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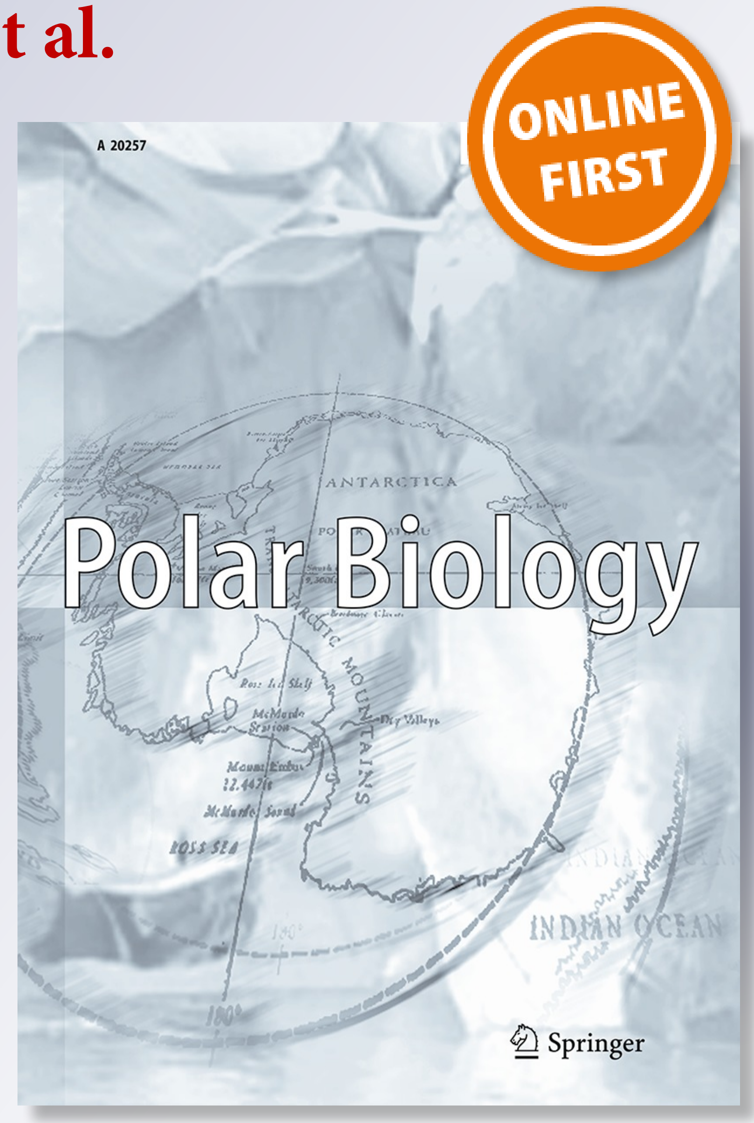

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Micro- and mesozooplankton responses during two contrasting summers in a coastal Antarctic environment

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Abstract Rapid climate-driven melting of coastal glaciers may control plankton dynamics in the Western Antarctic Peninsula. It is known that in Potter Cove, 25 de Mayo/King George Island, phytoplankton is tightly coupled to meltwater input. However, no information on zooplankton is available in this regard. The aim of this study was therefore to examine the structure and dynamics of microzooplankton and mesozooplankton in two zones (the inner and outer Potter Cove) differently impacted by glacier melting during two contrasting austral summers (2010 and 2011). Microzooplankton composition differed between the two zones and years analyzed, and its total biomass was observed to be highest far from the glacier influence and during 2010. Mesozooplankton composition and biomass were similar in the two zones and years analyzed. Colder than usual conditions in the summer of 2010 prevented glacier melting, thus favoring the development of an exceptional micro-sized diatom bloom (~ 190 µg C l^{-1} and >15 µg l^{-1} chlorophyll *a*), which was tightly followed by a maximum in large copepod abundance. After the bloom and in coincidence with intense glacier melting, large diatoms and large copepods were observed to be replaced by nanophytoplankton and microzooplankton (aloricate ciliates and dinoflagellates), respectively. In 2011, low phytoplankton abundance, probably controlled by high tintinnid biomass, was observed as a result of warmer temperatures than 2010 and low-salinity waters. Large copepods appeared to have exerted a high grazing pressure on aloricate ciliates and heterotrophic dinoflagellates in 2011. Our results suggest that whereas the joint effect of water temperature, salinity and phytoplankton availability as well as composition could be of primary relevance in structuring micro- and mesozooplankton community, zooplankton could be of secondary relevance in controlling phytoplankton biomass in Potter Cove during the two summers analyzed.

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Introduction

The current changes observed in Antarctic coastal areas as a result of climate change evidence the high environmental vulnerability of this region (Joughin and Alley 2011; Miles et al. 2013). The Western Antarctic Peninsula (WAP) is, in particular, experiencing variations in sea ice advance/retreat and glacier melting rhythms (Turner et al. 2005; Stammerjohn et al. 2008; Rückamp et al. 2011). This, in turn, promotes changes in the environmental conditions of the adjacent coastal habitats, which could challenge the adaptability of pelagic communities. Several effects of climate warming on pelagic communities have been registered, such as changes in phyto- and zooplankton abundance, distribution and phenology, and shifts in their physiological and ecological mechanisms (Ducklow et al. 2006; Montes-Hugo et al. 2009).

Potter Cove, which is located in the southwestern sector of 25 de Mayo/King George Island, has been impacted by intense glacier melting in the last years (Dominguez and Eraso 2007; Rückamp et al. 2011). In this area, phytoplankton productivity is modulated by the combined influence of several factors, such as water column stratification, surface freshening and light availability (Schloss et al. 2002, 2014). Wind stress is one of the main factors in controlling water column structure, while glacier melting is the main responsible for surface freshening and water turbidity increase, the latter of which, in turn, limits light availability. The analysis of a 19-year time series dataset evidences that due to the fact that chlorophyll *a* (Chl *a*) concentration in Potter Cove was coupled to the Southern Annular Mode (SAM) and El Niño Southern Oscillation (ENSO) signals, global climate is also modulating phytoplankton productivity (Schloss et al. 2012; Bers et al. 2013). Furthermore, as coldest water temperature favors rapid phytoplankton growth, exceptional blooms occur as it was the case in the summer of 2010. This was not the case in 2011, a year which was characterized by a more typical, poor phytoplankton assemblage and warmer conditions (Schloss et al. 2014). The role of planktonic predators in controlling phytoplankton biomass (i.e., top-down regulation) under these contrasting conditions still remains hypothetical.

Phytoplankton shifts affect the dynamics of consumers and therefore modify the entire ecosystem (Quetin and Ross 2001; Smith et al. 2001). Marine micro- and mesozooplankton communities respond dynamically (in space and time) to food availability and environmental conditions. As a result of their specific individual turnover rates and the subsequent functional growth and numerical responses, each predator species or group shows specific potential to controlling phytoplankton development and biomass accumulation (Valiela 1995). On the other hand, whereas microzooplankton has high duplication rates, close to those of phytoplankton cells (1–2 dupl. d^{-1}, Fenchel and Finlay 1983), crustacean and other mesozooplankton metazoan have by far lower duplication rates and longer life developmental cycles (Calbet 2008). In addition, in polar environments, slow growth rates and low grazing rates have been estimated for microzooplankton, which could result in a consequent reduction in their potential top-down control of phytoplankton at critical periods, such as pre-bloom conditions (Rose and Caron 2007).

