1  **Beyond a single patch: local and regional processes explain diversity patterns in a seagrass**
2  **epifaunal metacommunity**
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57

## 58    Abstract

59    Ecological communities are jointly structured by dispersal, density-independent responses to

60    environmental conditions and density-dependent biotic interactions. Metacommunity ecology

61    provides a framework for understanding how these processes combine to determine community

62    composition among local sites that are regionally connected through dispersal. In 17 temperate

63    seagrass meadows along the British Columbia coast, we tested the hypothesis that eelgrass

64    (*Zostera marina* L.) epifaunal invertebrate assemblages are influenced by local environmental

65    conditions, but that high dispersal rates at larger spatial scales dampen effects of environmental

66    differences. We used hierarchical joint species distribution modelling to understand the

67    contribution of environmental conditions, spatial distance between meadows, and species co-

68    occurrences to epifaunal invertebrate abundance and distribution across the region. We found

69    that patterns of taxonomic compositional similarity among meadows were inconsistent with

70    dispersal limitation and meadows in the same region were often no more similar to each other

71    than meadows over 1000 km away. Abiotic environmental conditions (temperature, dissolved

72    oxygen) explained a small fraction of variation in taxonomic abundances patterns across the

73    region. We found novel co-occurrence patterns among taxa that could not be explained by shared

74    responses to environmental gradients, suggesting the possibility that interspecific interactions

75    influence seagrass invertebrate abundance and distribution. Our results add to mounting evidence

76    that suggests that the biodiversity and ecosystem functions provided by seagrass meadows reflect

77    ecological processes occurring both within meadows and across seascapes, and suggest that

78    management of eelgrass habitat for biodiversity may be most effective when both local and

79    regional processes are considered.

80

81    **Key words:** Hierarchical Modelling of Species Communities, priority effects, dispersal, niche

82    filtering, British Columbia, *Zostera marina*

83

84    **Introduction**

85        Understanding how local environmental conditions, regional connectivity by dispersal and

86    biotic interactions jointly structure the composition of communities is a central challenge in

87    ecology (Ricklefs and Schluter 2003, Vellend 2010, Leibold and Chase 2017). Metacommunity

88    ecology (Leibold et al. 2004, Leibold and Chase 2017, Thompson et al. 2020) offers a

89    framework for understanding community assembly processes across spatial scales. In recent

90    years, applications of the metacommunity framework have emphasized the underlying processes

91    that give rise to abundance and diversity patterns (Brown et al. 2017, Leibold and Chase 2018,

92    Thompson et al 2020). Thompson et al. (2020) framed the metacommunity concept based on

93    three fundamental processes that together govern the dynamics of populations and communities:

94    1) Density-independent responses to environmental conditions, 2) Density-dependent biotic

95    interactions (ie. inter and intra-specific competition, predation or facilitation influencing

96    population growth and co-existence), and 3) Dispersal influencing connectivity across a

97    landscape or seascape. We apply this framework to understand the contribution of these

98    processes to a seagrass-associated invertebrate metacommunity.

99        Many coastal environments that host high biodiversity occupy spatially structured habitats

100   (e.g. coral reefs, kelp forests, seagrass meadows), and many marine species have dispersing life

101   histories that link populations in distinct habitat patches. The importance of interspecific

102   interactions (Berlow 1999, Sala and Graham 2002), and dispersal-driven population dynamics

103   (Levin and Paine 1974, Gaines and Roughgarden 1985) in coastal and marine communities has

104   long been recognized.  These combined roles of dispersal, the local environment, and biotic

105   interactions suggest patterns of marine biodiversity reflect metacommunity processes (Boström

106   et al. 2006).

107    Seagrasses are foundation species that support high productivity and faunal diversity (Orth et

108   al. 1984, Duffy et al. 2015). They form meadows separated by deeper water, un-vegetated

109   seafloor, or other vegetated habitats, and associated fauna disperse among meadows (Boström et

110   al. 2006, 2011). Diverse invertebrate assemblages including snails, amphipods, isopods, and

111   polychaete worms live among seagrass leaves, providing food sources for larger invertebrates,

112   fish, and birds (Best and Stachowicz 2014, Huang et al. 2015). The grazers within this group

113    consume detritus, macroalgae, or the seagrass itself (Valentine and Heck 1999), and many taxa

114    exert top-down control on epiphytic microalgae that compete with the seagrass for light and

115    nutrients (Sand-Jensen 1977, Duffy and Stachowicz 2006). Seagrass-associated epifauna exhibit

116    a range of dispersal modes (fast swimming by isopods; slow crawling by snails; permanent

117    attachment in bivalves) and reproductive strategies (brooding versus broadcast spawning) which

118    influence dispersal rates and the distances over which meadows are demographically connected.

119    Seagrass meadows occur in a wide range of temperature, salinity and hydrodynamic

120    environments, such that meadows may differ in their suitability for various invertebrate taxa

121    (Yamada et al. 2007, 2014).  Evidence for the importance of environmental filtering -- or the

122    tendency for taxa to exist where local environmental conditions are ideal -- has been reported in

123    several seagrass-associated fish and invertebrate systems (Baden et al. 2010, Robinson et al.

124    2011, Iacarella et al. 2018).

125    Though interspecific interactions among seagrass-associated invertebrates are not extensively

126    documented, there is some evidence of competition and predation influencing community

127    structure (Nelson 1979, Best and Stachowicz 2014). Predation can reduce abundances of

128    vulnerable invertebrate taxa, allowing others to increase in abundance (Nelson 1979, Baden et al.

