A community approach to understanding patterns and processes on rocky subtidal reefs in the Salish Sea

Derek Smith

A dissertation
submitted in partial fulfillment of the
requirements for the degree of

Doctor of Philosophy

University of Washington
2018

Reading Committee:
Kenneth P. Sebens, Chair
Megan N. Dethier
Jennifer L. Ruesink

Program authorized to award degree:
Biology

University of Washington

Abstract

A community approach to understanding patterns and processes on rocky subtidal reefs in the Salish Sea

Derek Smith

Chair of the Supervisory Committee:
Professor Kenneth P. Sebens
Department of Biology

The structuring of marine benthic communities is driven by a diverse set of ecological factors, each exerting its influence to differing degrees across all spatial and temporal scales. Here we've leveraged a decade of ecological data of the algal, sessile invertebrate, and mobile fauna assemblages on rocky subtidal reefs to present a community approach to understanding the patterns and underlying processes shaping the subtidal seascape in the Salish Sea (inland waters of Washington State). Specifically, we investigated at multiple spatial scales the structure of these communities along a depth gradient, on surfaces with diverse substrate orientations, and across a spectrum of flow regimes to reveal the associations of hundreds of organisms interacting in a mosaic of patchy habitats. We also strongly advocated for the continued efforts to quantify ecological change in our coastal oceans and its long-term consequences.

In the first chapter, we compared the rocky subtidal communities of the San Juan Archipelago to similar temperate habitats worldwide and discovered similarities, such as the characteristic zonation patterns of a shallow subtidal macroalgal-dominated zone shifting to an epifaunal invertebrate-dominated deep subtidal zone. We hypothesized that sessile invertebrate communities would exhibit vertical zonation patterns in diversity and percent cover across a depth gradient and now provide evidence for depth as a strong ecological axis in determining community composition. Contrary to our further hypothesis, the mobile fauna assemblages showed very little evidence of strong zonation patterns across depth in either abundance or diversity; this is perhaps the most surprising result from this study.

After our initial bottom-up approach to understanding depth zonation patterns on our reefs, we took a top-down approach to investigating scale-dependent patterns and processes in the second chapter. Starting first with the big picture at the habitat scale (hundreds of meters), then at the individual substrate-slope scale, and finally focusing in to sub-meter reef features, we now see a highly nuanced image of the communities across the underwater seascape. Assemblages on horizontal surfaces change much more dramatically with increasing depths than those found on vertical surfaces, although the diversity and abundance of taxa across all substrate orientations on converges in the deep zone, a condition referred to as the 'depth emergence' phenomenon. Regardless of depth, assemblages at the extreme ends of the substrate orientation spectrum (i.e. horizontal vs. vertical) have significantly different community structure owing largely to the increased cover of crustose coralline and foliose red algae on horizontal surfaces. And sub-meter vertical features in shelf habitats took on the characteristics of the surrounding surfaces, a pattern we did not expect to find but lends more evidence to the overall identification of light levels as a strong driver of community composition in all habitat types, substrate orientations, and at all spatial scales.

Lastly, at all 60 transect locations, we deployed alabaster dissolution blocks in an effort to connect small-scale localized flow patterns to community composition. In the third chapter we designed flow-mediated species response models and then fit long term ecological monitoring data of algal and invertebrate assemblages to these models to characterize the communities along the flow regime spectrum. As we suspected, differences in community structure are greatest between the lowest and the highest flow rates, with little overlap in the taxa found in the lowest and highest flow rates. Coherent species curves were generated and show clear abundance patterns related to local flow regimes with the taxa found together having the strongest association to each other in terms of showing a similar type of response (abundance in this case). We did not previously identify habitat-wide patterns of zonation in the mobile fauna, but abundance patterns in these taxa do appear to be flow related due in large part to an organism's ability to adhere to the substrate and its phenotypic plasticity. In conclusion, we found that many subtidal benthic species flourish in particular flow conditions and fit within predicted flow-mediated response curves based largely on organismal body plans, attachment to and elevation from the substrate, and feeding strategies.

This study encompasses multiple years, sites, and community components and as such we anticipate this study will contribute to a better understanding of subtidal community patterns locally and provide comparisons globally for years to come, especially as we have barely scraped the surface of the massive underlying data set. We believe we have created a solid foundation for quantifying ecological change in our coastal oceans and its long-term consequences.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Dedicated to my mother,

Patricia Ann Smith,

for instilling in me the true belief I can do anything

ACKNOWLEDGEMENTS

I wish to thank my Ph.D. advisor, Ken Sebens, for allowing me to explore so many research avenues during my time as his graduate student, especially the collection and analysis of the Sebens Lab long term ecological data set from which this dissertation was realized. This document would not be complete without also showing tremendous gratitude to Megan Dethier and Jen Ruesink, whose belief in me was unwavering, even in the darkest of hours. Peter Lape and Terrie Klinger also ensured the process was fair and the University's highest standards were met from beginning to end. Given these mentor's approval, I am so proud of my accomplishments and will forever be grateful to the University of Washington.

Fieldwork, especially subtidal fieldwork, takes a highly skilled cast of characters to conduct. Between 2006 and 2018, many people spent countless hours underwater collecting data and in the lab analyzing photographs in order to provide the foundation for one of, if not the, largest ecological data sets in the world. Tim Dwyer, Robin Elahi, Megan Mach, Kevin and Autumn Turner, Jessica Nordstrom, Kenan Matterson, Megan Cook, Heather Denham, Avery Paxton, Heidi Wilkin, and Breck McCollum, along with so many others, lent their time and expertise to this effort both above and below the waterline and deserve the lion's share of the thanks. We would not have been able to complete all the diving safely without oversight from Pema Kitaeff, one of the hardest working Diving Safety Officers I know and one of my dearest friends. Kristy Kull also ensured we were able to get out on the water in the first place, a feat not without its own share of difficulties she always handled professionally and graciously.

Considering the research focus of the University of Washington, nothing would get done if it weren't for the administrative staff in the Biology department and at Friday Harbor Laboratories. Billie Swalla, Scott Schwinge, Fred Ellis, Aimee Urata, Kathy Cowell, Vicky Daucinas, Bern Holthuis, Stacy Markman, Craig Staude, Alan Cairns, Jeannie Meredith, Sarah Ohara, Marissa Adamczyk, and Krista Klouser work tirelessly to ensure faculty and students have incredible and nearly frictionless experiences in the program. Although Emily Carrington and David Duggins weren't formally involved with my dissertation, they are my family and provided invaluable insights and support.

I am tremendously thankful for my fellowship in the National Science Foundation GK-12 program during my first two years in the graduate program. This teaching opportunity formed the foundation for my involvement in community-wide efforts to offer the next generation of scientists amazing opportunities both in the classroom and out in the field. I will cherish my lifelong friendships with teachers Nick Frazee, Marc Vermeire, Jesse Visciglia, and David Crain and would like to say thanks to Tansy Clay and all the other program administrators and staff.

In addition to conducting research in the Salish Sea, I also spent a substantial portion of my graduate time initiating research projects and teaching classes in several countries surrounding the Mediterranean Sea. I discovered a second father in George Robb, Jr. and will forever be grateful for the guidance and friendship he has shown me and for the opportunities he has given me. The time I have spent with Howard Phoenix, Lee Pape, Peter Campbell, Chris Begley, Graham Nickerson, Auron Tare, Michael Blades, Elliot Mercieca, Edwin Vella, Gerry Villanueva, and Jeff Royal has been phenomenal and I hope will continue far into the future.

I wouldn't be the person I am today without my family; Patricia, Blake, Liz, Gloria, Ann, Terry, Thom, and the rest of the Carmichael Clan. I owe my daily happiness and love to Brook, Sky, Stella, and the newest addition to our family, Livia. I don't know what I'd do without them.

This research was funded by the University of Washington Biology Department, Friday Harbor Laboratories, the National Science Foundation (NSF) GK-12 (DGE 0742559), and NSF Biological Oceanography (DGE 0850809).

CHAPTER 1

Benthic community structure and patterns along a depth gradient on subtidal rocky reefs in the San Juan Archipelago, Washington, USA.

Abstract

Despite the limited number of comprehensive and long-term subtidal ecological studies, there is evidence that predictable gradients of environmental, physical, and biotic factors produce recurring patterns of community structure at multiple spatial and temporal scales. In this study, we quantified benthic community structure to identify patterns of vertical zonation and to compare the rocky subtidal communities of the San Juan Archipelago to similar temperate habitats worldwide. We discovered these communities exhibit characteristic zonation of a shallow subtidal macroalgal-dominated zone shifting to an epifaunal invertebrate-dominated deep subtidal zone. We also provide evidence that sessile invertebrate communities exhibit vertical zonation patterns in diversity and percent cover across a depth gradient. Perhaps the most surprising result from this study is that unlike the sessile flora and fauna, the mobile fauna assemblages showed very little evidence of strong zonation patterns across depth in either abundance or diversity. Most importantly, we anticipate this study will contribute to a better understanding of subtidal community patterns locally and provide comparisons globally. Taken as a whole, this data set encompasses multiple years, sites, and community components and constitutes a solid background for quantifying ecological change in our coastal oceans and its consequences.

Introduction

Comprehensive studies investigating ecological patterns and processes in rocky subtidal marine communities have lagged behind the extensive body of research conducted at intertidal sites worldwide. Much of the literature investigating basic patterns of subtidal community zonation was published in the 1960s through the early 1990s. Few comprehensive long-term subtidal studies have been attempted, although these provide the foundation on which many subsequent observational and experimental studies can be built. Rocky subtidal community zonation has been described from South Africa (Field et al. 1980), New Zealand (Grange et al. 1981; Choat and Schiel 1982; Witman and Grange 1998; Smith 1999), Chile (Santileces 1991), the Northeast Pacific (Neushul 1967), the Sea of Japan (Golikov and Scarlato 1968), and the Northeast (Earll and Erwin 1983) and Northwest Atlantic (Witman 1985, 1987; Mathieson et al. 1991).

Important theories and conceptual models borrowed from terrestrial systems (Whittaker 1960; Ohmann and Spies 1998; Ruesink et al. 2002) and early intertidal studies (Hatton 1938; Connell 1961; Paine 1966) shape our current understanding of the dynamics of subtidal community structure and lend strength to the notion that terrestrial, intertidal, and subtidal systems share basic processes. The maintenance of clear zonation patterns in any environment, such as altitudinal zonation in terrestrial habitats, depends on both physical and biological factors including, but certainly not limited to, temperature regimes and competition in those environments.

Several factors contribute to benthic community structure at the mesoscale level (tens to hundreds of kilometers) in shallow subtidal marine habitats worldwide. The effects of physical factors such as temperature, salinity, and currents combine to form patchy, complex distributions of communities often exhibiting latitudinal as well as local gradients (de Forges et al. 2000; Connell and Irving 2008). Processes driven by prevailing environmental conditions, such as dispersal of asexual propagules and planktonic larvae and the spread of pathogens, are important across all spatial and temporal scales (Ayling 1981, Dayton et al. 1992; Palmer et al. 1996; Scheibling and Hennigar 1997; Witman 1998; Witman and Dayton in Bertness 2001). Disparity in the biomass of plankton in surface waters also contributes to patterns in benthic communities worldwide via mechanisms of benthic-pelagic coupling resulting in dense populations of benthic suspension feeders occurring in plankton-rich upwelling regions (Field et al. 1980; Branch and Griffiths 1988). Dayton and Tegner (1984) connected oceanographic processes to large-scale variability in nutrient supply and recruitment to subtidal communities and Menge (1992) and Bustamente et al. (1996) proposed that upwelling-driven areas of high productivity have a ‘bottom-up’ influence on adjacent rocky intertidal food webs.

At local scales of tens to hundreds of meters, small-scale environmental factors interact with biological controls to determine the diversity, community structure, and distribution of organisms (Sebens 1985, 1986; Archambault and Bourget 1996; Underwood and Chapman 1996; Benedetti-Cecchi 2001). Despite the limited number of comprehensive and long-term subtidal ecological studies, there is evidence that predictable gradients of environmental, physical, and biotic factors produce recurring patterns of community structure. In temperate regions, the subtidal macroalgal-dominated zone generally extends as deep as there is sufficient light for photosynthesis (Golikov and Scarleto 1968; Dayton 1975), often to depths of 10 meters of seawater (msw) to 25 msw, with large brown algae in the orders Laminariales and Fucales as the community dominants (Neushul 1967; Kain 1971; Shepard and Womersley 1970; North 1971; Dayton 1975, 1985; Velimirov et al. 1977; Duggins 1980; Field et al. 1980; Choat and Schiel

1982; Santileces and Ojeda 1984; Witman 1985, 1987; Johnson and Mann 1988; Mathieson et al. 1991; Bologna and Steneck 1993). Under the kelp canopy, foliose red and green algae are mixed with low beds of *Laminaria* and *Agarum* (Britton-Simmons 2006) with much of the primary space on hard substrate occupied by crustose coralline algae (Sears and Cooper 1978; Steneck 1986).

At depths beneath the macroalgal zone, sessile and mobile invertebrates are the most abundant community members (Peres and Molinier 1957; Hiscock and Mitchell 1980). These communities consist largely of suspension feeders such as sponges, bryozoans, ascidians, sea cucumbers, anthozoans, and brachiopods (Zenkevitch 1983; Dayton et al. 1974; Konnecker 1977; Hiscock and Mitchell 1980; Sebens 1986; Witman and Sebens et al. 1988). Macroalgae and large invertebrates both occupy primary space and create vertical relief, thus they are examples of foundation species, capable of modifying their habitat by altering patterns of water movement (Jackson and Winant 1983; Patterson 1984; Eckman et al. 1989, Nelson and Craig 2011) which in turn influences the supply of food and larvae (Genin et al. 1986; Eckman and Duggins 1991; Wildish and Kristmanson 1997; Gill and Coma 1998) and provides refuges from predation (Witman 1985; Stachowicz and Hay 1999; Bruno and Bertness in Bertness 2001). The existence of an algal canopy can either benefit or inhibit other species of algae and invertebrates and thus is a major factor determining the composition and diversity of understory communities. This may also be true of thickets of large invertebrates such as sea anemones, sponges, and ascidians.

An important driver of local-scale subtidal community pattern is the composition, texture, and angle of the substrate, with shallow horizontal and sloping substrates dominated by macroalgae and vertical substrates supporting more epifaunal invertebrates (Pequenat 1964; Lundalv 1971;

Velimirov et al. 1977; Witman et al. 1980; Hulbert et al. 1982; Sebens 1985, 1986; Vance 1978; Witman and Sebens 1988; Mathieson et al. 1991; Bruno and Witman 1996; Uriz et al. 1998; Witman and Grange 1998). On horizontal and sloping substrates in temperate regions, the abundance of sessile invertebrates increases and the abundance of macroalgae decreases with depth. This trend has been documented in studies where the densities of brachiopods on horizontal surfaces doubled between 33 msw and 42 msw (Witman et al. 1980; Hulbert et al. 1982; Witman and Cooper 1983) and the percent cover of sponges increased fourfold between 28 msw and 45 msw (Witman and Sebens 1988). Yet, because vertical surfaces typically harbor sessile invertebrates regardless of water depth, differences in invertebrate community structure on horizontal and vertical substrates are reduced with increasing depth; this is referred to as the 'depth emergence' phenomenon. While decreased light levels affect the community structure either as a result of increasing depth or substrate angle, biological processes such as predation, recruitment, sedimentation, and flow dynamics play a strong role in determining small scale community structure (Witman and Cooper 1983; Witman 1998; Sebens et al. 1988; Leichter and Witman 1997; Genovese 1996; Genovese and Witman 1999) and likely drive this phenomenon. As substrate angle is a fundamental determinant in the structure of local communities, it is important to consider this when designing long-term subtidal studies to adequately quantify benthic sessile and mobile communities across larger heterogeneous habitats and as distinct communities at small scales (Chapter 2).

Ecological processes, such as facilitation and spatial subsidies, influence one or more of the critical species and thus contribute to benthic community structure in the San Juan Archipelago. The red urchin *Mesocentrotus franciscanus* and lined chitons *Tonicella* spp. are two morphologically dissimilar consumers that work in tandem to generate and maintain available space (rock and crustose algae) on vertical rock walls (Elahi and Sebens 2012). Fluxes of energy and nutrients between adjacent habitats in the form of kelp detritus supplement autochthonous sources and can have important population-level effects on recipient species such as suspension feeders and urchins (Duggins and Eckman 1994, 1997; Britton-Simmons et al. 2009).

In this study, we quantified benthic community structure in the subtidal zone of San Juan Channel, part of the Salish Sea, in 3 m depth intervals, from 3 m to 27 m depth below mean lower low water (MLLW), to identify patterns of vertical zonation and to compare the rocky subtidal communities of the San Juan Archipelago to similar temperate habitats worldwide. We hypothesized that our study sites would exhibit characteristic zonation of a shallow subtidal macroalgal-dominated zone shifting to an epifaunal invertebrate-dominated deep subtidal zone. We also hypothesized that sessile invertebrate communities would exhibit vertical zonation patterns in diversity and percent cover across a depth gradient. Third, we hypothesized that both small (<3 cm) and large (≥3 cm) mobile fauna communities would exhibit strong vertical zonation patterns in response to available food sources across depth gradients.

Study Area

The islands of the San Juan Archipelago, Washington, USA are situated north of Puget Sound at the confluence of the Strait of Juan de Fuca and the Strait of Georgia (Figure 1), within the Salish Sea. The smooth and rounded landscape of the emergent islands is the result of the eroding forces of a Pleistocene glacier, which advanced south from the mountains of western British Columbia 18,500-15,000 years ago. During this period, known as the Fraser glaciation event, channels between the islands and the continental United States were deepened and scoured by the advancing glacier, leaving submerged vertical walls associated with the shorelines and submerged rocky outcrops throughout channels in the region. Some of the strongest tidal currents in the world flow past these bathymetric features helping to support diverse algal and invertebrate communities (Chapter 3).

Methods

At the outset of this study in 2006, five sites were selected in San Juan Channel near the Friday Harbor Laboratories on San Juan Island (Figure 2). Sites were chosen because they share similar hard substrate types but have a wide variation in substrate angle. Two more (high flow) sites, at nearby Reid Rock and Turn Island, were added in 2011 to expand the range of flow environments in the study. Benthic community data were collected using diver surveys between 2006 and 2015. Annually between September and December (in some years sampling extended later), the benthic communities were quantified at 45-60 discrete transect locations at 3 m depth intervals, ranging from 3 m to 27 m below the mean lower low tide datum, with permanently installed stainless steel pins and numbered plastic tags as transect starting points.

Four data collection methods were used to quantify the percent cover of algal and sessile invertebrate taxa, the abundances of mobile invertebrate taxa, and the percent cover of two non-organismal categories (bare rock and sediment). When the resulting data sets include only organismal classifications ranging from phylum to species-level, we use the term ‘taxa’ to refer to any discussion of the entire data set or any subset thereof. When the data set includes organismal and non-organismal categories, we use the broad term ‘categories’ in the same context.

Coarse community quantification and kelp canopies: Line-intercept transects

At each transect location, a diver collected line-intercept data points of algae, sessile invertebrates, and bare rock/sediment at 10 cm intervals along a 10 m transect (Figure 3) for a total of 100 points on each transect to capture a ‘fishes’ eye’ view of the habitat (*sensu* Turner

2015). The permanent pin at the start of the transect ensured that we were sampling approximately the same transect location each year, as long as divers kept the deployment depth equal all along the transect. Because the transect was laid out with some variation in position, it is unlikely that the intercepts hit exactly the same area in subsequent years.

Because shallow areas had a high percent cover of kelp canopy, often lying on the bottom directly above other algae and invertebrates and totally obscuring the benthos below, these transects were designed to quantify the percent cover of undisturbed kelp canopy before taking photographs of the underlying rock surface below the canopy. The organism located at each point was identified to the lowest possible taxon and the percent cover of each calculated (1 pt. = 1%). Easily identifiable and ubiquitous species (e.g. *Agarum fimbriatum* and *Metandrocarpa taylori*) were quantified at the species level across all years to facilitate a more detailed analysis of these important contributors to overall community structure. When *in situ* species identification was not possible, phylum or a descriptive category was used to maintain consistency across divers/transects (e.g. sponge, encrusting red algae, *Metridium* spp.). As not all transects stayed within discrete substrate angle designations (i.e. all horizontal or all vertical habitats), notes taken along with photos on the same transect were used to designate a substrate angle for each transect for each year (see below photo quadrat method). When at least eight of the ten photos taken on any given transect were designated as 'horizontal' or a combination of 'horizontal' and 'sloping', the transect was given a 'horizontal' designation. When at least eight of the ten photos taken on any given transect were designated as 'vertical', the transect was given a 'vertical' designation. Any other combination of horizontal, sloping, or vertical photo designations resulted in a 'mixed' designation for that transect.

All line-intercept transect data between 2006 and 2014 were analyzed for a total of 378 transects representing 37,800 data points. For the analysis of this data collection method, a ‘sample group’ refers to the entire set of percent cover estimates on each transect (i.e. a transect assemblage).

Benthic sessile community quantification: Benthic photo quadrats

A second diver on each survey used a photo quadrat with an Olympus 8080 Wide Zoom 8-megapixel digital camera and Ikelite strobe to capture 10 photos of the benthic communities along the transect tape at intervals determined randomly at the beginning of each sampling season. The photo quadrat setup had a framer dimension of 35 cm x 25 cm. Additionally, the visually estimated angle for each photo was classified as either horizontal (<15°), sloping (15° - 75°), or vertical (>75°) by the diver when taking the photo.

Using ImageJ image analysis software from the National Institutes of Health, the photos were cropped to remove the framer, color corrected for accurate organism identification, and divided into a grid of 24 identical squares for percent cover analysis. Each category was assigned a percent cover rating for each of the 24 boxes (0: not present, 1: <1%, 2: 1-19%, 3: 20-39%, 4: 40-59%, 5: 60-79%, 6: 80-99%, 7: >99%). Each percent cover rating was then converted to the decimal mean for each range (e.g. a percent cover rating of 4 becomes 0.5, method modified from Dethier et al. 1993, Elahi and Sebens 2012, 2013). The decimal means for each organism across each of the 24 squares were summed and then divided by 24 to arrive at a final percent cover for each organism over the entire substrate area captured in each photo. Although time consuming, this method has been shown to increase percent cover accuracy versus some point overlay methods and ensures the identification and quantification of every species present in every photo, including rare species, which are often missed with point overlays (Dethier et al. 1993).

All photos from 2007-2009 as well as a representative sample from 2006, 2010, and 2013 were analyzed for a total of 1626 photos representing over two million data points used in the overall analysis. In this analysis, a ‘sample group’ refers to the entire set of percent cover estimates in each photograph (i.e. a photo assemblage).

Small mobile fauna quantification: Benthic photo quadrats

The same photos used for the benthic sessile invertebrate quantification were also used to determine abundance and size of small mobile fauna (<3 cm). These were identified to the lowest possible taxon, counted, and measured using ImageJ image analysis software. All photos from 2007-2009 as well as a representative sample from 2010, 2013, and 2014 for a total of 1262 photos representing 7758 individual organisms across 96 taxa were used in the overall analysis. In this analysis, a ‘sample group’ refers to the entire set of abundances of all taxa in each photograph (i.e. a photo assemblage).

Large mobile fauna quantification: 1 m x 10 m swath counts

Divers identified all large mobile fauna (≥3 cm) to the lowest possible taxon, counted, and measured all individuals 0.5 m above and 0.5 m below the 10 m transect line for a total area of 10 m^2 on each transect. All swath counts between 2006 and 2011 were used for a total of 288 transects representing 3105 individual organisms across 40 taxa. In this analysis, a ‘sample group’ refers to the entire set of abundances of all taxa in each swath count (i.e. a swath assemblage). After 2008, divers began recording large mobile fauna as separate photographs of each individual along the transect, with scale for measurement at a later time.

Analyses

Percent cover and population density

For purposes of visualizing trends across the depth axis, mean values of abundance or percent cover were calculated for major taxonomic groups based on samples collected at each depth, keeping horizontal/sloping and vertical substrate orientations separate. Percent cover of all categories were calculated for each line-intercept transect, all photo quadrats on each transect, and for all sites, years, and depths. Mean densities for small mobile fauna in benthic photo quadrats and large mobile fauna were calculated across all swath counts for all sites, years, and depths.

Shannon diversity

Similar to abundance/cover of major taxonomic groups, diversity was visualized as mean values at each depth, treating horizontal/sloping and vertical categorizations separately. Shannon diversity indices were calculated for all line-intercept transects, benthic photo quadrats, and swath counts across all sites, years, and depths. For each depth, all year and site replicates were averaged keeping horizontal/sloping and vertical classifications separate for each data collection method.

Multivariate analysis

Percent cover from line-intercept and benthic photo quadrats as well as mobile fauna abundances were analyzed separately using multivariate analysis software, PRIMER v7 (PRIMER-E Ltd. Plymouth, UK; Clarke and Warwick, 2001). All data were square-root transformed before analysis. Ordination of samples by non-metric Multi-Dimensional Scaling (nMDS, Kruskal fit scheme 1, restarts=50, minimum stress=0.01), derived from S17 Bray-Curtis similarity matrices, were used to visualize similarities/dissimilarities between sample groups. Sample groups from each data collection method were compared between 3 m depth intervals to determine if differences exist from shallow to deep assemblages and to identify possible transition zones.

Differences between assemblages across all depths were further tested for significance using one-way analysis of similarity (ANOSIM). Contributions of taxa to similarities between assemblages were analyzed between each 3 m depth contour using one-way Similarity Percentages (SIMPER) tests, derived from the square root transformed percent cover and abundance data for each type of data collection method. Where the ANOSIM analysis seeks to providence evidence of where similarities or differences occur, SIMPER analysis provide evidence of how sample groups are similar or different, i.e. which taxa or categories contribute and at what level.

We also formally tested the hypothesis of no differences in community structure among depths and substrate orientations using PERMANOVA, a routine for testing the simultaneous response of one or more variables to one or more factors in an analysis of variance experimental design on the basis of our Bray-Curtis resemblance measure, using permutation methods.

Results

Seasonal temperature fluctuations

Temperatures at each depth are compared to temperature at the deepest site, 27 m, in Figure 4. The Y axis is the slope of the regression line comparing temperatures at the same half hour measurement interval. A slope of 25 represents a 25% increase in temperature at any site, for every degree of temperature increase at the 27 m site (slope of 1.25). During the summer months, these slopes are much higher because the shallower sites experience pulses of warmer, less saline water. During the fall months, there is very little difference among depths. This continues to be the case through winter and spring. Temperatures from June 7 to December 2, 2017 at each depth at Cantilever Point, at the north end of Friday Harbor, WA are compared in Figure 5. Note the concurrent peaks of temperature during the summer months, which appear at each depth. These peaks represent pulses of warm, less saline, water originating from the Fraser River north of this site. Regressions of temperature at 2m depth versus that at 27 m depth during summer and fall months are shown in Figure 6 for each half hour sampling interval. Note that temperatures at the two depths are essentially identical in the fall, but that temperatures at 2m get much higher in summer months.

Substrate orientation grouping justification

The reefs at these study sites consist of complex heterogeneous rocky habitat, presenting difficulties in ensuring individual transects are capturing the community composition of a particular substrate angle. Divers conducting the photo quadrat surveys classified individual photos *in situ*, with substrates having less than a fifteen-degree angle listed as ‘horizontal’ and greater than a 75-degree angle listed as ‘vertical’, which still left a large proportion of the samples with angles in between these listed as ‘sloping’. In the field, sloping surfaces appeared most similar to horizontal surfaces, based on community composition, and vertical surfaces had distinctly different species composition and thus appearance. We compared the benthic sessile community data across all sites in three depth zones to determine if the assemblages documented on sloping substrates were more similar to those on horizontal or vertical substrates. The visual and statistical results provide justification for grouping the horizontal and sloping assemblage data together in the shallow and mid zones (Chapter 2), although at the deepest sites all three substrate angles were very similar.

Percent cover and population density

The algal and invertebrate communities quantified with line-intercepts on horizontal/sloping transects show a pattern of high percent cover of large brown algae in shallow depths decreasing gradually from 6 m to 18 m and becoming absent at 21 m. Percent cover of invertebrates increases gradually from 3 m to 15 m and there is a dramatic increase in cover after 15 m depth with a maximum of approximately 90% cover at 24 m. Crustose coralline and other red algae increase steadily from 3 m to a maximum of approximately 20% cover at 15 m and then decrease in cover down to 27 m depth (Figure 7a).

In contrast, on vertical transects the percent cover of large brown algae is generally low and decreases more rapidly with depth than on horizontal/sloping transects, becoming nearly absent at 15 m. Percent cover of invertebrates steadily increases with depth from 3 m to 27 m. Crustose corallines and other red algae follow a similar pattern as in the horizontal/sloping transects, increasing steadily from 3 m to a maximum of approximately 20% cover at 15 m and then decreasing in cover down to 27 m depth (Figure 7b).

The benthic sessile assemblages in horizontal/sloping photo quadrats show a pattern of high percent cover of coralline algae and other encrusting red algae in shallow depths decreasing gradually after 12 m and encrusting and short erect invertebrate percent cover increasing from shallow to greater depths. Foliose algae and bare space percent covers remain relatively constant in shallow depths, decreasing slightly with increasing depth. Tall erect invertebrate percent cover increases with increasing depth (Figure 8a).

In vertical substrate photo quadrats, the percent cover of crustose corallines and other encrusting red algae varies between 30-40% in shallow depths, decreasing gradually after 15 m. The percent cover of encrusting and short erect invertebrates is much higher in shallow depths in vertical than in horizontal/sloping photo quadrats. Percent covers of foliose algae, tall erect invertebrates, and bare space show similar patterns to those on horizontal/sloping communities (Figure 8b).

Unlike for the other community elements, most of the small mobile fauna in horizontal/sloping photo quadrats show little depth zonation, with most individual species and larger grouped categories distributed approximately equally across all depths. The exceptions are that the mean density of chitons in the genus *Tonicella* increases steadily from 3 m with a maximum density of approximately 50 individuals/m^2 at 15 m, then decreases to nearly zero at 27 m. Hermit crabs have nearly double the mean density in shallow depths than at greater depths (Figure 9a).

In vertical photo quadrats, there is also little evidence of depth zonation patterns in small mobile fauna, with many taxa keeping a relatively constant mean density across depths. *Tonicella* spp. have a similar pattern to those on horizontal surfaces at shallow depths but decrease gradually after 15 m to nearly zero at 27 m (Figure 9b).

Mean densities of large mobile fauna from horizontal/sloping swath counts also show little evidence of depth zonation patterns, with the exception of the large red urchin (*Mesocentrotus franciscanus)*, which increases dramatically after 6 m with a maximum of approximately 25 individuals/10 m^2 at 12 m. Mean density of *M. franciscanus* drops sharply after 12 m decreasing to nearly zero at 27 m (Figure 10a).

On vertical swath transects, there is also little evidence of depth zonation patterns in large mobile fauna, with most taxa keeping a relatively constant mean density across depths. The mean densities of *M. franciscanus* follow a similar pattern as for the horizontal/sloping swath counts, but the maximum mean density of 25 individuals/10 m^2 has shifted deeper to 15 m (Figure 10b).

Shannon diversity

The algal and invertebrate assemblages quantified from point count and benthic photo quadrats on vertical substrates had higher mean diversity indices than the comparable communities on horizontal/sloping substrates in shallow depths. The horizontal/sloping communities show a dramatic increase in diversity starting at 15 m depth with the diversity indices converging at greater depths (Figures 11 and 12). This appears to be due to the inclusion of more invertebrate species on the horizontal/sloping surfaces as depth increases.

The small and large mobile fauna community diversity indices do not provide evidence of strong differences in diversity between horizontal/sloping and vertical substrates across any depths, with overlapping trends of increasing and decreasing diversity across depths in each substrate type (Figures 13 and 14).

nMDS and ANOSIM analysis

Ordination of sample groups by nMDS and ANOSIM analyses for the line-intercept transects used to quantify algal (including kelp canopy) and invertebrate communities showed significant differences in community composition across horizontal/sloping and vertical transects across nearly all pairwise depth comparisons (Figure 15a: Global R=0.53, p=0.001; Figure 15b: Global R=0.416, p=0.001; Table 1: R-statistics for all pairwise depth comparisons). There is a visual grouping of community similarity for shallow versus deeper sites with a distinct transition at 15-18 m depth.

There were also significant differences in benthic sessile community composition comparing photo quadrats along horizontal/sloping and vertical transects across nearly all depths (Figure 16a: Global R=0.34, p=0.001; Figure 16b: Global R=0.284, p=0.001; Table 2: R-statistics for all pairwise depth comparisons). There is again a visual grouping in community similarity between shallow and deeper sites with a distinct transition at 15-18 m depth.

The small mobile fauna community composition across horizontal/sloping and vertical transects showed differences in nearly all pairwise depth comparisons (Figure 17a: Global R=0.103, p=0.001; Figure 17b: Global R=0.083, p=0.001; Table 3: R-statistics for all pairwise depth comparisons). However, while the R-statistics were statistically significant due to the large sample size, the lack of any visual pattern in the nMDS plots and the relatively low R values of the correlations provide little evidence of genuine structure to the small mobile fauna communities across all depths.

Ordination of swath counts used to quantify large mobile fauna showed few significant differences in community composition along horizontal/sloping and vertical transects across all pairwise depth comparisons (Figure 18a: Global R=0.083, p=0.001; Figure 18b: Global R=0.173, p=0.001; Table 4: R-statistics for all pairwise depth comparisons). As with the small mobile fauna, the lack of any visual pattern in the nMDS plots and the relatively low values of the correlations suggest a lack of structure to the large mobile fauna communities across depths.

Similarity Percentages (SIMPER) analysis

SIMPER analysis of line-intercept transects identifies the individual/grouped species that characterize the transects, i.e. that contribute to community similarities across each depth (Figures 19 and 20). On horizontal/sloping transects, the largest contributors to community similarity on the 3 m through 12 m depths are kelps in the order Laminariales (*Agarum fimbriatum*, *Saccharina* spp.) and crustose coralline algae, with a combined contribution of nearly 80%. At 15 m and below, crustose coralline algae continue to contribute to community similarity, but there is a sharp decrease in large brown algal species and an increase in other encrusting and filamentous red algae. Sessile invertebrates also begin to contribute to community similarity at depths below 15 m with erect and encrusting bryozoans, hydroids, tunicates, and sponges dominating the subtidal landscape.

On vertical transects, the largest contributors to community similarity at the 3 m and 6 m depths are again kelps in the order Laminariales (*Agarum fimbriatum*, *Saccharina* spp.) and crustose coralline algae with a combined contribution of approximately 65%. We note that the high percent cover of kelps at shallow depths is due primarily to kelp blades draping down over the vertical surfaces, from plants attached on horizontal or sloping surfaces nearby; there are few, if any, kelp attached on vertical surfaces. The large brown algal species decrease sharply at 9 m and 12 m and are absent at 15 m and below. Crustose coralline algae continue to contribute to community similarity at all depths, but unlike for the horizontal/sloping transects, there are contributions from encrusting and filamentous red algae at all depths. Also unlike for the horizontal/sloping transects, sessile invertebrates contribute to community similarity at all depths; these include erect and encrusting bryozoans, hydroids, tunicates, sponges, and the social ascidian *Metandrocarpa taylori*.

SIMPER analysis of benthic photo quadrats, used to quantify sessile invertebrate communities, provides the individual/grouped species contributions to community similarities across each depth (Figures 21 and 22). In horizontal/sloping photos, the largest contributors to community similarity on the 3 m through 15 m depths are crustose coralline algae, other encrusting and foliose red algae, a complex of hydroids and bryozoans, and bare space. Combined, these groups make up more than 80% of the community similarities between 3 m and 15 m depths. At 18 m and below, the crustose coralline algae contribution to community similarity decreases and is absent at 27m, with sponges, tube worms, encrusting bryozoans, and the erect bryozoan *Diapoeroecia californica* increasing in contribution with increasing depth.

In vertical photos, the largest contributors to community similarity on the 3m through 15 m depths are crustose coralline algae, other encrusting and foliose red algae, a complex of hydroids and bryozoans, and bare space. The individual contribution to community similarity in these groups at each depth is decreased compared to the horizontal/sloping communities, with erect and encrusting bryozoans increasing in contribution with increasing depth. Sponges and the social ascidian *Metandrocarpa taylori* contribute to community diversity across all depths from shallow to deep.

For small mobile fauna in horizontal/sloping photos (Figures 23 and 24), the largest contributors to community similarity on the 3 m through 18 m depths are hermit crabs, chitons in the genus *Tonicella*, and shrimp. Combined, these groups make up more than 70% of the community similarities between 3 m and 18 m depths. At 21 m and below, shrimp continue to contribute to community similarity and hermit crab contributions decrease sharply, with *Tonicella* species absent. *Calliostoma* spp. and other snails contribute approximately 40-50% of community similarity at these depths.

In vertical photo quadrats, the largest contributors to community similarity on the 3 m through 18 m depths are again hermit crabs, chitons in the genus *Tonicella*, and shrimp. The individual contribution to community similarity in these groups at each depth is less compared to the horizontal/sloping communities, with *Calliostoma* spp. and other snails also contributing to community similarity at all depths. *Tonicella* spp. are again absent below 18 m depth.

For large mobile fauna in horizontal/sloping photo quadrats (Figures 25 and 26), the largest contributors to community similarity on the 3 m through 21 m depths are *Henricia* spp., *Pycnopodia helianthoides*, *Cryptochiton stelleri*, and *Mesocentrotus franciscanus*. Combined, these species make up approximately 60% of the community similarities between 3 m and 21 m depths. At 24 and 27 m, *Henricia* spp. contributions are nearly double those of shallower depths. The holothurian *Parastichopus californicus* contributes to community similarity at all depths except 3 m.

In vertical photos, only four large mobile fauna species contribute to community similarity across all depths. *Henricia* spp. and *Mesocentrotus franciscanus* contribute 70-90% of community similarity between 6 m and 21 m, with an increasing contribution of *Henricia* spp. at 24m and 27m depths.

Discussion

Our results are partially consistent with other studies of temperate zone rocky subtidal communities, providing evidence for strong depth zonation patterns, with distinct differences between communities on horizontal/sloping and vertical substrates. The benthic communities in the San Juan Islands are dominated by macroalgal cover (kelp and others) in shallow depths from the low intertidal zone to ~12 m and give way to epifaunal invertebrate communities as depth increases. There is a transition zone dominated by foliose red and coralline algae, but lacking the large, understory kelp. This is also the zone where the urchins *M. franciscanus* reach their highest densities. Much of the literature points toward light availability as the factor driving this pattern, although factors such as thermoclines, freshwater input from local watersheds, substrate aspect, and biological interactions (e.g. competitive dominance of macroalgal species) certainly play a role in shaping these communities and warrant further investigation. Large vertical rock wall habitats generally experience decreased light availability, decreased sediment loading, and sometimes increased flow rates relative to horizontal shelf habitats. Temperature regimes also shift gradually from our deepest to shallowest sites, with shallow sites experiencing over 30 percent greater mean temperatures in summer, and with spikes of higher temperatures that correlate with lower salinities. Although there is no sharp break that might coincide with the observed sessile zonation, it is certainly true that some of the component species will do better under colder summer conditions, and others (possibly with a more southern distribution) will be favored by these summer conditions. Sea surface warming has resulted in an average change of greater than one degree Celsius over the past 50 years, which is enough to affect growth rates, spawning, and larval development. Despite this documented change in the local conditions, vertical rock wall communities at around 15 m depth have not changed much over four decades (Elahi et al. 2014).

The effects of macroalgae on invertebrate assemblages at these sites is well established. One clear correlate with substrate angle in our study is that while the dominant macroalgal species were found throughout the shallow zones at every site, their percent cover was always much lower on vertical walls. Clearly, the factors cited above allowed the benthic sessile invertebrate communities to dominate vertical substrates even at shallower depths. Despite the dominance of macroalgal cover in shallow depths, the understory algae and benthic sessile invertebrates in this zone still provide strong contributions to overall diversity. Diversity indices of algal and invertebrate communities were higher on shallow vertical substrates than on shallow horizontal substrates. As depth increases, the diversity indices converge to become nearly equal at the greatest depth of 27 m. One of the primary factors that contributes to community diversity, light availability, decreases and becomes more similar across substrate orientations with increasing depth and likely helps drive this depth emergence phenomenon.

At the shallowest depth at all sites, the percent cover of crustose corallines and other encrusting red algae are approximately the same between horizontal and vertical surfaces. On horizontal surfaces, the percent cover of crusts increases down to 12 m, but then steadily declines to nearly zero at the deepest depth. On vertical surfaces, the percent cover of crusts is relatively high but variable down to 15 m and then steadily decreases to nearly zero at depth. Although macroalgal cover decreased with increasing depth in both types of habitats, there are fewer invertebrate competitors on the horizontal surfaces than on the vertical, allowing these crusts, which are poor competitors with other algae and with invertebrates (Sebens 1985, 1986, Steneck and Dethier 1994) to occupy more space.

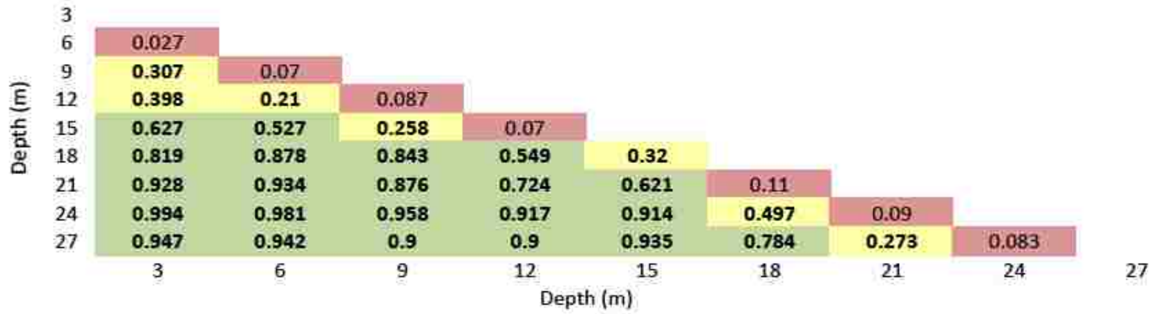
Perhaps the most surprising result from this study is that unlike the sessile flora and fauna, the mobile fauna assemblages showed very little evidence of strong zonation patterns across depth in either abundance or diversity. Many of the species surveyed, both large and small mobile fauna, are specialist consumers, often foraging for and feeding on specific prey species or particular phyla. Given the strong pattern of depth zonation of the benthic sessile communities, we expected to see a stronger zonation of the mobile species dur to pairing of sessile and mobile prey and predators. Of the few examples of zonation we did see in the mobile species, red urchins (*M. franciscanus*) were the most prominent with a large increase in mean densities at intermediate depths, then dropping to nearly zero in the deep zone, although they do occupy even deeper habitats (Britton-Simmons 2006)

Red urchins are voracious omnivores and appear in the greatest densities at depths where the macroalgal community begins to disappear (Tegner and Dayton 1991, Britton-Simmons et al. 2009). Very strong currents on some of these reefs can create a whiplash effect of kelp fronds on sessile and mobile species in close proximity to these large macroalgal blades (Kennelly 1989, Connell 2003, Morrow and Carpenter 2008). Given their morphology, it would be advantageous for urchins to remain clear of these areas. Extensive studies have provided evidence that red urchins benefit from spatial subsidies in the form of decaying drift kelp being delivered to them via strong currents (Britton-Simmons et al. 2009). Some of the strongest flow rates we measured near Friday Harbor Laboratories were at the 15 m depth where macroalgal cover is substantially reduced (to almost zero on vertical transects) and these correlate to high densities of red urchins.

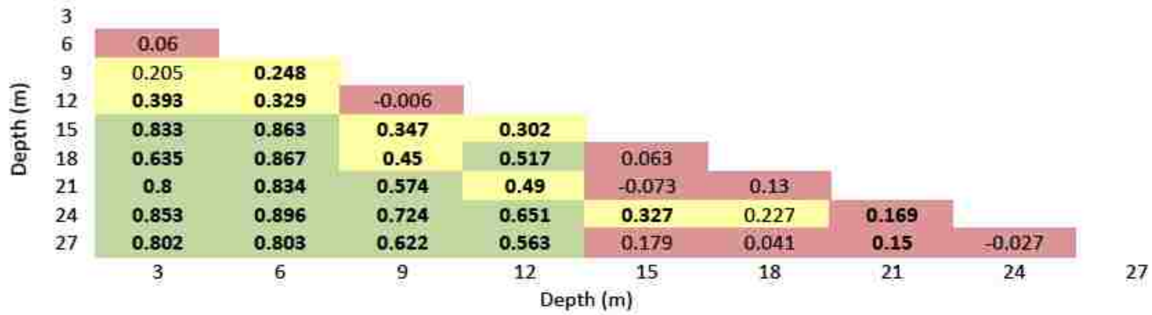
We anticipate this study will contribute to a better understanding of subtidal community patterns locally and provide comparisons globally. Because our data sets encompass multiple years, sites, and community components, they constitute a solid background for quantifying ecological change in our coastal oceans and its consequences. Quantification of pattern, as we have done here, is a critical first step in any ecological investigation and raises testable hypotheses about important processes, some of which are addressed in subsequent chapters.

Tables

Table 1. ANOSIM R-statistics for all pairwise depth comparisons of algal and invertebrate assemblages from horizontal/sloping (top) and vertical (bottom) line-intercept transects. Bolded values indicate significance at $p<0.05$.



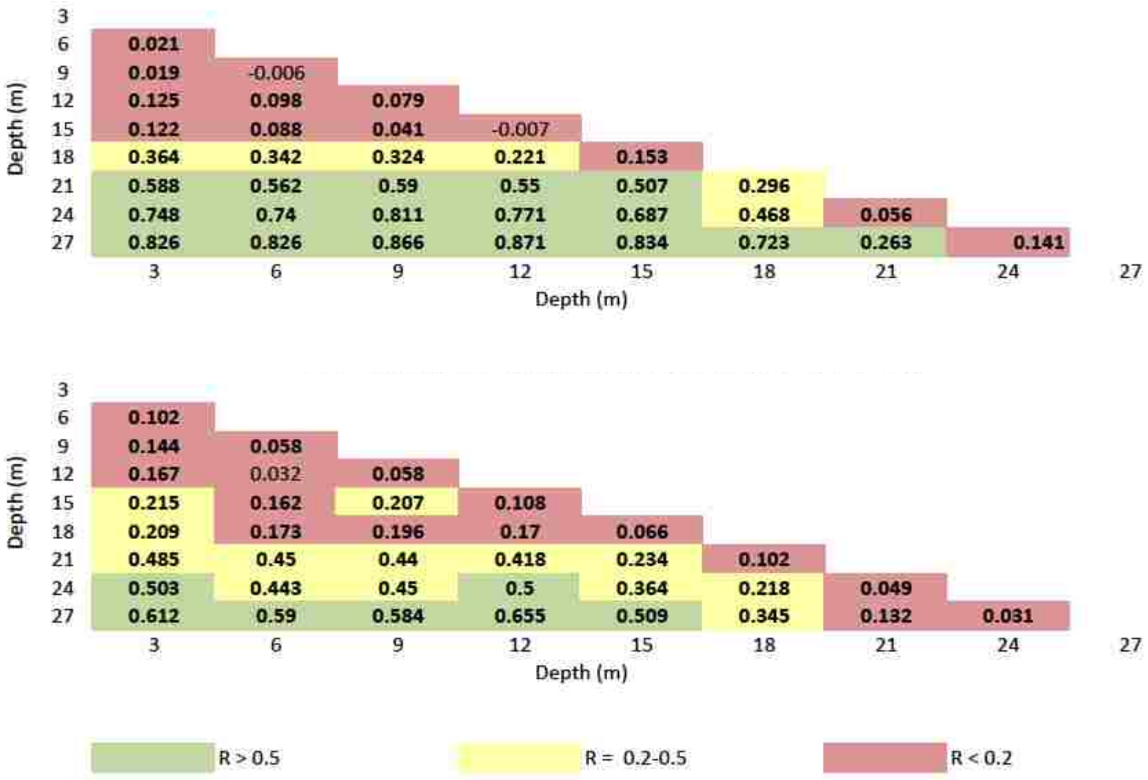
Depth (m)	3	6	9	12	15	18	21	24	27
3									
6	0.027								
9	**0.307**	0.07							
12	**0.398**	**0.21**	0.087						
15	**0.627**	**0.527**	**0.258**	0.07					
18	**0.819**	**0.878**	**0.843**	**0.549**	**0.32**				
21	**0.928**	**0.934**	**0.876**	**0.724**	**0.621**	0.11			
24	**0.994**	**0.981**	**0.958**	**0.917**	**0.914**	**0.497**	0.09		
27	**0.947**	**0.942**	**0.9**	**0.9**	**0.935**	**0.784**	**0.273**	0.083	



Depth (m)	3	6	9	12	15	18	21	24	27
3									
6	0.06								
9	0.205	**0.248**							
12	**0.393**	**0.329**	-0.006						
15	**0.833**	**0.863**	**0.347**	**0.302**					
18	**0.635**	**0.867**	**0.45**	**0.517**	0.063				
21	**0.8**	**0.834**	**0.574**	**0.49**	-0.073	0.13			
24	**0.853**	**0.896**	**0.724**	**0.651**	**0.327**	0.227	**0.169**		
27	**0.802**	**0.803**	**0.622**	**0.563**	0.179	0.041	**0.15**	-0.027	

🟩 R > 0.5
🟨 R = 0.2-0.5
🟥 R < 0.2

Table 2. ANOSIM R-statistics for all pairwise depth comparisons of benthic sessile assemblages from horizontal/sloping (top) and vertical (bottom) photo quadrats. Bolded values indicate significance at $p<0.05$.

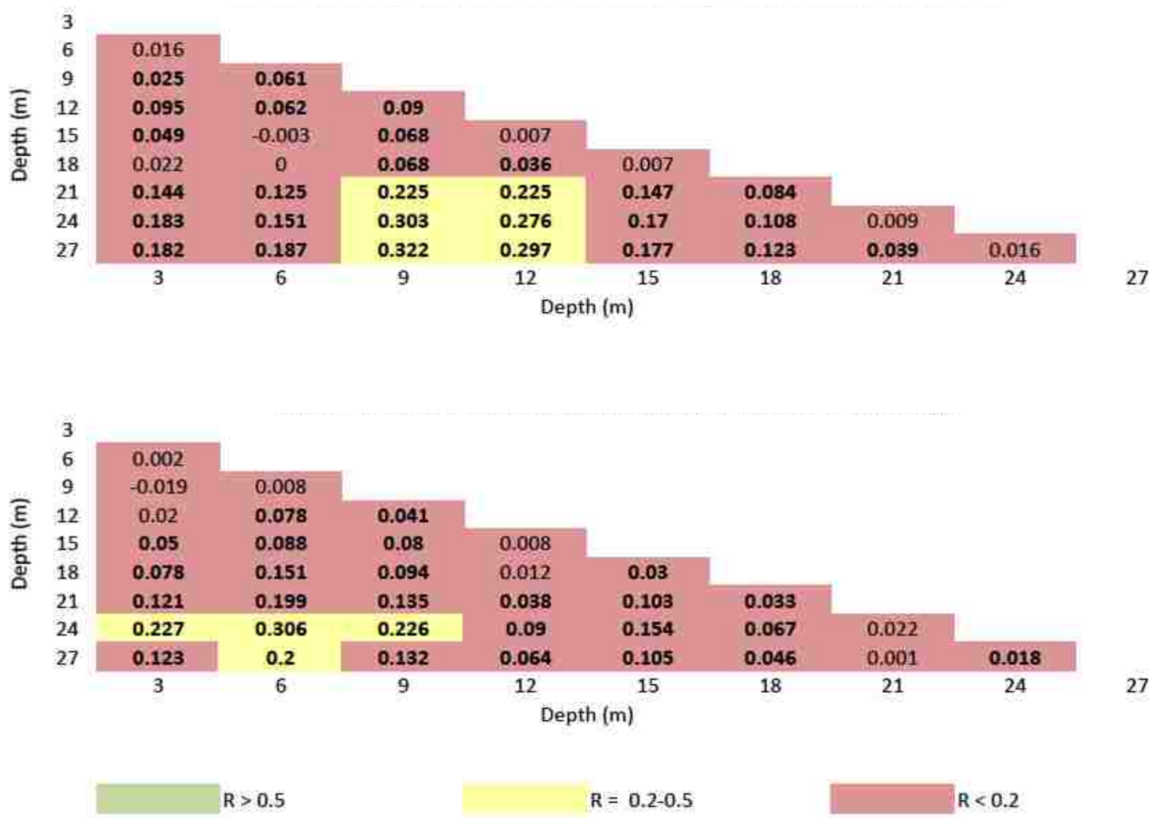


Depth (m)	3	6	9	12	15	18	21	24	27
3									
6	**0.021**								
9	**0.019**	-0.006							
12	**0.125**	**0.098**	**0.079**						
15	**0.122**	**0.088**	**0.041**	-0.007					
18	**0.364**	**0.342**	**0.324**	**0.221**	**0.153**				
21	**0.588**	**0.562**	**0.59**	**0.55**	**0.507**	**0.296**			
24	**0.748**	**0.74**	**0.811**	**0.771**	**0.687**	**0.468**	**0.056**		
27	**0.826**	**0.826**	**0.866**	**0.871**	**0.834**	**0.723**	**0.263**	**0.141**	

Depth (m)	3	6	9	12	15	18	21	24	27
3									
6	**0.102**								
9	**0.144**	**0.058**							
12	**0.167**	0.032	**0.058**						
15	**0.215**	**0.162**	**0.207**	**0.108**					
18	**0.209**	**0.173**	**0.196**	**0.17**	**0.066**				
21	**0.485**	**0.45**	**0.44**	**0.418**	**0.234**	**0.102**			
24	**0.503**	**0.443**	**0.45**	**0.5**	**0.364**	**0.218**	**0.049**		
27	**0.612**	**0.59**	**0.584**	**0.655**	**0.509**	**0.345**	**0.132**	**0.031**	

🟩 R > 0.5 🟨 R = 0.2-0.5 🟥 R < 0.2

Table 3. ANOSIM R-statistics for all pairwise depth comparisons of small mobile fauna communities from horizontal/sloping (top) and vertical (bottom) photo quadrats. Bolded values indicate significance at p<0.05.



Depth (m)	3	6	9	12	15	18	21	24	27
3									
6	0.016								
9	**0.025**	**0.061**							
12	**0.095**	**0.062**	**0.09**						
15	**0.049**	-0.003	**0.068**	0.007					
18	0.022	0	**0.068**	**0.036**	0.007				
21	**0.144**	**0.125**	**0.225**	**0.225**	**0.147**	**0.084**			
24	**0.183**	**0.151**	**0.303**	**0.276**	**0.17**	**0.108**	0.009		
27	**0.182**	**0.187**	**0.322**	**0.297**	**0.177**	**0.123**	**0.039**	0.016	

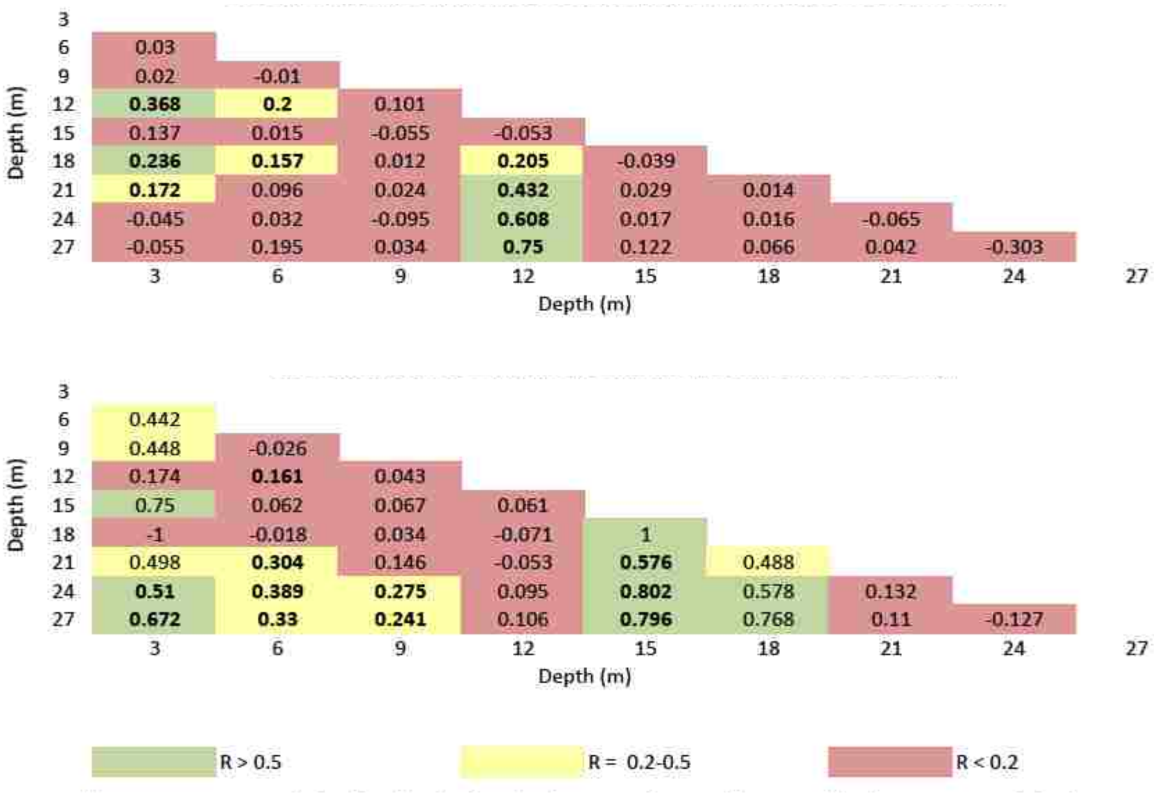
Depth (m)	3	6	9	12	15	18	21	24	27
3									
6	0.002								
9	-0.019	0.008							
12	0.02	**0.078**	**0.041**						
15	**0.05**	**0.088**	**0.08**	0.008					
18	**0.078**	**0.151**	**0.094**	0.012	**0.03**				
21	**0.121**	**0.199**	**0.135**	**0.038**	**0.103**	**0.033**			
24	**0.227**	**0.306**	**0.226**	**0.09**	**0.154**	**0.067**	0.022		
27	**0.123**	**0.2**	**0.132**	**0.064**	**0.105**	**0.046**	0.001	**0.018**	

🟩 R > 0.5

🟨 R = 0.2-0.5

🟥 R < 0.2

Table 4. ANOSIM R-statistics for all pairwise depth comparisons of large mobile fauna communities from horizontal/sloping (top) and vertical (bottom) swath counts. Bolded values indicate significance at p<0.05.



