Title: Grazer dominance of eelgrass epifaunal communities increases along a watershed gradient in a clementsian faunal metacommunity

Patterns of biodiversity reflect processes operating across local and regional scales, creating complex relationships between habitats, biodiversity and their functional relationship across landscapes. In metacommunities, local communities are structured by species interactions, resource supply, or abiotic stress, but effects of local processes on biodiversity patterns across a landscape depend on their context within networks of communities linked by dispersal. *Problem statement*: Our aim was to determine the spatial scales over which biodiversity and functional traits of eelgrass-associated epifaunal assemblages vary in a coastal marine system to support a broader understanding of the scale of processes that determine community structure and ecosystem function in these systems. We used a hierarchical field sampling scheme to test the hypothesis that faunal biodiversity associated with the foundation species *Zostera marina* show patterns of overdispersion within meadows consistent with local species interactions, but among meadows vary with abiotic conditions related to position along a watershed gradient. We collected 16 eelgrass samples from each of 9 subtidal meadows across a watershed gradient in Barkely Sound, British Columbia. We found non-random diversity patterns within and among meadows, consistent with fine-scale negative species interactions and coherent species turnover among meadow-scale species assemblages. Meadow-scale variation is consistent with Clementsian metacommunity structure along a gradient shared by taxa in the community, though this gradient is not consistent with gradients in meadow size or estuarine position. Two types of faunal assemblage emerged: a ‘grazer-dominated’ species assemblage in more marine meadows, and a ‘grazer-detritovore’ assemblage in meadows nearer the freshwater source. In eelgrass fauna, localized negative interactions within meadows appear to give way to regional-scale drivers of biodiversity such as abiotic conditions related to productivity, energy flow and abiotic conditions across sets of meadow clusters. Potentially large functional differences among meadow epifaunal communities, such as the numerical dominance of grazer taxa, may have minimal effects on presence-absence based community indices in a system with likely high dispersal among meadows. These patterns highlight a multi-scale nature to biodiversity and its conservation in this coastal marine system.

[we can use the edgar method to estimate biomass of grazers as an indicator of potential energy flow and productivity?]

**Introduction:**

How are marine faunal communities structured in space? Small animals living in structured spaces – insects in bracken, infauna in sediments, epifauna in plants…; use the foundation species but their abundance in space and time also reflects demographic processes and their responses to biotic and abiotic attributes of the habitat patch of the foundation species. These faunal assemblages often form metacommunities, or sets of local communities connected by dispersal. In metacommunities, biodiversity patterns at local and regional scales are determined both by local factors (species interactions, abiotic and biotic conditions) as well as the regional environment and conditions for dispersal. In metacommunities, regional biodiversity is often more stable over time due to dispersal dynamics, even when local communities experience substantial variation or disturbance in biodiversity.

There are several types of metacommunities, reflecting a different relative importance of the underlying metacommunity processes. Species sorted, mass effects, etc. Despite a growing theory of metacommunity ecology, applying this theory to empirical observations has been extraordinarily difficult. One solution is to identify patterns consistent with the underlying processes, and infer from these patterns the likely structuring dynamics. These patterns include random, nested, gleasoninan, clementsian, etc.

Biodiversity in coastal marine systems is largely associated with foundation species such as seagrass, corals, and kelp. Seagrass meadows host vast biodiversity that fuels immense secondary production (fish food), and has become a model system for testing hypotheses about biodiversity and ecosystem function () and climate change impacts (). Further, eelgrass is of primary conservation value because it supports such a diverse fauna. Despite the importance of eelgrass-associated biodiversity, the processes that structure it in nature are largely not understood. The processes that structure this community encompass a range spatial scales, from species interactions on a single blade to meadow-scale biotic and abiotic conditions to regional scale connectivity and climate.

A general understanding of metacommunities and the specific understanding of seagrass ecology support the following expectations: among meadows, we expect non-random spatial structure in diversity and species composition; within meadows, we expect patterns of negative co-occurrence among habitat patches reflecting species interactions (predation, competition). We hypothesize that non-random structure among meadows is driven by one or more of the following factors: position on a watershed abiotic gradient, meadow area, or eelgrass density.

[notes]

- seagrass epifauna are diverse, productive and important. They have become a model system for biodiversity and ecosystem function work. Despite their employment in mesocosms and their presence in the stomach’s of fish, relatively little is know about their distribution and abundance in nature, and the processes that might be driving such patterns.

- our aims are to describe the patterns of grazer biodiversity in these systems, in the context of biodiversity of other epifauna in at two spatial scales within a region.

How to explain among-meadow patterns: H1a) differences in abiotic tolerances among species lead to turnover among meadows along an abiotic gradient, H1b) biotic conditions such as eelgrass density, epiphyte abundance and time, meadow size or predation (fish diversity) may alter epifaunal diversity among meadows, H1c) if abiotic tolerances and biotic conditions are similar, meadows may be very similar in biodiversity, or may vary over time may reflecting demographics and stochastic variation.

