Seasonal similarity in rates of protistan herbivory in fjords along the Western Antarctic Peninsula

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Abstract

We quantified phytoplankton growth and protistan grazing rates during late austral autumn 2013 and late austral spring 2014, in several glacio-marine fjords and connecting channels along the Western Antarctic Peninsula (WAP). During austral autumn, low and declining chlorophyll $a$ (Chl $a$) concentrations ($\leq 0.4$ $\mu$g L$^{-1}$) were almost entirely composed of pico/nanophytoplankton, whereas during austral spring, high but patchy Chl $a$ concentrations in the fjords (up to 18.5 $\mu$g L$^{-1}$) reflected a diatom bloom. These contrasting dynamics were associated with high seasonal differences in irradiance, but not temperature, and were consistent with the balance resulting from lower phytoplankton growth rates in autumn ($-0.01$ d$^{-1}$ to $0.19$ d$^{-1}$) than in spring (0.06–0.93 d$^{-1}$) but similar magnitudes of herbivorous grazing in both seasons. Grazing was either absent or low (0.11–0.26 d$^{-1}$) and restricted to the picophytoplankton and nanophytoplankton. In the productive fjords lining the WAP, a fraction of primary production was channelled through a persistent and across-seasons equally active microbial food web, while during spring an increasing fraction of organic carbon shifted from trophic transfer and recycling to an export pathway.

In most of the global ocean, microzooplankton have been established as the primary consumers of marine phytoplankton (Sherr and Sherr 2002; Calbet and Landry 2004), their grazing impact accounting on average for 60–70% of primary production (PP, Steinberg and Landry 2017). Through their feeding, these dominantly protistan herbivores occupy a pivotal position in pelagic food webs as nutrient recyclers (Gaul et al. 1999; Sherr and Sherr 2002; Strom 2002), important trophic links (Schmidt et al. 2006; Saiz and Calbet 2011), and key agents of biogeochemical cycles (Strom 2008; Buitenhuis et al. 2010).

In contrast, the Antarctic food chain has traditionally been viewed as a simple system dominated by krill efficiently transferring diatom-dominated PP to whales and other megafauna (Hart 1934; Huntley et al. 1991). Yet evidence has been gathered that phagotrophic protists can be as abundant in Antarctic waters as at lower latitudes. Their distribution, however, can be patchy (Garrison 1991; Dennet et al. 2001; Landry 2002; Garzio and Steinberg 2013), and their biomass maxima sometimes occur at intermediate depths within the mixed layer (Burkill et al. 1995; Umani et al. 1998; Calbet et al. 2005). Although scarce, protistan grazing rates reported from the Southern Ocean (SO) vary widely among studies and locations. Some investigations have shown grazing exerting a strong impact on PP, at times consuming >100% PP (Tsuda and Kawaguchi 1997; Pearce et al. 2008; Yang et al. 2016), whereas others have measured low grazing rates or a low proportion of PP consumed (Burkill et al. 1995; Froneman and Perissinotto 1996; Caron et al. 2000).

As in other regions of the world, little is known about how protistan herbivory varies seasonally, as current knowledge is primarily based on measurements restricted to spring and/or summer, i.e., seasons of ample prey availability (Schmoker et al. 2013). This knowledge gap is due in large part to the prohibitive winter weather conditions, but it also stems from a prevalent view that winter halts ecosystem functions to a dormant stage, in which biological activities are reduced to a minimum (Smetacek and Nicol 2005). Yet it has been shown that small but diverse eukaryotic microbial communities are able to remain active during the dark arctic winter, presumably surviving on minimal feeding and reduced metabolism (Levinsen et al. 2000). New insights gained from Arctic studies (Berge et al. 2015) suggest that the classical paradigm of winter quiescence in polar systems needs to be revised, as it is detrimental to understanding the temporal dynamics of pelagic ecosystems and hinders predictions of ecosystem responses to climate-induced changes in temperature and sea ice cover.

In the SO, the few measurements of protistan herbivory made outside the productive season have yielded conflicting conclusions. On the East Antarctic coastline, measurements made throughout the year yielded grazing rates that varied seasonally (Pearce et al. 2008), whereas in the Ross Sea, the...
majority of experiments conducted during four separate cruises covering three different seasons yielded no grazing (Caron et al. 2000). The general variability in the grazing rates reported by prior studies is likely due in part to the wide diversity of marine systems represented in the vast SO, each with its unique hydrology, dynamics of nutrients and PP (Treguer and Jacques 1992).

Here, we report measurements of phytoplankton growth and protistan grazing rates in several scarcely studied glaciomarine fjords lining the northern part of the WAP known as the Danco Coast and in the adjacent Gerlache Strait, during two cruises aboard the R/V Nathaniel B. Palmer. These fjords are sites of exchange between the cryosphere and the ocean, and are influenced by glacial discharge. Thus they may be particularly sensitive to the WAP region’s warming (Turner 2016), as an increase in glacial melt-water input would likely affect the hydrography and biology of these systems (Dierssen et al. 2002). The timing of the cruises created the rare opportunity to make measurements during two contrasting seasons, once in 2013 during the poorly characterized late austral autumn, and a second time during late austral spring 2014. We expected large seasonal differences in environmental conditions, and our main objective was to assess how much these differences would be reflected in differences in the importance of protistan grazing as a factor governing the fate of primary production.

**Materials and methods**

**Study sites**

We quantified rates of phytoplankton growth and protistan grazing from 17 May 2013 to 06 June 2013 and again from 07 December 2014 to 24 December 2014, in four glaciomarine fjords fringing the northern part of the WAP known as the Danco Coast and in the adjacent Gerlache Strait, during two cruises aboard the R/V Nathaniel B. Palmer. These fjords are sites of exchange between the cryosphere and the ocean, and are influenced by glacial discharge. Thus they may be particularly sensitive to the WAP region’s warming (Turner 2016), as an increase in glacial melt-water input would likely affect the hydrography and biology of these systems (Dierssen et al. 2002). The timing of the cruises created the rare opportunity to make measurements during two contrasting seasons, once in 2013 during the poorly characterized late austral autumn, and a second time during late austral spring 2014. We expected large seasonal differences in environmental conditions, and our main objective was to assess how much these differences would be reflected in differences in the importance of protistan grazing as a factor governing the fate of primary production.

**Environmental conditions**

At each station, hydrographic data of total depth, temperature, and salinity were collected with a SBE911Plus Seabird Electronics Inc. CTD equipped with sensors of chlorophyll fluorescence (WET Labs AFLT) and PAR (Biophysical Instruments Licor Chelsea). The average of the 10% highest PAR values recorded over the daylight hours of each experiments’ duration was determined from the ship’s continuous data of mast PAR and used to characterize the intensity of incoming irradiance. Mixed layer depth was calculated from a density (sigma-t) difference criterion of 0.03 kg m$^{-3}$ (Dong et al. 2008), using as reference the near surface (5 m) density values.