Depth (m)	3	6	9	12	15	18	21	24	27
3									
6	0.03								
9	0.02	-0.01							
12	**0.368**	**0.2**	0.101						
15	0.137	0.015	-0.055	-0.053					
18	**0.236**	**0.157**	0.012	**0.205**	-0.039				
21	**0.172**	0.096	0.024	**0.432**	0.029	0.014			
24	-0.045	0.032	-0.095	**0.608**	0.017	0.016	-0.065		
27	-0.055	0.195	0.034	**0.75**	0.122	0.066	0.042	-0.303	

Depth (m)	3	6	9	12	15	18	21	24	27
3									
6	0.442								
9	0.448	-0.026							
12	0.174	**0.161**	0.043						
15	0.75	0.062	0.067	0.061					
18	-1	-0.018	0.034	-0.071	1				
21	0.498	**0.304**	0.146	-0.053	**0.576**	0.488			
24	**0.51**	**0.389**	**0.275**	0.095	**0.802**	0.578	0.132		
27	**0.672**	**0.33**	**0.241**	0.106	**0.796**	0.768	0.11	-0.127	

🟩 R > 0.5 🟨 R = 0.2-0.5 🟥 R < 0.2

Figures

Figure 1. Location of the San Juan Archipelago in the Salish Sea (inland waters of Washington State). Inset images from Google Earth.

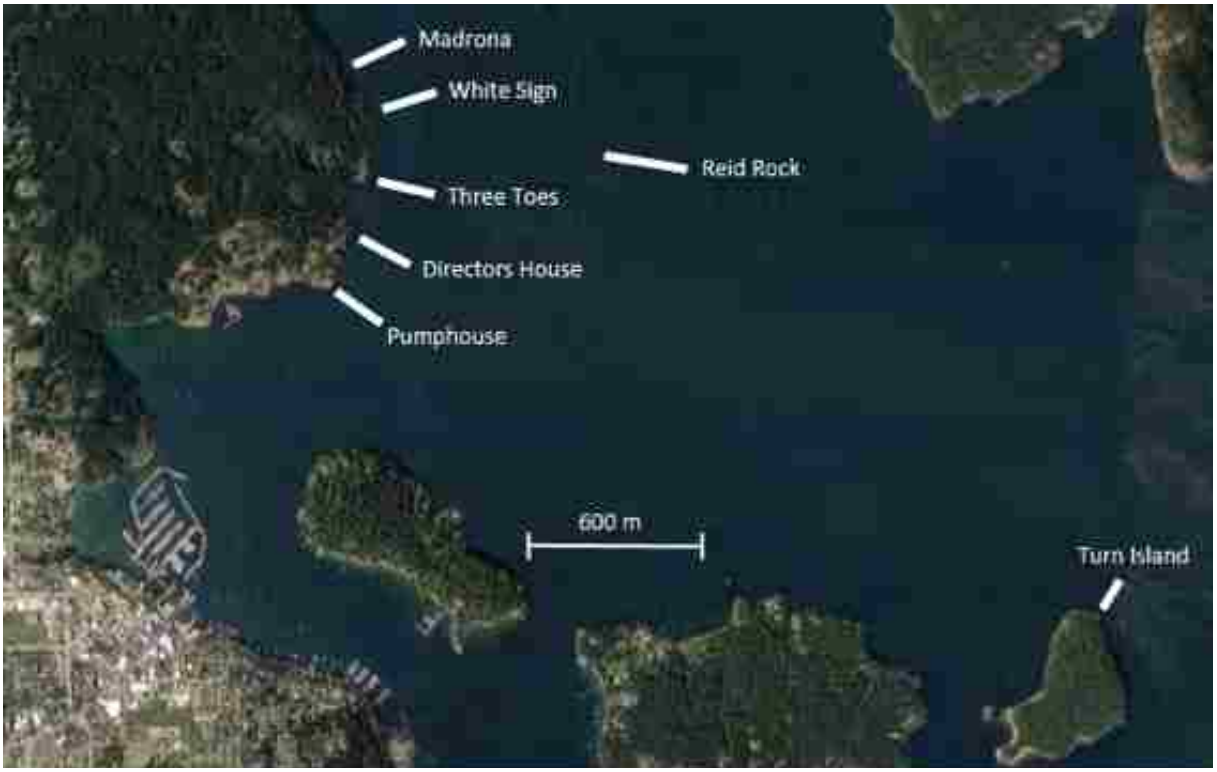


Figure 2. Study site locations in the San Juan Channel. Map image from Google Earth.

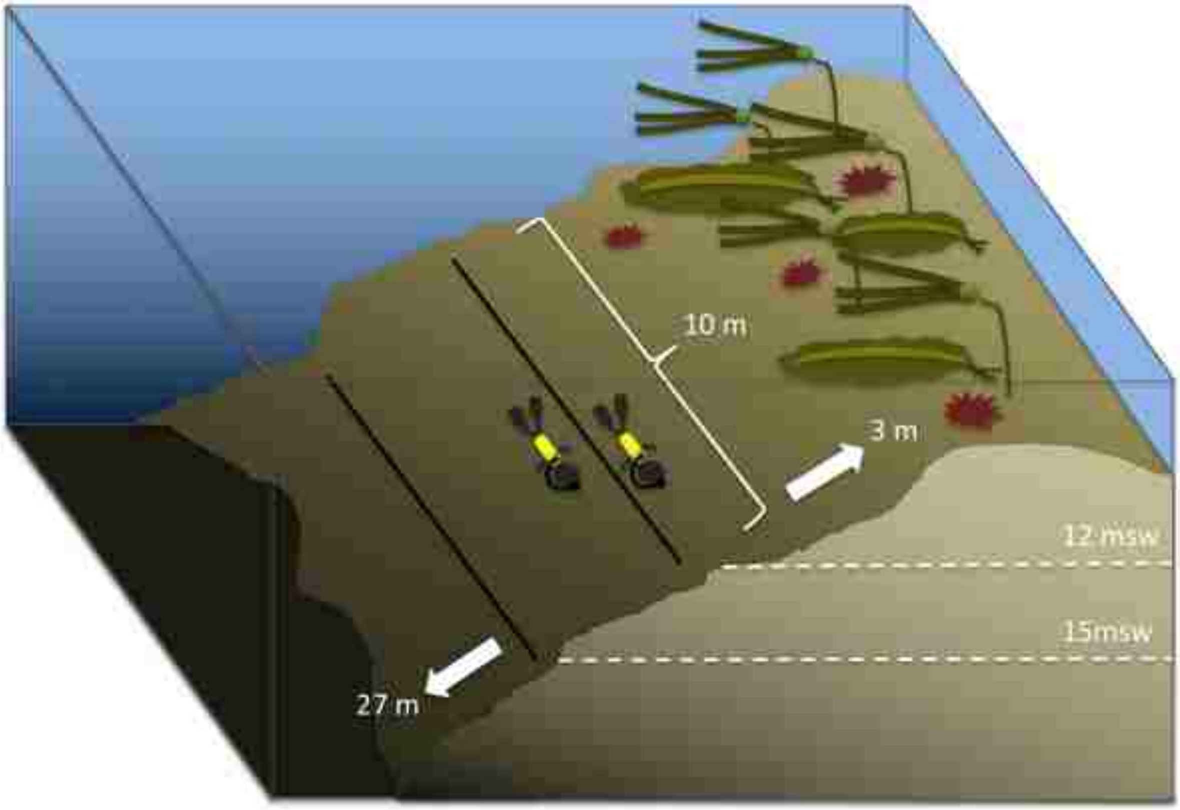


Figure 3. Typical study site layout, with semi-permanent 10 m depth contour transects placed at 3 m depth intervals, ranging from 3 m to 27 m below the mean lower low tide datum, with permanently installed stainless steel pins and numbered plastic tags as transect starting points.

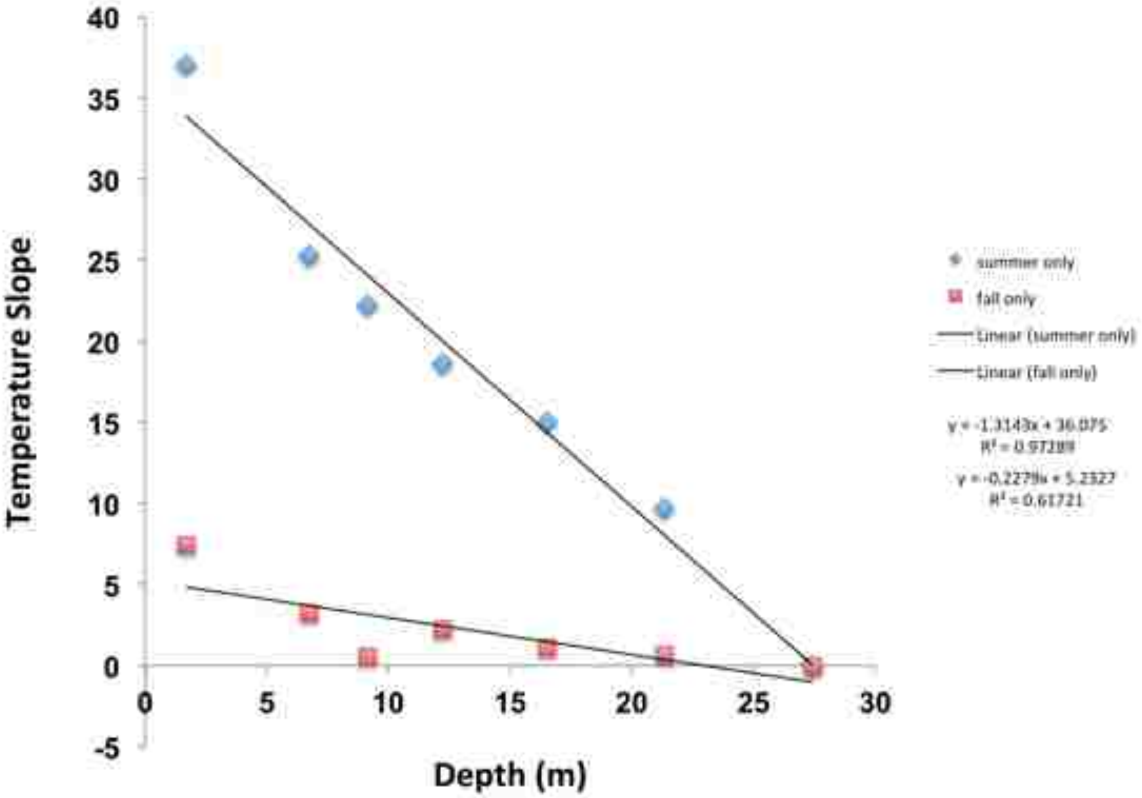


Figure 4. Temperatures at each depth compared to temperature at the deepest site (27 m). The y-axis is the slope of the regression line comparing temperatures at the same half hour measurement interval. A slope of 25 represents a 25% increase in temperature at any shallow site, for every degree of temperature increase at the 27 m site (slope of 1.25).

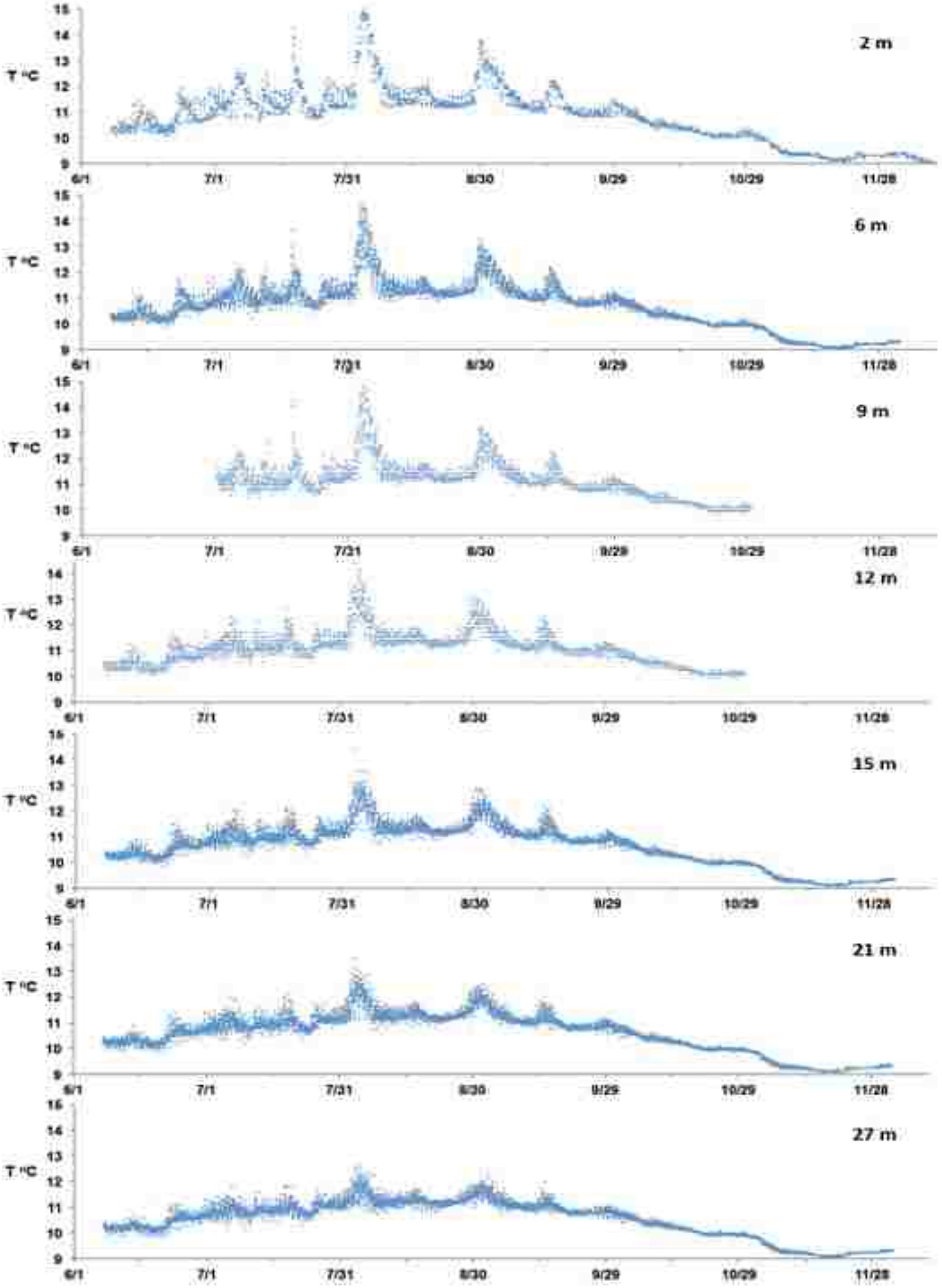


Figure 5. Temperatures from June 7 to December 2, 2017 at each depth at Cantilever Point (Pumphouse), at the north end of Friday Harbor, WA. Note the concurrent peaks of temperature during the summer months, which appear at each depth. These peaks represent pulses of warm, less saline, water originating from the Fraser River north of this site.

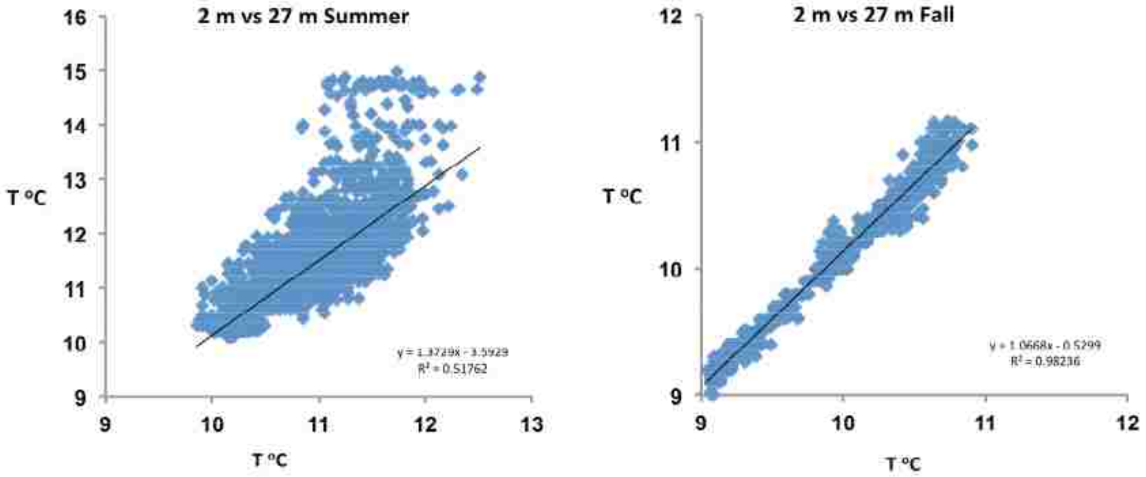


Figure 6. Regressions of temperature at 2m depth versus that at 27 m depth during summer and fall months for each half hour sampling interval.

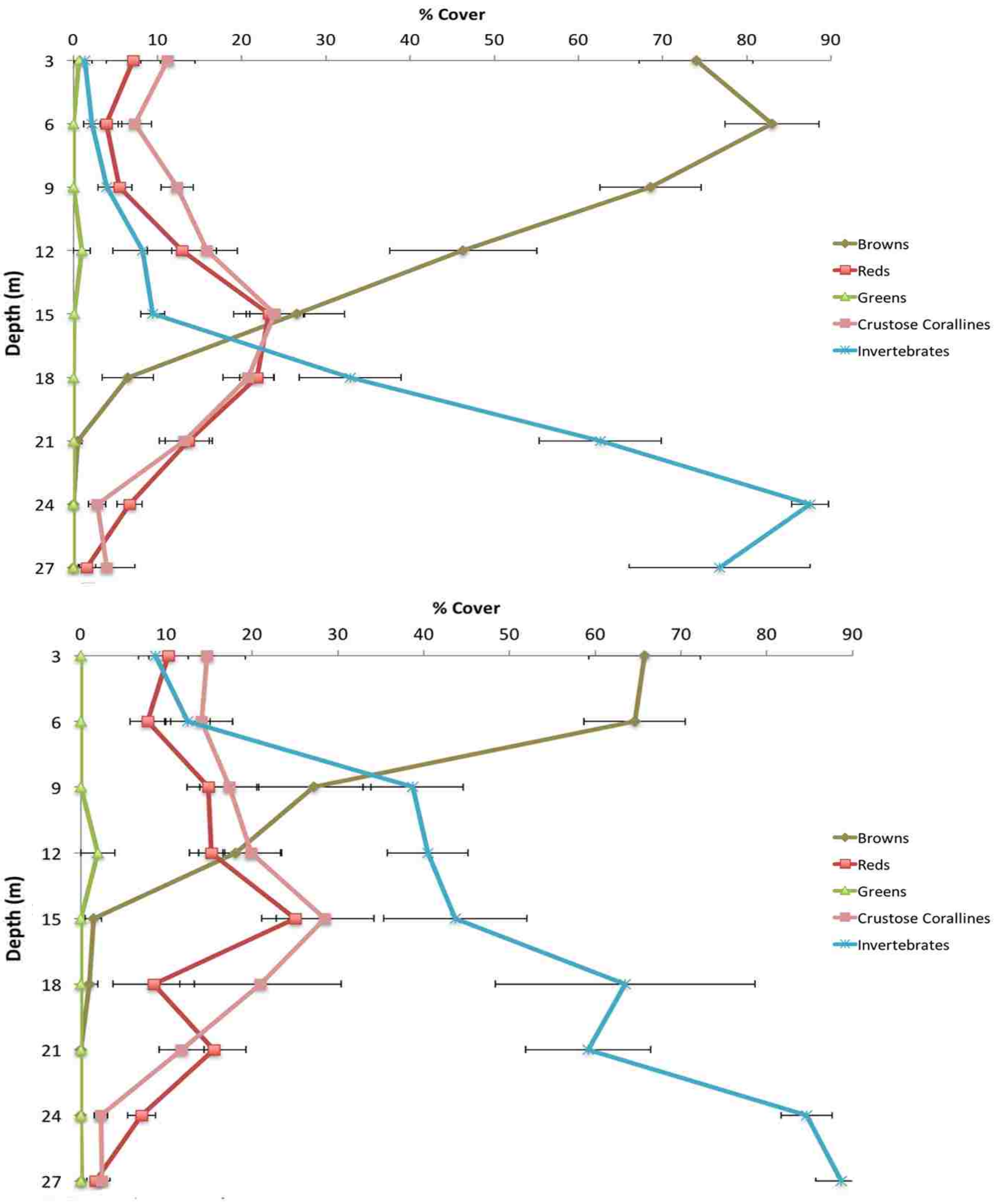


Figure 7. Percent cover of algal and invertebrate assemblages by depth on horizontal/sloping surfaces (top) and vertical surfaces (bottom). Bars are standard error.

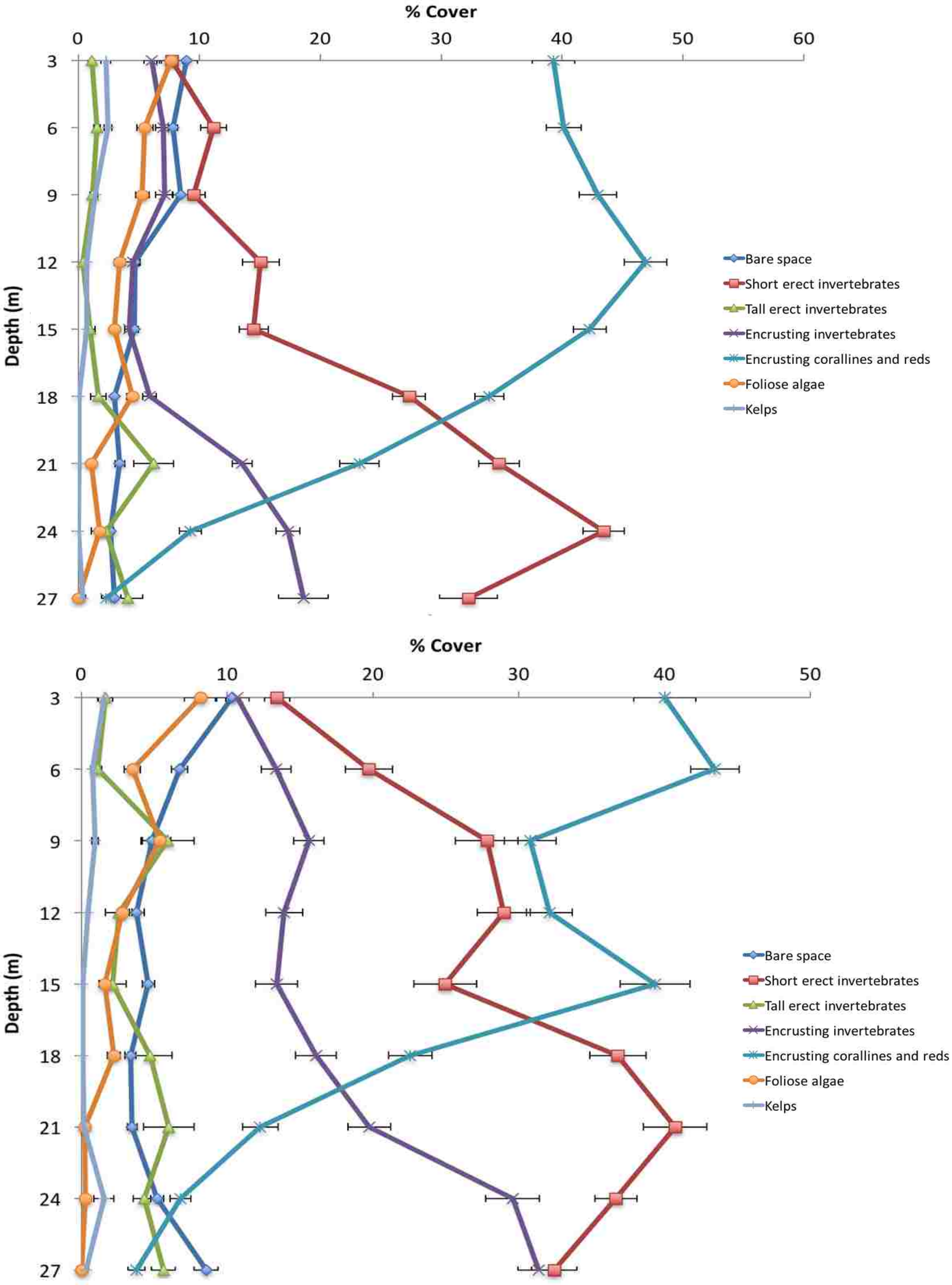


Figure 8. Percent cover of benthic sessile invertebrate assemblages by depth on horizontal/sloping surfaces (top) and vertical surfaces (bottom). Bars are standard error.

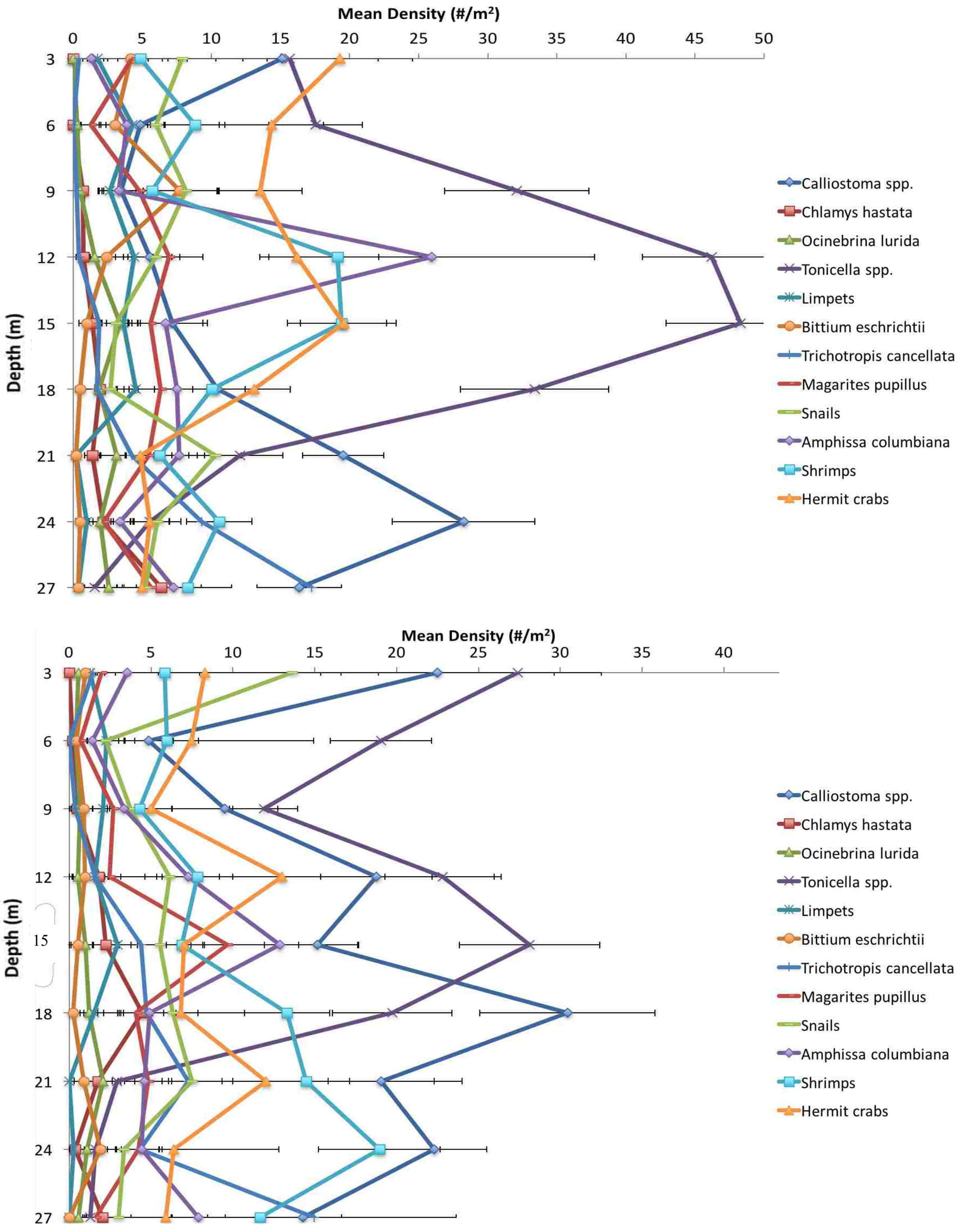


Figure 9. Mean density of small mobile fauna assemblages by depth on horizontal/sloping surfaces (top) and vertical surfaces (bottom). Bars are standard error

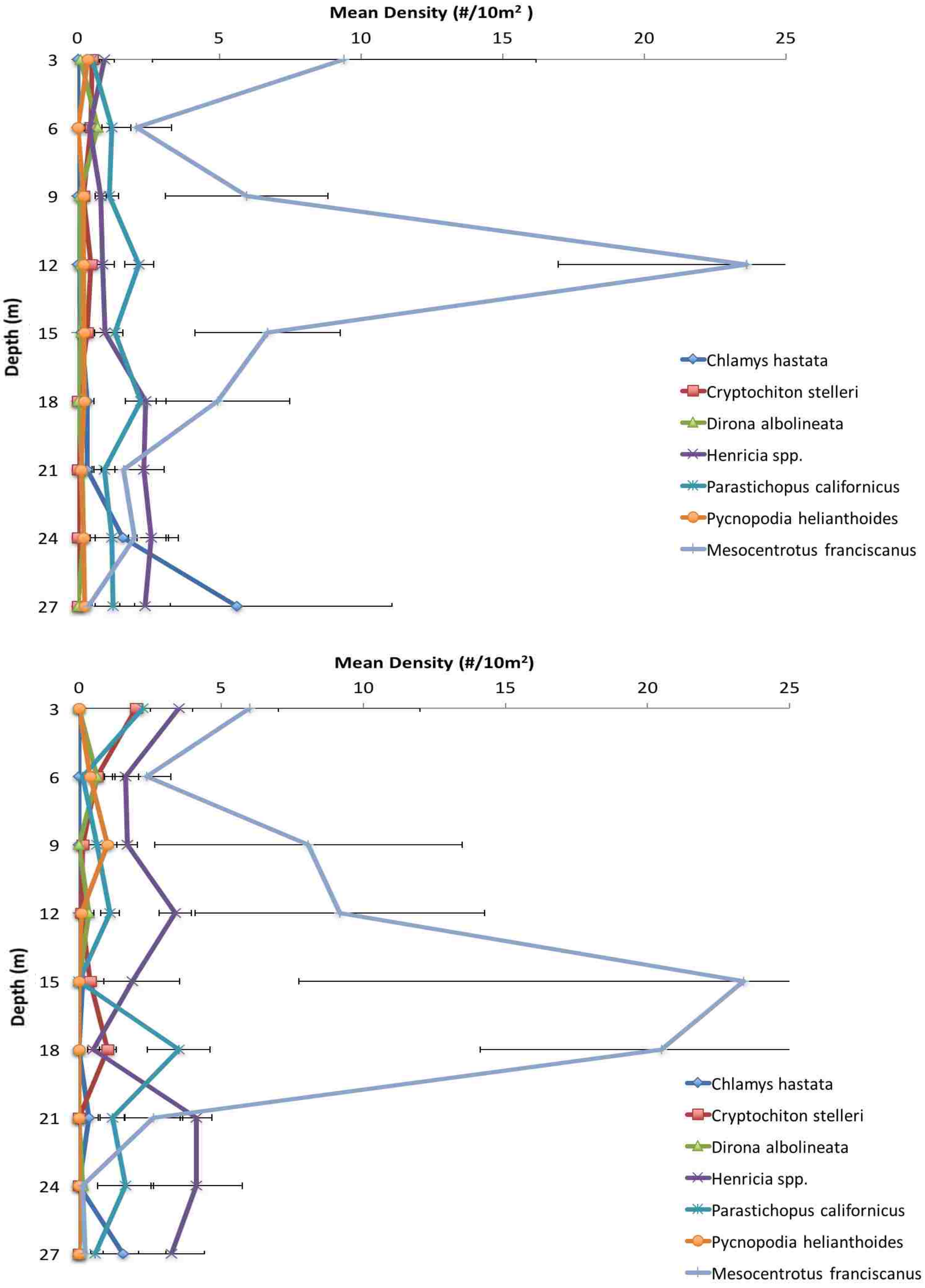


Figure 10. Mean density of large mobile fauna assemblages by depth on horizontal/sloping surfaces (top) and vertical surfaces (bottom). Bars are standard error.

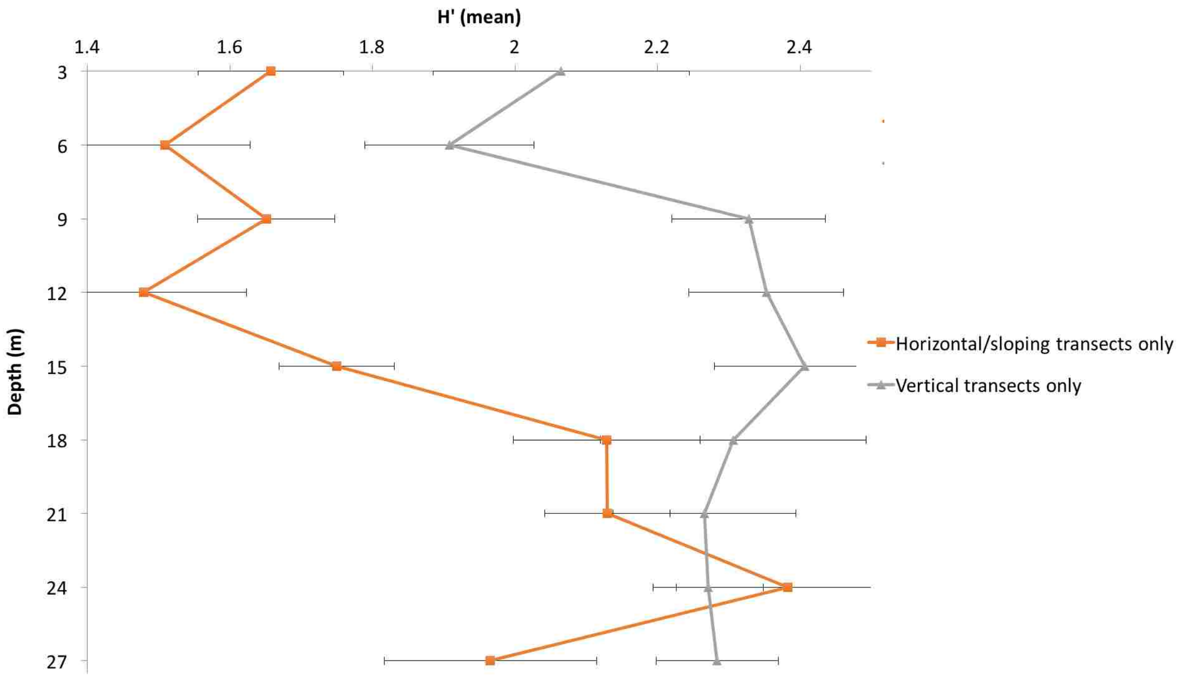


Figure 11. Plot of average Shannon diversity (H') for algal and invertebrate assemblages on horizontal/sloping and vertical transects. Bars are standard error.

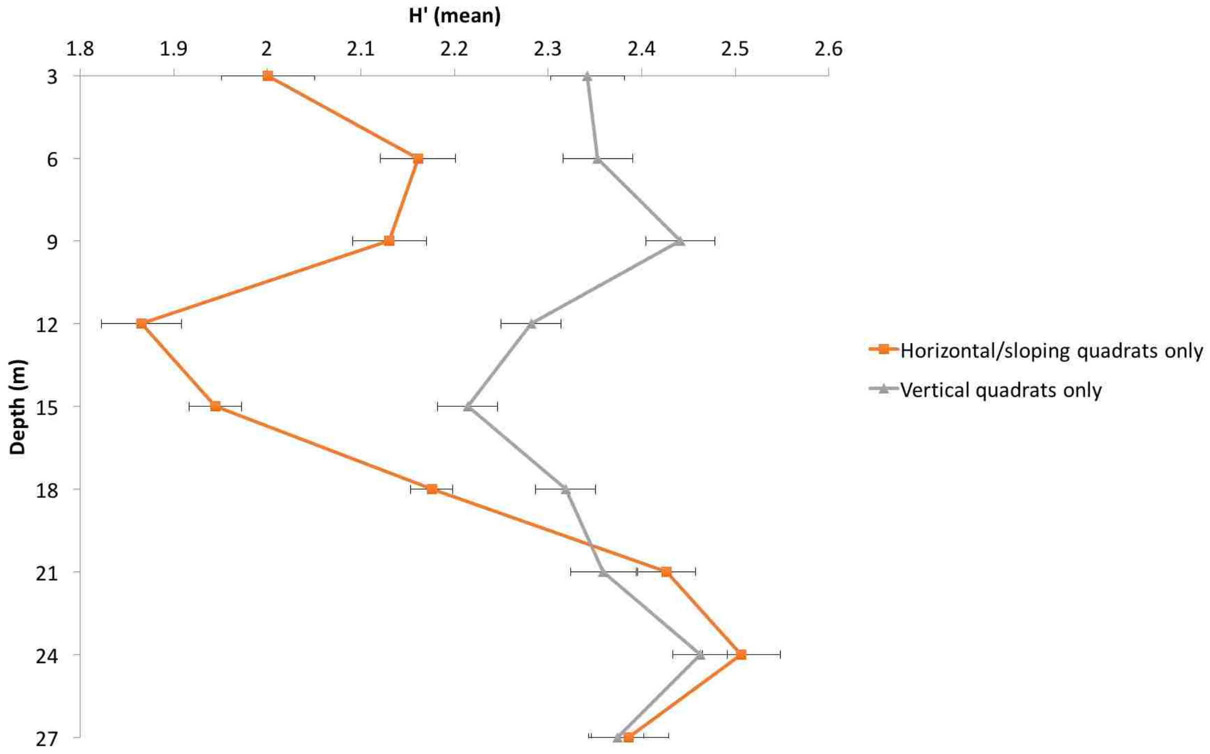


Figure 12. Plot of average Shannon diversity (H') for benthic sessile invertebrate assemblages on horizontal/sloping and vertical transects. Bars are standard error.

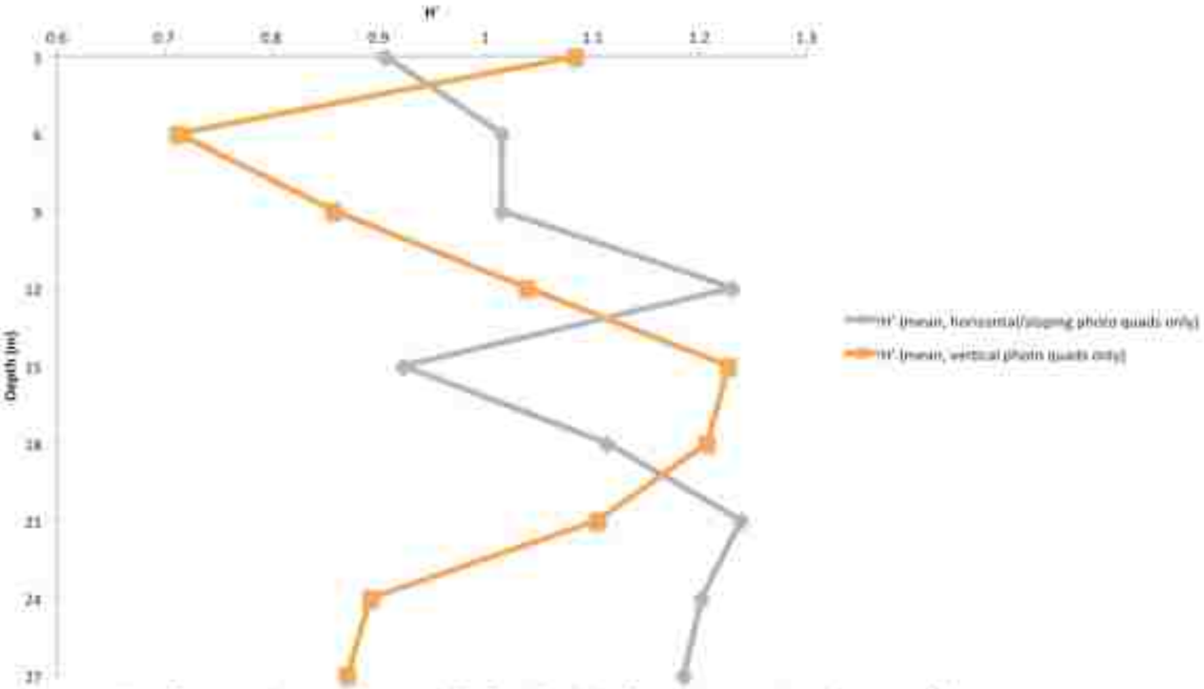


Figure 13. Plot of average Shannon diversity (H') for small mobile fauna assemblages on horizontal/sloping and vertical photo quadrats.

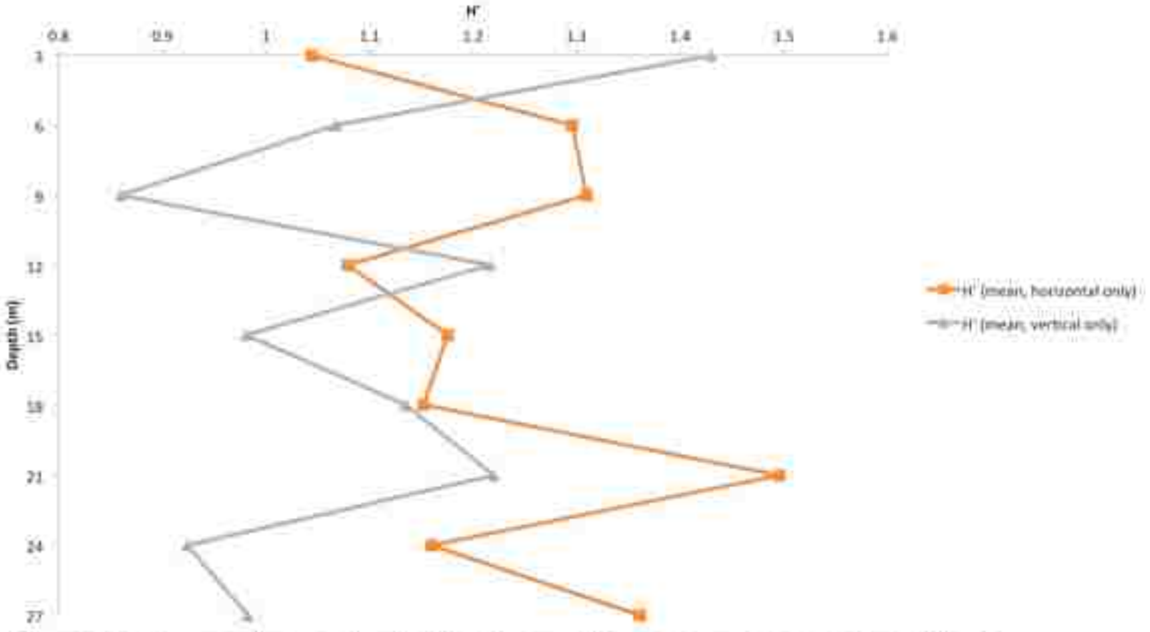


Figure15 Plot of average Shannon diversity (H') of large mobile fauna communities on horizontal/sloping and vertical transects

Figure 14. Plot of average Shannon diversity (H') for large mobile fauna assemblages on horizontal/sloping and vertical swath counts.

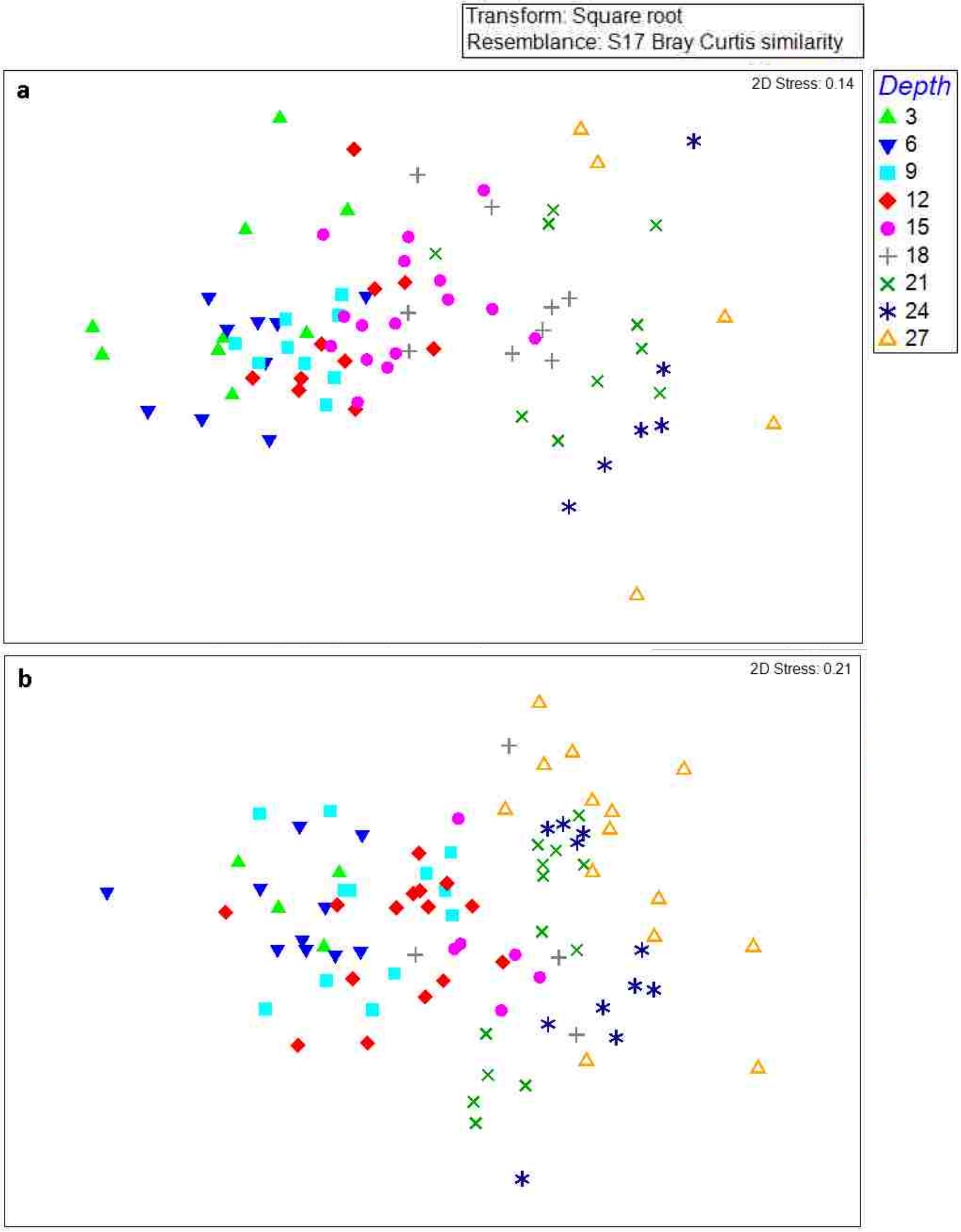


Figure 15. nMDS plots of algal and invertebrate assemblages by depth on a) horizontal/sloping and b) vertical transects.

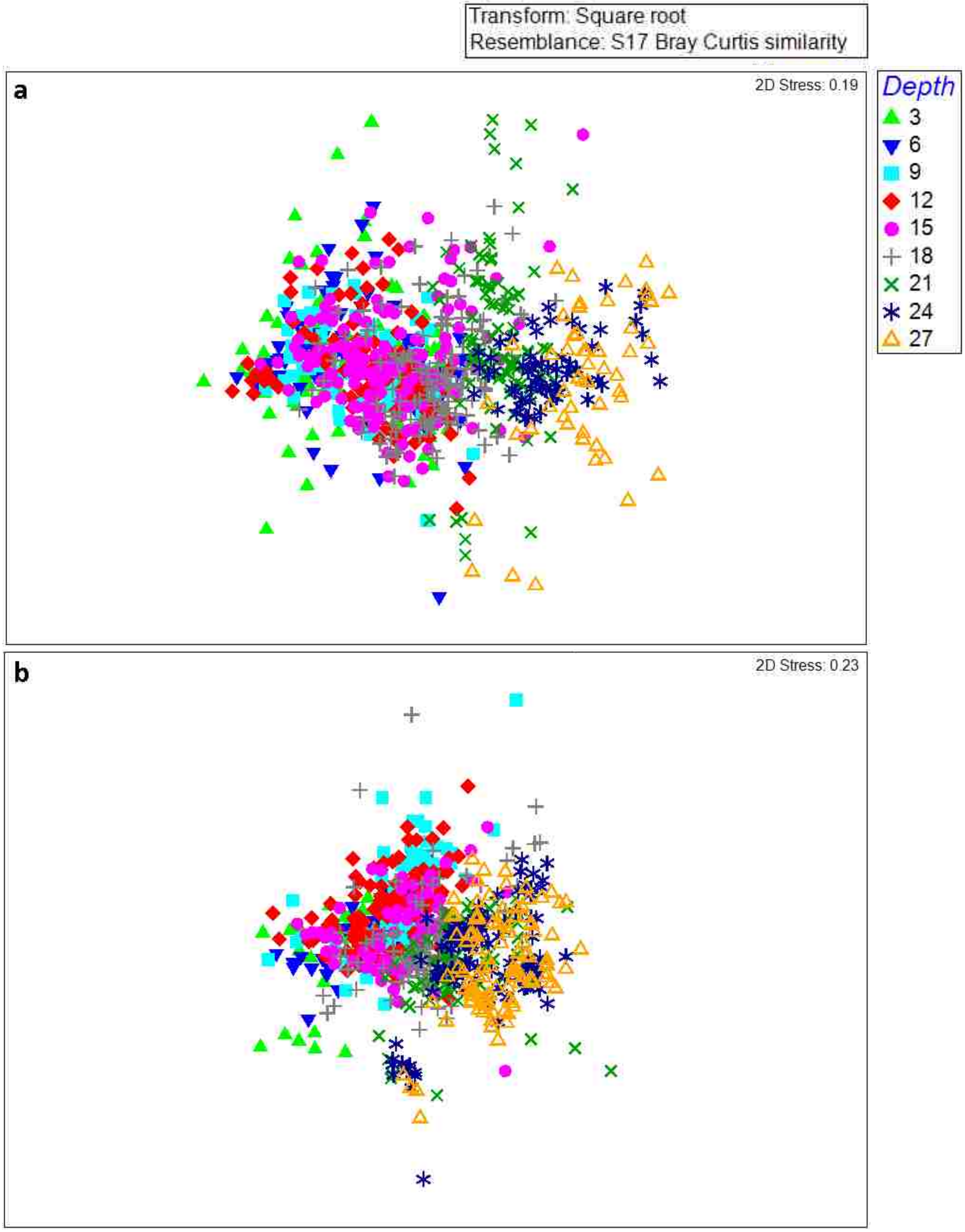


Figure 16. nMDS plots of benthic sessile invertebrate assemblages by depth on a) horizontal/sloping and b) vertical transects.

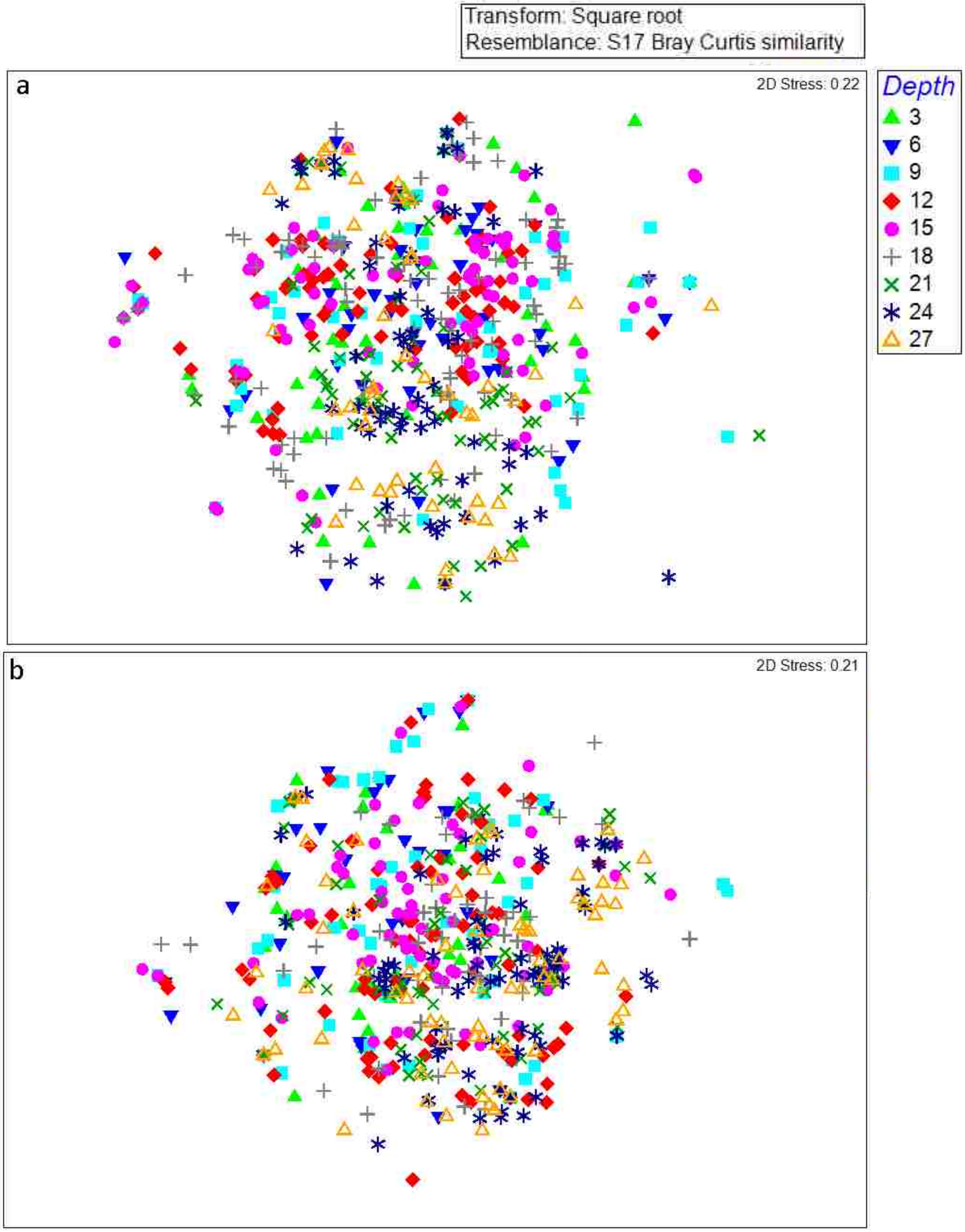


Figure 17. nMDS plots of small mobile fauna assemblages by depth on a) horizontal/sloping and b) vertical photo quadrats.

