind m^{-3}) and biomass (14075 µg C m^{-3}) were found next to an Adélie penguin breeding area (2014), while the highest Shannon index values were found next to a glacier in both summers. Multivariate analyses based on species abundance showed two main groups of sites, one of them encompassing all summer 2014 samplings and the other comprising all summer 2015 samplings. The positive correlation between *O. similis* and the 2–10 µm Chl-*a* fraction suggests that summer 2014 represented optimal conditions—in terms of food—for the growth and development of this species. Experimental studies based on natural prey assemblages revealed that *O. similis* feeds on flagellates rather than on diatoms.

Keywords Mesozooplankton · *Oithona similis* · *Fritillaria borealis* · Biomass · Community structure · Feeding rates

✉ Mariela L. Spinelli
marielaspinelli@bg.fcen.uba.ar

[1] CONICET- Universidad de Buenos Aires, Instituto de Biodiversidad y Biología Experimental y Aplicada, (IBBEA), Intendente Güiraldes 2160 - Ciudad Universitaria, C1428EGA Buenos Aires, Argentina

[2] Laboratorio de Zoplancton Marino, Departamento de Biodiversidad y Biología Experimental, Facultad de Ciencias Exactas y Naturales, Intendente Güiraldes 2160 - Ciudad Universitaria, C1428EGA Buenos Aires, Argentina

[3] Instituto Antártico Argentino, Dirección Nacional del Antartico, 25 de Mayo 1143, San Martín, Buenos Aires, Argentina

[4] Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Intendente Güiraldes 2160 - Ciudad Universitaria, C1428EGA Buenos Aires, Argentina

[5] CONICET- Universidad de Buenos Aires, Instituto de Ecología, Genética y Evolución de Buenos Aires, (IEGEBA), Intendente Güiraldes 2160 - Ciudad Universitaria, C1428EGA Buenos Aires, Argentina

Introduction

Zooplankton plays a key role in marine ecosystems given their capacity to control phytoplankton populations, to generate nutrients, and to export biogenic matter downward (Wallis et al. 2015). Copepods are generally the dominant zooplanktonic group in the pelagic realm (Verity and Smetacek 1996). Because of their body length (100 µm to 10 mm) and feeding habits (on ~ 5 µm cells up to other metazoans several mm long), they contribute to the food web in multiple ways, being the major link between phytoplankton and fish larvae when krill abundance is low (Murphy et al. 2007). Nevertheless, the relative contribution of different preys to copepod diets depends on the trophic state of the system.

Climate change is altering marine ecosystems in general (e.g., Doney et al. 2012) and marine planktonic communities in particular (e.g., Francis et al. 2012). Temperature influences water column stability, nutrient enrichment, the degree of new production, and thus the abundance, size composition, diversity, and trophic efficiency of zooplanktonic organisms (Richardson 2008). The coastal regions of high latitudes are subject to more pronounced seasonal variations in their conditions (duration of photoperiod, nutrient availability, annual change in sea ice extent and duration) than middle and low latitude environments (Clarke and Harris 2003). Moreover, several effects of climate warming on pelagic communities have been reported for Antarctic ecosystem (mainly in the West Antarctic Peninsula), such as changes in phyto- and zooplankton abundance distribution and shifts in their physiological and ecological mechanisms (Ducklow et al. 2007; Montes-Hugo et al. 2009). Fluctuations observed in Antarctic coastal areas where zooplankton was extensively investigated denote the high environmental vulnerability of this region (e.g., Sicinski et al. 1996; Calbet et al. 2002). In Antarctic environments, copepods are the dominant zooplanktonic group in terms of biomass and abundance, but they are exceeded by the euphausid *Euphausia superba* or the salp *Salpa thompsoni* in some regions and years (Daponte et al. 2001; Atkinson et al. 2012). Polar zooplankton can feed on phytoplankton and also on other sources of carbon (e.g., protozoans and metazoans) to meet metabolic demands, especially in low chlorophyll conditions or in offshore and slope regions (Gleiber 2014).

The knowledge on the mesozooplankton from the archipelagos of the Scotia Ridge is quite uneven. The South Georgia islands, located in the northern branch of the Ridge, have been exhaustively investigated (Atkinson 1994, 1998; Atkinson et al. 2012; Ward et al. 2012a, b). The South Orkney archipelago, located approximately 600 km north-east of the Antarctic Peninsula, comprises four main islands and several smaller ones. Waters surrounding this archipelago are subject to seasonal and interannual changes in the extent of sea ice across the Scotia Sea and Weddell Sea, to multiple frontal processes, and to fluctuations in the circulation of the Antarctic Circumpolar Current. Previous studies in nearshore environments of the South Orkney archipelago include those addressing avian and mammal krill predators of Signy and Laurie islands (Casaux et al. 2009; Coria et al. 2011; Dunn et al. 2016) and those focused on terrestrial systems (Walton 1982; Lewis Smith 1990), sub-littoral epifauna (Barnes 1995), and the marine microbial communities (Whitaker 1982; Leakey et al. 1994; Clarke and Leakey 1996) of Signy Island in particular. However, mesozooplankton biodiversity, abundance, and biomass fluctuations in nearshore waters of Laurie Island had remained practically unknown until now.

In this context, an ecological study of mesozooplankton was conducted for the first time at southern coastal waters of Laurie Island (South Orkney) during two consecutive summers. The primary goals of this study were: (1) to analyze the mesozooplankton community of Scotia Bay as to its abundance, biomass, structure and species diversity in relation to phytoplankton (size-fractioned chlorophyll-a) and temperature, as well as its variations both at different locations within the bay and at different time scales; (2) to experimentally explore the importance of key nano- and microplanktonic organisms as a food source for the dominant copepod species, and to estimate the feeding rates and selectivity of the latter on natural assemblages. In this respect, we propose the hypothesis that the abundance of the dominant mesozooplanktonic species is determined by the size and concentration of the potential food available.

Materials and methods

Sampling was conducted from a Zodiac boat at different sites within Scotia Bay during two consecutive summers (February–March 2014 and 2015; Fig. 1). Sampling sites were selected considering similar bottom depths (15–20 m) and dissimilarities as to other environmental features such as proximity to a penguin colony (S1), the input of glacier melting (S3), and distance to the shoreline taking Orcadas Station as reference (S4: 0.33 km; S8: 1.08 km; S2: 3.00 km). In summer 2014, samples were collected at three of these sites (S1, S3, S4), while collection sites in summer 2015 were four (S2, S3, S4, S8). In order to analyze short-term temporal fluctuations, S4 was sampled twice in 2014, while S8 was sampled four times in 2015. A total of 11 quantitative samplings were performed, always in the morning. At each site, subsurface seawater temperature was measured, and samples were collected in the water column to analyze

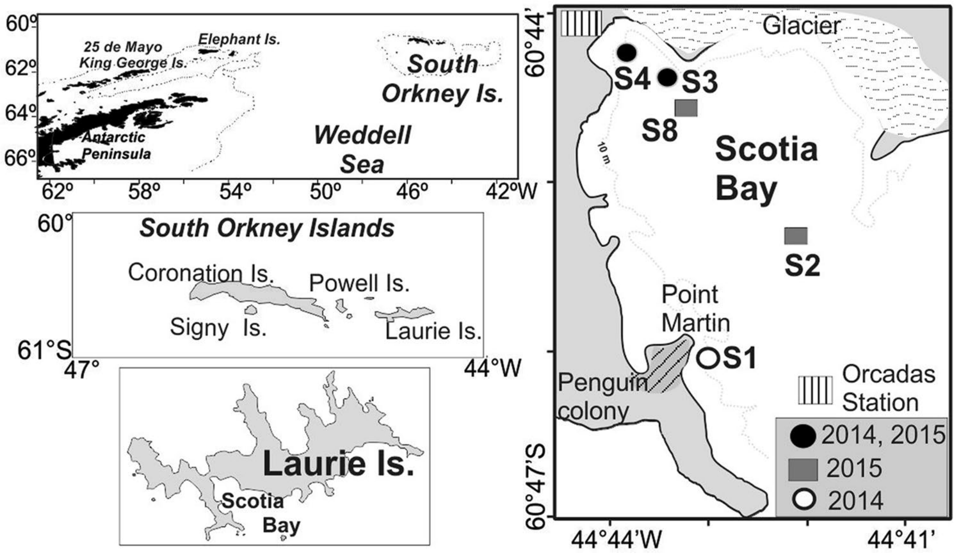


Fig. 1 Location of sampling sites in Scotia Bay, Laurie Island (South Orkney, Antarctica) during summers of 2014 and 2015

size-fractioned chlorophyll-*a* and total mesozooplankton density, biomass, and species abundances.

Chlorophyll samples were collected by means of a Niskin bottle. A total of 650 ml (average) of water was filtered by Whatman GF/F and polycarbonate filters of 2 and 10 µm arranged in series so as to obtain size-fractioned chlorophyll (0.7–2 µm, 2–10 µm, and > 10 µm). Filters were kept in dark at − 20 °C. Pigments were extracted in 90% acetone during 24 h at 4 °C and measured in a spectrophotometer. Chlorophyll *a* (Chl-*a*) concentrations were estimated according to Jeffrey and Humphrey (1975).

Mesozooplankton samples were taken with a plankton net (200-µm mesh, 48-cm opening diameter) by performing oblique hauls from near-bottom to surface. Samples were preserved in 5% seawater formalin. The volume of filtered water was measured using a mechanical flowmeter. Each sample was fractionated into 20 ml aliquots for counting purposes; aliquots were examined sequentially under stereomicroscope and counted until reaching 300 individuals for each group. For the least abundant taxa, counting was performed on the entire sample. Appendicularians and copepods were identified to the species level by following the taxonomic criteria of Esnal (1999) and Bradford-Grieve et al. (1999), respectively. Developmental stages (adults, copepodites I–III and IV–V) and sex (male/female) were identified for *Oithona similis*. Stages of *Fritillaria borealis* (mature or juvenile) were identified according to Presta et al. (2015). Measures of the length of the trunk (appendicularians) and cephalothorax (nauplii, calanoids, and cyclopoids) were taken for size and structure analysis purposes ($n = 30$–50 for each group per sample). Biomass was estimated from body measurements of each specimen. Wet weights of nauplii and copepods (cyclopoids and calanoids) were calculated according to Gradinger et al. (1999) and Nozais et al. (2001). The conversion factor for nauplii was 360, whereas that for copepodites and adult copepods depended on their body shape (C: 560 for semicylindrical shapes; C: 400 for pyriform shapes). Dry weight was estimated as 22.5% of the corrected wet weight (Gradinger et al. 1999), while carbon concentration was assumed to be 40% of the dry weight (Feller and Warwick 1988). Appendicularian biomass was estimated by using the relationships described in Jasper et al. (2009). For appendicularians and copepods, a factor of 30% was applied to correct for weight loss due to formaldehyde (Böttger-Schnack 1985).

