WILEY ECOSPHERE

Epifaunal diversity patterns among eelgrass meadows suggest metacommunity structure

Journal:	*Ecosphere*
Manuscript ID	Draft
Wiley - Manuscript type:	Article
Date Submitted by the Author:	n/a
Complete List of Authors:	Whippo, Ross; University of British Columbia, Zoology; Smithsonian Institution, Tennenbaum Marine Observatories Network Knight, Nicole; University of British Columbia, Zoology; McGill University, Department of Biology; Smithsonian Tropical Research Institute Prentice, Carolyn; University of British Columbia, Zoology; Simon Fraser University, School of Resource and Environmental Management Cristiani, John ; University of British Columbia, Zoology Siegle, Matthew; The University of British Columbia, Zoology O'Connor, Mary; University of British Columbia, Zoology
Abstract:	In coastal seascapes, spatial habitat structure can support high animal diversity and secondary productivity. Still, seascape-scale connectivity among eelgrass meadows is an often-overlooked dimension of their ecological and conservation value. We tested whether eelgrass-associated biodiversity patterns are consistent with spatial processes such as abiotic habitat filtering or metacommunity dynamics. In Barkley Sound, British Columbia, we quantified epifaunal biodiversity on eelgrass (Zostera marina) among nine meadows to test three hypotheses: taxonomic diversity and composition i) vary randomly within meadows but ii) vary systematically among meadows reflecting seascape position and metacommunity dynamics, and iii) patterns are stable over time. We sampled epifaunal invertebrate biodiversity in a systematic spatial grid within 9 eelgrass meadows along a spatial gradient. We used univariate and multivariate diversity metrics to test for spatial and temporal diversity patterns. Though we identified two high-diversity meadows, epifaunal diversity varied as much over a few meters within the same meadow as among meadows separated by kilometers and of different sizes and exposures. This variation was not clearly explained by seascape position. Community similarity increased from May to August. These findings leave open the possibility that seascape scale metacommunity dynamics influence eelgrass-associated epifaunal biodiversity and its persistence in spatially patchy seascapes.

SCHOLARONE™
Manuscripts

1   **Epifaunal diversity patterns among eelgrass meadows suggest**

2   **metacommunity structure**

3   Running head: Epifaunal diversity in seagrass

4

5   Ross Whippo[1,2], Nicole S. Knight[1,3,4], Carolyn Prentice[1,5], John Cristiani[1], Matthew R. Siegle[1],

6   Mary I. O'Connor[1†]

7

8   †Corresponding author: oconnor@zoology.ubc.ca

9

10   1.   Department of Zoology and Biodiversity Research Centre, University of British

11   Columbia, 2212 Main Mall, V6T 1Z4, Vancouver, Canada

12   2.   Smithsonian Institution, Tennenbaum Marine Observatories Network, 647 Contees

13   Wharf Rd, Edgewater, MD, 21037, USA

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

15   1B1, Montreal, Canada

16   4.   Smithsonian Tropical Research Institute, Apartado Balboa 0843-03092, Ancon, Republic

17   of Panama

18   5.   School of Resource and Environmental Management, Simon Fraser University, 8888

19   University Drive, V5A 1S6, Burnaby, Canada

20

21

22   ABSTRACT

23

24   In coastal seascapes, spatial habitat structure can support high animal diversity and secondary

25   productivity. Still, seascape-scale connectivity among eelgrass meadows is an often-overlooked

26   dimension of their ecological and conservation value. We tested whether eelgrass-associated

27   biodiversity patterns are consistent with spatial processes such as abiotic habitat filtering or

28   metacommunity dynamics. In Barkley Sound, British Columbia, we quantified epifaunal

29   biodiversity on eelgrass (*Zostera marina*) among nine meadows to test three hypotheses:

30   taxonomic diversity and composition i) vary randomly within meadows but ii) vary

31   systematically among meadows reflecting seascape position and metacommunity dynamics, and

32   iii) patterns are stable over time. We sampled epifaunal invertebrate biodiversity in a systematic

33   spatial grid within 9 eelgrass meadows along a spatial gradient. We used univariate and

34   multivariate diversity metrics to test for spatial and temporal diversity patterns. Though we

35   identified two high-diversity meadows, epifaunal diversity varied as much over a few meters

36   within the same meadow as among meadows separated by kilometers and of different sizes and

37   exposures. This variation was not clearly explained by seascape position. Community similarity

38   increased from May to August. These findings leave open the possibility that seascape scale

39   metacommunity dynamics influence eelgrass-associated epifaunal biodiversity and its

40   persistence in spatially patchy seascapes.

41

42   Key words: biodiversity; estuary; foundation species; grazer; invertebrate; metacommunity;

43   seagrass; seascape ecology; *Zostera marina*.

2

44   INTRODUCTION

45

46   Understanding species' distribution and abundance is essential to understanding

47   ecological communities and to making informed decisions about seascape management and

48   biodiversity conservation. In highly diverse coastal marine habitats, understanding can be limited

49   by a lack of basic information about where and when species occur and the spatial scales over

50   which dominant diversity-influencing processes operate (Gaston 2000, Boström et al. 2006).

51   Coastal foundation species such as seagrass and kelp are often targeted for conservation for the

52   biodiversity they harbor and the ecosystem services they provide. Yet, how exactly these habitats

53   support the high and productive animal assemblages, and the role of spatial arrangement of

54   habitats, remains poorly understood.

55   While a spatially discrete habitat patch such as a seagrass meadow or a kelp bed may

56   appear to host a complete or representative local faunal community, habitat provision by

57   foundation species is just one of several processes that influence biodiversity of a patch:

58   population dynamics and species interactions structure species assemblages at finer (within

59   meadow) and broader (seascape) spatial scales in spatially structured 'metacommunities'

60   (Leibold et al. 2004, Boström et al. 2006, Pillai et al. 2011). Rates of colonization and rescue

61   effects from source-sink dynamics can play a major role in maintaining the species composition

62   and functional integrity of an ecosystem, and understanding these dynamics is critical for

63   successful management (Gerber et al. 2014, Furrer and Pasinelli 2016).

64   The purpose of this study is to explore potential metacommunity structure among

65   eelgrass-associated epifaunal species as a first step to assess the most informative spatial scale

3

66   for understanding how eelgrass meadows support biodiversity and its associated ecosystem

67   functions. Specifically, our aim was to target epifaunal biodiversity among spatial scales in a

68   seagrass meadow seascape to determine whether individual meadows, or a set of meadows, are

69   representative spatial units for biodiversity (i.e. – groupings of habitat that reflect regional

70   patterns of diversity). Spatial variation in biodiversity is influenced by the spatial scales of

71   ecological processes (e.g.- local predation pressure vs. regional dispersal patterns) that affect

72   species' relative abundance and presence or absence (Leibold et al. 2004, Ricklefs 2004,

73   Boström et al. 2006). Across a region, evolutionary and colonization history produce a shared

74   regional species pool (*gamma diversity*). At finer scales, meadow- or host plant-scale biotic

75   interactions (predation, competition, facilitation, resource provision) and abiotic conditions

76   (temperature, salinity, etc.) filter species from the regional pool to a subset of regional diversity,

77   called *alpha diversity* (DeTroch et al. 2001, Crist and Veech 2006, Sanders et al. 2007). Between

78   local and regional scales, dispersal and colonization dynamics connect populations among

79   habitat patches to produce metacommunities. In metacommunities, abundance and diversity vary

80   among local sites, producing patterns of spatial turnover or variation, forms of *beta diversity*

81   (Anderson et al 2011), that are jointly influenced by local and regional process (Leibold and

82   Mikkelson 2002, Leibold et al. 2004, Crist and Veech 2006, Henriques-Silva et al. 2013).

83   Eelgrass-associated epifauna are the critical links in the food web that connect high

84   eelgrass related algal primary production to fish production in the food chain (Hemminga and

85   Duarte 2000). Biogeographic variation in eelgrass-associated epifaunal diversity influences the

86   strength of top down control in eelgrass meadows, and is central to many of the ecosystem

87   services provided by these systems (Duffy et al. 2003, 2015, Amundrud et al. 2015).

88   Epifaunal diversity can vary substantially within and among meadows (Hemminga and

89   Duarte 2000, Boström et al. 2006, Yamada et al. 2007, Carr et al. 2011, Barnes and Ellwood

90   2012, Barnes 2013). Within meadows, alpha diversity at fine scales ($0.5 - 1$ m^2) is typically

91   relatively consistent among patches within the same meadow and much lower than meadow-

92   scale species diversity (Carr et al. 2011, Barnes and Ellwood 2012, Barnes 2013). This pattern

93   suggests that compositional differences, one form of beta diversity, should be high and a

94   relatively important component of seagrass associated biodiversity within meadows. Though

95   studies of variation in species distribution have reported high turnover at moderate spatial scales

96   (< 150 m, Barnes and Ellwood 2012), few studies specifically assess beta diversity at the same

97   scale. Among meadows, variation in species composition and diversity is in some cases

98   explained partially by wave energy or exposure (e.g., fetch; Boström et al. 2006, Robinson et al.

99   2011) or salinity (Yamada et al. 2007, Boström et al. 2014, Barnes and Ellwood 2013). Still, in

100   some cases diversity patterns are not readily explained by abiotic attributes (e.g., Carr et al. 2011,

101   Barnes and Elwood 2012).

102   Here, we test the hypothesis that non-random spatial patterns in species composition and

103   turnover within and among meadows distinguish meadows within a seascape and provide insight

104   as to potential importance of abiotic factors and community dynamics in driving regional-scale

105   epifaunal diversity patterns. Specifically, we hypothesize that 1) alpha (quadrat-scale) epifaunal

106   diversity is the same among meadows, but within-meadow species composition varies in space to

107   produce patterns of beta diversity that also vary among eelgrass meadows, and 2) spatial

108   variation in species composition is consistent with i) local filtering of species based on abiotic

109   conditions, or ii) metacommunity-scale processes that involve dispersal among meadows. We

5

110   also tested 3) whether patterns of diversity vary over time, and whether variation over time could

111   provide insight to possible drivers of diversity patterns. To test these hypotheses, we used a

112   nested sampling design to quantify spatial structure in seagrass-associated epifaunal biodiversity

113   among nine meadows in British Columbia, Canada.

114

115   METHODS

116

117   *Study system*

118   We sampled epifaunal biodiversity in eelgrass *Zostera marina* meadows in summer of

119   2012 in Trevor Channel, Barkley Sound, where *Z. marina* is the only meadow-forming seagrass

120   species (Figure 1A). In this region, *Z. marina* forms primarily subtidal, perennial meadows that

121   range in size from $< 10 \text{ m}^2$ to $> 25,000 \text{ m}^2$ (Mason et al. 2015). A rich epifaunal assemblage of

122   gastropods, crustaceans and other taxa live on and among eelgrass blades. Epifauna consume

123   epiphytic algae growing on seagrass, detritus and each other, forming the base of a highly

124   productive food web (Hemminga and Duarte 2000, Heck Jr. and Valentine 2006).

125

126   *Structure and abiotic conditions*

127   We quantified several biotic attributes of eelgrass meadows that could explain variation

128   in eelgrass associated invertebrate biodiversity: shoot density, leaf area, epiphyte load, and

129   meadow area. Shoot density and leaf area were estimated from three or four 0.28 m^2 quadrats

130   collected outside each corner of a 4 x 4 m grid demarcated for community sampling (described

131   below) at each site concurrent with epifaunal sampling. For all meadows in all time periods, we

6

132 removed a shoot from each corner quadrat, dried and weighed eelgrass and its associated

133 epiphytes, and standardized epiphyte dry mass to eelgrass dry mass. Additionally, we sampled

134 epiphytes more thoroughly at three sites during low-tide periods (< 0.5 m) in mid and late

135 summer, by collecting 15 shoots per meadow from three tidal heights. We separated bladed

136 epiphytes from periphyton and again standardized epiphyte mass to eelgrass mass. We estimated

137 leaf area using methods described by Borg et al., 2010. We did not estimate quadrat-level density

138 or leaf area for the same quadrats from which we sampled epifaunal biodiversity.

139   To quantify meadow-scale abiotic conditions, we measured temperature and salinity

140 using a hand-held temperature/salinity sensor (YSI Inc., OH USA). Measurements were taken

141 throughout the tidal cycle on biodiversity sampling days, and opportunistically on other days.

142 We represented the estuarine abiotic gradient of salinity and temperature by quantifying the

143 geographic position from the nearest freshwater input of each meadow. Position was estimated as

144 linear distance in kilometers from the nearest freshwater source (Sarita River or Alberni inlet,

145 Figure 1A). We estimated exposure to wave energy (using fetch as a proxy) by calculating the

146 distance to nearest land from the eelgrass meadow in 10 degree increments around a centroid

147 point and summed the distance.