129    2010, Best and Stachowicz 2014, Amundrud et al. 2015, Huang et al. 2015). Despite some

130    evidence for competition among epiphytic grazers for shared food sources (Edgar 1990, Bruno

131    and O'Connor 2005) there is no evidence of competitive dominance to the point of exclusion in

132    the field (Nelson 1979, Best and Stachowicz 2014).

133    While research in past decades has found evidence for direct and indirect influences of local

134    characteristics such as habitat complexity (Orth et al. 1984), primary biomass (Cébrian and

135    Duarte 1998, Gullström et al. 2012), and nutrient availability (Virnstein and Howard 1987) on

136      faunal diversity and abundance, recent studies have focused more on regional scale or multi-

137      meadow processes such as dispersal (Whippo et al. 2018, Lefcheck et al. 2016, Stier et al. 2019,

138      Yeager et al. 2019), and have found that the influence of local-scale factors are often overriden

139      by regional patterns of inter-meadow connectivity (Lefcheck et al. 2016, Stier et al. 2019, Yeager

140      et al. 2019). This pattern has been attributed to relatively rapid life histories and high inter-

141      meadow dispersal in seagrass-associated organisms (Lefcheck et al. 2016).

142      We designed this study to better understand the contributions of dispersal, local

143      environmental conditions, and interspecific interactions with the largest spatially explicit (in

144      geographic extent) dataset of seagrass metacommunity diversity. Drawing upon metacommunity

145      theory, we tested the hypotheses that: (H1) Spatial distance *per se* within a region does not

146      confer community dissimilarity because meadows are well-connected by dispersal, even at larger

147      spatial scales (*dispersal limitation hypothesis*); (H2) Differences in local-scale environmental

148      factors such habitat structure, temperature, and salinity drive some differences in invertebrate

149      presence and abundance owing to differences in environmental niches among taxa, however the

150      contribution of environmental factors is smaller than the contribution of spatial distance/

151      dispersal (*environmental filtering hypothesis*); (H3) No clear patterns of spatial co-occurrence

152      among epifaunal species emerge because high dispersal and environmental responses override

153      signatures of biotic interactions (predation, competition) that would produce such patterns (*biotic*

154      *interactions hypothesis*).

155

156      **Methods**

157      *Study sites*

158      We sampled epifaunal invertebrate diversity in 17 *Zostera marina* (L.) meadows

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159    spanning the entire coast of British Columbia (approximately 1000 km distance) from late June

160    through August of 2017. Within five regions that each contain numerous eelgrass meadows, we

161    sampled a few meadows for our study (Fig. 1a): Haida Gwaii (two meadows); the central coast

162    of BC near Calvert Island (four meadows); southern Clayoquot Sound (three meadows); Barkley

163    Sound on the West coast of Vancouver Island (three meadows); the Southern Gulf Islands (five

164    meadows). Meadows varied in environmental conditions, such as seagrass shoot size and

165    density, hydrological regimes, and freshwater outflow influencing salinity.

166

167    *Field sampling*

168        We sampled three subtidal meadows with SCUBA in the Barkley Sound (SA, DC, RB)

169    and Central Coast (TB, TB, CI, CS) regions.  All others were sampled by wading or snorkeling

170    at low tide. We conducted collections within a six-week period of peak seagrass growth. We

171    used 0.25 m x 0.25 m quadrats to collect all above-ground eelgrass, epifaunal invertebrates,

172    eelgrass detritus, and macroalgae in each sample, following Whalen et al. (2013). Six quadrats

173    were arranged in a 15 m x 30 m array (Appendix 1: Fig. S1) in the middle of the meadow to

174    avoid edge effects. We uprooted eelgrass shoots at the first node, leaving rhizomes to avoid

175    sampling infauna that live in the sediments, removed all other above-ground biomass (detritus,

176    macroalgae, associated epifauna) within each quadrat by hand, and immediately placed all the

177    contents into a 300 μm mesh or plastic Ziploc bag for transport to the lab.

178

179    *Environmental data*

180        We acquired water quality data from regional data sources. The abiotic water quality data

181    were annual means pulled from Bio-ORACLE (Assis et al. 2018), including oxygen, nitrates,

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182    phosphates, silicates, salinity, maximum current velocity and sea surface temperature. Bio-

183    ORACLE is a database of marine environmental layers gathered from several satellite and in-situ

184    sources at a spatial resolution of 0.08°, and has been shown to accurately model distributions of

185    shallow-water invertebrate species (Tyberghein et al. 2012, Assis et al. 2018). Sea surface

186    temperature layers were taken from the Aqua-MODIS satellite, and values for nitrates, dissolved

187    oxygen, and salinity were interpolated from in-situ measurements reported in the World Ocean

188    Database (Tyberghein et al. 2012). All meadows were situated in distinct spatial cells, and thus

189    had distinct values for the aforementioned variables. We excluded phosphate and silicate

190    concentrations from our final analysis, as they strongly covaried with nitrates.

191        In each quadrat sample, we measured four biotic attributes summarizing habitat structure

192    and food availability: eelgrass leaf area index (LAI), and eelgrass, eelgrass detritus, and algal dry

193    mass. To quantify LAI, we measured leaf length, width, and blade number in five haphazardly-

194    chosen shoots from each quadrat, and multiplied the average blade area per shoot by the quadrat-

195    level shoot density. We dried eelgrass, detritus, and macroalgae in a desiccator oven (60° C for

196    48 hours) to measure ash-free dry mass.

197

198    *Invertebrate identification*

199        Immediately after collection, we rinsed eelgrass shoots with fresh water, passing the

200    water through a 500 μm sieve to remove epifaunal invertebrates. Invertebrates were preserved in

201    95% EtOH for identification with light microscopy (10x magnification). We identified

202    invertebrates to the lowest taxonomic level possible using keys in the Light and Smith manual

203    (Carlton 2007) and Kozloff (1996). In many cases, the lowest taxonomic resolution possible was

204    family or genus, therefore our biodiversity survey likely underestimates full species diversity.

