Diversity and structure of subtidal rock walls in the Salish Sea: the roles of grazing, oceanography, and long-term change

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Abstract

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The assembly and structure of communities is dictated by a number of ecological processes at a variety of spatial scales. Here I present an 'ecology of places', to emphasize the need for both intensive, small-scale experimentation and the larger-scale context from which to interpret the importance of less easily manipulated processes. Specifically, I investigated the roles of local-scale grazing, mesoscale oceanography, and decadal-scale variation on the diversity and structure of benthic communities on subtidal rock walls in the Salish Sea (inland waters of Washington State).

In the first chapter, I tested the hypothesis that consumers mediate natural variation in the relationship between prey richness and resource use on epilithic communities. Ecological theory and previous experimental work in dock communities predicted that resource (space) use is a negative, linear function of the number of sessile

species present. Contrary to these predictions, a three-month field experiment demonstrated that the relationship between prey richness and resource use was dependent on urchin density, because urchins control the structure of this community by grazing spatially dominant clonal ascidians and facilitating smaller consumers.

Following this work, I tested the effects of consumer identity and the predictions of a structural equation model I had developed in chapter one. Namely, do urchins exert indirect effects by facilitating other consumers? In a year-long factorial field experiment, I reduced the densities of urchins and chitons and discovered that the removal of both consumers resulted in unexpected, non-additive changes in community structure. These results suggest that facilitation and redundancy among consumers contribute to the resiliency of species-depauperate habitat dominated by encrusting algae, even if urchins are transient and do not persist indefinitely.

To place the local-scale experiments into a broader geographic context, I quantified the effect of mesoscale (10 – 100km) oceanographic variation on the diversity of epilithic communities in my third dissertation chapter. I used a hierarchical sampling design to survey 18 sites, nested within five distinct oceanographic seascapes in Washington. The most striking variation in diversity and composition was observed between seascapes with high and low water retention. Three abiotic correlates of water retention (sediment cover, mass flux, temperature) support the qualitative generalization that waterways and inlets represent distinct physical environments, and consequently harbor unique subtidal biota. Larval delivery and post-settlement mortality are likely to be important mechanisms related to the covarying effects of reduced water flow, sedimentation, and light limitation in high-retention sounds and fjords.

Long-term datasets provide a baseline for evaluating temporal variation in biodiversity and are critical for distinguishing between natural and anthropogenic mechanisms of change. My last dissertation chapter tested the hypothesis that the diversity and composition of contemporary (2006-2011) epilithic communities on subtidal rock walls in the San Juan Islands, WA, USA, have changed over thirty years. Despite changes in seawater temperature and chemistry, univariate and multivariate analyses suggest limited differences between historic and modern communities. Historic communities were more even, and characterized by a high percent cover of available space, suggestive of urchin grazing. Despite the initiation of urchin no-take restrictions in 1984, our data indicate that contemporary urchin densities are lower than urchin densities in the 1970's. Declines in biological disturbance (i.e., urchin grazing) will accentuate the naturally low physical disturbance levels on vertical surfaces in subtidal habitats. Although rock walls serve as natural refuges for many invertebrates, a lack of disturbance may allow 'weedy' species to dominate and reduce the local diversity of these subtidal communities.

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Dedicated to my grandfather,
Václav Hrubec,
for his inspirational wanderlust and curiosity

Věnováno mému dědečkovi,
Václavu Hrubcovi,
pro jeho inspirativní cestovní vášeň a zvědavost

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CHAPTER 1

Consumers mediate natural variation between prey richness and resource use on subtidal rock walls

Abstract

Space is the limiting resource for sessile organisms on marine rocky substrata, and the availability of space is decreased by recruitment and growth but increased through senescence, physical disturbance and consumption. In the present study, we examined whether consumers mediate variation in the relationship between prey richness and resource (space) use in subtidal epifaunal communities. First, we used surveys to identify relationships between prey richness, consumer richness, consumer identity, and consumer abundance with available space. As predicted, available space was correlated inversely with sessile prey richness, and positively with consumer richness. However, a model selection approach identified the abundance of sea urchins and chitons specifically as the best predictors of available space, suggesting that the proportion of available space is a reasonable indicator of recent disturbance. Next, we manipulated urchin density in the field to test the hypothesis that urchins control the structure of this community by grazing sessile taxa and facilitating smaller consumers. Diet analyses and structural equation models together indicate that urchins generate available space directly by consuming macroscopic sessile prey, and indirectly by facilitating chitons which maintain patches of space free of microscopic algae and recruits of larger sessile taxa. The significant interaction between prey richness and experimental urchin density on available space suggests that prey richness may buffer the impacts of urchin grazing. More generally, we highlight the need to study the effects of species richness on the structure of communities in the context of relevant ecological processes.

Introduction

Although ecologists have long investigated the causes of species richness (MacArthur & Wilson 1963, Connell 1978), more recently the focus has shifted to the consequences of richness within an ecosystem function framework (Hooper et al. 2005, Stachowicz et al. 2007). An accumulating body of experiments has demonstrated a positive effect of genotypic, species, and functional diversity on various ecosystem functions, including productivity, biomass, resource use, and resistance to environmental perturbations (Balvanera et al. 2006). However, the effect of diversity inferred from a carefully controlled experiment may be overwhelmed by other processes (Grace et al. 2007), such as propagule supply (Levine 2000) and disturbance (Cardinale et al. 2005). Consequently, researchers are now examining the effects of biodiversity change in the field (Stachowicz et al. 2008, Spooner & Vaughn 2009), and in the context of environmental factors known to affect the structure and function of communities (e.g., herbivory; Parker et al. 2010, Bracken et al. 2011).

In particular, interpreting the consequences of richness within a trophic context is imperative to conservation because species are being lost at upper trophic levels through extinctions, but gained at lower trophic levels through introductions (Byrnes et al. 2007). The manipulation of consumer abundance and/or diversity has revealed strong top-down control in some marine and terrestrial systems, which can ultimately impact ecosystem function (Paine 2002). In marine communities the effects of mobile consumers are ubiquitous (Connell 1961, Paine 1966, Lubchenco 1978, Underwood et al. 1983) and operate to restart succession through the provision of available space. Space on primary substrata is considered to be the limiting resource for sessile algae and filter-feeding invertebrates in rocky intertidal (Dayton 1971) and subtidal (Sebens 1986b, Vance 1988) habitats. Fluctuations in available space are buffered by greater numbers of sessile species, leading to increased stability and reduced invasibility in experimental marine communities (Stachowicz et al. 2002a).

Hard-bottom marine communities are tractable systems in which to test the relative importance of grazing and richness on resource use because the resource – available space – is easily quantified as a percentage of total space cover. We focused on epifaunal communities on subtidal vertical rock surfaces (walls) because they harbor an impressive diversity of sessile taxa that occupy the relatively two-dimensional and homogeneous space (Witman et al. 2004, Miller & Etter 2011). Importantly, subtidal rock walls are exposed to minimal physical disturbance, unlike more commonly studied rocky intertidal shores or shallow subtidal reefs (Witman & Dayton 2001). Consequently, the dynamics of space occupation are determined primarily by the recruitment and growth of sessile taxa and counteracted by their death, caused primarily by intrinsic factors, competition or predation. In particular, grazing by a variety of generalist and specialist consumers including mollusks, crustaceans, and echinoderms provides newly available space (Sebens 1986a, Miller & Etter 2011).

Classic field experiments have highlighted the effects of consumer identity (Paine 1992) and density (Underwood et al. 1983). More recent studies testing the role of consumer richness have also found strong support for the role of particular species (Duffy et al. 2001, Duffy et al. 2003, Byrnes & Stachowicz 2009). Urchins and chitons are 2 well-studied but functionally dissimilar consumers, each of which can exert strong effects in hard-bottom marine communities. In the San Juan Islands, Washington, USA, red urchins (*Strongylocentrotus franciscanus*) and lined chitons (*Tonicella* spp.) are conspicuous on subtidal rock walls. Red urchins attain large sizes (test diameter >18 cm) and eat primarily kelp (Vadas 1977), but will feed opportunistically on invertebrates (Duggins 1981, Epelbaum et al. 2009). Notably, their removal does not lead to changes in kelp communities (Carter et al. 2007) observed in similar experiments on shallow reefs elsewhere (Duggins 1980). It is likely that these urchins do not graze heavily upon attached algal thalli, but capture drift kelp transported by strong tidal currents (Britton-Simmons et al. 2009). In comparison, lined chitons are small (< 3cm) and have been reported to feed on crustose coralline algae (Demopulos 1975) and diatoms (Latyshev et al. 2004). However, the ecological effects of these 2 consumers on invertebrate-dominated vertical rock surfaces are unknown, and are likely to differ from those on algal-dominated horizontal rocky substrata.

The primary goal of this study was to examine how grazing pressure influences the relationship between sessile prey richness and space availability on subtidal rock walls. With respect to grazing, we evaluated the role of consumer richness, consumer identity, and consumer density. Using field surveys, we first identified urchins and chitons as potentially ‘strong’ interactors in this community from a suite of diverse consumers (e.g., molluscs, arthropods, and echinoderms) based on their abundances and known categories of prey. Then we examined relationships between sessile prey richness, mobile consumer richness, urchin and chiton densities, and available (cleared) space. We hypothesized that the percent cover of available space would relate inversely with prey richness (Stachowicz et al. 1999) but positively with consumer richness and density (Byrnes & Stachowicz 2009). A field experiment tested the role of urchins in creating the observed patterns from our surveys, and changes in the relative abundances of sessile taxa were compared with the gut contents of urchins and chitons. Finally, we used structural equation modeling (Grace et al. 2010) to test the hypothesis that urchins exert indirect effects on space availability by facilitating chitons.

Methods

Field surveys

We established a hierarchical sampling design of permanent quadrats on subtidal rock walls at 3 sites with the explicit goal of relating spatial variation in diversity and resource availability of the sessile prey community to the abundance of mobile consumers. The sites, Shady Cove (San Juan Island; 48°33′08″N, 123°00′20″W), Point George (Shaw Island; 48°33′33″N, 122°59′18″W) and O'Neal (O'Neal Island; 48°36′17″N, 123°05′33″W), are 2 - 8 km apart within San Juan Channel, Washington, USA. They are characterized by steep walls ranging in size from 2 to 10 m in height, interspersed with horizontal and sloping rock substrata.

In December 2007, permanent horizontal transects (2.5 m long, $n = 6$) separated by at least five meters were installed haphazardly on rock walls between 12 and 18 m depth at each site. Quadrats (0.09 m^2, $n = 4$) were positioned randomly along transects with corners marked with marine epoxy to enable repeated sampling of the benthos. Photographs of quadrats were taken using an Olympus C-8080 digital camera with an Ikelite strobe attached to a 36 × 25 cm aluminum frame, allowing identification of organisms ≥3 mm in diameter. These photographs were used to quantify percent cover of sessile taxa, as well as the densities of chitons and other 'small' (< 3 cm adult size) consumers. Concurrently, the abundance of 'large' (> 3 cm adult size) consumers was quantified within 1 m above and below each transect. In this paper we describe patterns of sessile prey richness and space availability from photographs taken in July 2008. Because of their high mobility, consumer densities in quadrats and on transects were estimated over 3 time points (December 2007, March 2008 and July 2008). Consumers were defined here as those mobile macro-invertebrates capable of scraping invertebrates or algae off rock surfaces, or able to consume whole or parts of sessile organisms such that space is made available for recruitment. Occupied space is generally not available for recruitment, but may be available to certain competitively superior species by direct overgrowth (Sebens 1986b).

Field experiment

We conducted a field experiment to test hypotheses related to the effects of the red urchin, *Strongylocentrotus franciscanus* (hereafter referred to as ‘urchin’) on the benthic community. Specifically, we were interested in the effect of urchins on space availability, prey richness, consumer richness, and the density of lined chitons, *Tonicella* spp. (hereafter referred to as ‘chitons’). Approximately 20 urchins (4 urchins m^{-2}) were added to 3 new permanent transects (2.5 m) on rock walls (12 – 18 m depth) at each site. At Shady Cove, one transect was interspersed within the original permanent transects, and one was placed at either end. At O’Neal and Point George, 2 transects were placed at one end, and the third at the other end of the original transects. The experimental target density of urchins was within the natural range of densities (0 - 5.2 urchins m^{-2}) observed during monitoring dives. These experimental transects (hereafter “addition” transects) were compared with 3 transects without the addition of urchins (hereafter “control” transects) from the permanent monitoring study (see above), using a before-after, control-impact design. Ten to 12 photographs were taken within 1 m of each transect immediately before the addition of urchins (27 June 2009), and at the end of the experiment (24 September 2009). Six photographs from each transect were selected randomly for the analysis of mobile and sessile species richness and cover (see below). Approximately every 2 weeks (6 observations during the experiment), we quantified the density of urchins on all transects, and added urchins as necessary to maintain the target density on addition transects. Urchin collections were focused ~3 m above and below target transects, and care was taken to ensure that urchins were not collected from the vicinity of neighboring transects.

Urchin and chiton diets

To determine whether the diets of the 2 major consumers reflected our field observations of prey removal, we quantified the gut contents of urchins and chitons from the rock wall communities. Urchins (n = 36) and chitons (n = 29) were collected for gut content analysis from permanent monitoring transects at O’Neal, Point George and Shady Cove in April 2009. All consumers were taken to the University of Washington’s Friday Harbor Laboratories for dissection, and gut contents were isolated and frozen (-20°C) for subsequent analysis. For urchin gut contents, we used a protocol modified from Cobb and Lawrence (2005) to estimate the proportions of several food categories. After thawing, urchin samples were mixed thoroughly and a representative layer of contents was spread evenly into a Petri dish. Contents were viewed using a dissecting scope (10 x magnification), and the proportion of prey was estimated from 50 random points. A 6 × 6 mm grid was placed under the dish and food items at 10 random intersections within each of 5 haphazard fields of view were identified to the lowest possible taxonomic level. Rare taxa viewed in scans of the entire Petri dish were assigned arbitrary values of 0.5%.

The diet of chitons was also quantified visually (Demopulos 1975, Fulton 1975, Robb 1975, Latyshev et al. 2004). In summary, we extracted the contents from the chiton foregut onto a glass slide, and observed them using a compound microscope (×200 magnification). We used a point count method using 10 equally spaced points on the ocular micrometer for 10 haphazard fields of view (100 points per chiton). Food items were classified into the following categories: microalgae, diatoms, crustose red algae, multi-cellular algae (filamentous and foliose), and other (unidentified materials and animal parts).

Analysis

The percent cover of sessile organisms was quantified from photographs using a visual-based method (Dethier et al. 1993). A grid of 20 rectangles was superimposed onto each image and the percent cover of sessile taxa was scored for each rectangle as follows: 0 = absence, 1 < 1%, 2 = 10%, (1 – 19%), 3 = 30% (20 – 39%), 4 = 50% (40 – 59%), 5 = 70% (60 – 79%), 6 = 90% (80 – 99%) and 7 > 99%. The sum of scores for each organism was expressed as a percentage of the total sum for the quadrat. Taxa were scored only if they were attached to rock or encrusting algae. Epibiotic taxa were not quantified because they do not occupy primary space and because habitat-forming ‘foundation’ species that might facilitate secondary space holders (Stachowicz & Byrnes 2006) were rare at the study sites. Organisms were identified to the lowest possible taxon and were assigned unique pseuodonyms when species identification was not possible.

We defined available space as the substratum available for the recruitment and growth of macroalgae and sessile invertebrates (Dayton 1971), including bare rock, calcified encrusting algae, and non-calcified encrusting algae (as in Sebens 1986a).

Encrusting algae are included in the definition of space because there is very little bare rock in shallow hard-bottom subtidal habitats, and most invertebrates can settle on or overgrow coralline and non-calcified algal crusts (Sebens 1986b). In so doing we assumed that these algal crusts are functionally equivalent, in part for simplicity, but also because the extent to which various species of encrusting algae facilitate (Morse et al. 1988) or inhibit (Breitburg 1984) the settlement of other sessile taxa is poorly understood in this community. Because we considered encrusting algae to be available space, we did not include them in our estimates of richness and diversity.

We used a linear mixed effects model and Akaike's Information Criterion corrected for small sample size (AIC_c) to infer the best model (Burnham & Anderson 2002) predicting the percent cover of available space (logit transformed). For the surveys completed in 2008, we tested the relative importance of sessile prey richness, consumer richness, density of red urchins, and the density of chitons. These 2 morphologically dissimilar consumers were selected because only their densities exhibited significant positive relationships to available space (Table S1 in the supplement), and because they were relatively abundant at the study sites (Fig. S1 in the supplement). Transect was nested within site and both were treated as random effects; quadrats were treated as the unit of replication.

To determine whether urchin abundance was related causally to the patterns of the other independent predictors of available space in the 2008 surveys, we tested the fixed effects of experimental treatment (control and urchin addition) on changes in sessile functional groups (percent cover), prey richness, prey evenness, consumer richness, and chiton density (no. m^{-2}) over the 3 mo experiment. We calculated the mean of each dependent variable for each transect (n = 6 quadrats) at the beginning and end of the 3 mo experiment. We then used a linear mixed effects model to test for change in dependent variables. Site was treated as a random effect; transects were treated as the unit of replication.

To test whether urchins change the relationship between available space and prey richness, we capitalized on variation in the manipulated urchin densities during the course of the 2009 experiment. Urchins were not restricted in their movement to or from transects, resulting in some overlap in densities between treatments, especially at O'Neal

(Table S2 in the supplement). Therefore, we treated the mean density of urchins (per transect) as a continuous variable, and used a linear mixed effects model to test the effect of urchin density, prey richness (in quadrats at the end of the experiment), and their interaction on available space in quadrats at the end of the experiment. Transect was nested within site and both were treated as random effects; quadrats were treated as the unit of replication. The mean density of urchins was calculated from the number of urchins remaining on transects 2 wk after every urchin addition (Table S2 in the supplement). Therefore, our estimates of mean urchin density throughout the manuscript can be considered conservative.

For all of our linear mixed effects models, we used a Monte Carlo markov chain resampling method to test the significance of fixed effects because the number of degrees of freedom in the denominator of a linear mixed-effects model is uncertain (Baayen et al. 2008). Residuals were inspected visually for normality and homoscedasticity. Note that because of the limitation of species identification from high-resolution quadrat photographs, both prey richness and consumer richness include categories that comprise not only species, but also higher taxa, which comprise several species. We consider this limitation to be acceptable, because the same categories were used across surveys and experiments.

Quantile regression was used to illustrate the relationships between available space and its predictors (sessile prey richness, consumer richness, lined chiton density, red urchin density), because we were interested in testing the upper and lower limits of the response variable distribution (Cade & Noon 2003), not just the mean response. Furthermore, some of the bivariate distributions (e.g., space vs. prey richness) violated the assumption of homoscedasticity for ordinary least squares (OLS) regression (Cade & Noon 2003), and the quantile approach provided a uniform testing approach for all regressions. For the survey data (2008), we calculated the 15th and 85th quantiles (τ = 0.15 and 0.85, respectively) to estimate the upper and lower bounds to the relationship between available space and the independent variables, as well as median quantiles (τ = 0.5) across all 3 sites. For data collected at the end of the experiment (September 2009), we calculated median quantiles for three ranges of urchin densities (0 – 0.2, 0.2 – 1.2, and 1.2 – 4.4 urchins m^{-2}; n = 36 for each range), but included all quadrats to estimate 10th and 90th quantiles ($\tau = 0.1$ and 0.9, respectively). We used slightly more extreme quantiles because of the increased sample size ($n = 108$ as opposed to $n = 72$) for the regressions ($n > 10/\tau$; Scharf et al. 1998). Lastly, to investigate potential mechanisms driving variation between available space and prey richness, we calculated median quantile regressions between the percent cover of macroalgae and clonal ascidians (both response variables) as a function of prey richness (predictor) before and after the addition of urchins to experimental transects ($n = 54$ for each time point). Statistical analyses were conducted using the packages 'lme4' (Bates et al. 2011) and 'quantreg' (Koenker 2011) in R 2.13 (R Development Core Team 2012).

Structural equation modeling

The analysis of our observational and experimental data, together with the literature on the effects of consumers on sessile prey in marine systems, led to the development of structural equation models (SEMs; Grace et al. 2010). The use of SEMs allowed us to distinguish between alternative hypotheses representing the direct (i.e., consumption of sessile prey) and indirect effects of urchin grazing (i.e., facilitation of chitons) on benthic community structure. We did not include consumer richness in our SEMs for simplicity, and because it was strongly correlated with chiton density ($r > 0.71$) in both datasets.

The saturated model, SEM A, represented the direct effects of urchin and chiton grazing on the sessile community, as well as the indirect effects of urchins mediated through chiton grazing. We included a path from urchin density to available space and prey richness because urchin grazing clears space and affects prey richness (Paine & Vadas 1969, Sebens 1986a). A path from urchin density to chiton density represented facilitation (Dethier & Duggins 1984) by urchins. Paths from chiton density to prey richness and available space represented the direct effect of chiton grazing on sessile prey (Duggins & Dethier 1985, Paine 1992). We included a covariance term between prey richness and available space because it is uncertain which variable is causal, and because both are likely to be affected by consumers simultaneously.

In SEM B, both urchins and chitons exert direct effects on the sessile community through grazing, but urchins do not facilitate chitons. This model was identical to SEM A, except that it lacked the path from urchin density to chiton density. In SEM C, urchins exert direct effects on sessile taxa and facilitate chitons, but chitons do not exert measurable effects on the sessile community. This model was identical to SEM A, except that it lacked the paths from chiton density to prey richness and available space. In SEM D, urchins (but not chitons) exert direct effects on the sessile community, and do not facilitate chitons. This last model was identical to SEM A, but lacked paths from urchin density to chiton density, as well as paths from chiton density to prey richness and available space.

In all SEMs, urchin and chiton density were log (x + 1) transformed and available space was logit transformed to improve normality. Nevertheless, the data failed to meet the assumption of multivariate normality, therefore we used maximum likelihood estimation with robust standard errors and a Satorra-Bentler scaled test statistic to calculate the fit of our models. We used a model selection approach (AIC_c) to identify the best model for the survey and experimental data separately. The best-fit model was then used in a multi-group analysis (Grace & Pugesek 1998) to test whether the magnitude and direction of the causal paths differed between the survey and experimental data. All analyses were conducted using the 'lavaan' package (Rosseel et al. 2011) in R.

Results

In surveys (2008) across the three sites, available space was correlated negatively with sessile prey richness and positively with consumer richness, lined chiton density, and urchin density (Fig. 1). Quantile regression revealed upper and lower limits to the amount of available space as a function of consumer richness, lined chiton density, and urchin density (Fig. 1, Table S3 in the supplement). In contrast, there was an upper, but not lower, limit, to the amount of available space as a function of sessile richness, resulting in a triangular relationship. Of these four variables, the density of lined chitons was the best single predictor of space (Table 1). The two best predictors of space were lined chiton density and urchin density, a model considerably better than the full model including all four predictors (Δi = 10.45, Table 1).

During the field experiment (2009), the urchin addition treatment effectively increased the density of urchins relative to the control treatment (2.3 ± 1.5 vs. 0.3 ± 0.3 urchins m^{-2}, mean ± 1 SD; n = 9 transects per treatment), despite the fact that urchins were free to move. Consequently, urchin grazing on addition transects caused a significant increase in available space (bare rock and encrusting algae), consumer richness, and chiton density (Fig. 2, Table S4 in the supplement). Urchin addition did not significantly affect prey richness, but control transects gained an average of two species per quadrat by the end of the experiment (Fig. 2b, Table S4). The magnitude of the grazing effect on available space was contingent upon the number of sessile species within quadrats, indicated by the urchin density × prey richness interaction (Table S5). Notably, at the end of the experiment, the median regression between available space and prey richness was significant for quadrats exposed to intermediate and high urchin densities, but not low urchin densities (Fig. 3, Table S3). In support of the triangular relationship observed in the survey results, there was an upper limit (i.e., the 90th quantile) to available space as a declining function of richness, but no lower limit (Fig. 3, Table S3).

Urchin grazing caused changes in the relative abundances of sessile taxa by September 2009, the end of the field experiment. After urchin addition the percent cover of macroalgae (primarily red algae) and clonal ascidians decreased significantly, uncovering bare rock and algal crusts (Fig. 2, Table S4). Solitary invertebrates, which occupied very little space (8.3 ± 5.1 % cover, mean ± SD, n = 108) relative to clonal invertebrates (41.1 ± 17.5 % cover, mean ± SD, n = 108) and macroalgae (14.5 ± 10.7 % cover, mean ± SD, n = 108) in June 2009, actually increased in response to urchin grazing (Fig. 2, Table S4). In contrast, hydroid cover increased on control transects (Fig. 2, Table S4). The decline of the spatially dominant sessile taxa (algae, clonal ascidians) on urchin transects corresponded with an increase in prey evenness (Fig. 2c). After the addition of urchins to experimental transects, the percent cover of clonal ascidians became positively correlated with prey richness, but the percent cover of macroalgae remained uncorrelated with prey richness (Fig. 4, Table S3). The observed reduction in macroalgae and clonal ascidians in the field experiment was consistent with the two most abundant prey found in urchin guts (Fig. 5a). Second to algae, the most abundant food item found in urchins was the clonal ascidian *Metandrocarpa taylori* (Fig. 5a), which was also the most abundant sessile invertebrate species across the three study sites before urchin addition (8.5 ± 7.6 % cover, mean ± SD, n = 108). In contrast, chitons cannot eat macroalgae and ascidians due to their smaller size, and thus their diet is composed primarily of microalgae and diatoms (Fig. 5b), which are ubiquitous on encrusting algae and “bare” rock.

The saturated structural equation model (SEM A) best fit the observed data for the survey and experiment (Table 2). The unsaturated SEMs lacking the facilitation of chitons by urchins, and/or chiton grazing, did not fit the observed covariance matrices ($p < 0.01$, Table 2), and were far worse than SEM A ($\Delta i > 14$). Therefore, we used SEM A in a multi-group context to test whether the magnitude and direction of causal paths were consistent between the survey and experimental data. We constructed a model identical to SEM A, but constrained the path coefficients to be identical for both datasets. We focused on the results of the constrained multi-group model because it fit the data nearly as well as SEM A without constraints ($\Delta i = 1.4$) and it adequately reproduced the observed covariance matrix ($\chi^2 = 7.6$, df = 5, $p = 0.18$); we were able to test the fit of the constrained model because the equality constraints across the survey and experimental data produced 5 degrees of freedom.

All of the hypothesized causal paths in the multi-group, constrained SEM were statistically significant ($p < 0.05$), although there was considerable variation in the magnitude of the path coefficients. The SEM explained variation in available space ($R^2 = 0.46 – 0.64$) better than the variation in prey richness ($R^2 = 0.06 – 0.11$), and the direct effects of consumer densities were stronger on available space than prey richness (Fig. 6). The magnitude of indirect effects is calculated as the product of standardized regression coefficients. With respect to available space, urchins exerted a stronger direct effect (0.35 – 0.58) relative to the indirect effect (0.10 – 0.17) mediated via chiton density. Similarly, urchins exerted a stronger direct effect (~ -0.15) on prey richness relative to the indirect effect (~ -0.05) mediated via chiton density. We did not constrain the covariation between prey richness and available space, and we observed significant residual covariance between these endogenous variables in the experimental dataset only.

Discussion

In this study, we demonstrate that natural variation between the number of sessile prey species and resource use on subtidal rock walls is a function of urchin grazing. Urchins mediate this relationship directly by altering the relative abundances of sessile taxa (Fig. 2a), and indirectly by facilitating chitons and their grazing activities (Fig. 2d, Fig. 6). The mechanisms underlying dynamic variation between richness and available space use in epifaunal communities on natural substrata are critical to understanding the relevance of previous biodiversity-ecosystem function research in epifaunal communities on man-made structures (e.g., 'fouling' communities on docks). Given that we studied prey richness by observing natural gradients, it is surprising that its inverse relationship with available space was more concordant with experimental manipulations of sessile richness (Stachowicz et al. 1999, 2002a), than with observational approaches in fouling communities. In contrast, available space increased with sessile diversity in unmanipulated, epifaunal dock assemblages, a consequence of high mortality rates of necessarily small colonies (Dunstan & Johnson 2004). This mechanism of size-specific mortality could become irrelevant in an artificially assembled community, yet our field observations support a negative relationship between richness and available space.

In addition to artificial assembly, we propose that grazing is another mechanism that negates the advantage that large invertebrate colonies possess in low diversity, competitive arenas associated with relatively undisturbed habitats (e.g., docks; Dunstan & Johnson 2004). Red urchins removed the spatial dominants (other than corallines and other crustose algae), though not necessarily the competitive dominants, such as large cnidarians, sponges and ascidians (Sebens 1986a, b). Urchins thus contributed to the variation in available space at low levels of prey richness (Figs. 1a and 3). It is unclear whether urchins were selectively foraging for macroalgae (mostly red algae) and clonal ascidians, or whether they were simply consuming the most abundant prey available; red urchins are generally thought to prefer kelp (Vadas 1977). Regardless, in the absence of grazing disturbance clonal ascidians and red algae are capable of monopolizing space on these rock walls, resulting in a triangular relationship (supported by quantile regression) between prey richness and available space. Both the survey and experimental data revealed that although there was an upper limit (significant upper quantile), there was no lower limit (non-significant lower quantile) to available space as a function of richness. In other words, quadrats with many (> 20) taxa had very little open space, but the amount of space was not necessarily high at low richness (Fig. 1). The absence of a lower limit is a consequence of the interaction between dominant space occupiers and the most abundant consumers.

The densities of two morphologically dissimilar consumers – urchins and chitons – together best explained patterns of available space in the surveys (Table 1). The positive correlation between consumer richness and open space (Fig. 1b) may have been related to the increased likelihood of including a chiton (Byrnes & Stachowicz 2009), rather than a ‘true’ diversity effect (e.g., complementarity). Most importantly, the manipulation of urchins demonstrated mechanistically that they uncover new patches of available space on rock walls, accompanied by increases in chiton density and consumer richness (Fig. 2). Together, the survey and experimental data suggest that an instantaneous measure of free space, defined in this way, provides a snapshot of recent grazing disturbance (Sebens 1986a). It is likely that the density of chitons increased in response to urchin grazing because chitons cannot adhere effectively to the soft bodies of sessile invertebrates and thalli of red algae. Further, chiton diet was composed primarily of microalgae and diatoms (Fig. 5), which rapidly colonize encrusting algae and bare substrata (O'Neill & Wilcox 1971, Dethier & Duggins 1984). We hypothesize that the increase in consumer richness reflects a similar response, as we identified 4 species of *Tonicella*, 2 species of the chiton *Mopalia*, the chiton *Lepidozona mertensii*, and several other mollusks (e.g., *Margarites* spp., *Acmaea* spp., *Lottia* spp.) which may require encrusting algae as a suitable substratum for attachment and/or grazing (i.e., "foraging space"; Dethier & Duggins 1984). Our results indicate that red urchins, as generalist consumers of both macroalgae and sessile invertebrates, facilitate the diversity and abundance of chitons and other specialized consumers, in a manner similar to the “indirect commensalism” observed between *Katharina* chitons and acmaeid limpets on intertidal rocky shores (Dethier & Duggins 1984). In the latter study, small specialist limpets were dependent on the larger, generalist *Katharina* to remove macroalgae and provide the appropriate substratum for microalgal growth.

It is unlikely that urchins were solely responsible for the creation of available space, because structural equation models lacking paths from chiton density to available space and prey richness fit the observed data poorly (Table 2). Furthermore, the effect of urchin grazing on the sessile community appears partially mediated through a facilitative effect on chitons, because incorporating a path from urchin density to chiton density greatly improved the fit of the model (SEM A; Table 2). Indeed, removing urchin facilitation (SEM B), chiton grazing (SEM C), or both (SEM D) resulted in poor model fit for both datasets (Table 2). Despite the inherent differences between the survey data (which integrate ecological effects over a longer time scale) and experimental data (which emphasize the top-down effects of a three-month 'pulse' disturbance), our multi-group analysis (Grace & Pugesek 1998) suggests that the strength and direction of direct and indirect effects were similar across the two studies. While the structural equation models permit a richer ecological interpretation of our data than the linear mixed effects models alone, the role of chiton grazing as a causal mechanism must be viewed as a hypothesis to be tested in future manipulations (Wootton 1994).

The experimental treatment period coincided with summer recruitment in the San Juan Islands, thus the trend of increased richness on control transects in September (Fig. 2b) may have been manifested through chiton grazing on early life stages of sessile taxa (Nydam & Stachowicz 2007). However, the effects of these two consumers on prey richness were relatively weak (Fig. 6), and grazing primarily affected the relative abundances of taxa (Fig. 2a). Any negative effects on prey richness would likely manifest only when red urchins occupy a specific area on rock walls for extended periods of time. In the San Juan Islands, we occasionally observe temporally stable (> 5 years), and dense (~ 18 m^{-2}), aggregations of red urchins on rock walls that are effectively barren, with few sessile species except for encrusting calcified algae (as in Sebens 1986a). Such species-poor walls are uncommon (Elahi, pers. obs.), and may reflect a nonlinear threshold as described for kelp forest-urchin barrens community shifts (Watanabe & Harrold 1991, Arkema et al. 2009). The extent to which communities dominated by encrusting algae are maintained by the positive feedback of urchin-mediated chiton grazing remains to be determined.

Although prey richness was independent of grazing at the end of the experiment, there was an interaction between urchin density and prey richness (Fig. 3), indicating that the upper bound of the relationship between available space and richness was related causally to the grazing effects of urchins. Similarly, the presence of upper trophic levels enhanced the effects of diversity on ecosystem function in seagrass (Duffy et al. 2005) and terrestrial plant (Parker et al. 2010) communities. Although red urchins ate a variety of prey, their diets were composed primarily of macroalgae and clonal ascidians (Fig. 5), and thus reflected the significant reductions in these two functional groups of sessile taxa after the experimental addition of urchins. The decline in cover of clonal ascidians (but not macroalgae) was consistent with the urchin-mediated variation in available space and prey richness. Namely, the significant median regression between clonal ascidian cover and prey richness after the addition of urchins appeared to be driven by disproportionately lower cover within quadrats harboring fewer taxa (Fig. 4b). In contrast, macroalgal cover was lower across all quadrats after urchin addition, regardless of prey richness, which may be related to urchin preference for algae.

