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Independent effects of grazing and tide pool habitats on the early colonisation of an intertidal community on western Antarctic Peninsula

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Abstract

Background: Prevailing environmental conditions can modulate the structuring role of biotic interactions. In intertidal habitats, less stressful environmental conditions and/or higher grazer densities may allow grazing effects to be stronger in tide pools than on emergent rocks. To test this hypothesis, we conducted a manipulative experiment on an intertidal rocky shore in Fildes Bay, King George Island, in which the effect of the dominant grazer *Nacella polaris* on the structure of benthic periphyton communities was compared between emergent rock and tide pool habitats. Also, we determined the spatial variation in density, weight, and maximum length of individuals of *N. polaris* in both habitats.

Results: The density of *N. polaris* was significantly larger in tide pools than on emergent rocks. Contrarily, we observed no significant differences in morphological parameters of *N. polaris* between both habitats or between intertidal elevations. In the manipulative study, we observed a greater taxonomic richness, diversity, and abundance of periphyton on emergent rocks than in tide pools. These variables also showed, in comparison with control areas, significantly higher values in experimental areas where herbivores were excluded by means of stainless-steel fences. The effects of habitat and grazer exclusion treatments were independent of each other, as no statistically significant interaction between both factors was observed.

Conclusions: Our results showed significant, but independent, effects of tide pool habitats and grazing on the early colonisation of these assemblages. Albeit the grazing effects of other herbivores such as amphipods and small gastropods cannot be ruled out, we suggest that traits of *N. polaris,* such as high mobility and circadian activity, allow this species to exert a firm control on the intertidal Antarctic assemblages across local environmental conditions.

Keywords: Antarctica, Environmental stress model, Grazing, Herbivory, Intertidal, *Nacella polaris*, Periphyton

Background

The interplay between biotic interactions and environmental factors is gaining higher relevance in basic and applied ecology, due to the rapid environmental changes that can be observed worldwide (e.g. [1]). The Antarctic ecosystems are showing the world's fastest responses to climate change, but the study of biotic interactions in these habitats has lagged behind other ecosystems [2]. The Antarctic intertidal habitats are constantly exposed to disturbances, such as ice scour, and wide fluctuations in temperature [3, 4]. In general, the availability of microhabitats with more benign environmental conditions, like shelters, might offer an opportunity to a number of species to establish in harsh environments, as shown in temperate regions [5, 6]. Accordingly, biotic interactions like competition, predation, and herbivory can be

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intensified in these microhabitats [7]. The analysis of the effects of biotic interactions on community structure across environmental conditions in Antarctica can be helpful to inform predictive models on how these fragile ecosystems will change in the near future.

Herbivory is defined as the effects that animals cause on populations and communities of plants, and is considered one of the most important ecological processes in marine and terrestrial environments [8–12]. In marine systems, herbivores can determine the spatial and temporal distribution of algae in both intertidal and subtidal habitats, as they can also affect the succession of entire benthic communities [8]. Theoretical models predict that the effects of herbivory and other interactions heavily depend on prevailing environmental stress levels, and it is expected that consumer activity of predators and herbivores should decrease when they are subjected to high environmental stress [7, 13]. In intertidal systems, which are generally characterised by prevailing harsh conditions for marine organisms due to exposure to atmospheric conditions, habitat heterogeneity in terms of crevices and tide pools provides ameliorated environmental conditions and shelter for a suite of organisms [14]. Accordingly, intertidal herbivores have been shown to have significant effects on the structure of tide pool communities, especially by controlling the abundance of fast-growing, nutrient-limited macroalgae (e.g. [14–16]).

Along intertidal and shallow subtidal Antarctic shores, the gastropod *Nacella polaris* (hereafter referred to as *Nacella*) is likely the most abundant grazer in terms of biomass on the Antarctic Peninsula and adjacent islands [17]. This herbivore is adapted to conditions of low temperatures and even freezing to which is exposed during winter [18]. In the Antarctic coast, the populations of *Nacella* are divided into a fraction that remains submerged in the subtidal habitat and another that migrates during summer months to the intertidal habitat [19, 20]. The seasonal migration of *Nacella* matches the re-colonisation of the intertidal zone by algal assemblages after ice retreat [21]. Therefore, it is likely that the migration activity of *Nacella* species is related with a higher resource availability and lower exploitation competition in the intertidal zone during the austral summer.

