Different ecological mechanisms lead to similar grazer controls on the functioning of periphyton Antarctic and sub-Antarctic communities

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ABSTRACT

The processes underpinning the differences between Antarctic and sub-Antarctic ecological communities are still unclear. Dispersal, drift, speciation, and abiotic environmental filtering have been considered to explain these differences; biotic interactions, however, have received less attention. Antarctic intertidal assemblages of macrobenthic grazers are characterised by numerically abundant populations of a single species, *Nacella concinna*. In contrast, sub-Antarctic habitats display a diverse assemblage of herbivores like chitons, keyhole limpets, and several species of *Nacella*. Thus, it was hypothesised that herbivores would have significant density-dependent effects of a single species on benthic primary productivity in Antarctica, but stronger effects of the whole assemblage in the sub-Antarctic. Field grazer inclusion-exclusion experiments showed that chlorophyll-*a* (chl-*a*) concentration was one order of magnitude lower in Fildes Bay (King George Island, Antarctica) than in the Strait of Magellan (Chilean South Patagonia). Still, grazers had significant and negative effects on chl-*a* accrual, a proxy for productivity, in both sites. In Fildes Bay, these effects were similar between experimental levels or grazer density. Accordingly, evidence for negative density dependence of per capita interaction strength was detected in this region. In the Strait of Magellan, only the open access treatments, exposed to the diverse assemblage of grazers, significantly decreased chl-*a* accrual. Grazers negatively affected the relative abundance of browns (i.e. diatoms, dinoflagellates, and early stages of brown algae) and cyanobacteria at both sites, but favoured green algae and bare substratum in Fildes Bay and Strait of Magellan, respectively. These results suggest that different mechanisms, such as negative density dependence and resource partitioning, can lead to similar grazing controls of the productivity of Antarctic and sub-Antarctic periphyton communities. Herbivory should be incorporated as a local biotic filter into a comprehensive model of community structure and functioning for these ecosystems.

1. Introduction

Polar and sub-polar regions currently show the fastest responses to climate change on earth (e.g. Blunden et al., 2013). This scenario compels us to improve our mechanistic understanding of the structure and functioning of local natural communities in these regions (Kennicutt et al., 2014). In particular, explaining the differences and similarities between Antarctic and sub-Antarctic communities remains as a central aim of polar ecology (Kaiser et al., 2013). For example, dispersal and neutral stochasticity, two fundamental processes in the theory of island biogeography (MacArthur and Wilson, 1967), are suggested to explain

the comparatively high diversity of marine intertidal species in King George Island (Griffiths and Waller, 2016). Selective pressure derived from nutrient inputs and glacier impacts has been suggested as a relevant factor reducing sub-Antarctic coastal diversity (e.g. Pugh and Davenport, 1997; Kim, 2001; Barnes et al., 2006). However, local biotic interactions, such as consumption, have received less attention in the quest for explaining ecological differences and similarities between both regions (McClintock et al., 2008; Amsler et al., 2012; Andrade and Brey, 2014; Chown et al., 2015). Coastal Antarctic and sub-Antarctic habitats harbour differing assemblages of macrobenthic consumers (Hogg et al., 2011; Griffiths and Waller, 2016), which can have contrasting effects on community structure and also on relevant ecosystem

properties such as productivity, as shown in other regions of the world (Gamfeldt et al., 2015).

Herbivory is a key form of consumption with deterministic effects on ecosystem processes and community structure across latitudes, species pools, and abiotic conditions (e.g. Lubchenco and Gaines, 1981; Hawkins and Hartnoll, 1983; Coleman et al., 2006; Poore et al., 2012). Evidence from several latitudes indicates that grazing can explain, in part, broad-scale patterns of community structure (Coleman et al., 2006; Poore et al., 2012; Aguilera et al., 2016). For example, grazing by benthic intertidal gastropods can affect the range limit of primary producers, influencing their broader-scale distribution patterns (Aguilera et al., 2016). At the local scale, grazers have been shown to modify the spatiotemporal variability in the abundance of primary producers and invertebrates (Benedetti-Cecchi, 2000; Orostica et al., 2014; Tejada-Martinez et al., 2016). Importantly, herbivory impacts relevant ecosystem processes that account for the transferring of primary production outcomes to higher trophic levels in the food web (e.g. Gamfeldt et al., 2015). This consumptive interaction, therefore, might well constitute part of the local selective forces (i.e. a "biotic filter"; HilleRisLambers et al., 2012) that influence not only the structure, but also the functioning of coastal Antarctic and sub-Antarctic communities.

Ecosystem functions (or properties) are aggregate, emergent estimations that account for fluxes of energy, nutrients, and organic matter across a given environment (reviewed in Cardinale et al., 2012). These properties can be used to compare communities between regions characterised by different species pools and environmental conditions, like Antarctic and sub-Antarctic areas. Primary productivity is an example of ecosystem property, which can be represented as the accrual of chlorophyll-*a* (chl-*a*) over time. In the case of intertidal rocky-shore habitats, chl-*a* accrual of periphyton communities defines a key bottom-up input of energy that propagates through the assemblage (e.g. Bustamante et al., 1995; Hillebrand, 2003; Liess and Hillebrand, 2004). Functionally distinct macrobenthic grazers habiting species-rich rocky shores can have different effects on the structure of local periphyton communities (Aguilera et al., 2013), hinting at some degree of resource partitioning among these consumers. Accordingly, different assemblages of grazers from Antarctic and sub-Antarctic coastal communities might encompass different top-down forces, which in turn could drive broad-scale differences in chl-*a* accrual between these regions.

The diversity of grazers, and species in general, can have positive effects on resource use through niche partitioning (Duffy et al., 2017). In general, laboratory and field experiments demonstrate that resource use is less efficient in depauperate communities relative to speciose communities of consumers (O'Connor and Crowe, 2005; Griffin et al., 2009; Duffy et al., 2017), supporting predictions from niche theory (MacArthur and Levins, 1967; Lehman and Tilman, 2000). On Antarctic intertidal rocky-shores, dense populations of a single grazer species, *Nacella concinna*, dominate the macrobenthic assemblages (e.g. Valdivia et al., 2014). The populations of *N. concinna* have been demonstrated to have significant effects on periphyton and macroalgal communities (Kim, 2001), independently of abiotic environmental conditions such as varying UV radiation and air exposure (Zacher et al., 2007; Segovia-Rivera and Valdivia, 2016). In contrast, sub-Antarctic communities show a comparatively high diversity of macrograzers, which include chitons, keyhole limpets, and several *Nacella* spp. (Griffiths and Waller, 2016). According to the general consensus about the significant role of biodiversity in resource utilisation and ecosystem functioning (Griffin et al., 2009, 2010; Cardinale et al., 2012), we could thus hypothesise that grazers would have significant density-dependent effects on periphyton community structure and productivity in Antarctica, but stronger effects of the species-rich assemblage in the sub-Antarctic region.