The decline of spatially dominant prey was associated with an increase in prey evenness at the end of the experiment (Fig. 2c). Intermittent urchin grazing within the range of densities observed in this study may therefore act as a mechanism promoting coexistence of sessile taxa (Lubchenco 1978). In particular, solitary invertebrates suffer a clear disadvantage against clonal invertebrates with respect to competition for space (Jackson 1977). Urchins indirectly facilitated the significant increase in percent cover of solitary invertebrates (e.g., barnacles), probably by reducing the cover of clonal invertebrates (Fig. 2a). In addition to consuming clonal ascidians, urchins appear to have exerted negative effects on hydroid colonies, but these were likely not related to grazing (Fig. 5a). Perhaps non-trophic impacts, such as spine abrasion, prevented hydroids from increasing their percent cover on urchin addition transects (Fig. 2a).

In summary, our results indicate that urchin feeding on spatially dominant ascidians is one specific mechanism that drives variation in the triangular relationship between open space and richness. The availability of space is a useful metric of community structure (Paine 1984) and an important corollary of at least one ecosystem function: invasibility (Stachowicz et al. 2002a, Clark & Johnston 2011). The susceptibility of rocky shores to invasions of exotic sessile taxa at local scales ($< 1 \text{ m}^2$) is likely a consequence of the indirect effects of grazing on resource availability and prey richness, in addition to the direct effects of biological disturbance (or lack thereof) on exotic species (Simoncini & Miller 2007, Shinen et al. 2009, Grey 2010). Further, if we accept available space to be a reasonable index of recent grazing disturbance, the significant correlation between space and richness observed in the presence of urchins is consistent with the hypothesis that high prey richness buffers the impacts of grazing disturbance (Hillebrand & Cardinale 2004, Edwards et al. 2010). Of course, correlations are always open to interpretation and we acknowledge the limitations of studying natural gradients in diversity. Even the static outcomes of ecological experiments may provide limited insight into the mechanisms of observed change (Wootton 1994). Our manipulation of urchins caused an increase in available space, but the role that chitons may play in the creation of space was not revealed until we applied a structural equation model to the data. A combination of approaches was necessary to uncover the potential for feedback among consumers and their prey.

Tables

Table 1. A linear mixed effects model including the densities of chitons and urchins best predicts the percent cover of available space (logit transformed) in permanent quadrats surveyed in 2008. Transect was nested within site; both were treated as random effects. Candidate models are listed with the number of parameters (*K*), corrected AIC (AIC_c), the difference in AIC between the candidate model and the best model (Δi) and Akaike weights (w_i).

Model	***K***	**AIC_c**	**Δi**	**w_i**
Prey richness (PR)	5	247.66	35.03	0.0000
Consumer richness (CR)	5	234.93	22.30	0.0000
Chiton density (CD)	5	215.50	2.88	0.1772
Urchin density (UD)	5	235.27	22.65	0.0000
PR + CR	6	237.45	24.82	0.0000
PR + CD	6	221.94	9.31	0.0071
PR + UD	6	238.48	25.85	0.0000
CR + CD	6	217.52	4.89	0.0647
CR + UD	6	231.60	18.98	0.0001
CD + UD	**6**	**212.63**	**0.00**	**0.7469**
PR + CR + CD + UD	8	223.08	10.45	0.0040

Table 2. χ^2 likelihood ratio tests and model selection results examining the fit of structural equation models to observed covariance matrices for survey and experimental data. We report Satorra-Bentler corrected χ^2 test statistics, corrected AIC (AIC_c), the difference in AIC between the candidate model and the best model (Δi), and Akaike weights (w_i).

Model	**df**	χ^2	***P***	**AIC_c**	**Δi**	w_i
Survey (2008)						
A	0	NA	NA	1003.7	0.0	1.0
B	1	6.89	**0.009**	1018.2	14.5	0.0
C	2	13.57	**0.001**	1025.3	21.6	0.0
D	3	27.43	**< 0.001**	1039.9	36.2	0.0
Experiment (2009)						
A	0	NA	NA	1340.7	0.0	1.0
B	1	11.21	**0.001**	1363.3	22.7	0.0
C	2	14.60	**0.001**	1365.1	24.4	0.0
D	3	36.44	**< 0.001**	1387.9	47.2	0.0

	Model description
A	Urchin facilitation, chiton grazing (saturated model)
B	No facilitation, chiton grazing
C	Urchin facilitation, no chiton grazing
D	No facilitation, no chiton grazing

Figures

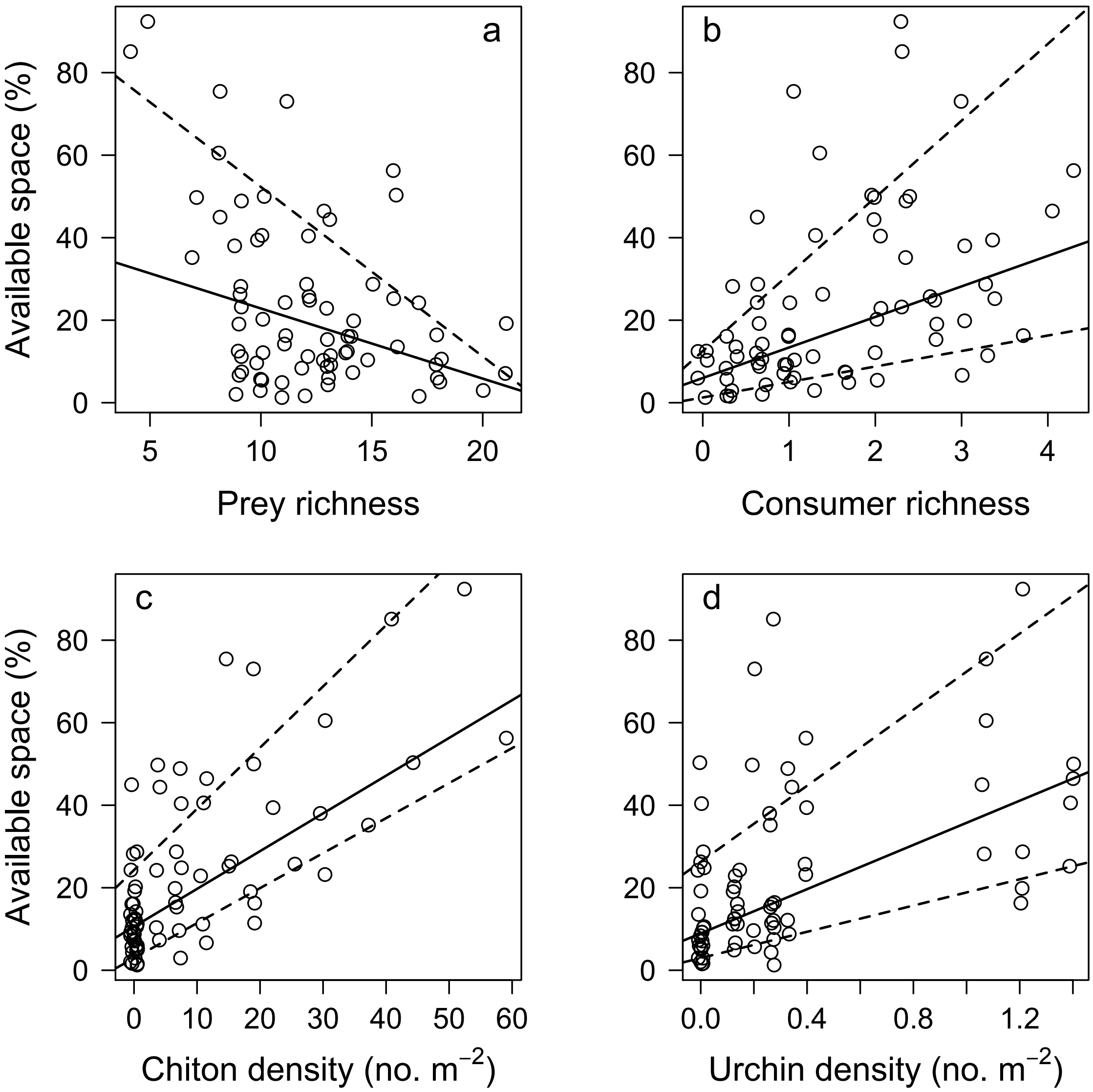

Figure 1. The percent cover of available space in quadrats plotted as a function of the richness of sessile prey taxa in quadrats (a), richness of consumer taxa in quadrats (b), density of the chiton *Tonicella* spp. in quadrats (c), and the density of the urchin *Strongylocentrotus franciscanus* on transects (d) surveyed in 2008. Black lines show the median (50th quantile) relationship between space and the independent variable, and dashed lines show the upper and/or lower bounds (85th and 15th quantile, respectively) of the relationship when significant ($P < 0.05$). Note the lack of a lower limit to space only when plotted against prey richness (a).

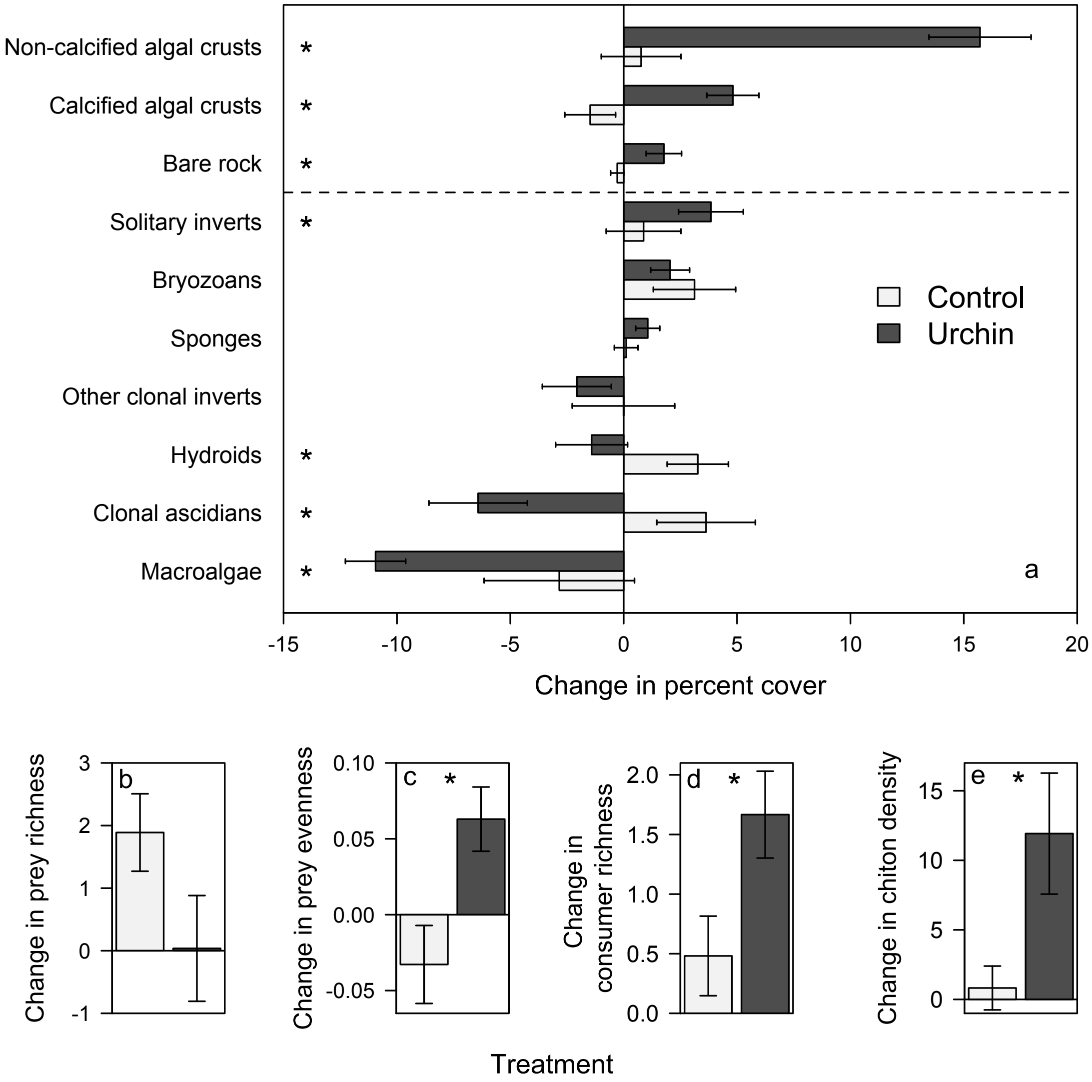

Figure 2. The change in mean (±1 SE) percent cover of functional groups (a), prey richness (b), prey evenness (c), consumer richness (d), and chiton density (no. m^{-2}; e) on transects ($n = 9$) in control and urchin addition treatments from June to September 2009 (pre and post-treatment, respectively). In (a), the three functional groups above the dashed line together represent available space. Asterisks denote the significance of a treatment effect in linear mixed effects models.

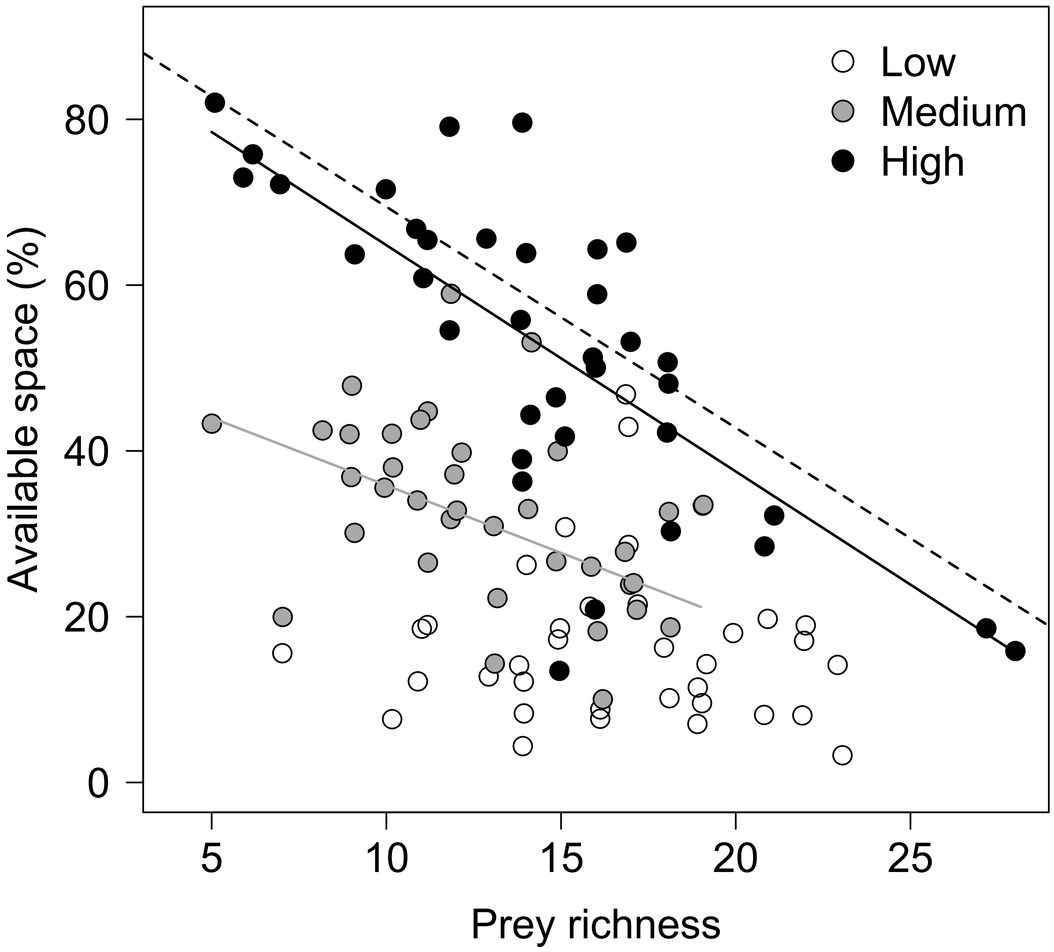

Figure 3. Available space declines with increasing richness, but only in the presence of urchin grazing at the end of the 2009 experiment. Points represent quadrats subjected to low (0 – 0.2 urchins m^{-2}; open symbols), medium (0.2 – 1.2 urchins m^{-2}; grey symbols), and high (1.2 – 4.4 urchins m^{-2}; black symbols) urchin densities (n = 36 quadrats per density). Solid lines depict the median (50th quantile) regression for each urchin density, where significant ($P < 0.05$). The dashed line represents the upper bound (90th quantile) to space as a function of richness for all quadrats combined. Note that there is no lower limit to space (10th quantile), and no relationship between space and richness at low urchin densities, resulting in a triangular relationship between space and richness.

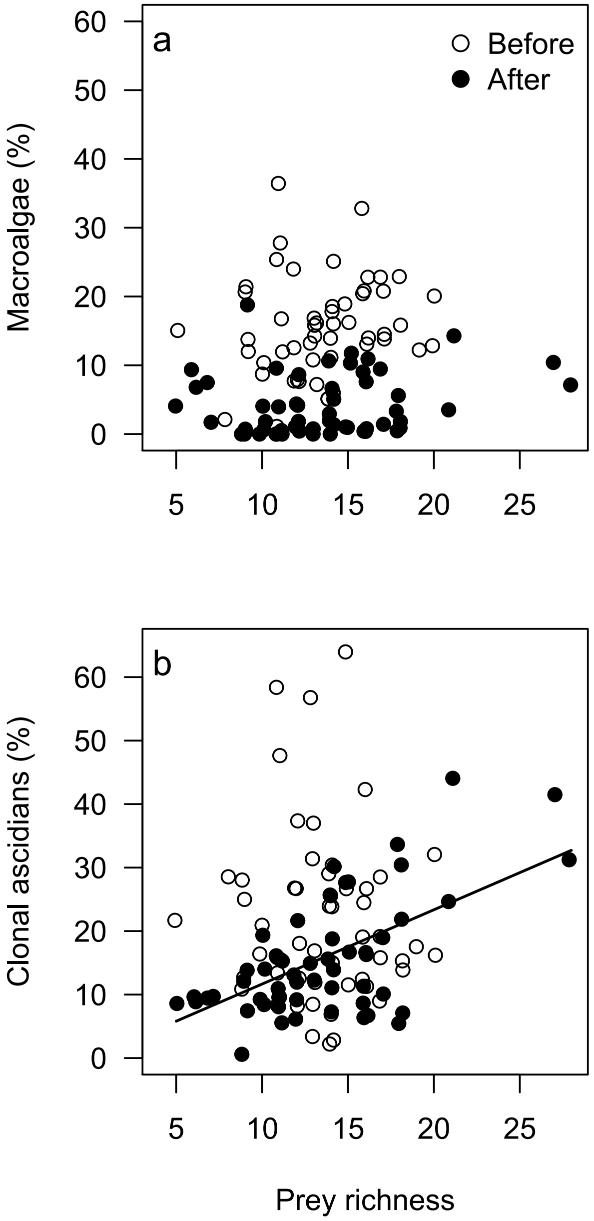

Figure 4. The percent cover of macroalgae (a) is not related to prey richness, but the percent cover of clonal ascidians (b) increases with prey richness after the addition of urchins. Points represent quadrats from urchin transects, before (open circles) and after (filled circles) the addition of urchins during the 2009 experiment. The line represents a significant (*P* < 0.05) median regression.

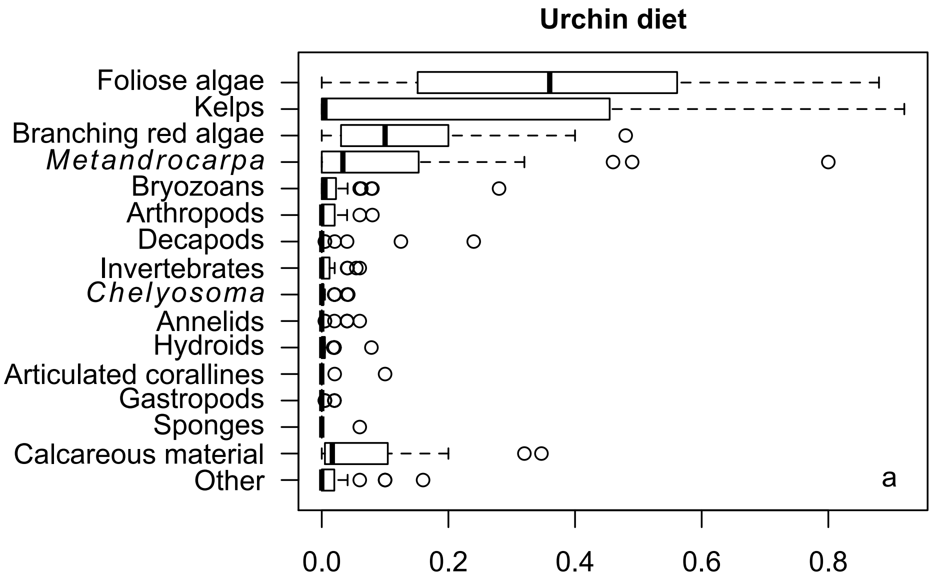

Figure 5. Macroalgae and a clonal ascidian, *Metandrocarpa taylori*, constitute the majority of red urchin diets (a), whereas microalgae and diatoms are the most abundant food items found in the intestines of *Tonicella* chitons (b). *Chelyosoma* is a solitary ascidian. Boxplots display the median and interquartile range (IQR) of data, with outliers plotted as circles beyond whiskers when the values are 1.5 times the IQR from the first or third quartile.

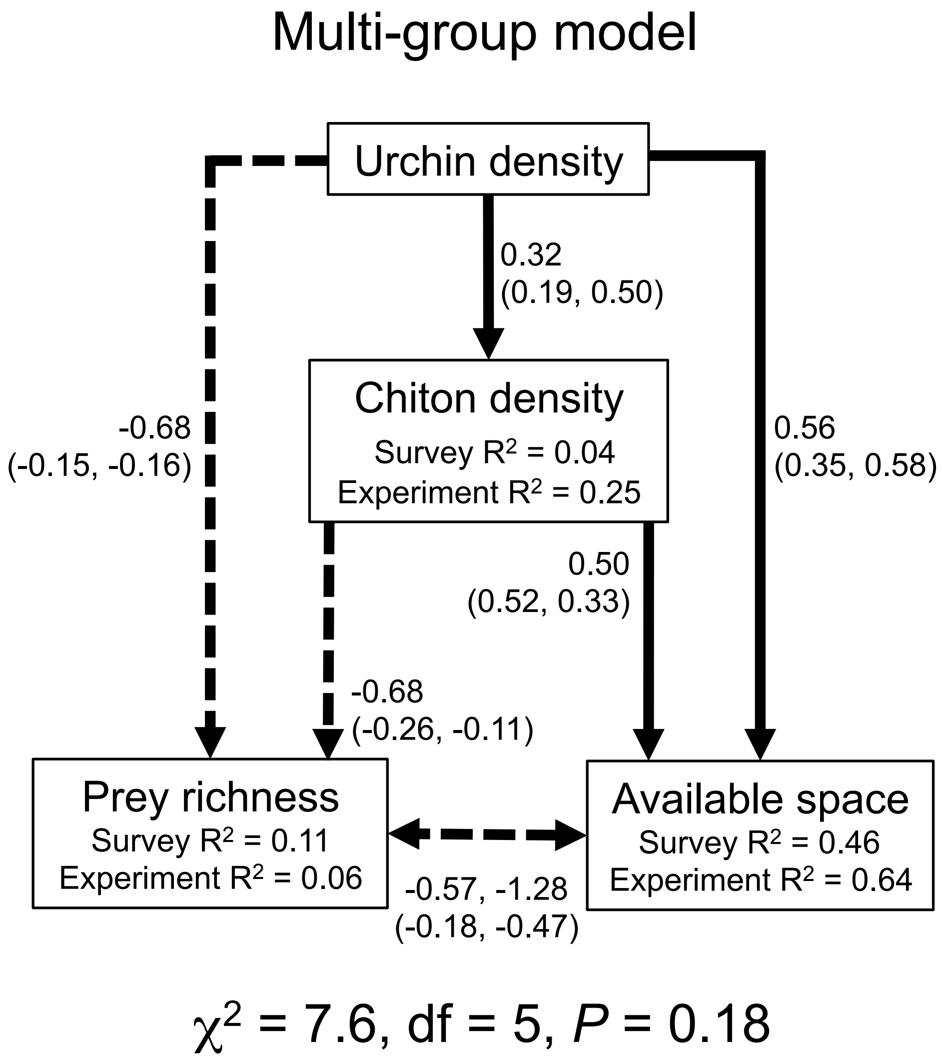

Figure 6. Path diagram estimating the strength of direct and indirect effects of urchins. The covariance matrix of the combined survey and experimental data is adequately represented by a multi-group structural equation model with equality constraints for each of the five causal paths. Solid and dashed lines represent positive and negative relationships, respectively. All causal paths are significant (*P* < 0.05); the number beside each path is the unstandardized path coefficient. The covariance between prey richness and available space was allowed to vary freely, and thus the two numbers below this path represent the unstandardized coefficients for the survey and experimental datasets, respectively. Likewise, the two numbers inside parentheses are the standardized coefficients for the survey and experimental datasets, respectively. The covariance between prey richness and available space was only significant for the experimental dataset.

Supplementary material

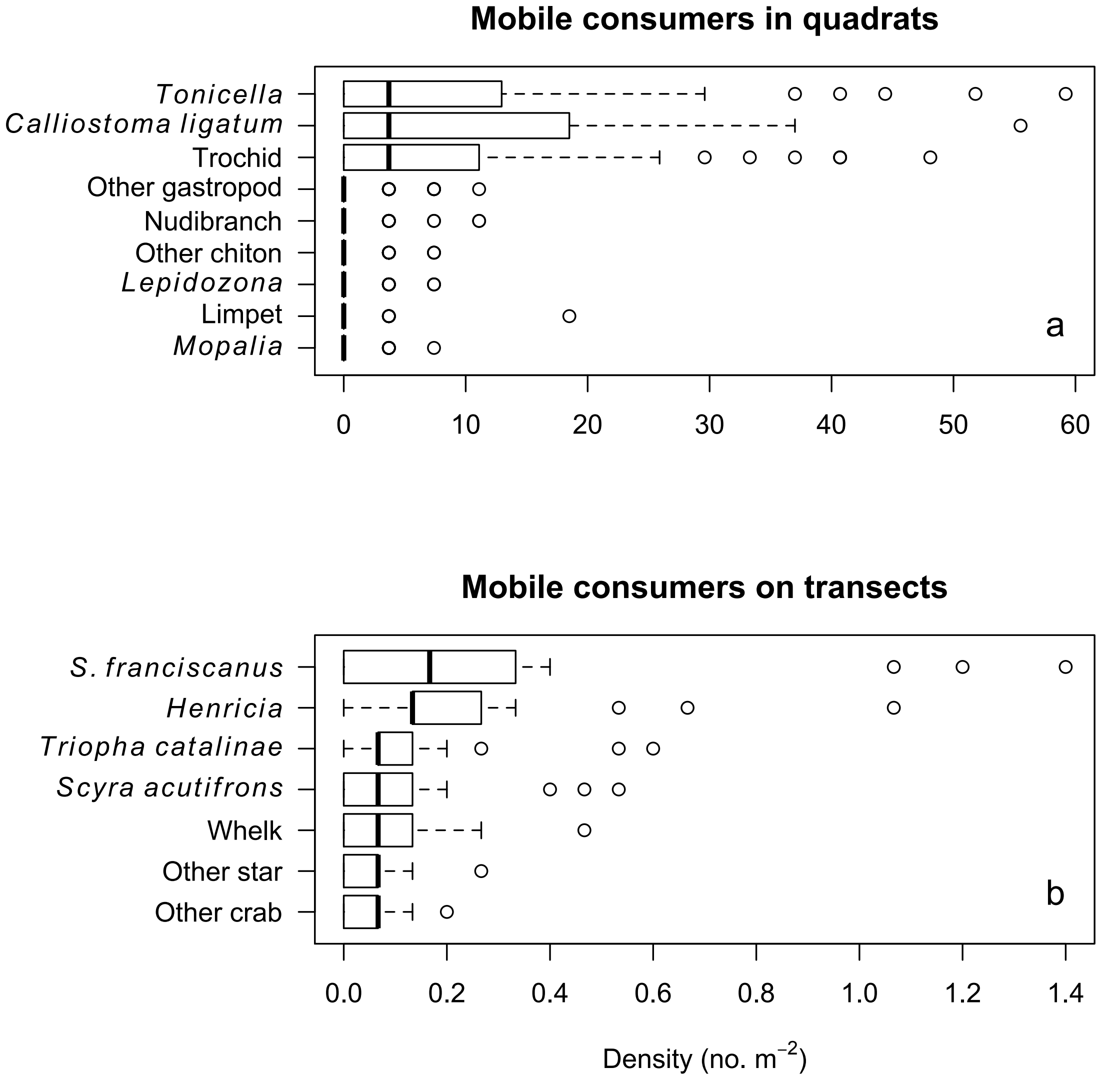

Figure S1. The density of mobile consumers in quadrats (a) and on transects (b). Boxplots display the median and interquartile range (IQR) of data, with outliers plotted as circles beyond whiskers when the values are 1.5 times the IQR from the first or third quartile. *Tonicella*, *Lepidozona* and *Mopalia* are chitons. *Strongylocentrotus franciscanus*, *Henricia*, *Triopha catalinae* and *Scyra acutifrons* are urchins, sea stars, sea slugs and crabs, respectively.

Table S1. We used a linear mixed effects model to assess the strength and direction of the relationship between available space and consumer density in the 2008 surveys. Percent cover of space (logit-transformed) was the response, and the independent predictors were the abundance (log [x + 1] transformed) of *Tonicella* spp., *Calliostoma ligatum*, trochid snails, *Strongylocentrotus franciscanus*, *Henricia* spp., *Triopha catalinae*, and *Scyra acutifrons*. Transect was nested within site; both were treated as random effects. We used a Monte Carlo markov chain (MCMC) resampling procedure (n = 5000) to assess the significance of the predictors in linear mixed effects models; when the 95% confidence intervals of the estimate did not include zero, we considered the estimate to be significant. The density of *Tonicella* spp. and *S. franciscanus* was positively correlated with available space, suggesting that these consumers play a role in the provision of space. However, the density of *C. ligatum* correlated negatively with space, suggesting that this snail associates with sessile invertebrates and/or macroalgae, the space occupiers in this community.

	Estimate	Standard error	t value	MCMC lower limit	MCMC upper limit	significance
Tonicella spp.	0.545	0.104	5.250	0.343	0.760	*
Calliostoma ligatum	-0.328	0.100	-3.279	-0.513	-0.106	*
Trochid snails	0.118	0.110	1.071	-0.076	0.368	ns
S. franciscanus	1.597	0.566	2.820	0.363	2.590	*
Henricia spp.	0.209	0.772	0.270	-1.152	1.899	ns
Triopha catalinae	-0.371	1.095	-0.339	-2.499	1.756	ns
Scyra acutifrons	0.638	1.263	0.505	-2.068	3.339	ns

Table S2. The density (±1 SD, n = 6 time points) of red urchins (*Strongylocentrotus franciscanus*) on experimental and control transects during the course of the 2009 experiment. Urchins were added to each transect at O'Neal, Pt. George, and Shady Cove at approximately 2-weekly intervals to achieve a target density of 20 urchins per transect (4 urchins m^{-2}). Estimates of density on urchin addition transects do not include urchin counts concurrent with manipulations and thus can be considered conservative. Transects are ordered by ascending numerical density, and categorical densities correspond to those in Fig. 3.