148

149 *Biodiversity sampling*

150   To estimate epifaunal biodiversity and characterize variation within meadows, we used a

151 4 x 4 m grid of 16 standard quadrats (0.28 m^2), each separated by 1 m, in each meadow (Figure

152 1B; after Sanders et al. 2007, Duffy et al. 2015). Repeated sampling within meadows was rotated

153 90° around a central reference point at a distance of 1-2 m so that seagrass removed at one time

7

154   period would not impact the density of seagrass and associated epifaunal at subsequent

155   samplings. This sampling design allowed for comparison of diversity among quadrats and

156   meadows while standardizing for total area sampled and the spatial arrangement of samples. We

157   placed sampling grids within contiguous meadows at least 2 m from any meadow edge. In each

158   quadrat, we cut away eelgrass at the sediment-water interface and placed it into a 250 µm mesh

159   bag, collecting all eelgrass and epifauna. All sampled areas were at least 1 m below lower low

160   water large tide (LLWLT) but not deeper than 3 m below LLWLT. Samples were then

161   transported back to the lab in seawater, where all invertebrates were removed and preserved in

162   70% EtOH within 24 hours of collection.

163   To estimate variation in diversity among meadows, we sampled nine meadows between

164   the open coast and Alberni Inlet in Trevor Channel (Figure 1; Table 1). We chose these

165   meadows among the subset of known meadows in Trevor Channel (n ~ 20) because they are

166   evenly distributed along the channel, they are large meadows (i.e., 0.12 – 11.33 ha), and they

167   represent many of the shallow areas where eelgrass might occur. To determine whether spatial

168   biodiversity patterns varied through time, we sampled five of these meadows three times, in May

169   (early summer, time A), June/July (midsummer, time B) and August (late summer, time C) of

170   2012.

171   We identified every invertebrate > 1 mm to the lowest taxonomic resolution possible

172   using light microscopy. Though many of our identifications are to species level, many other taxa

173   are identified to higher levels (Family or Order). Consequently, our taxonomic diversity

174   estimates should be considered minimum estimates. We classified invertebrate species to broad

175   trophic groups (grazer, predator, filter feeder, detritivore) based on our observations and

176   published information (Light and Carlton 2007, Macdonald et al. 2010).

177

178   *Biodiversity estimation*

179   To estimate diversity within and among meadows, we created species-quadrat and

180   species-site matrices with abundance data using information on every individual collected from

181   each quadrat (Gotelli and Colwell 2011). We estimated multiple biodiversity metrics: species

182   richness (number of species observed), their relative abundance, and the likelihood that

183   additional taxa were present but unobserved in estimating and comparing biodiversity among

184   samples and meadows. We estimated alpha (quadrat-scale) diversity by rarifying (ENS) and

185   using species richness values (R), Shannon diversity (H'), and Simpson evenness (S). The

186   effective number of species (ENS) is derived from the probability of an interspecific encounter

187   (PIE; Dauby and Hardy 2012). ENS is a standard metric that can help distinguish changes in

188   diversity from changes in abundance and can be interpreted as the number of equally-abundant

189   species that would exist in a sample of a given diversity value (Jost 2006). We used the R

190   package vegan (Oksanen et al. 2007, R Core Team 2016).

191   We quantified beta diversity in two ways. First, we estimated beta diversity (β_{BC}) *within*

192   each meadow using the Bray-Curtis dissimilarity metric, which accounts for relative abundance

193   of species and estimates differences among samples as their average distance from a group

194   (meadow-level) centroid (Tuomisto 2010, Anderson et al. 2011). This allows comparison of

195   quadrats to all other quadrats within the meadow. Second, we used a null model approach

196   developed by Chase et al. (2011) to evaluate possible mechanisms that influence community

9

197   similarity *among* meadows and to distinguish differences in beta diversity that reflect underlying

198   patterns of community structure rather than random differences in alpha diversity among sites.

199   The model uses the Raup-Crick beta diversity metric, β_{RC}, to compare pairwise dissimilarities

200   between samples with a null expectation. This metric uses presence/absence of species and their

201   relative occurrence among samples to assign probabilities that community samples are less

202   similar (>0), more similar (<0) or no different ($=0$) than expected by chance. We analyzed

203   patterns in community composition among all nine sites sampled at all time periods for both

204   intra-meadow and inter-meadow variation.

205

206   *Statistical diversity analyses*

207   To test our first hypothesis that alpha diversity (quadrat-level species diversity) does not

208   vary among quadrats we used one-way ANOVA on univariate diversity metrics among nine

209   meadows sampled in July (midsummer, time B). To explore possible explanations for variation

210   in diversity within and among meadows, we tested whether spatial patterns in grazer diversity

211   varied with season, distance from each other, and meadow attributes. We conducted linear

212   regression analyses using sampling date, distance among quadrats, meadow area, fetch and

213   distance from freshwater inputs as predictors. We tested for correlations among these variables.

214   Abundance and ENS were log-transformed to meet the assumption of homoscedasticity.

215   To test our second hypotheses that beta diversity within meadows varies among

216   meadows, we compared beta diversity estimates with null expectations as described above. Beta

217   and alpha diversity patterns can differ if species are aggregated within meadows (as opposed to

10

218   randomly distributed throughout the meadow), or if aggregation varies among species and

219   dominance varies among meadows. We estimated aggregation within meadows using

220   standardized Morisita's index (I), and then compared aggregation scores for species in each

221   meadow with their rank. We specifically tested for aggregation within meadows, whether it is

222   driven by the most abundant species, and whether the most abundant species are the same among

223   meadows.

224   For all model comparisons, we ranked models using AICc, and compared them using

225   likelihood ratio tests, δ_{aic} and Akaike weights (w). Models with a $\delta_{aic} < 2$ can be considered

226   equivalent to the best model (Burnham and Anderson 2003). In the case of multiple highly

227   ranked models, we selected the set of models that produced a cumulative $w > 0.95$, representing

228   our confidence (95%) that the set includes the best model, and we averaged these models to

229   produce coefficients of effects (Burnham and Anderson 2003). We examined residual plots for

230   deviations from the assumptions of linearity or homoscedasticity (with the exception of parallel

231   lines in a plot of the models' fitted values vs. residuals). This phenomenon resulted from

232   including repeated values of position in the estuary in the model (Searle 1988). We tested

233   hypotheses on a subset of our full dataset - the meadows sampled at all three time points - to

234   conservatively test for an effect of temporal variation.

235

236   *Elements of metacommunity methods*

237   To test whether biodiversity patterns among meadows are consistent with

238   metacommunity processes operating at the seascape scale, we applied the elements of

239   metacommunity (EMS) framework (Leibold and Mikkelson 2002, Presley et al. 2010). This

11

240   analysis first tests for coherence in species distributions among meadows by comparing observed

241   species distributions with expected distributions based on a null model. If positive coherence is

242   identified, spatial patterns can be further tested to identify patterns consistent with individualistic

243   species distributions across the seascape (a Gleasonian model of species distributions), or

244   clumped species distributions (Clementsian structure), or random, providing insight to possible

245   types of community structure (Leibold and Mikkelson 2002, Presley et al. 2010, Henriques-Silva

246   et al. 2013). We analyzed metacommunity structure for the nine meadows sampled in July 2012

247   using the R package Metacom (Dallas 2014). We used a null model that fixed species richness

248   within sites ('fixed row') but allowed composition to vary based on their marginal probabilities

249   (method = "R1").

250

251   RESULTS

252

253   *Meadow attributes*

254   We collected 71 samples for seagrass structural metrics. Meadows increased in shoot

255   densities (+0.27 shoots/km) and associated leaf area (+240.73 cm^2/km) with increasing proximity

256   to the Pacific Ocean (Table S1). Shoot density and leaf area increased between May and August

257   at meadows near freshwater but remained relatively high all summer at the seaward meadows

258   (Table S1). Distance from fresh water input captured correlations with other variables:

259   temperature, salinity, shoot density (Table S2). Salinity increased and temperature declined with

260   distance from freshwater inputs, though these changes were relatively small in magnitude (Table

261   S3). Epiphyte load was highly variable between meadows, uncorrelated with position in the

12

262 estuary and epiphyte abundances and the type of epiphytes present (periphyton vs. bladed algae)

263 varied spatially and temporally (Table S4). The bladed brown epiphyte *Punctaria* sp. was

264 abundant at two of the marine sites (DC and WI), and absent from the fresher NB.

265

266 *Epifauna summary*

267 We collected 304 seagrass samples with associated epifauna and identified approximately

268 81,500 invertebrates (47 taxa in 42 families). Of these, 30 taxa are considered epifaunal, meaning

269 they regularly or always occur on the blades of eelgrass (rather than associated with sediment)

270 (Table 2). We observed between 0 and 1200 individuals per 0.28 m^2 of seagrass meadow. Mean

271 total abundance of all taxa at the quadrat scale did not vary among meadows in May, but did

272 increase over the summer such that by August abundance was 2-3 times higher in seaward

273 meadows (DC, WI, RP) compared to meadows nearer Alberni Inlet in which abundance was

274 relatively stable over time (CB, NB; Table S5). The seasonal abundance increase in seaward

275 meadows is clear in small (1-2 mm) and large (>2 mm) size fractions.

276 Of the 30 epifaunal taxa observed, 17 taxa are herbivorous or omnivorous consumers of

277 epiphytic algae, classified as "grazers". These comprised approximately 72% of all individuals.

278 On average, in each meadow 6.0 ($\pm$ 0.15) grazer taxa (isopods, harpacticoid copepods,

279 amphipods, and gastropods) were detected. Among all samples, epifaunal assemblages were

280 dominated by small (1-2 mm) invertebrates, which made up ~83% of individuals, whereas large

281 invertebrates (> 8 mm) such as crabs, sea stars and urchins made up less than 3% of individuals.

282

283 *Spatial biodiversity patterns*

13

284   Between 10 and 22 epifaunal taxa (of the 30 observed) occurred in each meadow. Thus,

285   there was substantial variation in observed diversity among meadows (Tables 1, 2, S5). We

286   found that alpha diversity did not vary systematically among meadows with any predictor we

287   tested (Figure 2, Table S5). Quadrat-level species richness [R] varied as much within meadows

288   as among meadows (Figure 2A), with the exception of high species richness (alpha diversity) at

289   RP and BI (F = 8.9, df = 8, 136, P < 0.001). We observed similar patterns in Shannon diversity

290   (F = 4.6, df = 8, 136, P < 0.001) and Simpson diversity (F = 3.8, df = 8, 136, P < 0.001), though

291   for these metrics BI is not different, and DC has lower within-quadrat evenness than other

292   meadows (Figure 2D). Rarified diversity estimates were more variable among meadows (Figure

293   2B; F = 3.62, df = 8, 120, P = 0.002). The higher diversity of RP, lower S of DC, and differences

294   in ENS were not explained by meadow-scale predictors such as distance from fresh water input,

295   shoot density, meadow area or fetch (Table S5).

296   Beta diversity within meadows, reflecting similarity in relative abundance and

297   composition of species from each of the 16 sampled quadrats, varied substantially among

298   meadows (Figure 3E-F, Table S6). Comparison with the null model showed that both inter- and

299   intra- meadow beta diversity (β_{RC}) was always less than expected by chance indicating that

300   meadow epifauna were more similar than would be expected if species were distributed among

301   meadows randomly (Figure 4A, Figure S7). A permutation test of multivariate homogeneity of

302   group dispersions showed that within-meadow beta diversity varied among meadows, but beta

303   diversity did not vary predictably by distance from fresh water input or with other abiotic and

14

304   biotic factors. Finally, analyses of aggregation indicated that individuals within species were

305   spatially aggregated within meadows for most species (>80% in 7 of 9 meadows, Table 1).

306   Spatial variation in species composition was consistent with metacommunity-scale

307   processes structuring biodiversity patterns. Among all nine meadows in July, elements of

308   metacommunity structure (EMS) analysis based on presence/absence data suggested a

309   checkerboard pattern of species distribution among meadows, indicating differences among

310   meadows that were non-random. For all epifaunal taxa (30 taxa), EMS suggested negative spatial

311   coherence (86 embedded absences relative to 56.17 ± 6.53 expected by the null model, $z = -$

312   4.57, $P <0.01$). For grazers (17 taxa), we observed a similar pattern of negative coherence (29

313   embedded absences relative to 16.42 ± 3.76 expected by the null model, $z = - 3.35$, $P <0.01$).

314

315   *Temporal biodiversity patterns*

316   Over time, quadrat-scale (alpha) richness increased, primarily between July and August,

317   except at RP where richness spiked mid-summer (Figure 3A). Shannon diversity and Simpson's

318   evenness did not vary systematically over time (Figure 3C-D), while ENS declined slightly

319   overall between May and June (Figure 3B). By August, there was a trend toward lower quadrat-

320   scale observed richness and lower ENS, which increased from marine to fresher meadows

321   (Figure 3B).

