

Spatial variation in keystone predation on foundation species drives local and landscape-scale diversity patterns

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Data availability statement

Our scripts and data on Zenodo can be accessed by reviewers at the following link

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Abstract

The proposition that keystone predators increase biodiversity has been criticized for failing to consider the species facilitated by, rather than outcompeted by, dominant prey. Here, we revisit the relationship between the original keystone species, *Pisaster ochraceus*, and the diversity of rocky intertidal communities inclusive of competitively dominant prey, competitively subordinate space-holders, and the many taxa facilitated by both. Using a system of beach-bounded rocky headlands, we document landscape-scale variation in predation pressure, with lower *Pisaster* densities and lower mid-intertidal mussel consumption rates along landward segments of headlands where low intertidal rocky refugia for sea stars were unavailable due to the higher level of the sandy beach surface. Landward (low predation) segments hosted expansive mid-intertidal beds of the competitively dominant mussel *Mytilus californianus*, which were rare or absent on seaward (high predation) segments. Compared to consistent dominance of *M. californianus* on landward segments, seaward segments were dominated by a patchwork of habitat-forming barnacle and seaweed species, which resulted in higher within-plot (alpha) and among-plot (beta) diversity of primary space-holders. Of these various biogenic habitat types, mussel beds hosted the greatest number of unique taxa. However, the total richness was similar between landward and seaward segments because pronounced among-plot variation in the identity of competitively inferior foundation species led to higher beta diversity for the entire community where predation was high and mussels were rare. When *M. californianus* beds were compared to beds of the barnacle *Semibalanus cariosus*, which often dominated high-*Pisaster* areas, we found that both epizotic and total richness were higher for *S. cariosus* beds at the plot level (alpha diversity), but that beta diversity was higher within *M. californianus* beds when all associated species were considered. Our results suggest that relationships between keystone

predators and biodiversity depend on the spatial scale studied and the identity and diversity of foundation species that replace competitive dominants. Because many taxa may preferentially or even uniquely associate with either competitively dominant or competitively subordinate habitat-forming species, total biodiversity will be maximized not “with” or “without” a keystone predator, but when predation pressure varies across a landscape.

Introduction

Not all species have the same influence over ecological processes in their respective ecosystems. Rather, some species play particularly important roles either because they are abundant, in many cases determining the physical structure of the greater ecosystem (Dayton 1972, Ellison 2019), or because they have particularly strong per capita effects (Paine 1992, Power et al. 1996, Jones et al. 1997). Identifying species with especially consequential impacts can greatly aid in efforts to manage ecological systems and forecast the outcomes of ongoing environmental and ecological change (Kroeker and Sanford 2022).

The keystone species concept was developed as one way to distinguish species that are particularly important, and was originally applied to species with an outsized role in determining local species composition and maintaining ecological stability (Paine 1969). The term was subsequently refined to describe species that have a large impact on a community or ecosystem trait (e.g., species richness, nutrient or energy flow, the relative dominance of different foundation species, etc.) despite representing a relatively small fraction of a community’s total individuals or biomass (Power et al. 1996). While this definition allows for community importance to be considered on a variety of axes, perhaps the most pervasive paradigm to arise from this work is that of the keystone predator promoting biodiversity. This relationship can

emerge when the predator prevents a competitive dominant from monopolizing the primary limiting resource, as in the original example of the sea star *Pisaster ochraceus* controlling the mussel *Mytilus californianus*, the dominant competitor for space (Paine 1966, 1969, 1974). Although the keystone-diversity relationship was first documented in a rocky intertidal system with a strong competitive dominant, this concept has since been applied to a variety of ecosystems and now encompasses additional pathways of ecological interaction (Estes and Palmisano 1974, Power et al. 1996, Peterson et al. 2008, Letnic et al. 2012, Terborgh 2015).

Since Paine's pioneering work, the ecological dogma of keystone predators as biodiversity-promoting heroes has been called into question (Bruno et al. 2003, Lafferty and Suchanek 2016). While competitively dominant prey species can exclude other species in the absence of a keystone predator, those same competitive dominants can also act as ecosystem engineers (Jones et al. 1997), providing important biogenic habitat for an array of associated species. In the canonical example explored by Paine, the predatory sea star *Pisaster ochraceus* (hereafter; *Pisaster*) consumes mussels (*Mytilus californianus*) that would otherwise overgrow other benthic invertebrates and macroalgae with which mussels compete for primary substratum (Paine 1966, 1974). However, mussel beds also provide a diversity of microhabitats that are cool, damp, and sheltered from wave forces on otherwise highly stressful rocky shores (Tsuchiya 1983, Carrington et al. 2008, Jurgens and Gaylord 2018, Jurgens et al. 2022) and can serve as secondary substratum on which other organisms can grow (Lohse 1993). Consequently, beds of *Mytilus* spp. contain dozens — even hundreds — of associated species (Suchanek 1979, 1992, Smith et al. 2006, Scrosati and Ellrich 2024, Longman et al. 2025). Thus, if one considers all taxa within the community rather than just those that compete directly with the competitively dominant mussels for space, *Pisaster* predation might actually decrease diversity by removing

important biogenic habitat (Harley 2011). These studies have led to debate over the true impacts of keystone species when negative interspecific interactions (predation, competition) are considered alongside positive interactions such as facilitation by a competitive dominant (Bruno et al. 2003, Lafferty and Suchanek 2016). However, empirical tests to assess the overall effects of keystone predation on the diversity of the entire community, rather than specific subwebs, functional groups, or biogenic habitat types, are generally lacking.

The debate around the role of keystone predators in shaping biodiversity remains unsettled in part because it suffers from two important shortcomings: 1) a failure to consider taxa associated with the competitively inferior foundation species that replace the competitive dominant once the latter has been removed by predators; and 2) a near-exclusive focus on plot-scale diversity. In the *Pisaster* example, predator-induced mussel loss will negatively impact the species associated with mussel beds, but will likely benefit the many species (quantified by neither Paine nor Suchanek) that are associated with the seaweeds, barnacles, and other habitat-formers that occupy primary space in the absence of mussels. Local diversity of all taxa, both algal and invertebrate primary space-holders and their associated communities, has not been adequately quantified to allow direct comparisons between the predator-present state and the predator-absent state. Furthermore, by reducing our scale of inference to mean diversity within plots (alpha diversity), we may neglect meaningful turnover in species composition among plots (beta diversity), an important component of overall community biodiversity (Anderson et al. 2011, Socolar et al. 2016). Given well-established species-area relationships in a variety of systems (Lomolino 2000), including *M. californianus* beds (Suchanek 1979), the plot scale will rarely be large enough to fully capture diversity within a habitat type at the landscape scale. Furthermore, because the species-area relationship in one habitat may have a steeper initial slope

but plateau earlier than a curve from another habitat (Roswell et al. 2021), estimated diversity differences among habitats can be scale-dependent. Finally, the presence of a predator may shift a habitat-forming monoculture (e.g., mussels) to a patchy polyculture of other habitat-forming species (e.g., seaweeds, barnacles, and sponges) (Paine 1966). In such a scenario, there may be a greater number of taxa when predators are present because the more diverse suite of competitively subordinate ‘replacement’ taxa provides food and habitat for a higher diversity of associated species. Asking only whether plot-level mean species richness is higher or lower in the presence of a keystone consumer fails to account for patterns of species turnover among plots, and thus may not measure a consumer’s true effect on landscape-scale biodiversity. Characterizing diversity more holistically by incorporating more taxa and scales of inference will improve our efforts to understand, manage, and conserve biodiverse and resilient ecosystems.

Here, we use natural and manipulative experiments to explore the interplay between keystone predation, competition, and facilitation as drivers of biodiversity patterns at local to landscape scales. Specifically, we examine the classic *Pisaster* – *Mytilus* system as it plays out on rocky headlands bounded by sandy beaches. *Pisaster* are generally restricted to hard substrata (Rogers and Elliott 2013) and require rocky substrata both where they forage (mid-intertidal at high tide) and where they shelter (low intertidal at low tide; Robles et al. 1995). On rocky headlands that run perpendicular to gently-sloping sandy beaches, mid-intertidal rock is available along a wide stretch of shore, whereas low intertidal rock is available towards the seaward end of a headland but not at the landward end (Fig. 1). We propose that this geomorphological pattern generates natural variation in predator densities between seaward (high *Pisaster* density) and landward (low *Pisaster* density) areas, with likely consequences for the mid-intertidal community across the entire headland (Fig. 1). In other words, low intertidal rock contiguous

with mid-intertidal rock could enable access to the mid-intertidal zone for *Pisaster*, while the absence of contiguous low intertidal rock could restrict or preclude *Pisaster* access. Headlands thus present a useful system for comparing the diversity of mid-intertidal shores that are either highly accessible or minimally accessible to *Pisaster* without requiring the 5–25-year manual *Pisaster* removal experiments conducted in the Paineian tradition (Paine 1974, Paine and Trimble 2004).

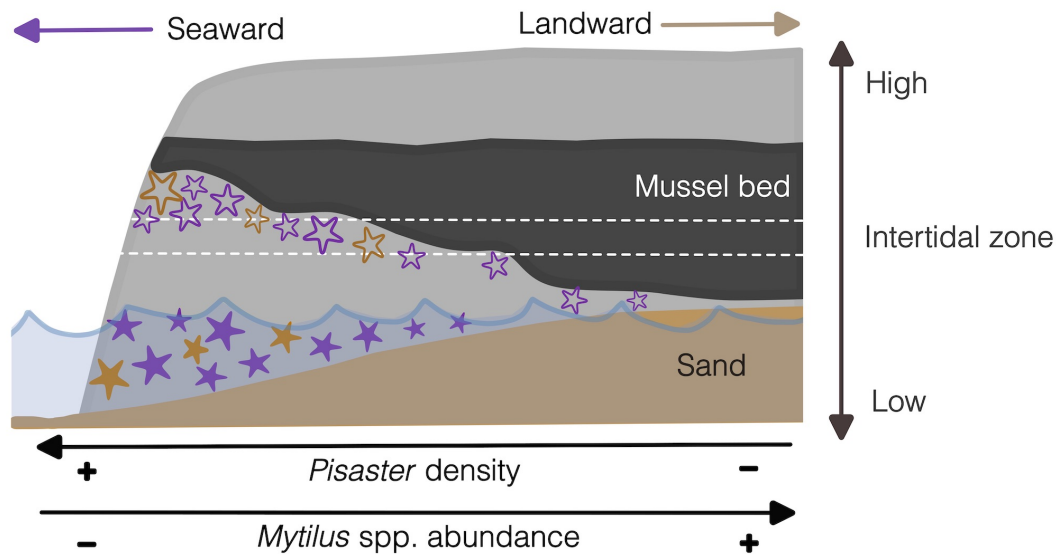


Figure 1. Schematic of hypothesized zonation patterns on a headland as viewed from the adjacent beach. The vertical position of the sand-rock interface gradually increases when going from the seaward to the landward segment of a rocky headland, resulting in a progressive loss of low intertidal refugia for predatory *Pisaster* (shaded stars = position at low tide, outline only = foraging range at high tide). We hypothesize that this pattern could contribute to differences in the density of *Pisaster* and the vertical extent of *Mytilus* spp. along the seaward-to-landward headland gradient. Space-holding species that replace mid-intertidal mussels in the presence of *Pisaster* are not depicted in this schematic, but could include a variety of barnacles, seaweeds, and other primary space-holders. The approximate position of mid-intertidal biodiversity sampling is shown by the white dashed horizontal lines.

To document this landscape-scale pattern and test its underlying causes, we conducted surveys and experiments along landward and seaward segments of replicate headlands. We recorded *Pisaster* densities and mussel bed zonation patterns, predicting that *Pisaster* would be

more abundant on seaward segments of headlands because they rely on low intertidal hard substratum for access to the mid-intertidal zone, and less abundant on more landward areas that lack a contiguous low intertidal refuge. We subsequently predicted that the lower limit of the mussel bed should occur higher on the shore at the seaward end of a headland due to higher *Pisaster* predation pressure, and lower on the shore at the landward end due to reduced predation pressure. Predation pressure in both areas was measured experimentally with mid-intertidal mussel outplants; we predicted that because of higher *Pisaster* densities on the seaward segment of headlands, predation pressure would also be higher in seaward compared to landward segments. We then sought to rule out other potential differences between headland segments (e.g., wave exposure and sand scour) by examining the position of *Mytilus* upper limits (which are related to wave exposure) and species richness and composition of scour-vulnerable sessile taxa present on the basal species *Semibalanus cariosus*, which occurred on both landward and seaward segments. Once these spatial patterns of foundation species and their likely causes were established, we were able to compare the biogenic habitats and associated communities found in landward and seaward segments of headlands to determine the effect of *Pisaster* predation on both plot-scale and landscape-scale biodiversity. For sessile species that require primary space, we predicted richness would be higher in the presence of *Pisaster* due to competitive release from mussels as was found by Paine (1966, 1974). In contrast, when considering *all* taxa, we predicted that plot-scale diversity would be highest where *Pisaster* was rare or absent due to the known facilitative effects of mussel beds on other taxa (Suchanek 1992, Commito et al. 2008, Koivisto and Westerborn 2010, Silliman et al. 2011, Bogdanski et al. 2024), which we anticipated would overwhelm the indirect diversity benefits of *Pisaster* on other primary space-holders (Paine 1966). However, we also predicted that the biodiversity “cost” of the predator

would be partially or fully offset by higher among-plot diversity in areas where *Pisaster*, by removing mussels, facilitated a suite of replacement foundation species whose domination of space — unlike a contiguous mussel bed — may be more variable from one plot to the next.

Methods

Study site and species

This work was conducted on Calvert Island on the central coast of British Columbia, Canada. The Heiltsuk Nation and the Wuikinuxv Nation hold Indigenous rights to their territories, where all data were collected. Our work was done under formal agreements with each Nation. The western shore of Calvert Island features semi-exposed to fully-exposed granitic rocky shorelines interspersed with sandy beaches (Fig. S1). Here, rocky intertidal communities are broadly similar to those of well-studied coastlines in Oregon, Washington, and elsewhere in British Columbia. Sessile invertebrates, especially the California mussel, *M. californianus*, and the thatched barnacle, *Semibalanus cariosus*, dominate the mid-intertidal zone, along with a diverse algal assemblage (Hesketh and Harley 2023, Whalen et al. 2023). These foundation species provide habitat for other sessile organisms and numerous small, motile fauna. The sea star *Pisaster ochraceus*, which exhibits strong top-down control at other intertidal sites in the broader region (Paine 1966, Menge et al. 1994, Harley 2011), is a conspicuous benthic predator. Although sea star wasting disease is present on Calvert Island, *Pisaster* numbers did not decline as precipitously here as they did further south, and *Pisaster* population density during our study was relatively stable and similar to pre-outbreak density (Gehman and Harley, unpublished data).