Here, we test the hypothesis that the differing levels of diversity between Antarctic and sub-Antarctic assemblages of macrograzers lead to different top-down controls of local periphyton productivity between both regions. From this hypothesis we deduce the predictions that, in Antarctic shores, larger densities of a single grazer species, *N. concinna*, will have stronger and more negative effects on chl-*a* accrual (Prediction 1); and, in sub-Antarctic shores, the entire assemblage of grazers would have stronger effects on chl-*a* accrual than a single species at varying densities (Prediction 2). These predictions were tested through field exclusion-inclusion experiments replicated in Fildes Bay (West Antarctic Peninsula) and Strait of Magellan (Chilean South Patagonia).

2. Material and methods

2.1. Study sites

The study was conducted in Fildes Bay, King George Island, Antarctica, and Strait of Magellan, Chilean South Patagonia. In each locality, we selected a wave-sheltered intertidal site that spanned ca. 100 m of the shore and was characterised by large benches of emergent rock (Fig. 1A and B). The experiments were set-up along the mid-low intertidal zone and were visited during diurnal low-tide hours. The studies were conducted between January and February 2017 in Fildes Bay, and between December 2016 and February 2017 in Strait of Magellan. Thus, both experiments overlapped during the austral summer season.

The Antarctic site was located in the north-eastern part of Fildes Bay (−62.18S, −58.8W). The assemblage of grazers in this site was largely dominated in terms of biomass by *N. concinna*, followed by small-sized littorinid snails such as *Laevilittorina antarctica* and *Laevilacunaria umbilicata* (see also Valdivia et al., 2014; Segovia-Rivera and Valdivia, 2016). The dominant intertidal seaweed at this site was the brown alga *Adenocystis utricularis*, followed by the red alga *Iridaea cordata* and the green alga *Urospora penicilliformis*. Recent studies have shown a relatively high diversity of periphyton taxa in the study site (Segovia-Rivera and Valdivia, 2016). The grazer species used in the experiments in Fildes Bay was *N. concinna*.

The sub-Antarctic site was located in a south-western section of the Strait of Magellan (−53.61S, −70.93W). Although important previous accounts have reported the structure of subtidal communities in the Strait of Magellan (e.g. Dayton, 1985), data on intertidal communities are still scarce (but see Benedetti-Cecchi and Cinelli, 1997; Ríos and Mutschke, 1999; Aldea and Rosenfeld, 2011; Griffiths and Waller, 2016; Fica et al., 2017). Several species characterise the mid-intertidal assemblage of grazers, including siphonarid, scurrinid, and keyhole limpets, several polyplacophorans, and at least three species of the genus *Nacella: N. flammea*, *N. magellanica*, and *N. deaurata* (Benedetti-Cecchi and Cinelli, 1997; Rosenfeld et al., 2013; Griffiths and Waller, 2016)—several other species of *Nacella* can be found in low intertidal and shallow subtidal habitats (Aldea and Rosenfeld, 2011; Gonzalez-Wevar et al., 2011). We used individuals of *N. deaurata* in the inclusion treatments of the Strait of Magellan experiment.