Hypotheses: because meadows are relatively small, homogenous and discrete in this region, we hypothesized 1a) A decline in diversity in fresher sites, and species turnover among meadows consistent with a *nested community structure* in which marine sites contained more species and fresher sites contained a subset of taxa, or 1b) if biotic processes such as connectivity or species interactions prevail, communities would exhibit clementsian structure that is not necessarily correlated with the abiotic gradient (for SI) and random / no structure of connectivity prevails. 2) We expected variation among plots within meadows, reflecting local-scale processes. (*can I do a checkerboard for plots within meadows?*), and 3) we did expect these patterns to vary over time due to demographic processes (recruitment events, population cycles).

Localized experiments have shown that predation and dispersal are important; we know abundance and biodiversity vary with latitude, and along salinity gradients (refs). We don’t know how these processes interact, and whether they vary at the scale of a meadow, a habitat patch or a region.

Previous efforts to describe spatial patterns in biodiversity have suggested that species richness is oven relatively stable over space and less than the regional pool, and composition varies substantially even within meadows. These patterns have not been linked to the underlying drivers through experiments or sem…

intro to seagrass: foundation species, epifaunal biodiversity is more than one narrow group (e.g., gastropods, bats, birds, etc) and may be competing for space, food, or not interacting. Other EMS applications to date have not been for such diverse assemblages (or marine).

**Methods:**

*Study area an organisms:*

Barkely Sound, description of watershed gradient (figure 1). Differences along the gradient.

The epifauna: polyphyletic, resembles other regions.

*Biodiversity sampling:*

16 plots, X meadows, 3 times.

*Quantitative analyses:*

Methods: Willig et al 2011 oikos pooled plots within strata, which would be analogous to us pooling plots within meadows

EMS analysis…

Calculate species accumulation curves for plots within meadows (heino et al 2015) using vegan random. I did this for time C using vegan random, and all site curves saturate.

**Results:**

We observed and identified X individuals, and classified them into 47 taxonomic groups, comprising benthic crustaceans (x), gastropods (x) and others. Abundance and species richness of invertebrates varied among meadows (Table 1), and increased from spring to late summer (Table of regression results). Species richness saturated in our sampling within meadows (SAC plots, probably in SOM).

*Spatial structure in biodiversity among meadows*

* Position on the watershed gradient and area did not explain trends in diversity. (neither did seagrass attributes?)
* EMS (July, 9 sites) suggests clementsian structure along a shared gradient, but this gradient is not the watershed gradient or a gradient of meadow area (check this) (Table 2). Those gradients, when imposed, produce significant checkerboard patterns. Checkerboard also shows up among grazers along the watershed gradient.
* Temporal variation in structure is apparent (univariate patterns vary, gleasonian structure in July, random in May, and almost gleasonian in august.
* Do we see any patterns for potential food competitors (grazers), or w/in taxonomic groups (crustaceans, gastropods)

Two types of community emerge when we consider abundance-based metrics (NMDS; figure 2). Among meadows, composition is similar across groups of meadows (Figure 3 nmds). More marine influenced sites were dominated by grazers, while fresher sites were much more variable in functional composition and not clearly dominated by grazers.

[Can I estimate relative abundance of different trophic groups in each meadow? So for each plot, estimate the numeric relative abundance of grazers…]

[EMS analysis on plots suggests nested structure, but only at the end of the summer (plots at time E). When we add in all times and all sites, E does generally stand out as different; other sites /times are nested within time E, showing that species were essentially added throughout the summer. ]

*We expected variation among plots within meadows, reflecting local-scale processes. (can I do a checkerboard for plots within meadows?)*

* beta diversity vs null model suggests higher than expected aggregation within meadows, suggesting species interactions or demography, esp emerging over summer. (figure 3)

**Discussion:**

1. At what scales (plot, meadow) does epifaunal biodiversity vary? – maybe this is for the discussion.

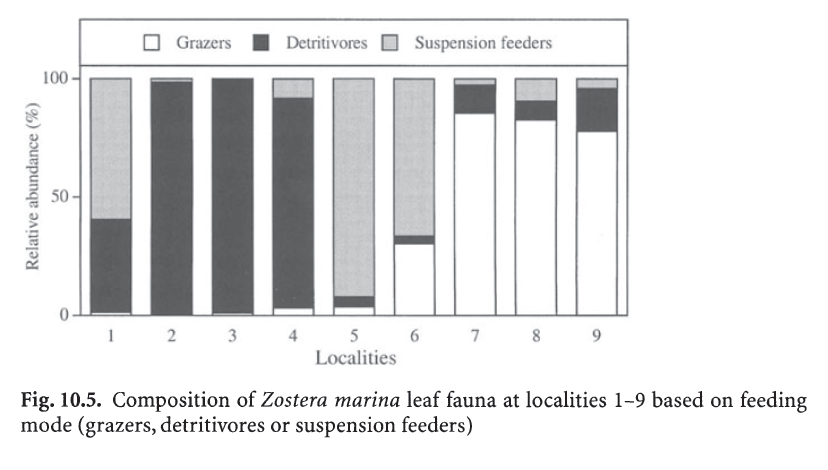
Overall, suggests low environmental heterogeneity wrt species tolerances, and that biotic processes like dispersal and demography are likely important structuring processes in this system.

