

**How wave exposure and heatwave related mass mortality impacts barnacle's
(*Balanus glandula*) facilitatory role on *Littorina* spp. snails**

by

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Abstract

Climate change is causing an increase in the frequency and severity of heatwaves, particularly along intertidal coastlines in the Pacific Northwest. This greatly impacts the many sessile ecosystem engineer species, specifically the barnacle species *Balanus glandula*, which inhabit the high intertidal habitat. These ecosystem engineer species play vital roles as biological facilitators, providing habitat for other small intertidal invertebrates. One well understood example of this is the relationship between *B. glandula* and *Littorina* spp. snails. Their relationship through heatwave related mortality across different exposure types is unknown. Thus, in this study we aim to better understand the effects different wave exposures can have on this relationship in the face of extreme climatic events. We hypothesized *Littorina* abundance, at sites with different environmental wave exposure types, would react differently to heatwave related mass mortality of *B. glandula*, due to the differing protectional needs of *Littorina* at these sites. We predicted that the mass mortality of *B. glandula* will initially result in increased *Littorina* abundance, but through time the degradation of the remaining barnacle habitat will cause decreases in *Littorina* abundance; these effects are expected across all wave exposure types. Secondly, we anticipate that these previous predictions will be amplified at wave exposed sites, relative to wave sheltered sites. To address this research question, four sites, two exposed and two sheltered, were subjected to 15x15 centimeter treatment plots of mass mortality, cleared, or an unmanipulated control. The abundance of *Littorina* were monitored throughout time to quantify the effects of the different stages of heatwaves. Our study provided insignificant evidence to prove that *Littorina* abundance increased at mass mortality plots. However, it did display that at cleared plots, which are likely to be the inevitable outcome of heatwaves, *Littorina* abundance significantly decreased. Finally, the relationship between *B. glandula* and *Littorina* was insignificantly impacted by different exposure conditions. Regardless of the effect of wave exposure, these findings display that the loss of *Littorina* in intertidal habitats could elicit negative impacts and decrease ecosystem stability. Thus, understanding the impact of heatwaves is crucial to motivate protection and ask critical questions about how these multifaceted intertidal systems are affected by a changing climate.

Keywords

climate change, ecosystem engineer, biological facilitation, habitat degradation, habitat roguistisity

Introduction

Mean global temperatures and the frequency of extreme weather events has been rapidly increasing due to human activities (IPCC, 2021). Further, the climatic state has also become more variable and severe as a result of anthropogenic impacts on climate. In particular, heatwaves along marine fronts are becoming increasingly prevalent which can have large consequences to organisms living in intertidal habitats (Harley, 2008; Oliver et al., 2018; Sorte, 2019).

Marine heatwaves can impact intertidal communities on multiple trophic scales which has broad implications for those who rely on the system. For example, Oliver et al. (2019) suggest that marine heatwaves can impact our fisheries and aquaculture practices directly, as a result of physiological stress, and indirectly because intertidal biodiversity loss can cause trophic cascading effects. Heatwaves have also been reported to negatively impact intertidal habitats and their inhabitants in many ways (Tsuchiya, 1983; Harley, 2008; Weitzman, et al., 2021). As intertidal habitat represents a large component of biodiversity in marine systems (Gray, 1997), we can see how heatwaves impacting these habitats at increased rates may have unknown consequences on this system. Heatwaves have killed intertidal organisms in the past (Tsuchiya, 1983; Harley, 2008; Mieszkowska et al., 2021), but the long-term consequence of many large-scale heatwaves occurring with increased frequency is yet to be determined.

The increased severity and frequency of marine heatwaves is evident now, and has caused mass mortality events for organisms who live in intertidal systems. In the recent 2021 heatwave that affected the Pacific Northwest, more than a billion intertidal organisms were described to have been killed as temperatures reached above 50°C on the substrate (Migdal, 2021). Further, certain species of barnacles were reported to suffer mortality which was declared as “much worse than normal” in areas hit by the heatwave (Harley, In Prep 2021). This recent event shows how heatwaves can profoundly impact intertidal systems, especially ecologically important sessile organisms. Importantly, one of the less well-studied mechanisms

through which heatwaves could impact intertidal ecosystems is by modifying interspecific interactions, such as biological facilitation.

Biological facilitation is the promotion one species has on the survival and growth of a different species, which often leads to an enhancement of the overall community function (Bruno et al., 2003). Silva et al. (2015) described facilitation as a community structuring force which can be compared to competition and predation in importance. Biological facilitation is a characteristic trait of ecosystem engineering species. Ecosystem engineers modify or create habitat through physically altering the abiotic or biotic habitat around them (Harley & O'Riley, 2011; Hölker et al., 2015). As a result, many ecosystem engineers have high ecological importance biologically facilitating one or many species in the environment through their habitat manipulations.