Landscape-scale patterns of predator abundance and top-down control

The alternating pattern of steep-sided headlands and gently sloping sandy beaches on Calvert Island provides a replicated system of shorelines that vary in the presence and extent of low intertidal rocky substratum suitable for *Pisaster*. At the seaward end, the steep walls of these headlands extend downwards into the low intertidal or subtidal zone before reaching the sandy bottom. As one follows the headland wall towards its landward terminus, the sandy beach gradually rises in elevation and lower intertidal rocky substratum is progressively lost (Fig. 1), excluding hard substratum-dependent low intertidal species from the landward segment of a headland. Despite being above the level of sand inundation, community structure differs within the mid-intertidal zone, with mussels (*M. californianus*) becoming increasingly common towards the landward segment (Fig. S2A). We propose that this seaward-landward pattern of mussel distribution is due to variation in the abundance of *Pisaster*, which generally occupy a rocky low intertidal refuge during low tide and move into the mid-intertidal zone to feed at high tide (Robles et al. 1995). If this conceptual model is correct, headlands provide an ideal, replicated system for comparing the diversity of adjacent sections of mid-intertidal shore that are either readily accessible or minimally accessible to *Pisaster*.

To confirm that *Pisaster* abundance was higher on seaward segments of headlands, and that this difference resulted in a broader mussel (*M. californianus*) vertical distributional extent and higher mussel cover on landward segments due to reduced *Pisaster* predation pressure, we used a combination of surveys and experiments to test the following specific hypotheses: 1) *Pisaster* will be more abundant at the seaward segments of headlands than at landward segments where the low intertidal zone is inundated by sand; 2) as a result, predation pressure on mussels will be higher at the seaward segments; 3) the differences in predation pressure will result in the lower limit of mussel beds being higher on the shore on seaward segments; 4) the upper limits of

M. californianus will be similar on landward and seaward segments (an indicator that wave exposure and other abiotic factors are similar among segments); 5) as a consequence of hypotheses 3 and 4, the vertical extent of the mussel bed will be narrower on the seaward segments of headlands; and 6) *M. californianus* cover within the mid-intertidal zone would be higher — and thus the diversity of primary space-holders lower — at landward segments compared to seaward segments.

To determine how *Pisaster* density varied along headlands, we conducted replicate *Pisaster* surveys along landward and seaward segments of 11 headlands (see Table S1 for site details) in eight different years (N = 42 total visits). Surveyed areas were located on continuous stretches of rocky shore facing roughly the same direction within a site. Local topography prevented this from being done at Third Beach, so the west-facing landward subsite was paired with a safely accessible north-facing seaward shore. Surveys were conducted on 8–20 m linear stretches of shore, with all *Pisaster* counted within the survey areas. Because *Pisaster* moves vertically up the shore to feed, often along the linear margin of the lower distributional limit of their prey, their density is best expressed as number per linear meter of shore on steeply sloping surfaces such as these. These surveys were conducted from 2017–2023 and in 2026, although not every site was surveyed each year (Table S1).

We tested how predation pressure varied between seaward and landward segments of these headlands by outplanting mussels in the mid-intertidal zone following established methods (Gehman and Harley 2019). Briefly, the rock surface was cleared with a hammer and chisel and rinsed, a lag bolt was anchored to the rock, and a ~3 x 15 cm "hoagie" of A-788 Splash Zone Compound (Z-spar; Pettit Paint, Rockaway, NJ) was installed, including the lag bolt as an additional anchor point. Five mussels (*M. californianus*, 35–50 mm in length) were pressed into

each Z-spar hoagie by their right valve such that they were securely attached but could still open their shells to feed (Fig. S2B–C). Five mussel hoagies, separated by ~1–4 m along the shore, were outplanted within each segment (landward and seaward) at each of six headlands at shore levels 2.0–2.5 m above Canadian chart datum (N = 300 mussels). These experiments were conducted at various times and monitored for days (three sites) to months (three sites) as dictated by logistical constraints (see Table S1). Background mortality rates using this technique are generally low (Gehman & Harley 2019). We treated empty or missing mussels as evidence of *Pisaster* predation because *Pisaster* were able to consume outplanted mussels *in situ* and remove them from the Z-spar (CH, personal observation; see Fig. S2D–E), almost all of the tissue was missing for all mussels that were killed within 1–5 days of deployment (suggesting that it was not heat-induced mortality, where soft tissue can persist for a week or more), no shells were found to be broken (i.e., no evidence of damage by floating logs), and no other benthic predators of large *M. californianus* were present.

To test how *Pisaster* predation shapes the vertical extent of *M. californianus* prey, we measured the upper and lower limits of mussel beds and their vertical extent at different times and sites throughout the study period. In 2017 and 2022, we used a rotating laser level to measure the vertical positions of the upper and lower limit of the contiguous mussel bed, along with the vertical position of the beach surface, at five approximately evenly-spaced locations within six headlands surveyed for *Pisaster* densities (Table S1). Note that the position of the lower limit of the mussel bed varies with *Pisaster* predation pressure (Robles et al. 2009), whereas differences in the upper limit within a headland would be indicative of differences in wave exposure or temperature (Harley & Helmuth 2003). Measurements were standardized to Canadian chart datum (the approximate height of the lowest astronomical tide) by measuring the

still water level of the tide at a given time (two or three measurements per site visit) and referencing those measurements against predicted water level (Xtide, Egg Island BC station). Additional measurements were made at a further five headlands in 2023 (Table S1). For these, only the vertical extent (distance between the upper and lower limits) of mussel beds was measured with a stadia rod and a hand level at five locations in each segment (landward or seaward) at each site. In total, we made 57 and 33 upper limit measurements, 58 and 26 lower limit measurements, and 84 and 82 vertical extent measurements at landward and seaward headland segments, respectively. Fewer seaward zonation measurements were made because mussel beds were often absent in these areas. In a few cases, isolated individuals were present at the upper distributional limit. For these, we recorded an upper limit but not a lower limit, and the vertical extent for these cases, along with areas lacking mussels entirely, was recorded as zero.

To confirm that *M. californianus* cover was lower and benthic space-holder diversity was higher in the presence of *Pisaster* as previously established elsewhere (Paine 1966, 1969, 1974), we surveyed the percent cover of primary space-holders in the mid-intertidal zone at the landward and seaward ends of five headlands (Fig. S1, Table S1) in May 2025. At each headland, the *Pisaster* survey area (see above) was subdivided into five equal subsections, and a 20 x 20 cm quadrat was placed at a randomly determined point along each subsection. The shore level of these quadrats coincided with the vertical position of the outplanted mussels in the predation experiment (2.0–2.5 m above chart datum; see above). The percent cover of all primary space-holders occupying >1% cover was visually estimated. Secondary cover was often high on *M. californianus* and the thatched barnacle *S. cariosus*; therefore, the identity and percent cover of sessile species growing directly on these two basal species was also recorded. Because *S. cariosus* was present in both landward and seaward segments, we were able to

compare species growing on this basibiont to determine whether sand scour played a strong role in limiting potentially vulnerable taxa like macroalgae.

Biodiversity surveys

To survey patterns of species diversity associated with spatial variation in *Pisaster* predation, inclusive of both habitat-forming and habitat-associated species, we destructively sampled mid-intertidal habitats at the seaward and landward segments of five headlands (Fig. S1, Table S1). Diversity surveys were conducted in conjunction with an extensive Bioblitz held on Calvert Island in August 2017 (Lambert 2019). Samples were collected from 2.0–2.5 m above Canadian chart datum, and we collected all biota within 20x20 cm areas from each of two haphazardly located plots on both the seaward and landward segments. Our 400 cm² plot size is above the size at which the mussel bed area-richness relationship began to level off in earlier work (Suchanek 1979). This design resulted in ten samples dominated by *M. californianus* from landward segments, and ten samples dominated by various other foundation species (*Semibalanus cariosus*, n = 3; *Chthamalus dalli*, n = 3; fleshy macroalgae, n = 3, articulated coralline algae, n = 1) from seaward segments. Each sample represented a complete clearance of all organisms down to bare rock, and all animal and algal species > 2 mm in length were identified to the lowest taxonomic resolution possible by expert taxonomists to yield presence/absence data for each habitat type. Hereafter, we refer to these as "Bioblitz samples".

Preliminary observations revealed that *S. cariosus* was a surprisingly strong promoter of species richness, potentially exceeding the facilitative effect of the better-studied *M. californianus*. To further investigate this pattern, additional sampling was conducted on a gently sloping (< 20°), wave-exposed mid-intertidal bench approximately 300 m from the nearest sandy

beach (Fig. S1), where a patchy mosaic of *M. californianus* and *S. cariosus* could be found. Note that, unlike our steep-sided headlands, *Pisaster* does not forage as high on gently sloping shores. Six samples (15x15 cm) were collected from well-interspersed areas with either >90% cover of *M. californianus* or >90% cover of *S. cariosus* (12 samples total), all at approximately the same shore level and within a few meters of one another. Other than the smaller size of the sampled plots, the sampling methods were identical to those described above. Hereafter, we refer to these as "targeted samples".

Statistical analyses

All statistical analyses were performed in R (version 4.4.0; R Core Team, 2024). Sand levels, *Pisaster* densities, *Pisaster* feeding data, and the lower limit, upper limit, vertical extent, and cover of mussel beds on headlands were modeled as a function of headland segment (landward vs. seaward) using (generalized) linear mixed models. We included random effects of survey year nested within site for models of sand levels, *Pisaster* density, and mussel bed upper and lower limits to account for repeated measures at headlands through time. For modeling feeding data, site was included as a random effect. For mussel bed vertical extent, where surveys were repeated at some, but not all, sites through time, we included separate random effects of site and year. Linear models of sand levels and mussel bed upper and lower limits were constructed under a Gaussian distribution and tested by ANOVA (*lme4* and *lmerTest* packages). We modeled *Pisaster* density, feeding data, and mussel bed vertical extent and cover and tested models using Type II ANOVAs (*glmmTMB* and *car* packages). We modeled *Pisaster* density under a Tweedie distribution and feeding data under a binomial distribution, and the proportional cover of mussels under a beta distribution, with cover adjusted to fall in the interval (0,1) (Smithson and Verkuilen

2006). For mussel bed vertical extent, we modeled zero inflation as a function of headland segment, and for mussel cover, we modeled dispersion as a function of headland segment. Model assumptions were checked for all models (*DHARMA* package).

We next tested for differences between the structure and diversity of communities associated with different headland segments and habitat-forming species. Richness was modeled under a Poisson distribution using generalized linear models (*glmmTMB* package) with a random intercept effect of site for collections that occurred at multiple locations, and models were tested using Type II AN(C)OVAs (*car* package). The total richness of Bioblitz samples and the richness of primary space-holders were modeled as a function of headland segment. The total richness of Bioblitz samples from all seaward biogenic habitats, targeted samples of *M. californianus* and *S. cariosus* beds, and secondary cover communities on *M. californianus* and *S. cariosus* were modeled as a function of biogenic habitat type. For Bioblitz samples of seaward biogenic habitats, we compared the richness of different habitats using a Tukey post-hoc pairwise comparison (*emmeans* package). For the model of associated secondary richness, we included basal species cover as a covariate. Community structure differences among headland segments and biogenic habitats for primary space-holder samples, Bioblitz samples, and targeted samples were analyzed using a constrained principal coordinates analysis (function *capscale* in the *vegan* package). We used Bray-Curtis indices for analyses of primary space-holder communities, where percent cover was quantified, and Jaccard indices for analyses of Bioblitz and targeted samples, where only presence-absence data were collected. PERMDISP tests were used to examine how the heterogeneity (beta diversity) of communities varied between headland segments (using primary space-holder samples) and habitat types (using Bioblitz and targeted samples). Constrained PERMANOVAs were used to test how community structure depended

upon habitat type, with accompanying post-hoc pairwise comparisons (*multiconstrained* function in the *biodiversityR* package).

Results

Low intertidal refugia, Pisaster abundance, and Pisaster feeding rates

We first sought to determine how the vertical elevation of the sandy beach surface along headlands affected the abundance of *Pisaster*. As expected, the shore level of the sand bordering seaward segments of headlands (85 ± 8 cm; mean $\pm$ SE above Canadian chart datum) was lower than the level of the sand bordering landward segments (147 ± 6 cm), a significant difference (Type I ANOVA; $F_{1,100} = 76.43$, $df = 1$, $P < 0.001$). The density of *Pisaster* on the shore was correspondingly several times higher on seaward segments of the headlands than on adjacent landward segments (Fig. 2A; ANOVA; $\chi^2 = 117.9$, $df = 1$, $P < 0.001$). When *M. californianus* feeding experiments were conducted on headlands, predation rates were higher on seaward segments, where *Pisaster* were more abundant, compared to landward segments during both months-long (Fig. 2B; Type II ANOVA; $\chi^2 = 50.45$, $df = 1$, $P < 0.001$) and days-long feeding experiments (Fig. 2C; Type II ANOVA; $\chi^2 = 22.01$, $df = 1$, $P < 0.001$).