In Antarctic shores and elsewhere, the re-colonisation of the intertidal zone begins with the arrival of benthic microalgae (e.g. diatoms and cyanophytes) and macroalgal spores; these early colonists are collectively called periphyton [22]. Periphyton is one of the main sources of food for benthic herbivores and in many cases is critical for the establishment of benthic macroalgae [23]. Grazing often has negative effects on the biomass accrual and productivity of this group [24]. In Antarctic coast, intertidal *Nacella* feeds on periphyton that is mainly comprised by microalgae and small filamentous algae [17]. Although herbivores play an important role in determining algal composition and biomass in intertidal pools elsewhere [11, 14, 25], there has been little attention to the grazing activity on different intertidal habitats on western Antarctic Peninsula (but see [26]).

In this work, we test the hypothesis that less stressful environmental conditions and/or higher grazer densities may result in that grazing effects are intensified in tide pools, which has significant consequences for the re-colonisation of benthic communities. From this hypothesis, we deduced the predictions that (1) tide pools should harbour higher densities and larger individuals of the herbivore *Nacella*, and (2) that the grazing effect of *Nacella* on the dynamic of periphyton communities is stronger in tide pools than on emergent rocks. The study was conducted on an intertidal rocky shore at Fildes Bay, King George Island, Antarctica. The information of biotic interactions across environmental conditions could be helpful to understand the processes structuring the natural communities in dynamic environments such as the Antarctic intertidal habitat.

Methods
Study sites and model species
The study was conducted on an intertidal rocky shore located northeast of Fildes Bay, King George Island (62.18 S, 58.88 W; Fig. 1), and took place between December 2013 and February 2014; in situ observations and samplings were conducted during diurnal low-tide periods. Tide pools in the study site are of ca. eight meters long, showing temperatures and salinity values ranging between 9.3 and 11.2 ° C and 34 and 35 psu, respectively.

The study area is characterised by red macroalgae such as *Iridaea cordata* and crustose algae, which are found
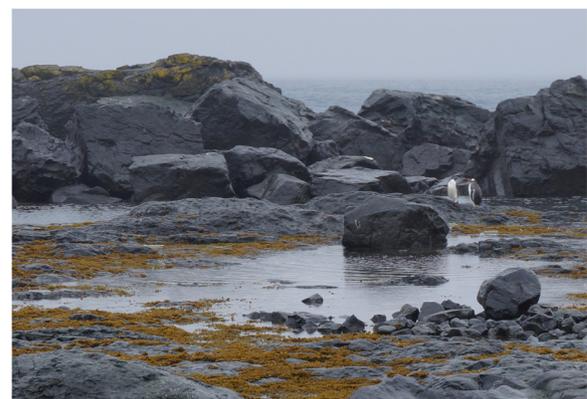
Fig. 1 Study site in NE Fildes Bay, King George Island, Antarctica. The photo was taken during low tide. The dominant macroalgal species around the tide pool in the centre of the picture is *Adenocystis utricularis* (brown alga). Photo credit: Lilian Villanueva

mainly in tide pools; *Adenocystis utricularis*, brown seaweed that is mainly distributed on emergent rock and mid-high intertidal elevations; and the filamentous algae *Urospora penicilliformis* and *Ulothrix* sp., which occur in higher abundance in emergent rock habitats (Additional file 1: Figure S1). The assemblage of invertebrate species is dominated by *Nacella*, followed by the small-sized littorinid snails *Laevilittorina antarctica* and *Laevilacunaria umbilicata*.

The study consisted of two parts, an observational study and a manipulative experiment. In the observational study we determined the spatial patterns of occurrence and body size of *Nacella* as functions of shelter availability (i.e. emergent rock vs. tide pools) and intertidal elevations (i.e. mid- and low intertidal zones). In the manipulative experiment we tested the interactive effect of grazer removal and tide pool habitats on the dynamics of periphyton communities.

Tidal elevation was determined by using the green alga *Ulothrix* sp. and the red alga *Pyropia endiviifolia*, as indicators of the upper limit of the intertidal zone [27]. The low limit of the intertidal zone was defined according to chart datum. Once the upper boundary was determined on the shore, we divided the intertidal range in three zones of equal vertical extent (high, mid-, and low zones). Samplings of *Nacella* were restricted to the mid- and low intertidal zones, because of the lack of individuals at higher elevations.

Observational study

For each intertidal height (i.e. mid- and low intertidal zones), ten individuals were collected from haphazardly selected tidal pools and ten from emerging rocks. The organisms were labelled and transported to the laboratory at the Base Antártica Julio Escudero (INACH), where wet weight (0.001 g precision) and maximum shell length (0.01 mm precision) were determined.