**Experimental set-up**

Rates of phytoplankton growth and protistan grazing were quantified using the Landry and Hassett dilution method (Landry and Hassett 1982). The method is designed to estimate the mortality of phytoplankton due to grazing by microzooplankton. Although the term “microzooplankton” technically describes 20–200 μm organisms (Sieburth et al. 1978), including multicellular grazers such as copepod nauplii, rotifers, and mesozooplankton, the group is predominantly represented by phagotrophic protists such as ciliates and dinoflagellates, as well as heterotrophic nanoflagellates. Thus in our and many other studies, the grazing measured was principally due to protistan grazers (Calbet 2008).

We conducted 11 and 13 dilution experiments during austral autumn and austral spring, respectively (Table 1). We further refer to these experiments as “dilution series” (DS). Water for the experiments was collected using the CTD rosette sampler from a depth of 5 m (autumn 2013), and from the depth of the CTD fluorescence maximum (spring 2014), the latter varying between 5 m and 12 m but always occurring within the surface mixed layer (Table 1).

Additionally, to investigate the depth-dependent variability of rates, on three occasions during autumn 2013 we used a 2-point modification of the dilution method (Worden and Binder 2003; Chen 2015; Morison and Menden-Deuer 2017). This abbreviated method allowed us to perform simultaneous measurements using water collected from three different depths (5 m, 18 m, and 80 m) during the same CTD cast. During spring, a 2-point approach was also used in one experiment performed in the Gerlache Strait (Table 1).

Source water was gently transferred from the Niskin bottles into 10 L or 20 L carboys through a silicone tube to which a 200 μm mesh was affixed to screen out mesozooplankton. We refer to this < 200-μm water as whole seawater (WSW). Filtered seawater (FSW) was obtained by filtering water collected from the same depth as WSW directly from the Niskin bottles through a 0.2 μm capsule filter ( Pall).

For the DS, WSW and FSW were combined to obtain four dilution levels each containing 10%, 20%, 40%, 70% WSW in addition to the 100% WSW treatment. The 2-point experiments included a 100% WSW treatment and either a 25% WSW (autumn) or a 10% WSW (spring). Each dilution level was prepared as a single stock in a carboy and further siphoned into either 2.4 L (autumn) or 1.2 L (spring) polycarbonate bottles. Bottle volumes were determined based on in situ chlorophyll $a$ (Chl $a$) concentration. During autumn, both the larger bottles and the larger proportion of WSW used in the 2-point were meant to ensure enough biomass to obtain a measurable Chl $a$ signal in the diluted fraction.

Dilutions were incubated in duplicate. During autumn, however, we increased the replication to three bottles for the
highest dilution and the undiluted treatment (including in the 2-point experiments), to increase our ability to constrain rates despite the low biomass.

In situ nutrient concentrations are not well characterized for the autumn season, but we suspected that macronutrients might have been depleted by the large spring and summer phytoplankton blooms that occur in the WAP marginal ice zones (Kim and Ducklow, 2016). Therefore, replicates of all dilution levels were amended with macronutrients to a final concentration of 10 μM and 1 μM for nitrate and phosphate, respectively, and a set of undiluted duplicates was prepared without added nutrients to serve as a nutrient control. In the spring, macronutrients are usually high (Ducklow et al. 2012) and melting sea-ice enriches seawater with iron (van der Merwe et al. 2011). Excess nutrients can negatively affect phytoplankton growth rates (Stoecker et al. 2014 and ref. therein), thus during spring no nutrients were added to the dilutions, and to control for nutrient limitation, a set of undiluted duplicates were amended with 10 μM nitrate, 1 μM phosphate, 10 μM silicate, and a solution of f/2 trace metals corresponding to a final concentration of 1 nM iron.

To provide gentle agitation, bottles were vertically suspended in the deck-board incubators, and incubations were maintained for 24 h at ambient temperature with ship supplied, flow-through surface seawater water. Temperature was recorded at 15 min intervals using Hobo data loggers. To recreate the ambient in situ light environment, the deck incubators were covered with an optical filter (light blue #118 LEE™), which was chosen to best represent the light attenuation and spectral quality within the mixed layer by transmitting light in the 400–570 nm range and removing longer wavelengths (Daniels et al. 2015 and references within). Based on comparisons between the on-deck incoming irradiance and the light intensity inside the screened incubator measured with a Biospherical QSL-2101 light meter, the filter reduced the overall light to ca. 20%. Although this standard light reduction did not always replicate the in situ % of incoming irradiance, it was representative of light attenuation in the upper water column. Due to the cruises’ CTD deployment schedules, during autumn, incubations started after sunset whereas in the spring, incubations started in late morning.

Estimation of phytoplankton growth and grazing mortality rates

For all experiments, rates of phytoplankton growth (μ) and protistan-grazing mortality (g) were estimated following Landry and Hassett (1982) from changes in total extracted Chl a. During spring, rate estimates were also determined for the >
20 μm Chl a a fraction measured in the 10% and 100% WSW dilution levels, except for experiments performed in Wilhelmina Bay and Crystal sound, where all Chl a was < 20 μm.

For each experiment, initial (P₀) and final (Pₜ) Chl a concentrations were determined from triplicate subsamples of each dilution stock and of each replicate bottle respectively, in volumes that varied between 60 mL and 500 mL depending on Chl a concentration. Chl a extraction and determination followed Graff and Rynearson (2011), except that extraction took place at room temperature for 12 h in 96% ethanol (Jespersen and Christoffersen 1987). Apparent phytoplankton growth rate (k, d⁻¹) in each bottle was estimated using the equation $k = 1/t \ln (Pₜ - P₀)$, where t is the incubation time in days.

The DS method assumes that k is a linear function of the dilution factor. To verify that this critical assumption was met,

### Table 1. Environmental characteristics of stations where water was collected for dilution experiments conducted along the Western Antarctic Peninsula during austral autumn 2013 and austral spring 2014. Mixed layer depth (MLD) was calculated from a density difference criterion of 0.03 kg m⁻³, using 5 m density values as reference. Temperature and salinity data are from depth of sample collection. Photosynthetically available radiation (PAR) values represent the average 10% highest values of daylight hours over the duration of the experiment. Day length = sunrise to sunset. Site locations are shown in Figure 1.

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<th>Total depth (m)</th>
<th>MLD (m)</th>
<th>T (°C)</th>
<th>Salinity (PSU)</th>
<th>PAR (μE m⁻² s⁻¹)</th>
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*Morison and Menden-Deuer Antarctic seasonal protistan herbivory*
the linear regression of $k$ vs. the dilution factor for each DS experiment was tested for deviations from linearity using ANOVA on the residuals of the regression at an alpha level of 0.05 (Zar 2010). We determined $\mu$ and $g$ according to Morison and Menden-Deuer (2017) as follows:

1. If no deviation from linearity was detected, we tested the null hypothesis that the regression slope = 0. If the regression slope was significantly different from 0, the rates were estimated from the linear regression coefficients ($g$ from the negative slope and $\mu$ from the $y$-intercept) following Landry and Hassett (1982). If the regression slope was not significantly different from 0, $g$ was set to 0 and $\mu$ was calculated as the average of $k$ across all dilution levels (Murrell et al. 2002; Chen et al. 2009).

