

Mesoscale variability in oceanographic retention sets the abiotic stage for subtidal benthic diversity

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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 mensurative 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 5 distinct oceanographic seascapes in the Salish Sea (Northeast Pacific Ocean). Three of the seascapes are waterways, and 2 of the seascapes 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 5 seascapes, primarily between waterways and inlets. Namely, sites nested in waterways exhibited greater diversity at the quadrat and site scales than did sites within inlets. Multivariate analyses of community composition reflected a similarly conspicuous separation between waterway and inlet sites. Four abiotic correlates (predicted current speed, alabaster dissolution rate, temperature, and sediment cover) of water retention supported the qualitative generalization that waterways and inlets represent distinct abiotic environments and are associated with unique subtidal biota. We hypothesize that reduced larval delivery and increased post-settlement mortality, related to the covarying effects of water flow and quality, are the potential drivers of low diversity in high-retention sounds and fjords.

KEY WORDS: Biodiversity · Epibiota · Spatial scale · Temperate rocky reef assemblages · Water low

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INTRODUCTION

Compelling evidence implicates biological diversity as a critical component of ecosystem function and change (Hooper et al. 2012). 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 useful over large spatial scales, where experimental manipulations are not feasible (Sagarin & Pauchard 2010).

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, high variability at local scales is a common feature of ecological systems (Fraschetti et al. 2005) and is related to temporal variability in the interplay between abiotic and biotic processes (Benedetti-Cecchi et al. 2000). These endpoints of spatial scale are of limited practical use to resource managers because the design of marine protected areas is conducted between the local and regional scales.

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Oceanographic variability at the ‘mesoscale’ (10 to 100 km) structures both intertidal (Roughgarden et al. 1988, 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 features dictate the direction and magnitude of currents. Current speed is typically diminished in semi-enclosed bodies that tend to retain water and the reduction in flow is associated with changes in other abiotic factors, including temperature and sedimentation (Lirman et al. 2003, Jokiel & Brown 2004, Kaufmann & Thompson 2005).

The importance of water flow is apparent at multiple levels of biological organization. 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 deliver particulate food to sessile (Sebens 1984, Witman et al. 1993, Lesser et al. 1994) 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) 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 to 10 km; Leonard et al. 1998).

In this study, we tested the hypothesis that meso-scale oceanographic features dictate the biodiversity and composition of subtidal benthic communities using a hierarchical sampling design across 4 spatial scales. Hierarchical designs permit the quantification of variability at each scale and are a powerful tool for identifying salient patterns and suggesting relevant causal processes for future study (Underwood & Chapman 1996). In addition to the analysis of hierarchical spatial pattern, which encompassed a wide range of potential ecological processes, we focused our attention on physical gradients related to water retention at the mesoscale. 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. We compared sites within distinct oceanographic bodies (hereafter referred to as ‘seascapes’) of the Salish Sea in the Northeast Pacific Ocean. Although the seascapes can

potentially receive larvae from the same regional species pool, they are subject to different physical environments. In addition to biotic surveys, we quantified 4 correlates of water retention to examine empirically the qualitative generalization of high versus low retention.

MATERIALS AND METHODS

Field surveys

We focused on epifaunal communities on subtidal vertical rock surfaces (walls) because they harbor an impressive diversity of sessile taxa that occupy the relatively 2-dimensional and homogeneous space (Witman et al. 2004, Miller & Etter 2011). Subtidal rock wall communities were sampled at 18 sites (Fig. 1, Table S1 in the Supplement at www.int-res.com/articles/suppl/m498p117_supp.pdf) with the explicit goal of partitioning variation in the richness of sessile and mobile taxa at 4 spatial scales. The 4 hierarchical spatial scales that we investigated included seascape (10 to 100 km), site (1 to 10 km), transect (5 to 50 m), and quadrat (<2.5 m), which span 6 orders of magnitude. Although the spatial scales of seascape and site overlap (Fig. 1), the influence of seascape was meant to reflect *a priori* hypothesized differences in oceanographic features, specifically with respect to water retention. The 5 seascapes included were Haro Strait (Haro; n = 4 sites), San Juan Channel (Channel; n = 4), Lopez Sound 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 mariners and divers for their rapid tidal currents. Haro Strait is on the west side of the San Juan Islands, and of the 3 waterways is the deepest (>350 m) and most exposed to windswell. Rosario Strait (~50 to 100 m depth) lies to the east of the San Juan Islands, and separates the archipelago from mainland Washington. San Juan Channel (~100 to 150 m depth) is the main passage separating San Juan Island from the other islands in the archipelago, and is the narrowest (2 to 5 km) of the 3 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