Site	Treatment	Transect	Density (urchins m^{-2})	Categorical density
Shady Cove	Control	SC_C_1	0	low
Shady Cove	Control	SC_C_2	0	low
Shady Cove	Control	SC_C_3	0	low
O'Neal	Control	ON_C_1	0.07 ± 0.52	low
Pt. George	Control	PG_C_1	0.20 ± 0.89	low
Pt. George	Control	PG_C_2	0.20 ± 1.26	low
O'Neal	Addition	ON_A_1	0.27 ± 1.75	medium
O'Neal	Control	ON_C_3	0.27 ± 0.52	medium
O'Neal	Addition	ON_A_3	0.47 ± 1.86	medium
Pt. George	Control	PG_C_3	0.76 ± 1.72	medium
O'Neal	Control	ON_C_2	0.90 ± 3.39	medium
O'Neal	Addition	ON_A_2	1.13 ± 4.68	medium
Pt. George	Addition	PG_A_2	1.27 ± 3.78	high
Pt. George	Addition	PG_A_1	2.60 ± 3.03	high
Pt. George	Addition	PG_A_3	2.83 ± 5.85	high
Shady Cove	Addition	SC_A_2	3.63 ± 1.47	high
Shady Cove	Addition	SC_A_3	3.9 ± 0.55	high
Shady Cove	Addition	SC_A_1	4.33 ± 1.86	high

Table S3. Quantile regression models estimating relationships between available space (percent cover) and 4 predictors (untransformed) in surveys of permanent quadrats in 2008 (n = 72), and at the end of the experiment in September 2009 (n = 108). Because of the increased sample size in 2009, we estimated slightly more extreme quantiles to better illustrate the limits to the relationship between available space and prey richness. We also estimated median regressions between the percent cover of macroalgae and clonal ascidians as a function of prey richness for quadrats in the urchin treatment before and after the experimental addition of urchins. Significant ($P < 0.05$) regressions are indicated in bold type.

	n	intercept (SE)	slope (SE)	*P*
Survey (2008)				
Space vs. prey richness				
85th quantile	72	93.38 (14.85)	-4.11 (0.96)	**< 0.001**
50th quantile	72	39.85 (10.77)	-1.70 (0.67)	**0.013**
15th quantile	72	8.28 (5.33)	-0.18 (0.37)	0.622
Space vs. consumer richness				
85th quantile	72	12.51 (7.99)	18.62 (5.22)	**< 0.001**
50th quantile	72	5.98 (2.60)	7.40 (2.13)	**< 0.001**
15th quantile	72	1.26 (1.42)	3.76 (1.46)	**0.013**
Space vs. chiton density				
85th quantile	72	24.29 (5.21)	1.48 (0.47)	**0.002**
50th quantile	72	10.57 (1.60)	0.91 (0.26)	**< 0.001**
15th quantile	72	2.93 (1.28)	0.85 (0.13)	**< 0.001**
Space vs. urchin density				
85th quantile	72	26.28 (6.31)	46.09 (14.92)	**0.003**
50th quantile	72	8.93 (1.52)	26.80 (6.89)	**< 0.001**
15th quantile	72	2.96 (1.19)	15.90 (3.96)	**0.002**
Experiment (2009)				
Space vs. prey richness				
Low urchin density, 50th quantile	36	21.31 (7.21)	-0.19 (0.40)	0.637
Intermediate urchin density, 50th quantile	36	52.15 (5.97)	-1.63 (0.48)	**0.002**
High urchin density, 50th quantile	36	92.12 (3.65)	-2.73 (0.24)	**< 0.001**
All urchin densities, 90th quantile	108	96.11 (5.73)	-2.67 (0.40)	**< 0.001**
All urchin densities, 10th quantile	108	20.21 (5.68)	-0.57 (0.33)	0.080
Macroalgae vs. prey richness				
Urchin treatment, before addition; 50th quantile	54	10.15 (5.70)	0.32 (0.41)	0.446
Urchin treatment, after addition; 50th quantile	54	-1.12 (2.77)	0.25 (0.19)	0.209
Clonal ascidians vs. prey richness				
Urchin treatment, before addition; 50th quantile	54	23.17 (7.95)	-0.30 (0.52)	0.573
Urchin treatment, after addition; 50th quantile	54	-0.04 (3.53)	1.12 (0.26)	**< 0.001**

Table S4. Results of linear mixed effects models testing the fixed effect of treatment on transect-scale change in dependent variables over the course of the 3 mo experiment. Site was treated as a random effect. A Monte Carlo markov chain (MCMC) resampling procedure (n = 5000) assessed the significance of treatment; when the 95% confidence intervals of the parameter estimate did not include zero, the estimate was considered to be significant.

	Estimate	Standard error	t value	MCMC lower limit	MCMC upper limit	significance
Non-calcified algal crusts						
Treatment	14.945	2.856	5.232	9.057	20.975	*
Calcified algal crusts						
Treatment	6.293	1.605	3.920	2.850	9.446	*
Bare rock						
Treatment	2.055	0.685	3.001	0.604	3.610	*
Solitary inverts						
Treatment	2.971	0.985	3.018	0.131	5.549	*
Bryozoans						
Treatment	-1.074	2.007	-0.535	-5.147	2.877	ns
Sponges						
Treatment	0.950	0.745	1.276	-0.570	2.455	ns
Other clonal inverts						
Treatment	-2.057	2.725	-0.755	-7.848	3.618	ns
Hydroids						
Treatment	-4.682	1.814	-2.581	-8.497	-0.672	*
Clonal ascidians						
Treatment	-10.052	3.072	-3.273	-16.417	-3.739	*
Macroalgae						
Treatment	-8.104	3.290	-2.463	-15.157	-1.320	*
Prey richness						
Treatment	-1.852	1.047	-1.769	-3.889	0.344	ns
Prey evenness						
Treatment	0.096	0.028	3.455	0.036	0.159	*
Consumer richness						
Treatment	1.185	0.494	2.398	0.171	2.228	*
Chiton density						
Treatment	11.100	4.506	2.464	1.915	20.496	*

Table S5. Results of a linear mixed effects model testing the effects of urchin density and prey richness on available space (logit transformed) in quadrats at the end of the experiment in 2009. Transect was nested within site; both were treated as random effects. A Monte Carlo markovchain (MCMC) resampling procedure (n = 5000) assessed the significance of the predictor when the 95% confidence intervals of the parameter estimate did not include zero, the estimate was considered to be significant.

	Estimate	Standard error	t value	MCMC lower limit	MCMC upper limit	significance
Urchin density (UD)	1.014	0.175	5.804	0.654	1.336	*
Prey richness (PR)	-0.024	0.025	-0.947	-0.078	0.022	ns
UD x PR	-0.033	0.009	-3.482	-0.051	-0.013	*

CHAPTER 2

Non-additive consequences of consumer loss on subtidal community structure and variability

Abstract

Declines in global biodiversity have prompted ecologists to investigate the role of diversity in providing functional redundancy in communities. We tested the effects of consumer identity and functional diversity on subtidal rock wall epifauna. In a factorial field experiment replicated at three sites, we reduced the densities of urchins and chitons and quantified changes in community structure and variability over a two-year period, including a year of recovery after the cessation of experimental removals. The removal of each functional group in isolation had no effect on the epilithic community, but the removal of both consumers caused a decrease in available space and an increase in the cover of clonal ascidians. At the end of the experiment, quadrats subjected to the removal of both consumers exhibited significantly greater variation in community composition. These two consumers appear to be important in canalizing the potential variation in the sessile community, because a year after the cessation of treatments, community variability returned to pre-treatment levels. Our data suggest that urchins and chitons are complementary in the maintenance of available space, and that the loss of multiple consumers results in unexpected, non-additive ecological consequences. Facilitation and redundancy among consumers may contribute to the resiliency of urchin-mediated ‘barrens’, even if urchins are transient and do not persist indefinitely.

Introduction

In light of the rising number of local and global anthropogenic threats to ecosystems, there is a growing need to understand the interactive effects of stressors (Darling & Côté 2008). Biodiversity loss, whether arising from habitat destruction, human extraction, or global climate change, is a major concern. One of the hypothesized benefits of a biologically rich community is the potential for different species to perform similar functions, a form of 'biological insurance' (Yachi & Loreau 1999). Redundancy among species can even mask the degradation of an ecosystem until a 'tipping point' is reached. A prime example related, in part, to the sequential loss of consumers has been well documented on Jamaican coral reefs. Chronic overfishing of herbivorous fishes, followed by a region-wide mortality of herbivorous sea urchins, contributed to a shift from coral-dominated reefs to algal-dominated reefs (Hughes 1994). Such 'ecological surprises' (Paine et al. 1998) arising from species loss may be better predicted if researchers conduct appropriate, well-replicated removal experiments in the field (Díaz et al. 2003).

There is an emerging consensus that the biodiversity of primary producers has a positive effect on ecosystem functioning (Cardinale et al. 2006), but fewer studies have manipulated diversity at higher trophic levels, despite the greater threat of extinction to consumers (Duffy et al. 2007). The smaller sample size of studies precludes the ability to draw broad generalizations, but the idiosyncratic effects of predator richness on prey are also likely due to interactions between predators (Bruno & Cardinale 2008). For instance, the extent to which two predators suppress prey more than a single predator depends on the level of intra-guild predation (Vance-Chalcraft et al. 2007). Prior to the emphasis on biodiversity *per se*, numerous studies examined 'multiple-predator effects' using 2 x 2 factorial experiments, especially in terrestrial invertebrate and freshwater systems (Sih et al. 1998). By comparison, factorial manipulations of herbivores and predators in marine systems are few (Vance-Chalcraft et al. 2007), but with considerable support for non-additive (Martin et al. 1989, Navarette & Menge 1996, Crowder et al. 1997, Siddon & Witman 2004, Burkepile & Hay 2008) responses to multiple consumers.

Urchins are large and abundant consumers in many marine environments, and exert strong top-down control on algal (Paine & Vadas 1969) and sessile invertebrate

(Witman 1985) populations. Consequently, they are an integral component of food webs and can mediate trophic cascades upon release from predation (Estes & Duggins 1995). Two immediate anthropogenic threats to urchin populations include the extraction of adults for fisheries (Pfister & Bradbury 1996), and the detrimental impacts of climate change on echinoid development (Byrne et al. 2011, Chan et al. 2011). Therefore, it is critical to understand the extent to which the community-wide effects of urchin loss will be buffered by the diverse set of coexisting marine consumers. Chitons are ubiquitous molluscan mesograzers on hard rocky substrata in nearshore marine environments, and like urchins, are capable of structuring benthic communities (Duggins & Dethier 1985). Through grazing, these consumers restart succession on benthic rocky substrata by clearing space, a limiting resource for sessile taxa (Paine 1984).

In this study, we ask whether experimental removals of red urchins (S*trongylocentrotus franciscanus*) and lined chitons (*Tonicella* spp.) lead to non-additive consequences for benthic communities in the San Juan Islands, WA, USA. Although these two consumers often coexist, it is unlikely that they compete for resources because red urchins typically are larger and consequently eat macroalgae and sessile invertebrates (Chapter 1). In fact, red urchins appear to facilitate lined chitons and other molluscan mesograzers (Chapter 1), by providing 'foraging space' (Dethier & Duggins 1984). Although the morphological dissimilarities (e.g., size, mouthparts) between urchin and chitons are reflected in their ability to consume mature sessile invertebrates and macroalgae, the extent to which these consumers complement one another in the maintenance of available space is unclear. In a factorial field experiment replicated at three sites, we reduced the densities of urchins and chitons and quantified changes in community structure and variability over a two-year period, including a year of recovery after the cessation of experimental removals.

Methods

We tested for non-additive effects of urchins and chitons using a factorial removal of these two consumers. The evidence for non-additivity was considered to be a statistical model that included a significant interaction between urchin and chiton removal for a given dependent variable. The effects of consumer removal were studied in the context of natural temporal variation by examining changes in community structure for two years, during and after a 9-month removal experiment.

In December 2007 (prior to the removal of grazers), permanent transects (2.5 m long, $n = 6$ site^{-1}) and quadrats (0.09 m^2, $n = 4$ transect^{-1}) were established on subtidal rock walls (12 – 18 m depth) at three sites in the San Juan Islands, WA, USA (details in Chapter 1). These permanent study sites were suited ideally for the manipulation of grazers at scales relevant to the consumer. Using a split-plot design, we removed urchins from transects (whole-plot factor), and removed chitons from quadrats (within-plot factor).

At each of three sites, urchins were removed from three transects, and three other transects served as controls. The six permanent transects at each site were arranged linearly and parallel to shore, and for the purposes of urchin removal, adjacent transects were paired (to stratify the removal treatments throughout the site). For each pair of transects, the removal treatment was assigned to the transect with higher urchin density (quantified from six surveys between December 2007 and March 2009). Within each transect, the quadrats with the highest, and third highest, density of chitons (quantified from three surveys between December 2007 and March 2009) were assigned to removal treatments. The remaining two quadrats were not manipulated. The systematic method by which we targeted higher densities of consumers ensured that the removal treatments were meaningful (i.e., so that removal treatments were, on average, actually removing consumers), but not completely biased (i.e., control treatments did experience some grazing pressure).

Consumer removals began on 18 April 2009 and continued every two weeks until 24 January 2010. Logistical difficulties associated with winter SCUBA diving in the San Juan Islands prevented the removal treatments to continue through March, one year after the initial photographs. Photographs of quadrats were taken at nine time points between 20 March 2009 and 14 March 2011.

Analysis

The percent cover of sessile organisms was quantified from photographs using a visual-based method (details in Chapter 1). Taxa were scored only if they were attached to rock or encrusting algae, i.e., epibiotic taxa do not occupy primary space and thus were not quantified. We defined available space as the substratum available for the recruitment and growth of macroalgae and sessile invertebrates (Dayton 1971), which included bare rock, calcified encrusting algae, and non-calcified encrusting algae . Encrusting algae are included in the definition of available space because there is very little bare rock in shallow hard-bottom subtidal habitats, and most invertebrates can overgrow coralline and non-calcified algal crusts (Sebens 1986b). In so doing we assumed that these algal crusts are functionally equivalent, in part for simplicity, but also because the extent to which various species of encrusting algae facilitate (Morse et al. 1988) or inhibit (Breitburg 1984) the settlement of other sessile taxa is poorly understood in this community. Because we considered encrusting algae to be available space, we did not include them in our estimates of richness and Shannon-Weaver diversity.

We used mixed effects models to address three hypotheses with our data. First, we tested the hypothesis that the effects of consumer removal would change during the course of the year-long experimental period because sessile taxa would need time to respond to the release from predation. Second, we hypothesized that consumer removal would result in an increase in clonal ascidians and a concomitant decrease in the cover of available space. Third, we tested the effects of consumer removal on the variability in community composition.

We studied temporal variation in the sessile community during the course of the experiment (20 March 2009 – 22 March 2010) and during one year of recovery after the experiment (22 March 2010 – 14 March 2011). Specifically, we quantified the percent cover of sessile invertebrates and macroalgae, along with the richness, Shannon-Weaver diversity, and evenness of sessile taxa in quadrats. We designed a set of six nested, ecologically relevant models for the data collected during the experiment (March 2009 –

March 2010). All models included site, transect and quadrat as random effects. The fixed effects varied between the models, and these details are listed for each model description (Table 1). The cover of sessile invertebrates and macroalgae was logit transformed. In models with taxon richness as a dependent variable, we used a generalized linear model with a poisson error family.

To address the hypothesis that the removal of consumers would change the cover of clonal ascidians and concomitantly affect the cover of available space, we quantified annual changes in these functional groups during (March 2009 – March 2010; experiment) and after (March 2010 – March 2011; recovery) the experimental treatment. The effects of consumer removal were then tested using a set of linear mixed effects models (Table 2). All models included site and transect as random effects.

To test for the effects of consumer removal on the variability of the epilithic community, we analyzed the homogeneity of treatment dispersions (variances) using the multivariate analog of a Levene's test for univariate analysis (Anderson 2006). First, we created a Bray-Curtis dissimilarity matrix of the 72 permanent quadrats based on nine functional groups for March 2009 (pre-experiment), March 2010 (experiment), and March 2011 (recovery). The Bray-Curtis distances between quadrats and treatment centroids for each dataset were then reduced to principal coordinates and the first two axes were used as the dependent variable in a set of linear mixed effects models (Table 3) identical to those used for the change in cover of clonal ascidians and available space. Dissimilarity matrices were based on nine functional groups: available space, macroalgae, sponges, hydroids, bryozoans, complex, clonal ascidians, solitary invertebrates, and other clonal invertebrates. Complex was defined as a mixed assemblage composed primarily of hydroids, red macroalgae, sediment, and occasional bryozoans. We chose to use functional groups in our analysis, rather than species (or lowest possible taxonomic groupings) to minimize the influence of uncommon species and site-specific differences in species composition. To identify which functional groups were driving the differences in dispersion at the end of the experiment, we subtracted the average standard deviation in percent cover of the control, urchin removal, and consumer removal from the standard deviation of the double removal treatment. We used the same approach to calculate the difference in mean percent cover of the double removal treatment relative to the three other treatments for each functional group.

We compared models using the Akaike Information Criterion corrected for small sample size (Burnham & Anderson 2002), and the two best models were also compared using a likelihood ratio test. Residuals were inspected visually for normality and homoscedasticity, and maximum likelihood was used to estimate parameters in all mixed effects models. Statistical analyses were conducted using the packages 'lme4' (Bates et al. 2011) and 'vegan' (Oksanen et al. 2011) in R 2.13 (R Development Core Team 2012).

Results

Despite not using cages, we successfully reduced both urchin and chiton densities in the removal treatments (Fig. 1). This reduction in consumer pressure significantly affected temporal variation in the cover of sessile invertebrates from March 2009 – March 2010 (Fig. 2). The full model, including a three-way interaction, (Table 1) best fit the observed data, and was marginally better than the next best model (likelihood ratio test, $P < 0.07$; Table 1). The three-way interaction is most apparent at the end of the experiment (March 2010), when the cover of clonal invertebrates in quadrats subjected to both urchin and chiton removal (hereafter referred to as the 'double removal' treatment) was 27 – 55% higher relative to the other three treatments (Fig. 2). After one year of the removal of both consumers, absolute invertebrate cover increased by 13% (a 37% relative increase, Fig. 2). In contrast, macroalgal cover varied temporally but did not respond to consumer manipulations (Fig. 2). Sessile biodiversity in quadrats (richness, Shannon-Weaver diversity, evenness) responded to neither experimental treatments nor time (Table 1).

Best-fit models for the change in cover of both clonal ascidians and available space included a significant interaction between urchin and chiton removal (Table 2), driven by the conspicuous changes in the double removal treatment (Fig. 3). For example, the removal of both consumers triggered a ~10% increase in the cover of clonal ascidians (Fig. 3a) relative to the other treatments, corresponding to a ~75% change relative to initial starting conditions. The most common clonal ascidian at the three sites, *Metandrocarpa taylori*, exhibited a 2.3 fold increase in percent cover (~ 8%) in response to the removal of both consumers (Table 4). Likewise, the cover of available space decreased by 5% in the double removal treatment, but increased by 4 – 9% in the other three treatments (Fig. 3b). To summarize, neither urchin nor chiton removal in isolation caused a change in either the cover of clonal ascidians or available space, while the double removal did, thereby illustrating the non-additivity of these consumer effects.

When we stopped removing consumers, the densities of urchins and chitons recovered to similar densities found in control areas (Fig. 1). The time course of the recovery was rapid, with the total cover of sessile invertebrates in the double removal treatment dropping to levels comparable to the other treatments within approximately three months (June 2010; Fig. 2). The cover of clonal ascidians dropped by ~13% in the double removal treatment, compared with losses of only 1 – 3% in the other treatments (Fig. 3c). In particular, *M. taylori* decreased in cover by 10% in the former treatment, a 69% relative drop (Table 4). In contrast, the null model best fit the data for the recovery of available space (Table 3), despite available space increasing the most in the double removal treatment (Table 3, Fig. 3d).

The mean dispersion (i.e., variability) of treatment groups demonstrated similar non-additive effects of consumer removal (Table 3). At the end of the experiment (March 2010), communities subjected to both urchin and chiton removal exhibited greater variability (distance to the group centroid) than others (Fig. 4). Prior to the experiment (March 2009), and after a year of recovery (March 2011), there was no difference in the dispersion of treatment groups (Fig. 4, Table 3). The double removal treatment exhibited greater variability (standard deviation, σ) than the average variability of the three other treatments for six of the functional groups, especially for clonal ascidians, available space and hydroids (Fig. 5). Despite having the second largest difference in standard deviation, the mean cover of available space was very similar among the four treatments (Fig. 5, Table 5).

Discussion

We have presented field evidence that morphologically dissimilar consumers can serve a similar functional role in a benthic marine community. Removal of only one of the consumers did not cause changes to the epifauna on subtidal rock walls (Fig. 2). However, reducing the natural densities of both of these common consumers caused an increase in the cover of sessile invertebrates, in particular clonal ascidians (Fig. 3). Our data contribute to the growing consensus that the effects of multiple stressors can be non-additive (Darling & Côté 2008) and lead to 'ecological surprises' (Paine et al. 1998). In particular, field experiments in terrestrial (Davidson et al. 2010, Allen & Crawley 2011), freshwater (González & Tessier 1997, Steinmetz et al. 2008), and marine (Siddon & Witman 2004, Burkepile & Hay 2008) habitats have documented the non-additive impacts of consumers.

After one year of experimental removals, quadrats subjected to reductions in the densities of both urchins and chitons exhibited significantly greater variation in community composition, but no obvious clustering of treatments in ordination space (Fig. 4). At first glance, the lack of distinct clusters is surprising because two of the functional groups used in the ordination were clonal ascidians and available space, both of which exhibited significant quadrat-scale change (over time) in response to the simultaneous reduction of urchin and chiton densities. We interpret the discrepancy between quadrat-scale change and multivariate composition across treatments a consequence of the naturally high within- and between-site variation in the composition of these rock wall communities (Table 6). The mean cover of available space was remarkably similar among all four treatments (Table 5), but the relative difference in variability of available space in double removal quadrats (relative to the three other treatments) was the second highest among functional groups (Fig. 5). This observation suggests that the consequences of consumer removal on the availability of space are dependent on the taxa present in quadrats. Indeed, clonal taxa capable of rapidly usurping space through vegetative propagation (e.g., ascidians, hydroids, bryozoans) exhibited the greatest variability in the double removal treatment, as opposed to more slowly growing clonal invertebrates (e.g., sponges, zoanthids) (Fig. 5).

Against the backdrop of high natural variation, perhaps it is to be expected that the successional trajectories of quadrats responding to consumer loss are idiosyncratic and depend on initial starting conditions (Berlow 1997) such as species composition (Benedetti-Cecchi 2000) and resource availability (Dudgeon & Petraitis 2001). Furthermore, no single species or functional group monopolizes space on subtidal rock walls (Sebens 1986a) to the extent that is commonly observed on shallow (horizontal) reefs (e.g., kelps), rocky intertidal benches (e.g., mussels), prairies (e.g., grasses), temperate forests (e.g., trees), and other habitats. Therefore, we do not consider it likely that a longer experiment would have permitted quadrats subjected to both urchin and chiton removals to become sufficiently distinct from the other treatments above and beyond site- and transect-scale variation in community composition.

The return of urchins and chitons into experimental transects and quadrats (Fig. 1) caused a decrease in the cover of clonal ascidians which matched the temporary increase (~ 10%) caused by consumer removal (Fig. 3). Urchin grazing likely reversed the effects of the year-long removal experiment, because red urchins at these sites eat the clonal ascidian *Metandrocarpa taylori* (Chapter 1), and this species in particular exhibited a pronounced increase, then decrease, in response to the removal and recovery of grazing pressure (Table 4). After a year of consumer recovery, the communities no longer exhibited significant variability in the composition of sessile taxa by treatment group (Fig. 4c). Therefore, these two consumers appear to be important in canalizing the potential variation in the sessile community (Berlow 1997). We hypothesize that persistent grazing disturbance, together with temporal variation in the recruitment of sessile invertebrates (Stachowicz & Byrnes 2006, Grey 2010), is partly responsible for preventing a species or functional group from monopolizing space on subtidal rock walls.

The removal of neither urchins nor chitons in isolation caused any shifts in the diversity or composition of the sessile community (Table 1, 2) on subtidal rock walls. This is most surprising with respect to the urchin treatment, because urchins are generally regarded to have strong impacts on benthic community structure (Paine & Vadas 1969). However, in the San Juan Islands, the removal of red urchins does not result in changes to shallow (~10 m depth) kelp communities (Carter et al. 2007). It is possible that the abundance of drift algae in the San Juan Islands (Britton-Simmons et al. 2012) reduces active foraging and thus, benthic impacts of red urchins. Red urchins are relatively inactive and tend not to form 'feeding fronts' in the San Juan Islands (Carter et al. 2007, Elahi pers. obs.) which are often associated with urchin 'barrens' devoid of kelp (Breen & Mann 1976, Scheibling et al. 1999). Finally, Carter et al. (2007) speculated that chitons and other mesograzers prevented the colonization of available substratum by kelp recruits. Our data support this hypothesis, but with respect to clonal ascidians on rock walls, rather than kelp on horizontal reefs. The increase in clonal ascidians was likely not due to sexual recruitment, but rather clonal growth which is particularly well-suited to rapid colonization of available space (Sebens 1986b). Macroalgal cover (primarily red algae) did increase during summer months, but not in response to the reduction in consumer pressure (Fig. 2). Both of these observations are consistent with light-limitation on vertical rock surfaces, which confers a competitive advantage to sessile invertebrates (Miller & Etter 2008).

We suggest that *Strongylocentrotus franciscanus* and *Tonicella* spp., at their natural densities, can be redundant components with respect to the maintenance of the limiting resource in this community, available space. The experimental design, however, cannot distinguish between the effects of consumer diversity and density (Byrnes & Stachowicz 2009). Because we were interested primarily in the consequences of ecological extinction of these two consumers, we did not attempt to manipulate diversity while maintaining density constant. Further, it is difficult to speculate on the absolute equivalence of these two consumers because we did not control for differences in biomass or consumption rate. On an individual basis, it is unlikely that these two consumers are exchangeable, even after controlling for biomass, because they possess different mouthparts (Aristotle's lantern vs. radula). Size, however, is a key ecological trait (Emmerson & Raffaelli 2004) and a primary determinant of prey capture (Scharf et al. 2000). Whereas urchins are capable of clearing space through the consumption of macroalgae (Paine & Vadas 1969) and sessile invertebrates (Witman 1985, Chapter 1), small chitons (e.g., *Tonicella*) eat primarily microalgae and diatoms (Chapter 1). Larger chitons (e.g., *Mopalia muscosa*) likely have a stronger effect on macroscopic taxa (Nydam & Stachowicz 2007) and can even maintain higher levels of unoccupied space than urchins in experimental fouling communities (Byrnes & Stachowicz 2009).

Therefore, with respect to the regeneration of available space, the morphological dissimilarities (e.g., relative size and mouthparts) of the consumers used in our study are reflected as functional differences. Our results may extend to other benthic marine communities, including kelp forests, and have implications for the persistence of crustose-coralline dominated barrens, which are initiated by intense urchin grazing. Through grazing, urchins facilitate chitons by providing foraging space (Chapter 1). Our experiment suggests that the facilitation of chiton grazing by urchins may promote the stability of urchin ‘barrens’ through functional redundancy, even if urchins are transient and do not persist indefinitely.

Tables

Table 1. Results of linear mixed effects models testing the fixed effects of urchin removal, chiton removal, and time on dependent variables measured in quadrats over the course of the one-year experiment (March 2009 – March 2010). Site, transect, and quadrat were treated as random effects. Candidate models are listed with the number of parameters (*K*), corrected AIC (AIC_c), the difference in AIC_c between the candidate model and the best model (Δi), the log-likelihood (logLik), and Akaike weights (w_i). Candidate models with Δi < 2 are listed in bold. In addition, the two best models were compared using likelihood ratio tests; bold type indicates a significant difference between the two models.

Model	*K*	AIC_c	Δi	logLik	w_i	Test	Ratio	*P*
Invertebrate cover								
1	**14**	**790.91**	**0.00**	**-381.98**	**0.49**	1 vs 3	8.75	0.068
2	13	795.84	4.93	-385.37	0.04			
3	**10**	**792.15**	**1.25**	**-386.35**	**0.26**			
4	10	796.16	5.25	-388.35	0.04			
5	8	794.28	3.38	-389.32	0.09			
6	7	794.68	3.78	-390.48	0.07			
Macroalgal cover								
1	14	1547.93	4.81	-760.24	0.06			
2	13	1551.22	8.10	-762.84	0.01			
3	10	1546.56	3.44	-763.42	0.11			
4	10	1545.86	2.75	-763.07	0.16			
5	**8**	**1543.12**	**0.00**	**-763.65**	**0.63**	4 vs 5	1.15	0.562
6	7	1549.60	6.49	-767.87	0.02			
Available space cover								
1	14	666.42	7.87	-319.84	0.01			
2	13	665.39	6.83	-320.24	0.02			
3	**10**	**659.83**	**1.28**	**-320.25**	**0.30**			
4	10	662.30	3.75	-321.48	0.09			
5	**8**	**658.55**	**0.00**	**-321.49**	**0.58**	3 vs 5	2.49	0.288
6	7	675.93	17.38	-331.13	0.00			
Richness (glmer, family = poisson)								
1	13	272.67	2.57	-124.65	0.07			
2	**11**	**270.92**	**0.82**	**-125.42**	**0.16**			
3	**9**	**271.35**	**1.25**	**-127.33**	**0.13**			
4	**9**	**270.36**	**0.26**	**-126.84**	**0.21**			
5	**7**	**270.68**	**0.58**	**-128.75**	**0.18**			
6	**6**	**270.10**	**0.00**	**-129.36**	**0.24**	4 vs 6	5.04	0.169
Diversity								
1	14	167.47	2.15	-72.14	0.11			
2	13	167.82	2.50	-73.00	0.09			
3	**10**	**167.07**	**1.75**	**-74.82**	**0.14**			
4	**10**	**166.44**	**1.13**	**-74.51**	**0.19**			
5	**8**	**166.95**	**1.64**	**-76.32**	**0.14**			
6	**7**	**165.32**	**0.00**	**-76.32**	**0.33**	4 vs 6	3.63	0.304
Evenness								
1	14	-546.62	10.41	288.08	0.00			
2	13	-547.88	9.14	287.61	0.01			
3	10	-552.50	4.53	286.65	0.06			
4	10	-552.93	4.10	286.87	0.08			
5	**8**	**-555.30**	**1.73**	**285.91**	**0.25**			
6	**7**	**-557.03**	**0.00**	**285.72**	**0.60**	5 vs 6	0.39	0.534

Model	**Description and R syntax for fixed effects***
1	Full model - the effects of urchin and chiton removal on dependent variable are non-additive and vary with time y ~ urchin + chiton + time + urchin:chiton + urchin:time + chiton:time + urchin:chiton:time
2	The effects of urchin and chiton removal on dependent variable are additive and vary with time y ~ urchin + chiton + time + urchin:time + chiton:time
3	The effect of urchin removal on dependent variable varies with time y ~ urchin + time + urchin:time
4	The effect of chiton removal on dependent variable varies with time y ~ chiton + time + chiton:time
5	Dependent variable varies with time y ~ time
6	Null model (intercept only) y ~ 1

* random effects are identical for all models, specified as:
(1|site) + (1 + urchin|site:transect) + (1|site:transect:quad)

Table 2. Results of linear mixed effects models testing the fixed effects of urchin and chiton removal on the change in quadrat-scale cover of clonal ascidians and available space after one year of experimental removal (March 2010), and one year of recovery after the cessation of experimental treatments (March 2011). Site and transect were treated as random effects. Candidate models are listed with the number of parameters (*K*), corrected AIC (AIC_c), the difference in AIC_c between the candidate model and the best model (Δi), the log-likelihood (logLik), and Akaike weights (w_i). Candidate models with Δi < 2 are listed in bold. In addition, the two best models were compared using likelihood ratio tests; bold type indicates a significant difference between the two models.

Model	*K*	AICc	Δi	logLik	w_i	Test	Ratio	*P*
Experiment; Change in clonal ascidians								
1	**9**	**540.43**	**0.00**	**-261.55**	**0.89**	**1 vs 2**	**8.14**	**0.004**
2	8	546.72	6.28	-265.62	0.04			
3	7	547.95	7.51	-267.18	0.02			
4	7	547.20	6.76	-266.80	0.03			
5	6	548.39	7.96	-268.35	0.02			
Experiment; Change in available space								
1	**9**	**574.81**	**0.00**	**-278.71**	**0.60**	**1 vs 3**	**4.94**	**0.026**
2	8	577.87	3.07	-281.18	0.13			
3	7	577.80	2.99	-282.09	0.14			
4	7	579.32	4.51	-282.85	0.06			
5	6	579.22	4.41	-283.75	0.07			
Recovery; Change in clonal ascidians								
1	**9**	**548.22**	**0.00**	**-265.44**	**0.95**	**1 vs 2**	**9.28**	**0.002**
2	8	555.64	7.42	-270.08	0.02			
3	7	558.01	9.79	-272.21	0.01			
4	7	556.11	7.89	-271.25	0.02			
5	6	558.43	10.21	-273.37	0.01			
Recovery; Change in available space								
1	**9**	**563.13**	**1.60**	**-272.88**	**0.13**			
2	**8**	**562.58**	**1.05**	**-273.54**	**0.17**			
3	**7**	**562.33**	**0.80**	**-274.36**	**0.19**			
4	**7**	**561.80**	**0.27**	**-274.10**	**0.24**			
5	**6**	**561.53**	**0.00**	**-274.91**	**0.28**	4 vs 5	1.64	0.201

Model	Description and R syntax for fixed effects*
1	Full model - the effects of urchin and chiton removal on dependent variable are non-additive y ~ urchin + chiton + urchin:chiton
2	The effects of urchin and chiton removal on dependent variable are additive y ~ urchin + chiton
3	Urchin removal affects dependent variable y ~ urchin
4	Chiton removal affects dependent variable y ~ chiton
5	Null model (intercept only) y ~ 1

* random effects are identical for all models, specified as:
(1|site) + (1 + urchin|site:transect)

Table 3. Results of linear mixed effects models testing the fixed effects of urchin and chiton removal on the variability in community composition of quadrats (measured as the distance of each quadrat to the centroid for its treatment group in principal coordinate ordination space; Figure 3) before the experiment (March 2009), after the experiment (March 2010), and after one year of recovery (March 2011). Site and transect were treated as random effects. Candidate models are listed with the number of parameters (*K*), corrected AIC (AIC_c), the difference in AIC_c between the candidate model and the best model (Δi), the log-likelihood (logLik), and Akaike weights (w_i). Candidate models with Δi < 2 are listed in bold. In addition, the two best models were compared using likelihood ratio tests; bold type indicates a significant difference between the two models.