Spearman Rank Correlation (r_s) test was used to relate the abundances of the groups and of the species of copepods and appendicularians with temperature and with total and size-fractioned Chl-*a* ($p < 0.05$).

ANOVA tests were performed in order to detect possible statistically significant differences in the sizes of each mesozooplankton group between (a) the different sites explored in each summer, and (b) the two sites explored in both summers (S3 and S4). Homoscedasticity and normality of residuals in all analyses were tested graphically (Zuur et al. 2009). Since all groups showed normally distributed residuals, the models used were all of the general linear type. The assumption of homogeneity of variance was satisfied in all cases except for the size of calanoids in 2014, so an ordinary least squares estimation was used in the analysis. Non-homogeneity of variances in the size of calanoids during 2014 was addressed by using generalized least squares (GLS) fit by Restricted Maximum Likelihood Estimation (REML) and the VarIdent function, which allows different variances per treatment (Zuur et al. 2009). Tukey's Honestly Significant Difference test was used to determine differences among sites when an effect proved significant (F ratio, $p < 0.05$). All statistical analyses were performed using the statistical softwares R (R Development Core Team 2017) and InfoStat (Di Rienzo et al. 2013).

Shannon diversity index (*H*) (Shannon and Weaver 1949) was used to estimate diversity, while the evenness of samples was assessed by the Pielou index (*J*) (Pielou 1969).

A multivariate analysis technique of numerical classification was used to define groups of sites based on the abundance values of copepod and appendicularian species. Hierarchical agglomerative clustering was carried out using the Bray–Curtis similarity index (Bray and Curtis 1957) coupled with group average. To identify an appropriate number of groups, we use two criteria according to Balzarini et al. (2008) and Borcard et al. (2011): (1) plotting the fusion level values (the dissimilarity values where a fusion between two branches of a dendrogram occurs); (2) draw a cut line at a distance equal to 50% at the maximum observed distance. These criteria allow identifying reasonably well-balanced, without outliers, and well-delimited groups. To examine the contribution of each taxon both to the degree of similarity within a group and to the degree of dissimilarity between groups, an analysis of similarity percentage (SIMPER) was applied using the Bray–Curtis similarity index. PRIMER 5.0 software package (Clarke and Warwick 2001) was used for data analysis.

Feeding experiment and clearance rate of *Oithona similis*

This experiment was carried out on materials collected in the site nearest to Orcadas Station (S4) on 03/05/2104. Seawater samples were taken from a 10 m depth by means of Niskin bottles. A volume of 500 mL was preserved in 2% formaldehyde for the quantitative analysis of nano- and microplanktonic organisms. A volume of 20 mL was filtered by duplicate in black polycarbonate filters of 0.8 µm pore size and stained with DAPI (f.c. 5 µg mL^{-1}) according to Porter and Feig (1980) for estimations of nanoflagellate abundance. Filters were kept frozen in darkness until examination. For the identification of diatom species, subsamples were processed according to Simonsen (1974) for eliminating the organic matter from frustules, and the specimens were further mounted onto glass slides using Naphrax. The rest of the volume was filtered through a sieve of 200-µm mesh to exclude metazoan grazers, and used as natural food source for the experiment.

In turn, mesozooplankton was sampled by slow vertical hauls with a plankton net (mesh size 200 µm) in the upper 10 m. Immediately after collection, the content of the net was transferred to a thermobox and taken to Orcadas Station. The copepod species chosen for the experiments was *O. similis*, as it was found to be the dominant one in a preliminary analysis of the materials. Within 1 h after collection, undamaged individuals were sorted under a stereomicroscope and removed with a wide-mouth pipette. Five individuals were placed into 500 ml experimental bottles ($n = 6$) previously filled with natural seawater, and incubated for 24 h at 1–2 °C. Control bottles (without copepods, $n = 6$) were incubated in the same way. All bottles were regularly rotated/shaken in order to prevent food sedimentation. After incubation, individuals were checked for survival, verified as to their level of activity, and removed from the bottles. The volume of water at the final time was immediately preserved for quantitative analyses of nanoflagellates and other nano- and microplanktonic components. At the beginning and at the end of the experiment, water samples of both control and experimental bottles were preserved (following the procedure described below) and examined under an inverted microscope according to the Utermöhl (1958) technique for the counting of nano- and microplanktonic cells ($n = 12$), and under an upright fluorescence microscope for the counting of nanoflagellates (by duplicate, $n = 24$). Clearance rate of *O. similis* was calculated from the density of cells before and after incubation in both experimental and control bottles using the equations proposed by Kiørboe et al. (1982). Concentration of each food item in the final time was compared between treatments (with/without copepods) by using the Student *t* test. The selectivity coefficient (*W*) and electivity index (*E*) of *O. similis* for each food item available was calculated according to Vanderploeg and Scavia (1979).

Results

Environmental features, mesozooplanktonic community structure, and species abundance

Summer 2014

Tables 1 and 2, and Fig. 2a–d summarize the environmental features and the biotic variables of the main mesozooplanktonic groups. Average values found for surface seawater temperature and total Chl-*a* were above 1 °C (Max: 1.3 °C) and around 5 mg Chl-*a* m^{-3}, respectively, with little variation between sites. Most of the Chl-*a* (up to 95%) was in the > 10 µm fraction, followed by the 2–10 µm fraction (~ 3%). The 0.7–2 µm fraction was undetectable. According to in situ observations, the sea ice retreated in October 2013.

The mesozooplanktonic community was represented by copepods, nauplii and appendicularians. The mean contribution of these groups to abundance was 68, 18 and 14%, respectively. Cyclopoids were dominant (57%) over calanoids (11%) in almost all sites. Mean biomass of total mesozooplankton was 7667 µg C m^{-3}. The mean contribution of calanoids and cyclopoids to the total was 81.6 and 18% (6258 µg C m^{-3} and 1377 µg C m^{-3}) while that from

Table 1 Temperature (°C), total and size-fractioned chlorophyll-*a* (mg Chl-*a* m^{-3}), and abundance (ind m^{-3}) of total mesozooplankton, appendicularians, cyclopoids, calanoids and nauplii in Scotia Bay during summer 2014

	Mean ± SE	Range
Surface temperature	1.13 ± 0.17	0.9–1.3
Total Chl-*a*	4.7 ± 0.47	4.26–5.26
Chl-*a* > 10 μm	4.58 ± 0.51	4.11–5.11
Chl-*a* 2–10 μm	0.12 ± 0.08	0–0.20
Chl-*a* 0.7–2 μm	0	0
Mesozooplankton and species abundance		
Total	1338 ± 749	671–2111
Appendicularians		
Fritillaria borealis	189 ± 60	133–272
Cyclopoids	755 ± 548	226–1464
Oithona similis	453 ± 359	49–900
Oithona frigida	302 ± 203	111–564
Oncaea sp.	47 ± 46	0–107
Calanoids	151 ± 117	41–302
Calanoides acutus	14 ± 15	4–37
Calanus propinquus	17 ± 10	7–31
Rhincalanus gigas	2 ± 5	0–10
Calanus simillimus	44 ± 63	4–136
Microcalanus pygmaeus	5 ± 9	0–18
Metridia sp.	14 ± 18	0–37
Clausocalanus brevipes	9 ± 15	0–31
Nauplii	243 ± 312	73–711

appendicularians and nauplii represented 0.3 and 0.1% (26 and 6 μg C m^{-3}) respectively.

The size structure of each mesozooplankton group was roughly similar between sites (Fig. 2c) with the exception of site S4 (ANOVA: F calanoids (3,196) = 60.7, $p < 0.0001$; F cyclopoids (3,196) = 13.24, $p < 0.0001$; F appendicularians (3,196) = 7.53, $p < 0.0001$).

A total of eleven species were found in the bay during summer 2014 (between 7 and 11 at the different sites): Three species of cyclopoids (*Oithona similis*, *Oithona frigida* and *Oncaea* sp), seven species of calanoids (*Rhincalanus gigas*, *Calanoides acutus*, *Calanus simillimus, Calanus propinquus, Microcalanus pygmaeus, Metridia* sp, and *Clausocalanus brevipes*), and one species of appendicularians (*Fritillaria borealis*). The H index ranged from 1.2 to 1.84, with equitability values being quite similar between sites (0.63–0.83).

The dominant species in terms of abundance at most sites was *O. similis* (mean: 4.5 × 10^2 ind m^{-3}), which showed a high contribution of females (average: 30.7%) with ovisacs and an average female:male ratio of 1.73. The most evenly distributed species was *F. borealis* (mean: 1.89 × 10^2 ind m^{-3}; Fig. 2c), with an average mature:juvenile ratio of 0.62.

A comparative analysis of summer 2014 sampling sites based on the spatial variability of mesozooplankton showed the following trends:

The site next to the penguin colony (S1) hosted both highest densities and highest biomass of total mesozooplankton (2111 ind m^{-3}; 14076 μg C m^{-3}). This is accounted for by the contribution of calanoids (88.35%, 12435 μg C m^{-3}), which were here more abundant than elsewhere, and were represented mainly by *C. simillimus, C. propinquus* and *R. gigas* (136, 19 and 10 ind m^{-3}, respectively), with the latter species being found only at this site.

The site close to the glacier (S3) showed the highest values of diversity (H: 1.84) jointly with lowest total mesozooplankton abundances (671 ind m^{-3}) and approximately half of the biomass found at S1 (6434 μg C m^{-3}). The abundance of calanoids, appendicularians and cyclopoids showed a similar range: 184–226 ind m^{-3}. S3 also exhibited the following exclusive features: (a) *O. frigida* prevailed in abundance over *O. similis* (177 ind m^{-3} vs. 49 ind m^{-3}); (b) calanoids showed largest sizes (1992 ± 734 μm, $n = 50$, Fig. 2c); (c) copepodits I–III of *O. similis* reached their highest contribution; (d) *Oncaea* sp was absent.