In each site, we monitored grazer density on mid-intertidal benches and daily maximum wave velocity. Wave velocity was estimated by means of inexpensive dynamometers (Bell and Denny, 1994) used in several studies on wave exposure and intertidal ecology (e.g. Castilla et al., 1998; Molis et al., 2015). Grazer densities were estimated in ten 0.125 m² (Fildes Bay) and 0.25 m² (Strait of Magellan) quadrats in each study site. Mean (standard error of the mean) grazer densities were 41 (17.4) and 26 (7.5) ind m^{-2} for Fildes Bay and Strait of Magellan, respectively (Fig. 2, see also *Results*). The grazer inclusion treatments were adjusted to cover a range of densities from below and above these mean values; that is, one, two, or three limpets per experimental unit, equating to 16, 32, or 48 ind m^{-2}, respectively (see next section).
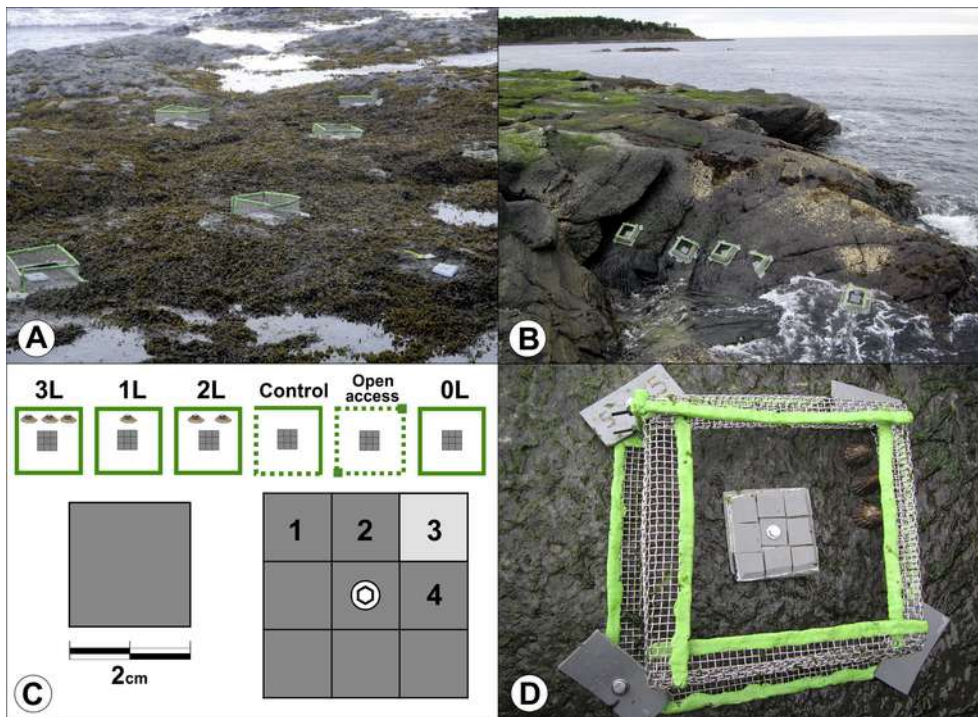
Fig. 1. Study sites, experimental design, and set-up. Examples of randomised blocks in Fildes Bay (A) and Strait of Magellan (B). Outline of treatment allocation of blocks in panel B and artificial settlement plate deployed in the middle of each experimental unit (C). We used Velcro™ to fix the sub-plates on the PVC plates; four sub-plates were sequentially sampled at uniform time intervals in this study. Close-up of a stainless-steel fence utilised in the three-limpet treatment (D). In panel C, the codes 0L, 1L, 2L, and 3L stand for zero-, one-, two-, and three-limpet treatments. Fences were 25 cm wide × 25 cm long × 6 cm high.
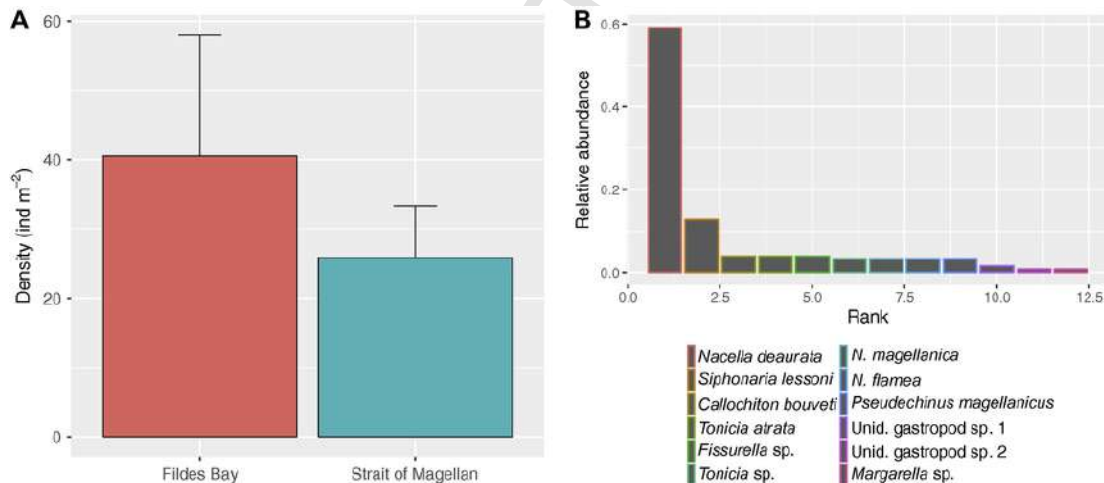

Fig. 2. Mean (Standard Error of the Mean) density of *Nacella* spp. on intertidal rocky shores in Fildes Bay (West Antarctic Peninsula) and Strait of Magellan (Chilean South Patagonia) (A). Mid-low intertidal grazer assemblages were dominated by *N. concinna* (Fildes Bay) and *N. deaurata* (Strait of Magellan). Rank-abundance distribution of grazer species in Strait of Magellan rocky intertidal (B).

2.2. Experimental design and set-up

A grazer exclusion-inclusion field experiment was arranged in a randomised block design in each site. The design included "treatment" as a fixed factor with six levels: zero, one, two, or three limpets, open access, and control; and "block" as a random factor with five levels, yielding a total of 30 experimental units for each site. Each block consisted of a haphazardly selected area of ca. 5 m² composed of six 25 × 25 cm plots (Fig. 1A and B). Blocks were restricted to flat and gently sloped areas lacking large crevices in order to reduce the variation related to local spatial heterogeneity. In each block, each of the six ex-

perimental treatments was randomly allocated to a given plot (see example in Fig. 1C). For each of the zero-, one-, two-, and three-limpet treatments, we used a 25 × 25 × 6 cm (width, length, and height) stainless-steel fence that was fixed to the rock with stainless screws to prevent grazers to enter or exit the plot (Fig. 1D). The open access treatment consisted of a plot that was delimited with screws to allow all grazers access. The control treatment consisted of an experimental plot that was fenced on two sides to allow grazers to access the plot, and at the same time, to generate the potential effects of fencing on confounding factors. All plots were scraped clean with a paint scraper and a steel brush mounted onto a drill to remove macroalgae and invertebrates. In the inclusions—i.e. one-, two-, and three-limpet treatments—

we used individuals of *N. concinna* with a mean shell length of 3.34 cm (range = 2.50–3.90 cm) in Fildes Bay and *N. deaurata* with mean shell length of 4.27 cm (4.00–4.53 cm) in Strait of Magellan.

In the centre of each plot, we fixed a 10×10 cm polyvinyl chloride (PVC) plate to the rock with a stainless screw. On top of this plate, we used Velcro™ to fix a set of four 4-cm² plates ("sub-plates" hereafter; see Fig. 1C). The surface of each sub-plate was roughened (grain size 60) to improve periphyton settlement. In addition, the edges of the plates and sub-plates were ground to form a ramp that allowed the grazers to access the plates. The same experimental device has been previously used to estimate significant effects of benthic grazers on Antarctic periphyton diversity and structure (Segovia-Rivera and Valdivia, 2016). Each sub-plate was replaced every seven and fourteen days in Fildes Bay and Strait of Magellan, respectively, until completing four sampling times. The difference in sampling intervals was adopted to account for the difference in colonising periods between these systems: in Fildes Bay settlement substratum is available during a short period of time due to ice cover in winter, whereas in Strait of Magellan settlement substratum may be available for a longer period.