In Potter Cove, whereas small copepods (i.e., <1 mm of total length), such as *Oithona similis* and *Oncaea curvata*, tend to dominate within mesozooplankton during summer, large copepods (i.e., >1 mm in total length), such as *Calanus propinquus*, *Calanoides acutus* and *Metridia gerlachei*, and juveniles euphausiid (caliptopes and furcilia) are less frequent and abundant (Elwers and Dahms 1998; Fuentes and Hoffmeyer 2005; Fuentes 2006). Taking into account their known feeding habits, small copepods may cope with nanoplankton and other trophic items, such as fecal pellets and detritus particles (Pond and Ward 2011). In contrast, large copepods and euphausiids graze mainly on large diatoms and microzooplankton (Atkinson et al. 1996). Microheterotrophs, on the other hand, can graze on nano- and microplankters, such as diatoms, flagellates and other groups (Calbet and Landry 2004). However, it is still unclear how these different zooplankton assemblages respond to the contrasting conditions (temperature, salinity, phytoplankton conditions) co-occurring in the same environment, as it was the case during the austral summers of 2010 and 2011.

In the present work, we have studied the structure and temporal dynamics of micro- and mesozooplankton assemblages related to phytoplankton abundance in two areas of Potter Cove, which are differently impacted by glacier melting during the austral summers of 2010 and 2011. Based on Schloss et al.'s proposal (2014), we have hypothesized that different temperatures, meltwater influence and phytoplankton availability and composition could be, on the one hand, directly translated into changes in the composition and structure of micro- and mesozooplankton assemblages and indirectly translated into their top-down role in controlling phytoplankton development, on the other.

Materials and methods

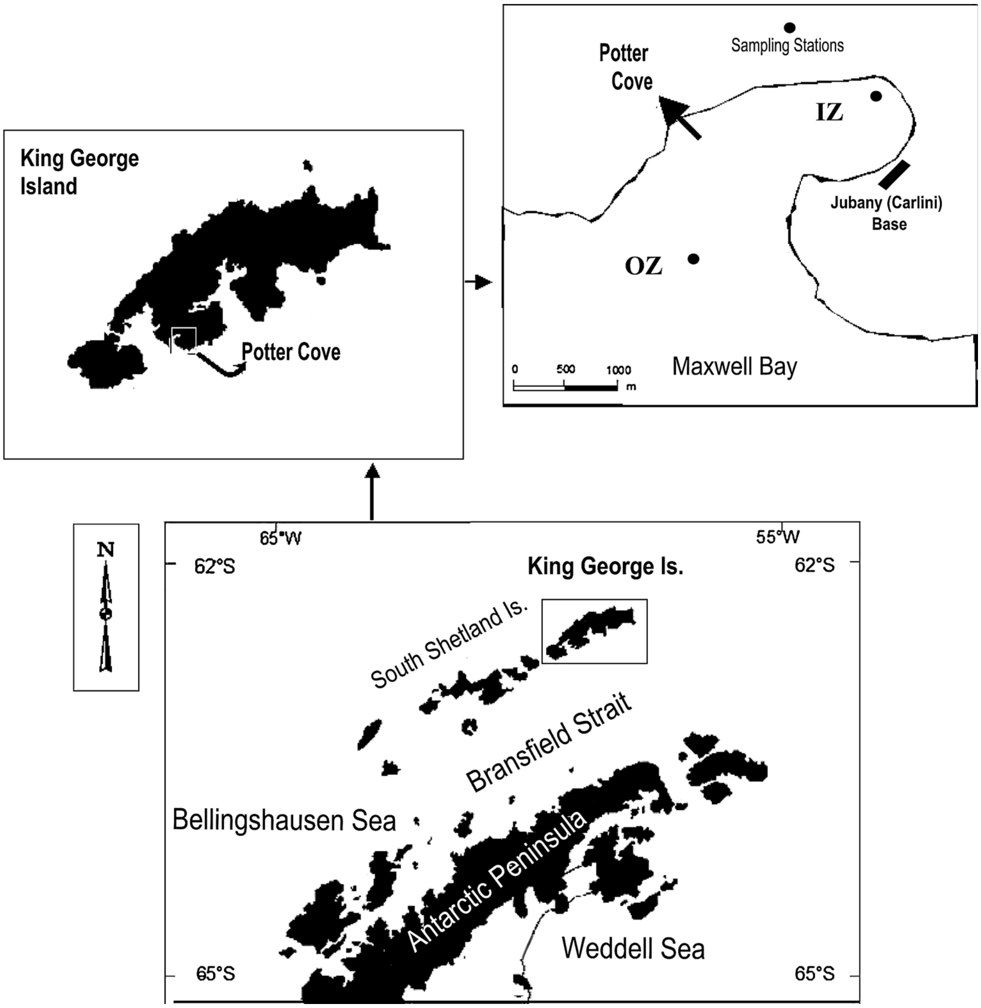
This study was carried out in Potter Cove (25 de Mayo/King George Island, South Shetland Islands, Antarctica, 62°14′S, 58°38′W) (Fig. 1) during the austral summers of

2010 (January 7–February 25) and 2011 (January 4–March 5). The cove is a shallow coastal environment. Depths at the sampling sites are ~30 m in the inner zone (IZ) and 80 m in the outer zone (OZ). During austral summer, these areas are characterized by the presence of a very shallow pycnocline (at ~3 m depth) around which phytoplankton develops. The system was typically mixed, and a continuously stratified water column was evident during the majority of the days of the present study (Online Resource 1). Two sampling stations representing different zones of the cove were studied. Both zones are usually differently impacted by glacier melting, and the features of the entire water column in these areas vary depending on mixing or stratification periods (Schloss and Ferreyra 2002). The sampling station in the IZ was located close to the base of Fourcade Glacier at the cove's head, which is consistently exposed to glacial meltwater inputs, whereas the sampling station in the OZ was located at the mouth of the cove close to Maxwell Bay. Both zones are approximately 4 km apart from each other.

Sampling was carried out weekly from 9 a.m. to 6 p.m. At each sampling event, water conductivity, density, temperature and turbidity profiles from close to the bottom to the surface were obtained using a Seabird CTD (19 plus V2). Sea water was collected from a Zodiac boat using a 5-l Niskin bottle from depths below the pycnocline, at ~5 and 10 m depth in the IZ and OZ, respectively, to the surface, to encompass the depth of maximal phytoplankton biomass. Chlorophyll *a* (Chl *a*) concentrations were determined on 0.5–1 l seawater filtered onto Whatman GF/F filters kept frozen until analysis, which was performed within 1 week of sampling. Photosynthetic pigments were extracted during 24 h at 4 °C and dark conditions with 90 % acetone and read on a Shimadzu UV160A spectrophotometer. Chl *a* concentration was estimated following the method of Strickland and Parsons (1972).

Sea water samples (250–500 ml) were preserved with acid Lugol's solution (2 % final concentration) for quantitative analyses of nanophytoplankton, microphytoplankton and microzooplankton. Microplankton samples for

Fig. 1 Map of the study area



qualitative analyses were additionally obtained using 20-μm mesh net and horizontal tows. Mesozooplankton samples were collected by means of 5-min horizontal tows at 2-knot speed at the same depths, using a 200-μm mesh net with a flow meter fixed to the net's mouth. These samples were preserved in 4 % neutralized formaline (4 % final concentration).

