NOTE

Effects of trampling on intertidal mussel beds: importance of disturbance intensity

María M. Mendez[1,2,*], Juan P. Livore[1], Gregorio Bigatti[1,2,3]

[1]Laboratorio de Reproducción y Biología Integrativa de Invertebrados Marinos (IBIOMAR-CCT CONICET CENPAT), U9120ACV Puerto Madryn, Argentina
[2]Universidad Nacional de la Patagonia San Juan Bosco, Sede Puerto Madryn, U9120ACV Puerto Madryn, Argentina
[3]Universidad Espíritu Santo, 092301 Samborondón, Ecuador

ABSTRACT: Trampling is one of the most frequent forms of human disturbance on rocky shores. This activity may directly reduce the abundance of dominant species, indirectly promote changes in the abundance of associated species and ultimately affect biological interactions. We assessed the effects of different intensities of human trampling on *Brachidontes* spp. mussel beds, a dominant feature on rocky intertidal flats of southwestern Atlantic coasts. We experimentally applied 6 levels of trampling intensity on a Patagonian rocky shore. Simulated trampling intensity ranged from 0 to 600 tramples per day, and plots were disturbed replicating local usage patterns (i.e. austral summer weekend recreation). By the end of the experiment, *Brachidontes* spp. coverage decreased as a result of increasing intensities of trampling and mostly replaced by bare rock. Even the lowest experimental intensity produced a loss of more than 40% of coverage. Changes in coverage were generally immediate and occurred after the first 2 trampling events, regardless of disturbance intensity. Our findings highlight that as few as 5 people walking on the mid-intertidal flat can produce a decline of the mussel bed cover in a specific area. Our findings also alert to the urgency of implementing effective management actions in this and other frequented areas dominated by similar habitat-forming species.

KEY WORDS: Disturbance · Trampling · Mussel beds · Rocky shores · Southwestern Atlantic

INTRODUCTION

The effect of different forms of anthropogenic perturbation on coastal habitats has been studied in detail in recent decades (Davenport & Davenport 2006). Human use of coasts has grown exponentially in the last century, driven in part by the development of the tourism industry (Davenport & Davenport 2006). People perform a variety of activities on rocky shores that have the potential to alter the benthic communities by modifying the abundance of key species (Addessi 1994, Smith & Murray 2005, Araújo et al. 2012). Despite its ubiquity and effects, trampling by humans has often been overlooked, although it is considered one of the most frequent types of anthropogenic disturbance on rocky shores (Milazzo et al. 2004, Plicanti et al. 2016). Trampling is an important ecological disturbance, and its effects are likely to intensify as the use of shore areas increases (Casu et al. 2006, Davenport & Davenport 2006).

Studies have investigated the effects of trampling on benthic organisms, highlighting that vulnerability to trampling is usually influenced by its intensity and the characteristics of the organisms affected (Povey & Keough 1991, Milazzo et al. 2004). Trampling may

directly reduce the abundance of dominant species and indirectly promote changes in the abundance (both increases and decreases) of other associated species, thus affecting biological interactions (Brosnan & Crumrine 1994, Schiel & Taylor 1999). Along with the reduction in coverage by the dominant benthic organisms, the proportion of bare rock increases and opportunistic species can colonize this space (Van De Werfhorst & Pearse 2007, Araújo et al. 2012). Notwithstanding that long-lasting effects on communities may occur even with relatively low trampling intensities, there are few regulations specifically developed to mitigate its effects on benthic assemblages (Milazzo et al. 2004, Casu et al. 2006).

On the southwestern Atlantic coast, mussel beds are a distinctive feature of intertidal rocky shores (Bertness et al. 2006, Silliman et al. 2011). The tiny mussels *Brachidontes rodriguezii* and *B. (Perumytilus) purpuratus* form a dense matrix of organisms that dominate the mid-intertidal rocky shores of Argentinean Patagonia (41−55° S, 63−70° W). *Brachidontes* spp. beds provide habitat, shelter and food for associated organisms, including more than 30 species (Silliman et al. 2011, Bagur et al. 2016). Hence, understanding how *Brachidontes* spp. respond to any kind of disturbance will provide useful information about the conservation status of the whole intertidal community.

Mussel beds in Argentinian Patagonia are frequently and intensely used for recreation (Mendez et al. 2017). Península Valdés, a UNESCO World Heritage site, attracts thousands of tourists every year. In 2016, more than 300 000 people visited the natural reserve (https://peninsulavaldes.org.ar/ingresos-a-peninsula-valdes/). Most of these visitors also use surrounding coastal areas and perform different recreational activities (Mendez et al. 2017). Initial studies revealed that during summer these activities modify the abundance of benthic species (Mendez et al. 2017). Along the coast, the mid-intertidal flat is the most frequently visited zone and its mussel bed is severely impacted by human trampling (Mendez et al. 2017). By the end of summer, mussel cover decreases from 95% in control plots to less than 5% in trampled ones (Mendez et al. 2017).

