Investigating the environmental and anthropogenic drivers of temperate reef grazers and developing a grazer-based metric for assessing reef health

by

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Abstract

Grazers structure ecosystems by consuming primary producers. Recently, human-induced predator loss has caused destructive overgrazing of foundational species by grazers. Kelp forests are one critical ecosystem that has been affected, where red sea urchin (*Mesocentrotus franciscanus*) grazers have overconsumed many areas, resulting in barren habitats. Importantly, not all grazers in these ecosystems remove the kelp canopy; species such as the red turban snail (*Pomaulax gibberosus*) merely graze on biofilms or remove small patches leaving the kelp blades intact. Given the disruptions (*e.g.*, predator loss) to normal grazer controls, identifying key factors regulating grazer populations is crucial to inform conservation action. We investigated potential environmental and recreational fishing drivers of red sea urchin and red turban snail density on rocky reefs. We predicted that temperature and wave exposure would negatively affect grazer density, and that grazer density would be lower on loose seafloor. We also predicted lower urchin density and higher snail density in protected areas, where limited fishing promotes higher trophic levels and larger-bodied predators. We found a strong negative relationship between turban snail density and wave exposure, suggesting turban snails may be impacted by increases in wave energies. Conversely, urchin density was not significantly associated with any of the environmental variables tested, supporting that this species tolerates a wide range of environmental conditions and can maintain high densities over diverse regions without management intervention. Indeed, we found that protected areas with reduced fishing pressure returned significantly higher snail-to-urchin ratios, translating into healthier ecosystems and intact kelp forest communities. Reduced fishing pressure likely contributed to more complete predator communities in protected areas, which can improve urchin control, leading to increased macroalgal growth and snail densities. Our results support the role of protection from fishing as a key management strategy that can regulate damaging urchin populations and promote healthier reef communities.

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Introduction

Crucial trophic interactions are being disrupted by human activities (Estes & Palmisano, 1974; Hamilton & Caselle, 2015; R. A. Myers et al., 2007). One of the most important trophic interactions affected is the top-down control of primary producers by herbivorous grazers, which is a driving force in structuring ecosystems (Poore et al., 2012; Smith et al., 2010). Grazers consume primary producers, regulating their abundance and diversity (Carson & Root, 2000; Paine & Vadas, 1969). Predators, in turn, help control grazer population sizes, but this control has been disrupted following predator population declines due to hunting (Kenyon, 1969), fishing (Hamilton & Caselle, 2015), and climate change (Hamilton et al., 2021; Schultz et al., 2016; Vásquez et al., 2006). Predator loss can lead to complete degradation of ecosystems as herbivores are released from predation pressure and overgraze much of the available primary producers (Estes & Palmisano, 1974). Destructive overgrazing reduces food for other grazer species and the extent and quality of habitat provisioned by foundational producer species (Filbee-Dexter & Scheibling, 2014). Thus, identifying the drivers controlling grazer populations and preventing damaging overgrazing is critical to conserving ecosystems where predator populations have decreased.

One of the most well-studied examples of an ecosystem impacted by destructive overgrazing is kelp forest communities (Filbee-Dexter & Scheibling, 2014). Kelp forests are diverse subtidal ecosystems where large, canopy-forming macroalgal species such as bull kelp (*Nereocystis luetkeana*) and giant kelp (*Macrocystis pyrifera*) provide complex, three-dimensional habitats for a wide array of species (Graham et al., 2007). Kelp forests are crucial ecosystems as many of the species that benefit from the provided habitat are ecologically, economically, and culturally significant, such as Pacific herring and Pacific salmon (Graham, 2004; Shaffer et al., 2023). Under normal circumstances, kelp forests host many different grazers (Graham, 2004; McLean, 1962) that enact top-down regulation of the macroalgal communities (Davenport & Anderson, 2007) and are, in turn, controlled by predators such as sea otters (*Enhydra lutris*) and California sheephead fish (*Bodianus pulcher*) (Cowen, 1983; Estes & Palmisano, 1974).

In many northeast Pacific kelp forests, the red sea urchin (*Mesocentrotus franciscanus*) is a dominant grazer species (Dayton, 1985). Red sea urchins are voracious, echinoderm grazers of many forms of macroalgae, but they prefer to feed on large kelp species such as giant kelp (Leighton, 1966). Typically, urchins feed on detached pieces of drift kelp on the seafloor and do not directly graze on intact kelp (Harrold & Reed, 1985). However, if urchin densities increase or the amount of drift kelp becomes limiting, urchins will begin actively feeding on the attached kelp (Breen & Mann, 1976; Harrold & Reed, 1985). This is especially damaging and can lead to the removal of kelp and a transition to a barren ecosystem state referred to as an urchin barren (Harrold & Reed, 1985). Urchin barrens are highly stable and can persist for many years due to two crucial adaptations of red sea urchins; they can live for hundreds of years (Ebert & Southon, 2003) and can shut down their metabolism in the absence of food (Schuster & Bates, 2023; Spindel et al., 2021), preventing starvation and effectively decoupling the abundance of urchins from ecosystem primary productivity levels. Any kelp or other macroalgae that attempt to colonize this habitat are immediately consumed by the urchins that are still present, maintaining the urchin barren ecosystem state (Spindel et al., 2021). The persistence of these barren habitats is a major problem, given the importance of kelp forests for many essential species (Shaffer et al., 2023).

Unfortunately, urchin barrens are increasingly observed from Alaska to southern California, where many red sea urchin predators have experienced significant population declines (Durham & Wagner, 1980; Harvell et al., 2019; Kenyon, 1969). For example, an important predator of red sea urchins, the sea otter (Estes & Palmisano, 1974), was hunted to near extinction along most of its range on the west coast of North America during the eighteenth and nineteenth centuries for the fur trade (Kenyon, 1969). The lack of otters contributed to the overgrazing of many kelp forests by urchins (Estes & Duggins, 1995; Estes & Palmisano, 1974). Still, many forests remained intact due to the persistence of other urchin predators, such as sunflower stars (*Pycnopodia helianthoides*) (Duggins, 1983) and California sheephead fish (Cowen, 1983). However, predation pressure has recently decreased in some areas following the decline of sunflower stars due to sea star wasting disease (Harvell et al., 2019), and the decline of sheephead populations due to overfishing (Hamilton & Caselle, 2015). Losses of these predators have permitted higher urchin densities and the expansion of urchin barrens (Schultz et al., 2016).

While the impacts of grazing from certain herbivores, such as red sea urchins, can be incredibly damaging to ecosystems, grazing by other species can benefit their communities (Guidone et al., 2010). One such grazer found living alongside red sea urchins throughout much of their range is the red turban snail, *Pomaulax gibberosus* (Alf, 2019; Durham & Wagner, 1980). Turban snails prefer to graze on larger kelp species such as *M. pyrifera* (Mazariegos-Villarreal et al., 2017), but in contrast to urchins, they do not overgraze the kelp (Watanabe, 1984). They do this by only consuming small patches of kelp blades, or biofilms growing on the blades (Mazzillo et al., 2013). Turban snails can benefit macroalgal communities by grazing on these biofilms or small epiphytic algae that foul kelp blades (Guidone et al., 2010), or by excreting high levels of nutrients, such as ammonium, which are essential for macroalgal growth (Bracken et al., 2018). In addition to the benefits turban snails provide to macroalgae, snails also receive benefits from macroalgae such as predation refugia (Watanabe, 1984) and food (Mazariegos-Villarreal et al., 2017). Turban snail densities are also associated with site-level macroalgal productivity (Shears & Babcock, 2003). This association provides a method to estimate local kelp and macroalgal productivity based on turban snail density and, in turn, offers a way to investigate the health and productivity of rocky reef trophic webs through the abundance of turban snail grazers.

An effective tool for marine ecosystem managers to build healthy, intact trophic webs that offer natural controls of detrimental species (*e.g*., *M. franciscanus*) and promote beneficial species (*e.g*., *P. gibberosus*) is through the protection of areas from human activities (Shears & Babcock, 2003). There are different types of protected areas, each with slightly different restrictions, but two of the most common types include marine protected areas (MPAs), which are long-term protected areas created through specific government legislation, and harvest refugia, which are created through less rigorous legislation and lack the extended timescales of MPAs (Robb et al., 2011). Human activities such as fishing are restricted within both MPAs and harvest refugia to preserve biodiversity, maintain the sustainability of ecosystems, and restore overfished populations (Carr & Reed, 1993; Pomeroy et al., 2005). A third, even more restrictive type of protected area is marine reserves, where there is zero fishing or wildlife removal permitted (Agardy et al., 2003). For the purposes of this study, MPAs, harvest refugia, and marine reserves will be grouped under the general term, “protected area”, as they all offer protections to ecosystems from fishing activity.

Protected areas have been shown to reduce the substantial impacts of recreational fishing on grazer populations (Shears & Babcock, 2003), which can include the removal or deterrence of predators (Hamilton & Caselle, 2015; Hughes et al., 2019), the input of nutrients/waste (Leon &

Warnken, 2008), and the disruption of seafloor habitats (Flynn & Forrester, 2019). Even so, to ensure that protected areas successfully promote healthy ecosystems, it is crucial that they be well-enforced and implemented for extended periods of time (Edgar et al., 2014). It is also important that the effectiveness of protected areas at maintaining healthy communities be evaluated frequently to confirm whether or not further action needs to be taken to improve the success of the protected areas (Pomeroy et al., 2005). There are different metrics for assessing the success of protected areas, but various measures of fish biomass or species richness from SCUBA surveys are commonly used (Edgar et al., 2014). These metrics can be effective in clear, tropical waters but are more difficult in productive, temperate waters where low visibility makes accurately identifying and counting mobile fish more challenging. These challenges are compounded where cryptic and nocturnal species are common, causing divers to miss species that are present. Additionally, divers can scare fish away (E. M. V. Myers et al., 2016), further making fish-based ecosystem health metrics difficult to apply in some contexts and pointing to the need for alternative metrics. Common reef invertebrates such as red turban snails and red sea urchins are potential alternative species to be used in reef health metrics as they are slow-moving (Diaz et al., 2011; Mattison et al., 1977) and are not scared away by divers, making them easy to identify and count even in murky water. Further, their slow movement means that individuals are nearby regardless of whether it is day or night, limiting variation in the number of individuals observed at different times of day. Therefore, the use of new, invertebrate-grazer-based methods of assessing the health of ecosystems within protected areas is a promising alternative to the problematic fish-based metrics.