An example of a facilitatory ecosystem engineer in the intertidal zone are barnacles, particularly the species *Balanus glandula* (Darwin, 1758) which are prevalent along the west coast of North America (Possingham & Roughgarden., 1990). These barnacles create important habitat for many other organisms by increasing surface rugosity and providing cracks and crevices for smaller recruiting species (Jernakoff, 1985). When barnacles are killed due to physiological stress (e.g., thermal stress) their opercular plates, the top valves which they open and close to feed, eventually weaken and detach. This leaves their outer calcareous casing (the lateral test) which can remain in the ecosystem for months (Silva et al., 2015). Once the barnacle has been killed, however, the leftover lateral test is no longer being structurally reinforced by growth and this important habitat is more susceptible to being lost (Silva et al., 2015). The loss of habitat in general can be negative for many intertidal invertebrates and biodiversity (Hanski, 2011). Therefore, barnacle mortality temporarily increases the available habitat space for other organisms, such as *Littorina spp.* snails, as the rugosity of the system increases, but the implications of losing barnacles overtime can be negative.

Littorina spp. are small abundant grazing herbivores and an important prey species that can often be found in high densities in barnacle beds of intertidal communities

(Silva et al., 2015). *Littorina* utilize barnacle tests as microhabitat shelter from many potential abiotic and biotic conditions (Harley & O'Riley, 2011). *Littorina* are found in higher abundance in barnacle beds with high numbers of dead barnacles (Harley & O'Riley, 2011; Silva, 2015) suggesting that *Littorina* can more effectively utilize the dead barnacles as cover to protect themselves from predators, desiccation, and wave action. When considering how barnacle mortality may affect *Littorina* abundance, wave exposure is another factor that needs to be evaluated.

Wave action has the ability to damage and displace both organisms and their habitat from the environment (Bertness, 1989 & Catesby & McKillup, 1998). For example, waves can directly disturb *Littorina* and thus impede snail access to feeding grounds (Harley & O'Riley, 2011; Silva et al., 2015). Further, strong wave action is responsible for *Littorina* mortality, especially in autumn and winter when seasonal storms are present (Harley & O'Riley, 2011). Additionally, barnacles can also be removed by the strong force of wave action (Chan et al., 2006). The manner in which *Littorina* interact with barnacles is well documented (Harley & O'Riley, 2011; Silva et al., 2015; Boulding & Harper 1998), yet the ways wave action may interact with intertidal habitat is multifaceted and few studies have identified the effects on this system. Researching these effects, whilst addressing the heatwave related mortality of *B. glandula*, provides a novel outlook on how different intertidal habitats may be impacted in our future.

In this study, we aim to address how mass mortality of an important barnacle facilitator species affects the abundance of *Littorina*. Furthermore, we explore how this facilitatory role may differ between varying levels of wave exposure. We hypothesize that heatwave related mass mortality of *B. glandula* affects *Littorina* abundance differently under varying wave exposure due to differential protection needs of *Littorina*. We predict that *Littorina* abundance will increase directly after a *B. glandula* mass mortality event but decrease thereafter once the remaining *B. glandula* habitat degrades. Additionally, we expect the previous predictions to be significantly amplified at wave exposed sites, relative to wave sheltered sites.

Materials and Methods

Study System

We conducted this study on rocky intertidal shores near Bamfield Marine Science Center (BMSC), British Columbia, Canada. The experimental locations were situated on granite substrate, in the high intertidal, exposed to mixed diurnal tides. We selected two wave exposed and two wave sheltered sites. The wave exposed sites, Brady's Point (48°49'48.3"N 125°09'05.7"W) and Scott's Bay (48°50'01.1"N 125°08'55.3"W), are located on the Northwest side of Bamfield. These localities are directly impacted by swell and wind from Trevor Channel and the open ocean (Fig. 1). The wave sheltered sites, Rance Island (48°49'17.9"N 125°08'20.4"W) and Strawberry Point (48°49'57.8"N 125°07'45.6"W), are located in Bamfield Inlet and Grappler Inlet respectively. These inlets are physically protected from the conditions of Trevor Channel, thus, the incoming swell is interrupted and reduced here. The exposure level of each site was cross referenced to another study which quantified wave exposure in Bamfield, BC (Starko et al., 2019).

We implemented treatments at each wave exposed and wave sheltered site on separate dates, which was then followed by abundance surveys two and four weeks after (Table S1). For data collection and consistency, we assigned numbers sequentially (1-12) to each quadrat and marked them using epoxy/putty.