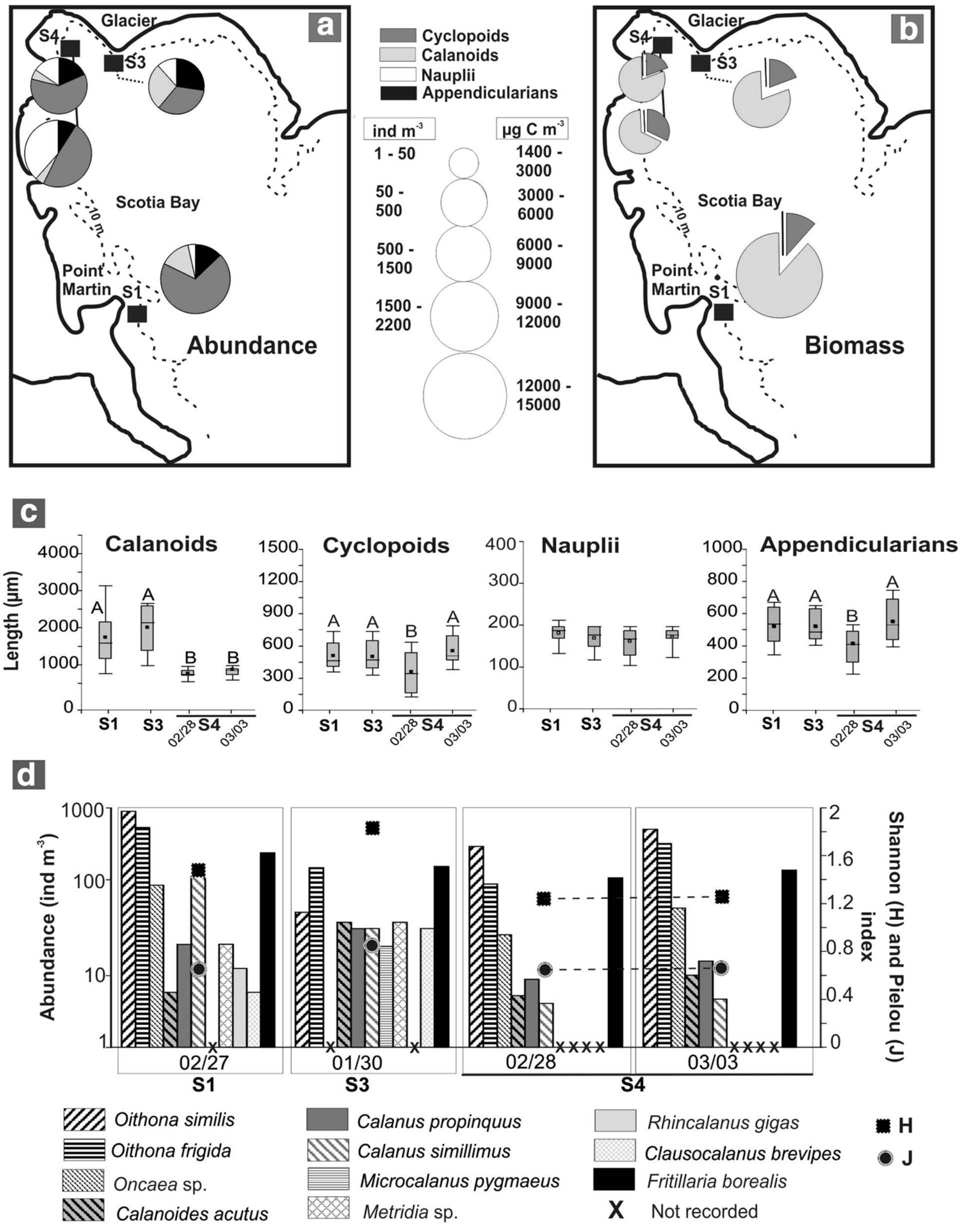
The site near Orcadas station (S4) stood out for the dominance of adult stages (mainly females) of *O. similis* jointly with the absence of *Metridia* sp., *M. pygmaeus, R. gigas*, and *C. brevipes*. This site, which was sampled twice within a 4-day period (02/28 and 03/03), revealed pronounced short-term fluctuations in abundances: Highest percentage of females of *O. similis* with ovisacs (Table 2), smallest sizes (496 ± 96 μm, $n = 50$) and lowest biomass values (902 μg C m^{-3}) of both cyclopoids and *Fritillaria borealis* (75% of juveniles) were recorded on 02/28.

Table 2 Relative abundance (%) of copepodites (CI–III; IV–V) and adults (female, male) of *Oithona similis*, and of mature and juvenile individuals of *Fritillaria borealis* in Scotia Bay during summer 2014

Site	Date	*Oithona similis*					*Fritillaria borealis*		
		Female	Male	Female:Male	CI–III	CIV–V	Mature	Juvenile	Mature:Juvenile
1	02/27	20*	14.2	1.41	35.8	30	41	59	0.69
3	03/03	18*	10.6	1.70	44	27.4	35	65	0.54
4	02/28	45*	23	1.96	18	14	25	75	0.33
4	03/03	39.8	21.3	1.87	24.6	14.3	48	52	0.92
Average		30.7	17.27	1.73	30.6	21.43	37.25	62.75	0.62

Asterisk indicates > 50% contribution of *Oithona similis* females with ovisacs

Fig. 2 Summer 2014 in Scotia Bay: **a** Abundance (ind m^{-3}), **b** biomass (μg C m^{-3}); **c** size structure of each mesozooplanktonic group (different letters indicate significant differences between sites, $p < 0.05$); **d** species abundance (log scale), Shannon index (*H*) and Pielou index (*J*)



Contrastingly, on 03/03 there was a twofold increase in the abundance and biomass of cyclopoids, a twofold increase in the abundance of calanoids, and a sevenfold increase in the abundance of nauplii. Nauplii abundances observed at site S4 on this date are the highest of all summer 2014 records (711 ind m^{-3}), and are likely to represent a reproductive peak of *O. similis*.

The analysis of the mesozooplanktonic community as a function of environmental variables during summer 2014 revealed that both the abundance and the biomass of cyclopoids correlate negatively with total and > 10 μm Chl-*a* (Spearman rank correlation, $r_s = -0.8$, $n = 4$, $p = 0.04$; $r_s = -0.96$, $n = 4$, $p = 0.01$, respectively), while the abundance of *O. similis* correlates positively with the 2–10 μm Chl-*a* fraction (Spearman rank correlation, $r_s = 0.76$, $n = 4$, $p = 0.02$).

Summer 2015

Tables 3 and 4, and Fig. 3a–d summarize the trends observed for this period. Average values of seawater temperature and total Chl-*a* were equal or below 0.5 °C and around 1.53 mg Chl-*a* m^{-3}, respectively. The mean contribution of the different Chl-*a* fractions was 49% for > 10 μm, 43% for 2–10 μm and 9% for 0.7–2 μm (Table 3). In this summer, the seasonal sea ice persisted in the bay until January.

On average, total zooplankton abundances (125 ind m^{-3}) were one order of magnitude lower than in 2014, with a

Table 3 Temperature (°C), total and size-fractioned chlorophyll-*a* (mg Chl-*a* m^{-3}), and abundance (ind m^{-3}) of total mesozooplankton, appendicularians, cyclopoids, calanoids, nauplii and other taxa in Scotia Bay during summer 2015

	Mean ± SE	Range
Surface temperature	0.19 ± 0.28	− 0.2 to 0.5
Total Chl-*a*	1.53 ± 0.98	0.93–3.54
Chl-*a* > 10 µm	0.76 ± 0.89	0–2.64
Chl-*a* 2–10 µm	0.64 ± 0.37	0.22–1.15
Chl-*a* 0.7–2 µm	0.14 ± 0.12	0–0.37
Mesozooplankton and species abundance		
Total	125 ± 111	23–360
Appendicularians		
Fritillaria borealis	8 ± 11	0–29
Cyclopoids	48 ± 42	9–133
Oithona similis	37 ± 31	7–102
Oithona frigida	11 ± 12	2–30
Calanoids	25 ± 21	3–68
Calanoides acutus	2 ± 2	0–8
Calanus propinquus	8 ± 7	0–19
Rhincalanus gigas	10 ± 6	3–21
Calanus simillimus	2 ± 3	0–10
Microcalanus pygmaeus	1 ± 1	0–3
Metridia sp.	1 ± 1	0–2
Clausocalanus brevipes	2 ± 3	0–8
Nauplii	41 ± 36	2–115
Other	3 ± 6	1–15

Other: Siphonophora, Polychaeta, Cladocera, Chaetognatha, and Nemertea

dominance of copepods (mean: 59%, cyclopoids 39%, calanoids: 20%) followed by nauplii (33%) and appendicularians (6%). Mean biomass of total mesozooplankton reached 5283 µg C m^{-3}. The mean contribution of calanoids to the total was 95% (5035 µg C m^{-3}), followed by cyclopoids (4.5%, 239 µg C m^{-3}), appendicularians and nauplii (< 0.5%, 6 and 4 µg C m^{-3}, respectively).

Size structures of nauplii and appendicularians were similar between sites. However, those of cyclopoids and calanoids (Fig. 3c) proved to be significantly different, presumably due to the (smallest) sizes found at S8 (ANOVA: F cyclopoids (6,295) = 16.27, $p < 0.0001$; F calanoids (6,295) = 2.93, $p = 0.0087$).

The number of species (between 3 and 10 at the different sites) and the values of the H index (0.62–1.64) and equitability (0.56–0.92) were found to be more variable than in 2014. Copepod and appendicularian species' compositions were roughly the same as summer 2014 except for *Oncaea* sp (not recorded in 2015) and *Rhincalanus gigas* (recorded at all sites in 2015) (Fig. 3d).

As in 2014, *O. similis* was dominant in all sites; however, females were not observed with ovisacs in 2015, and the mean female:male ratio was slightly higher (1.96). The mature:juvenile ratio of *F. borealis* increased substantially in 2015 (average: 12.84), with ~ 90% of the individuals being mature (Table 4).

