**Invertebrate beta diversity varies among eelgrass meadows**

R. Whippo1,2, N.S. Knight1,3, C. Prentice1,4 , M. Siegle1, M. I. O’Connor1\*

\*Corresponding author: [oconnor@zoology.ubc.ca](mailto:oconnor@zoology.ubc.ca)

1. Department of Zoology and Biodiversity Research Centre, University of British Columbia, 2212 Main Mall, V6T 1Z4, Vancouver, Canada

2. Smithsonian Institution, Tennenbaum Marine Observatories Network, 647 Contees Wharf Rd, Edgewater, MD, 21037, USA

3. Department of Biology, McGill University, 1205 Avenue du Docteur-Penfield, H3A

1B1, Montreal, Canada

4. School of Resource and Environmental Management, Simon Fraser University, 8888 University Drive, V5A 1S6, Burnaby, Canada

**Running head:** Variation in epifaunal eelgrass diversity

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ABSTRACT: Seagrass habitats form spatially heterogeneous landscapes that support high secondary productivity and biodiversity. The spatial structure of seagrass landscapes could support high biodiversity through metacommunity dynamics of seagrass-associated animals. Here, we tested whether spatial patterns of eelgrass-associated invertebrate biodiversity are consistent with metacommunity processes across meadows. For 9 meadows in Barkley Sound, British Columbia, we quantified epifaunal biodiversity on eelgrass *Zostera marina*, and tested the following hypotheses: after controlling for depth and edge effects, epifaunal diversity and composition i) vary randomly within meadows but ii) vary systematically among meadows reflecting abiotic factors and metacommunity dynamics. Finally, we hypothesized that differences among meadows reflect their position in the landscape, and therefore persist throughout the season such that iii) variation among meadows is consistent through time over a single summer. We found that within meadows, invertebrates were non-randomly distributed, showing signals of greater intra-specific aggregation than expected by chance. Non-random distributions of epifauna are consistent with checkerboard patterns, but we did not detect a clear signal of other predictors (*but maybe of fetch…grazer abundance increased with exposure).* *Grazer / fetch pattern was stable over time, though signals of recruitment events by mussels are strong.*

Faunal assemblages are temporally dynamic and vary substantially within meadows, and we have shown here that meadows can be similar to each other in patterns that suggest that wave energy and dispersal may be important controls on biodiversity.

**INTRODUCTION**

Understanding the distribution and abundance of species is a central goal of ecological research. Achieving this goal for spatially structured habitats is essential to not only understanding ecological communities but also to making informed decisions about landscape management and biodiversity conservation. In coastal marine habitats, rich in biodiversity, knowledge of how biodiversity is structured across spatial scales is limited by a lack of basic information about where and when species occur, and how species are distributed across habitat patches (Bostrom et al 2006, Guichard or Baskett papers?, Gaston 2000). While a spatially discrete habitat patch such as a seagrass meadow or a kelp bed may appear to represent the local community, the habitat or resources provided by that foundation species is one of several processes that influence biodiversity of a local patch. In addition, population dynamics and species interactions structure species assemblages at finer (within meadow) and broader (landscape) spatial scales (Leibold et al 2004, Bostrom et al 2006, Pillai et al 2011).

The purpose of this study is to quantify faunal biodiversity across scales in a seagrass meadow seascape to determine whether individual seagrass meadows, or a set of meadows in a landscape, represent meaningful spatial units for associated faunal biodiversity. Spatial variation in biodiversity is related to the spatial scales of ecological processes that influence the relative abundance and presence or absence of species (Ricklefs 2004, Liebold et al 2004, Bostrom et al 2006). Over broad spatial scales evolutionary and dispersal processes (immigration) influence the regional species pool, while at finer scales local species diversity reflects biotic interactions (predation, competition, facilitation, resource provision) and abiotic conditions (gradients, disturbance, stochastic variation). Between local and regional scales, dispersal and colonization dynamics connect species populations among habitat patches, leading to mesoscale diversity patterns that reflect local processes and dispersal (Shurin). These mesoscale patterns have been described by metacommunity dynamics (Leibold and Mikkelson, Liebold et al).

Diversity at fine scales ('alpha' diversity, often described for a sample of a habitat) can reflect the regional availability of species, the quality of the habitat, species interactions, and the propensity for like individuals to aggregate in space (). Fine scale diversity is often the easiest to sample, and therefore is often reported, yet this measure does not fully describe diversity patterns in a spatially structured community. Comparison of alpha diversity estimates among sites or studies can make inference or comparisons across spatial scales challenging (Azaele et al. 2015, Chase and Knight 2013). Missing from alpha diversity estimates is the variation of diversity present in the region, but not captured in a particular patch or sample, known as ‘beta’ diversity. For example, dispersal and connectivity among patches promote biodiversity at the landscape scale if patches host different species assemblages so that in total lead to a greater regional species pool (gamma diversity) than observed in any habitat patch (Crist & Veech 2006).

In coastal marine systems, faunal biodiversity is distributed among patchy seascapes comprised of foundation species such as seagrass or kelp. Despite the apparent similarity of these habitats from patch to patch, the biodiversity of animals living among the shoots or stipes can vary substantially from place to place (seagrass diversity refs). For invertebrates and small vertebrates, seagrasses provide a physically complex and resource rich habitat, often in the form of disjunct meadows creating a heterogenous landscape of meadow and non-meadow areas (Bostrom et al 2006, etc). Within meadows, alpha diversity at 0.5 – 1 m2 is typically relatively constant and much lower than meadow-scale species diversity (Barnes 2013, Barnes and Elwood 2012, etc). The processes responsible for low and consistent sample-scale alpha diversity are not known, and leading theoretical explanations of competition have been not strongly supported (Nelson, Barnes 2013). This pattern suggests that beta diversity should be high and a relatively important component of seagrass associated biodiversity within meadows, yet there are few reports of beta diversity from seagrass systems. Among meadows, variation in species composition and diversity has been reported, though it is not readily explained by abiotic attributes (Carr et al, etc), though a few studies report effects of fetch or some measure of energy (Bostrom et al JEMBE 2006, Robinson et al 2011 for fish in this region), or salinity (Baden).

Here, we test the hypotheses that i) alpha diversity does not vary systematically among meadows, but beta diversity does vary among eelgrass meadows, and ii) spatial variation in species composition is consistent with metacommunity-scale processes structuring biodiversity. To test these hypotheses, we quantified spatial structure in eelgrass-associated epifaunal biodiversity across nine meadows to answer the following questions for a system of discontinuous eelgrass (*Zostera marina*; eelgrasses are seagrasses in the genus *Zostera*) meadows in British Columbia, Canada. When possible, we attempted to test possible biotic and abiotic drivers of biodiversity patterns within and among meadows.