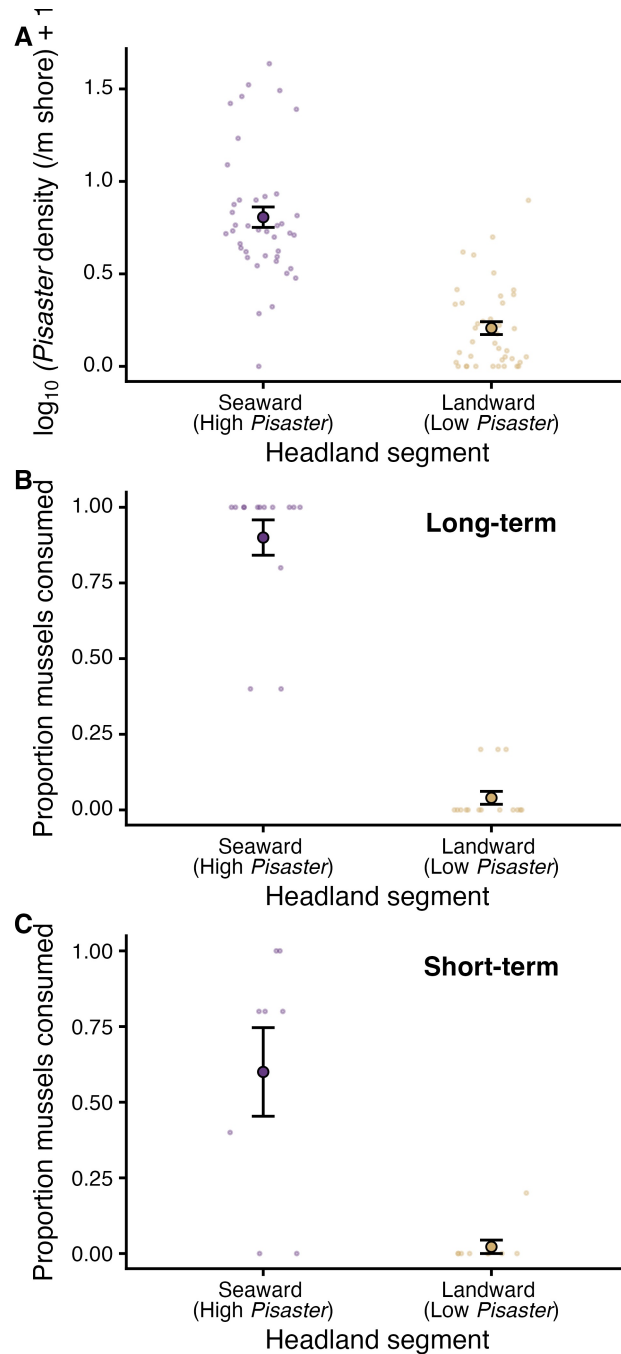


Figure 2. Spatial differences in predator abundance and predation rates between the seaward and landward segments of headlands on Calvert Island, British Columbia. **(A)** Differences in the density of *Pisaster* sea stars between segments of headlands (log transformed for visualization, $n=42$). **(B)** Long-term differences in the consumption of outplanted clusters of *M. californianus* mussels between segments of headlands, as determined using a months-long feeding experiment at three sites from 2020–2021 ($N = 30$ clusters). **(C)** Short-term differences in the consumption of outplanted *M. californianus* mussels between segments of headlands, as determined using a 4-day long feeding experiment at three sites in 2019 and 2026 ($N = 30$ clusters). Error bars represent the standard error about the mean, and raw data are plotted in the background.

Mytilus distribution on headlands

Predation by *Pisaster* shaped the distribution of *M. californianus* prey on shore. The lower limit of mussel beds was lower on landward segments of headlands than on seaward segments (Fig. 3A; Type II ANOVA; $F_{1,74} = 92.15$, $P < 0.001$). The position of the upper limit, meanwhile, remained consistent along the headland predation gradient (Fig. 3B; Type I ANOVA; $F_{1,78} = 2.63$, $P = 0.109$). The vertical extent of the mussel bed was greater at landward segments of headlands, where sea stars were less abundant (see Fig. 2A), compared to seaward segments (Fig. 3C; Type II ANOVA; $\chi^2 = 103.80$, $df = 1$, $P < 0.001$). Mid-intertidal mussel cover (mean $\pm$ SE) was substantially higher on landward segments ($87.4 \pm 5.2\%$) compared with seaward segments ($0.8 \pm 0.3\%$), a significant difference (Fig. 3D; Type II ANOVA; $\chi^2 = 325.78$, $df = 1$, $P < 0.001$).

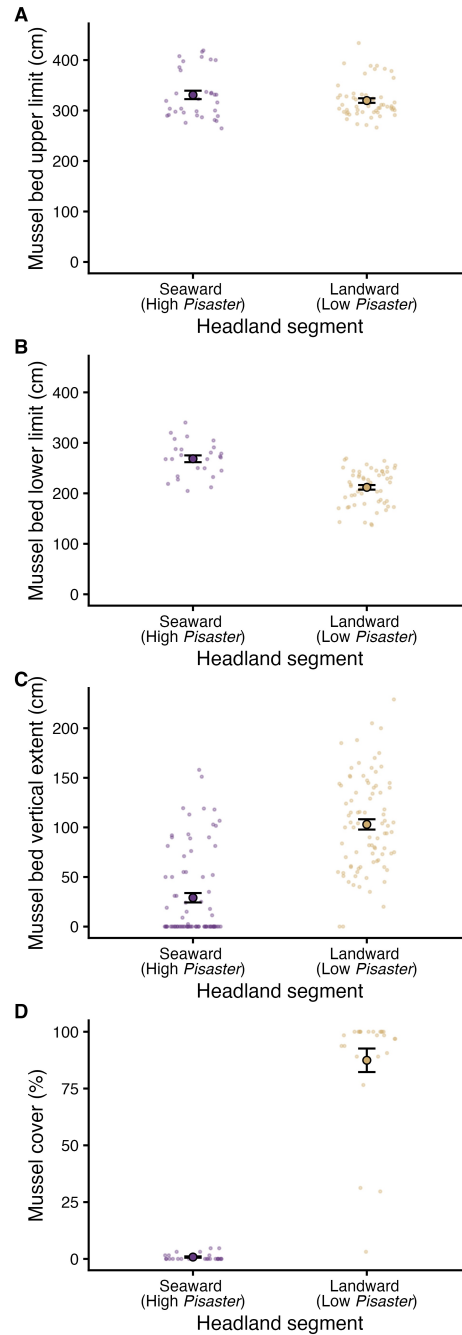


Figure 3. Patterns in the distribution of *M. californianus* beds on seaward and landward segments on the rocky headlands of Calvert Island, British Columbia, in terms of their (A) upper limit, (B) lower limit, (C) vertical extent (upper limit minus lower limit), and (D) mid-intertidal percent cover. Vertical positions in A and B are expressed relative to Canadian chart datum. Data in panels A and B derive from five headlands sampled in each of two years ($n=5$ replicates per segment per headland per year). Data in panel C include data from A and B plus additional single-year sampling at six more headlands (11 headlands in total). Data in panel D were recorded during a single year at five headlands ($n=5$ replicates per segment per headland). Error bars represent the standard error about the mean, and raw data are plotted in the background.

Patterns of diversity

Our sampling revealed a highly diverse intertidal community composed of 167 total identified taxa (Table S2). Sessile taxa included mussels, barnacles, sea anemones, and a host of green, red, and brown seaweeds. Mobile species included crustaceans, gastropods, polychaete worms, nemertean worms, echinoderms, insects, and others.

The diversity and composition of primary space-holders varied strikingly across the landward-to-seaward headland gradient. The plot-scale richness (alpha diversity) of the primary space-holder community was higher on seaward segments of headlands (Fig. 4A; Type II ANOVA; $\chi^2 = 33.34$, $df = 1$, $P < 0.001$) where sessile taxa including barnacles, seaweeds, macroalgae, and anemones persisted in the presence of *Pisaster* (Fig. S5). By comparison, plot-scale richness was lower on landward segments where *Pisaster* were rare and mussels dominated (Fig. S5). The beta diversity of these sessile taxa was also higher on seaward segments, with larger among-plot differences in community structure than on landward segments (Fig 4B; PERMDISP; $F_{1,48} = 32.16$, $P < 0.001$). The composition of primary space-holder communities differed significantly between seaward and landward headland segments (PERMANOVA; $F_{1,44} = 34.60$, $P = 0.001$) and among the five headlands surveyed (PERMANOVA; $F_{4,44} = 2.75$, $P = 0.002$).

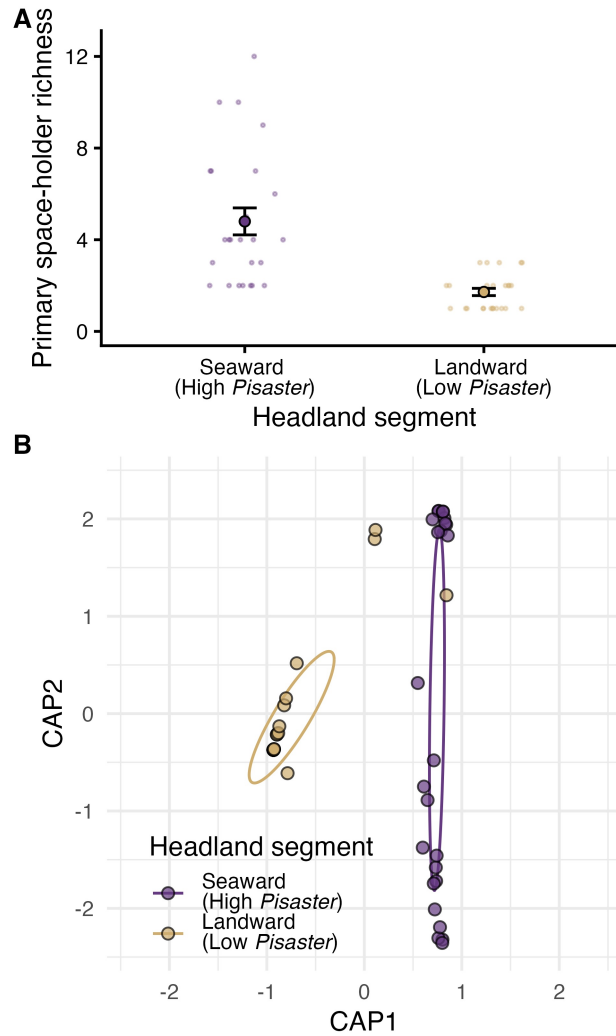


Figure 4. Diversity and community structure of primary space-holding species on seaward and landward segments on the rocky headlands of Calvert Island, British Columbia, in terms of their (A) species richness and (B) community structure expressed in two-dimensional ordination space using a Constrained Analysis of Principal Coordinates (CAP) with Bray-Curtis indices as non-Euclidean distances. Data derive from five plots per headland segment across five headlands.

We next broadened our perspective to consider the composition and richness of the entire community present in Bioblitz and targeted samples, including all motile and sessile taxa > 2 mm (Table S2). For all headlands, mid-intertidal plots on landward segments were dominated by the mussel *M. californianus*, whereas mid-intertidal plots on seaward segments were dominated by a variety of barnacle and macroalgal species (Fig. S2). Contrary to our prediction, total plot-

scale species richness in Bioblitz samples was not consistently higher in landward segments, where *Pisaster* was rare and mussels dominated, as compared to seaward segments. Rather, average plot-scale richness was similar between headland segments (Type II ANOVA; $\chi^2 = 0.89$, $df = 1$, $P = 0.346$), but varied among plots within seaward segments depending on what foundation species dominated the available space (Fig. S2; Type II ANOVA; $\chi^2 = 21.46$, $df = 4$, $P < 0.001$). Specifically, *Chthamalus dalli* barnacle beds facilitated lower richness communities compared to most other biogenic habitats (*emmeans*; $P < 0.05$; see also Figs. S2 and S3). Richness did not differ significantly among the other biogenic habitat types, but note the low samples sizes for these comparisons.

Different biogenic habitats harbored distinct communities (Fig. 5A; PERMANOVA; $F_{4,11} = 3.14$, $P = 0.001$) with similar beta diversity among plots in each habitat (PERMDISP; $F_{3,15} = 0.48$, $P = 0.701$). Post-hoc pairwise comparisons showed that compositional differences were almost entirely driven by dissimilarities between mussel-associated communities and those associated with all other biogenic habitats (*multiconstrained*; $P = 0.001$; Table S3). In total, 102 taxa were associated with mussel beds ($n=10$ plots), 51 of them unique (Fig. S3). When all non-mussel habitats were considered collectively ($n=10$ plots), they contained 98 taxa, 47 of which were not found in mussel beds. The composition of communities also differed among sampled headlands (PERMANOVA; $F_{4,11} = 1.57$, $P = 0.005$). Because all landward habitats sampled were *M. californianus* beds, habitat type and headland segment were perfectly collinear. However, when communities associated with non-mussel seaward habitats were collectively compared to those of landward mussel habitats, seaward, non-mussel habitats had higher beta diversity (PERMDISP; $F_{1,18} = 8.83$, $P = 0.00819$) and these groups differed in their composition (Fig. 5B; PERMANOVA; $F_{1,18} = 3.17$, $P = 0.001$).

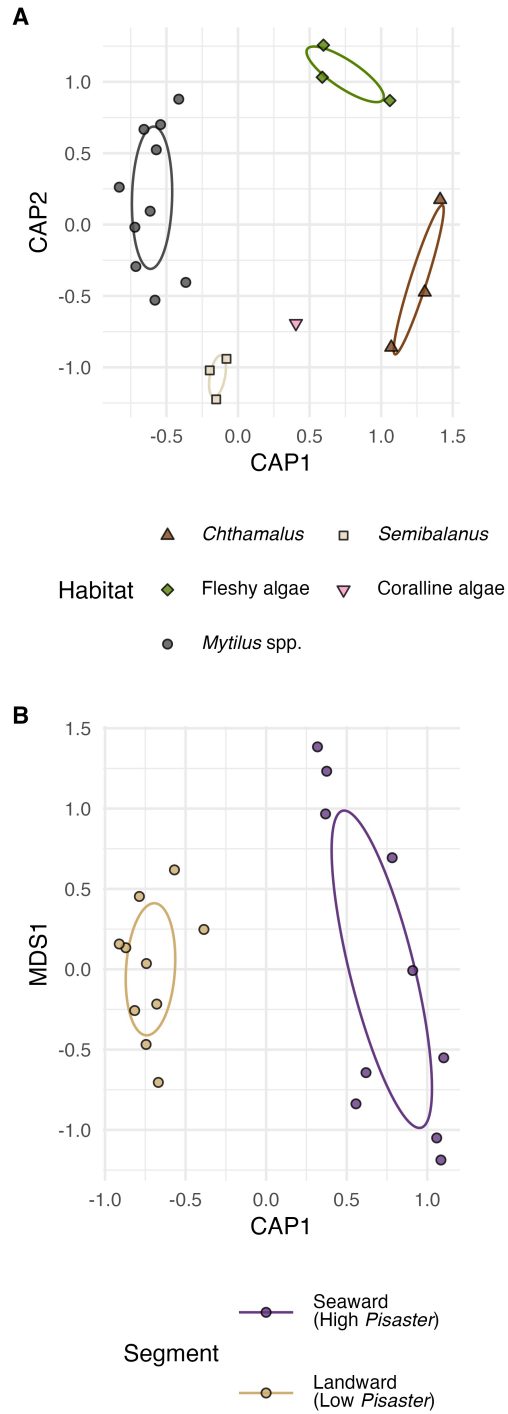


Figure 5. Constrained Analysis of Principal Coordinates (CAP) plots of community composition associated with Bioblitz samples of **(A)** different biogenic habitats and **(B)** seaward non-mussel versus landward mussel habitats collected from rocky headlands of Calvert Island, BC (N=20). Ordinations used Jaccard indices as non-Euclidean distances and are plotted along the two primary axes.