Phytoplankton samples were examined qualitatively using phase contrast and differential interference contrast under two Leica DM 2500 microscopes. For diatom frustules observation, organic material was removed from net subsamples using sodium hypochlorite as described in Almandoz et al. (2011). Clean material was subsequently dried onto cover glasses for mounting in Naphrax following Ferrario et al. (1995). Further scanning electron microscopy observations of selected samples were made with a JEOL JSM-6360 LV. For quantitative estimations, cells were enumerated with a phase contrast Leica DMIL LED inverted microscope according to the procedures described by Utermöhl (1958). Subsamples of 50 and 100 ml were left to settle for 24 and 48 h, respectively, in a sedimentation chamber. At least 100 cells of the most abundant taxa were counted in one or more strips of the chamber at 250 or 400×, depending on their concentration and size. The whole chamber bottom was also scanned at 100× to count large and sparse species. Cell biovolumes and carbon content were estimated as in Almandoz et al. (2011).

Microzooplankton samples were stored in the dark at room temperature and were analyzed within 3 months after the sampling date. After gentle mixing, 50 ml of the subsample was removed and left for sedimentation for at least 72 h prior to the analysis using an inverted microscope (Hasle 1978). Aloricate ciliate volumes were estimated by associating the shape of each ciliate with standard geometric configurations (Montagnes et al. 1988; Leakey et al. 1992). Individual carbon biomass was estimated by converting cell volume into carbon weight using a factor of 0.19 pg C μm^{-3} (Putt and Stoecker 1989) and was expressed as μg C l^{-1}. Tintinnids were identified according to Kofoid and Campbell (1929) and Barría de Cao (1987) and enumerated following the same procedure as that for aloricate ciliates. Biovolumes were calculated by assigning standard geometric shapes to the organisms. Biomass in carbon terms was estimated using the linear regression equation: C (pg) = 444.5 + 0.053 lorica volume (μm^3) (Verity and Langdon 1984).

Mesozooplankton samples were qualitatively and quantitatively examined under stereo microscopes WILD M 5 and Nikon SMZ645. To estimate mesozooplankton biomass, the individual dry/wet weight of the dominant component in the samples was either taken from the literature (e.g., Omori and Ikeda 1984; Boysen-Ennen and Piatkowski 1988; Kiørboe and Sabatini 1995; Mayzaud et al. 2002; Kaufmann et al. 2003; Fuentes 2006; Lukáč 2006) or calculated by applying body size–carbon content relationship equations (e.g., Siegel 1986; Mayzaud et al. 2002; Almeda et al. 2011). For the rest of the components, it was assumed that individual dry/wet weight was equal to that of other components of similar size. Carbon values, in turn, were derived applying conversion factors from the literature (Ikeda 1984; Schnack 1985; Ikeda and Kirkwood 1989).

Data analyses

Abundance and biomass of nanophytoplankton (2–20 μm), microphytoplankton and microzooplankton (20–200 μm) and mesozooplankton (200 μm–20 mm; all size classes after Sieburth et al. 1978) were estimated and classified in different size planktonic groups and subgroups according to taxonomy (see Table 2). Data of abiotic and these biotic variables were firstly analyzed in order to detect spatial (IZ vs OZ) and temporal (2010 vs 2011) differences using two-way analysis of variance (ANOVA) and multiple comparison LSD test (Sokal and Rohlf 1995). In the absence of interaction between factors, comparisons were made using the mean values of all treatments (zones × year) separately.

Secondly, in order to determine predictive relationships within each zone of Potter Cove along time and for each summer analyzed, forward stepwise multiple linear regression analysis (MLRA) was applied. In order to reduce the number of variables and to simplify the interpretation of the models considered, only three dependent variables (in terms of biomass) were selected. Each of them included more than one subgroup from those primitively established (Table 2). These variables representing the main fraction of plankton consumers were microzooplankton (Mi, zooplankton b (20 and 200 μm), including tintinnids, heterotrophic dinoflagellates and aloricate ciliates), small mesozooplankton (SMe, mesozooplankton <1 mm, including small copepods) and large mesozooplankton (LMe, mesozooplankton >1 mm, including large copepods, adventitious, meroplankton and other holozooplankton). As explanatory (independent) variables, we considered the following: temperature, salinity, turbidity, and nanophytoplankton (NP, phytoplankton between 2 and 20 μm, including diatoms and other nanophytoplankton taxa) and microphytoplankton (MP, phytoplankton between 20 and 200 μm, including diatoms and other microphytoplankton taxa) which, in terms of our hypothesis, respectively, were the main abiotic and food-item variables. All variables were log transformed [log $(x + 1)$], and statistical analyses were subsequently performed using STATISTICA version 7 and InfoStat (free version) software packages.

Results

Dynamics of abiotic conditions

Sea water temperature was lower in the summer of 2010 than in 2011 while salinity showed an opposite trend. Although sea surface temperature (SST) was lower in the IZ than in the OZ during the two summer periods analyzed except on January 10, 2011, it followed, in general, a similar trend during the two summer periods analyzed (Fig. 2a, b; Table 1). In addition, in the two austral summers of 2010 and 2011, salinity was lower in the IZ than in the OZ (Fig. 2c, d; Table 1), thus showing a similar trend to that of temperature. During the summer of 2011, salinity in the IZ was significantly lower than in the OZ, with values below 32 on some days (January 10, in coincidence with high SST, January 31, February 20 and March 5). Turbidity showed an opposite trend to that of salinity in the two summer periods analyzed (Fig. 2e, f; Table 1), with values consistently higher in the IZ than in the OZ. ANOVA revealed significant differences in temperature and salinity between the two summer periods analyzed and in salinity and turbidity between the two zones analyzed (Table 1).

Features and dynamics of plankton group assemblages

In terms of cell numbers, cryptophytes, prasinophytes, prymnesiophytes, silicoflagellates, autotrophic dinoflagellates and other unidentified nanoflagellates (collectively represented as nanophytoplankton-other taxa) largely contributed to total phytoplankton density (65.8 and 69.5 % on average during 2010 and 2011). However, in terms of phytoplankton carbon, microplanktonic diatoms (MDiat) biomass accounted—on average—for 82.2 % (in 2010) and 85.9 % (in 2011) of total phytoplankton (Table 2). Centric diatom species, mainly *Porosira glacialis* and *Thalassiosira antarctica*, dominated this group during the two summers analyzed, reaching maximum values on January 18, 2010 in the IZ and decreasing on January 25 in the OZ (Fig. 3a, b). A lower phytoplankton peak dominated by nanophytoplankton (mainly cryptophytes) was observed at the end of February 2010. In 2011, three minor peaks in phytoplankton biomass were observed in the OZ and two in the IZ, all of which were dominated by microplanktonic diatoms (Fig. 4a, b).