Given that red sea urchin and red turban snail grazers have important diverging impacts on producer communities, and that typical predator controls on grazers have been impaired, identifying how each of these species is controlled by environmental and anthropogenic drivers is critical for ecosystem conservation. Environmental variables that could potentially affect the density of *M. franciscanus* and *P. gibberosus* are temperature, wave exposure, and seafloor type. High temperatures can decrease the survival and fitness of urchins (Wong & Hofmann, 2020; Zhan et al., 2019) and snails, although urchins are more resistant than turban snails (Schuster & Bates, 2023). Wave exposure can be damaging to urchins and snails as waves can reduce foraging efficiency or dislodge grazers or the kelp they require for food (Etter, 1996; Graham et al., 2007; Siddon & Witman, 2003). Seafloor type can impact these grazers as soft or loose sediments can make attachment to the seafloor more difficult during wave events and are known to deter urchins by impairing their movement (Kawamata et al., 2011; Laur et al., 1986). An anthropogenic driver that could influence the density of *M. franciscanus* and *P. gibberosus* is recreational fishing, given the substantial impacts of recreational fishing on grazer populations, such as predator removal (Hamilton & Caselle, 2015; Hughes et al., 2019). Crucially, fishing can differentially affect urchins and turban snails, as the release of urchins from predation can lead to the removal of macroalgae and subsequent adverse effects on turban snails (Shears & Babcock, 2003).

Understanding the impacts of these environmental and anthropogenic drivers on the densities of red sea urchins and red turban snails is crucial in informing management practices and estimating how these populations may shift as climate change increases ocean temperatures (Su et al., 2023) and wave forces (Reguero et al., 2019), and humans continue to fish recreationally. With knowledge of what drives these species, managers can identify sites or regions that should be targeted to reduce harmful urchin populations and maintain turban snail populations, thus promoting healthy rocky reef ecosystems.

The objectives of this study were threefold. First, to better understand the environmental drivers of red turban snail and red sea urchin population density, we investigated temperature, wave exposure, and seafloor type, hypothesizing that these variables would influence the density of red sea urchins and red turban snails by affecting the survival and fitness of these species. We predicted temperature would be negatively related to grazer density due to the adverse effects of elevated temperatures on survival for red sea urchins and red turban snails, but that the effect would be weaker for urchins as they are more resistant to temperature. Further, we predicted wave exposure would be negatively related to grazer density as stronger or more frequent waves can negatively affect these species through dislodgment or reduced effective foraging time. Additionally, we predicted that grazer density would be higher on solid seafloor as movement and attachment are impaired on softer, looser sediments.

Second, to illuminate the influence of anthropogenic impacts on these grazers, we investigated protection from fishing. We hypothesized that fishing, or the lack thereof, would impact the density of red sea urchins and red turban snails indirectly by influencing community composition. We predicted that urchin density would be higher in fished habitats where predator removal and deterrence are increased, whereas snail density would be higher in protected areas where predators keep urchins in check and permit macroalgal growth.

Third, to further inform the management of rocky reefs, we explored the influence of protection from fishing on the relative densities of these two species. We hypothesized that the ratio of red turban snails to red sea urchins would differ between sites inside and outside of protected areas based on the differential impacts of fishing on these species. We predicted that the snail-to-urchin ratio would be higher in protected areas where intact predator communities restrict urchin densities, allowing for increased macroalgal growth and elevated turban snail densities.

Methods

Study region

Here, we surveyed shallow (3-11 m depth), rocky reef sites (n = 26) located throughout the central and eastern regions of Barkley Sound, BC, Canada (Figure 1). Barkley Sound is an inlet on the west coast of Vancouver Island that is approximately 30 km wide by 20 km long, with multiple diverse island groups. Within the sound are various areas with differing levels of protection from anthropogenic activities. There was a mix of sites located in openly fished areas and within protected areas with restrictions on fishing activities (*e.g.* Broken Group Islands, Baeria Rocks Ecological Reserve) (Table S1). We classified sites as having some level of protection or unprotected (*i.e.*, open to fishing and other human activities) (Table 1) using the ProtectedSeas Level of Fishing Protection system (ProtectedSeas, n.d.). We further grouped these sites into regions based on distinct island groupings (Deer Group/Bamfield, Broken Group, Deep Imperial Eagle Channel, Numukamis Bay) (Figure 1).

Data sets analyzed

Reef Life Survey data

Reef sites for monitoring were selected based on the Reef Life Survey (RLS) criteria: at least 90% hard substratum, extending at least 50 m along a given depth contour, and at depths reachable by SCUBA divers (Edgar & Stuart-Smith, 2014). At each survey location within Barkley Sound, dive surveys were conducted following the RLS methods for sampling rocky and coral reef communities (Edgar & Stuart-Smith, 2014). Survey dates, depths, and locations are summarized in Table S1. A 50 m transect line was laid along a defined depth contour at each location. A first pass of the transect by a diver identified and counted any mobile fish in two 5 m wide by 5 m high bands. Next, a second pass along the transect identified and counted all macroinvertebrates and cryptic fishes in two 1 m wide by 2 m high bands, resulting in a density of each species (number of individuals/m^2). Finally, photo-quadrats were taken of the seafloor at 2.5 m intervals along the transect, with the camera held approximately 0.5 m above the seafloor. Density data on red sea urchins and red turban snails resulting from the RLS surveys in Barkley Sound (April and May of 2024) were obtained from https://reeflifesurvey.com/survey-data/.

To characterize the seafloor/substrate type of each transect, we individually analyzed the photo-quadrats imaged as part of the RLS protocol. We scored the dominant substrate type in each photo as either kelp/macroalgae, sandy/soft substrate, loose rubble substrate, or solid substrate. We adapted the sediment size categories from Wentworth (1922) for substrate classification (Table 2). Sandy/soft substrate consisted of silt and sand, loose rubble substrate was a combination of shell hash, granules, pebbles, and cobbles, and solid substrate was a combination of boulders and solid rock slabs. The dominant seafloor type in each image was whichever type made up the greatest area within the photo. We used the dominant seafloor type that appeared the most within each transect to characterize the transect overall. To limit bias in scoring the dominant seafloor type of each transect, we randomized the order in which we analyzed the transects and did not check where each was located within Barkley Sound before analysis.

Sea surface temperature

We used the Global Ocean OSTIA Sea Surface Temperature and Sea Ice Analysis product from the Copernicus Marine Service (European Union-Copernicus Marine Service, 2015) to obtain sea surface temperature (SST) data covering all of Barkley Sound (Figure 2). This database uses satellite measurements from microwave and infrared radiometers to calculate SST daily at a spatial resolution of 0.05º latitude x 0.05º longitude (~6 km). We took the daily raw temperature data for the year before sampling began, including the sampling days (2023-04-22 to 2024-05-03), and averaged the temperature within each 0.05º x 0.05º cell. We used the

GPS coordinates of the survey sites to extract the average SST of the cell within which each site was located.

Site wave exposure/openness

To estimate the exposure of each site to waves and turbulence, we used a fetch-based metric called "openness" developed by Hill et al. (2010). Fetch is the distance over water to the nearest wind-breaking landform in a given direction. Openness considers the fetch in all directions around a site to estimate a site's exposure to wind-generated waves (Hill et al., 2010). We calculated openness following the methods of Hill et al. (2010). This involved measuring the fetch in meters around each study site at 7.5º increments with a maximum fetch of 650 km allowed. We chose this maximum because this distance has been estimated to be the maximum distance under which winds can increase the size of waves (Hill et al., 2010). To calculate the fetch increments around each site, we used the "waver" (v0.3.0) package (Marchand & Gill, 2023) and a high-resolution shapefile of Vancouver Island, BC, Canada (Government of British Columbia, 2018). We summed the 48 fetch values at each site and normalized the openness by dividing the summed value by the largest sum across all the sites. Ultimately, a site with higher openness meant fewer wind/wave-breaking landforms nearby. This relates to higher wave exposure and more frequent and stronger waves, as the size of waves is partially determined by the open-water distance over which wind can blow unimpeded by landforms (Denny, 1988).

DFO flyover data

To quantify fishing impacts within Barkley Sound, we obtained recreational fishing boat location data (Fisheries and Oceans Canada, 2024b) from Fisheries and Oceans Canada (DFO). DFO creel surveyors completed aerial flyover surveys of Barkley Sound twice weekly (one weekday and one weekend day) from June 1 to September 30 of 2021-23. During these surveys, the locations and numbers of recreational boats fishing were recorded. The flight route (Figure 3) allowed all of Barkley Sound to be visible, and if boats could not be identified, the plane diverted to ensure that all boats were properly characterized and counted.

We used the DFO flyover counts of recreational boats actively fishing to calculate the mean number of recreational boats fishing within a given radius of each site per year. To do this, we constructed circular polygons around each site (radii = 1.0 km, 1.5 km, 2.0 km) and merged these polygons with the DFO recreational boat counts to extract how many boats were spotted within the radius each year (Figure 3). We recorded the number of boats fishing within the radius of each site in each year and averaged the counts across the three years of data (2021, 2022, 2023) to calculate the mean number of recreational boats fishing around each site per year. We omitted aerial surveys where parts of Barkley Sound were obscured by fog.

We used the mean number of recreational boats fishing within 1.0, 1.5, and 2.0 km of the RLS sites per year to assess whether fishing impacts were higher at unprotected sites and to support the use of protection status as a measure of fishing effort. We used a Wilcoxon rank sum test to compare the rank sums of the mean number of recreational boats fishing around protected and unprotected sites per year. The Wilcoxon rank sum tests (Table 3) all indicated that the rank sums were significantly lower for protected sites compared to unprotected sites (Figure 4). This supported the use of protection status as an indicator of fishing activity, as more boats impacted the ecosystems around unprotected sites.