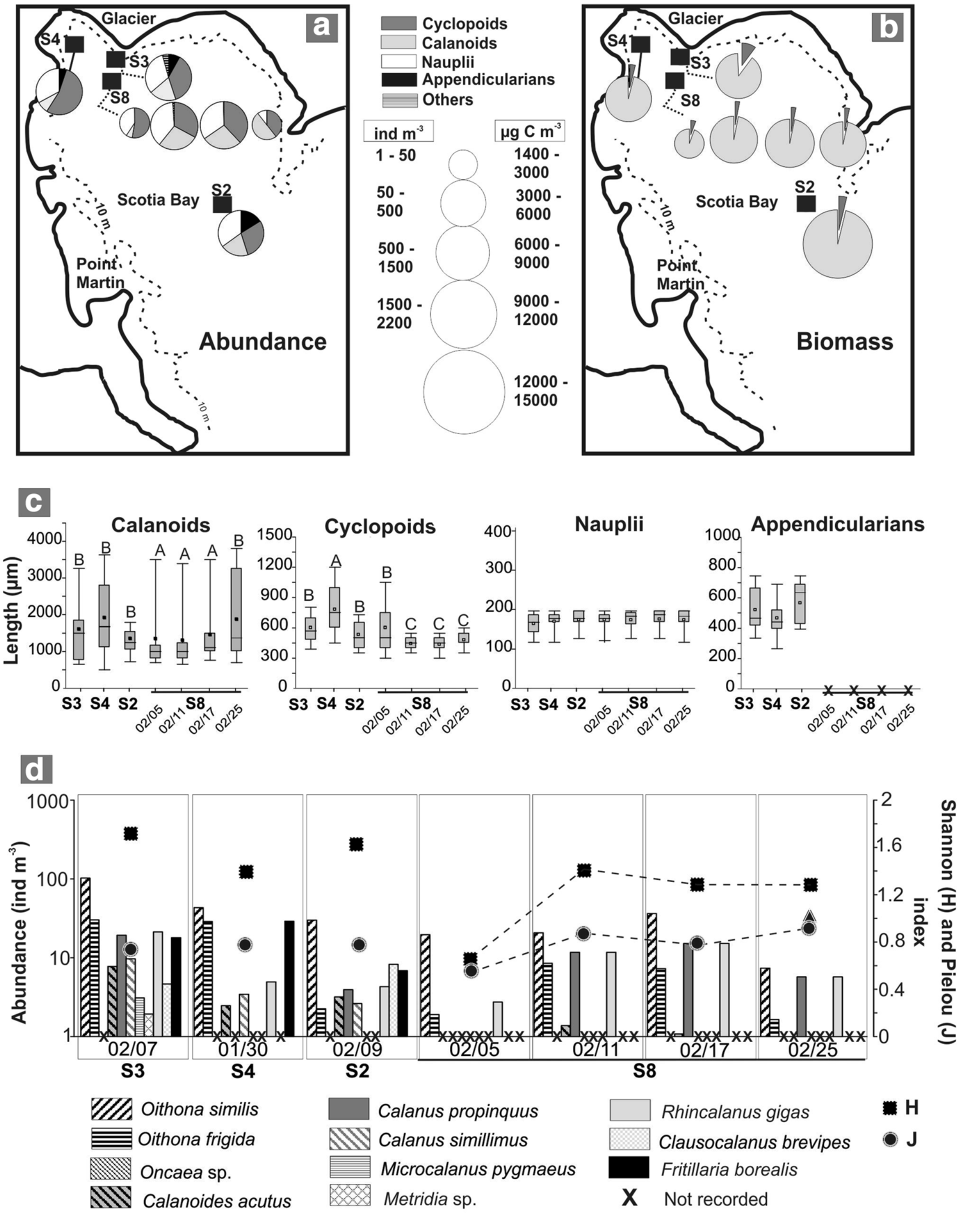
The waters surrounding the glacier (site S3) exhibited the highest number of species and Shannon index, as well as the maximun abundances of total mesozooplankton (360 ind m^{-3}) and of cyclopoids in particular (133 ind m^{-3}). This site was also marked by the presence of other mesozooplanktonic groups in low densities (< 1% of total mesozooplankton abundance), such as Amphipoda, Siphonophora, Polychaeta, Cladocera, Chaetognatha, andNemertea (Fig. 3a, Table 3).

Short-term fluctuations (weekly sampling during one month) were explored at Site S8 in 2015 (Fig. 4). The mesozooplanktonic community (Fig. 3d, 4) was represented only by copepods (cyclopoids, calanoids and nauplii), with no records of either *Calanus simillimus*, *C. brevipes* or the appendicularian *Fritllaria borealis*. An increase in all groups present was observed toward the 3rd week (twofold for cyclopoids and nauplii; one order of magnitude for calanoids), with a subsequent decrease during the 4th week of the survey. In parallel with this trend, total Chl-*a* decreased toward the second and 3rd weeks with null records of the > 10 µm fraction during the latter, in coincidence with the peaking of the three groups. This trend was confirmed by the highly significant negative correlation found at this site

Table 4 Relative abundance (%) of copepodites (CI–III; IV–V) and adults (female, male) of *Oithona similis*, and mature and juvenile individuals of *Fritillaria borealis* in Scotia Bay during summer 2015

Station	Date	*Oithona similis*					*Fritillaria borealis*		
		Female	Male	Female:Mature	CI–III	CIV–V	Mature	Juvenile	Mature:Juvenile
3	02/07	24.8	12.6	1.97	26.2	36.4	91	9	10
4	01/30	32	25	1.28	18	25	95	5	19
2	02/09	22.6	12	1.88	27	38.4	90.4	9.6	9.4
	02/05	42	18	2.33	8	32	0	0	
8	02/11	35	20	1.75	15	30	0	0	
	02/17	33	17.5	1.89	31.5	18	0	0	
	02/25	27.6	10.4	2.65	35.8	26.2	0	0	
Average		31	16.5	1.96	23.07	29.43	92.13	7.87	12.84

Fig. 3 Summer 2015 in Scotia Bay: **a** Abundance (ind m^{-3}), **b** total biomass (µg C m^{-3}), **c** size structure of each mesozooplanktonic group (different letters indicate significant differences between sites, $p < 0.05$) and **d** species abundance (log scale), Shannon index (H) and Pielou index (J)



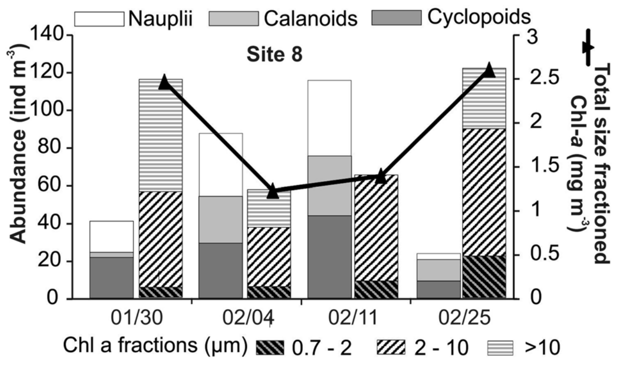


Fig. 4 Abundance (ind m^{-3}) of nauplli, cyclopoids and calanoids, and total and size-fractioned chlorophyll-*a* (mg Chl-*a* m^{-3}) in site S8 during the four sampling dates of summer 2015

for calanoid and nauplii numbers vs. total and > 10 µm Chl-*a* (Spearman rank correlation $r_s = -0.93$, $n = 4$, $p = 0.04$; and $r_s = -0.97$, $n = 4$, $p = 0.04$; respectively). Also during the 3rd week (02/25), the similar contribution of different species to abundance (~ 7 ind m^{-3}) resulted in the highest value of equitability.

Sites S4 and S2 were separated 3 km from each other, the former being located on inshore waters and the latter farther into outer waters. Despite their similar total mesozooplankton abundances (134 and 112 ind m^{-3}), S4 and S2 differed widely in other aspects: S4 showed the highest Chl-*a* concentrations of summer 2015 (3.54 vs. 0.47 mg Chl-*a* m^{-3}) jointly with the dominance of cyclopoids (87% in abundance), mostly of large sizes. On the other hand, site S2 exhibited quite similar contributions of calanoids and cyclopoids (59 and 41% in abundance), but total mesozooplanktonic biomass reached the highest values within the whole bay (Max: 9322 μg C m^{-3}), mainly attributable to calanoids (8961 μg C m^{-3}) (Fig. 3a).

Results from Spearman rank correlation (r_s) between environmental variables and mesozooplanktonic groups and species revealed that temperature correlated negatively with total mesozooplankton biomass ($r_s = -0.73$, $n = 7$, $p = 0.02$), cyclopoid biomass ($r_s = -0.84$, $n = 7$, $p = 0.02$), calanoid sizes ($r_s = -0.91$, $n = 30$, $p = 0.001$), calanoid abundance ($r_s = -0.86$, $n = 7$, $p = 0.004$), and the abundance of *R. gigas* and *C. propinquus* ($r_s = -0.76$, $n = 7$, $p = 0.04$; and $r_s = -0.79$, $n = 7$, $p = 0.03$, respectively).

Summer 2014 versus summer 2015

Based on the abundance of the species recorded at all sites in both 2014 and 2015, the cluster analysis revealed two main groups of sites (Fig. 5): Group I, comprising all summer 2014 sites, and Group II, comprising all summer 2015 sites. The MDS analysis confirmed the cluster assemblages. In summer 2014 (Group I), *O. similis, O. frigida,* and *F. borealis* had similar contribution in abundances (35, 29.6, and 28%, respectively). In summer 2015, there were changes in the species structure and abundances (one order of magnitude lower than that in 2014): *O. similis* was the dominant species (58%) followed by *R. gigas* (16%) and *O. frigida* (11%).

On the other hand, based on the sizes of copepod species and appendicularians, it was found that both calanoids and *F. borealis* reached sizes significantly larger (ANOVA: F calanoids $(1,500) = 7.36$, $p = 0.0069$; *F Fritillaria borealis* $(1,335) = 8.78$; $p = 0.0033$) at the lower temperatures of summer 2015. Cyclopoids were also larger in 2015, yet not significantly (ANOVA, $F(1,500) = 0.24$, $p = 0.6246$).

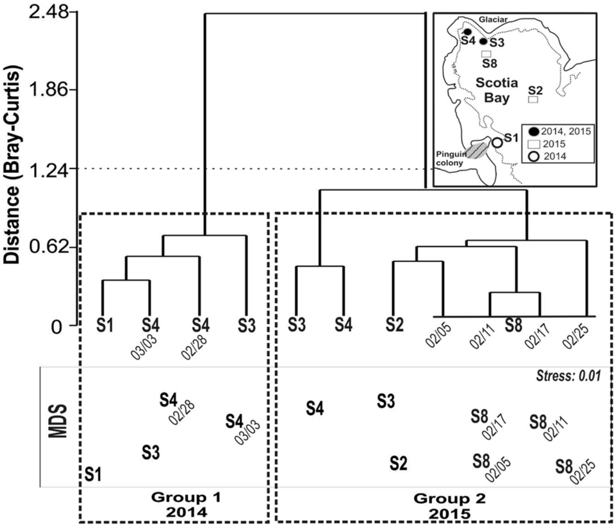


Fig. 5 Cluster analysis and multidimensional scaling (MDS) based on copepod and appendicularian species abundances at all sites during summers, 2014 and 2015, in Scotia Bay

Finally, a comparison restricted only to the sites sampled in both 2014 and 2015 (S3 and S4) revealed for these two places the same trend of all other sites investigated, i.e., higher values of temperature, total Chl-*a,* and total mesozooplankton abundances in 2014 as compared to 2015 (Table 5). Total biomass, however, was not found to vary substantially from one year to another.