To test whether mussels may be facilitating, rather than restricting, diversity by providing shell surface for other species to colonize (Lohse 1993), we compared the diversity of epizoic sessile species (secondary cover) associated with *M. californianus* with that of the barnacle *S. cariosus*, the most common mid-intertidal spatial dominant found in areas of higher *Pisaster* predation pressure (see Fig. S4). Epizoic richness scaled with basal species cover (Type II ANCOVA; $\chi^2 = 8.59$, $df = 1$, $P = 0.00338$), reflecting expected positive species-area relationships. Independent of basal species area, more epizoic species were found on *S. cariosus* tests than on *M. californianus* shells (Fig. 6A; $\chi^2 = 10.21$, $df = 1$, $P = 0.00139$), most of them algae (see Table S4). When considering *S. cariosus* alone, the richness of the epizoic community again scaled with primary cover (Type II ANCOVA; $\chi^2 = 9.84$, $df = 1$, $P = 0.00171$) but was similar between landward and seaward segments ($\chi^2 = 1.50$, $df = 1$, $P = 0.221$). We found similar results for community composition on *S. cariosus* tests, which differed depending on within-plot percent cover of *S. cariosus* (PERMANCOVA; $F_{1,19} = 2.18$, $P = 0.016$), but was similar between headland segments ($F_{1,19} = 1.28$, $P = 0.225$). Together, these trends indicate no apparent effect of vertical proximity to sand. Epizoic beta diversity was higher on *S. cariosus* compared to *M. californianus* beds (Fig. 6B; PERMDISP; $F_{1,45} = 12.03$, $P = 0.00117$), and community composition differed significantly between the two habitat types (Fig. 6B; PERMANOVA; $F_{1,41} = 9.94$, $P = 0.001$) and among headlands ($F_{4,41} = 2.82$, $P = 0.001$).

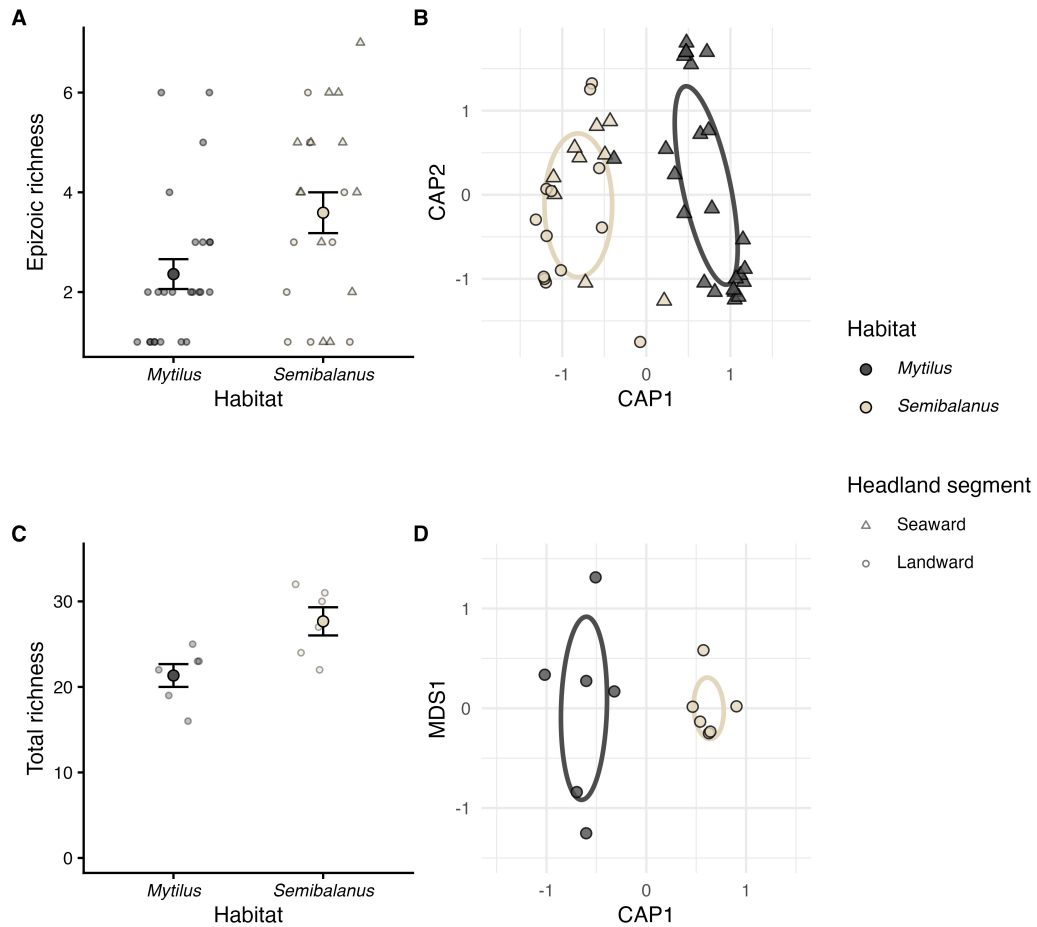


Figure 6. Differences in species richness and composition of communities associated with two different biogenic habitat types, *M. californianus* mussel beds and *S. cariosus* barnacle beds. **(A)** Richness of epizoic species. **(B)** Constrained Analysis of Principal Coordinates (CAP) plot of epizoic community composition. **(C)** Total richness across all taxa. **(D)** Constrained Analysis of Principal Coordinates (CAP) plot of the composition of the full community. Data in (A) and (B) were derived from surveys on seaward and shoreward segments of the five focal headlands (unlike shoreward-restricted *M. californianus*, *S. cariosus* could be found in both segments). In (C) and (D), targeted samples (n=6) were collected from a single intertidal bench far from the nearest sand. Note that in (A) and (C), error bars represent the standard error about the mean richness across all plots.

Through additional, targeted sample collection at a single intertidal site, we also more robustly compared the diversity of full communities (motile plus sessile taxa) associated with *M. californianus* and *S. cariosus*, using similar methods as the full biodiversity surveys but different

plot and sample sizes. A total of 48 taxa, 13 of them unique, were found in both *M. californianus* and *S. cariosus* bed targeted samples. Plot-scale richness was significantly higher in plots dominated by *S. cariosus* compared to *M. californianus* (Fig. 6C; Type II ANOVA; $\chi^2 = 4.93$, $df = 1$, $P = 0.0265$). The opposite pattern held for beta diversity; communities associated with *M. californianus* were more beta-diverse than communities associated with *S. cariosus* (Fig. 6D; PERMDISP; $F_{1,10} = 10.28$, $P = 0.00939$). The communities facilitated by *M. californianus* and *S. cariosus* beds also differed significantly in terms of their composition (Fig. 6D; PERMANOVA; $F_{1,10} = 3.80$, $P = 0.001$).

Discussion

Understanding the processes that determine patterns of biodiversity has been a motivating goal of ecologists since the dawn of the discipline (Darwin 1859, Hutchinson 1959). While large-scale patterns of diversity are influenced by long-term and biogeographic scale drivers including speciation-extinction dynamics (Schluter and Pennell 2017), variation in primary productivity (Waide et al. 1999), and environmental stability (Chesson and Huntly 1997), local species interactions can also exert strong control over diversity (Paine 1966, 1974). Over ecological time scales, diversity is enhanced by forces that promote species persistence either directly — for instance, facilitation by foundation species (McIntire and Fajardo 2014) — or indirectly — for instance, top-down forces disrupting competitive exclusion (Terborgh 2015). However, the effects of key species can be complex and more than strictly positive or negative, especially once indirect effects are considered. Thus, determining the true relationship between ecologically important species and biodiversity remains an important goal for understanding natural ecosystems and prioritizing conservation efforts.

For the community in which the term ‘keystone species’ was coined, the sea star *Pisaster ochraceus* enhanced the diversity of species that require primary space on the substratum for attachment by preventing overgrowth by a competitively dominant prey species, *Mytilus californianus* (Paine 1966). The notion that keystone predators promote diversity has since been applied to additional interaction pathways (e.g., trophic cascades) and to a variety of different ecosystems (Estes and Palmisano 1974, Power et al. 1996, Peterson et al. 2008, Letnic et al. 2012, Terborgh 2015). However, the paradigm that predators enhance biodiversity, exemplified by the *Pisaster*–*Mytilus* example but extending more broadly, has been called into question (Bruno et al. 2003, Lafferty and Suchanek 2016). These authors rightly point out that Paine did not enumerate all species in his surveys and suggest that the total diversity of the system might actually be *reduced* by *Pisaster* due to the important facilitative role *M. californianus* plays for non-space-holding species (Bruno et al. 2003, Lafferty and Suchanek 2016).

To address these countervailing effects of keystone predation on biodiversity, we revisited the original keystone species interaction web to simultaneously consider the indirect effects of *Pisaster* on both primary space-holders that may be outcompeted by *M. californianus* and species facilitated by mussels and/or other foundation species (barnacles and macroalgae) that replace mussels as spatial dominants in the presence of *Pisaster*. This approach allows for a full comparison of biodiversity in areas with and without high densities of the keystone predator. To explore these ecological relationships, we took advantage of landscape-scale patterns in *Pisaster* abundance along beach-bounded headlands related to differences in hard substratum availability on the low shore. The presence of low shore rocky refugia resulted in significantly higher mid-shore predation pressure at the seaward end of headlands, as *Pisaster* requires a low-intertidal refuge from which to access and forage in the mid-intertidal zone. Landscape-scale

heterogeneity in predation pressure has also been related to the spatial distribution of refugia for consumers in other systems. In grasslands, predation on wading bird nests is higher for nests located nearer to forested habitats, which act as a non-foraging refuge for red fox predators (Kaasiku et al. 2022). In coral reef systems, grazing halos on sandy bottoms reflect the extent to which herbivorous fish forage away from patch reef refugia (DiFiore et al. 2019). In salt marshes, distance from a low shore or subtidal refuge for benthic predators was correlated with reduced predator encounter rates and increased prey abundance (Lewis and Eby 2002).

As a result of higher predation pressure, the lower intertidal limit of the mussel bed was higher on the shore and both the total vertical extent of the mussel bed and mid-intertidal mussel cover were reduced at the seaward relative to the landward end of our headlands. Other mussel-dominated shores show similar effects related to the connectivity to and/or availability of low intertidal or subtidal habitat for predators. Connectivity to low-shore predator refugia determines the abundance of mussels (*Mytilus* spp.) in Norway; for instance, tree branches that hang down into the intertidal zone are only likely to support mussel populations if they do not come into contact with the substratum where mobile predators like dogwhelks are common (Meister et al. 2023). On rocky shores in New Zealand, important predators of mussels (e.g., labrid fish) require subtidal rocky habitat, but can forage in nearby intertidal habitats at high tide. As a result, intertidal benches adjacent to subtidal rocky reefs (high predator access) featured high mussel predation rates and low mussel cover, whereas intertidal benches bordered by subtidal soft sediment habitat (low predator access) featured lower predation rates and higher mussel cover (Rilov and Schiel 2006b, 2006a).

As with these other habitats with variable proximities to or connectivity with predator refugia (e.g., Rilov and Schiel 2006a, 2006b), the mid-intertidal zone on beach-bounded

headlands in British Columbia represents a useful system for comparing habitats that differ in predator access. Given the comparative nature of this system, it is important to consider other potentially important differences between landward and seaward headland segments. Landward and seaward segments within a headland were separated by as little as 2 m up to ~50 m and in most cases faced the same direction, reducing the likelihood that solar insolation or substrate temperature drove observed biological patterns. Sand burial and sand scour can be important structuring forces on rocky shores (Littler et al. 1983, McQuaid and Dower 1990), and landward segments were closer, vertically, to the beach surface. However, even our landward sampling plots were located high enough on the headland wall to avoid burial. There were no obvious signs of sand abrasion on invertebrates or exposed seaweeds on the landward segments, and the community composition and diversity of epizoic taxa living on *S. cariosus* tests did not differ between seaward and landward headland segments. Furthermore, we did not find appreciable amounts of sand in any of our biodiversity samples, which were collected down to bedrock. This suggests that the infauna inhabiting these near-vertical headland walls were fairly protected from excessive sand accumulation within the habitat matrix provided by foundation species. There may also have been wave exposure differences between landward and seaward segments of the headlands, although the fact that most study areas were oriented parallel to the incoming wave direction should reduce this effect. Indeed, for two headlands, the landward section was likely more rather than less wave exposed, related to swells overtopping the “landward” tombollo in one case, and protection from an outlying islet in another. Our biological zonation measurements support our contention that there was no general wave exposure gradient within headlands. The upper limits of *M. californianus* closely track wave exposure (Harley and Helmuth 2003), and we found no differences in the position of the upper limit of *M. californianus* within our

headlands. The basic within-headland pattern of *Pisaster* abundance and top-down effects were consistent despite the fact that some headlands were considerably more exposed than others, suggesting that the basic influence of low intertidal rocky refugia is generalizable across the wave exposure gradient. The role of wave exposure and other environmental gradients in determining the identity and diversity of foundation species that dominate in the absence of mussels would be an interesting topic for future study. Finally, we note that the diversity patterns identified in our headland surveys were similar to those found in the targeted *Mytilus* vs. *Semibalanus* surveys. The latter surveys were conducted in closely interspersed plots of essentially identical wave exposure and far from the nearest source of sand, suggesting that the identity of the foundation species alone is sufficient to drive diversity patterns.

Despite potential nuances associated with abiotic conditions, the most notable ecological differences within headlands appear to be driven by the higher abundance of *Pisaster* and therefore lower abundance of mussels at the seaward end. As documented in Paine's original studies in Washington State (Paine 1966, 1969, 1974), we found that areas inaccessible to *Pisaster* had higher mussel cover and lower richness of primary space-holders relative to areas where *Pisaster* foraged. Whereas Paine found 15 primary space-holder species in areas with *Pisaster* vs. only eight where *Pisaster* had been removed, we found 22 in areas with high *Pisaster* density vs. only five in areas with low *Pisaster* density. The spatial distribution of these primary space-holders was quite heterogenous, with some plots dominated by little brown barnacles (*Chthamalus dalli*), others by the larger thatched barnacles (*S. cariosus*), and still others by mixed beds of macroalgae. The reasons why particular seaward segments, or plots sampled within them, are dominated by a particular group of species is likely due to variation in orientation, wave exposure, and local *Pisaster* abundance. For example, while *Pisaster* does

consume *S. cariosus* (Harley et al. 2006) and may largely eliminate it from some areas (e.g., the seaward sections of North Island Notch, North Beach, and Third Beach; see also Harley 2011), it would appear that *S. cariosus* can still dominate mid-intertidal space in cases where *Pisaster* predation pressure is not too high (e.g., West Beach), or is focused on more desirable mussels that persist in a narrow band higher on the shore due to high wave exposure (e.g., Seventh Beach). These patterns are worthy of further study, as our sample sizes are too small to draw definitive conclusions regarding their causes.