The purpose of this study was to understand the effects of the main recreational activity on Patagonian intertidal mussel beds during the summer season. To address this goal, we experimentally evaluated the effects of varying intensities of trampling on the mussel bed during the disturbance period. We tested the hypothesis that mussel cover will decrease with increasing trampling intensity.

MATERIALS AND METHODS

Study site

The study was performed on a wave-protected shore at Punta Loma Natural Reserve (PL; 42°48′ S, 64°53′ W), on the west coast of Golfo Nuevo, southwestern Atlantic coast. Westerly winds are predominant, persistent and intense all year round (Paruelo et al. 1998) with an annual mean speed of 24.5 km h^{-1} and annual mean air temperature of 15.2°C (absolute minimum: −0.9°C; absolute maximum: 41.5°C; meteorologia.appm.com.ar) in 2017. Tides are semidiurnal with a mean amplitude of ~4 m, exposing a sedimentary rock platform (consolidated limestone). The mid-intertidal level is dominated by a single-layer matrix of *Brachidontes* spp. mussels, and visitor access to the shore has been prohibited for the last 30 yr, ensuring that no recent anthropogenic disturbances took place in the experiment area.

Experimental design

Plots (20 × 20 cm) were established in the mussel bed and trampled during 2 consecutive days once per week in January and February 2017 during diurnal low tides (n = 12 disturbance events, 6 wk). This temporal pattern was specifically chosen to replicate local usage of coastal areas during summer weekends (Mendez et al. 2017). Six levels of disturbance intensity were simulated, ranging from 0 to 600 tramples per event (n = 5 plots per treatment). A trample was defined as one uniform step of a single person (mean weight 70 kg) wearing rubber footwear. Thus, intensity was considered here as the repetition of tramples in an experimental plot. Level 1 had an intensity of 0 tramples (control plots). Levels 2 to 6 were trampled 10, 50, 100, 300 and 600 times, respectively. Levels 2, 3 and 4 were observed usage patterns recorded for a nearby public-access coastal area (Mendez et al. 2017), whilst levels 5 and 6 corresponded to increased visitor frequency.

Photographs of the plots were taken before the start of the experiment and after each trampling week (t_0–t_6), using a digital camera equipped with a frame that standardized distance from the substrate. Photographs were analyzed using Coral Point Count with Excel extensions (CPCe v4.1; Kohler & Gill 2006). One hundred equidistant points were placed over each image to estimate percentage cover of benthic organisms using a point-intercept method. All organisms were identified to the lowest possible taxonomic level.

Differences in *Brachidontes* spp. cover among plots before the experimental manipulation (t_0) were tested with a 1-way (intensity level) ANOVA. Normality and homogeneity of variance assumptions were evaluated with Kolmogorov-Smirnov and Levene tests, respectively. Variations in mussel cover throughout the experiment were tested using a generalized linear mixed model (GLMM). Analyses were carried out in the R software (R Development Core Team 2015) using the 'lme4' package (Bates et al. 2014). All the steps of the adopted procedure were conducted following Zuur & Ieno (2016). The full model included time and intensity level as fixed factors and plot as random effect, with a binomial distribution. The full model was the following:

$$cov_{ijk} \sim Bin(\pi_{ijk}, n_{ijk}) \qquad (1)$$

$$\log\left(\frac{\pi_{ijk}}{1-\pi_{ijk}}\right) = \alpha_i + INTENSITY_j + TIME_k \qquad (2)$$

where cov_{ijk} is percentage cover for the ith plot, in the jth intensity level and at the kth time, π is the proportion of mussel cover, n the number of observations, and α the intercept. In order to evaluate the significance of intensity level we compared the full model with a simplified model that did not incorporate this factor (chi-squared test). The simplified model is the following:

$$\log\left(\frac{\pi_{ik}}{1-\pi_{ik}}\right) = \alpha_i + TIME_k \qquad (3)$$

Finally, we compared the full model with a reduced model generated by grouping those intensity levels with similar intercepts and overlapping confidence intervals. The reduced model is the following:

$$\log\left(\frac{\pi_{ijk}}{1-\pi_{ijk}}\right) = \alpha_i + INTENSITY_j + TIME_k \qquad (4)$$

with $j = 4$ levels (see 'Results' for grouped intensities) and times as above ($k = 7$: t_0-t_6). Model assumptions were verified by plotting residuals versus fitted values, and versus each covariate in the model to perform a visual inspection of residual patterns for each model. GLMM analyses were carried out only for mussels and bare rock, as no other item exceeded 12% coverage at any given time.