In the vicinity of the glacier (site S3), 100% of the total Chl-*a* in summer 2014 was provided by the > 10 μm fraction, in coincidence with the high values of abundance and biomass of total mesozooplankton. In 2015, there was an increase in the contribution of both the 0.7–2 and 2–10 μm Chl-*a* fractions jointly with a change in the structure of the mesozooplanktonic community, as this period was marked by the presence of other mesozooplanktonic groups in low

Table 5 Comparison of temperature (°C), total Chl-*a* (mg Chl-*a* m^{-3}), relative contribution of size-fractioned Chl-*a* (%), abundance (A, ind m^{-3}), biomass (B, μg C m^{-3}), and size (S, μm) of total mesozooplankton, appendicularians, cyclopoids, calanoids and nauplii in Scotia Bay at sites S3 and S4 in summer 2014 and 2015

Site	S3		S4	
Year	2014	2015	2014	2015
Surface temperature	1.3	− 0.2	1.05	0.5
Total Chl-*a*	4.92	1.08	4.81	3.54
Chl-*a* > 10 μm (%)	100	63	96	75
Chl-*a* 2–10 μm	–	21%	4%	25%
Chl-*a* 0.7–2 μm	–	16%	–	–
Total mesozooplankton				
A	671	360	1285	134
B	6434	5401	5079	4331
Appendicularians				
A	184 (27%)	29 (8%)	149 (12%)	7 (5%)
B	33	25	25	7
S	464	522	456	565
Cyclopoids				
A	226 (34%)	133 (37%)	665 (52%)	72 (54%)
B	1236	544	1329	166
S	570	601	464	781
Calanoids				
A	184 (27%)	68 (19%)	60 (5%)	11 (8%)
B	5185	4820	3720	4154
S	1993	1617	799	1917
Nauplii				
A	78 (12%)	115 (32%)	412 (32%)	44 (33%)
B	7	11	5	3
S	169	169	167	174

The contribution of each group to total mesozooplankton abundance is shown in brackets densities. The sizes of appendicularians were significantly larger in 2015 (ANOVA, $F(1,99) = 4.64$, $p = 0.0336$). Remarkably, site S3 showed both the lowest and highest temperature values recorded during the survey. The temperature maximum was registered during summer 2014 (1.3 °C) in association with the shared dominance of *F. borealis* and *O. frígida* (32 and 30%, respectively). On the other hand, the temperature minimum corresponded to summer 2015 (− 0.2 °C), with the clear dominance of *O. similis* (47%).

In the vicinity of Orcadas Station (site S4), the 0.7–2 µm Chl-*a* fraction was negligible in both summers, but the contribution of the 2–10 µm fraction was higher in 2015. The sizes of calanoids, cyclopoids and appendicularians, on the other hand, were significantly larger in 2015 (ANOVA, F calanoids $(1,148) = 77.04$, $p < 0.0001$; F cyclopoids $(1,148) = 53.37$, $p < 0.0001$; and F appendicularians $(1,148) = 7.78$, $p = 0.006$).

Table 6 Abundance of diatoms and nanoflagellates in experimental (EB, Cell L^{-1}) and control bottles (CB, Cell L^{-1}) at the final time (Tf) during a feeding experiment on *Oithona similis*, with Student *t* (*T*) and *p* values

	N	Trophic item	
		Diatoms	Nanoflagellates
Tf (EB)	6	99831	824688
Tf (CB)	6	102883	1326506
T		− 0.45	− 4.9
p		0.6595	**0.0006**
F mean + SE (range)		0.18 ± 0.34 (− 0.24 to 0.59)	2.96 ± 1.32 (1.45–4.50)
W		0.13	0.86
E		− 0.51	0.63

E values < 0 indicate no food selection

F Oithona similis feeding rate (ml ind^{-1} h^{-1}), *W* selectivity coefficient, *E* electivity index

Bold values = statistically significant ($p < 0.05$)

Feeding experiments on *Oithona similis*

During summer 2014, food items in situ and in the experimental bottles at the initial time of the experiment were nanoflagellates (contribution to abundance: 95.63%), diatoms (4.25%), silicoflagellates (0.08%), ciliates (0.03%), and tintinnids (0.01%). Given that the abundance of silicoflagellates, ciliates and tintinnids was extremely low and could lead to inaccurate estimations, the analysis was restricted to nanoflagellates and diatoms. Table 6 summarizes the results of the mean final concentrations in the 6 replicates of the control and 6 experimental bottles, the filtration rate (F), the selectivity coefficient (W) and the electivity index (E). Two main trends were observed at the end of the experiment: (1) nanoflagellates showed concentrations significantly different from initial ones jointly with a high filtration rate, a selectivity coefficient close to 1, and a positive electivity index; (2) the average abundance of diatoms in the experimental and control bottles was not significantly different, and in three of the replicates no filtration rates was observed on diatoms (Fig. 6a). In addition, the selectivity coefficient for diatoms was much lower than that for nanoflagellates and the electivity index was negative, thus indicating that *O. similis* rather avoided feeding on diatoms. From the 26 diatom species identified at the beginning of the experiment, three of them (*Thalassiosira tumida*, *Odontella weissflogii*, and *Pseudo-nitzschia* cf *lineola*) represented 74% of total abundance.

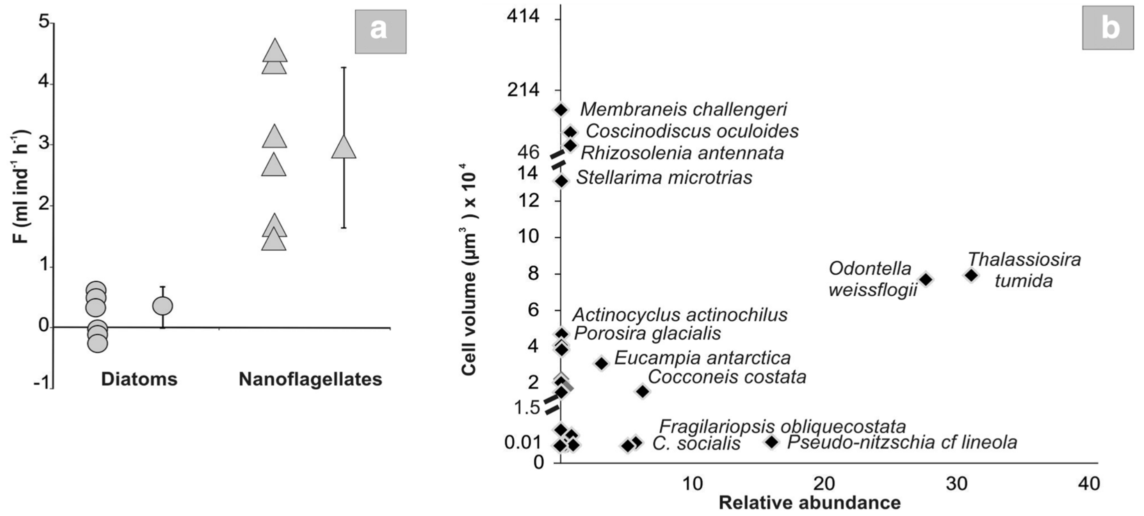


Fig. 6 Clearance rate (F: ml ind^{-1} h^{-1}) of *Oithona similis* on diatoms and nanoflagellates (**a**) and relative abundance (%) of diatom species versus cell volume ($µm^3$) (**b**)

The cell volume ranged from ca. 100 µm^3 to 629 × 10^4 µm^3, with over 50% of the cells having a mean volume above 2 × 10^4 µm^3 (Fig. 6b). Within the range of smaller volumes (< 2 × 10^4 µm^3), ca. 70% of the diatoms corresponded to solitary forms such as *Asteromphalus*. *Cylindrotheca*, and benthic taxa—like *Cocconeis* and *Licmophora*. The remaining ~ 30% formed chains or filaments (*Chaetoceros criophilus, C. socialis, Fragilariopsis obliquecostata, F. curta, F. sublinearis, Pseudo-nitzschia heimii,* and *P. lineola*).

Discussion

Spatial and annual fluctuations of mesozooplankton assemblages

Copepods were the dominant mesozooplanktonic group during the two summers and in all sites investigated, in coincidence with previous observations made on other Antarctic marine environments (Atkinson 1998). Whereas the abundance of Antarctic copepod species has been a major research topic since the first expeditions, data comparisons among the various sources are hampered by the different units used (e.g., ind m^{-2} vs. ind m^{-3}), the different methods applied for biomass estimations, the type and mesh-size of nets, the sampling depth, and the time of year, as concluded by Atkinson et al. (2012). Nevertheless, the methods applied on some Antarctic coastal areas allow some comparisons; for instance, summer abundance of copepods in Potter Cove (25 de Mayo/King George Island, South Shetland) ranged from 8 to 40 ind m^{-3} (García et al. 2015), while the orders of magnitude in Terra Nova Bay (Ross Sea) are the same as in our study (range: 45.2–3965.3 ind m^{-3}; Pane et al. 2004). Coincidentally, *O. similis* was the dominant species in both areas.

Studies on the mesozooplankton of South Orkney nearshore marine environments in particular are extremely scarce, with just a few—mainly taxonomic—articles restricted to Signy Island. For example, Gee and Fleeger (1986) describe two species of harpacticoid copepods, and Stanwell-Smith et al. (1997) address the tunicates found in their study on invertebrate larvae. In this context, the current study is the first for nearshore environments of Laurie Island, and may also be the first in providing ecological information on the coastal mesozooplankton of the South Orkney Archipelago. The fact that there might exist inaccessible publications from early expeditions precludes us from confirming this fact.

Environmental conditions, species specific-assemblages, and the structures of copepod and appendicularian communities in Scotia Bay all show a clear difference between summer 2014 and summer 2015 (Table 1, 3, 5; Figs. 2, 3). Summer 2014 was characterized by higher temperatures and Chl-*a* concentrations, jointly with abundances that were one order of magnitude higher for all groups of copepods and two orders of magnitude for appendicularians compared with summer 2015. The decrease in numbers found in summer 2015 was offset by a statistically significant increase in the size of both calanoids and appendicularians (calanoids contribution to total biomass: 95%), resulting in non differences between both summers in terms of total mesozooplankton biomass. This suggests that the ecosystem remained quite stable in its carbon content despite the shift in species composition and environmental conditions.

Temperature, like sea ice dynamics and the quantity, quality and size of food, plays a key role in the life cycle of zooplankton. Low temperatures result in organisms with larger sizes (such as in summer 2015) and also in longer egg hatching times and stage durations (Ward and Shreeve 1998; Shreeve et al. 2002; Hirst and Bunker 2003), thus increasing the mortality of slower growing instars (Kiørboe and Hirst 2008).