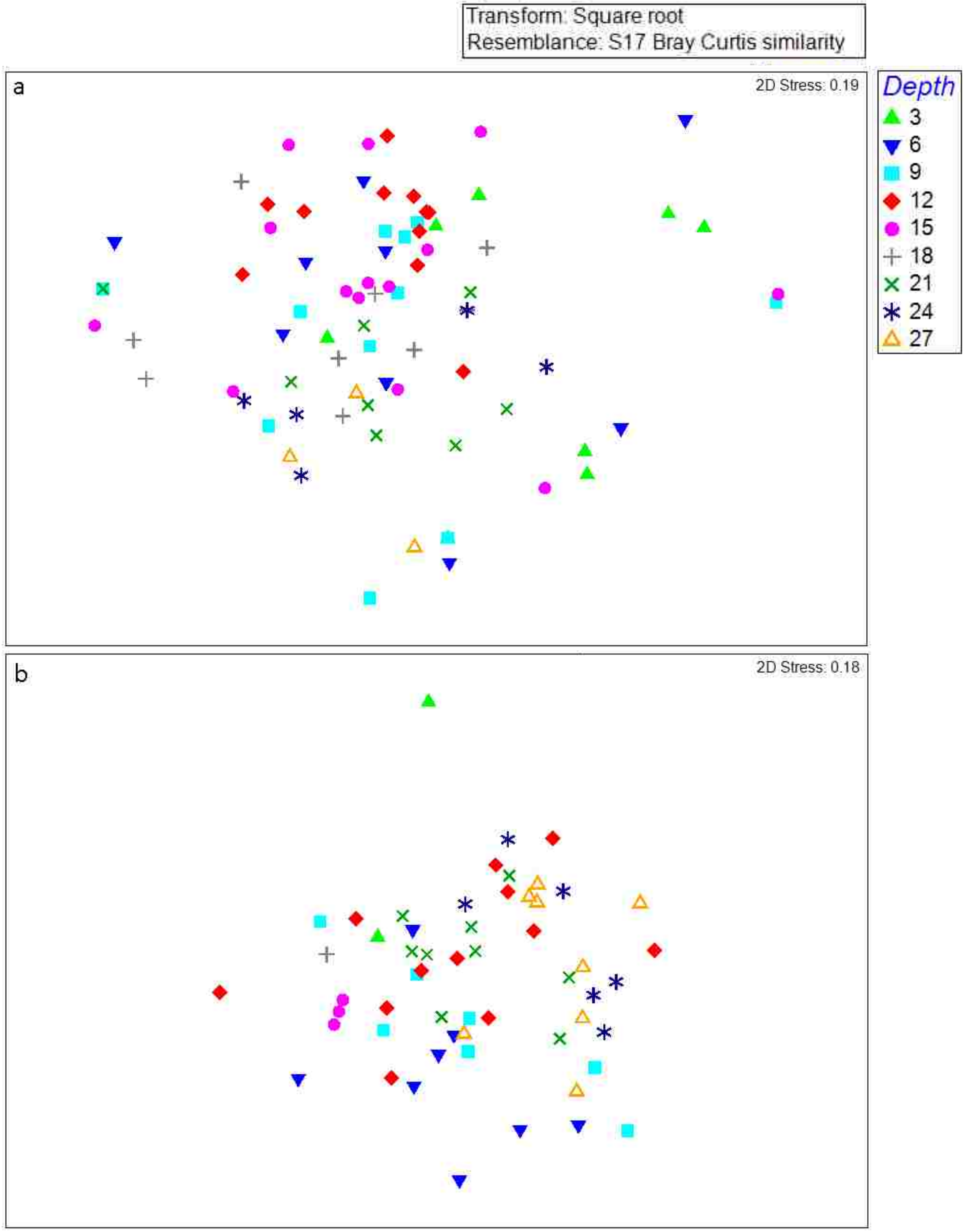


Figure 18. nMDS plots of large mobile fauna assemblages by depth on a) horizontal/sloping and b) vertical photo quadrats.

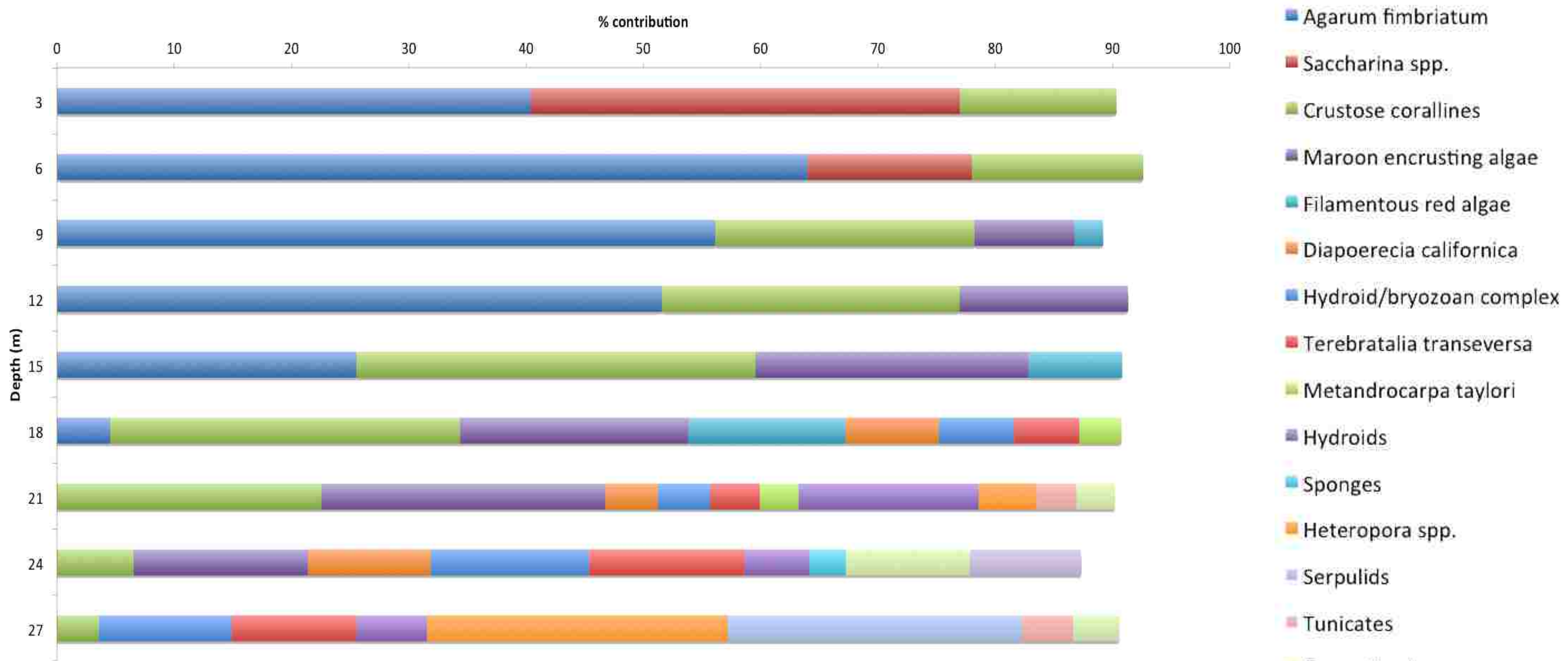


Figure 19. SIMPER contributions to algal and invertebrate assemblage similarity by depth from horizontal/sloping line-intercept transects.

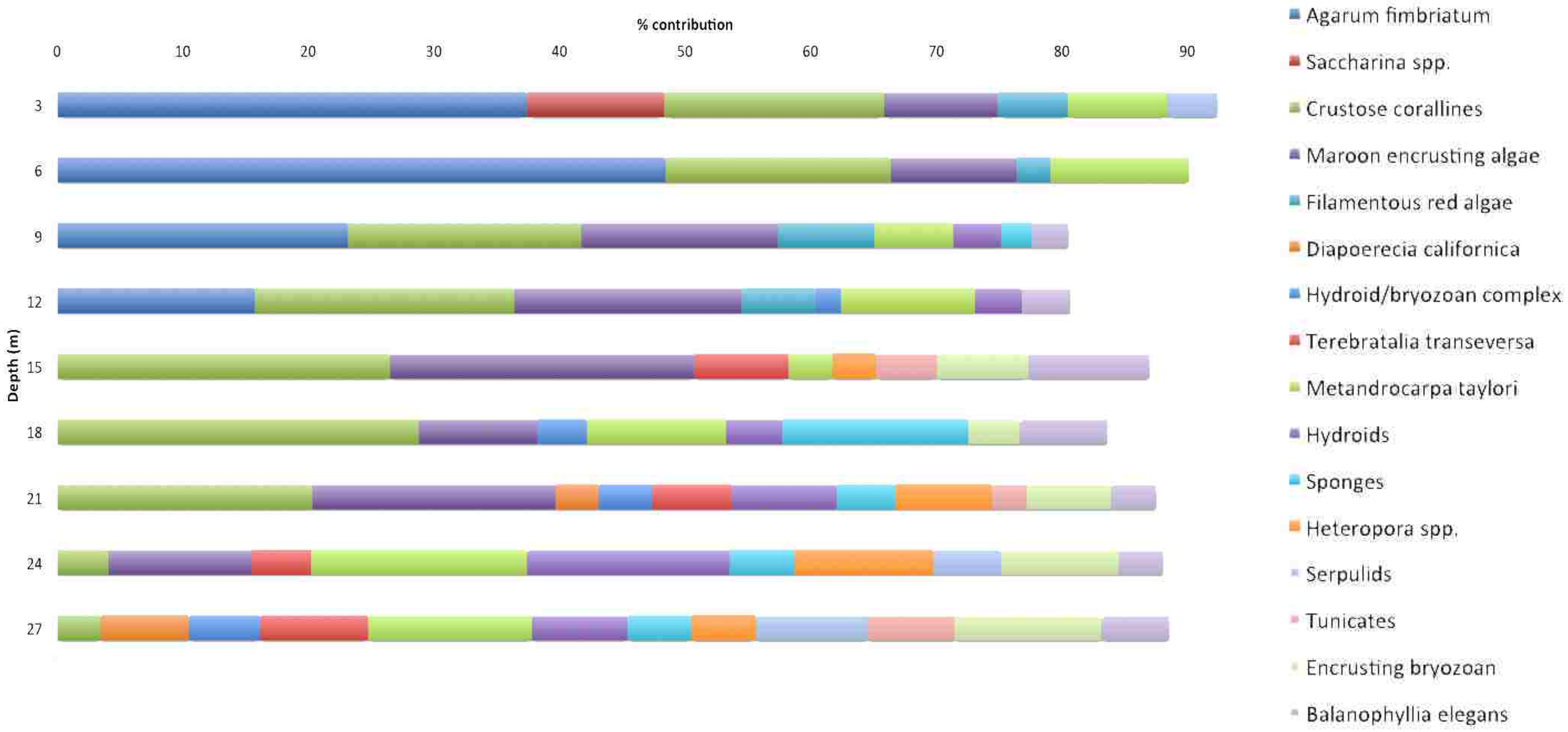


Figure 20. SIMPER contributions to algal and invertebrate assemblage similarity by depth from vertical line-intercept transects.

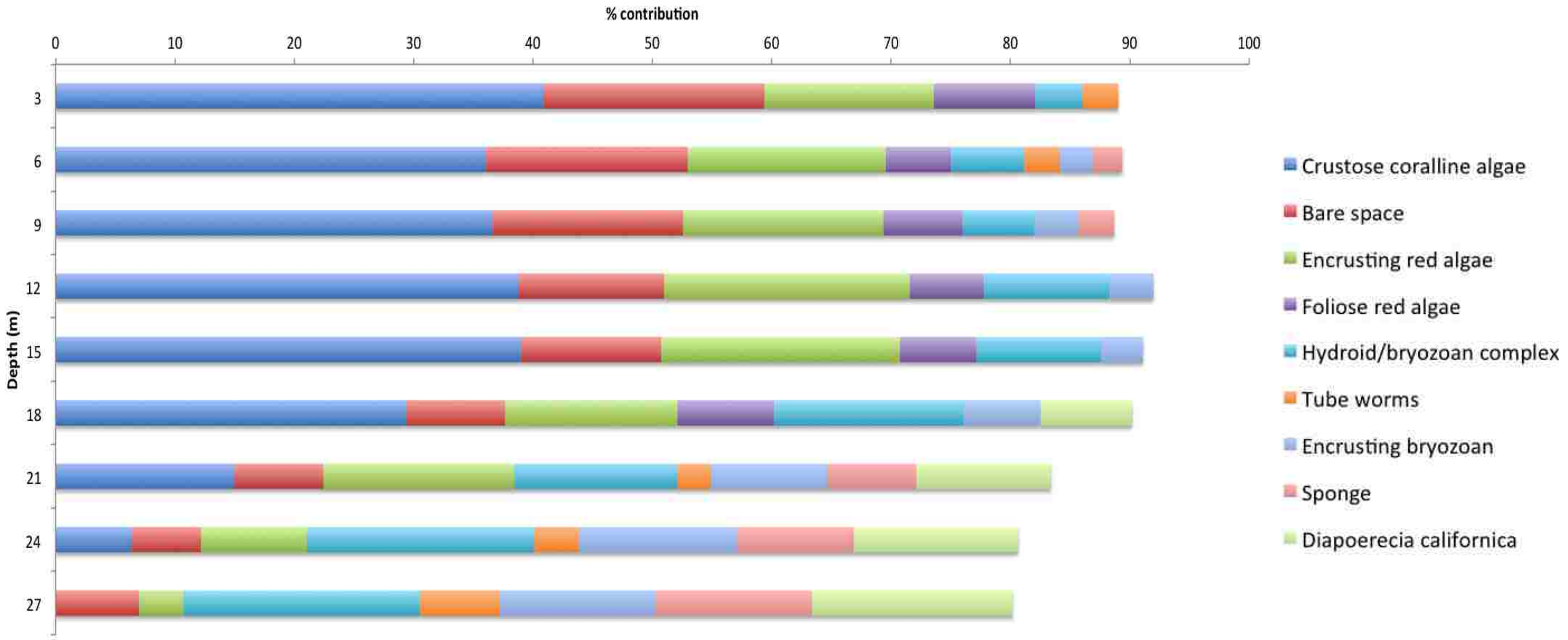


Figure 21. SIMPER contributions to benthic sessile invertebrate assemblage similarity by depth from horizontal/sloping photo quadrats.

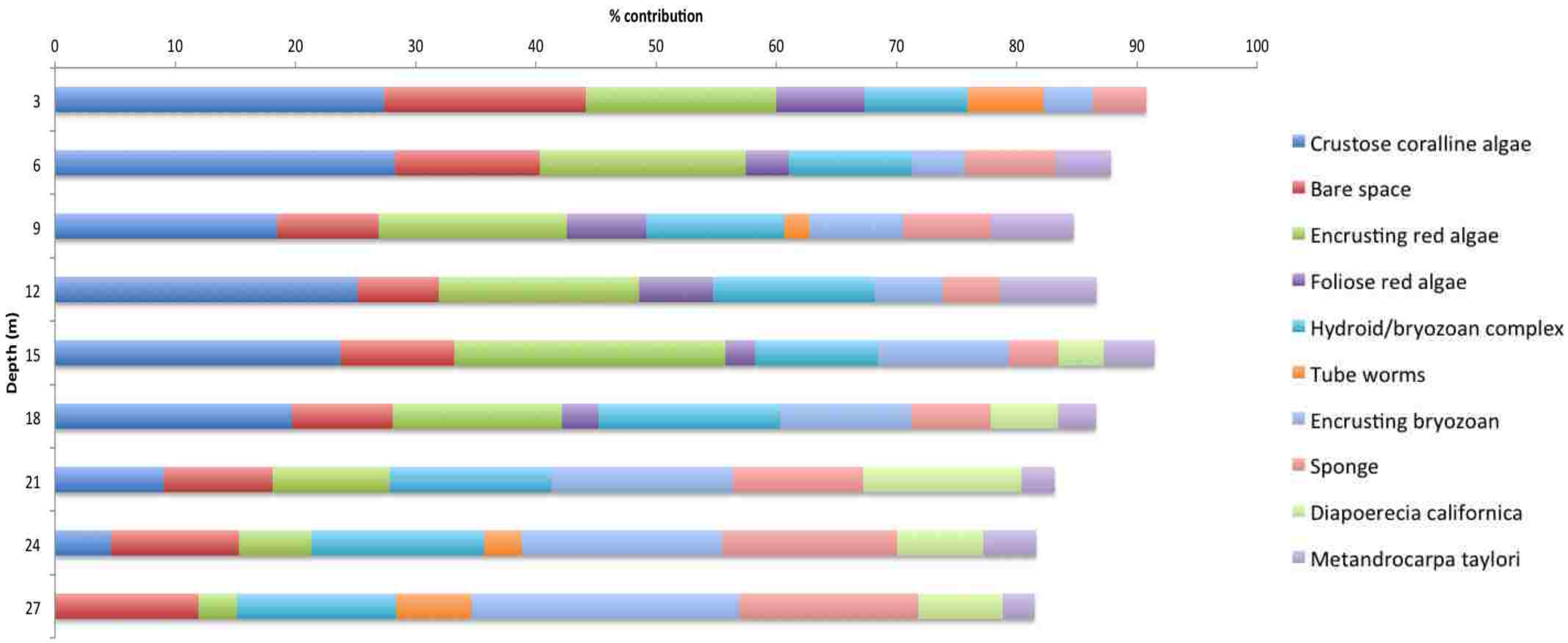


Figure 22. SIMPER contributions to benthic sessile invertebrate assemblage similarity by depth from vertical photo quadrats.

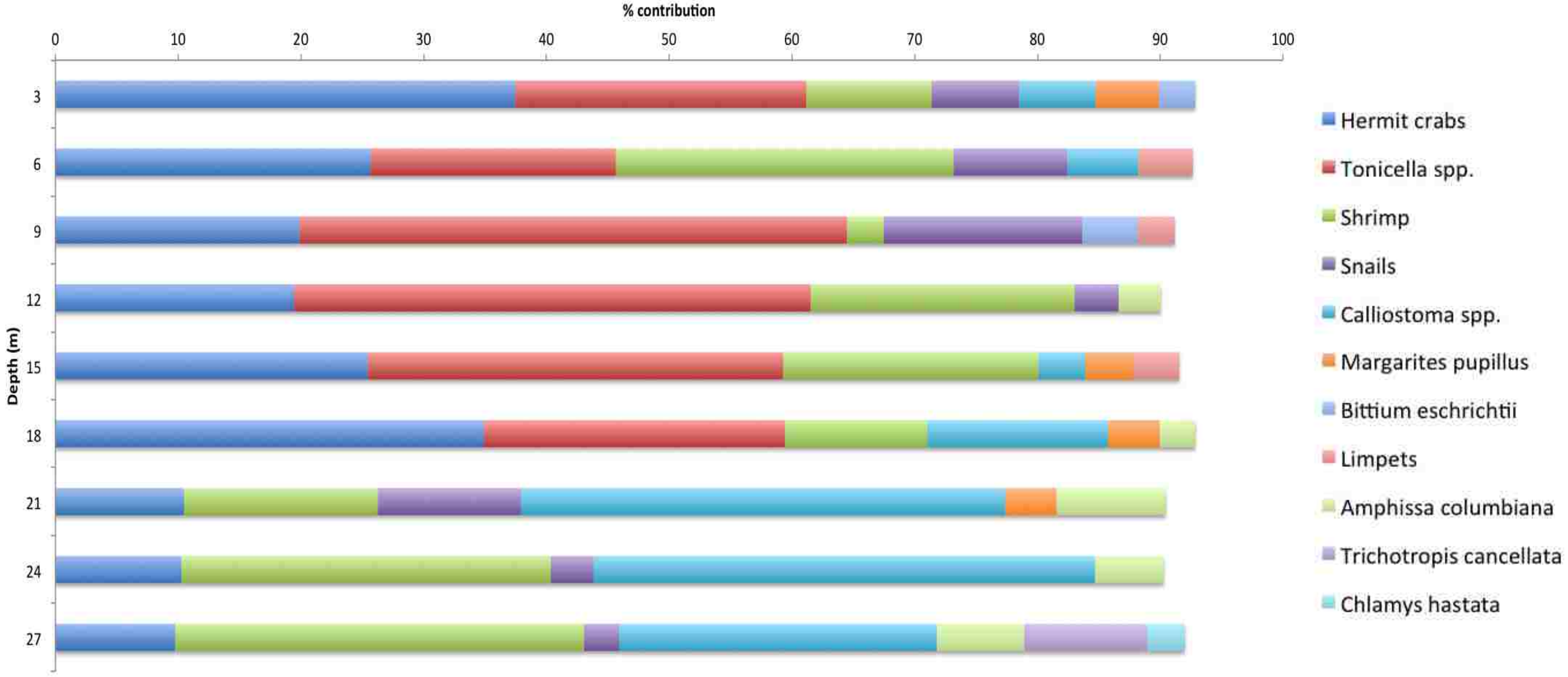


Figure 23. SIMPER contributions to small mobile fauna assemblage similarity by depth from horizontal/sloping photo quadrats.

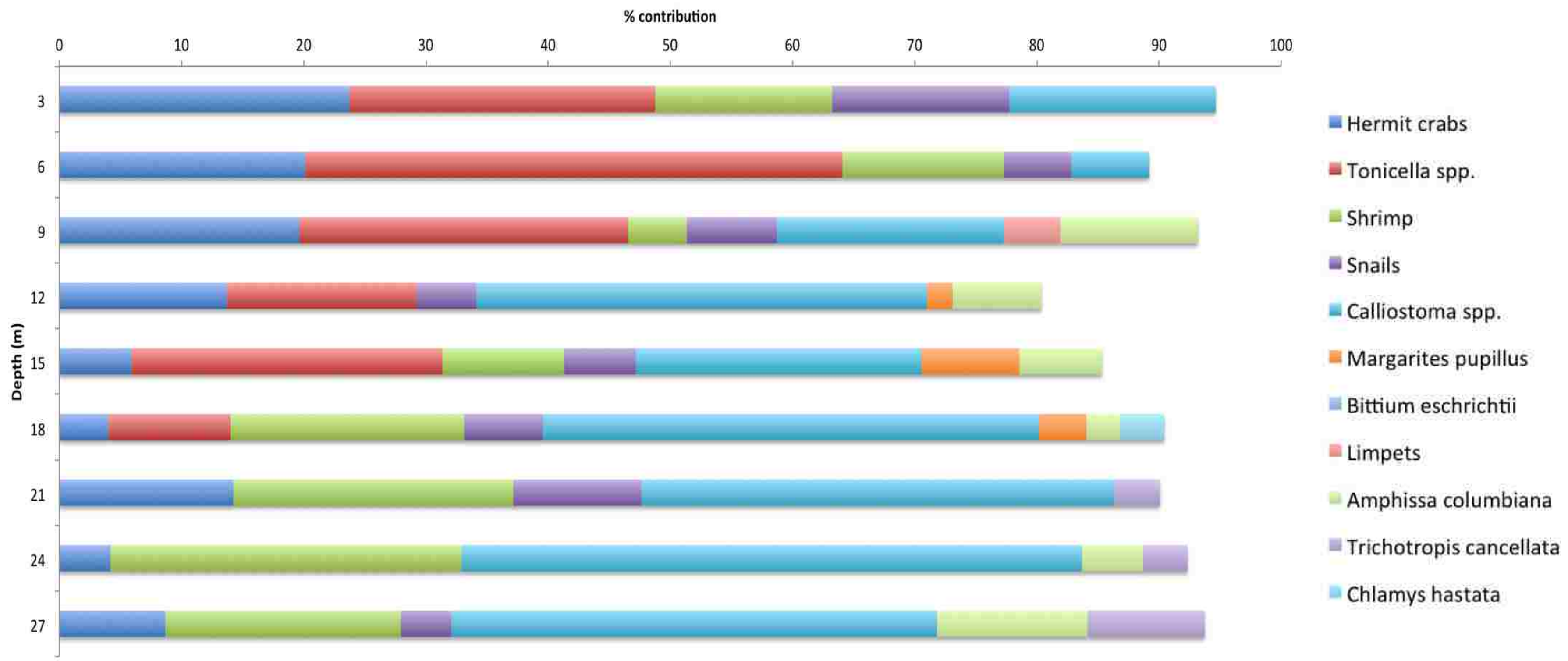


Figure 24. SIMPER contributions to small mobile fauna assemblage similarity by depth from vertical photo quadrats.

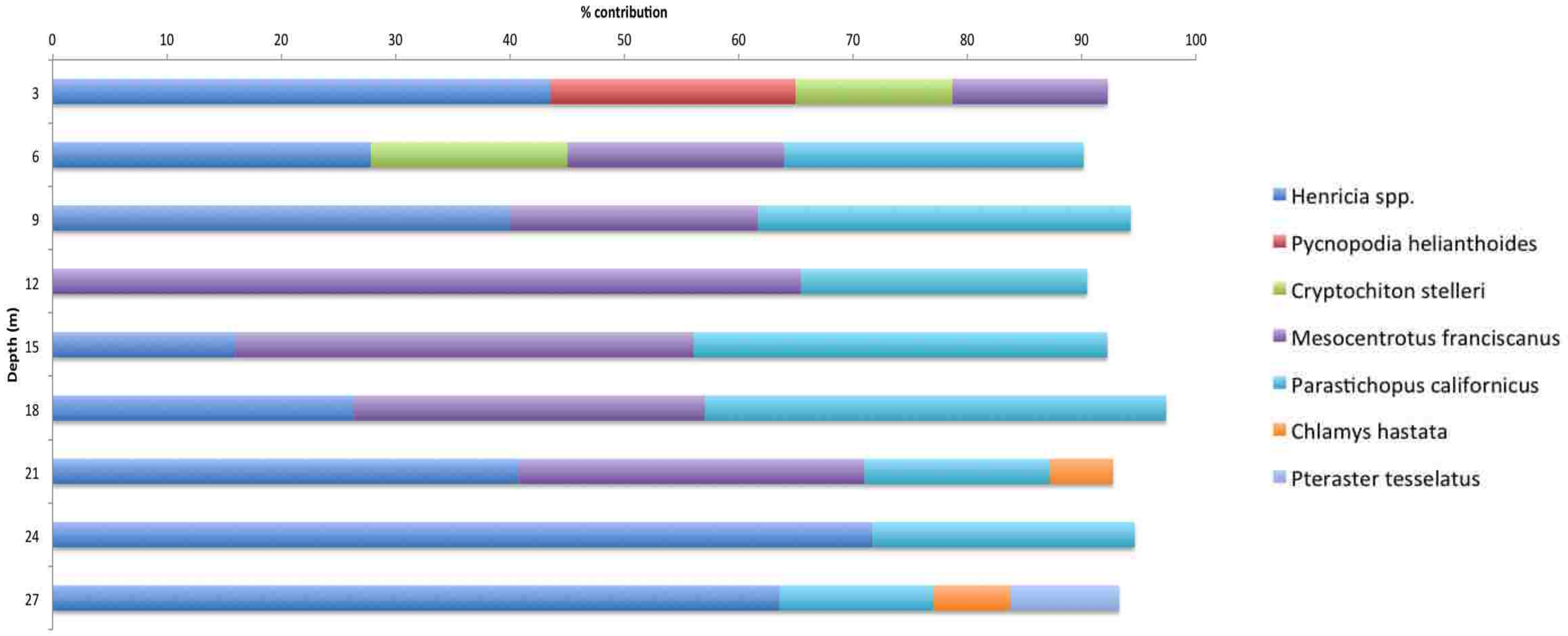


Figure 25. SIMPER contributions to large mobile fauna assemblage similarity by depth from horizontal/sloping swath counts.

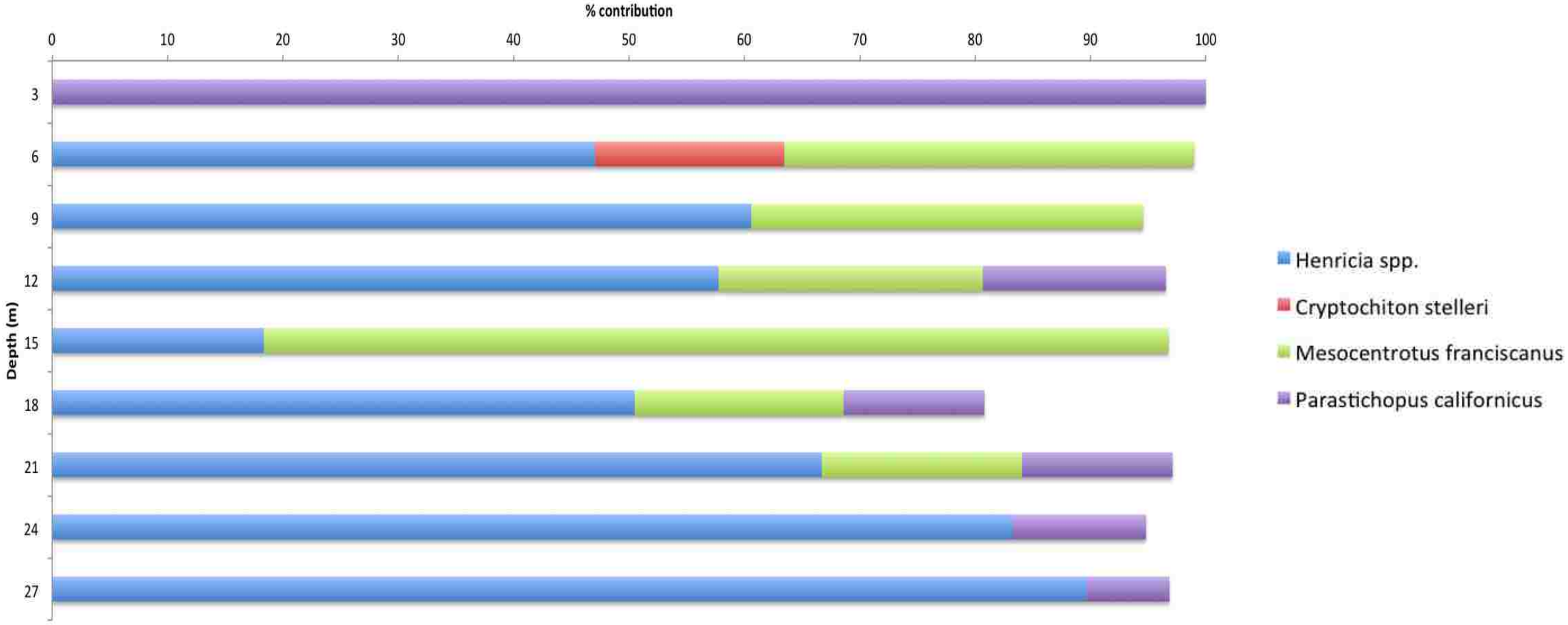


Figure 26. SIMPER contributions to large mobile fauna assemblage similarity by depth from vertical swath counts.

Supplemental Material

Alphabetical category/taxa lists for each data collection type

Line-intercept:

Non-organismal categories

Bare rock
Sediment
Shell/rock

Taxa

Agarum fimbriatum
Alaria marginata
Aplidium solidum/californicum
Balanophyllia elegans
Balanus crenatus
Balanus nubilis
Bivalve (unidentified)
Branching bryozoan
Clavelina huntsmani
Cliona californiana
Costaria costata
Crassadoma gigantea
Cribrinopsis spp.
Crisia spp.
Crustose corallines
Cystodytes lobatus
Desmarestia munda
Diapoeroecia californica
Didemnum carnulentum
Distaplia occidentalis
Dodecaceria concharum
Encrusting bryozoan (unidentified)
Epizoanthus scotinus
Eudistoma purporpunctatum
Eurystomella bilabiata
Fauchea laciniata
Filamentous green algae
Filamentous red algae
Fucus distichus
Heteropora alaskensis/pacifica
Hydroid/bryozoan complex
Hydroids (unidentified)
Kelp (sporeling, unidentified)
Laminaria complanata
Maroon encrusting algae
Metandrocarpa taylori
Metridium spp.
Myxicola infundibulum
Nereocystis luetkeana
Pileolaria spp.
Pododesmus macrochisma
Psolus chitonoides
Pycnoclavella stanleyi
Pyura haustor
Saccharina latissima
Saccharina subsimplex
Sargassum muticum
Schizoporella unicornis
Serpullid (unidentified)
Sponges (unidentified)
Styela spp.
Stylantheca spp.
Sycon spp.
Terebratalia transversa
Terebratulina unguicula
Tube complex
Tunicates (unidentified)
Ulva spp.
Urticina spp.

Benthic photo quadrats:

Non-organismal categories

Bare space
Rubble/Debris/Shell hash
Sediment

Taxa

Abietinaria spp.
Agarum fimbriatum
Aplidium solidum
Ascidia paratropa
Balanophyllia elegans
Balanus crenatus
Balanus nubilis
Boltenia villosa
Bryozoan (branching, unidentified)
Bryozoan (encrusting)
Chelyosoma spp.
Chondracanthus exasperatus
Clavelina huntsmani
Clavularia spp.
Cliona californiana
Cnemidocarpa finmarkiensis
Corella spp.
Costaria costata
Crassadoma gigantea
Cribrinopsis fernaldi
Crisia spp.
Crustose corallines
Cystodytes lobatus
Dendrobeania lichenoides
Desmarestia viridis
Diapoeroecia californica
Didemnum spp.
Distaplia occidentalis
Dodecaceria concharum
Encrusting algae (maroon, unidentified)
Epizoanthus scotinus
Eudistoma purpuropunctatum
Eurystomella bilabiata
Fucus distichus
Halocynthia igaboja
Heteropora pacifica
Hydroid spp.
Hydroid/Bryozoan complex
Kelp (unidentified)
Lafoeia spp.
Laminaria complanata
Leucilla nuttingi
Leucosolenia spp.
Metandrocarpa taylori
Metridium farcimen
Myxicola infundibulum
Nereocystis luetkeana
Phidolopora pacifica
Pododesmus machrochisma
Psolidium bidiscum
Psolus chitonodes
Pycnoclavella stanleyi
Pyura haustor
Red algae (unidentified)
Red algae (coralline, erect)
Saccharina bongardiana
Saccharina latissima
Sargassum muticum
Schizoporella unicornis
Serpulid (unidentified)
Spirorbid (unidentified)
Spiochaetocerus costarum
Sponge (unidentified)
Stenogramme interrupta
Styela spp.
Stylantheca spp.
Suberites montiniger
Synoicum parfustis
Terebratalia transversa
Terebratalia unguicula
Tube worm (complex)
Tube worm (unidentified)
Tunicate (colonial, unidentified)
Tunicate (solitary, unidentified)
Ulva spp.
Urticina columbiana
Urticina crassicornis

Small mobile fauna photos:

Taxa

Acanthodoris nanaimoensis
Acanthodoris spp.
Acmaea mitra
Agonopsis vulsa
Amphissa columbiana
Astyrss gausapata
Bittium eschrichtii
Bivalve, unidentified
Boreotrophon multicostatus
Cadlina luteomarginata
Calliostoma annulatum
Calliostoma ligatum
Calliostoma, unidentified
Ceratostoma foliatum
Chirolophis nugator
Chiton, unidentified
Chlamys hastata
Clinocardium spp.
Crab, unidentified
Cranopsis cucullata
Cranopsis multistriata
Crepidula spp.
Cryptochiton stelleri
Cryptolithodes spp.
Dendronotus albus
Dendronotus diversicolor
Dermasterias imbricata
Diaulula sandiegensis
Diodora aspera
Dirona albolineata
Doris montereyensis
Doris odhneri
Doris spp.
Eggs (unidentified)
Eupentacta quinquesemita
Evasterias troschelii
Flabellina spp.
Flabellina trilineata
Flabellina triophina
Flabellina verrucosa
Fusitriton oregonensis
Geitodoris heathi
Henricia spp.
Hermissenda crassicornis
Hermit crab, unidentified
Janolus fuscus
Jordania zonope
Katharina tunicata
Limacia cockerelli
Limpet, unidentified
Lopholithodes mandtii
Loxorhynchus crispatus
Magarites pupillus
Mesocentrotus franciscanus
Mopalia kennerleyi
Mopalia spectabilis
Mopalia spp.
Nucella spp.
Nudibranch, unidentified
Nudibranch, unidentified dorid
Ocinebrina lurida
Ophiuroid, unidentified
Oregonia gracilis
Oregonia spp.
Orthasterias koehleri
Pandalus danae
Pandalus platyceros
Parastichopus californicus
Peltodoris spp.
Pholis laeta
Phyllolithodes papillosus
Placetron wosnessenskii
Pteraster tesselatus
Pugettia gracilis
Pycnopodia helianthoides
Rhinogobiops nicholsii
Rhinolithodes wosnessenkii
Scyra acutifrons
Sebastes emphaeus
Sebastes maliger
Shrimp, unidentified
Snail, unidentified
Solaster dawsoni
Strongylocentrotus droebachiensis
Tonicella insignis
Tonicella lineata
Tonicella spp.
Tonicella undocaerulea
Tonicella venusta
Trichotropis cancellata
Triopha catalinae
Tritonia festiva

Large mobile fauna swath counts:

Taxa

Ceratostoma foliatum
Chlamys hastata
Glebocarcinus oregonensis
Cancer productus
Cryptochiton stelleri
Dendronotus albus
Dirona albolineata
Dendronotus dalli
Dendronotus diversicolor
Dermasterias imbricata
Enteroctpous dofleini
Eupentacta quinquesemita
Evasterias troschelii
Fusitriton oregonensis
Henricia spp.
Haliotis kamtschatkana
Mediaster aequalis
Nucella spp.
Oregonia gracilis
Orthasterias koehleri
Pisaster brevispinus
Parastichopus californicus
Pugettia gracilis
Pycnopodia helianthoides
Pteraster militaris
Phyllolithodes papillosus
Pugettia producta
Pteraster tesselatus
Placetron wosnessenskii
Rhinolithodes wosnessenkii
Scyra acutifrons
Solaster dawsoni
Strongylocentrotus droebachiensis
Mesocentrotus franciscanus
Strongylocentrotus purpuratus
Solaster stimpsoni
Triopha catalinae
Tritonia festiva

DGPS coordinates for study sites

Site name	Lat (ddº mm.mmm´)	Lon (ddº mm.mmm´)
Pumphouse (PUMP)	48º 32.773´ N	123º 00.428´ W
Director's House (DIRE)	48º 32.839´ N	123º 00.396´ W
Three Toes (3TOE)	48º 33.012´ N	123º00.330´ W
White Sign (WHIT)	48º 33.140´ N	123º 00.358´ W
Madrone Tree (MADR)	48º 33.173´ N	123º 00.396´ W
Reid Rock (REID)	48º 32.907´ N	122º 59.562´ W
Turn Island (TURN)	48º 32.807´ N	122 º 58.923´ W

CHAPTER 2

Scale-dependent patterns and processes in a rocky subtidal community in the San Juan Archipelago, Washington, USA.

Abstract

Previously, we took a bottom-up approach to studying our subtidal rocky habitat in the San Juan Archipelago by using individual transects and photo quadrats to provide insights into more complex systems at the habitat level. Here, we take a top-down approach to understanding the relationships between observed pattern, underlying processes, and spatial scale, starting first with the big picture at the habitat scale (hundreds of meters), then at the individual substrate-slope scale, and finally focusing in to sub-meter features in the underwater seascape. This three-tiered analysis allowed us to make predictions at each scale and identify areas of overlap in both pattern and process. As expected from our prior results, benthic assemblages become increasingly dissimilar with increasing depth in both the shelf and wall habitat types and again represent a shift from an algal-dominated shallow zone to an epifaunal-dominated deep zone. We provide evidence these changes with depth are much more remarkable for the shelf than for wall habitats. We structured our analysis using three distinct depth zones and discovered the strongest differences in community structure appear between the mid and deep zones, with a dramatic decrease in the cover of crustose coralline and foliose red algae in the deep zone. Within each depth zone, comparing the extreme ends of the substrate angle spectrum (i.e. horizontal vs. vertical) showed a significant difference in the community structure, again largely driven by a decrease in the cover of crustose coralline and foliose red algae on vertical substrates. Lastly, we reveal that in the shallow and mid zones, the benthic sessile assemblages on small vertical patches of substrate are more similar to assemblages in the surrounding shelf habitat than to those typically found on large vertical walls where the opposite is true of the small horizontal patches within a wall habitat. Although the patchy, heterogeneous nature of the habitat we sampled makes it difficult to assign clear roles to any single abiotic factor, these results strongly point to the importance of light and of water flow to structuring benthic sessile communities.

Introduction

Studies on the composition of invertebrate communities in temperate rocky subtidal systems have increased steadily over the past three decades (Witman and Dayton 2001). As for these communities, our understanding of their importance and function at different spatial scales remains patchy at best (Connell and Irving 2008). Given that the occupiable surface area of shallow subtidal seascapes is at least an order of magnitude greater and far less accessible than their intertidal counterparts, the lack of long-term community datasets capable of describing entire communities and ecosystems is understandable. Yet within the available literature, there are recognizable patterns arising from shared mechanisms and processes that persist across local (tens to hundreds of meters) and mesoscale (few to many kilometers) ranges. From Chapter 1, we have provided evidence that such patterns include depth as an important ecological axis in determining community composition, with a shift from a macroalgal-dominated shallow zone to an epifaunal-dominated deep zone, and a 'depth emergence' phenomenon where the diversity and abundance of organisms on horizontal and vertical surfaces start to converge at greater depths.

Abiotic factors such as light, sedimentation, temperature, and disturbance usually co-vary along depth gradients and may relate to community patterns, but the strength of these factors on shaping communities may differ among spatial scales. There are currently few studies in the published literature that attempt to describe the relationship of local and mesoscale community patterns with key processes at different scales. Assessing the impacts that variation in these abiotic factors might have at different spatial scales, accompanied with further studies of biotic factors regulating community composition, provides us with a more complete assessment of shallow subtidal communities and can enhance conservation and management of these critically important habitats. Here, we investigate how the rocky subtidal communities of the San Juan Archipelago can contribute to this area of inquiry.

When examining any ecological system, it is critically important to define at what spatial scale the patterns observed align with the underlying processes that drive them, as most ecological processes are scale-dependent (Steele 1978, Dayton and Tegner 1984, Wiens 1989, Jackson 1991). Where to draw the lines between spatial scales has been a moving target, largely because processes at all spatial scales interact to produce the dynamics of local communities (Levin 1992, Witman and Dayton in Bertness 2001). In terms of many pre- and post-settlement abiotic factors, we could loosely define spatial scale to be the distance one would have to travel before environmental conditions change enough to affect the structure or function of the local community. Even with this loose definition, depending on the environmental conditions being measured and their resulting effects on individuals or entire communities, spatial scale remains relative to the observer and the questions being asked.

Differences in diversity and abundance of invertebrate cover between horizontal and vertical surfaces is one of the most striking and general features of rocky subtidal communities worldwide (Witman and Dayton in Bertness 2001). The distribution and abundance of species based on the paradigm of substrate angle is modified by environmental variables such as, flow regime, sedimentation, light, salinity, aspect, distance from shore, habitat complexity, and substrate aspect as it affects consumer foraging. Horizontal and sloping rock surfaces are typically characterized by macroalgae, encrusting colonial invertebrates (Jackson 1977, Estes and Duggins 1995) and aggregations of solitary invertebrates such as barnacles and mussels

(Paine 1976, Velimirov et al. 1977) while vertical surfaces are characterized by short, erect invertebrates, colonial invertebrates, and a lack of macroalgal cover.

Although terrestrial and marine ecosystems are largely studied separately, topographic features such as the angle of substrate (slope) and the direction of orientation (aspect) of these features have been shown to influence community composition in terrestrial systems (Whittaker 1960; Ohmann and Spies 1998). Studies of marine subtidal communities in temperate regions have shown differences in community composition between horizontal and vertical substrates (Sebens 1985 and 1986, Baynes 1999; Glasby 2000; Miller and Etter 2011), lending strength to the notion that terrestrial and marine subtidal systems share this feature in common. One area of technological advance that holds great promise toward predictive capability in marine ecosystems is multibeam and sidescan sonar, which have been used in bathymetric mapping of seafloor features to create accurate marine navigation charts for decades. Recent studies using bathymetry maps to assess and predict subtidal community assemblages have improved our understanding of community structure and dynamics from regional to local spatial scales (deMoustier and Matsumoto 1993; Clarke et al. 1996; Witman and Dayton 2001; Beaman and Harris 2007; Greene et al. 2007; Shotwell et al. 2007; Whitmire et al. 2007; Wedding et al. 2008; Miller and Etter 2008, Brown and Blondel 2009). However, such surveys often miss the shallow subtidal habitats closest to shore.

In Chapter 1, we took a bottom up approach to studying our subtidal rocky habitat in the San Juan Archipelago by using individual transects and photo quadrats to provide insights into more complex systems at the habitat level. In this framework, we identified distinct depth zonation patterns in the macroalgae and epifaunal invertebrates but few such patterns in the mobile fauna.

This descriptive approach was useful in the initial analysis of these data and for giving further direction to analyses at both broader and finer spatial scales.

In this chapter, we take a top-down approach to understanding the relationships between observed pattern, underlying processes, and spatial scale, starting first with the big picture at the habitat scale (hundreds of meters), then at the individual substrate-slope scale, and finally focusing in to sub-meter features in the underwater seascape. This three-tiered analysis allows us to make predictions at each scale and identify areas of overlap in both pattern and process. At the broad habitat scale, we hypothesize the differences in community composition between shelf and wall habitats will be most pronounced in the shallow zone, with community assemblages on horizontal and sloping surfaces characterized by species/groups most likely to rely on increased light levels. Further, at the local substrate scale, we hypothesize individual substrate orientation will have less of an effect among each designation within each depth zone than within each designation between depth zones. Lastly, we hypothesize that even at small spatial scales, the community assemblages on sub-meter features will more closely resemble those found on analogous larger structures than the assemblages inhabiting the surrounding habitat.

Methods

To characterize the patterns of community similarities across multiple spatial scales in our study area, we used photo quadrats of the benthic sessile and small mobile fauna community from the data collection described in Chapter 1. These photo quadrats have inherent scale-independent metadata such as site and depth, but they also include an *in situ*, semi-quantitative, diver estimate of substrate angle which does not exist for the line-intercept and swath counts. We used the same analysis techniques on these data sets as in Chapter 1, including calculating percent cover for each taxon in the benthic sessile communities and population densities for the small mobile fauna. Multivariate analyses included non-metric Multidimensional Scaling (nMDS), Analysis of Similarities (ANOSIM), and Similarity Percentages (SIMPER) on both data types. The nMDS plots are a visual representation of similarities (or differences) among sample groups with corresponding R-statistics providing a statistical test of separation among sample groups. R-statistics range in value from 0 to 1, with higher values representing larger separation (i.e. greater dissimilarity) among sample groups. The SIMPER analyses quantify the contribution of individual species/groups to similarities within any sample group, or dissimilarities between sample groups. In Chapter 1, we tested the relationships between pairwise comparisons of each three-meter depth interval and found the farther apart the depth interval, the more dissimilar the photo quadrat assemblages on each transect. Here, we group the three-meter depth intervals into three distinct zones for analysis; the ‘shallow’ zone from 3 msw to 9 msw, the ‘mid’ zone from 12 msw to 18 msw, and the ‘deep’ zone from 21 msw to 27 msw. These depth zone designations are used throughout the results.

We have divided our analysis and results into three sections that examine patterns on increasingly smaller scales. In the first section, we characterize community similarities within, and differences between, large areas of homogenous habitat type. Where in Chapter 1 we separated horizontal/sloping and vertical assemblages into discreet analyses among three-meter depth intervals, here we integrate samples from all substrate orientations to discuss typical assemblages at a larger scale. Disregarding any other photo designation (e.g. site, depth, substrate orientation), we categorized each transect (and hence all of the photo quadrats taken on that transect) into one of two large-scale designations, 'shelf' or 'wall', to describe the broad habitat type where each photograph was taken. With a transect length of 10 m, individual transects didn't cross between shelf and wall habitats. However, all sites contained transects with both shelf and wall designations. The shelf designation was used when the overall area within which sites and transects were nested had a substrate slope between 0°- 75°. The wall designation was used when the overall substrate slope was >75° and had a contiguous vertical height of at least two meters and a contiguous horizontal width of at least ten meters. We then compared communities in each of the two large habitat categories among each of the three depth zones, as well as between shelf and wall habitats within each of the three depth zones (Figure 1).

In the second section, we categorize the data not by broad habitat type but by the slope of individual photo quadrats regardless of location. We explore the influence of substrate orientation (H≤15°, S=15°-75°, and V≥75°) on community assemblages within each depth zone (Figure 2). This allows us to focus on patterns and processes at a more local scale, examining what individual species/groups are characteristic of each substrate orientation as well as where there is overlap between communities.

In the third section, we investigate whether patterns, and thus ecological processes, might change at very small spatial scales. Knowing how slope and depth alter large-scale community patterns, we tested the hypothesis that meter-scale differences in slope affect local biotic communities more than does the surrounding broad habitat type. We compared four small-scale conditions that exist in the study habitats: 1) how the assemblages found on small vertical patches (<1 m) in an otherwise shelf habitat compare to the surrounding assemblages on horizontal surfaces; 2) how these small vertical assemblages compare to those on vertical surfaces in wall habitats; 3) how the assemblages on small horizontal patches (<1 m) in an otherwise wall habitat compare to the surrounding assemblages on vertical surfaces; and 4) how these small horizontal assemblages compare to those on horizontal surfaces in shelf habitats (Figure 3). In these analyses, we aim to discover at what spatial scale the assemblage's characteristic of horizontal and vertical surfaces appear.

We also analyzed the benthic sessile assemblage similarities between years and sites using the grouped depth zones and substrate orientations. These analyses are detailed in the Supplemental Materials.

Results

Section 1: Broad Habitat (Wall vs Shelf) scale

Chapter 1 illustrated the striking differences between benthic sessile communities at each sampling depth. Here, we compared entire shelf and wall communities (all substrate angles) among depth zones and within each depth zone and found further evidence of community differences among depth zones and habitat types. Benthic assemblages are increasingly dissimilar with increasing depth in both the shelf and wall habitat types (Figures 4 and 5). Although there are substantial differences among depth zones within each habitat type, these changes with depth are much more remarkable for the shelf than for wall habitats. Differences in both habitat types are representative of the shift from an algal-dominated shallow zone to an epifaunal-dominated deep zone.

The shelf assemblages in the shallow and mid zones are characterized by crustose coralline algae, foliose red algae, other encrusting red algae, and bare space, which together constitute the majority of the similarity (Figures 6 and 7). By contrast, the shelf assemblages in the deep zone are more diverse, including the frequent presence of *Diapoeroecia californica*, *Balanophylia elegans*, and *Heteropora pacifica*. Although kelp canopy cover is not quantified in these benthic photographs, it similarly declines sharply with depth (Chapter 1). Comparing shelf and wall habitats, benthic assemblages in the wall habitat are more diverse than the assemblages in the shelf habitat among all three depth zones. Characteristic wall species/groups include the suspension feeders *Diapoeroecia californica*, encrusting bryozoans, hydroid/bryozoan complex, *Terebratalia transversa*, sponges, *Balanophylia elegans*, and *Heteropora pacifica*.

Metandrocarpa taylori and *Didemnum* spp. also contribute to similarities within the wall assemblages.

Comparing shelf and wall assemblages within each depth zone, the shallow and mid zones have distinct benthic sessile communities, with the strongest separation between assemblages in the mid zone (Figures 8 and 9). In the deep zone, there is no difference between shelf and wall assemblages (Figure 10), again providing evidence for the 'depth emergence' phenomenon seen in Chapter 1.

In the shallow and mid zones, crustose coralline and other encrusting red algae, foliose red algae, and bare space are more characteristic of the shelf habitat, whereas sponges are more characteristic of the wall habitat (Figures 11 and 12). Both *Metandrocarpa taylori* and *Terebratalia transversa* were absent in the shallow shelf habitat but were present and contributed to community similarity in the shallow wall habitat. In the mid zone, *Diapoeroecia californica*, *Terebratalia transversa*, *Metandrocarpa taylori*, and *Didemnum* spp. were all absent in the shelf habitat but were present and contributed to community similarity in the wall habitat.

Among all depth zones and broad habitat types, there are very few differences in the small mobile fauna communities (Figures 13 and 14). The only evidence of depth zonation patterns emerges when comparing between the shallow and deep zones in each habitat type, but these differences are weak considering the strong pattern in the benthic sessile communities. There are also no differences in the communities when comparing between habitat types within each of the depth zones (Figures 15 - 17).

In the shallow and mid zones, the shelf assemblages are characterized by hermit crabs, *Tonicella lineata* and other *Tonicella* spp., and shrimp (Figure 18). The communities in the deep zone are characterized by the dominance of *Calliostoma ligatum* and the presence of *Trichotropus cancellata* and by the absence of *Tonicella lineata* and other *Tonicella* spp.

In the wall habitat, hermit crabs are more representative of the shallow zone than either the mid or deep zones, shrimp dominate the deep zone, and again *Tonicella lineata* and other *Tonicella* spp. are absent from the deep zone (Figure 19).

Section 2: Patterns of community structure with depth and local substrate orientation

Section 1 illustrated that large-scale broad shelf and wall habitats have different benthic assemblages, although these assemblages converge with depth. Here we focus on the role of local slope (on the photo quadrat scale) and test how patterns are altered by differences in substrate orientation regardless of surrounding habitat type. When comparing the assemblages among and within substrate orientation types and grouped depth zones, four clear patterns emerge:

1) Within each of the three substrate orientations, there are no ecologically relevant differences between typical community assemblages in the shallow versus mid zones. However, for each substrate orientation, there is a significant difference between communities in the mid versus deep zones (Figures 20 - 22).

2) The differences in typical community assemblages between the shallow and deep zones are greatest on horizontal substrates and progressively less on sloping and vertical substrates (Figures 20 - 22). Thus overall, community assemblages on vertical substrates are more similar in species/group composition across depth zones than on either the horizontal or sloping substrates.

Examining the species that drive these patterns, the transition from the mid to the deep zones for all substrate orientations is largely driven by a decrease in crustose coralline and other encrusting red algae, foliose red algae, and bare space. For all orientations, deeper zones are characterized by the suspension feeders *Diapoeroecia californica*, *Terebratalia transversa*, *Balanophylia elegans*, *Heteropora pacific*, sponges, and encrusting bryozoans (Figures 23 - 25).

3) Comparing the biota on different slopes within each of the depth zones, there are no differences in the typical benthic assemblages between horizontal versus sloping substrates or between sloping versus vertical substrates (Figures 26 - 28).

4) However, there are differences between assemblages in the horizontal and vertical substrate orientations in the shallow and mid zones. These differences in the typical communities at the extreme ends of substrate orientation get smaller with increasing depth (Figures 26 - 28).

In the shallow and mid zones, assemblages on horizontal surfaces are characterized by the large contribution of crustose coralline algae whereas the assemblages on vertical surfaces are characterized by *Diapoeroecia californica*, *Terebratalia transversa*, *Metandrocarpa taylori*, and sponges (Figures 29 and 30).

Unlike in the benthic sessile communities, there were no patterns when comparing the small mobile fauna communities within each substrate orientation among grouped depth zones, or among substrate orientations within each depth zone.

Section 3: Small-scale patches

Section 2 illustrated that substrate orientation broadly affects benthic assemblages, although these differences depend strongly on depth. Here we focus on meter-scale patterns and processes, testing how assemblages change on isolated patches whose slope differs from that of the surrounding habitat.

In the shallow and mid zones, the benthic sessile assemblages on small vertical patches of substrate are more similar to assemblages in the surrounding shelf habitat than to those typically found on large vertical walls (Figures 31 - 34). The opposite is true of the small horizontal patches within a wall habitat; the assemblages on these patches are more similar to those found on horizontal substrate in the shelf habitat than those in the surrounding wall habitat (Figures 35 and 36).

In the deep zone, however, the differences disappear and the assemblages on small vertical patches, small horizontal patches, and large vertical walls become more similar and predictable (Figures 37 and 38). Assemblages on horizontal surfaces in the shelf habitat were least similar to all other sample groups (Figures 39 and 40).

While there are many similarities in the assemblages between small vertical patches and large vertical walls, *Metandrocarpa taylori* and *Didemnum* spp. are more likely to be found on large vertical walls and have a greater contribution to community similarity. There is also a sharp decrease in crustose coralline algae on large vertical walls compared to small vertical patches (Figures 41 and 42).

The abundance of *Metandrocarpa taylori* and *Didemnum* spp., and the low importance of crustose coralline algae on vertical assemblages in the wall habitat also drives differences with the assemblages on nested small horizontal patches (Figure 43).

Similar to prior results from Chapter 1 and previous sections of this manuscript, there are few distinct small-scale patterns in the small mobile fauna communities. Of all the comparisons between small and large horizontal and vertical substrates, only the assemblages found on small horizontal patches in wall habitats differed significantly from what is found on large horizontal substrate in the shelf habitat (Figure 44). This difference was due in large part to a striking contribution from shrimp in the small horizontal patches (Figure 45).

Discussion

In this chapter, we analyzed the benthic sessile and small mobile fauna community data across multiple scales with finer resolution than in Chapter 1. In the benthic sessile communities, we found strong evidence of the same vertical zonation pattern as noted in Chapter 1, although we are now able to determine at what scale and in what habitat context these shifts in the community occur. At the broadest spatial scale analyzed, assemblages in shelf habitats exhibit stronger differentiation between shallow and deep sites than do assemblages in wall habitats. The shallow and middle depth shelf habitats are characterized by a high cover of encrusting and foliose red algae, especially crustose coralline algae, and more bare space than in the deep shelf habitat. As available light for photosynthesis decreases with depth, the abundance of primary producers also decreases (Golikov and Scarleto 1968, Dayton 1975). The depth to which light can penetrate is a function of water clarity and turbidity and can differ dramatically between tropical and temperate nearshore systems. Substrate slope and aspect can also affect light; vertical surfaces, especially those facing north, have even less available sunlight each day regardless of depth due to the arc of the sun across the southern sky and the relatively high latitude in the San Juan archipelago. This results in a predictable decrease in the abundance of foliose and encrusting algal species on steep surfaces and allows a more diverse assemblage of epifaunal invertebrates to proliferate, thus resembling assemblages from the deeper, light-limited depths.