While mussels monopolized primary space in the absence of *Pisaster*, this does not necessary preclude other species from forming secondary cover (i.e., growing on mussel shells). Further south in Oregon and California, Lohse (1993) found that most but not all species found living directly on rock substrata in the absence of mussels were also found, at least occasionally, living on mussel shells as well. Although abundances often differed between habitats and there were important differences in richness patterns among sites, Lohse's results suggest that epizoism can reduce the likelihood of complete competitive exclusion by mussels. In our surveys, of the 17 sessile species found growing on the rock in areas with many *Pisaster* but *not* in areas with few *Pisaster*, many (65%) but not all of these species could be found growing on secondary substrata instead. Interestingly, much of this secondary space-holder diversity was actually facilitated by *S. cariosus* growing in small disturbance patches, rather than by the mussels that dominated the vast majority of plots at the landward end of headlands.

The predator-driven differences in mussel dominance in the mid-intertidal zone allowed us to move beyond the primary space-holders explored by Paine and test the effects of *Pisaster* on the diversity of the entire mid-intertidal community. Given earlier work by Suchanek and others (Suchanek 1979, 1992, Smith et al. 2006, Commito et al. 2008, Koivisto and Westerbom

2010, Silliman et al. 2011, Bogdanski et al. 2024), we were unsurprised by the large number of species present in mussel-dominated plots. Indeed, the plot-level *M. californianus* bed richness we observed was broadly similar to that reported from California in 2002 (Smith et al. 2006), although the sample plots in the Smith et al. study were larger and only considered animals. What was somewhat surprising was that plots lacking mussels as facilitators were nonetheless often highly speciose. Beds of thatched barnacles (*Semibalanus cariosus*) and seaweeds hosted similar species richness to *M. californianus* beds in our headland surveys. Targeted sampling on a gently sloping rocky bench where patches of *M. californianus* and *S. cariosus* were intermixed at the scale of centimeters to meters — likely as a result of patch-dynamics related to wave disturbance (Paine and Levin 1981) — revealed that the average number of species per plot (alpha diversity) was actually higher in *S. cariosus* beds. This latter result paralleled our plot-scale epizoid (secondary cover) richness result for *S. cariosus* on the focal headlands, where these barnacles provided secondary substrate for considerably more sessile species than did *M. californianus* both at the plot level and in total. The highly rugose, "thatched" barnacle shell surfaces provide advantageous opportunities for seaweed recruitment (e.g., Johnson 1994), and recesses and cavities within shells, among individuals, or in empty tests provide a variety of dwelling spaces for small invertebrates (e.g., Barnes 2000). *Semibalanus cariosus* has also been shown to provide habitat for a diverse species assemblage elsewhere in British Columbia (Hesketh and Harley 2023), and it would seem that this barnacle's influence as an autogenic ecosystem engineer may be underappreciated relative to the better-studied mytilid mussels.

Considering both positive and negative interactions allows for a more fulsome assessment of the impacts of keystone predators. Lafferty and Suchanek (2016) contend that to generalize from Paine's original (1966) results to other systems "requires the assumption that

either the competitive dominant is not also a foundational species or species facilitated by the dominant are not counted in the tally of biodiversity.” We find this view to be incomplete, as other foundation species may dominate the space made available by a keystone consumer removing the competitive dominant, and these subordinate species may themselves support high diversity. Unless we know the diversity of species associated with both the competitively dominant foundation species and its competitively inferior replacement(s), we do not have a complete picture of how keystone predation influences total biodiversity within a system. Indeed, we found that these subordinate foundation species can in fact support diverse communities of associated species, with richness and composition depending on the identity of the subordinate species and the scale of investigation. Compared to mussels, the structurally complex beds of the large barnacle *S. cariosus* supported a similar or greater number of species at the plot scale depending on the comparison, while beds of the diminutive little brown barnacle (*Chthamalus dalli*) supported fewer. Similar patterns may apply in other keystone scenarios, including those involving trophic cascades. For instance, sea otters indirectly support the presence of biodiverse kelp forests — and reduce the presence of alternative urchin barren or mussel and barnacle-dominated states — through their voracious consumption of sea urchins (Estes and Palmisano 1974). However, considerations of otter-mediated effects on kelp-associated species generally focus on fish and large invertebrates (e.g., Gregr et al. 2020). It is unclear whether the replacement of kelp forests by alternate ecosystem states would decrease overall diversity once more diminutive taxa are considered, as both urchin barrens (Coleman and Kennelly 2019) and algal turf meadows (Dijkstra et al. 2017) elsewhere have been found to harbor a greater biodiversity of small algae and invertebrates than nearby kelp forests. More holistic diversity

surveys in areas with and without cascade-causing keystones such as sea otters, described above, or wolves (Ripple and Beschta 2012) would be an interesting avenue of future study.

While mean species richness patterns at the plot scale in our study suggest that areas with higher *Pisaster* predation pressure feature higher primary space-holder diversity but similar overall diversity relative to areas where *Pisaster* are rare, this limited scale of comparison fails to tell the whole story. For example, although plot-scale richness within mussel beds was actually lower than *S. cariosus* beds in our targeted comparison of these two taxa, species turnover (beta diversity) was higher and there were more unique species found in mussel beds. While dispersion also appeared to be somewhat higher with mussel bed plots in the headlands surveys, it was statistically comparable to other biogenic habitats (*S. cariosus*, *C. dalli*, or various macroalgae) that persisted in the presence of *Pisaster*, a result that may be due to low, unbalanced sample sizes among habitat types. Nevertheless, when considered collectively, the communities facilitated by these subordinate foundation species at the seaward end of the headlands had higher beta diversity than landward mussel bed communities. These competitively inferior space-holders supported different community types, and each biogenic habitat type (*S. cariosus*, *C. dalli*, and macroalgae) contained at least one unique species.

These results suggest that we may have been approaching the predation-diversity debate through too narrow of a lens, that of alpha diversity. Patterns of biodiversity are inherently scale-dependent (Chase et al. 2018), but with regards to predator effects on biodiversity, patterns beyond plot-scale averages are often overlooked. Historically, the popularity of ANOVA-based experimental designs has resulted in many comparisons of the mean richness or diversity of plots in areas with or without predators; this limited viewpoint is something of which we ourselves have been guilty (Harley 2011). However, plot-scale inferences are not the only, or even the best,

scale at which to address patterns of biodiversity (Chase et al. 2019). Such a simplistic approach ignores potentially substantial species turnover among plots, and different foundation species, or combinations of foundation species, may have higher or lower beta diversity. Taken together, our results demonstrate that keystone predator effects on biodiversity are scale-dependent, and suggest that — as with many patterns in biodiversity — a more complete understanding of the predation-biodiversity relationship requires a careful consideration of both local-scale richness and species composition differences among plots.

In summary, the relationship between *Pisaster*, the original keystone species, and diversity at the plot scale depends on what foundation species replace the mussels that *Pisaster* consumes. For example, a bed of the small barnacle *C. dalli* is a considerably poorer habitat than a mussel bed, but beds of the larger barnacle *S. cariosus* may actually support higher species richness at the plot scale. Widening our viewpoint to consider among-plot variation within a site (the targeted *M. californianus* vs. *S. cariosus* comparison), we found the mussel beds had higher turnover among plots and thus higher beta diversity that balanced out lower alpha diversity and resulted in an equal number of species in both habitats. Scaling up further to consider multiple headlands, *Pisaster* predation transformed a near mussel monoculture to a patchwork of other biogenic habitat types, and the beta diversity among plots was higher where *Pisaster* was an important ecological force. Our original goal was to determine whether a particularly well-studied predator truly does have a positive effect on overall biodiversity in addition to the diversity of primary space-holders originally considered by Paine. While we now have a more complete species richness tally across the entire macroscopic community (the total number of species found in areas with and without *Pisaster* was relatively similar at 98 vs. 102, respectively), our results indicate that the true answer to this question is both nuanced and scale-

dependent. In many ways, our results suggest that we may not have been asking the right question at all. All biogenic habitats, even the poorest, supported at least one unique species in our samples. Biodiversity is therefore not maximized by the presence of *Pisaster*, or by its absence, but by a landscape mosaic that allows *Pisaster* to control a competitively dominant facilitator in some places but not others. We encourage further holistic work on predator-diversity relationships, as different keystone predators, particularly those that may lack strong direct or indirect links to foundation species (e.g., largemouth bass in lakes; Mittelbach et al. 1995) or have been introduced (Doherty et al. 2016, Mollot et al. 2017), may drive different patterns. By incorporating a landscape-scale perspective into studies of predator-prey interactions and foundation species effects, we will better understand the forces that promote and maintain diversity across a variety of spatial and temporal scales.

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Conflict of interest statement

The authors declare no conflicts of interest.

Literature cited

- Anderson, M. J., T. O. Crist, J. M. Chase, M. Vellend, B. D. Inouye, A. L. Freestone, N. J. Sanders et al. 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist: Roadmap for beta diversity. *Ecology Letters* 14:19–28.
- Barnes, M. 2000. The use of intertidal barnacle shells. *Oceanography and Marine Biology: an Annual Review* 38:157–187.
- Bogdanski, D., L. Marcos-Almansa, and A. A. V. Flores. 2024. Intertidal mussels as ecosystem engineers: maintenance of invertebrate assemblages amid intertidal stress gradients. *Oikos* 2024:e10304.
- Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution* 18:119–125.
- Carrington, E., G. M. Moeser, S. B. Thompson, L. C. Coutts, and C. A. Craig. 2008. Mussel attachment on rocky shores: the effect of flow on byssus production. *Integrative and Comparative Biology* 48:801–807.

- Chase, J. M., McGill, B. J., McGlinn, D. J., May, F., Blowes, S. A., Xiao, X., Knight, T. M., Purschke, O., and N.J. Gotelli. 2018. Embracing scale-dependence to achieve a deeper understanding of biodiversity and its change across communities. *Ecology Letters* 21:1737–1751.
- Chase, J. M., B. J. McGill, P. L. Thompson, L. H. Antão, A. E. Bates, S. A. Blowes, M. Dornelas et al. 2019. Species richness change across spatial scales. *Oikos* 128:1079–1091.
- Chesson, P., and N. Huntly. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *The American Naturalist* 150:519–553.
- Coleman, M. A. and S.J. Kennelly. 2019. Microscopic assemblages in kelp forests and urchin barrens. *Aquatic Botany* 154: 66–71.
- Comito, J. A., S. Como, B. M. Grupe, and W. E. Dow. 2008. Species diversity in the soft-bottom intertidal zone: Biogenic structure, sediment, and macrofauna across mussel bed spatial scales. *Journal of Experimental Marine Biology and Ecology* 366:70–81.
- Darwin, C. 1859. On the origin of species by means of natural selection, or, the preservation of favoured races in the struggle for life. J. Murray, London.
- Dayton, P. K. 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. In *Proceedings of the Colloquium on Conservation Problems in Antarctica*. Allen Press, Blacksburg, VA.
- DiFiore, B., S. Queenborough, E. Madin, V. Paul, M. Decker, and A. Stier. 2019. Grazing halos on coral reefs: predation risk, herbivore density, and habitat size influence grazing patterns that are visible from space. *Marine Ecology Progress Series* 627:71–81.

- Dijkstra, J. A., Harris, L. G., Mello, K., Litterer, A., Wells, C., and C. Ware. 2017. Invasive seaweeds transform habitat structure and increase biodiversity of associated species. *Journal of Ecology* 105: 1668–1678.
- Doherty, T. S., A. S. Glen, D. G. Nimmo, E. G. Ritchie, and C. R. Dickman. 2016. Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences* 113:11261–11265.
- Ellison, A. M. 2019. Foundation species, non-trophic interactions, and the value of being common. *iScience* 13:254–268.
- Estes, J. A., and J. F. Palmisano. 1974. Sea otters: Their role in structuring nearshore communities. *Science* 185:1058–1060.
- Gehman, A.-L. M., and C. D. G. Harley. 2019. Symbiotic endolithic microbes alter host morphology and reduce host vulnerability to high environmental temperatures. *Ecosphere* 10:e02683.
- Gregg, E. J., Christensen, V., Nichol, L., Martone, R. G., Markel, R. W., Watson, J. C., Harley, C. D. G., Pakhomov, E. A., Shurin, J. B., and K. M. A. Chan. 2020. Cascading social-ecological costs and benefits triggered by a recovering keystone predator. *Science* 368:1243–1247.
- Hakai Institute. 2026. Observations from the 2017 Hakai MarineGEO Bioblitz (v1.0) [Data set]. Hakai Institute. <https://doi.org/10.21966/0jfr-7b65>
- Harley, C. D. G., Pankey, M. S., Wares, J. P., Grosberg, R. K., and M. J. Wonham. 2006. Color polymorphism and genetic structure in the sea star *Pisaster ochraceus*. *Biological Bulletin* 211:248–262.

- Harley, C. D. G. 2011. Climate change, keystone predation, and biodiversity loss. *Science* 334:1124–1127.
- Hesketh, A. V., and C. D. G. Harley. 2023. Extreme heatwave drives topography-dependent patterns of mortality in a bed-forming intertidal barnacle, with implications for associated community structure. *Global Change Biology* 29:165–178.
- Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? *The American Naturalist* 93:145–159.
- Johnson, L. E. 1994. Enhanced settlement on microtopographical high points by the intertidal red alga *Halosaccion glandiforme*. *Limnology and Oceanography* 39:1893–1902.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78:1946–1957.
- Jurgens, L. J., L. W. Ashlock, and B. Gaylord. 2022. Facilitation alters climate change risk on rocky shores. *Ecology* 103:e03596.
- Jurgens, L. J., and B. Gaylord. 2018. Physical effects of habitat-forming species override latitudinal trends in temperature. *Ecology Letters* 21:190–196.
- Kaasiku, T., R. Rannap, and P. Männil. 2022. Predation-mediated edge effects reduce survival of wader nests at a wet grassland-forest edge. *Animal Conservation* 25:692–703.
- Koivisto, M. E., and M. Westerborn. 2010. Habitat structure and complexity as determinants of biodiversity in blue mussel beds on sublittoral rocky shores. *Marine Biology* 157:1463–1474.
- Kroeker, K. J., and E. Sanford. 2022. Ecological leverage points: Species interactions amplify the physiological effects of global environmental change in the ocean. *Annual Review of Marine Science* 14:75–103.