Model	*K*	AICc	Δi	logLik	w_i	Test	Ratio	*P*
March 2009 (pre-experiment)								
1	9	-92.56	5.93	57.19	0.02			
2	8	-95.31	3.18	57.15	0.09			
3	**7**	**-96.70**	**1.78**	**56.51**	**0.19**			
4	**7**	**-97.19**	**1.30**	**56.74**	**0.24**			
5	**6**	**-98.49**	**0.00**	**56.10**	**0.46**	4 vs 5	1.29	0.256
March 2010 (post-experiment)								
1	**9**	**-116.71**	**0.00**	**68.89**	**0.80**	**1 vs 4**	**9.53**	**0.009**
2	8	-110.99	5.72	64.79	0.05			
3	7	-109.60	7.11	62.82	0.02			
4	7	-112.25	4.46	64.12	0.09			
5	6	-110.79	5.92	62.16	0.04			
March 2011 (post-recovery)								
1	9	-119.66	6.73	70.32	0.02			
2	8	-121.56	4.83	69.96	0.05			
3	7	-123.91	2.47	69.86	0.17			
4	7	-124.11	2.27	69.96	0.19			
5	**6**	**-126.38**	**0.00**	**69.86**	**0.58**	4 vs 5	0.20	0.655

Model	Description and R syntax for fixed effects*
1	Full model - the effects of urchin and chiton removal on dependent variable are non-additive y ~ urchin + chiton + urchin:chiton
2	The effects of urchin and chiton removal on dependent variable are additive y ~ urchin + chiton
3	Urchin removal affects dependent variable y ~ urchin
4	Chiton removal affects dependent variable y ~ chiton
5	Null model (intercept only) y ~ 1

* random effects are identical for all models, specified as:
(1|site) + (1 + urchin|site:transect)

Table 4. Percent cover (mean ± SE) of the three most common clonal ascidian species and the sum of other clonal ascidians in four experimental treatments. We report values prior to the experiment (pre-experiment; March 2009), after the experiment (post-experiment; March 2010), and one year after the cessation of experimental removals (post-recovery; March 2011).

Treatment	**Period**	***Metandrocarpa taylori***	***Didemnum carnulentum***	***Pycnoclavella stanleyi***	**Other clonal ascidians**
Control	Pre-experiment	3.5 ± 1.1	2.9 ± 1.2	1.9 ± 0.9	0.7 ± 0.3
Control	Experiment	6.4 ± 2.5	2 ± 0.7	1.1 ± 0.5	0.2 ± 0.1
Control	Recovery	2.6 ± 1	3.2 ± 1.3	0.6 ± 0.4	0.2 ± 0.1
Chiton removal	Pre-experiment	3.2 ± 1.6	4.1 ± 1.5	2.3 ± 1.1	0.9 ± 0.4
Chiton removal	Experiment	5.2 ± 2.4	2.6 ± 1	1.1 ± 0.6	0.3 ± 0.2
Chiton removal	Recovery	2.5 ± 1.2	4.4 ± 1.7	0.7 ± 0.4	0.2 ± 0.1
Urchin removal	Pre-experiment	4.5 ± 1.6	1.1 ± 0.5	1.7 ± 1.7	0.2 ± 0.1
Urchin removal	Experiment	6.1 ± 2.1	1.1 ± 0.5	0.5 ± 0.5	0.1 ± 0.1
Urchin removal	Recovery	3.1 ± 1.2	2.5 ± 1.3	0.3 ± 0.3	0.1 ± 0.1
U & C removal	Pre-experiment	6.8 ± 2.1	4.6 ± 2.1	1.5 ± 1.1	0.2 ± 0.2
U & C removal	Experiment	15.3 ± 5.2	5.4 ± 2.9	1.8 ± 1.3	0.3 ± 0.2
U & C removal	Recovery	4.8 ± 1.6	4 ± 2.3	0.7 ± 0.5	0.1 ± 0.1

Table 5. Percent cover (mean ± SD) of the nine functional groups in four treatments at the end of the experiment (March 2010).

Functional group	**Control**	**Urchin removal**	**Chiton removal**	**U & C removal**
Clonal ascidians	9.8 ± 15.2	7.8 ± 10	9.2 ± 14.4	22.9 ± 28.5
Space	36.2 ± 15.7	38.9 ± 16.3	38.3 ± 15.8	37.1 ± 22.7
Hydroids	1.2 ± 2.9	0.9 ± 2.5	0.5 ± 1.2	2.8 ± 7.7
Complex	0.9 ± 1.9	0.6 ± 1.8	0.3 ± 0.7	2.2 ± 4.7
Bryozoans	11 ± 11.5	6.7 ± 5.4	10.3 ± 8.8	7.9 ± 10.6
Solitary inverts	7.8 ± 3.9	10.3 ± 11.4	6.7 ± 5.2	8.1 ± 7.6
Sponges	8.1 ± 10.3	3.2 ± 3.2	6.8 ± 8.3	5.3 ± 7.2
Macroalgae	2 ± 3.2	4 ± 5.3	2.9 ± 4.3	2.2 ± 3.2
Clonal inverts	0.5 ± 2.1	2.7 ± 8.1	1.4 ± 3.7	0.8 ± 2

Table 6. Results of a nested permutational analysis of variance on the composition of nine functional groups (see Methods) of sessile taxa at three spatial scales (site, transect, quadrat) on subtidal rock walls in March 2009 (prior to the experiment). We report the degrees of freedom (DF), sums of squares (SS), and variance. The percentage of variance attributable to each spatial scale is calculated as its SS divided by the total SS.

	DF	**SS**	**Variance**
Site	2	2.08	24.6%
Transect	15	3.63	43.0%
Quadrat (residuals)	54	2.73	32.3%
Total	71	8.44	

Figures

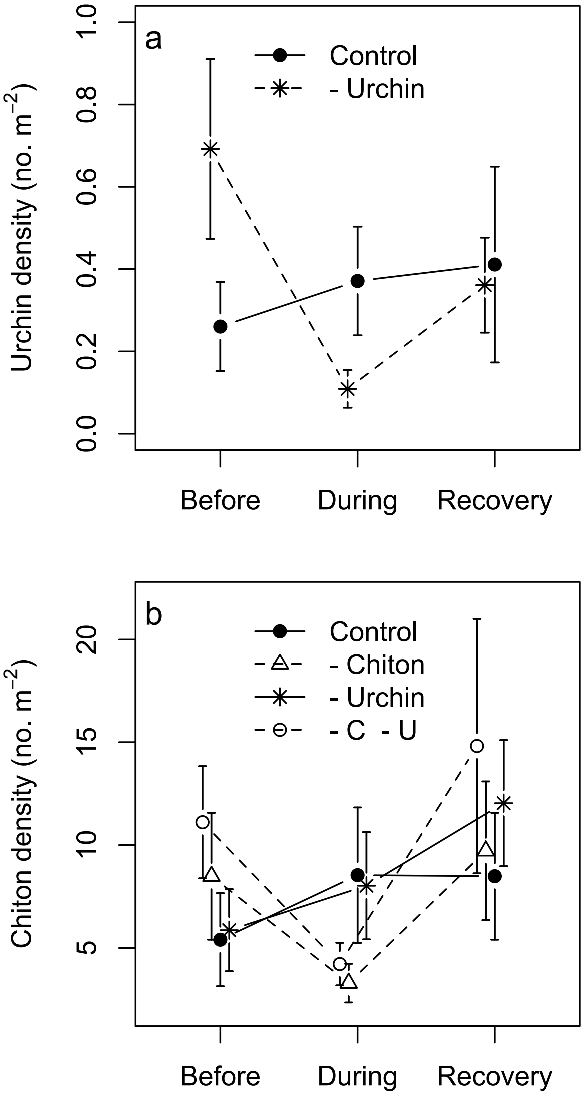

Figure 1. The density (mean ± SE) of urchins (a) and chitons (b) before (March 2008 – March 2009) and during (March 2009 – March 2010) the experiment, and after the recovery (March 2010 – March 2011) of these two consumers.

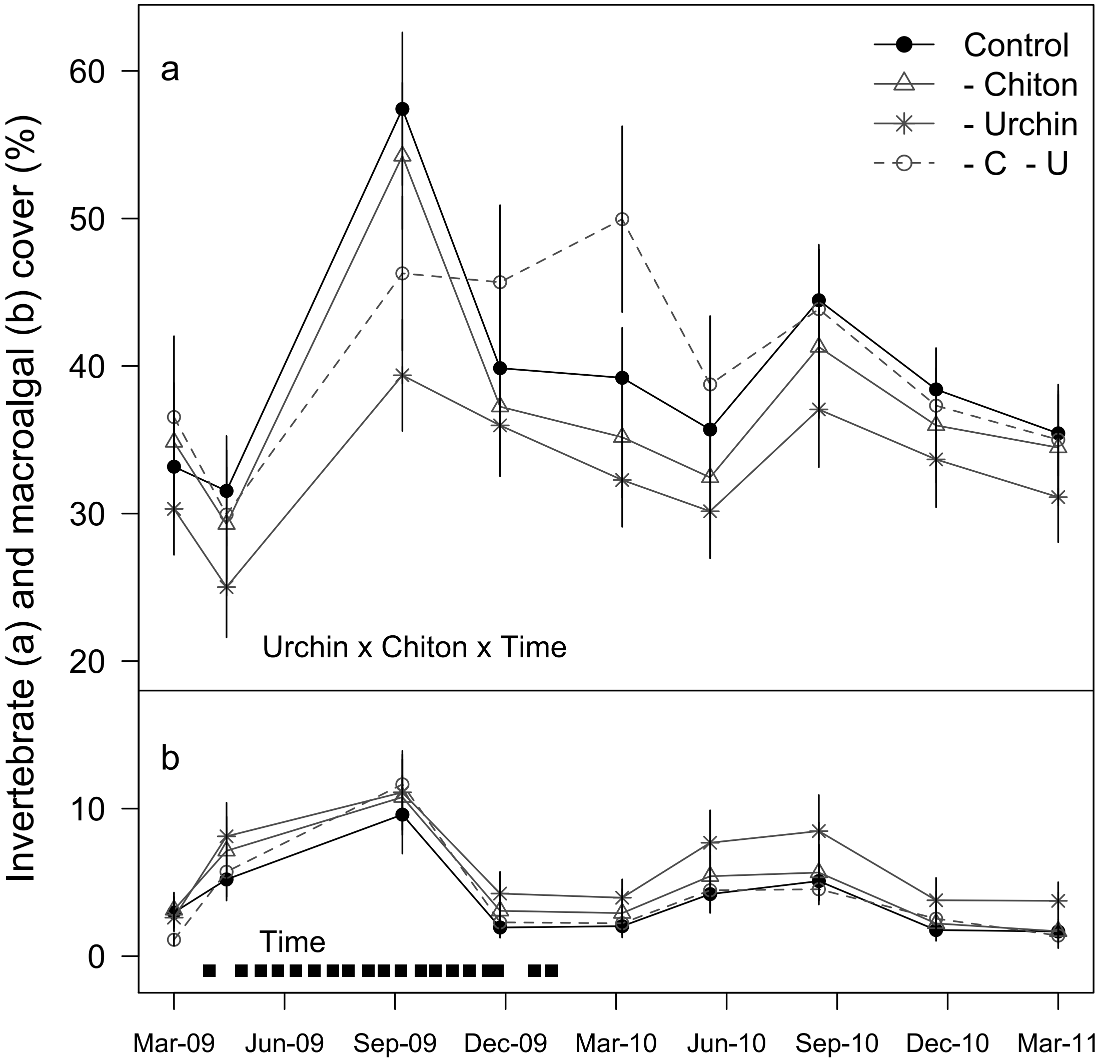

Figure 2. The percent cover (mean ± SE) of invertebrates (a) during the experimental period (March 2009 – March 2010) depended on the interaction between urchin treatment, chiton treatment, and time. Note that the percent cover of invertebrates was indistinguishable among experimental treatments after one year of recovery (March 2011). In contrast, the percent cover of macroalgae (b) depended only on time. Black squares indicate the dates of consumer removal. The best model (Table 1) is indicated for each panel, except when no candidate model was better than the null model.

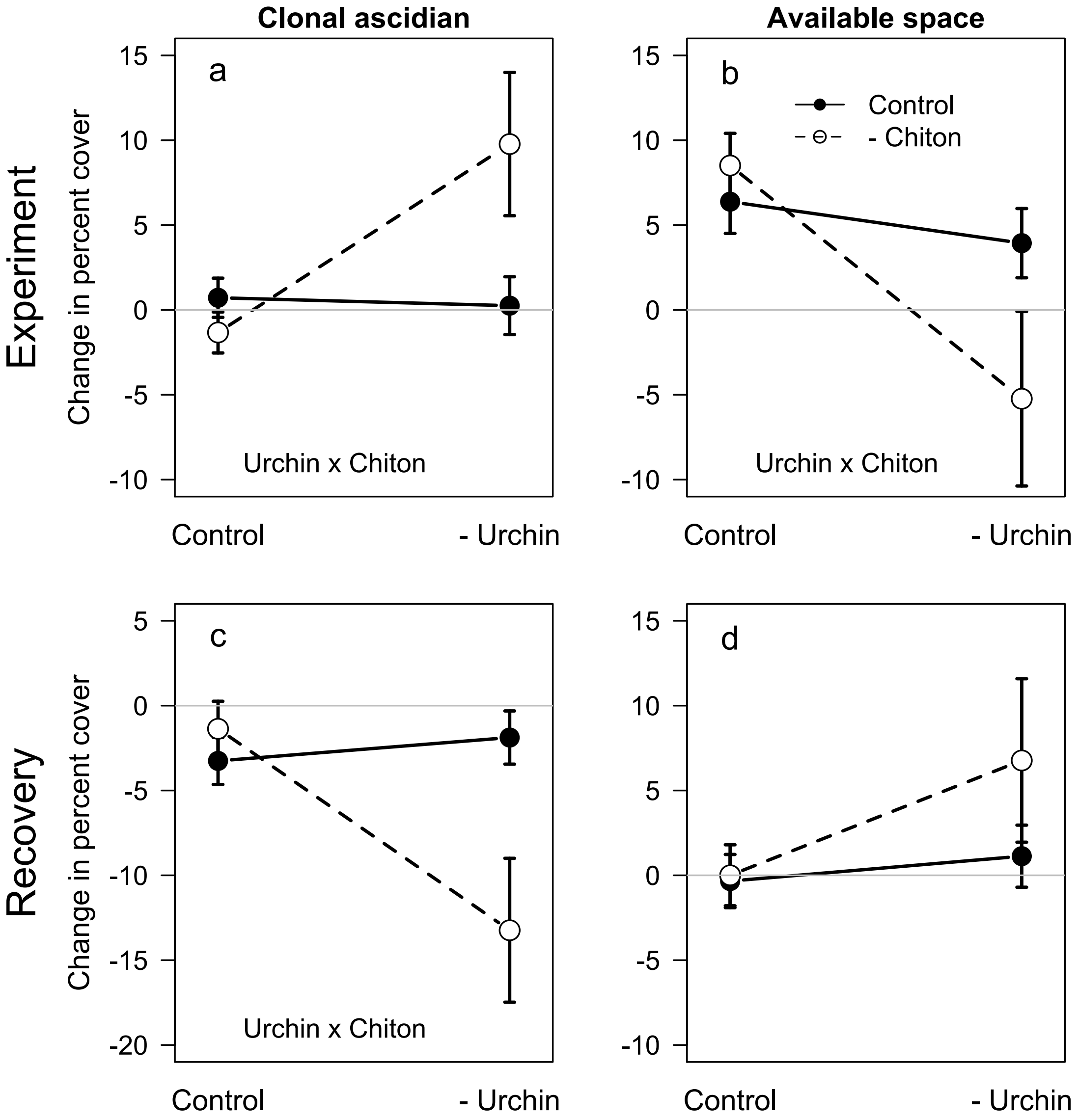

Figure 3. The experimental removal of both urchins and chitons caused an increase in the percent cover (mean ± SE) of clonal ascidians (a), and a decrease in available space (b) in quadrats. After a year of recovery, the percent cover of clonal ascidians (c) decreased in quadrats previously subjected to both urchin and chiton removal. In contrast, the effects of consumer removal did not affect the recovery of space (d). The best model (Table 2) is indicated for each panel, except when no candidate model was better than the null model.

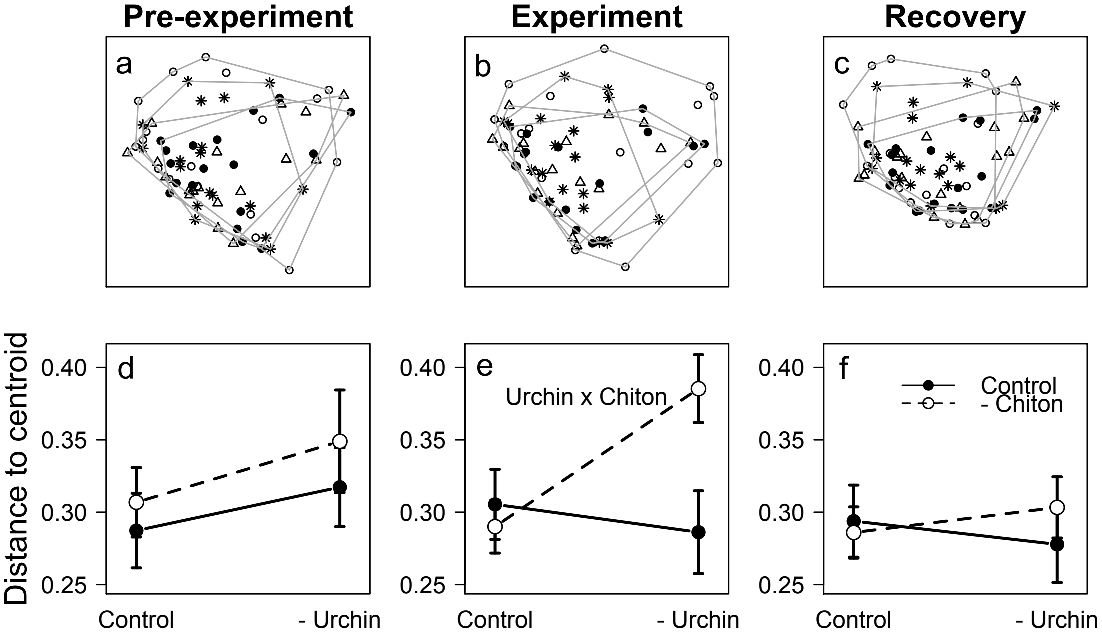

Figure 4. Ordination plots of nine functional groups of sessile taxa before (March 2009; a) the experimental removal of consumers, after one year of consumer removal (March 2010; b), and one year after the cessation of experimental treatments (March 2011; c). In (a) – (c), treatments are represented as follows: control (closed circles), chiton removal (triangles), urchin removal (asterisks), and urchin and chiton removal (open circles). Polygons enclose all quadrats within a single treatment. The distance (mean ± SE) from each quadrat to the centroid of its treatment group increased in response to both urchin and chiton removal after the experiment in March 2010 (e). The best model (Table 3) is indicated for each panel, except when no candidate model was better than the null model.

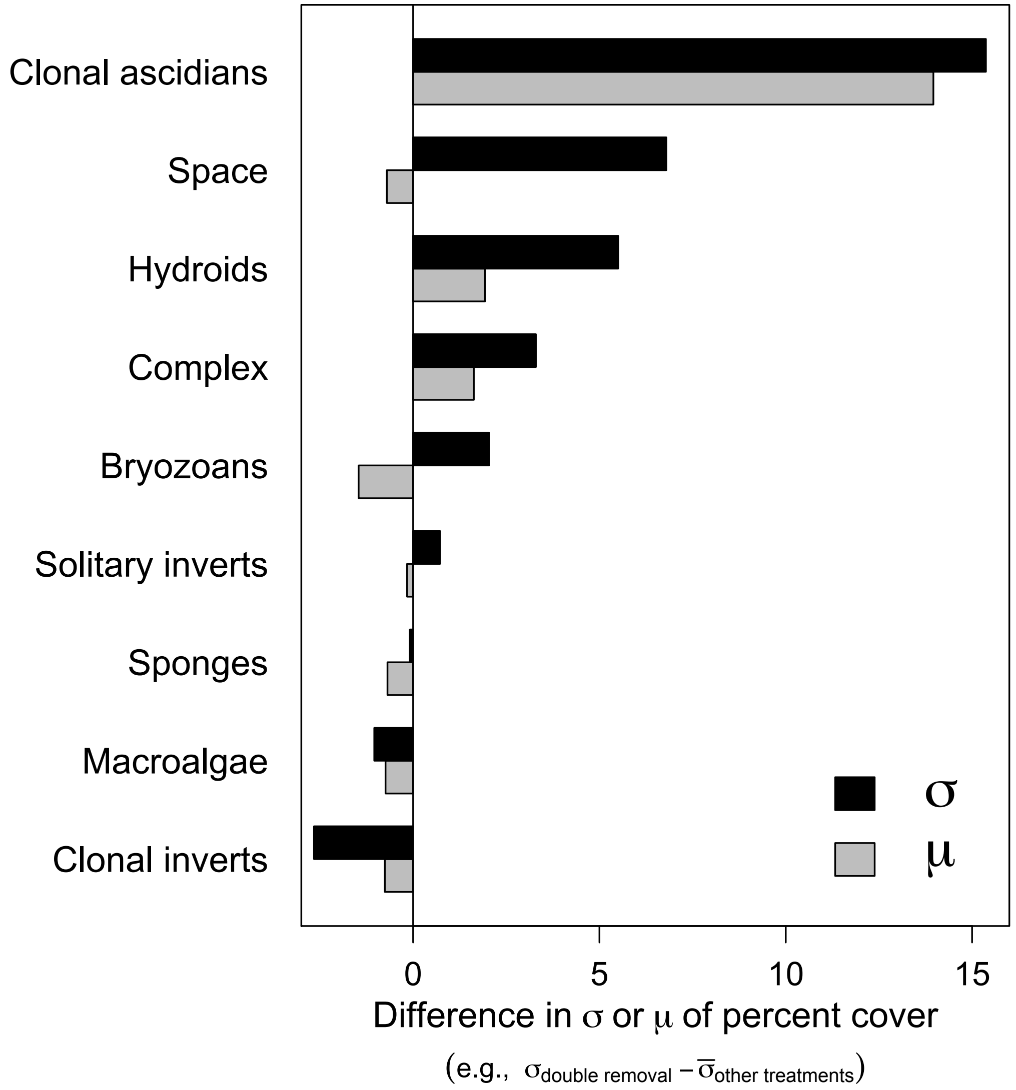

Figure 5. The percent cover of six functional groups used in the ordination plots (Fig. 3) exhibited greater variability (standard deviation, σ) in double removal quadrats relative to the average variability of the three other treatments (control, single removals) at the end of the experiment (March 2010). In contrast, the percent cover (mean, μ) of the functional groups was similar between double removal quadrats and the average percent cover of the three other treatments for all functional groups, except for the large increase of clonal ascidians. See Table 5 for the percent cover (μ ± σ) data for the functional groups used in this analysis.

CHAPTER 3

Mesoscale oceanographic variability in water retention dictates benthic biodiversity

Abstract

Understanding the relative importance of ecological processes at different spatial scales is an issue central to both ecological theory and conservation efforts. In this study, we quantified the role of mesoscale oceanographic variation on the structure of subtidal (~15 m depth) rock wall communities. We used a hierarchical sampling design to survey 18 sites, nested within five distinct oceanographic seascapes in Washington State. Three of the seascapes (Haro Strait, San Juan Channel, Rosario Strait) are waterways, and two of the seascapes (Lopez and East Sounds, Hood Canal) are restricted inlets. Waterways and inlets are categorically different in their relative levels of water retention and tidal currents; sites in waterways tend to exhibit lower water retention and stronger tidal currents. The most striking variation in diversity was observed between the five seascapes, primarily between waterways and inlets. Namely, sites nested within the Haro Strait, San Juan Channel, and Rosario Strait seascapes exhibited greater diversity at the quadrat and site scales than did sites within Lopez Sound, East Sound, and Hood Canal. Multivariate analyses of community composition reflected a similarly conspicuous separation between waterway and inlet sites. We quantified three abiotic correlates (sediment cover, alabaster dissolution rates, temperature) of water retention at a subset of sites, and the data support the qualitative generalization that waterways and inlets represent distinct oceanographic environments, and consequently harbor unique subtidal biota. We hypothesize that larval delivery and post-settlement mortality are important mechanisms related to the covarying effects of reduced water flow, sedimentation, and light limitation in high-retention sounds and fjords.

Introduction

Compelling evidence implicates biological diversity as a critical component of ecosystem change (Hooper et al. 2012) and functioning (Balvanera et al. 2006). Thus, there is an urgent need to document patterns of species diversity at a variety of spatial scales, to match patterns of abundance and distribution with the processes that maintain them (Underwood et al. 2000, Connell & Irving 2008). Observational approaches that include matching patterns with relevant environmental covariates are particularly important over large spatial scales, where experimental manipulations are not feasible (Sagarin & Pauchard 2009).

At one extreme, biogeographic variation in regional (>1000 km) species pools is a consequence of historical and evolutionary processes, and has a positive, linear (i.e., non-saturating) effect on local (< 10 m) richness (Karlson et al. 2004, Witman et al. 2004). At the opposite extreme, large variability at local scales is a common feature of ecological systems (Fraschetti et al. 2005) and is associated with biotic (e.g., competition, predation) and abiotic (e.g., temperature, desiccation) causes (e.g., Connell 1961). These endpoints of spatial scale are of little practical use to resource managers because the design of marine protected areas is conducted between the local and regional scales.

Oceanographic variability at the "mesoscale" (10 – 100 km) structures both intertidal (Menge et al. 1997) and subtidal (Witman et al. 2010) benthic communities. This intermediate scale of observation is a prime candidate for study because oceanographic processes deliver food, disperse larvae and set the abiotic stage for local processes on the benthos. In this paper, we explored mesoscale variation in the biodiversity of two distinct oceanographic features. Waterways (e.g., straits, channels) and inlets (e.g., fjords, sounds) are categorically different in their relative levels of water retention and flow. Waterways are open bodies of water and tend to exhibit low retention and high flow, whereas inlets are restricted bodies of water typified by high retention and low flow.

The importance of water flow is ubiquitous in marine systems. It dictates the physiological rates (Patterson et al. 1991, Fabricius et al. 1995) and shapes the morphology (Sebens et al. 1997, Kaandorp 1999) of individuals. Currents transport particulate food to sessile (Lesser et al. 1994, Witman et al. 2003) and mobile (Britton-

Simmons et al. 2009) consumers. Water flow affects community assembly by mediating larval dispersal and recruitment (Roughgarden et al. 1988, Palardy & Witman 2011, Knights et al. 2012) and subsequent post-settlement processes, including grazing behavior (Siddon & Witman 2003) and predator-prey interactions (Powers & Kittinger 2002). Altogether, these multiple effects of flow on bottom-up and top-down processes ultimately influence the distribution of species at small scales (< 1 m; Leichter & Witman 1997), and the structure of communities at larger scales (1 - 10 km; Leonard et al. 1998).

We tested the hypothesis that mesoscale oceanographic features dictate the biodiversity and community composition of subtidal benthic communities.

We focused on epifaunal communities on subtidal vertical rock surfaces (walls) because they harbor an impressive diversity of sessile taxa that occupy the relatively two-dimensional and homogeneous space (Witman et al. 2004, Miller & Etter 2011). We used a hierarchical sampling design to quantify the percentage of variation attributable to four spatial scales, ranging from the local to mesoscale. We compared sites within distinct areas of the Salish Sea (Fig. 1), which we shall refer to as seascapes. We focus on the following seascapes: Haro Strait, San Juan Channel, Rosario Strait, Lopez Sound and East Sound, and Hood Canal. Although all of these seascapes can potentially receive larvae from the same regional species pool, they are subject to different physical environments, especially with respect to water retention. Therefore, these seascapes are oceanographically distinct but overlap in evolutionary history. In addition to biotic surveys, we quantified three correlates of water retention – sediment cover, alabaster dissolution, and seawater temperature – to examine empirically the qualitative generalizations of high versus low retention.

Methods

Field surveys

We established a hierarchical sampling design of random quadrats on subtidal rock walls at 18 sites (Fig. 1, Table 1) with the explicit goal of partitioning variation in the richness of sessile and mobile taxa at four spatial scales. The four hierarchical spatial scales that we investigated included seascape (10 – 100 km), site (1 – 10 km), transect (5 – 50 m), and quadrat (< 2.5 m), which span six orders of magnitude. Although the spatial scale of seascape and site overlap (Fig. 1), the influence of seascape was specifically meant to reflect *a priori* hypothesized differences in oceanographic features, specifically with respect to water retention. The five seascapes included were Haro Strait (Haro; n = 4 sites), San Juan Channel (Channel; n = 4), Lopez and East Sound (Sound; n = 4), Rosario Strait (Rosario; n = 3), and Hood Canal (Hood; n = 3).

Haro Strait, Rosario Strait and San Juan Channel are waterways connecting the Strait of Georgia and the Strait of Juan de Fuca in the Salish Sea (Fig. 1). These narrow passages are well known to sailors and divers for their rapid tidal currents. Haro Strait is on the west side of the San Juan Islands, and of the three waterways is the deepest (> 350 m) and most exposed to windswell. Rosario Strait (~50 – 100 m depth) lies to the east of the San Juan Islands, and it separates the archipelago from mainland Washington. San Juan Channel (~100 – 150 m depth) is the main passage separating San Juan Island from the other islands in the archipelago, and is the narrowest (2 – 5 km) of the three waterways.

In contrast, East Sound and Lopez Sound are nestled within the San Juan Islands and do not connect directly to the surrounding straits. Consequently, they experience restricted water motion. East Sound is a shallow (~30 m) fjord, and a partial sill restricts tidal exchanges even further (Menden-Deuer 2008) from the adjacent Lopez Sound. Lopez Sound is also relatively shallow (~30 – 60 m), and water is flushed to Rosario Strait through several narrow passes (e.g., Obstruction Pass, Thatcher Pass).

About 80 km to the south of the San Juan Islands, Hood Canal is a long (90 km) and narrow (1 – 4 km) fjord and forms one of the four major basins of Puget Sound. Water retention is high, due to a shallow (50 m) sill which precedes the deep (120 – 180 m) fjord (Ebbesmeyer et al. 1988, Babson et al. 2006). Hypoxia in southern Hood Canal has become more prevalent in the past five decades, and is a consequence of both natural (minimal water exchange) and anthropogenic causes (e.g., eutrophication) (Newton et al. 2007). Fish kills in southern Hood Canal, a result of hypoxia, have been recorded in 2003, 2006, 2010, and 2011 (Bargmann 2003, Palsson 2003, Palsson et al. 2008, Dunagan 2010, 2011).

Between July and September 2010, horizontal transects (2.5 m long, *n* = 6) separated by at least five meters were sampled haphazardly on rock walls (≥ 2m in height) between 12 and 19 m depth at each site. Quadrats (0.09 m^2, *n* = 4) were positioned randomly along transects, and photographs of quadrats were taken using an Olympus C-8080 digital camera with an Ikelite strobe attached to a 36 × 25 cm aluminum frame, allowing identification of organisms ≥3 mm in length. These photographs were used to quantify the richness (number of taxa) and composition of sessile and mobile taxa. Organisms were identified to the lowest possible taxon and were assigned unique pseuodonyms when species identification was not possible. Concurrently, the abundance of 'large' (> 3 cm adult size) mobile fauna (e.g., echinoderms) was quantified within 1 m above and below each transect.

Correlates of water retention

To test the hypothesis that waterways and inlets are categorically different with respect to water retention, we quantified three correlates of water flow – sediment cover, alabaster dissolution, and temperature. For all five seascapes, we quantified the percent cover of sediment in quadrats because sedimentation rates are related inversely to water flow (Genovese & Witman 1999, Lenihan 1999). The percent cover of sediment was quantified from photographs using a visual-based method (Dethier et al. 1993). A grid of 20 rectangles was superimposed onto each image and the percent cover of sediment was scored for each rectangle as follows: 0 = absence, 1 < 1%, 2 = 10%, (1 – 19%), 3 = 30% (20 – 39%), 4 = 50% (40 – 59%), 5 = 70% (60 – 79%), 6 = 90% (80 – 99%) and 7 > 99%. The sum of scores was expressed as a percentage of the total sum for the quadrat. Due to the extreme homogeneity of variances for sediment cover (unit of replication = quadrat), we used a Kruskal-Wallis non-parametric test to test the fixed effect of seascape and thus omitted the nested, random effects of site and transect.

In addition, we selected the Channel and Sound seascapes for the quantification of alabaster dissolution and temperature measurements. These two seascapes were chosen because they exhibited striking differences in both diversity and sediment cover, and because their relative proximity to Friday Harbor Laboratories made repeated visits logistically feasible. The dissolution of gypsum (or other materials) is a practical means of quantifying integrated water motion (Doty 1971, Thompson & Glenn 1994). We used blocks (5.9 × 5.5 × 1.2 cm) of cut alabaster to integrate dissolution over a longer time period, because preliminary trials indicated that balls made from ground gypsum dissolved within ~48 hours at the highest flow sites. Three alabaster blocks were deployed at least 5 m apart on rock walls (12 – 17m depth) at each of the Channel and Sound sites between 27 July and 6 August 2012. The change in dry weight of each block was normalized to the number of days (7 – 9) in the field. Dissolution data were balanced, and thus a nested analysis of variance (ANOVA) was used to test the effects of seascape (fixed) and site (random) on alabaster dissolution (unit of replication = transect). Dissolution was natural log transformed to meet the assumptions of normality and homogeneity of variances.

With respect to temperature, we hypothesized that seascapes with higher water retention would exhibit higher and/or more variable seawater temperatures due to water stratification (Ebbesmeyer et al. 1988), especially during summer months. We deployed a HOBO® temperature logger (Onset Computer Corporation) at each site in Channel and Sound seascapes between 29 July and 7 September 2012, which logged temperature every half hour. For analysis, mean daily temperatures were calculated from the raw data. A repeated-measures ANOVA tested the effect of seascape (fixed) on temperature in the San Juan Islands (unit of replication = site).

Diversity - univariate analyses

We defined richness as the number of species (or lowest possible taxon) per quadrat. Broader functional groups (e.g., hydroids) were used when necessary, and thus all of our estimates of biodiversity should be regarded as conservative (see Tables S1 and S2 for taxa). Taxa were scored only if they were attached to rock or encrusting algae.

Epibiotic taxa were not quantified because they do not occupy primary space. Organisms obscured by sediment were also omitted.