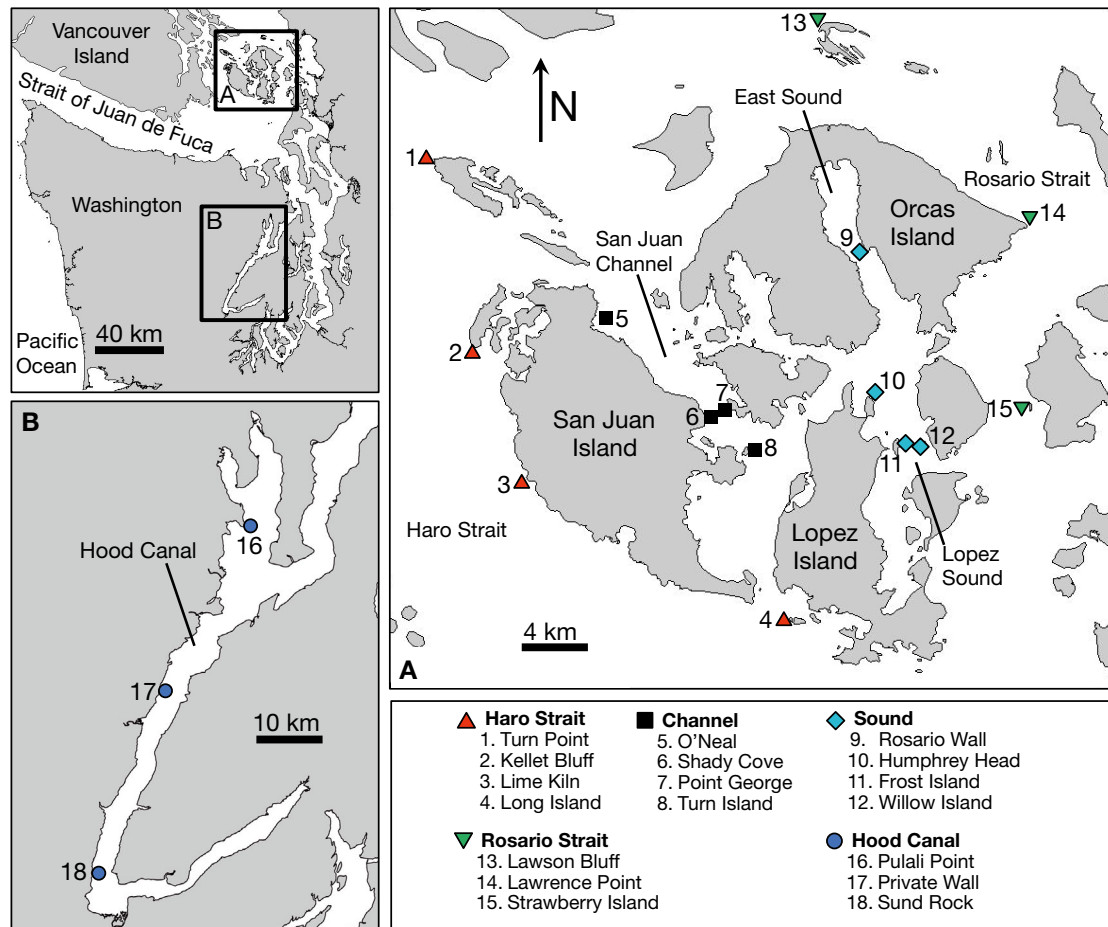


Fig. 1. Map of the Salish Sea showing the seascapes and sites characterized in this study. See Table S1 in the Supplement at www.int-res.com/articles/suppl/m498p117_supp.pdf for coordinates

tidal exchanges even further (Menden-Deuer 2008) from the adjacent Lopez Sound. Lopez Sound is also relatively shallow (~30 to 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 to 4 km) fjord and forms one of the 4 major basins of Puget Sound. Water retention is high, due to a shallow (50 m) sill that precedes the deep (120 to 180 m) fjord (Babson et al. 2006). Hypoxia in the southern Hood Canal has become more prevalent in the past 5 decades, and is a consequence of both natural (minimal water exchange) and anthropogenic causes (e.g. eutrophication) (Newton et al. 2007). Fish kills in the southern Hood Canal, a result of hypoxia, have been observed 4 times between 2003 and 2011 (Palsson 2003, Palsson et al. 2008, Dunagan 2011).

Between July and September 2010, horizontal transects (2.5 m long, $n = 4$ to 6) separated by at least 5 m were sampled haphazardly on rock walls (≥ 2 m 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 pseudonyms 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 seascapes were different with respect to water retention, we quantified 4 abiotic factors: predicted current speed, alabaster

dissolution, temperature, and sediment cover. These factors were hypothesized to be indicators of water retention, or movement, over a range of spatial scales (quadrat to site).

Due to the hazardous conditions imposed by strong tidal fluctuations, most, if not all, maritime activities (including scientific diving) in Washington State are planned carefully in accordance with current predictions provided by the National Current Observation Program (www.tidesandcurrents.noaa.gov). To illustrate differences in water flow among the seascapes, we calculated the daily average of peak current predictions at 14 current stations (Table S2 in the Supplement) in the San Juan Islands and Hood Canal for August 2012 (to match alabaster deployment; see below). The strength of this comparison lies in its wide geographic coverage. However, the current stations were not located directly at our sites and thus may not reflect actual water motion at the benthos.

To address this issue, we quantified alabaster dissolution (a measure of mass flux) at 8 sites. The dissolution of gypsum (or other materials) is a practical means of quantifying water motion (Doty 1971, but see Porter et al. 2000). We used blocks ($5.9 \times 5.5 \times 1.2$ 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 h at the highest flow sites. Sites within the Channel and Sound seascapes were chosen because they were relatively close to Friday Harbor Laboratories, and thus the simultaneous deployment of alabaster blocks was logistically feasible. In addition to practicality, these sites spanned a considerable range of the variability in predicted current speed, diversity, and sediment cover. Three alabaster blocks were deployed at least 5 m apart on rock walls (12 to 17 m 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 to 9) in the field. One alabaster block from Point George, which exhibited $2.1 \text{ mg cm}^{-2} \text{ d}^{-1}$ mass loss, was not included in data analysis because it was an outlier (>3 SD from the overall mean). Such a high dissolution rate may have been the result of urchin grazing, mechanical failure, or an acceleration of dissolution due to changes in the shape of the block. The exclusion of this outlier did not change the significance of statistical tests. Due to the unbalanced nature of the dissolution data, a linear mixed effects model was used to test the effects of seascape (fixed) and site (random) on alabaster dissolution (unit of replication = transect). A linear regression

tested the relationship between alabaster dissolution and predicted current speed.

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, 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 30 min. 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).

Sedimentation rates are related inversely to water flow (Genovese & Witman 1999, Lenihan 1999) and sediment tends to accumulate in sheltered habitats (Airoldi 2003). A simple and commonly used method to quantify the accumulation of sediment is to measure the percent cover of sediment in quadrats (reviewed in Airoldi 2003). Although this method cannot estimate sedimentation rate, or the sediment mass per unit area, it is an ecologically relevant metric on subtidal rock walls. Sessile taxa on walls require available space (encrusting algae and bare rock) for recruitment and growth (Sebens 1986), and accumulated sediment thus reduces the 2-dimensional cover of appropriate substratum. We quantified the percent cover of sediment 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 was expressed as a percentage for each quadrat. A linear mixed effects model was used to test the effects of seascape (fixed), site (random), and transect (random) on logit-transformed sediment cover (unit of replication = quadrat).

Diversity — univariate analyses

We chose to focus on sessile taxa that occupied primary space and mobile fauna within quadrats. Epibiotic taxa were not quantified because they do not occupy primary space (rock or encrusting algae). Richness was defined as the number of species (or lowest possible taxon) per quadrat. Broader functional groups (e.g. hydroids) were used when neces-

sary, and thus all of our estimates of biodiversity should be regarded as conservative. Organisms obscured by sediment were necessarily omitted. To quantify the extent to which sediment cover may have obscured the presence of taxa, and thus affect our estimates of richness, we compared quadrats before and after the removal of sediment. On 2 July 2013, haphazardly selected quadrats (separated by at least 5 m lateral distance) at Frost Island ($n = 6$), Humphrey Head ($n = 6$), Rosario Wall ($n = 2$), and Willow Island ($n = 6$) were photographed. These sites were selected because they exhibited relatively high levels of sediment cover in the San Juan Islands. Holding the quadrat in place, divers flushed any loosely attached sediment out of the frame with their hands and waited for currents to carry away sediment before photographing the quadrat a second time. Richness and the percent cover of sediment was quantified (as described above) from photographs taken before and after the sediment removal. A paired t -test was used to test the effect of sediment removal on sediment cover and richness.