205

206    *Analysis*

207         All statistical analyses were conducted in R (version 3.6.0; R Development Core Team

208    2019. We followed the Hierarchical Modelling of Species Communities (HMSC) framework

209    (Ovaskainen et al. 2017) using the 'Hmsc-R' package (Tikhonov et al. 2019) to fit a hierarchical

210    joint species distribution model (JDSM) with Bayesian inference. The framework uses traditional

211    single-species distribution modelling by estimating species responses (presence or abundance) to

212    environmental covariates across samples, but does so for all species simultaneously. It can use

213    residual variation in occurrences to infer species co-occurrence patterns that do not result from

214    shared responses to environmental covariates in the model (Ovaskainen et al. 2017). HMSC can

215    also account for spatially hierarchical sampling structures. In these ways, the HMSC framework

216    overcomes statistical limitations of previous methods used in metacommunity studies (Gilbert and

217    Bennett 2010, Tuomisto et al. 2012, Brown et al. 2017).

218         Each individual species distribution model within the JDSM is a generalized linear model

219    that describes the abundance of species $j$ (where $j = 1\dots n$), where $y_{ij}$ is the abundance of species $j$

220    in sample $i$, $D$ is the statistical distribution of the abundance data (Poisson distribution in this study),

221    $L_{ij}$ is the linear predictor to link species' presence with environmental covariates, and $\sigma^2_j$ is a

222    variance term for the abundance of species $j$:

223                                         $$y_{ij}^D \sim D(L_{ij}, \sigma_j^2).$$

224
225    The linear predictor $L_{ij}$ is described by fixed ($F$) and random ($R$) effect terms:

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227                                         $$L_{ij} = L^F_{ij} + L^R_{ij},$$

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229    The fixed effect term $L^F_{ij}$ is modelled as a regression:

230                                        $$L^F_{ij} = c_{jk}x_{ik}$$

231

232    where $x_{ik}$ represents the measured value for environmental covariate $k$ for a given sample $i$ (e.g.,

233    biomass in quadrat $i$), and parameter $\beta$ represents the relationship between environmental

234    covariate $k$, and the abundance of species $j$.

235    The random effect term $L^R_{ij}$, captures the variation in species abundances that cannot be explained

236    by the measured covariates. It is further denoted as:

237                              $$L^R_{ij,} = \varepsilon_{ij}{}^Q + \varepsilon_{ij}{}^S + \varepsilon_{ij}{}^R + \varepsilon_{ij}{}^D$$

238    where the terms describe three random effects associated with our spatially nested sampling

239    scheme ($\varepsilon_{ij}{}^Q$, $\varepsilon_{ij}{}^S$, $\varepsilon_{ij}{}^R$ for Quadrat (sample), Site (meadow), and Region), as well as a fourth spatially

240    explicit random effect (spatial autocorrelation in species abundances). The spatially explicit

241    random effect $\varepsilon_{ij}{}^D$ was calculated with latent factor analysis that takes into account spatial distance

242    between all pairwise combinations of samples (see Ovaskainen et al. 2016a for details).

243         The three non-spatial random effect terms are assumed to have multivariate normal

244    distributions $\varepsilon_{ij}{}^Q \sim N(0, \Omega^Q)$, $\varepsilon_{ij}{}^S \sim N(0, \Omega^S)$, $\varepsilon_{ij}{}^R \sim N(0, \Omega^R)$. Variance terms $\Omega^Q$, $\Omega^S$, $\Omega^R$, are

245    variance-covariance matrices (square matrices containing all taxa in the model), where the

246    diagonal elements give species-specific residual variance in occurrences among samples, and the

247    off-diagonal elements give residual co-variances between species pairs. The term "residual" refers

248    to the fact that it is the variance unexplained by environmental covariates in the fixed effects

249    predictor described above. These variance-covariance matrices ($\Omega^Q$, $\Omega^S$, $\Omega^R$, and $\Omega^D$) are

250    parameters estimated using a latent variable approach described in Ovaskainen et al. (2016b). They

251    were used to represent co-occurrence matrix R, where $j_1$ and $j_2$ refer to two species within the

252    model, and $R_{j1j2} = \Omega_{j_1 j_1} / \sqrt{\Omega_{j_1 j_1} \Omega_{j_2 j_2}}$ . R describes the extent to which a given species pair co-

253    occurs more positively or negatively than by chance, after controlling for possible shared responses

254    to the same environmental covariates.

255    We estimated parameters with Markov chain Monte Carlo. Markov chains were run to

256    200 000 iterations, a burn-in length of 1000 iterations, and was thinned to retain every $10^{th}$

257    sample of the posterior distributions. We confirmed that Markov chains were well-mixed by

258    visually inspecting trace plots. Estimates of parameter $\beta$ (environmental responses across taxa)

259    and $\Omega$ (variance-covariance matrices used to visualize species co-occurrence patterns

260    independent of the environment) were extracted as 95% credible intervals. We evaluated the

261    model fit ($R^2$ and Root-Mean-Square Error or RMSE) using 4-fold cross-validation.

262    To test our three hypotheses, we visualized different aspects of the parametrized JDSM.

263    To test for dispersal limitation (H1), we looked for increased pairwise community dissimilarity

264    among samples with increased pairwise spatial distance. We predicted species abundances in

265    every sample using our trained model, then calculated pairwise Bray-Curtis dissimilarity index

266    (Bray and Curtis 1957) on these predicted abundances. We then conducted log-linear regression

267    of predicted pairwise dissimilarity against pairwise spatial distance (km) on a logarithmic scale.