Proxy for reef health

The relative densities of red turban snails and red sea urchins were assessed as a potential metric indicating the health of rocky reef ecosystems in coastal, temperate waters. The relative densities of these species can provide an estimate of reef health as higher densities of urchins are damaging (Breen & Mann, 1976), while turban snail densities give an estimate of the local kelp productivity (Shears & Babcock, 2003), which could balance out the effects of high urchin densities (Harrold & Reed, 1985). To use this metric, we calculated the log ratio of the number of red turban snails to the number of red sea urchins counted along a transect (Equation 1). The log ratio centers the metric around zero, with positive numbers indicating relatively greater snail density and negative numbers indicating relatively greater urchin density. Additionally, the log ratio means that an equivalent difference in the species' densities in either direction results in the same ratio magnitude. As there were zero counts for each species at some sites, we added one to the count of each species (Equation 1) to ensure that all values were positive and non-zero. By having the ratio be snails to urchins, higher values indicated a healthier site.

$$Snail - to - Urchin\ ratio = \log_{10}\left(\frac{Red\ turban\ snail\ count + 1}{Red\ sea\ urchin\ count + 1}\right) \qquad \text{Eq. 1}$$

Statistical analyses

To test the effects of the environmental drivers of mean SST, wave exposure (openness), and dominant seafloor type on red turban snail and red sea urchin density, we used the "gam" function from the "mgcv" (v1.9-1) package (Wood, 2023) to fit a generalized additive model (GAM) for snails and a generalized additive mixed model (GAMM) for urchins. We used the Restricted Maximum Likelihood method for smoothing parameter estimation as this produces stable, reliable results (Marra & Wood, 2011). Additionally, we employed the double penalty selection within both models, which enables a penalty to be applied to each smooth, allowing terms with little effect to be reduced to a constant term and effectively be removed from the model (Marra & Wood, 2011). Furthermore, we scaled and centred both mean SST and openness to ensure no problems with them being on different scales.

To assess the impact of site protection status on the density of red sea urchins, the density of red turban snails, and reef health, we used linear models (LMs) and linear mixed-effects models (LMMs) fitted with the "glmmTMB" (v1.1.10) package (Brooks et al., 2024). We used the snail-to-urchin ratio as a proxy for reef health. All LMs and LMMs were fitted with the same package for consistency.

In building all models, we used a Gaussian distribution. To test for spatial autocorrelation between the survey sites, we performed a Moran's I test on the model residuals using the "spdep" (v1.3-8) package (Bivand et al., 2025) (Appendix). When necessary, we used a random intercept effect of region (based on our site regional groupings as seen in Figure 1) to account for the spatial autocorrelation and compared each model with and without the random effect. We used Akaike information criterion (AIC) analysis to identify that the random effect should be included in the environmental and protection status urchin density models and the snail-to-urchin ratio model but not in the environmental and protection status snail density models. Within the urchin environmental GAMM, region was fit as a random intercept using a random effect smooth term (s(region, bs = "re")). We confirmed that the trends in the fixed effects were consistent with and without the random effect, considering the fixed effects showed some correlation with the random effect. Furthermore, we removed non-significant interaction terms following AIC analysis. To check that the model assumptions of homoscedasticity and normality of residuals were met, we assessed the residuals visually and used the "DHARMa" (v0.4.7) package (Hartig et al., 2024). To produce acceptable fits and ensure that model assumptions were met, we found that it was necessary to log-transform the snail density in the environmental GAM (0.01 was added to the snail density to remove densities of 0 snails/m^2) and square-root-transform the snail density in the protection status LM (Appendix). Additionally, we tested the GAM and GAMM variables to ensure no problems arose from concurvity, which is an extension of collinearity where predictors can be correlated with each other non-linearly (Wood, 2008). High concurvity can lead to model interpretability problems and unstable parameter estimates, as it is difficult for the model to distinguish between the effects of the correlated predictors on the response variable.

We used R 4.4.1 (R Core Team, 2024) for all data collation and statistical analyses performed above. The code and all data used for analyses are available as supporting material.

Results

Environmental drivers

Log-transformed snail density was significantly negatively related to openness (Figure 5) but did not respond to either mean SST or dominant seafloor type (Table 4). None of the three environmental predictors were significantly related to the red sea urchin density (Table 5); however, there was a trend of higher urchin density on solid substrate and a trend of decreasing urchin density with increasing openness, driven by the densities observed at higher openness values (Figure 6). Additionally, the random effect of region was significant in the urchin model (Table 5), indicating that region explained a significant amount of the variation in urchin density.

Protected area effects

The densities of red turban snails and red sea urchins were not significantly related to protection status (Table 6 and Table 7). However, there were trends of higher snail density (square-root-transformed) and lower urchin density in protected sites (Figure 7A and B). The mean (all means shown with ± Standard Error) red turban snail densities for protected and unprotected sites were 1.44 ± 0.34 snails/m^2 and 1.02 ± 0.30 snails/m^2, respectively. For urchins, the mean density for protected sites was 2.63 ± 0.72 urchins/m^2 and for unprotected sites was 3.61 ± 0.32 urchins/m^2. Moreover, the random effect of region explained 21.6% of the total variance in the urchin densities (Intraclass Correlation Coefficient = 0.22), indicating substantial variation in urchin density between regions.

Additionally, we observed intact kelp forests on 3 transects in protected areas, while kelp forests were not observed at unprotected sites (Table S2). There were stark contrasts in the red sea urchin density between sites with and without kelp, with mean urchin densities of 0.02 ± 0.02 urchins/m^2 and 3.64 ± 0.28 urchins/m^2, respectively. Red turban snails showed an opposite trend of higher mean density at sites with kelp (1.74 ± 0.46 snails/m^2) compared to sites lacking kelp (1.08 ± 0.25 snails/m^2).

The analysis of the snail-to-urchin ratio between protected and unprotected sites showed a significant effect of protection status on the ratio, with a trend of higher ratios at protected sites (Figure 7C; Table 8). In fact, the average snail-to-urchin ratio for protected sites (0.09 ± 0.42) was approximately 15 times higher than for unprotected sites (–1.08 ± 0.16). Additionally, the model showed that the random effect of region explained 38.9% of the variation in the snail-to-urchin ratio (Intraclass Correlation Coefficient = 0.39), suggesting that the ratio varies substantially between regions.

<u>*Density summary*</u>

Overall, red turban snail densities were variable, with some sites having densities as high as 6.45 snails/m^2, while snails were absent at others (Table S2). The mean snail density across all sites was 1.14 ± 0.23 snails/m^2. The maximum density across all sites was similar for urchins (7.09 urchins/m^2), while the mean (3.33 ± 0.31 urchins/m^2) was slightly higher (Table S2).

Discussion

Here we find support for the effectiveness of protection from fishing, as well as crucial information on the effects of environmental and anthropogenic drivers on the densities of the red urchin (*M. franciscanus*) and red turban snail (*P. gibberosus*), two important reef grazers. We developed the snail-to-urchin ratio as a proxy for reef health and found that rocky reef ecosystems within protected areas in Barkley Sound had significantly higher snail-to-urchin ratios than nearby unprotected sites. The elevated ratios within protected areas indicate improved health as there were relatively fewer damaging urchin grazers and more turban snails, suggesting higher local kelp productivity (Shears & Babcock, 2003), which can balance out the detrimental effects of urchins (Harrold & Reed, 1985). Improved reef health within protected areas was paired with lower human activities related to fishing at protected sites (*i.e.*, fishing restrictions were respected by fishers), as evidenced by significantly lower numbers of boats fishing around protected sites. Red turban snail density was strongly negatively related to wave exposure, suggesting that wave exposure may be an essential environmental control for this species. Conversely, red sea urchin densities were not significantly related to any of the environmental variables tested, highlighting urchins' effectiveness at surviving varied conditions and contributing to their role as a widespread damaging grazer. However, there were some sites having few to no urchins and visible kelp.

Protected area effects on species density and ecosystem health

The findings of this study were consistent with our predictions on the effect of protection from fishing on the ratios of red turban snails to red sea urchins on rocky reefs, and support the effectiveness of protected areas in the temperate coastal waters of British Columbia. Rocky reefs located within protected areas were healthier than nearby, unprotected sites, as evidenced by the higher ratio of turban snail to urchin grazers at protected sites. Notably, this trend was observed between different types of protected areas, each with differing levels of protection. The sites with the highest ratios were found in the Broken Group Rockfish Conservation Area (Protection Level 4), which has year-round restrictions on commercial and recreational fishing of finfish (*e.g.*, rockfish, salmon), and the Numukamis Bay Finfish Closure Area (Protection Level 2), which only has finfish fishing closures during August and September (Fisheries and Oceans Canada, 2023, 2024a). The differences in restrictions may not result in behavioural differences among recreational fishers, with fishers avoiding both areas for fear of penalties. Our analysis supported the explanation that fishers avoid fishing within protected areas as we identified that fishers in Barkley Sound fish significantly less around protected sites compared to unprotected sites.

The reduced fishing effort within the protected areas may have led to higher snail-to-urchin ratios and healthier reefs due to several mechanisms. For instance, decreased recreational boat activity may have limited nutrient inputs from the dumping of boat sewage or waste, which could decrease phytoplankton productivity (Lohrenz et al., 1997) and restrict urchin recruitment (Birkeland, 1982; Strathmann, 1978). However, the most likely mechanism is due to fishing activity, and we focus on the role of fishing and its impacts on predation pressure as the primary drivers of differences in the snail-to-urchin ratio and reef health between protected and unprotected sites.

