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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

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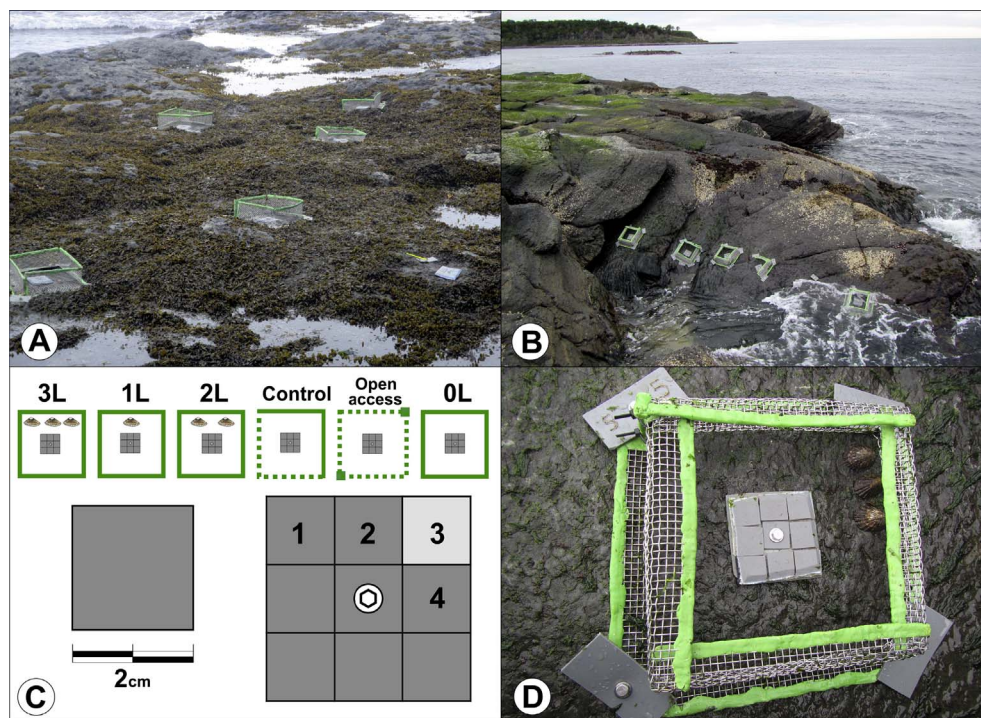


Fig. 1. Study sites, experimental design, and set-up. Examples of randomised blocks in Fildes Bay (A) and Strait of Magellan (B). Outline of treatment allocation of blocks in panel B and artificial settlement plate deployed in the middle of each experimental unit (C). We used Velcro™ to fix the sub-plates 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.

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; Oróstica 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).

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