268    Increased community dissimilarity could reflect dispersal limitation due to prohibitively far

269    dispersal distances, *or* due to increasing differences in environmental conditions with increasing

270    spatial scale. To distinguish between these possibilities, we compared a regression of predicted

271    dissimilarity based on the full JDSM (including environmental covariates) with the predicted

272    dissimilarity calculated from the same trained model, but with no effect of the environment (all

273    environmental covariates were set to their mean values).

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274    To test the environmental filtering hypothesis (H2), we analyzed $\beta$ for each combination

275    of species and environmental covariate to determine whether they had a positive or negative

276    relationship. We also partitioned the variance in abundance explained by environmental

277    covariates, spatial autocorrelation, and sampling design random effects.

278    To test the biotic interactions hypothesis (H3), we represented co-occurrence matrix R as

279    a correlation plot for each random effect level, demonstrating the extent to which species pairs

280    co-occurred more negatively or positively than predicted by their modelled correlation with

281    environmental covariates at each spatial scale (Ovaskainen et al. 2017, Aivelo and Norberg

282    2018).

283

284    **Results**

285    *Taxonomic abundance and distribution patterns*

286    We identified 52 282 individuals representing at least 50 taxa across the region

287    (Appendix 2: Table 2).  Of these, 3% of individuals were bivalves, 12% were gastropods (snails

288    and limpets), 14% were copepods, 41% were polychaetes (most of which were calcifying

289    polychaetes *Spirorbis* sp.), 13% were gammarid amphipods, 6% were caprellid amphipods, and

290    the remaining 11% included other crustaceans (isopods, tanaids, cumaceans, crabs, shrimp).

291    These taxa span several phyla, diet types (herbivores, detritivores, suspension feeders), and

292    dispersal strategies (brooding, broadcast spawning). Mean meadow-level taxonomic richness

293    was 20 taxa per 0.0625 m$^2$ of seagrass area.

294    Several taxa were present at all 17 meadows: harpacticoid copepods *Porcellidium* sp.

295    (4% of all individuals across the entire region), snails *Lacuna* spp. (7%), and tanaids *Leptochelia*

296    sp. (10%). We found genera *Mytilus* sp. (mussel) and *Nereis* sp. (polychaete worm) in all

297 meadows, however we were not confident the same species were present at each meadow. Ten

298 taxa were present in every region, but not necessarily every meadow: isopod *Pentidotea*

299 *resecata,* gammarid amphipods *Monocorophium insidiosum, Ampithoe valida, Pontogeneia*

300 *rostrata, Ampithoe dalli, Aoroides* spp*.,* snails *Amphissa columbiana* and *Alia carinata,* and

301 limpet *Lottia pelta*.

302      We excluded rare species (those found in fewer than 5% of samples, or fewer than 5 out

303 of 102 quadrats) from our JDSM, leaving 33 taxa in our modelling analysis (Appendix 1: Table

304 S2). This was necessary to avoid statistically over-inflating the importance of model covariates.
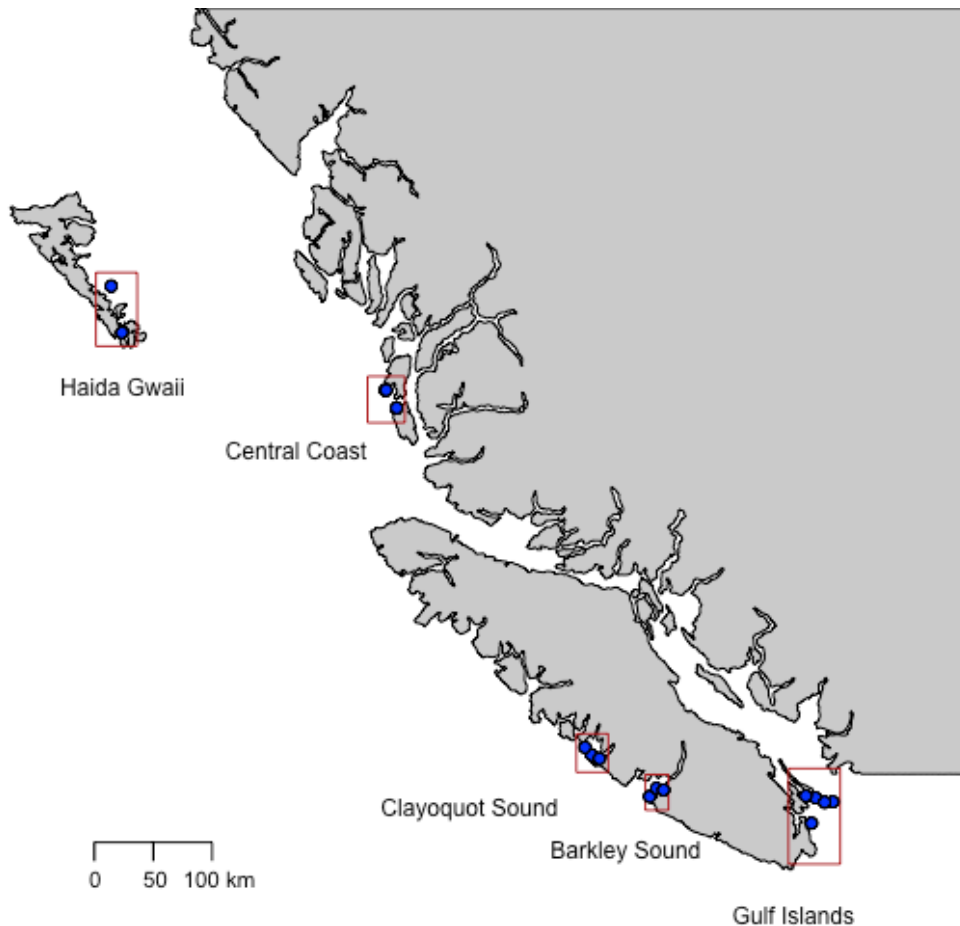


305

306 **Fig. 1A** Map of coastal British Columbia showing eelgrass meadow sites in Haida Gwaii (HL, RA), Clayoquot Sound (DK, EB, IN), Barkley
307 sound (SA, DC, RB), near Calvert island in the central coast (TB, TN, CS, CI), and the southern gulf islands (GB, JB, CB, LH, SS).