Experimental Design and Data Collection

The experimental design was modified from Harley and O'Riley (2011), and Silva et al. (2015). In brief, we examined two wave-exposed and two sheltered sites and quantified habitat associations between *Balanus glandula* and *Littorina spp.* snails. To avoid confounds in our experimental design we haphazardly selected plots with dense *B. glandula* coverage, low mortality of *B. glandula*, and little to no *Fucus distichus* presence. In cases where dense *F. distichus* cover was present, we placed the bottom edge of the quadrat along the upper growth limit of *F. distichus* to isolate *B. glandula*'s facilitator effects from that of *F. distichus*'. Since *F. distichus* visually

covered the *B. glandula* beds, this logistically allowed us to take clear photos of the barnacles within each plot and accurately survey *Littorina*. Photos were taken of each plot to measure the initial *B. glandula* percent cover.

Before we implemented treatment at each site, an initial *Littorina* survey was completed in each plot. We counted the abundance of *Littorina* in 10x10 cm plots centered within the 15x15 cm quadrats (n = 12 plots per site; Fig. 2). This was done to ensure that the snails counted were actively selecting the treated plots as habitat, and not randomly on the margin of treated and non-treated areas.

After surveying, we randomly applied one of three different treatments. These treatments included a no treatment control, 100% mortality of *B. glandula* (experimentally killed), and a bare rock treatment where all organisms, including algae, were scraped off. We placed twelve 15 x15 centimeter quadrats at each site (n = 4 per treatment, 12 plots per site; N = 48 total) near the upper growth limit of *B. glandula* parallel to the shore. Experimental kills were executed using either blunt probes or tweezers to puncture the opercular plates of the barnacles. The 100% mortality treatments were used to simulate the effects on *B. glandula* after an extreme heat event. The purpose of the control plots was to compare how increased rugosity of the 100% mortality treatment, and decreased rugosity of the cleared treatment changed *Littorina* abundance.

Two weeks post treatment the plots were re-surveyed to analyze *Littorina* abundance changes in the manipulated and non-treated plots at both wave exposed, and wave sheltered sites. This was repeated four weeks post treatment for the final data collection (Table S1).

Data Analysis

To compare barnacle bed communities between all sites, percent *B. glandula* cover was quantified and a Shapiro-Wilk test was used to check for normality assumptions in the data; the percent cover data was non-normal (Shapiro & Wilk, 1965). Thus, a non-parametric Kruskal-Wallis and Dunn's Test analyzed differences between sites

of the same wave exposure and across the different exposure levels (Kruskal & Wallace, 1952; Dinno, 2015).

Using a Shapiro Wilk's test we also determined our response variable, the total number of *Littorina* snails, was not normally distributed (Shapiro and Wilk, 1965). To address this, we used the function *fitDist* from the *gamlss* package (Rigby & Stasinopoulos, 2005) to determine that the Geometric family distribution best fit our response variable distribution of total *Littorina*. Further, both the Double Poisson distribution and the Negative Binomial distribution were also well fit to other count data (Gurmu, 1998; Allison & Waterman, 2002). Therefore, to describe the terms driving the variation in the total *Littorina* count at each plot, considering our multiple continuous and categorical explanatory variables, we created three full Generalized Additive Models for Location, Scale and Shape (GAMLSS) using the aforementioned distributions. Our full model was as follows:

$$Total\ Snails \sim treatment * survey * wave\ exposure + random(site)$$

We ran a backward model selection against these models to determine which model was the best fit for the observed data (determined by the model with the lowest AIC value). Using the Generalized Akaike Information Criterion (GAIC) function, the model with the lowest AIC value was fit to the negative binomial distribution. All the analyses conducted were done in R (V 4.0.5, R Core Team, 2021).

Results

Barnacle Bed Density

The *Balanus glandula* percent cover between test sites significantly differed (Kruskal-Wallis, $\chi^2 = 35.69$, $df = 3$, $p\text{-value} = 8.69e-08$). Brady's Point and Scott's Bay (the exposed sites) had similar barnacle cover (DunnTest, $Z = -0.57$, $p\text{-adj} = 1.00$; Fig. 3). Rance Island and Strawberry Point's (the sheltered sites) also had equal barnacle cover (DunnTest, $Z = -0.28$, $p\text{-adj} = 0.78$; Fig. 3). Importantly, Brady's

Point had significantly more *B. glandula* cover than both Rance Island (DunnTest, $Z = 4.05$, $p\text{-adj} = 2.01\text{e-}04$; Fig. 3), and Strawberry Point (DunnTest, $Z = 3.78$, $p\text{-adj} = 4.75\text{e-}04$; Fig. 3). This was also true for Scott's Bay compared to Rance Island (DunnTest, $Z = -4.62$, $p\text{-adj} = 2.26\text{e-}05$; Fig. 3), and Strawberry Point (DunnTest, $Z = 4.35$, $p\text{-adj} = 6.91\text{e-}05$; Fig. 3).