Microzooplankton composition and species number were different in the two zones and periods studied. The number of species was higher in 2010 (19–27 species in the IZ and OZ, respectively) than in 2011 (11–12 species in the IZ and OZ, respectively). In the summer of 2010, in the OZ, two main microzooplankton biomass peaks were observed on January 25 and on February 25, both of which were formed by heterotrophic dinoflagellates and aloricate ciliates (Fig. 3c, d). In 2011, a single biomass peak of microzooplankton was observed on February 20 in the IZ, which was dominated by tintinnids (Fig. 4c, d; Table 2). *Gyrodinium* spp. were the most abundant heterotrophic dinoflagellates in both zones and years, while *Strombidium* spp. dominated the aloricate ciliates. *Cymatocylis affinis/convallaria* and *Codonellopsis balechi* were the dominant tintinnids (Tin) in 2010 and 2011, respectively (Online Resource 2).

In contrast to our observations on microzooplankton, mesozooplankton composition and species number were similar in the two zones and summer periods studied (except for the high biomass of adventitious mesozooplankton and meroplankton groups in 2011). The number of species identified was 13 and 16 in the IZ in 2010 and 2011, respectively, and 13 and 17 in the OZ in 2010 and 2011, respectively. High abundances and biomasses were observed in the IZ on January 25, 2010, and on January 15, 2011, although values were similar between the two summer periods studied (Table 2). The assemblages were numerically dominated by the small copepod *O. similis*, which was the most abundant species in the IZ, with abundances varying between 0 and 210 ind m^{-3} in 2010 and between 0 and 195 in 2011, and relative abundances of 89.3 and 77.7 %, respectively. However, in terms of biomass, the large copepods *Rhincalanus gigas* in 2010 (797 µg C m^{-3}, on January 25, Fig. 3e, f) and *C. propinquus* in 2011 (619 µg C m^{-3}, on January 15, Fig. 4e, f) both in the IZ (Online Resource 2) showed the highest values, being responsible for 81.6 and 60.7 % of total relative biomass, respectively (Table 2). In 2011, a second peak of total mesozooplankton biomass was observed on January 4 in the OZ, which was mainly represented by adventitious zooplankton and meroplankton (Fig. 4e, f).

The comparison of biotic variables for 2010 and 2011 via ANOVA revealed significant differences in non-diatom microphytoplankton taxa and aloricate ciliates density and biomass as well as in adventitious and meroplankton groups in terms of biomass (Table 3). The MLRA for the IZ and OZ in the summers of 2010 and 2011 resulted in seven models plus three global models (considering data from both summers) in which statistical significance was recorded for at least one of the variables within the model and in which more than 45 % of total variance was explained (Table 4). In the summer of 2010, microzooplankton biomass was positively related to nanophytoplankton (significantly in the OZ but not significantly in the IZ) and negatively related to salinity, turbidity and microphytoplankton (in the IZ). Furthermore, in the IZ large mesozooplankton was positively and significantly related to temperature, while in the OZ small

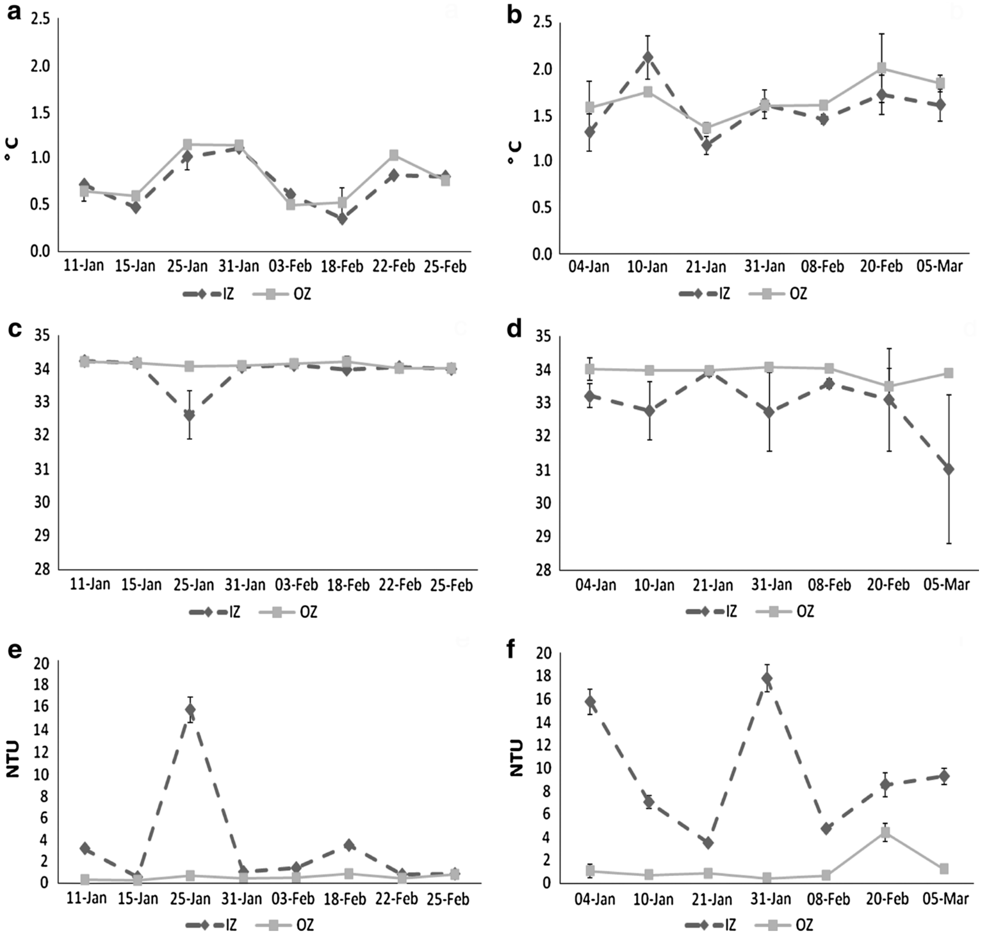


Fig. 2 Temporal variability of surface temperature (**a**, **b**), salinity (**c**, **d**) and turbidity (**e**, **f**) at both sampling stations: inner zone (IZ) and outer zone (OZ) in Potter Cove during the two summer periods studied. *Left panel* 2010; *right panel* 2011. Mean and standard deviation (indicated in *error bars*)

mesozooplankton was negatively related to nanophytoplankton. In the summer of 2011, microzooplankton was significantly and positively related to temperature in the OZ and to nanophytoplankton in the IZ. In the OZ, small mesozooplankton was negatively and significantly related to temperature but positively related to biomasses of microzooplankton and microphytoplankton. In general terms, microzooplankton was significantly and positively related to salinity and nanophytoplankton. Small mesozooplankton was, in turn, significantly and negatively related to nanophytoplankton and turbidity, and large mesozooplankton was significantly and positively related to temperature.

Discussion

Summer environmental conditions and dynamics of plankton groups

Significant differences in environmental conditions at the sea surface waters (below 5 and 10 m in the IZ and OZ, respectively) of Potter Cove were found between the summers of 2010 and 2011. The exceptional phytoplankton bloom—in terms of cell density and phytoplankton carbon (corresponding to chlorophyll *a* concentrations of ~15 mg m^{-3})—recorded in the summer of 2010 was related to low sea water temperature, water column stratification and high water transparency (low turbidity) and salinity. Previous research has described in detail this phenomenon in the complete water column (Schloss et al. 2014). On the other hand, mean water temperature was significantly higher during January and February 2011 with respect to the summer of 2010. This seems to have boosted glacier melting, which could have, in turn, added low-salinity waters to the system and affected water transparency in the adjacent coastal habitat. In addition, as proposed by Schloss et al. (2014), strong westerly winds during the summer of 2011 (data not shown) seem to have disrupted the structure of the water column, while in the summer of 2010 the prevailing easterly and low-speed winds seem to have contributed to maintaining water column stratification.