13

308

309    *Spatial connectivity via dispersal driving community similarity*

310         The highest Bray-Curtis dissimilarity value was 0.99 for a pair of sites spaced 787 km

311    apart (HL in Haida Gwaii and SA in Clayoquot Sound). The two communities at the highest

312    pairwise distance (997 km, RA in Haida Gwaii and SS in the Gulf Islands) had a dissimilarity

313    index of 0.8. The lowest dissimilarity index value was 0.59 at a pairwise spatial distance of 0.6

314    km (LH and SS in the Gulf Islands). A log-linear regression of Bray-Curtis dissimilarity

315    calculated from predicted abundances using the JDSM showed that community dissimilarity

316    increased with increased spatial distance (Fig. 1b, $y = 0.75 + 0.023\log(x)$, n = 272, $R^2 = 0.16$).

317    The maximum and minimim pairwise dissimilarity values were reduced when the effect of the

318    environment was removed ($y = 0.74 + 0.021\log(x)$, n = 272, $R^2 = 0.07$), suggesting

319    environmental variables drive some dissimilarity in species composition with increased spatial

320    distance.

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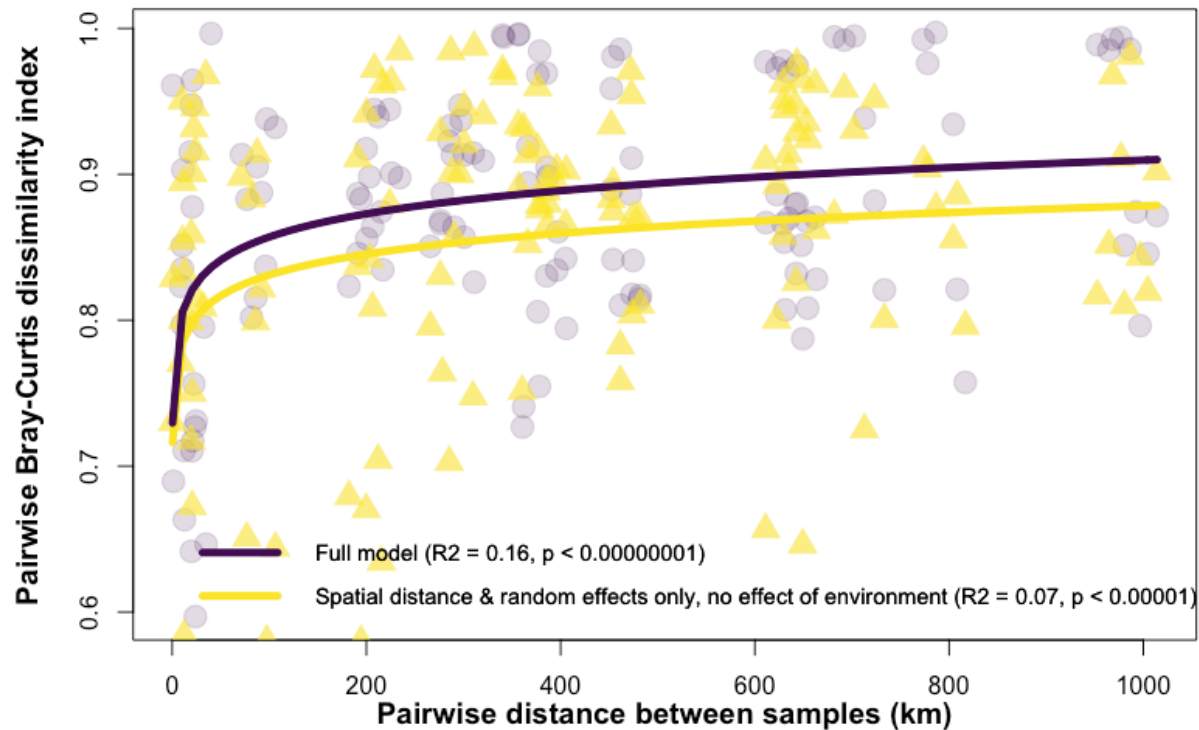
**Figure 1b.** Bray-Curtis pairwise community dissimilarity index as a function of spatial distance (Euclidean) between every pairwise combination of meadows in our study. The purple points and line show pairwise dissimilarity predicted by the full joint species distribution model using the original environmental and spatial data. The yellow points and line show pairwise dissimilarity predicted by the same trained model, but the effect of all environmental variables has been removed (set to their mean values). The yellow points and line show calculated pairwise dissimilarity based on the raw abundance data.

*Environmental conditions*

The assessment of model fit and variance partitioning analysis both showed that the importance of environmental covariates differed among taxa, and that overall the environment explained relatively a low proportion of variation in species abundances across the region (Fig 2a). While the mean $R^2$ across individual species distribution models was 0.27, individual $R^2$ values varied (0 to 0.68, Appendix 1: Table A2) indicating variability in model fit.