2.3. Sampling and estimation of chl-*a* accrual

The sub-plates were wrapped with aluminium foil immediately after collection in the field and kept at −20 °C in the laboratory. The chl-*a* concentration of each sub-plate was determined by means of ethanol-based spectrophotometry. The attached algal material was gently removed from the sub-plate with a spatula and rinsed with ca. 0.22 μm of filtered seawater (the exact amount depended on the amount of periphyton). The sample was used to estimate the composition of algal groups with the PHYTO-PAM-II Phytoplankton Analyser (Heinz Walz GmbH, Germany; see next paragraph) and to determine the total concentration of chl-*a* according to the standard method from ethanol extracts (ISO, 1992). For the chl-*a* determination, 0.5 μm of the diluted sample was filtered on a 24 mm-diameter glass-fibre filter (GA-55, Advantec, Japan). The filter was submerged in 90% ethanol (v/v) (4–6 ml) in a test tube that was then closed to avoid evaporation and contact with air. The test tubes were wrapped with foil for dark conditions. For the extraction of chl-*a*, the test tubes were placed in a water bath (Memmert, Germany) at 75 °C for 5 min. The samples were allowed to cool down to room temperature and were then filtered with a sterile syringe membrane filter (0.45 μm MCE membrane, BIOFIL®) to clarify the sample. Absorbance of the extracts was read with an UV/Vis spectrophotometer (OPTIZEN POP, Mecasys, Korea) at 665 nm and at 750 nm for turbidity correction. The concentration of chl-*a* was calculated considering the area of the plate surface (4 cm²).

The PHYTO-PAM-II (Compact version) chlorophyll fluorometer (Heinz Walz GmbH, Germany) was used to estimate the relative composition of algal groups on the sub-plates. The excitation of an algal sample with five pulse-modulated measuring light wavelengths (440, 480, 540, 590, 625 nm) generates five chl-*a* fluorescence signals that allow separating four functional types on the basis of the transfer of excitation energy of their characteristic antenna pigments. Thus, the instrument is designed to discriminate between algae containing phycoerythrin (e.g. cryptophytes and rhodophytes), cyanobacteria, green algae, and chl *c*-containing algae (e.g. diatoms, dinoflagellates, and early stages of brown algae; hereafter referred to as "browns" for simplicity). Calibration (based on fluorescence reference excitation spectra) provided by the PhytoWin software was used. Additionally, we cross-calibrated the identification of these functional types by means of microscopy-aided cell identification. Thus, we believe that this cross-calibration, in addition to the company-provided calibration spectra, allowed us obtaining a reliable estimation of the functional types.

Because the analysis of frozen samples did not permit measurements of the parameters related to *in vivo* photosynthetic characteristics, only the chlorophyll content was measured. Considering the methodological challenges to reliable chlorophyll estimation with these techniques (Jakob et al., 2005), in the present study, chlorophyll data were used to estimate relative algal composition (%) instead of absolute concentrations.

Accrual of chl-*a* and relative abundances of green algae, browns, and cyanobacteria were estimated by calculating the integral of the area under the curve (AUC) of a graph between each dependent variable (y-axis) with time (x-axis). This transformation was done for each plot separately and allowed us to describe and compare among experimental groups the temporal patterns in chl-*a* concentration and community composition. For example, and since all plots started from a clean surface, larger AUCs indicated larger chl-*a* accrual.

To assess the effects of treatments on community composition, the AUCs of relative abundances of greens, browns, and cyanobacteria were combined in a principal component analysis (PCA). The first principal component (PC1) accounted for 86.4% of the variation in the dataset. Green algae, browns, and cyanobacteria displayed Pearson product-moment correlations of 0.33, −0.99, and −0.86, respectively, with PC1. The PC1 was then used for statistical analyses as proxy for community composition. For instance, a positive effect of grazing on PC1 translated into positive effects on the relative abundance of green algae, but negative effects on those of browns and cyanobacteria.

2.4. Statistical analysis

General and Generalised Linear Mixed Models (LMM and GLMM, respectively) were used to test our predictions separately on chl-*a* accrual and PC1. The Antarctic and sub-Antarctic datasets were also analysed separately. Grazer treatment and block were included in the models as fixed and random factors, respectively. Model parameters were estimated through Maximum Likelihood. The degrees of freedom of the fixed effect terms were estimated through the Kenward-Roger approximation, and the hypothesis test was done on the basis of conditional t-tests (Pinheiro and Bates, 2004). Random effects were assessed as Best Linear Unbiased Prediction (BLUP) estimations for each block. Standardised residual-vs-fitted values and quantile-quantile plots were used to check homogeneity of variances. A visual inspection of residuals showed the most suitable model for all variables was a LMM (Gaussian distribution of errors and identity link), excepting chl-*a* accrual in Strait of Magellan, which was analysed with a GLMM with Gamma distribution of errors and log link. Due to broad heterogeneity in the distributions of residuals, adjusted means of chl-*a* for both sites were weighted with the respective standard deviations. The "treatment" contrast—in which a reference group (zero-limpet treatment in this case) is compared against all other groups—was used to estimate effect coefficients. Thus, significant effects of inclusion treatments in Fildes Bay would provide evidence supporting Prediction 1, and significant effects of open access and control treatments in Strait of Magellan would support Prediction 2.

Finally, per capita interaction strength was estimated separately for each density (inclusion) treatment and site. We used the Berlow et al. (1999) Dynamic Index as:

$$DI_i = \frac{\ln\left(\frac{N_i}{D}\right)}{Y_i t}$$

where DI_i is the Dynamic Index for the *i*-th grazer-inclusion treatment, N_i is the mean chl-*a* accrual of that treatment, D is the mean chl-*a* accrual of the zero-limpet (reference) group, Y_i is the number of grazers in the *i*-th inclusion treatment, and *t* is the time in days. Boot-

strapped DI_i and bias-corrected confidence intervals were estimated after 1000 resamples (Davison and Hinkley, 1997).

All analyses were done in R programming environment version 3.3.3 ("Another Canoe"). The *MESS*, *lme4*, and *boot* packages were used for computing AUC, (G)LMMs, and bootstrapped DI_i, respectively (Bates et al., 2015; Canty and Ripley, 2016; Ekstrøm, 2016). The *ggplot2*, *sjPlot*, *plyr*, *cowplot*, *grid*, and *gridExtra* were used for graphics (Wickham, 2009, 2011; Auguie, 2016; Wilke, 2016; Lüdecke, 2017).