Density of *Nacella* was quantified in a 12-m alongshore transect placed in the mid-intertidal zone. The number of *Nacella* individuals was quantified in 0.25×0.25 m quadrats placed every 0.5 m along the transect. Also, the percentage cover of tide pools in each quadrat was estimated.

Manipulative experiment
Experimental design and setup

We used a randomized block design to distribute a 2×3 factorial experiment with "habitat" (two levels: tide pool or emergent rock) and "treatment" (three levels: total exclusion, control, and procedural control) as fixed and crossed factors. In the study site, we haphazardly located four blocks. In each block, we haphazardly selected a tide pool and an area of emergent rock (ca. 1 m²). In each tide pool and emergent rock area, we haphazardly

located three areas of 0.20×0.20 m. The small size of the experimental area (i.e. experimental unit) was chosen to minimise the impact on the natural assemblages. Each area was randomly assigned to one of the following three treatments: (1) total exclusion (TE), in which a stainless-steel fence of $20 \times 20 \times 8$ cm (width, length, and height) was fixed to the rock with stainless screws to exclude grazers; (2) control (C), in which the area was delimited with screws in order to allow the access to grazers; and (3) procedural control (PC), in which the experimental area was fenced on two sides in order to allow grazers to access the plot, and at the same time, to generate the potential effects of fencing on confounding factors (Fig. 2). Before installing fences, each plot was scraped with a paint scraper and a steel brush in order to remove macroalgae and mobile invertebrates. Crustose algae were not removed due to logistical constraints.

In the centre of each treatment, we fixed to the substrate with a stainless screw a 10×10 cm polyvinyl chloride (PVC) plate. On top of this plate, we used Velcro (TM) to fix a set of four small plates of equal size ("sub-plates" hereafter). The surface of each sub-plate was roughened (grain size 60) in order to benefit the settlement of periphyton. In addition, the edges of plates and sub-plates were grinded in order to form a ramp that allowed the grazers to access the plates. Each sub-plate was replaced every ten days, after completing four sampling times.

Sampling

In the laboratory at Base Antártica Julio Escudero, settled periphyton was extracted from each sub-plate by means of 4 % formalin and a sterilised tooth brush [23]. The sub-plate was hydrated with 0.5 ml of 4 % formalin, and then the periphyton was extracted by gently scraping with horizontal, vertical, and circular movements the surface of the sub-plate with the brush. This procedure was repeated three times for each sub-plate. A dropper was used to drip onto the plate additional 0.5 ml of 4 % formalin, and then to transfer the material to a 10 ml flask. The samples were subsequently transferred to the Laboratorio de Ecología Litoral, UACH (Valdivia), for further processing.

Periphyton samples (10 μl) were poured on a Neubauer chamber and observed under an epifluoresence microscope (60x). Periphyton taxa were identified to the lowest level possible (genus) on the basis of morphological characteristics. The identification was made using taxonomic descriptions [28–32]. We used species (genus)-accumulation curves to determine the minimum number of sub-samples for each sub-plate—the number of taxa stabilised at four sub-samples. Each periphyton taxon was quantified in one sector of the Neubauer camera and then algal concentration was calculated as:
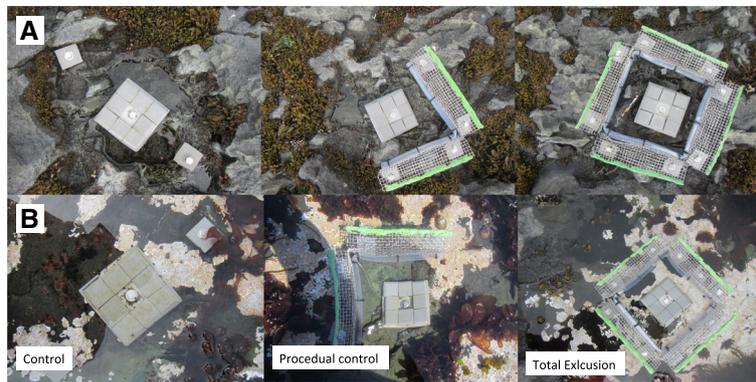
Fig. 2 Experimental setup. Control, procedural control, and herbivore total exclusion treatments were deployed in tide pools (panels **a**) and on emergent rocks (panels **b**)

Algal concentration (cells ml^{-1}) = (Total cells counted in sector × 10,000)/number of sectors. Taxon richness (i.e. the number of genus in each experimental unit) and diversity were then calculated from the genus abundance data. Diversity was expressed as the Shannon' diversity index H, which combines taxon richness the relative abundance of taxonomic identities. A higher value of the index indicates a greater taxonomic diversity.