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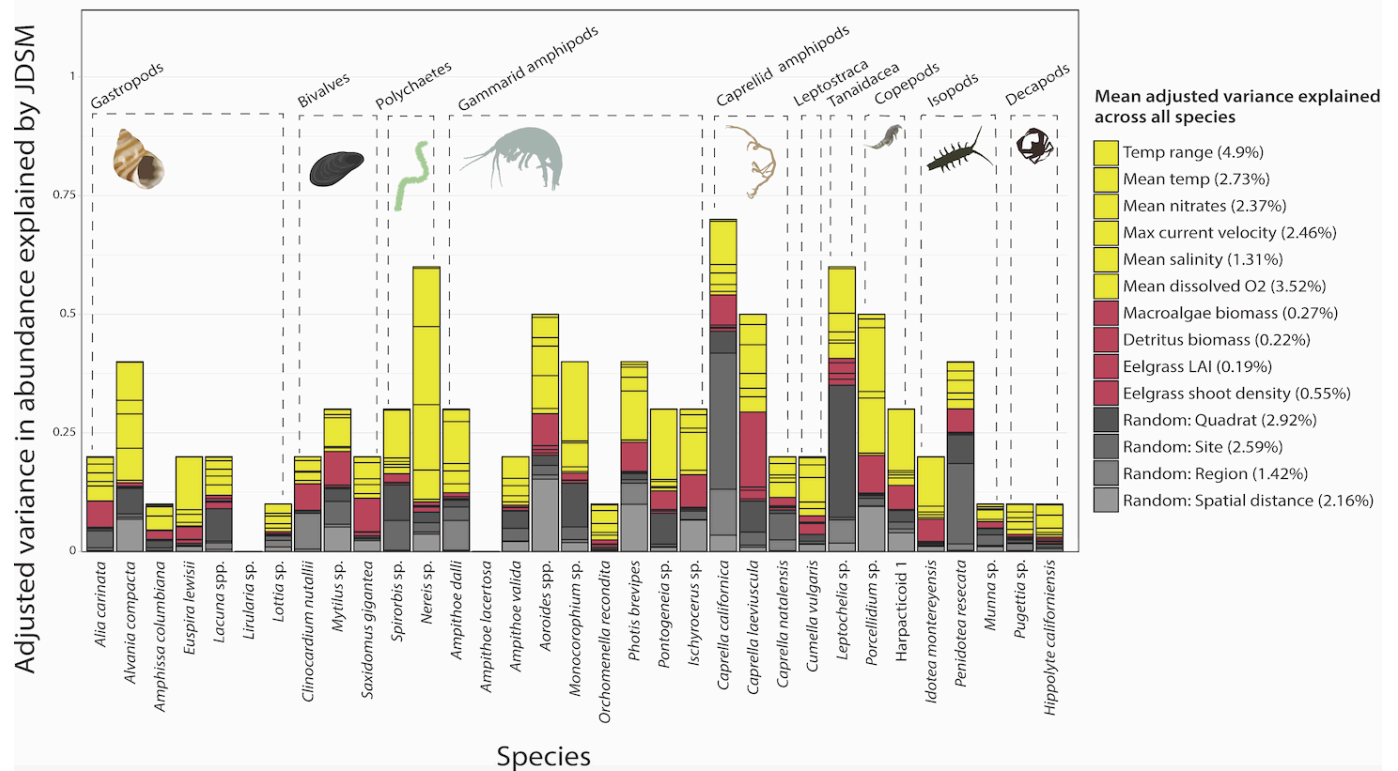
**Figure 2a.** Variation partitioning of fixed and random effects within the joint species distribution model. Variances explained have been adjusted to reflect the model fit (Multiplied by Pseudo $R^2$). An unadjusted version of the variance partitioning analysis can be found in Appendix 1, Fig. S3 of the Supplementary Information. Dashed lines indicate broad invertebrate taxonomic groupings. Grey cells represent the contribution of random effects associated with the sampling design. Yellow cells represent abiotic water quality covariates. Pink cells represent biotic covariates (food availability, habitat structure). The percentages next to the legend labels indicate mean variation explained by that covariate/ random effect across all species distribution models.

Overall, abiotic water quality variables explained more variation than biotic variables (Fig. 2a). Mean and range of sea surface temperatures and dissolved oxygen explaining the largest proportions of variation on average. Herbivore food availability (seagrass, algae biomass) and habitat structure (seagrass shoot density and LAI) had lower influence on abundance (pink bars, Fig. 2a). The importance of some environmental covariates differed markedly among taxa; for example, nitrate levels explained approximately 27% of variance in the abundance of gastropod *Alvania compacta* across meadows, but only 5% of variance in gastropod *Alia carinata* (Fig 2a). The mean variance in taxon abundance explained by spatial autocorrelation

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351    was 2.2% (pale gray bars, Fig. 2a), and other hierarchical random effects associated with the

352    sampling design explained 2.92% (quadrat-level), 2.59 (meadow or site-level), and 1.42%

353    (region-level) of variation.

354        The strength and directionality of responses to environmental variables also differed

355    among taxa, based on inspection of the $\beta$ parameters that estimate the relationships between

356    environmental covariates and species abundances (Fig. 2b). None of the taxa in our study

357    showed statistically supported responses ($\beta$ within 95% credible interval) to all environmental

358    variables. The few that showed a significant response to eelgrass LAI responded positively

359    (higher LAI meant higher abundances). Thirteen taxa responded negatively to higher temperature

360    ranges, and two responded positively (Fig. 2b). The majority of taxa (22 out of 33) had

361    significant responses to dissolved oxygen levels. Of these, 8 responded negatively (high

362    dissolved $O_2$ yields lower abundances), and 14 responded positively (high dissolved $O_2$ yields

363    lower abundances).