3. Results

Both sites harboured different densities of grazers along mid-low intertidal fringes. The density of *N. concinna* in Fildes Bay was, on average, 57% larger than the density of *Nacella* spp. in Strait of Magellan (Fig. 2A). Twelve taxa composed the grazer assemblage in Strait of Magellan, which was numerically dominated by *N. deaurata* (Fig. 2B). Daily maximum wave velocities in the study sites were comparable to those of wave-sheltered southern Pacific shores (e.g. Castilla et al., 1998), with values ranging between 1.8 and 4.2 m s^{-1} (n = 10) in Fildes Bay, and between 3.6 and 4.3 m s^{-1} (n = 5) in Strait of Magellan.

Mean (standard error of the mean) chl-*a* concentrations on artificial settlement substrata were 1.04 (0.06) µg m^{-2} and 9.40 (0.78) µg m^{-2} in Fildes Bay and Strait of Magellan, respectively. Periphyton communities reached maximum chl-*a* concentrations of 3.7 µg m^{-2} after 28 days of colonisation in Fildes Bay and 54.1 µg m^{-2} after 47 days in

Strait of Magellan. Browns, followed by cyanobacteria and then green algae, numerically dominated the periphyton assemblages in the Fildes Bay experiment. A similar pattern was observed in Strait of Magellan, with the exception that green algae made no contribution to the assemblage. In both regions, we observed increasing values of chl-*a* concentration over time (Fig. 3A and B). In addition, the communities showed trajectories from the dominance of greens (Fildes Bay) or bare substratum (Strait of Magellan) toward a mixture of browns and cyanobacteria (both sites), evidenced by decreasing PC1 scores over time (Fig. 3C and D).

The experimental treatments significantly affected chl-*a* accrual and composition across sites (Fig. 4). In Fildes Bay, all treatments, excepting the open access treatment, significantly reduced chl-*a* accrual (Fig. 4A). In Strait of Magellan, on the other hand, only the open access and control treatments showed statistically significant negative effects on chl-*a* accrual (Fig. 4B), indicating an effect of the entire, species-rich grazer assemblage on this ecosystem. Chl-*a* accrual displayed small differences between open access and control treatments. The exception was the relatively smaller effect of the open access treatment in Fildes Bay. Yet, a large overlap between the confidence intervals of control and open treatments was observed, suggesting a small artefact effect of fences on chl-*a* accrual.

Community composition followed a similar pattern to that described above for chl-*a* accrual (Fig. 4C and D). In Fildes Bay, positive effects of grazer treatments on the relative abundance of green algae
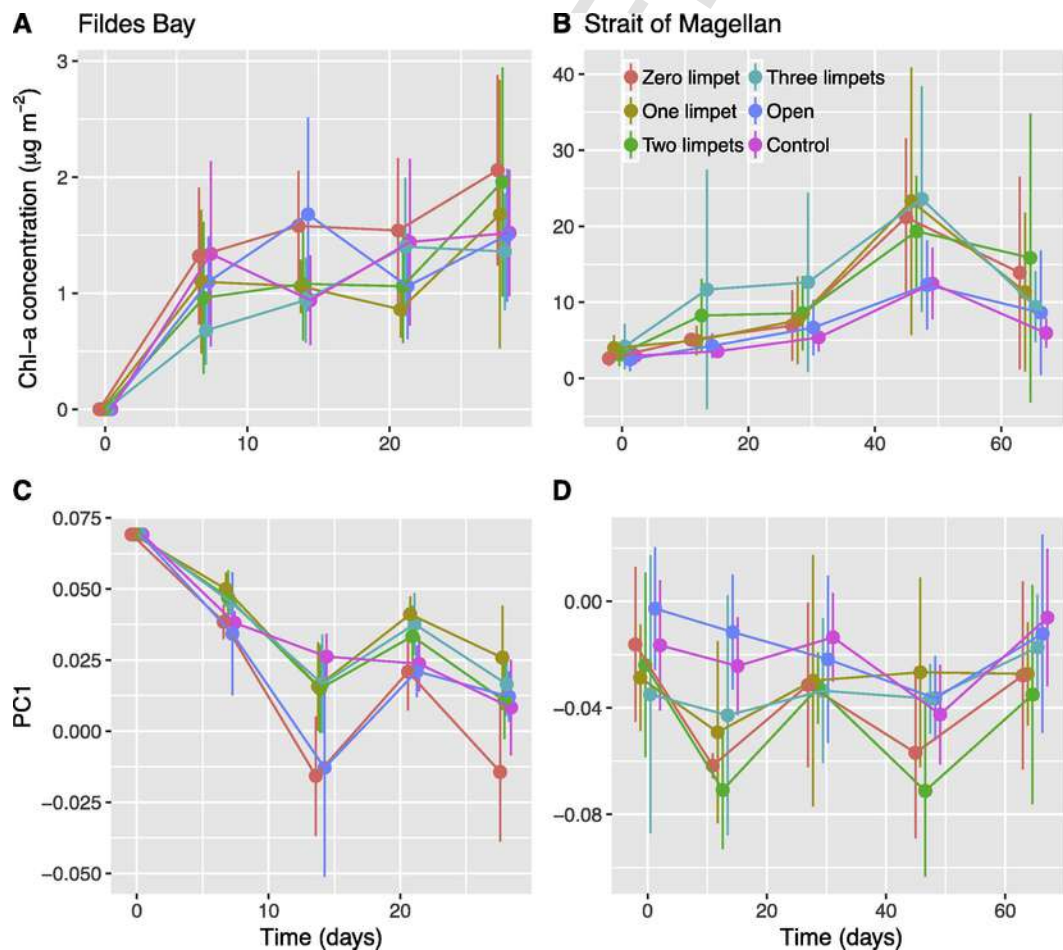