Available bare space is more common on horizontal and sloping surfaces in the shallow and mid zones than in the deep zone and is maintained largely through two consumers, red urchins (*Mesocentrotus franciscanus*) and chitons in the genus *Tonicella* (Elahi and Sebens 2012). The populations of *Tonicella* we found in shallow and mid zones, combined with higher densities of *M. franciscanus* at these depths (see Chapter 1), corroborate the importance of consumer-mediated natural variation on different slopes. Vertical surfaces have less bare space because algal and epifaunal organisms there are less susceptible to consumption by *M. franciscanus,* as urchins' ability to attach to vertical surfaces covered with soft-bodied creatures is limited (Sebens 1985). If they cannot attach tube feet to hard surfaces, they are easily dislodged by currents.

In Chapter 1, we compared communities on transects at three-meter depth intervals and discovered that the further apart in depth they were, the more dissimilar were their assemblages. In that framework, there appeared to be a continuous transition from the shallowest to the deepest zones. By grouping the depths into three zones, we were still able to detect some differences between the shallow and mid zones, but they are far more similar to each other than either is to the deep zone. The biggest shift in community composition occurs in the transition from the mid to deep zone (between 18 msw and 21 msw). The reduced cover of encrusting and foliose algae in the wall habitat among all depths, combined with the dominance of suspension feeders on these surfaces, suggest that flow regimes may work together with reduced available light to keep wall habitats similar across depths. We investigate this process further in Chapter 3. It is likely that in addition to available light, biotic factors we did not quantify such as recruitment (Sebens et al. 1988), predation (Witman and Cooper 1983, Witman 1998), and the combined effects of flow, sedimentation, and competition for space (Genovese 1996, Genovese and Witman 1999) all play important roles in shaping these deep communities. More experimental work needs to be done to determine the nature and strength of these interactions.

Given the inherently patchy nature of the glacier-carved subtidal rocky reef habitat in the San Juan Islands, it would be difficult to run a transect that only traversed one substrate orientation with no anomalous surfaces. Thus, our transects had varying slopes at the individual photograph level. This variability enabled us to discern that the assemblages on sloping substrates are a hybrid of overlapping species/groups found typically on both horizontal and vertical substrates. Furthermore, substrate orientation drives the largest differences in the assemblages at the extreme ends of the spectrum (i.e. between H and V) in the shallow and mid zones but plays less of a role in the deep zone, where assemblages on all three substrate types converge. If the primary process creating different assemblages with substrate slope is light availability, then it would be logical that slope effects would diminish in the deep zone where light is greatly reduced.

In what might have been considered annoying outliers in the data set, we instead captured meter-scale variation and attempted to identify if small patches of horizontal and vertical substrate are more representative of assemblages in their larger analogous habitat or of assemblages in their surrounding habitat. The organisms on small horizontal patches are most similar to those in larger shelf habitats rather than to assemblages on the walls surrounding them. Conversely, while assemblages on small vertical patches may include organisms characteristic of larger walls, they more closely resemble assemblages in the surrounding shelf habitat. One explanation for this might be that small vertical surfaces do not offer the same protection from urchin foraging as do the larger vertical walls. A second explanation would be that propagules from the nearest microhabitat patches seed nearby surfaces no matter their orientation. This does not explain why small horizontal features are very unlike the vertical walls around them. Here, it is possible that sedimentation or increased light availability are important.

Many studies have documented the co-occurrence of mobile consumers with their resources (Estes and Palmisano 1974, Paine 1980, Allison et al. 1995, Estes and Duggins 1995, Huntly 1995, Duffy and Hay 2001, Duffy 2002), in particular epifaunal invertebrate and algal assemblages (Hayward 1980, Lubchenko and Gaines 1981, Menge 1995, Elahi and Sebens 2012), and we expected this reliance on resources to result in depth zonation of mobile fauna in our analysis as well. However, few differences existed in mobile fauna at any depth or scale in our study area. While some of the local species are opportunistic feeders, many such as gastropod molluscs have specific food requirements due to their feeding anatomy (Bloom 1976, Blinn et al. 1989), dietary preference (Nybakken and Eastman 1977, Fernandez and Boudouresque 1998), habitat preference (Bloom 1981, Hawkins et al. 1989), feeding behaviors (Hawkins et al. 1989), temporal appearance of the food resource (Yoshioka 1986), and recruitment cues (Lambert and Todd 1994, Pechenik et al. 1995, Hadfield and Paul 2001). Many small mobile fauna also have limited range due to their size and low mobility, likely spending their entire adult life in a patch of habitat only tens of meters in area. The lack of spatial pattern in the mobile fauna is evidence that even though there are recognizable and predictable assemblages of food resources, most mobile fauna are generalists across these sessile communities or have mobility that extends beyond the borders of wall or shelf habitat patches. Only two of the consumer species showed a strong depth pattern, red urchins and chitons, which are known to co-occur; chitons may benefit from urchin predation on large algae and invertebrates, thus favoring the crustose algae that chitons utilize (Elahi and Sebens 2013). Chiton zonation might thus be due to habitat selection by urchins, which can move to all depths, although they often remain almost stationary for long periods (Lowe et al. 2015).

Although the patchy, heterogeneous nature of the habitat we sampled makes it difficult to assign clear roles to any single abiotic factor, this second chapter strongly points to the importance of light and of water flow to the benthic sessile communities. Evidence for the role of flow is discussed in greater detail in Chapter 3.

Figures

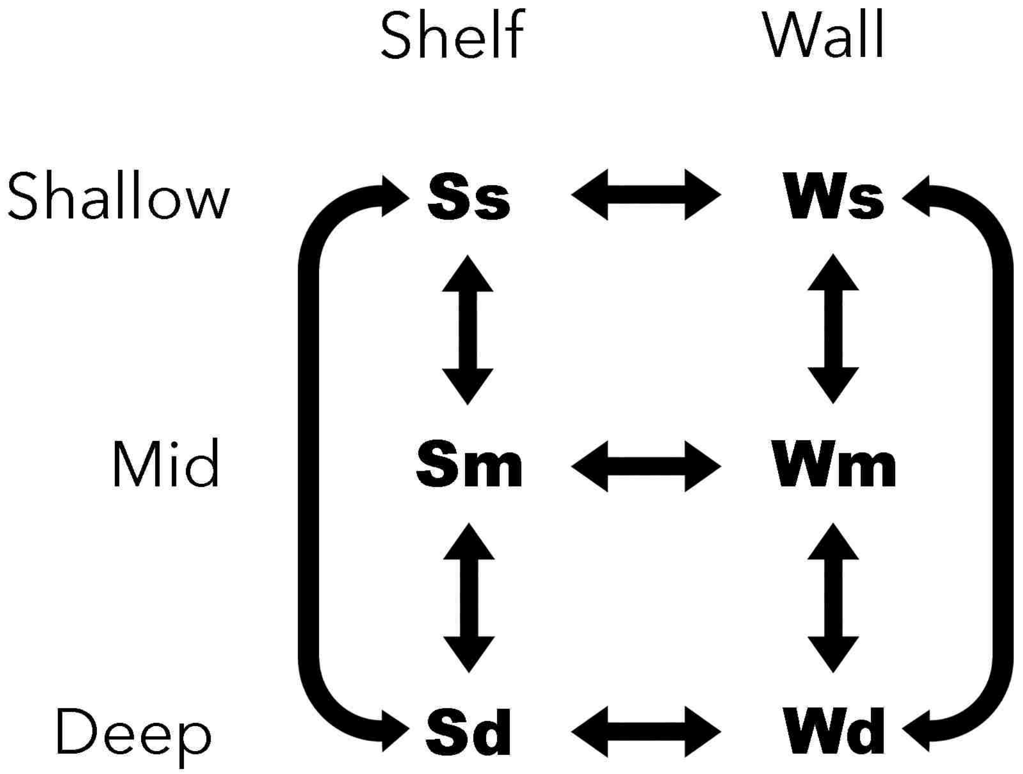


Figure 1. Section 1 comparisons of assemblages in each of the two large habitat categories (Shelf and Wall) among each of the three depth zones (Shallow, Mid, and Deep), as well as between shelf and wall habitats within each of the three depth zones.

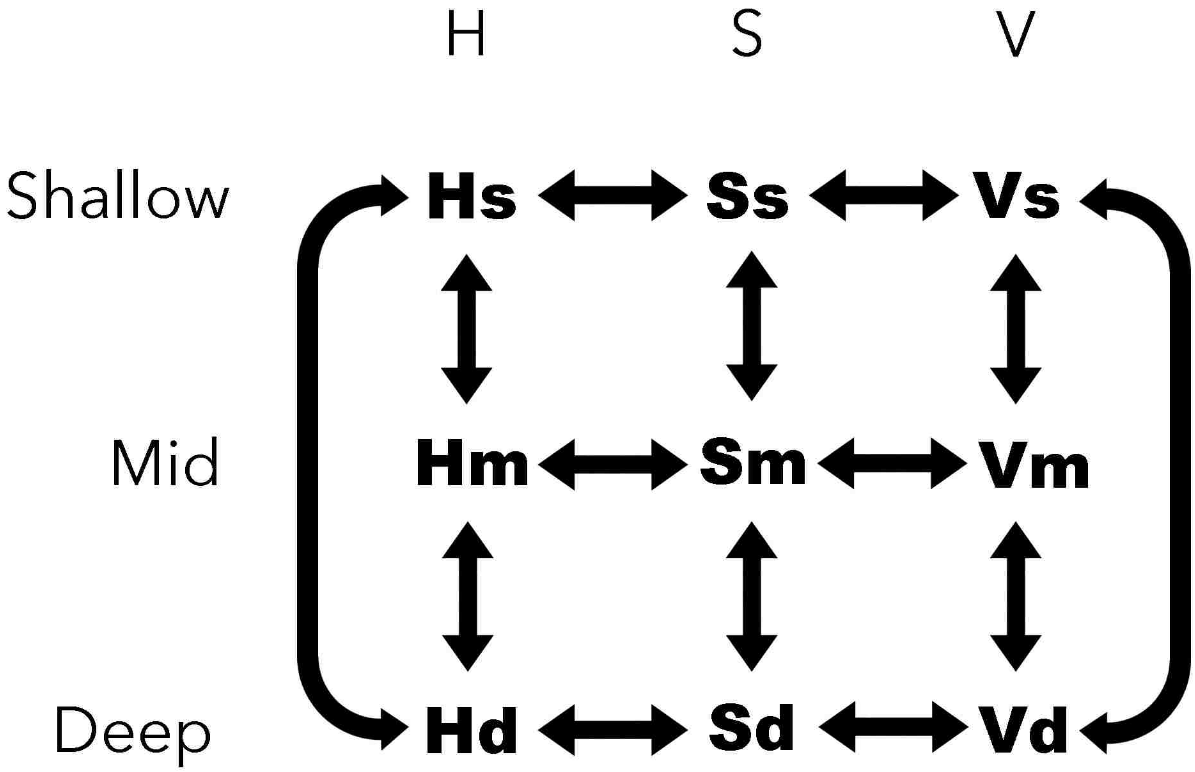


Figure 2. Section 2 comparisons of assemblages in each of the substrate orientation categories (Horizontal, Sloping, and Vertical) among each of the three depth zones (Shallow, Mid, and Deep), as well as between substrate orientations within each of the three depth zones.

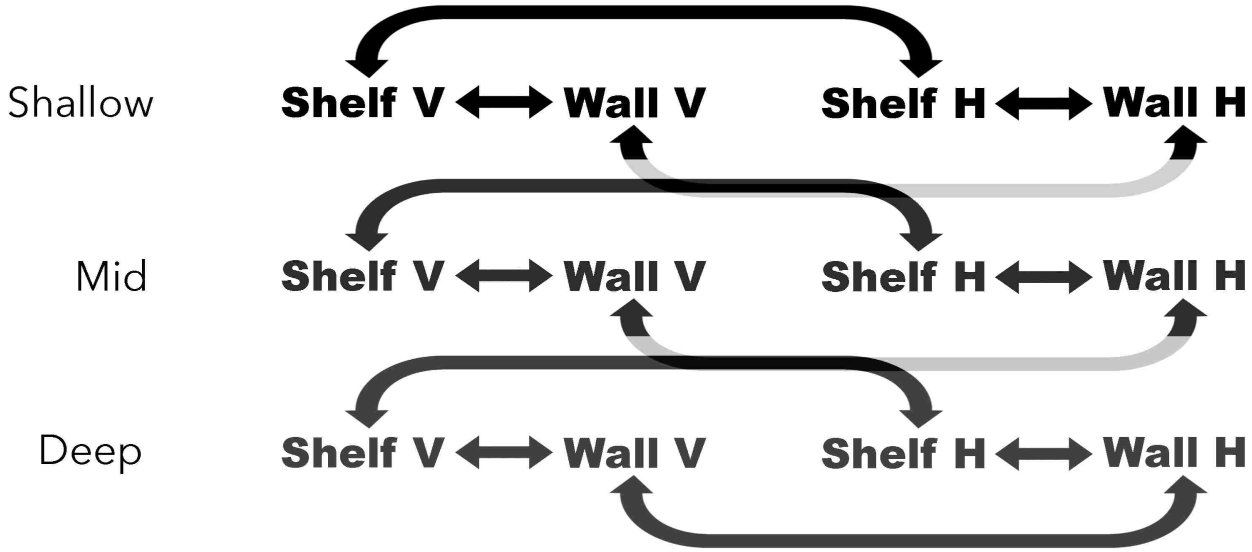


Figure 3. Section 3 investigates how the assemblages found on small vertical patches in an otherwise shelf habitat compare to the surrounding assemblages on horizontal surfaces, how these small vertical assemblages compare to those on vertical surfaces in wall habitats, how the assemblages on small horizontal patches in an otherwise wall habitat compare to the surrounding assemblages on vertical surfaces, and how these small horizontal assemblages compare to those on horizontal surfaces in shelf habitats.

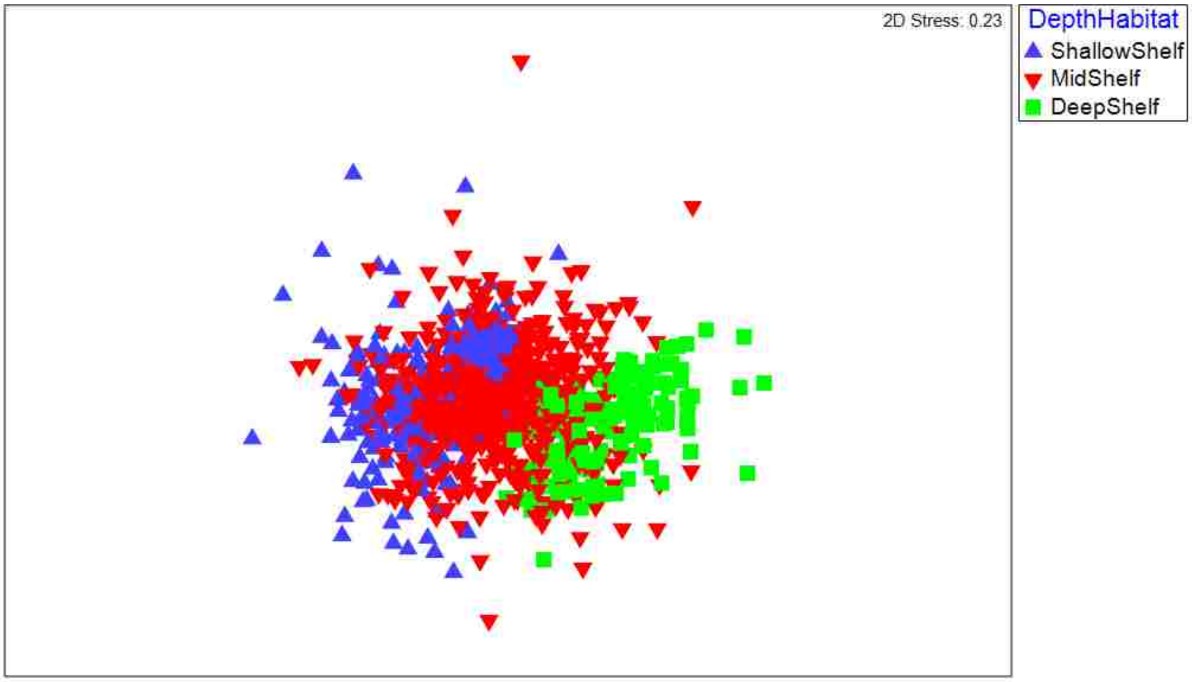


Figure 4. nMDS plot of benthic sessile assemblage similarities among grouped depth zones in the shelf habitat. Global R-statistic: 0.287 (ShallowShelf, MidShelf: 0.21; MidShelf, DeepShelf: 0.426; ShallowShelf, DeepShelf: 0.71).

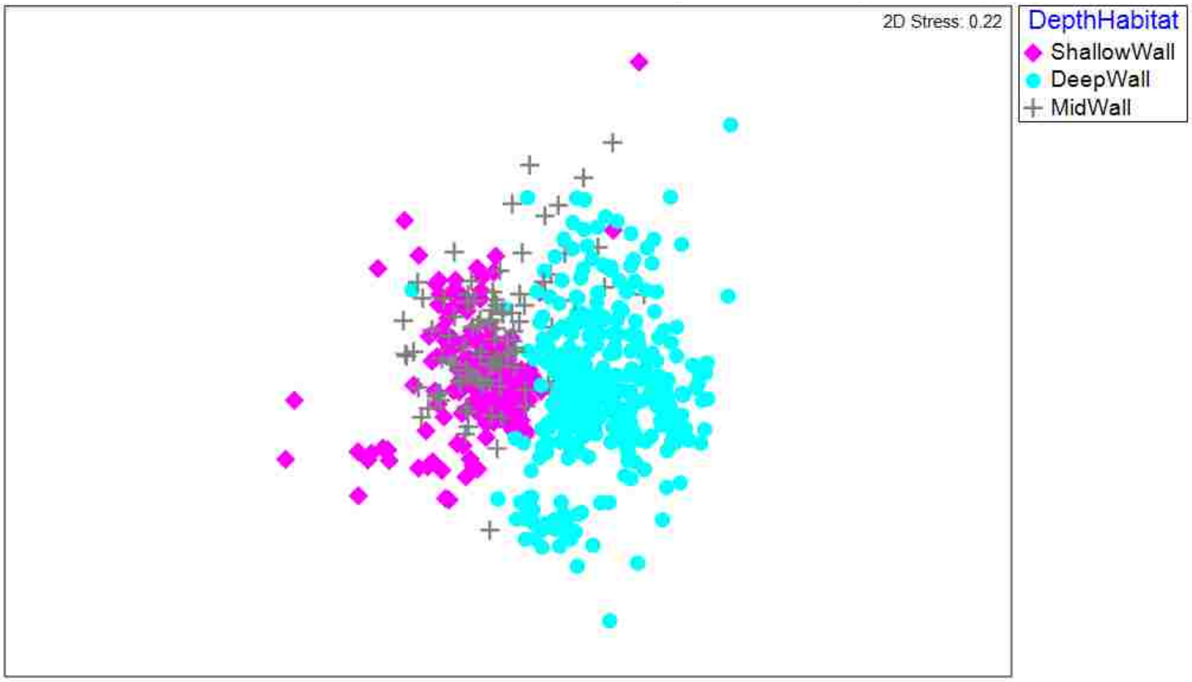


Figure 5. nMDS plot of benthic sessile assemblage similarities among grouped depth zones in the wall habitat. Global R-statistic: 0.33 (ShallowWall, MidWall: 0.225; MidWall, DeepWall: 0.382; ShallowWall, DeepWall: 0.363).

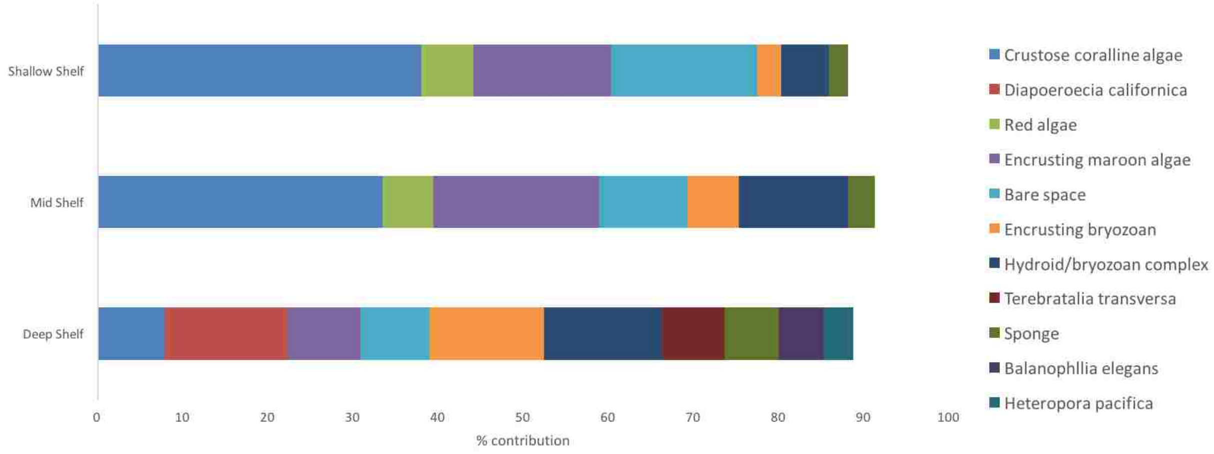


Figure 6. Contribution to benthic assemblage similarity among grouped depths in the shelf habitat. Shallow: 3 m to 9 m; Mid: 12 m to 18 m; Deep: 21 m to 27 m.

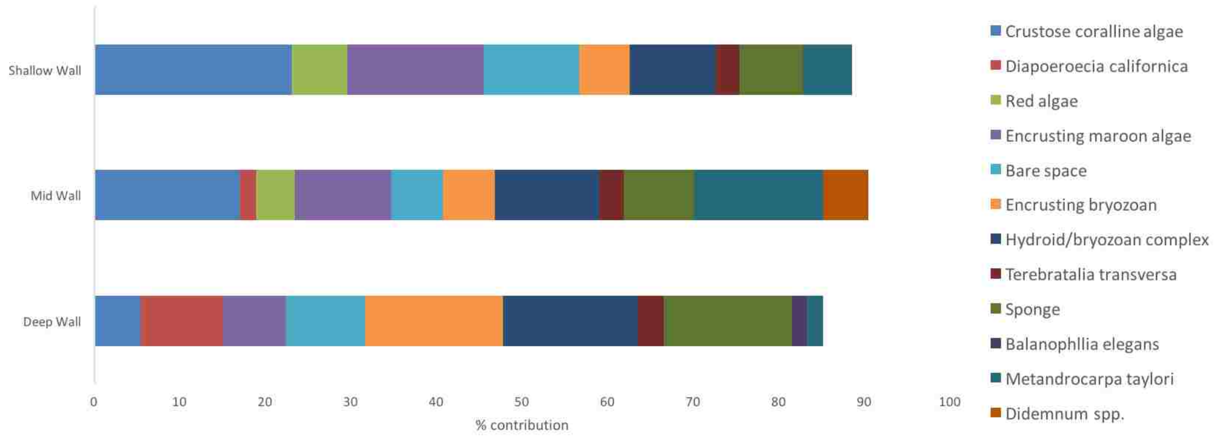


Figure 7. Contribution to benthic assemblage similarity among grouped depths in the wall habitat. Shallow: 3 m to 9 m; Mid: 12 m to 18 m; Deep: 21 m to 27 m.

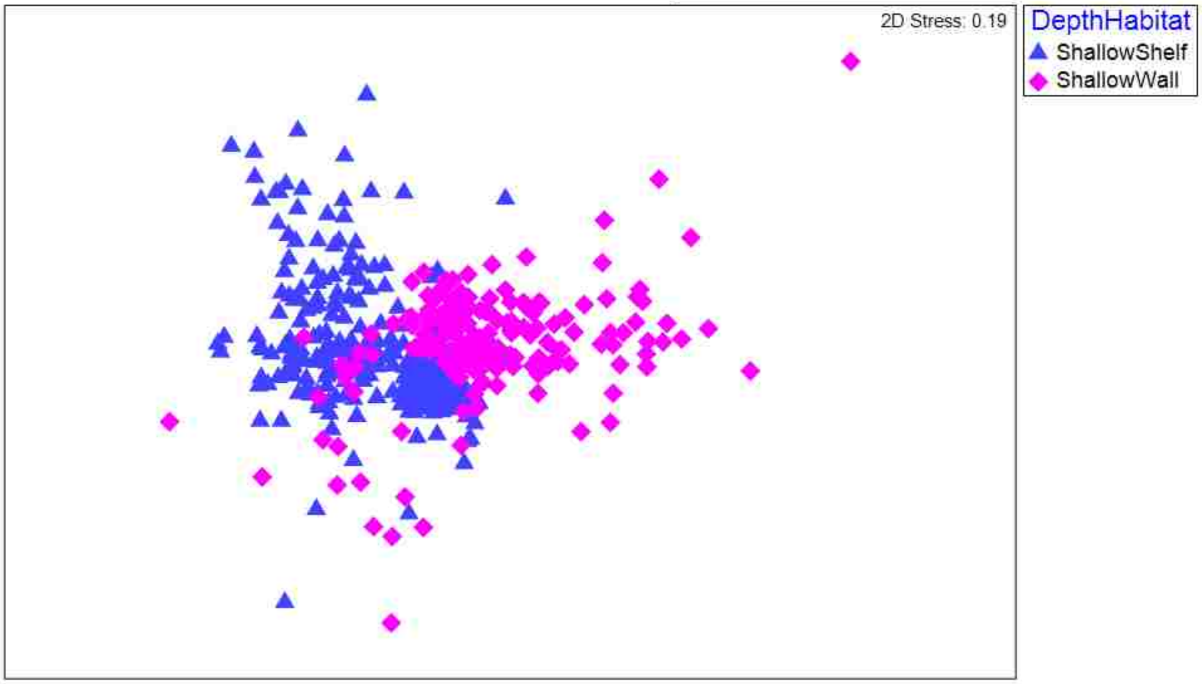


Figure 8. nMDS plot of benthic sessile assemblage similarities among the shelf and wall habitats in the shallow zone (3 m to 9 m). R-statistic: 0.274.

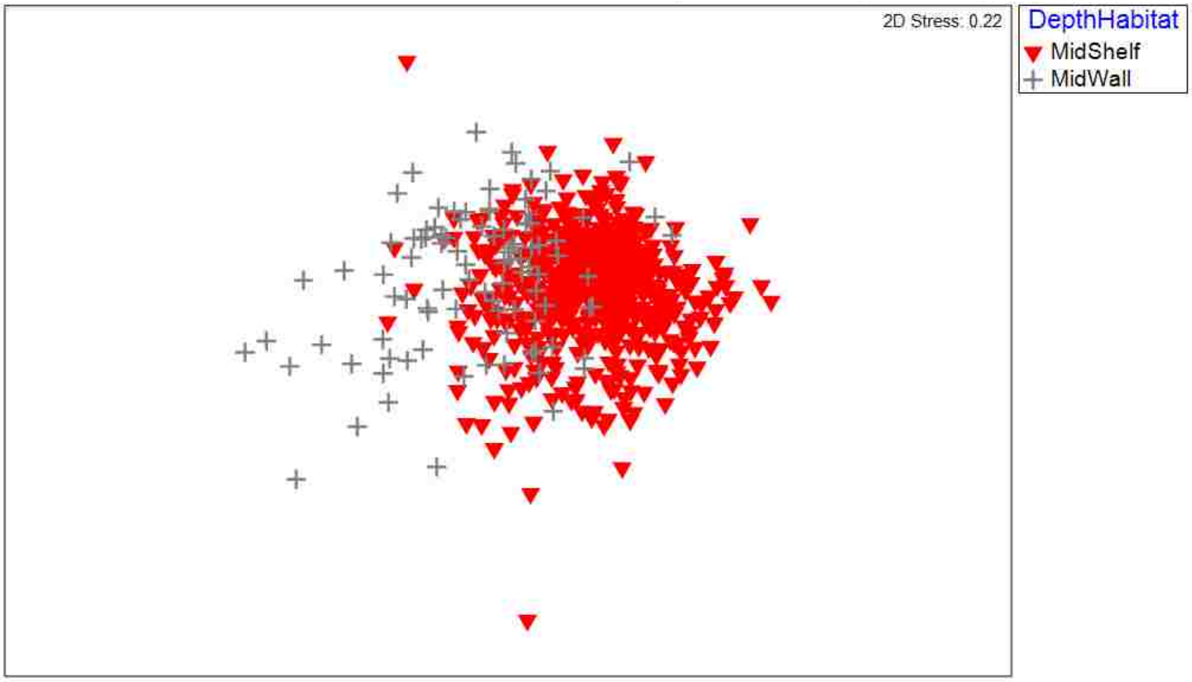


Figure 9. nMDS plot of benthic sessile assemblage similarities among shelf and wall habitats in the mid zone (12 m to 18 m). R-statistic: 0.46.

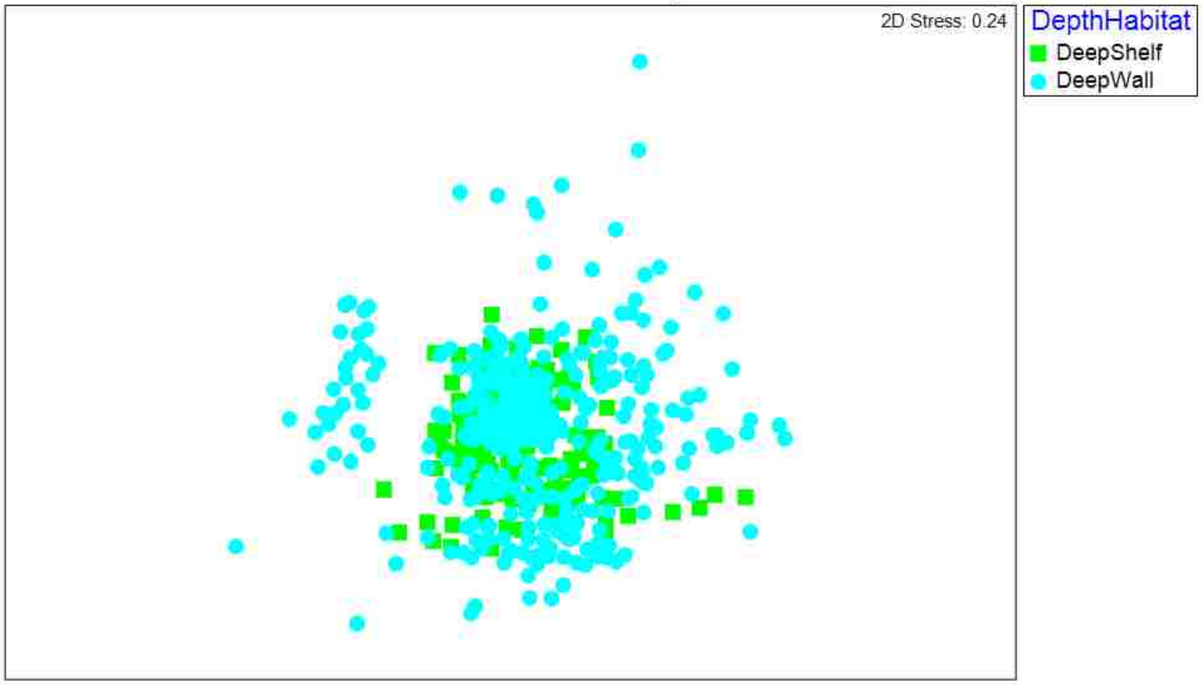


Figure 10. nMDS plot of benthic sessile assemblage similarities among shelf and wall habitats in the deep zone (24 m to 27 m). R-statistic: -0.018.

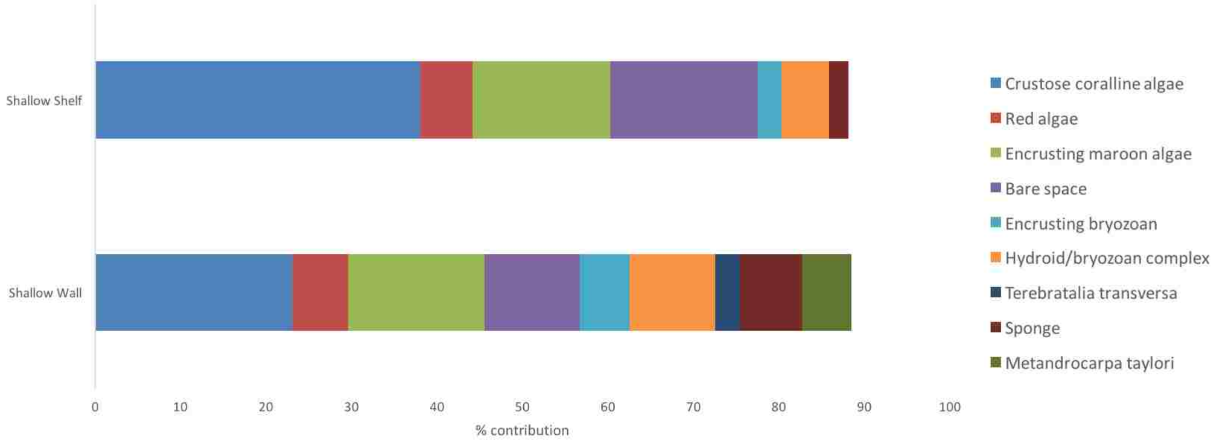


Figure 11. Contribution to benthic sessile assemblage similarity among shelf and wall habitats in the shallow zone (3 m to 9 m).

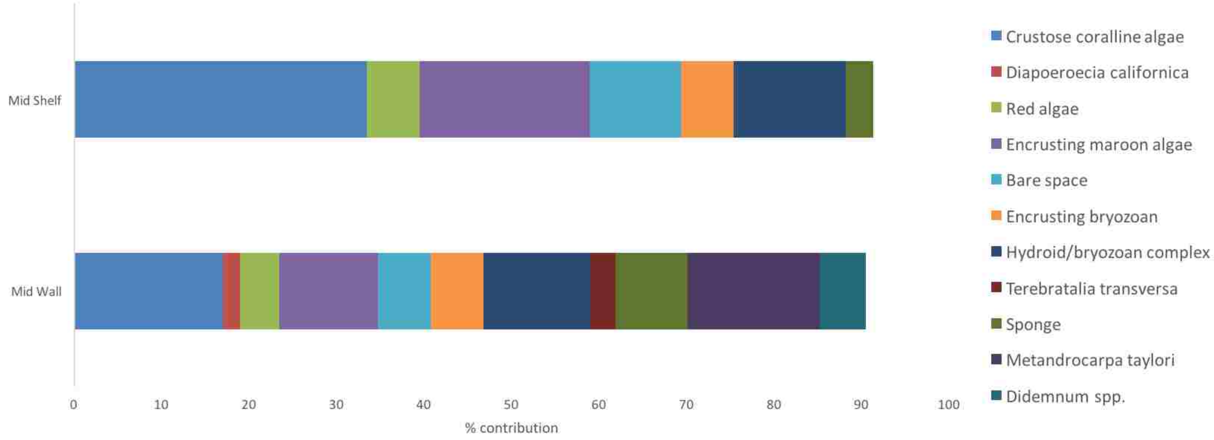


Figure 12. Contribution to benthic sessile assemblage similarity among shelf and wall habitats in the mid zone (12 m to 18 m).

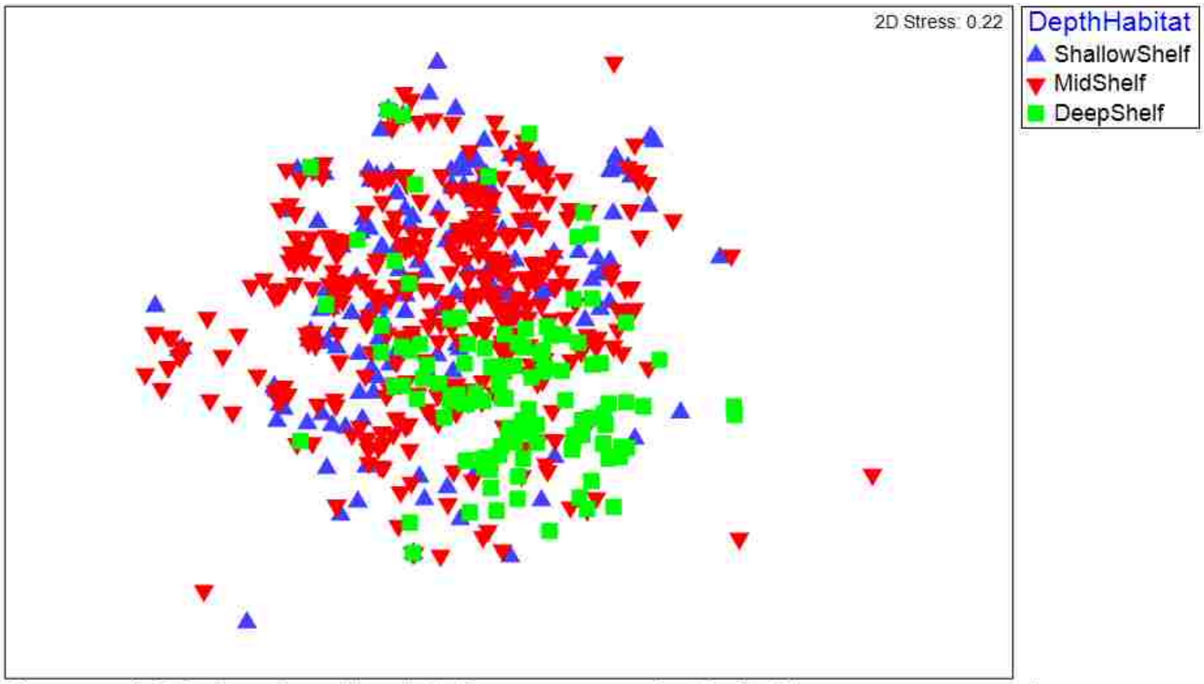


Figure 13. nMDS plot of small mobile fauna assemblage similarities among grouped depth zones in the shelf habitat. Global R-statistic: 0.092 (ShallowShelf, MidShelf: 0.031; MidShelf, DeepShelf: 0.106; ShallowShelf, DeepShelf: 0.275).

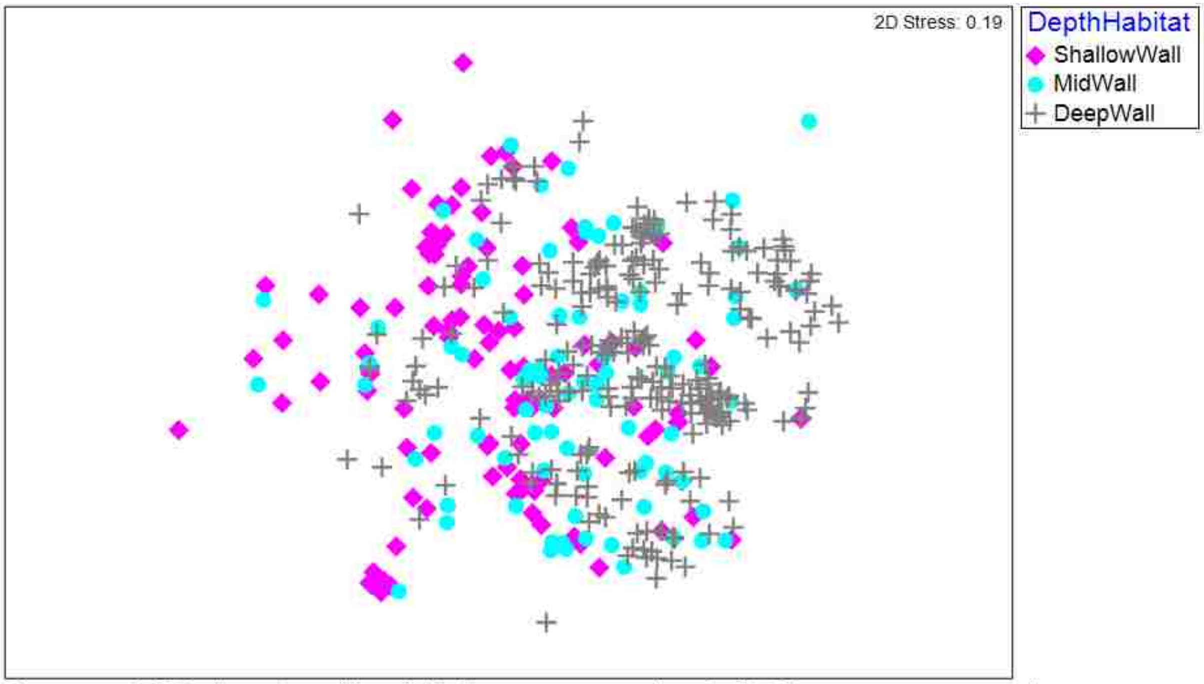


Figure 14. nMDS plot of small mobile fauna assemblage similarities among grouped depth zones in the wall habitat. Global R-statistic: 0.161 (ShallowWall, MidWall: 0.039; MidWall, DeepWall: 0.122; ShallowWall, DeepWall: 0.212).

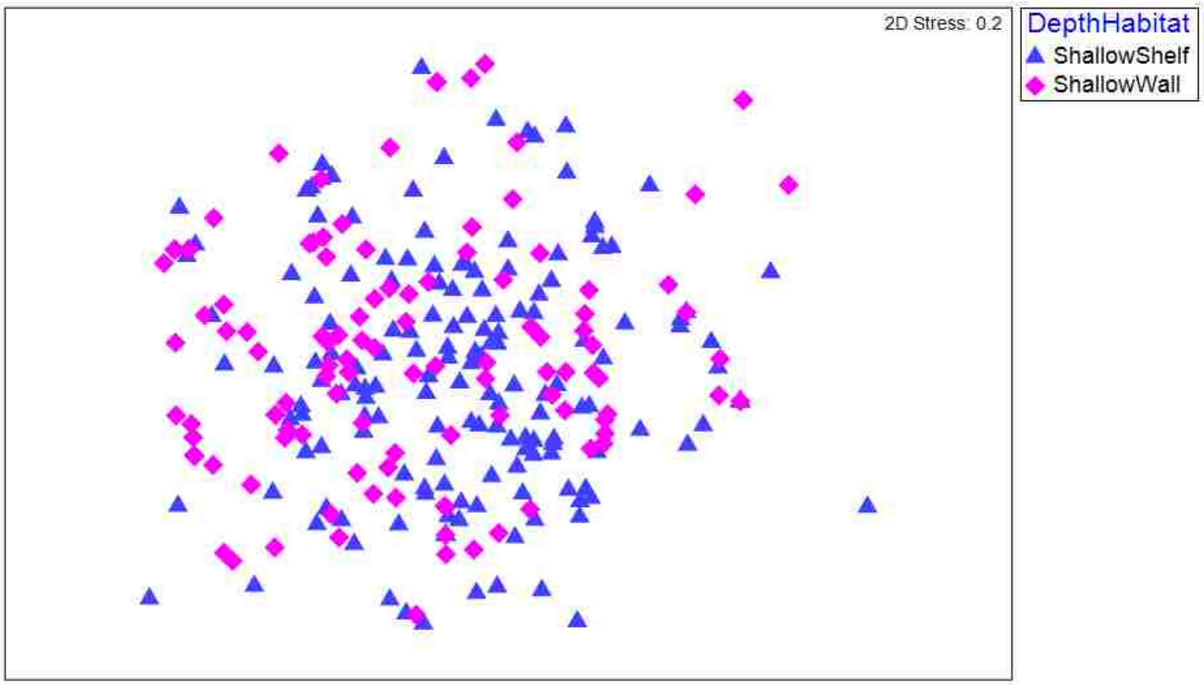


Figure 15. nMDS plot of small mobile fauna assemblage similarities among shelf and wall habitats in the shallow zone (3 m to 9 m). R-statistic: 0.075.

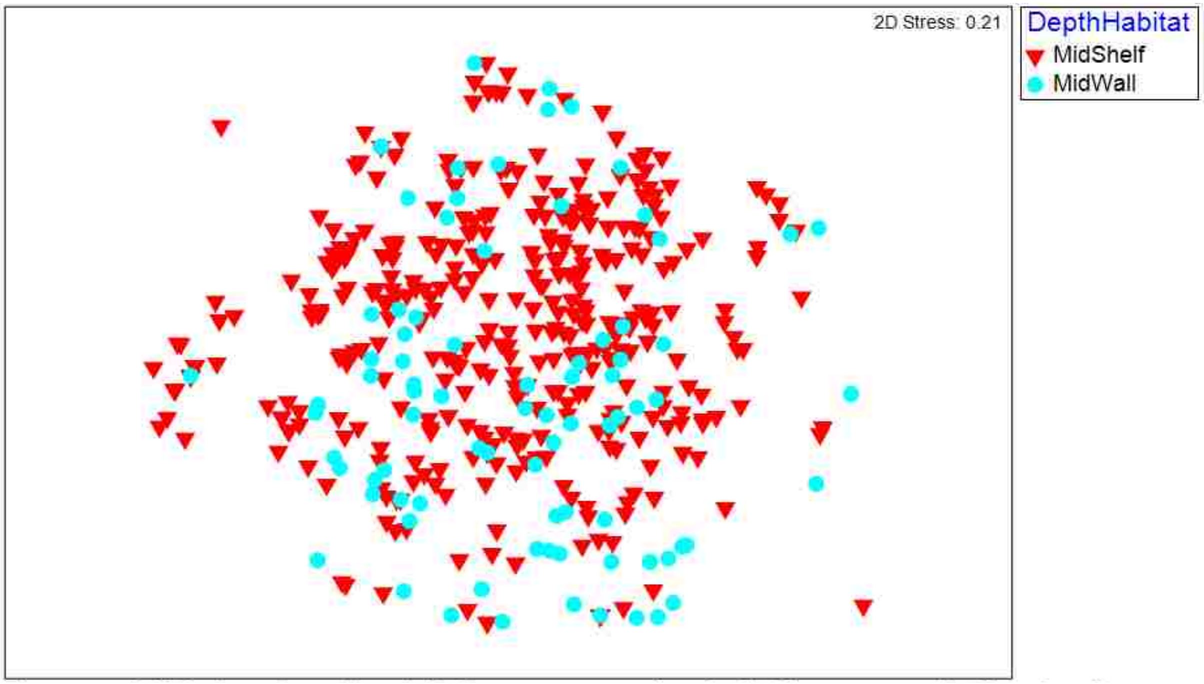


Figure 16. nMDS plot of small mobile fauna assemblage similarities among shelf and wall habitats in the mid zone (12 m to 18 m). R-statistic: 0.089.

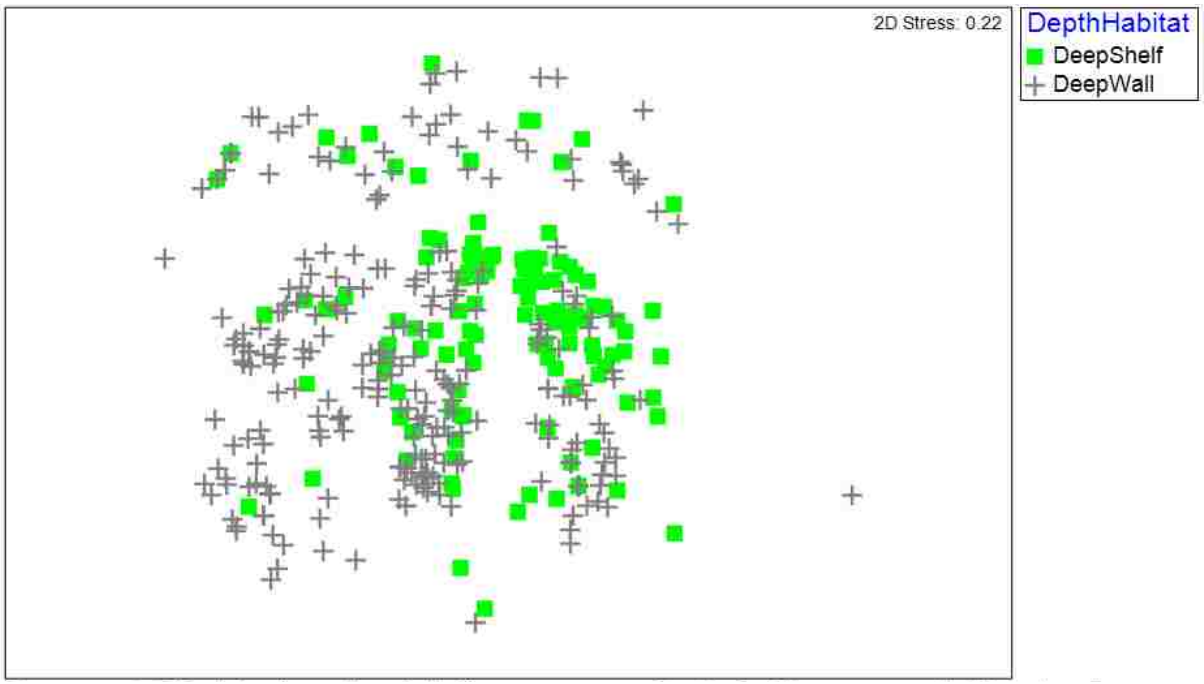


Figure 17. nMDS plot of small mobile fauna assemblage similarities among shelf and wall habitats in the deep zone (24 m to 27 m). R-statistic: 0.061.

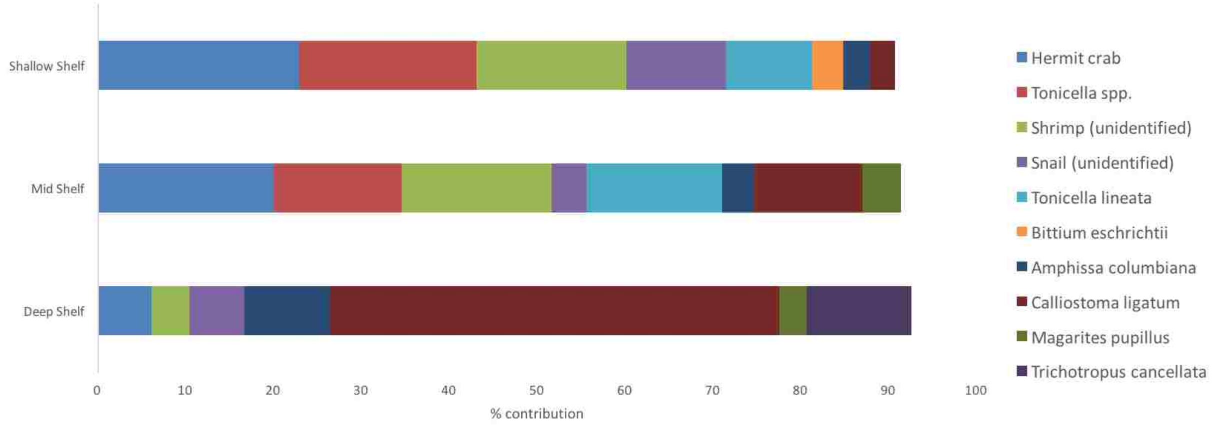


Figure 18. Contribution to small mobile fauna assemblage similarity among grouped depths in the shelf habitat. Shallow: 3 m to 9 m; Mid: 12 m to 18 m; Deep: 21 m to 27 m.

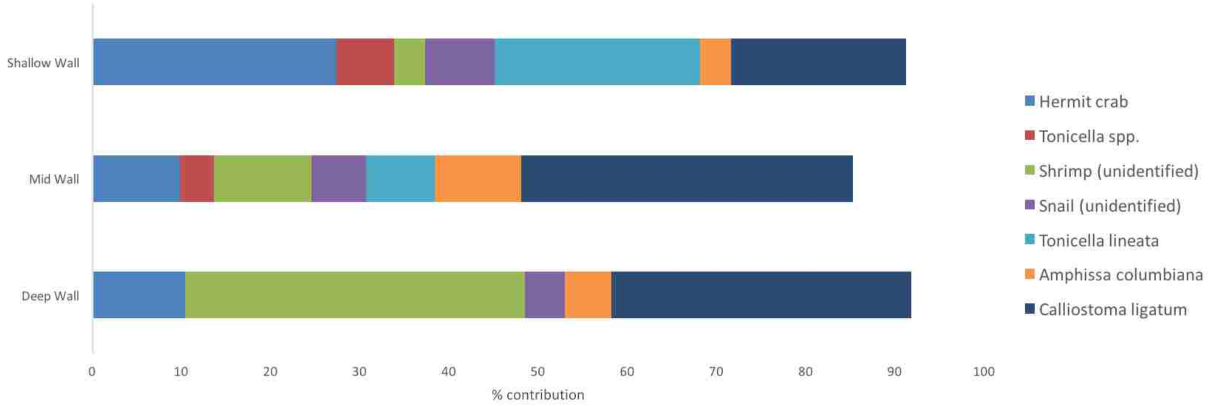


Figure 19. Contribution to small mobile fauna assemblage similarity among grouped depths in the wall habitat. Shallow: 3 m to 9 m; Mid: 12 m to 18 m; Deep: 21 m to 27 m.

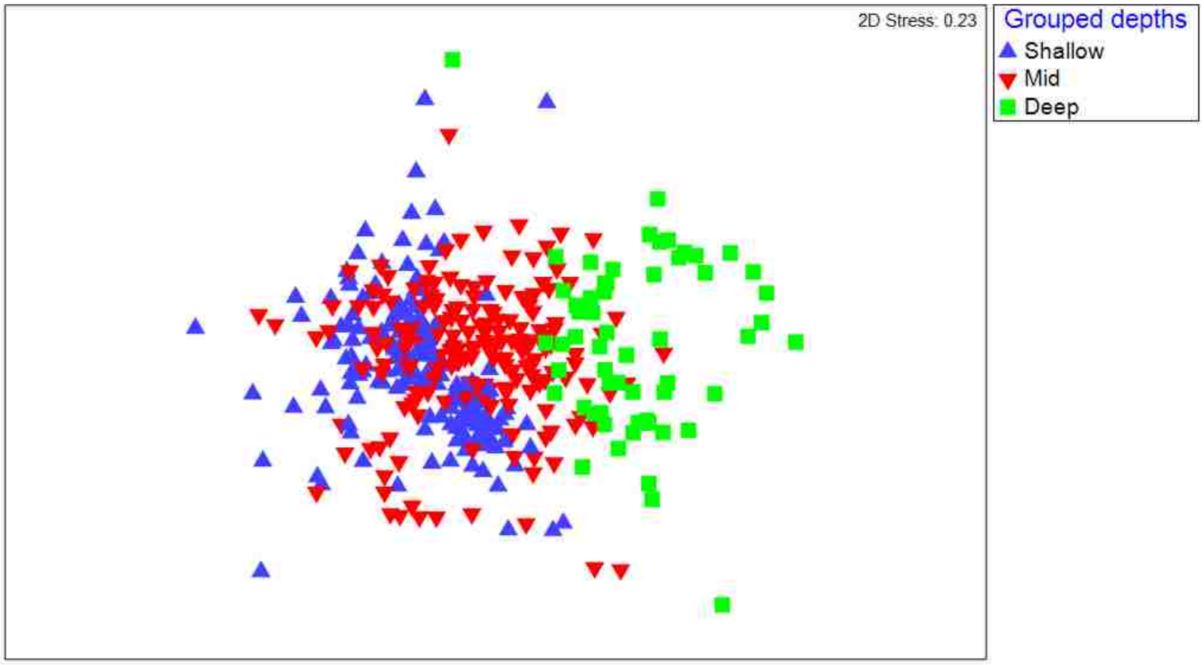


Figure 20. nMDS plot of benthic sessile assemblage similarities among grouped depths on horizontal substrate. Global R-statistic: 0.294 (Shallow, Mid: 0.1; Mid, Deep: 0.503; Shallow, Deep: 0.718).

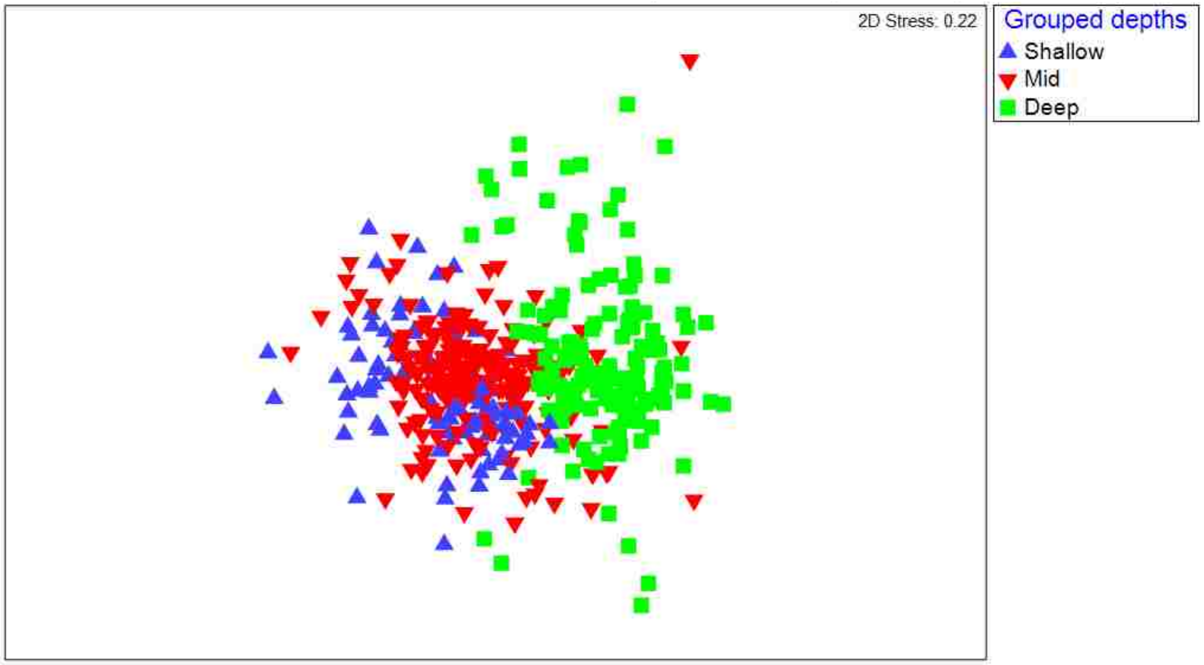


Figure 21. nMDS plot of benthic sessile assemblage similarities among grouped depths on sloping substrate. Global R-statistic: 0.397 (Shallow, Mid: 0.151; Mid, Deep: 0.495; Shallow, Deep: 0.533).