2. When deviations from linearity were detected (three autumn and one spring experiments), rates were estimated using the linear portion of the data only, which was determined by applying a piecewise regression model using the R package “stats.” Breakpoints dividing the original linear regression into segments were identified as the dilution at which the model has the minimum residual standard error (Crawley 2013). For nonlinear data, we thus estimated $g$ as the $y$-intercept of the new linear regression through the linear portion of the data, and $g$ was then estimated as $g = \mu - k_1$, where $k_1$ is the average apparent phytoplankton growth in the undiluted bottles. In some cases, no adjustment was possible (no linear data subset), and $g$ was then labeled as “undetectable” and $\mu$ was estimated as the average of $k$ across all dilution levels.

For the 2-point experiments, a $t$-test was used to test the null hypothesis that the regression slope = 0 comparing the mean $k$ of the diluted and undiluted treatments. When the diluted treatment used in the 2-point experiment only represented a 10% fraction of WSW (one experiment during spring), $k_d$ was used as a conservative estimate of $\mu$ (Worden and Binder 2003; Strom and Fredrickson 2008; Lawrence and Menden-Deuer 2012), and $g$ was determined using the equation $g = k_d - k_1$. This approach could not be used when the diluted fraction had a higher biomass of 25% WSW (autumn). For such experiments, $g$ was estimated using the equation $g = (k_d - k_1) / (1 - D)$, where the subscript $d$ corresponds to the diluted treatment and $D$ represents the dilution factor in the diluted treatment, and $\mu$ was then calculated as $\mu = g + k_1$ (Landry et al. 2008).

Three experiments conducted during spring yielded negative grazing rates. Noteworthy is that these experiments were associated with exceedingly high Chl $a$ concentrations, suggesting allelopathy as a plausible mechanism (Stoecker et al. 2015), which we did not however attempt to verify. Negative grazing rates were set to 0, and $\mu$ was then calculated as the average $k_1$ value.

In both the DS and 2-point methods, we applied realized dilution factors as determined from measured initial Chl $a$ concentrations in the dilutions, which varied from the target dilutions by an average of 3%. In either season, we found no significant difference ($t$-test) between treatments incubated with and without nutrients and thus all undiluted replicates regardless of nutrient treatment were included in the calculation of rates. Neither phytoplankton growth nor grazing rates from the autumn experiments were significantly different whether estimated from a regression analysis of the DS, or calculated using only the highest dilution and the nondiluted treatments ($p = 0.97$, mean of the difference = 0.0009 $d^{-1}$ $\pm$ 0.07 SD and $p = 0.41$, mean of the difference = 0.014 $d^{-1}$ $\pm$ 0.06 SD, for $\mu$ and $g$, respectively), reconfirming that the two types of experiments conducted in this study yield undistinguishable results (Chen 2015; Morison and Menden-Deuer 2017).

Predicted accumulation rates ($d^{-1}$) were estimated using the equation $r = \mu - g$, and grazing impact on phytoplankton as the proportion of PP consumed was estimated using the equation $\%$ PP grazed = $g/\mu$ (Calbet and Landry, 2004). The latter was not estimated when instantaneous phytoplankton growth rates were equal or less than 0.

**Spatial and size distribution of Chl $a$**

To characterize the concentration and distribution of Chl $a$ across the sampling region, Chl $a$ measurements were performed at additional locations to supplement measurements made for the dilution experiments (Fig. 1). For each geographic area sampled during the two cruises, Chl $a$ was extracted from a total of 18 (2013) and 11 (2014) water samples collected from a depth of 5 m with the CTD rosette at 11 and nine separate sites respectively. To characterize the size distribution of the phytoplankton community, Chl $a$ was measured in 2–5 size fractions from ~0.7 (GF/F) to 20 $\mu$m, in all 2013 samples. In 2014, a total of six samples for Chl $a$ fractionation were collected from the CTD fluorescence maximum, which varied between 5 m and 15 m, and fractionated measurements were also performed three times (in Antvord, Wilhelmina, and Paradise bays) with water collected from 5 m for dilution experiments.

**Phytoplankton community composition**

To obtain a qualitative description of the nanophytoplankton and microphytoplankton community, live subsamples of the source water used in dilution experiments were analyzed using FlowCAM®, an imaging instrument that provides rapid characterization of plankton composition, typically at a group level. Depending on plankton size composition, samples were analyzed using 300 $\mu$m and 100 $\mu$m flow cells at 4X and 10X magnifications. In late autumn 2013, samples were analyzed sporadically, as low in situ biomass dominated by picoplankton necessitated large volumes of water (up to 10 L) to be concentrated so less abundant larger cells could be detected. In 2014, we analyzed duplicate or triplicate subsamples of undiluted source water used in the dilution experiments until 1000
images per sample were obtained. Phytoplankton were identified to major taxon following Thronsden et al. (2007) and Kraberg et al. (2010).

**Protistan grazer community composition and biomass**

To determine the species composition and biomass of the grazer community, well mixed subsamples of the undiluted plankton assemblage were collected at the beginning of each experiment and preserved with a 2% acidified Lugol’s solution (Menden-Deuer et al. 2001). All 2013 samples were analyzed but one from Wilhelmina. For 2014, biomass estimates were generated for at least one sample collected from each fjord. When a fjord was sampled both at the beginning and the end of the sampling period (Table 1), a second sample was analyzed for temporal comparison.

Phagotrophic protists (> 10 μm) were enumerated following the Utermöhl (1958) method. In 2013, a settled volume of 100 mL was used. Due to high phytoplankton abundance in the Utermöhl method results in underestimates (Davis et al. 2002) for ciliates, and others were categorized into morphotypes. Although many dinoflagellates and ciliates function as mixotrophs (Flynn et al. 2013), because of their phagotrophic capacity, we categorized all dinoflagellates as herbivorous. Since enumeration of heterotrophic nanoflagellates using the Utermöhl method results in underestimates (Davis and Sieburth 1982), these organisms were not counted, although they were included in the incubations and thus contribute to measured grazing rates.

Linear cell dimensions were measured using ImageJ software (National Institute of Health) of at least 50 or all imaged individuals per morphotype. Cell volumes were calculated from linear dimensions using appropriate geometric shape algorithms. Biomass for each morphotype was estimated by converting biovolumes into carbon content (μg C L⁻¹) applying published conversion factors specific to dinoflagellates and other general plankton groups (Menden-Deuer and Lesard 2000) or to tintinnid ciliates (Verity and Langdon 1984).