Fig. 3. Temporal patterns of chl-*a* concentration (A and B) and composition (C and D) of periphyton communities growing on artificial settlement panels in Fildes Bay (A and C) and Strait of Magellan (B and D). Panels C and D show the first axis of a principal component analysis (PC1, 86.4%) of microalgae, cyanobacteria, and browns. Greens and bare substratum were positively correlated with PC1; cyanobacteria and browns were negatively correlated with PC1. Values are given as mean±standard deviation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
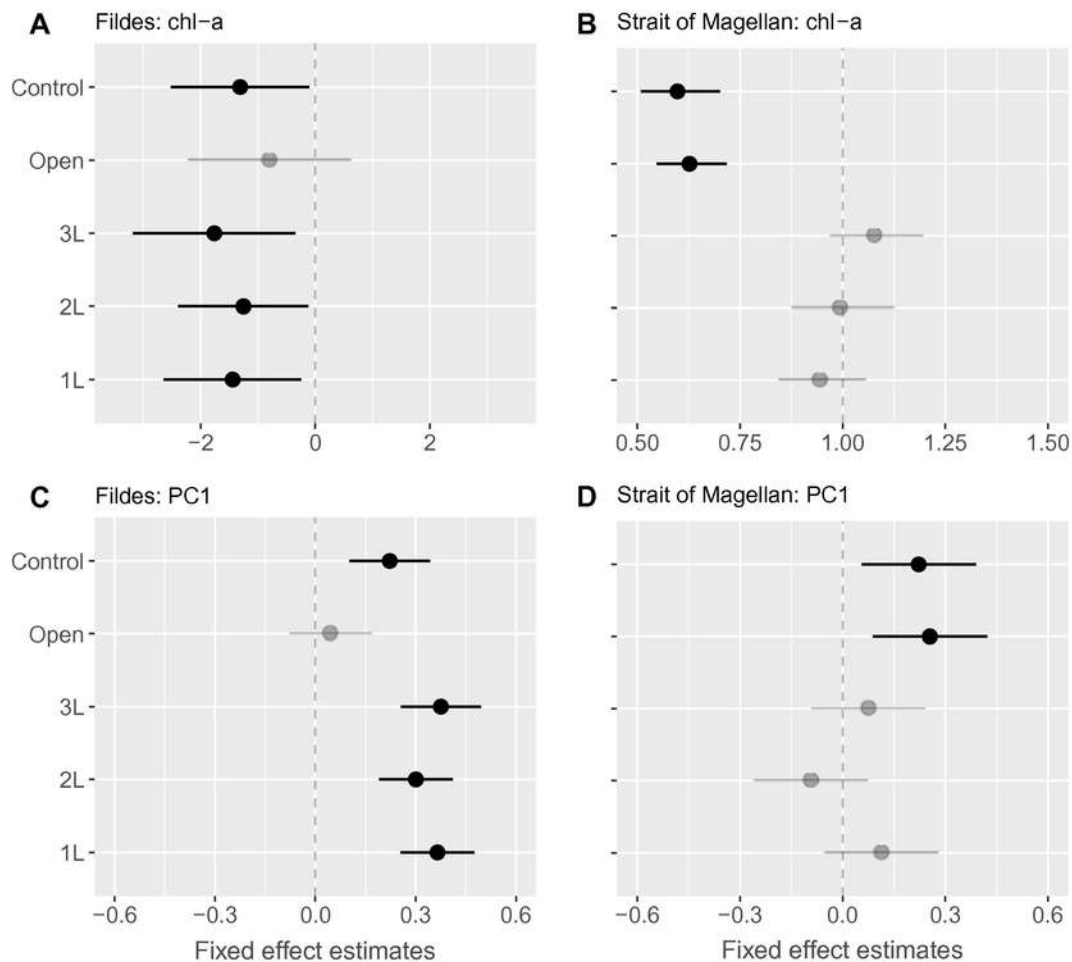
Fig. 4. Estimated fixed effects and confidence intervals of grazer treatments on chl-*a* accrual (A and B) and composition (C and D) of periphyton communities from Fildes Bay (A and C) and Strait of Magellan (B and D). Faded symbols indicate statistically non-significant effects. All effects were estimated as differences from the reference treatment of zero limpets. Treatment codes are as in Fig. 1. Effects in panel B are in log scale, so that 1 indicates no effect. In panels C and D, greens and bare substratum correlated positively with PC1, and cyanobacteria and browns correlated negatively with PC1.

and negative effects on those of cyanobacteria and browns were detected (i.e. positive trends of PC1 in Fig. 4C). PC1 exhibited a comparatively small systematic change in the open access treatment in relation to the reference treatment in Fildes Bay, with an overlap of half CI with the controls (Fig. 4C). In Strait of Magellan, PC1 followed the same pattern of chl-*a* accrual in the open access and control plots, with significant positive effects on bare substratum and negative effects on the relative abundance of browns and cyanobacteria (Fig. 4D).

Random effects were similar across sites, with two blocks having significant (positive or negative) effects on chl-*a* accrual and PC1 quantified in the reference groups (intercepts in Fig. 5). A different pattern of PC1 was observed in Strait of Magellan, where the five blocks significantly affected the estimations of taxonomic-group relative abundances (Fig. 5D). Finally, the patterns of per capita interaction strength (DI_i) concurred with those of density-dependent and main grazing effects on chl-*a* accrual (Fig. 6). In Fildes Bay, per capita interaction strength tended to decrease (i.e. approached zero) with increasing grazer densities in the inclusion plots (Fig. 6A). In Strait of Magellan, per capita interaction strength was statistically non-significant (Fig. 6B), according to the lack of effects observed for chl-*a* accrual.

4. Discussion

The results of our study suggest that grazer assemblages from Antarctic and sub-Antarctic rocky shores exert different forms of top-

down controls, but similar effects, on the functioning of benthic communities: whereas in Fildes Bay the experimental densities of *N. concinna* led to significant and similar reductions in chl-*a* accrual (a proxy for productivity), in Strait of Magellan the open access and control treatments, which allowed a species-rich grazer assemblage to access the experimental plots, showed significantly lower chl-*a* accrual than the reference treatments. Thus, while the presence of single grazer species was relevant for local productivity in Fildes Bay, the entire assemblage of grazers largely defined productivity in Strait of Magellan. In both regions, however, grazers significantly reduced the abundances of browns and cyanobacteria, and in both experiments, grazers showed similar amounts of local spatial variation in productivity. In the following, we discuss the role of intraspecific competition and resource partitioning as likely mechanisms underpinning deterministic effects of grazers on community composition and productivity of Antarctic and sub-Antarctic coastal communities.