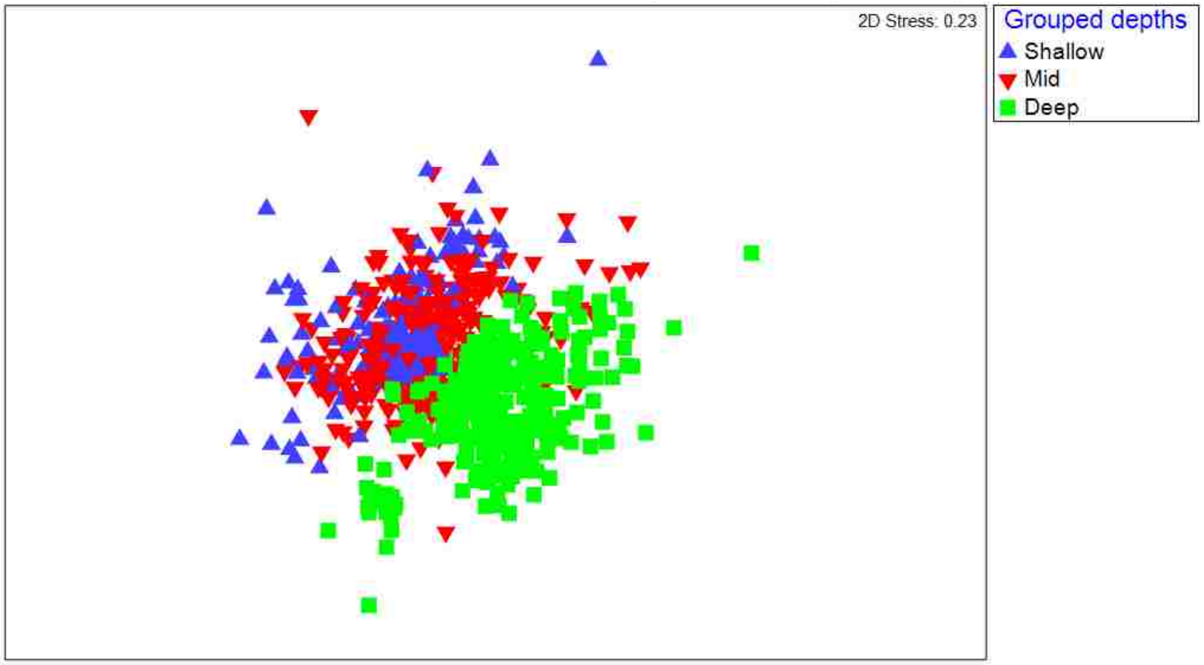


Figure 22. nMDS plot of benthic sessile assemblage similarities among grouped depths on vertical substrate. Global R-statistic: 0.278 (Shallow, Mid: 0.0.073; Mid, Deep: 0.31; Shallow, Deep: 0.436).

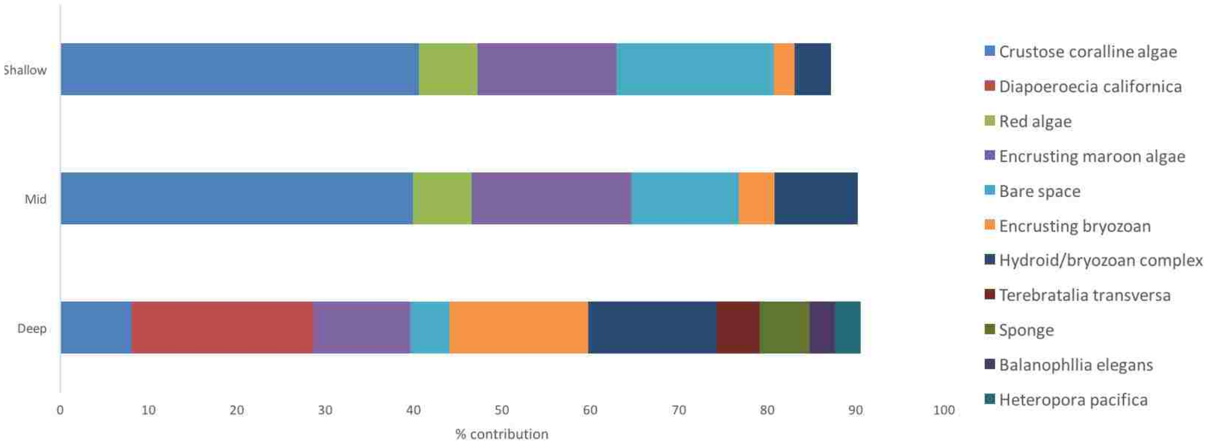


Figure 23. Contribution to benthic assemblage similarity among grouped depths on horizontal substrate. Shallow: 3 m to 9 m; Mid: 12 m to 18 m; Deep: 21 m to 27 m.

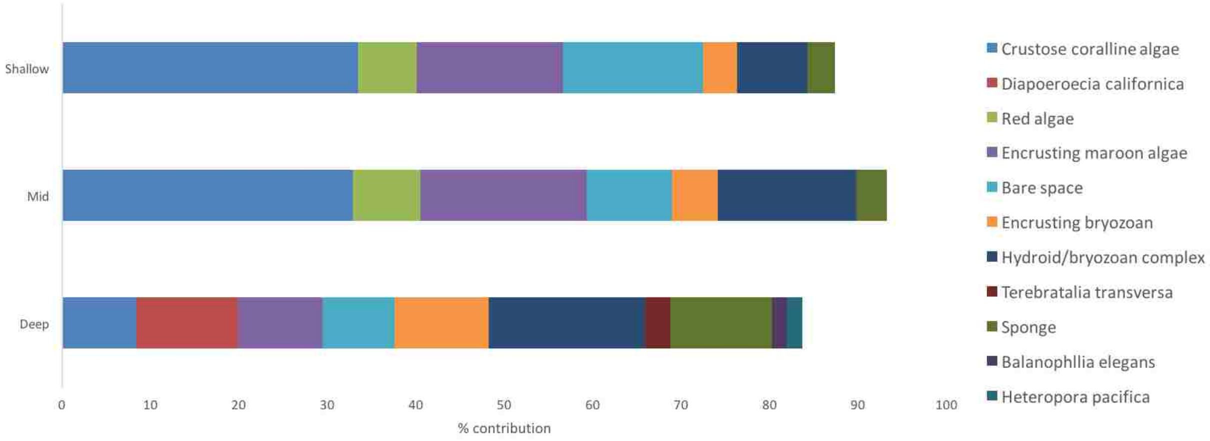


Figure 24. Contribution to benthic assemblage similarity among grouped depths on sloping substrate. Shallow: 3 m to 9 m; Mid: 12 m to 18 m; Deep: 21 m to 27 m.

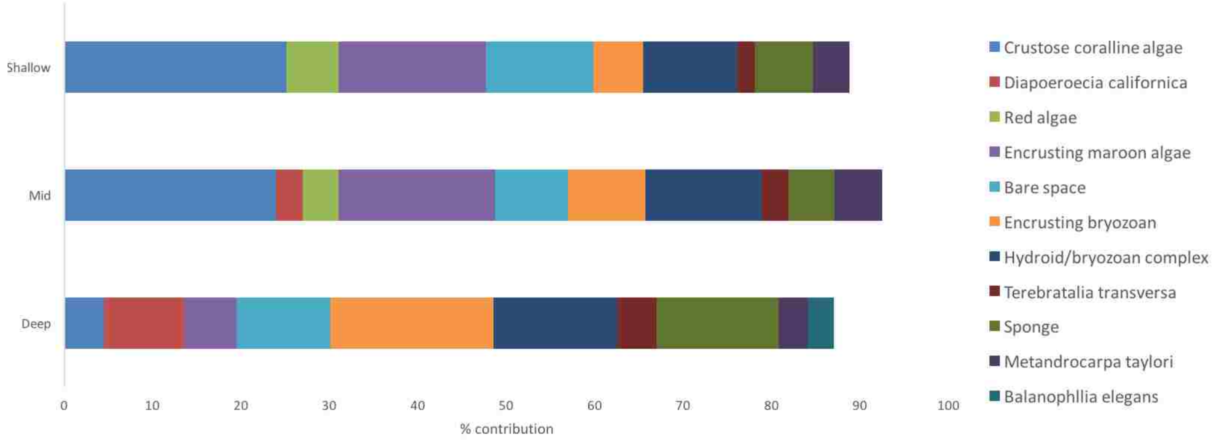


Figure 25. Contribution to benthic assemblage similarity among grouped depths on vertical substrate. Shallow: 3 m to 9 m; Mid: 12 m to 18 m; Deep: 21 m to 27 m.

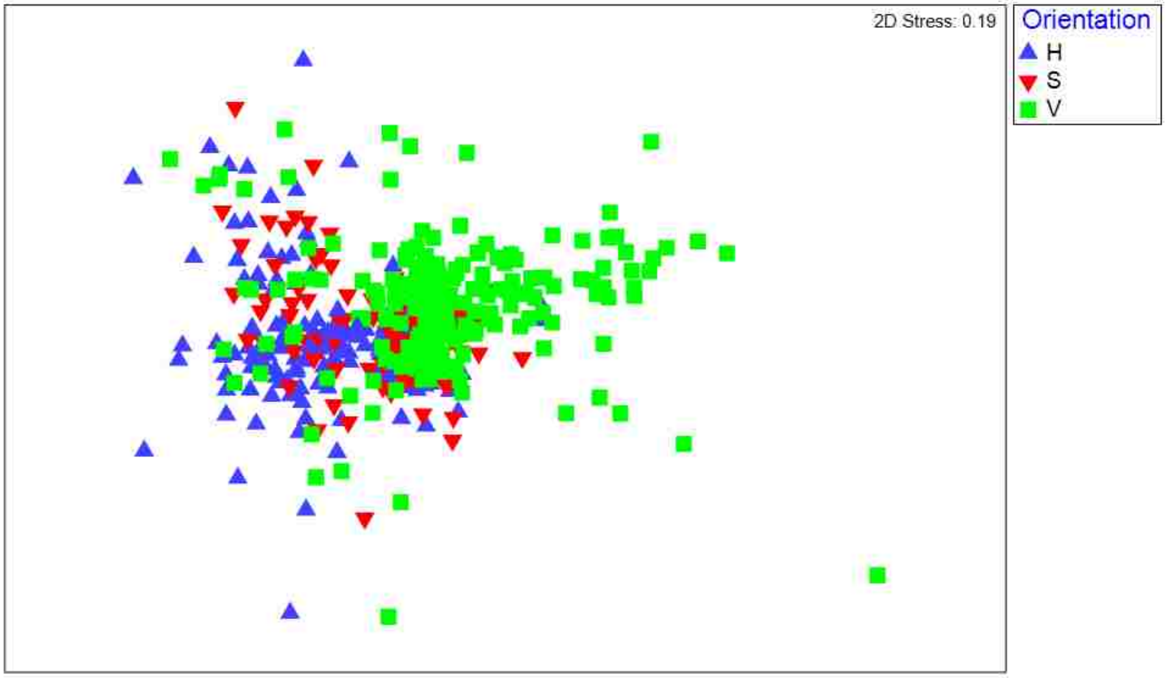


Figure 26. nMDS plot of benthic sessile assemblage similarities among horizontal, sloping, and vertical substrates in the shallow zone (3 m to 9 m). Global R-statistic: 0.124 (H, S: 0.037; S, V: 0.048; H, V: 0.21).

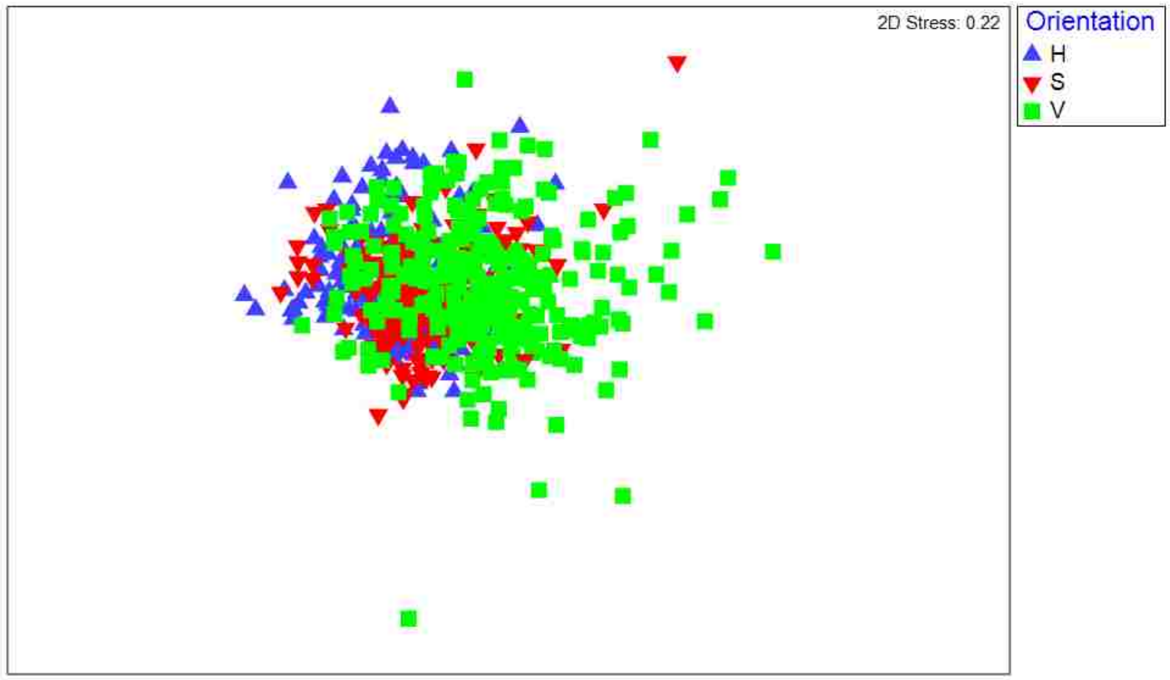


Figure 27. nMDS plot of benthic sessile assemblage similarities among horizontal, sloping, and vertical substrates in the mid zone (12 m to 18 m). Global R-statistic: 0.086 (H, S: 0.029; S, V: 0.0.092; H, V: 0.134).

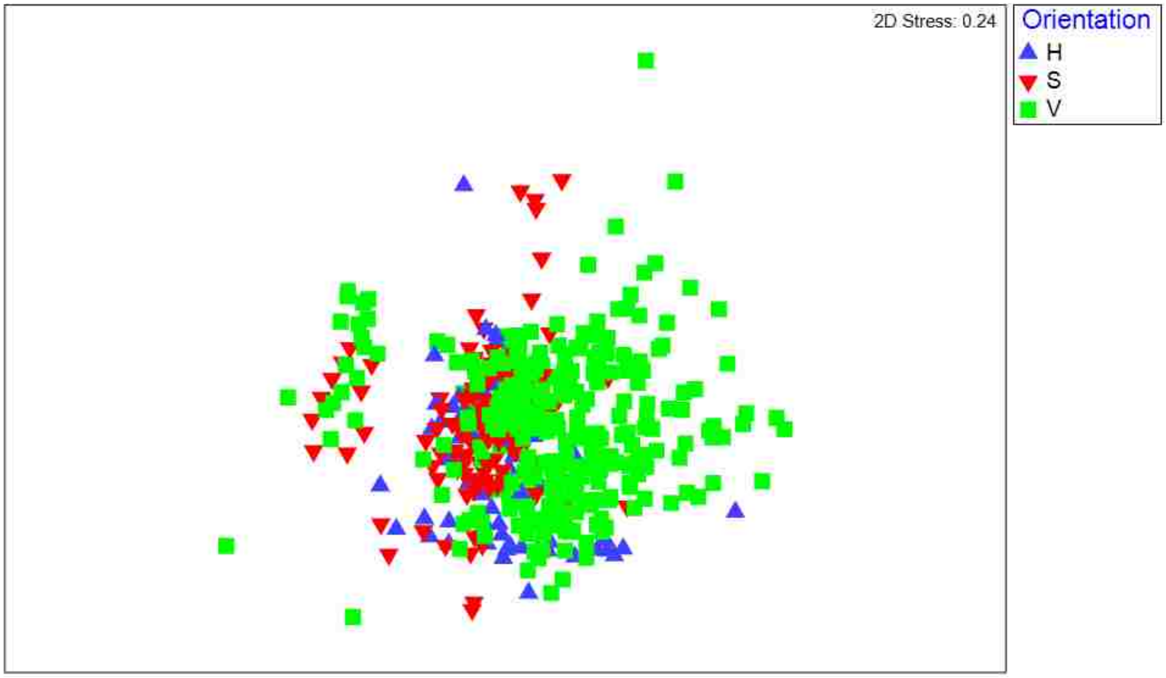


Figure 28. nMDS plot of benthic sessile assemblage similarities among horizontal, sloping, and vertical substrates in the deep zone (21 m to 27 m). Global R-statistic: 0.041 (H, S: 0.143; S, V: 0.0.028; H, V: 0.068).

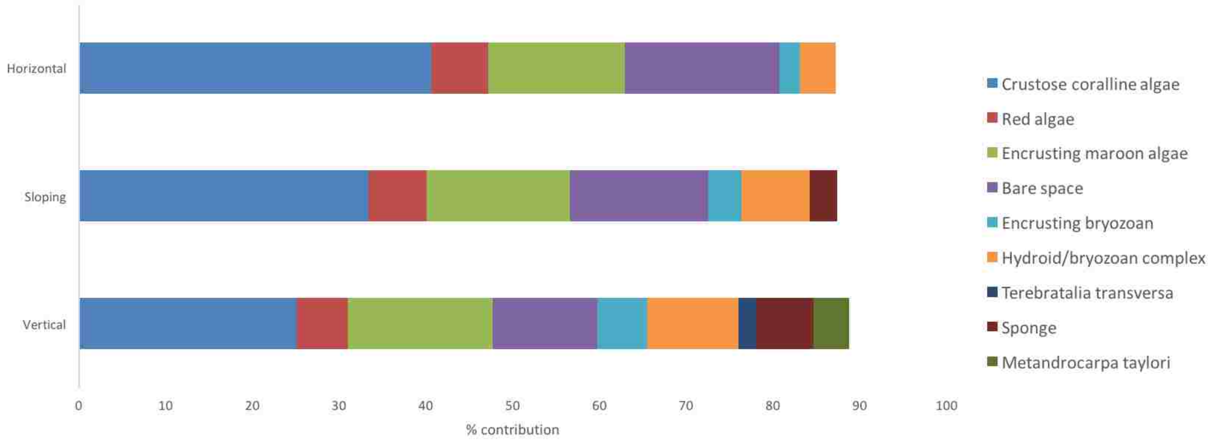


Figure 29. Contribution to benthic sessile assemblage similarity among substrate orientations in the shallow zone (3 m to 9 m).

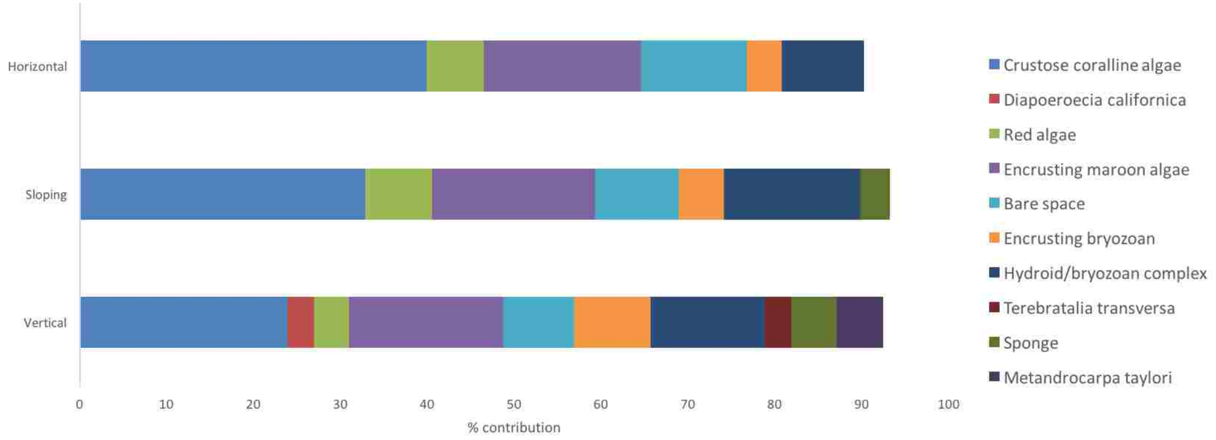


Figure 30. Contribution to benthic sessile assemblage similarity among substrate orientations in the mid zone (12 m to 18 m).

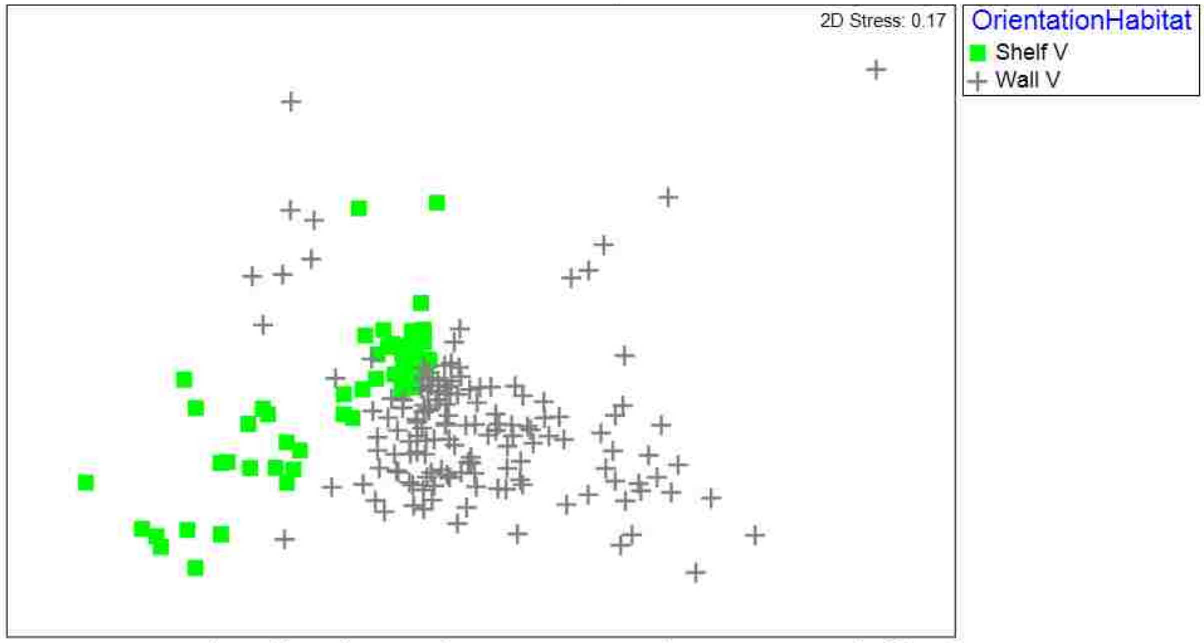


Figure 31. nMDS plot of benthic sessile assemblage similarities among shelf and wall habitats on vertical substrates in the shallow zone (3 m to 9 m). R-statistic: 0.261.

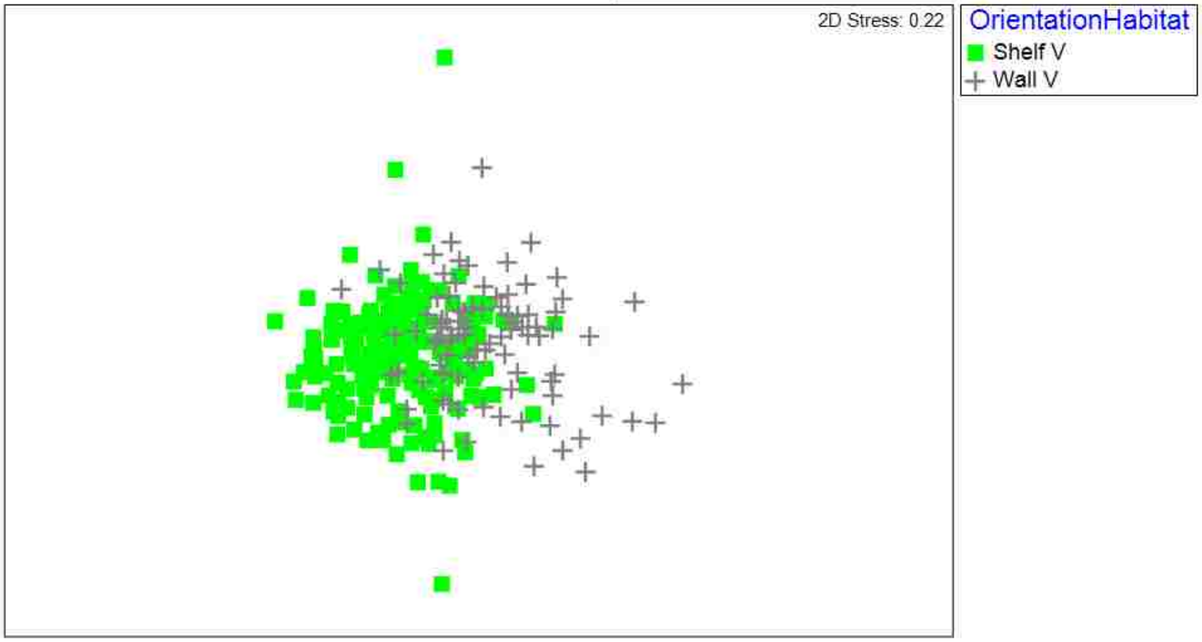


Figure 32. nMDS plot of benthic sessile assemblage similarities among shelf and wall habitats on vertical substrates in the mid zone (12 m to 18 m). R-statistic: 0.283.

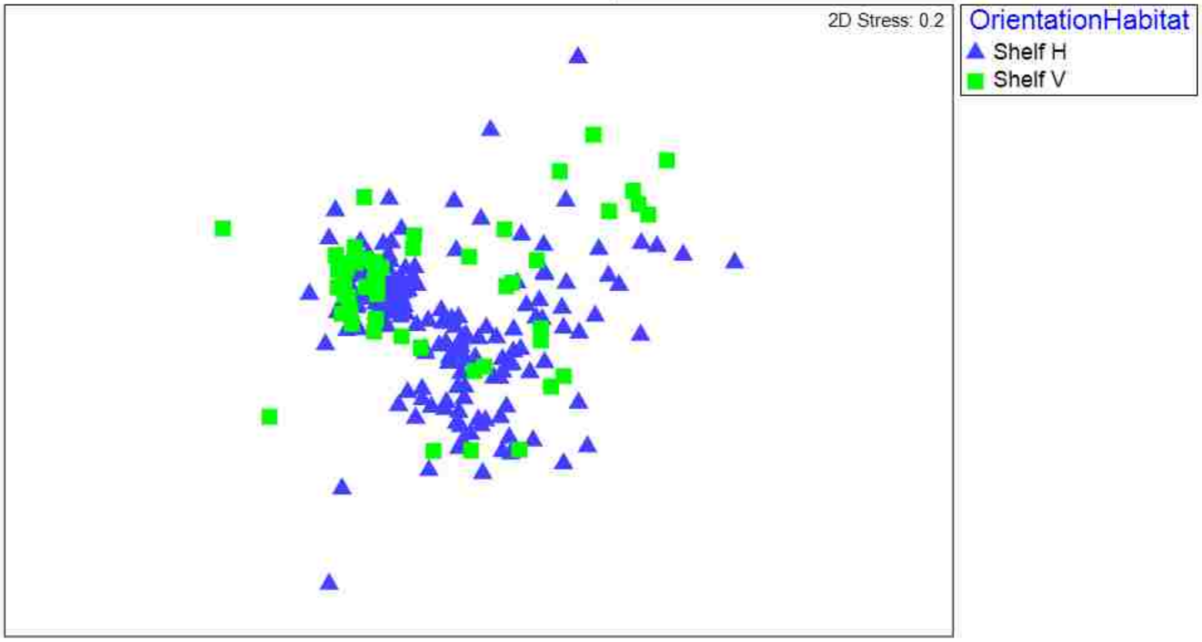


Figure 33. nMDS plot of benthic sessile assemblage similarities among horizontal and vertical substrates within the shelf habitat in the shallow zone (3 m to 9 m). R-statistic: 0.122.

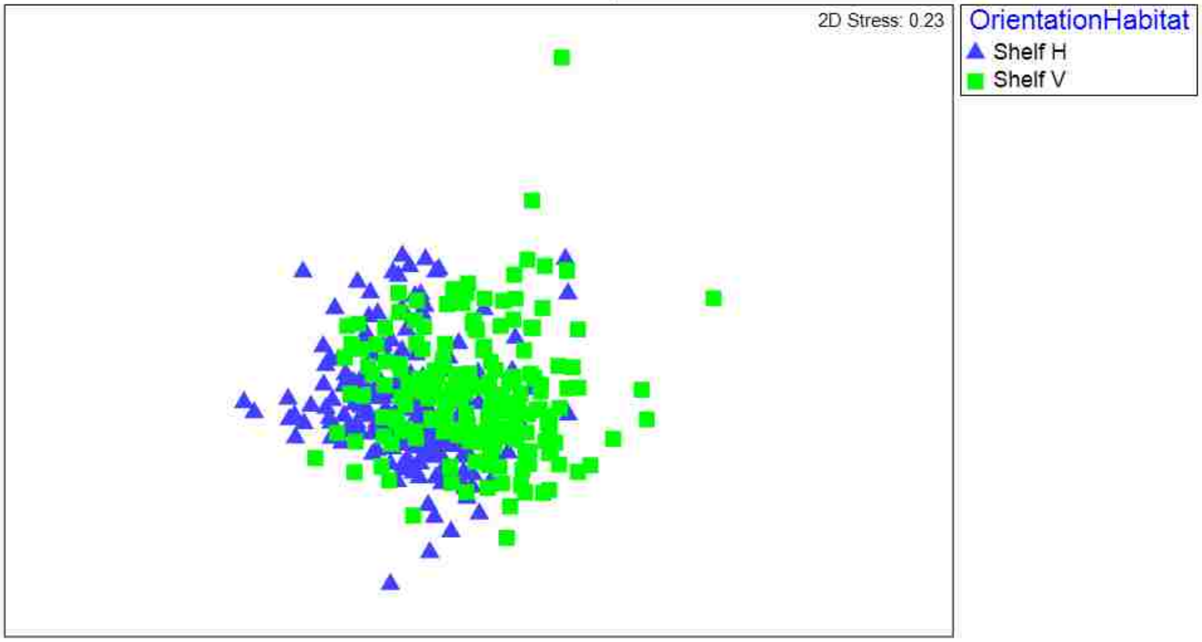


Figure 34. nMDS plot of benthic sessile assemblage similarities among horizontal and vertical substrates within the shelf habitat in the mid zone (12 m to 18 m). R-statistic: 0.138.

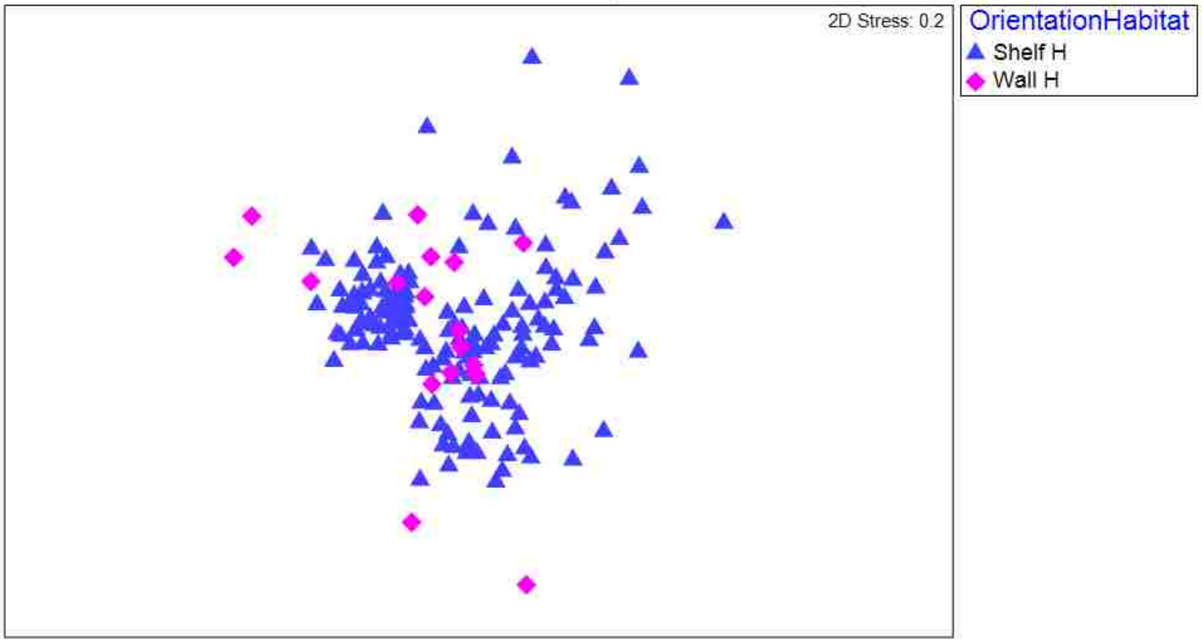


Figure 35. nMDS plot of benthic sessile assemblage similarities among shelf and wall habitats on horizontal substrates in the shallow zone (3 m to 9 m). R-statistic: 0.082.

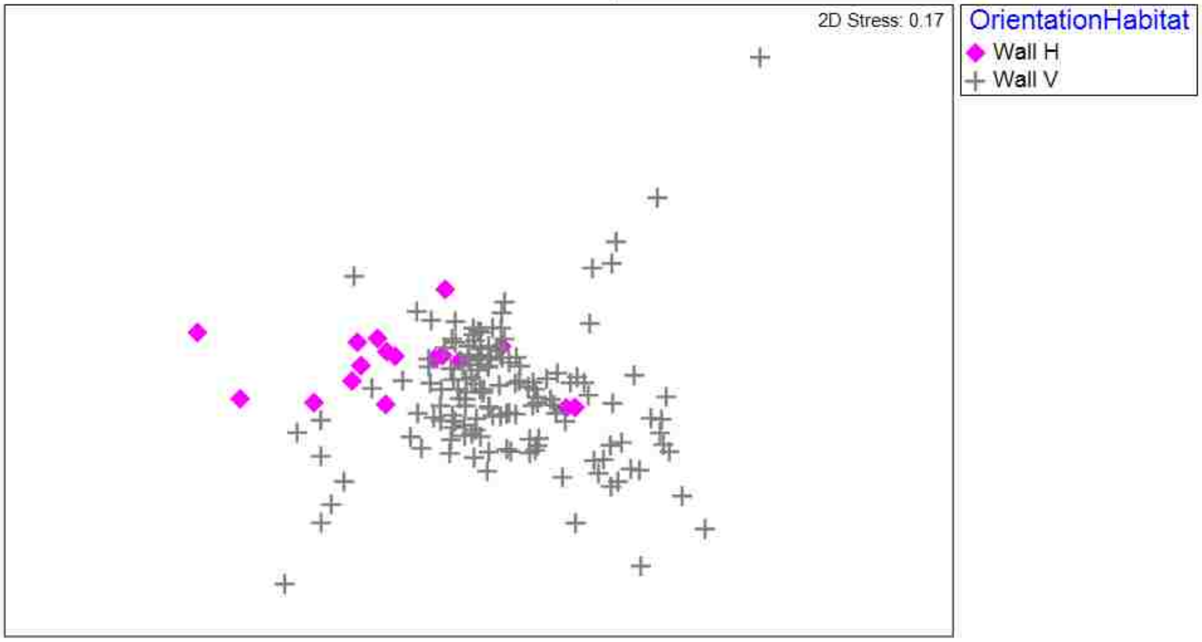


Figure 36. nMDS plot of benthic sessile assemblage similarities among horizontal and vertical substrates within the wall habitat in the shallow zone (3 m to 9 m). R-statistic: 0.189)

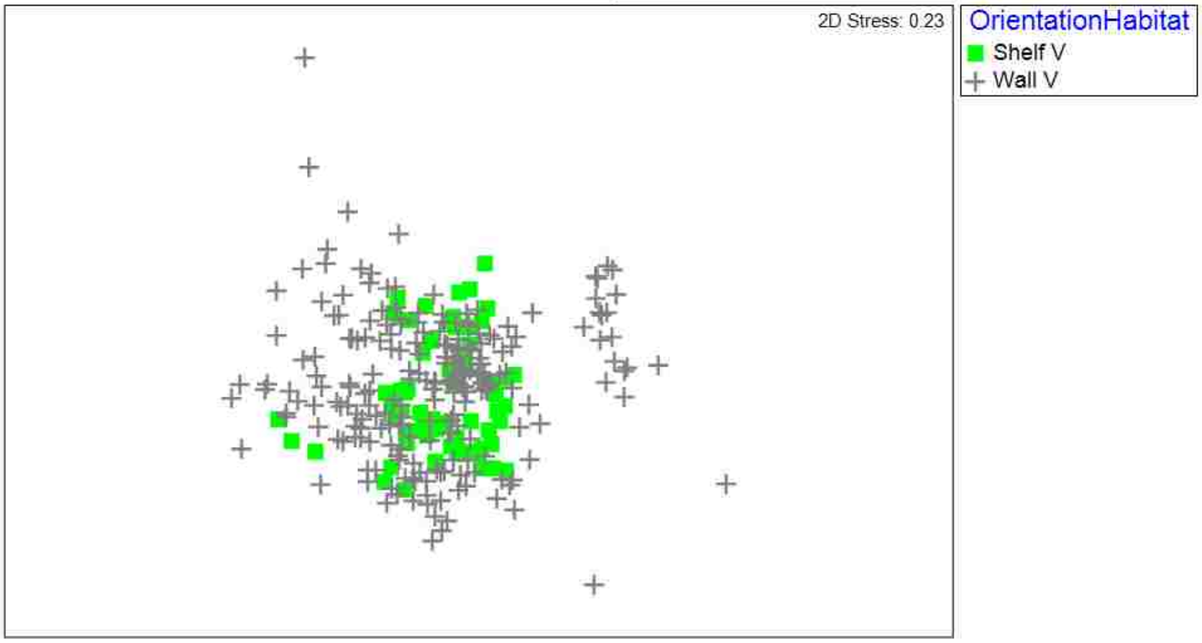


Figure 37. nMDS plot of benthic sessile assemblage similarities among shelf and wall habitats on vertical substrates in the deep zone (21 m to 27 m). R-statistic: -0.05.

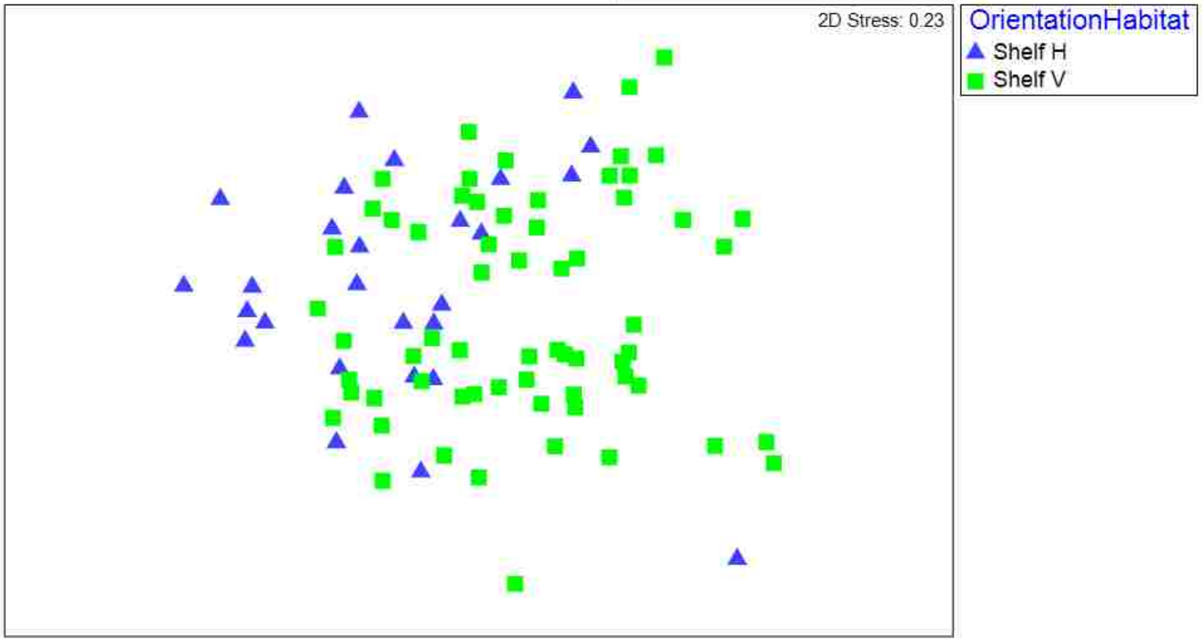


Figure 38. nMDS plot of benthic sessile assemblage similarities among horizontal and vertical substrates within the shelf habitat in the deep zone (21 m to 27 m). R-statistic: 0.184.

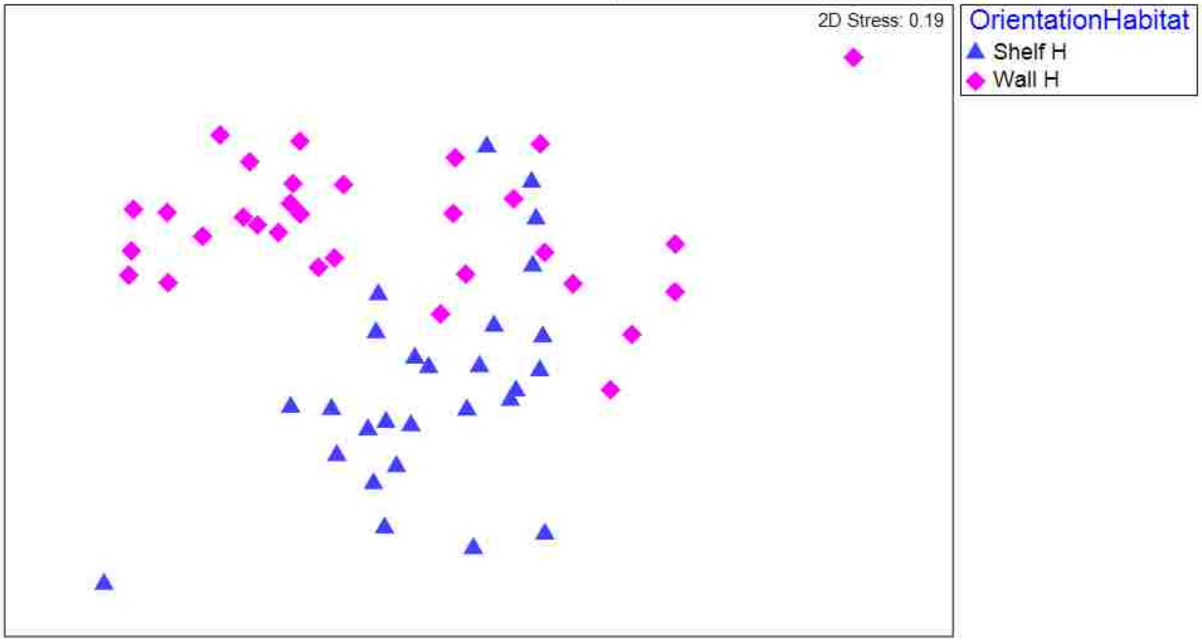


Figure 39. nMDS plot of benthic sessile assemblage similarities among shelf and wall habitats on horizontal substrates in the deep zone (21 m to 27 m). R-statistic: 0.284.

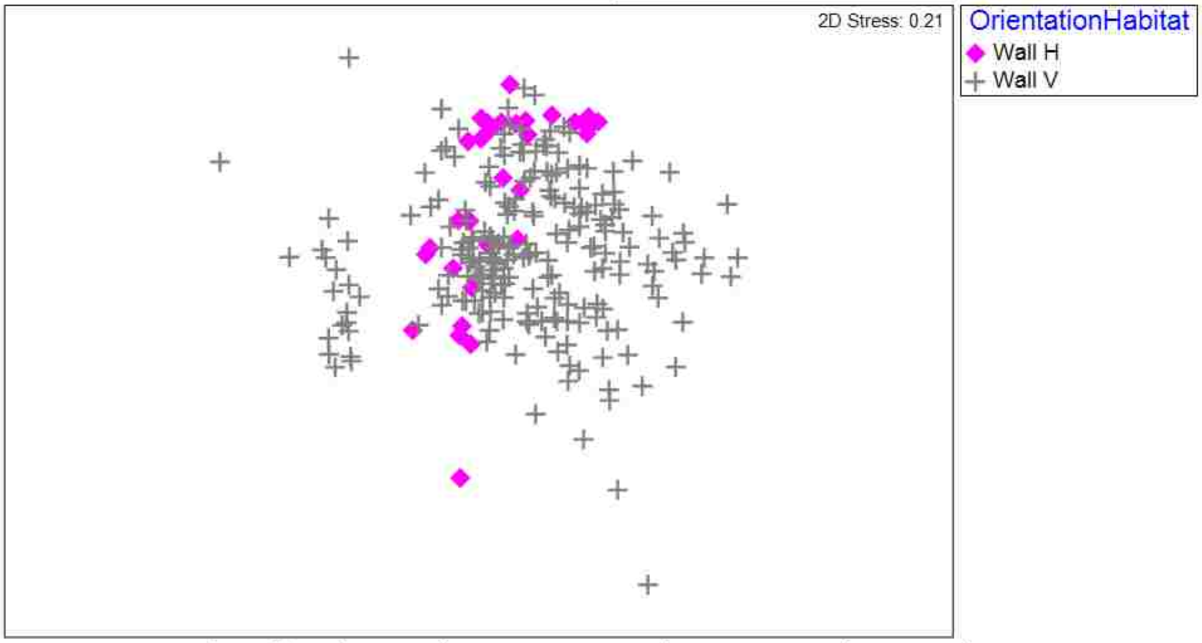


Figure 40. nMDS plot of benthic sessile assemblage similarities among horizontal and vertical substrates within the wall habitat in the deep zone (21 m to 27 m). R-statistic: 0.052.

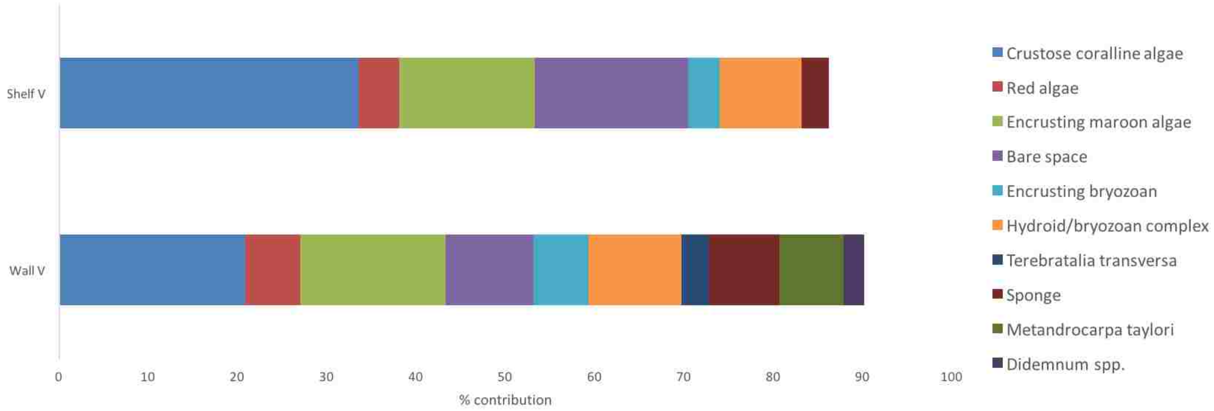


Figure 41. Contribution to benthic sessile assemblage similarity among shelf and wall habitats on vertical substrates in the shallow zone (3 m to 9 m).

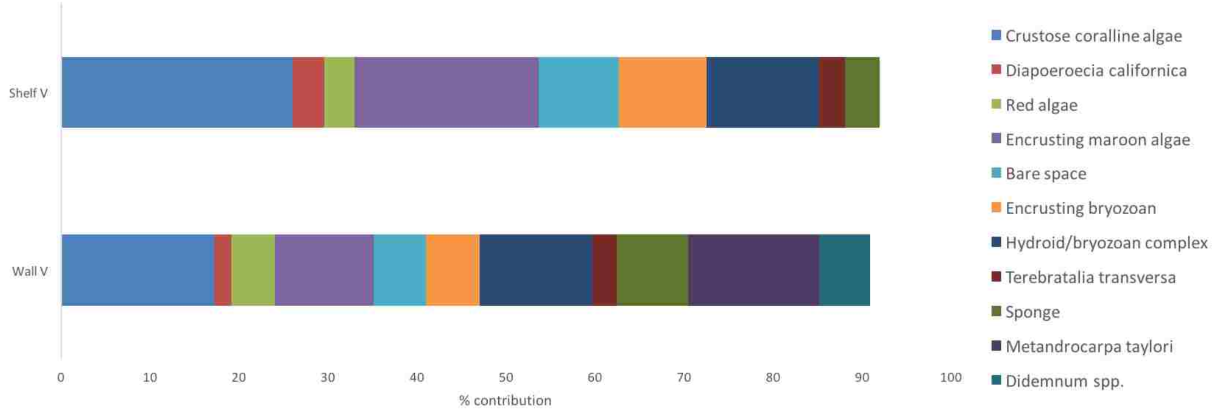


Figure 42. Contribution to benthic sessile assemblage similarity among shelf and wall habitats on vertical substrates in the mid zone (12 m to 18 m).

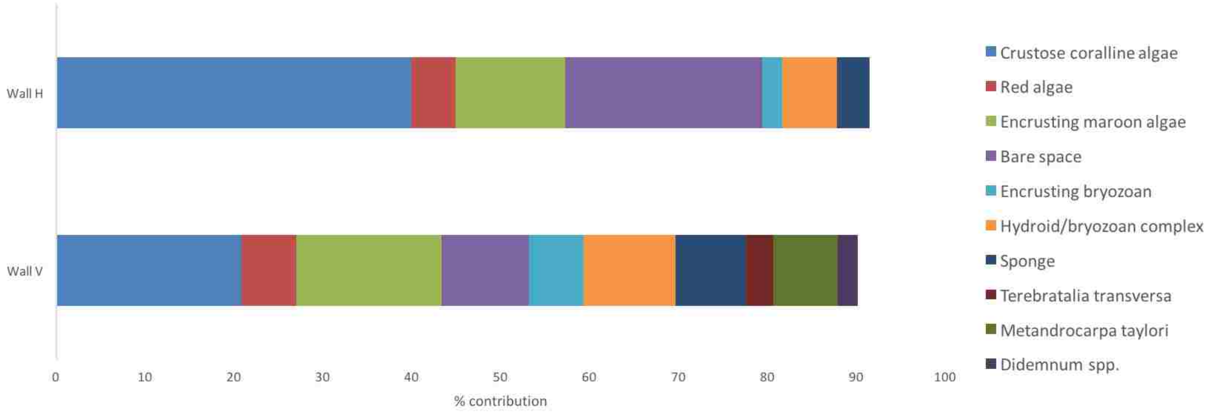


Figure 43. Contribution to benthic sessile assemblage similarity among horizontal and vertical substrates within the wall habitat in the shallow zone (3 m to 9 m).

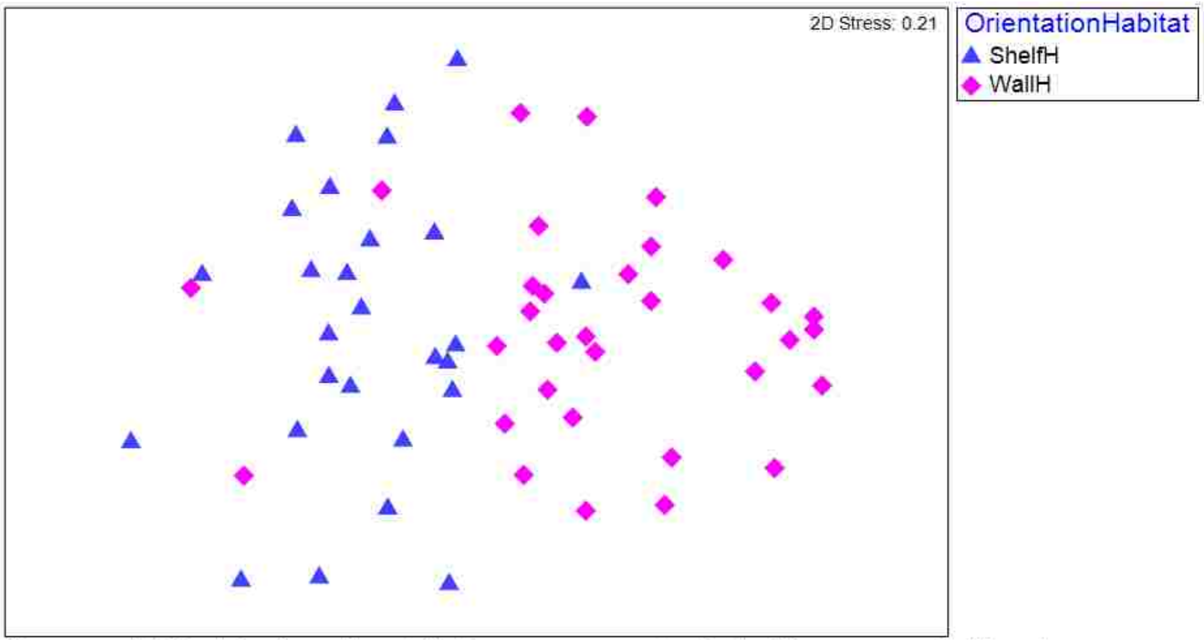


Figure 44. nMDS plot of small mobile fauna assemblage similarities among the shelf and wall habitats on horizontal substrates in the deep zone (21 m to 27 m). R-statistic: 0.382.

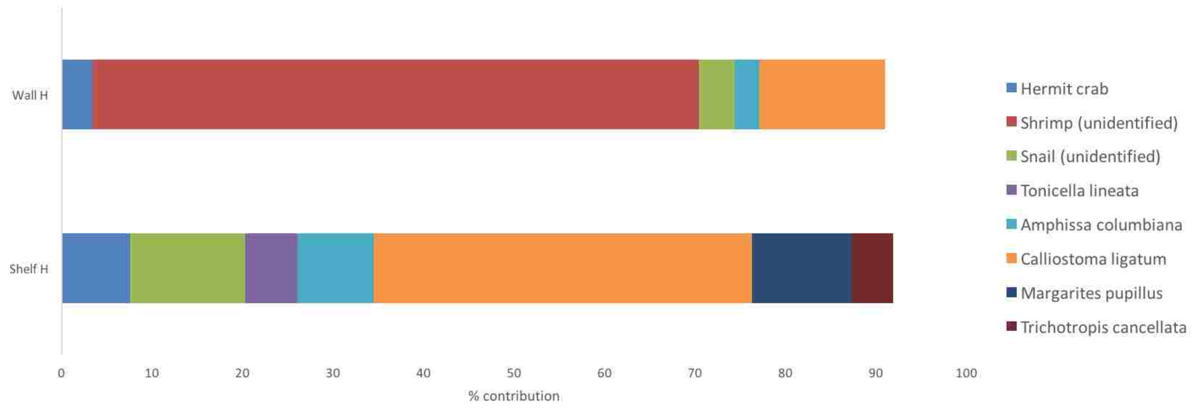


Figure 45. Contribution to small mobile fauna assemblage similarity among shelf and wall habitats on horizontal substrates in the deep zone (21 m to 27 m).

Supplemental Material

Three separate analyses were used to determine to what degree community composition dissimilarities emerged from inter-depth, site, and annual variation. Depth zonation patterns showed the strongest relationship with benthic community dissimilarity, both visually using nMDS plots (Chapter 1, Figure 16), and statistically using ANOSIM values. R-Statistics (Chapter 1, Table 2) illustrate the degree of separation between communities in samples; a low R-Statistic (near 0) indicates great overlap in species and relative abundances whereas an R-Statistic near 1 indicates completely different communities. Because depth emerged as such an overriding key factor (with high R-Statistics illustrating community differentiation among depths) and because all our sites are relatively close (within 3 km), in subsequent analyses we used site transects as replicates within depths to investigate community dissimilarities.

Visual and statistical results also showed evidence of patchy community dissimilarities driven by both inter-annual and inter-site variation (consistently low R-Statistics in among-year and among-site comparisons). A recent study by Elahi and Sebens (2014) also found little evidence of inter-annual variation on vertical surfaces in the mid zone, even when compared to a study conducted 40 years ago on the same local reefs. Thus, for this study, we have used transects across years as replicates to investigate community dissimilarities across depths. Although the transects have a fixed starting point, the position of the quadrats on each transect is randomly determined before the start of each season. As none of the datasets are generated from fixed quadrats, we consider quadrat data from different years as functionally independent.