Restrictions on fishing can support healthier reefs by limiting urchin recruitment. In tropical regions, protected areas reduce the recruitment of a different harmful echinoderm species, the Crown-of-Thorns Starfish (*Acanthaster* spp.) (Kroon et al., 2021). Like red sea urchins, the Crown-of-Thorns Starfish is a damaging grazer that can reduce the cover of reef-building corals (De'ath et al., 2012), resulting in severe ecosystem impacts such as loss of critical habitats (Wilson et al., 2008). Protected areas can reverse these negative impacts from the sea star by promoting high biomass of fish communities, which predate upon the sea star's larval and juvenile stages (Kroon et al., 2020, 2021). Enhanced fish predator biomass within protected areas and subsequent regulation of damaging grazers have also been observed in temperate systems. For instance, within marine reserves in New Zealand, predatory fish populations are increased due to protection from fishing, and predation on juvenile urchins is significantly higher than in nearby areas where fishing is allowed (Babcock et al., 1999; Shears & Babcock, 2002). This increased predation led to reduced urchin densities and improved macroalgal communities, which were associated with increased densities of turban snails (Shears & Babcock, 2002, 2003). A similar process may be present in Barkley Sound, in which reduced fishing activity within the protected areas promotes larger populations of fish (*e.g.*, black rockfish (*Sebastes melanops*) or wolf eels (*Anarrhichthys ocellatus*)), which can feed on the pelagic urchin larvae or recently settled juveniles (Armstrong, 1996; Love et al., 2002). The increased predation of urchin larvae and juveniles would reduce urchin recruitment and density at the protected reefs and allow for the growth of healthy kelp forests and the trend of higher snail densities that we observed in the protected areas.

Aside from explicitly harvesting predators from reefs, fishing activity may also deter urchin predators such as the sea otters present in Barkley Sound (Hughes et al., 2019), causing the otters to spend more time in protected areas away from boats. Currently, there are a few otters present within the sound (A. Jones, personal observation), though large established populations are not present (Watson & Estes, 2011). If otters preferentially spend their time in protected areas away from fishing boats, they could contribute to the reduced urchin densities and healthier reefs in protected areas through predation (Estes & Palmisano, 1974). Additionally, by lowering urchin numbers and thus promoting kelp growth (Estes & Palmisano, 1974), otters could contribute to the trend of increased snail densities within protected areas (Shears & Babcock, 2003) and higher snail-to-urchin ratios.

Interestingly, one of the protected areas within Barkley Sound, the Baeria Rocks Ecological Reserve, had urchin barrens and lower reef health (based on lower snail-to-urchin ratios) compared to the other two protected areas examined. This occurred despite the reserve having the strictest regulations (Protection Level 5), with no human access allowed except for permitted researchers (BC Parks, 2025). It does not appear that fishers are fishing illegally within this reserve, as the recreational boat fishing location analysis showed negligible numbers of boats fishing near these sites, implicating the role of other mechanisms supporting urchin barrens within this reserve. Potentially, the ocean currents around Baeria Rocks promote high urchin recruitment (Farina et al., 2018), or the higher mean SST in this protected area negatively impacts kelp survival (Luning & Freshwater, 1988), thus hurting turban snail survival. Additionally, it is possible that predation pressure on urchins is lower within this reserve than in the other protected areas due to factors other than fishing, such as increased abundance of higher trophic level predators (*e.g*., lingcod; *Ophiodon elongatus*) which consume the predators of the urchins (Beaudreau & Essington, 2007). Further research within this reserve is needed to elucidate the forces leading to lower reef health.

An important next step in the evaluation of the protected areas within Barkley Sound is to investigate whether there are differences in the predator communities between protected and unprotected sites that could explain the trends in the snail-to-urchin ratio that we observed. One aspect of this analysis could involve tracking the sea otters within the sound to see which areas they prefer to stay in and feed. An additional manipulation could be tethered predation experiments, where urchins are fixed in place on different reefs, and the predation mortality is observed to quantify the predation pressure on urchins (Shears & Babcock, 2002). The quantification of the predation levels between the protected and unprotected sites in Barkley Sound would provide explicit evidence of the effect of fishing on predator communities and, subsequently, on the snail-to-urchin ratios and reef health.

Environmental drivers of species density

The results of this study highlighted how various environmental factors are related to the density of red turban snails on rocky reefs. Consistent with our predictions, we found that the log-transformed snail densities were significantly negatively related to openness, a proxy for the wave exposure of the reef. Stronger and/or more frequent waves may negatively impact red turban snails by dislodging them or reducing the time when conditions are calm enough for them to forage (Etter, 1996). This can have major implications on the populations of this species as reductions in foraging time for related species have been shown to decrease individual growth rates (Etter, 1996). Slower growth rates can lead to lower densities of snails as smaller snails are more vulnerable to predation (Richardson & Brown, 1992) and produce fewer offspring (Spight & Emlen, 1976). Additionally, powerful waves can dislodge kelp (Graham et al., 2007), which the snails rely on for food (Mazariegos-Villarreal et al., 2017) and as a refuge to escape benthic predation (Watanabe, 1984). Dislodgment, loss of food, and increased predation may be the driving causes of lower red turban snail density with increasing wave exposure.

Notably, the relationship between red turban snail density and openness is only linear after log-transforming snail density, suggesting the effects of increasing wave exposure are more severe initially before levelling off. A possible rationalization for this is that as wave exposure increases and more kelp is removed, there is eventually a point where the majority of the available kelp has been dislodged and further increases in wave exposure do not translate into an equivalent removal of food and protection for the snails. This interpretation is supported by research demonstrating that kelp loss shows a saturating relationship with increasing wave height, suggesting there is a point where further wave exposure does not lead to equivalent kelp losses (Cavanaugh et al., 2011).

We also found that red sea urchin density was not significantly related to any of the environmental drivers tested, although trends were observed for some of the environmental variables. There was a trend of higher urchin density on solid substrate, possibly because loose substrates have been shown to deter urchins and impair their movement (Kawamata et al., 2011; Laur et al., 1986). Urchins move with appendages called tube feet, which are most effective on solid, flat seafloor and are not as efficient on soft, loose sediments (Laur et al., 1986). Furthermore, loose sediments can make it harder for urchins to secure themselves to the seafloor during strong waves, leading to increased mortality (Laur et al., 1986).

One possible reason the observed trend was insignificant is due to the sampling site selection. Under the RLS methodology, survey sites were selected based on them consisting of ~90% hard substratum. Thus, even though areas of seafloor dominated by sand and kelp were observed, the transects overall consisted of primarily loose rubble (shell hash, granules, pebbles, cobbles) and solid (boulders, solid rock slabs) substrates. While loose rubble substrate may make it more difficult for urchins to move and increase their mortality in high flow conditions (Laur et al., 1986), the differences in conditions between loose rubble and solid substrate would likely not be as pronounced as for sand and solid substrate. During photo-quadrat analysis, urchins appeared to be qualitatively less dense on sandy sediments, but the methodology could not distinguish fine-scale, within-transect variations. Future surveys may benefit from including some new sites with more significant proportions of fine sediments to further investigate the effect of seafloor type on red sea urchin density. Additionally, it may be helpful to include an analysis of the seafloor surrounding the sampled reefs. For example, one of the sites with the fewest urchins and healthiest kelp forest was surrounded by sandy bottom (J. M. Schuster, personal observation), even though the reef where the sampling occurred was dominated by solid substrate. Potentially, the seafloor types around a particular reef can deter urchin movement onto the reef, leading to lower urchin densities.

Additionally, there was a trend of decreasing urchin density with increasing openness, but only after the openness reached intermediate levels. This trend suggests that red sea urchins may be resistant to wave exposure up until a point where they cannot secure themselves any longer, and dislodgment reduces the population density. Previous tests have shown that the proportion of green sea urchins dislodged by waves/currents is exponentially related to water velocity (Siddon & Witman, 2003), meaning the number of urchins dislodged by waves is negligible at lower water velocities but rapidly increases at higher velocities. This exponential relationship between urchin dislodgment and water velocity could contribute to the observed trend in urchin density, where density only starts to decrease at high wave exposure. Furthermore, the urchins' ability to shut down their metabolisms even if waves remove their kelp food (Schuster & Bates, 2023; Spindel et al., 2021) suggests that only when waves become so powerful as to remove the urchins is there a decline in density.

One potential reason that the relationship between urchin density and wave exposure was not significant may be related to seasonal movements of red sea urchins within Barkley Sound. Red sea urchins in Barkley Sound are known to migrate to deeper waters in the winter to avoid powerful storms and return to the shallows in the summer when wave strength declines (Pace, 1975). This behaviour could allow urchins to persist at sites with higher wave exposure as they can avoid the most damaging wave events and limit their time on reefs to when conditions are calmer. It may be beneficial to complete multiple surveys throughout the year at the RLS sites within Barkley Sound to see if this migratory behaviour is contributing to the presence of urchins at more exposed sites.

In contrast to our expectations, mean SST was found not to be related to the densities of either red turban snails or red sea urchins, even though temperature has previously been shown to affect each of these species on an individual level (Schuster & Bates, 2023; Wong & Hofmann, 2020). The lack of a relationship between temperature and the densities of these grazers may be because the temperatures observed within Barkley Sound were not high enough to cause an effect on these species (Schuster & Bates, 2023; Wong & Hofmann, 2020). Another potential explanation relates to the specific temperature data used. Satellite measurements of SST may be too coarse to piece apart the temperature regimes these grazers experience at depth at the different survey sites. As annual RLS surveys continue in Barkley Sound, installing temperature loggers on the seafloor where the transects are laid could provide accurate, *in situ* measurements of the temperatures experienced by the rocky reef communities. Potentially, these *in situ* measurements may improve our ability to tease apart the effects of temperature on snail and urchin density and prove more useful than SST data derived from remote sensing and modelling approaches.

Conclusions

Overall, this study provides important insights that could have far-reaching implications for both the present and future of rocky reef conservation. We found evidence of the environmental drivers controlling the density of a beneficial (red turban snail) and a detrimental (red sea urchin) grazer species. Wave exposure appears to be a decisive controlling factor of the density of red turban snails, a finding that is especially critical in the face of future changes to temperature and wave energies. Climate change is increasing the wave power within the oceans (Reguero et al., 2019), which may reduce the sites where red turban snails can live in high densities. Additionally, as ocean temperatures rise due to climate change (Su et al., 2023), the ability of red turban snails to grip the seafloor may be reduced (Clayman & Seebacher, 2019), putting them at elevated risk of dislodgment during wave events. The combination of increased wave action and decreased attachment strength may significantly reduce the areas where red turban snails can survive. This is particularly important for rocky reef ecosystem structure given that losses of red turban snails could negatively affect macroalgal communities through reductions in nutrient recycling (Bracken et al., 2018) and grazing of harmful epiphytic algae (Guidone et al., 2010).