322   Beta diversity as gamma/alpha and mean Bray-Curtis dissimilarity generally decreased

323   over the summer, meaning quadrats within the same meadow became more similar. However,

324   Bray-Curtis beta spiked at RP and CB in midsummer, likely due to a numerical increase in

325   *Caprella* spp. and *Phyllaplysia taylori* at RP, and *Mytilus trossulus* at CB. These decreases in

15

326   beta diversity over the course of the summer are reflected in comparisons to null predictions

327   (Figure 4), which found that among- and within-meadow beta diversity exhibited less

328   dissimilarity than predicted values, a trend that strengthened on both scales over the course of the

329   summer. This indicates that meadows were becoming more similar across small (<1 m) and large

330   (>10 km) scales simultaneously. This trend can be attributed to the observed recruitment events

331   by increasingly common mesograzers that occurred as the summer progressed.

332

333   *Patterns in composition and dominance*

334   Increasing similarity within and among meadows over time co-occurred with increases in

335   abundance in common taxa, rather than by changes in their presence in meadows (Table 2,

336   Figure 3). For example, *Caprella* spp. abundance increased more than ten-fold (from an average

337   of 16 individuals/quadrat to 237 individuals/quadrat) from early to mid-summer, but by late

338   summer a recruitment event of *Phyllaplysia taylori* led this species to outnumber *Caprella* spp.

339   at RP and DC. However, changes in abundance were not consistently observed among sites. For

340   example, the *P. taylori* recruitment event occurred at two sites, while a major mussel recruitment

341   event occurred at other sites including NB and CB later during the same period, causing the

342   species composition of these two sites to diverge from the others. Many species were rare but

343   present at most sites and times, yet no species was common everywhere at all times (Table 2).

344   Nearly half of epifaunal taxa analyzed (12) were common – five taxa were detected at every site

345   and sampling time.

346   Meadow-scale patterns in species number and compositional variation were more similar

347   among meadows than expected by chance, even though we observed different numbers and

16

348 combinations of species in each meadow. For example, samples collected within meadows mid-

349 summer were typically more similar to samples from the same meadow than to samples from

350 other meadows. These distinctive meadow species compositions reflected differences in

351 numerically dominant species, rather than less striking differences in species presence or

352 absence. However, while dissimilarity was greater among sites than within sites at the beginning

353 of the summer compared to null expectations, the reverse was true by the end of the summer

354 (Figure 4A).

355   Among all meadows, five taxa accounted for > 80% of invertebrates collected: the

356 caprellid amphipods *Caprella* spp. (*C. laeviuscula* and *C. californica*), the sea hare *Phyllaplysia*

357 *taylori* (primarily juveniles), the mussel *Mytilus trossulus* (primarily juveniles), the polychaete

358 worm *Platynereis bicanaliculata*, and the sea spider *Pycnogonum* sp. However, abundances of

359 these species were not consistently high among all meadows and all sampling periods.

360

361 DISCUSSION

362   Seagrass meadows host vast biodiversity, and this biodiversity is part of the immense

363 ecological and economic value associated with seagrass ecosystems (Hemminga and Duarte

364 2000, Duffy et al. 2015, Heck and Williams 2000). Generalities and drivers of spatial patterns in

365 eelgrass associated fauna are not well documented or understood (Boström et al. 2006). In an

366 unprecedented spatially explicit description of the epifaunal biodiversity of British Columbia

367 seagrass meadows over a summer season, we found that non-random spatial patterns in species

368 composition and turnover distinguished meadows within the Trevor Channel seascape. In

369 contrast, alpha diversity (species richness and ENS) was varied little over space and time.

17

370   Differences in meadow area, fetch and distance from freshwater input did not explain variation

371   in diversity. These patterns suggest that species interactions and population dynamics are playing

372   out across meadows in this region, and seagrass meadow communities may form larger

373   metacommunities linked by dispersal.

374   Spatial patterns in epifauna suggest possible metacommunity structure, indicating that

375   biodiversity may be maintained at the seascape scale rather than the meadow scale. Among

376   meadows, species exhibited patterns consistent with a checkerboard distribution. Checkerboard

377   patterns have been interpreted to reflect negative species interactions such that pairs of species

378   do not occur together. Although this pattern could also reflect shared environmental affinities

379   among groups of species (Leibold and Mikkelson 2002, Presley et al. 2010, Henriques-Silva et

380   al. 2013), the metacommunity analysis found no evidence for spatially nested or clumped

381   community patterns that would have been more consistent with groups of species sharing

382   environmental affiliations. This suggestion is also supported by the lack of an observed effect of

383   meadow area or other abiotic predictors in this study. Absence of a signal of meadow area on

384   diversity could indicate high connectivity (low isolation) among meadows. However, we only

385   surveyed a small proportion of the larger meadows, so it is possible that higher diversity may be

386   found in the larger meadows if sampled more extensively. Average quadrat scale diversity (7-20

387   species, Figure 3) and meadow-scale gamma diversity (Chao2 index estimate: 16 species per

388   meadow + sd 3.39) was in all cases much lower than regional species diversity (47 observed

389   taxa). Together, these patterns suggest that some processes limit the presence of regional taxa in

390   all meadows, and that within-meadow communities may be maintained by a balance between

391   habitat filtering and biological connectivity that maintains population connections among nearby

392   meadows. Such connectivity could maintain higher diversity in smaller meadows than expected

393   based only on their size.

394   Contrary to some studies in other regions (Yamada et al. 2007, Barnes and Ellwood

395   2012), we did not observe a clear signal of continuous species turnover along the biotic and

396   abiotic gradients associated with distance from fresh water input (Figure 2, Figure 3A-C), until,

397   possibly, late summer (Figure 3D). We observed only weak, trends in invertebrate abundance

398   and diversity with estuarine position (correlated with salinity and eelgrass structure). This may

399   be indicative of the salinity regime of the sites sampled by Barnes (2013) and Yamada et al.

400   (2007), which spanned a greater range in salinity (< 5 - 35 ppt and 6.2 – 32.2 ppt, respectively)

401   than did ours (~14 - 28 ppt), and may have captured physiologically stressful, low-salinity

402   conditions with a stronger influence on invertebrate assemblages.

403   Our findings are consistent with other studies that suggest that species compositional

404   turnover in space is the main component of biodiversity in these systems. Quadrat-scale diversity

405   seems to be quite constrained to a small number of species, regardless of meadow biotic or

406   abiotic attributes. Thus, the processes that underlie spatial turnover are the ones that facilitate the

407   high diversity of this system. Our study reveals spatial aggregation of most species within

408   meadows. Aggregation can indicate micro-habitat variation, species interactions such as

409   competition, predation or facilitation, or historical effects such as recovery from disturbance or

410   stochastic events. We also observed turnover in composition among meadows that suggests a

411   role for seascape-scale dispersal (>10 km), asynchronous community trajectories, or historical

412   events such as disturbance and associated recovery.

413   Our study contributes to a limited number of existing beta diversity estimates for

414   seagrass-associated epifauna. These studies have typically focused on turnover, i.e., directional

415   change in beta diversity along some gradient, finding that beta diversity in seagrass beds can be

416   driven by variation in salinity, seagrass species, tidal height, and sub-habitat type (e.g., seagrass

417   shoots or sediment; De Troch et al. 2001, 2003, Barnes and Ellwood 2012, Knight et al. 2015).

418   However, we know very little about non-directional variation in beta diversity within seagrass

419   meadows, and (to our knowledge) no study has attempted to distinguish observed patterns in beta

420   diversity from null expectations (Kraft et al. 2011). The comparison of null expectations to

421   empirical datasets allowed us to infer whether random processes such as chance colonization and

422   extinction, or deterministic processes like environmental filtering or competition are likely

423   causes of observed patterns in community composition (Chase and Myers 2011).

424   Over the summer season, species turnover within and among meadows declined,

425   reflecting demographic changes that increased the abundance and prevalence of several

426   numerically dominant species. These demographic changes were driven by very different

427   specific processes: annual recruitment pulses by the weakly-dispersing seagrass specialist

428   *Phyllaplysia taylori* in RP and DC in August, recruitment by the pelagic dispersing and

429   cosmopolitan mussel *Mytilus trossulus* at other sites, and population increases by benthic

430   eelgrass-dwelling caprellid amphipods. These increases were similar among quadrats, but each

431   reflects a temporary increase that is expected to change over time with juvenile mortality and

432   population dynamics. Grazer taxa such as amphipods and isopods with continuous population

433   dynamics and overlapping generations increased between May and July at all sites except NB.

434   This latter pattern suggests some site-level factors such as food availability, seasonal warming,

20

435   or reduction in predation between May and July that was then reversed in DC, CB and NB by

436   August. Despite this variation in univariate metrics and the identities of dominant species,

437   multivariate metrics suggested composition overall was relatively stable through time,

438   suggesting that the differences in abundance and richness are reflecting changes in dominance,

439   consistent with observations in other systems (Douglass et al. 2010, Thom et al. 1995, Best and

440   Stachowicz 2014). Still, the potential role of species interactions such as competition or

441   predation in the temporal dynamics of these communities is not well understood.

442

443   CONCLUSIONS

444   Seagrass communities are known for their high epifaunal diversity and productivity, and

445   fine-scale variation in species composition appears to be a critical component of this diversity.

446   Understanding spatial and temporal variation is essential to linking the abiotic and biotic features

447   of a marine seascape to the ecosystem functions that promote biodiversity as well as secondary

448   productivity that emerges at higher trophic levels including fish, wading birds, and marine

449   mammals. As anthropogenic pressure on valuable coastal ecosystems continues to accelerate at

450   local and regional scales, it is more important than ever that we develop a baseline understanding

451   of how biodiversity in seagrass meadows is maintained across ecologically relevant scales.

452   In this comprehensive assessment of eelgrass-associated biodiversity, we have shown that

453   species diversity and abundance vary among seagrass meadows within a region, and that the

454   variation is not clearly predictable from an estuarine gradient and related biotic and abiotic

455   predictors. Although *Z. marina* provides relatively homogenous habitat, each *Z. marina* meadow

456   appears to host a subset of epifaunal species observed in the larger region. These patterns are

457   indicative of a metacommunity system, and suggest that processes that maintain diversity in

458   eelgrass communities may reflect a seascape of many meadows connected through dispersal. If

459   true, the conservation of eelgrass systems will require a network approach that preserves

460   numerous meadows within the region. Examining biodiversity patterns across a seascape has

461   expanded our view of seagrass biodiversity, and additional research is required to address the

462   challenges of understanding how spatial turnover in diversity is related to the function and

463   resilience of these ecosystems.

464

465   ACKNOWLEDGMENTS

466

476

477

478

479   LITERATURE CITED

480

481   Amundrud, S. L., D. S. Srivastava, and M. I. O'Connor. 2015. Indirect effects of predators

482   control herbivore richness and abundance in a benthic eelgrass (Zostera marina) mesograzer

483   community. Journal of Animal Ecology 84:1092–1102.

484   Anderson, M. J., T. O. Crist, J. M. Chase, M. Vellend, B. D. Inouye, A. L. Freestone, N. J.

485   Sanders, H. V Cornell, L. S. Comita, K. F. Davies, S. P. Harrison, N. J. B. Kraft, J. C.

486   Stegen, and N. G. Swenson. 2011. Navigating the multiple meanings of beta diversity: a

487   roadmap for the practicing ecologist. Ecology Letters 14:19–28.

488   Barnes, R. S. K. 2013. Distribution patterns of macrobenthic biodiversity in the intertidal

489   seagrass beds of an estuarine system, and their conservation significance. Biodiversity and

490   Conservation 22:357–372.

491   Barnes, R. S. K., and M. D. F. Ellwood. 2012. Spatial variation in the macrobenthic assemblages

492   of intertidal seagrass along the long axis of an estuary. Estuarine Coastal and Shelf Science

493   112:173–182.

494   Borg, J. A., A. A. Rowden, M. J. Attrill, P. J. Schembri, and M. B. Jones. 2010. Spatial variation

495   in the composition of motile macroinvertebrate assemblages associated with two bed types

496   of the seagrass Posidonia oceanica. Marine Ecology Progress Series 406:91–104.

497   Boström, C., S. Baden, A. C. Bockelmann, K. Dromph, S. Fredriksen, C. Gustafsson, D. Krause-

498   Jensen, T. Moller, S. L. Nielsen, B. Olesen, J. Olsen, L. Pihl, and E. Rinde. 2014.

499   Distribution, structure and function of Nordic eelgrass (Zostera marina) ecosystems:

500   implications for coastal management and conservation. Aquatic Conservation-Marine and

501   Freshwater Ecosystems 24:410–434.

502 Boström, C., K. O'Brien, C. Roos, and J. Ekebom. 2006. Environmental variables explaining

503   structural and functional diversity of seagrass macrofauna in an archipelago landscape.

504   Journal of Experimental Marine Biology and Ecology 335:52–73.

505 Burnham, K. P., and D. R. Anderson. 2003. Model selection and multimodel inference: a

506   practical information-theoretic approach. Springer Science & Business Media.