Species accumulation curves were plotted as the number of species observed at each site (S_{obs}), and the estimated number of species per site (S_{Chao2}) was calculated using the *Chao2* estimator (Colwell & Coddington 1994). We used linear mixed-effects models to test the fixed effect of seascape on richness, S_{obs}, and S_{Chao2} separately for sessile and mobile taxa. Mixed effects models were used rather than nested ANOVA because transects were not uniformly replicated across sites, nor were sites uniformly replicated within seascape (i.e., data were not balanced). For richness, we treated site and transect as random effects; quadrat was treated as the unit of replication (residual error). For S_{obs} and S_{Chao2} we tested the effects of seascape (fixed) and site (random); transect was treated as the unit of replication (residual error). In addition to inferring differences between seascapes, we calculated the percentage of explained variation (PEV) attributable to each spatial scale. PEV was calculated as the variance (for each spatial scale) divided by the total variance using the results of mixed-effects models treating each spatial scale (including seascape) as random. PEV was calculated similarly for dissolution and temperature data. Assumptions of normality and homogeneity of variances for parametric testing were met by graphical inspection; when necessary a log transformation was used (mobile richness, mobile S_{Chao2}). We used the R package 'lmer' to fit linear mixed-effects models, and the R package 'languageR' to implement a Monte Carlo Markov chain resampling method for significance tests of fixed effects.

Community composition - multivariate analyses

We used non-metric multi-dimensional scaling (nMDS) ordinations to visualize patterns in the community composition of subtidal rock walls from the different seascapes. Rather than plot each quadrat (n = 400), we plotted the centroids for each site (n = 18) to emphasize the differences between sites and seascapes, following the methodology of Anderson (2001) and Terlizzi et al. (2005). In brief, principle coordinates were calculated from the Bray-Curtis dissimilarity matrix of the original presence-absence matrix of 132 observed taxa. Next, a Euclidean dissimilarity matrix was calculated using the arithmetic average of the principal coordinates for each site, and used as the input dissimilarity matrix for the nMDS analysis. The same approach was applied to large mobile fauna on transects, but 22 transects were omitted because no organisms were observed and thus the Bray-Curtis index was undefined for pairs of blank samples (empty transects). We chose not to use a ‘dummy species’ to calculate dissimilarities for blank samples because we did not have a single, common, *a priori* ecological explanation for blank transects (Clarke et al. 2006).

As a complement to ordination, we used a hierarchical cluster analysis to identify which sites were most similar to each other, and thus compare the utility of our *a priori* designations of seascape to post-hoc clusters. The same input dissimilarity matrix for the nMDS algorithm (above) was used for the cluster analysis using the hclust function in R, with the method of Ward’s minimum variance. The optimum number of clusters was identified using the Calinski-Harabasz criterion (Calinski & Harabasz 1974). Following the identification of the two best clusters for taxa in quadrats, we used indicator species analysis (Dufréne & Legendre 1997, Bakker 2008) to identify the taxa that best characterized each cluster. Cluster 1 contained all but one of the waterway (Haro, Channel, Rosario) sites, and cluster 2 was comprised of the inlet sites and O’Neal Island (Channel).

Differences in the community composition of quadrats (sessile and mobile taxa) and transects (mobile taxa) were tested using permutation analysis of variance (PERMANOVA) on Bray-Curtis dissimilarity matrices of presence/absence data (quadrat) and untransformed abundance data (transect). For quadrat data, the model included the effects of seascape, site, and transect; the model for transect data included the effects of seascape and site. To determine whether differences in multivariate community composition were attributable to dispersion among seascapes (rather than location), the group dispersion to seascape centroids (i.e., multivariate beta diversity or species turnover; Anderson 2006) was compared using permutational analysis of dispersion (PERMDISP). Significance was evaluated using 1000 permutations for PERMANOVA and PERMDISP. Seascape was treated as a fixed effect; all other effects as random (as for ANOVA’s). PERMANOVA and PERMDISP were performed in Primer 6 (Clarke & Gorley 2006); all other analyses were conducted using the vegan (Oksanen et al. 2011) and stats packages in R 2.14 (R Development Core Team 2012).

Results

Correlates of water retention

Sites within restricted inlets (Sound, Hood) exhibited significantly higher (Kruskal-Wallis $\chi^2 = 308.3$, df = 4, $P < 0.001$) percent cover of sediment in quadrats in restricted inlets (Sound, Hood) than quadrats in waterways (Haro, Channel, Rosario). No accumulation of sediment was observed at sites in Haro Strait, and limited sediment cover in San Juan Channel and Rosario Strait (Fig. 2a). Sound and Hood sites were highly variable in sediment cover (Fig. 2a), and an increasing southward gradient of sediment cover was observed in Hood Canal (Table 1).

Using alabaster dissolution as a proxy for water flow, we detected significantly (Table 3) higher flow at Channel sites than Sound sites (Fig. 2b). The effect of seascape explained 63% of the variance, and the effect of site was less important (27%). However, O'Neal Island in San Juan Channel exhibited similar dissolution rates to sites in Lopez Sound (Table 1). Flow was greatest, and most variable, at Point George (1.6 ± 0.4 mg cm^{-2} day^{-1} mass loss), in part due to one block that exhibited 2.1 mg cm^{-2} day^{-1} mass loss.

Overall, seawater temperatures at Channel sites were significantly (Table 3) lower than Sound sites (Fig. 3a). However, the mean temperature of O'Neal Island was more similar to Sound sites (Table 1), than Channel sites. Temperatures were also highly variable (72% unexplained variance, Table 5). Much of this variability was due to tidal fluctuations in phase with the lunar cycle (Fig. 3a). For example, the lowest temperatures and sharpest decreases were observed during full (1 and 31 August) and new (17 August) moons, when tidal exchanges typically are greatest. During quarter moons (10 and 24 August), higher temperatures were associated with the smaller tidal exchanges. The most variable sites were Rosario Wall in East Sound, and O'Neal Island in San Juan Channel (Fig. 3a). The mean temperature of sites was highly correlated with mean dissolution rates, with O'Neal Island plotted among Sound sites (Fig. 3b).

Community structure in quadrats

Seventy-three sessile and fifty-nine mobile taxa were identified in a total of 400 quadrats. Species accumulation curves more closely approached their asymptotes for sessile taxa than mobile taxa (Fig. 4), indicating that sessile taxa were sampled more efficiently than mobile taxa in quadrats. All three measures of diversity (richness, S_{obs}, and S_{Chao2}) for sessile and mobile taxa in quadrats were highest at sites in waterways (Haro, Channel, Rosario) compared to sites in restricted inlets (Sound, Hood) (Fig. 5, Table 4). With respect to sessile taxa, the spatial scale of seascape explained the greatest amount of variation for all measures of diversity (Table 5). However, the largest percentage of variance for mobile richness was explained by quadrat (50%), followed by seascape (31%;); seascape explained a larger percentage of variance than site for S_{obs}, and S_{Chao2} (Table 5).

The ordination of presence/absence data (community composition) for sessile and mobile taxa in quadrats suggests differences in both location and dispersion among waterway vs inlet sites (Fig. 6). All four scales (seascape – quadrat) of spatial variation explained significant, and roughly equivalent (21 – 33%), proportions of the total variance in community composition using PERMANOVA (Table 6). Notably, pairwise tests indicated significant differences between the Haro, Channel, Rosario seascapes (waterways) and the Sound and Hood seascapes (inlets) (Table 6). Indeed, the centroids of Haro, Channel and Rosario group together in the ordination (Fig. 6a), and cluster together in the dendrogram (Fig. 6b). The only exception was O'Neal Island, which clustered with the Willow Island and Frost Island sites from Lopez Sound (Fig. 6b). These latter three sites displayed similar alabaster dissolution rates (0.77 – 0.92 g dissolution day^{-1}), with O'Neal Island exhibiting the slowest dissolution of the four Channel sites (Table 1).

The inlet sites and O'Neal Island (Cluster 2) were best characterized by two species – the bivalve *Pododesmus macrochisma* (jingle shell) and barnacle *Balanus crenatus*, both of which are solitary, possess an exoskeleton, and are capable of active filter feeding (ISA; Table 7). In contrast, Cluster 1 (waterway sites) was characterized by a number of taxa, many of which were clonal, lacked exoskeletons, and filtered water passively (Table 7). The ordination axes of community composition were significantly related to the percent cover of sediment ($F = 62.2$, estimated d.f. = 7.9, $P < 0.001$, adj. $R^2 = 0.97$), displayed visually as sediment contours in Figure 6.

In addition to the striking differences between waterway and inlet sites, the sites in Haro Strait were distinct from those Rosario Strait (Table 6, Fig. 6), and corresponded to differences in diversity (Fig. 5) and sediment cover (Fig. 2). The significant difference in community composition between Haro and Rosario sites is likely related, in part, to the frequency and percent cover of the clonal tubeworm, *Dodecaceria fewkesii* (pers. obs). Despite their geographic distance, Sound and Hood sites were not significantly different from each other (Table 6), likely due to the high dispersion exhibited by both seascapes (Fig. 6b). Group deviations from centroids (i.e., community variability) differed significantly among seascapes (Table 6), with all but two pairwise comparisons (Haro-Channel, Haro-Sound) exhibiting significant differences.

Community structure on transects

The abundances of eight common mobile fauna were quantified on 100 transects, with the red urchin, *Strongylocentrotus franciscanus*, and blood star, *Henricia* spp., the most abundant species (Table 8). Three species, including the red urchin, were absent on transects at inlet (Sound, Hood) sites. Furthermore, red urchins were never observed at the Sound sites (23 dives, 2010 – 2012) or in Hood Canal (16 dives in 2010, including four additional sites – Octopus Hole, Jorsted Creek, Flagpole Point, and Pinnacle). These striking differences in mobile fauna were reflected in the ordination (Fig. 7) and statistical analyses.

The scale of seascape explained a significant proportion of the variance (29%; Table 9) in transect fauna, with five of the six significant pairwise comparisons between inlet and waterway sites (Table 9). In addition, Sound and Hood seascapes were different from each other (Table 9). A permutation test of the average group dispersion from seascape centroids was significant (Table 9), and thus variation in species turnover (i.e., beta diversity) contributed to the significant differences tested by the PERMANOVA. Specifically, two significant pairwise tests (Channel-Hood, Haro-Hood) contributed to the overall effect (Table 9).

Similar to the ordination of taxa in quadrats (Fig. 6a), waterway seascapes grouped together, while the Sound and Hood seascapes occupied different sections of the multivariate space (Fig. 7). The percent cover of sediment was again significantly related to the response surfaces of the ordination axes ($F = 16.8$, estimated d.f. $= 8.1$, $P = 0.001$, adj. $R^2 = 0.90$). The cluster analysis algorithm (Calinski = 5.65) identified three clusters, corresponding to the waterway sites (except Strawberry Island), Hood sites and Strawberry Island, and the Sound sites (Fig. 7b). The first split corresponded to clusters 1 and 2 from the quadrat taxa, generally separating waterway and inlet sites.

Discussion

The most striking variation in biodiversity was observed between seascapes characterized by high versus low retention of water. Haro Strait, San Juan Channel and Rosario Strait are waterways that connect the Strait of Juan de Fuca and Strait of Georgia. Sites within these passages are thus subject to strong tidal currents, high flow and low retention of water. In contrast, Lopez Sound, East Sound and Hood Canal are restricted inlets with weak tidal currents, low flow and high retention. We measured three correlates of water retention in the San Juan Islands, and all three provided empirical support for the generalization of high versus low retention (Fig. 2, 3). These three abiotic factors covary, in that sediment cover is associated with low alabaster dissolution (Fig. 2), and the latter correlates strongly with high seawater temperatures (Fig. 2b). We did not measure light, but our field observations suggest that light availability is comparatively low at Sound and Hood sites. During periods of high tidal exchange (new and full moons), water temperatures at all Channel and Sound sites decrease, but this change is especially prominent at all sites in San Juan Channel relative to East and Lopez Sound (Fig. 3a). Altogether, these results support the premise that tidally forced flushing in waterways is subdued in restricted inlets, resulting in a distinct abiotic environment.

The abiotic correlates of water retention corresponded to conspicuous differences in diversity and composition. We show that variation in subtidal biodiversity is strongly influenced by mesoscale oceanography, at a spatial scale intermediate to local (< 10 m) and regional (1000s of km) scales. The 10 – 100 km scale of seascapes defined in this study explained 48 - 82% and 27 - 73% of the diversity (richness, S_{obs}, and S_{Chao2}) of sessile and mobile taxa, respectively. The effect of seascape also explained a significant, albeit smaller (20 – 29%), proportion of community composition in quadrats and transects. Thus, univariate metrics of biodiversity (richness, S_{obs}, and S_{Chao2}) were best explained by the largest scale of observation (seascape), but multivariate indicators of community structure (composition and dispersion) were best explained by the smallest scales of observation (quadrat or transect). This discrepancy is likely due to the idiosyncrasies of multivariate community composition at small spatial scales (Fraschetti et al. 2005).

There are three covarying mechanisms related to water flow for the disparity in diversity between the seascapes. First, larval delivery correlates with flow and can increase local richness by increasing the abundance of rare species (Palardy & Witman 2011). The higher mean dissolution rates of alabaster blocks at the sites in San Juan Channel (Fig. 1, Fig. 2) is consistent with the hypothesis that flow, and thus propagule supply, are higher in San Juan Channel than East/Lopez Sound. These low flow sites in the Sound also exhibited high percent cover of sediment, suggesting a non-exclusive mechanism to the reduced delivery of propagules in low flow situations. It is well known that sedimentation has consequences for benthic community structure (Daly & Mathieson 1977, Salinas & Urdangarin 1994, Carballo et al. 1996, Roberts et al. 1998, Irving & Connell 2002a, Airoldi 2003), with strong negative effects on sessile invertebrates (Gerrodette & Flechsig 1979, Young & Chia 1984, Irving & Connell 2002b). Sedimentation rates correlate inversely with flow (Genovese & Witman 1999, Lenihan 1999), and thus the already depauperate settler community at low-flow sites is potentially subjected to strong post-settlement mortality. Teasing apart the interrelated effects of flow and sedimentation is complicated further by the effect of turbidity on light availability to the benthos (Irving & Connell 2002b). High retention sites exhibited poor visibility (R.E., pers. obs.) and it is likely that the negative effects of shading on algae (Glasby 1999) influenced the differences in community composition between inlets and waterways (Table 6).

Reductions in flow and increases in sedimentation could also influence the competitive hierarchies among sessile taxa, which compete strongly for available space, the limiting resource on hard bottom communities (Paine 1984, Sebens 1986b). In addition to reproductive propagules, currents deliver food to the suspension feeding invertebrates that tend to dominate deeper subtidal rocky habitats (i.e., below the kelp zone) and vertical rocky substrata (Miller & Etter 2011). One might expect, for example, that passive suspension feeders (e.g., anemones, pedal sea cucumbers) would be more prevalent in high flow habitats, because they rely on particle flux for nutrition (Lesser et al. 1994). In support of this hypothesis, passive suspension feeders were significant indicators of high flow sites only (Table 7). In contrast, the high-retention, low-flow, sites were characterized by a bivalve jingle shell (*Pododesmus macrochisma*) and a barnacle (*Balanus crenatus*). Bivalves are active filter feeders, while barnacles switch to active filtering in low-flow situations (Trager et al. 1990). Indeed, the barnacles we observed in low-flow sites were often actively filtering (R.E., pers. obs.). Furthermore, high levels of suspended sediment at low-flow sites can supplement the growth of actively feeding bivalves (Lesser et al. 1994). These latter two solitary species also possess an exoskeleton, which presumably is an appropriate defense against the smothering effects of sediment (Jackson 1977).

The ordination and dendrogram of larger mobile fauna on transects exhibited similar patterns to those from taxa in quadrats. Namely, the largest divide existed between waterway sites and inlet sites (Fig. 6). However, the mechanisms driving these patterns are not likely to be the same, because these transect fauna are mobile consumers (e.g., echinoderms), rather than sessile filter feeders. In part, a diverse sessile and mobile community in quadrats may support a diverse and abundant suite of larger consumers on transects. The complete absence of red urchins (*Strongylocentrotus franciscanus*) at inlet sites likely drives the clustering observed in Figure 6b, but we can only speculate as to why red urchins were found exclusively in waterways.

The presence of other echinoderms with planktonic larvae (e.g., *Pycnopodia helianthoides*, *Parastichopus californicus*) suggests that dispersal is not limiting the distribution of red urchins. However, species-specific tolerance to physiological stresses, including sedimentation (Airoldi 2003), may play a role in mediating patterns of post-settlement mortality among echinoderms. Errant sea cucumbers (e.g., *P. californicus*) are deposit feeders, and thus may benefit from sedimentation. Sunflower stars (*P. helianthoides*) feed on bivalves and barnacles, including those that characterize inlets (*P. macrochisma* and *B. crenatus*). Red urchins prefer to eat bull kelp, *Nereocystis luetkeana* (Vadas 1977), but this canopy-forming species is rare in low-flow inlets (pers. obs; Duggins et al. 2001). Together with the general lack of macroalgae and sessile invertebrates (Table 5), feeding constraints arising from the indirect effects of sediment cover may limit the survivorship of juvenile red urchins at low-flow sites. We have observed wolf eels and octopus, the primary predators of red urchins in the Salish Sea, in Sound and Hood Canal seascapes, and thus we cannot rule out predation as another contributor to the absence of red urchins.

In addition to variability at the seascape scale, there was considerable variation between sites within seascapes. Notably, O'Neal Island in San Juan Channel exhibited a physical environment (Fig. 3) and biotic community (within quadrats) most similar to sites in Lopez Sound (Fig. 6). It is likely that the slower flow at O'Neal Island is related to the wide north end of San Juan Channel and the small bay in which it is situated (Rocky Bay). Despite being closer to the other Channel sites, the rock walls at O'Neal more closely resemble those at Willow Island in Lopez Sound, suggesting that abiotic conditions are more important than geographic proximity for the structure of these subtidal communities.

Hood Canal also displayed considerable within-seascape variability. The three sites displayed a north-south gradient of sediment cover (Table 1) and richness (Table 2). Although we did not measure alabaster dissolution, we expect that tidal currents and water flow are minimal at Sund Rock in the southern portion of the fjord. The increased prevalence of anoxic events in southern Hood Canal, are thought to be related primarily to the low flushing rates (Newton et al. 2007). A variety of anthropogenic stressors, including eutrophication (Steinberg et al. 2010) and invasive species (Lambert 2005), may contribute further to the low species richness in quadrats at Sund Rock in southern Hood Canal. However, invasive tunicates were absent from the quadrats in this study, despite their documented dominance in 2007 (Cornwall 2007). Specifically, *Ciona intestinalis* was reported to cover large swaths of rock, but we observed only isolated individuals at deeper depths (25 – 30 m) than those used in the quantitative portion of this study. Further surveys will be required to confirm the apparent population crash of this introduced species.

Given the overwhelming evidence for the importance of diversity for community structure and ecosystem function (Balvanera et al. 2006, Hooper et al. 2012), the results of this study could help inform the placement of marine protected areas. If biodiversity is, or becomes, a priority for managers in the Salish Sea, selecting sites within waterways should guarantee relatively high levels of species richness, without the need for extensive diving surveys. However, the protection of specific organisms, rather than diversity *per se*, often guides the design of reserves. In the San Juan Islands, the utility of reserves is often judged on the abundance and size of rockfish (Palsson et al. 2009). Sites in southern Hood Canal are protected (Sund Rock, Octopus Hole), and recreational divers enjoy these sites due to ease of access and the relatively high frequency of octopus, lingcod and wolf eel sightings. We argue that an understanding of spatial pattern provides a basis for prediction, an important practical goal for ecologists and resource managers whose task is to identify areas of conservation priority.

Tables

Table 1. Summary of site locations and abiotic correlates of water retention (mean ± SD).

Site number	Site name	Site code	Region	Transects (n)	Depth (m)	Latitude	Longitude	Sediment cover (%)	Dissolution (mg cm^{-2} day^{-1})	Temperature (°C)
1	Turn Point	TP	Haro	6	15.5 ± 2.6	48°41'11"N	123°14'14"W	0 ± 0	NA	NA
2	Kellet Bluff	KB	Haro	6	14.4 ± 1.3	48°35'19"N	123°12'09"W	0 ± 0	NA	NA
3	Lime Kiln	LK	Haro	6	15.1 ± 2	48°30'58"N	123°09'11"W	0 ± 0	NA	NA
4	Long Island	LI	Haro	6	15.6 ± 1.7	48°26'30"N	122°55'53"W	0 ± 0	NA	NA
5	O'Neal Island	ON	Channel	6	15 ± 1.5	48°36'17"N	123°05'34"W	2.5 ± 3.8	0.91 ± 0.1	11.23 ± 0.81
6	Shady Cove	SC	Channel	6	13.7 ± 1.2	48°33'08"N	123°00'20"W	0 ± 0	1.12 ± 0.14	10.77 ± 0.52
7	Point George	PG	Channel	6	15 ± 0.7	48°33'33"N	122°59'18"W	0 ± 0	1.64 ± 0.42	10.79 ± 0.47
8	Turn Island	TI	Channel	6	14.6 ± 1.7	48°32'05"N	122°58'10"W	0 ± 0	1.16 ± 0.1	10.65 ± 0.40
9	Rosario Wall	RW	Sound	6	13.7 ± 1.4	48°38'41"N	122°52'30"W	37.4 ± 23.9	0.62 ± 0.05	11.46 ± 0.81
10	Humphrey Head	HH	Sound	4	15 ± 2.3	48°33'58"N	122°52'12"W	59.1 ± 28.5	0.72 ± 0.02	11.38 ± 0.42
11	Frost Island	FI	Sound	4	14.6 ± 1.8	48°32'25"N	122°50'34"W	37.5 ± 18.5	0.92 ± 0.07	11.13 ± 0.37
12	Willow Island	WI	Sound	6	15.4 ± 1.8	48°32'23"N	122°49'24"W	23.3 ± 14.7	0.77 ± 0.06	11.24 ± 0.44
13	Lawson Bluff	LB	Rosario	6	16.7 ± 1.7	48°45'59"N	122°55'09"W	2.6 ± 2.5	NA	NA
14	Lawrence Point	LP	Rosario	6	14.6 ± 1.7	48°39'41"N	122°44'32"W	3.2 ± 5.4	NA	NA
15	Strawberry Island	SI	Rosario	5	15.3 ± 1.6	48°33'48"N	122°44'12"W	5.2 ± 6.3	NA	NA
16	Pulali Point	PP	Hood	6	14.4 ± 1.3	47°44'15"N	122°51'05"W	24.5 ± 20.7	NA	NA
17	Private Wall	PW	Hood	4	15 ± 2.6	47°33'43"N	123°01'07"W	61.3 ± 23.6	NA	NA
18	Sund Rock	SR	Hood	5	15.7 ± 2.6	47°26'07"N	123°07'14"W	99.3 ± 1.2	NA	NA

Table 2. Diversity of sessile and mobile taxa in quadrats at each site, as well as the density (mean ± SD) of red urchins (*Strongylocentrotus franciscanus*).

		Sessile			**Mobile**			
Site number	Region	S_{obs}	S_{Chao2} (± SE)	Richness (mean ± SD)	S_{obs}	S_{Chao2} (± SE)	Richness (mean ± SD)	Urchin density (no. m^{-2})
1	Haro	61	98.5 ± 29.7	12.7 ± 14.8	27	52 ± 24.2	1.6 ± 2.3	0.03 ± 0.08
2	Haro	59	69.7 ± 10.3	16.8 ± 9.4	34	52 ± 14.4	2.9 ± 4.8	0.87 ± 0.99
3	Haro	51	54 ± 3.2	10.9 ± 5.6	36	164 ± 143.6	3.6 ± 2.7	0.23 ± 0.39
4	Haro	57	71.4 ± 11.2	11.3 ± 16.9	31	35.2 ± 4.9	3.9 ± 6	0.27 ± 0.47
5	Channel	45	53.1 ± 7.1	10.2 ± 4.7	28	44 ± 16.5	2.1 ± 3.2	0.77 ± 0.75
6	Channel	56	58.3 ± 2.5	12.4 ± 10.4	27	39.3 ± 13.2	2.2 ± 1.7	0 ± 0
7	Channel	41	73 ± 39.6	9.2 ± 8.5	28	44 ± 16.5	3.5 ± 3.5	0.4 ± 0.25
8	Channel	59	63 ± 3.7	15.3 ± 10.1	28	48.3 ± 20.2	2.3 ± 2.3	0.3 ± 0.56
9	Sound	29	35.3 ± 7.6	6.4 ± 3.8	20	20.4 ± 0.9	1.2 ± 1.3	0 ± 0
10	Sound	22	23.5 ± 2.3	4.4 ± 3.5	17	23.3 ± 7.6	0.8 ± 0.5	0 ± 0
11	Sound	32	35.1 ± 3.7	6.5 ± 3.7	21	25.2 ± 4.9	1.3 ± 1	0 ± 0
12	Sound	41	45.9 ± 4.8	8.8 ± 4.6	30	30 ± 0	2.4 ± 2.2	0 ± 0
13	Rosario	41	65.5 ± 31.1	10.1 ± 6.1	27	30.1 ± 3.7	2.7 ± 1.9	0.1 ± 0.17
14	Rosario	48	52.9 ± 4.8	13.4 ± 2.7	35	47.1 ± 9.7	3.3 ± 2.2	0.07 ± 0.1
15	Rosario	45	55 ± 8.4	10.2 ± 7	30	42.5 ± 10.7	2.6 ± 2.1	0.04 ± 0.09
16	Hood	29	31.3 ± 3.4	6.6 ± 3.3	21	25.2 ± 4.9	0.7 ± 0.7	0 ± 0
17	Hood	28	31 ± 3.2	3.2 ± 2.2	15	16 ± 1.9	0.6 ± 0.4	0 ± 0
18	Hood	25	31.4 ± 5.9	2.6 ± 1.6	12	12 ± 0	0.3 ± 0.3	0 ± 0

Table 3. Results of nested analysis of variance (ANOVA) for alabaster dissolution and repeated-measures ANOVA for temperature data. In both analyses, seascape was treated as a fixed effect, and site as a random effect. Date was treated as a fixed effect in the repeated-measures ANOVA.

Source of variation	df	MS	F	P
Dissolution (mg cm^{-2} day^{-1}; ln(x))				
Seascape	1	1.1834	9.41	**0.022**
Site	6	0.1257	8.83	**0.000**
Transect (residual)	16	0.0142		
Temperature (°C)				
Error: Site				
Seascape	1	15.88	2.52	**0.025**
Site (residual)	6	1.78		
Error: Within				
Date	1	0.78	2.52	0.114
Seascape × Date	1	0.33	1.08	0.300
Residual	318	0.31		

Table 4. Results of linear mixed-effects models testing the variation in the number of taxa in quadrats (richness), and the results of linear models testing the variation in the observed number of species per site (S_{obs}), and the estimated number of species per site (S_{Chao2}) for both sessile and mobile taxa. Seascape was treated as a fixed effect; all other sources of variation were treated as random. Significance of levels was assessed with a Monte Carlo Markov Chain resampling (n = 10000) procedure for mixed effects models. Bold types indicate significant differences (P < 0.05).

Seascape	Estimate	SE	t value	*P*
Sessile taxa				
Richness				
Haro (intercept)	12.75	1.06	12.04	**0.000**
Channel	-0.81	1.35	-0.60	0.260
Georgia	-1.51	1.70	-0.89	0.161
Sound	-6.19	1.57	-3.93	**0.000**
Hood	-8.58	1.71	-5.02	**0.000**
S_{obs}				
Haro (intercept)	57.00	3.10	18.42	**0.000**
Channel	-6.75	4.38	-1.54	0.147
Georgia	-12.33	4.73	-2.61	**0.022**
Sound	-26.00	4.38	-5.94	**0.000**
Hood	-29.67	4.73	-6.28	**0.000**
S_{Chao2}				
Haro (intercept)	73.39	5.52	13.31	**0.000**
Channel	-11.55	7.80	-1.48	0.162
Georgia	-15.59	8.43	-1.85	0.087
Sound	-38.45	7.80	-4.93	**0.000**
Hood	-42.18	8.43	-5.01	**0.000**
Mobile taxa				
Richness (ln(x) + 1)				
Haro (intercept)	1.24	0.11	11.13	**0.000**
Channel	-0.15	0.15	-0.96	0.282
Georgia	0.02	0.17	0.14	0.907
Sound	-0.48	0.16	-2.97	**0.004**
Hood	-0.91	0.18	-5.17	**0.000**
S_{obs}				
Haro (intercept)	32.00	2.04	15.72	**0.000**
Channel	-4.25	2.88	-1.48	0.164
Georgia	-1.33	3.11	-0.43	0.675
Sound	-10.00	2.88	-3.47	**0.004**
Hood	-16.00	3.11	-5.15	**0.000**
S_{Chao2} **(ln(x))**				
Haro (intercept)	4.14	0.19	22.15	**0.000**
Channel	-0.36	0.26	-1.37	0.194
Georgia	-0.47	0.29	-1.65	0.123
Sound	-0.94	0.26	-3.57	**0.003**
Hood	-1.31	0.29	-4.60	**0.001**

Table 5. The percentage of explained variance (PEV) attributable to each spatial scale for the number of taxa in quadrats (richness), the observed number of species per site (S_{obs}), and the estimated number of species per site (S_{Chao2}) for both sessile and mobile taxa. In addition, PEV is presented for alabaster dissolution and temperature. Variances were estimated using linear mixed-effects models that treated all scales of variation as random effects.

Source	PEV (%)	PEV (%)
Biotic responses	*Sessile taxa*	*Mobile taxa*
Richness		
Seascape	51.1	31.4
Site	19.3	8.5
Transect	10.4	9.9
Quadrat (residual)	19.2	50.2
S_{obs}		
Seascape	79.5	69.9
Site (residual)	20.5	30.1
S_{Chao2}		
Seascape	70.8	61.5
Site (residual)	29.2	38.5
Abiotic responses		
Dissolution (mg cm^{-2} day^{-1}; ln(x))		
Seascape	63.2	
Site	26.6	
Transect (residual)	10.2	
Temperature (°C)		
Seascape	19.9	
Site	8.3	
Residual	71.8	

Table 6. Results of permutational multivariate analysis of variance, permutational analysis of multivariate dispersion, and post-hoc comparisons between seascapes for 73 sessile and 59 mobile taxa in quadrats. Bold types indicate significant differences (P < 0.05).

Source of variation	df	SS	Pseudo-F	P (perm)
Seascape	4	218270	2.99	**0.001**
Site	13	240940	5.95	**0.001**
Transect	82	255490	2.73	**0.001**
Quadrat (residual)	300	342560		
Total	399	1053900		

Pairwise test between seascapes	t	P (perm)
Channel, Haro	0.92	0.6
Channel, Rosario	1.37	0.071
Channel, Sound	1.75	**0.014**
Channel, Hood	1.99	**0.011**
Haro, Rosario	1.61	**0.015**
Haro, Sound	1.89	**0.008**
Haro, Hood	1.89	**0.013**
Rosario, Sound	2.02	**0.022**
Rosario, Hood	2.06	**0.016**
Sound, Hood	1.50	0.08

Deviations from centroid	Pseudo-F	P (perm)
Seascape	18.73	**0.001**

Pairwise test of deviation from centroid between seascapes	t	P (perm)
Channel, Haro	0.70	0.501
Channel, Rosario	4.53	**0.001**
Channel, Sound	0.17	0.864
Channel, Hood	6.12	**0.001**
Haro, Rosario	4.57	**0.001**
Haro, Sound	0.34	0.711
Haro, Hood	5.10	**0.001**
Rosario, Sound	3.20	**0.007**
Rosario, Hood	8.12	**0.001**
Sound, Hood	4.33	**0.001**

Table 7. Indicator values, significance levels, percent occurrence (B) of sessile and mobile taxa in quadrats associated with the two clusters in Figure 6. Only taxa with significant ($P < 0.05$) indicator values > 20 are included in this table. Percent occurrence for each listed taxon in the other cluster is shown for comparison, as well as the ratio of occurrence in each cluster ($B/B_{\text{other cluster}}$). Each taxon is identified to phylum/class, feeding mode, presence/absence of exoskeleton, and whether it is solitary or clonal. With respect to feeding, sessile invertebrates are categorized as either passive, or active filter feeders (Gili & Coma 1998, Riisgård & Larsen 2010). However, we acknowledge this to be an oversimplification, because many active filter feeders orient to the predominant current direction or change their morphology to maximize the passive capture of particles. *Metridium farcimen* is strictly solitary aclonal**, whereas *M. senile* is clonal and can replicate asexually via pedal laceration (Kramer & Francis 2004). The majority of deeper (> 10 m) *Metridium* are believed to be *M. farcimen* (based on their large size) but has not been determined empirically.

Table 7.