RESULTS

A total of 9 taxa were recorded in the experimental plots: 3 algae, 2 bivalves, 2 gastropods, 1 barnacle and 1 anemone. Excluding *Brachidontes* spp., coverage of all taxa was consistently less than 5% (with

the exception of the green alga *Ulva prolifera*, 11.4% at t_6). *Brachidontes* spp. was the only taxon with an average coverage higher than 5% at all sampling times.

No differences were found in *Brachidontes* spp. cover among experimental plots at t_0 ($F = 1.82$, df = 5, p > 0.1). Disturbance generated with the 6 intensities of trampling decreased *Brachidontes* spp. cover and this reduction in coverage increased with intensity level ($\chi^2 = 142.81$, df = 5, p < 0.05; Fig. 1A). At t_0, mean *Brachidontes* spp. cover across all experimental plots was 95.4% (SD = 1.9), whilst at t_6 it decreased to 30.6% (SD = 31.8). Most of this loss was observed after the first 2 trampling events (t_1 and t_2; Fig. 1A). The decline in *Brachidontes* spp. cover produced by level 2 of trampling intensity (10 tramples) was no different from the trend registered for control plots (0 tramples). In contrast, the patterns registered for level 3 to level 6 were different to control plots. Analysis of
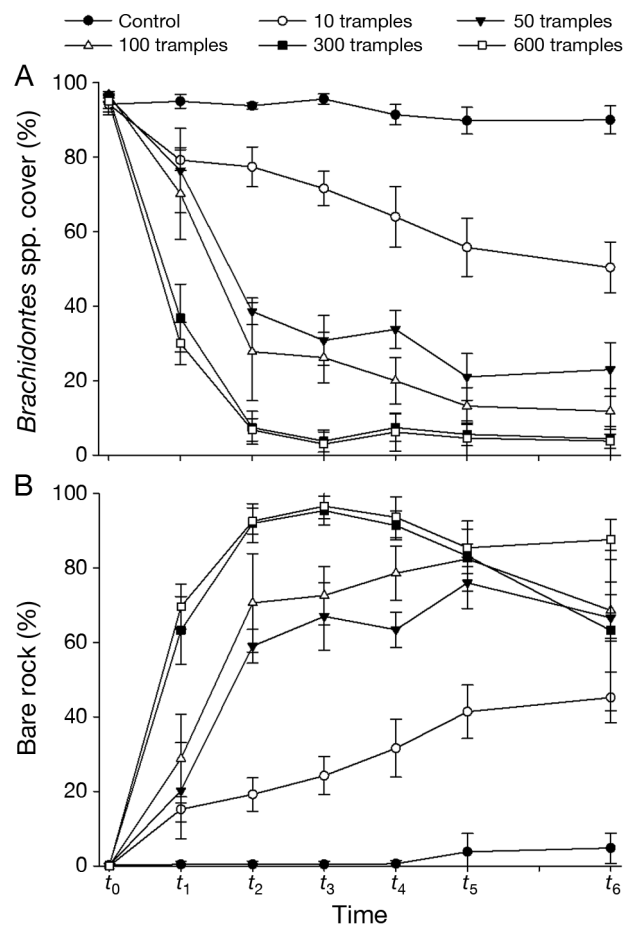

Fig. 1. Mean (±SD) (A) percentage cover of *Brachidontes* spp. and (B) percentage of bare rock for the different intensities of trampling at the 7 times studied (t_0, before the experiment started, and t_1 to t_6 at the end of each experiment week)

GLMM intercepts showed that levels 3 and 4 (50 and 100 tramples) produced a similar reduction of mussel cover. The same was observed for levels 5 and 6 (300 and 600 tramples). In fact, no significant differences were found when full and grouped models were compared ($\chi^2 = 0.027$, df = 5, p > 0.05).

Concurrently, trampling increased the proportion of bare rock in all the treatments, and this increase was related to the intensity level (except for the control, $\chi^2 = 138.73$, df = 5, p < 0.05; Fig. 1B). At t_0 mean proportion of bare rock across all experimental plots was 0.1% (SD = 0.3) whilst at t_6 it increased to 56% (SD = 28.1). A decrease in the proportion of bare rock was detected in the 50 and 100 tramples treatment by the end of the experiment due to the recruitment of the opportunistic green alga *Ulva prolifera* (Fig. 1B). As in the *Brachidontes* spp. temporal analysis, most of the change (in this case, increase in the proportion of bare rock) was observed after the first 2 trampling events (t_1 and t_2). Again, analysis of GLMM intercepts showed that levels 3 and 4 (50 and 100 tramples) produced a similar increase in the proportion of bare rock, and the same was observed for levels 5 and 6 (300 and 600 tramples). No significant differences were found when full and grouped models were compared ($\chi^2 = 1.35$, df = 5, p > 0.05).