507 Carr, L. A., K. E. Boyer, and A. J. Brooks. 2011. Spatial patterns of epifaunal communities in

508   San Francisco Bay eelgrass (Zostera marina) beds. Marine Ecology-an Evolutionary

509   Perspective 32:88–103.

510 Chase, J. M., N. J. B. Kraft, K. G. Smith, M. Vellend, and B. D. Inouye. 2011. Using null models

511   to disentangle variation in community dissimilarity from variation in α-diversity. Ecosphere

512   2:art24.

513 Chase, J. M., and J. A. Myers. 2011. Disentangling the importance of ecological niches from

514   stochastic processes across scales. Philosophical Transactions of the Royal Society B-

515   Biological Sciences 366:2351–2363.

516 Crist, T. O., and J. A. Veech. 2006. Additive partitioning of rarefaction curves and species-area

517   relationships: unifying alpha-, beta- and gamma-diversity with sample size and habitat area.

518   Ecology Letters 9:923–932.

519 Dallas, T. 2014. metacom: an R package for the analysis of metacommunity structure.

520   Ecography 37:402–405.

521 Dauby, G., and O. J. Hardy. 2012. Sampled-based estimation of diversity sensu stricto by

522   transforming Hurlbert diversities into effective number of species. Ecography 35:661–672.

24

523   DeTroch, M., F. Fiers, and M. Vincx. 2001. Alpha and beta diversity of harpacticoid copepods in

524   a tropical seagrass bed: the relation between diversity and species' range size distribution.

525   Marine Ecology Progress Series 215:225–236.

526   DeTroch, M., F. Fiers, and M. Vincx. 2003. Niche segregation and habitat specialisation of

527   harpacticoid copepods in a tropical seagrass bed. Marine Biology 142:345–355.

528   Douglass, J. G., K. E. France, J. P. Richardson, and J. E. Duffy. 2010. Seasonal and interannual

529   change in a Chesapeake Bay eelgrass community: Insights into biotic and abiotic control of

530   community structure. Limnology and Oceanography 55:1499–1520.

531   Duffy, J. E., P. L. Reynolds, C. Boström, J. A. Coyer, M. Cusson, S. Donadi, J. G. Douglass, J.

532   S. Eklof, A. H. Engelen, B. K. Eriksson, S. Fredriksen, L. Gamfeldt, C. Gustafsson, G.

533   Hoarau, M. Hori, K. Hovel, K. Iken, J. S. Lefcheck, P. O. Moksnes, M. Nakaoka, M. I.

534   O'Connor, J. L. Olsen, J. P. Richardson, J. L. Ruesink, E. E. Sotka, J. Thormar, M. A.

535   Whalen, and J. J. Stachowicz. 2015. Biodiversity mediates top-down control in eelgrass

536   ecosystems: a global comparative-experimental approach. Ecology Letters 18:696–705.

537   Duffy, J. E., J. P. Richardson, and E. A. Canuel. 2003. Grazer diversity effects on ecosystem

538   functioning in seagrass beds. Ecology Letters 6:637–645.

539   Furrer, R. D., and G. Pasinelli. 2016. Empirical evidence for source–sink populations: a review

540   on occurrence, assessments and implications. Biological Reviews 91:782–795.

541   Gaston, K. J. 2000. Global patterns in biodiversity. Nature 405:220–227.

542   Gerber, L. R., M. Del Mark Mancha-Cisneros, M. O'Connor, and E. R. Selig. 2014. Climate

543   change impacts on connectivity in the ocean: Implications for conservation. Ecosphere 5:1–

544   18.

545   Gotelli, N. J., and R. K. Colwell. 2011. Estimating species richness. Biological diversity:

546   frontiers in measurement and assessment 12:39–54.

547   Heck Jr., K. L., and J. F. Valentine. 2006. Plant–herbivore interactions in seagrass meadows.

548   Journal of Experimental Marine Biology and Ecology 330:420–436.

549   Hemminga, M. A., and C. M. Duarte. 2000. Seagrass ecology. Cambridge University Press.

550   Henriques-Silva, R., Z. Lindo, and P. R. Peres-Neto. 2013. A community of metacommunities:

551   exploring patterns in species distributions across large geographical areas. Ecology 94:627–

552   639.

553   Jost, L. 2006. Entropy and diversity. Oikos 113:363–375.

554   Knight, N. S., C. Prentice, M. Tseng, and M. I. O'Connor. 2015. A comparison of epifaunal

555   invertebrate communities in native eelgrass Zostera marina and non-native Zostera japonica

556   at Tsawwassen, BC. Marine Biology Research 11:564–571.

557   Kraft, N. J. B., L. S. Comita, J. M. Chase, N. J. Sanders, N. G. Swenson, T. O. Crist, J. C.

558   Stegen, M. Vellend, B. Boyle, M. J. Anderson, H. V Cornell, K. F. Davies, A. L. Freestone,

559   B. D. Inouye, S. P. Harrison, and J. A. Myers. 2011. Disentangling the Drivers of beta

560   Diversity Along Latitudinal and Elevational Gradients. Science 333:1755–1758.

561   Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D.

562   Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The

563   metacommunity concept: a framework for multi-scale community ecology. Ecology Letters

564   7:601–613.

565   Leibold, M. A., and G. M. Mikkelson. 2002. Coherence, species turnover, and boundary

566   clumping: elements of meta-community structure. Oikos 97:237–250.

26

567 Light, S. F., and J. T. Carlton. 2007. The Light and Smith manual: intertidal invertebrates from

568   central California to Oregon. Univ of California Press.

569 Macdonald, T. A., B. J. Burd, V. I. Macdonald, and A. Van Roodselaar. 2010. Taxonomic and

570   feeding guild classification for the marine benthic macroinvertebrates of the Strait of

571   Georgia, British Columbia. Page Canadian Technical Report of Fisheries and Aquatic

572   Sciences.

573 Mason, B., R. Knight, and L. Boyer. 2015. Eelgrass Community Mapping Network.

574   http://cmnmaps.ca/EELGRASS/.

575 Oksanen, J., R. Kindt, P. Legendre, B. O'Hara, M. H. H. Stevens, M. J. Oksanen, and M.

576   Suggests. 2007. The vegan package. Community ecology package 10:631–637.

577 Pillai, P., A. Gonzalez, and M. Loreau. 2011. Metacommunity theory explains the emergence of

578   food web complexity. Proceedings of the National Academy of Sciences of the United

579   States of America 108:19293–19298.

580 Presley, S. J., C. L. Higgins, and M. R. Willig. 2010. A comprehensive framework for the

581   evaluation of metacommunity structure. Oikos 119:908–917.

582 R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for

583   Statistical Computing, Vienna, Austria.

584 Ricklefs, R. E. 2004. A comprehensive framework for global patterns in biodiversity. Ecology

585   Letters 7:1–15.

586 Robinson, C. L. K., J. Yakimishyn, and P. Dearden. 2011. Habitat heterogeneity in eelgrass fish

587   assemblage diversity and turnover. Aquatic Conservation-Marine and Freshwater

588   Ecosystems 21:625–635.

589   Sanders, N. J., J. P. Lessard, M. C. Fitzpatrick, and R. R. Dunn. 2007. Temperature, but not

590   productivity or geometry, predicts elevational diversity gradients in ants across spatial

591   grains. Global Ecology and Biogeography 16:640–649.

592   Searle, S. R. 1988. Parallel lines in residual plots. American Statistician 42:211.

593   Tuomisto, H. 2010. A diversity of beta diversities: straightening up a concept gone awry. Part 1.

594   Defining beta diversity as a function of alpha and gamma diversity. Ecography 33:2–22.

595   Yamada, K., M. Hori, Y. Tanaka, N. Hasegawa, and M. Nakaoka. 2007. Temporal and spatial

596   macrofaunal community changes along a salinity gradient in seagrass meadows of Akkeshi-

597   ko estuary and Akkeshi Bay, northern Japan. Hydrobiologia 592:345–358.

598

599

Table 1: Landscape attributes, diversity and aggregation estimates for epifaunal taxa in nine eelgrass meadows in Barkley Sound. Fetch was estimated by calculating the distance to nearest land from the eelgrass meadow in 10 degree increments around a centroid point and summing the distances. Diversity at the site level is reported as the number of epifaunal species (30 possible taxa, Table 2) observed in each meadow (γ_{site}) and diversity (R_{site}) estimated from extrapolated rarified estimates to 2x minimum following Chao et al (2014). Estimates of spatial aggregation (I_m) for epifaunal species (mean $\pm$ se) with significant aggregation across species are indicated in bold (95% CIs do not include 0.5). The proportion of species in meadows with significant I based on X^2 tests is given.

Site name	Abbr.	Fetch (km)	Diversity (γ_{site})	Aggregation (I_m)	Diversity R_{site}	Proportion of species with significant I
Dodger Channel	DC	32.05	17	0.47 (0.34 – 0.59)	18.2 (10.0, 26.4)	91
Wizard Islet	WI	50.53	18	0.41 (0.25 – 0.57)	19.8 (11.5, 27.8)	83
Bald Eagle Cove	BE	58.97	17	0.5 (0.34 – 0.65)	22.2 (4.78, 39.7)	90
Ellis Island	EI	97.17	13	0.44 (0.28 – 0.60)	12.3 (7.6, 16.9)	82
Robber's Passage	RP	50.55	22	**0.57** (0.51 – 0.64)	29.4 (19.6, 39.2)	93
Numukamis Bay	NB	68.72	16	0.46 (0.28 – 0.64)	19 (10.7, 27.3)	88
Crickitt Bay	CB	24.85	14	0.53 (0.37 – 0.69)	14 (9.0, 20.0)	89
Boyson Islands	BI	51.59	17	0.38 (0.21 – 0.55)	17 (12.4, 21.6)	77
Crow Cove	CC	29.41	10	**0.23** (0.03 – 0.40)	9 (8.0, 10.9)	67

29

Table 2: Relative abundance of epifaunal taxa in meadows sampled at multiple times (May [M], June/July [J], and August [A], first panel), and once (June/July [J], second panel). Numbers indicate the rank of abundances relative to other species observed in that meadow at that time. T is overall rank for each species considering all meadows. Species with significant spatial intraspecific aggregation within the meadow, estimated as Morisita's Index, are indicated in bold. Significance determined by chi-squared tests and $P < 0.05$. Grazers indicated with *.

Species	T	DC M	DC J	DC A	WI M	WI J	WI A	RP M	RP J	RP A	NB M	NB J	NB A	CB M	CB J	CB A
Crustacean																
Caprella spp.*	1	1	**1**	2	9	**5**	2	1	**1**	2	11	11	6	3	**6**	4
Aoroides columbiae￼*	7	2	**2**	3	5	11	7	3	**8**	5	--	7	8	--	**7**	13
Pentidotea resecata	8	4	**4**	5	7	**3**	5	6	**9**	8	1	**3**	4	2	**5**	8
Leptochelia dubia	9	--	16	10	10	--	--	5	**5**	7	7	**5**	12	5	**4**	2
Photis brevipes￼*	12	5	**3**	8	4	**7**	6	9	**6**	9	5	8	3	8	**8**	5
Monocorophium achersicum￼*	13	6	**6**	6	14	9	14	--	**18**	--	9	--	9	12	9	6
Unknown amphipod	15	--	**8**	--	18	15	--	10	--	--	--	--	--	7	--	--
Pontogeneia rostrata￼*	16	9	**5**	--	2	--	8	--	15	--	8	15	15	10	13	--
Harpacticoid copepod￼*	17	12	13	16	11	12	18	--	**11**	12	3	--	5	13	--	10
Eogammarus confervicolus	18	7	12	--	12	--	16	--	--	--	13	12	--	--	--	--
Ampithoe spp.*	19	11	--	15	13	14	13	--	**16**	--	14	9	10	--	--	--
Balanus spp.	21	--	--	18	--	--	15	--	**20**	16	16	14	14	--	--	17
Cirolana harfordi	23	--	15	--	8	13	17	--	**21**	--	--	--	--	--	--	--
Pugettia richii	24	13	11	11	--	--	21	--	--	15	--	--	--	--	--	--
Pandalidae	26	--	--	14	--	--	20	--	**17**	10	--	--	--	--	--	--
Pagurus quaylei	29	14	--	--	16	--	22	--	--	--	--	--	--	--	--	--
Nebalia sp.	30	--	--	--	--	--	--	--	--	--	15	--	--	--	--	15
Gastropod																
Phyllaplysia taylori￼*	2	3	10	1	15	--	9	4	**2**	1	--	13	--	--	--	--
Mytilus trossulus	3	--	14	7	--	**1**	1	--	**3**	4	4	**2**	1	14	**1**	1