Year and site: Horizontal and shallow only

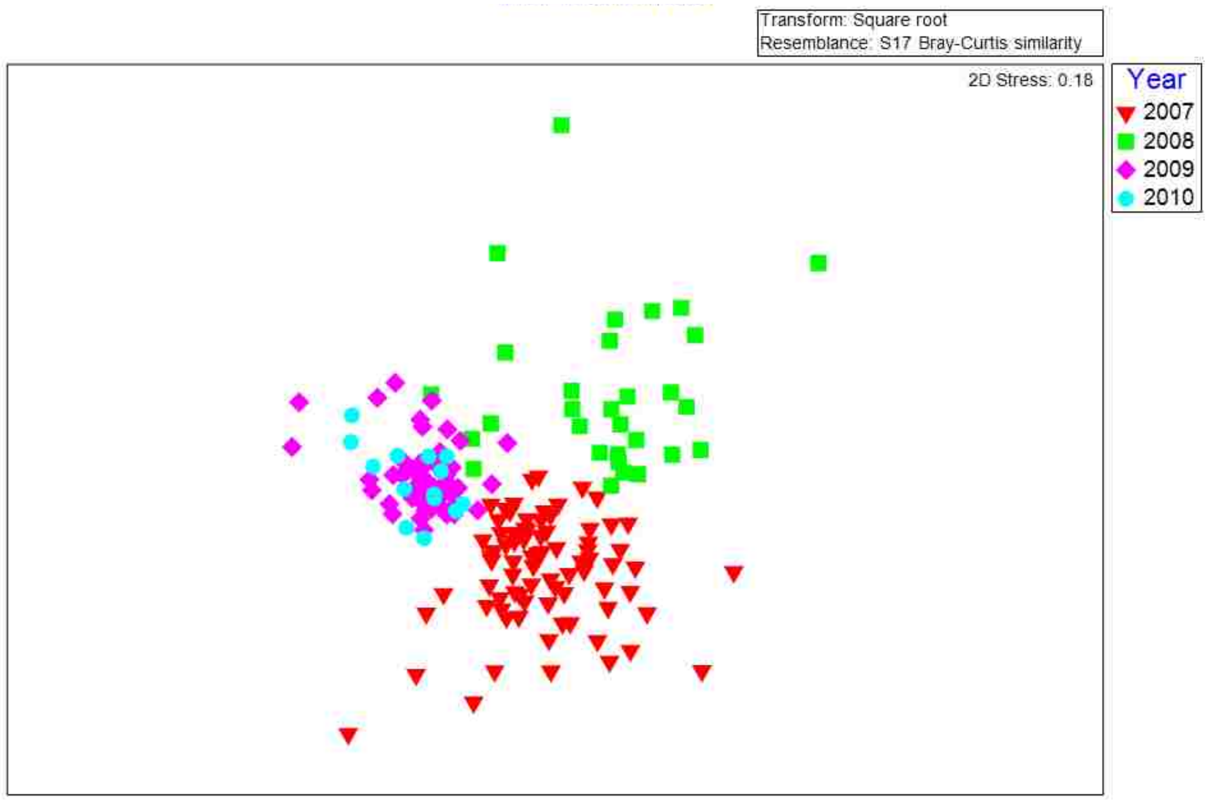


Figure S1. nMDS plot of benthic sessile assemblage similarities between years on horizontal surfaces in the shallow zone (3 m to 9 m). Global R-statistic: 0.573.

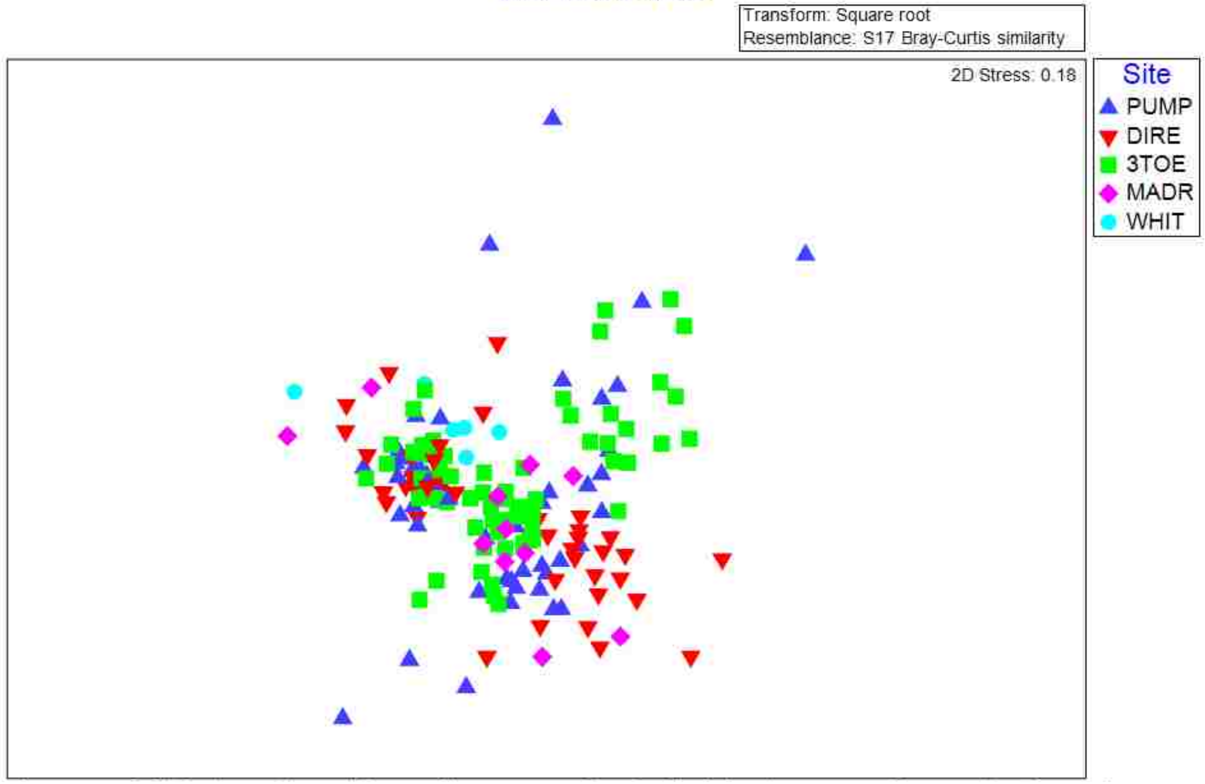


Figure S2. nMDS plot of benthic sessile assemblage similarities between sites on horizontal surfaces in the shallow zone (3 m to 9 m). Global R-statistic: 0.084.

Year and site: Horizontal and mid only

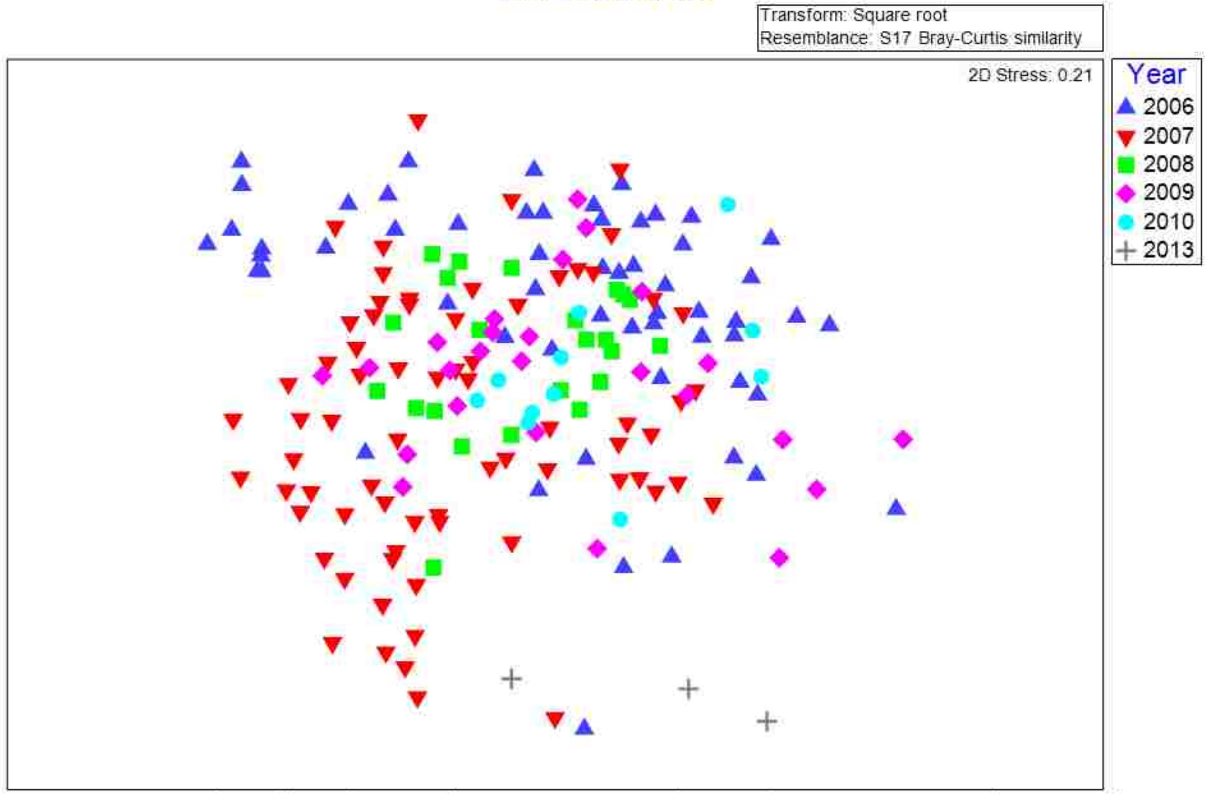


Figure S3. nMDS plot of benthic sessile assemblage similarities between years on horizontal surfaces in the mid zone (12 m to 18 m). Global R-statistic: 0.132.

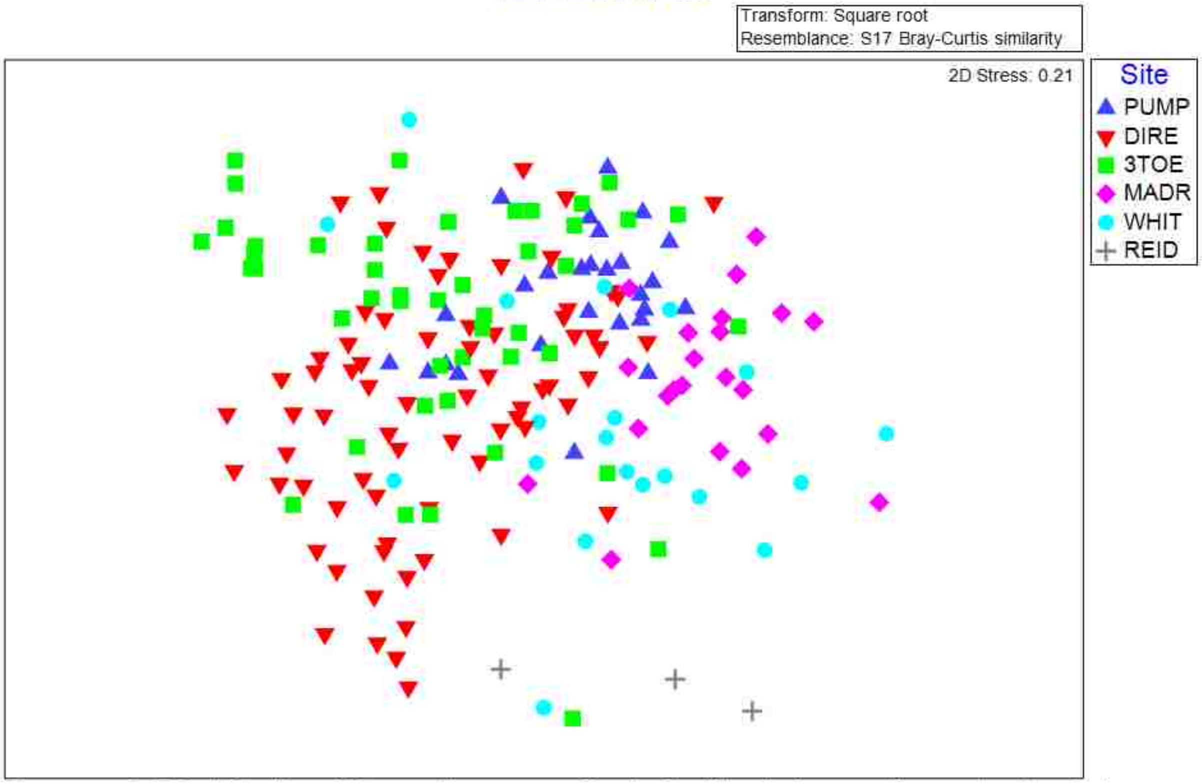


Figure S4. nMDS plot of benthic sessile assemblage similarities between sites on horizontal surfaces in the mid zone (12 m to 18 m). Global R-statistic: 0.29.

Year and site: Horizontal and deep only

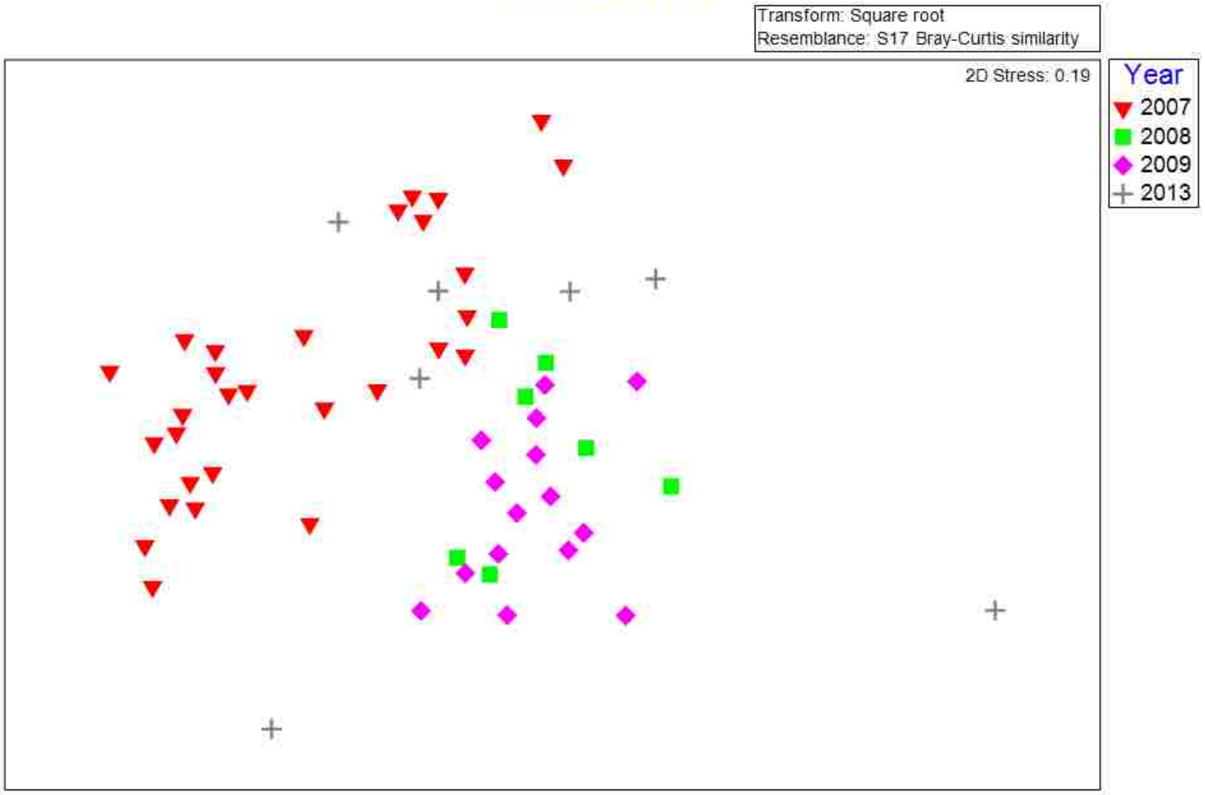


Figure S5. nMDS plot of benthic sessile assemblage similarities between years on horizontal surfaces in the deep zone (21 m to 27 m). Global R-statistic: 0.497.

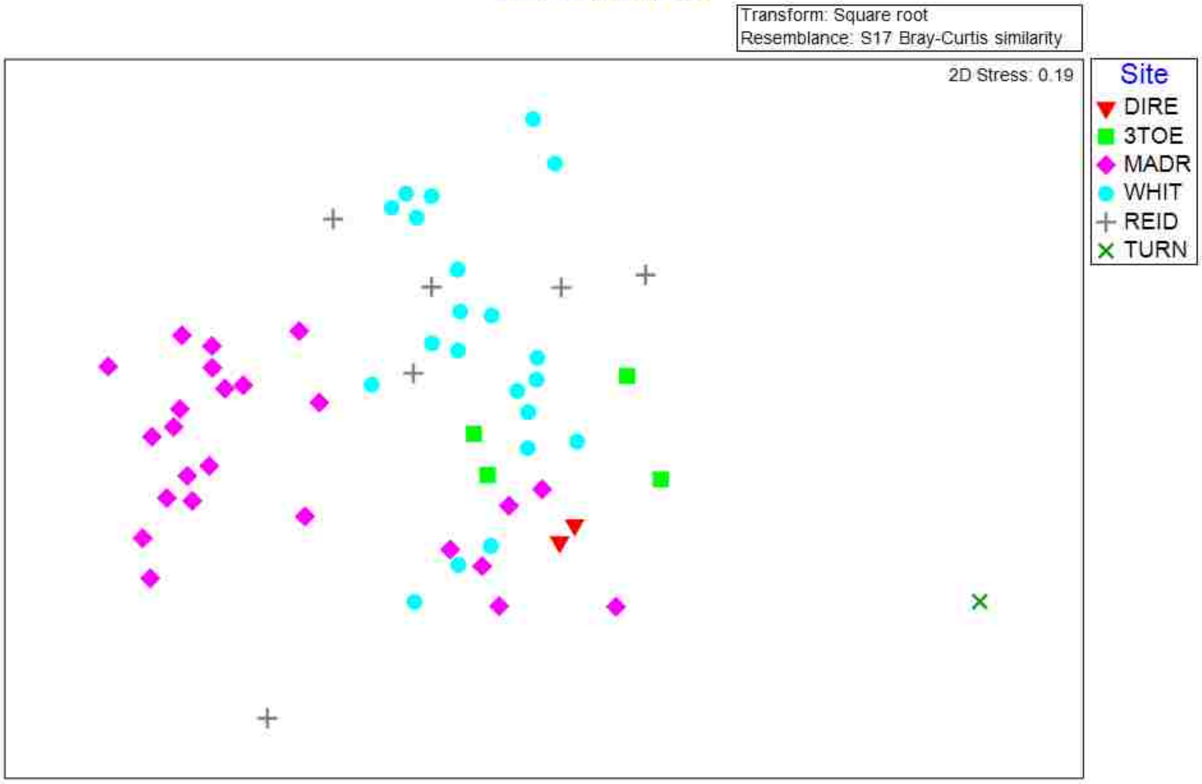


Figure S6. nMDS plot of benthic sessile assemblage similarities between sites on horizontal surfaces in the deep zone (21 m to 27 m). Global R-statistic: 0.49.

Year and site: Sloping and shallow only:

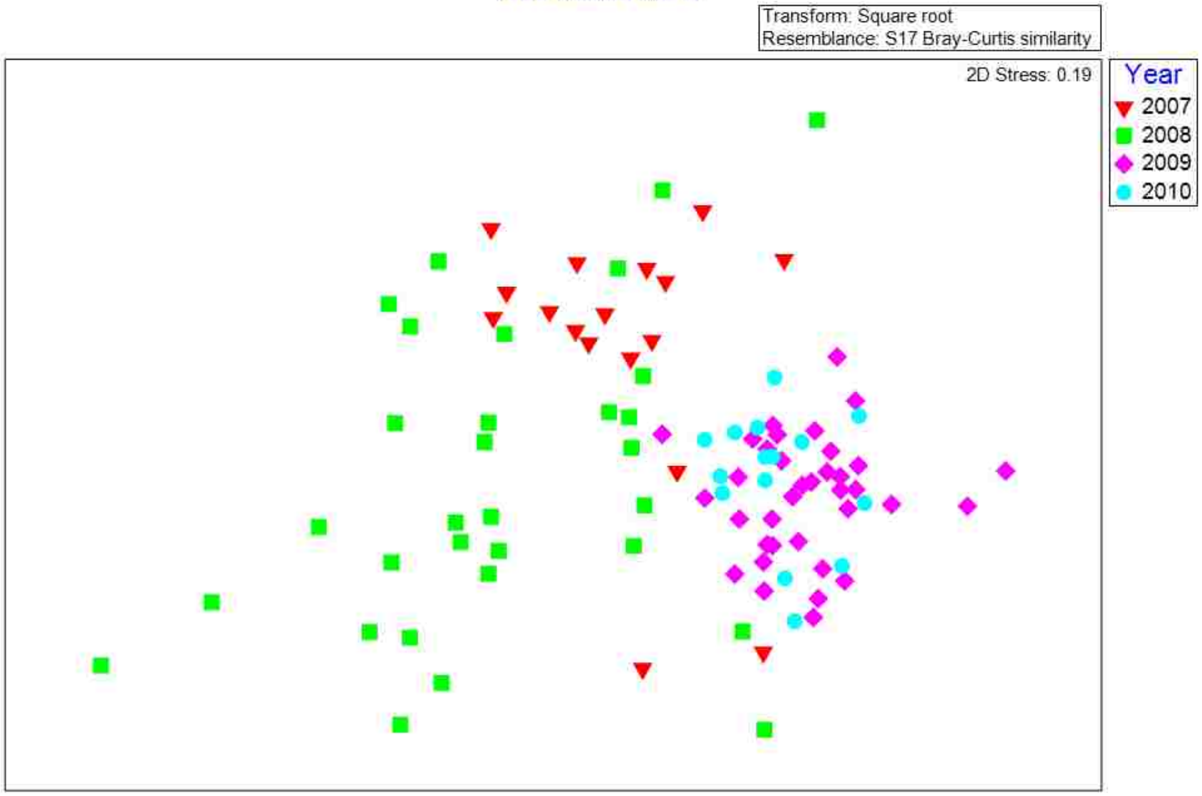


Figure S7. nMDS plot of benthic sessile assemblage similarities between years on sloping surfaces in the shallow zone (3 m to 9 m). Global R-statistic: 0.467.

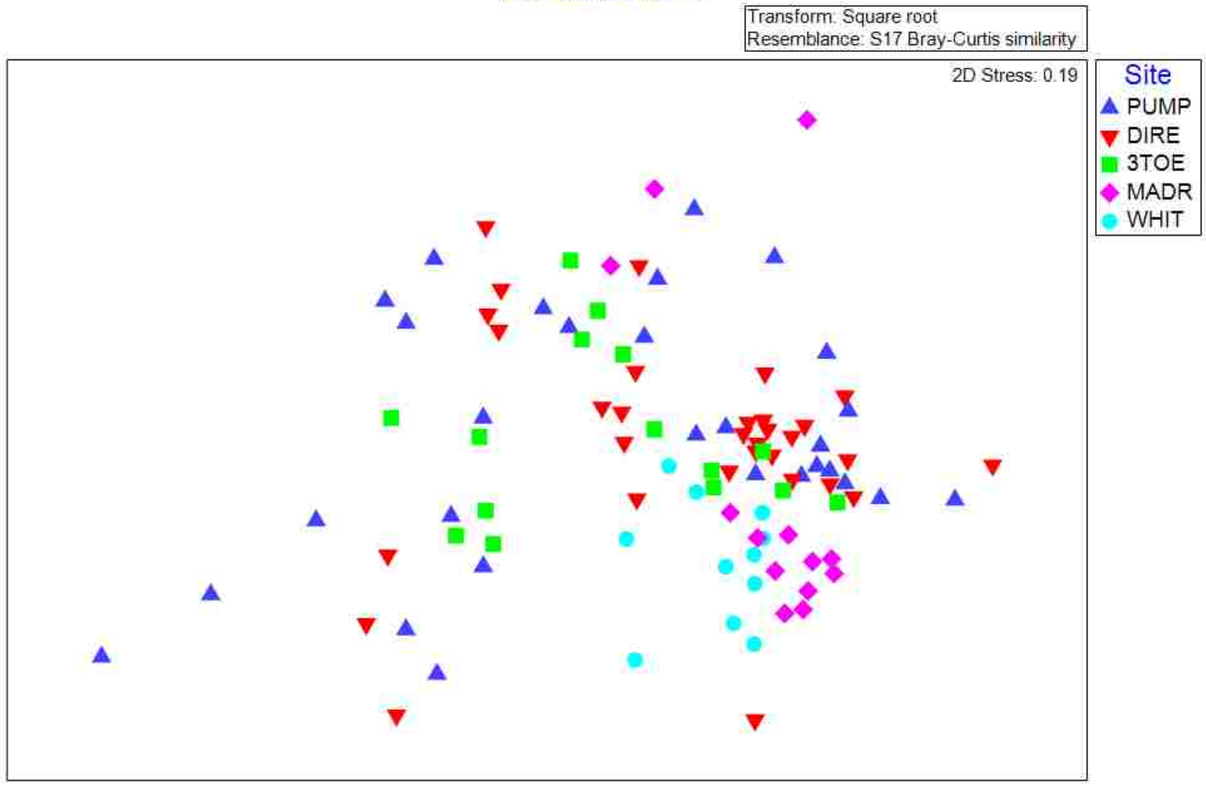


Figure S8. nMDS plot of benthic sessile assemblage similarities between sites on sloping surfaces in the shallow zone (3 m to 9 m). Global R-statistic: 0.048.

Year and site: Sloping and mid only

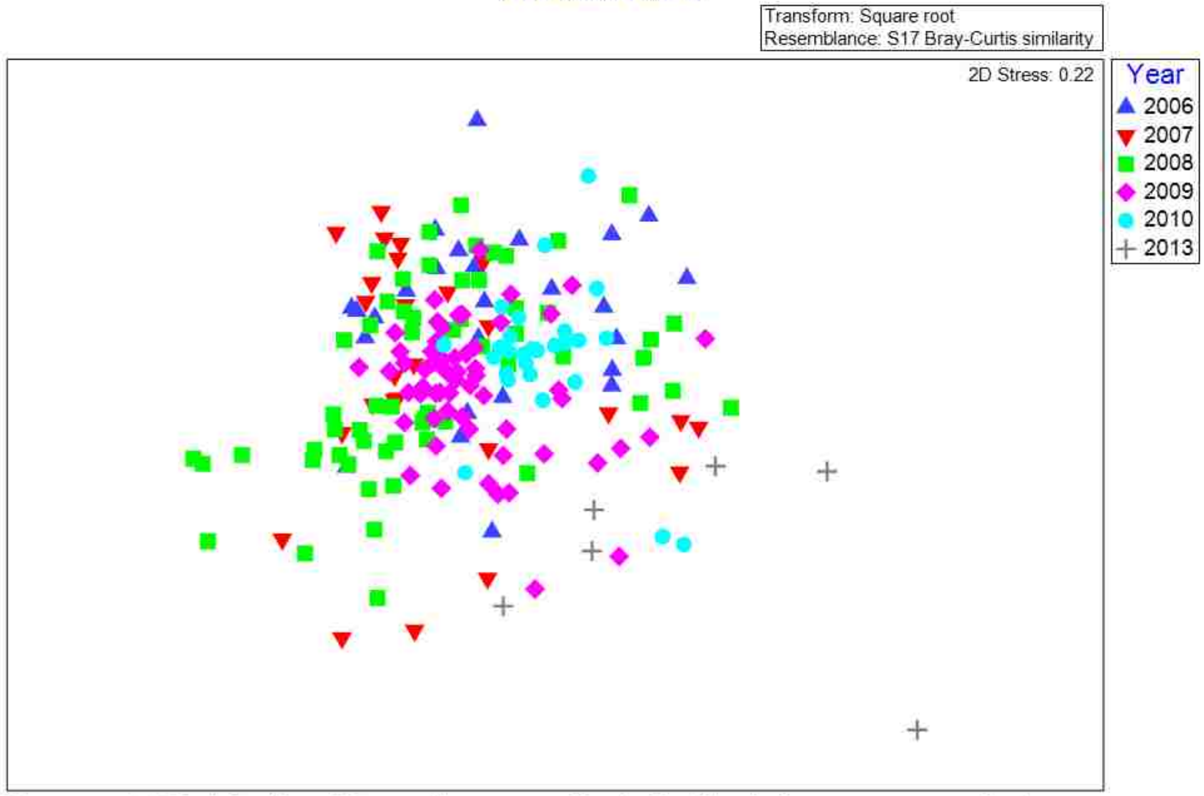


Figure S9. nMDS plot of benthic sessile assemblage similarities between years on sloping surfaces in the mid zone (12 m to 18 m). Global R-statistic: 0.235.

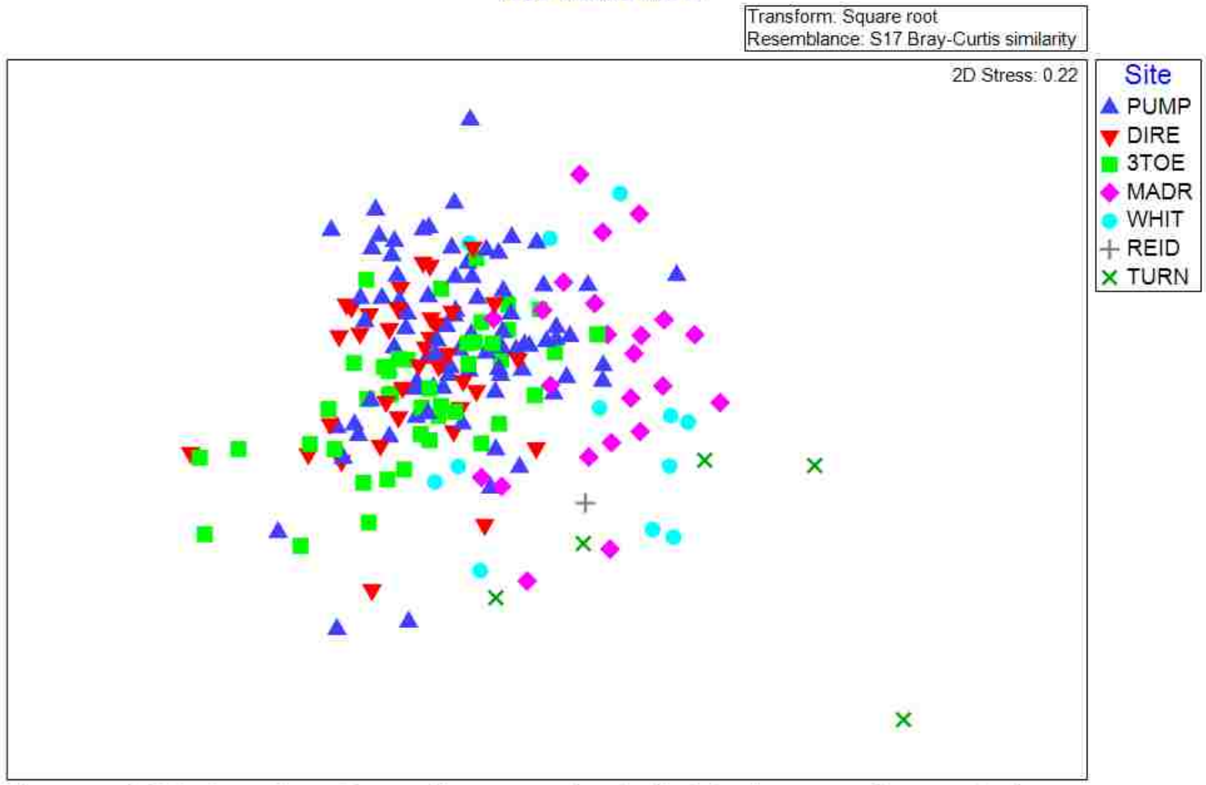


Figure S10. nMDS plot of benthic sessile assemblage similarities between sites on sloping surfaces in the mid zone (12 m to 18 m). Global R-statistic: 0.288.

Year and site: Sloping and deep only

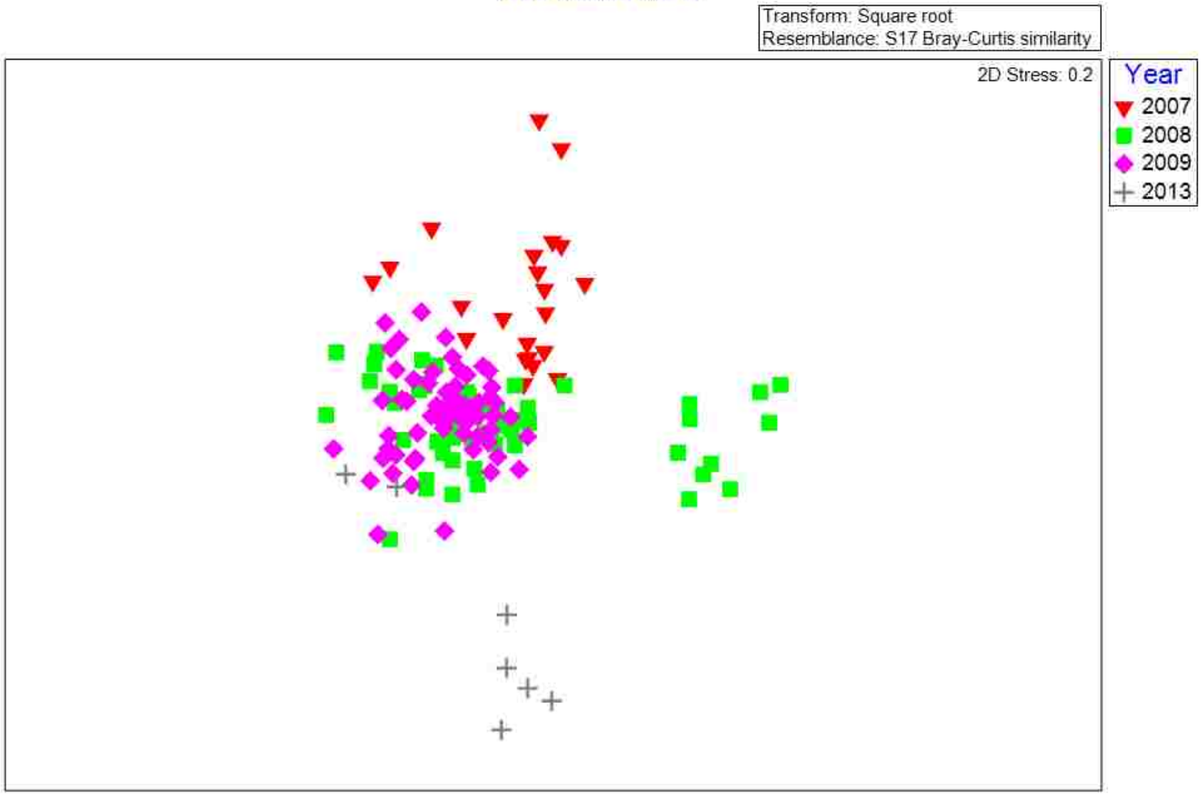


Figure S11. nMDS plot of benthic sessile assemblage similarities between years on sloping surfaces in the deep zone (21 m to 27 m). Global R-statistic: 0.355.

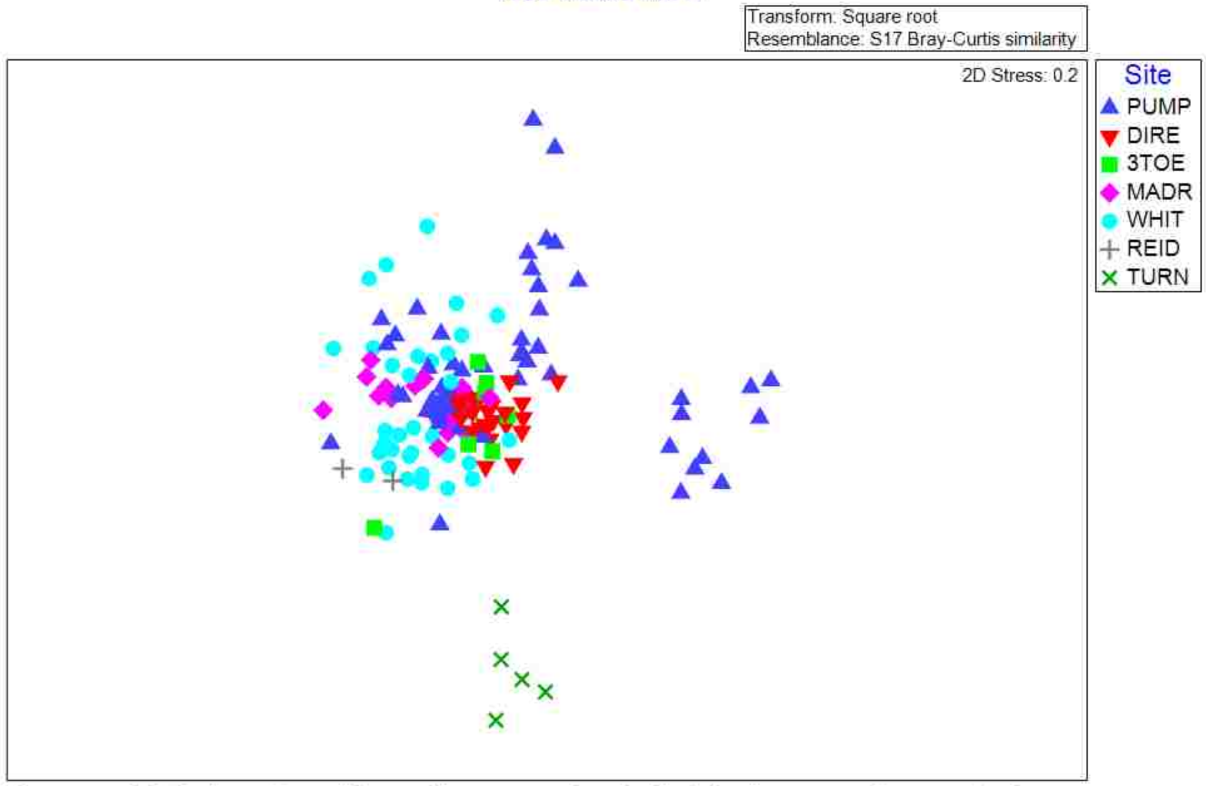


Figure S12. nMDS plot of benthic sessile assemblage similarities between sites on sloping surfaces in the deep zone (21 m to 27 m). Global R-statistic: 0.129.

Year and site: Vertical and shallow only

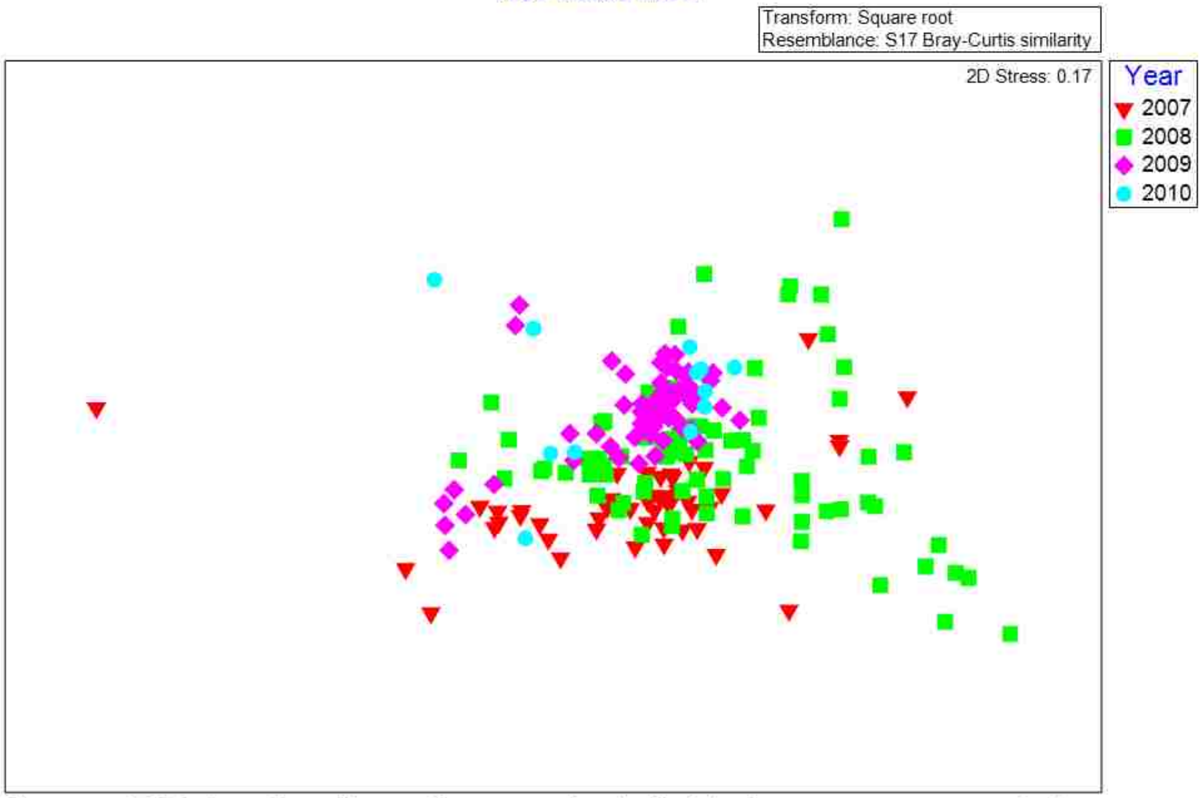


Figure S13. nMDS plot of benthic sessile assemblage similarities between years on vertical surfaces in the shallow zone (3 m to 9 m). Global R-statistic: 0.182.

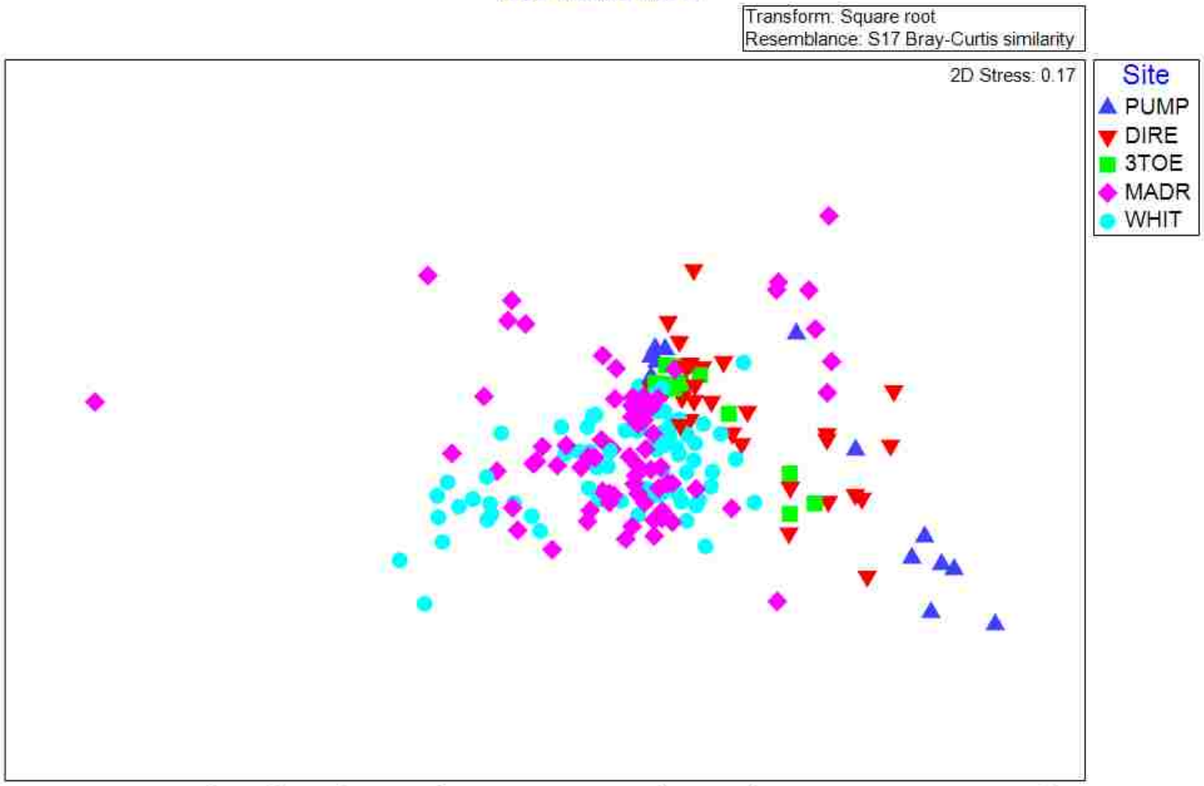


Figure S14. nMDS plot of benthic sessile assemblage similarities between sites on vertical surfaces in the shallow zone (3 m to 9 m). Global R-statistic: 0.247.

Year and site: Vertical and mid only

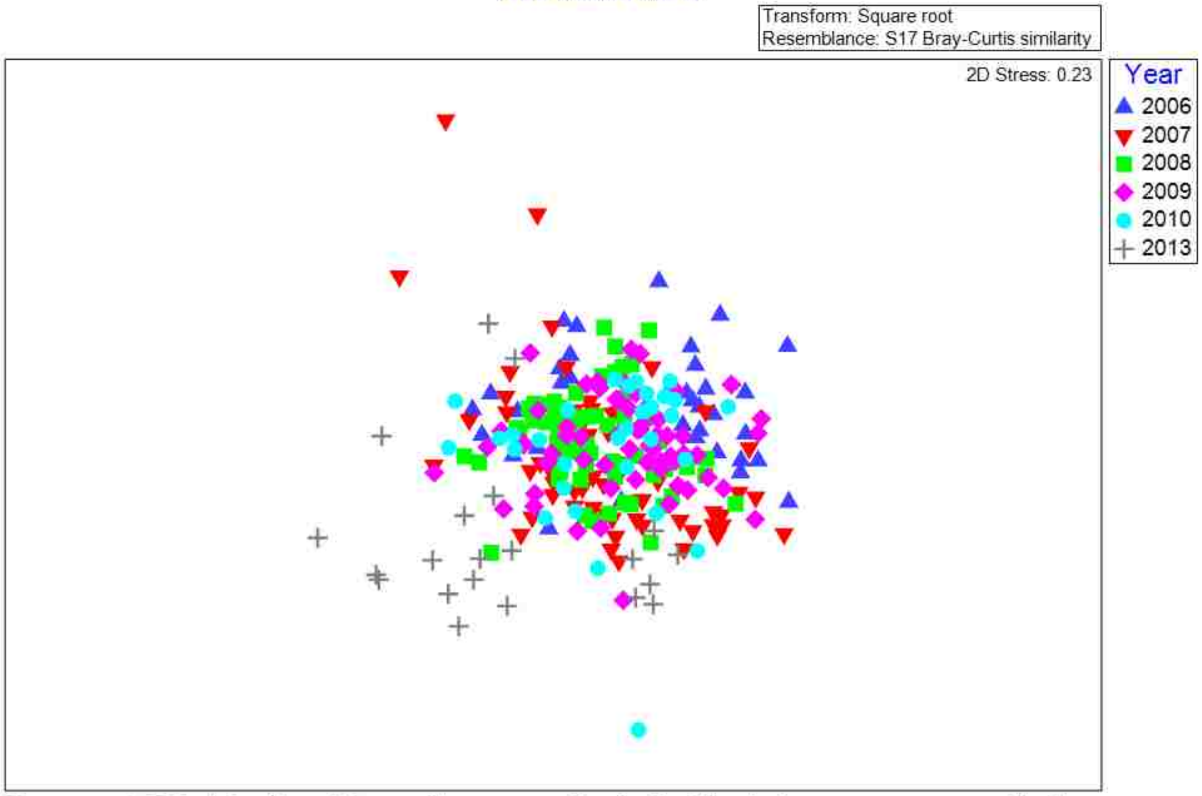


Figure S15. nMDS plot of benthic sessile assemblage similarities between years on vertical surfaces in the mid zone (12 m to 18 m). Global R-statistic: 0.288.

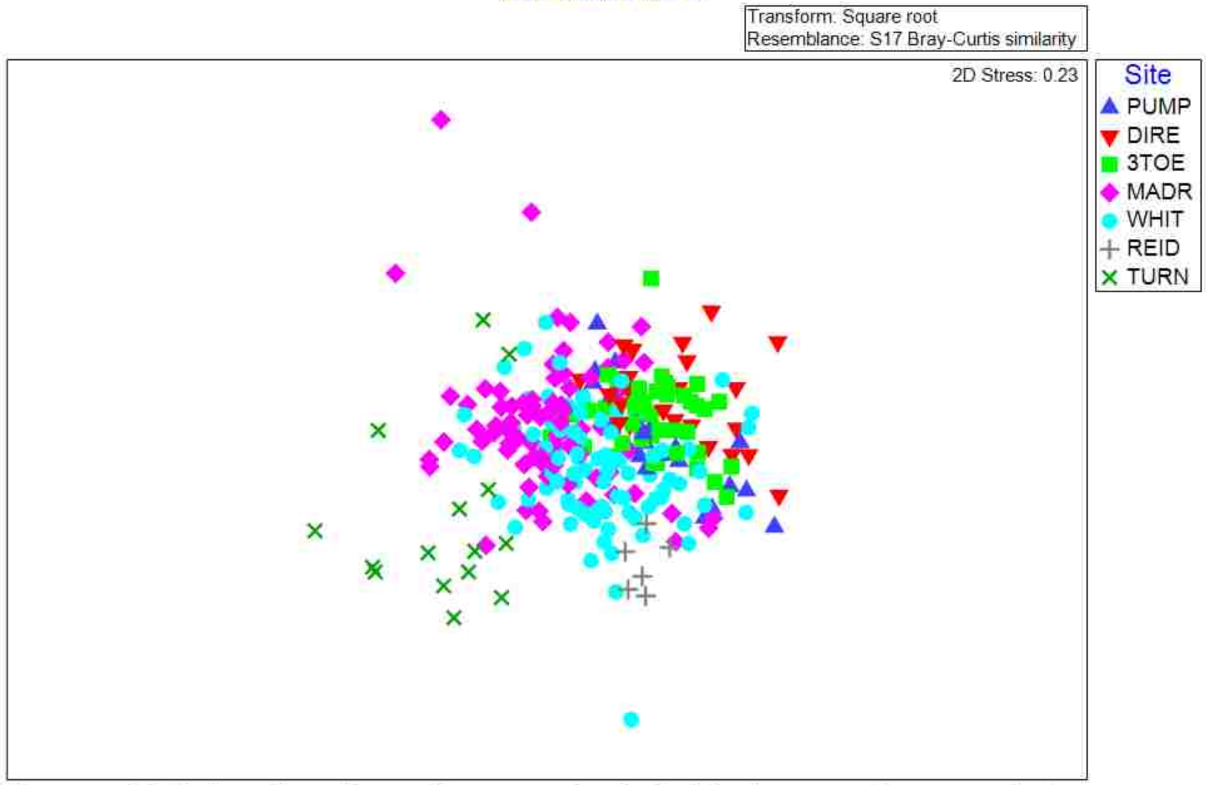


Figure S16. nMDS plot of benthic sessile assemblage similarities between sites on vertical surfaces in the mid zone (12 m to 18 m). Global R-statistic: 0.328.

Year and site: Vertical and deep only

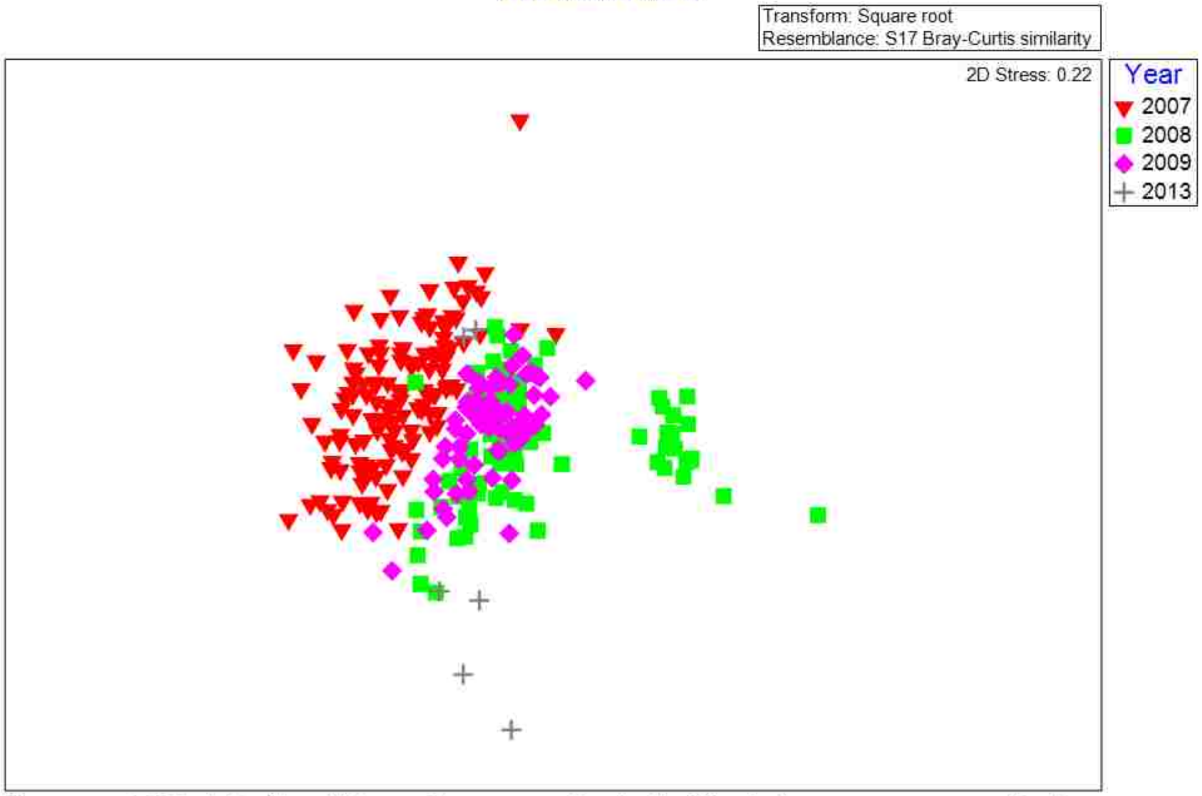


Figure S17. nMDS plot of benthic sessile assemblage similarities between years on vertical surfaces in the deep zone (21 m to 27 m). Global R-statistic: 0.321.

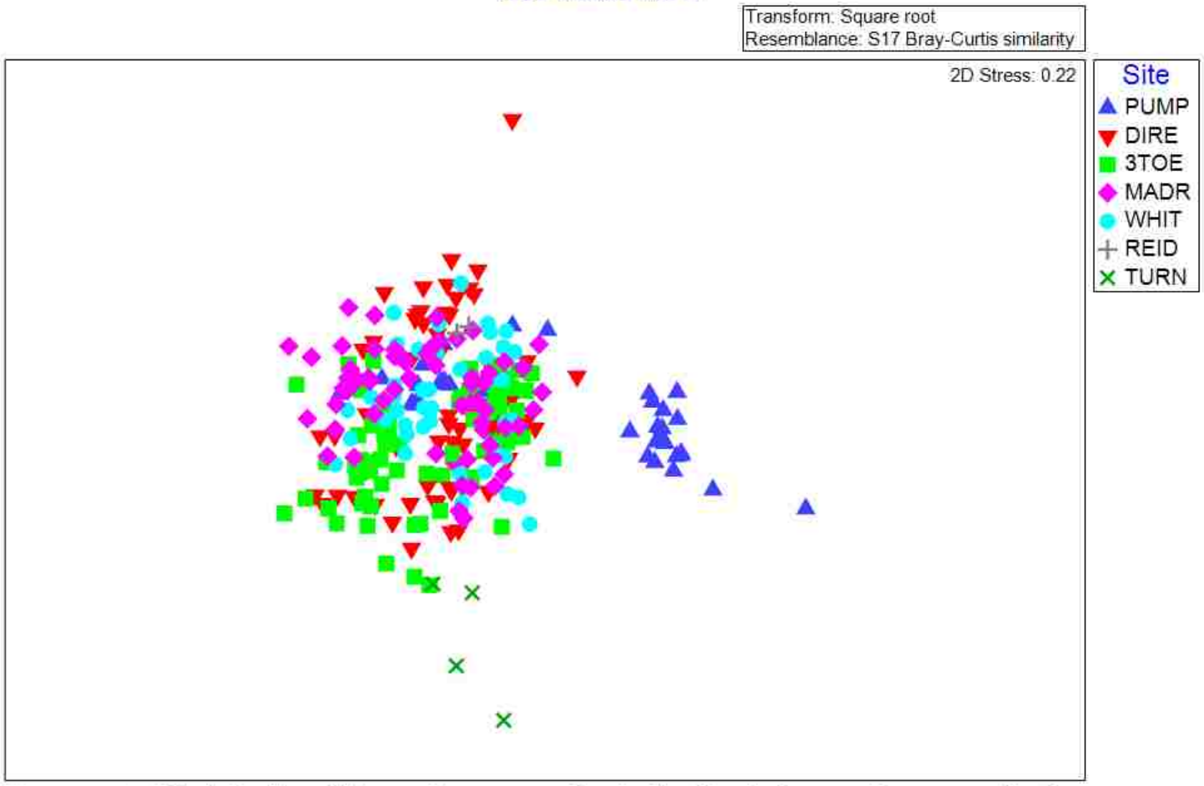


Figure S18. nMDS plot of benthic sessile assemblage similarities between sites on vertical surfaces in the deep zone (21 m to 27 m). Global R-statistic: 0.267.