**MATERIALS AND METHODS**

**Study system**

We sampled epifaunal biodiversity in eelgrass *Zostera marina* meadows in Trevor Channel, Barkley Sound, British Columbia, where *Z. marina* is the only meadow-forming seagrass species (Figure 1).  In this region, *Z. marina* forms primarily subtidal, perennial meadows that range in size from < 10 m2 to > 25,000 m2 (Mason et al 2015). *Zostera*, like other seagrasses, hosts a rich faunal assemblage of gastropods, crustaceans and annelids that live on and among the eelgrass blades. These epifauna consume epiphytic algae growing on seagrass, detritus and each other, forming the base of a highly productive food web.

We quantified biotic attributes of eelgrass meadows that could explain variation in eelgrass associated invertebrate biodiversity. We estimated shoot density, leaf area index (LAI), and meadow area. Shoot density and LAI were estimated from four 0.28 m2 quadrats collected outside each corner of a 4 x 4 m grid demarcated for community sampling (described below) in May and August at each of our main sites (i.e., the five sites that we sampled three times; Figure 1, Table 1) concurrently with epifaunal sampling. We removed, dried and weighed eelgrass and its associated epiphytes, and standardized epiphyte mass to eelgrass mass. To estimate LAI, we counted the number of blades per eelgrass shoot and measured the longest blade for length (from top of sheath to tip of blade) and width (at the midpoint). We then multiplied the width and length of the longest blade by the number of blades for each shoot (after Borg et al. 2010).

To quantify meadow-scale abiotic conditions, we monitored temperature and salinity using a hand held temperature/salinity probe (YSI Inc., OH USA). Measurements were taken throughout the tidal cycle on biodiversity sampling days, and opportunistically on other days. Three stations were established at each site representing approximately the center and furthest edges of the largest contiguous meadow. At each station we recorded temperature and salinity at the surface, 2 m below the surface, and directly above the bottom. If the bottom was at 2 m, we only recorded surface and 2 m depth. If the bottom was shallower than 2 m, we recorded the bottom depth and took surface and bottom measurements. No measurements were taken below 5 m or taken in the intertidal zone. We used position in the watershed to represent the estuarine gradient of salinity and temperature. Position was estimated as linear distance in kilometers from the nearest freshwater source (Sarita or Alberni inlet). We estimated fetch by calculating the distance to nearest land from the eelgrass meadow (is there a Gregr ref for this?)

**Biodiversity sampling**

To estimate epifaunal biodiversity and characterize variation within meadows, we used a 4 x 4 m grid of 16 standard plots (0.28 m2), each separated by 1 m, in each meadow (after Sanders 2007). This sampling design allowed for comparison of diversity among plots and meadows while standardizing for total area sampled and the spatial arrangement of samples. We placed sampling grids within contiguous meadows at least 2 m from any meadow edge.  In each plot, we cut away eelgrass at the sediment-water interface and placed it into a 250 µm mesh bag, collecting all eelgrass and epifauna. All sampled areas were at least 1 m below lower low water large tide (LLWLT), and did not vary in depth by more than a meter at any given site. We collected samples using SCUBA, then transported to the lab in seawater, where all invertebrates were removed and preserved in 70% EtOH within 24 hours of collection.

To estimate variation in diversity among meadows, we sampled nine meadows spanning a watershed gradient beginning near the open coast and moving inland towards Alberni Inlet (Figure 1; Table 1).  We chose these meadows among the subset of known meadows in Trevor channel (n ~ 20) because they are evenly distributed along Trevor Channel (Figure 1), they are large meadows (i.e., min 0.25 ha, not fringing), and they capture many of the shallow areas where eelgrass might occur. To determine whether spatial biodiversity patterns varied through time, we sampled five of these meadows three times, in May (early summer, time A), June/July (midsummer, time B) and August (late summer, time C) of 2012 (Table 1).

We sorted invertebrate collections by size into the following fractions: 1-2 mm, 2-4 mm, 4-8 mm, and > 8 mm. We identified every invertebrate > 1mm in each sample to the lowest taxonomic resolution possible using light microscopy. Though many of our identifications are to species level, many other taxa are identified to higher levels (family or order). Each of these groups possibly includes numerous species; consequently our reference to taxa below reflects varying resolution, and our taxonomic diversity estimates should be considered minimum estimates. We did not include egg masses or colony-forming species (e.g., bryozoans) in our analyses. We classified invertebrate species to broad trophic groups (grazer, predator, filter feeder, detritivore) based on our observations and published information (MacDonald et al. 2010, Light and Smith). The grazer functional group includes organisms that consume micro- or macro-algae, including biofilms, growing on eelgrass.

**Biodiversity estimation**

To estimate diversity within and among meadows, we created species-plot and species-site matrices with abundance data for each taxon, using information on every individual collected from each plot (no subsampling; Gotelli and Colwell 2010). We estimated multiple biodiversity metrics: species richness (number of species observed), their relative abundance, and the likelihood that additional taxa were present but unobserved in estimating and comparing biodiversity among samples and meadows. We estimated alpha diversity by rarifying (ENS) and using raw richness values (R), Shannon diversity (H’), and Simpson evenness (S). The effective number of species (ENS) is derived from the probability of an interspecific encounter (PIE), to characterize diversity at the plot scale (Dauby & Hardy 2012). ENS can be interpreted as the number of equally-abundant species that would exist in a sample of a given diversity value (Jost 2006). We used the R package vegan (Oksanen et al. 2013) for biodiversity analyses.

We quantified beta diversity in two ways. First, beta diversity can defined as the difference between alpha and gamma (regional) diversity (Veech oikos). We estimated beta diversity for each meadow by subtracting the mean alpha (R) from the estimated meadow-scale gamma (*chao2? Or just observed?*). Other definitions of beta diversity capture the magnitude of compositional turnover among samples or habitat patches (Anderson et al. 2006, 2010). We estimated variation in species composition and turnover with a Bray-Curtis dissimilarity matrix by measuring multivariate homogeneity of group dispersions (Anderson et al. 2006, 2010). We compared differences among meadows at each sampling period with a permutational test for homogeneity of multivariate dispersions that generated pairwise comparisons based on 999 permutations. This method excludes joint absences and focuses on relative abundance among data sets, and is well suited to zero-rich community data. [*is this accurately capturing the approach for the comparison with the null model?*]

Spatial patterns in beta diversity can be used to infer the possible role of underlying ecological processes that could structure communities in space, or alternatively, can indicate random distributions of species not clearly explained by a particular ecological model (Liebold and Mikkelson 2002). We used a null model to test whether observed patterns of species turnover whether different from an expectation based on random distributions. To generate null models of beta diversity for each meadow, we created a statistical function in the program R (R Core Team 2013) that permutes observed community composition using the *permat* function from the vegan package (Oksanen 2013).  Beta diversity was calculated within each meadow with a Bray-Curtis dissimilarity matrix, and resampled 999 times to generate null expectations based on observed compositions. The resulting mean value of the median was used to represent the expected null value for multivariate dispersion, correcting for underestimation bias (Stier et al. 2013).