Lacuna spp.*	14	10	9	--	6	**2**	11	8	**12**	11	10	10	13	15	10	12
Margarites helicinus*	20	--	--	12	--	--	10	--	--	--	--	--	--	--	--	--
Lottia pelta*	22	--	--	9	17	--	19	--	--	--	--	--	--	11	--	--
Haminoea spp.*	27	--	--	--	--	--	--	--	**19**	13	--	--	--	--	--	16
Alia carinata*	28	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Annelid																
Platynereis bicanaliculata	4	8	**7**	4	1	**4**	4	2	**4**	3	6	**6**	7	4	12	7
Janua pagastecheri	10	--	--	--	--	8	3	7	7	6	--	--	--	9	--	--
Other																
Nematode	5	--	--	13	3	15	--	--	**10**	--	12	**1**	2	--	**2**	3
Pycnogonum sp.	6	--	--	17	--	**6**	--	--	14	14	--	--	--	1	11	9
Halacard mite	11	--	--	--	--	10	--	--	13	--	2	**4**	--	6	**3**	11
Nemertea	25	--	--	--	--	--	--	--	--	17	17	--	11	--	--	14

Species	BE J	EI J	BI J	CC J
Crustacean				
Caprella spp.*	**1**	**4**	14	4
Aoroides columbiae*	10	**6**	**8**	--
Pentidotea resecata	**3**	11	**6**	5
Leptochelia dubia	16	--	**4**	7
Photis brevipes*	5	**7**	--	--
Monocorophium achersicum*	--	--	12	9
Unknown amphipod	**2**	--	**5**	3
Pontogeneia rostrata*	14	12	10	--
Harpacticoid copepod*	--	--	--	--
Eogammarus confervicolus	**8**	9	--	--
Ampithoe spp.*	--	--	15	--
Balanus spp.	--	10	--	--

Cirolana harfordi	15	--	--	--
Pugettia richii	--	--	--	--
Pandalidae	17	--	--	--
Pagurus quaylei	--	--	16	--
Nebalia sp.	--	--	--	--
Gastropod				
Phyllaplysia taylori*	9	**3**	--	--
Mytilus trossulus	**7**	**1**	**2**	1
Lacuna spp.*	**4**	--	**7**	--
Margarites helicinus*	--	--	--	--
Lottia pelta*	--	--	13	--
Haminoea spp.*	--	--	--	--
Alia carinata*	--	--	**9**	--
Annelid				
Platynereis bicanaliculata	**6**	**5**	11	--
Janua pagastecheri	12	--	--	--
Other				
Nematode	--	--	**1**	6
Pycnogonum sp.	13	**2**		8
Halacard mite	11	**8**	**3**	2
Nemertea	--	--	--	--

Table 3: Comparisons of univariate diversity metrics over time using two-way ANOVA with site and sampling time as main effects. *P < 0.01, **P < 0.001

Model	Main Effect	df	Sum Sq	Mean Sq	F
Alpha	Site	4	58.57	14.64	**2.99×10^{-4}
	Time	2	53.5	26.75	**6.47×10^{-5}
	Site*time	8	122.92	15.37	**1.15×10^{-5}
	Residuals	191	503.41	2.64	--
H'	Site	4	4.41	1.1	**3.48×10^{-5}
	Time	2	0.16	0.08	0.6
	Site*time	8	5.43	0.68	**1.06×10^{-4}
	Residuals	191	30.65	0.16	--
S	Site	4	1.91	0.3	**4.42×10^{-5}
	Time	2	0.09	0.05	0.36
	Site*time	8	1.23	0.15	**9.55×10^{-4}
	Residuals	191	8.51	0.04	--
ENS	Site	4	3.23	0.81	**1.70×10^{-5}
	Time	2	1.91	0.96	*1.18×10^{-3}
	Site*time	8	3.65	0.46	*1.38×10^{-3}
	Residuals	191	26.18	0.14	--

33

Figure 1: **A)** Seagrass is found at the coastal margins of Trevor Channel (approximately 200m deep), one of three

channels in Barkley Sound that connect freshwater sources in Alberni Inlet and Numukamis Bay with the open

Pacific Ocean. Eelgrass meadows sampled during summer 2012 between Alberni Inlet and the Pacific Ocean

southwest of Dodger Channel (DC). Five meadows were sampled in May, July and August, while four additional

meadows were sampled once in midsummer (asterisk). Site names as in Table 1. BMSC = Bamfield Marine

Sciences Centre. **B)** In each meadow, 16 plots were sampled in a grid, at least two meters from the meadow edge,

and >1 m depth. Samples were cut at the substrate (dashed line, inset).

A)
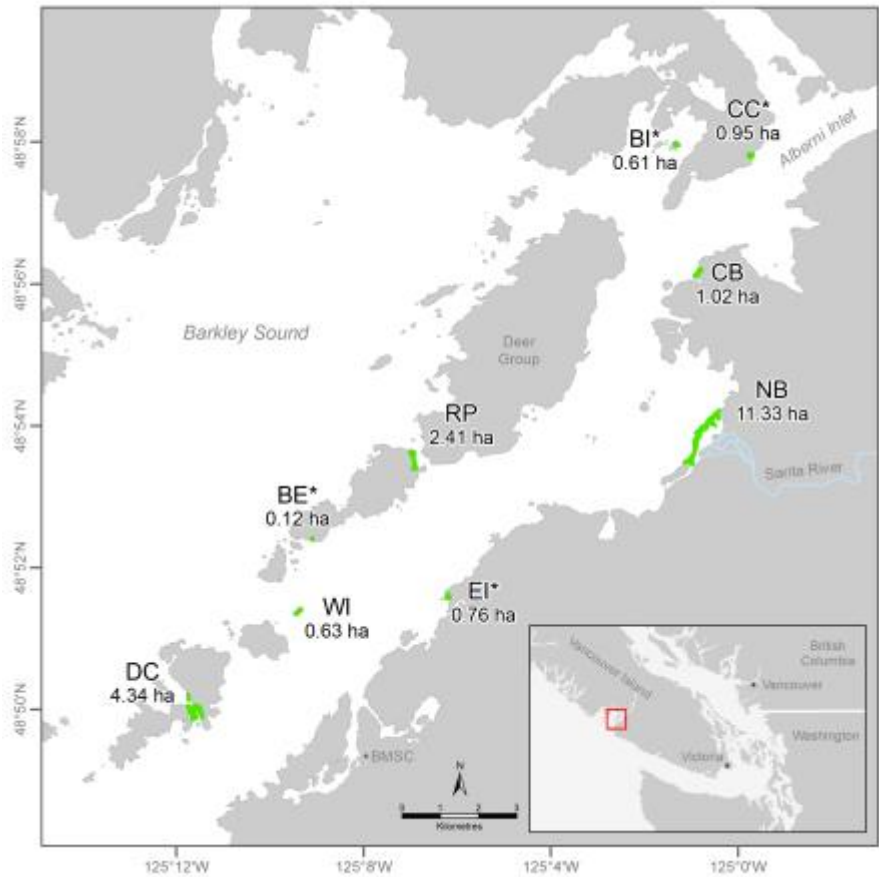
B)
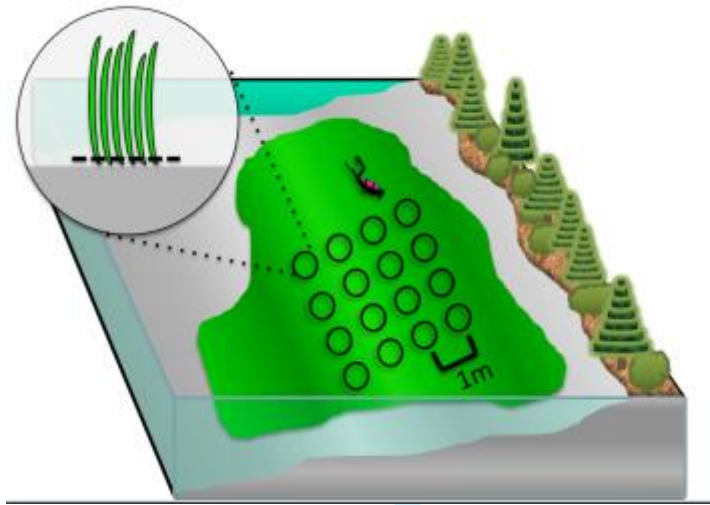
Figure 2: Fine-scale epifaunal diversity estimated from sampled plots (0.28 m², n = 16) in nine eelgrass meadows in Trevor Channel, British Columbia, in midsummer 2012. Asterisks indicate significant differences (P < 0.01) among sites, based on a one-way ANOVA. Sites are arranged left to right in terms distance from a freshwater source, with DC being the most marine and farthest from a freshwater source (Figure 1).

A)

B)

C)

D)
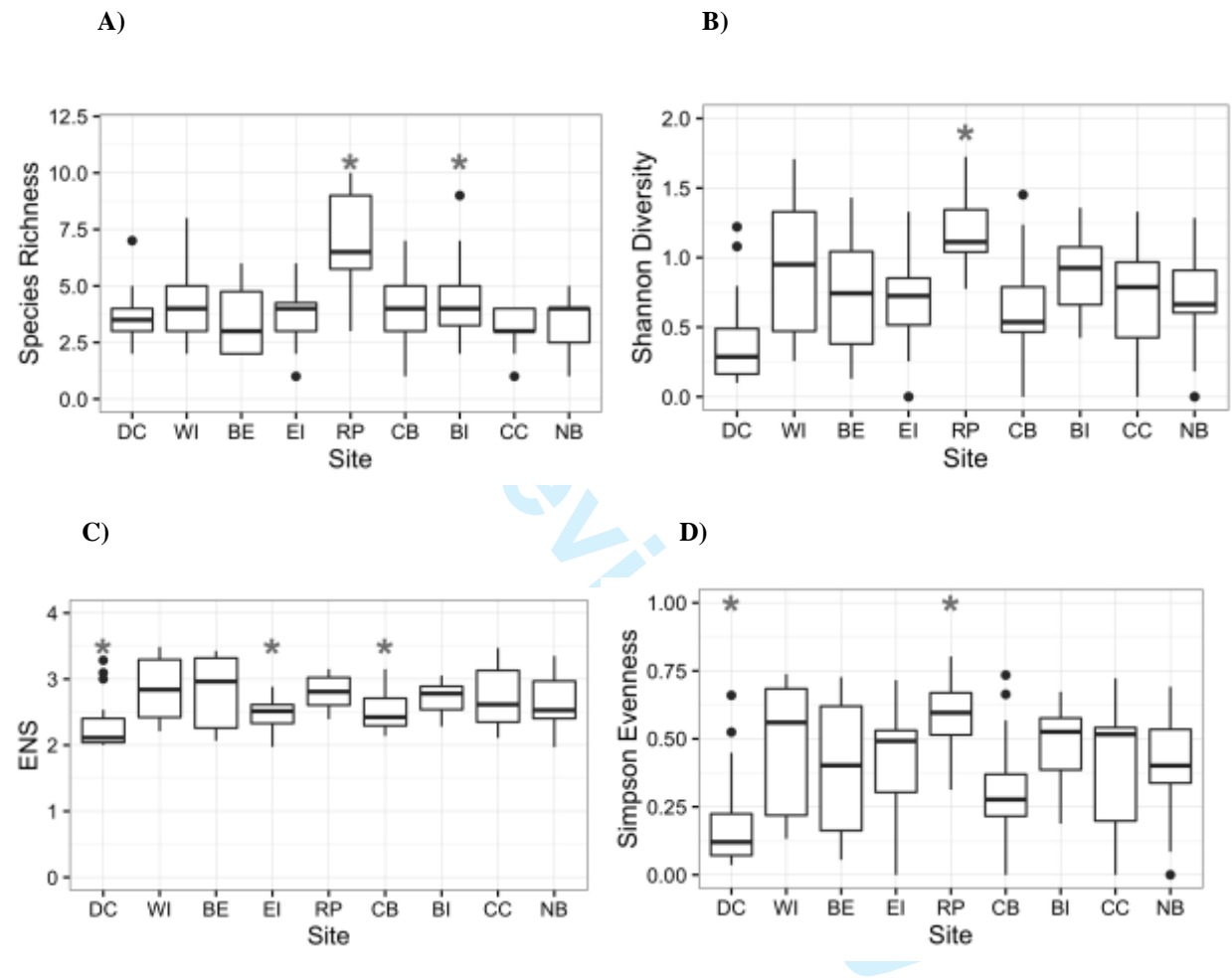
Figure 3: Temporal trends in rarified richness **(A)**, effective number of species **(B)**, shannon diversity **(C)**, simpson evenness **(D)**, and beta diversity as gamma/alpha **(E)** and mean Bray-Curtis distance **(F)** within all sites and time periods in May ("A"), June/July ("B"), and August ("C"). Site abbreviations as in Table 1.

A)

B)

C)

D)

E)

F)

Figure 4: A) Beta diversity (species composition) within and among meadows varied less than expected. Expected

beta diversity (rescaled Raup-Crick Probabilities, B_{RC}) = 0, values approaching 1 show greater dissimilarity than

null predictions, values approaching -1 show less dissimilarity than null predictions, with values at 0 being no

different from the null predictions. Comparisons show among- and within-site probabilities for 5 (light green) and 9

(dark green) meadows. Comparisons across meadows pool all meadows within each sampling time, comparisons

within meadows are pooled within each individual meadow. Box plots embedded with violin plots show median and

quartiles, and width of violin plots show kernel probability density of those variables, with wider portions being

more likely than narrower portions. **B)** nMDS of community composition and abundance in mid-summer across all

sites using Bray-Curtis metric. 2-D stress = 0.23.