	IV	*P*	B	$B_{\text{other cluster}}$	$B/B_{\text{other cluster}}$	Phylum/Class	Feeding mode	Exoskeleton	Solitary/Clonal
Cluster 1									
Encrusting coralline algae	51.78	0.000	0.90	0.77	1.2	Rhodophyceae	Producer	no	Clonal
Encrusting bryozoan	51.73	0.000	0.76	0.35	2.1	Bryozoa	Active filter	no	Clonal
Encrusting non-calcified red algae	49.09	0.000	0.91	0.67	1.4	Rhodophyceae	Producer	no	Clonal
Terebretalia transversa	45.51	0.000	0.55	0.12	4.8	Brachiopoda	Active filter	yes	Solitary
Metridium spp.	44.85	0.000	0.47	0.02	25.5	Anthozoa	Passive filter	no	Solitary**
Psolus chitonoides	42.89	0.000	0.48	0.06	7.9	Echinodermata	Passive filter	no	Clonal
Balanophyllia elegans	39.42	0.000	0.57	0.25	2.3	Anthozoa	Passive filter	no	Clonal
Calliostoma ligatum	38.71	0.000	0.44	0.12	3.8	Prosobranchia	Mobile consumer	yes	Solitary
Diapoeroecia californica	36.91	0.000	0.46	0.11	4.2	Bryozoa	Active filter	no	Clonal
Didemnum carnulentum	34.15	0.000	0.35	0.01	57.0	Ascidiacea	Active filter	no	Clonal
Sponge other	33.13	0.000	0.53	0.32	1.7	Porifera	Active filter	no	Clonal
Trochid snail	30.05	0.000	0.32	0.02	17.4	Prosobranchia	Mobile consumer	yes	Solitary
Foliose and bladed red algae	29.02	0.008	0.50	0.37	1.4	Rhodophyceae	Producer	no	Clonal
Schizoporella japonica	28.41	0.000	0.37	0.11	3.4	Bryozoa	Active filter	no	Clonal
Abietinaria spp.	27.74	0.000	0.31	0.03	10.0	Hydrozoa	Passive filter	no	Clonal
Amphissa spp.	27.13	0.000	0.31	0.05	6.4	Prosobranchia	Mobile consumer	yes	Solitary
Crisia spp.	24.01	0.010	0.41	0.29	1.4	Bryozoa	Active filter	no	Clonal
Filamentous red algae	23.96	0.000	0.37	0.21	1.8	Rhodophyceae	Producer	no	Clonal
Haliclona spp. 2	23.90	0.000	0.27	0.04	7.4	Porifera	Active filter	no	Clonal
Hydroid other	23.69	0.032	0.42	0.32	1.3	Hydrozoa	Passive filter	no	Clonal
Distaplia occidentalis	23.56	0.000	0.24	0.01	39.6	Ascidiacea	Active filter	no	Clonal
Antho lambei	21.94	0.000	0.24	0.02	9.9	Porifera	Active filter	no	Clonal
Tonicella spp.	21.83	0.000	0.28	0.09	3.3	Polyplacophora	Mobile consumer	no	Solitary
Aglaophenia spp.	21.02	0.000	0.22	0.01	35.4	Hydrozoa	Passive filter	no	Clonal
Pycnoclavella stanleyi	20.59	0.000	0.21	0.01	34.7	Ascidiacea	Active filter	no	Clonal
Dodecaceria fewkesii	20.34	0.000	0.20	0.00	NA	Polychaeta	Active filter	yes	Clonal
Pileolaria spp.	20.09	0.000	0.25	0.05	4.5	Polychaeta	Active filter	yes	Solitary
Cluster 2									
Pododesmus macrochisma	31.76	0.000	0.38	0.08	4.8	Mollusca	Active filter	yes	Solitary
Balanus crenatus	21.47	0.000	0.27	0.08	3.6	Cirripedia	Active filter	yes	Solitary

Table 8. Mean (± SD) densities (no m^{-2}) of the eight most common mobile fauna counted on transects used in ordination (Fig. 5).

Species	Haro	Channel	Georgia	Sound	Hood
Cryptochiton stelleri	0.04 ± 0.08	0.07 ± 0.15	0 ± 0	0 ± 0	0 ± 0
S. franciscanus	0.35 ± 0.63	0.37 ± 0.53	0.07 ± 0.12	0 ± 0	0 ± 0
Henricia spp.	0.18 ± 0.27	0.33 ± 0.34	0.36 ± 0.47	0.02 ± 0.06	0.01 ± 0.05
Dermasterias imbricata	0.02 ± 0.06	0 ± 0	0.11 ± 0.44	0.04 ± 0.1	0 ± 0
Evasterias troschelii	0 ± 0	0.01 ± 0.04	0 ± 0	0.06 ± 0.15	0 ± 0
Pycnopodia helianthoides	0.01 ± 0.04	0.03 ± 0.08	0.01 ± 0.05	0.1 ± 0.12	0.03 ± 0.07
Solaster stimpsoni	0.12 ± 0.19	0.01 ± 0.04	0 ± 0	0 ± 0	0 ± 0
Parastichopus californicus	0 ± 0	0.12 ± 0.21	0.05 ± 0.11	0.01 ± 0.04	0.25 ± 0.26

Table 9. Results of permutational multivariate analysis of variance, permutational analysis of multivariate dispersion, and post-hoc comparisons between seascapes for eight mobile fauna (see Table 6) on transects. Bold types indicate significant differences ($P < 0.05$).

Source of variation	df	SS	Pseudo-F	P (perm)
Seascape	4	79104	4.77	**0.001**
Site	13	55917	1.93	**0.001**
Transect (residual)	82	133770		
Total	300	273620		

Pairwise test between seascapes	t	P (perm)
Channel, Haro	1.08	0.355
Channel, Rosario	1.00	0.455
Channel, Sound	2.87	**0.037**
Channel, Hood	2.87	**0.031**
Haro, Rosario	1.29	0.060
Haro, Sound	2.58	**0.024**
Haro, Hood	2.98	**0.024**
Rosario, Sound	2.24	**0.006**
Rosario, Hood	1.88	0.112
Sound, Hood	3.09	**0.005**

Deviations from centroid	Pseudo-F	P (perm)
Seascape	3.04	**0.042**

Pairwise test of deviation from centroid between seascapes	t	P (perm)
Channel, Haro	1.70	0.134
Channel, Rosario	0.34	0.797
Channel, Sound	0.06	0.962
Channel, Hood	2.49	**0.027**
Haro, Rosario	0.89	0.437
Haro, Sound	1.15	0.315
Haro, Hood	3.68	**0.003**
Rosario, Sound	0.20	0.866
Rosario, Hood	2.02	0.100
Sound, Hood	1.81	0.131

Figures

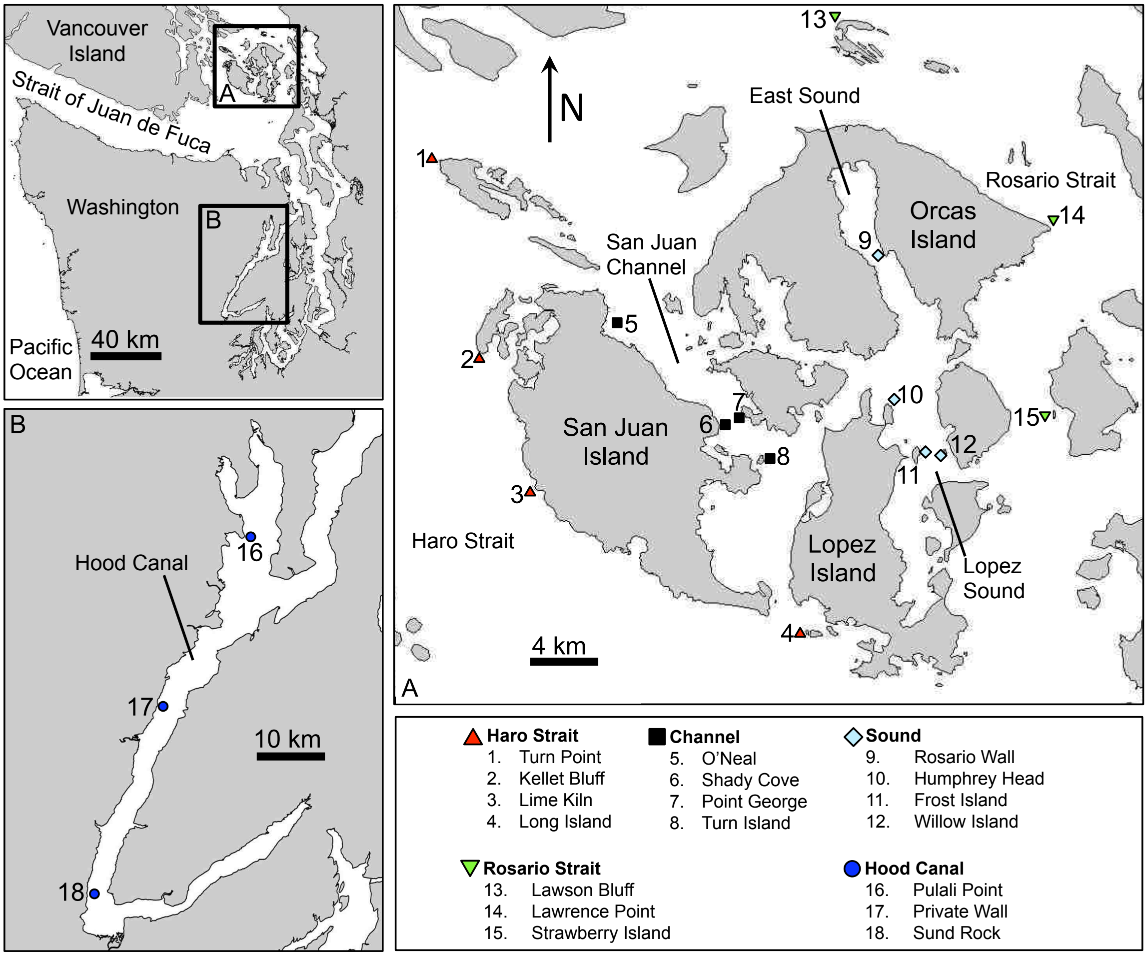

Figure 1. Map of the Salish Sea showing the seascapes and sites characterized in this study. See Table 1 for coordinates.

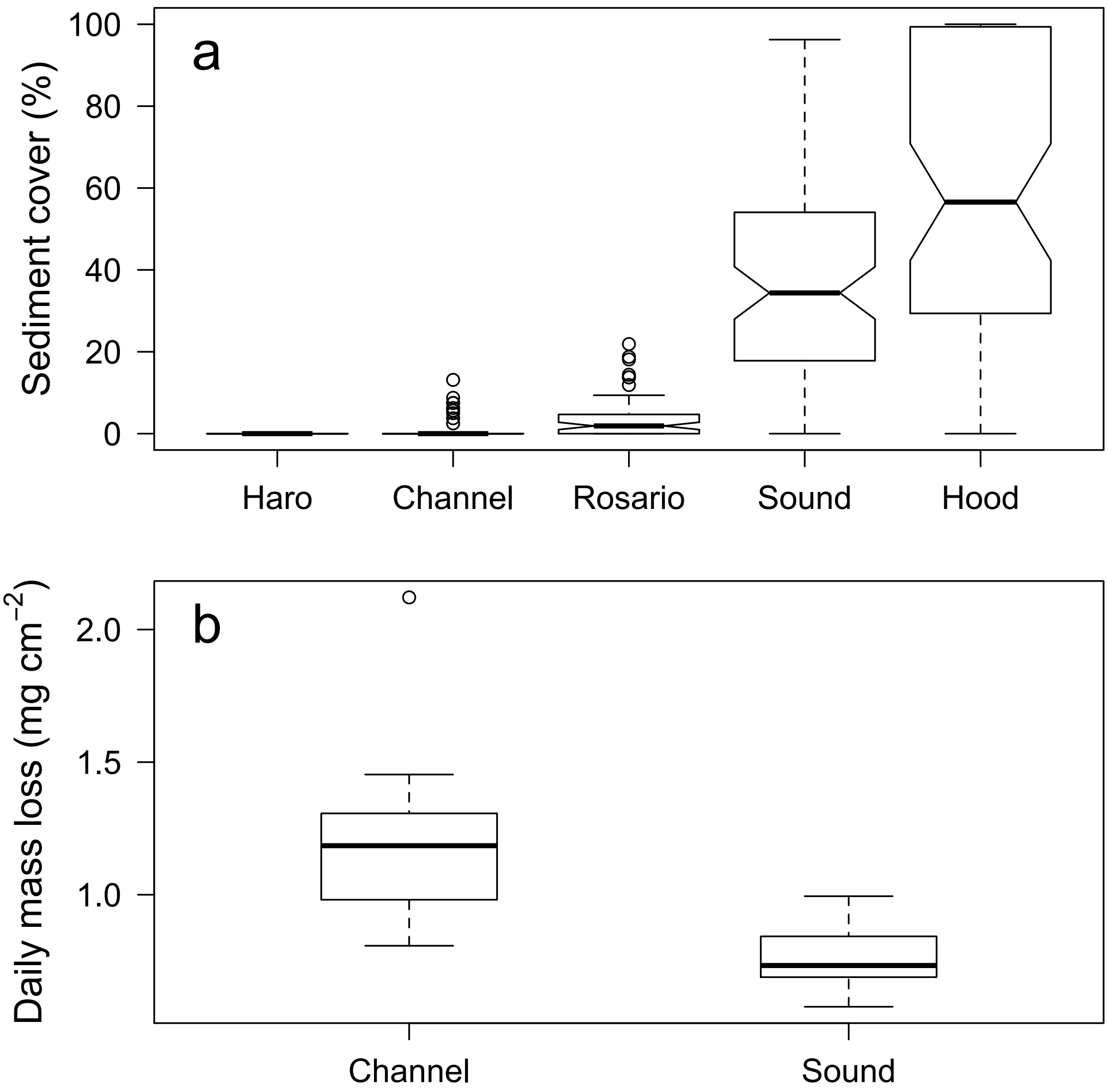

Figure 2. Boxplots of the percent cover of sediment in quadrats (a), and the daily dissolution of alabaster blocks (b). The sample size for sediment cover (a) was relatively high (n = 400), and thus we display boxplots using notches that can be used to interpret significant differences between medians – if notches do not overlap, the medians are different. All boxplots display the median and interquartile range (IQR) of data, with outliers plotted as circles beyond whiskers when the values are 1.5× IQR from the first or third quartiles.

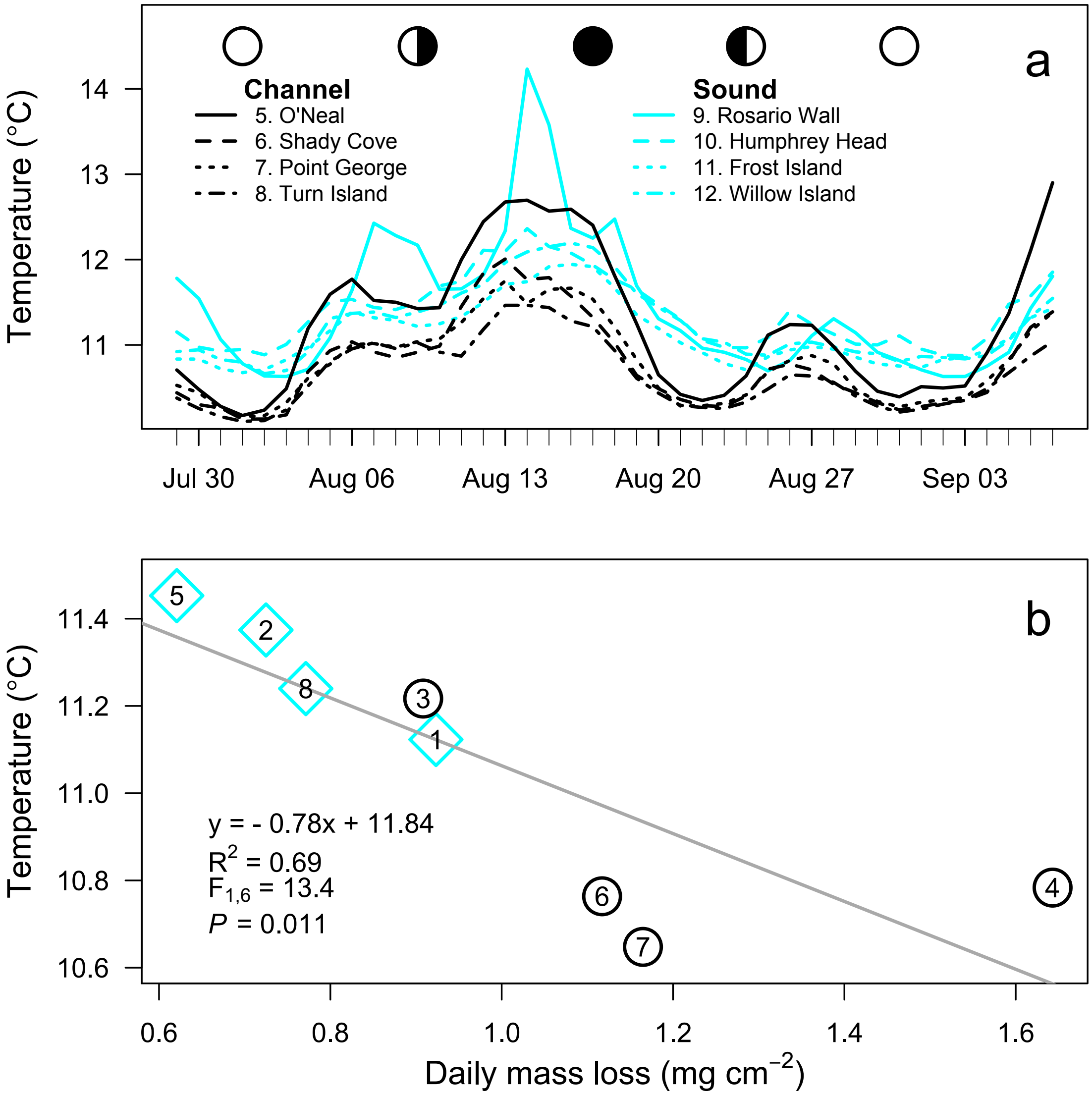

Figure 3. Mean daily temperatures at four Channel sites and four Sound sites over one complete tidal cycle (a), and mean temperature plotted against the mean dissolution of alabaster blocks at the same sites. Circles in panel (a) represent moon phases. Standard deviations for panel (b) are reported in Table 1.

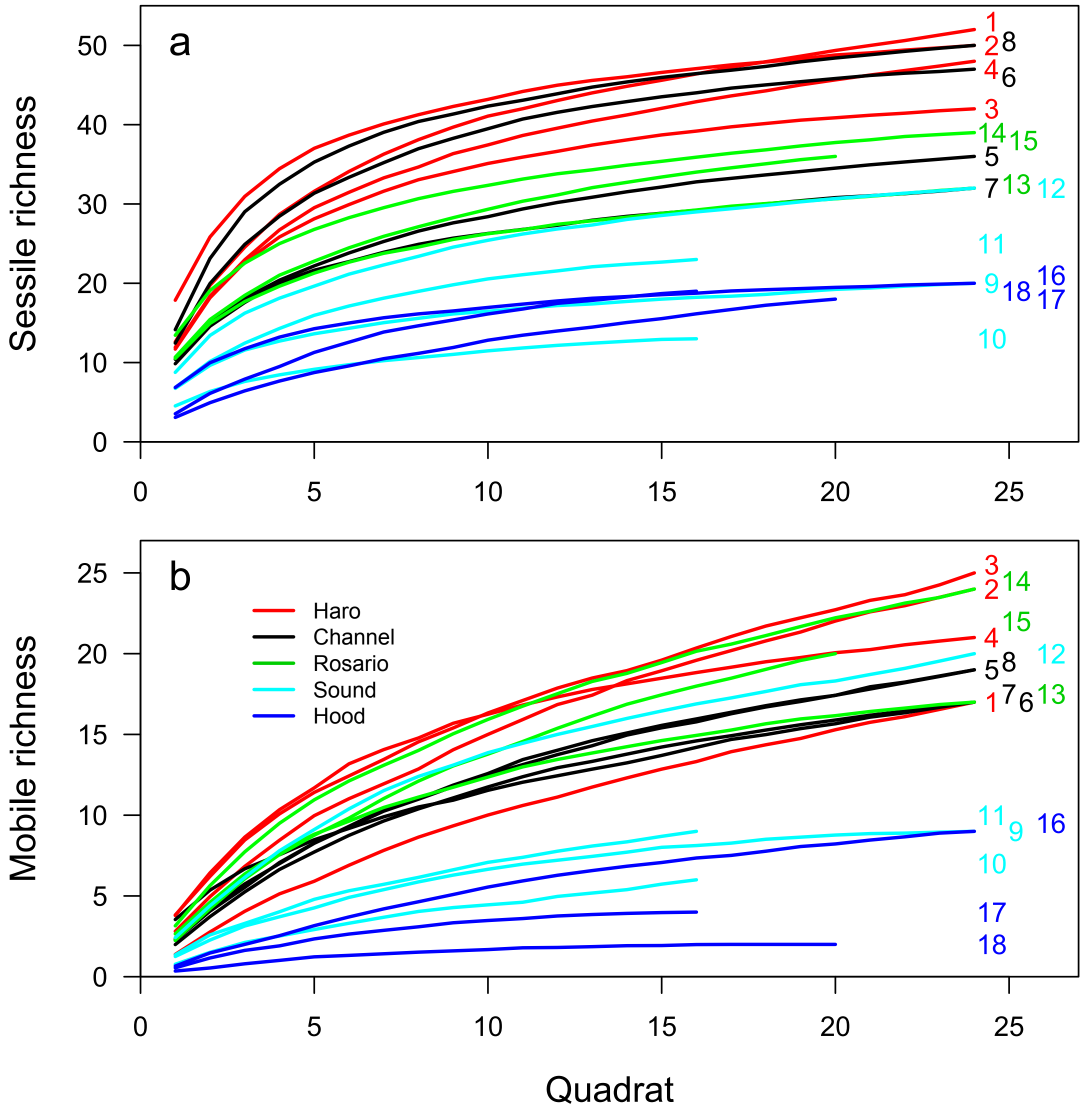

Fig. 4. Species accumulation curves for the number of sessile (a) and mobile (b) taxa in quadrats. Numbers beside curves correspond to sites in Figure 1 and Table 1.

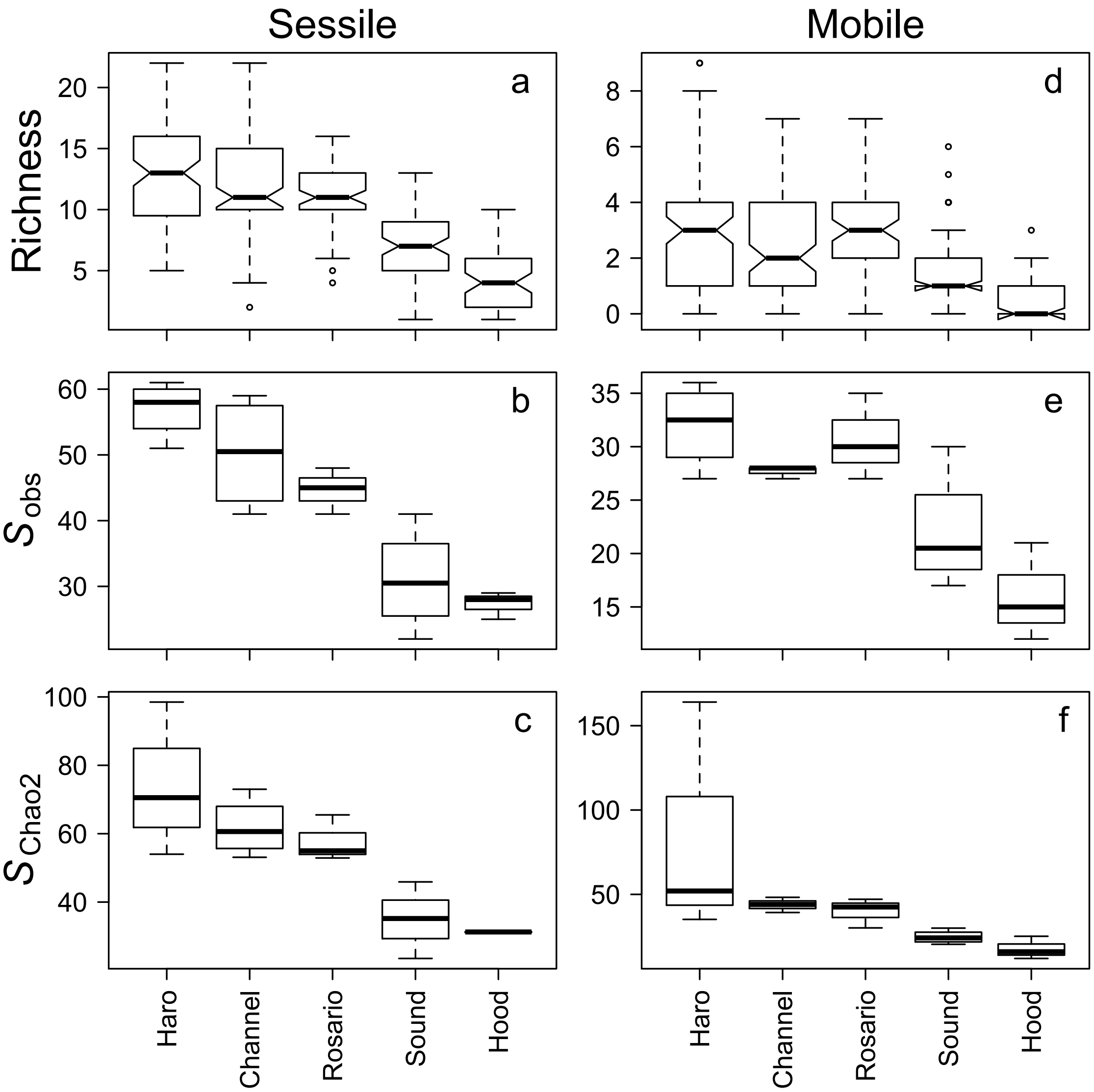

Figure 5. Boxplots of richness, the number of observed sessile taxa per site (S_{obs}), and the number of estimated sessile taxa per site (S_{Chao2}) for sessile (a – c) and mobile (d – f) taxa in quadrats. The sample size for richness (a, d) were relatively high (n = 400), and thus we display boxplots using notches that can be used to interpret significant differences between medians – if notches do not overlap, the medians are different. All boxplots display the median and interquartile range (IQR) of data, with outliers plotted as circles beyond whiskers when the values are 1.5× IQR from the first or third quartiles.

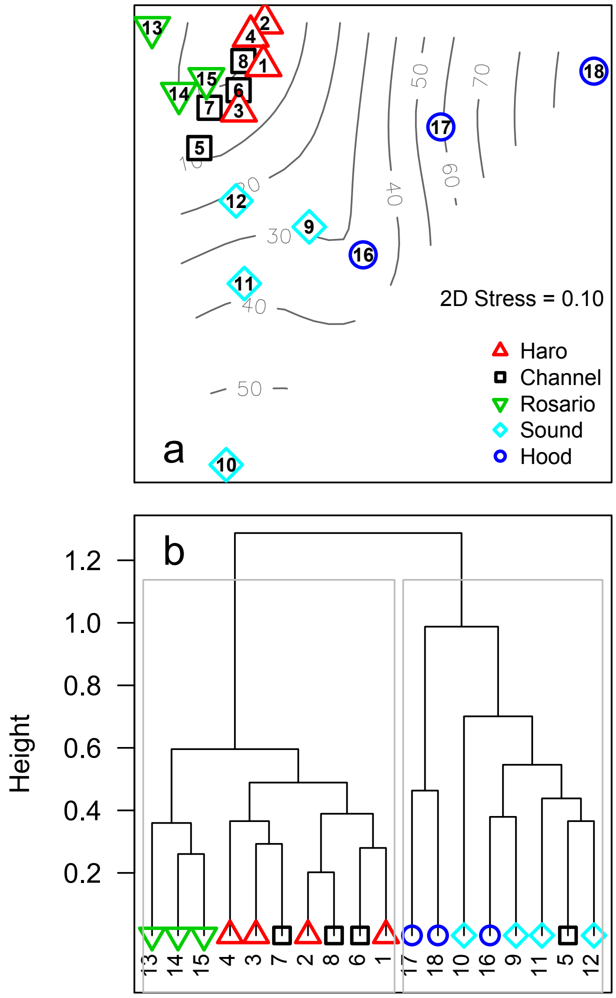

Figure 6. In (a), a plot of the first two axes of a non-metric multi-dimensional scaling analysis of community composition (presence/absence) of 73 sessile taxa and 59 mobile taxa in quadrats with response surfaces for the percent cover of sediment. Points represent the centroids for each site, and are coded by region. In (b), a cluster analysis arising from the same matrix used in panel (a). Grey boxes outline the optimum number of clusters.

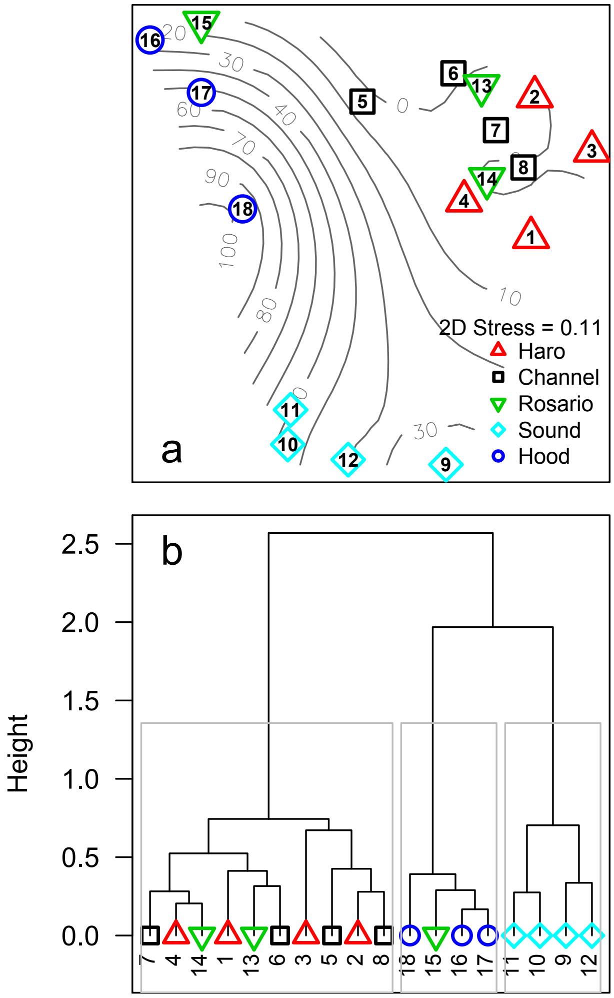

Figure 7. In (a), a plot of the first two axes of a non-metric multi-dimensional scaling analysis of untransformed abundances of the eight most common large mobile fauna on transects with response surfaces for the percent cover of sediment. Points represent the centroids for each site, and are coded by region. In (b), a cluster analysis arising from the same matrix used in panel (a). Grey boxes outline the optimum number of clusters.

Supplemental material

Table S1. Sessile species list

	Phaeophyceae
AGFI	*Agarum fimbriatum*
	Porifera
Hal1	*Haliclona* spp. 1
Hal2	*Haliclona* spp. 2
ANLA	*Antho lambei*
SYSP	*Sycon* spp.
SYAM	*Syringella amphispicula*
CLCE	*Cliona cellata*
XEHI	*Xestospongia hispida*
MYLA	*Myxilla lacunosa*
Leuc	*Leucosolenia* spp.
POPA	*Polymastia pacifica*
SPOT	Sponge other
	Hydrozoa
Abie	*Abietinaria* spp.
Agla	*Aglaophenia* spp.
Lafo	*Lafoea* spp.
HYSP	Hydroid other
	Anthozoa
EPSC	*Epizoanthus scotinus*
BAEL	*Balanophyllia elegans*
Metr	*Metridium* spp.
CRFE	*Cribrinopsis fernaldi*
Urti	*Urticina* spp.
EPLI	*Epiactis lisbethae*
GERU	*Gersemia rubiformis*
Alcy	*Alcyonium* spp.
	Polychaeta
DOCO	*Dodecaceria concharum*
DOFE	*Dodecaceria fewkesii*
PSCO	*Pseudochitinopoma occidentalis*
PHCL	*Phyllochaetopterus claparedii*
PISP	*Pileolaria* spp.
TUCA	Calcareous tube
TUOT	Other tube

	Bryozoa
EUBI	*Eurystomella bilabiata*
SCUN	*Schizoporella japonica*
DELI	*Dendrobeania lichenoides*
DICL	*Diapoeroecia californica*
Cris	*Crisia* spp.
CEDI	*Cellaria diffusa*
HEPA	*Heteropora pacifica*
PHPA	*Phidolopora pacifica*
DEMU	*Dendrobeania murrayana*
BREN	Encrusting bryozoan
BRER	Erect bryozoan
	Brachiopoda
TETR	*Terebratalia transversa*
	Ascidiacea
META	*Metandrocarpa taylori*
DICA	*Didemnum carnulentum*
DIOC	*Distaplia occidentalis*
PYST	*Pycnoclavella stanleyi*
PEAN	*Perophora annectans*
CLHU	*Clavelina huntsmani*
APCA	*Aplidium californicum*
APSO	*Aplidium solidum*
Trid	*Trididemnum* spp.
Chel	*Chelyosoma spp.*
Core	*Corella spp.*
CNFI	*Cnemidocarpa finmarkiensis*
HAIG	*Halocynthia igaboja*
Stye	*Styela spp.*
ASPA	*Ascida paratropa*
PYHA	*Pyura haustor*
BOVI	*Boltenia villosa*
TCOT	Colonial tunicate other
TSOT	Solitary tunicate other
	Echinodermata
PSCH	*Psolus chitinoides*

Table S2. Mobile species list

Code	**Polyplacophora**	**Code**	**Echinodermata**
CST	*Cryptochiton stelleri*	SFR	*Strongylocentrotus franciscanus*
Ton	*Tonicella* spp.	SDR	*Strongylocentrotus droebachiensis*
Mop	*Mopalia* spp	Hen	*Henricia* spp.
LME	*Lepidozona mertensii*	PHE	*Pycnopodia helianthoides*
Chi	Chiton other	SST	*Solaster stimpsoni*
		ETR	*Evasterias troschelii*
	Prosobranchia	PTE	*Pteraster tesselatus*
Lot	*Lottia* spp.	Oph	Ophiuroid
AMI	*Acmae mitra*	PCA	*Parastichopus californicus*
CCU	*Cranopsis cucullata*	EQU	*Eupentacta quinqesimita*
Lim	Limpet other	CPI	*Cucumaria piperata*
CLI	*Calliostoma ligatum*	PLU	*Pseudocnus lubricus*
CAN	*Calliostoma annulatum*	Cuc	Cucumber other
CAL	*Calliostoma* spp.		
Tro	Trochid snail		**Crustacea**
Amp	*Amphissa* spp.	SAC	*Scyra acutifrons*
GA1	Gastropod spp. 1	COR	*Cancer oregonensis*
OLU	*Ocinebrina lurida*	LMA	*Lopholithodes mandtii*
TCAn	*Trichotropis cancellata*	MQU	*Munida quadrispina*
CFO	*Ceratostoma foliatum*	Her	Hermit crabs
FOR	*Fusitriton oregonensis*	Shr	Shrimp
NUC	*Nucella* spp.		
BMU	*Boreotrophon multicostatus*		**Osteichthyes**
GAS	Gastropod spp other	JZO	*Jordania zonope*
		AHA	*Artedius harringtoni*
	Nudibranchia	Gun	Gunnel
ACO	*Aldisa cooperi*		
GHE	*Gheitodoris heathi*		
DSA	*Dialula sandiegensis*		
CMO	*Cadlina modesta*		
LCO	*Limacia cockerellii*		
CLU	*Cadlina luteomarginata*		
ANA	*Acanthodoris* spp.		
Dorid	Dorid spp other		
TFE	*Tritonia festiva*		
JFU	*Janolus fuscus*		
DAL	*Dirona albolineata*		
HCR	*Hermissenda crassicornis*		
DDI	*Dendronotus diversicolor*		

CHAPTER 4

Rock walls as refugia: relative constancy in the diversity, structure, and stability of subtidal communities after three decades

Abstract

Long-term ecological datasets provide a critical baseline for distinguishing between natural and anthropogenic mechanisms of temporal change in an age of rapid human modification of the biosphere. A unique archive (1969-1974) of photographs permitted a test of the hypothesis that the diversity and composition of contemporary (2006-2011) epilithic communities on subtidal rock walls in the San Juan Islands, WA, USA, have changed over thirty years. Despite a 0.9°C rise in temperature and increased protection of sea urchins and bottomfishes over the intervening three decades, univariate and multivariate analyses suggest limited differences between historic and contemporary communities. Historic communities were more even, and characterized by a high percent cover of bare rock and noncalcified enrusting algae, suggestive of urchin grazing. Despite the initiation of urchin no-take restrictions in 1984, our data indicate that contemporary urchin densities are lower than urchin densities in the 1970's. Although we detected subtle variation in the communities driven primarily by less abundant taxa (e.g., brachiopods, pedal sea cucumbers), it is difficult to ascribe these differences to temporal, rather than spatial, variation. Consistent with the predicted effects of ocean acidification, non-calcifying taxa increased in cover whereas calcifying taxa declined, but this difference was not significant. We suggest that subtidal rock walls may serve as refuges from biodiversity loss, and emphasize the need for long-term ecological monitoring with consistent methodology.