1. energetic influences may be changing along estuarine gradient toward grazers of algae, and more abundant epifauna in general. Bottom up factors would include seagrass shoot density and LAI (we know this increases with salinity, increased epifaunal productivity (biomass isn’t clearly covary-ing).

**how our observations compare with others:**

Baden and Bostrom in the Baltic: abundance of epifauna decreased from high (250 x 10^3/m2) to 1.15 x 10^3/m2 from marine to fresher water. Marine sites crustaceans dominated by detritivorous amphipods; moderate salinity sites crustaceans dominated by idotea balthica; only one amphipod at the fresher sites. Marine sites gastropods were dominated by hydrobia, rissoa, littorina and gibbula (grazers). They found, like us, more epifauna / m2 in marine sites.

Baden and Bostrom did look at how dominant feeding type varies, but found that grazers took over at fresher sites.

****

“with increasing exposure the Zostera beds change from detritus sinks to detritus sources (Fonseca et al 1983, Fonseca and Fisher 1986, Bostrom and Bonsdorff 2000). Hence due to such differing current regimes (Gambi et al 1990) the amounts of organic matter available as food resources or building matirals for the leaf fauna differ among regions studied.”

High current areas are detritus sources, and low current areas are sinks. Fonseca et al 1986 suggested that in higher flow meadows, life histories might need to reflect this higher shear environment, and predation may be more intense in the low flow meadows. We are seeing fewer grazers in the low flow environments, possibly consistent with the predation hypothesis.

**Table 1:** Modeled effects of time (t) and position within the watershed (P) on plot-scale diversity estimates of invertebrate assemblages. Model comparisons for mixed effects models with meadow as a random effect. AICc, AIC weight (*w*) and δAIC values, and results of likelihood ratio tests (P-values) that compare the model in one row with model Basic 1 (first row). The best model has the lowest AICc value, and likelihood ratio tests facilitate interpretation of differences in models with similar AICc values (\* P < 0.05 for a comparison of the best model with other models in the set)

*Add in grazers as additional rows? Re-analyze this, maybe just for july all 9?*

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Model** | | ***w*** | **df** | **logLik** | δAIC | Time | Pos | T\*P |
| **Ln(Abundance)** | |  |  |  |  |  |  |  |
| **A3\*** | **ln(N) = t + P + t\*P** | **0.824** | **8** | **-90.05** | **0.00** | 0.03  [-0.06, 0.11] | -0.01  [-0.04, 0.01] | **0.02**  [0.01, 0.02] |
| A1 | ln(N) = t | 0.115 | 6 | -94.15 | 3.93 |  |  |  |
| A2 | ln(N) = t + P | 0.060 | 7 | -93.74 | 5.23 |  |  |  |
| Rarified Richness | |  |  |  |  |  |  |  |
| **B2\*** | **RR = t + P** | **0.569** | **7** | **-726.32** | **0** | **1.42**  [0.34, 2.50] | 0.04  [-0.15, 0.24] | 0.00  [-0.12, 0.13] |
| B1 | RR = t | 0.232 | 4 | -730.37 | 1.79 |  |  |  |
| B3 | RR = t + P + t\*P | 0.198 | 8 | -726.30 | 2.11 |  |  |  |
| Simpson’s Index | |  |  |  |  |  |  |  |
| **C2\*** | **SI = t + P + t\*P** | **0.687** | **8** | **85.42** | **0** | **0.08**  [0.03, 0.12] | 0.01  [-0.01, 0.02] | 0.00  [-0.01, 0.00] |
| C1 | SI = t | 0.160 | 6 | 81.83 | 2.92 |  |  |  |
| C3 | SI = t + P | 0.153 | 7 | 82.85 | 3.01 |  |  |  |

**Table of EMS results:** for 9 sites at time C, we see: Clementsian

* 5 sites at each time, only time C do we see something (gleasonian). But, for other months the matrix makes it looks like there should be a pattern but there isn’t.
* 5 sites pooled across times – random
* for plots time E shows structure that we could assess by forcing meadow order.

**Figure 1**: figure of univariate metrics like Jon’s (less complex). Stats in text?

**Figure 2**: nmds results

**Appendix Figure 1**: Eelgrass meadows sampled during summer 2012 between Alberni Inlet (red star) and the Pacific Ocean southwest of Dodger Channel (DC). Five meadows were sampled in May, July and August (red dots), while four additional meadows were sampled once in midsummer (yellow dots).   WI = Wizard Islet, BE = Bald Eagle Cove, EI = Ellis Island, RP = Robber’s Passage, NB = Numukamis Bay, CB = Crickett Bay, BI = Boyson Islands, CC = Crow Cove. BMSC = Bamfield Marine Sciences Centre.

****