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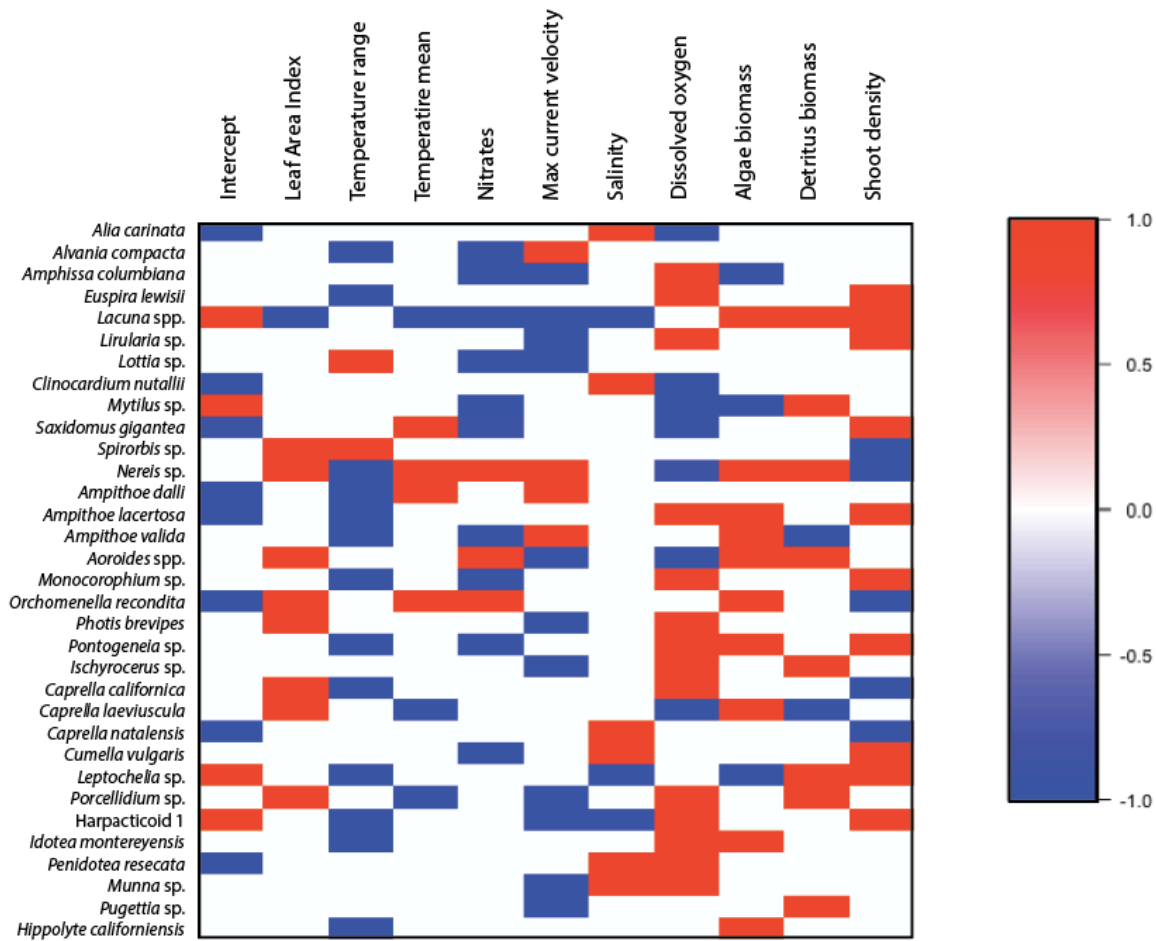
**Figure 2b.** Heat plot summarizing beta (β) parameters, or responses to all environmental covariates in the joint species distribution model. Coloured cells indicate that the response is statistically supported (β falls within 95% credible interval). Red cells indicate positive responses to a given environmental covariate (higher abundance correspond with higher values of the environmental covariate), whereas blue cells indicate negative responses (lower abundance with higher values of the environmental covariate).

*Co-occurrence patterns*

Co-occurrence patterns were less strong at the between-quadrat and between-region spatial scales (Fig 3a, 3c). In comparisons among quadrats, we observed more positive species co-occurrences than negative co-occurences (Fig. 3a). In comparisons among meadows, we identified, *post hoc*, two main species co-occurrence groupings (Fig. 3b). Members of the first

18

376     group (hereafter referred to as *Leptochelia* group) included *Leptochelia* sp. (tanaid), *Photis*

377     *brevipes* (gammaridean amphipod), *Amphissa columbiana* (snail), *Spirorbis* sp. (calcifying

378     polychaete), *Nereis* sp. (polychaete worm), *Caprella laeviuscula* and *Caprella natalensis*

379     (caprellid amphipods) (Fig. 3b). These taxa positively co-occurred more often than expected by

380     chance or by environmental filtering. They negatively co-occurred with members of the second

381     group, which included a harpacticoid copepod species, *Mytilus* sp. (mussel), *Porcellidium* sp.

382     (copepod), *Ischyrocerus* sp. (gammarid amphipod), and *Penidotea resecata* (isopod) (hereafter

383     referred to as harpacticoid group). *Alvania compacta* and *Lirularia* sp. (snails) positively co-

384     occurred with each other but did not strongly co-occur with members of the two main groups.

385     Remaining taxon pairs did not exhibit strong positive or negative co-occurrence patterns.

386          The two co-occurrence groups were represented at all meadows, suggesting that members

387     from these groups can be simultaneously present (Fig. 3d). However, their abundances tended to

388     negatively co-vary; at meadows JB, HL, CB, RA, EB, DC, and DU, members of the *Leptochelia*

389     group were most abundant, whereas Harpacticoid group members were most abundant at SS, SA,

390     LH, GB and RB. Meadow HL was an outlier, as it was strongly dominated by *Spirorbis* sp. The

391     emergent species groupings identified in Fig. 3b do not clearly correspond with geographical

392     structure because the cluster analysis did not group meadows by region membership (black

393     symbols, Fig. 3d).