In contrast to the turban snail results, no significant relationships existed between red sea urchin density and the environmental variables tested. Red sea urchins appear to tolerate a wide range of environmental conditions and are not tightly controlled by environmental factors. This could be due in part to the urchins' ability to go into metabolic shutdown to prevent starvation (Schuster & Bates, 2023; Spindel et al., 2021) or that they have been too widely released from predation throughout their range (Hamilton & Caselle, 2015; Harvell et al., 2019; Kenyon, 1969). These findings suggest that without management intervention, red sea urchins can continue to be a damaging grazer species at high densities across vast regions, enacting strong top-down control of rocky reef ecosystems and creating barren habitats.

Our results show that an effective management strategy for promoting lower urchin densities and healthier reefs is the use of protected areas. The protected areas in Barkley Sound reduced fishing activities at protected sites, presumably leading to reduced fishing pressure. Reduced urchin densities at protected sites were paired with increased snail densities and the presence of healthy, intact kelp forests at some sites, highlighting the effects that grazers can have on ecosystem structure. Ultimately, protected areas can restore trophic interactions that humans have disrupted, leading to proper top-down control of rocky reef communities and renewal of natural ecosystem structuring.

Figures

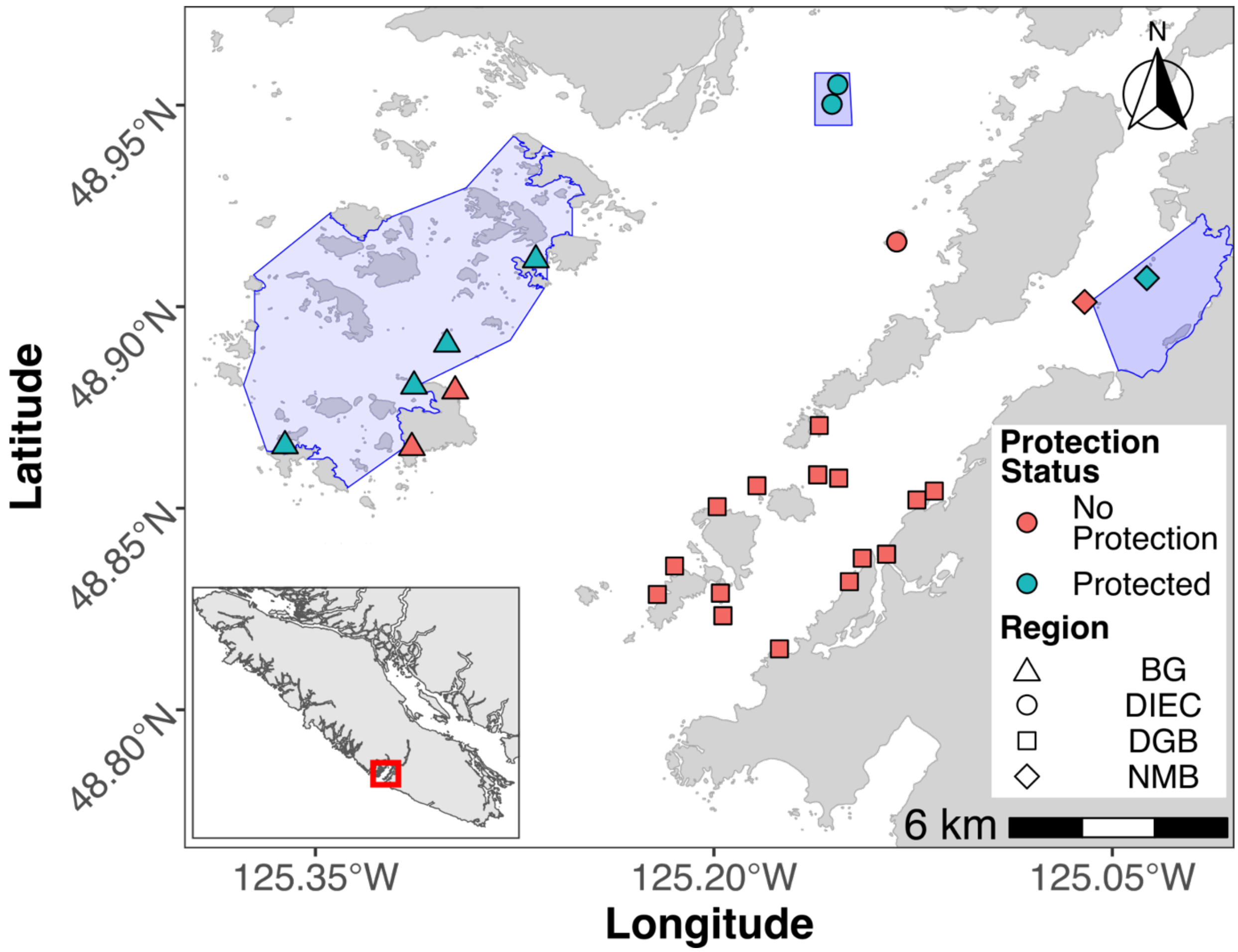

Figure 1. Locations of Reef Life Survey study sites (n = 26) within Barkley Sound, BC, Canada, which were sampled in April and May of 2024. The colours indicate the protection-from-fishing status of each site. Some sites have been shifted slightly to prevent overlap. Region classifications are indicated by the shapes with the region codes corresponding to: BG = Broken Group, DIEC = Deep Imperial Eagle Channel, DGB = Deer Group/Bamfield, and NMB = Numukamis Bay. Areas protected from fishing are shown with blue shade: farthest west = Broken Group Rockfish Conservation Area, central north = Baeria Rocks Ecological Reserve, farthest east = Numukamis Bay Finfish Closure Area. Inset is a map of Vancouver Island illustrating the location of Barkley Sound (red square).

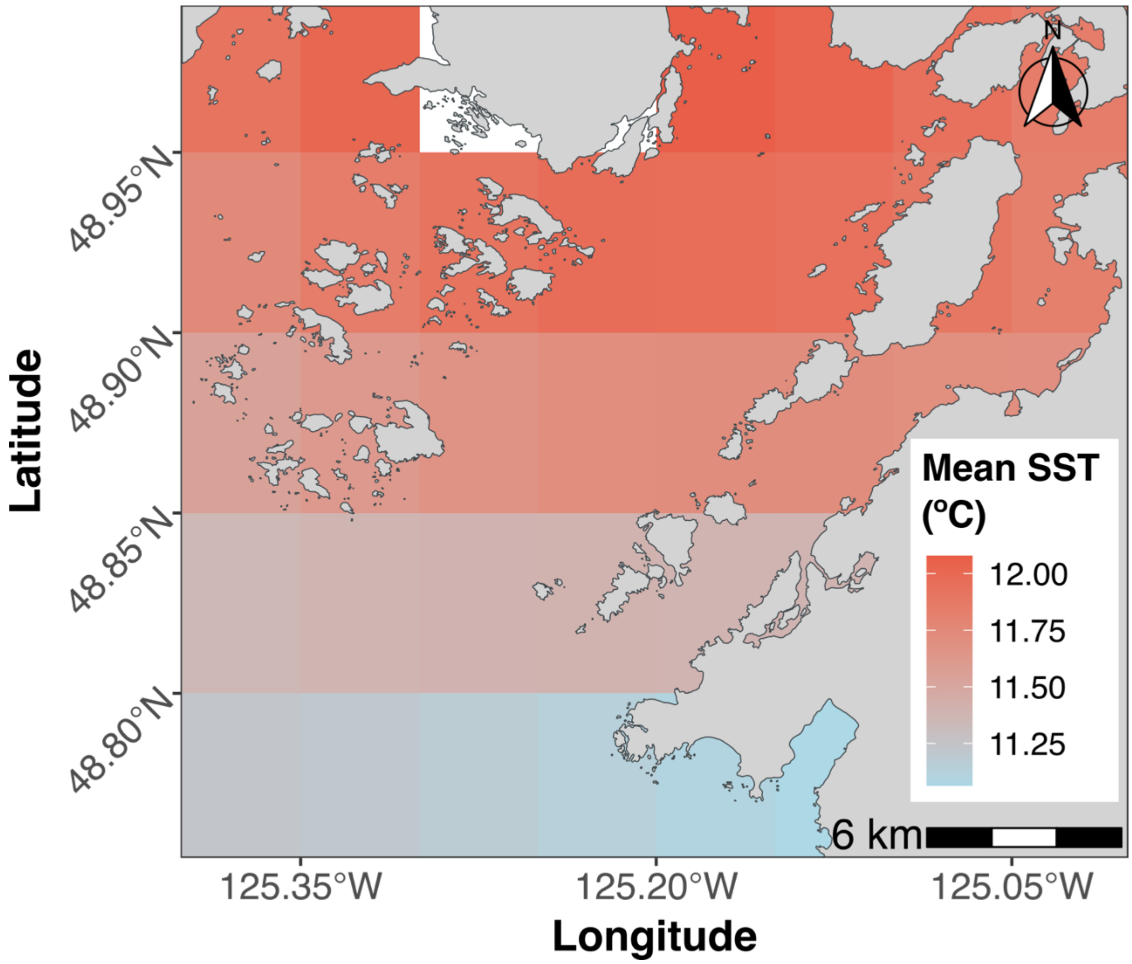

Figure 2. Mean sea surface temperature (SST) in Barkley Sound, BC, Canada, from daily temperature measurements from the Global Ocean OSTIA Sea Surface Temperature and Sea Ice Analysis product (European Union-Copernicus Marine Service, 2015). Mean SST was calculated by averaging the daily temperatures within 0.05º latitude x 0.05º longitude cells for the year before Reef Life Survey subtidal surveys within Barkley Sound in April and May of 2024 (2023-04-22 to 2024-05-03).