- Lafferty, K. D., and T. H. Suchanek. 2016. Revisiting Paine's 1966 sea star removal experiment, the most-cited empirical article in the *American Naturalist*. *The American Naturalist* 188:365–378.
- Lambert, G. 2019. The Ascidiacea collected during the 2017 British Columbia Hakai MarineGEO BioBlitz. *Zootaxa* 4657.
- Letnic, M., E. G. Ritchie, and C. R. Dickman. 2012. Top predators as biodiversity regulators: the dingo *Canis lupus dingo* as a case study. *Biological Reviews* 87:390–413.
- Lewis, D. B., and L. A. Eby. 2002. Spatially heterogeneous refugia and predation risk in intertidal salt marshes. *Oikos* 96:119–129.
- Littler, M., D. Martz, and D. Littler. 1983. Effects of recurrent sand deposition on rocky intertidal organisms: Importance of substrate heterogeneity in a fluctuating environment. *Marine Ecology Progress Series* 11:129–139.
- Lohse, D. P. 1993. The importance of secondary substratum in a rocky intertidal community. *Journal of Experimental Marine Biology and Ecology* 166:1–17.
- Lomolino, M. V. 2000. Ecology's most general, yet protean pattern: The species-area relationship. *Journal of Biogeography* 27:17–26.
- Longman, E. K., S. Merolla, S. A. Talke, N. Trautman, J. L. Largier, L. Harris, and E. Sanford. 2025. Evaluating historical changes in a mussel bed community in northern California. *Scientific Reports* 15:1930.
- McIntire, E. J. B., and A. Fajardo. 2014. Facilitation as a ubiquitous driver of biodiversity. *New Phytologist* 201:403–416.
- McQuaid, C. D., and K. M. Dower. 1990. Enhancement of habitat heterogeneity and species richness on rocky shores inundated by sand. *Oecologia* 84:142–144.

- Meister, N., T. Langbehn, Ø. Varpe, and C. Jørgensen. 2023. Blue mussels in western Norway have vanished where in reach of crawling predators. *Marine Ecology Progress Series* 721:85–101.
- Menge, B. A., E. L. Berlow, C. A. Blanchette, S. A. Navarrete, and S. B. Yamada. 1994. The keystone species concept: Variation in interaction strength in a rocky intertidal habitat. *Ecological Monographs* 64:249–286.
- Mittelbach, G. G., Turner, A. W., Hall, D. J., Rettig, J. E., and C. W. Osenberg. 1995. Perturbation and resilience: A long-term, whole-lake study of predator extinction and reintroduction. *Ecology* 76:2347–2360.
- Mollot, G., J. H. Pantel, and T. N. Romanuk. 2017. The effects of invasive species on the decline in species richness. *Advances in Ecological Research* 56:61–83.
- Paine, R. T. 1966. Food web complexity and species diversity. *The American Naturalist* 100:65–75.
- Paine, R. T. 1969. A note on trophic complexity and community stability. *The American Naturalist* 103:91–93.
- Paine, R. T. 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* 15:93–120.
- Paine, R. T. 1992. Food-web analysis through field measurement of per capita interaction strength. *Nature* 355:73–75.
- Paine, R. T., and S. A. Levin. 1981. Intertidal landscapes: Disturbance and the dynamics of pattern 51:145–178.

- Paine, R. T., and A. C. Trimble. 2004. Abrupt community change on a rocky shore — biological mechanisms contributing to the potential formation of an alternative state. *Ecology Letters* 7:441–445.
- Peterson, C. N., S. Day, B. E. Wolfe, A. M. Ellison, R. Kolter, and A. Pringle. 2008. A keystone predator controls bacterial diversity in the pitcher-plant (*Sarracenia purpurea*) microecosystem. *Environmental Microbiology* 10:2257–2266.
- Power, M., D. Tilman, J. Estes, B. Menge, W. Bond, L. Mills, G. Daily, J. Castilla, J. Lubchenco, and R. Paine. 1996. Challenges in the quest for keystones. *BioScience* 46:609–620.
- R Core Team. 2024. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Ripple, W. J., and R. L. Beschta. 2012. Trophic cascades in Yellowstone: The first 15 years after wolf reintroduction. *Biological Conservation* 145:205–213.
- Robles, C., Sherwood-Stephens, R., and M. Alvarado. 1995. Responses of a key intertidal predator to varying recruitment of its prey. *Ecology* 76:565–579.
- Robles, C. D., Desharnais, R. A., Garza, C., Donahue, M., and C. A. Martinez. 2009. Complex equilibria in the maintenance of boundaries: experiments with mussel beds. *Ecology* 90:985–995.
- Rogers, T. L., and J. K. Elliott. 2013. Differences in relative abundance and size structure of the sea stars *Pisaster ochraceus* and *Evasterias troschelii* among habitat types in Puget Sound, Washington, USA. *Marine Biology* 160:853–865.
- Roswell, M., J. Dushoff, and R. Winfree. 2021. A conceptual guide to measuring species diversity. *Oikos* 130:321–338.

- Schluter, D., and M. W. Pennell. 2017. Speciation gradients and the distribution of biodiversity. *Nature* 546:48–55.
- Scrosati, R. A., and J. A. Ellrich. 2024. Changes in the composition of invertebrate assemblages from wave-exposed intertidal mussel stands along the Nova Scotia coast, Canada. *PeerJ* 12:e17697.
- Silliman, B. R., M. D. Bertness, A. H. Altieri, J. N. Griffin, M. C. Bazterrica, F. J. Hidalgo, C. M. Crain, and M. V. Reyna. 2011. Whole-community facilitation regulates biodiversity on Patagonian rocky shores. *PLoS ONE* 6:e24502.
- Smith, J. R., P. Fong, and R. F. Ambrose. 2006. Dramatic declines in mussel bed community diversity: Response to climate change? *Ecology* 87:1153–1161.
- Smithson, M., and J. Verkuilen. 2006. A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. *Psychological Methods* 11:54–71.
- Socolar, J. B., J. J. Gilroy, W. E. Kunin, and D. P. Edwards. 2016. How should beta-diversity inform biodiversity conservation? *Trends in Ecology & Evolution* 31:67–80.
- Suchanek, T. 1979. The *Mytilus californianus* community: Studies on the composition, structure, organization and dynamics of a mussel bed. PhD dissertation, University of Washington.
- Suchanek, T. 1992. Extreme biodiversity in the marine environment: Mussel bed communities of *Mytilus californianus*. *The Northwest Environmental Journal* 8:150–152.
- Terborgh, J. W. 2015. Toward a trophic theory of species diversity. *Proceedings of the National Academy of Sciences* 112:11415–11422.
- Tsuchiya, M. 1983. Mass mortality in a population of the mussel *Mytilus edulis* L. caused by high temperature on rocky shores. *Journal of Experimental Marine Biology and Ecology*.

- Waide, R. B., M. R. Willig, C. F. Steiner, G. Mittelbach, L. Gough, S. I. Dodson, G. P. Juday, and R. Parmenter. 1999. The relationship between productivity and species richness. *Annual Review of Ecology and Systematics* 30:257–300.
- Whalen, M. A., S. Starko, S. C. Lindstrom, and P. T. Martone. 2023. Heatwave restructures marine intertidal communities across a stress gradient. *Ecology* 104: e4027.

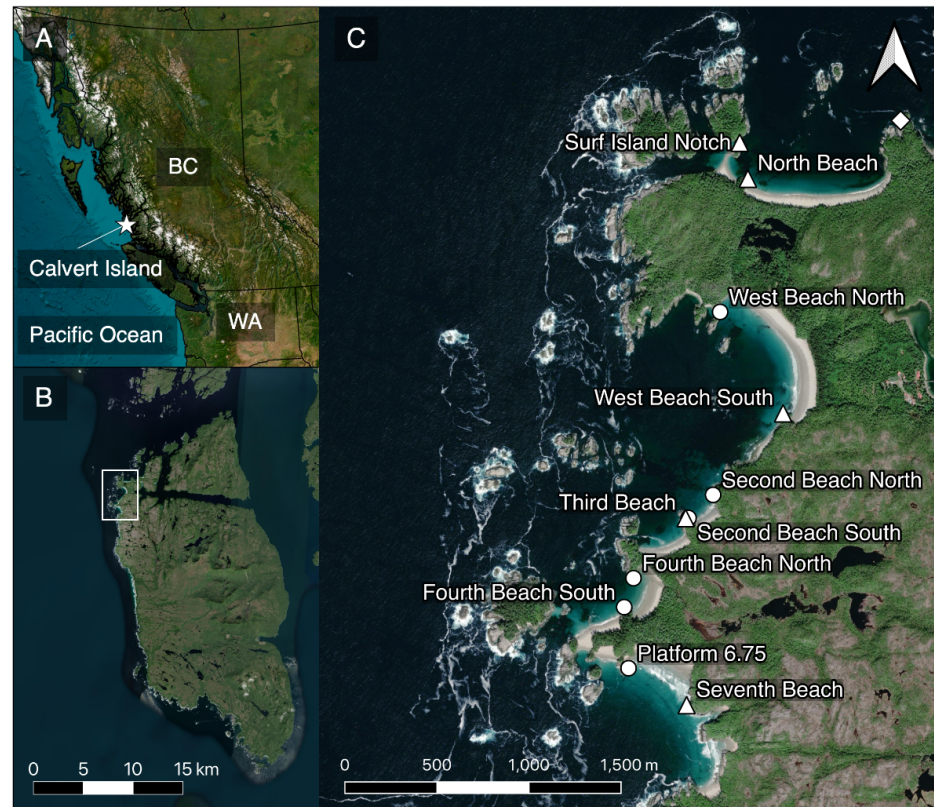


Figure S1. Map of headlands used in the present study. Surveys were conducted on (A) Calvert Island in British Columbia, Canada (B) on the island's northwestern coast, where 11 headlands were surveyed (C) to test the effect of *Pisaster* presence on plot-scale and landscape-scale intertidal biodiversity. Circular points indicate locations of zonation surveys. Triangular points indicate the five sites where biodiversity sampling and primary space-holder surveys occurred in addition to zonation surveys. *Pisaster* feeding trials were conducted at these same five sites along with Second Beach North. The northernmost diamond point indicates where *S. cariosus* and *M. californianus* beds were sampled for targeted biodiversity comparisons in 2017. Satellite imagery © ESRI.

9 **Table S1.** Site locations, site characteristics, and sampling dates for Calvert Island headland comparisons.

Site (wave exposure)	Headland segment	Latitude (°N)	Longitude (°W)	Aspect	Sand level (m)	Dates of <i>Pisaster</i> censuses	Dates of feeding experiment (start; end)	Dates of zonation surveys
Surf Island (semi-exposed)	landward	51.66528	-128.14685	NW	2.04	2017-04-29 2017-08-06 2017-09-21 2019-07-13	2021-05-27 2021-08-20	2017-04-29
	seaward	51.66545	-128.14627	NW	0.44	2021-05-26 2022-05-17		
North Beach (semi- exposed)	landward	51.66358	-128.14541	E	1.52	2017-04-29 2017-08-06 2017-09-21 2019-07-13	2021-07-13 2021-07-18	2017-04-29
	seaward	51.66373	-128.14543	E	1.02	2020-08-21 2021-05-26 2022-05-17		
West Beach North (semi-exposed)	landward	51.65736	-128.14692	E	N/A	2023-06-04	N/A	2023-06-04
	seaward	51.65715	-128.14687	E	N/A			
West Beach South (semi-exposed)	landward	51.65235	-128.14138	W	1.91	2017-08-09 2018-06-16 2019-07-13 2020-08-21	2020-08-21 2021-05-24	2017-09-24 2022-05-15
	seaward	51.65243	-128.14138	W	1.56	2021-05-24 2022-05-13 2023-06-04		

Site (wave exposure)	Headland segment	Latitude (°N)	Longitude (°W)	Aspect	Sand level (m)	Dates of <i>Pisaster</i> censuses	Dates of feeding experiment (start; end)	Dates of zonation surveys
Second Beach North (exposed)	landward	51.64794	-128.14641	W	N/A	2023-06-03 2026-08-13	2026-08-13 2026-08-17	2023-06-03
	seaward	51.64822	-128.14641	W	N/A			
Second Beach South (semi-exposed)	landward	51.6470	-128.14796	N	N/A	2023-06-03	N/A	2023-06-03
	seaward	51.64701	-128.1482	N	N/A			
Third Beach (exposed)	landward	51.64647	-128.14865	W	1.53	2017-04-30 2017-09-20 2018-06-17 2019-07-14 2020-08-21 2021-05-25 2022-05-18	2021-05-29 2021-08-19	2017-04-30
	seaward	51.64699	-128.14843	N	(subtidal)			
Fourth Beach North (semi-exposed)	landward	51.64399	-128.15196	N	N/A	2023-06-03	N/A	2023-06-03
	seaward	51.64389	-128.15218	N	N/A			
Fourth Beach South (semi-exposed)	landward	51.64249	-128.15245	S	N/A	2023-06-03	N/A	2023-06-03
	seaward	51.64245	-128.15275	S	N/A			
Platform 6 ¾ (exposed)	landward	51.63973	-128.15165	E	1.54	2017-04-26 2022-05-18	N/A	2017-04-27

Site (wave exposure)	Headland segment	Latitude (°N)	Longitude (°W)	Aspect	Sand level (m)	Dates of <i>Pisaster</i> censuses	Dates of feeding experiment (start; end)	Dates of zonation surveys
	seaward	51.63949	-128.15207	E	0.47			
Seventh Beach (very exposed)	landward	51.63852	-128.14730	W	1.65	2017-05-01	2017-07-14	2017-05-01
						2017-09-20	2017-07-18	
						2018-06-17		
						2019-07-14		
						2020-08-21		
						2021-05-28		
						2022-05-18		
	seaward	51.63789	-128.14732	W	0.90			



Figure S2. Photographs taken during field work showing: **(A)** differences in mussel bed extent observed between the seaward segment (foreground, note the abundant *Semibalanus cariosus* and the presence of *Pisaster*) and landward segment (background, note the extensive mussel bed) of the rocky headland at Second Beach North, surveyed in 2023 (Fig. S1; Table S1); **(B)** *M. californianus* outplanted to the landward segment of a headland after 82 days (note that all mussels have survived and laid down byssus); **(C)** *M. californianus* outplanted on a seaward segment after 3 days, with empty, clean shells providing evidence of predation by *Pisaster*; **(D)** a seaward outplant block with one mussel consumed and one mussel entirely removed within 24 hours of outplanting; **(E)** a nearby *Pisaster* feeding on the removed mussel from panel D the morning after it was outplanted; there were no naturally-occurring adult mussels close to these outplants. All photographs by CGDH.