A)

B)

PCoA 1
method = "bray"
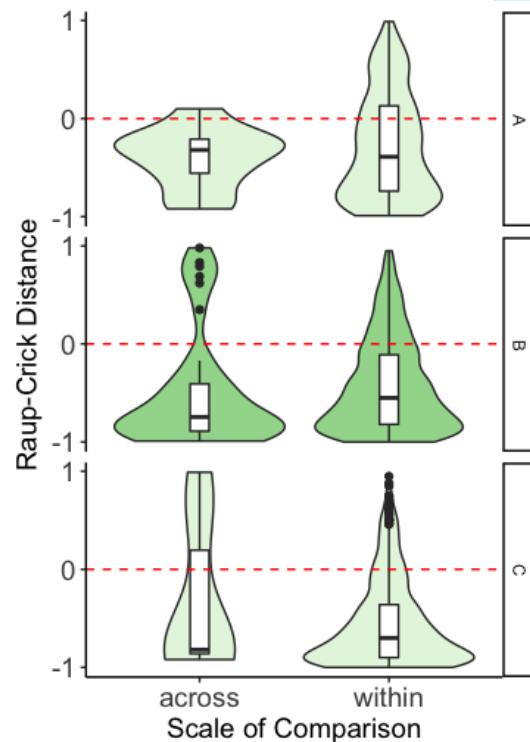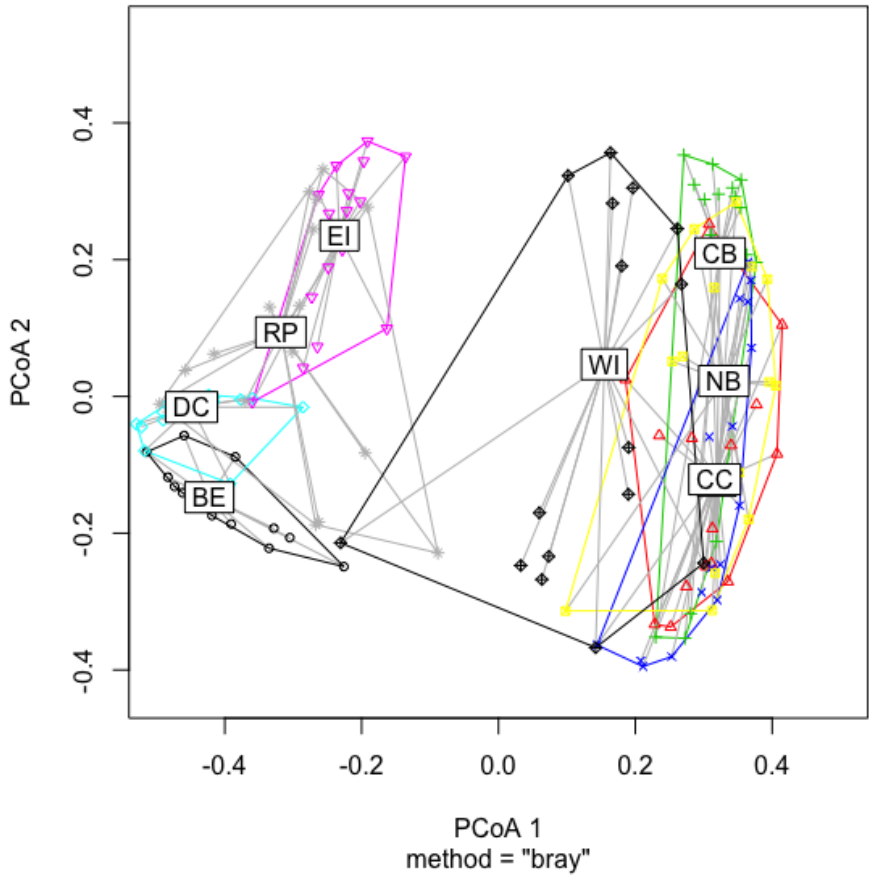
Appendix

Table S1: Mean shoot density and leaf area (cm^2) with standard error (SE), and mean epiphyte load standardized as grams of epiphyte per gram of seagrass (dried weight) for patches of eelgrass meadow (0.28m^2) sampled in May, July, and August 2012.

Month	Site	Mean Shoot Density	SE Shoot Density	Mean Leaf Area	SE Leaf Area	Mean Epiphyte Load
May	DC	12.3	±1.4	8037	±2229	0.02
	WI	8	±2.3	3928	±1866	0.11
	RP	7.7	±1.5	2245	±5	0.16
	NB	6.5	±0.3	1593	±476	0.09
	CB	4	±1.0	1903	±704	0.05
July	DC	14.8	±2.0	9257	±1493	0.07
	WI	12.5	±1.8	5608	±1223	0.15
	BE	7	±1.5	2542	±787	0.04
	EI	12.5	±1.2	6246	±1078	0.03
	RP	10.3	±1.8	4372	±1576	0.04
	NB	8.3	±3.1	5062	±2285	0.09
	CB	6.5	±0.9	2885	±381	0.04
	BI	5.5	±1.4	2811	±1315	0.05
	CC	6	±2.2	3576	±1736	0.02
August	DC	12.7	±1.9	7902	±1213	0.01
	WI	7.8	±1.8	4611	±392	0.08
	RP	8	±1.8	4514	±781	0.03
	NB	9.5	±0.6	4302	±1216	0.06
	CB	7.3	±1.1	3562	±537	0.02

41

Table S2: Model results for tests of relationships between abiotic and biotic meadow attributes. In all models, intercepts were allowed to vary randomly among meadows: dfw – distance from fresh water input.

Model	df	logLik	AICc	Delta	Wt
Salinity					
Y ~ dfw	**4**	**-418.12**	**844.5**	**0**	**0.629**
Y ~ temp+dfw	**5**	**-417.64**	**845.7**	**1.18**	**0.343**
Y ~ temp*dfw	6	-419.04	850.7	6.17	0.028
Y ~ temp	4	-422.87	854.0	9.50	0.005
Y ~ 1	3	-424.32	854.8	10.27	0.004
Y ~ temp+dfw+fetch	6	-428.54	869.7	25.16	0.000
Y ~ fetch	4	-434.09	876.5	31.94	0.000
Temperature					
Y ~ dfw	**4**	**-328.31**	**664.9**	**0**	**0.434**
Y ~ 1	**3**	**-329.69**	**665.5**	**0.64**	**0.315**
Y ~ Sal	**4**	**-329.23**	**666.7**	**1.84**	**0.173**
Y ~ Sal + dfw	5	-328.97	668.4	3.47	0.076
Y ~ Sal*dfw	6	-332.06	676.7	11.83	0.001
Y ~ fetch	4	-340.49	689.3	24.35	0.000
Y ~ Sal+dfw+fetch	6	-340.05	692.7	27.80	0.000
Shoot Density					
Y ~ dfw	**4**	**-92.90**	**195.2**	**0**	**1.000**
Y ~ 1	3	-105.79	218.3	23.15	0.000
Leaf Area					
Y ~ dfw	**4**	**-306.82**	**623.0**	**0**	**0.998**
Y ~ 1	3	-314.42	635.6	12.62	0.002
Epiphytes					
Y ~ 1	**3**	**6.87**	**-2.9**	**0**	**0.999**
Y ~ dfw	4	3.01	12.0	14.92	0.001

Table S3: Mean summer temperature and salinity values (May – August 2012) with standard error (SE).

Site	Mean Temperature	SE Temperature	Mean Salinity	SE Salinity
DC	12.6	±0.2	25.7	±0.6
WI	13.7	±0.2	21.7	±0.5
RP	14.1	±0.3	22.4	±0.4
NB	14.9	±0.4	16.6	±0.5
CB	14.8	±0.5	17.3	±0.5

Table S4: Mean epiphyte loads ± standard error at the three sites in June (period B) and August (period C) 2012.

Epiphyte load is standardized to seagrass dry weight in grams. Bladed epiphytes are *Punctaria* sp.

Site	Bladed epiphyte load		Periphyton load	
	<u>Jun</u>	<u>Aug</u>	<u>Jun</u>	<u>Aug</u>
DC	0.45 ± 0.05 (14)	0.15 (1)	0.56 ± 0.06 (15)	0.56 ± 0.05 (15)
WI	0.04 ± 0.03 (7)	0.43 ± 0.12 (13)	0.61 ± 0.07 (15)	0.57 ± 0.04 (15)
NB	--	0.12 (1)	0.87 ± 0.08 (15)	1.05 ± 0.12 (15)

Table S5: Model selection results for a set of candidate models predicting plot-level (n = 9) univariate richness indices across nine eelgrass meadows in July 2011. The top-ranked model is listed first in each group; models with delta > 2 are considered to have little support by the data.

Model			df	logLik	AICc	Delta	Wt
Alpha							
	G	Y ~ site	10	-234.49	490.8	0	1
	D	Y ~ 1	2	-262.61	529.3	38.46	0
	.	Y ~ area	3	-261.96	530.1	39.26	0
	B	Y ~ dfw	3	-262.25	530.7	39.83	0
	A	Y ~ fetch	3	-262.6	531.4	40.54	0
	C	Y ~ dfw*fetch	5	-262.23	534.9	44.1	0
	F	Y ~ area*fetch	5	-262.35	535.2	44.33	0
H'							
	G	Y ~ site	10	-51.28	124.4	0	0.999
	C	Y ~ dfw*fetch	5	-64.17	138.8	14.39	0.001
	B	Y ~ dfw	3	-67.36	140.9	16.48	0
	F	Y ~ area*fetch	5	-65.66	141.8	17.37	0
	A	Y ~ fetch	3	-68.52	143.2	18.8	0
	D	Y ~ 1	2	-69.96	144	19.58	0
	.	Y ~ area	3	-69.69	145.6	21.15	0
S							
	G	Y ~ site	10	27.76	-33.7	0	0.945
	C	Y ~ dfw*fetch	5	18.67	-26.9	6.81	0.031
	F	Y ~ area*fetch	5	17.93	-25.4	8.29	0.015
	B	Y ~ dfw	3	14.96	-23.7	9.94	0.007
	A	Y ~ fetch	3	13.35	-20.5	13.16	0.001
	D	Y ~ 1	2	11.63	-19.2	14.5	0.001
	.	Y ~ area	3	12.21	-18.2	15.45	0
ENS							
	G	Y ~ site	10	-52.19	126.2	0	0.628
	C	Y ~ dfw*fetch	5	-59.21	128.9	2.66	0.166
	F	Y ~ area*fetch	5	-59.78	130	3.8	0.094
	.	Y ~ area	3	-62.56	131.3	5.07	0.05
	B	Y ~ dfw	3	-63.13	132.4	6.2	0.022

| A | Y ~ fetch | 3 | -63.13 | 133.1 | 6.8 | 0.016 |
| D | Y ~ 1 | 2 | -64.88 | 133.9 | 7.62 | 0.011 |

Table S6: Values of beta diversity within each site per time period expressed as gamma/mean alpha, and mean

Bray-Curtis dissimilarity

Site	Beta (gamma/alpha)			Beta (Bray-Curtis)		
	A	B	C	A	B	C
DC	5.5133	5.7523	3.5714	0.4012	0.4041	0.2908
WI	4.4519	4.295	2.214	0.7253	0.6442	0.4167
BE	NA	6.0095	NA	NA	0.3683	NA
EI	NA	3.9396	NA	NA	0.4152	NA
RP	6.7528	2.0041	3.1348	0.3616	0.5112	0.3318
NB	5.8785	5.6306	4.9355	0.5185	0.5407	0.4779
CB	7.8462	6.6667	3.1566	0.3915	0.6733	0.6062
BI	NA	4.1469	NA	NA	0.5719	NA
CC	NA	7.6588	NA	NA	0.5486	NA

FIGURE S7: Beta diversity (species composition) within and among meadows varied less than expected. Expected beta diversity (rescaled Raup-Crick Probabilities, B_{RC}) = 0, values approaching 1 show greater dissimilarity than null predictions, values approaching -1 show less dissimilarity than null predictions, with values at 0 being no different from the null predictions. Comparisons show among-site probabilities for 9 meadows over the course of summer 2012 (May = A, June/July = B, August = C). Box plots embedded with violin plots show median and quartiles, and width of violin plots show kernel probability density of those variables, with wider portions being more likely than narrower portions.