For each model, visual inspection of residuals revealed uniform dispersion and no evident patterns, confirming that the models comply with underlying assumptions.

DISCUSSION

Disturbance generated by 6 consecutive events of trampling by humans affected the mid-intertidal assemblage by drastically decreasing the coverage of the *Brachidontes* spp. bed. The magnitude of the trampling effect increased with its intensity, but even the lowest level produced a loss of more than 40% of mussel coverage. Furthermore, the greatest loss of mussel cover occurred after 2 trampling events at all disturbance levels. This study shows that as few as 5 people taking the same path to travel to (and return from) the intertidal flat on the first 2 weekends of summer can produce a decline of the mussel bed cover in a specific area, potentially affecting tens of species living in it.

Community susceptibility to recreational trampling differs depending on inherent characteristics, such as species composition or the form of organisms involved (Brosnan & Crumrine 1994, Milazzo et al. 2004, Plicanti et al. 2016). In the current experiment,

all the simulated intensities of trampling produced a severe decline of *Brachidontes* spp. cover. Loss of mussels was due to the direct crushing of individuals or their dislodgment, most likely caused by the weakening of the byssus attachment to the substrate. As for other intertidal species of macroalgae and invertebrates, the effects of trampling registered in this study were dependent on the intensity of the disturbance (Fletcher & Frid 1996, Smith & Murray 2005). A noteworthy result was the timing of response (i.e. loss of mussel bed) which was practically independent of trampling intensity. The maximum effect of this disturbance occurred after the second trampling event (2 days of trampling in 2 consecutive weeks) in all the treatments.

Trampling intensity also affects the later temporal recovery of assemblages (Brosnan & Crumrine 1994, Brown & Taylor 1999, Smith & Murray 2005). In our experiment, the size of the patches generated by the loss of mussels was related to the trampling intensity (i.e. larger patches as the number of tramples increased). Small patches have been shown to recover quickly due to the encroachment of adjacent mussels (Paine & Levin 1981, Sousa 1984). Large gaps, on the other hand, need successful recruitment events, and full recovery can take up to several decades (Paine & Levin 1981, Sousa 1984). Recovery of *Brachidontes* spp. mussel beds after strong disturbances most likely takes several years, but this information is currently lacking for the study area. Thus, we aim to continue observation of the experimental plots to describe the exact recovery pattern and to evaluate the effect of trampling intensities on recovery.

Trampling not only affects dominant species. It also produces changes in species associated with them (Brown & Taylor 1999, Schiel & Taylor 1999, Casu et al. 2006). *Brachidontes* spp. mussel beds provide habitat, food and shelter to other invertebrate species (Silliman et al. 2011, Bagur et al. 2016). Consequently, the decline of the mussel bed cover also brings with it the loss of the associated species, therefore leading to a decrease in species diversity at the respective site.

One of the most evident consequences of trampling is the emergence of bare rock (Brosnan & Crumrine 1994, Fletcher & Frid 1996, Van De Werfhorst & Pearse 2007). We registered in our experiment that the proportion of bare rock increased. Bare rock became available for colonization by early succession organisms, such as opportunistic algae and barnacles that do not require secondary space for larval settlement (Povey & Keough 1991). In this sense, trampling may shift the community to an alternate state, with *Brachidontes* spp. being replaced by barnacles and

turf or encrusting algae. In fact, this switch in species dominance could last several years, since long periods of time are required for the recovery of mussel beds. Although the *Brachidontes* spp. cover also changed naturally, as seen in the changes observed on control plots, the proportion of bare rock generated by trampling was vastly greater.

In the Patagonian region, mussel beds are very popular among local people, becoming attractive recreation sites every summer, and they are consequently exposed to intense and frequent trampling. The present work provides the first experimental study on the effects of different intensities of human trampling on *Brachidontes* spp.. Mussel beds subjected to regular trampling may develop adaptive traits that would not be present in the studied population, hence caution is advised when generalizing our findings. From a conservation perspective, regulating the number of visitors could be an appropriate action to mitigate trampling effects and should be accompanied by other management strategies, such as periodic rotation of trails, suitable signage advocating conservation of the ecosystem, and educational programs. Furthermore, our findings and conclusions can be useful for other locations where similar habitat-forming species are dominant.

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