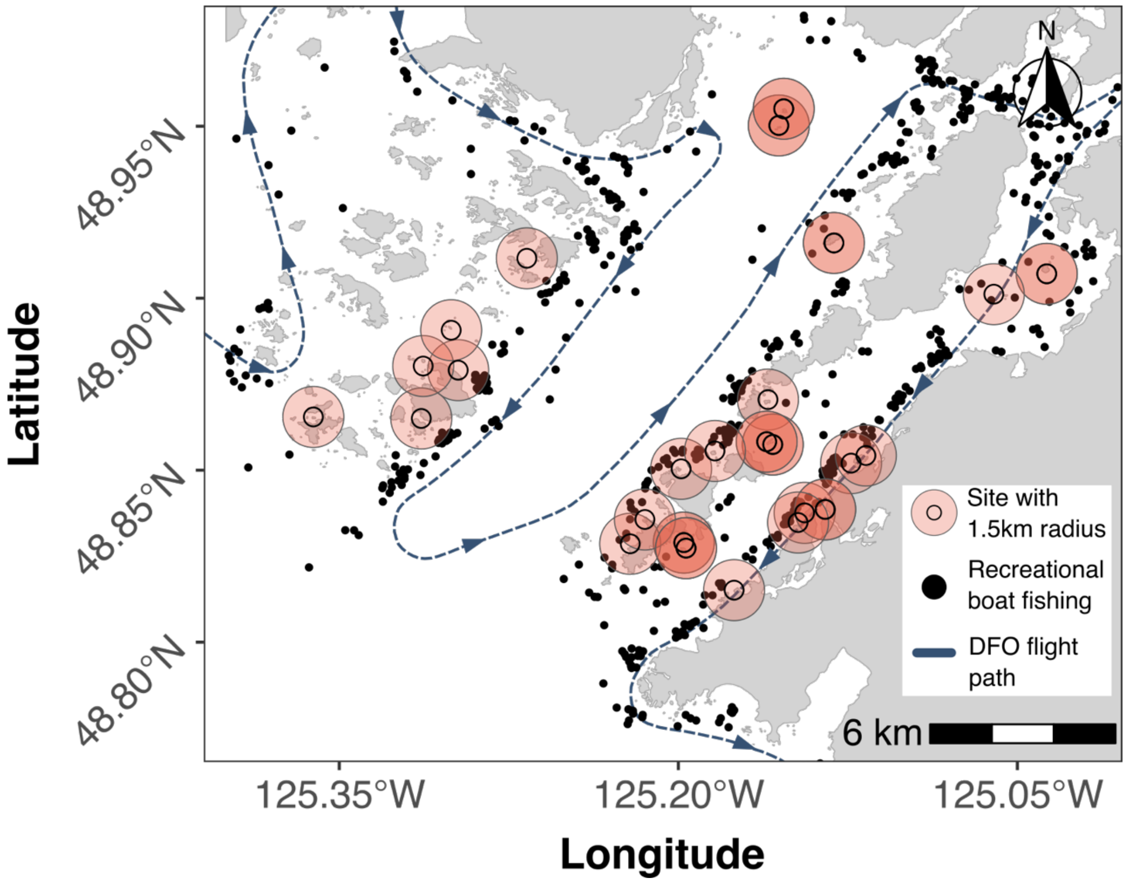

Figure 3. Example of the raw data from DFO flyover surveys (June 1–September 30, 2023) indicating the locations of recreational boats fishing (black dots) with 1.5 km radii (red-filled circles) around each Reef Life Survey site (open black dots) in Barkley Sound, BC, Canada. Subtidal surveys were conducted at each site in April and May of 2024. The DFO surveys sometimes grouped boats that were close together as one point, so some points indicate multiple boats, but this has been omitted for ease of viewing. The flight path taken by DFO surveyors is shown (dashed blue line) with arrows showing the direction of flight. DFO surveys were completed in the summers of 2021-23. The mean numbers of recreational boats fishing within 1.0, 1.5, and 2.0 km radii per year were calculated to compare fishing activity between protected and unprotected sites.

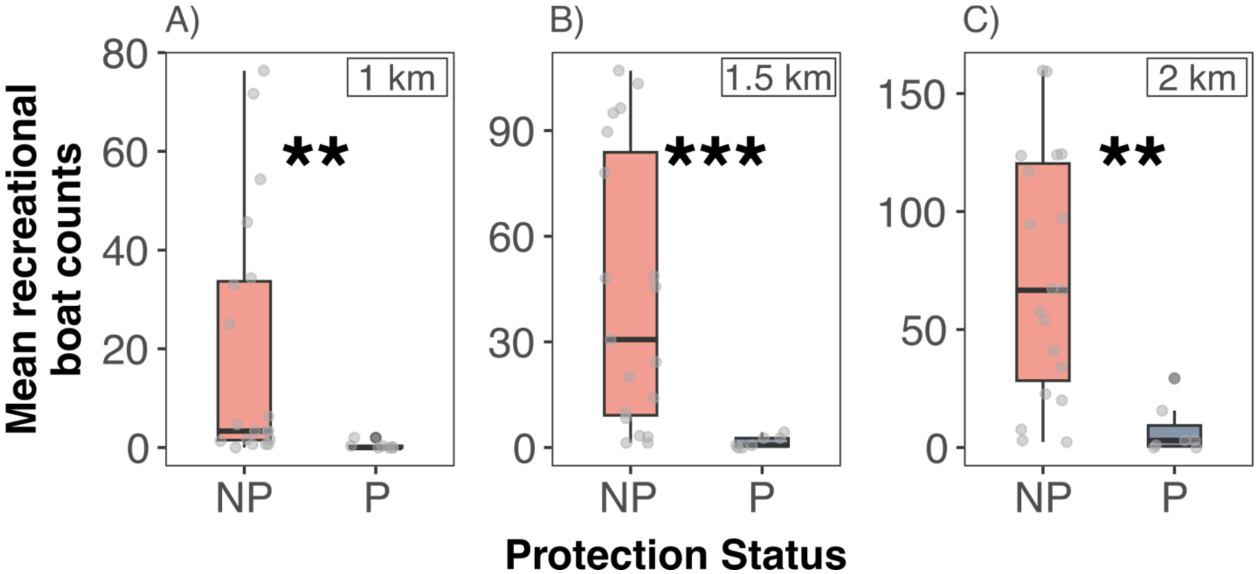

Figure 4. Distributions of the mean number of recreational boats fishing (per year) within A) 1.0, B) 1.5, and C) 2.0 km of Reef Life Survey sites in Barkley Sound, BC, Canada, separated by protection-from-fishing status (NP = No Protection, P = Protected). Raw data are shown with grey circles and have been jittered across the x-axis for ease of viewing. Means were calculated from DFO flyover survey data of recreational fishing boat locations from 2021-23. Asterisks indicate level of significance based on Wilcoxon rank sum tests (* = P < 0.05, ** = P < 0.01, *** = P < 0.001).

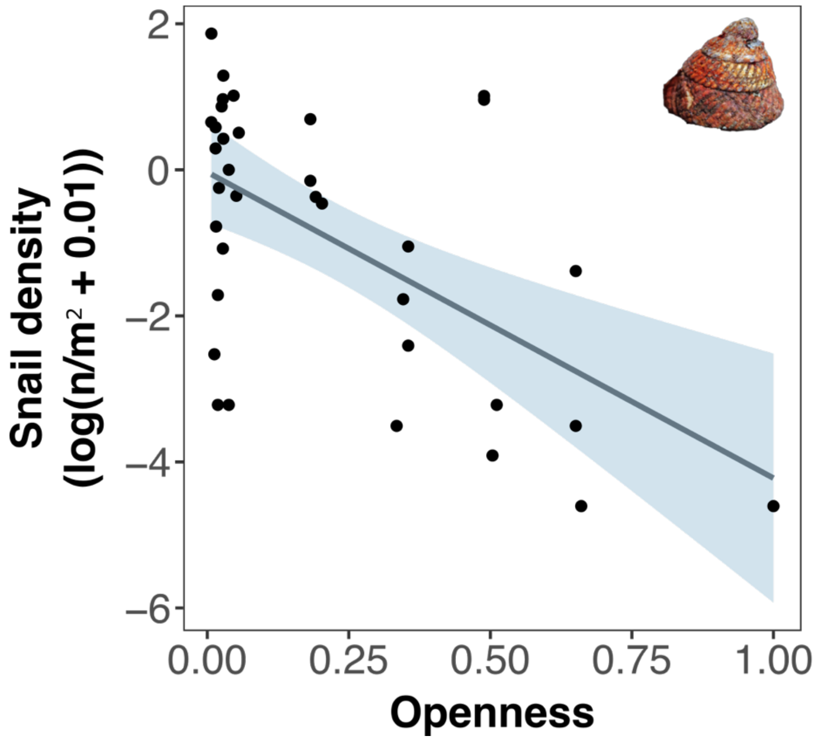

Figure 5. The relationship of openness (normalized) with the log-transformed red turban snail (*P. gibberosus*) density from Reef Life Survey sites in Barkley Sound, BC, Canada, in April and May of 2024. Raw data (black points) are shown with a line of best fit (blue line) and 95% confidence intervals (blue shade).