**Results**

**Environmental conditions**

During late autumn, daily average sea surface temperature (SST) varied from −1.5 to 0.7 °C and water temperature at collection depth varied from −1.4 to 0 °C (Table 1). During late spring, SST varied over a similar range, from −1.7 to 1 °C (Table 1), yet below-zero temperatures were only recorded in the channels and during transit to and from Crystal Sound (latitude 66° 54′ S). The average temperature at collection depth (5 m) was −0.98 (± 0.34) °C in autumn compared to 0.18 (± 0.65) °C in spring. During both seasons, mixed layer depth (MLD) at sampling sites within the fjords was shallow. During late autumn, MLD in the fjords varied from 7 m to 30 m but reached 60 m in the Bismarck Strait (Table 1). Stratification was driven by the presence of a layer of fresher but colder water at the surface. During late spring, MLD ranged from 6 m to 20 m (Table 1). In the fjords, stratification resulted from warmer but fresher water at the surface, but in the Straits and Crystal Sound, surface water was both fresher and up to 1 °C colder than at a depth of 100 m.

The most striking seasonal contrast in environmental conditions was the difference in irradiance. Between the beginning and the end of the austral autumn sampling period, day length decreased from ~ 6 h to ~ 4 h (Table 1). Autumn was marked by very few sunny days, the sky was generally overcast, and heavy snow fell on several occasions. These conditions, together with a low sun angle, contributed to overall low PAR: day-light daily averages of Mast PAR ranged from 11 to 131 (average 45 ± 36) μmol photons m⁻² s⁻¹ and averages of 10% highest PAR measurements ranged from 30 μmol photons m⁻² s⁻¹ to 426 μmol photons m⁻² s⁻¹ (Table 1). In contrast, during austral spring, there was no period of total darkness (Table 1). Daily averages of Mast PAR measurements ranged from 252 to 941 (average 538 ± 210) μmol photons m⁻² s⁻¹ with large variation around the daily mean (75–114% coefficients of variation), and averages of the 10% highest PAR values ranged from 882 μmol photons m⁻² s⁻¹ to 1775 μmol photons m⁻² s⁻¹ (Table 1). On average, irradiance (expressed as daily light integral) during austral spring was 40-fold greater than during austral autumn.

**Chl a concentration, phytoplankton growth, and grazing mortality rates**

In late austral autumn, Chl a concentrations were low throughout. Chl a measured at the beginning of each experiment varied from 0.14 (± 0.01) to 0.40 (± 0.02) μg L⁻¹, with lowest concentrations measured in Wilhelmina Bay at the end of the sampling season (Table 2). Phytoplankton growth and grazing mortality rates estimated from water collected at 5 m were low. Phytoplankton growth rates ranged from −0.1 d⁻¹ to 0.19 d⁻¹ (Table 2). Grazing was detected in only six out of the 14 experiments, with rates ranging from 0.11 d⁻¹ in Wilhelmina to 0.26 d⁻¹ in Antvord (Table 2). There was no relationship between temperature and grazing rates’ magnitude (Fig. 2). When grazing was detected, the measured rates of growth and mortality were either closely coupled, or g exceeded μ.

For the experiments performed in Wilhelmina Bay using water collected from 18 m to 80 m, both growth and grazing rates (if detected) were generally low (< 0.2 d⁻¹) except on June 4th for the experiment using water collected from 80 m, which yielded growth and grazing rates of 0.61 ± 0.1 d⁻¹ (Table 2). Although these rates are remarkably high and resulted from the detection of changes in minimal Chl a concentration,
their variation calculated from triplicate incubations was consistent with the typical error associated with such measurements (see Morison and Menden-Deuer 2017), and analysis of samples from the 80 m depth revealed the presence of potential grazers such as dinoflagellates (1180 L$^{-1}$) and aloricate ciliates (161 L$^{-1}$).

During late austral spring, initial Chl $a$ varied from 0.2 $\mu$g L$^{-1}$ in Crystal Sound to 18.5 $\mu$g L$^{-1}$ in Flandres Bay (Table 3). Phytoplankton growth rates ranged from 0.06 d$^{-1}$ to 0.31 d$^{-1}$ and averaged 0.18 d$^{-1}$, not including one growth rate of 0.93 d$^{-1}$ measured in Antvord Bay did not substantially alter the spring average accumulation rate (0.12 d$^{-1}$), nor the average PP consumed (44%).

In the experiments in which rates were estimated based both on total and >20 $\mu$m Chl $a$, phytoplankton growth rates for the >20 $\mu$m fraction ranged from −0.11 d$^{-1}$ to 0.92 d$^{-1}$ (Table 3) and were significantly higher than corresponding estimates based on total Chl $a$ (t-test, t = 2.185, DF = 9, p = 0.03). Mean growth rate (0.37 ± 0.02 d$^{-1}$) in the >20 $\mu$m fraction exceeded the total growth rate on average by 0.12 (±0.17) d$^{-1}$ (Fig. 4). Overall, the >20 $\mu$m size fraction did not appear to be subject to grazer-induced mortality. Grazing for the >20 $\mu$m fraction was detected in only one out of 10 experiments (Andvord Bay, $g = 0.33 ± 0.10$ d$^{-1}$; Table 3).

### Phytoplankton abundance and species composition

At all sites sampled during late autumn, on average 91% of surface Chl $a$ was contributed by cells <10 $\mu$m (Fig. 5A), and an average of 47% was contributed by cells <2 $\mu$m (data not

<table>
<thead>
<tr>
<th>Date</th>
<th>Site</th>
<th>Chl $a$ (µg L$^{-1}$)</th>
<th>$\mu$ (d$^{-1}$)</th>
<th>$g$ (d$^{-1}$)</th>
<th>$r$ (d$^{-1}$)</th>
<th>% PP</th>
</tr>
</thead>
<tbody>
<tr>
<td>17 May</td>
<td>W2</td>
<td>0.39 (0.01)</td>
<td>0.18 (0.02)</td>
<td>0.16 (0.03)</td>
<td>0.02 (0.04)</td>
<td>89</td>
</tr>
<tr>
<td>20 May</td>
<td>W3</td>
<td>0.38 (0.01)</td>
<td>−0.01 (0.06)</td>
<td>Undetectable</td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td>21 May</td>
<td>W1</td>
<td>0.31 (0.01)</td>
<td>0.01 (0.03)</td>
<td>0</td>
<td>0.01 (0.03)</td>
<td>n/a</td>
</tr>
<tr>
<td>22 May</td>
<td>W1</td>
<td>0.28 (0.01)</td>
<td>0.03 (0.04)</td>
<td>0.13 (0.06)</td>
<td>−0.10 (0.07)</td>
<td>433</td>
</tr>
<tr>
<td>23 May</td>
<td>A3</td>
<td>0.35 (0.01)</td>
<td>−0.07 (0.08)</td>
<td>0</td>
<td>−0.07 (0.08)</td>
<td>n/a</td>
</tr>
<tr>
<td>24 May</td>
<td>A1</td>
<td>0.28 (0.03)</td>
<td>0.15 (0.05)</td>
<td>0.26 (0.08)</td>
<td>−0.11 (0.09)</td>
<td>173</td>
</tr>
<tr>
<td>25 May</td>
<td>A1</td>
<td>0.34 (0.01)</td>
<td>0.05 (0.02)</td>
<td>0</td>
<td>0.05 (0.02)</td>
<td>0</td>
</tr>
<tr>
<td>27 May</td>
<td>A1</td>
<td>0.23 (0.03)</td>
<td>0.10 (0.08)</td>
<td>0</td>
<td>0.10 (0.08)</td>
<td>0</td>
</tr>
<tr>
<td>29 May</td>
<td>F2</td>
<td>0.24 (0.01)</td>
<td>0.06 (0.08)</td>
<td>Undetectable</td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td>30 May</td>
<td>F1</td>
<td>0.23 (0.02)</td>
<td>0.19 (0.03)</td>
<td>0.19 (0.05)</td>
<td>0.00 (0.04)</td>
<td>100</td>
</tr>
<tr>
<td>31 May</td>
<td>B5</td>
<td>0.40 (0.02)</td>
<td>−0.08 (0.04)</td>
<td>0</td>
<td>−0.08 (0.04)</td>
<td>n/a</td>
</tr>
</tbody>
</table>