ID	Functional group	Taxon	Bioblitz samples					Targeted samples	
			Landward	Seaward				Off-headland	
			<i>Mytilus</i>	<i>Chthamalus</i>	Fleshy algae	<i>Semibalanus</i>	Coralline algae	<i>Mytilus</i>	<i>Semibalanus</i>
1	SI	<i>Abietinaria filicula</i>	1	0	0	0	0	0	0
2	A	<i>Acrosiphonia coalita</i>	0	0	0	0	1	0	0
3	MI	<i>Aeolidia papillosa</i>	1	0	0	0	0	0	0
4	SI	<i>Alcyonidium</i> sp.	1	0	0	0	0	0	0
5	SI	<i>Amathia gracilis</i>	1	0	0	0	0	0	0
6	MI	<i>Americorophium brevis</i>	0	0	1	0	0	0	0
7	MI	Amphipoda (unidentified)	0	0	0	1	0	1	1
9	MI	<i>Amphiporus formidabilis</i>	0	0	0	0	0	1	1
10	MI	<i>Ampithoe dalli</i>	1	0	1	0	1	0	0
11	MI	<i>Anelepus japonicus</i>	1	0	1	0	0	0	0
12	SI	<i>Anthopleura elegantissima</i>	1	0	1	1	1	1	1
13	SI	<i>Anthopleura xanthogrammica</i>	1	0	0	0	0	0	0

ID	Functional group	Taxon	Bioblitz samples				Targeted samples		
			Landward	Seaward			Off-headland		
				<i>Mytilus</i>	<i>Chthamalus</i>	Fleshy algae	<i>Semibalanus</i>	Coralline algae	<i>Mytilus</i>
14	MI	<i>Aoroides exilis</i>	1	0	0	0	0	0	0
15	MI	<i>Apohyale anceps</i>	1	0	1	1	1	1	1
16	MI	Arachnida (unknown mites)	1	0	0	1	0	1	1
17	MI	<i>Armandia brevis</i>	1	0	0	0	0	0	0
18	SI	<i>Balanus crenatus</i>	1	0	0	0	0	0	0
19	SI	<i>Balanus glandula</i>	1	1	1	1	1	1	1
20	MI	<i>Boccardia columbiana</i>	0	0	0	1	0	0	0
21	A	<i>Bossiella</i> sp.	1	0	0	0	0	0	0
22	SI	<i>Bowerbankia</i> sp.	1	0	0	0	0	0	0
23	MI	<i>Branchiomaldane simplex</i>	1	0	0	0	0	0	0
24	SI	Bryozoa (unidentified)	1	0	0	0	0	1	0
25	A	<i>Callithamnion pikeanum</i>	0	0	0	0	1	0	0

ID	Functional group	Taxon	Bioblitz samples					Targeted samples	
			Landward	Seaward				Off-headland	
			<i>Mytilus</i>	<i>Chthamalus</i>	Fleshy algae	<i>Semibalanus</i>	Coralline algae	<i>Mytilus</i>	<i>Semibalanus</i>
26	MI	Caprellidae	1	0	0	0	0	0	0
27	A	<i>Ceramothamnion coulteri</i>	1	0	0	0	0	0	0
28	A	<i>Ceramothamnion pacificum</i>	0	0	0	0	1	0	0
29	A	<i>Chamberlainium tumidum</i>	0	0	1	0	1	0	0
30	MI	Chironomidae 1 (larva)	0	1	0	0	0	0	0
31	MI	Chironomidae 2 (larva)	0	0	0	1	0	0	0
32	MI	Chironomidae 3 (larva)	0	1	0	0	0	0	0
33	MI	Chironomidae 4 (larva)	0	0	0	1	1	0	0
34	MI	Chironomidae 5 (larva)	0	0	0	1	0	0	0
35	A	Chlorophyta 1 (unidentified)	1	0	0	0	0	0	0
36	A	Chlorophyta 2 (unidentified)	1	0	0	1	0	0	0
37	SI	<i>Chthamalus dalli</i>	1	1	1	1	1	1	1

ID	Functional group	Taxon	Bioblitz samples					Targeted samples	
			Landward	Seaward				Off-headland	
			<i>Mytilus</i>	<i>Chthamalus</i>	Fleshy algae	<i>Semibalanus</i>	Coralline algae	<i>Mytilus</i>	<i>Semibalanus</i>
38	MI	<i>Cirolana harfordi</i>	1	0	0	0	0	1	0
39	MI	Cirolanidae (unidentified)	1	0	0	0	0	0	0
40	A	<i>Cladophora columbiana</i>	1	0	0	1	1	1	1
41	A	<i>Colpomenia peregrina</i>	0	0	1	1	1	0	0
42	A	<i>Corallina officinalis</i>	1	0	1	0	0	0	0
43	A	<i>Corallina</i> sp.	0	0	0	0	0	1	1
44	A	<i>Corallina vancouveriensis</i>	1	0	0	1	1	0	0
45	A	Corallinophycidae (unidentified)	0	0	1	0	0	1	1
46	SI	<i>Crucigera zygophora</i>	1	0	0	0	0	0	0
47	A	<i>Cryptosiphonia woodii</i>	0	0	1	0	0	0	0
48	SI	<i>Cucumaria pseudocurata</i>	1	0	0	0	0	1	0
49	SI	<i>Cucumaria</i> sp.	1	0	0	0	0	0	0

ID	Functional group	Taxon	Bioblitz samples				Targeted samples		
			Landward	Seaward				Off-headland	
				<i>Mytilus</i>	<i>Chthamalus</i>	Fleshy algae	<i>Semibalanus</i>	Coralline algae	<i>Mytilus</i>
50	SI	<i>Cucumaria vegae</i>	1	0	0	0	0	0	0
51	SI	<i>Cyanoplax dentiens</i>	0	0	0	1	0	0	0
52	MI	<i>Cyanoplax fernaldi</i>	1	0	1	0	0	0	0
53	MI	<i>Diaulula sandiegensis</i>	1	0	0	0	0	0	0
54	MI	Diptera (unidentified)	0	0	0	1	1	0	0
55	MI	<i>Dynamene benedicti</i>	0	0	1	0	1	0	0
56	MI	<i>Dynamenella sheareri</i>	0	0	0	1	0	1	1
57	MI	<i>Emplectonema gracile</i>	1	0	0	1	0	1	1
58	A	<i>Endocladia muricata</i>	1	1	0	1	1	1	1
59	SI	<i>Eudistylia vancouveri</i>	1	0	0	0	0	0	0
60	MI	<i>Eulalia quadrioculata</i>	1	0	0	1	0	0	0
61	A	<i>Fucus distichus</i>	1	1	1	0	0	1	1

ID	Functional group	Taxon	Bioblitz samples					Targeted samples	
			Landward	Seaward				Off-headland	
			<i>Mytilus</i>	<i>Chthamalus</i>	Fleshy algae	<i>Semibalanus</i>	Coralline algae	<i>Mytilus</i>	<i>Semibalanus</i>
62	MI	Gastropoda 1 (unidentified)	1	0	0	0	0	0	0
63	MI	Gastropoda 2 (unidentified)	0	0	0	0	0	1	0
64	MI	Gastropoda 3 (unidentified)	0	0	0	0	0	1	0
65	A	<i>Gloiopeltis</i> sp.	0	0	0	1	0	0	0
66	SI	<i>Haliclona</i> sp.	1	0	0	0	0	0	0
67	A	<i>Halosaccion glandiforme</i>	0	0	1	0	0	0	0
68	MI	<i>Hemigrapsus nudus</i>	1	0	0	1	0	1	1
69	MI	<i>Hemioniscus balani</i>	0	1	0	0	0	0	0
70	A	<i>Herpochondria borealis</i>	0	0	0	0	1	0	0
71	SI	<i>Hiatella arctica</i>	1	0	0	1	0	0	0
72	A	<i>Hildenbrandia</i> sp	0	1	1	0	1	0	0
73	A	<i>Hymenena</i> sp.	0	0	0	0	1	0	0

ID	Functional group	Taxon	Bioblitz samples					Targeted samples	
			Landward	Seaward				Off-headland	
			<i>Mytilus</i>	<i>Chthamalus</i>	Fleshy algae	<i>Semibalanus</i>	Coralline algae	<i>Mytilus</i>	<i>Semibalanus</i>
74	MI	Insecta 1 (unidentified larva)	0	0	0	0	0	0	1
75	MI	Insecta 2 (unidentified larva)	0	0	0	0	0	1	1
76	MI	Isopoda (unidentified)	1	0	0	1	0	0	0
77	MI	Isopoda 2 (unidentified)	0	0	0	1	0	1	0
78	MI	<i>Katharina tunicata</i>	1	0	0	0	1	0	0
79	SI	<i>Kurtiella tumida</i>	0	0	1	0	0	1	1
80	SI	<i>Lasaea rubra</i>	0	0	0	1	1	0	0
81	SI	<i>Lasaea</i> sp.	0	0	1	1	0	0	0
82	SI	<i>Leukoma staminea</i>	1	0	0	0	0	0	0
83	MI	<i>Littorina plena</i>	1	1	1	0	0	0	1
84	MI	<i>Littorina scutulata</i>	1	1	1	1	0	0	1
85	MI	<i>Littorina sitkana</i>	0	1	1	0	0	0	0

ID	Functional group	Taxon	Bioblitz samples					Targeted samples	
			Landward	Seaward				Off-headland	
			<i>Mytilus</i>	<i>Chthamalus</i>	Fleshy algae	<i>Semibalanus</i>	Coralline algae	<i>Mytilus</i>	<i>Semibalanus</i>
86	MI	<i>Lottia digitalis</i>	1	1	0	1	0	1	1
87	MI	<i>Lottia paradigitalis</i>	1	1	1	1	1	1	1
88	MI	<i>Lottia pelta</i>	1	1	0	1	0	1	1
89	MI	<i>Lottia scutum</i>	0	0	1	0	0	0	0
90	A	<i>Mastocarpus</i> sp.	1	1	1	0	1	0	1
91	SI	<i>Membranipora</i> sp.	1	0	0	0	0	0	0
92	SI	Metazoa (unidentified)	1	0	0	0	0	0	0
93	SI	Metazoa 2 (unidentified)	0	0	0	0	0	0	1
94	SI	<i>Metridium</i> sp.	1	0	0	0	0	1	0
95	SI	<i>Modiolus</i> sp.	1	0	1	0	0	1	0
96	SI	<i>Mysella</i> sp.	0	0	1	0	0	0	0
97	SI	<i>Mytilus californianus</i>	1	1	1	1	1	1	1

ID	Functional group	Taxon	Bioblitz samples				Targeted samples		
			Landward	Seaward				Off-headland	
				<i>Mytilus</i>	<i>Chthamalus</i>	Fleshy algae	<i>Semibalanus</i>	Coralline algae	<i>Mytilus</i>
98	MI	<i>Naineris uncinata</i>	1	0	0	0	0	0	
99	A	<i>Nemalion elminthoides</i>	1	0	1	1	0	0	1
100	MI	Nematoda (unidentified)	1	0	1	0	1	1	1
101	MI	Nemertea (unidentified)	1	0	0	1	0	0	0
102	MI	<i>Nereis vexillosa</i>	1	0	1	1	0	1	1
103	MI	<i>Notoplana</i> sp.	1	0	1	1	1	1	1
104	MI	<i>Nucella ostrina</i>	1	0	1	1	0	1	1
105	A	<i>Odonthalia floccosa</i>	0	0	0	0	0	1	1
106	MI	<i>Oedoparena</i> sp.	0	1	1	0	0	0	0
107	MI	Oligochaeta (unidentified)	1	0	1	0	0	0	0
108	MI	<i>Oligochinus lighti</i>	1	0	0	0	0	0	1
109	MI	<i>Onchidella carpenteri</i>	1	0	0	1	0	1	1

ID	Functional group	Taxon	Bioblitz samples				Targeted samples		
			Landward	Seaward				Off-headland	
				<i>Mytilus</i>	<i>Chthamalus</i>	Fleshy algae	<i>Semibalanus</i>	Coralline algae	<i>Mytilus</i>
110	MI	<i>Pagurus granosimanus</i>	1	0	0	0	0	0	0
111	MI	<i>Pagurus hirsutiusculus</i>	1	0	1	0	0	0	0
112	MI	<i>Pancolus californiensis</i>	0	0	1	1	1	0	0
113	SI	<i>Paradexiospira vitrea</i>	1	0	0	0	0	0	0
114	MI	<i>Paranemertes peregrina</i>	1	0	0	1	0	1	1
115	MI	<i>Pentidotea vosnesenskii</i>	1	0	1	1	0	0	0
116	MI	<i>Petrolisthes cinctipes</i>	1	0	0	0	0	1	0
117	SI	<i>Phascolosoma agassizii</i>	1	0	0	0	0	1	0
118	MI	Phoxichilidiidae (unidentified)	1	0	0	0	0	0	0
119	MI	<i>Pisaster ochraceus</i>	1	0	0	0	1	0	0
120	MI	<i>Platynereis bicanaliculata</i>	1	0	0	0	0	0	0
121	A	<i>Plocamium</i> sp.	0	0	0	1	1	0	0

ID	Functional group	Taxon	Bioblitz samples					Targeted samples	
			Landward	Seaward				Off-headland	
			<i>Mytilus</i>	<i>Chthamalus</i>	Fleshy algae	<i>Semibalanus</i>	Coralline algae	<i>Mytilus</i>	<i>Semibalanus</i>
122	SI	<i>Pollicipes polymerus</i>	1	0	0	1	1	1	1
123	MI	Polychaeta 1 (unidentified)	0	0	0	0	0	1	1
124	MI	Polychaeta 2 (unidentified)	0	0	0	0	0	1	1
125	MI	Polychaeta 3 (unidentified)	0	0	0	0	0	0	1
126	MI	Polycladida (unidentified)	0	0	0	0	1	0	0
127	SI	Polyplacophora	1	0	1	1	0	0	1
128	A	<i>Polysiphonia</i> sp.	0	0	0	1	1	0	0
129	SI	Porifera (unidentified)	1	0	0	0	0	0	0
130	MI	<i>Proceraea okadai</i>	1	0	0	0	0	0	0
131	MI	<i>Protohyale oclairi</i>	0	0	1	0	0	0	0
132	SI	<i>Psuedocna</i> sp.	1	0	0	0	0	0	0
133	A	<i>Pterosiphonia</i> sp	0	0	0	0	0	0	0

ID	Functional group	Taxon	Bioblitz samples				Targeted samples		
			Landward	Seaward				Off-headland	
				<i>Mytilus</i>	<i>Chthamalus</i>	Fleshy algae	<i>Semibalanus</i>	Coralline algae	<i>Mytilus</i>
134	A	<i>Pyropia falex</i>	0	1	1	0	0	0	0
135	A	<i>Pyropia fusicola</i>	0	1	0	0	0	0	0
136	A	<i>Pyropia</i> sp. (unidentified)	0	1	0	0	0	0	1
137	A	Rhodophyta (unidentified)	1	0	0	1	1	1	1
138	SI	<i>Schizobranchia insignis</i>	1	0	0	0	0	0	0
139	MI	<i>Scoletoma zonata</i>	1	0	0	0	0	0	0
140	SI	<i>Scrupocellaria</i> sp.	1	0	0	0	0	0	0
141	A	<i>Scytosiphon</i> sp.	0	0	1	0	0	0	0
142	SI	<i>Semibalanus cariosus</i>	1	1	1	1	1	1	1
143	SI	Serpulidae	1	0	0	0	0	0	0
144	SI	<i>Sertularella rugosa</i>	1	0	0	0	0	0	0
145	SI	<i>Sertularia</i> sp.	1	0	0	0	0	0	0