Littorina abundance

From backwards model selection, our final model included treatment, survey time, wave exposure, and the interactions between treatment and time as well as wave exposure and time. Site of collection as a random effect was also included (i.e., reduced model: $\text{total} \sim \text{treatment} + \text{survey} + \text{wave_exposure} + \text{treatment:survey} + \text{survey:wave_exposure} + \text{site}$, where random effects are signified with italicized text). The random effect was insignificant in our model. At both exposure levels, the mass mortality plots showed increases in *Littorina spp.* snail abundance relative to the control plots, though this trend was not statistically significant ($p = 0.73$; Table 1, Fig. 4). In the mass mortality treatment at wave exposed sites, there was an initial increase in abundance, followed by a decrease. Conversely, abundance in mortality treatments at sheltered sites increased over time (Fig. 4), however these trends through time were not statistically significant ($p = 0.15$; Table 1, Fig. 4). The control plots proportionally followed the same trends seen in the mass mortality plots at both exposure levels (Fig. 4). Our model proved that cleared plots, relative to control plots, decreased significantly in *Littorina* abundance at both wave exposed, and wave sheltered sites ($p = 5.09\text{e-}05$; Table 1, Fig. 4). This decrease in *Littorina* abundance at cleared plots was maintained over time ($p = 1.29\text{e-}12$; Table 1, Fig. 4). There were significantly more *Littorina* at wave exposed sites relative to wave sheltered sites ($p = 3.50\text{e-}11$; Table 1; Fig. 4). The interaction between survey time and wave exposure type was significant ($p = 0.01\text{e-}01$; Table 1).

Discussion

Our study investigated how the mass mortality of *Balanus glandula* would impact their facilitatory role on *Littorina spp.* snail abundance through differing levels of wave

exposure in Bamfield, BC. We hypothesized that heatwave related mass mortality of *B. glandula* would have unique impacts on *Littorina* abundance at the different exposure types, due to *Littorina*'s different protectional needs at these sites. Our hypothesis was not supported as the distinct exposure types showed insignificant differences in *Littorina* abundance at mass mortality and cleared plots compared to control plots. Interestingly, following our general expectations for cleared plots, *Littorina* did dramatically decrease across all sites. Between the two different exposure types, *B. glandula* beds were found to be significantly denser at exposed sites. We observed patterns of increasing *Littorina* abundance at mass mortality plots across exposure types, though statistically insignificant. However, we found that at our cleared plots, *Littorina* abundance significantly decreased across all exposure types, but the magnitude of this decrease did not differ between environments. The decrease in *Littorina* abundance at all cleared plots demonstrates the eventual negative impacts heatwaves can cause in many environments.

Our analysis of the barnacle bed densities between exposure types indicated that the *B. glandula* populations of the two exposure types differed, and exposed sites had higher percent cover (Fig. 3). This provides a potential explanation as to why the count data for *Littorina* are relatively higher at the exposed sites throughout the experiment, and why exposure type proved to be a significant term in our model. This is ecologically intuitive as barnacles can survive in higher densities with increased flow conditions as this provides adequate food for the population (Nilcéa & Vallarino, 2001). Notably, this increase in barnacle cover can provide more habitat for *Littorina* snails (Silva et al., 2015) and likely better support a larger population.

Littorina are known to actively select complex microhabitats which are high in available surface area (Jones & Boulding, 1999). This suggests that our pattern of increased *Littorina* abundance at all exposure types in mass mortality plots relative to control plots could show that *Littorina* preferentially inhabit the more rugous environment, though the trend was statistically insignificant (Fig. 4). Further, the effect of mass mortality plots on *Littorina* abundance across exposure types through time displayed a variable trend (Fig. 4). The differences in these trends between exposure types, and the control plots following these trends proportionally, is difficult

to biologically explain. The effects of wave action increasing in intensity and frequency throughout the fall (Harley & O'Riley, 2011) could describe why exposed sites saw decreases later in the experiment, and why control plots proportionally followed these patterns. Nevertheless, this trend is statistically insignificant. However, the difference in the direction of these trends across wave exposures through time helps explain why the interaction term between wave exposure and survey time was significant. Overall, with increased surveys, time, or sample size, these trends could have had the potential to be significant relative to the control conditions. Supporting our trends, Harley and O'Riley (2011), and Silva et al., (2015) found that increasing barnacle habitat surface area through mortality has resulted in increases in *Littorina* abundance. Further, Mazzuco et al. (2020) explain that increasing available habitat surface area can provide benefits, such as increased abundance and diversity, for other intertidal organisms. As such, the severe heatwaves expected in our future may elicit a temporary positive effect on the small intertidal invertebrates who utilize the barnacle habitat. Importantly, however, the preservation of this temporary increase in habitat (when *B. glandula*'s lateral tests are still present in the environment), likely varies depending on many conditions. Nevertheless, we found limited knowledge surrounding these details in literature. The eventual removal of barnacles is important as *B. glandula* live higher than other intertidal biological facilitator species who cannot tolerate these environments (Bushek, 1988). As such, after the barnacle tests are removed this habitat will likely remain barren. As a result of their physiological ability to live in the high intertidal, *B. glandula* can potentially be exposed to severe heatwaves conditions longer than other organisms (Berger & Emlet, 2007), displaying the potential for these sites to eventually become cleared.