### Table 2. Initial Chl $a$ concentration (Chl $a$, µg L$^{-1}$), as well as rates (d$^{-1}$) of phytoplankton growth ($\mu$), grazing mortality ($g$), phytoplankton accumulation ($r$), and grazing impact as proportion of primary production consumed (% PP) estimated from dilution experiments conducted in the Western Antarctic Peninsula during austral autumn 2013. Rates are given ± one standard deviation of the mean rate obtained from duplicate or triplicate incubation bottles (in parentheses). Site locations shown in Fig. 1.
shown). Detritus was frequent in all autumn samples. In Wilhelmina Bay, cells > 10 μm almost entirely consisted of cryptophytes. There were few diatoms, yet despite diatoms’ low abundance, this group was represented by diverse genera including *Thalassiosira*, *Rhizosolenia*, *Guinardia*, *Chaetoceros*, *Pseudonitzschia*, and *Thalassiothrix*. *Corethron* was present in all the bays sampled in various stages of reproduction (Fig. 6A).

During the spring, Chl a concentrations indicated a phytoplankton bloom. Phytoplankton biomass distribution within each fjord was patchy, as evidenced by large variations in Chl a depending on sampling location (Table 3). In Antvord Bay,
the Chl \(a\) concentration doubled over the 10 d separating repeated sampling, reflecting a rapid development of a diatom bloom, whereas in Flandres Bay, katabatic winds blowing down the glaciers mixed the water column, likely contributing to an observed decrease in surface Chl \(a\) with time (Table 3).

Of the bays, Wilhelmina had the lowest Chl \(a\) concentration (3.4 \(\pm\) 0.5 \(\mu\)gL\(^{-1}\)), 90% of which was measured in the < 5 \(\mu\)m fraction. In all the other fjords, and at sites in Gerlache Strait where size distribution was assessed (G1 and G2), an average of 76% of Chl \(a\) was contributed by cells > 20 \(\mu\)m (Fig. 5B). In contrast in Bismarck Strait, up to 81% of Chl \(a\) was found within the < 2 \(\mu\)m fraction. Species composition of the phytoplankton community varied among sites (Fig. 6A). In Wilhelmina Bay and Bismarck Strait, the > 6 \(\mu\)m phytoplankton consisted mostly of cryptophytes, an observation previously reported for the northern subregion of the Antarctic Peninsula (Garibotti et al. 2003). In contrast diatoms characterized the phytoplankton community in Andvord, Flandres, and Paradise bays. Whereas in Andvord Bay long chains of Chaetoceros spp. were most abundant, long chains of Detonula pumila, Thalassiosira spp. and other centric diatoms dominated the two other bays, together with species of Corethron. Both in Flandres and Paradise, prasinophytes identified as Pyramimonas sp. were also abundant. The microphytoplankton community was most diverse in Gerlache strait, composed of all the different diatom species present in the bays. Colonies of Phaeocystis antarctica were sometimes present in samples, but never abundant.

**Grazer biomass and species composition**

During autumn, grazer biomass in the fjords varied from a bay average of 3.3 (\(\pm\) 0.9) \(\mu\)g C L\(^{-1}\) in Andvord Bay to a bay average of 6.0 (\(\pm\) 1.1) \(\mu\)g C L\(^{-1}\) in Flandres Bay (Fig. 7A). In Wilhelmina Bay, grazer biomass decreased between the beginning and the end of the sampling period, from an average of 4.3 (\(\pm\) 0.4) \(\mu\)g C L\(^{-1}\) to an average of 2.2 (\(\pm\) 0.9) \(\mu\)g C L\(^{-1}\). In Bismarck strait, grazer biomass was 17.6 \(\mu\)g C L\(^{-1}\), 4.5 times greater than the fjords’ overall average biomass. Spring grazer biomass varied over an order of magnitude, from 6.2 \(\mu\)g C L\(^{-1}\) in Andvord Bay on December 10\(^{th}\), to 52.3 \(\mu\)g C L\(^{-1}\) in Flandres Bay (Fig. 7C). In three of the fjords where sampling...
occurred twice 7–14 d apart, total grazers’ biomass increased by 40–250% (Fig. 7C).

In both sampling seasons, the protistan grazer community was dominated by athecate dinoflagellates (Fig. 7). In the fjords, thecate dinoflagellates were rare and tintinnid ciliates were almost absent. Dinoflagellates dominated the autumn grazer community both in abundance and biomass, representing an average of 77% of both the numerical abundance and the total biomass in the fjords (Fig. 7B), ¼ of which could be attributed to numerous athecate forms, principally of the genera *Gyrodinium* and *Gymnodinium* (Fig. 6B). Oligotrich ciliates accounted for ¼ of total biomass in the fjords. In Bismarck strait, the ratio of dinoflagellates to ciliates was similar to that in the fjords, with dinoflagellates dominating the grazer community both in numerical abundance (82%) and biomass (69%), but dinoflagellate thecate forms were more predominant than in the fjords, contributing 53% of the dinoflagellate biomass (Fig. 7B). Noteworthy was the presence of cells tentatively identified as cysts (Fig. 6B).

During spring, the numerical abundance of protistan grazers was similar to their abundance during autumn, but their biomass was greater, reflecting a ~ 2-fold increase in the average size of grazers. Similarly to observations made during autumn, athecate dinoflagellates generally dominated the grazer community during spring, with <20 µm gymnoid forms being particularly abundant on the first visit to Wilhelmina Bay. In Flandres Bay, however, a few large *Protoperidinium* spp. and tintinnid ciliates contributed most of the biomass (Fig. 6B). In general, there were few aloricate ciliates, except in Paradise Bay where a few but large *Strombidium*-type oligotrichs contributed 91% of the biomass (Fig. 7D).