Statistical analyses

Nacella' body weights (g) and lengths (cm) were analysed separately using two-way Analyses of Variance (ANOVA) in the R environment v. 3.1.2 [33]. The analysis included intertidal zone (either mid- or low zone) and habitat (either emergent rock or tide pool) as crossed and fixed factors. The assumptions of homogeneity of variances were tested through Levene's tests. In addition, we assessed the correlation between *Nacella*' density and the percentage cover of tide pools by means of a Cross Correlation Function (CCF) analysis in R. In this way, we were able to analyse the spatial structure of *Nacella* as a function of the availability of tide pools.

For periphyton taxonomic richness and diversity, we separately calculated the area under the curve (AUC) of the relationship between each dependent variable (y-axis) with time (x-axis). In this way, we integrated each dependent variable over time, avoiding the problems of autocorrelation in the repeated measures. In addition, this transformation allowed us to describe and compare among experimental groups the temporal patterns in species colonisation. For example, and since all plots started from a clean surface, larger AUCs indicated faster re-colonisation patterns. Then, we used a mixed-model ANOVA to determine the separate and interactive effects of treatments (fixed factor with three levels: TE, C, or PC), habitat (fixed factor; either emergent rock or tide pool), and block (random factor) on the temporal trajectories of taxon richness and diversity.

A significant interaction between grazer treatment and habitat would be seen as evidence supporting our prediction that the effects of herbivory are stronger in tide pools than emergent rocks. A Student-Newman-Keuls (SNK) post hoc analysis was used for the treatment factor in order to contrast the exclusion (TE) and control (C) treatments, as well as to determine whether there was an artefact effect of fences (i.e. C vs. PC treatments).
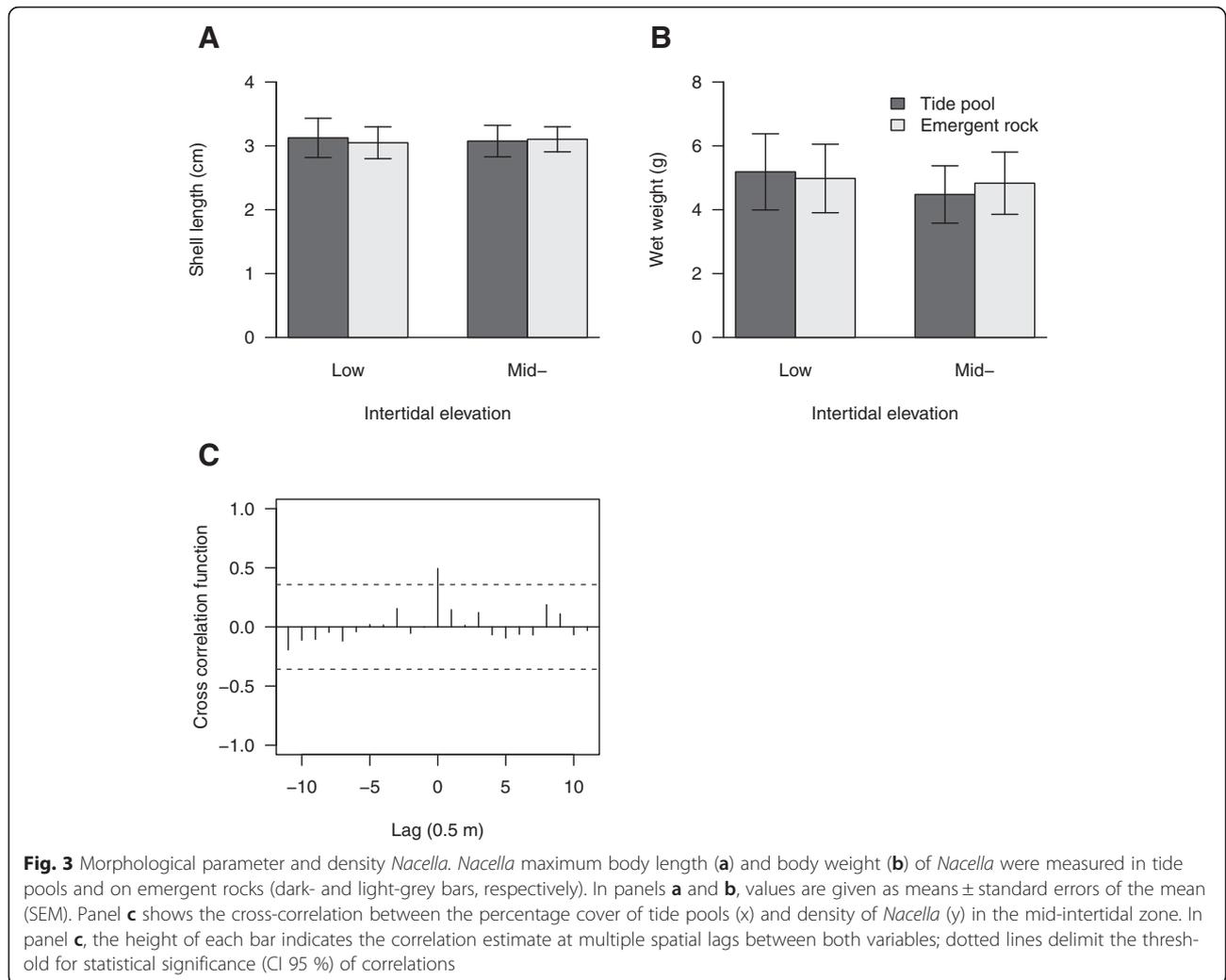
A non-multidimensional metric scaling (MDS), based on Bray-Curtis dissimilarities, was used to display multivariate patterns of abundances of periphyton. In addition, we tested the effects of treatment, habitat, and block on the multivariate structure of periphyton by means of permutational analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarities calculated from the AUC matrix. Finally, an analysis of percentage similarity (SIMPER) for treatment and habitat was performed to determine the relative contribution of taxa to the differences between groups. Multivariate analyses were performed in PRIMER with PERMANOVA software v. 6 [34,35]. All null-hypothesis significance tests were performed with α = 0.05.