We used sampling curves to estimate site-level taxonomic richness because the number of sampled quadrats was not the same across sites (Gotelli & Colwell 2001). 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 replicated uniformly across sites, nor were sites replicated uniformly 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 variance (PV) attributable to each spatial scale. PV 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. PV was calculated similarly for sediment cover, dissolution, and temperature data. Last, we used mass flux (i.e. alabaster dissolution) and predicted current speed as continuous predictors of all 3 diversity metrics in linear regression models. Assumptions of normality and homo-

geneity 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 'lme4' (Bates et al. 2011) to fit linear mixed-effects models, and the R package 'languageR' to implement a Monte Carlo Markov chain (MCMC) resampling method for significance tests of fixed effects.

Community composition — multivariate analyses

Differences in the community composition of quadrats (sessile and mobile taxa) and transects (mobile taxa) were tested using permutational multivariate analysis of variance (PERMANOVA) on Bray-Curtis dissimilarity matrices of presence and 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 2006a) was compared using permutational multivariate analysis of dispersion (PERMDISP). Significance was evaluated using 10 000 permutations for PERMANOVA and PERMDISP. Seascape was treated as a fixed effect; all other effects as random (as for ANOVAs). When using the Bray-Curtis dissimilarity measure, the square root of components of variation based on PERMANOVA can be interpreted directly as a percentage of the total variation (Anderson et al. 2008) in a manner analogous to the PV described above for univariate richness. PERMANOVA and PERMDISP were performed in Primer 6 (Anderson et al. 2008); all other analyses were conducted using the 'vegan' (Oksanen et al. 2011) and 'stats' packages in R 2.14 (R Development Core Team 2012).

We used non-metric multidimensional 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). To test the hypothesis that the percent cover of sediment was correlated with community composition, we used the function 'ordisurf' in the vegan package to fit nonlinear response surfaces for sediment cover to each ordination (see Bennion et al. 2012 for another application of 'ordisurf'). This method used a generalized additive model to fit sediment cover using a 2-dimensional smooth of the nMDS scores for the first 2 axes as the predictor variable. We used indicator species analysis (Bakker 2008) to identify which taxa best characterized waterways (Haro, Channel, Rosario) and inlets (Sound, Hood). The percent occurrence (number of quadrats in which a species was present divided by the total number of quadrats for a given site) of 6 indicator species was then tested against predicted current speed using linear regression.

RESULTS

Correlates of water retention

Predicted current speeds for August 2012 exhibited considerable variability among 14 current stations in the inland waters of Washington (Fig. 2a). The most conspicuous difference was the relatively low flow speed predicted at current stations in the Sound and Hood seascapes (Fig. 2a).

Using alabaster dissolution as a proxy for mass flux, Channel sites exhibited significantly higher (estimate = 0.39, t -value = 3.26, $p_{MCMC} < 0.001$) flux than Sound sites (Fig. 2b). The effect of seascape was associated with 67% of the variance, and the effect of site was less important (25%). Notably, O'Neal Island in San Juan Channel exhibited similar dissolution rates to sites in Lopez Sound (Table S1 in the Supplement). Average mass flux (per site) was correlated positively with average predicted current speed at nearby current stations (Fig. 2c).

Overall, seawater temperatures at Channel sites were significantly lower (repeated measures ANOVA,

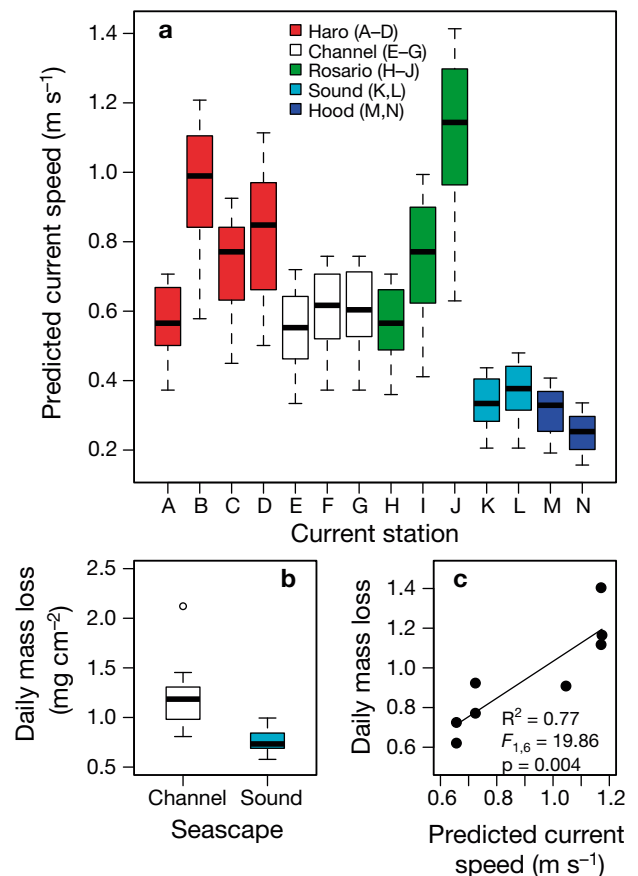


Fig. 2. (a) Boxplots of peak predicted current speed (daily averages in August 2012) from current stations in the 5 seascapes; (b) boxplots of the daily dissolution of alabaster blocks; and (c) the relationship between average daily dissolution and average predicted current speed for 8 sites. All boxplots display the median and interquartile range (IQR) of data, with outliers plotted as circles beyond whiskers when the values are $1.5 \times$ IQR from the first or third quartiles. The single outlier for alabaster dissolution in (b) was removed for all analyses, but did not change the significance of statistical tests. See Table S2 in the Supplement for current station names, coordinates, and closest sites

$F_{1,6} = 8.91$, $p = 0.025$) than Sound sites (Fig. 3a). However, the mean temperature of O'Neal Island (Channel) was more similar to Sound sites (Table S1), than Channel sites. Temperatures were also highly variable (72% unexplained variance, Table 1). Much of this variability was likely due to tidal fluctuations in phase with the lunar cycle (Fig. 3a). For example, the lowest temperatures and sharpest declines were observed during full (1 and 31 August) and new (17 August) moons, when tidal exchanges are typically 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