**Discussion**

Measurements of rates of phytoplankton growth and grazer-induced mortality are essential to quantify how much of the organic carbon fixed by phytoplankton is either recycled or transferred to higher trophic levels in surface
waters or available for export to deeper waters, and therefore to understand ocean trophic linkages and biogeochemical cycling (Le Fèvre et al. 1998; Smetacek et al. 2004). In the global ocean, predation by phagotrophic protists represents the major fate of marine phytoplankton (Steinberg and Landry 2017). In the SO, marginal ice zones such as those in the WAP are seasonally highly productive (Smith and Nelson 1986; Vernet et al. 2008) and act as a sink for CO₂ (Ducklow et al. 2007). Yet as in the rest of the SO, where environmental conditions are subject to extreme variations, seasonal data on the dynamics of phytoplankton and the factors regulating its mortality are scarce, and it is commonly assumed that biological activity of plankton ceases during winter.

A major finding of the work presented here was the absence of a sizable seasonal difference in the magnitude of protistan herbivory rates. Grazer-induced phytoplankton mortality rates followed a similar pattern irrespective of season, with either no grazing or low grazing rates that rarely exceeded 0.1 d⁻¹. This similarity was measured against a backdrop of environmental conditions that did not drastically differ between seasons, except for an extraordinary increase in irradiance during spring. This increase in available radiation
relieved light limitation on phytoplankton growth obviously imposed by low winter irradiance levels, and consequently induced an increase not only in phytoplankton abundance, but also in the composition and the size structure of the phytoplankton community. Frequency of absent and low grazing rates was similar across seasons at Chl $\alpha$ concentrations that ranged over two orders of magnitude, underscoring that bulk prey abundance, as assessed by measurements of Chl $\alpha$ concentration, was not a determinant of grazing magnitude. This conclusion is consistent with the observations from many other studies of protistan herbivory (Lawrence and Menden-Deuer 2012 and references within), yet it conflicts with a generally observed functional response of zooplankton, i.e., that ingestion rates increase, albeit not always linearly, with prey density (Ivlev 1955; Holling 1959; Frost 1972). The observed lack of seasonality in grazing rates implies that the functions traditionally used to describe zooplankton grazing in plankton models (Franks 2002; Li et al. 2011; Leles et al. 2016) may not be universally applicable to microzooplankton grazing, especially when bulk indices of prey abundance such as chlorophyll are used.

Whereas Chl $\alpha$ concentration was not a predictor of grazing magnitude, phytoplankton size structure was one common factor to the occurrence of grazing in both seasons. Grazing was generally prevalent, when picoplankton and nanoplankton dominated phytoplankton abundance. Grazing on these small cells may also have been occurring during spring where and when diatoms dominated, but could have escaped detection due to opposing dynamics of different Chl $\alpha$ fractions. We base our suggestion on the fact that the > 20 μm phytoplankton fraction generally grew at rates up to twofold to threefold higher than those measured for total Chl $\alpha$. Thus any decrease in Chl $\alpha$ that would result from grazing on the pico- or nano-size fraction may have been offset by an
increase in Chl $a$ due to growth of the $> 20 \mu m$ size fraction, and measurements based on total Chl $a$ would have underestimated grazing rates. To resolve internal plankton population dynamics, future studies should include a detailed analysis of changes in the abundance of different size fractions, especially when the size spectrum of the phytoplankton stock is broad.

Our observations suggest that springtime grazing was directed at the picophytoplankton and/or nanophytoplankton, and thus the larger phytoplankton size fraction presumably remained available for predation by mesozooplankton or sedimentation, which would be consistent with patterns observed in marginal ice zones (Ducklow et al. 2007 and references therein). The in situ build up of a diatom dominated bloom suggests predation by larger predators did not balance growth in the $> 20 \mu m$ size fraction.

Remarkably, a fraction of primary production was recycled within the microbial food web irrespective of season. Other Antarctic studies have found substantial grazing to be associated with small phytoplankton cell size (Garrison et al. 1993; Froneman and Perissinotto 1996; Froneman 2004; Safi et al. 2007; Garzio et al. 2013). As climate-driven changes in water temperature and salinity along the WAP are predicted to favor the dominance of smaller phytoplankton types (Moline et al. 2004; Montes-Hugo et al. 2009), phytoplankton losses due to protistan grazing could intensify, with consequences for the transfer of primary production through the food web and the cycling of carbon.

Average grazing rates for polar (i.e., both Arctic and Antarctic) regions are generally reported to be low ($\sim 0.15 d^{-1}$; Calbet and Landry 2004; Schmoker et al. 2013; Menden Deuer et al. 2018). While our rate data agree well with this average,

### Table 4. Summary of published rates of phytoplankton growth and protistan grazing measured using the dilution method in the Southern Ocean (SO).