Introduction

Humans are modifying the biosphere at an alarming rate, through global impacts on climate and local effects on habitats and organisms (Hooper et al. 2012). Identifying shifts in the diversity and composition of communities is a necessary first step towards developing a mechanistic understanding of the natural and anthropogenic drivers of ecosystem change. Long-term ecological datasets (Dayton et al. 1998), especially those that extend beyond the typical careers of individual scientists (Connell et al. 2008), are critical in this respect. Once such datasets have been compiled for a variety of ecosystem, we can identify those habitats that are susceptible to change, and those that are resilient, and thus inform the management of natural resources.

Recognizing this priority, ecologists have used long-term datasets to detect decadal-scale community shifts (Magurran et al. 2010), including changes consistent with the predicted effects of climate warming (Parmesan 2006, Moritz et al. 2008, Myers et al. 2009). In the marine realm, long-term changes related to climate (Sagarin et al. 1999, Wootton et al. 2008, Harley 2011), overfishing (Jackson et al. 2001, Steneck et al. 2002, Myers & Worm 2003) and pollution (Connell et al. 2008) have been particularly well-documented. Synergistic effects of multiple stressors have contributed to the demise of coral reefs (Gardner et al. 2003, Pandolfi et al. 2003, Bruno & Selig 2007), kelp forests (Steneck et al. 2002, Connell et al. 2008), and seagrass beds (Steneck et al. 2002) worldwide over the last five decades. A recurring theme in the degradation of these latter ecosystems is the transition from a structurally complex habit to a simpler community dominated by turf algae (Connell et al. 2011).

One common challenge in the aforementioned studies is the unification of disparate datasets, especially when multiple investigators have employed similar, but not identical, sampling designs. We addressed this challenge in the present study, in which we compared benthic communities at one site in 1969 – 1974, to the same site, and additional sites, in 2006 – 2011. We studied nearshore habitats in the San Juan Islands (Washington, USA), which are well known to harbor a rich variety of life (Kozloff 1993). The San Juan Islands comprise an archipelago at the confluence of the Strait of Juan de Fuca and the Strait of Georgia. Many sites within San Juan Channel, a narrow passage connecting the larger straits, are characterized by strong currents driven by daily tidal exchanges (Duggins et al. 2003). Shallow water rocky habitats in San Juan Channel support a diverse suite of algal (Vadas 1977, Duggins et al. 2001, Britton-Simmons 2004), invertebrate (Mauzey et al. 1968, Young 1985, Bruno & Witman 1996) and vertebrate (Norton 1991, Beaudreau & Essington 2007) species. In this study we focused primarily on the sessile and mobile invertebrates on subtidal rock walls, which exhibit high local diversity relative to nearby rocky reefs (Miller & Etter 2011).

A unique archive of photographs permitted a test of the hypothesis that benthic communities on subtidal rock walls have changed over three decades. Specifically, we asked the following questions. How has the diversity and stability of these communities changed? Has the composition of the community changed, and are these changes consistent with the predicted effects of marine protected areas and/or climate change? For example, do changes in sessile taxa reflect changes in predator (bottomfish) and consumer (e.g., urchin) densities? Does seawater warming homogenize communities by facilitating non-native species (Stachowicz et al. 2002b, Sorte et al. 2010)? Or do changes in seawater chemistry exert disproportionately negative effects on calcifying taxa (Wootton et al. 2008)?

Methods

Hypothesized drivers of change

To evaluate the comparison of historic and modern communities in the context of climate change, we extracted daily surface seawater temperatures from a long-term dataset (1921 – current) collected at the Race Rocks lighthouse (48°17'52"N, 123°31'53"W) in the Strait of Juan de Fuca, Canada (http://www.racerocks.com/racerock/abiotic/temperature/seatemperature.htm). Analogous data on other seawater parameters (e.g., pH) were not available, but a shorter time series in a nearby location (outer coast of Washington State) suggests that seawater chemistry in the San Juan Islands has also changed (Wootton et al. 2008) . A factorial analysis of variance tested the fixed effects of era (historic vs. modern), daily variation (Julian day), and their interaction. Daily averages were calculated for historic and modern six-year periods (1969 – 1974, 2006 – 2011) from the Race Rocks dataset. A linear regression tested for a relationship between the temperature of surface water (10 Dec 2007 – 16 Sept 2011) at Race Rocks to daily averages of seawater at 15 m depth at Shady Cove (HOBO® temperature logger, Onset Computer Corporation), the primary study site.

To evaluate the comparison of historic and modern communities in the context of grazing and predation, we quantified the densities of red sea urchins (*Strongylocentrotus franciscanus*) and bottomfish (lingcod *Ophiodon elongatus* and copper rockfish *Sebastes caurinus*) in the San Juan Islands. Marine protected areas were established for sea urchins (in 1984; Carter & VanBlaricom 2002) and bottomfish (in 1990; Palsson et al. 2009), and thus we predicted higher densities of these animals in contemporary communities with potentially larger trophic impacts. Densities of red urchins were quantified from quadrats at Shady Cove (historic study) or transects at Shady Cove and additional sites (contemporary studies) described below. Historic data for fish densities were not available at Shady Cove, and thus we compared our contemporary (2008 – 2011) fish data to historic (1974 – 2000) fish data from a nearby site, Point George. I collected contemporary fish data at three sites in San Juan Channel using the methods described in Chapter 1, and additional fish data were provided by Kevin R. Turner (unpublished data). Historic data were compiled from two theses (Moulton 1977, Eisenhardt 2001) and an unpublished Friday Harbor Labs class paper (Miller 1991).

Study designs

We compared epilithic communities on subtidal rock walls in 1969 – 1974 at one site (Shady Cove, Fig. 1) in San Juan Channel, WA, to rock walls at several sites (including Shady Cove) in San Juan Channel in 2006 – 2011. To minimize the influence of seasonality, we restricted our analysis to fall - winter months (September – March). In the following paragraphs, we describe the three study designs (summarized in Table 1).

In 1968, four permanent quadrats (0.25 m^2) were established on a vertical rock wall at 13 – 15 m depth at Shady Cove (Fig. 1) by Charles Birkeland. Each of these quadrats (hereafter referred to as 'composite' quadrats) was divided into four contiguous quadrats (hereafter referred to as 'subquadrats'), the corners of which were marked using epoxy. Despite their spatial proximity, we treat each of these subquadrats as a replicate in our analyses. Photographs of subquadrats were taken using a Nikonos camera and strobe, and film slides were digitized prior to analysis. For the purposes of our historical comparison, we included only photographs taken between October and February, from 1969 – 1974.

In 2006, a single permanent horizontal transect (10 m long) was established at 3, 6, 9, 12, 15, 18 and 21 m depth at each of five sites located between Pumphouse and Shady Cove (Fig. 1) by Kenneth Sebens. These transects were established haphazardly on bedrock and encompassed vertical, sloping, and horizontal rock surfaces. Ten photographs of randomly spaced quadrats (0.09 m^2) were taken along each transect annually (September – February). In addition, red urchins were counted within 0.5 m of each side of each transect. For the purposes of our historical comparison, we included only photographs of vertical substrata at 12 and 15 m depth, from 2006 – 2009.

In 2007, permanent horizontal transects (2.5 m long, $n = 6$) separated by at least five meters were installed haphazardly on rock walls between 12 and 18 m depth at Shady Cove, O'Neal and Point George in San Juan Channel (Fig. 1) by Robin Elahi. Quadrats (0.09 m^2, $n = 4$) were positioned randomly along transects with corners marked with marine epoxy to enable repeated sampling of the benthos. Photographs of quadrats were taken using an Olympus C-8080 digital camera with an Ikelite strobe attached to a 36 × 25 cm aluminum framer, allowing identification of organisms ≥3 mm diameter. In addition, red urchins were counted within 1 m of each side of each transect. For the purposes of our historical comparison, we included only photographs taken between December and March, from 2008 – 2011.

Univariate analysis

The multivariate community matrix was used to calculate richness, Shannon-Weaver diversity, and evenness to examine temporal and spatial variation in these univariate metrics of community structure. To test for differences, we restricted our comparisons of historic and modern communities to permanent quadrats at Shady Cove, because we desired to limit the inherent spatial variation due to site selection (O'Neal, Point George) and the placement of quadrats randomly along transects each year (Sebens study). Specifically, we tested the effect of era (historic vs. modern), year, and era × year using linear mixed effects models. The era × year interaction was of particular interest, because it tested whether annual variation differed between historic and modern communities, and thus this effect was independent of the placement of permanent quadrats (a potential confounding effect). Block (composite quadrat or transect) and quadrat were treated as random effects.

To test the effect of era on the stability of epilithic communities, we calculated the coefficient of variation (CV) of richness, diversity and evenness across three years in historic (Birkeland study; 1969, 1970, 1972) and modern communities (Elahi study; 2008, 2009, 2011). We did not include 2010 data because some of the quadrats were being subjected to a consumer removal experiment (Elahi unpublished). Although the treatments had no significant effect on richness, diversity or evenness (Elahi unpublished), we omitted these data to achieve a more conservative test of the hypothesis. We chose to remove the 1974 data because only 12 of the 16 quadrats were sampled in this year (Table 1), and because we wished to achieve a consistent temporal sample (3 samples over 4 years) across both eras. In contrast to the linear model described above for richness, diversity and evenness, we included all three modern sites with fixed quadrats (Shady Cove, O'Neal, Point George), because the dependent variable (CV) is a proportion that incorporates site-to-site variation in absolute levels of richness, diversity, and evenness. Therefore, block (composite quadrat or transect) was nested within site; both were treated as random effects. CV was logit-transformed to improve normality and homogeneity of variances.

In all linear models, a Monte Carlo markov chain (MCMC) resampling procedure (n = 5000) assessed the significance of the predictor when the 95% confidence intervals of the parameter estimate did not include zero, the estimate was considered to be significant. All analyses were conducted using R (R Development Core Team 2012), using the packages vegan (Oksanen et al. 2011) and lme4 (Bates et al. 2011).

Multivariate analysis

To visualize differences in the community composition of sessile taxa between historic and modern epilithic communities, we used a non-metric multidimensional scaling approach. The percent cover of sessile organisms was quantified from photographs using a visual-based method (Chapter 1), and we identified organisms to the lowest possible taxonomic resolution among the historic and modern photos; 42 sessile taxa (Table S1) and bare rock were included in the analyses. Densities of red urchins were also quantified from historic photos for comparison to urchin densities from contemporary transects.

First, to compare quadrats at Shady Cove only, we conducted two ordinations; one used the raw, untransformed percent cover data, and the second used a square root transformation. The use of a square root transformation prior to the application of a non-metric multi-dimensional scaling analysis of a community matrix tends to reduce the importance of the most abundant species (Clarke & Green 1988), and thus emphasize the importance of taxa that do not occupy a large proportion of space. We included a total of 60 samples from the Birkeland study (each subquadrat was sampled four times, except for 4 subquadrats which were sampled thrice; 1969, 1970, 1972, 1974), 72 samples from the Elahi study (each quadrat sampled three times; 2008, 2009, 2011), and 81 samples from the Sebens study (quadrats sampled randomly over a four year period; 2006 – 2009).

Second, to place the observed variation among historic and modern quadrats at Shady Cove into a broader context, we conducted two more ordinations (with untransformed and square root transformed) using the data from all sites (Table 1). We included a total of 60 samples from the Birkeland study (each subquadrat was sampled four times, except for 4 subquadrats which were sampled thrice; 1969, 1970, 1972, 1974), 216 samples from the Elahi study (each quadrat sampled three times; 2008, 2009, 2011), and 97 samples from the Sebens study (quadrats sampled randomly over a four year period; 2006 – 2009).

In all cases, Bray-Curtis dissimilarity was used to construct the distance matrix. Upon inspection of a scree plot (McCune & Grace 2002), we chose to use ordinations with three dimensions ($k = 3$) to achieve acceptable stress (< 0.2) with a minimum number of dimensions.

Indicator species analysis (Dufréne & Legendre 1997, Bakker 2008) was used to identify the sessile taxa that best characterized each era (historical or modern) at Shady Cove. We included 60 samples from the Birkeland dataset, 72 samples from the Elahi dataset, and 81 samples from the Sebens dataset; raw, untransformed percent cover data was used for this analysis. To visualize the relative changes in the most common taxa we calculated the log change in percent cover (ln(modern cover/historic cover)). The mean cover value across years for historic (Birkeland) and contemporary (averaged across Sebens and Elahi quadrats) quadrats was calculated for taxa that were present in at least 5% of both historic and contemporary photographs. Taxa were categorized as either calcifying, non-calcifying, or components of available space. Complex was defined as a mixed assemblage composed primarily of hydroids, red macroalgae, sediment, and occasional bryozoans. Tube was primarily composed of calcareous tube dwelling annelids, but also included sessile, tube dwelling gastropods. Although encrusting algae can be calcified or non-calcified, they are often overgrown by sessile invertebrates and macroalgae and thus we consider them as available space in subtidal communities (Chapter 1). Using a one-way analysis of variance, we tested whether the log change in percent cover differed among calcified and non-calcified taxa.

Results

On average, seawater surface temperature at Race Rocks was 0.9°C warmer during the modern (2006 – 2011) period than the historic (1969 – 1974) period (MS = 106.72, $F_{1,726}$ = 75.77, $P < 0.001$). Surface temperatures varied significantly throughout the year (MS = 257.98, $F_{1,726}$ = 183.15, $P < 0.001$), but there was no interaction between Julian day and era (MS = 0.65, $F_{1,726}$ = 0.46, P = 0.50). The range of mean daily temperatures for historic and modern periods was 6.6 – 10.9 and 7.4 – 12.1, respectively (Fig. 2a). Seawater temperature at 15m depth at Shady Cove was significantly correlated with surface seawater temperature at Race Rocks (Fig. 2b).

The density of red urchins was highest in the 1970's, although some contemporary transects appeared to harbor similarly high urchin densities (Table 2). However, red urchins were sometimes removed prior to photography in the historic samples (evidenced by red urchin tube feet in some photographs), and thus we consider our historic estimates of urchin density to be conservative. In contrast, the densities of bottomfish have increased an order of magnitude since the 1970's at Point George (Table 3).

The univariate statistical comparisons of fixed quadrats at Shady Cove revealed significantly higher sessile richness, but lower evenness in modern quadrats (Fig. 3, Table S2). However, richness in modern random quadrats at Shady Cove, and other sites in San Juan Channel, displayed qualitatively similar taxon richness relative to historic fixed quadrats (Fig. 3a, b). In contrast, evenness was consistently lower at all modern sites (Fig. 3f) relative to the historic quadrats (Fig. 3e) at Shady Cove. A significant year × era interaction was observed for sessile diversity and evenness in fixed quadrats at Shady Cove (Table S2). No measures of stability (logit-transformed coefficient of variation) for sessile taxa differed between historic quadrats at Shady Cove and modern, fixed quadrats at three sites (Fig. 4, Table S3).

Historic (1969 – 1974) rock wall communities at Shady Cove appeared to harbor a subset of the community variation exhibited by the larger spatial extent of modern samples at Shady Cove (Fig. 5). Relative to the analysis of untransformed percent cover data (Fig. 5a), the ordination of square root transformed data (Fig. 5b) suggests less overlap between historic and modern communities at Shady Cove.

Against the larger backdrop of variation among five sites in San Juan Channel, historic communities at Shady Cove exhibited considerable overlap in ordinations based on untransformed percent cover data (Fig. 6), but less overlap based on square root transformed data (Fig. 7). Modern fixed quadrats at Shady Cove, arguably the most robust comparison to the historic data, exhibited the largest difference in community composition (Fig. 7a). In contrast, random quadrats at Shady Cove exhibited the most overlap with the historic communities (Fig. 7b). Fixed quadrats at O'Neal exhibited minimal overlap with the historic communities, but fixed quadrats on two transects at Point George clustered with historic samples (Fig. 7c,d).

Historic samples were characterized by a high cover of bare rock and encrusting non-calcified red algae (Table 4). Additional indicator taxa for historic communities included encrusting bryozoans (including *Eurystomella bilabiata*), as well as pedal sea cucumbers (*Psolus*), and brachiopods (*Terebratalia*) (Table 4, Fig. 8). By comparison, modern communities displayed a high cover of encrusting calcified red algae and the ascidian *Didemnum carnulentum* (Fig. 8). Other taxa indicative of modern quadrats included complex, sponges, and upright red algae (Table 4, Fig. 8). Importantly, there were no taxa unique to historic samples (Table S1). There was no significant difference ($F_{1,17} = 1.4$, $P = 0.25$) in the log change of percent cover between calcified and non-calcified taxa (Fig. 8).

Discussion

Our comparison of epilithic taxa on subtidal rock walls indicates remarkable constancy over three decades. Despite the establishment of urchin reserves in 1984 (Carter & VanBlaricom 2002) and bottomfish reserves in 1990 (Palsson et al. 2009), increases in regional seawater temperature (Fig. 2) and acidity (Wootton et al. 2008, Kim et al. 2010), the biodiversity and composition of sessile invertebrates and algae on rock walls now encompass the variability observed in the 1970's. For example, an ordination of the untransformed percent cover of sessile taxa in historic and modern quadrats revealed substantial overlap, suggesting that the relative abundances of the dominant space-occupying taxa have not changed in three decades. Further, two of three metrics of biodiversity (richness and diversity) and all three metrics of stability (richness, diversity, evenness) were not appreciably different between historic and modern samples. The lack of a conspicuous change in our study is surprising in the context of many decadal-scale studies of benthic marine communities (e.g., Hughes 1994, Sagarin et al. 1999, Connell et al. 2004, Paine & Trimble 2004, Connell et al. 2008, Wootton et al. 2008, Colvard & Edmunds 2011, Harley 2011, Sorte & Stachowicz 2011).

Despite the overall constancy of historic and modern communities, we did observe some subtle variation in community composition driven primarily by less abundant species. For example, brachiopods (*Terebratalia* spp.) and pedal sea cucumbers (*Psolus* spp.) are both solitary invertebrates that were significant indicators of the historic community (Table 2). These taxa, along with other calcifiers, exhibited a relative decrease in cover to non-calcifying taxa, but this trend was not statistically significant. Other significant indicators of the historic data included bare rock and non-calcified encrusting red algae, both of which increase in communities subjected to red urchin grazing (Chapter 1). Indeed, the densities of urchins in historic quadrats were generally higher than urchin densities observed in the modern studies (Table 2). Importantly, we did not observe any unique taxa to the historic photos (Table S1), suggesting that taxa have not gone locally extinct in the last four decades. Moreover, to the best of our knowledge, only one species (bryozoan *Schizoporella japonica*) on contemporary walls is not native. In contrast, contemporary fouling communities on man-made docks are often dominated by non-native species (Grey 2009, Sorte & Stachowicz 2011).

In addition to the subtle differences in community composition, we highlight the significantly higher evenness in historic fixed quadrats relative to modern fixed quadrats. Urchin grazing increases the evenness of these sessile communities by removing spatially dominant ascidians and macroalgae (Chapter 1). Indeed, the densities of urchins in historic quadrats were higher than most modern sites (Table 2). In Washington, commercial harvesting of red urchins began in 1971 and peaked in the 1980's, but an urchin reserve was established in San Juan Channel in 1984 (Carter & VanBlaricom 2002). Outside of the reserve, urchin populations declined between 1984 and 1993 as a consequence of harvesting (Pfister & Bradbury 1996). Our limited data on rock walls within the reserve suggest modest reductions in urchin density over the last three decades (Table 2). Although reserves have benefitted rockfish and lingcod at Point George (Table 3), increased densities of bottomfish appear to not have any cascading effects on the sessile rock wall community, probably in part to their demersal habits of occupying rock ledges and reefs.

Across eras, univariate metric of diversity did not vary annually, but a significant era × year interaction for both the diversity and evenness of sessile taxa suggests that modern quadrats at Shady Cove exhibited greater annual variation. We quantified a specific measure of stability, the coefficient of variation (CV), for all three metrics of univariate biodiversity to further explore annual variation within quadrats. No significant differences in stability were observed between eras, but there is a pattern of higher stability (i.e., lower CV) in the diversity of historic communities. Given that the design of modern studies encompassed a broader spatial scale than the historic study (Table 1), the extent to which these patterns represent real temporal changes in stability or natural spatial variation is unclear. The difficulty in comparing modern and historic datasets with different designs highlights the need for consistency and repeatability in existing long-term studies to best interpret community shifts (or lack thereof) over time.

In our opinion, the relative constancy of these epilithic communities should be viewed with guarded optimism, in part because subtidal rock walls are local-scale hotspots of invertebrate biodiversity (Miller & Etter 2011). We hypothesize that these communities are resilient to the chronic effects of global change stressors (e.g., temperature, acidification) due to the near-absence of local-scale stressors, including species invasions and physical disturbances. Indeed, the interplay between multiple stressors often triggers unexpected ecological consequences (Crain et al. 2008, Darling & Côté 2008), including synergistic effects among warming, invasion, and disturbance (Britton-Simmons 2006, Sorte et al. 2010).

The phase-shifts observed on coral reefs, kelp forests and seagrass meadows are often associated with physical disturbance (e.g., hurricanes), followed by the preemption of available space and light by 'weedy' algae (Connell et al. 2011). Due to their vertical topography, rock walls are less susceptible to physical disturbances, both natural (e.g., sedimentation, waves, log damage) and human-induced (e.g., trawling, bottomfishing). Furthermore, reduced light availability contributes to sessile invertebrate dominance on vertical surfaces (Glasby 1999, Miller & Etter 2008). The potential for subtidal rock walls to serve as natural refuges and source populations in future scenarios of habitat degradation warrants further investigation. More generally, the identification of natural refuges in other ecosystems should become a conservation priority in light of today's rapid anthropogenic change.

Tables

Table 1. Details of the three studies used to compare historic (1969 – 1974) and modern (2006 – 2011) epilithic communities in San Juan Channel.

Primary investigator	Site	Latitude, longitude	Depth (m)	Study design	Quadrat size (m^2)	Spatial arrangement	Composite quadrats or transects per site (n)	Temporal sampling Year (n)	total N
Birkeland	Shady Cove	48°33’08”N, 123°00’20”W	13 - 16	16 permanent quadrats	0.06	4 contiguous quadrats form a 'composite' quadrat	4	1969 (16), 1970 (16), 1972 (16), 1974 (12)	60
Sebens	Shady Cove	48°33’08”N, 123°00’20”W	12 - 15	Random quadrats	0.09	10 non-contiguous quadrats spaced randomly along 10 m permanent transect	4	2006 (14), 2007 (28), 2008 (19), 2009 (20)	81
	Colins Cove	48°33’01”N, 123°00’19”W	15	Random quadrats	0.09		1	2006 (4), 2008 (1), 2009 (5)	10
	Pumphouse	48°32’47”N, 123°00’26”W	12	Random quadrats	0.09		1	2007 (6)	6
Elahi	Shady Cove	48°33’08”N, 123°00’20”W	12 - 16	24 permanent quadrats	0.09	4 non-contiguous quadrats spaced randomly along 2.5 m permanent transect	6	2008 (24), 2009 (24), 2010 (24), 2011 (24)	96
	O'Neal	48°36’17”N, 123°05’34”W	13 - 18	24 permanent quadrats	0.09		6		96
	Point George	48°33’33”N, 122°59’18”W	14 - 17	24 permanent quadrats	0.09		6		96

Table 2. Densities (no. m^{-2}) of red urchins (*Strongylocentrotus franciscanus*) at each site, with the number of spatial replicates in parentheses. Urchin density for each spatial replicate was calculated from 3 – 14 surveys conducted over 4 – 6 years (temporal replicates). For sites in the Elahi study, each of six spatial replicates was observed 10 times.

Site	Years	Investigator	Replicate size (m^2)	Density ± SD (no. m^{-2})	Number of temporal replicates
Shady Cove	1968 - 1974	Birkeland	0.25	1.18 ± 1.03 (4)	12, 11, 14, 9
Shady Cove	2006 - 2009	Sebens	10	1.04 ± 1.72 (3)	4, 2, 3
Shady Cove	2007 - 2011	Elahi	5	0.09 ± 0.12 (6)	10
Colins Cove	2006 - 2009	Sebens	10	0.1	1
Pumphouse	2006 - 2009	Sebens	10	0.47	1
O'Neal	2007 - 2011	Elahi	5	0.86 ± 0.66 (6)	10
Point George	2007 - 2011	Elahi	5	0.38 ± 0.3 (6)	10

Table 3. Densities (no. ha^{-2}) of copper rockfish (*Sebastes caurinus*) and lingcod (*Ophiodon elongatus*) at Point George. Data from 1974 – 2000 were compiled from theses and class papers.

Species	Years	Investigator	Replicate size (m^2)	Density (fish ha^{-1}) ± SD (no. of replicates)
S. caurinus	1974 - 1976	Moulton	675 - 2302	0.004 ± 0.004 (32)
	1991	Miller		0.003 ± 0.001 (6)
	1999	Eisenhardt		0.007 ± 0.001 (11)
	2000	Eisenhardt	600 - 1200	0.045 ± 0.020 (4)
	2007 - 2011	Elahi	5	0.058 ± 0.146 (15)
	2009 - 2012	Turner	450 - 540	0.022 ± 0.018 (14)
O. elongatus	1974 - 1976	Moulton	675 - 2302	0.001 ± 0.001 (32)
	1991	Miller		0.0002 ± 0.0003 (6)
	1999	Eisenhardt		0.001 ± 0.001 (11)
	2000	Eisenhardt	600 – 1200	0.005 ± 0.002 (4)
	2007 - 2011	Elahi	5	0.007 ± 0.014 (15)
	2009 - 2012	Turner	450 - 540	0.004 ± 0.004 (14)

Table 4. Indicator values, significance levels, and percent cover (mean ± SE) of sessile taxa associated with each study period at Shady Cove. Only taxa with significant ($P < 0.05$) indicator values > 20 are included in this table. Percent cover for each listed taxon during the other study period is shown for comparison. See Table S1 for full list.

	Indicator value	*P*	Percent cover	Percent cover (in other study period)
1969 - 1974				(2006 - 2011)
Bare rock	87.07	0.000	12.72 ± 0.94	1.89 ± 0.25
Encrusting bryozoan	72.92	0.000	14.46 ± 0.97	5.37 ± 0.60
Psolus spp.	72.60	0.000	5.68 ± 0.84	0.32 ± 0.06
Encrusting non-calcified red algae	54.87	0.030	25.87 ± 1.65	21.28 ± 1.37
Epizoanthus scotinus	47.78	0.000	2.8 ± 0.58	0.42 ± 0.13
Terebratalia spp.	46.91	0.029	1.16 ± 0.11	0.9 ± 0.13
Aplidium solidum	27.12	0.000	1.03 ± 0.34	0.05 ± 0.02
Eurystomella bilabiata	24.22	0.003	1.78 ± 0.4	0.92 ± 0.28
2006 - 2011				(1969 - 1974)
Calcareous tube	62.56	0.000	1.6 ± 0.19	0.41 ± 0.09
Encrusting calcified red algae	59.64	0.001	18.01 ± 1.21	12.19 ± 0.77
Complex	59.16	0.000	5.63 ± 0.73	0.03 ± 0.03
Sponge	57.97	0.000	2.88 ± 0.32	0.98 ± 0.30
Didemnum carnulentum	43.96	0.001	9.34 ± 0.85	5.10 ± 1.09
Foliose red algae	39.17	0.000	0.36 ± 0.07	0.03 ± 0.02
Diaperoecia californica	32.68	0.000	0.68 ± 0.18	0 ± 0
Pycnoclavella stanleyi	26.13	0.001	1.71 ± 0.35	0.34 ± 0.17
Filamentous red algae	22.22	0.000	0.64 ± 0.14	0 ± 0

Figures

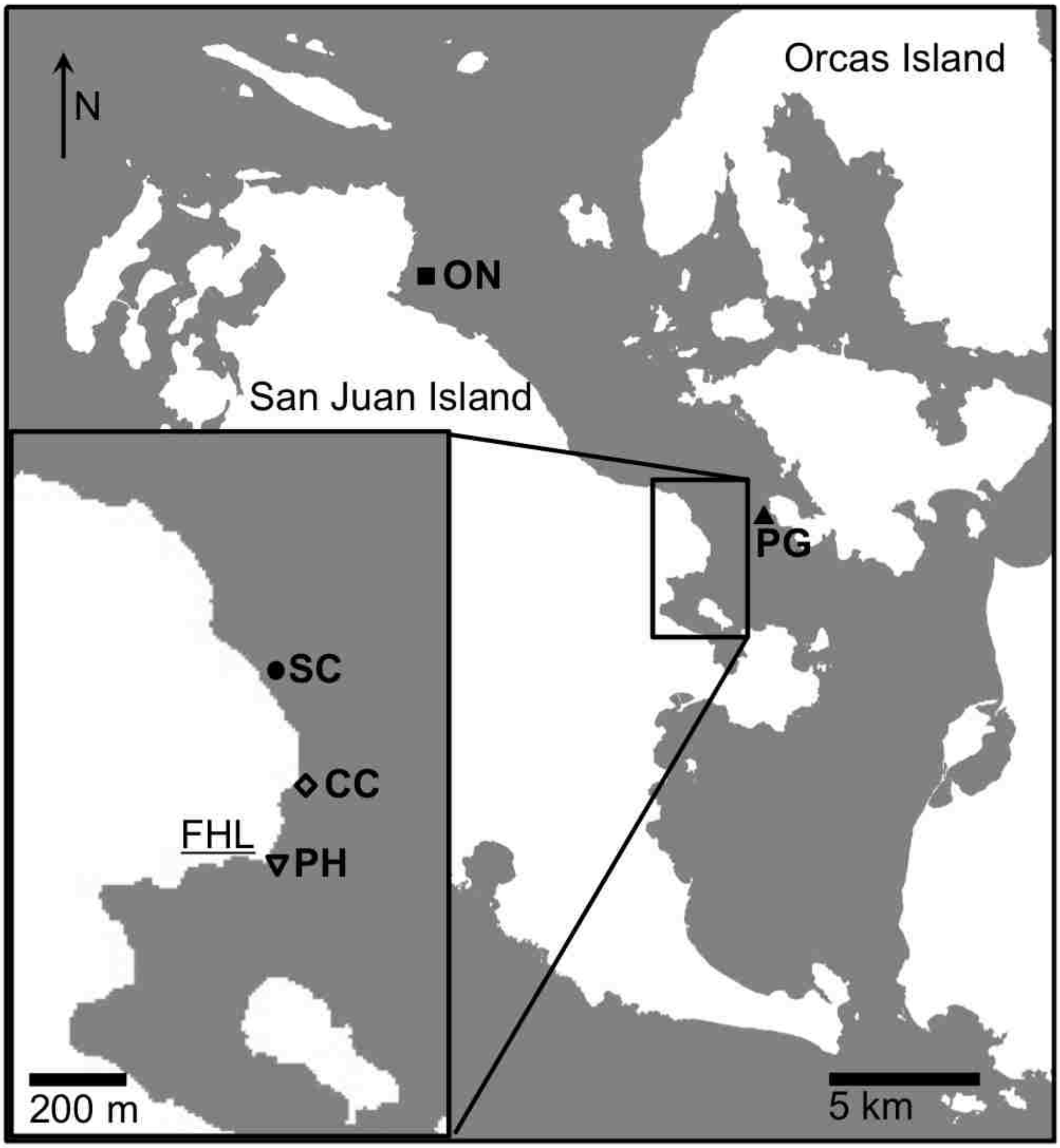

Fig. 1. Map of the San Juan Islands showing the study sites (Shady Cove, SC; Colins Cove, CC; Pumphouse, PH; O'Neal, ON; Point George, PG) sampled by Birkeland (SC; 1969 – 1974), Elahi (ON, PG, SC; 2008 – 2011), and Sebens (SC, CC, PH; 2006 – 2009). Friday Harbor Laboratories (FHL) is labeled for reference. See Table 1 for coordinates.