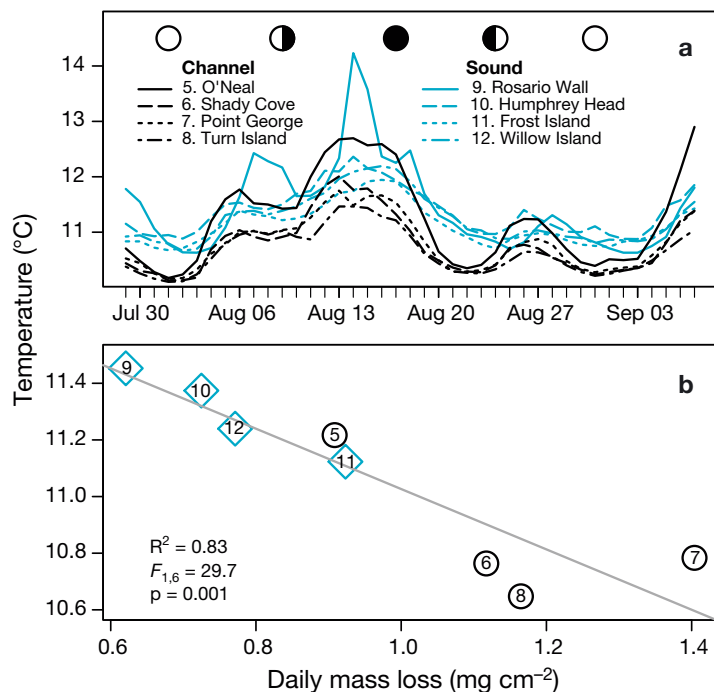


Fig. 3. (a) Mean daily temperatures at 4 Channel sites and 4 Sound sites over one complete tidal cycle between 29 July and 7 September 2012; and (b) mean temperature plotted against the mean dissolution of alabaster blocks at the same sites. Circles in (a) represent moon phases. Standard deviations for (b) are reported in Table S1 in the Supplement

Channel (Fig. 3a). The mean temperature of sites was correlated negatively with mean dissolution rates, with O'Neal Island plotted among Sound sites (Fig. 3b).

Sites within restricted inlets (Sound, Hood) exhibited significantly higher (Table S4 in the Supplement) percent cover of sediment in quadrats than

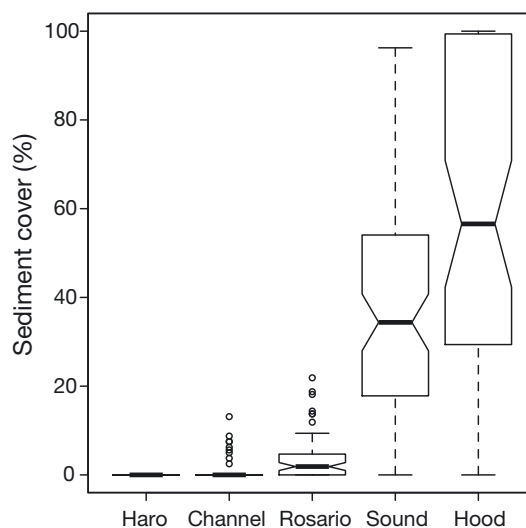


Fig. 4. Boxplots of the percent cover of sediment in quadrats. Due to the high number of quadrats ($n = 400$), we display boxplots using notches that can be used to interpret significant differences between medians—if notches do not overlap, the medians are different. All boxplots display the median and interquartile range (IQR) of data, with outliers plotted as circles beyond whiskers when the values are $1.5 \times$ IQR from the first or third quartiles

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. 4). Sound and Hood sites were highly variable in sediment cover (Fig. 4), and an increasing southward gradient of sediment cover was observed in Hood Canal (Table S1).

Table 1. Percentage of variance (PV) 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, PV is presented for alabaster dissolution, sediment cover, and temperature. Variances were estimated using linear mixed-effects models that treated all scales of variation as random effects

Source	Biotic responses		Source	Abiotic responses PV (%)
	Sessile taxa PV (%)	Mobile taxa PV (%)		
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		
Dissolution (mg cm⁻² d⁻¹)				
Seascape			67.4	
Site			25.4	
Transect (residual)			7.2	
Sediment cover (%)				
Seascape			70.2	
Site			18.4	
Transect			6.2	
Quadrat (residual)			5.3	
Temperature (°C)				
Seascape			19.9	
Site			8.3	
Residual			71.8	

Community structure in quadrats

In a total of 400 quadrats, 73 sessile and 59 mobile taxa were identified. Species accumulation curves more closely approached their asymptotes for sessile taxa than mobile taxa (Fig. S1 in the Supplement), indicating that sessile taxa were sampled more efficiently than mobile taxa in quadrats. All 3 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 with sites in restricted inlets (Sound, Hood) (Fig. 5, Tables S3 & S4). Across 4 Sound sites, the removal of $35 \pm 14\%$ cover of sediment revealed an additional 1.4 ± 1.6 sessile taxa and 0.5 ± 1.1 mobile taxa in a haphazard sample of 20 quadrats (values are means \pm SD). Although the change in sessile richness (but not mobile richness) was statistically significant (Table S5), the ecological significance of ~ 1.4 taxa is small

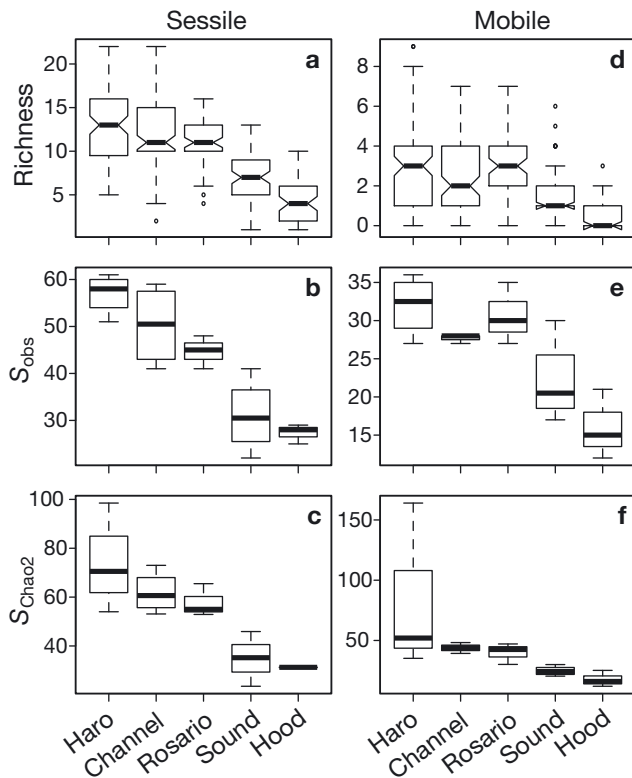


Fig. 5. Boxplots of richness, the number of observed taxa per site (S_{obs}), and the number of estimated taxa per site (S_{Chao2}) for (a–c) sessile and (d–f) mobile taxa in quadrats. The sample sizes for richness (a, d) were relatively high ($n = 400$), and thus we display boxplots using notches that 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 $1.5 \times$ IQR from the first or third quartiles

relative to the larger difference in taxon richness observed between sites from waterways and inlets (Table S3).