General trends of Antarctic sea ice coverage during the time of this study are not clear (Eisenman et al. 2014). There is little evidence of a decline in sea ice in this region over the last 30–50 years (Murphy et al. 2014). The scarcity of previous investigations on the area of this study hinders the analysis of the effects of sea ice extent and winter persistence on food availability and mesozooplankton abundances. Nevertheless, and according to in situ observations, the sea ice retreat in Scotia Bay during 2014 occurred earlier than in 2015 (October 2013 and January 2015), thus possibly accelerating the advent of the phytoplanktonic bloom and favoring the reproduction and the increase of mesozooplanktonic abundances. On the other hand, regions such as the Western Antarctic Peninsula are currently showing significant changes in their macrozooplankton and copepod community structure as a result of an increase in air and sea surface temperature, and a decrease in sea ice coverage (Atkinson et al. 2012; Gleiber et al. 2012; Gleiber 2014; Steinberg et al. 2015). Based on a long-term temporal series, Gleiber (2014) concluded that higher abundances of copepods are related to high chlorophyll and low sea ice conditions. When applying this trend to Scotia Bay, the significant changes in mesozooplankton abundances from a warmer, richer summer in 2014 to a colder, poorer summer in 2015 could be indirectly related to atmospheric conditions and an earlier sea ice retreat. Incidentally, the results from Scotia Bay stress the relevance of biomass measurements to understand the role of environmental changes in the carbon dynamics of planktonic communities.

Oithonid and Oncaeid cyclopoids occur worldwide in high abundances. Their biomass levels in Antarctic waters can reach the same order of magnitude as calanoids (Metz 1996, 1998; Schnack-Schiel et al. 1998). Despite its numeric dominance in Scotia Bay, cyclopoids (mainly oithonids) showed low (18%) to very low (4.5%) levels of average biomass in 2014 and 2015, respectively (Fig. 2, 3). Instead, the bulk of biomass was mostly due to calanoids, the contribution of which increased from 82% in 2014 to 95% in 2015. Among these, *R. gigas* was the only species with a rise in abundance in 2015 (Fig. 3d). Such an increment is thought to respond to changes in the water circulation pattern that favor the proliferation of this species in the bay, in accordance with Zmijewska and Yen (2003), and/or to the significant decrease in sea water temperature from 2014 to 2015, as suggested by the highly significant negative correlation between *R. gigas* numbers and sea temperature. Calanoids of larger sizes were also found in colder waters, in agreement with trends previously reported (Chinnery and Williams 2004; Hansen et al. 2010).

Spatial distribution

The mesozooplankton community of Scotia Bay was found to show a certain degree of spatial heterogeneity in terms of abundance, biomass and diversity. In the first place, highest levels of total mesozooplankton biomass and abundance were observed next to the Adélie penguin breeding areas –site sampled in summer 2014 only. This finding may respond to aloctonous organic matter from the colony fueling the food web with higher amounts of more diverse food items. The diet of the Adélie penguin, recently explored in East Antarctica on the basis of DNA sequences (Jarman et al. 2013), is composed mainly by krill (40%) and followed by fish and calanoid copepods. The latter were found in association with fish (28%) rather than with krill (23%), thus suggesting that copepods actually represent a case of secondary predation (i.e., from the consumption of fish that have eaten copepods). Given the importance of copepods in the diet of fish, and the importance of fish (such as notothenioids) in the diet of Adélie penguins—the numbers of which are in decline at most locations (Dunn et al. 2016)—, the link between these communities will have to be further explored in connection with Weddell Sea offshore waters.

Secondly, during both summers the waters next to the glacier hosted the highest diversity (H) of copepods and appendicularians jointly with the largest number of zooplankton groups. This finding suggests that local features associated with the presence of the glacier result in an environment more heterogeneous than the rest of the sampling sites, thus shaping the community structure in a special way and favoring the increase in planktonic diversity. Although our results do not provide a causal explanation to this trend, they might lead to future investigations. To date, studies addressing the impact of melting glaciers on planktonic organisms and diversity have proven controversial (Sommaruga 2015). Suggested effects range from loss of diversity in benthic communities (Sahade et al. 2015) to phytoplanktonic increase due to iron enrichment (Hawkings et al. 2014).

Finally, along the ca. 3 km distance spanning between the site nearest to the shore and the middle of the bay (S4–S8 and S2) there were clear changes in species richness (six, four, and eight species, respectively). Such richness and diversity variations at small spatial scales is attributable to top-down control processes exerted by some copepod species, as will be treated below.

Abundance fluctuations at short time scales

The results of the weekly analysis performed during one month at site S8 (approx. 1.33 km away from the coastline) in summer 2015 (Fig. 4) suggest that variations in mesozooplankton abundances respond to specific strategies related with the life cycle of dominant species (reproductive pulses reflected in nauplii increase) as well as to biotic interactions (grazing pressure and type of food availability in terms of Chl-*a*). The decoupling between the maximum abundance of nauplii and calanoid copepods (mainly *R. gigas* and *C. propinquus*) and the decrease of total and > 10 µm Chl-*a* is evinced by the inverse relationship between these variables and calanoid abundances. The diet of *C. propinquus*, in particular, is known to include both protozoans and metazoans, and to show a high degree of carnivory mainly when phytoplanktonic food is scarce (Pasternak and Schnack-Schiel 2001). As regards *R. gigas*, it has been reported to modify its diet according to spatial and temporal variations in the type of food (Ward et al. 1996). Recently, Gleiber (2014) observed that *R. gigas* changed its feeding from mostly phytoplankton in high-bloom conditions at the coast to other carbon sources (i.e., metazoans and protozoans) in lower Chl-*a* conditions at offshore stations. The feeding activity of both species, seemingly high during summer, can partially explain the decrease in total Chl-*a* and the null records of > 10 µm Chl-*a*, mostly represented by diatoms.

Among the different sites sampled in Scotia Bay during both summers, S8 was the only one where *Fritillaria borealis* was absent. This species, however, was recorded in low concentrations at those sites next to S8 (S4 and S3, located 0.8 km and 0.42 km away, respectively). No clear explanation to this finding emerges from the results of this study, as our sampling design was not conceived for such a possible patchy distribution pattern. *F. borealis* in particular -and appendicularians in general- usually exhibits a heterogeneous spatial distribution (Gorsky et al. 2005) determined primarily by environmental conditions such as temperature, circulation dynamics and wind intensity and direction (Wyatt 1973; Greve et al. 2004) rather than by grazing pressure. Nevertheless, and given its relevance as a prey item for fish, calanoids, nauplii and other pelagic organisms, the absence of *F. borealis* at S8 may also be due to preying by the calanoids *C. propinquus* and *R. gigas*, which, as previously pointed out, were dominant at this sampling site.

Occurrence of *Fritillaria borealis* at Scotia Bay in summer

Appendicularians represent an important food item for copepods, jellyfish and fish larvae (Gorsky et al. 2005), and play a key role in both the formation of marine snow and the flow of organic matter. Despite this relevance, previous ecological studies reporting data on the abundance and biomass of appendicularians in Antarctic waters have been sporadic and either spatially restricted or limited to the genus or family levels, mainly because of their fragility and the selectivity of the nets commonly used for mesozooplankton (Atkinson et al. 2012). In this context, the present study allowed discerning the following ecological aspects of appendicularians from Antarctic nearshore environments.

In Scotia Bay, the group was represented by one single, cosmopolitan species, *Fritillaria borealis*, which reached maximum abundances (average: 189 ind m^{-3}) in summer 2014. Different Antarctic coastal environments explored during an annual cycle at Potter Cove, Shetland islands (Aguirre 2015) were found to host similar mean abundances of this species (290 ind m^{-3}; 100-μm mesh; late summer) jointly with very low abundances of *Oikopleura gaussica*. A study on the appendicularians from the seasonal ice zone of East Antarctica (Tsujimoto et al. 2007) reported *Fritillaria* spp with an abundance of > 300 ind m^{-3} (270-μm mesh), while Ward et al. (2005) found mean abundances of 127 ind m^{-3} (200-μm mesh, as in our study) in the Scotia Sea during January–February. Lindsay (2012) presented detailed abundance records of appendicularian genera from three distinct zones within Eastern Antarctica waters, reporting average abundances one order of magnitude lower than those in Scotia Bay, with maximum values in the Sea Ice Zone (49.7 ind m^{-3}). On the other hand, by covering an ample sector of Eastern Antarctica in the framework of the SCAR SO-CPR Survey 1991–2008, McLeod et al. (2010) provided valuable information on the relative abundances of both *Fritillaria* spp. and *Oikopleura* spp. The analyses of this information suggest that *Oikopleura* occurs mainly in open waters and presents a rather homogeneous distribution, while *Fritillaria* tends to concentrate in ice-covered coastal and shelf waters. This dissimilar spatial distribution suggests niche separation and would account for the absence of *Oikopleura* in Scotia Bay. Nevertheless, the likely occurrence of a succession process should also be taken into account, since *F. borealis* is known to precede the occurrence of *Oikopleura* in nearly 2 months, as per the conclusions of Greve et al. (2004) for the North Sea.

F. borealis numbers were found to increase both at higher temperatures and higher > 10 μm Chl-*a* concentrations. The simultaneous finding of lower abundances and a higher mature:juvenile ratio in summer 2015 suggests that a certain time span had elapsed since the last reproductive pulse (Table 4). Instead, the higher numbers and lower mature:juvenile ratio registered during the warmer summer of 2014 (Table 2) is indicative of a recent reproductive event. This is in accordance with the experimental observations made by Lombard et al. (2009) on *Oikopleura*, who report an inverse relationship between temperature and the proportion of mature appendicularians.

Appendicularians are known to respond rapidly to an increase in phytoplankton, and their abundance maxima are usually detected in coincidence with phytoplanktonic blooms (Båmstedt et al. 2005). It is evident that summer 2014 conditions stimulated its reproduction and, possibly, the replacement of "houses." While temperature is known to regulate both house production and the clogging rate of filtering systems, the predominance of large food particles can involve a greater investment in house production in relation to food ingestion (Lindsay 2012). In this context, the higher temperatures and the larger phytoplankton (> 10 μm) recorded in summer 2014 (Table 1) may have caused both the clogging of filters and the discarding of houses, together with increased rates of growth and house renewal, as it was suggested for *O. dioica* (Sato et al. 2001). Gelatinous species are indicators of ecosystem performance and change. In the light of this, temporal/spatial trends in appendicularian abundances and its discarded houses need to be further explored in Antarctic coastal environments and marginal ice-zones.