**Statistical analyses**

To test our first hypothesis that faunal beta diversity (turnover among samples) varies among meadows but alpha diversity (sample-level species diversity) does not, we used one-way anova on univariate diversity metrics among nine meadows sampled in July (midsummer, time B). To explore possible explanations for variation in diversity within and among meadows, we tested whether spatial patterns in grazer diversity varied with season, distance, biotic and abiotic meadow attributes. We conducted linear regression analyses using sampling date, distance among plots, meadow area, fetch and position in the watershed as predictors. We explored correlations among predictors (*and found that density and LAI also varied along this gradient?).* Abundance and ENS were log-transformed to meet the assumption of homoscedasticity.

Beta and alpha diversity patterns can differ if species are aggregated within meadows (as opposed to randomly distributed throughout the meadow), or if aggregation varies among species and dominance varies among meadows. We estimated aggregation within meadows using standardized Morisita’s index (I), and then compared aggregation scores for species in each meadow with their rank. We specifically asked, *a)* is there aggregation within meadows, is it driven by the most abundant species, and are the most abundant species the same across meadows? (*do species I scores vary among meadows? b) do morisita scores vary with species rank?*.)

To determine whether spatial patterns of biodiversity are consistent with metacommunity processes, we applied the elements of metacommunity (EMS) framework (Leibold and Mikkelson) using the implementation in the R package Metacom (Presley et al). This analysis first tests for coherence in species distributions, random distributions or… If coherence is identified, subsequent tests allow determination of whether patterns are consistent with nested community structures, clementsian or gleasonian (refs). We analyzed metacommunity structure for the 9 meadows sampled in July 2012.

We ranked models using AICc, and compared them using likelihood ratio tests, δaic and Akaike weights (*w*).Models with a δaic < 2 can be considered equivalent to the best model (Burnham & Anderson 2002). In the case of multiple highly ranked models, we selected the set of models that produced a cumulative *w* > 0.95, representing our confidence (95%) that the set includes the best model, and we averaged these models to produce coefficients of effects (Burnham & Anderson 2002).  We examined residual plots for deviations from the assumptions of linearity or homoscedasticity, (*with the exception of parallel lines in a plot of the models’ fitted values vs. residuals*).  This phenomenon resulted from including repeated values of position in the estuary in the model (Searle 1988). We tested hypotheses on a subset of our full dataset - the meadows sampled at all three time points - to conservatively test for an effect of temporal variation. We then repeated the analysis with the full dataset (including the four sites sampled only once).

**RESULTS**

*Biodiversity summary and meadow attributes*

We collected 304 eelgrass samples, and identified of approximately 81,500 epifaunal invertebrates, representing at least 47 epifaunal taxa in 42 families, across the nine eelgrass meadows, five of which were sampled three times (Table 1). We observed between 0 and 1200 individual epifauna per 0.28 m2. The position in watershed predictor captured correlations with other variables: temperature, salinity, shoot density (appendix, table?). Moving from Alberni Inlet to the ocean, meadows increased in shoot densities (0.27 shoots/km) and associated LAI (240.73 cm2/km) (Tables 1, 2; Appendix 2). Shoot density and LAI increased between May and August at the fresher sites but remained relatively high all summer at the seaward meadows (Appendix 2; Tables 1, 2). Epiphyte load was highly variable between meadows, and did not change predictably with position in the estuary (Appendix 2; Tables 1, 2). Epiphyte abundances and the type of epiphytes present (periphyton vs. bladed algae) varied both spatially and temporally (Appendix 3). The bladed brown epiphyte *Punctaria* *sp.* was abundant at two of the marine sites (Dodger Channel and Wizard Islet), and absent from the fresher Numukamis Bay.

Mean total abundance of all taxa at the plot scale did not vary among meadows in May, but did increase over the summer such that by August abundance was 2-3 times higher in seaward meadows (DC, WI, RP) compared to meadows nearer Alberni Inlet in which abundance was stable over time (CB, NB; Tables 2, 3; Figure 2). The seasonal increase in seaward meadows is clear in both the small (1-2 mm) and large (>2 mm) size fractions.

*Hypothesis 1: alpha diversity does not vary systematically among meadows, but beta diversity does vary among eelgrass meadow.* We found that plot-level alpha diversity [R, *ENS?*] differed as much within meadows as among meadows, with the exception of high diversity at Robbers Passage (*anova results*). We observed similar patterns in Shannon diversity (*anova results*) and Simpson diversity (*anova results*). Observed plot-level diversity did / did not vary due to changes in plot-level density ().We did not have plot-level data on other biotic and abiotic attributes (shoot density, temperature, salinity, etc) to test for drivers of variation in alpha diversity among plots. The higher richness of Robbers Passage was not explained by meadow-scale predictors such as position in the watershed, shoot density, meadow area or fetch.

In contrast to the apparent spatial stability of alpha diversity, beta diversity did vary among meadows. *Beta diversity patterns. Then can get into aggregation as one explanation of this.* Aggregation and species rank results (Table 3): Within meadows, there is evidence of spatial aggregation of taxa consistent with clumping of species in space more than expected based on a random spatial distribution of species within the meadow (Figure 3). When the composition of each of the 16 plots is compared with the median composition, the average distance to the median serves as a metric of meadow-scale beta diversity. Average distance to median ranged from 0.20 to 0.49 across all sites and times (Appendix 5). In all cases, observed beta diversity exceeded the null expectation from <1% to >19%, with an average difference of 9.7% (Figure 3, Appendix 5).

We observed slightly higher beta-diversity among plots, suggesting greater spatial aggregation within meadows, in meadows nearer Alberni Inlet (Figure 3). Further, comparing within-meadow estimates of beta diversity across time suggested that beta diversity declined slightly toward the end of the summer (May - 0.33, June/July - 0.34, August - 0.29). However, these trends were not statistically significant. Although beta diversity did not vary predictably along the watershed gradient, a permutation test of multivariate homogeneity of group dispersions showed that meadows did have significantly different values of beta diversity (Appendix 6).

*Hypothesis ii: spatial variation in species composition is consistent with metacommunity-scale processes structuring biodiversity*

*Composition: NMDS results, include temporal dimension.*

*Summarize general composition: dominance Table 3.* Of these, 24 taxa are herbivorous or omnivorous consumers of epiphytic algae, and therefore belong to the functional group “grazers” (Appendix 1). These comprised approximately 72% of all individuals; and 6.0 (± 0.15) grazer taxa (isopods, harpacticoid copepods, amphipods, and gastropods) were detected on average in each meadow. Grazers include (Appendix 1). Other functional groups include predators (polychaetes, crabs, free-living mites, two species of amphipod), filter feeders (bivalves), and deposit feeders/detritivores (shrimp). Across all samples, epifaunal assemblages were dominated by small (1-2 mm) invertebrates, which made up ~83% of individuals, whereas large invertebrates (> 8 mm) such as crabs, sea stars and urchins made up less than 3% of individuals.