<table>
<thead>
<tr>
<th>Study region</th>
<th>Time of year</th>
<th>$T \ (^{\circ}C)$</th>
<th>Chl $a$ ($\mu g \ L^{-1}$)</th>
<th>$\mu$ ($d^{-1}$)</th>
<th>$g$ ($d^{-1}$)</th>
<th>Reference</th>
<th>Map ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bellingshausen Sea</td>
<td>Nov/Dec</td>
<td>-1.8 to -1.0</td>
<td>0.05-1.42</td>
<td>n/a</td>
<td>0.03-0.52</td>
<td>Burkill et al. (1995)</td>
<td>1</td>
</tr>
<tr>
<td>SO Atlantic sector</td>
<td>Jan/Feb</td>
<td>&lt;1.0</td>
<td>1.01</td>
<td>0.24</td>
<td>0.04</td>
<td>Froneman and Perissinotto (1996)</td>
<td>2</td>
</tr>
<tr>
<td>SO Atlantic sector</td>
<td>Jan/Feb</td>
<td>&lt;1.0</td>
<td>1.88</td>
<td>1.68</td>
<td>0.22</td>
<td>Froneman and Perissinotto (1996)</td>
<td>2</td>
</tr>
<tr>
<td>SO Atlantic sector</td>
<td>Jan/Feb</td>
<td>1.00-5.00</td>
<td>0.10-0.68</td>
<td>0.51-1.86</td>
<td>0.06-0.33</td>
<td>Froneman and Perissinotto (1996)</td>
<td>2</td>
</tr>
<tr>
<td>Lazarev Sea</td>
<td>Dec/Jan</td>
<td>-1.65 to -1.0</td>
<td>0.23-0.51</td>
<td>0.0 to -0.09</td>
<td>0.0-0.07</td>
<td>Froneman et al. (1997)</td>
<td>3</td>
</tr>
<tr>
<td>Lazarev Sea</td>
<td>Dec/Jan</td>
<td>-0.32 to 0.29</td>
<td>0.28-0.48</td>
<td>0.0 to -0.08</td>
<td>0.0 to -0.06</td>
<td>Froneman et al. (1997)</td>
<td>3</td>
</tr>
<tr>
<td>WAP</td>
<td>Dec/Jan</td>
<td>0.5-2.0</td>
<td>0.75-2.28</td>
<td>0.0 to -0.42</td>
<td>&lt;0.0 to 0.29</td>
<td>Tsuda and Kawaguchi (1997)</td>
<td>4</td>
</tr>
<tr>
<td>Polar front</td>
<td>Dec/Jan</td>
<td>-0.9 to 0.0</td>
<td>0.08-0.25</td>
<td>-0.03 to 0.66</td>
<td>0.0-0.69</td>
<td>Tsuda and Kawaguchi (1997)</td>
<td>5</td>
</tr>
<tr>
<td>Ross Sea</td>
<td>Oct/Nov</td>
<td>-1.9 to -1.8</td>
<td>0.04-0.71</td>
<td>n/a</td>
<td>0.0-0.26</td>
<td>Caron et al. (2000)</td>
<td>6</td>
</tr>
<tr>
<td>Ross Sea</td>
<td>Jan/Feb</td>
<td>-0.5 to 0.5</td>
<td>0.65-5.8</td>
<td>n/a</td>
<td>0.0-0.11</td>
<td>Caron et al. (2000)</td>
<td>6</td>
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<tr>
<td>Ross Sea</td>
<td>Apr</td>
<td>-1.9 to -1.8</td>
<td>0.02-0.08</td>
<td>n/a</td>
<td>0.00</td>
<td>Caron et al. (2000)</td>
<td>6</td>
</tr>
<tr>
<td>Polar front</td>
<td>Oct/Nov</td>
<td>-0.02-4.5</td>
<td>0.24-0.86</td>
<td>0.0 to -0.30</td>
<td>0.10-0.23</td>
<td>Landry et al. (2001)</td>
<td>7</td>
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<tr>
<td>Polar front</td>
<td>Dec</td>
<td>-1.06 to 3.66</td>
<td>0.17-1.51</td>
<td>0.0-1.00</td>
<td>0.00-0.55</td>
<td>Selph et al. (2001)</td>
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<tr>
<td>Prydz Bay</td>
<td>Dec/Jan</td>
<td>0.29-4.10</td>
<td>-2.00 to 1.50</td>
<td>0.11-2.60</td>
<td>0.11-1.06</td>
<td>Li et al. (2001)</td>
<td>9</td>
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<tr>
<td>SO Atlantic sector</td>
<td>Dec/Jan</td>
<td>n/a</td>
<td>0.40-0.44</td>
<td>0.27-0.63</td>
<td>0.0 to -0.09</td>
<td>Froneman (2004)</td>
<td>10</td>
</tr>
<tr>
<td>SO Atlantic sector</td>
<td>Dec/Jan</td>
<td>n/a</td>
<td>0.10-0.12</td>
<td>0.74-0.81</td>
<td>0.19-0.28</td>
<td>Froneman (2004)</td>
<td>10</td>
</tr>
<tr>
<td>SO Atlantic sector</td>
<td>Dec/Jan</td>
<td>n/a</td>
<td>0.23-0.32</td>
<td>0.19-0.62</td>
<td>0.04-0.08</td>
<td>Froneman (2004)</td>
<td>10</td>
</tr>
<tr>
<td>Polar front/ACC</td>
<td>Nov</td>
<td>n/a</td>
<td>0.09-0.69</td>
<td>0.19-0.33</td>
<td>0.18-0.43</td>
<td>Safi et al. (2007)</td>
<td>11</td>
</tr>
<tr>
<td>Near Davis Station</td>
<td>Feb/Mar</td>
<td>-1.82 to 0.34</td>
<td>3.69-9.88</td>
<td>0.50-0.81</td>
<td>0.27-0.55</td>
<td>Pearce et al. (2008)</td>
<td>12</td>
</tr>
<tr>
<td>Near Davis Station</td>
<td>Apr/Jun</td>
<td>-2.00 to -1.84</td>
<td>0.06-0.75</td>
<td>-1.93 to 0.09</td>
<td>0.00-0.15</td>
<td>Pearce et al. (2008)</td>
<td>12</td>
</tr>
<tr>
<td>Near Davis Station</td>
<td>Jul/Sept</td>
<td>-2.03 to -2.00</td>
<td>0.03-0.06</td>
<td>-1.11 to 0.44</td>
<td>0.00-1.54</td>
<td>Pearce et al. (2008)</td>
<td>12</td>
</tr>
<tr>
<td>Near Davis Station</td>
<td>Oct/Nov</td>
<td>-2.11 to -2.01</td>
<td>1.70-6.79</td>
<td>-0.55 to -2.82</td>
<td>&lt;0.00</td>
<td>Pearce et al. (2008)</td>
<td>12</td>
</tr>
<tr>
<td>Near Prytz Bay</td>
<td>Jan-Mar</td>
<td>n/a</td>
<td>0.30-2.40</td>
<td>0.28-1.77</td>
<td>0.31-2.36</td>
<td>Pearce et al. (2010)</td>
<td>13</td>
</tr>
<tr>
<td>WAP PaLTER grid</td>
<td>Jan</td>
<td>-0.7 to 1.2</td>
<td>0.48-12.70</td>
<td>0.13-0.50</td>
<td>0.00-0.26</td>
<td>Garzio et al. (2013)</td>
<td>14</td>
</tr>
<tr>
<td>WAP Palmer</td>
<td>Feb/Mar</td>
<td>1.1-1.5</td>
<td>0.64-4.33</td>
<td>0.33-0.55</td>
<td>0.10-0.31</td>
<td>Garzio et al. (2013)</td>
<td>14</td>
</tr>
<tr>
<td>Amundsen Sea</td>
<td>Dec/Jan</td>
<td>-1.49 to -0.82</td>
<td>0.26-0.76</td>
<td>0.29-0.43</td>
<td>0.0-0.32</td>
<td>Yang et al. (2016)</td>
<td>15</td>
</tr>
<tr>
<td>Amundsen Sea</td>
<td>Dec/Jan</td>
<td>-1.80 to -1.34</td>
<td>0.27-1.73</td>
<td>0.27-0.33</td>
<td>0.0-0.23</td>
<td>Yang et al. (2016)</td>
<td>15</td>
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<tr>
<td>Amundsen Sea</td>
<td>Dec/Jan</td>
<td>-1.65 to -0.36</td>
<td>3.43-12.17</td>
<td>0.30-0.40</td>
<td>0.22-0.41</td>
<td>Yang et al. (2016)</td>
<td>15</td>
</tr>
<tr>
<td>WAP fjords</td>
<td>May/Jul</td>
<td>-1.4 to -0.4</td>
<td>0.14-0.40</td>
<td>-0.08 to 0.19</td>
<td>0.0-0.26</td>
<td>Present study</td>
<td>16</td>
</tr>
<tr>
<td>WAP fjords</td>
<td>Dec</td>
<td>-1.2 to 1.3</td>
<td>0.20-18.50</td>
<td>0.06-0.93</td>
<td>&lt;0.0 to 0.11</td>
<td>Present study</td>
<td>16</td>
</tr>
</tbody>
</table>
we found that even the highest rates we measured correspond to the low end of the range of rate magnitudes reported for Antarctica (Table 4). Similarly, the average proportion of PP grazed estimated from the present study (40%) was lower than that estimated from other studies conducted in polar regions (53–59%). Studies performed in the SO are sparse, and span several different marine habitats from polynyas and marginal ice zones to the polar front and open waters of the ACC (Fig. 8). This diversity of habitats likely contributes to the variability in reported grazing rates (Table 4). Nonetheless vast regions remain either unsampled (e.g., Weddell Sea) or have been characterized by few studies (Table 4), making it difficult to identify common factors that influence grazing loss processes to build a predictive understanding of the role of microzooplankton in the SO.