Figure 1: A) Seagrass is found at the coastal margins of Trevor Channel (approximately 200m deep), one of three channels in Barkley Sound that connect freshwater sources in Alberni Inlet and Numukamis Bay with the open Pacific Ocean. Eelgrass meadows sampled during summer 2012 between Alberni Inlet and the Pacific Ocean southwest of Dodger Channel (DC). Five meadows were sampled in May, July and August, while four additional meadows were sampled once in midsummer (asterisk). Site names as in Table 1. BMSC = Bamfield Marine Sciences Centre.
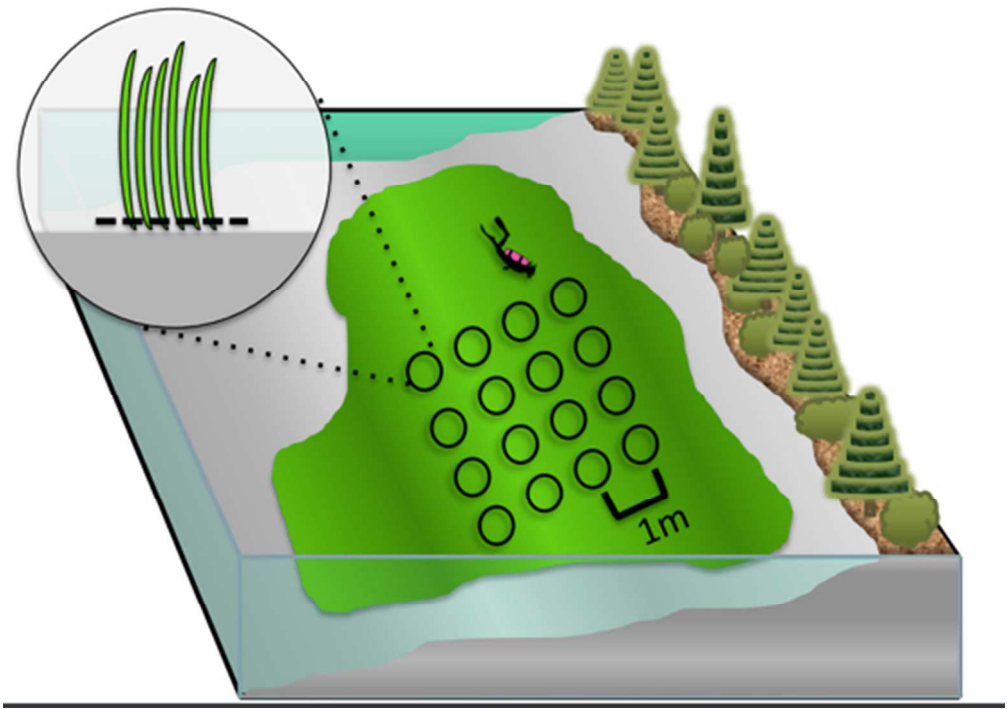
Figure 1: . B) In each meadow, 16 plots were sampled in a grid, at least two meters from the meadow edge, and >1 m depth. Samples were cut at the substrate (dashed line, inset).
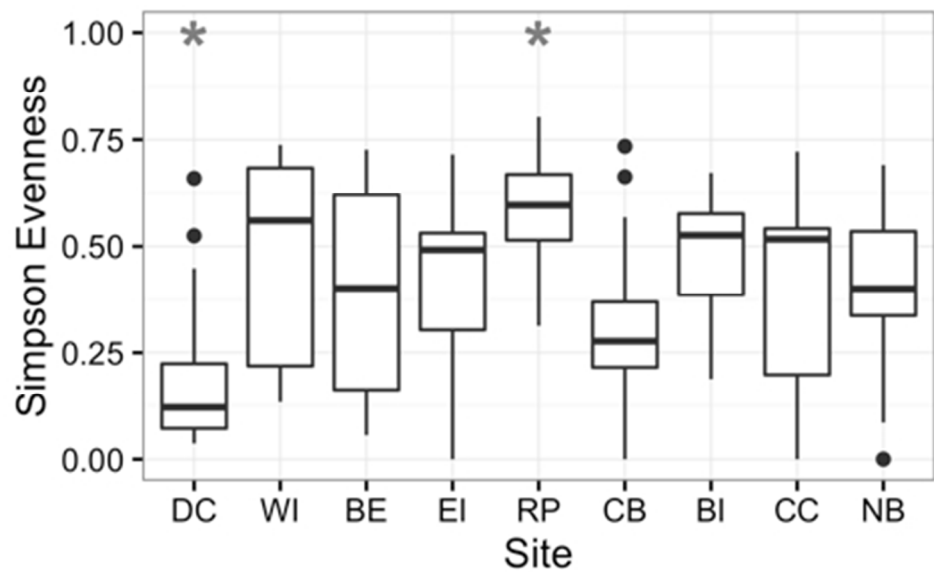
Figure 2: Fine-scale epifaunal diversity estimated from sampled plots (0.28 m2, n = 16) in nine eelgrass meadows in Trevor Channel, British Columbia, in midsummer 2012. Asterisks indicate significant differences (P < 0.01) among sites, based on a one-way ANOVA. Sites are arranged left to right in terms distance from a freshwater source, with DC being the most marine and farthest from a freshwater source (Figure 1).
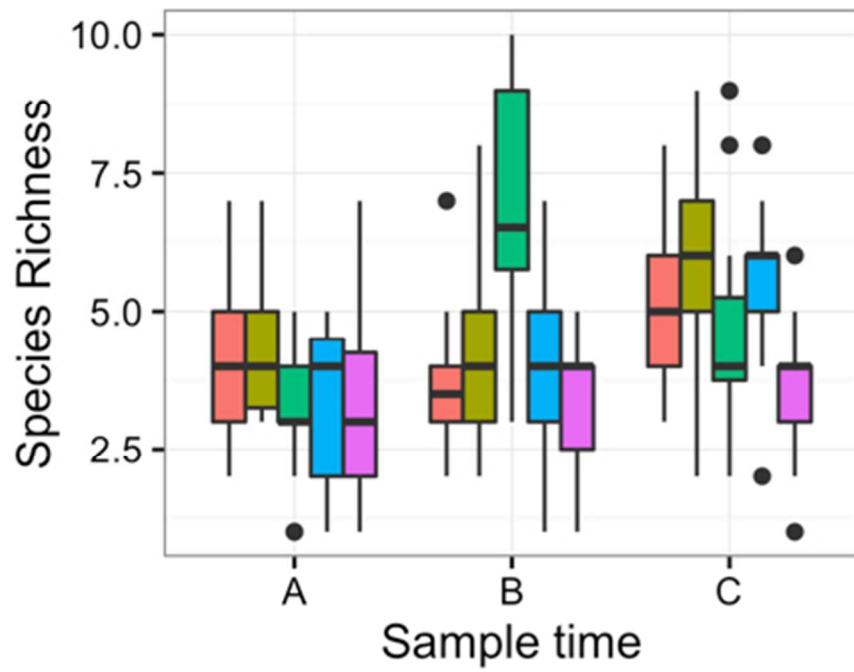
Figure 2: Fine-scale epifaunal diversity estimated from sampled plots (0.28 m2, n = 16) in nine eelgrass meadows in Trevor Channel, British Columbia, in midsummer 2012. Asterisks indicate significant differences (P < 0.01) among sites, based on a one-way ANOVA. Sites are arranged left to right in terms distance from a freshwater source, with DC being the most marine and farthest from a freshwater source (Figure 1).

Figure 2: Fine-scale epifaunal diversity estimated from sampled plots (0.28 m2, n = 16) in nine eelgrass meadows in Trevor Channel, British Columbia, in midsummer 2012. Asterisks indicate significant differences (P < 0.01) among sites, based on a one-way ANOVA. Sites are arranged left to right in terms distance from a freshwater source, with DC being the most marine and farthest from a freshwater source (Figure 1).

Figure 2: Fine-scale epifaunal diversity estimated from sampled plots (0.28 m2, n = 16) in nine eelgrass meadows in Trevor Channel, British Columbia, in midsummer 2012. Asterisks indicate significant differences (P < 0.01) among sites, based on a one-way ANOVA. Sites are arranged left to right in terms distance from a freshwater source, with DC being the most marine and farthest from a freshwater source (Figure 1).