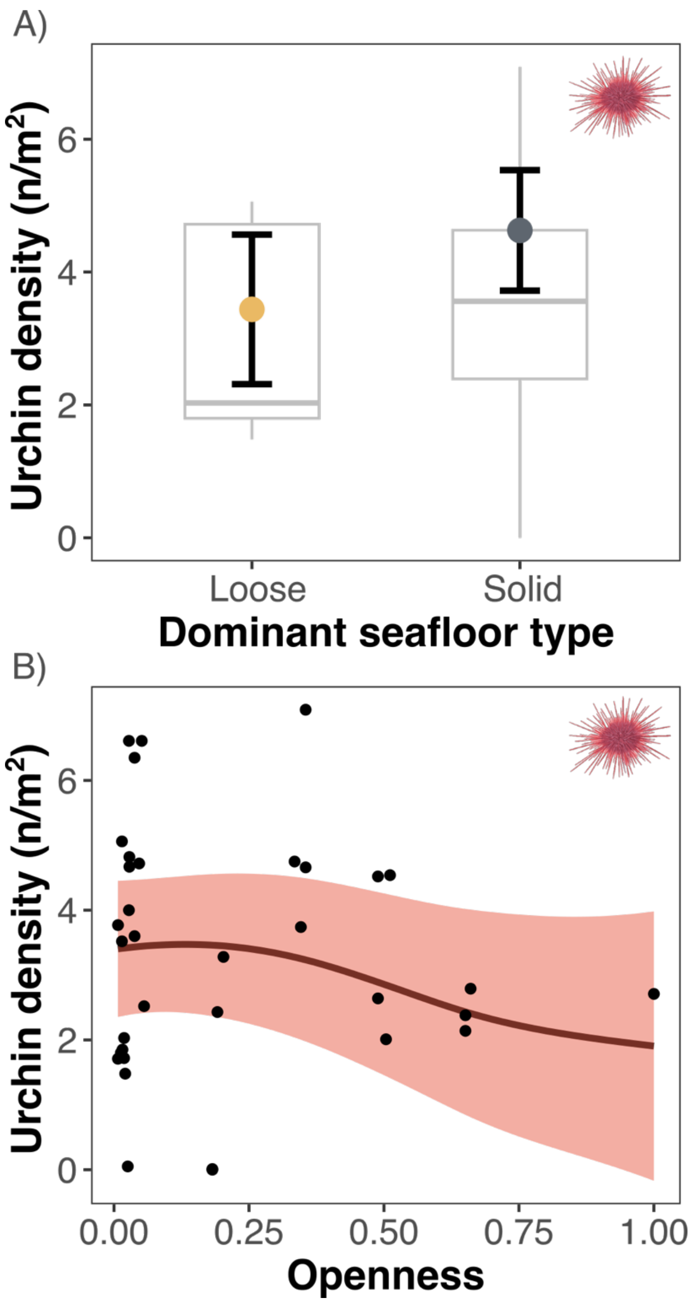

Figure 6. A) Distributions of red sea urchin (*M. franciscanus*) density between seafloor types (Loose = loose rubble substrate and solid = solid rock substrate) with model predictions (coloured points) and 95% confidence intervals (black error bars) from a generalized additive mixed model (GAMM). B) Relationship of red sea urchin density and openness (normalized) with raw data (black points) and GAMM predictions (black line) with a 95% confidence interval (red shade) shown. Predictions made by holding other continuous variables at their mean, and categorical and random variables at their reference level. For openness predictions, a sequence of 100 openness values was generated. Urchin densities were obtained from subtidal Reef Life Surveys at sites in Barkley Sound, BC, Canada, in April and May of 2024.

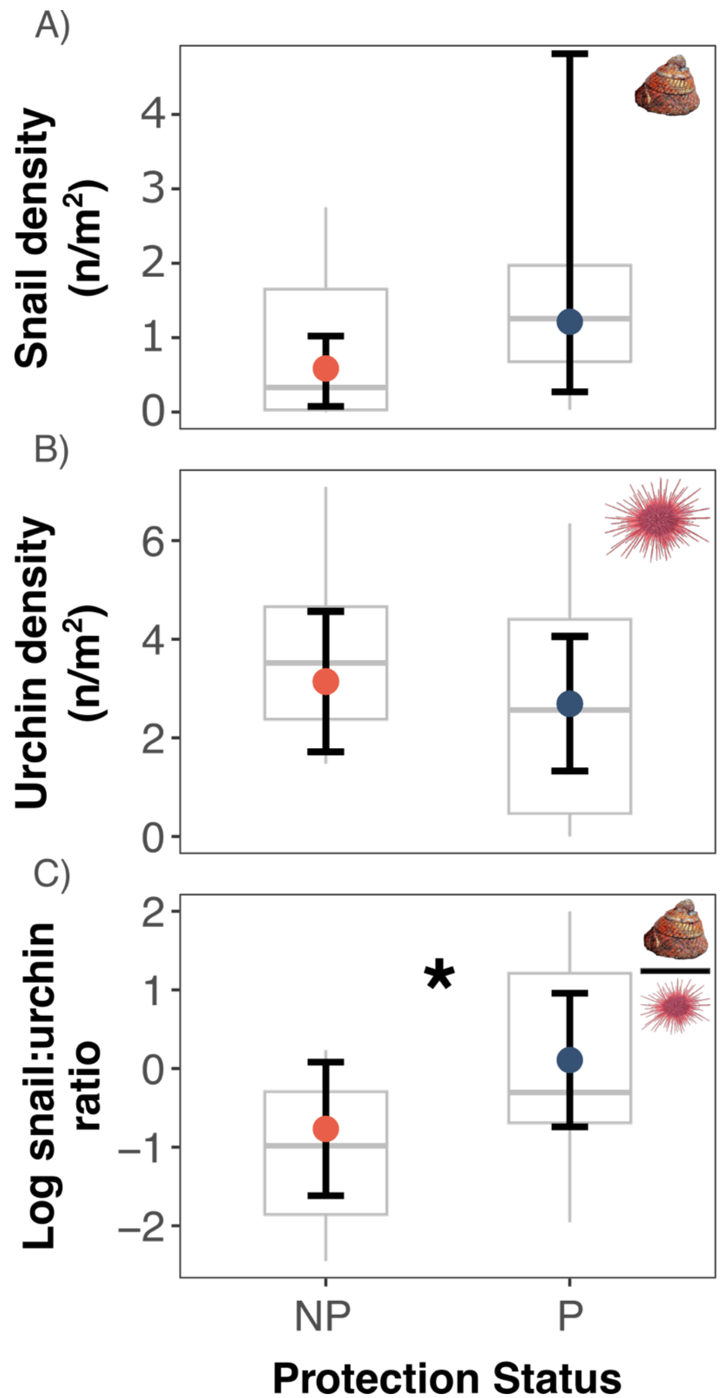

Figure 7. Distributions of the A) red turban snail (*P. gibberosus*) density, B) red sea urchin (*M. franciscanus*) density, and C) log snail-to-urchin ratios at Reef Life Survey sites in Barkley Sound, BC, Canada, separated by protection-from-fishing status (NP = No Protection, P = Protected). Coloured points are model predictions (A = linear model with square-root-transformed response, B and C = linear mixed-effects models) with 95% confidence intervals (black error bars), and the asterisk indicates $P < 0.05$. Predictions in B) and C) were averaged over the levels of the random effect of region. One outlier was removed in A).

Tables

Table 1. Site protection classifications adapted from the ProtectedSeas Level of Fishing Protection system (ProtectedSeas, n.d.) used to classify Reef Life Survey sites in Barkley Sound, BC, Canada, as either protected or unprotected from fishing.

Protection score	Description	RLS protection status
1 – Least Restrictive	No known restrictions on marine life removal beyond national or subnational generally applicable restrictions	Unprotected
2 – Less Restrictive	At least one species- or gear-specific restriction applies beyond generally applicable restrictions	Protected
3 – Moderately Restrictive	Several species- or gear-specific restrictions apply	Protected
4 – Heavily Restrictive	Marine life removal is mostly prohibited, with few exceptions	Protected
5 – Most Restrictive	Marine life removal is prohibited or entry is prohibited	Protected

Table 2. Seafloor/substrate categories based on sediment sizes adapted from the Wentworth (1922) scale. The substrate scores were used to classify the dominant substrate type of photo-quadrats taken during Reef Life Survey surveys in Barkley Sound, BC, Canada, in 2024.

Adapted Wentworth size class	Size Range (mm)	Substrate Score
Silt/sand	< 2.00	Sandy/soft
Granule/pebble/cobble	2.00 – 256	Loose rubble
Boulder/solid rock	256 <	Solid

Table 3. Results of Wilcoxon rank sum tests of the mean number of recreational boats fishing (per year) within the specified radii of each Reef Life Survey site in Barkley Sound, BC, Canada. Bold text indicates significance, and asterisks indicate the level of significance (* = P < 0.05, ** = P < 0.01, *** = P < 0.001).

Radius tested	W value	P–value
1.0 km	122	**1.39×10^{-3} ** **
1.5 km	125	**7.93×10^{-4} *** **
2.0 km	122	**1.46×10^{-3} ** **

Table 4. Summary of the predictors used in the environmental generalized additive model for log-transformed red turban snail (*P. gibberosus*) density at Reef Life Survey sites within Barkley Sound, BC, Canada, in 2024. The intercept used for dominant seafloor type was "loose rubble substrate". Bold text indicates significance, and asterisks indicate the level of significance (* = P < 0.05, ** = P < 0.01, *** = P < 0.001). Model sample size was n = 35.

Variable	Parametric/smooth	Estimate	EDF	Test statistic	P–value
(Intercept)	Parametric	–1.58	N/A	t = –3.06	**4.40×10^{-3} ** **
Dominant seafloor type (Solid)	Parametric	0.865	N/A	t = 1.43	0.163
Openness	Smooth	N/A	0.949	F = 2.08	**1.01×10^{-4} *** **
Mean SST (ºC)	Smooth	N/A	2.02×10^{-5}	F = 0.00	0.746

Table 5. Summary of the predictors used in the environmental generalized additive mixed model for red sea urchin (*M. franciscanus*) density at Reef Life Survey sites within Barkley Sound, BC, Canada, in 2024. The intercept used for dominant seafloor type was "loose rubble substrate," and the region variable was fit as a random effect (denoted RE below). Bold text indicates significance, and asterisks indicate the level of significance (* = P < 0.05, ** = P < 0.01, *** = P < 0.001). Model sample size was n = 35.

Variable	Parametric/smooth	Estimate	EDF	Test statistic	P–value
(Intercept)	Parametric	1.66	N/A	t = 1.58	0.125
Dominant seafloor type (Solid)	Parametric	1.19	N/A	t = 1.93	0.0638
Openness	Smooth	N/A	1.21	F = 0.645	0.0859
Mean SST (ºC)	Smooth	N/A	0.401	F = 0.484	0.195
Region	Smooth (RE)	N/A	2.59	F = 6.77	**2.82×10^{-4} *****

Table 6. Summary of the predictors used in the protection status linear model for square-root-transformed red turban snail (*P. gibberosus*) density at Reef Life Survey sites within Barkley Sound, BC, Canada, in 2024. The intercept used for protection status was "No Protection." Bold text indicates significance, and asterisks indicate the level of significance (* = P < 0.05, ** = P < 0.01, *** = P < 0.001). Model sample size was n = 35.