In the cleared plots *Littorina* abundance significantly decreased displaying the severity of the eventual loss of *Littorina* habitat (Fig. 4). This could be attributed to *Littorina* being important prey to many organisms and thus seeking adequate cover to protect themselves from their predators (Harley & O'Riley, 2011; Silva et al., 2015). However, despite Harley and O'Riley (2011) providing evidence that barnacle cover was important for preventing negative impacts on *Littorina* by wave action, in our study, the cleared plots' *Littorina* abundance did not decrease more severely at

exposed sites relative to sheltered sites. This could potentially be due to the fact that, unlike in a heatwave scenario, only a small 15x15 centimeter plot of habitat was cleared. As such, at both exposure types, *Littorina* could simply avoid the habitat, acquiring safety in cover from predators in the adjacent barnacles (which is a large pressure at both exposure types) without ecological downfalls like grazing competition. Without the ability to avoid post heatwave barren habitat, we suspect there would be greater decreases in *Littorina* abundance at more wave exposed sites. Overall, *B. glandula* habitat removal caused large decreases in *Littorina* abundance and alluded to the potential implications of losing an entire upper bed of this important ecosystem engineer.

The impact of heatwaves increasing available habitat space through the mass mortality of *B. glandula* could not only positively impact *Littorina* but also positively impact other high intertidal invertebrate inhabitants such as many amphipod species (Gibson & Barnes, 2003). Critically, after mortality, *B. glandula*'s lateral tests are temporary habitats that will eventually be removed, leaving high intertidal habitat which is difficult to inhabit by other biological facilitators (Bushek, 1988). Our data shows this loss of *B. glandula* can greatly decrease invertebrate prey abundance at these sites. Crucially, the loss of important prey species can impact food webs causing trophic cascades which can have profound impacts on entire marine ecosystems (Ilić et al., 2021). Lindberg et al. (1998) describe an example of an intertidal trophic cascade where the removal of limpets from their habitat elicits a change in species diversity and abundance at the manipulated plots. Knowing the effects of trophic cascades, mitigating the potential negative effects of heatwaves on intertidal systems is essential, not only for intertidal organisms, but also for subtidal and marine ecosystems. An example of this is the indirect effect of heatwaves on aquaculture and fisheries as they depend on ecosystem stability which is jeopardized through the loss of lower trophic levels (Oliver et al., 2019). This helps to display how the effects of heatwave mortalities, impacting organisms and their habitat, are broad and can trickle down to affect whole ecosystems and all those who rely on it (Oliver et al., 2019; Bernhardt & O'Connor, 2021). Importantly, we've only addressed the potential indirect stress of heatwaves through the loss of *B. glandula*.

The direct stress of heatwaves on the system as a whole adds another layer of complexity to our question.

Limitations & Future Research

A limitation of this experiment was that we only considered the direct thermal impact of heatwaves on *B. glandula* and not on *Littorina*. This should be further addressed to gain a more holistic view of this species interaction through heatwaves, as *Littorina* are impacted directly by increased temperatures altering their behaviour and habitat selection (Chappon et al., 2017). Additionally, our study was constrained by a six week time period and limited in our availability to conduct field work. Ideally, the study could have been conducted over a longer period of time to more accurately understand the full cycle of *B. glandula* as a biological facilitator after a heatwave. Furthermore, having an increased sample size, more sites measured, and more frequent abundance surveys could have provided the statistical power needed to better address how wave exposure and the effects of increased habitat rugosity are tied into the many impacts of marine heatwaves. Both Harley and O'Riley (2011), and Silva et al. (2015) allude to knowledge gaps surrounding these topics, however, our findings showed limited support to address them. Important follow up research could address these shortcomings and help piece together the unknown impacts of heatwaves, on the *B. glandula* and *Littorina* relationship, in the future.

To further our study, future work could track and quantify how *B. glandula* percent cover changes at mass mortality plots, relative to control, at different exposure types through time. This could also include measuring recruitment in both cleared and mass mortality plots at different wave exposure levels through time. For example, at multiple sites eight weeks after treatment implementation, we observed *B. glandula* habitat degradation (Fig. S1). Conducting a study on this degradation would advance the current understanding of how severely this habitat will be impacted through time under the increased frequency and intensity of heatwaves. In a broad sense, researching which habitat types are impacted by heatwaves more severely could provide insight into where conservation efforts should be allocated towards in our future.