Abundance, population structure, and feeding rates of *Oithona similis*

O. similis was the most abundant copepod species at Scotia Bay in both summers (Fig. 2d, 3d). The direct relationship found in 2014 between this species and the 2–10 μm Chl-*a* fraction suggests optimal conditions (in terms of food quality and quantity) for its growth and development during this period. Previous investigations have reported oithonids as showing both a decrease in their fecundity in low temperature conditions and a direct increase in their numbers with temperature and Chl-*a* (Ward and Hirst, 2007; Dvoretsky and Dvoretsky, 2009). While no correlation was found between temperature and *O. similis* in Scotia Bay, in summer 2014—characterized by significantly higher temperatures and Chl-*a* concentrations as compared to 2015—the population of *O. similis* seemed to experience a reproductive pulse, as suggested not only by its significantly higher abundances but also by the occurrence of mature females with eggs retained in their ovisacs (Table 2, 4). This species reproduces continuously throughout its annual cycle (Atkinson 1998), yet peaking at different times of year according to location: early spring in the Weddell Sea (Fransz 1988) or late summer at Potter Cove, Shetland Islands (Elwers and Dahms 1998). In Potter Cove, the spring–summer population shows a predominance of adult females and copepodites V, whereas the autumn population is dominated by earlier stages (Aguirre 2015). The above findings suggest that *O. similis* has the capability of adjusting the intensity of its reproductive activity according to environmental conditions.

O. similis represents an important link between microbial food webs and higher trophic levels. It has an omnivorous diet but exhibits preference for motile prey (Atkinson et al. 1996; Lischka and Hagen 2007) like ciliates and heterotrophic dinoflagellates (Nielsen and Sabatini 1996; Nishibe et al. 2010). Depending on their abundance and distribution in a given environment, diatoms have been reported either as not being ingested by *O. similis* (western sub-arctic Pacific; Nishibe et al. 2010) or as an important component of its diet (Scotia Sea; Pond and Ward 2011). The ingestion rates reported herein for *O. similis* are high for flagellates and low or almost null for diatoms in agreement with the trend observed by Nishibe et al. (2010). In turn, the low electivity index suggests avoidance of (or inaccessibility to) diatoms. In the current study, most diatoms ranged in size from 33 to 100 µm, which may in part account for the almost null consumption of these phytoplankters. The low motility of diatoms and the fact that *O. similis* uses hydraulic signals to detect its preys (Svensen and Kiørboe 2000) can further explain these results. In contrast with *O. similis*, *O. frigida*—the second most abundant species in Scotia Bay—is morphologically adapted to the consumption of diatoms (Pond and Ward 2011). The high abundances of these two species (Fig. 2a), together with the current experimental results on the feeding of *O. similis* on natural prey assemblages, suggest that oithonids at Scotia Bay are one of the main pelagic channels linking the microbial loop and the classic food chain while transferring organic carbon to higher trophic levels through sinking fecal pellets.

Conclusions

Dominated by copepods such as oithonids, summer mesozooplankton in nearshore waters of Laurie Island seems to play an important role in controlling nanoflagellate abundance, and probably also in linking the microbial loop with secondary consumers. Sampling at short temporal scales (weekly and daily frequencies) allowed a close tracking of the changes in the community structure in relation to different size fractions of Chl-*a*. A clear change in mesozooplanktonic abundances was observed from summer 2014 to summer 2015: colder sea water conditions and lower levels of Chl-*a* during summer 2015 were associated with lower abundances; yet, total biomass remained practically stable due to increased numbers of larger calanoids. Future studies should be focused on determining through which mechanisms and to what extent the changes in spatial and interannual mesozooplankton abundance are the result of either physical processes such as tidal mixing and water circulation between the bay and the Weddell Sea, or other processes such as the timing of ice retreat and its triggering effect on the seasonal phytoplankton bloom in the Scotia Bay ecosystem.

Acknowledgements We thank M. Yaya, I. Hoermann, S. Gorini, and J. Zocatelli (Dirección Nacional del Antártico) for their assistance during sampling. Thanks are due also to the Instituto Antártico Argentino and Dirección Nacional del Antártico for providing logistic support, to the Orcadas Base personnel for their cooperation, and to the reviewers for helping to improve the manuscript. This study was supported by a fellowship granted to M.S. by CONICET, Argentina, and by funds assigned to V.A.'s project PICT-O 2010-0128 (FONCYT and Instituto Antártico Argentino).

References

Aguirre G (2015) Ecología del mesozooplancton marino en ambientes costeros de altas latitudes: Canal Beagle (extremo sur de Sudamérica) y Caleta Potter (Isla 25 de Mayo, Antártida). Dissertation, University of Buenos Aires

Atkinson A (1994) Diets and feeding selectivity among the epipelagic copepod community near South Georgia in summer. Polar Biol 14:551–560

Atkinson A (1998) Life cycle strategies of epipelagic copepods in the Southern Ocean. J Mar Syst 15:289–311

Atkinson A, Ward P, Murphy EJ (1996) Die1 periodicity of subantarctic copepods: relationships between vertical migration, gut fullness and gut evacuation rate. J Plankton Res 18:1387–1405

Atkinson A, Ward P, Hunt BPV et al (2012) An overview of Southern Ocean zooplankton data: abundance, biomass, feeding and functional relationships. CCAMLR Sci 19:171–218

Balzarini MG, Gonzalez L, Tablada M et al (2008) Manual del Usuario. Editorial Brujas, Argentina

Båmstedt U, Fyhn HJ, Martinussen MB et al (2005) Seasonal distribution, diversity and biochemical composition of appendicularians in Norwegian fjords. In: Gorsky G, Youngbluth M (eds) Response of marine ecosystem to global change: ecological impact of appendicularians. GB Scientific Publisher, pp 233–259

Barnes DKA (1995) Sublittoral epifaunal communities at Signy Island, Antarctica. I. The ice-foot zone. Mar Biol 121:555–563

Borcard D, Gillet F, Legendre P (2011) Numerical ecology with R. Springer, New York

Böttger-Schnack R (1985) Untersuchungen zur Verteilung der kleinen Metazoa im Plankton des Roten Meeres, unter besonderer Beru¨cksichtigung cyclopoider und harpacticoider Copepoden. Dissertation, University of Hamburg

Bradford-Grieve JM, Markhaseva EL, Rocha CEF, Abiahy B (1999) Copepoda. In: Boltovskoy D (ed) South Atlantic Zooplankton. Backhuys Publishers, Leiden, pp 869–1098

Bray RJ, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. Ecol Monogr 27:325–349

Calbet A, Alcaraz M, Atienza DE, Broglio E (2002) Vaqué D (2005) Zooplankton biomass and distribution patterns along the western Antarctic Peninsula. J Plankton Res 27:1195–1203

Casaux R, Carlini A, Corbalán A et al (2009) The diet of the Weddell seal *Leptonychotes weddellii* at Laurie Island, South Orkney Islands. Polar Biol 32:833–838

Chinnery FE, Williams JA (2004) The influence of temperature and salinity on *Acartia* (Copepoda: Calanoida) nauplii survival. Mar Biol 145:733–738

Clarke A, Harris CM (2003) Polar marine ecosystems: major threats and future change. Environ Conserv 30:1–25

Clarke A, Leakey RJG (1996) The seasonal cycle of phytoplankton, macronutrients, and the microbial community in a nearshore antarctic marine ecosystem. Limnol Oceanogr 41:1281–1294

Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation, 2nd edn. Primer-E, Plymouth

Coria NR, Montalti D, Rombola EF et al (2011) Birds at Laurie Island, South Orkney islands, Antarctica: breeding species and their distribution. Mar Oornithol 39:207–213

Daponte MC, Capitanio FL, Esnal GB (2001) A mechanism for swarming in the tunicate *Salpa thompsoni* (Foxton, 1961). Antarct Sci 13:240–245

Di Rienzo JA, Casanoves F, Balzarini MG et al (2013). InfoStat versión 2013. Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina. http://www.infostat.com.ar

Doney SC, Ruckelshaus M, Duffy JE et al (2012) Climate change impacts on marine ecosystems. Ann Rev Mar Sci 4:11–37

Ducklow HW, Baker K, Martinson DG et al (2007) Marine pelagic ecosystems: the West Antarctic Peninsula. Philos Trans R Soc B 362:67–94

Dunn MJ, Jennifer A, Jackson JA et al (2016) Population size and decadal trends of three penguin species nesting at Signy Island. South Orkney Islands PLoS One. https://doi.org/10.1371/journal.pone.0164025

Dvoretsky VG, Dvoretsky AG (2009) Spatial variations in reproductive characteristics of the small copepod *Oithona similis* in the Barents Sea. Mar Ecol Prog Ser 386:133–146

Eisenman I, Meier WN, Norris JR (2014) A spurious jump in the satellite record: has Antarctic sea ice expansion been overestimated? Cryosphere 8:1289–1296

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 299:150–155

Esnal GB (1999) Appendicularia. In: Boltovskoy D (ed) South Atlantic Zooplankton. Backhuys Publishers, Leiden, pp 1375–1399

Feller RJ, Warwick RM (1988) Energetics. In: Higgins RP, Thiel H (eds) Introduction to the study of meiofauna. Smithsonian Institution Press, Washington, pp 181–196

Francis TB, Scheuerell MD, Brodeur RD, Levin PS et al (2012) Climate shifts the interaction web of a marine plankton community. Glob Change Biol 18:2498–2508

Fransz HG (1988) Vernal abundance, structure and development of epipelagic copepod populations of the eastern Weddell Sea (Antarctica). Polar Biol 9:107–114

Garcia MD, Hoffmeyer MS, López Abbate MC, Barría de Cao MS et al (2015) Micro and mesozooplankton responses during two contrasting summers in coastal Antarctic environment. Polar Biol 39:123–137

Gee JM, Fleeger JW (1986) Two new species of harpacticoid copepod from the South Orkney Islands, Antarctica, and a redescription of *Idyellopsis typica* Lang (Tisbidae). Zool J Linn Soc Lond 88:143–165

Gleiber M (2014) Long-term change in copepod community structure in the Western Antarctic Peninsula: Linkage to climate and implications for carbon cycling. Dissertation, The Faculty of the School of Marine Science

Gleiber MR, Steinberg DK, Ducklow HW (2012) Time series of vertical flux of zooplankton fecal pellets on the continental shelf of the western Antarctic Peninsula. Mar Ecol Prog Ser 471:23–36

Gorsky G, Youngbluth MJ, Deibel D (2005) Response of marine ecosystems to global change: ecological impact of appendicularians. Editions Scientifiques, Paris

Gradinger R, Friedrich C, Spindler M (1999) Abundance, biomass and composition of the sea ice biota of the Greenland Sea pack ice. Deep Sea Res Part II 46:1457–1472

Greve W, Reiners F, Nast J, Hoffmann S (2004) Hoffmann Helgoland Roads meso- and macrozooplankton time-series 1974 to 2004: lessons from 30 years of single spot, high frequency sampling at the only off-shore island of the North Sea. Helgol Mar Res 58:274–288