Results

Observational study

Maximum shell length and wet weight of *Nacella* ranged from 1.5 to 4.6 cm and 0.5 to 12.8 g, respectively. Body lengths (Fig. 3a) and weights (Fig. 3b) showed similar values between habitats (i.e. tide pools or emergent rocks) and intertidal zones (i.e. low or mid-intertidal zones). Accordingly, the 2-way ANOVA showed no significant effect of habitat and intertidal zone on both body-size variables ($P > 0.05$).

On the other hand, *Nacella* densities ranged from 0 to 32 ind. m^{-2} and 0 to 176 ind. m^{-2} on emergent rocks and in tide pools, respectively. Mean density values were ca. 2 ind. m^{-2} and ca. 42 ind. m^{-2} on emergent rocks and in tide pools, respectively. The CCF analysis showed a

Fig. 3 Morphological parameter and density *Nacella*. *Nacella* maximum body length (**a**) and body weight (**b**) of *Nacella* were measured in tide pools and on emergent rocks (dark- and light-grey bars, respectively). In panels **a** and **b**, values are given as means ± standard errors of the mean (SEM). Panel **c** shows the cross-correlation between the percentage cover of tide pools (x) and density of *Nacella* (y) in the mid-intertidal zone. In panel **c**, the height of each bar indicates the correlation estimate at multiple spatial lags between both variables; dotted lines delimit the threshold for statistical significance (CI 95 %) of correlations

significant and positive correlation between the percentage of cover of tide pools and *Nacella*' density at lag 0, indicating a strong "instantaneous" correlation between both variables (Fig. 3c); that is, the density of *Nacella* was higher in areas with larger tide pool covers.

Manipulative experiment

We identified a total of eight periphyton taxa (Table 1). *Licmophora, Cocconeis, Fragilaria, Actinocyclus, Navicula,* and *Grammtophora* were the first taxa to colonise the settlement panels after ten days of exposure (Table 1). *Nitzschia* and *Amphora* colonised the plates after 20 days of colonisation. Recruits of the macroalgae *Palmaria* (red) and *Adenocystis utricularis* (brown) were observed after 40 days of exposure to colonisation (Table 1).

Taxon richness peaked after 20 days of colonisation of plates; this peak was lower in tide pools than on emergent rocks (compare Fig. 4a and b). In average, diversity showed an overall decrease after 30 days and a further

Table 1 Periphyton occurrence. Order in which benthic microalgae and macroalgal propagules occurred on settlement plates during the experiment