Extending the comparisons to across meadows, we found that samples collected within meadows were typically more similar to samples from the same meadow than to samples from other meadows, suggesting meadow-scale aggregation and similarity in faunal assemblages (Figure 4). This species turnover among meadows was driven by both shifts in relative abundance, and by species turnover (Figure 4). Although many species were rare but present at most sites and times, no species was common everywhere at all times. Five taxa were detected at every site and sampling time (the grazers *Pentidotea resecata*, *Caprella* spp., and *Aoroides* *columbiae*; the predator *Eogammarus confervicolus*; and the filter-feeding *Mytilus trossulus*), and eight additional taxa were detected at all sites but one. Conversely, four species were only detected at one time and place (*Alia carinata* at BI, *Strongylocentrotus* sp.at WI, *Solaster* sp.at CB, and *Dinophilus* sp. at DC; Appendix 1), and eight taxa were observed only twice. Whether a species was present at a site was fairly consistent through time. For example, *Photis brevipes*, *Pontogeneia* sp., *Platynereis bicanaliculata* and *Lacuna* sp. were not observed at Crow Cove at any of the three sampling times (48 samples in total).

Across all meadows, five taxa accounted for > 80% of invertebrates collected: the caprellid amphipods *Caprella* spp. (*C. laeviuscula* and *C. californica*), the sea hare *Phyllaplysia taylori* (primarily juveniles), the mussel *Mytilus trossulus* (primarily juveniles), the polychaete worm *P*. *bicanaliculata*, and the sea spider *Pycnogonum* sp.  However, the abundances of these species were not consistently high across all meadows and all sampling periods.  For example, in the midsummer sampling period the number of caprellids ranged from 488 individuals/plot in Numukamis Bay to less than 0.1 individual/plot at Ellis Island.

NMDS visualization reveals a community dominated by epiphyte grazers (*Caprella spp*., amphipods *A. columbiae, P*. *brevipes*, the isopod *Pentidotea resecata,* the sea hare *P. taylori*) in meadows toward the ocean end of Trevor Channel, and a community dominated by filter feeders (primarily mussels), *Pycnogonum* sp. and nematodes at meadows toward the Inlet (Figure 4). These differences are conserved through time, except at Wizard Islet (which resembled marine sites until a major recruitment of mussels in July; Figure 4).

The identity of dominant taxa varied through time. We observed large temporal changes in the abundance of many common species: for example, *Caprella* spp. abundance increased more than ten-fold (from an average of 16 individuals/plot to 237 individuals/plot) from early to mid-summer, but by late summer a recruitment event of *P. taylori* let this species to outnumber *Caprella* spp*.* at Robbers Bank and Dodger Channel (at the marine end of the estuary).  However, these changes in abundance were not consistently observed across sites. For example, the *P. taylori* recruitment event occurred at two sites, while a major mussel recruitment event occurred at other sites including Numukamis Bay and Crickitt Bay later during the same period.

The grazer species composition varied among meadows. *Pentidotea resecata*, amphipods *A. columbiae* and *Caprella* spp.*,* were observed in every meadow (Appendix 1), but tended to be less abundant in the meadows nearer Alberni Inlet. The eelgrass specialist *P. taylori* was not observed in every meadow (e.g., never at CC, and only 2 individuals observed at NB), but numerically dominated the fauna in some meadows (DC, RP and EI).

*EMS results*

**DISCUSSION**

We found that invertebrate biodiversity and abundance observed associated with foundation species can vary substantially between habitat patches and over the course of a season. A watershed gradient of salinity and eelgrass shoot density did not explain variation in alpha (meadow-scale) diversity or species turnover among meadows. However, differences in species composition suggest that meadows nearer the ocean in Trevor Channel host grazer-dominated assemblages, while meadows nearer Alberni Inlet are dominated by filter feeders and other non-grazer taxa. This pattern suggests oceanographic circulation and dispersal among meadows might play a role in influencing species composition, even in the absence of clear trends in total diversity and a continuous effect of salinity, temperature or shoot density on total diversity.

Estimated species richness at the meadow scale varied by a factor of four from 13 to 53 species, and plot-level invertebrate abundance ranged over three orders of magnitude. However, we emphasize again that because we did not identify every individual to species, our estimates of diversity are minimums and the true diversity in these meadows is likely higher.

**Spatial variation in biodiversity**

Contrary to our expectations, we did not observe a clear signal of continuous variation in biodiversity along the biotic and abiotic gradients associated with the watershed. The lack of a clear signal of salinity in the epifaunal community contrasts with previous findings in other seagrass systems. Barnes (2013) found that invertebrate assemblages in an extensive seagrass meadow in Knysna Bay (South Africa) respond strongly to estuarine gradients, with significant reductions in species diversity and richness at the fresh end of the estuary.  Yamada et al (2007) also found a positive relationship between salinity and invertebrate diversity. In contrast, we observed only weak, temporally inconsistent trends in invertebrate abundance and diversity with estuarine position (correlated with salinity and eelgrass structure).  However, the sites sampled by Barnes (2013) and Yamada et al. (2007) spanned a greater range in salinity (< 5 - 35 ppt and 6.2 – 32.2 ppt, respectively) than did ours (~14 - 28 ppt), and may have captured physiologically stressful, low-salinity conditions with a stronger influence on invertebrate assemblages.

Variation in species diversity at the plot- or meadow-scale could also be explained by meadow area. Larger meadows would be expected to host more species per area than smaller meadows. We only have area estimates for five of the meadows we sampled, and the low sample size (n = 5) and low variation in meadow area prevent robust statistical analysis of area as a predictor. Numukamis Bay (NB) was by far the largest meadow (72 ha), while the others were on the order of <1 to several hectares (Table 1). However, species diversity patterns do not suggest vastly greater species richness in NB than other sites, nor are there fewer species at the smallest (< 1 ha) meadows (Figure 2). Further, average plot scale diversity (7-20 species, Figure 3) and meadow-scale alpha diversity (Chao2 index estimate: 28 species per meadow) was in all cases much lower than regional species diversity (gamma diversity = 47 observed taxa), suggesting that some processes limit the presence of all regionally-present taxa in all meadows.