Conclusions & Implications

This study aimed to address the many ways heatwaves, causing mass mortality in *B. glandula*, could impact *Littorina* abundance, especially at different wave exposure types. The impact of wave exposure on the mass mortality of *B. glandula* was insignificant in our results, however, the three treatment types in tandem allowed for a unique view on the timeline of this system through heatwaves. Specifically, our study portrayed the negative impacts of habitat loss on *Littorina*, as they decreased drastically in abundance at cleared habitats. Knowing the mortality of *B. glandula* will eventually result in habitat degradation from the substrate, and understanding if this habitat will be reinhabited quickly, or how this differs between sites, will be critical in protecting this ecosystem in a changing climate.

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Tables and Figures

Table 1. Summary output for the backwards step Gamlss model displaying significant and non-significant explanatory variables. P-value terms with “*, **, or ***” are variables that were found to be significantly different in comparison to the intercept with a value of 0.05 or lower, 0.01 or lower, and 0.001 or lower respectively.

| | Estimate | Std.Error | t value | p value |
|----------------------------------|----------|-----------|---------|--------------|
| Intercept | 4.42 | 0.21 | 20.84 | <2.00e-16*** |
| Mass Mortality Treatment | -0.09 | 0.27 | -0.35 | 0.73 |
| Cleared treatment | 1.30 | 0.31 | 4.19 | 5.09e-05*** |
| Survey Time | -0.08 | 0.10 | -0.78 | 0.44 |
| Sheltered (wave exposure) | -1.80 | 0.25 | -7.22 | 3.50e-11*** |
| Mass Mortality: Survey | 0.18 | 0.12 | 1.44 | 0.15 |
| Cleared treatment: Survey | -1.32 | 0.17 | -7.83 | 1.29e-12*** |

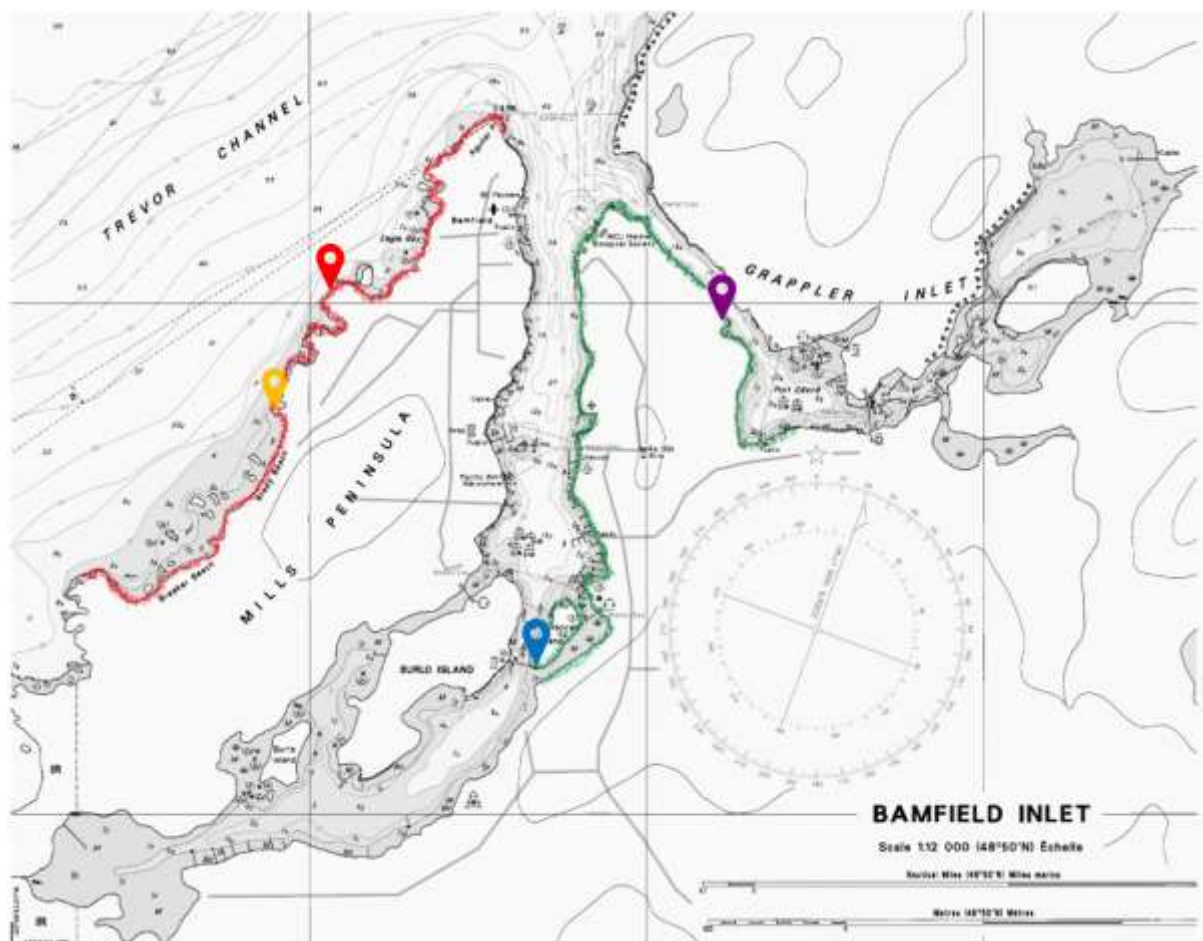


Fig. 1. Map of the wave-exposed (shore outlined in red) and wave-sheltered (shore outlined in green) study sites situated near the Bamfield Marine Science Centre, British Columbia, Canada. Yellow represents Brady's point, red represents Scott's Bay, blue represents Rance Island, and purple represents Strawberry point