Variable	Estimate	Std. Error	z–value	P–value
(Intercept)	0.765	0.123	6.24	**4.32×10^{-10} *****
Protected status (Protected)	0.337	0.229	1.47	0.142

Table 7. Summary of the predictors used in the protection status linear mixed-effects model for red sea urchin (*M. franciscanus*) density at Reef Life Survey sites within Barkley Sound in 2024. The intercept used for protection status was "No Protection." Random effects, residual variance, and standard deviation are shown below. Bold text indicates significance, and asterisks indicate the level of significance (* = P < 0.05, ** = P < 0.01, *** = P < 0.001). Model sample size was n = 35.

Variable	Estimate	Std. Error	z–value	P–value
(Intercept)	3.14	0.726	4.33	**1.52×10^{-5} *** **
Protected status (Protected)	–0.450	0.872	–0.516	0.606

Random effects

Groups	Variance	St. Dev.
Region	0.738	0.859
Residual	2.68	1.64

Table 8. Summary of the predictors used in the linear mixed-effects model for the red turban snail (*P. gibberosus*)-to-red sea urchin (*M. franciscanus*) ratio at Reef Life Survey sites within Barkley Sound, BC, Canada, in 2024. The intercept used for protection status was "No Protection." Random effects, residual variance, and standard deviation are shown below. Bold text indicates significance, and asterisks indicate the level of significance (* = P < 0.05, ** = P < 0.01, *** = P < 0.001). Model sample size was n = 35.

Variable	Estimate	Std. Error	z–value	P–value
(Intercept)	–0.768	0.433	–1.77	0.0765
Protected status (Protected)	0.876	0.435	2.02	**0.0439 ***

Random effects

Groups	Variance	St. Dev.
Region	0.436	0.660
Residual	0.684	0.827

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Appendix

Site Information

Table S1. Summary of sites (n = 26) sampled during the Reef Life Survey sampling in Barkley Sound, BC, Canada, in April and May of 2024. Region classifications were based on distinct island groupings (BG = Broken Group, DIEC = Deep Imperial Eagle Channel, DGB = Deer Group/Bamfield, and NMB = Numukamis Bay). The sites with two depth values correspond to sites where two separate transects were done. Protection score was scored according to the ProtectedSeas Level of Fishing Protection categories (descriptions available at https://navigatormap.org/methodology/).

Site code	Site name	Region	Date	Depth (m)	Location	Protection score
BMSC1	Dodger Channel	DGB	2024-04-25	5.0, 6.5	48.82895 N, 125.1976 W	1
BMSC2	Kirby	DGB	2024-04-29	4.0	48.85040 N, 125.1988 W	1
BMSC3	Ohiat	DGB	2024-04-29	6.0	48.85558 N, 125.1838 W	1
BMSC4	Kii xin	DGB	2024-04-29	8.5	48.81512 N, 125.1753 W	1
BMSC5	Taylor Rock	DGB	2024-04-23	6.0, 6.5	48.82733 N, 125.1966 W	1
BMSC6	Baeria Rocks South Island	DIEC	2024-04-22	8.0, 11.0	48.95023 N, 125.1555 W	5
BMSC8	Baeria Rocks North Island Northside	DIEC	2024-04-22	7.5, 8.5	48.95508, N 125.1534 W	5
BMSC9	Eagle Bay	DGB	2024-04-23	6.5	48.83479 N, 125.1470 W	1
BMSC10	Ross Islets Slug Island	DGB	2024-04-26	4.5	48.87052 N, 125.1603 W	1

BMSC11	Wizard Island South	DGB	2024-04-26	5.0, 7.5	48.85747 N, 125.1582 W	1
BMSC12	Wizard Island North	DGB	2024-04-26	4.5, 7.0	48.85828 N, 125.1609 W	1
BMSC13	Effingham West	BG	2024-05-01	3.0	48.86503 N, 125.3137 W	2
BMSC14	Effingham Archipelago	BG	2024-05-01	6.0	48.87908 N, 125.2974 W	2
BMSC15	Raymond Kelp Rock	BG	2024-05-01	6.5	48.88028 N, 125.3129 W	4
BMSC16	Faber Islets	BG	2024-05-02	7.5	48.89070 N, 125.3005 W	4
BMSC17	Wouwer Channel	BG	2024-05-02	5.8	48.86548 N, 125.3615 W	4
BMSC18	Eussen Rock	BG	2024-05-02	8.5	48.91162 N, 125.2670 W	4
BMSC19	Ed King SW Pyramid	DGB	2024-04-25	8.5	48.82860 N, 125.2213 W	1
BMSC20	Ed King East	DGB	2024-04-25	6.7	48.83567 N, 125.2148 W	1
BMSC21	Dixon SW	DGB	2024-04-30	6.5	48.85205 N, 125.1236 W	1
BMSC22	Dixon Inside	DGB	2024-04-30	5.5	48.85427 N, 125.1170 W	1
BMSC23	Aguilar Point	DGB	2024-05-03	6.7	48.83759 N, 125.1441 W	1

BMSC24	Swiss Boy	DIEC	2024-04-24	5.5, 10.5	48.91607 N, 125.1312 W	1
BMSC25	Goby Town	DGB	2024-04-23	5.5, 6.0	48.83859 N, 125.1350 W	1
BMSC26	Hosie South	NMB	2024-04-24	6.5, 8.0	48.90710 N, 125.0370 W	2
BMSC27	San Jose North Island	NMB	2024-05-03	8.5	48.90118 N, 125.0604 W	1

Raw density and ratio data

Table S2. The raw red turban snail (*P. gibberosus*) and red sea urchin (*M. franciscanus*) densities (# of individuals/m^2) and log snail-to-urchin ratio from Reef Life Survey sampling at sites in Barkley Sound, BC, Canada, in April and May of 2024. The protection-from-fishing status for each site is also indicated, along with if there was extensive kelp present at the site.

Site code	Depth (m)	Snail density	Urchin Density	Snail-to-urchin ratio	Protection status	Kelp present
BMSC1	5.0	2.74	4.52	–0.22	No protection	No
BMSC1	6.5	2.60	2.64	–0.01	No protection	No
BMSC10	4.5	0.07	1.80	–1.35	No protection	No
BMSC11	5.0	2.62	6.61	–0.40	No protection	No
BMSC11	7.5	0.33	4.00	–1.07	No protection	No
BMSC12	4.5	0.08	7.09	–1.90	No protection	No
BMSC12	7.0	0.34	4.66	–1.13	No protection	No
BMSC13	3.0	6.45	3.77	0.23	No protection	No
BMSC14	6.0	1.65	2.52	–0.18	No protection	No
BMSC15	6.5	2.37	0.05	1.60	Protected	Yes
BMSC16	7.5	0.62	3.28	–0.72	Protected	No

BMSC17	5.8	1.91	1.71	0.05	Protected	No
BMSC18	8.5	0.45	1.85	–0.61	Protected	No
BMSC19	8.5	0.00	2.71	–2.43	No protection	No
BMSC2	4.0	2.75	4.72	–0.23	No protection	No
BMSC20	6.7	0.02	4.75	–2.20	No protection	No
BMSC21	6.5	0.16	3.74	–1.34	No protection	No
BMSC22	5.5	0.77	1.48	–0.28	No protection	No
BMSC23	6.7	0.03	4.54	–2.06	No protection	No
BMSC24	10.5	0.24	2.38	–0.98	No protection	No
BMSC24	5.5	0.02	2.14	–1.86	No protection	No
BMSC25	5.5	0.03	2.03	–1.71	No protection	No
BMSC25	6.0	0.17	1.72	–0.98	No protection	No
BMSC26	6.5	0.85	0.00	1.93	Protected	Yes
BMSC26	8.0	1.99	0.01	2.00	Protected	Yes
BMSC27	8.5	0.68	2.43	–0.55	No protection	No
BMSC3	6.0	0.69	6.61	–0.98	No protection	No
BMSC4	8.5	0.00	2.79	–2.45	No protection	No
BMSC5	6.0	1.33	5.06	–0.58	No protection	No
BMSC5	6.5	1.78	3.52	–0.30	No protection	No
BMSC6	11.0	0.03	3.60	–1.96	Protected	No
BMSC6	8.0	0.99	6.35	–0.80	Protected	No
BMSC8	7.5	3.62	4.82	–0.12	Protected	No
BMSC8	8.5	1.52	4.67	–0.49	Protected	No

BMSC9	6.5	0.01	2.01	–2.00	No protection	No

Statistical Analyses

Model formulae

The models used in this analysis were fit as seen below:

Environmental models (GAM and GAMM)

Log(Red turban snail density + 0.01) ~ s(Mean SST) + s(Normalized openness) + Dominant seafloor type

Red sea urchin density ~ s(Mean SST) + s(Normalized openness) + Dominant seafloor type + s(Region, bs = "re")

Protection status models (LM and LMM)

Square-root(Red turban snail density) ~ Protection status

Red sea urchin density ~ Protection status + (1 | Region)

Snail-to-urchin ratio model (LMM)

Red turban snail to red sea urchin ratio ~ Protection status + (1 | Region)

Testing distributions for the snail data

When modelling the red turban snail density in the generalized additive model, we initially attempted to use the raw density data with a Gaussian distribution. The residuals indicated this was not valid, so we tried other distribution families (Gamma, Tweedie, Scat), but none provided acceptable fits. We then tried a simple log transformation of the snail density with a Gaussian distribution, and the fit was much improved. We ran into similar problems when making the red turban snail protection status linear model. However, in this case, the log transformation resulted in the violation of the assumption of homoscedasticity. We then tried a square-root transformation and this produced the best fit.

Moran's I test for spatial autocorrelation

To check that there was not an unacceptable level of spatial autocorrelation between sites in the models, we used a Moran's I test of the model residuals. To increase our confidence in the results, we tried two separate methods of calculating the spatial weights matrix used in the Moran's I test. The first method was a simple neighbour matrix, with only transects from the same sites considered neighbours in the weight matrix. We also tried the test with neighbours from farther distances and found the same results. The second method involved using an inverse distance weight matrix for the Moran's I test. A small constant was added to the transects from the same sites so they were considered to be a few meters away from each other. We used two-sided Moran's I tests and all final models had insignificant results of the Moran's I tests on the model residuals, indicating the spatial autocorrelation had been adequately accounted for.