Hansen BW, Drillet G, Kozmer A, Madsen KV, Pedersen MF, Sørensen TF (2010) Temperature effects on copepod egg hatching: does acclimatization matter? J Plankton Res 32:305–315

Hawkings JR, Wadham JL, Tranter M, Raiswell R et al (2014) Ice sheets as a significant source of highly reactive nanoparticulate iron to the oceans. Nat Commun. https://doi.org/10.1038/ncomms4929

Hirst A, Bunker A (2003) Growth of marine planktonic copepods: Global rates and patterns in relation to chlorophyll *a*, temperature, and body weight. Limnol Oceanogr 48:1988–2010

Jarman SN, McInnes JC, Faux C et al (2013) Adélie penguin population diet monitoring by analysis of food DNA in scats. PLoS ONE. https://doi.org/10.1371/journal.pone.0082227

Jaspers C, Nielsen TG, Garstensen J, Hopcroft RR, Møller EF (2009) Metazooplankton distribution across the Southern Indian Ocean with emphasis on the role of Larvaceans. J Plankton Res 31:525–540

Jeffrey SW, Humphrey GF (1975) New spectrophotometric equations for determining chlorophylls a, b, c1 and c2 in higher plants, algae and natural phytoplankton. Biochem Physiol Pflanz 167:191–194

Kiørboe T, Hirst AG (2008) Optimal development time in pelagic copepods. Mar Ecol Prog Ser. https://doi.org/10.3354/meps07572

Kiørboe T, Møhlenberg F, Nicolajsen H (1982) Grazing rate and gut clearance in the planktonic copepod *Centropages hamatus* (Lilljeborg) in relation to food concentration and temperature. Ophelia 21:181–194

Leakey RJG, Fenton N, Clarke A (1994) The annual cycle of planktonic ciliates in nearshore waters at Signy Island, Antarctica. J Plankton Res 16:841–856

Lewis Smith RI (1990) Signy Island as a paradigm of biological and environmental change in Antarctic terrestrial ecosystems. In: Kerry KR, Hempel G (eds) Antarctic ecosystems: ecological change and conservation. Springer, Berlin, pp 32–50

Lindsay MC (2012) Distribution and abundance of Larvaceans in the Southern Ocean. Dissertation, University of Tasmania

Lischka S, Hagen W (2007) Seasonal lipid dynamics of the copepods *Pseudocalanus minutus* (Calanoida) and *Oithona similis* (Cyclopoida) in the Arctic Kongsfjorden (Svalbard). Mar Biol 150:443–454

Lombard F, Renaud F, Sainsbury C, Sciandra A, Gorsky G (2009) Appendicularian ecophysiology. I: food concentration dependent clearance rate, assimilation efficiency, growth and reproduction of *Oikopleura dioica*. J Mar Syst 78:606–616

McLeod DJ, Hosie GW, Kitchener JA, Takahashi KT et al (2010) Zooplankton atlas of the Southern Ocean: the SCAR SO-CPR survey (1991-2008). Polar Sci 4:353–385

Metz C (1996) Lebensstrategien dominanter antarktischer *Oithonidae* (Cyclopoida, Copepoda) und *Oncaeidae* (Poecilostomatoida, Copepoda) im Belllngshausenmeer. Dissertation, Ber Polarforsch 207:l–123

Metz C (1998) Feeding of *Oncaea curvata* (Poecilostomatoida, Copepoda). Mar Ecol Prog Ser 169:229–235

Montes-Hugo M, Doney SC, Ducklow HW et al (2009) Recent changes in phytoplankton communities associated with rapid regional climate change along the western Antarctic Peninsula. Science 323:1470–1473

Murphy EJ, Watkins JL, Trathan PN et al (2007) Spatial and temporal operation of the Scotia Sea ecosystem: a review of large-scale links in a krill centred food web. Philos Trans R Soc B 362:113–148

Murphy EJ, Clarke A, Abram NJ, Turner J (2014) Variability of sea-ice in the northern Weddell Sea during the 20th century. J Geophys Res Oceans 119:4549–4572

Nielsen TG, Sabatini M (1996) Role of cyclopoid copepods *Oithona* spp in North Sea plankton communities. Mar Ecol Prog Ser 139:79–93

Nishibe Y, Kobari T, Ota T (2010) Feeding by the cyclopoid copepod *Oithona similis* on the microplankton assemblage in the Oyashio region during spring. Plankton Benthos Res 5:74–78

Nozais C, Gosselin M, Michel C, Gugliemo T (2001) Abundance, biomass, composition and grazing impact of sea-ice meiofauna in the North Water, northern Baffin Bay. Mar Ecol Prog Ser 217:235–250

Pane L, Feletti M, Francomacaro B, Mariottini GL (2004) Summer coastal zooplankton biomass and copepod community structure near the Italian Terra Nova Base (Terra Nova Bay, Ross Sea, Antarctica). J Plankton Res 26:1479–1488

Pasternak AF, Schnack-Schiel SB (2001) Seasonal feeding patterns of the dominant Antarctic copepods *Calanus propinquus* and *Calanoides acutus* in the Weddell Sea. Polar Biol 24:771–784

Pielou EC (1969) An introduction to mathematical ecology. Wiley, New York

Pond DW, Ward P (2011) Importance of diatoms for *Oithona* in Antarctic waters. J Plankton Res 33:105–118

Porter KG, Feig YS (1980) The use of DAPI for identifying and counting aquatic microflora. Limnol Oceanogr 25:943–948

Presta ML, Hoffmeyer MS, Capitanio FL (2015) Population structure and maturity stages of *Fritillaria borealis* (Appendicularia, Tunicata): seasonal cycle in Ushuaia Bay (Beagle Channel). Braz J Oceanogr 63:279–288

Richardson AJ (2008) In hot water: zooplankton and climate change. ICES J Mar Sci 65:279–295

Sahade R, Lagger C, Torre LF et al (2015) Climate change and glacier retreat drive shifts in an Antarctic benthic ecosystem. Sci Adv. https://doi.org/10.1126/sciadv.1500050

Sato R, Tanaka Y, Ishimaru T (2001) House production by *Oikopleura dioica* (Tunicata, Appendicularia) under laboratory conditions. J Plankton Res 23:415–423

Schnack-Schiel SB, Hagen W, Mizdalski E (1998) Seasonal carbon distribution of copepods in the eastern Weddell Sea, Antarctica. J Mar Syst 17:305–311

Shannon CE, Weaver W (1949) The mathematical theory of communication. The University of Illinois Press, Urbana

Shreeve RS, Ward P, Whitehouse MJ (2002) Copepod growth and development around South Georgia: relationships with temperature, food and krill. Mar Ecol Prog Ser 233:169–183

Sicinski J, Rozycki O, Kittel W (1996) Zoobenthos and zooplankton of Herve Cove, King George Island, South Shetland Islands, Antarctic. Pol Polar Res 17:221–238

Simonsen R (1974) The diatom plankton of the Indian Ocean expedition of RV Meteor 1964–1965. Meteor-Forschungsergebnisse, Reihe, Berlin

Sommaruga R (2015) When glaciers and ice sheets melt: consequences for planktonic organisms. J Plankton Res 3:509–518

Stanwell-Smith D, Hood A, Peck LS (1997) A field guide to the pelagic invertebrate larvae of the maritime Antarctic. British Antarctic Survey, Cambridge

Steinberg DK, Ruck KE, Gleiber MR, Garzio LM et al (2015) Long-term (1993-2013) changes in macrozooplankton off the Western Antarctic Peninsula. Deep-Sea Res Part I 101:54–70

Svensen C, Kiørboe T (2000) Remote prey detection in *Oithona similis*: hydromechanical vs chemical cues. J Plankton Res 22:1155–1166

Tsujimoto M, Takahashi KT, Hirawake T, Fukuchi M (2007) U–nusual abundance of appendicularians in the seasonal ice zone (140°E) of the Southern Ocean. Polar Biosci 19:133–141

Utermöhl H (1958) Zur Vervollkommnung der quantitativen Phytoplankton Methodik. Mitt Int Ver Theor Angew Limnol 9:1–38

Vanderploeg HA, Scavia D (1979) Two electivity indices for feeding with special reference to zooplankton grazing. Can J Fish Aquat Sci 36:362–365

Verity PG, Smetacek V (1996) Organism life cycles, predation, and the structure of marine pelagic ecosystems. Mar Ecol Prog Ser 130:277–293

Wallis JR, Swadling KM, Everett JD, Suthers IM et al (2015) Zooplankton abundance and biomass size spectra in the East Antarctic sea-ice zone during the winter–spring transition. Deep Sea Res Part II 131:170–181

Walton DWH (1982) The Signy Island terrestrial reference sites. XV. Microclimate monitoring, 1972–74. Br Antarct Surv Bull 55:111–126

Ward P, Hirst AG (2007) *Oithona similis* in a high latitude ecosystem: abundance distribution and temperature limitation of fecundity rates in a sac spawning copepod. Mar Biol 151:1099–1110

Ward P, Shreeve RS (1998) Egg hatching times of Antarctic copepods. Polar Biol 19:142–144

Ward P, Shreeve RS, Cripps GG (1996) *Rhincalanus gigas* and *Calanus simillimus*: lipid storage patterns of two species of copepod in the seasonally ice-free zone of the Southern Ocean. J Plankton Res 18:1439–1454

Ward P, Shreeve R, Whitehouse M, Korb B et al (2005) Phyto- and zooplankton community structure and production around South Georgia (Southern Ocean) during summer 2001/02. Deep Sea Res Part I 52:421–441

Ward P, Atkinson A, Tarling G (2012a) Mesozooplankton community structure and variabilityin the Scotia Sea: a seasonal comparison. Deep Sea Res Part II 60:78–92

Ward P, Atkinson A, Venables HJ, Tarling GA et al (2012b) Food web-structure and bioregions in the Scotia Sea: a seasonal synthesis. Deep-Sea Res PTII 60:253–266

Whitaker TM (1982) Primary production of phytoplankton off Signy Island, South Orkneys, the Antarctic. Proc R Soc Lond Ser B 214:169–189

Wyatt T (1973) The biology of *Oikopleura dioica* and *Fritillaria borealis* in the Southern Bight. Mar Biol 22:137–158

Zmijewska MI, Yen J (2003) Seasonal and diel changes in the abundance and vertical distribution of the Antarctic copepod *Calanoides acutus*, *Calanus propinquus, Rhincalanus gigas, Metridia gerlachei* and *Euchaeta antarctica* (Calanoida) in Croker Passage (Antarctic Peninsula). Oceanologia 35:101–127

Zuur AF, Ieno EN, Walker NJ et al (2009) Dealing with heterogeneity. In: Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (eds) Mixed effects models and extensions in ecology with R. Springer, New York, pp 71–100