4.1. Potential mechanisms explaining the consumptive effects of grazers on periphyton communities

Intraspecific competition and resource partitioning could explain the patterns of consumption described herein. In the Antarctic sites, the results did not support our Prediction 1 of density-dependent grazing effects on productivity. Despite the significant effects of grazers, the lack of density-dependent effects can be explained by the decrease in
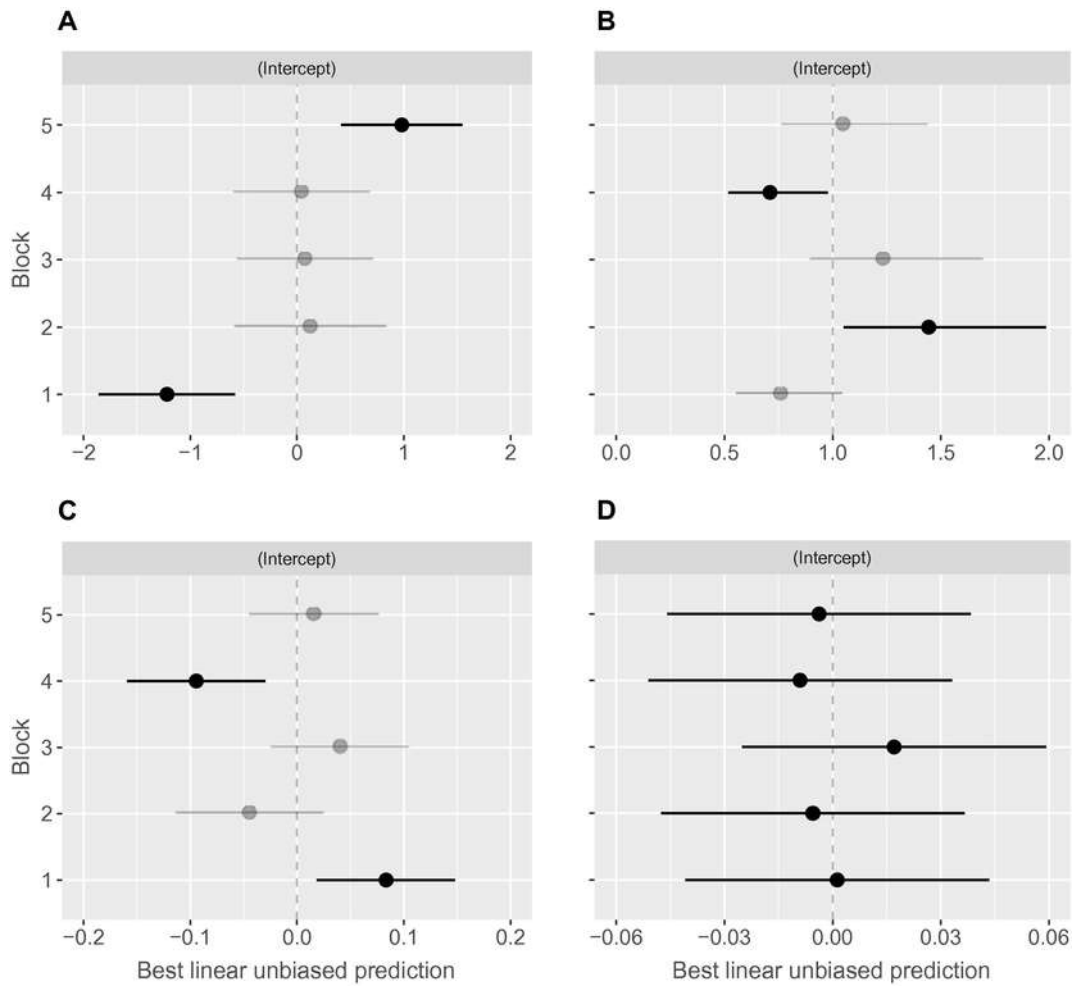
Fig. 5. Estimated random effects and confidence intervals of grazer treatments on chl-*a* accrual (A and B) and composition (C and D) of periphyton communities from Fildes Bay (A and C) and Strait of Magellan (B and D). Faded symbols indicate statistically non-significant effects. In Panels C and D, greens and bare substratum correlated positively with PC1, and cyanobacteria and browns correlated negatively with PC1.Treatment codes and effect contrasts are as in Figs. 1 and 4, respectively.
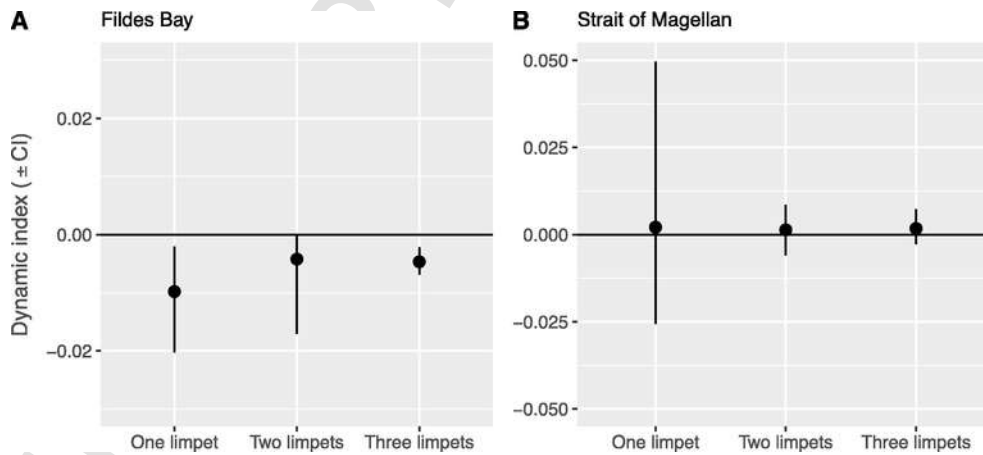

Fig. 6. Per capita interaction strength (Dynamic Index) for each grazer inclusion treatment and experiment replicated in Fildes Bay (A) and Strait of Magellan (B). Mean bootstrapped Dynamic Index and bias-corrected confidence intervals (CI) were estimated from chl-*a* accrual values after 1000 resamples.

the per capita interaction strength as densities were experimentally increased. Increased intraspecific competition likely reduced grazer's per capita consumption, which might have compensated for the overall effects on chl-*a* accrual of experimental populations. Although external trophic subsidies via detritus material can increase grazers' carrying capacity (Notman et al., 2016), the comparatively low chl-*a* concentra-

tions observed during the experiment suggest that trophic resources were highly limited in Fildes Bay, which might have enhanced the strength of intraspecific competition and, thus, negative density-dependence (Vellend, 2016). Theoretical work supports these explanations (e.g. Chesson, 2000; Berryman, 2003), and intraspecific competition is a well-established mechanism of population control in limpets (Creese

and Underwood, 1982; Boaventura et al., 2003). For instance, negative density-dependence has been suggested to allow for the coexistence between *Patella vulgata* and *P. depressa* populations on Portuguese shores (Boaventura et al., 2002). Thus, it can be suggested that, for this single-species assemblage of macrograzers, density-dependent competition might have acted as a "stabilising" mechanism that maintained a steady-state level of resource consumption.