CHAPTER 3

Flow-mediated community structure on subtidal rocky reefs in the San Juan Archipelago, Washington, USA.

Abstract

Complex flow patterns exert a strong influence on the distribution and abundance of individual organisms in subtidal coastal habitats and likely play a role in structuring community composition across all spatial scales. Given the importance of water movement, there are likely to be predictable responses to increasing flow speed. Few studies to date have investigated the effect of flow regime on entire communities *in situ* or how flow affects communities differently across shifting habitat types or substrate orientations. In this study, we first present flow-mediated species response models and then fit long term ecological monitoring data of algal and invertebrate assemblages to these models so we can characterize the communities along the flow regime spectrum. We found that differences in community structure are greatest between the lowest and the highest flow rates, with little overlap in the taxa found in the lowest and highest flow rates. While there is not a linear relationship between increasing flow rates and the strength of this community separation, benthic sessile community assemblages always showed a significant break between High and Very High flow designations, indicating that very high flow rates exert the strongest influence on the communities in both the shelf and wall habitats and across depths. Taxa characterized by low abundance/densities in low flow rates and high abundance/densities in high flow rates are nearly all short erect or encrusting invertebrates such as *Abietinaria spp.*, *Balanus spp.*, and bryozoans as well as small mobile invertebrates capable of avoiding periods of very high flow such as the echinoderms *Psolidium bidiscum* and *Psolus chitonoides*. Taxa characterized by decreasing abundance/densities with increasing flow rates include macroalgal species providing canopy cover such as *Agarum fimbriatum*, *Laminaria complanata,* and *Saccharina subsimplex* as well as relatively tall, erect invertebrates such as *Boltenia villosa* and *Cnemidocarpa finmarkiensis*. Taxa characterized by low abundance/densities in both low and high flow rates and high abundance/densities in

intermediate flow rates are a mix of short and tall erect invertebrates such as tunicates, anemones, and sponges. These and other characteristics may go a long way toward describing the patterns of abundance of these sessile and mobile taxa, but flow is only one of many critical environmental factors. Continued research, both in the lab and in the field, is needed to provide evidence of the strength of other environmental factors as well as biological interactions in shaping the subtidal community seascape.

Introduction

Complex flow patterns in subtidal coastal habitats exert a strong influence on the distribution and abundance of individual organisms and likely play a structuring role in community composition at both small spatial scales and along contiguous habitat at larger spatial scales. Early studies recognized the importance of water movement (Kitching 1939, 1941, Kitching et al. 1952) including a study on siltstone reefs (Pequenat 1964) suggesting high densities of invertebrates on the top of the reef were being driven by greater availability of food due to more water movement. Seminal studies on the effects of flow-enhanced food supply on population and community structure led to many other studies of flow effects (Sebens 1984, Genin et al. 1986, Duggins 1988, Eckman et al. 1989, Lesser et al. 1994, Leichter and Witman 1997, Genovese and Witman 1999).

Few studies to date have investigated the effect of flow regime on entire communities or how flow affects communities differently across shifting habitat types or substrate orientations. Partially due to logistical and resource constraints, it is very difficult to simultaneously deploy equipment at multiple sites to adequately measure flow rates or mass transfer on even relatively small spatial scales and to couple these measurements with robust quantification of benthic communities. Thus, many studies have focused on individual species responses to a relevant range of flow speeds, both in the laboratory and in the field. These studies form a solid foundation for our understanding of how the movement of fluids interacts with individual organisms' morphology, plasticity, physiology, and behavior, both pre- and post-settlement. This body of work includes the effects of water motion on external fertilization (Levitan 1995, Serrao et al. 1996, Pearson and Brawley 1998), the ability of an organism to settle either via efficacy of settlement cues or arrival of larvae to habitat (Jumars and Nowell 1984; Turner et al. 1994;

Wright and Boxshall 1999; Gaylord and Gaines 2000), the recruitment via planktonic larvae (Wing et al. 1995, 1998), the delivery of nutrients to macroalgae (Koehl and Alberte 1988), the flux of particulate matter to suspension feeding animals (Shimeta and Jumars 1991), diverse organisms' feeding ability and growth (Sebens 1984; Okamura 1992; Arkema 2009), as well as on their morphology (Koehl et al. 2008; Ferrier and Carpenter 2009).

Foundation species can alter flow patterns (Jackson and Winant 1983, Patterson 1984, Eckman et al. 1989) and thus play an important role as habitat modifiers. This modification can exert a strong influence on the food and larval supply to adjacent patches and organisms (Genin et al. 1986, Eckman and Duggins 1991, Wildish and Kristmanson 1997, Gill and Coma 1998). At the population level, high water flow over aggregations of mussels and barnacles means they experience narrower temperature ranges than adjacent solitary individuals (Bertness 1989, Helmuth 1998) while macroalgal communities modify the rates of transport of heat, mass, and momentum within their canopies (Eckman et al. 1989, Leonard 2000).

Water movement and transport, although arguably one of the strongest determining factors of ecological patterns, is still only one of many factors that affect the distribution and abundance of marine plants and animals. The ways in which morphology, physiology, and behavior of organisms interact with these factors is important in understanding ecological patterns and processes.

Flow-mediated species response models

Given the importance of water movement, there are likely to be predictable responses to increasing flow speed. Figure 1 illustrates four possible responses; Type A describes species that increase in abundance/population density as flow increases, characteristic of organisms that can successfully stay anchored to the substrate and would not suffer catastrophic disturbance of their morphology in high flow conditions. These species likely benefit from increased water movement due to their feeding strategy, decreased sediment loads, and possibly due to a decrease in certain consumers which are unable to persist in high flow areas. Type B describes species that decrease in abundance/density as flow increases, characteristic of organisms that may become dislodged from the substrate and/or have reduced efficacy in prey capture at high flow velocities. Type C describes species that increase in abundance/density as flow increases, but then decrease as flow approaches maximum, and Type D describes species that show the opposite pattern. Prior to our analysis, we did not expect to see any individuals or groups in the community matching the Type D response curve. Species showing responses fitting the Type A, B, and C curves may be responding directly to varying flow rates across the spectrum, with both positive and negative effects on individual organisms. However, even high correlation values don’t lead us to discount indirect effects such as competition with species directly responding to flow or predation between individuals in all habitats.

With the expectation of individual species/functional groups having varying degrees of success across flow regimes, we hypothesize the largest differences in community assemblages will reveal themselves at the extreme ends of the flow spectrum, with low flow communities characterized by organisms fitting the Type A curve, high flow communities characterized by those fitting the Type B curve, and a large transitional group between these ends of the spectrum representing the Type C organisms.

We also anticipate many of the taxa will not show any structured response to different flow velocities across our study habitats (dotted line in Figure 1). This could be inherent to the large variation in morphological characteristics represented in the observed organisms, biological interactions such as competition and predation not measured in this study, and/or sampling artifacts; we only conduct subtidal surveys during slack tides and are reliant on flow tank experiments to directly observe the hydrodynamic effects of increasing water velocity on an organism's phenotypic plasticity.

Study area

Bathymetry strongly influences current patterns and flow regimes that can impact organisms at multiple spatial scales (Gaylord et al. 2007). Although multibeam and sidescan technologies have been used in bathymetric mapping of seafloor features to create accurate marine navigation charts for decades, only recently have these been used to investigate the influence of bottom topography on coastal subtidal ecosystems (De Moustier and Matsumoto 1993; Clarke et al. 1996; Whitmire et al. 2007; Brown and Blondel 2009). There is still much work to be done toward using bathymetry maps to predict and assess subtidal community assemblages, although recent studies have improved our understanding of community structure and dynamics from regional to local spatial scales (Witman and Dayton 2001; Beaman and Harris 2007; Greene et al. 2007; Shotwell et al. 2007; Wedding et al. 2008; Miller and Etter 2008).

The subtidal communities on rocky reefs in the San Juan Archipelago, Washington State, experience daily tidal shifts that create a dramatic range of flow regimes across a mosaic of patchy habitats. Subtidal communities change predictably with depth, dominated in the shallow zone by canopy-forming macroalgae and giving way to an epifaunal invertebrate dominated deep zone (Chapter 1). Given the complex bathymetry of the substrate at our study sites, with large shelf and vertical rock walls present in both the shallow and deep zones, there is considerable variation in the abundance of foundation species (such as barnacles, kelps, and ascidians) not just with depth, but along horizontal gradients parallel to shore.

Methods

Data from four data collection methods used to quantify the percent cover of algal and sessile invertebrate communities and the abundances of mobile invertebrate communities at seven study sites in the San Juan Archipelago were used in this analysis. For specific methods, see Chapter 1. Identification to the species level was carried out but was not always possible across all data collection methods. In the Results, we refer to the sample groups of species, genera, etc., collectively as 'taxa'.

Flow data

To calculate mean flow speeds across all study sites and relative flow regimes among eachstudy site, we used a combination of alabaster dissolution blocks, an InterOcean Systems S4 current meter, and a SonTek Hydra Acoustic Doppler Velocimeter (ADV). In addition to calibration of the alabaster block dissolution, S4 and ADV deployments of a few days to a few weeks were meant capture the maximum and minimum flow speeds during spring and neap tide cycles during various months of this study. Mean, high, and highest flow rates at all study sites can be seen in Table 1. Alabaster blocks measuring 5 cm x 5 cm x 2 cm were cut, rinsed, and dried in a drying oven at 60° C for 24 hours. Each block was numbered on the bottom and a small amount of enamel applied over the numbers to prevent fading while submerged. Each block was then weighed to the nearest 0.001 gram with a digital balance and photographed with a scale to calculate surface area of the top of each block. We then applied a 1.25 cm wide strip of painter's tape around each block so the top half of the 2 cm sides were covered by the tape, and glued the blocks to small acrylic plates using silicone caulk. Caulk was liberally applied to the edge where the block met the acrylic and up the exposed sides. Care was taken to avoid getting silicone caulk on the bottom side of each block so it would not need to be cleaned after retrieval. The painter's tape was then removed leaving a clean, exposed alabaster side wall approximately halfway up the block's 2 cm sides. The silicone was allowed to dry for 24 hours and then measurements were taken of each exposed side so total exposed alabaster surface area could be calculated. Cable ties were used to secure the alabaster/acrylic assembly to construction bricks for deployment (Figure 2). This placed all blocks approximately seven centimeters above the substratum, a height representative of many of the taller invertebrates and foliose algae in these communities.

Using a maximum allowable alabaster dissolution time of 10-12 days, three 10-day deployments started on November 5th, 2011. One alabaster assembly was deployed at each transect depth at each of the long-term monitoring sites for a total of 60 blocks deployed; we required three days of diving for deployment at all 7 sites. Each transect location has a permanent stainless-steel pin where the brick was placed so it would not become dislodged by the water flow. At each transect location, the assembly was placed so the 5 cm x 5cm top surface was oriented parallel to the average substrate angle. In vertical substrate areas, it was necessary to use cable ties to secure the assembly to the installed pin. The first set of alabaster blocks was retrieved and a new set deployed over a three-day period starting November 17th, 2011.The second set was retrieved and third set deployed over a three-day period starting November 27th, 2011, and the third set retrieved starting December 7th, 2011. Each alabaster block was carefully removed from the acrylic base and cleaned of any remaining silicone. Each block was then dried as before and re-weighed. The total dissolution can be calculated as: [(initial weight (g) – final weight (g))/surface area (initial; cm^2]/# of days, to give a dissolution rate of g/cm^2/day.

Dissolution rates were calculated for each of the 180 blocks and divided into six flow categories for use in analysis. Categories were created by calculating the mean dissolution rate and standard deviation and using two standard deviations above and below the mean to bin the individual block dissolution rates (Table 2). These categories were then assigned to each of the sample groups by data collection method; at the transect level for point counts and large mobile fauna swath counts and at the photo quadrat level for benthic sessile and small mobile fauna assemblages. All quadrats along an individual transect were assigned the same category value.

Average flow speeds can be estimated by measuring the dissolution rates of the alabaster blocks (Eckman et al. 1989, Santschi et al. 1991, Porter et al. 2000) since dissolution of alabaster in seawater is a transport-limited process (Berner 1978). Calibrated mean flow speeds for all alabaster dissolution blocks were calculated using data collected from the InterOcean S4 current meter simultaneously deployed with alabaster dissolution blocks in a no-flow environment (seawater holding tank in the lab) and at two field sites, and then creating a linear relationship model. Flow speed ranges for each of the six categories of flow regime are shown in Figure 3.

Analysis

All line-intercept, photo quadrats, and mobile fauna abundances were analyzed using multivariate analysis software, PRIMER v7 (PRIMER-E Ltd. Plymouth, UK; Clarke and Warwick 2001). All data were square-root transformed before analysis. Multivariate analyses included non-metric Multidimensional Scaling (nMDS) and Analysis of Similarities (ANOSIM) on all data types. The nMDS plots are a visual representation of similarities (or differences) among sample groups with corresponding R-statistics providing a statistical test of separation among sample groups. R-statistics range in value from 0 to 1, with higher values representing larger separation (i.e. greater dissimilarity) among sample groups. Using the percentage of total abundance over all samples for each of 204 unique taxa identifiers, we generated coherent species curves for all line-intercept transects, photo quadrats, and swath counts to look at the strength of the inter-taxa covariance in their response to varying flow regimes. Researchers have been drawing line plots of species responses over spatio-temporal gradients throughout the history of ecology, but they have usually been for single species or combinations that are subjectively selected. Our analysis using Type 3 SIMPROF tests groups line plots together in species sets that are statistically indistinguishable within sample groups but significantly different between sample groups (Clarke et al. 2014). In this framework, these coherent species curves allowed us to test the predicted species-flow response curve models against the community assemblage data.

In our initial analyses of the influence that flow exerts on community structure across all our sites, we found few patterns, probably because it is very unlikely that flow acts similarly across the entire study area (e.g. high flow over shelf versus wall habitats, or high flow over the same habitat type but at different depths). To better describe the effect of flow on individual organisms and community assemblages in an ecologically realistic way, we classified each transect into one of six possible habitat categories based on depth and larger scale substrate orientation (see Chapter 2, Section 1). These designations allow a more meaningful analysis of how flow regimes affect different subsets of the ecosystem. Although the results from each habitat type provide an interesting look at trends and patterns, we report here almost exclusively on the MidShelf habitat, as our database contains flow regimes across the entire spectrum for this habitat type, including all binned flow categories from Low to Very High (no sites were categorized as Very Low flow based on alabaster block deployment).

Results

Quantitative tidal current measurements

Flow measurements were made with an InterOcean S4 electromagnetic current meter and a Sontek Hydra ADV, each sampling at 0.5 m off the substratum. Figure 4 shows mean flow (each 0.5 s) at each site for the entire sampled period, compared to the mean flow during the sampled period with the highest flow (5 min, 600 points), and to the highest flow speeds recorded during the deployment (highest 0.1%). The shallow Reid Rock site was plotted separately for the highest flows because these values were much higher than the rest.

Figure 5 shows maximum flow speeds at each site (top 0.1 %) versus location of the site on an axis going from the middle of San Juan Channel (least obstructed tidal flow) toward Friday Harbor (more obstructed tidal flow). Mean flow, and the mean flow during the highest flow period, did not show significant relationships to distance from mid channel, but the highest flow speeds were significant (R^2=0.524, p=0.0011) with the fastest flow in the middle of the channel.

Regression lines of mean flow at each sampling period (5 min per hour) to the change in tidal height during that hour (tidal exchange rate) are shown in Figure 6. Tidal exchange can be considered the same for all sites in San Juan Channel and thus these regressions allow comparison over all time periods even when the number of days or time of year differ between deployments. Note the mid-channel Reid Rock site exhibits the highest flow speeds at maximum exchange, and sites inside the mouth of Friday Harbor have the lowest flow speeds.

Benthic community structure across flow regimes

The benthic sessile community data generated from photo quadrats comprises the data set with the highest resolution in the identification of individual species, so we use those data to discuss trends seen across all four data collection methods. Patterns in the macroalgae and small and large mobile fauna are presented later with coherence plots.

Overall, as predicted we found that differences in community structure are greatest between the lowest and the highest flow rates; high R-values from the ANOSIM analysis suggest there is little overlap in the taxa found in the lowest and highest flow rates in the MidShelf and DeepWall habitats. While there is not a linear relationship between increasing flow rates and the strength of this community separation, benthic sessile community assemblages always showed a substantial break between the High and Very High flow designations, indicating that very high flow rates exert the strongest influence on the communities in both the shelf and wall habitats and across depths (Table 3).

Coherent species curves were generated for each of the four data collection methods, resulting in 56 plots across all habitat types and depths. Here, we show curves generated from the sample groups found in the MidShelf habitat as we recorded all flow categories (low to very high) in that study area. In these plots, taxon abundance is expressed in relative terms as a percentage of total abundance for that taxon over all samples. The taxa found together in each plot have the strongest association to each other in terms of showing a similar type of response (abundance in this case) to varying flow regimes.

Type A response

Taxa that exhibit a Type A response, i.e. those characterized by low abundance/densities in low flow rates and high abundance/densities in high flow rates, are shown in Table 4. These 15 taxa are nearly all short erect or encrusting invertebrates such as *Abietinaria spp.*, *Balanus spp.*, and bryozoans as well as small mobile invertebrates capable (e.g., by being very low-profile or a strong foot for attachment) of avoiding periods of very high flow such as the echinoderms *Psolidium bidiscum* and *Psolus chitonoides*.

Although we originally predicted the Type A response curves would be linear, the species coherence plots reveal a more exponential response curve for these organisms, with a large increase in abundance/density occurring in the transition from High to Very High flow rates (Figures 7 - 9). In some taxa, there was a four to five-fold increase in abundance between Low and Very High flow rates.

Type B response

Taxa that exhibit a Type B response, i.e., those characterized by declining abundance/densities with increasing flow rates, are shown in Table 5. These include macroalgal species providing canopy cover such as *Agarum fimbriatum*, *Laminaria complanata,* and *Saccharina subsimplex* as well as relatively tall, erect invertebrates such as *Boltenia villosa* and *Cnemidocarpa finmarkiensis*.

The species coherence plots fit a more linear relationship between abundance/density and flow rates as anticipated in our model (Figures 10 and 11).

Type C response

Taxa that exhibit a Type C response, i.e. those expected to have low abundance/densities in both low and high flow rates and high abundance/densities in intermediate flow rates, are shown in Table 6. This response is a mix of short and tall erect invertebrates such as tunicates, anemones, and sponges. We predicted this response curve would be the result of biological interactions, e.g. between predators and prey or among competitors; the taxa exhibiting this response may be those where the strength of these interactions outweighs the effects of flow rates.

For the benthic sessile taxa in this response group, coherent species curves show a close resemblance to the predicted response curve, with low densities at either end of the flow spectrum and high densities in the Medium High and High flow categories (Figures 12 and 13). In some groups, such as sponges, the densities change ten to twenty-fold across the flow spectrum.

Discussion

Analyses of our extensive database show that many species and functional groups show clear abundance patterns related to local flow regimes, with the nature of these responses varying widely among organisms. Many different pre- and post-settlement factors can combine to determine whether any individual species or entire taxon will settle, survive and have reproductive success in a particular habitat. Without manipulative experimentation, we are unable to determine which of these variables actually control settlement of organisms in our system and affect community structure in the way we hypothesize. We thus focus our discussion on the organisms that have managed to recruit into our studied habitats; if they are there, it demonstrates that propagules have been successful. We thus are considering what their presence or absence from one habitat type or depth tells us about post-settlement processes, both abiotic and biotic.

Taxa that increase in abundance with increasing flow (Type A) must be able to overcome the tremendous physical forces of high flows in rocky subtidal communities. Flow velocities in the benthic boundary layer of deep rocky subtidal environments are often just a few cm/s (Hiscock 1983, Leichter and Witman 1997, Genovese and Witman 1999), yet in the San Juan Archipelago we have recorded mean velocities higher than 45 cm/s from the shallowest transects (three meters of sea water, msw) to the deepest transects (27 msw), with maxima over 1 m/s. To survive in these very high flows, species employ a variety of techniques. First, some permanently adhere to the substrate. *Balanus nubilis* and other barnacles are the only sessile crustaceans; they adhere using a complex series of processes including molting, epicuticular membrane development, calcification of the shell, and secretion of an underwater adhesive (Kamino 2016). The secure attachment of their base allows them to withstand strong daily tidal currents. High densities of *B. nubilis* on substrates experiencing very high flow may develop because they capture prey increasingly well in fast moving water. Some barnacle species have developed flow-dependent feeding structures that provide more surface area for prey capture in low flow conditions and shorter structures that are less susceptible to damage, but still maintain efficient prey capture, in high flow conditions (Marchinko and Palmer 2003). This phenotypic plasticity, coupled with their ability to outcompete other organisms in extreme wave-swept habitats, certainly contributes to their high densities. Serpulid worms attach using a chemical process that is substantially different from that of barnacles, but they are similar in securing themselves to the substrate, are able to withstand very high flow rates, and as suspension feeders may benefit from greater food delivery. Like barnacles, these tube-dwelling annelid worms have the ability to retreat into their solid, calciferous structures during periods of high flow.

Rather than relying on permanent attachment to the substrate, some mobile fauna are able to secure themselves to the substrate during periods of very high flow. Using their muscular foot and lowering their shell into direct contact with the substrate to form a more hydrodynamic shape, limpets are able to withstand the tremendous forces generated even in wave-swept habitats (Denny and Blanchette 2000). As limpets are not suspension feeders, it is unlikely that higher abundances in very high flow conditions are correlated to feeding strategy, but rather to their ability to physically persist in these conditions where their predators might not.

Another strategy organisms employ to survive in very high flow conditions is to keep a low profile, either by encrusting the substrate or having the ability to dramatically alter body shape in response to water movement. *Aplidium solidum*, a colonial tunicate, and *Stylantheca* spp., an encrusting hydrocoral, take the shape of the substrate they inhabit and present little of their anatomical structure to the water above the boundary layer. *Psolus chitonoides*, the armored sea cucumber, has the ability to retract its oral tentacles and form a structure similar to chitons, complete with calcareous plates to protect its body and reduce the coefficient of drag. These suspension feeders all presumably benefit from the regular food delivery in high-current areas, and their morphology allows them to withstand periods of extreme flow even if they cannot feed at those times.

It is harder to explain what survival strategies are being used by some other taxa that thrive in high flow. *Abietineria* spp., a small erect hydroid, as well as *Corella* spp. and *Cystodytes lobata*, both solitary ascidians, have morphological characteristics that would seem to be less flow-resistant (i.e. they are higher profile and relatively delicate). It is possible the increased densities of these organisms in very high flow conditions are due to a biological interaction, e.g. absence of a predator, rather than a physical environmental process. The decorator crab *Loxorhynchus crispatus* also has no special morphological characteristics enhancing survival in high flow habitats. As we only conduct subtidal surveys during slack tides, the observed occurrences of *L. crispatus* coincide with periods of low flow when it is safe to be actively moving in the environment. However, this species only showed a Type A response to flow, suggesting a genuine preference for high flow areas. This species often ‘decorates’ with encrusting sponges and colonial ascidians (pers. obs.); the high flow may benefit the growth of its epibionts, which do not result in the high drag that algal and hydroid epibionts can.

Taxa having high abundances/densities in low flow conditions (Type B) have a different set of environmental variables to contend with, some as detrimental to their survival as are conditions in very high flow areas. A characteristic attribute of low flow areas is an increased amount of sediment persisting on the substrate (Genovese and Witman 1999, Lenihan 1999, Airoldi 2003), which can easily suffocate benthic sessile organisms. A decreased amount of water transport in these areas also correlates with less food available for filter and suspension feeders. Both conditions translate into a need for benthic sessile organisms to achieve some elevation from the substrate and a way to efficiently remove small prey items and particulate matter from the water column. Macroalgae also benefit from getting up off the substrate into flow, both to avoid sediment and to have enough flow for gas and nutrient exchange.

Bladed macroalgae generally appeared only in Type B coherence plots; these included *Costaria costata*, *Saccharina subsimplex*, and *Laminaria complanata*, as well as the understory algae *Desmarestia munda* and *Ulva spp*. Algal blades offer a large amount of surface area and are susceptible to mechanical disturbance from increasing water flow. The holdfasts of *Nereocystis luetkeana* and a few other large brown algae can stay secured to the substrate during even the highest of tidal exchanges, but most other algae would be torn apart or swept away entirely, in some cases still attached to cobble or small boulders (pers. obs.). In stark contrast, there were no occurrences of macroalgal species in any of the Type A coherence plots, as predicted from the morphological characteristics of both canopy forming and understory algae.

Tall, erect invertebrates, such as some sponges and tunicates, lack streamlined shape. Although some species may thrive in higher flow environments in other geographic areas, many of our common taxa exhibit a Type B response and are nearly absent in areas that experience very high flow rates. These include sponges in the genera *Leucosolenia* and *Suberites*, and the tunicates *Chelyosoma* spp., *Distaplia occidentalis*, *Boltenia villosa*, and *Cnemidocarpa finmarkiensis*. This absence could also be due to pre-settlement barriers, such as reduced larval supply or an organism's ability to adhere in high flow conditions.

Many of our small mobile fauna species have limited mobility and small home ranges. We did not identify habitat-wide patterns of zonation in these species/groups (Chapters 1 and 2), but abundance patterns do appear to be flow related. Nudibranchs such as *Acanthodoris* spp. and *Hermissenda crassicornis* had much higher abundances in areas that only experience low flow rates and were nearly absent from high flow areas. While these organisms have some phenotypic plasticity, their soft bodies and fleshy appendages deform, and they are unable to stay secured to the substrate in high flow conditions (Wyeth and Willows 2005, Briones pers. comm.). Some other nudibranch species exhibited a Type C response indicating that they can persist, and even experience high abundances, in moderate flow conditions. However, most nudibranch species are specialist feeders, so the distribution of these species may relate most closely to their preferred food sources.

It is difficult to explain habitat preferences of many of the large mobile invertebrate taxa in this flow-mediated response framework, especially since we found no evidence of depth zonation (Chapters 1 and 2) in these organisms. Two of the large mobile fauna which exhibited only Type B response were the holothurian *Parastichopus californicus* and the sea star *Pteraster tesselatus*. Both can alter their body shape and stay secured to the substrate in moderate amounts of flow, but both are relatively stout-bodied and adhere weakly, so they likely are unable to persist in very high flow environments. *P. californicus* consumes benthic detritus and likely benefits from the increase in deposited particles in low flow areas.

As with the Type A response, there are taxa that exhibited only Type B response despite seeming to have characteristics that would lend themselves better to the Type A response. Previously discussed, Lottiid limpets have multiple strategies for thriving in very high flow environments. Yet other limpets, e.g. *Cranopsis cucullata* and *Diadora aspera,* exhibited only Type B response to the spectrum of flow conditions. Some limpet species are specialist feeders and it is possible their preferred food items are also better suited for areas that experience only low to moderate flow regimes. In contrast to *L. crispatus*, another decorator crab species, *Oregonia gracilis*, only exhibited a Type B response with the highest abundance in low flow habitats. Where *L. crispatus* may be 'tending' to epizoans on its exoskeleton that thrive in high flow areas, the same could be true of *O. gracilis* in low flow areas. While there is an abundance of literature about general community assemblages on decorator crabs, a study on use of different decorations in low and high flow habitats would be of interest.

A surprising member of the low-flow group is the jingle shell, *Pododesmus machrochisma*. A filter feeder with a low hydrodynamic profile and a tough byssus stalk to permanently attach to the substrate, this species appears better suited for high flow environments. At least one of the epizoans commonly found on these shells, the barnacle *Balanus nubilis*, was also found to exhibit only a Type A response to flow. Anecdotal evidence (Lamb and Hanby 2005) indicates *P. machrochisma* is very common in low-current locales in the Northwest and Northeast Pacific intertidal and subtidal zones. Settlement processes and feeding mechanisms of this common species warrant further study.

Having high densities/abundances in intermediate flow (Type C), suggests an organism benefits from some water movement but has decreased recruitment or survivorship in low and very high flow areas. This response curve may be driven in part by inter- and intraspecific biological interactions such as competition and facilitation. Unlike most macroalgal species that only exhibited a Type B response, we identified juvenile kelps in the Order Laminariales, along with the red alga *Stenogramme interrupta*, in the Type C response. Both benefit from water movement across their blades for sediment removal and nutrient exchange but are smooth-bladed and have a relatively small surface area, thus likely avoiding catastrophic mechanical destruction in intermediate flow areas. The presence of juvenile kelps in type C response coupled with the presence of adults of the same species in the Type B response may indicate a change in optimal habitat with size.

Benthic sessile taxa in the Type C group include tunicates, anemones, and a tube-dwelling annelid. The tunicates *Eudistoma purpuropunctatum*, *Clavelina huntsmani*, and *Halocynthia igaboja* all have more erect structures than the tunicates in the Type A response, which would account for the decrease in their abundance in areas that experience very high flow rates. These tunicates still have structures that attach them to the substrate as well as oral and atrial siphons, making them vulnerable to clogging with higher sediment loads in areas with low flow. The same explanations could apply for the two anemones in this response curve, *Epizoanthus scotinus* and *Urticina crassicornis*. The only annelid species in this group, *Myxicola infundibulum*, is often found in rock crevices or buried in soft sediments. In both habitats, individuals produce an erect slime tube that provides some elevation from the substrate for the suspension-feeding structure, a crown of mucus and cilia covered radioles. The slime tube allows for some protection of the worm while remaining flexible to withstand the forces of intermediate water movement.

We also identified small and large mobile fauna in the Type C group, including many nudibranch species. *Cadlina luteomarginata*, *Dendronotus dali*, *Doris montereyensis*, and *Janolus fuscus* have a range of body types, most of which do not hold up well in very high flow regimes. The abundance of these nudibranch species in areas that experience intermediate flow is likely due to individuals foraging on specific prey items within the limits of increasing water flow. The same is likely true of the snails *Amphissa columbiana* and *Ocenebrina lurida*. While many chitons are associated with high energy wave-swept shorelines, the gumboot chiton, *Cryptochiton stelleri*, is generally found in subtidal habitats and has the highest abundances in areas that experience intermediate flow in our study sites. Although *C. stelleri* is the largest of the chitons and has a relatively hydrodynamic shape, it has a surprisingly weak foot muscle and can be dislodged during periods of very high flow. It is known to feed on *Ulva* spp. and kelps in the Order Laminariales, both of which appear in this response curve and have their highest abundances in areas of intermediate flow.

Also in this response category are the echinoderms *Eupentacta quinquesemita* and *Henricia leviuscula*. *E. quinquesemita* is one of the smallest sea cucumbers in the Pacific Northwest region and is often found in crevices and under boulders, especially where there is vigorous water movement. A deposit and suspension feeder, these sea cucumbers would benefit from increased water movement and areas where there is some soft sediment persisting on the substrate. *H. leviuscula* is also one of the smaller species of sea stars, and although it has a relatively poor ability to adhere to the substrate, its streamlined shape helps make it capable of withstanding moderate flow rates. Another decorator crab, *Scyra acutifrons*, is in this response group and presents the same difficulty in describing the species/habitat relationship as the species with Type A and B responses.

In addition to taxa that exhibited the same type of response to increasing flow regimes, we also documented several taxa that responded differently depending on the habitat type where they were located. Two of the most ubiquitous members of the benthic sessile community across all sites are the tunicates *Metandrocarpa taylori* and *Didemnum carnulentum*. Although most abundant on vertical substrate, especially in large wall habitats, both are found on substrates of all angles and across all depths. In shallow and mid shelf habitats, both species exhibited Type A, B, and C responses, where in deep shelf and wall habitats they exhibited Type B response only. *M. taylori* is a social ascidian with clonal individuals in close association with each other. *D. carnulentum* is colonial and also takes the shape of the substrate it encrusts, likely increasing both species' success in all depths and habitats.

Arguably the most recognizable member of the subtidal benthic sessile community in the Pacific Northwest, the giant plumose anemone *Metridium farcimen* is found in aggregations on all substrate orientations, including overhanging ledges, and across all flow regimes. In shelf habitats across mid and deep depths, *M. farcimen* exhibited diverse Type A, B, and C responses, with no clear indication of a strong pattern of flow-mediated response. However as with the two ascidians discussed above, in deep wall habitats, *M. farcimen* exhibited a Type B response, with the highest densities found in areas that experience low flow rates. When combined with the difficulty of occupying space on vertical walls, individuals subjected to very high flow rates on these substrates may be unable to colonize or persist.

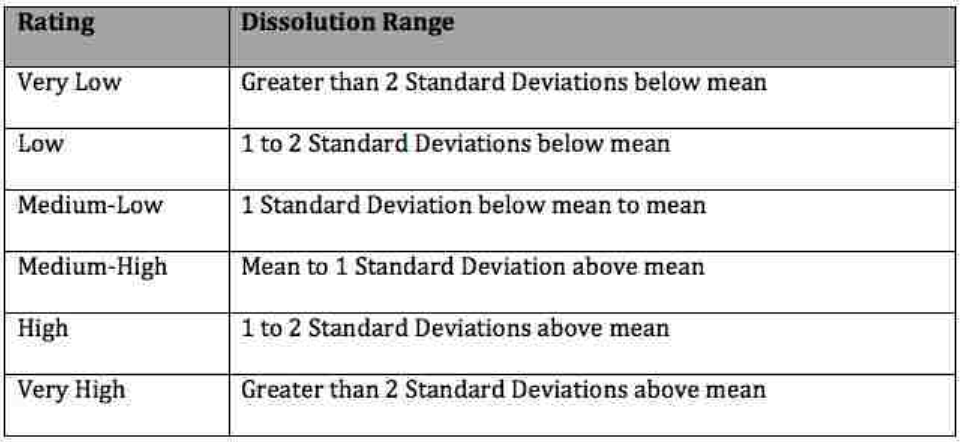
In conclusion, we found that many subtidal benthic species flourish in particular flow conditions and fit within predicted flow-mediated response curves based largely on organismal body plans, attachment to and elevation from the substrate, and feeding strategies. More research needs to be done to understand the underlying causes why certain taxa would respond differently to flow in different habitats. While these and other characteristics may go a long way toward describing the patterns of abundance of these sessile and mobile taxa, flow is only one of many critical environmental factors. Continued research, both in the lab and in the field, is needed to provide evidence of the strength of other environmental factors as well as biological interactions in shaping the subtidal community seascape.

Tables

Table 1. Mean flow rates (in cm/s) at all study sites. Mean is of all points in deployment (half second intervals). Mean High is of the highest block in deployment (5 min period). Mean 0.1 is mean of the top 0.1 percent of all points. SDev = Standard Deviation. Flow Categories: Mean (<8 low, 8-12 mod, 12.1-18 high, >18 very high).

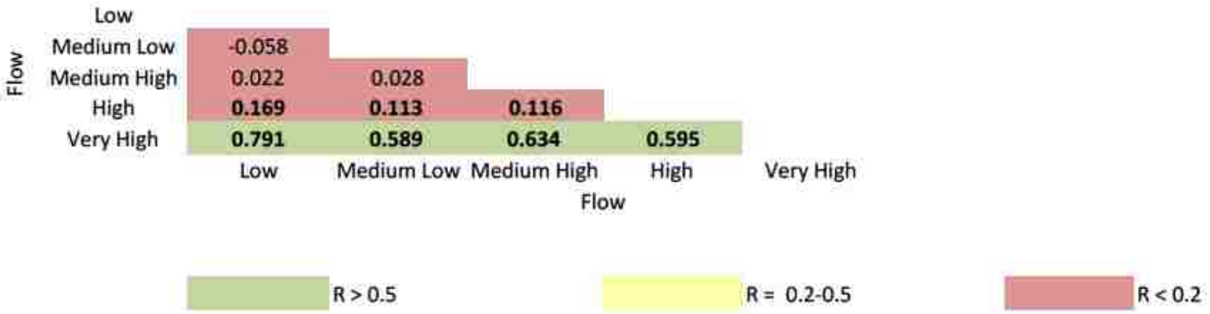
Site	Meter	Depth	Month	Days	Mean (cm/s)	SDev (cm/s)	Mean High (cm/s)	Sdev 0.1 (cm/s)	Mean 0.1 (cm/s)	Sdev 0.1 (cm/s)	Flow Cat. Mean	Flow Cat. Max 0.1
Pumphouse	S4	13m	Nov	13	6.68	5.39	20.48	17.72	31.76	1.49	LOW	LOW
Pumphouse	S4	13m	Nov	10	6.88	4.13	20.47	3.72	28.38	1.08	LOW	LOW
Director's House	S4	6m	June	11	12.10	10.40	44.10	8.20	56.00	1.90	MOD	MOD
Three Toes	Hydra	6m	Aug	7	14.50	14.00	55.90	15.20	79.70	18.20	MOD	HIGH
White Sign	S4	24m	Feb	18	30.39	15.10	80.53	23.27	106.37	11.18	V HIGH	V HIGH
White Sign	S4	24m	Mar	16	25.09	10.56	56.95	13.36	76.20	3.58	V HIGH	HIGH
White Sign	S4	24 m	Apr	14	25.26	13.46	56.07	14.79	84.37	5.74	V HIGH	V HIGH
Madrone Tree	Hydra	6m	Jun	30	7.25	5.24	27.72	10.04	40.71	3.66	LOW	MOD
Madrone Tree	Hydra	15m	Apr	30	7.76	5.97	20.29	8.41	54.88	10.19	LOW	MOD
Madrone Tree	Hydra	15m	May	30	7.25	5.24	27.72	10.04	40.71	3.66	LOW	MOD
Madrone Tree	Hydra	6m	May	30	9.02	6.78	33.89	7.48	50.01	3.38	MOD	MOD
Madrone Tree	Hydra	27m	Jan	30	18.90	12.75	57.77	7.59	79.98	8.71	HIGH	HIGH
Madrone Tree	Hydra	27m	Feb	31	15.12	10.04	44.00	6.74	63.81	6.74	HIGH	HIGH
Reid Rock	Hydra	12m	July	30	19.00	22.47	64.56	56.16	287.33	24.29	V HIGH	V HIGH
Reid Rock	Hydra	12m	August	31	12.06	12.07	37.50	32.35	186.23	58.83	V HIGH	V HIGH
Turn Island	S4	24m	Nov	18	11.59	6.76	40.85	12.84	64.35	5.72	MOD	MOD
Turn Island	S4	13m	Dec	35	24.92	14.31	59.48	13.16	98.99	10.96	V HIGH	V HIGH
Turn Island	S4	6m	Jan	33	19.93	12.73	68.61	18.97	95.03	5.91	V HIGH	V HIGH

Table 2. Flow categorizations based on standard deviations away from the mean dissolution rate.



Rating	**Dissolution Range**
Very Low	Greater than 2 Standard Deviations below mean
Low	1 to 2 Standard Deviations below mean
Medium-Low	1 Standard Deviation below mean to mean
Medium-High	Mean to 1 Standard Deviation above mean
High	1 to 2 Standard Deviations above mean
Very High	Greater than 2 Standard Deviations above mean

Table 3. ANOSIM R-statistics for all pairwise flow category comparisons of benthic sessile assemblages from MidShelf and DeepWall habitats. Bolded values indicate significance at $p<0.05$.

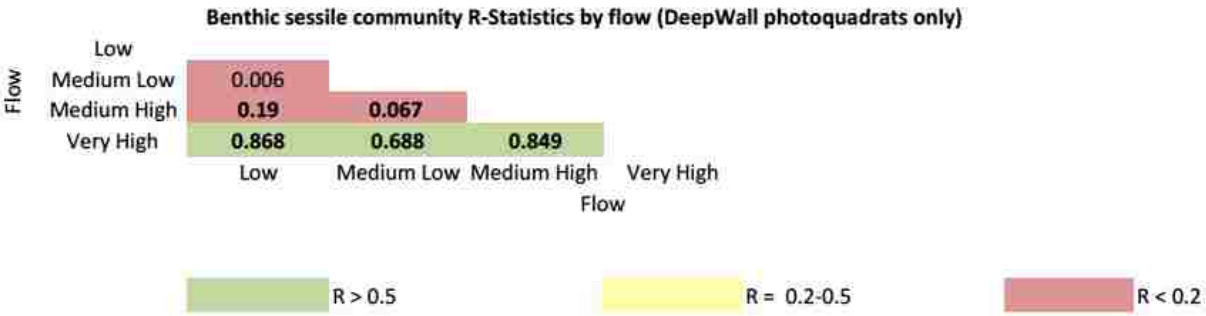


Flow	Low	Medium Low	Medium High	High	Very High
Low					
Medium Low	-0.058				
Medium High	0.022	0.028			
High	**0.169**	**0.113**	**0.116**		
Very High	**0.791**	**0.589**	**0.634**	**0.595**	

🟩 R > 0.5

🟨 R = 0.2-0.5

🟥 R < 0.2



Benthic sessile community R-Statistics by flow (DeepWall photoquadrats only)

Flow	Low	Medium Low	Medium High	Very High
Low				
Medium Low	0.006			
Medium High	**0.19**	**0.067**		
Very High	**0.868**	**0.688**	**0.849**	

🟩 R > 0.5

🟨 R = 0.2-0.5

🟥 R < 0.2

Table 4. Taxa exhibiting Type A response to flow in the MidShelf habitat.

Type A	Phylum	Functional Group
Abietinaria	Cnidaria	Short erect inverts
Balanophylia elegans	Cnidaria	Short erect inverts
Balanus nubilus	Arthropoda	Short erect inverts
Balanus crenatus	Arthropoda	Short erect inverts
Bryozoan (encrusting)	Bryozoa	Short erect inverts
Corella	Chordata	Tall erect inverts
Cribrinopsis fernaldi	Cnidaria	Mobile inverts
Cystodytes lobatus	Chordata	Short erect inverts
Heteropora pacifica	Bryozoa	Short erect inverts
Hydroids	Cnidaria	Short erect inverts
Metridium farcimen	Cnidaria	Tall erect inverts
Psolidium bidiscum	Echinodermata	Mobile inverts
Psolus chitinoides	Echinodermata	Mobile inverts
Stylantheca spp.	Cnidaria	Encrusting inverts
Terebratalia transversa	Brachiopoda	Short erect inverts

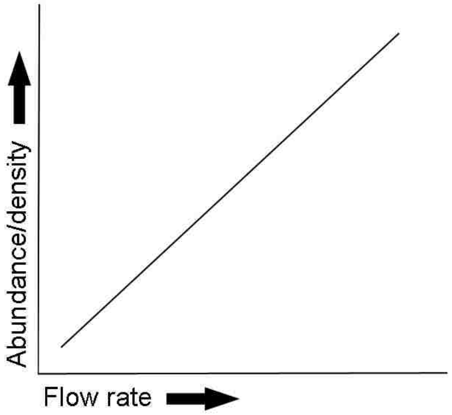


Table 5. Taxa exhibiting Type B response to flow in the MidShelf habitat.

Type B	Phylum	Functional Group
Agarum fimbriatum	Heterokonta	Brown algae
Boltenia villosa	Chordata	Tall erect inverts
Cnemidocarpa finmarkiensis	Chordata	Tall erect inverts
Laminaria complanata	Heterokonta	Brown algae
Pododesmus machrochisma	Mollusca	Short erect inverts
Saccharina latissima	Heterokonta	Brown algae
Spirorbid worms	Annelida	Encrusting inverts
Tunicates	Chordata	Short erect inverts

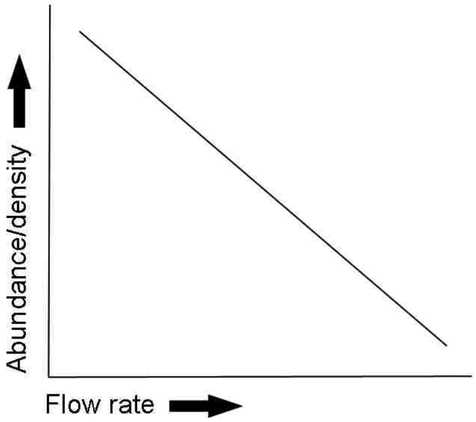
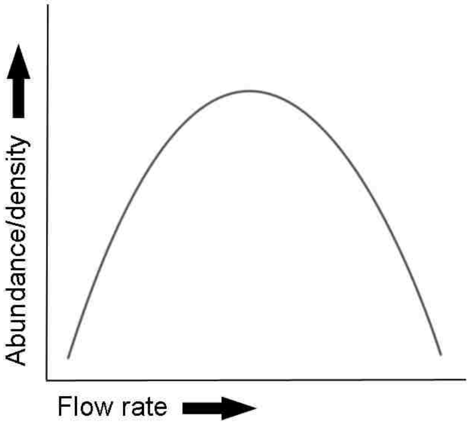


Table 6. Taxa exhibiting Type C response to flow in the MidShelf habitat.

Type C	Phylum	Functional Group
Cliona californiana	Porifera	Short erect inverts
Crassodoma gigantea	Mollusca	Short erect inverts
Crisia spp.	Bryozoa	Short erect inverts
Diapoeroecia californica	Bryozoa	Tall erect inverts
Epizoanthus scotinus	Cnidaria	Short erect inverts
Eurystomella bilabiata	Bryozoa	Short erect inverts
Halocynthia igaboja	Chordata	Tall erect inverts
Metandrocarpa taylori	Chordata	Short erect inverts
Pycnoclavella stanleyi	Chordata	Short erect inverts
Schizoporella unicornis	Bryozoa	Encrusting inverts
Terebratalia unguicula	Mollusca	Short erect inverts
Sponge (unidentified)	Porifera	Tall erect inverts



Figures

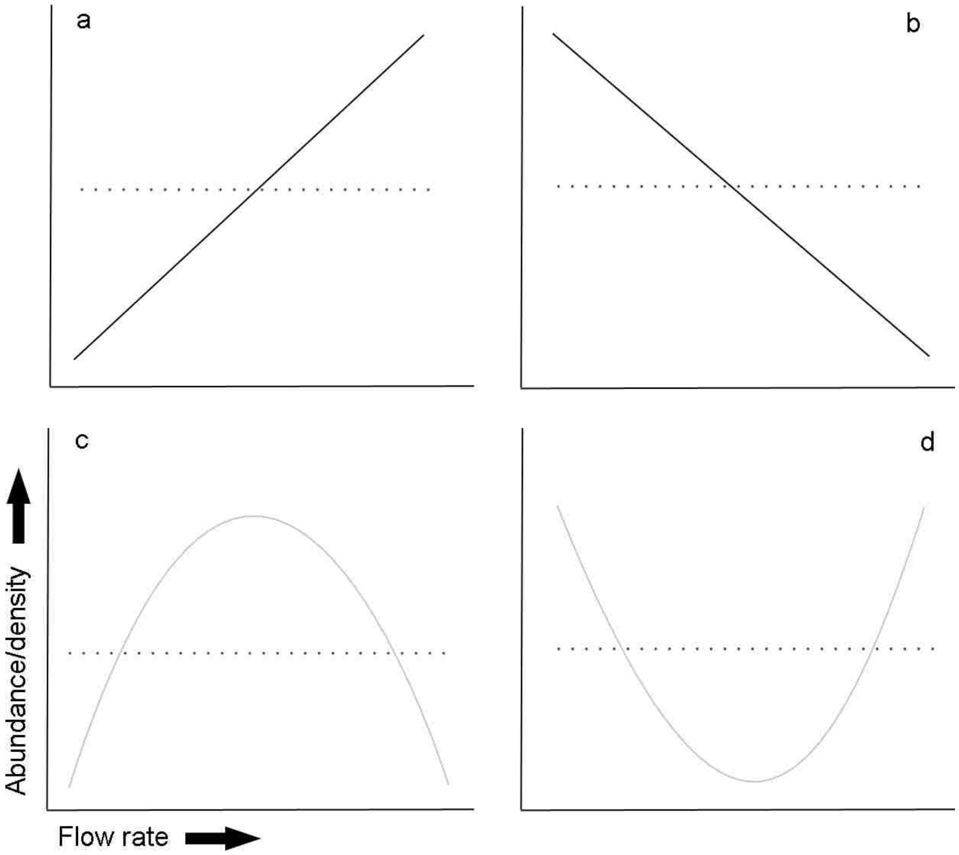


Figure 1. Predicted species' abundance/density responses to flow rates a) increase with increasing flow rates b) decrease with increasing flow rates c) increase with increasing flow but decrease as flow rate approaches maximum and d) decrease with increasing flow but increase as flow rate approaches minimum. Dotted lines represent the null condition (i.e. no flow-mediated response).

Figure 2. Completed alabaster dissolution block assembly, above and below the waterline.

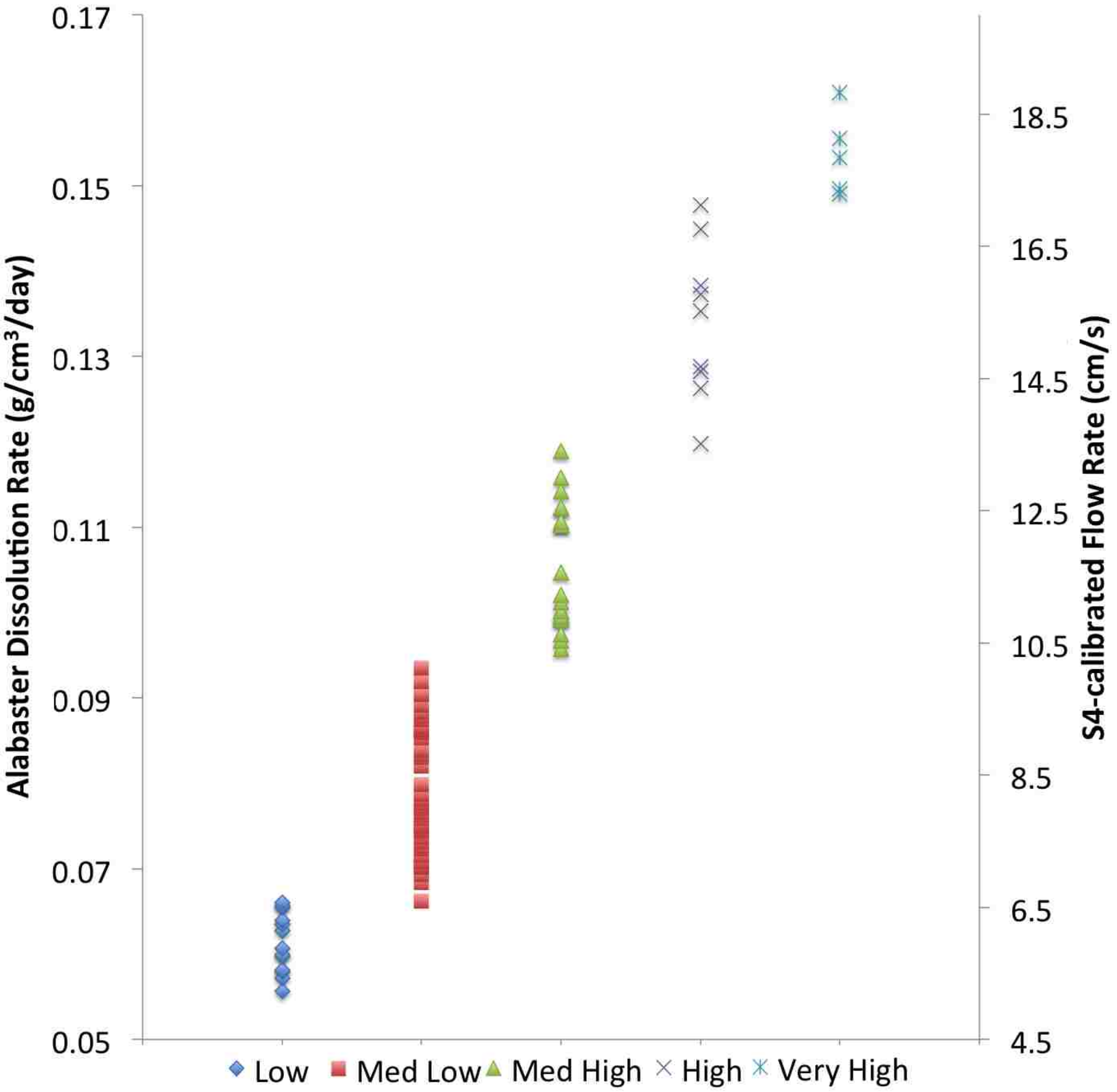


Figure 3. Alabaster dissolution rate plotted against S4-calibrated flow rate shows the relationship between the binned flow categories and actual flow speeds.

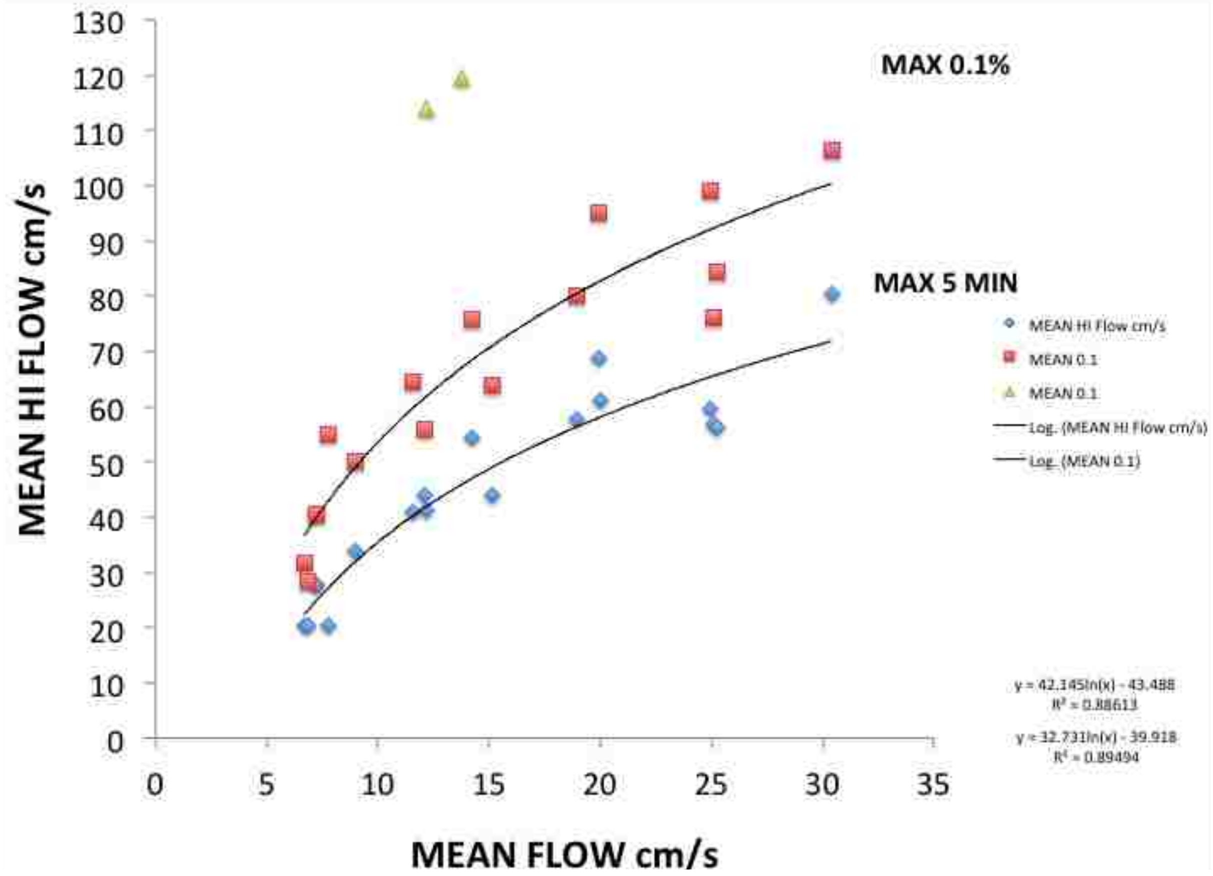


Figure 4. Mean flow (each 0.5 s) at each site for the entire sampled period, compared to the mean flow during the sampled period with the highest flow (5 min, 600 points), and to the highest flow speeds recorded during the deployment (highest 0.1%). The shallow Reid Rock site (in green) was plotted separately for the highest flows because these values were much higher than the rest.