Taxon/Days after start	10	20	30	40
Licmophora	x	x	x	x
Cocconeis	x	x	x	x
Fragilaria	x	x	x	x
Actinocyclus	x	x	x	x
Navicula	x	x	x	x
Grammatophora	x	x	x	x
Nitzschia		x	x	x
Amphora		x	x	
Ulothrix			x	x
Palmaria				x
Adenocystis				x
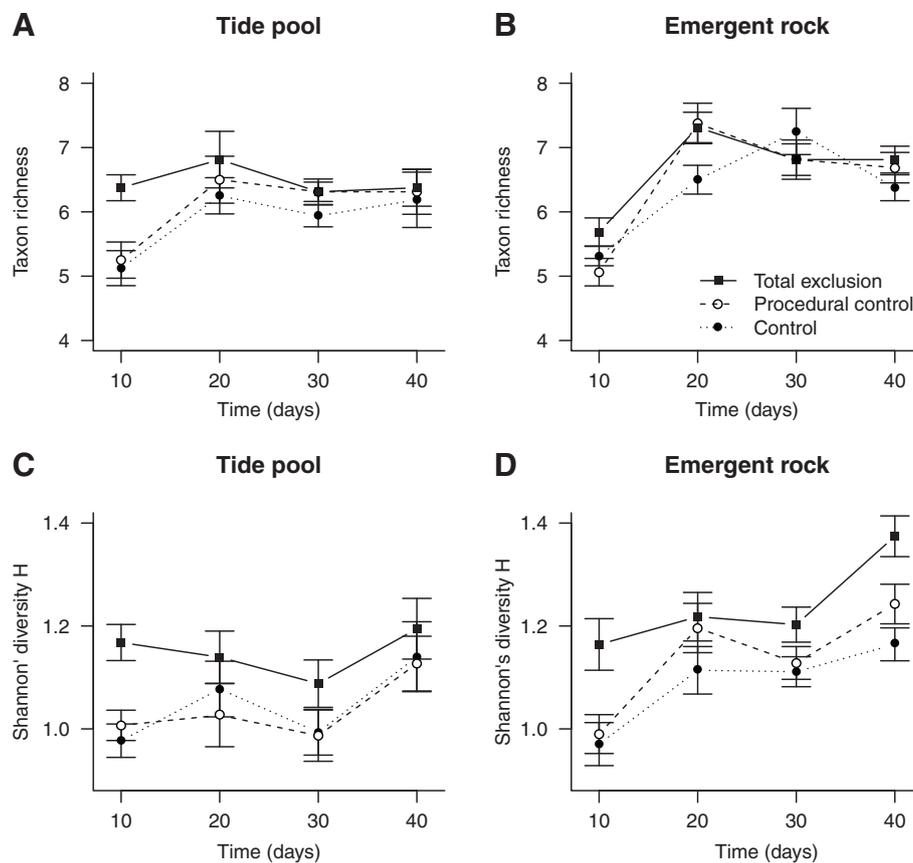
Fig. 4 Temporal patterns of richness (**a**, **b**) and Shannon' diversity (**c**, **d**) during the grazer-exclusion experiment. The experiment was replicated in tide pools (**a**, **c**) and on emergent rocks (**b**, **d**). Values are given as means ± standard errors of the mean (SEM)

increase after 40 days of colonisation (Fig. 4c and d). Exclusion treatment and habitat showed significant and independent effects on taxonomic richness and diversity; block accounted for a significant amount of variation in taxon richness (Table 2). Both, control (C) and procedural control (PC) treatments showed significantly lower number of taxa and diversity than the TE treatment (Fig. 4, SNK test: $P < 0.05$). The differences between the C and PC treatments were statistically non-significant for t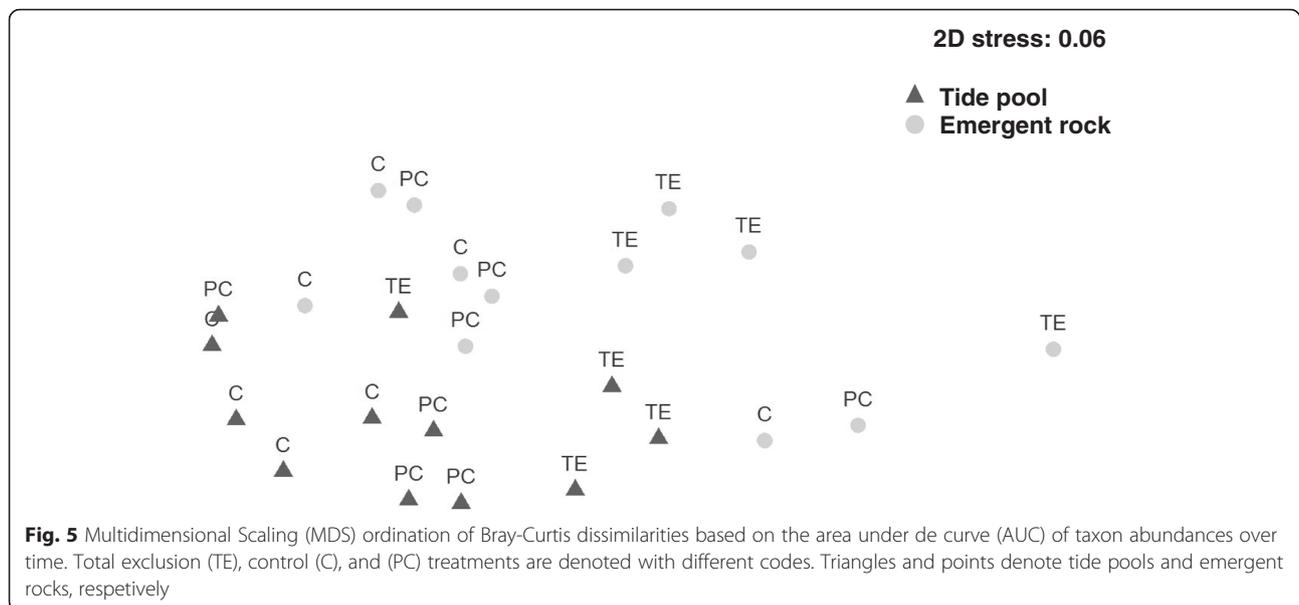axonomic richness and diversity (Fig. 4, SNK: $P >$ 0.05), indicating that confounding effects of fences on the colonisation patterns can be discarded. Taxonomic richness and diversity were significantly lower in tide pools than on emergent rocks (Fig. 4, Table 2).