On the other hand, in spite of the great differences in the total phytoplankton biomass recorded during the two summer periods studied, phytoplankton composition was

Table 1 Descriptive statistics of physicochemical variables and chlorophyll a measured in both zones and years

	2010		2011	
	IZ	OZ	IZ	OZ
Temperature (°C)	0.74 (±0.05)	0.814 (±0.05)	1.57 (±0.07)	1.68 (±0.14)
Salinity	33.86 (±0.27)	34.11 (±0.05)	32.90 (±0.78)	33.92 (±0.19)
Turbidity (UNT)	3.37 (±0.41)	0.57 (±0.01)	9.54 (±0.42)	1.37 (±0.29)
Chl *a* (μg l^{-1})	3.31 (±2.73)	4.07 (±3.62)	1.27 (±0.94)	0.73 (±0.47)

Factor	*F*	*p*	LSD test
Temperature (Temp)			
Year	82.77	**<0.0001**	2010 < 2011
Zone	0.54	0.4679	IZ = OZ
Salinity (Sal)			
Year	9.13	**0.0053**	2010 > 2011
Zone	10.06	**0.0037**	IZ < OZ
Turbidity (Tur)[a]			
Year	3.65	0.0766	2010 = 2011
Zone	28.17	**0.0001**	IZ > OZ
Chlorophyll *a* (Chl *a*)			
Year	6.24	**0.0186**	2010 > 2011
Zone	0.06	0.8059	IZ = OZ

Mean, standard deviation (indicated in parentheses) and ANOVA test values

[a] Variables interact between factors.

Bold indicates significant difference

observed to be similar. Also, while nanophytoflagellates were generally dominant in numerical abundance terms, large diatoms were dominant in terms of phytoplankton carbon. This had, in fact, been observed in other regions of the WAP (Garibotti et al. 2005). A temporal succession from diatoms to cryptophytes was also evident as observed in other Antarctic areas (Ducklow et al. 2007). In contrast, the haptophyte *Phaeocystis* sp., which has been reported as a typical bloom forming in low-salinity Antarctic environments (Estrada and Delgado 1990; Kang et al. 2001), did not reach high abundances during the present study. Local environmental factors, such as water column stratification derived from melting glacier (Piquet et al. 2011), competition for nutrients (Walsh et al. 2001) and selective grazing by zooplankton (Haberman et al. 2003), are all potential factors driving the succession of species in coastal habitats as observed in our study.

Microzooplankton, which has been studied in detail for the first time in this zone in the present work, was dominated by dinoflagellates and ciliates, as observed in studies carried out in other areas, such as Admiralty Bay (Wasik 1998), Weddell Sea (Barría de Cao 1987; Alder and Boltovskoy 1991; Petz et al. 1995) and Bellingshausen Sea (Balech 1976; Klöser 1990). On the other hand, a high abundance of small copepods was recorded at Potter Cove (Elwers and Dahms 1998; Fuentes 2006). According to Fuentes (2006), "resident mesozooplankton" in Potter Cove is likely to consist of copepod species, such as *O. similis*, *O. curvata* and *M. gerlachei* and larvae of benthic organisms. "Sporadic mesozooplankton" seems to be mainly represented by *Euphausia superba*, *Salpa thompsoni* and by large copepods, such as *C. acutus*, *C. propinquus* and *R. gigas*. The usual low abundance of phytoplankton in Potter Cove (Schloss et al. 2012) could favor the presence of omnivorous species (*O. similis*, *M. gerlachei*, *Ctenocalanus citer*, among others), which are able to graze on a wide range of particles, from small plankton to organic aggregates and fecal pellets (González et al. 1994; Kattner et al. 2003).

Trophic interactions among plankton assemblages

In the summer of 2010, micro- and mesozooplankton consumers were tightly coupled to both nano- and microphytoplankton biomass. This leads us to think of a resource control of consumer assemblages as well as of a top-down selective grazing control of different consumer groups. In Potter Cove, large copepods were probably partly responsible for the termination of the microplankton diatom bloom, as reported for other areas (Schnack 1985; Cushing 1989). Their increase in abundance coincided with a large freshwater input into the water column. Phytoplankton could have therefore been simultaneously controlled by both bottom-up (low salinity, poor light conditions) and

Table 2 Abundance and biomass average and standard deviation values for different plankton functional groups from both zones and during the two summer periods studied

Planktonic groups	2010							
	IZ				OZ			
	Abundance		Biomass		Abundance		Biomass	
	Mean (±SD)	%	Mean (±SD)	%	Mean (±SD)	%	Mean (±SD)	%
Microplanktonic diatoms (MDiat)	34,170 (61,793)	42.6	34 (64)	89.4	34,277 (44,362)	15.2	36 (50)	76.2
Nanoplanktonic diatoms (NDiat)	3045 (3116)	3.8	0.20 (0.21)	0.5	29,842 (27,057)	13.3	1.64 (1.73)	3.5
Microphytoplanktonic-other taxa (MOt)	575 (719)	0.7	0.17 (0.25)	0.4	2395 (3348)	1.1	0.77 (1.22)	1.6
Nanophytoplanktonic-other taxa (NOt)	42,490 (89,328)	52.9	3.69 (5.34)	9.6	158,571 (308,023)	70.4	8.71 (12)	18.6
Total phytoplankton (TPh)	80,281 (21,381)	100	39 (17)	100	225,085 (69,642)	100	47 (16)	100
Aloricate ciliates (AC)	287 (0.92)	26.7	0.66 (0.00)	37.7	990 (4.40)	31.0	2.40 (0.01)	52.6
Tintinnids (Tin)	17 (0.55)	1.6	0.03 (0.00)	1.4	22 (0.34)	0.7	0.06 (0.00)	1.3
Dinoflagellates (Din)	772 (26)	71.7	1.07 (0.05)	60.8	2184 (67)	68.3	2.10 (0.07)	46.1
Total microzooplankton (TMi)	1077 (2.54)	100	1.75 (0.00)	100	3197 (6.79)	100	4.56 (0.01)	100
Small copepods (SC)	37 (9.12)	89.2	43 (10)	4.1	19 (3.17)	89.5	21 (3.31)	12.4
Large copepods (LC)	3 (0.52)	6.9	841 (210)	81.7	0.95 (0.13)	4.5	138 (32)	80.5
Other holozooplankton (OH)	0.18 (0.04)	0.4	53 (15)	5.2	0.39 (0.10)	1.8	10 (2.73)	5.8
Adventitious and meroplankton (A&M)	1.43 (0.26)	3.4	92 (27)	9.0	0.87 (0.08)	4.2	2.04 (0.26)	1.2
Total mesozooplankton (TMe)	42 (9.6)	100	1029 (216)	100	21 (3.26)	100	171 (33)	100