With respect to sessile taxa, the spatial scale of seascape was associated with the greatest amount of variation for all measures of diversity (Table 1). However, the largest percentage of variance for mobile richness was associated with the quadrat scale (50%), followed by the seascape scale (31%); seascape was associated with a larger percentage of variance than site for S_{obs} and S_{Chao2} (Table 1). At the site scale, diversity metrics were correlated positively with both alabaster dissolution (Fig. 6a–c) and predicted current speed (Fig. 6d–f).

The ordination of presence and absence data (community composition) for sessile and mobile taxa in quadrats suggests differences in both location (i.e. central tendency) and dispersion (i.e. variability) among seascapes (Fig. 7a). In other words, sites representing waterway seascapes (Haro, Channel, Rosario) were aggregated together in a small portion of multivariate space, whereas sites representing inlet seascapes (Sound, Hood) occupied a different portion of the multivariate space and were more spread apart. The ordination axes were related significantly to the percent cover of sediment ($F = 62.2$, estimated $df = 7.9$, $p < 0.001$, adjusted $R^2 = 0.97$), displayed visually as sediment contours (Fig. 7a). All 4 scales (seascape to quadrat) of spatial variation were statistically significant, and contributed roughly comparable percentages (21 to 32%) of the total variance in community composition using PERMANOVA (Table S6). Notably, pairwise tests indicated significant differences between seascapes in waterways (Haro, Channel, Rosario) and seascapes in inlets (Sound, Hood) (Table S6). Indeed, the centroids of Haro, Channel and Rosario group together in the ordination (Fig. 7a).

Waterway sites were characterized by a number of taxa, as revealed by the indicator species analysis. The top 3 indicators of waterway sites were encrusting algae and bryozoans that could not be identified to genus, and the next 3 indicators were solitary sessile taxa (Table 2). The percent occurrence (at the site level) of these taxa, which included a brachiopod and 2 anthozoans, was correlated positively with predicted current speed (Fig. 8a–c). In contrast, the inlet sites were best characterized by the bivalve *Pododemus macrochisma* (jingle shell), as well as significant (but weaker) characterization by the barnacle *Balanus crenatus* and solitary tunicate *Cnemidocarpa finmarkiensis* (Table 2). The percent occurrence of these 3 species was not correlated signifi-

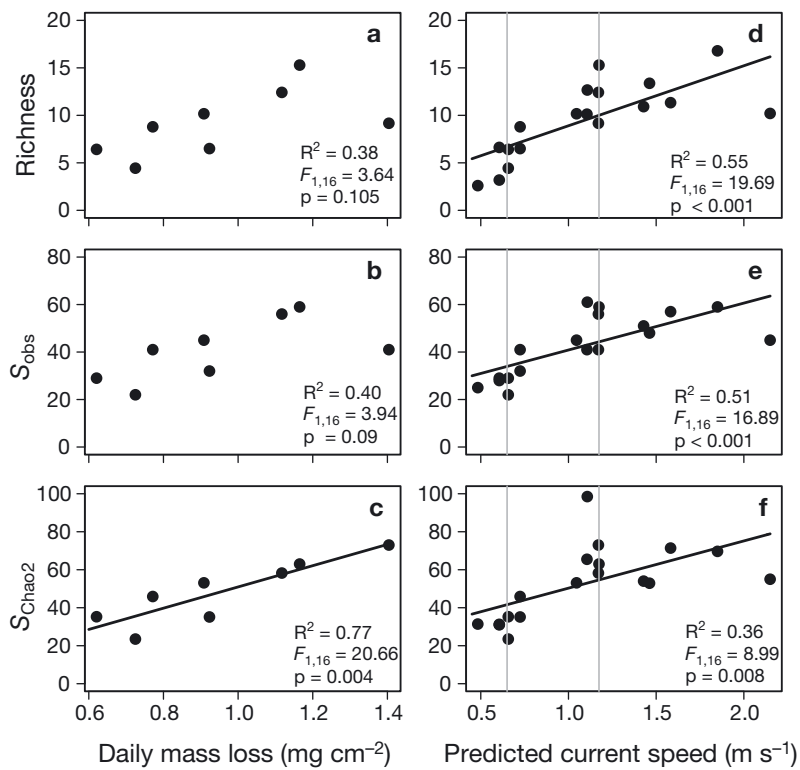


Fig. 6. Richness of sessile taxa in quadrats, number of observed taxa per site (S_{obs}), and number of estimated sessile taxa per site (S_{Chao2}) plotted against (a–c) the average dissolution of alabaster blocks, and (d–f) the daily average of peak predicted current speed in August 2012. The 8 sites at which alabaster dissolution was measured (a–c) are in between the vertical gray lines in (d–f)

cantly with predicted current speed, but all were more common at lower current speeds (Fig. 8d–f).

In addition to the pronounced differences between waterway and inlet sites, the sites in Rosario Strait displayed more subtle separation from Channel and Haro sites (Fig. 7a). Pairwise tests between Rosario and all the other seascapes were significant (Table S6 in the Supplement). The uniqueness of the Rosario sites is related, in part, to the high percent occurrence of the clonal tubeworm, *Dodecaceria fewkesii* (Table S7). In contrast, sites from Haro and Channel seascapes harbored very similar communities, evidenced by the non-significant pairwise test (Table S6). Despite their geographic distance, Sound and Hood sites were not significantly different from each other (Table S6), perhaps in part due to the high dispersion exhibited by both seascapes (Fig. 7a). However, the northernmost site in Hood Canal (Pulali Point) was most similar to Rosario Wall in East Sound (Fig. 7a). Group deviations from centroids (i.e. community variability) differed significantly among seascapes (Table S6), with all but 3 pairwise com-