Fig. 2. Visual depiction of a quadrat. *Balanus glandula* and *Littorina* spp. abundance surveyed in a centred 10x10 cm plot (white square). Treatment was applied in the 15x15 cm quadrat (red square).

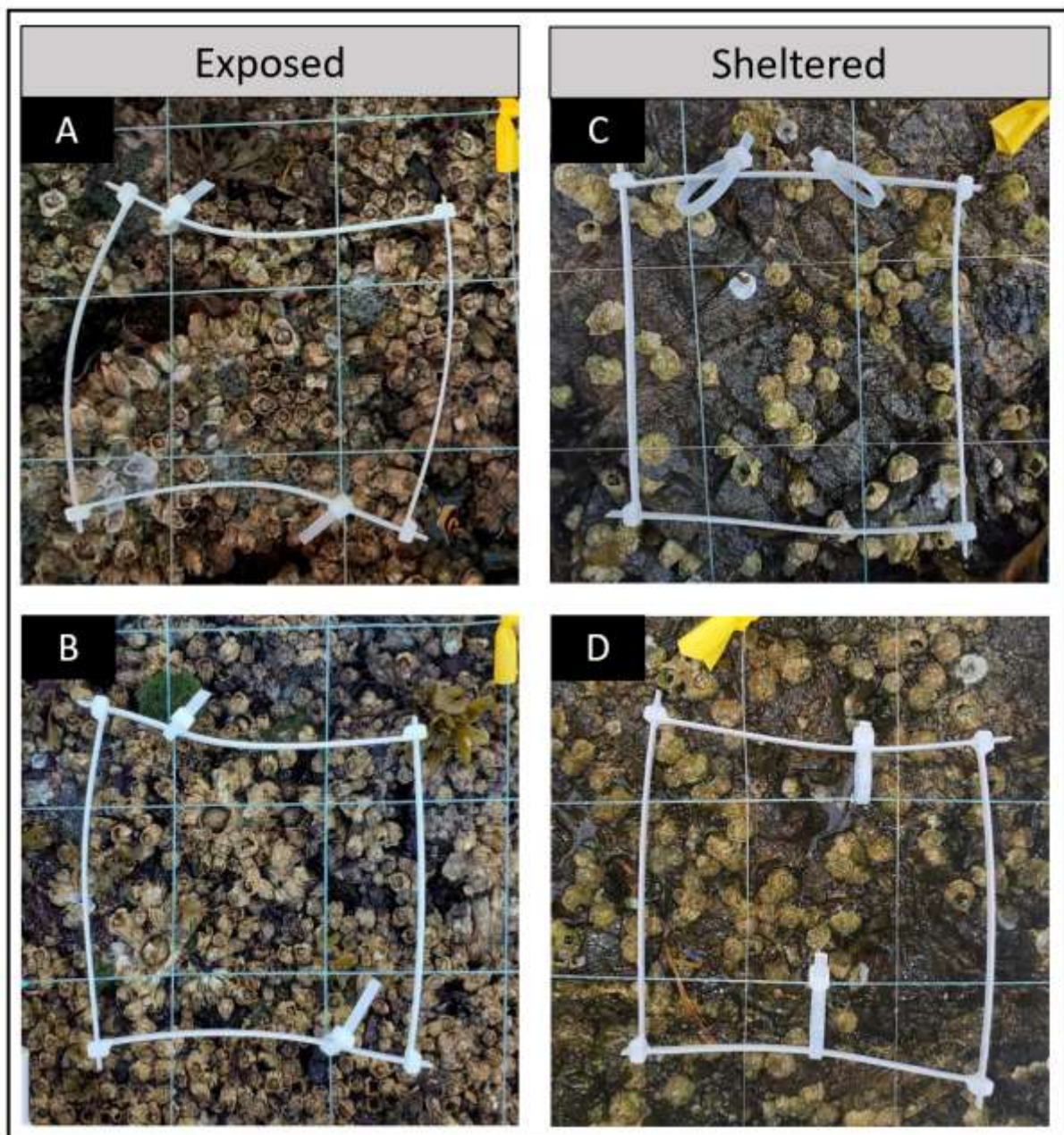


Fig. 3. Photographs illustrating barnacle bed density differences between exposed study sites a) Scott's Bay and b) Brady's Point, and sheltered study sites c) Rance Island and d) Strawberry Point.