Planktonic groups	2011							
	IZ				OZ			
	Abundance		Biomass		Abundance		Biomass	
	Mean (±SD)	%	Mean (±SD)	%	Mean (±SD)	%	Mean (±SD)	%
Microplanktonic diatoms (MDiat)	23,512 (28,633)	20.4	16 (19)	83.3	43,595 (39,645)	30.3	27 (26)	87.5
Nanoplanktonic diatoms (NDiat)	2835 (2474)	2.5	0.31 (0.28)	1.6	9035 (4104)	6.3	0.86 (0.53)	2.8
Microphytoplanktonic-other taxa (MOt)	37 (98)	0.0	0.01 (0.04)	0.1	29 (76)	0.0	0.01 (0.03)	0.0
Nanophytoplanktonic-other taxa (NOt)	89,068 (161,953)	77.1	2.96 (5.40)	15.0	91,161 (145,555)	63.4	3.06 (4.85)	9.8
Total phytoplankton (TPh)	115,452 (41,480)	100	20 (8)	100	143,821 (41,318)	100	31 (13)	100
Aloricate ciliates (AC)	71 (0.65)	13.4	0.32 (0.00)	12.4	54 (0.41)	33.9	0.34 (0.00)	44.2
Tintinnids (Tin)	271 (33)	51.1	1.65 (0.20)	63.3	51 (3.71)	32.1	0.25 (0.02)	32.1
Dinoflagellates (Din)	189 (2.55)	35.5	0.64 (0.02)	24.3	54 (0.73)	33.9	0.18 (0.00)	23.8
Total microzooplankton (TMi)	531 (2.39)	100	2.61 (0.01)	100	160 (0.33)	100	0.77 (0.00)	100
Small copepods (SC)	36 (11)	79.8	47 (15)	3.2	6.56 (1.41)	67.6	7.90 (1.58)	1.5
Large copepods (LC)	5.77 (1.89)	12.8	1017 (325)	69.9	1.11 (0.16)	11.5	187 (30)	35.3
Other holozooplankton (OH)	0.21 (0.06)	0.5	12 (4.46)	0.8	0.47 (0.11)	4.8	36 (10)	6.9
Adventitious and meroplankton (A&M)	3.14 (0.70)	6.9	378 (93)	26.0	1.56 (0.11)	16.1	298 (91)	56.3
Total mesozooplankton (TMe)	45 (14)	100	1,454 (334)	100	9.70 (1.57)	100	529 (102)	100

Abundance in cells l^{-1}, ind l^{-1}, and ind m^{-3} and biomass in μg C l^{-1}, μg C l^{-1} and μg C m^{-3} for phytoplankton, micro- and mesozooplankton, respectively

top-down (copepods' grazing) processes during the summer of 2010. The low abundances of microzooplankton in January 2010, particularly in the IZ, thus support the hypothesis about the negative impact of colder than average temperatures on microzooplankton (Rose and Caron 2007), which in turn resulted in a lower than usual control of phytoplankton by microzooplankton (Schloss et al. 2014). On the other hand, after the decay of the diatom bloom

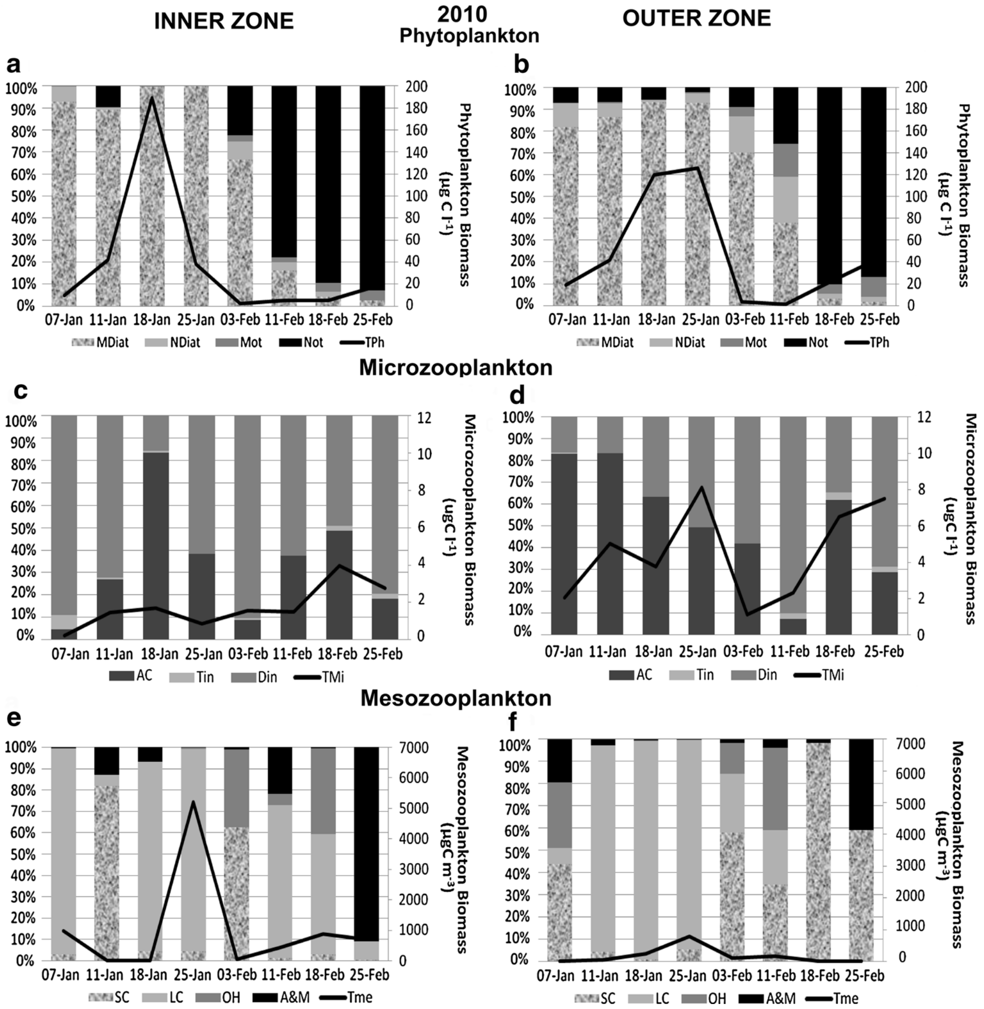


Fig. 3 Temporal variability of total biomass of phytoplankton (TPh) (**a**, **b**), microzooplankton (TMi) (**c**, **d**) and mesozooplankton (TMe) (**e**, **f**) and relative biomass (in percent) of the planktonic groups along the studied period during the summer of 2010. IZ on the *left panel*, OZ on the *right panel*. Planktonic groups of phytoplankton: *MDiat* microplanktonic diatoms, *NDiat* nanoplanktonic diatoms, *MOt* microphytoplanktonic-other taxa, *NOt* nanophytoplanktonic-other taxa. Planktonic groups of microzooplankton: *AC* aloricate ciliates, *Tin* tintinnid, *Din* heterotrophic dinoflagellates. Planktonic groups of mesozooplankton: *SC* small copepods, *LC* large copepods, *OH* other holoplanktonic taxa, and *A&M* adventitious and meroplanktonic taxa

recorded, microzooplankton cells (AC and Din) were coupled to (and probably controlled) nanophytoplankton cells, both in the IZ and OZ. Microzooplankton has been reported to significantly contribute to maintaining low phytoplankton biomass in several marine ecosystems (Calbet and Saiz 2005). Nevertheless, the percentage of the decrease in phytoplankton biomass as a result of microzooplankton grazing may be low in carbon terms in polar regions (Schmoker et al. 2013). This as well as the coldest summer conditions could give rise to a negligible control in this case.