The MDS ordination showed that experimental units located in tide pools and on emergent rock were well discriminated in terms of Bray-Curtis dissimilarities (Fig. 5). Within these two groups, the TE treatment clustered in the centre of the ordination, while the C and PC treatments clustered toward the left side (Fig. 5). In

Table 2 Summary of effects of habitat (either tide pool or emergent rock), grazing treatment (total exclusion, control, and procedural control), and randomly selected blocks on the temporal patterns of taxonomic richness, Shannon's diversity, and the structure of periphyton rocky-shore communities

Source	d.f.	Taxon richness		Shannon's diversity		Community structure	
		F	P	F	P	pseudo F	P (perm)
Habitat = H	1	10.501	0.005	7.252	0.017	19.257	0.001
Treatment = T	2	6.090	0.010	7.795	0.005	10.693	0.001
Block	3	17.240	0.039	16.531	0.051	6.879	0.001
H x T	2	0.991	0.400	0.319	0.731	1.396	0.252
Residual	15						

Taxon richness and Shannon's diversity were analysed with ANOVA; community structure was analysed with PERMANOVA, based on Bray-Curtis dissimilarities

Fig. 5 Multidimensional Scaling (MDS) ordination of Bray-Curtis dissimilarities based on the area under de curve (AUC) of taxon abundances over time. Total exclusion (TE), control (C), and (PC) treatments are denoted with different codes. Triangles and points denote tide pools and emergent rocks, respetively

agreement with the univariate analyses (see previous paragraph), the PERMANOVA showed significant responses in community structure to exclusion treatment, habitat, and block, but not to the interaction between habitat and treatments (Table 2). Pairwise multivariate analyses conducted between exclusion treatments showed that the differences between treatments C and PC were statistically non-significant; both control treatments were statistically different from the TE treatment.

According to similarity percentage (SIMPER) analyses, the 92 % of the multivariate differences between tide pools and emergent rocks were accounted for by the genera *Navicula, Licmophora, Fragilaria,* and *Cocconeis*. For grazer exclusion treatments, the differences between TE and C treatments were accounted for by the genera cited above in addition with *Actinocyclus*, which together accounted for 94.8 % of the average between-group dissimilarity. For these taxa, we observed higher abundances on emergent rocks than in tide pools, and in TE than C and CP treatments.

Discussion

These results suggest that intertidal tide pool habitats and grazing by the gastropod *Nacella polaris* (hereafter referred to as *Nacella*) had significant, albeit independent, effects on the structure of early-succession periphyton communities in a rocky shore on the western Antarctic Peninsula. Individuals of *Nacella* were found in higher densities in tide pools than on emergent rocks exposed to aerial conditions. Despite these spatial patterns of distribution, body sizes and weights remained similar across microhabitats. In addition, herbivore-exclusion treatments had positive effects on the richness, diversity, and abundances of periphyton taxa, in

agreement with previous manipulative work conducted in western Antarctic Peninsula [21, 36]. Also, there was a higher richness and diversity of periphyton taxa occurring on emergent rock than in tide pools. Finally, no significant response of periphyton community structure and diversity to the interactive effect of grazer treatments and habitat was observed. Below we discuss these results in the light of what is known about (1) the high mobility of *Nacella*, (2) the circadian activity of this species, and (3) the potential effect of other grazers on intertidal community structure on western Antarctic Peninsula.