Despite the absence of a clear signal of an abiotic gradient or meadow area effect, we were able to distinguish between the composition of invertebrate assemblages at the marine and fresh ends of the estuary (Figure 4). Invertebrate assemblages in meadows including and to the southwest of Robber’s Passage (at the marine end of the estuary) tended to clump together in the NMDS similarity plot (Figure 4), and were dominated by grazers (amphipods, caprellids, the sea hare *Phyllaplysia taylori*). At the northeast (fresh) end of the estuary, invertebrate assemblages were dominated by juvenile mussels and nematodes. The one exception to this pattern was the invertebrate assemblage at WI, which showed a composition intermediate to those of the more marine and freshwater meadows despite its position at the marine end of the estuary (Figure 4). The emergence of two invertebrate assemblages associated with spatial areas in Trevor Channel could be explained by differences in connectivity, or meadow-to-meadow colonization and movement, within the two regions of Trevor Channel. The position of the break in species composition corresponds to a large sill in the bottom of Trevor Channel, at which the bottom depth rises to only 30 m from approximately 200 m. This sill could restrict mixing between the seaward and upstream ends of the Channel. Restricted exchange of water could be associated with distinct abiotic properties that influence species’ ability to persist or dominate in these environments. An alternate explanation is that population connectivity could be reduced between these two regions, such that meadows within one of the regions are more demographically connected and therefore more similar in composition than meadows in the other region.

Like alpha diversity metrics, beta diversity did not vary predictably along the watershed gradient. However, our results show that non-directional beta diversity is significantly greater than expected by chance (Figure 3), suggesting aggregation of species within meadows is greater than expected at random. Spatial aggregation within meadows can indicate micro-habitat variation, species interactions such as competition, predation or facilitation, or historical effects such as recovery from disturbance. Despite this signal of aggregation, suggesting species turnover within meadows over fine scale, we observed greater turnover in composition among meadows than within meadows. Greater turnover among meadows could, again, reflect either spatial distance among samples, variation in meadow-scale properties (properties not measured in this study), connectivity, asynchronous community trajectories, or historical events such as disturbance and associated recovery.

To date, there are only a few other beta diversity estimates for seagrass-associated epifauna with which to compare our findings. These studies have typically focused on directional beta diversity, i.e., beta diversity along some gradient.  Previous research has shown that beta diversity in seagrass beds can be driven by variation in salinity, seagrass species, tidal height, and sub-habitat type (e.g., seagrass shoots or sediment; Barnes and Ellwood 2012, De Troch et al. 2001, De Troch et al. 2003, Knight et al. 2015). However, we know very little about non-directional beta diversity within seagrass meadows, and (to our knowledge) no study has attempted to distinguish observed patterns in beta diversity from null expectations (Kraft et al. 2011).  The comparison of null expectations to empirical datasets allows us to infer whether random processes such as chance colonization and extinction, or deterministic processes like environmental filtering or competition are generating observed patterns in community composition (Chase and Myers 2011).

Eelgrass meadows are known for their ability to support a high diversity of fish species (Robinson et al. 2011, Robinson & Yakimishyn 2008). In British Columbia, over 80 fish species occur in eelgrass meadows (Robinson & Yakimishyn 2008). However, not all eelgrass meadows support the same fish assemblages (Robinson et al. 2011), and salinity is one abiotic driver of differences in fish assemblage composition. Though we did observe differences in species assemblages of fish across the meadows, there was no clear correlation between fish composition or diversity and invertebrate abundance or diversity. One limitation to this test in our study is the limited sampling effort for fish diversity and thus low sample sizes. Based on other reports from the region, there likely were many more fish species in these meadows that we missed, and we consequently limit our inferences on fish as a driver of invertebrate composition at this time.

**Temporal trends**

Temporal variation in abundance and diversity within meadows balanced in magnitude the variation we observed over 30 km and nine distinct meadows. Rather than a directional seasonal in abundance or diversity within meadows, these metrics tended to peak in mid-summer (July) and decline again in August. Despite the observed variation, there was no clear overall directional trend through time (Table 3). Dominant species did shift through time, within meadows. These shifts through time reflected recruitment events of several species, notably *Phyllaplysia taylori* and *Mytilus trossulus*. Local reproductive events by the non-dispersing offspring of *P. taylori* dominated the marine sites RP and DC in August. At other sites, planktonic dispersing larvae of mussels colonized and dominated eelgrass assemblages. These trends suggest that reproductive events, regardless of dispersal type, characterize seasonal trends in epifauna diversity and abundance between May and August in this system. Other taxa shifted in abundance substantially, including an increase in nematode abundance at NB between May and July. Grazer taxa such as amphipods and isopods with continuous population dynamics and overlapping generations increased between May and July at all sites except NB. This latter pattern suggests some site-level factors such as food availability, seasonal warming, or reduction in predation between May and July that was then reversed in DC, CB and NB by August. Despite this variation in univariate metrics and the identities of dominant species, multivariate metrics suggested composition overall was relatively stable through time, suggesting that the differences in abundance and richness are reflecting changes in dominance (Figure 4).

The temporal patterns we observed are different from patterns reported epifauna in eelgrass meadows in the east coast of North America. In those systems, grazer and invertebrate abundance and diversity peaks in winter, and from May declines substantially until grazers are virtually absent in late summer (Nelson 1979). This trend has been attributed to seasonal fish predation that intensifies in June each year. In Chesapeake Bay eelgrass systems, epifaunal grazers remain relatively stable in abundance between May and August, though their relative abundance shifts from *Caprella* and *Gammarus* dominated assemblages to the amphipod *Erichsonella attenuata* (Douglass et al. 2010). Our observations are consistent with other reports of seasonal variation in epifaunal assemblages from Puget Sound, WA, showing increasing abundance of grazers (*P. resecata*, *Lacuna* sp., and *Caprella* sp.) between May and late summer (Thom et al. 1995). Best and Stachowicz (2014) also report peak abundance of epifaunal taxa in August, and that peak abundance can vary among habitat patches. These patterns are not clearly consistent with a major seasonal change in predation pressure in this system, despite fish assemblages that include seasonal juveniles (Robinson et al 2011).

**Conclusions**

Understanding spatial and temporal variation is essential to linking the abiotic and biotic features of a marine seascape to the ecosystem functions that promote biodiversity as well as secondary productivity that emerges at higher trophic levels including fish, wading birds, and marine mammals.  Although biodiversity patterns in seagrass meadows have been to date quantified primarily within individual, discrete meadows, many of the processes that influence these patterns, including potentially damaging processes such as eutrophication, the introduction of non-native species, and severe weather, operate across much larger spatial scales (Duarte 2002).  This disconnect between sampling scale and the spatial extent of disturbance has been shown to lead to conflicting and misleading conclusions about the effects of disturbance on ecosystems, particularly with respect to changes in local population persistence and species richness (Powell et al. 2013).  As anthropogenic pressure on valuable coastal ecosystems continues to accelerate, it is more important than ever that we develop a baseline understanding of how biodiversity in seagrass meadows is maintained across ecologically relevant scales. This study represents one of the first comprehensive assessments of eelgrass-associated biodiversity in the Pacific Northwest, and is perhaps the most comprehensive assessment and analysis of eelgrass-associated biodiversity on Vancouver Island.