At the sub-Antarctic site, on the other hand, only the treatments exposed to grazers from several species and at natural densities exhibited statistically significant effects on benthic productivity, supporting our Prediction 2 of herbivore assemblage effects. In addition, the single-species treatments showed no significant effect on chl-*a* and composition, neither in terms of collective or per capita levels. These results further agreed with previous work demonstrating that species-rich communities perform better than species-poor assemblages in both the laboratory and nature (Duffy et al., 2017). Resource complementarity has been suggested as a key mechanism sustaining diversity effects of grazers (e.g. Creese and Underwood, 1982; O'Connor and Crowe, 2005; Duffy et al., 2015) and other functional types (e.g. Hooper et al., 2005; Griffin et al., 2008). In the Strait of Magellan, the *N. deaurata* diet is mostly composed of brown and red algae, whereas that of *N. magellanica* consists of green algae, foraminifera, and micro-invertebrates (Andrade and Brey, 2014). These recent observations suggest a certain level of resource complementarity, at least between these two abundant species. However, resource complementarity can be absent even among grazers with different feeding mechanisms (Hawkins et al., 1989). Alternatively, "identity effects"—i.e. those effects derived from species with extreme functional traits—can also lead to more efficient communities, as reported for temperate intertidal grazers (Aguilera et al., 2013) and marine suspension feeders (Valdivia et al., 2009) among other communities (e.g. Hector et al., 1999). Indeed, resource complementarity and identity effects jointly contribute to ecosystem functioning (Hector et al., 1999). In either case, our results suggest that different biotic mechanisms (i.e. density-dependent competition and "diversity" effect) control the benthic productivity across the analysed regions.

Other environmental factors should, however, be further considered. For example, mesograzers, such as amphipods and small littorinid snails can be very abundant and account for significant changes in algal biomass in Antarctic shores (Zamzow et al., 2010; Amsler et al., 2014). In addition to grazing, abiotic factors such as UV radiation negatively affect algal succession (Zacher et al., 2007). When both factors act simultaneously, grazing can be affected due to UV-induced changes in the chemical composition of algae (Lotze et al., 2002; Obermuller et al., 2003), which can explain the nil effects of the single-species inclusion treatments on periphyton communities observed in the Strait of Magellan. Also, stronger seasonality with shorter growth seasons at higher latitudes, like in the Antarctic sites, can lead to harsh competition and negative density dependence among consumers (Thompson et al., 2004). Seasonality can fuel a significant latitudinal variation in herbivory, even within the same species (Jenkins et al., 2001). Moreover, differences in chemical defences, growth rates (Campana et al., 2009), and responses to changes in wave exposure (Thompson et al., 2005) within periphyton communities could also lead to idiosyncratic responses to grazing pressure. Manipulative and observational work will be needed to disentangle the suite of mechanisms by which the assemblage of grazers modulates the functioning of these coastal communities.

4.2. Similar effects of herbivores on Antarctic and sub-Antarctic periphyton communities

Despite the potentially different mechanisms discussed above, herbivores had similar negative effects on brown algae, diatoms, and cyanobacteria. Although we were unable to distinguish taxa to a finer resolution level, it is likely that the brown spectrum corresponded to late-successional groups in the periphyton assemblage. For instance, propagules of the brown macroalga *Adenocystis utricularis* can colonise the substratum after ca. 30 days of exposure to settlement in Fildes Bay (Segovia-Rivera and Valdivia, 2016). Moreover, the general trend of both communities toward assemblages dominated by browns and cyanobacteria further hints at a successional pathway. Thus, in both regions, grazers had a "delaying" effect on the succession and productivity rate of benthic communities (Hawkins, 1981; Underwood, 1984; Christofoletti et al., 2011), resembling the effect of some abiotic factors on algal succession (Campana et al., 2009).

The general negative grazer effect on cyanobacteria observed in this study contrasts with previous work showing a low palatability of this group owing either the presence of noxious compounds or low nutritional value (Hill and Hawkins, 1991; Liess and Hillebrand, 2004). However, and despite selectivity is rare among benthic grazers (Liess and Hillebrand, 2004), they can have very idiosyncratic and species-specific effects on cyanobacteria—sometimes negative, sometimes positive—and even within the same grazer assemblage (Aguilera et al., 2013). In some cases, top-down effect of grazing on cyanobacterial mats can be more important than bottom-up controls (e.g. grazing fish vs. nutrient enrichment; Flecker et al., 2002). Moreover, the net effect of increased grazing on cyanobacteria has been described as a shift from assemblages dominated by small- (e.g. cyanobacteria) to large-sized algae (e.g. diatoms and early phases of macroalgae; Tuchman and Stevenson, 1991; Caramujo et al., 2005). The common pattern of consumption on cyanobacteria raises the question of why grazer species from contrasting and seemingly disconnected habitats display similar adaptations to feed on unpalatable or nutrient-poor resources. Further research merging ecological (e.g. feeding preferences) and phylogeographic (e.g. genetic diversity) perspectives might open an avenue to improve our understanding of the natural communities in these austral ecosystems.

5. Conclusion

In summary, our results suggest that grazer assemblages can have similar controlling effects on productivity and structure across Antarctic and sub-Antarctic benthic communities. The mechanisms underpinning these effects, interestingly, seem to differ functionally between both regions, with negative density-dependence and resource complementarity (and probably identity effects) likely relevant in the former and latter ecosystem, respectively. More research is needed to integrate the role of biotic interactions, as a selective force, with those of dispersal, neutral drift, and speciation into a comprehensive model of community dynamics for the region. This aim gains special relevance in the current scenario of large- and fine-scale anthropogenic impacts on austral ecosystems.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.pocean.2018.01.008.

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