Figure 3: Temporal trends in rarified richness (A)
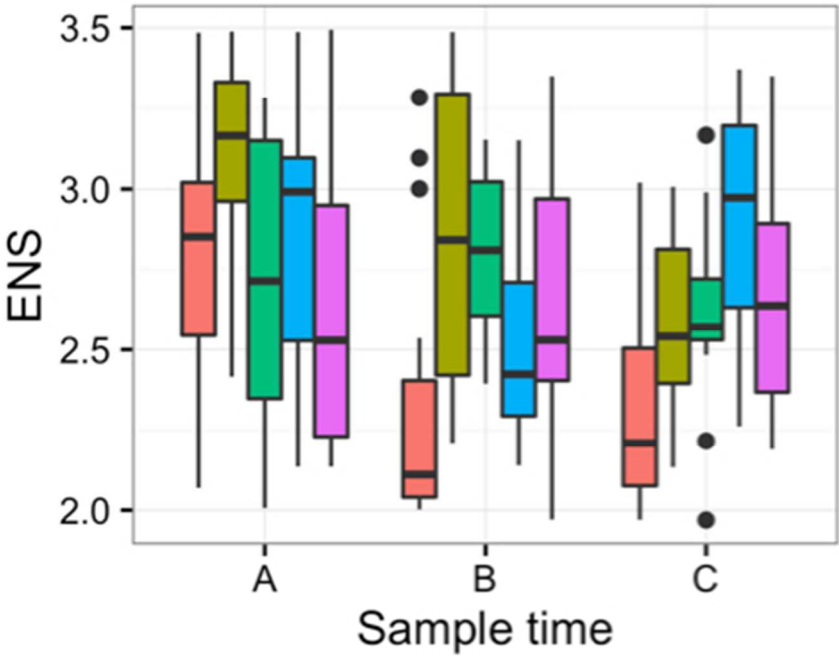
Figure 3: Temporal trends in effective number of species (B)
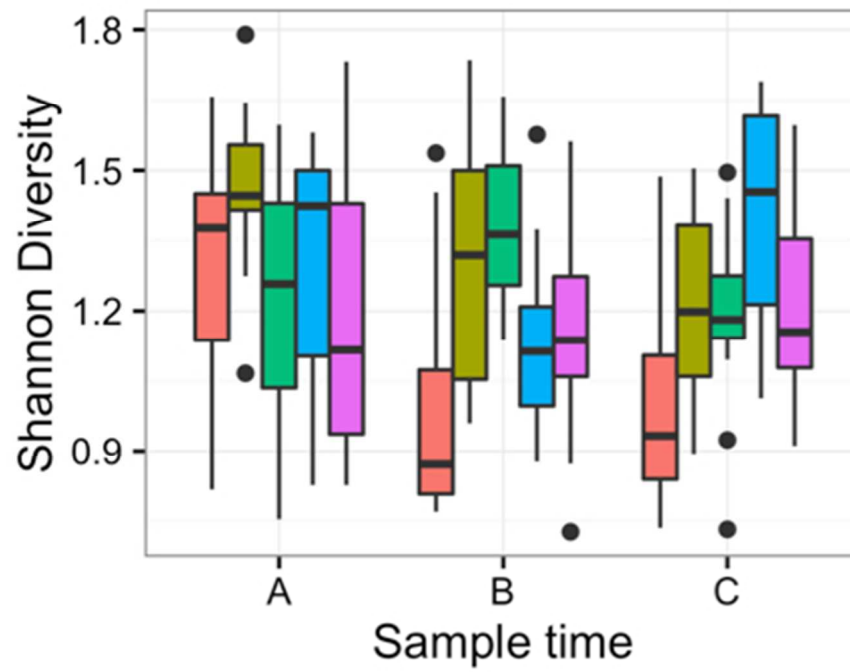
Temporal trends in Shannon diversity (C)
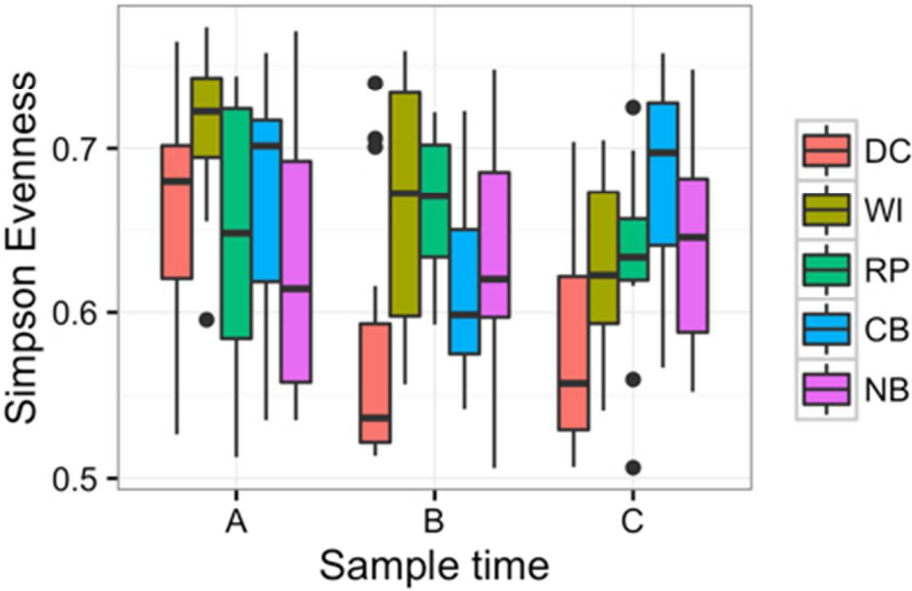
Temporal trends in Simpson evenness (D)
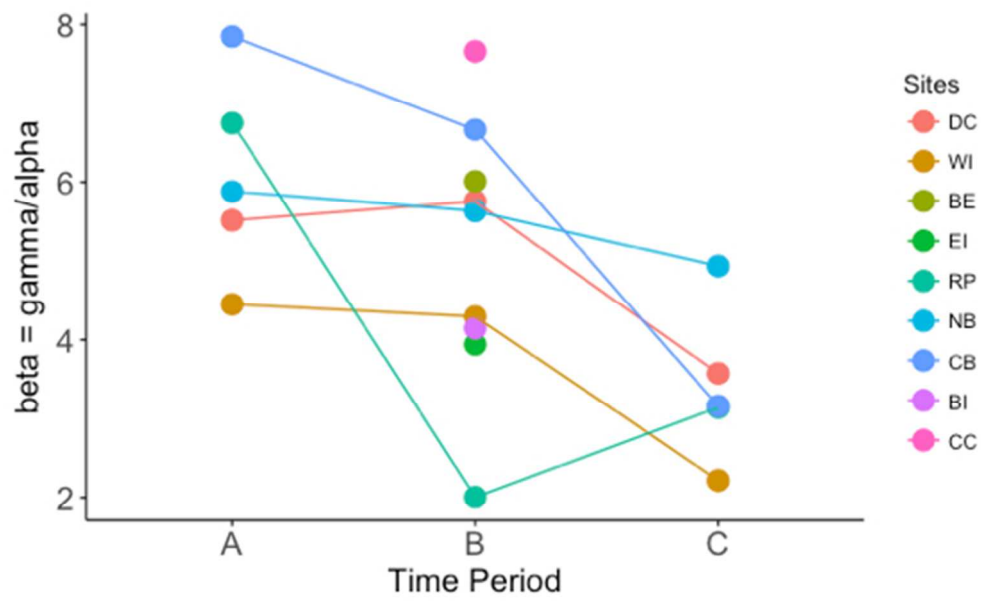
Temporal trends in beta diversity as gamma/alpha (E
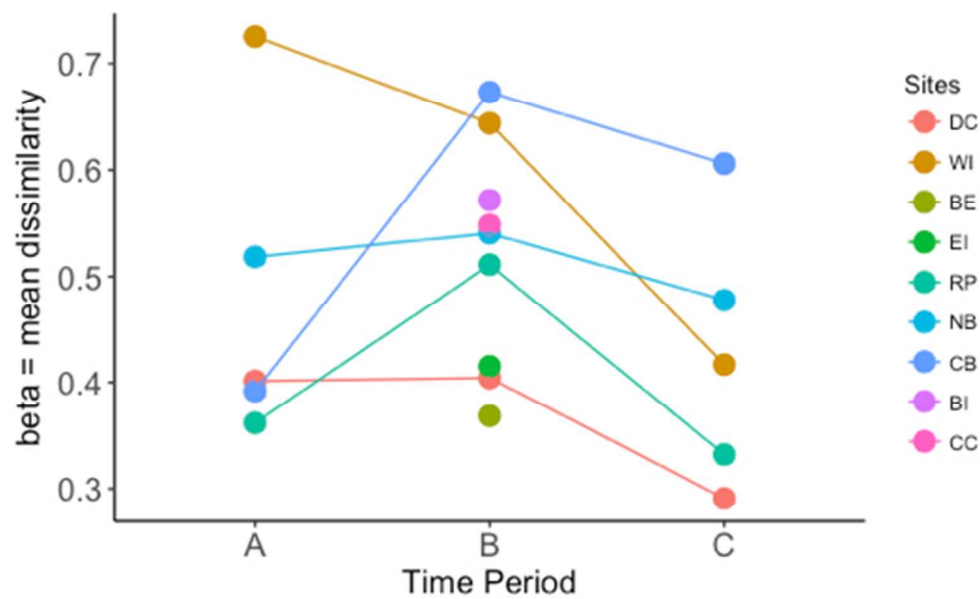
Temporal trends in mean Bray-Curtis distance (F) within all sites and time periods in May ("A"), June/July ("B"), and August ("C"). Site abbreviations as in Table 1.
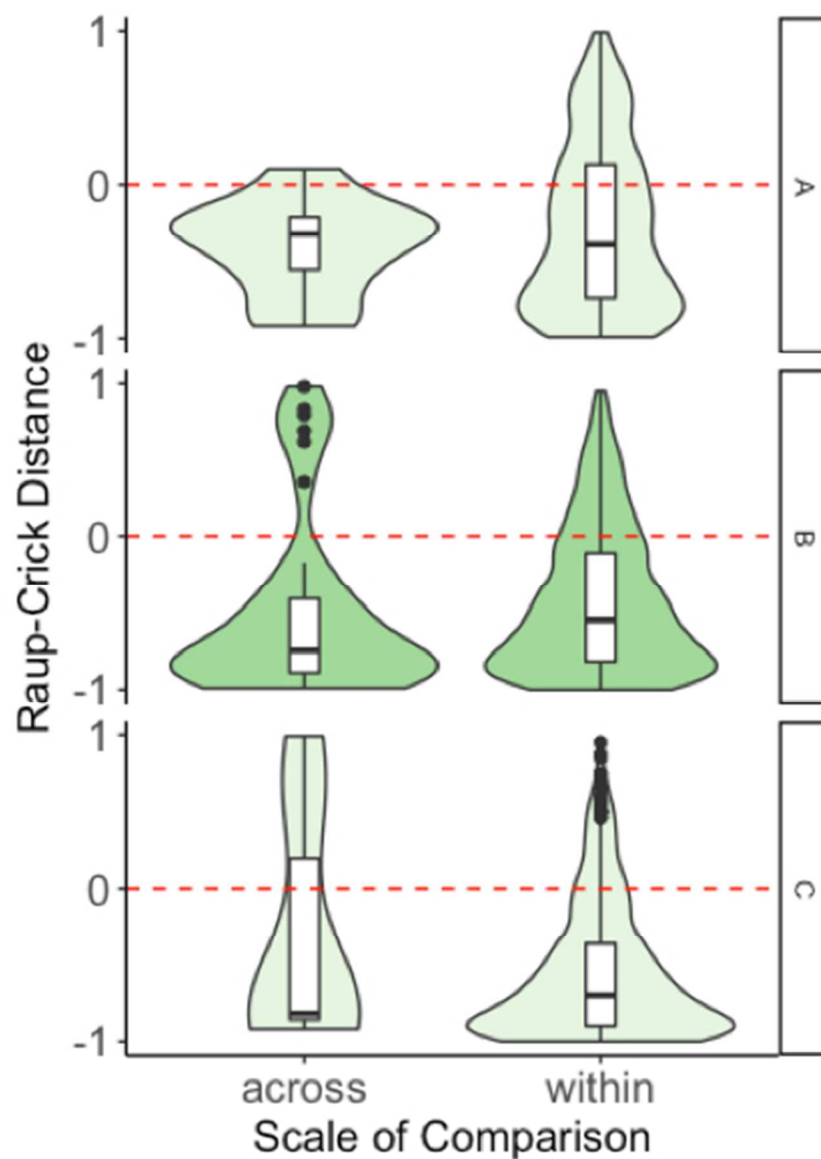
Figure 4: A) Beta diversity (species composition) within and among meadows varied less than expected. Expected beta diversity (rescaled Raup-Crick Probabilities, BRC) = 0, values approaching 1 show greater dissimilarity than null predictions, values approaching -1 show less dissimilarity than null predictions, with values at 0 being no different from the null predictions. Comparisons show among- and within-site probabilities for 5 (light green) and 9 (dark green) meadows. Comparisons across meadows pool all meadows within each sampling time, comparisons within meadows are pooled within each individual meadow. Box plots embedded with violin plots show median and quartiles, and width of violin plots show kernel probability density of those variables, with wider portions being more likely than narrower portions.
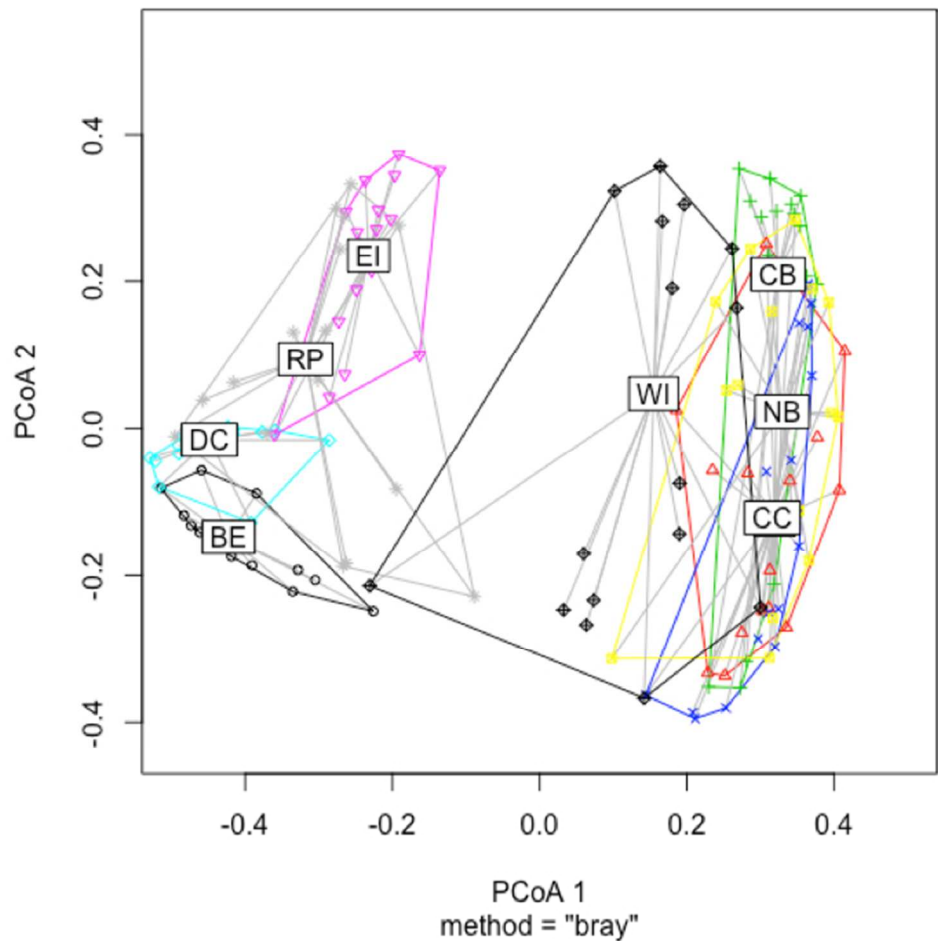
Figure 4: B) nMDS of community composition and abundance in mid-summer across all sites using Bray-Curtis metric. 2-D stress = 0.23.
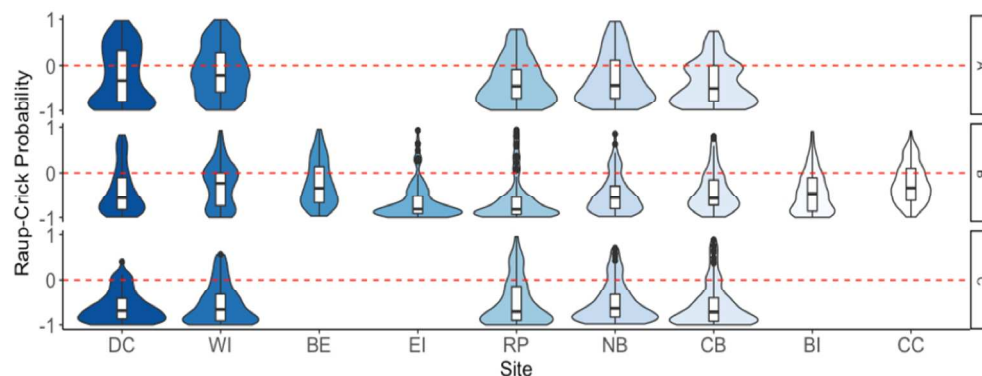
FIGURE S7: Beta diversity (species composition) within and among meadows varied less than expected. Expected beta diversity (rescaled Raup-Crick Probabilities, BRC) = 0, values approaching 1 show greater dissimilarity than null predictions, values approaching -1 show less dissimilarity than null predictions, with values at 0 being no different from the null predictions. Comparisons show among-site probabilities for 9 meadows over the course of summer 2012 (May = A, June/July = B, August = C). Box plots embedded with violin plots show median and quartiles, and width of violin plots show kernel probability density of those variables, with wider portions being more likely than narrower portions.