We have shown here that species diversity and abundance vary among seagrass meadows within a region, and that the variation is not clearly predictable based on an estuarine gradient and related predictors. Although *Z. marina* provides relatively homogenous habitat, *Z. marina* meadows host distinct communities, and each appears to host a subset of epifaunal species observed in the larger region. These patterns are indicative of a metacommunity system, and suggest that the processes that maintain diversity in eelgrass communities may reflect a seascape of many meadows connected through dispersal. If true, then conservation of eelgrass systems will require a network approach that preserves numerous meadows within the region. Examining biodiversity patterns across a seascape has expanded our view of seagrass biodiversity, and additional research is required to meet the challenges of understanding how spatial turnover in diversity is related to the function and resilience of these ecosystems.

**[outtakes from intro that might be useful here:** The diversity and composition of epifaunal grazers can influence ecosystem functions, including resilience to disturbance and control of algal epiphytes (Blake & Duffy 2012, Duffy et al. 2003, Duffy et al. 2015, Eklöf et al. 2012). Diversity of epifaunal grazers (algae-consumers) has been shown to stabilize trophic processes in seagrass meadows, with the additional effect of controlling epiphytic algal abundance and facilitating seagrass growth (Hughes et al. 2004). However, grazers are often analyzed as part of a larger pool of invertebrates that includes predators and detritivores, in large part because the natural history of many of these invertebrates is not well documented and consequently it is difficult to separate species into trophic groups. As a result, we have a limited understanding of how grazers vary in their distribution and abundance, and what proportion of invertebrates is actually contributing to algal consumption in seagrass meadows.

Seagrass habitat is considered an indicator of high biodiversity for assessments and prioritization schemes (Shokri & Gladstone 2013), yet seagrass-associated epifaunal diversity can vary substantially over relatively fine spatial and temporal scales (Boström et al. 2010, Carr et al. 2011, Robinson et al. 2011, Nelson 1979).  Seagrass meadows exist in discrete patches that range over several orders of magnitude in size (Mason et al. 2015), and are often separated by physical barriers such as deep water, fast currents, rocky substrates and human developments. Many factors can drive variation in diversity within meadows, including predation (Amundrud et al. 2015, Huang et al. 2015, Nelson 1979), productivity (De Troch et al. 2006), seagrass shoot density and phenotype (McCloskey & Unsworth 2015), and the regional species pool (Duffy et al. 2015, France & Duffy 2006). At the seascape scale, meadow size and abiotic factors including salinity (Yamada et al. 2007, Robinson et al. 2011), temperature (Barnes & Ellwood 2012), and connectivity (movement) among meadows (Boström et al. 2010, Tanner 2003) also influence biodiversity. ]

Patterns of species diversity and composition across scales reflect the distribution of individuals within species across space. A nearly-universal pattern in ecological communities is the rank-abundance distribution, or the pattern in which few species are common and most are rare. Another ubiquitous pattern is that of intraspecific aggregation in space. Together, these two attributes of how individuals are distributed in the environment mean that diversity at fine spatial scales – several orders of magnitude of the body size of individuals – can be decoupled from diversity at broader spatial scales over an environmental or spatial gradient.

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LITERATURE CITED

Altieri AH, Witman JD (2014) Modular mobile foundation species as reservoirs of

biodiversity.  Ecosphere 5:124

Amundrud SL, Srivastava DS, O’Connor MI (2015) Indirect effects of predators control herbivore

richness and abundance in a benthic eelgrass (*Zostera marina*) mesograzer community.  J Anim Ecol 84:1092-1102

Anderson MJ, Ellingsen KE, McArdle BH (2006) Distance-based test for homogeneity of

multivariate dispersions. Biometrics 62:245-253

Anderson MJ, Crist TO, Chase JM, Vellend M, Inouye BD, Freestone AL, Sanders NJ, Cornell HV,

Comita LS, Davies KF, Harrison SP, Kraft NJB, Stegen JC, Swenson NG (2010) Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. Ecol Lett 14:19-28

Angelini C, van der Heide T, Griffin JN, Morton JP, Derksen-Hooijberg M, Lamers LPM, Smolders AJP, and Silliman BR (2015) Foundation species’ overlap enhances biodiversity and multifunctionality from the patch to landscape scale in southeastern United States salt marshes. Proc Roy Soc B 282: 20150421

Azaele, S., Maritan, A., Cornell, S.J., Suweis, S., Banavar, J.R., Gabriel, D., and Kunin, W.E. 2015. Towards a unified descriptive theory for spatial ecology: Predicting biodiversity patterns across spatial scales. Methods in Ecology and Evolution. 6(3): 324-332. doi:10.1111/2041-210X.12319

Backman TWH (1991) Genotypic and phenotypic variability of *Zostera marina* on the west coast of

North America.  Can J Bot 69:1361-1371

Barnes RSK (2013) Distribution patterns of macrobenthic biodiversity in the intertidal seagrass beds

of an estuarine system, and their conservation significance.  Biodivers Conserv22:357-372

Barnes RSK, Barnes MKS (2011) Hierarchical scales of spatial variation in the smaller surface and

near-surface macrobenthos of a subtropical intertidal seagrass system in Moreton Bay,

Queensland.  Hydrobiologia673:169-178  
Barnes RSK, Ellwood MDF (2012) Spatial variation in the macrobenthic assemblages of intertidal

seagrass along the long axis of an estuary.  Estuar Coast Shelf S112:173-182

Best RJ, Stachowicz JJ (2014) Phenotypic and phylogenetic evidence for the role of food and

habitat in the assembly of communities of marine amphipods. Ecology 95: 775-786

Bishop MJ, Byers JE, Marcek BJ, Gribben PE (2012) Density-dependent facilitation cascades

determine epifaunal community structure in temperate Australian mangroves. Ecology 93:1388-1401

Blake RE, Duffy JE (2012) Changes in biodiversity and environmental stressors influence

community structure of an experimental eelgrass (*Zostera marina*) system. Mar Ecol Prog Ser 470:41-54

Borg JA, Rowden AA, Attrill MJ, Schembri PJ, Jones MB (2010) Spatial variation in the composition

of motile macroinvertebrate assemblages associated with two bed types of the seagrass *Posidonia oceanica.*  Mar Ecol Prog Ser 406:91-104

Boström C, Tomroos A, Bonsdorff E (2010) Invertebrate dispersal and habitat heterogeneity:

Expression of biological traits in a seagrass landscape.  J Exp Mar Biol Ecol 390:106-117

Bracken MES, Bracken BE, Rogers-Bennett L (2007) Species diversity and foundation

species: Potential indicators of fisheries yields and marine ecosystem functioning. California Cooperative Oceanic Fisheries Investigations Reports 48:82-91

Burnham KP, Anderson DR (2002) Model selection and multimodel inference. Springer-Verlag New York, NY

Byers JE, Cuddington K, Jones CG, Talley TS, Hastings A, Lambrinos JG, Wilson WG (2006) Using ecosystem engineers to restore ecological systems. Trends Ecol Evol 21:493-500

Carr LA, Boyer KE, Brooks AJ (2011) Spatial patterns of epifaunal communities in San Francisco Bay eelgrass (*Zostera marina*) beds. Mar Ecol-Evol Persp 32:88-103

Chao A, Bunge J (2002) Estimating the number of species in a stochastic abundance model.