In this study we observed higher abundances of *Nacella*, but similar body sizes and shell morphologies, when tide pools were compared with emergent rocks. The comparatively high mobility of this species might explain these patterns. For instance, studies on Signy Island described two *Nacella* groups: a group that migrates from the subtidal to the intertidal zone during the summer and a group that remain submerged. These two groups are distinguished by the morphology of the shell [19, 20]. Individuals larger than 20 mm primarily undergo vertical migration, probably as a method to prevent intraspecific competition in the subtidal zone [37]. In agreement with these patterns, significant differences in shell morphology between intertidal and subtidal *Nacella* have been described in King George Island [21]. Accordingly, the limpets analysed in our study—which was restricted to intertidal measurements—shared similar morphological conditions and body-size ranges. On the other hand, their comparatively high capacity to disperse at the local scale, reflected by vertical migrations, might allow *Nacella* individuals to move from benign (i.e. tide pools and crevices) to more adverse (i.e.

emergent rocks) environments in order to allocate food. Subtidal and intertidal Antarctic limpets move 50 and 17 cm a day, respectively (Kim), which can be considered relatively high if compared with limpets from temperate regions (e.g. [38]). Further observational and manipulative research in this region should focus on behavioural aspects of *Nacella*, including homing behaviour and circadian rhythms.

Despite that densities of *Nacella* were highest in tide pools, the grazing effects of this species on periphyton did not vary between microhabitats. Logistic constraints limited our observations to low tide and daylight hours, so we did not account for distributional patterns of *Nacella* during high tide and night. Herbivores can have differential activity during day and night, as shown in temperate regions [38]. For instance, in central Chile the pulmonate gastropod *Siphonaria lessoni* is characterised by diurnal activity, while larger herbivores such as *Chiton granosus* and *Fissurella crassa* by nocturnal activity [38]. In addition, predation risk can stimulate nocturnal activity in prey species. In Antarctica the kelp gull *Larus dominicanus* predominantly feeds in shallow water at low tide and daytime, and the number of seagulls looking for prey significantly increases as the extreme low tide approaches [39, 40]. Therefore, it might be hypothesised that *Nacella* shows differential day vs. night activity patterns, which might allow this species to forage on emergent rocks when predation risk is low.

We also observed a higher diversity and abundance of periphyton on emergent rocks than tide pools, irrespectively of the presence or absence of *Nacella*. Tide pools in the intertidal zone of the Antarctic Peninsula harbour, in addition to *Nacella*, an abundant assemblage of benthic grazing species. Amphipods that feed on periphyton are abundant in the Antarctic intertidal [41–43], and were numerous in tide pools at the experimental location of this study (V. Segovia-Rivera and N. Valdivia, pers. observations). Interesting, we observed a lower percentage cover of filamentous algae in tide pools than emergent rock (see Additional file 1: Figure S1). In shallow subtidal habitats in the Antarctic Peninsula, moreover, amphipod densities can reach more than 300,000 ind. m^{-2}, which are several orders of magnitude higher than densities recorded elsewhere [44]. Such assemblages show specific habitat-selection behaviours depending non-consumptive effects of shallow subtidal predators and algal host characteristics [45], and can be a major driver of, at least, subtidal macrobenthic assemblages [46, 47]. According to a global literature review that includes the western Antarctic Peninsula, small grazers like amphipods can have strong and significant effects on the structure of local communities [48]. Accordingly, populations of small meso-grazers associated to intertidal tide pools might have a strong effect on

benthic colonisation, and these effects could well be comparable to that of larger grazers.

Conclusions

In summary, the combination of observational and experimental approaches of our study allowed us to determine significant, but independent, effects of grazing and tide pool habitats on early-successional Antarctic communities. The role of meso-grazers such as amphipods and small littorinid snails should be also considered in order to increase the accuracy of predictive models of intertidal community structure. Nevertheless, we suggest that the comparatively high mobility of *Nacella* allows this species to strongly control the colonisation patterns of these Antarctic habitats, independently of local environmental conditions. The relevance of understanding how these ecosystems function—especially in the early stages of development—cannot be underestimated.

Additional file

Additional file 1: Figure S1 Percentage cover of dominant sessile species in King George Island. Percentage covers of each macrobenthic species were estimated in situ in 15 50 × 50 cm quadrats divided in 25 equal fields. Estimations were conduced on emergent rocks and in tide pools. (DOCX 57 kb)

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