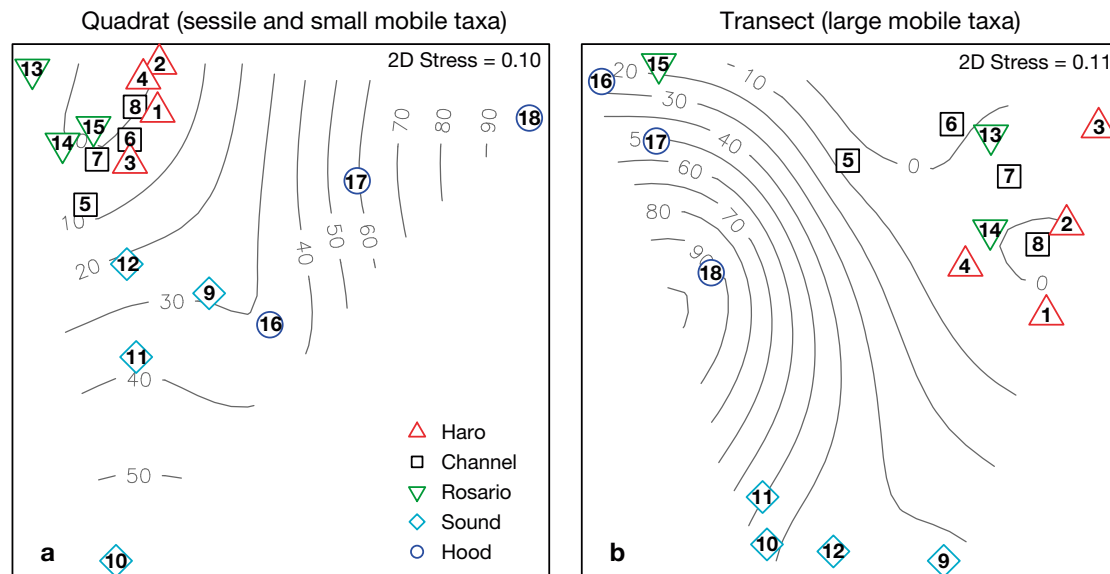


Fig. 7. (a) Non-metric multidimensional scaling analysis of community composition (presence and absence) of 73 sessile taxa and 59 mobile taxa in quadrats, and (b) non-metric multidimensional scaling analysis of untransformed abundances of the 8 most common large mobile fauna on transects. Points represent the centroids for each site and gray lines are the response surfaces for the percent cover of sediment

Table 2. Indicator values (IV), significance levels, and percent occurrence (B) of sessile and mobile taxa in quadrats associated with waterways and inlets. Only taxa with significant ($p < 0.05$) indicator values >18 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 ($B/B_{\text{other cluster}}$). NA = not applicable

	IV	p	B	$B_{\text{other cluster}}$	$B/B_{\text{other cluster}}$	Phylum or class
Waterways (Haro, Channel, Rosario)						
Encrusting bryozoan	59.6	<0.001	0.78	0.24	3.21	Bryozoa
Encrusting coralline algae	53.9	<0.001	0.91	0.62	1.46	Rhodophyceae
Encrusting non-calcified red algae	51.0	<0.001	0.92	0.73	1.26	Rhodophyceae
<i>Balanophyllia elegans</i>	46.4	<0.001	0.59	0.16	3.74	Anthozoa
<i>Terebretalia transversa</i>	44.4	<0.001	0.52	0.09	5.63	Brachiopoda
<i>Metridium</i> spp.	42.4	<0.001	0.43	0.01	60.31	Anthozoa
<i>Schizoporella japonica</i>	39.3	<0.001	0.40	0.01	56.00	Bryozoa
<i>Psolus chitonoides</i>	38.6	<0.001	0.44	0.06	6.88	Holothuroidea
<i>Calliostoma ligatum</i>	37.7	<0.001	0.42	0.04	9.69	Gastropoda
Sponge other	32.9	<0.001	0.52	0.30	1.73	Porifera
<i>Diaperoforma californica</i>	31.7	<0.001	0.42	0.13	3.23	Bryozoa
<i>Didemnum carnulentum</i>	30.8	<0.001	0.32	0.01	44.15	Ascidacea
<i>Abietinaria</i> spp.	29.6	<0.001	0.30	0.00	NA	Hydrozoa
<i>Haliclona</i> spp. 1	29.6	<0.001	0.30	0.00	NA	Porifera
Trochid snail	28.9	<0.001	0.30	0.01	41.46	Gastropoda
Filamentous red algae	28.0	<0.001	0.39	0.15	2.59	Rhodophyceae
Foliose and bladed red algae	27.5	0.024	0.49	0.38	1.29	Rhodophyceae
<i>Amphissa</i> spp.	27.4	<0.001	0.30	0.03	10.50	Gastropoda
Hydroid other	27.1	<0.001	0.44	0.27	1.62	Hydrozoa
<i>Antho lambei</i>	23.5	<0.001	0.23	0.00	NA	Porifera
<i>Distaplia occidentalis</i>	22.3	<0.001	0.22	0.00	NA	Ascidacea
<i>Tonicella</i> spp.	21.6	<0.001	0.27	0.07	3.82	Polyplacophora
<i>Haliclona</i> spp. 2	21.0	<0.001	0.25	0.04	5.74	Porifera
<i>Pileolaria</i> spp.	20.7	<0.001	0.24	0.04	6.68	Polychaeta
<i>Eurystomella bilabiata</i>	20.4	<0.001	0.22	0.02	10.41	Bryozoa
<i>Aglaophenia</i> spp.	20.0	<0.001	0.20	0.00	NA	Hydrozoa
<i>Pycnoclavella stanleyi</i>	19.6	<0.001	0.20	0.00	NA	Ascidacea
<i>Dodecaceria fewkesii</i>	18.5	<0.001	0.18	0.00	NA	Polychaeta
Inlets (Sound, Hood)						
<i>Pododesmus macrochisma</i>	38.7	<0.001	0.45	0.07	6.16	Bivalvia
<i>Balanus crenatus</i>	19.2	<0.001	0.26	0.10	2.64	Cirripedia
<i>Cnemidocarpa finmarkiensis</i>	18.5	<0.001	0.24	0.07	3.61	Ascidacea

parisons (Haro–Channel, Haro–Sound, Channel–Sound) exhibiting significant differences. Percent occurrences (at the seascape scale) for the most common sessile taxa in quadrats are listed in Table S7 in the Supplement, and mean densities of the most common mobile fauna in quadrats are given in Table S8.

Community structure on transects

Of 8 common mobile fauna quantified on 100 transects, the red urchin *Strongylocentrotus franciscanus* and blood star *Henricia* spp. were the most abundant taxa (Table S9). 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 to 2012) or in Hood Canal (16 dives in 2010, including 4 additional sites: Octopus Hole, Jorsted Creek, Flagpole Point, and

Pinnacle). These differences in mobile fauna were reflected in the multivariate statistical analyses.