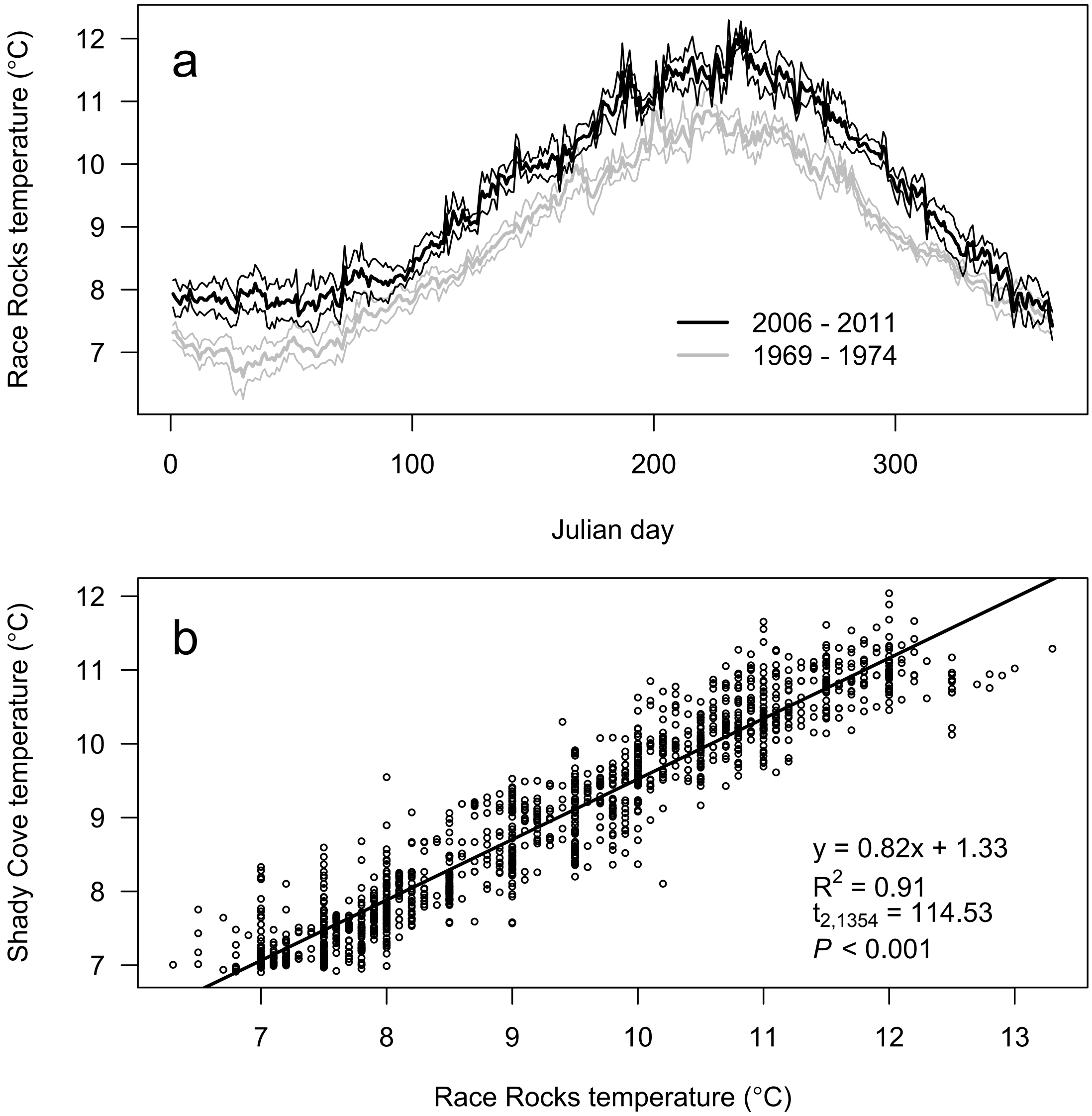

Fig. 2. Annual variation in surface seawater temperature (a) in 1969 – 1974 and 2006 – 2011 at Race Rocks, Canada. Thick and thin lines represent daily means ± SE, respectively. Modern (2008 – 2011) surface seawater temperatures at Race Rocks (Strait of Juan de Fuca) are highly correlated with seawater temperatures at 15m depth at Shady Cove (b).

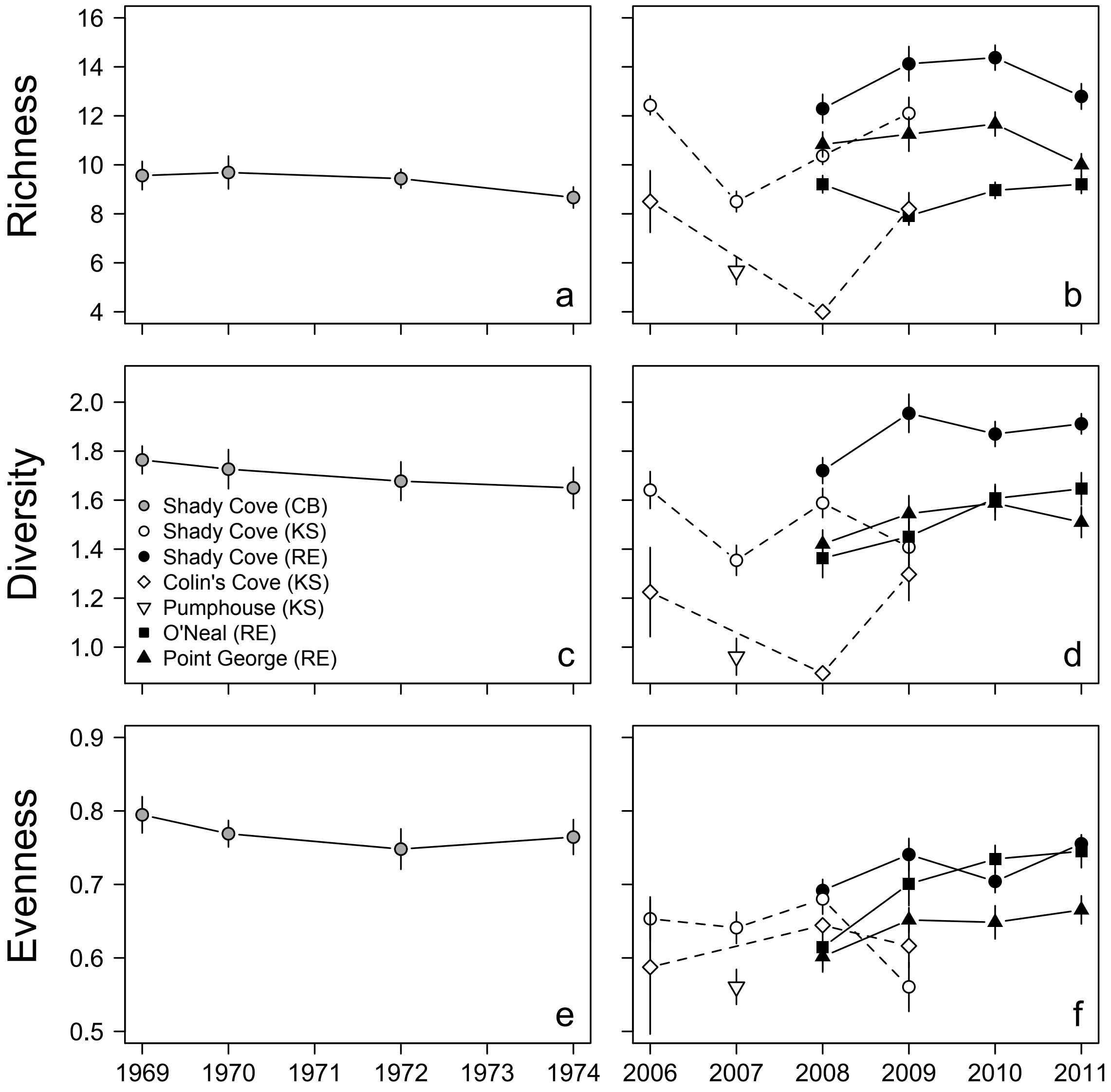

Fig. 3. Time series of mean (± SE) richness (a, b), diversity (c, d), and evenness (e, f) of sessile taxa in subquadrats at Shady Cove in 1969 – 1974 (a, c, e) and in quadrats at multiple sites in San Juan Channel in 2006 – 2011 (b, d, f).

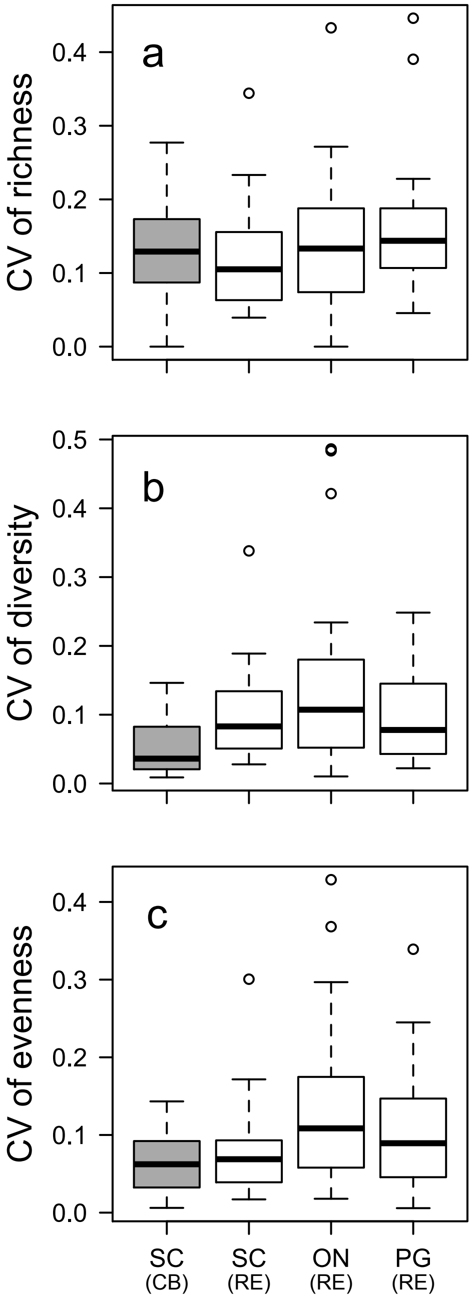

Fig. 4. Boxplots of coefficient of variation (CV) of richness (a), diversity (b), and evenness (c) of sessile taxa in historic permanent subquadrats (SC; gray boxplots) and in modern permanent quadrats (SC, ON, PG; white boxplots). Boxplots display the median and interquartile range (IQR) of data, with outliers plotted as circles beyond whiskers when the values are 1.5× IQR from the first or third quartiles.

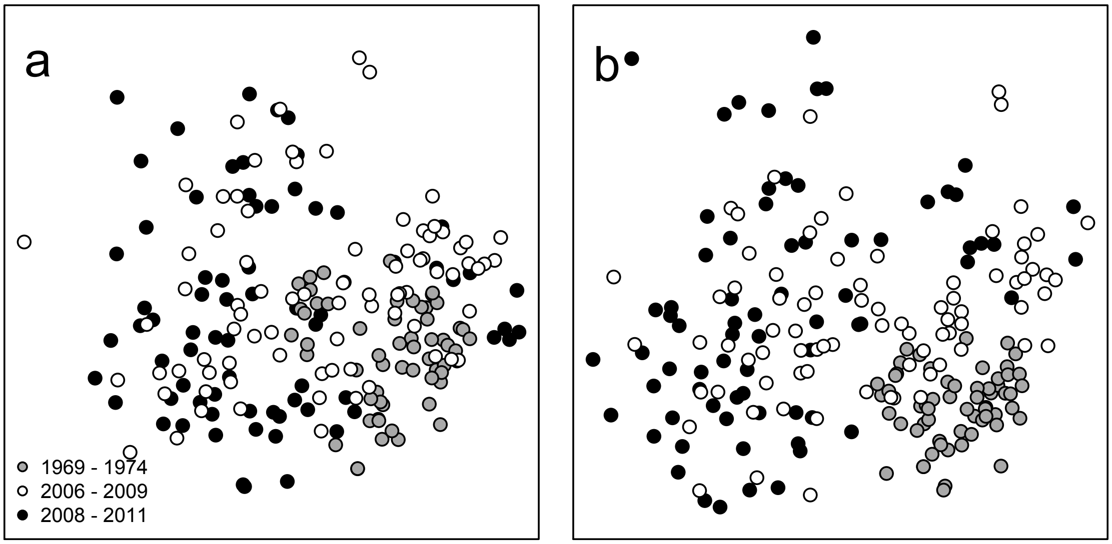

Fig. 5. Plot of the first two axes of a non-metric, multi-dimensional scaling analysis of untransformed (a) and square root transformed (b) percent cover of 42 sessile taxa and bare rock on subtidal rock walls at Shady Cove. Gray, white and black points represent quadrats from Birkeland (1969 – 1974), Sebens (2006 – 2009), and Elahi (2008 – 2011) studies, respectively. Each panel arises from a separate ordination. Stress equals 0.14 and 0.15 for (a) and (b) respectively.

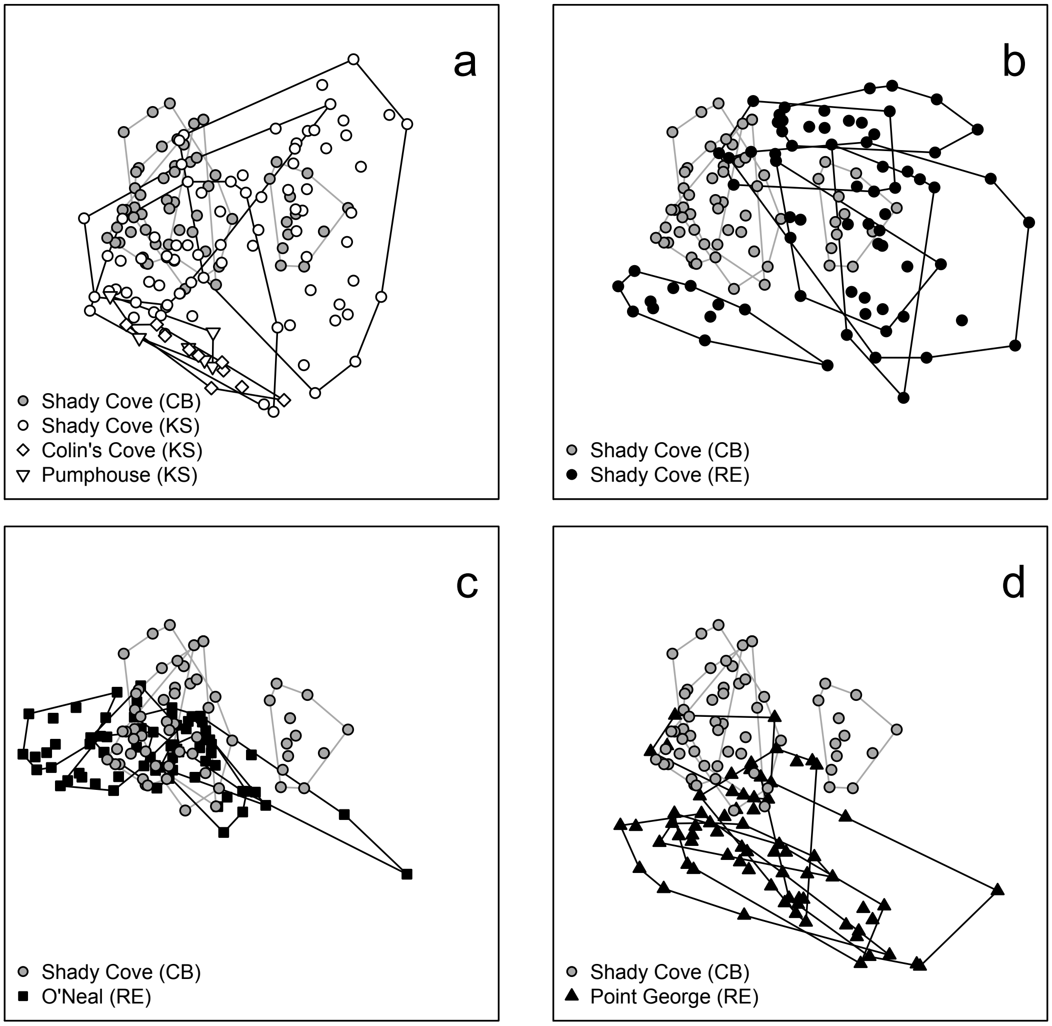

Fig. 6. Plot of the first two axes of a non-metric, multi-dimensional scaling analysis of untransformed percent cover of 42 sessile taxa and bare rock on subtidal rock walls. All panels arise from a single ordination (stress = 0.17), but have been separated to illustrate differences between Birkeland's fixed quadrats (CB; 1969 – 1974) at Shady Cove with (a) Sebens' random quadrats (KS; 2006 – 2009) at Shady Cove, and Colin's Cove, and Pumphouse, (b) Elahi's fixed quadrats (RE; 2008 – 2011) at Shady Cove, (c) Elahi's fixed quadrats (RE; 2008 – 2011) at O'Neal, and (d) Elahi's (RE; 2008 – 2011) fixed quadrats at Point George. Polygons enclose quadrats within each composite quadrat (1969 – 1974) or transect (2006 – 2011).

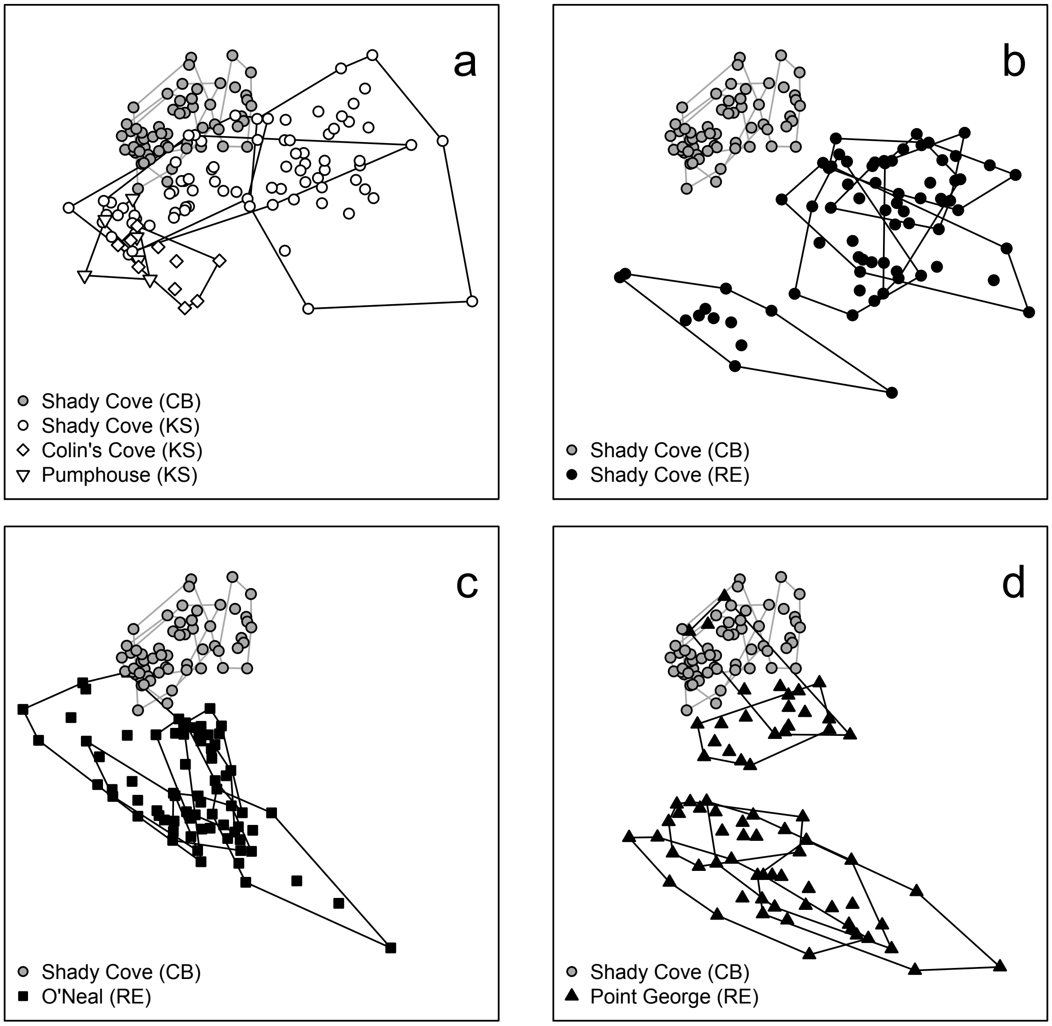

Fig. 7. Plot of the first two axes of a non-metric, multi-dimensional scaling analysis of square root transformed percent cover of 42 sessile taxa and bare rock on subtidal rock walls. All panels arise from a single ordination (stress = 0.18), but have been separated to illustrate differences between Birkeland's fixed quadrats (CB; 1969 – 1974) at Shady Cove with (a) Sebens' random quadrats (KS; 2006 – 2009) at Shady Cove, Colin's Cove, and Pumphouse, (b) Elahi's fixed quadrats (RE; 2008 – 2011) at Shady Cove, (c) Elahi's fixed quadrats (RE; 2008 – 2011) at O'Neal, and (d) Elahi's (RE; 2008 – 2011) fixed quadrats at Point George. Polygons enclose quadrats within each composite quadrat (1969 – 1974) or transect (2006 – 2011).

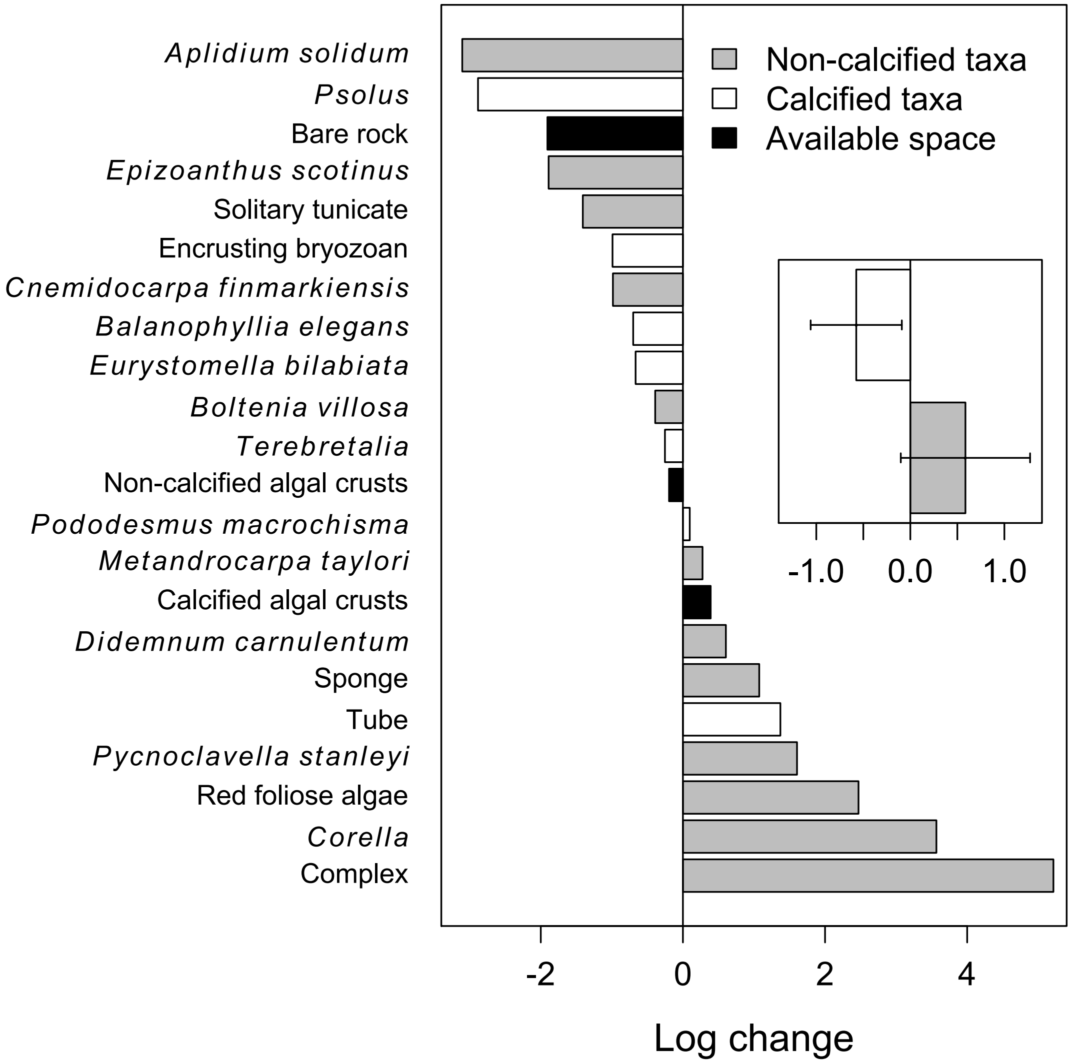

Fig. 8. Relative change in cover of common sessile taxa and bare rock (see Methods) on subtidal rock walls over three decades. Taxa are categorized as non-calcified, calcified, or as components of available space; the inset depicts the mean (± SE) log change for calcified and non-calcified sessile taxa growing upon available space on the rock walls (the trend is not significant).

Supplemental material

Table S1. Indicator values, significance levels, and percent cover (mean ± SE) of all sessile taxa associated with each study period at Shady Cove.

	Indicator value	*P*	Percent cover
1969 - 1974			
Bare rock	87.07	0.000	12.722 ± 0.937
Encrusting bryozoan	72.92	0.000	14.46 ± 0.973
Psolus spp.	72.60	0.000	5.681 ± 0.839
Encrusting non-calcified red algae	54.87	0.030	25.874 ± 1.653
Epizoanthus scotinus	47.78	0.000	2.797 ± 0.578
Terebratalia spp.	46.91	0.029	1.159 ± 0.112
Metandrocarpa taylori	42.43	0.322	9.858 ± 1.192
Encrusting calcified red algae	40.36	0.999	12.186 ± 0.77
Balanophyllia elegans	33.41	0.361	2.042 ± 0.322
Aplidium solidum	27.12	0.000	1.033 ± 0.338
Eurystomella bilabiata	24.22	0.003	1.784 ± 0.4
Didemnum carnulentum	13.54	1.000	5.102 ± 1.092
Sponge	12.73	1.000	0.982 ± 0.298
Boltenia villosa	11.93	0.280	0.219 ± 0.067
Solitary tunicate other	10.71	0.004	0.058 ± 0.023
Calcareous tube	9.11	1.000	0.407 ± 0.093
Cnemidocarpa finmarkiensis	8.49	0.090	0.087 ± 0.033
Halocynthia igaboja	6.44	0.006	0.083 ± 0.045
Pododesmus macrochisma	3.97	0.437	0.085 ± 0.042
Ascidia paratropa	1.25	0.276	0.007 ± 0.007
Pycnoclavella stanleyi	1.11	1.000	0.343 ± 0.174
Complex	1.00	0.000	0.031 ± 0.031
Eudistoma purpuratum	0.56	0.491	0.006 ± 0.006
Foliose red algae	0.26	1.000	0.031 ± 0.022
Corella spp.	0.05	1.000	0.006 ± 0.006
Opuntiella californica	0.00	1.000	0 ± 0
Filamentous red algae	0.00	1.000	0 ± 0
Agarum fimbriatum	0.00	1.000	0 ± 0
Brown foliose species	0.00	1.000	0 ± 0
Diaperoecia californica	0.00	1.000	0 ± 0
Crisia spp.	0.00	1.000	0 ± 0
Heteropora pacifica	0.00	1.000	0 ± 0
Phidolopora pacifica	0.00	1.000	0 ± 0
Bryozoan upright	0.00	1.000	0 ± 0
Hydroid spp.	0.00	1.000	0 ± 0
Metridium spp.	0.00	1.000	0 ± 0
Gersemia rubiformis	0.00	1.000	0 ± 0
Dodecaceria concharum	0.00	1.000	0 ± 0
Balanus crenatus	0.00	1.000	0 ± 0
Balanus nubilis	0.00	1.000	0 ± 0

Distaplia occidentalis	0.00	1.000	0 ± 0
Colonial tunicate other	0.00	1.000	0 ± 0
Chelyosoma spp.	0.00	1.000	0 ± 0
2006 - 2011			
Calcareous tube	62.56	0.000	1.605 ± 0.192
Encrusting calcified red algae	59.64	0.001	18.011 ± 1.215
Complex	59.16	0.000	5.631 ± 0.729
Sponge	57.97	0.000	2.876 ± 0.32
Encrusting non-calcified red algae	45.13	0.970	21.282 ± 1.374
Didemnum carnulentum	43.96	0.001	9.339 ± 0.851
Metandrocarpa taylori	41.62	0.348	12.99 ± 1.167
Foliose red algae	39.17	0.000	0.364 ± 0.067
Diaperoecia californica	32.68	0.000	0.68 ± 0.179
Terebratalia spp.	30.00	0.930	0.9 ± 0.127
Pycnoclavella stanleyi	26.13	0.001	1.709 ± 0.35
Encrusting bryozoan	24.78	1.000	5.369 ± 0.599
Balanophyllia elegans	22.56	0.994	1.014 ± 0.112
Filamentous red algae	22.22	0.000	0.638 ± 0.136
Corella spp.	19.70	0.000	0.229 ± 0.053
Hydroid spp.	18.95	0.000	0.603 ± 0.182
Agarum fimbriatum	17.65	0.000	0.917 ± 0.259
Crisia spp.	17.65	0.000	0.124 ± 0.036
Colonial tunicate other	15.03	0.000	0.24 ± 0.072
Dodecaceria concharum	13.07	0.001	0.374 ± 0.1
Chelyosoma spp.	12.42	0.002	0.067 ± 0.018
Distaplia occidentalis	11.11	0.003	0.126 ± 0.047
Bryozoan upright	9.80	0.007	0.099 ± 0.038
Metridium spp.	9.15	0.009	1.67 ± 0.672
Bare rock	8.37	1.000	1.89 ± 0.251
Boltenia villosa	7.65	0.784	0.148 ± 0.035
Balanus crenatus	7.19	0.022	0.124 ± 0.072
Eurystomella bilabiata	5.32	0.988	0.917 ± 0.279
Brown foliose species	5.23	0.068	0.007 ± 0.004
Pododesmus macrochisma	3.77	0.522	0.094 ± 0.032
Heteropora pacifica	3.27	0.179	0.001 ± 0.001
Phidolopora pacifica	3.27	0.180	0.014 ± 0.009
Cnemidocarpa finmarkiensis	2.13	0.949	0.033 ± 0.011
Opuntiella californica	1.96	0.367	0.011 ± 0.008
Epizoanthus scotinus	1.20	1.000	0.423 ± 0.125
Psolus spp.	1.18	1.000	0.318 ± 0.062
Eudistoma purpuratum	0.86	0.650	0.012 ± 0.011
Gersemia rubiformis	0.65	0.722	0.013 ± 0.013
Balanus nubilis	0.65	0.718	0.004 ± 0.004
Solitary tunicate other	0.51	0.992	0.014 ± 0.009
Aplidium solidum	0.17	1.000	0.046 ± 0.02
Ascidia paratropa	0.16	0.927	0.002 ± 0.002
Halocynthia igaboja	0.02	0.999	0.003 ± 0.003

Table S2. Results of a linear mixed effects model testing the effects of era (historic vs. modern), year and their interaction on the richness (natural log), diversity, and evenness (squared) of the sessile community in fixed quadrats at Shady Cove. Block (composite quadrat or transect) and quadrat were treated as random effects. A Monte Carlo markov chain (MCMC) resampling procedure (n = 5000) assessed the significance of the predictor when the 95% confidence intervals of the parameter estimate did not include zero, the estimate was considered to be significant.

	Estimate	Standard error	t value	MCMC lower limit	MCMC upper limit	significance
Richness (ln)						
Era	0.285	0.128	2.224	0.071	0.473	*
Year	-0.006	0.018	-0.321	-0.044	0.032	ns
Era × Year	0.023	0.022	1.059	-0.023	0.072	ns
Diversity						
Era	-0.026	0.148	-0.176	-0.269	0.221	ns
Year	-0.019	0.020	-0.923	-0.067	0.025	ns
Era × Year	0.067	0.025	2.679	0.008	0.125	*
Evenness (squared)						
Era	-0.162	0.058	-2.817	-0.272	-0.053	*
Year	-0.015	0.010	-1.475	-0.038	0.006	ns
Era × Year	0.036	0.013	2.831	0.008	0.063	*

Table S3. Results of a linear mixed effects model testing the effects of era (historic vs. modern) on the coefficient of variation (logit-transformed) of richness, diversity, and evenness of the sessile community in the historic (Birkeland; Shady Cove) and modern (Elahi; Shady Cove, O'Neal, Point George) studies. Block (composite quadrat or transect) was nested within site; both were treated as random effects. A Monte Carlo markov chain (MCMC) resampling procedure (n = 5000) assessed the significance of the predictor when the 95% confidence intervals of the parameter estimate did not include zero, the estimate was considered to be significant.

Dependent variable	Estimate	Standard error	t value	MCMC lower limit	MCMC upper limit	significance
CV of richness (logit)	0.065	0.115	0.568	-0.289	0.480	ns
CV of diversity (logit)	0.862	0.375	2.302	-0.012	1.773	ns
CV of evenness (logit)	0.517	0.348	1.488	-0.694	1.641	ns

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