Among environmental factors, the invariably low water temperature of Antarctic waters is typically proposed as the cause of low heterotrophic protist grazing pressure (Rose and Caron 2007) and low grazing rates (Archer et al. 1996; Caron et al. 2000). In the present study, we measured a range of grazing rates that varied irrespective of temperature. Irrespective of season in which we sampled, temperature was always low (≤ 1.3°C) and varied over a negligible range (1.4°C) across seasons. Several studies in the Antarctic have shown no relationship between herbivory rates and water temperature even when rates were measured under a wider range of temperatures than in the present study (Froneman and Perissinotto 1996; Tsuda and Kawaguchi 1997; Landry et al. 2001), whereas temperature-dependence of grazing rates was identified but over a relatively narrow temperature range (e.g., Burkill et al. 1995; Caron et al. 2000; Garzio et al. 2013). Furthermore, it has been shown that grazing impact on PP can be consistently high at freezing temperatures (Sherr et al. 2013; Yang et al. 2016), and high grazing rates comparable to or exceeding those measured in temperate waters have been measured in the Arctic (Franzé and Lavrentyev 2014; Menden Deuer et al. 2018). Thus it appears that additional factors beyond temperature govern the extent of phytoplankton losses due to grazing.

Low water temperature has also been postulated as a major factor limiting the growth rates and thus the accumulation of
grazers’ biomass sufficient to exert a grazing impact substantial enough to prevent blooms at high latitudes (Rose and Caron 2007). Nonetheless this suggestion conflicts with findings that polar athecate dinoflagellates and ciliates can achieve high growth rates at low in situ temperatures (Franzé and Lavrentyev 2014). While we did not measure grazers’ growth rate in the present study, their estimated biomass was similar during both seasons and at some sites greater than what has been reported for more forgiving locales, such as the North Atlantic in spring for example (Gifford et al. 1995; Morison and Menden-Deuer 2015). Thus low grazing pressure may not only be due to lack of grazers. We cannot completely rule out that some larger micrograzers, such as diatom-feeding large dinoflagellates, may have been excluded from the incubations by filtering of the seawater through a 200 μm mesh, resulting in underestimates of grazing rates during spring, but it is unlikely that this common practice introduced a substantial bias.

Lack of grazing and/or low grazing rates associated with substantial grazers’ biomass has been reported by previous SO studies (Caron et al. 2000; Garzio et al. 2013). This apparent paradox may be explained by the capacity of protistan grazers to sustain considerable periods of starvation (Anderson and Menden-Deuer 2016 and references within), and to retain minimal levels of activity, including feeding, via a reduction in metabolism (Levinsen et al. 2000). Alternatively it suggests that protistan grazers may have relied on other food sources such as bacteria (Garzio et al. 2013) or other grazers (Jeong et al. 2010).

During spring, the average biomass of phagotrophic protists in bays dominated by diatoms increased over the period of time (7–14 d) at the same location. Yet this increase reflected a ~ 2-fold increase in the average size of the grazers rather than an increase in their total numbers, suggesting a gradual appearance of new larger predator species presumably better suited to the progressively dominant large diatoms. Thus the observed development of diatom blooms in the fjords may have resulted not as much from a low grazers’ biomass due to low temperature, but rather from a temporal lag between the shift in the size composition of the phytoplankton community and that of a grazing community matched to the most available prey.

Although grazing rates were seasonally similar in magnitude, a marked seasonality of the phytoplankton growth was measured, resulting in a seasonal difference in the sign of the phytoplankton biomass accumulation rates. In the autumn, the measured rates predicted a decline in phytoplankton standing stock, generally a result of low or negative phytoplankton growth that was exceeded by grazing. In the spring, phytoplankton growth rates exceeded grazing rates in 85% of the experiments, which is consistent with previous measurements made during summer in the PAL LTER region (Garzio et al. 2013). Accumulation rates estimated from the experiments could not be compared directly with those in situ due to limited time spent at any one station and to Chl a patchiness within the bays. Yet rates of change in plankton abundance appeared consistent with the observed in situ Chl a temporal dynamics, i.e., autumn negative average accumulation rate corresponding to declining Chl a concentration, and spring positive average accumulation rate corresponding to observed phytoplankton biomass accumulation and bloom formation. Concurrent observations of whole water column distributions and individual motility behaviors of krill showed krill were actively moving in both seasons (Kane et al. 2018), and were feeding on phytoplankton during late austral spring (Cleary et al. 2018). This suggests that, quantitatively, krill removed less phytoplankton biomass than microzooplankton. Seasonal variations in phytoplankton growth rather than grazing pressure governed net accumulation rates, yielding the diatom blooms that characterize the seasonally high productivity of the marginal ice zones of the WAP system (Vernet et al. 2008).

In conclusion, the present study provides estimates of the role of herbivorous microzooplankton during two different seasons in the unique and climate-sensitive ecosystems of coastal fjords of the WAP, and contributes to further understanding of the seasonal dynamics of a fast warming region’s planktonic food web, and to assembling a baseline of process-rates necessary for detecting future potential climate-driven changes. We document order of magnitude seasonal differences in Chl a concentration and phytoplankton growth rate, and a lack of seasonal contrast in herbivorous protistan grazing. These dynamics undoubtedly are subject to interannual variability. Multiple at sea campaigns over several years are required to quantify both seasonal and interannual variability and establish their relative importance in driving southern ocean food web fluxes. Repeated measurements beyond one field study in each season would be essential to strengthen our understanding of plankton population dynamics in the studied region. Nevertheless the present results suggest that a proportion of PP is continuously funneled through the microbial food web irrespective of season, even during winter when the system may be expected to be dormant. In contrast, during spring an increasing fraction of organic carbon shifted pathways, from entering the microbial food web to being available for export. Overall, our study suggests that the division of plankton population dynamics into sharp seasonality needs revising, and that year-round measurements are needed to understand the factors that shape the structure and functioning of pelagic ecosystems.

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Conflict of interest

None declared.