In contrast, while in the summer of 2011, in the IZ, phytoplankton biomass was mostly related to adventitious and meroplanktonic (A&M) species, in the OZ no relation between phyto- and zooplankton was observed. The high biomass of large copepods as well as of adventitious and meroplankton species could have exerted a grazing pressure on aloricate ciliates and heterotrophic dinoflagellates, as proposed by Calbet and Saiz (2005), thus potentially allowing phytoplankton to increase via the control of their microzooplankton grazers. Concentrations of ~ 4 mg m^{-3} chlorophyll *a* were, in fact, detected (Schloss et al. 2014). According to Nejstgaard et al.'s findings (2001) derived from mesocosm experiments in Norway, phytoplankton standing stocks were controlled by microzooplankton grazing as is often the case in the field at least during the warmer seasons (Nielsen and Kiørboe 1994; Banse 1995; Putland 2000). Ciliates feed, in general, on small organisms (Jonsson 1986), and heterotrophic dinoflagellates (such as *Gyrodinium* spp.) can ingest prey ranging in size from ca. 1 µm (Jeong et al. 2005) to several times their body size (Sherr and Sherr 2007). Recent reviews have reported that microzooplankton can consume nearly 60 % of the daily primary productivity in Antarctic waters (Calbet and Landry 2004; Schmoker et al. 2013). However, because phytoplankton concentrations in 2011 were actually lower than in 2010, the effects of microzooplankton grazing that could have been yielded earlier in the season in this relatively warmer year before the present sampling started cannot be discarded.

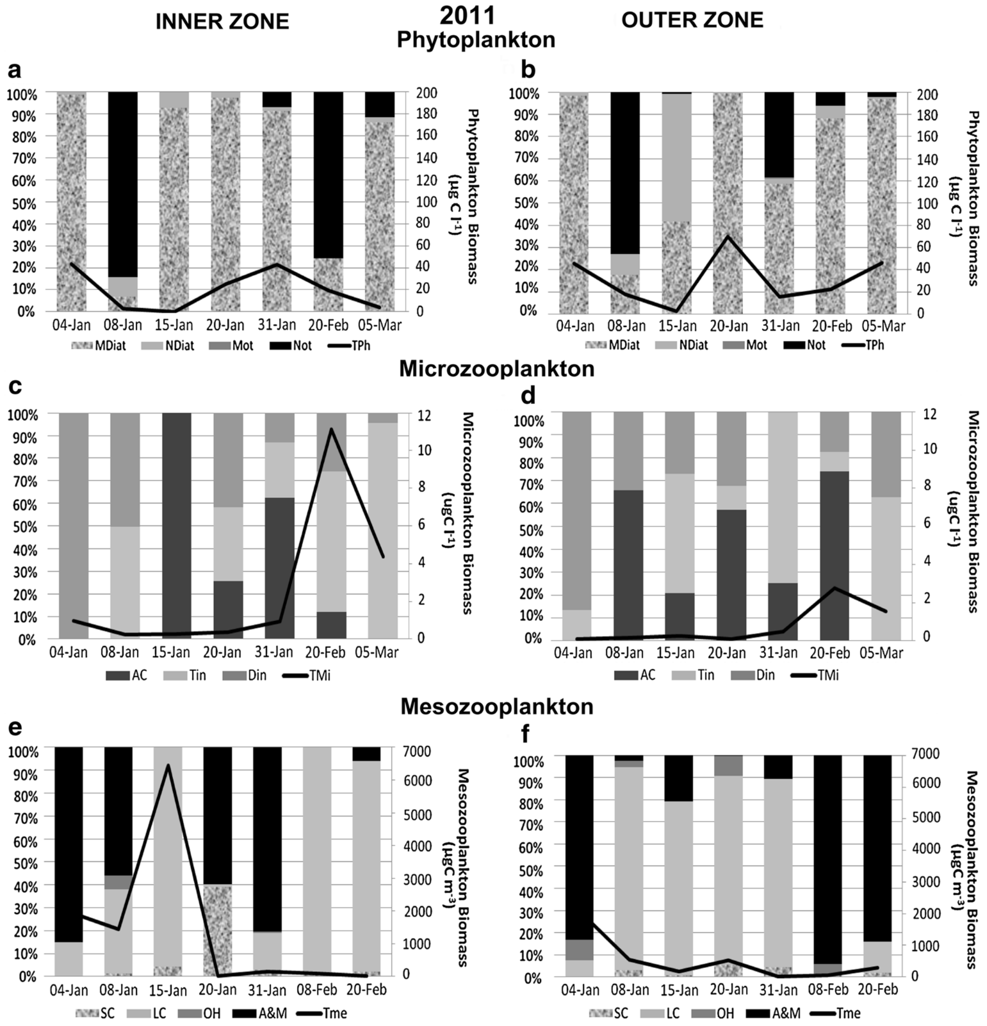


Fig. 4 Temporal variability of total biomass of phytoplankton (TPh) (**a**, **b**), microzooplankton (TMi) (**c**, **d**) and mesozooplankton (TMe) (**e**, **f**) and relative biomass (in percent) of planktonic groups along the period studied during the summer of 2011. IZ on the *left panel*, OZ on the *right panel*. Names of planktonic groups as in the legend of Fig. 3

Microzooplankton is additionally an important food source in the diet of mesozooplankton (Calbet and Saiz 2005) and meroplankton (Baldwin and Newell 1991) thanks to their nutritional quality and the characteristics of their swimming behavior (Stoecker and Capuzzo 1990; Broglio et al. 2004). Ciliates are within the optimal prey-size range of copepods (Berggreen et al. 1988), whereas many phytoplankton cells are either too small (i.e., in the picoplankton size range) or too large and unpalatable (e.g., chain-forming diatoms; Saiz and Calbet 2011). Heterotrophic dinoflagellates are also a significant food source for mesozooplankton (Sherr and Sherr 2007), which are sometimes cleared at higher rates than ciliates (Liu et al. 2005). It can thus be suggested that in our study area mesozooplankton predation on microzooplankters led to trophic cascades, releasing phytoplankton from microzooplankton grazing pressure.

Furthermore, taking into account the predator–prey interactions suggested by MLRA models as well as the effects of bottom-up control, the presence of microzooplankton (in both summers) seems to be strongly related to the presence of nanophytoplankton, thus implying that the presence of one group involves the presence of some other group, as proposed by Hansen et al. (1994). This and the negative relationship with microphytoplankton in the inner zone strongly support the hypothesis on the role of microzooplankton in controlling phytoplankton biomass, which additionally depends on temperature, turbidity and salinity conditions. In contrast, in the OZ during the summer of 2011, temperature appeared to be a good descriptor to microzooplankton biomass, which agrees with the fact that these organisms may benefit from relatively warmer conditions to increase their abundances (Rose and Caron 2007). This was also likely the case for large mesozooplankton in the IZ in the summer of 2010. For small mesozooplankton, the trophic interaction with nanophytoplankton explained their abundance in the OZ.