Biometrics 58:531-539

Chase JM, Myers JA (2011) Disentangling the importance of ecological niches from stochastic

processes across scales.  Philos T Roy Soc B 366:2351-2363

Colwell RK, Coddington JA (1994) Estimating terrestrial biodiversity through extrapolation.  Philos T Roy Soc B345:101-118

Crist TO, Veech JA (2006) Additive partitioning of rarefaction curves and species-area relationships: unifying α-, β-, and γ-diversity with sample size and habitat area. Ecol Lett 9:923-932

Dauby G, Hardy OJ (2012) Sampled-based estimation of diversity *sensu stricto* by transforming

Hurlbert diversities into effective number of species.  Ecography35:661-672

Dayton PK (1972) Toward an understanding of community resilience and the potential effects of

enrichments to the benthos at McMurdo Sound, Antarctica. Proceedings of the Colloquium on Conservation Problems 81–96. Allen Press, Lawrence, Kansas

De Troch M, Van Gansbeke D, Vincx M (2006) Resource availability and meiofauna in sediment of tropical seagrass beds: Local versus global trends. Mar Environ Res 61:59-73

De Troch M, Fiers F, Vincx M (2003) Niche segregation and habitat specialisation of harpacticoid

copepods in a tropical seagrass bed.  Mar Biol 142:345-355

De Troch M, Fiers F, Vincx M (2001) Alpha and beta diversity of harpacticoid copepods in a

tropical seagrass bed: the relation between diversity and species’ range size distribution. Mar Ecol Prog Ser 215: 225-236

Douglass JG, France KE, Richardson JP, Duffy JE (2010) Seasonal and interannual change in a

Chesapeake Bay eelgrass community: Insights into biotic and abiotic control of community structure. Limnol Oceanogr 55:1499-1520

Douglass JG, Duffy JE, Canuel EA (2011) Food web structure in a Chesapeake Bay eelgrass bed as determined through gut contents and C-13 and N-15 isotope analysis. Estuar Coast 34:701-711

Duarte CM (2002) The future of seagrass meadows. Environ Conserv 29:192-206

Duffy JE, Canuel EA, Richardson JP (2003) Grazer diversity and ecosystem functioning in seagrass beds. Ecol Lett 6:637-645

Duffy JE, Reynolds PL, Boström C, Coyer JA, Cusson M, Donadi S, Douglass G, Eklöf JS, Engelen AH, Eriksson BK, Fredriksen S, Gamfeldt L, Gustafsson C, Hoarau G, Hori M, Hovel K, Iken K, Lefcheck JS, Moksnes P, Nakaoka M, O’Connor MI, Olsen JL, Richardson JP, Ruesink JL, Sotka EE, Thormar J, Whalen MA, Stachowicz JJ (2015) Biodiversity mediates top–down control in eelgrass ecosystems: a global comparative-experimental approach.  Ecol Lett 18:696-705

Edgar GJ, Shaw C (1995) The production and trophic ecology of shallow-water fish assemblages

in southern Australia .3. General relationships between sediments, seagrasses, invertebrates and fishes.  J Exp Mar Biol Ecol 194:107-131

Eklöf JS, Alsterberg C, Havenhand JN, Sundbäck K, Wood HL, Gamfeldt L (2012)

Experimental climate change weakens the insurance effect of biodiversity. Ecol Lett, 15:864–872

France KE, Duffy JE (2006) Diversity and dispersal interactively affect predictability of ecosystem function. Nature 441:1139-1143

Gaston KJ 2000. Global patterns in biodiversity. Nature 405(6783): 220-227. doi:10.1038/35012228

Gedan KB, Kellogg L, Breitburg DL (2014) Accounting for multiple species in oyster reef

restoration benefits. Restor Ecol 22:517-524

Gotelli NJ, Colwell RK (2010) Estimating species richness. In: Magurran AE, McGill BJ (eds)

Biological Diversity: Frontiers in Measurement and Assessment. Oxford University Press, Oxford 39-54

Government of Canada (2010) Canadian Climate Normals: Bamfield East.

<http://climate.weather.gc.ca/climate_normals/results_1981_2010_e.html?stnID=231&lang=e&amp;StationName=Bamfield&amp;SearchType=Contains&amp;stnNameSubmit=go&dCode=5&dispBack=1>  (accessed 7/20/2015)

Haegele CW (1997) The occurrence, abundance, and food of juvenile herring and salmon in the

Strait of Georgia, British Columbia, in 1990 to 1994. Retrieved from the Department of Fisheries and Oceans Canada website: http://www.dfo-mpo.gc.ca/library/224393.pdf

Hansen JCR, Reidenbach MA (2013) Seasonal growth and senescence of a *Zostera marina* seagrass

meadow alters wave-dominated flow and sediment suspension within a coastal bay.  Estuar Coast 36:1099-1114

Heck KL, Wetstone GS (1977) Habitat complexity and invertebrate species richness and

abundance in tropical seagrass meadows. J Biogeogr 4:135-142

Huang AC, Essak M, O’Connor MI (2015) Top-down control by great blue herons *Ardea heroditas*

regulates seagrass-associated epifauna. OikosOnline (accessed 7/27/2015)

Hughes AR, Bando KJ, Rodriguez LF, Williams SL (2004) Relative effects of grazers and nutrients

on seagrasses: a meta-analysis approach. Mar Ecol Prog Ser 282:87-99

Idjadi JA, Edmunds PJ (2006) Scleractinian corals as facilitators for other invertebrates on a

Caribbean reef. Mar Ecol Prog Ser 319:117-127

Irving AD, Bertness MD (2009) Trait-dependent modification of facilitation on cobble beaches.

Ecology 90:3042-3050

Jackson EL, Rowden AA, Attrill MJ, Bossey SJ, Jones MB (2001) The importance of seagrass

beds as a habitat for fishery species.  Oceano Mar Biol 39:269-303

Jost L (2006) Entropy and diversity.  Oikos 113:363-375

Knight NS, Prentice C, Tseng M, O’Connor MI (2015) A comparison of epifaunal invertebrate

communities in native eelgrass *Zostera marina* and non-native *Zostera japonica* at Tsawwassen, BC.  Mar Biol Res 11:564-571

Kraft NJB, Comita LS, Chase JM, Sanders NJ, Sweson NG, Crist TO, Stegen JC, Vellend M,

Boyle B, Anderson MJ, Cornell HV, Davies KF, Freestone AL, Inouye BD, Harrison SP, Myers JA (2011) Disentangling the drivers of beta diversity along latitudinal and elevational gradients.  Science 333:1755-1758

Lannin R, Hovel K (2011) Variable prey density modifies the effects of seagrass habitat structure on

predator-prey interactions. Mar Ecol Prog Ser 442:59-70

Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB,

Law R, Tilman D, Loreau M, Gonzalez A (2004) The metacommunity concept: a framework for multi-scale community ecology. Ecol Lett 7:601-613

Macdonald TA, Burd BJ, Macdonald VI, van Roodselaar A (2010) Taxonomic and feeding

guild classification for the marine benthic macroinvertebrates of the Strait of Georgia, British Columbia. Canadian Technical Report of Fisheries and Aquatic Sciences 2874

Mason B, Knight R, Boyer L (2015) Community mapping network.