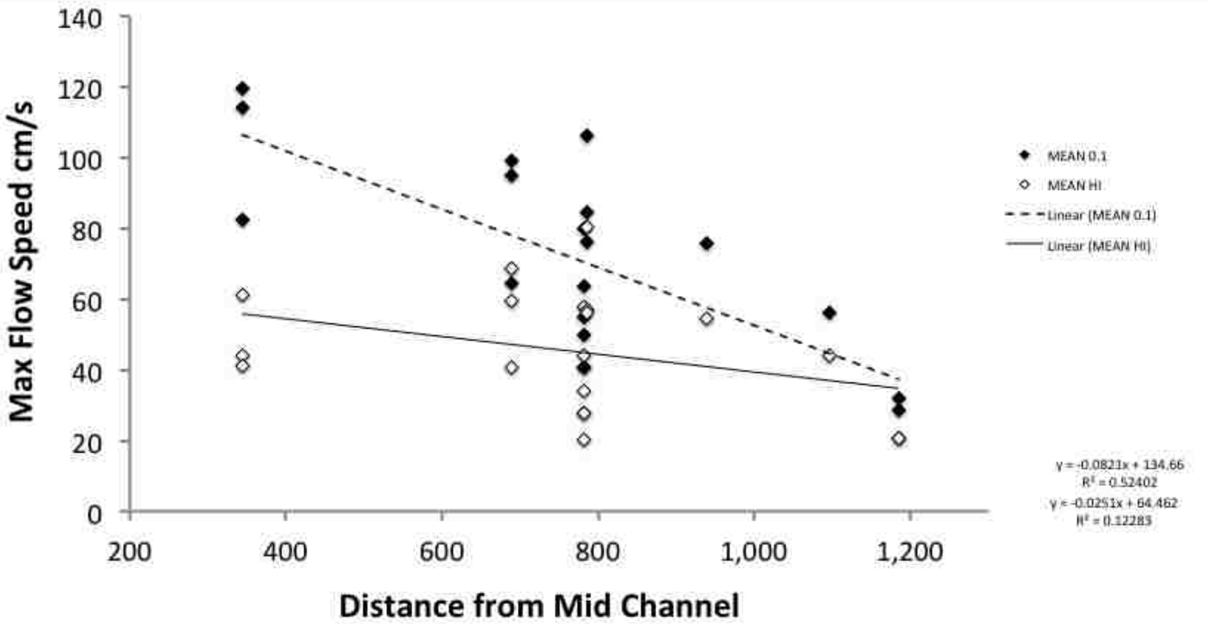


Figure 5. Maximum flow speeds at each site (top 0.1 %) versus location of the site on an axis going from the middle of San Juan Channel (least obstructed tidal flow) toward Friday Harbor (more obstructed tidal flow).

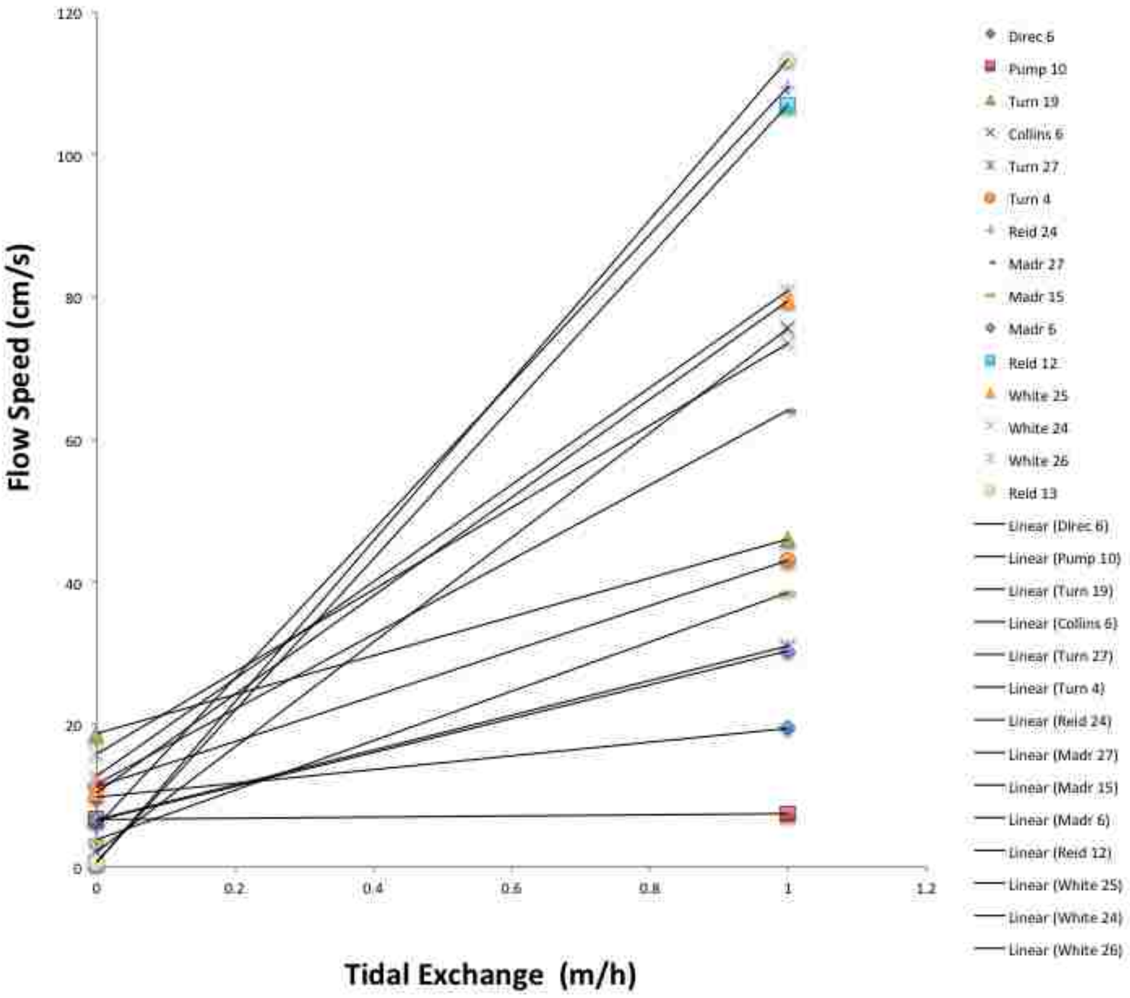


Figure 6. Regression lines of mean flow at each sampling period (5 min per hour) to the change in tidal height during that hour (tidal exchange rate). Tidal exchange can be considered the same for all sites in San Juan Channel and thus these regressions allow comparison over all time periods even when the number of days or time of year differ between deployments. Note the mid-channel Reid Rock site exhibits the highest flow speeds at maximum exchange, and sites inside the mouth of Friday Harbor have the lowest flow speeds.

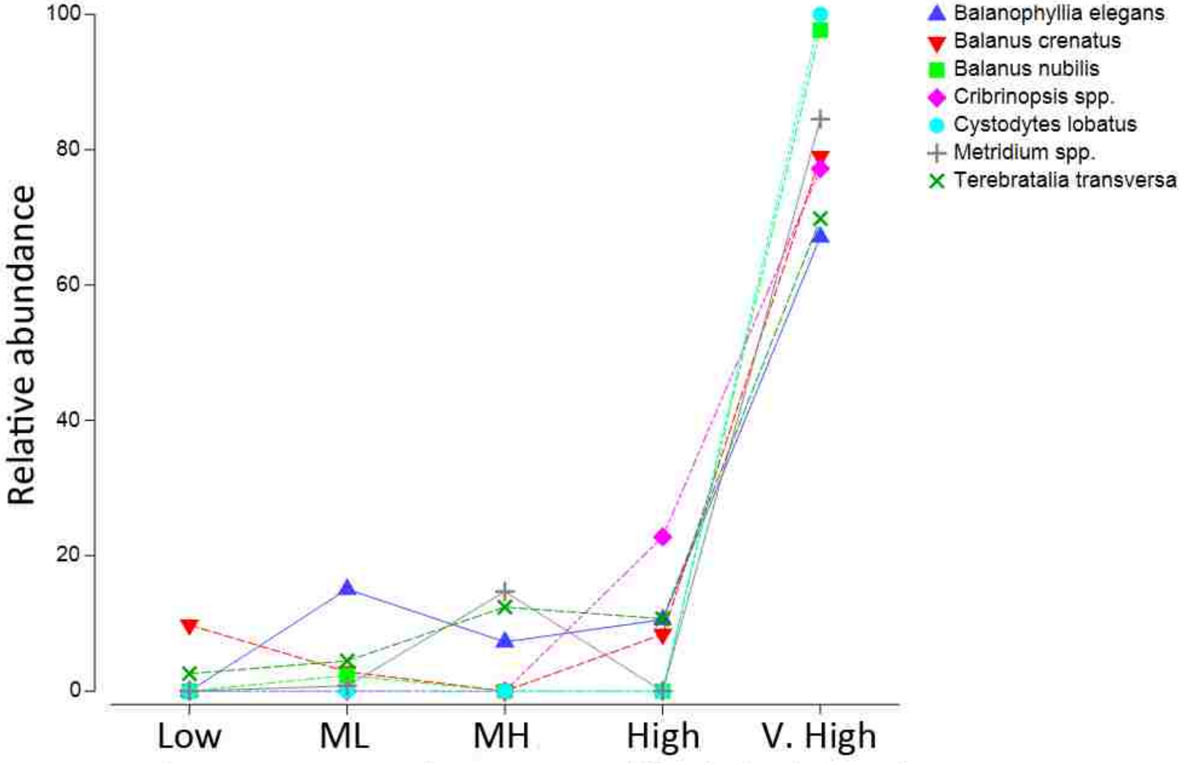


Figure 7. Coherent species curve (Type 3 SIMPROF) for algal and invertebrate assemblages in the MidShelf habitat.

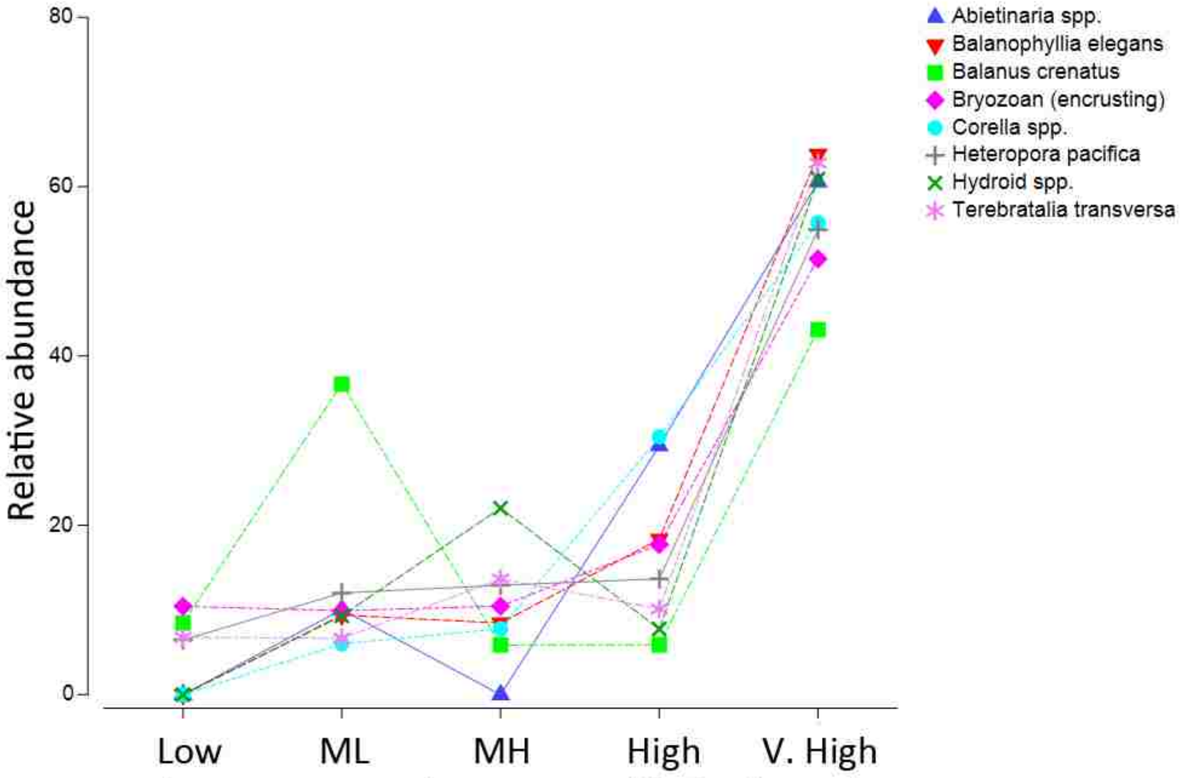


Figure 8. Coherent species curve (Type 3 SIMPROF) for benthic sessile assemblages in the MidShelf habitat.

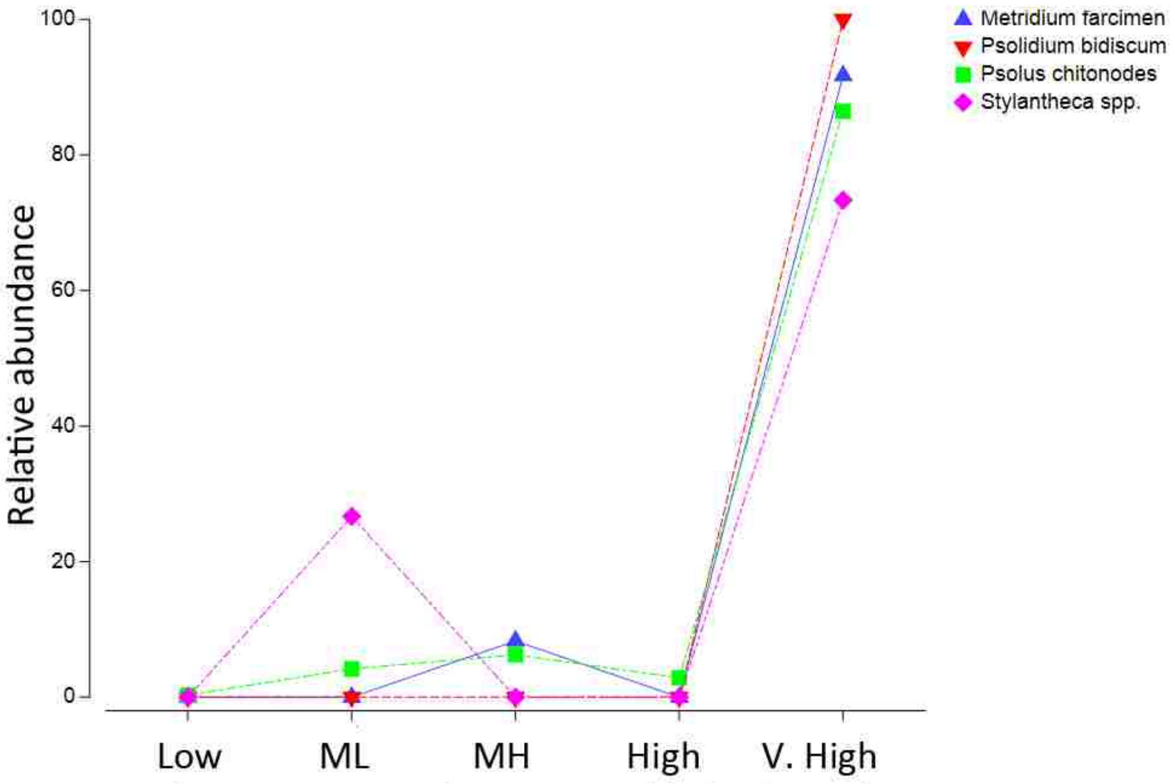


Figure 9. Coherent species curve (Type 3 SIMPROF) for benthic sessile assemblages in the MidShelf habitat.

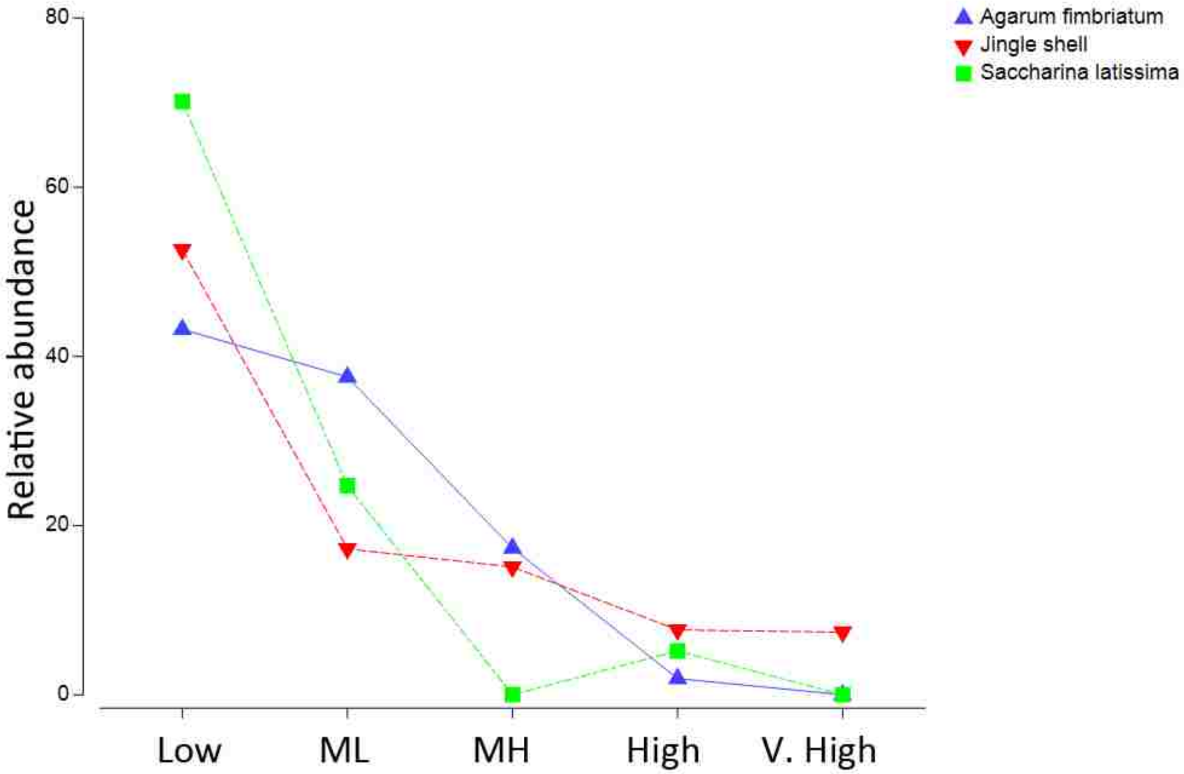


Figure 10. Coherent species curve (Type 3 SIMPROF) for algal and invertebrate assemblages in the MidShelf habitat.

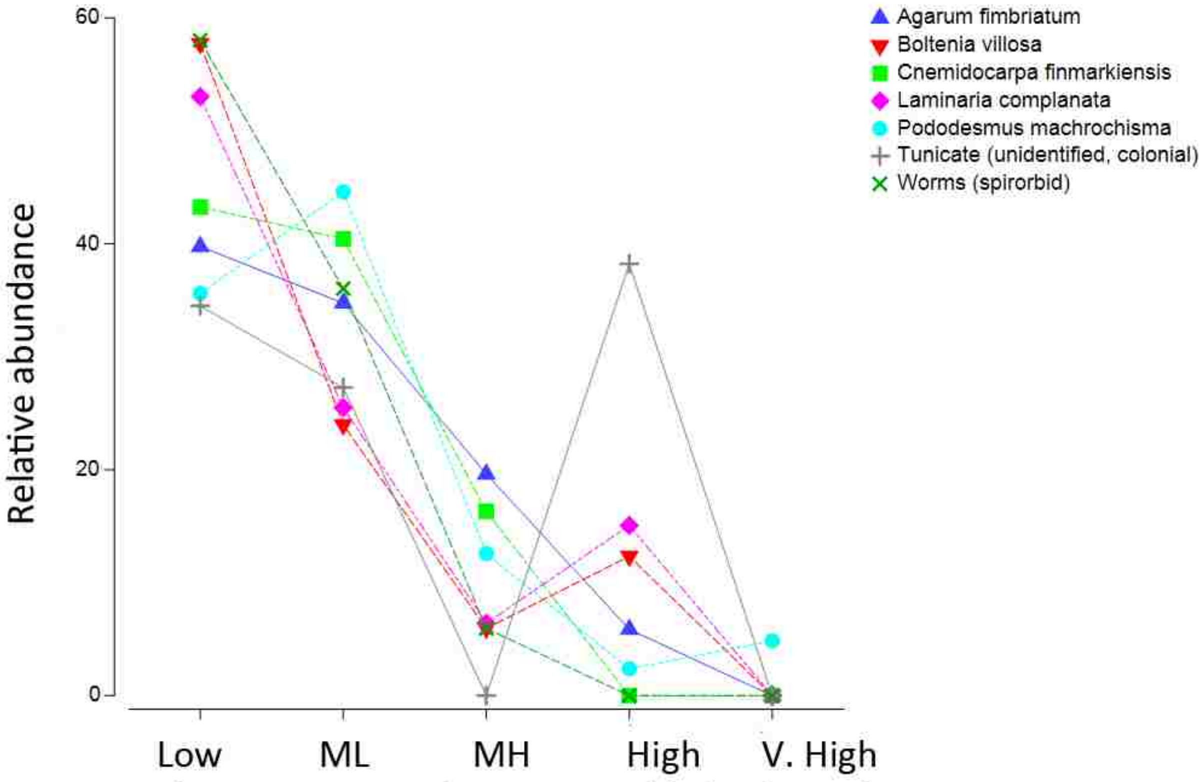


Figure 11. Coherent species curve (Type 3 SIMPROF) for benthic sessile assemblages in the MidShelf habitat.

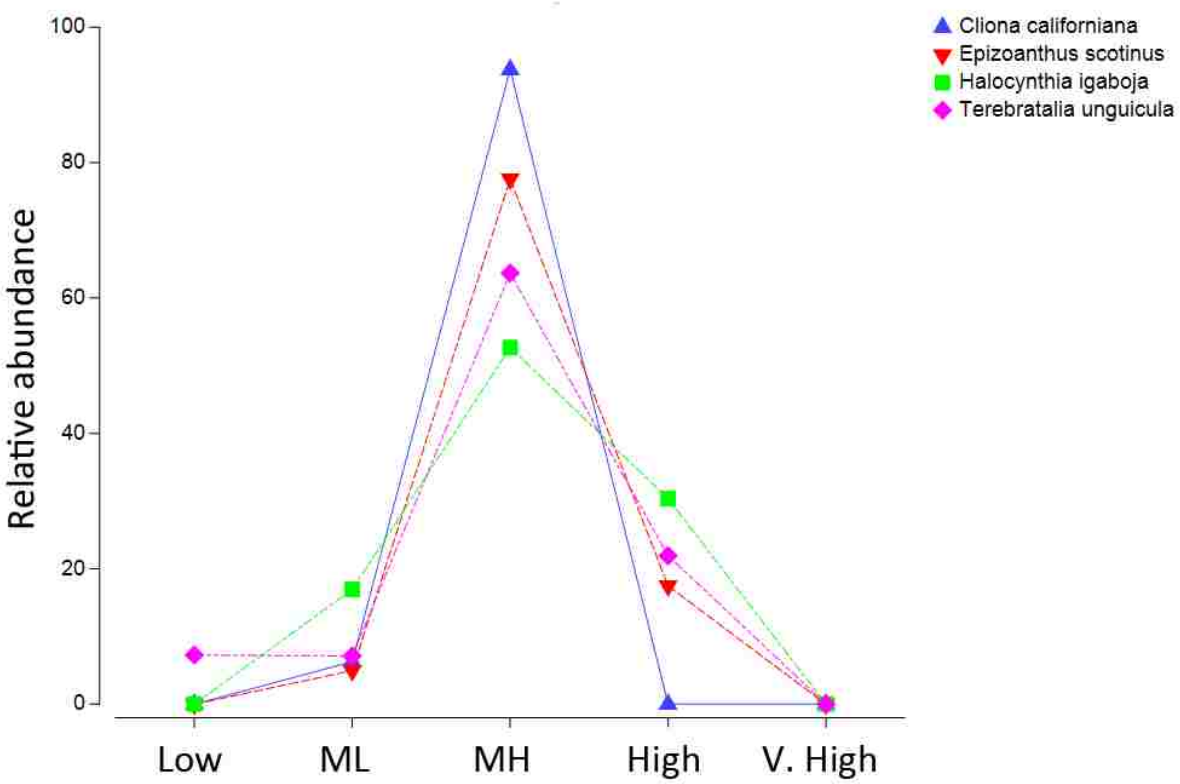


Figure 12. Coherent species curve (Type 3 SIMPROF) for benthic sessile assemblages in the MidShelf habitat.

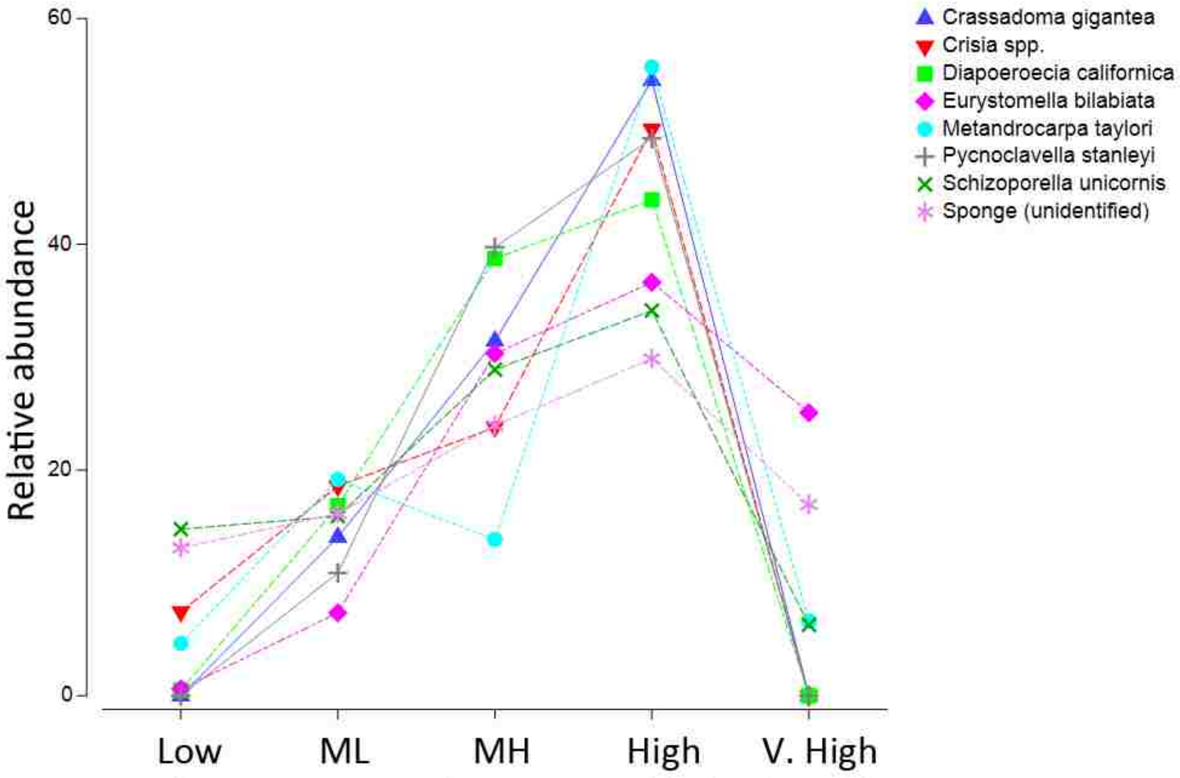


Figure 13. Coherent species curve (Type 3 SIMPROF) for benthic sessile assemblages in the MidShelf habitat.

Literature Cited

Airoldi, L. (2003) The effects of sedimentation on rocky coast assemblages. In Oceanography and Marine Biology, An Annual Review. Volume 41: 169-171

Allison, G. W., B.A. Menge, J. Lubchenco, S.A. Navarrete (1995) Predictability and uncertainty in community regulation: consequences of reduced consumer diversity in coastal rocky ecosystems. – In: Mooney, H. A., Cushman, J. H., Medina, E. et al (eds.), Functional roles of biodiversity: a global perspective. John Wiley and Sons pp. 371–392

Arkema K.K. (2009) Flow-mediated feeding in the field: consequences for the performance and abundance of a sessile marine invertebrate. Mar Ecol Prog Ser 388: 207-220

Archambault, P., E. Bourget (1996) Scales of coastal heterogeneity and benthic intertidal species richness, diversity and abundance. Mar Ecol Prog Ser 136: 111-121

Ayling, A. (1981) The role of biological disturbance in temperate subtidal encrusting communities. Ecology 62: 830-847

Baynes, T.W. (1999) Factors structuring a subtidal encrusting community in the southern Gulf of California. Bull of Mar Sci Volume 64: 419-450

Beaman, R. J., P.J. Harris (2007) Geophysical variables as predictors of megabenthos assemblages from the northern Great Barrier Reef, Australia. Geological Association of Canada.

Benedetti-Cecchi, L. (2001) Variability in abundance of algae and invertebrates at different spatial scales on rocky sea shores. Mar Ecol Prog Ser 215: 79-92

Berner R.A. (1978) Rate control of mineral dissolution under earth surface conditions. American Journal of Science 278: 1235-1252

Bertness, M. D. (1989) Intraspecific competition and facilitation in a northern acorn barnacle population. Ecology 70: 257-268

Blinn, W., R.E. Truitt, A. Pickart (1989) Feeding ecology and radular morphology of the freshwater limpet *Ferrissia fragilis*. J of the N Am Benthological Soc 8:237-242

Bloom, S. A. (1976) Morphological correlations between dorid nudibranch predators and sponge prey. Veliger 18: 289-301

Bloom, S. A. (1981) Specialization and noncompetitive resource partitioning among sponge-eating dorid nudibranchs. Oecologia 49: 305-315

Bologna, P.A., R.S. Steneck (1993) Kelp beds as habitat for American lobster *Homarus americanus*. Mar Ecol Prog Ser 100: 127-134

Branch, G.M., C.L. Griffiths (1988) The Benguela ecosystem. V. The coastal zone. Oceanogr Mar Bio Annu Rev 22: 429-523

Britton-Simmons, K.H. (2006) Functional group diversity, resource preemption, and the genesis of invasion resistance in a community of marine algae. Oikos 113: 395-401

Britton-Simmons, K.H., G. Foley, D. Okamoto (2009) Spatial subsidy in the subtidal zone: utilization of drift algae by a deep subtidal urchin. Aquat Biol 5: 233-243

Brown, C. J., P. Blondel (2009) Developments in the application of multibeam sonar backscatter for seafloor habitat mapping. Applied Acoustics 70: 1242-1247

Bruno, J. F., J.D. Witman (1996) Defensive mechanisms of scleractinian cup corals against overgrowth by colonial invertebrates. J Exp Mar Biol Ecol 207: 229-241

Bruno, J.F., M.D. Bertness (2001) Habitat Modification and Facilitation in Benthic Marine Communities. In: Bertness M, Gaines S, Hay M, (eds.) Marine Community Ecology. Sinauer, Sunderland, MA. pp. 339-366

Bustamente, R.H., G.M. Branch, S. Eekhout, B. Robertson, P. Zoutendyk, M. Shleyer, A. Dye, N. Hanekom, D. Keats, M. Jurd, C. McQuad (1996) Gradients of intertidal primary productivity around the coast of South Africa and their relationships with consumer biomass. Oecologia 102: 189-201

Choat, J.H., D.R. Schiel (1982) Patterns of distribution and abundance of large brown algae and invertebrates in subtidal regions on northern New Zealand. Journal of Experimental Marine Biology and Ecology 60: 129-162

Clarke, J. E. H., L.A. Mayer, D.E. Wells (1996) Shallow-water imaging multibeam sonars: a new tool for investigating seafloor processes in the coastal zone and on the continental shelf. Marine Geophysical Researches 18: 607-629

Clarke, K., R. Warwick (2001) Changes in marine communities: an approach to statistical analysis and interpretation. 2nd Edition. PRIMER-E: Plymouth, UK

Clarke, K. R., J.R. Tweedley, F.J. Valesini (2014) Simple shade plots aid better long-term choices of data pre-treatment in multivariate assemblage studies. J of the Mar Bio Assoc of the UK 94: 1-16

Connell, J.H. (1961) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology 42: 710-723

Connell, S. D. (2003) Negative effects overpower the positive of kelp to exclude invertebrates from the understorey community. Oecologia 137: 97-103

Connell, S.D., A.D. Irving (2008) Integrating ecology with biogeography using landscape characteristics: a case study of subtidal habitat across continental Australia. J of Biogeogr 35: 1608-1621

Dayton, P. K. (1975) Algal canopy interactions in a sea otter-dominated kelp community at Amchitka Island, Alaska Fish Bull 73: 670-684

Dayton, P.K. (1985) The structure and regulation of some South American kelp communities. Ecol Monogr 55: 447-468

Dayton, P.K., Tegner, M.J. (1984) The importance of scale in community ecology. In: P.W. Price et al. (eds.), A New Ecology, pp. 457-481

Dayton, P.K., M.J. Tegner, P.B. Parnell Edwards (1992) Temporal and spatial patterns of disturbance and recovery in a kelp forest community. Ecol Monogr 62: 421-445

Dayton, P.K., G.A. Robilliard, R.T. Paine, L.B. Dayton (1974) Biological accommodation in the benthic community at McMurdo Sound, Antarctica. Ecol Monogr 44: 105-128

de Forges, B.R., J.A. Koslow, G.C.B. Poore (2000) Diversity and endemism of the benthic seamount fauna in the southwest Pacific. Nature 405: 944-947

De Moustier, C., H. Matsumoto (1993) Seafloor acoustic remote sensing with multibeam echo-sounders and bathymetric sidescan sonar systems. Marine Geophysical Researches 15: 27-42

Denny, M. W., C.A. Blanchette (2000) Hydrodynamics, shell shape, behavior and survivorship in the owl limpet *Lottia gigantea*. J Exp Biol 203: 2623-2639

Dethier, M.N., E.S. Graham, S. Cohen, L.M. Tear (1993) Visual versus random-point percent cover estimations: 'objective' is not always better. Mar Ecol Prog Ser 96: 9

Duffy, J. E., M.E. Hay (2001) The ecology and evolution of marine consumer-prey interactions. In: Bertness, M. D., Hay, M. E. and Gaines, S. D. (eds)., Marine community ecology. pp. 131–157

Duffy, J. E. (2002) Biodiversity and ecosystem function: the consumer connection. Oikos, 99: 201-219

Duggins, D.O. (1980) Kelp beds and sea otters: An experimental approach. Ecology 61: 447-453

Duggins, D. O. (1988) The effects of kelp forests on nearshore environments: biomass, detritus, and altered flow. In The community ecology of sea otters pp. 192-201

Duggins, D.O., J.E. Eckman (1994) The role of kelp detritus in the growth of benthic suspension feeders in an understory kelp forest. J Exp Mar Biol Ecol 176: 53-68

Duggins, D.O., J.E. Eckman (1997) Is kelp detritus good food for suspension feeders? Effects of kelp species, age, and secondary metabolites. Mar Biol 128: 489-495

Earll, R., D.G. Erwin (eds.) (1983) Sublittoral Ecology. Clarendon Press, Oxford

Eckman, J.E., D.O. Duggins, A.T. Sewell (1989) Ecology of understory kelp environments: Effects of kelps on flow and particle transport near the bottom. J Exp Mar Biol Ecol 129: 173-187

Eckman, J.E., D.O. Duggins (1991) Life and death beneath macrophyte canopies: Effects of understory kelps on growth rates and survival of marine benthic suspension feeders. Oecologia 87: 473-487

Elahi, R., K.P. Sebens (2012) Consumers mediate natural variation between prey richness and resource use in a benthic marine community. Mar Ecol Prog Ser 452: 131-143

Elahi, R., K.P. Sebens (2013) Experimental removal and recovery of subtidal grazers highlights the importance of functional redundancy and temporal context. PloS one 8: 11

Elahi, R., T.R. Dwyer, K.P. Sebens (2014) Mesoscale variability in oceanographic retention sets the abiotic stage for subtidal benthic diversity. Mar Ecol Prog Ser 498: 117-132

Estes, J. A., J.F. Palmisano (1974) Sea otters: their role in structuring nearshore communities. Science 185: 1058–1060

Estes, J. A., D.O. Duggins (1995) Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. Ecological Monographs 65: 75-100

Fernandez, C., C.F. Boudouresque (1998). Evaluating artificial diets for small *Paracentrotus lividus* (Echinodermata: Echinoidea). Echinoderms: San Francisco pp. 651-657

Ferrier, G. A., R.C. Carpenter (2009) Subtidal benthic heterogeneity: flow environment modification and impacts on marine algal community structure and morphology. The Biological Bulletin 217: 115-129

Field, J.G., C.L. Griffiths, R.J. Griffiths, N. Jarman, P. Zuotendyk, B. Velimirov, A. Bowes (1980) Variation in structure and biomass of kelp communities along the South West Cape coast. Trans R Soc S Africa 44:145-203

Gaylord, B., S. D. Gaines (2000). Temperature or transport? Range limits in marine species mediated solely by flow. The American Naturalist 155: 769-789

Gaylord, B., J.H. Rosman, D.C. Reed, J.R. Koseff, J. Fram, S. MacIntyre, K. Arkema, C. McDonald, M.A. Brzezinski, J.L. Largier, S.G. Monismith (2007). Spatial patterns of flow and their modification within and around a giant kelp forest. Limnology and Oceanography 52: 1838-1852

Genin, A., P.K. Dayton, P.F. Lonsdale, F.N. Spies (1986) Corals on seamount peaks provide evidence of current acceleration over deep-sea topography. Nature 322: 59-61

Genovese, S.J. (1996) Regional and temporal variation in the ecology of an encrusting bryozoan in the Gulf of Maine. PhD Dissertation, Northeastern University, Boston

Genovese, S.J., J.D. Witman (1999) Interactive effects of flow speed and particle concentration on growth rates of an active suspension feeder. Limnol Oceanogr 44: 1120-1131

Gill, J.M., R. Coma (1998) Benthic suspension feeders: Their paramount role in littoral marine food webs. Trends Ecol Evol 13: 316-321

Glasby, T. M. (2000) Surface composition and orientation interact to affect subtidal epibiota. J Exp Mar Biol Ecol 248: 177-190

Golikov, A.N., O.A. Scarlato (1968) Vertical and horizontal distribution of biocoenoses in the upper zones of Japan and Okhotsk Seas and their dependence on the hydrological system. Sarsia 34: 109-116

Grange, K.R., R.J. Singleton, J.R. Richardson, P.J. Hill, W.D.L. Main (1981) Shallow rock-wall biological associations of some southern fiords of New Zealand. New Zealand Journal of Zoology 8: 209-227

Greene, H. G., J.J. Bizzarro, V.M. O'Connell, C.K. Brylinsky (2007) Construction of digital potential marine benthic habitat maps using a coded classification scheme and its application. Mapping the seafloor for habitat characterization: Geological Association of Canada Special Paper 47: 141-155

Hadfield, M. G., V.J. Paul (2001) Natural chemical cues for settlement and metamorphosis of marine invertebrate larvae. Marine chemical ecology pp. 431-461

Hatton, H. (1938) Essais de Bionomie explicative sur quelques especes intercotidales d'algues et d'animaux. Ann Inst Oceanogr Monaco 17: 241-348

Hawkins, S. J., D.C. Watson, A.S. Hill, S.P. Harding, M.A. Kyriakides, S. Hutchinson, T.A.Norton (1989) A comparison of feeding mechanisms in microphagous, herbivorous, intertidal, prosobranchs in relation to resource partitioning. Journal of Molluscan Studies 55: 151-165

Hayward, P. J. (1980) Invertebrate epiphytes of coastal marine algae. The shore environment 2: 761-787

Helmuth, B. S. (1998) Intertidal mussel microclimates: predicting the body temperature of a sessile invertebrate. Ecol Monog 68: 51-74

Hiscock, K., R. Mitchell (1980) The description and classification of sublittoral epibenthic ecosystems. In J.H. Price, D.E.G. Irvine, and W.F. Farnham (eds.), The Shore Environment 2: 323-370

Hulbert, A.W., K. Pecci, J.D. Witman, L.G. Harris, J.R. Sears, R.A. Cooper (1982) Ecosystem definition and community structure of the macrobenthos of the NEMP monitoring station at Pigeon Hill in the Gulf of Maine. NOAA Technical Memorandum NMFS-F/NEC 14

Huntly, N. (1995) How important are consumer species to ecosystem functioning? In: Jones, C. G. and Lawton, J. H. (eds.) Linking species and ecosystems. Chapman and Hall, pp. 72–83

Jackson, J. B. C. (1977) Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. The American Naturalist 111: 743-767

Jackson, G.A., C.D. Winant (1983) Effect of a kelp forest on coastal currents. Cont Shelf Res 2: 75-80

Jackson, J. B. (1991) Adaptation and diversity of reef corals. *BioScience* 475-482

Johnson, C., K. Mann (1988) Diversity, patterns of adaptation, and stability of Nova Scotian kelp beds. Ecol Monogr 58: 129-154

Jumars, P. A., A.R. Nowell (1984) Fluid and sediment dynamic effects on marine benthic community structure. American Zoologist 24: 45-55

Kain, J.M. (1971) Continuous recording of underwater light in relation to Laminaria distribution. In D.J. Crisp (ed.), Fourth European Marine Biology Symposium pp. 335-346

Kamino K. (2016) Barnacle Underwater Attachment. In: Smith A. (eds.) Biological Adhesives. Springer, Cham

Kennelly, S. J. (1989) Effects of kelp canopies on understory species due to shade and scour. Mar Ecol Prog Ser 50: 215-224

Kitching, J. A. (1939) The Physiology of Contractile Vacuoles: IV. A Note on the Sources of the Water Evacuated, and on the Function of Contractile Vacuoles in Marine Protozoa. Journal of Experimental Biology 16: 34-37

Kitching, J. A. (1941) Studies in Sublittoral Ecology: III. Laminaria Forest on the West Coast of Scotland; A Study of Zonation in Relation to Wave Action and Illumination. The Biological Bulletin 80: 324-337

Kitching, J. A., S.J. Lilly, S.M. Lodge, J.F. Sloane, R. Bassindale, F.J. Ebling (1952) The Ecology of the Lough Ine Rapids with Special Reference to Water Currents: III. The Effect of Current on Other Environmental Conditions. The Journal of Ecology 179-201

Koehl, M. A. R., R.S. Alberte (1988) Flow, flapping, and photosynthesis of *Nereocystis leutkeana*: a functional comparison of undulate and flat blade morphologies. Marine Biology 99: 435-444

Koehl, M. A. R., W.K. Silk, H. Liang, L. Mahadevan (2008) How kelp produce blade shapes suited to different flow regimes: a new wrinkle. Integrative and Comparative Biology 48: 834-851

Konnecker, G. (1977) Epibenthic assemblages as indicators of environmental conditions. In B.F. Keegan, P.O. Ceidigh, and P.J.S. Boaden (eds.), Biology of Benthic Organisms, pp. 391-395. Pergamon Press, Oxford

Lamb, A., B.P. Hanby, M.W. Hawkes, S.C. Byers (2005). Marine life of the Pacific Northwest: a photographic encyclopedia of invertebrates, seaweeds and selected fishes. Harbour Pub

Lambert, W. J., C.D. Todd (1994) Evidence for a water-borne cue inducing metamorphosis in the dorid nudibranch mollusc *Adalaria proxima* (Gastropoda: Nudibranchia). Marine Biology 120*:* 265-271

Leichter, J.J., J.D. Witman (1997) Water flow over subtidal rock walls: effects on distribution and growth of suspension feeders. J Exp Mar Biol Ecol 209: 293-307

Lenihan, H. S. (1999) Physical–biological coupling on oyster reefs: how habitat structure influences individual performance. Ecological Monographs 69: 251-275

Lesser, M. P., V.M. Weis, M.R. Patterson, P.L. Jokiel (1994) Effects of morphology and water motion on carbon delivery and productivity in the reef coral, *Pocillopora damicornis* (Linnaeus): diffusion barriers, inorganic carbon limitation, and biochemical plasticity. J Exp Mar Biol Ecol 178: 153-179

Levin, S.A (1992) The problem of pattern and scale in ecology. Ecology 73: 1943-1967

Levitan, D. R. (2000) Sperm velocity and longevity trade off each other and influence fertilization in the sea urchin *Lytechinus variegatus*. Proceedings of the Royal Society B: Biological Sciences 267: 531-535

Leonard, G. H. (2000) Latitudinal variation in species interactions: a test in the New England rocky intertidal zone. Ecology 81: 1015-1030

Lowe, A. T., R. Whippo, A.W. Galloway, K.H. Britton-Simmons, M.N. Dethier (2015) Sedentary urchins influence benthic community composition below the macroalgal zone. Marine Ecology 36: 129-140

Lubchenco, J. and Gaines, S. D. (1981) A unified approach to marine plant-herbivore interactions. I. Populations and communities. Annu Rev Ecol Syst*.* 12: 405–437

Lundalv, T. (1971) Quantitative studies on rocky-bottom biocoenoses by underwater photogrammetry. Thallasia Jugoslavica 7: 201-208

Marchinko, K. B., A.R. Palmer (2003) Feeding in flow extremes: dependence of cirrus form on wave-exposure in four barnacle species. Zoology 106: 127-141

Mathieson, A.C., C.A. Penniman, L.G. Harris (1991) Northwest Atlantic rocky shore ecology. In A.C. Mathieson and P.H. Nienhuis (eds.), Intertidal and Littoral Ecosystems, pp. 109-191. Ecosystems of the World, Vol 24. Elsevier, Amsterdam

Menge, B.A. (1992) Community regulation: Under what conditions are bottom-up factors important on rocky shores? Ecology 73: 755-765

Menge, B. A. (1995) Indirect effects in marine rocky intertidal interaction webs: patterns and importance. Ecol Monogr 65: 21–74

Miller, R. J., R.J. Etter (2008) Shading facilitates sessile invertebrate dominance in the rocky subtidal Gulf of Maine. Ecology 89: 452-462

Miller, R. J., R.J. Etter (2011) Rock walls: small-scale diversity hotspots in the subtidal Gulf of Maine. Mar Ecol Prog Ser 425: 153-165

Morrow, K., R. Carpenter (2008) Shallow kelp canopies mediate macroalgal composition: effects on the distribution and abundance of *Corynactis californica* (Corallimorpharia). Mar Ecol Prog Ser 361: 119-127

Nelson, M.L., S.F. Craig (2011) Role of the sea anemone Metridium senile in structuring a developing subtidal fouling community. Mar Ecol Prog Ser 421: 139-149

Neushul, M. (1967) Studies of subtidal marine vegetation in western Washington. Ecology 48: 83-94

North, W.J. (ed.) (1971) The biology of giant kelp (Macrocystis) in California. Nova Hedwigia 32: 1-600

Nybakken, J. J., J. Eastman (1977) Food preference, food availability and resource partitioning in *Triopha maculata* and *Triopha carpenteri* (Opisthobranchia: Nudibranchia). Veliger 19: 279-289

Ohmann, J.L., T.A. Spies (1998) Regional gradient analysis and spatial pattern of woody plant communities of Oregon forests. Ecol Monogr. 68: 151–182

Okamura, B. (1992) Microhabitat variation and patterns of colony growth and feeding in a marine bryozoan. Ecology 73: 1502-1513

Paine, R. T. (1966) Food web complexity and species diversity. Amer Nat 100: 65-75

Paine, R. T. (1976) Size-limited predation: an observational and experimental approach with the Mytilus-Pisaster interaction. Ecology 57: 858-873

Paine, R. T. (1980) Food webs: linkage, interaction strength and community infrastructure. J Anim Ecol 49: 667–685

Palmer, M.A., J.D. Allan, C.A. Butman (1996) Dispersal as a regional process affecting the local dynamics of marine and stream benthic invertebrates. Trends Ecol Evol 11: 322-326

Patterson, M.R. (1984) Patterns of whole-colony prey capture in the octocoral *Alcyonium siderium*. Biol Bull 167: 613-629

Pearson, G. A., S.H. Brawley (1998) A model for signal transduction during gamete release in the fucoid alga *Pelvetia compressa*. Plant physiology 118: 305-313

Pechenik, J. A., M.G. Hadfield, L.S. Eyster (1995) Assessing whether larvae of the opisthobranch gastropod *Phestilla sibogae* (Bergh) become responsive to three chemical cues at the same age. Journal of experimental marine biology and ecology, 191: 1-17

Pequenat, W.E. (1964) The epifauna of a California siltstone reef. Ecology 45: 272-282

Peres, J.M., R. Molinier (1957) Compte rendu du colloque tenue a genes par la comite du benthos de la Commission Internationale pour L'Exploration Scientifique de la Mer Mediterranee. Recl. Trav. Stn., Mar. Endoume 22: 5-15

Porter ET, LP Sanford and SE Suttles (2000) Gypsum dissolution is not a universal integrator of 'water motion.' Limnology and Oceanography 45: 145-158

Ruesink, J.L., K.E. Hodges, C.J. Krebs (2002) Mass-balance analysis of boreal forest population cycles: Merging demographic and ecosystem approaches. Ecosystems 5:138-158

Santschi PH, RF Anderson and W Bowles (1991) Measurements of diffusive sublayer thicknesses in the ocean by alabaster dissolution, and their implications for the measurements of benthic fluxes. Journal of Geophysical Research 96: 10641-10657

Santileces, B., F.P. Ojeda (1984) Population dynamics of coastal forests of *Macrocystis pyfrifera* in Puerto Toro, Isla Navarino, Southern Chile. Mar Ecol Prog Ser 14: 175-183

Santileces, B. (1991) Littoral and sublittoral communities of continental Chile. In A.C. Mathieson and P.H. Nienhuis (eds.), Intertidal and Littoral Ecosystems, pp. 347-370 Ecosystems of the World, Vol 24. Elsevier, Amsterdam

Scheibling, R.E., A.W. Hennigar (1997) Recent outbreaks in sea urchins *Strogylocentrotus droebachiensis* in Nova Scotia: Evidence for a link with large-scale meteorological and oceanographic events. Mar Ecol Prog Ser 152: 155-165

Sears, J.R., R.A. Cooper (1978) Descriptive ecology of offshore, deep-water benthic algae in the temperate western North Atlantic Ocean. Mar Biol 44: 309-314

Sebens, K. P. (1984) Water flow and coral colony size: interhabitat comparisons of the octocoral *Alcyonium siderium*. Proceedings of the National Academy of Sciences 81: 5473-5477

Sebens, K.P. (1985) Community ecology of vertical walls in the Gulf of Maine USA: Small scale processes and alternative community states. In P.G. Moore and R. Seed (eds.), The Ecology of Rocky Coasts. Hodder and Stoughton, Toronto

Sebens, K.P. (1986) Spatial relationships between encrusting marine organisms in the New England subtidal zone. Ecol Monogr 56: 73-96

Sebens, K.P., J.D. Witman, R.A. Allmon, E.J. Maney, Jr. (1988) Early community development experiments in rocky subtidal habitats (Gulf of Maine, 30 - 80 m). pp. 45 - 66. In. I. Babb and M. DeLuca (eds.) Benthic Productivity and Marine Resources in the Gulf of Maine. N.U.R.P. (N.O.A.A.) Research Report 88 - 3

Sebens, K. P. (1991) Habitat structure and community dynamics in marine benthic systems. In Habitat Structure pp. 211-234

Serrao, E. A., G. Pearson, L. Kautsky, S.H. Brawley (1996) Successful external fertilization in turbulent environments. Proceedings of the National Academy of Sciences 93: 5286-5290

Shepard, S.A., H.B.S. Womersley (1970) The sublittoral ecology of West Island, South Australia. I. Environmental features and algal ecology. Trans R Soc Austral 94: 105-137

Shimeta, J., P.A. Jumars (1991) Physical mechanisms and rates of particle capture by suspension feeders. Oceanogr Mar Biol Annu Rev 29: 191-257

Shotwell, S. K., J. Heifetz, D.L. Courtney, H.G. Greene (2007) Mapping marine benthic habitat in the Gulf of Alaska: Geological habitat, fish distributions, and fishing intensity. Mapping the seafloor for habitat characterization. Geol Assoc Can Spec Pap 47: 349-368

Smith, F. (1999) Subtidal landscapes of a New Zealand fjord: Patterns of species diversity, community structure, and recruitment processes. Ph.D. Dissertation, University of Otago, New Zealand

Stachowicz, J.J., M.E. Hay (1999) Reducing predation through chemically mediated camouflage: Indirect effects of plant defenses on herbivores. Ecology 80: 495-509

Steele, J. H. (1978) Some comments on plankton patches. In Spatial pattern in plankton communities pp. 1-20

Steneck, R.S. (1986) The ecology of coralline algal crusts: consequent patterns and adaptive strategies. Annu Rev Ecol Syst 17: 273-303

Steneck, R. S., M.N. Dethier (1994) A functional group approach to the structure of algal-dominated communities. Oikos 476-498

Tegner, M. J., P.K. Dayton (1991) Sea urchins, El Ninos, and the long term stability of Southern California kelp forest communities. Mar Ecol Prog Ser 77: 49-63

Turner, E. J., R.K. Zimmer-Faust, M.A. Palmer, M. Luckenbach, N.D. Pentchef (1994) Settlement of oyster (*Crassostrea virginica*) larvae: Effects of water flow and a water-soluble chemical cue. Limnology and Oceanography 39: 1579-1593

Turner, K.R. (2015) Effects of fish predation on benthic communities in the San Juan Archipelago. Ph.D. Dissertation, University of Washington, Seattle

Underwood, A.J., M.G. Chapman (1996) Scales of spatial patterns of distribution of intertidal invertebrates. Oecologia 107: 212-224

Uriz, M.J., M. Maldonado, X. Turon, R. Marti (1998) How do reproductive output, larval behavior, and recruitment contribute to adult spatial patterns in Mediterranean encrusting sponges? Mar Ecol Prog Ser 167: 137-148

Vance, R.R. (1978) A mutualistic interaction between a sessile marine clam and its epibionts. Ecology 59: 679-685

Velimirov, B., J.G. Field, C.L. Griffiths, P. Zoutendyk (1977) The ecology of kelp bed communities in the Benguela upwelling system. Helgolander wiss Meersunters 30: 495-518

Wedding, L. M., A.M. Friedlander, M. McGranaghan, R.S. Yost, M.E. Monaco (2008) Using bathymetric lidar to define nearshore benthic habitat complexity: Implications for management of reef fish assemblages in Hawaii. Remote Sensing of Environment 112: 4159-4165

Whitmire, C. E., R.W. Embley, W.W. Wakefield, S.G. Merle, B.N. Tissot (2007) A quantitative approach for using multibeam sonar data to map benthic habitats. Mapping the Seafloor for Habitat Characterization: Geological Association of Canada, Special Paper 47: 111-126

Whittaker, R.H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. Ecol Monogr 30:279–338

Wiens, J. A. (1989) Spatial scaling in ecology. Functional Ecology *3*: 385-397

Wildish, D., D. Kristmanson (1997) Benthic Suspension Feeders and Flow. Cambridge University Press, Cambridge

Wing, S. R., L.W. Botsford, J.L. Largier, L.E. Morgan (1995) Spatial structure of relaxation events and crab settlement in the northern California upwelling system. Mar Ecol Prog Ser 128: 199-211

Wing, S. R., L.W. Botsford, J.F. Quinn (1998) The impact of coastal circulation on the spatial distribution of invertebrate recruitment, with implications for management. Canadian Special Publication of Fisheries and Aquatic Sciences pp. 285-294

Witman, J.D. (1985.) Refuges, biological disturbance, and rocky subtidal community distribution in New England. Ecol Monogr 55:421-445

Witman, J.D, (1987) Subtidal coexistence: Storms, grazing, mutualism, and the zonation of kelps and mussels. Ecol Monogr 57: 167-187

Witman, J.D. (1998) Natural disturbance and colonization on subtidal hard substrate in the Gulf of Maine. In E.M. Dorsey and J. Pederson (eds.), Effects of Fishing Gear on the Sea Floor of New England, pp. 30-37. MIT Sea Grant publication 98-4

Witman, J.D., R.A. Cooper (1983) Disturbance and contrasting patterns of population structure in the brachiopod *Terebratulina septentrionalis* from two subtidal habitats. J Exp Mar Biol Ecol 73: 57-79

Witman, J. D., K.P. Sebens (1988) Benthic community structure at a subtidal rock pinnacle in the central Gulf of Maine. In I. Babb and M. De Luca (eds.), Benthic Productivity and Marine Resources of the Gulf of Maine, pp. 67-104. National Undersea Research Program Research Report 88-3

Witman, J.D., K.R. Grange (1998) Links between rain, salinity, and predation in rocky subtidal community. Ecology 79: 2429-2447

Witman, J.D., P.K. Dayton (2001) Rocky subtidal communities. In: Bertness M, Gaines S, Hay M, (eds.) Marine Community Ecology. Sinauer, Sunderland, MA. pp. 339-366

Witman, J.D., A.W. Hulbert, L.G. Harris, K. Pecci, K. McCarthy, R.A. Cooper (1980) Community structure of the macrobenthos of Pigeon Hill in the Gulf of Maine: A baseline report from the Ocean Pulse monitoring program. Ocean Pulse Tech. Report.

Wright, J. R., A.J. Boxshall (1999) The influence of small-scale flow and chemical cues on the settlement of two congeneric barnacle species. Mar Ecol Prog Ser 183: 179-187

Wyeth, R. C., A.D. Willows (2006) Field behavior of the nudibranch mollusc *Tritonia diomedea*. The Biological Bulletin 210: 81-96

Yoshioka, P. M. (1986) Competitive coexistence of the dorid nudibranchs *Doridella steinbergae* and *Corambe pacifica*. Mar Ecol Prog Ser pp. 81-88

Zenkevitch, L (1983) Biology of the Seas of the U.S.S.R. Allen and Unwin, London

VITA

Derek Smith was born on December 14, 1973 in Stanford, California. He attended St. Francis High School in Mountain View, graduating in 1991. He received a Bachelor of Arts in Marine Biology from the University of California at Santa Cruz in 1999 and an Master of Science in Zoology from the University of Hawaiʻi at Manoa in 2010. In 2018, Derek completed his Doctor of Philosophy in Biology with Kenneth P. Sebens at the University of Washington.