Global MLRA models (considering the summers of 2010 and 2011) revealed similar positive relationships between microzooplankton and nanophytoplankton as well

Table 3 Two-way ANOVA results for overall phytoplankton, microzooplankton and mesozooplankton density and biomass as well as for all the planktonic groups

Planktonic groups	Factor	Density		Biomass	
		p	LSD test	*p*	LSD test
Microplanktonic diatoms (MDiat)	Year	0.1666	2010 = 2011	0.5055	2010 = 2011
	Zone	0.9992	IZ = OZ	0.6715	IZ = OZ
Nanoplanktonic diatoms (NDiat)	Year	0.5998	2010 = 2011	0.5261	2010 = 2011
	Zone	**0.0001**	IZ < OZ	**0.0002**	IZ < OZ
Microphytoplanktonic-other taxa (MOt)	Year	**<0.0001**	2010 > 2011	**0.0063**	2010 > 2011
	Zone	0.3064	IZ = OZ	0.1253	IZ = OZ
Nanophytoplanktonic-other taxa (NOt)	Year	0.6014	2010 = 2011	0.5282	2010 = 2011
	Zone	0.4137	IZ = OZ	0.3853	IZ = OZ
Total phytoplankton (TPh)	Year	0.4713	2010 = 2011	0.3257	2010 = 2011
	Zone	0.1342	IZ = OZ	0.7133	IZ = OZ
Aloricate ciliates (AC)[a]	Year	**0.0005**	2011 < 2010	0.9289	IZ_2010 = IZ_2011 = OZ_2010 > OZ_2011
	Zone	0.2295	IZ = OZ	**0.0159**	
Tintinnids (Tin)	Year	0.0702	2010 = 2011	**0.0153**	2010 < 2011
	Zone	0.5198	IZ = OZ	0.1042	IZ = OZ
Dinoflagellates (Din)[a]	Year	**<0.0001**	IZ_2010 = IZ_2011 = OZ_2010 = OZ_2011	0.1664	IZ_2010 = IZ_2011 = OZ_2010 = OZ_2011
	Zone	0.7127		0.1547	
Total microzooplankton (TMi)[a]	Year	**<0.0001**	IZ_2010 = IZ_2011 = OZ_2010 = OZ_2011	0.0173	IZ_2010 = IZ_2011 = OZ_2010 > OZ_2011
	Zone	0.7858		**0.0001**	
Small copepods (SC)	Year	0.234	2010 = 2011	0.4429	2010 = 2011
	Zone	0.4393	IZ = OZ	0.2062	IZ = OZ
Large copepods (LC)	Year	0.9393	2010 = 2011	0.3994	2010 = 2011
	Zone	0.3581	IZ = OZ	0.4882	IZ = OZ
Other holozooplankton (OH)	Year	0.9312	2010 = 2011	0.9852	2010 = 2011
	Zone	0.368	IZ = OZ	0.5932	IZ = OZ
Adventitious and meroplankton (A&M)	Year	0.9312	2010 = 2011	**0.0182**	2010 < 2011
	Zone	0.368	IZ = OZ	0.7092	IZ = OZ
Total mesozooplankton (TMe)	Year	0.6693	2010 = 2011	0.3523	2010 = 2011
	Zone	0.3315	IZ = OZ	0.2970	IZ = OZ

[a] Variables interact between factors.

Bold indicates significant difference

Table 4 Multiple linear regression analysis (MLRA) models for three dependent variables: microzooplankton (zoopl. >20 µm) (Mi), small mesozooplankton (mesozoopl. <1 mm) (SMe) and large mesozooplankton (mesopl. >1 mm) (LMe,) for four studied periods: summers of 2010 and 2011 in the IZs and OZs

	R^2	R^2 adj	F	p
Summer 2010, inner zone				
Mi = 0.099 NP − **58.08 Sal** − **1.802 Turb** − 0.147 MP	0.927	0.829	9.476	**<0.047**
LMe = **3.202 Temp** + 25.190 Sal	0.635	0.489	4.354	ns
Summer 2010, outer zone				
Mi = **0.406 NP**	0.720	0.674	15.465	**<0.007**
SMe = **−0.059 NP** − 15.118 Sal + 0.048 Mi − 0.079 Temp	0.859	0.671	4.568	ns
Summer 2011, inner zone				
Mi = **1.284 NP** − 19.806 Sal − 12.915 Temp − 0.763 MP + 1.221 Turb	0.970	0.894	12.794	ns
Summer 2011, outer zone				
Mi = **4.748 Temp**	0.526	0.447	6.667	**<0.042**
SMe = **−0.532 Temp** + **0.054 Mi** + **0.025 NP** + 0.006 MP	0.904	0.776	7.080	ns
2010 + 2011				
Mi = **0.6676 Sal** + 0.2622 NP − 0.1389 LMe	0.842	0.825	51.389	**<0.001**
SMe = **−0.4409 NP − 0.3612 Tur** + 0.1511 LMe − 0.2104 MP	0.854	0.833	41.043	**<0.001**
LMe = −0.4183 NP **+ 1.1369 Temp** + 0.4550 SMe − 0.4251 Mi	0.362	0.271	3.968	ns

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

as a negative relationship between biomasses of small mesozooplankton and nanophytoplankton, which may, in turn, mean a cascade effect due to predation control over the former. These interactions were probably the strongest although the differences between this global approach and the previous individual cases for the two zones and periods analyzed highlight the great influence of both temporal and spatial variability in our study area. Further studies on this variability are therefore necessary for future sampling strategies. In addition, long-time data series are also necessary in order to eventually reach a more generalized, predictive and comprehensive model of spatial–temporal plankton interactions in Potter Cove, which could contribute to explaining our findings in other similar fjord polar systems.

Conclusions

Both bottom-up and top-down mechanisms were observed to have acted synergistically to structure planktonic assemblages in the summers of 2010 and 2011. Uncoupling between the maxima in predator and preys' abundance could give rise to the temporal window that allowed the rapid growth and development of phytoplankton blooming species, as observed during the summer of 2010. Large mesozooplankton (i.e., large copepods, other holoplankton and adventitious as well as meroplankton components) behaved as the main top-down control of phytoplankton further promoting a change in the relative abundance of phytoplankton forms. In the summer of 2011, which was warmer than that of 2010, the control exerted by microzooplankton prevented phytoplankton biomass accumulations. Small mesozooplankton predation seemed to play a potential role in controlling nanophytoplankton abundance. The contrast between the IZ and the OZ shows that abiotic factors, such as glacier melting, turbidity and changes in temperature and salinity, are more important as structuring factors of phytoplankton and microzooplankton in the IZ than in the OZ, thus favoring the presence of omnivorous copepods. On the other hand, in the OZ low mesozooplankton biomass and microzooplankton biomass and composition were mainly influenced by the kind of food (i.e., type of phytoplankton) available.

Taken together, our results suggest that apart from the important role of abiotic variables, micro- and mesozooplankton grazing was in part a potential factor that controlled phytoplankton biomass accumulation during the two summer periods studied. They also strongly suggest that once phytoplankton assemblage was established, its size structure and composition appeared to be of primary relevance in structuring zooplankton community size fractions within the pelagic habitat of Potter Cove. They also seem to be indicative of the fact that the grazing of some forms of micro- and mesozooplankton on other zooplankton, e.g., the copepods' grazing on aloricate ciliates and dinoflagellates, could indirectly favor phytoplankton accumulation.

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