<http://cmnmaps.ca/EELGRASS/> (accessed 7/15/2015)

McCloskey RM, Unsworth RKF (2015) Decreasing seagrass density negatively influences associated

fauna.  PeerJ 3:e1053

McFarlane GA, Ware DM, Thomson RE, Mackas DL, Robinson CLK (1997) Physical, biological

and fisheries oceanography of a large ecosystem (west coast of Vancouver Island) and implications for management. Oceanol Acta 20:191-200

Nagelkerken I, Blaber SJM, Bouillon S, Green P, Haywood M, Kirton LG, Meynecke JO, Pawlik J,

Penrose HM, Sasekumar A, Somerfield PJ (2008) The habitat function of mangroves for terrestrial and marine fauna: A review.  Aquat Bot 89:155-185

Nelson WG (1979) An analysis of structural pattern in an eelgrass (*Zostera marina* L.) amphipod community. J Exp Mar Biol Ecol 39:231-264.

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O’Hare RB, Simpson GL, Solymos P,

Stevens MHH, Wagner H (2013) vegan: Community Ecology Package. R package version

2.0-10

Pawlowicz R (2013) Barkley Sound Time Series.

<http://www.eos.ubc.ca/~rich/BSTS/bark_home.html> (accessed 7/20/2015)

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2014) nlme: Linear and Nonlinear Mixed

Effects Models. R package version 3.1-118

Powell KI, Chase JM, Knight TM (2013) Invasive plants have scale-dependent effects on diversity

by altering species-area relationships. Science 339:316-318

R Core Team (2013) R: A language and environment for statistical computing. R Foundation for

Statistical Computing, Vienna, Austria. URL: <http://www.R-project.org/>

Ricklefs, R.E. 2004. A comprehensive framework for global patterns in biodiversity. Ecology Letters. 7(1): 1-15. doi:10.1046/j.1461-0248.2003.00554.x

Robinson CLK, Yakimishyn J (2008) Monitoring for the ecological integrity of eelgrass beds *(Zostera marina*)in Canada’s coastal national parks of British Columbia. Western and Northern Service Centre Technical Report

Robinson CLK, Yakimishyn J, Dearden P (2011) Habitat heterogeneity in eelgrass fish assemblage diversity and turnover. Aquat Conserv 21:625-635

Robinson CLK, Yakimishyn J (2013) The persistence and stability of fish assemblages with eelgrass meadows (*Zostera marina*) on the Pacific coast of Canada. Can J Fish Aquat Sci 70:775-784

Sanders NJ, Lessard JP, Fitzpatrick MC, Dunn RR (2007) Temperature, but not productivity or

geometry, predicts elevational diversity gradients in ants across spatial grains. Global Ecol Biogeogr 16:640-649

Schindler, D.E., Armstrong, J.B., and Reed, T.E. 2015. The portfolio concept in ecology and evolution. Frontiers in Ecology and the Environment. 13(5): 257-263. doi:10.1890/140275

Searle SR (1988) Parallel lines in residual plots.  Am Stat42:211-211

Shokri MR, Gladstone W (2013) Limitations of habitats as biodiversity surrogates for conservation planning in estuaries.  Environ Monit Assess 184:3477-3492

Stier AC, Geange SW, Hanson KM,  Bolker BM (2013) Predator density and timing of arrival affect reef fish community assembly. Ecology 94, 1057–1068

Sturaro N, Lepoint G, Perez-Perera A, Vermeulen S, Panzalis P, Navone A, Gobert S (2014)

Seagrass amphipod assemblages in a Mediterranean marine protected area: a multiscale approach.  Mar Ecol Prog Ser 506:175-192

Sutherland TF, Elner RW, O’Neill JD (2013) Roberts Bank: Ecological crucible of the Fraser

River estuary.  Prog Oceanogr 115:171-80

Tanner JE (2003) Patch shape and orientation influences on seagrass epifauna are mediated by

dispersal abilities. Oikos 100:517-524

Thom R, Miller B, Kennedy M (1995) Temporal patterns of grazers and vegetation in a temperate seagrass system. Aquat Bot 50:201-205

Thomson RE (1981) Oceanography of the British Columbia Coast. Canadian Special Publications of Fisheries and Aquatic Sciences 56, 291pp.

Tuomisto H (2010) A diversity of beta diversities: straightening up a concept gone awry.  Part 1.  Defining beta diversity as a function of alpha and gamma diversity.  Ecography 33:2-22

van Katwijk MM, Bos AR, de Jonge VN, Hanssen LSAM, Hermus DCR, de Jong DJ (2009)

Guidelines for seagrass restoration: Importance of habitat selection and donor population, spreading of risks, and ecosystem engineering effects. Mar Pollut Bull 58:179-188

Veech JA, Crist TO (2010) Toward a unified view of diversity partitioning. Ecology91:1988-1992

Vizzini S, Sara G, Michener RH, Mazzola A (2002). The role and contribution of the seagrass

*Posidonia oceanica* (L.) Delile organic matter for secondary consumers as revealed by carbon and nitrogen stable isotope analysis. Acta Oecol 23:277-285

Waycott M, Duarte CM, Carruthers TJB, Orth RJ, Dennison WC, Olyarnik S, Calladne A,

Fourqurean JW, Heck KL, Hughes AR, Kendrick GA, Kenworthy WJ, Short FT, Williams SL (2009) Accelerating loss of seagrasses across the globe threatens ecosystems. P Natl Acad Sci USA 106:12377-12361

Williams SL (2007) Introduced species in seagrass ecosystems: Status and concerns. J Exp Mar Biol

Ecol 350:89–110

Williams SL, Ruckelshaus MH (1993) Effects of nitrogen availability and herbivory on eelgrass

(*Zostera marina*) and epiphytes. Ecology 74:904-918

Wonham M, Carlton J (2005) Trends in marine biological invasions at local and regional scales: The Northeast Pacific Ocean as a model system. Biol Invasions 7:369–92

Yamada K, Hori M, Tanaka Y, Hasegawa N, Nakaoka M (2007) Temporal and spatial macrofaunal community changes along a salinity gradient in seagrass meadows of Akkeshi-ko estuary and Akkeshi Bay, northern Japan. Hydrobiologia 592:345-358