ID	Functional group	Taxon	Bioblitz samples					Targeted samples	
			Landward	Seaward				Off-headland	
			<i>Mytilus</i>	<i>Chthamalus</i>	Fleshy algae	<i>Semibalanus</i>	Coralline algae	<i>Mytilus</i>	<i>Semibalanus</i>
146	A	<i>Sphacelaria rigidula</i>	0	0	1	1	0	0	0
147	SI	Spirorbidae	1	0	0	0	0	0	0
148	MI	Staphalinidae	0	0	0	0	0	1	1
149	MI	Staphalinidae (larva)	1	1	0	1	1	0	0
150	MI	<i>Syllis adamantea</i>	1	1	0	1	1	0	0
151	MI	<i>Syllis pigmentata</i>	1	0	1	1	0	0	0
152	SI	<i>Symplectoscyphus tricuspidatus</i>	1	0	0	0	0	0	0
153	MI	Tanaeidae	0	1	0	1	0	0	1
154	MI	<i>Tegula funebris</i>	1	0	0	0	0	1	0
155	SI	Terebellidae	1	0	0	0	0	0	0
156	MI	<i>Tetrastemma bilineatum</i>	0	0	0	0	0	1	0
157	MI	<i>Tetrastemma</i> sp. 1	0	0	0	1	1	0	0

ID	Functional group	Taxon	Bioblitz samples					Targeted samples	
			Landward	Seaward				Off-headland	
			<i>Mytilus</i>	<i>Chthamalus</i>	Fleshy algae	<i>Semibalanus</i>	Coralline algae	<i>Mytilus</i>	<i>Semibalanus</i>
158	MI	<i>Tetrastemma</i> sp. 2	0	0	0	1	0	0	0
159	A	<i>Ulva intestinalis</i>	1	0	1	0	0	0	1
160	A	<i>Ulva lactuca</i>	1	0	0	0	0	0	0
161	A	<i>Ulva</i> sp.	1	1	1	1	0	1	1
162	MI	<i>Uromunna ubiquita</i>	1	0	0	1	1	0	1
163	A	<i>Urospora</i> sp.	0	0	0	0	0	1	0
164	A	<i>Wildemanian norrisii</i>	0	1	0	0	0	0	0

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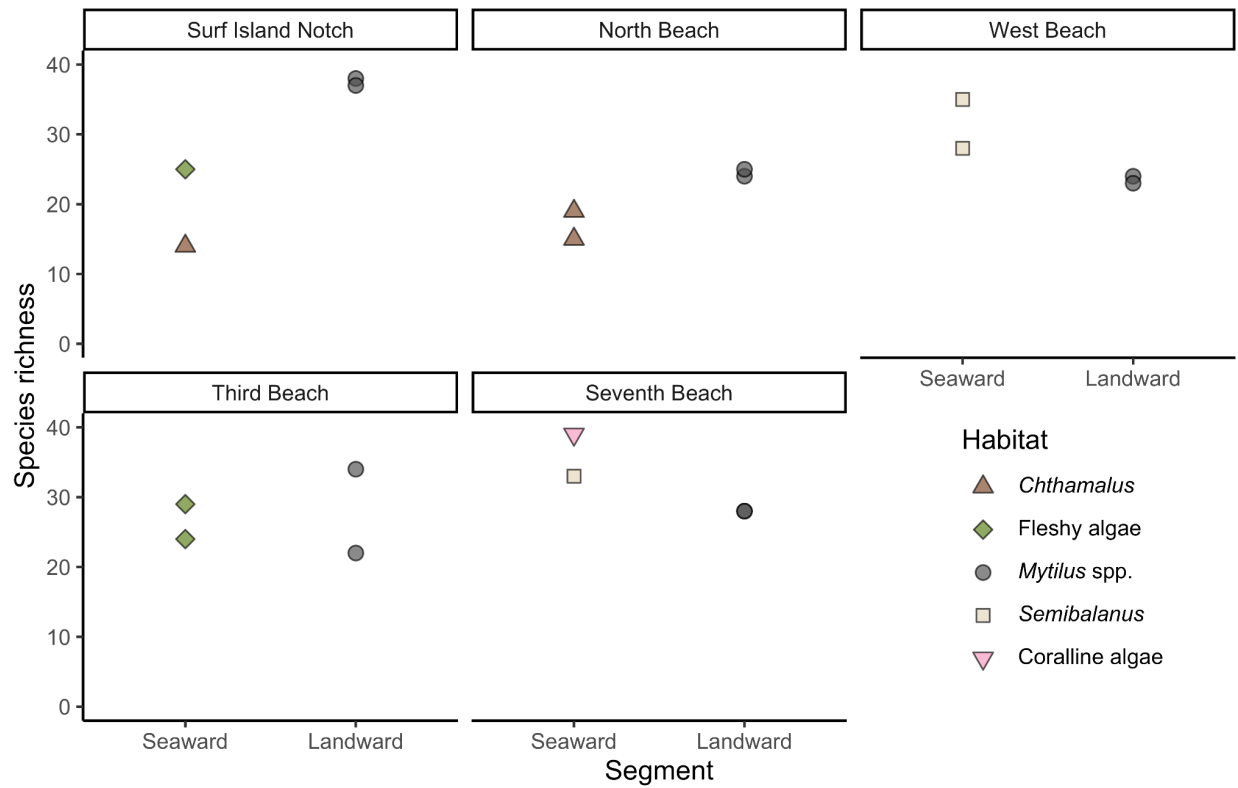


Figure S2. Species richness of individual plots from the seaward (high *Pisaster*) and landward (low *Pisaster*) segments of five headlands. “Habitat” refers to the habitat-forming sessile species with the highest percent cover in each plot.

Table S3. Post-hoc comparisons of community composition between different biogenic habitats ordinated using *capscale* analysis. Samples were collected from areas with and without *Pisaster* at five rocky headlands on Calvert Island, BC as part of a Bioblitz in 2017. Note that the minimum *P* value possible is 0.001, given that the default 999 permutations were used.

Comparison	Df	Sum of Squares	<i>F</i>	<i>P</i>
<i>Chthamalus</i> vs. Coralline algae	2	0.640	2.351	0.167
<i>Chthamalus</i> vs. Fleshy algae	3	0.934	1.524	0.156
<i>Chthamalus</i> vs. <i>Mytilus</i> spp.	5	2.097	2.431	0.001
<i>Chthamalus</i> vs. <i>Semibalanus</i>	3	1.049	2.351	0.022
Coralline algae vs. Fleshy algae	2	0.527	0.968	0.500
Coralline algae vs. <i>Mytilus</i> spp.	5	1.639	1.898	0.001
Coralline algae vs. <i>Semibalanus</i>	2	0.521	1.613	0.167
Fleshy algae vs. <i>Mytilus</i> spp.	5	1.866	1.936	0.001
Fleshy algae vs. <i>Semibalanus</i>	3	0.994	1.528	0.133
<i>Mytilus</i> spp. vs. <i>Semibalanus</i>	5	1.709	1.914	0.001

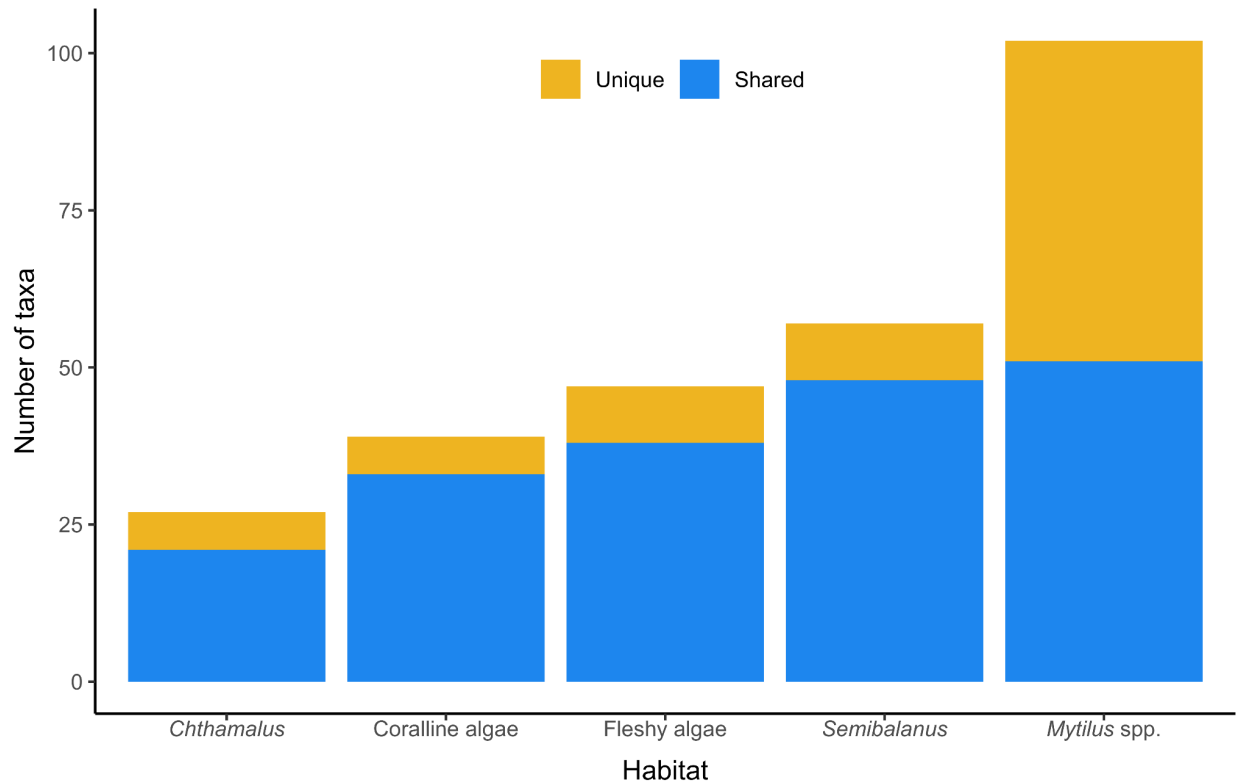


Figure S3. Number of taxa found in different habitat types created by intertidal foundation species surveyed during the 2017 Bioblitz on Calvert Island, British Columbia. The height of the bars indicates the total number of species among all plots sampled of that type, and the portion shaded yellow indicates the number of these that were unique to the habitat sampled. The number of plots sampled varied between habitat types; n=10 plots sampled for *Mytilus* spp., n=3 plots for *Semibalanus*, fleshy algae, and *Chthamalus*, and n=1 plot for coralline algae.

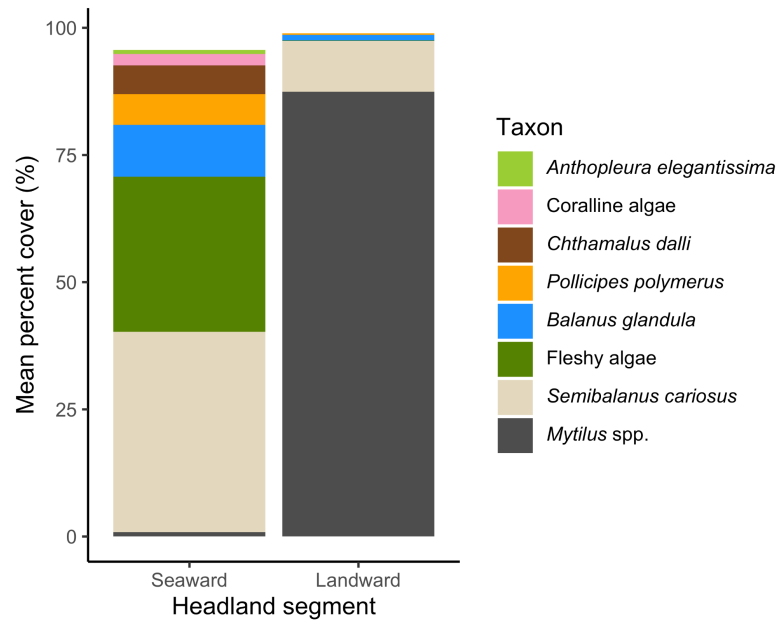


Figure S4. Stacked barplot showing the mean percent cover for primary space-holders along mid-intertidal transects surveyed at the seaward and landward segments of five headlands on Calvert Island, British Columbia, Canada in 2025 (n=5 per headland segment, N=50, see Fig S1 and Table S1 for site details).

98 **Table S4.** Epizoic species growing on *Semibalanus cariosus* and *Mytilus californianus* beds at
99 five headlands on Calvert Island, British Columbia, Canada in 2025 (across n=5 samples per
100 headland segment, see Fig. S1 and Table S1 for site details). The presence of species for each
101 habitat type and headland segment is shown by a 0 (absent) or 1 (present); there were no
102 instances of *M. californianus* habitat on seaward headland segments.

Species	Group	<i>Semibalanus cariosus</i>		<i>Mytilus californianus</i>
		Landward	Seaward	Landward
<i>Acrosiphonia coalita</i>	Green alga	1	1	0
<i>Alaria marginata</i>	Kelp	1	1	0
<i>Anthopleura elegantissima</i>	Anemone	1	1	1
<i>Balanus glandula</i>	Barnacle	1	1	1
<i>Chthamalus dalli</i>	Barnacle	0	0	1
<i>Corallina vancouveriensis</i>	Red alga	0	1	0
<i>Endocladia muricata</i>	Red alga	0	1	1
<i>Fleshy algal crust</i>	Red alga	1	1	0
<i>Fucus distichus</i>	Brown alga	1	1	1
<i>Halosaccion glandiforme</i>	Red alga	1	1	0
<i>Mazzaella affinis</i>	Red alga	1	1	0
<i>Mytilus californianus</i>	Mussel	0	1	
<i>Mytilus trossulus</i>	Mussel	0	1	0
<i>Pollicipes polymerus</i>	Barnacle	0	1	1
<i>Pyropia</i> spp.	Red alga	0	1	1
<i>Filamentous red</i>	Red alga	1	1	1
<i>Semibalanus cariosus</i>	Barnacle			1
<i>Ulva</i> spp.	Green alga	1	1	1

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