The scale of seascape was significant and associated with 33% of the variance in transect fauna (Table S10), with 5 of the 7 significant pairwise comparisons between inlet and waterway sites (Table S10). In addition, Sound and Hood seascapes were significantly different from each other, as were Haro and Rosario seascapes (Table S10). A permutation test of the average group dispersion from seascape centroids was significant (Table S10), and thus variation in species turnover (i.e. beta diversity) contributed to the significant differences tested by the PERMANOVA. However, only 2 significant pairwise tests (Channel–Hood, Haro–Hood) contributed to the overall effect (Table S10). Similar to the ordination of taxa in quadrats (Fig. 7a), waterway seascapes grouped together, while the Sound and Hood seascapes occupied different sections of the multivariate

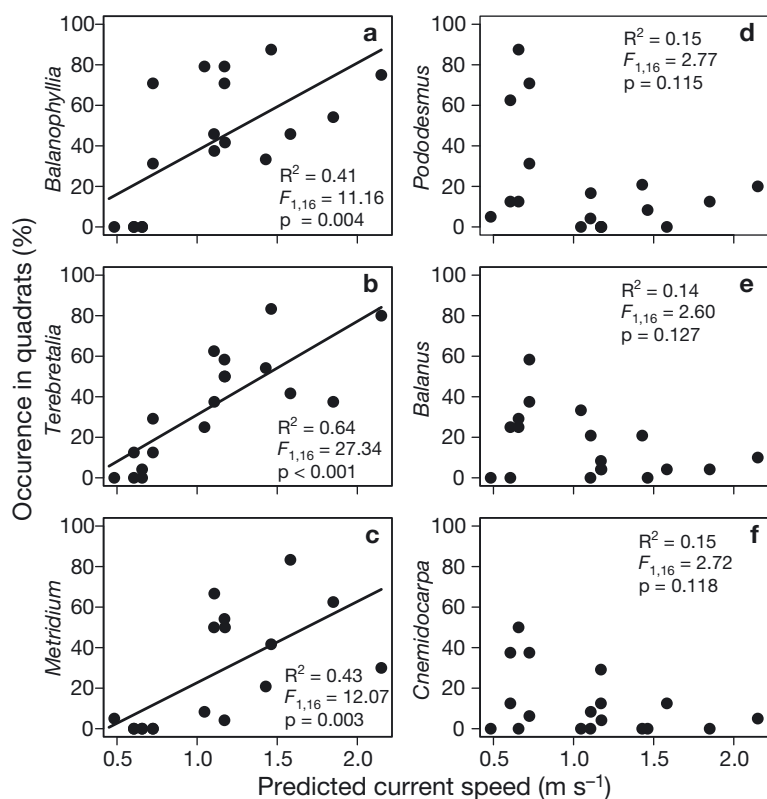


Fig. 8. Percent occurrence of sessile invertebrates in quadrats plotted against the average of peak predicted current speed in August 2012. These taxa were plotted because they were the top indicator species (or species complex in the case of *Metridium*) for low- and high-retention sites (Table 2). *Balanophyllia elegans* (cup coral), *Terebretalia transversa* (brachiopod), and *Metridium* spp. (anemone) are passive suspension feeders and indicators of low-retention, high-flow sites. *Pododesmus macrochisma* (bivalve jingle shell), *Balanus crenatus* (barnacle), and *Cnemidocarpa finmarkiensis* (solitary tunicate) are capable of active filter feeding and were significant indicators of high-retention, low-flow sites. Each point represents a single site

space (Fig. 7b). The percent cover of sediment was again significantly related to the response surfaces of the ordination axes ($F = 16.8$, estimated $df = 8.1$, $p = 0.001$, adjusted $R^2 = 0.90$).

DISCUSSION

Spatial variability in the biodiversity of sessile subtidal taxa in the Salish Sea was greatest at the scale of seascape (10 to 100 km). Given the correlative nature of our study, it is impossible to ascribe causation to this intermediate-scale pattern. The distribution and abundance of subtidal organisms on rocky reefs is a result of both abiotic (e.g. light, salinity, temperature, flow, upwelling, nutrients, disturbance) and biotic (e.g. dispersal, settlement, competition, predation, facilitation) processes and their inter-

actions (Witman & Dayton 2001). In the present study, the most striking variation in diversity was observed between seascapes characterized by high versus low retention of water, due primarily to differences in tidal current speeds. We present several lines of evidence consistent with the hypothesis that abiotic conditions related to oceanographic retention are in part responsible for the ecological patterns. From the outset, we emphasize that the potential mechanisms are not mutually exclusive, are likely to covary, may be modified by biotic interactions, and probably trigger both direct and indirect effects.

Haro Strait, San Juan Channel and Rosario Strait 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 4 correlates of water retention in the San Juan Islands, and all 4 provided empirical support for the generalization of high versus low retention. These abiotic factors covary, in that sediment cover is associated with low predicted current speed and alabaster dissolution, and alabaster dissolution correlates strongly with high seawater temperatures. We did not measure light, but our field observations

suggest that light availability is comparatively low at the Sound and Hood sites. During periods of high tidal exchange (new and full moons), water temperatures at all Channel and Sound sites decreased, but this change was especially prominent at all sites in San Juan Channel relative to East and Lopez sounds. It is worth noting that the observed higher seawater temperatures in East and Lopez sounds may only apply during summer months, when air temperature is higher than water temperature. In the northern Salish Sea (Strait of Georgia), seasonal heating is also more pronounced in areas with minimal tidal current, and the coolest areas are subject to strong tidal mixing and minimal stratification (Levings et al. 1983). Altogether, our 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 univariate metrics of diversity in quadrats. We show that variation in subtidal diversity is influenced strongly by processes at intermediate to local (<10 m) and regional (1000s of km) spatial scales. The 10 to 100 km scale of seascapes was associated with 51 to 80% and 31 to 70% of the variance in diversity (richness, S_{obs} , and S_{Chao2}) of sessile and mobile taxa, respectively. One important caveat is that high sediment cover likely obscured the presence of some taxa at high-retention sites. Although the removal of sediment resulted in a statistically significant increase in sessile richness, the magnitude (1.4) was small relative to the differences between inlet and waterway sites. Therefore, we consider the reduced biological diversity in inlets to be primarily an ecological effect, rather than an artifact of the photographic method.

There are at least 4 covarying mechanisms that may be contributing to the observed positive correlation between univariate metrics of biodiversity and proxies of water movement (alabaster dissolution and predicted current speed). First, larval delivery correlates with flow and can increase local richness by increasing the abundance of rare species (Palardy & Witman 2011). Second, low-flow sites 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 on rock surfaces (reviewed in Airoldi 2003), with strong negative effects on sessile invertebrates (Gerrodette & Flechsig 1979, Young & Chia 1984, Irving & Connell 2002). 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 blockage of potential settlement surfaces, for recognition and contact, as well as strong post-settlement mortality. Third, 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 2002). Fourth, oxygen and nutrient depletion in estuaries with limited tidal flux (Breitburg 1990, Newton et al. 2007, Perissinotto et al. 2010) may impose physiological constraints on epifauna and influence diversity and community structure (Jewett et al. 2005).