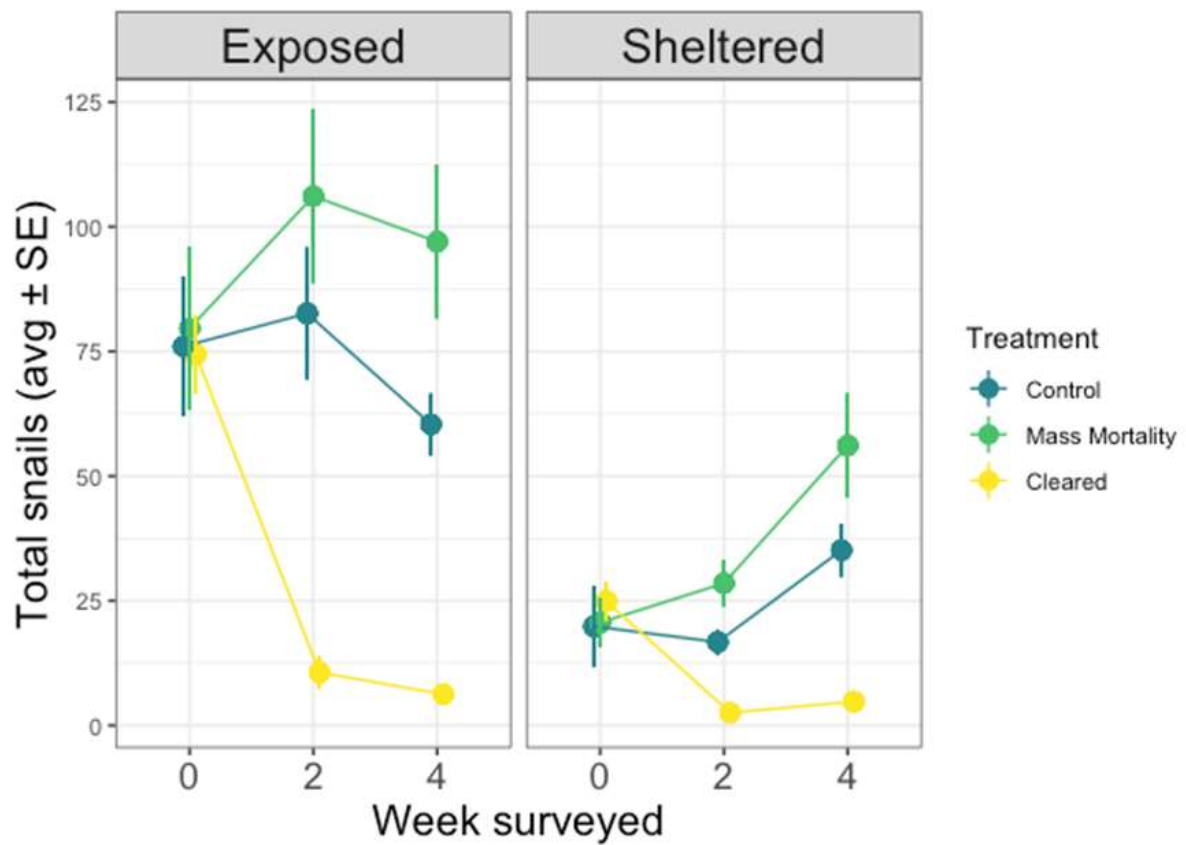


Fig. 4. The total abundance of *Littorina* spp., at wave exposed and wave sheltered sites, in control, mass mortality, and cleared treatment plots, sampled every two weeks over a four-week period. Error bars denote as standard error.

Supplementary

Table S1. Record of dates for treatment implementation and *Littorinia spp.* abundance surveys (prior and post treatment) at each of the four experimental sites.

| | Brady's Point | Scott's Bay | Rance Island | Strawberry Point |
|---|--------------------------|--------------------|---------------------|-------------------------|
| Implementation & Baseline Survey | Oct. 16th | Oct. 17th | Oct. 23rd | Oct. 24th |
| Week Two Survey | Oct. 30th | Oct. 31st | Nov. 6th | Nov. 7th |
| Week Three Survey | Nov. 13th | Nov. 14th | Nov. 20th | Nov. 21st |

Fig. S1. Photographs displaying barnacle bed coverage shift over an eight-week period between a wave-exposed (Brady's Point) and wave sheltered site (Strawberry Point). Letters A-D represent the initial barnacle cover and letters E-H represent barnacle cover eight weeks later. Images A, E, C, & G are quadrats from the wave exposed site Brady's Point. Images B, F, D, & H are quadrats from the wave sheltered site Strawberry Point.