With respect to multivariate community composition in quadrats and on transects, the effect of seascape was also significant, but associated with a smaller percentage of the variance (22 and 33% for taxa in quadrats and transects, respectively). Thus,

univariate metrics of biodiversity (richness, S_{obs} , and S_{Chao2}), or alpha diversity, were associated primarily with the largest scale of observation (seascape), but multivariate indicators of community structure (composition and dispersion) were correlated more strongly with the smallest scales of observation (quadrat or transect). In part, this is due to the idiosyncrasies of multivariate community composition at small spatial scales (Fraschetti et al. 2005) related to heterogeneity in abiotic microhabitats and species interactions (Benedetti-Cecchi et al. 2000). Small-scale patchiness is common on subtidal reefs, and is a consequence of variability along vertical (depth) and horizontal axes (Terlizzi et al. 2007, Konar et al. 2009). At the seascape scale the variance was attributable to both the position of site centroids, as well as the spread of centroids within a seascape (i.e. multivariate dispersion). Considering multivariate dispersion as a metric of beta diversity (Anderson 2006b), there is high species turnover in Sound and Hood seascapes, suggesting the presence of strong underlying gradients (abiotic, biotic, or both) among high-retention sites.

Waterways were characterized by a number of different taxa representing many functional groups, including algae and filter-feeding invertebrates. Algae may be limited by light availability within inlets, because high-retention sites exhibited relatively poor visibility (R. Elahi pers. obs.). Both algae and sessile invertebrates benefit from increased mass transfer under high-flow and turbulent conditions, but risk mechanical breakage and dislodgement under extreme conditions (Denny 1988, Patterson et al. 1991, Hurd 2000). Suspension-feeding invertebrates also depend on currents for the delivery of particulate food, and tend to dominate deeper subtidal rocky habitats (i.e. below the kelp zone) and vertical rocky substrata (Witman & Dayton 2001). Interestingly, passive suspension feeders (e.g. anthozoans, brachiopods, pedal sea cucumbers) were significant indicators of high-flow sites only (Table 2). In contrast, the high-retention, low-flow sites were characterized by the bivalve jingle shell *Pododesmus macrochisma*, the barnacle *Balanus crenatus*, and the solitary tunicate *Cnemidocarpa finmarkiensis*. Bivalves, barnacles, and tunicates are active filter feeders, although some barnacles switch to passive filtering in high-flow conditions (Trager et al. 1990). Indeed, the barnacles we observed in low-flow sites appeared to be actively filtering (R. Elahi pers. obs.). Passive suspension feeders may be more common in waterways because they rely on particle flux for nutrition (Sebens 1984, Lesser et al. 1994). Consistent

with this hypothesis, 3 passive suspension feeders were correlated positively with predicted current speed, but the jingle shell, barnacle, and tunicate exhibited negative (but not statistically significant) relationships with predicted current speed.

Similar to taxa in quadrats, the ordination of larger mobile fauna on transects revealed a separation between waterway and inlet sites. The suite of mechanisms driving this pattern at the transect scale are not likely to be the same, because transect fauna were large mobile consumers (e.g. echinoderms), rather than sessile invertebrates, algae, and small mesograzers. In part, a diverse assemblage of sessile and mobile taxa in quadrats may support a rich and abundant suite of larger consumers on transects. For example, high densities of blood stars *Henricia* spp. in waterway sites may be related to their sponge prey (Sheild & Witman 1993), which were relatively abundant and diverse at waterway sites. Beyond differences between waterway and inlet seascapes, species composition on transects was markedly different between Sound and Hood seascapes. Hood Canal is relatively isolated from the other seascapes in this study, and its unique biota suggests that the ecological processes responsible for reducing biodiversity in high-retention seascapes are not necessarily identical across inlets, or that benthic community similarity decreases with geographic distance (e.g. Nakaoka et al. 2006). These alternatives are not likely to be mutually exclusive, but greater replication of inlet seascapes will be necessary to evaluate their relative importance.

The absence of red urchins *Strongylocentrotus franciscanus* at inlet sites was surprising because these ecologically important grazers are common throughout the San Juan Islands (Pfister & Bradbury 1996). 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 a broad range of invertebrates such as bivalves and barnacles, including those that characterize inlets (*Pododesmus macrochisma* and *Balanus crenatus*). Red urchins prefer to eat bull kelp, *Nereocystis luetkeana* (Vadas 1977), but this canopy-forming species is rare in low-flow inlets (Duggins et al. 2001, R. Elahi pers. obs.). Together with the gen-

eral lack of macroalgae and sessile invertebrates, feeding constraints arising from the indirect effects of sediment cover may limit the survivorship of juvenile red urchins at low-flow sites. The observed presence of predators (e.g. sunflower stars, wolf eels, and octopus) in Sound and Hood seascapes may also contribute to the conspicuous absence of red urchins.

In addition to variability at the seascape scale, there was considerable variation among sites within seascapes. Notably, O'Neal Island in San Juan Channel exhibited a physical environment and biotic community (within quadrats) most similar to sites in Lopez Sound. 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). In the ordination, O'Neal Island is situated between waterway and inlet sites, suggesting that the rock wall community reflects the intermediate abiotic conditions. Barnacles *Balanus crenatus*, an indicator species of inlets, exhibit pulses of recruitment on O'Neal Island rock walls that were nearly absent at 2 other Channel sites (Shady Cove and Point George; R. Elahi pers. obs.).

Hood Canal also displayed considerable within-seascape variability. The 3 sites displayed a north-south gradient of sediment cover and richness. Although we did not measure alabaster dissolution there, 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 the 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 the 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 greater depths (25 to 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 importance of diversity for community structure and ecosystem function (Hooper et al. 2012), the results of this mensurative study could help inform the placement of marine protected areas. 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 the southern Hood Canal are protected (Sund Rock, Octopus Hole), and recreational divers enjoy these sites due to ease of access and the relatively frequent sightings of charismatic fauna (e.g. octopus, lingcod, wolf eel). If biodiversity is, or becomes, a priority for managers in the Salish Sea, selecting sites in waterways should guarantee relatively high levels of species richness, without the need for extensive diving surveys. However, elucidating the specific mechanisms responsible for the observed patterns in this study require further investigation.

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