394
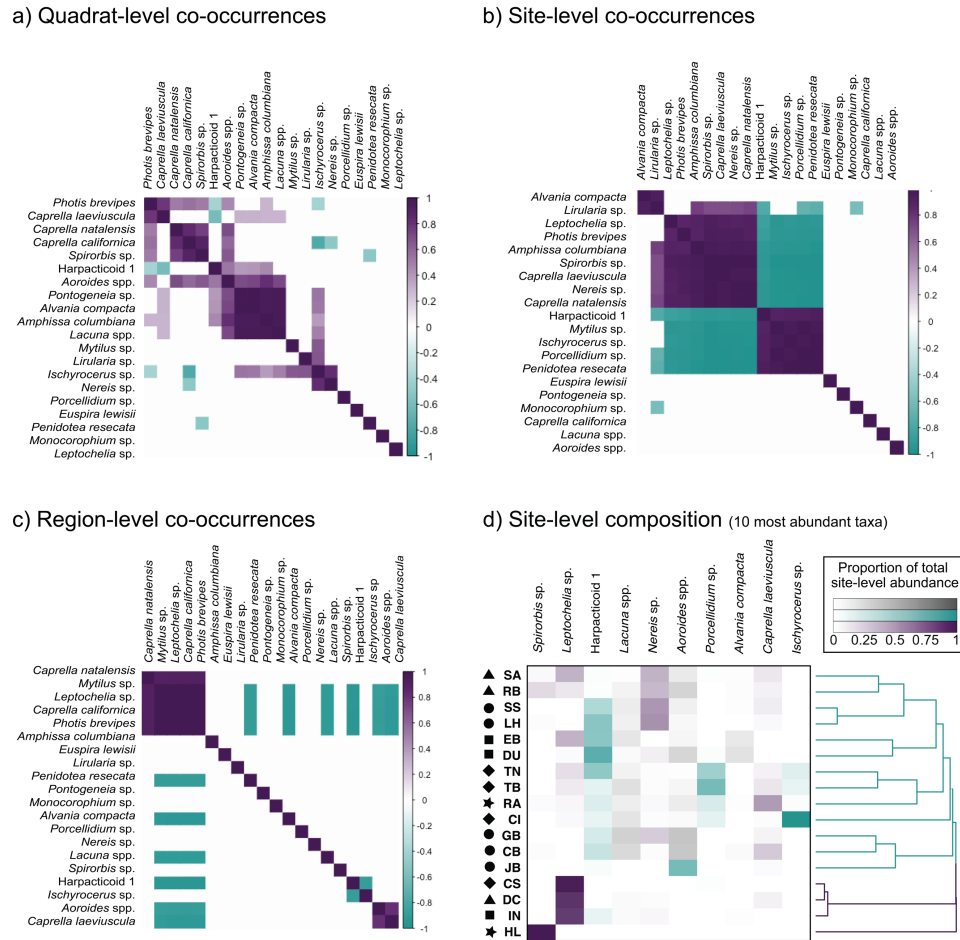
**Figure 3. a-c)** Correlation plots showing modelled a) quadrat-level, b) site-level, and c) region-level pairwise co-occurrences after removing the effect of shared responses to the environmental covariates in our model. Only the 20 most abundant species (according to total abundance across the metacommunity or study region) are represented. Purple cells represent positively co-occurring species pairs, and turquoise cells represent negatively co-occurring species pairs. Species names are ordered according to the output of hierarchical clustering with Ward's criterion on pairwise co-occurrence values. **d)** Heatmap and cluster dendrogram depicting species relative abundance and compositional similarity across sites. Species are ordered by decreasing abundance from left to right. Cell colours correspond to the two main site-level co-occurrence groupings shown in Fig. 3b: purple or "*Leptochelia*" group, and blue or "Harpacticoid" group. Cell shade strength indicates proportional abundance at a given site (darker means higher relative abundance). The black symbols to the left of the site abbreviations indicate region membership; stars indicate Haida Gwaii sites, diamonds indicate Central Coast sites, triangles indicate Barkley Sound sites, squares indicate Clayoquot Sound sites, and triangles indicate Southern Gulf Islands sites.

418    **Discussion**

419          With a biodiversity survey of 17 seagrass meadows across an approximately 1000km

420    spatial extent, we fitted a joint species distribution model to test hypotheses about the

421    contributions of dispersal, environmental filtering, and species interactions to epifaunal

422    invertebrate abundance and distribution. We also documented at least two previously

423    unrecognized species' associations in the region. This study is the largest (in geographical

424    extent) spatially explicit seagrass-based metacommunity study to our knowledge. We found little

425    support for complete dispersal limitation even across over 1000 km of coastline, some support

426    for the importance of environmental niche filtering, and co-occurrence patterns that might have

427    arisen from interspecific interactions. Overall, these results suggest that seagrass-associated

428    biodiversity patterns reflect ecological processes spanning local (meadow-scale) to regional

429    scales, and provide additional support for recent findings that eelgrass-associated diversity

430    reflects regional-scale ecological processes in addition to local scale processes (Lefcheck et al.

431    2016, Whippo et al. 2018, Stier et al. 2019, Yeager et al. 2019).

432

433    *Dispersal limitation is unlikely at this regional spatial scale*

434          Our findings that: 1) Many species were present in all regions or all meadows; 2) The

435    effect of spatial distance alone did not explain decay in community similarity (Fig. 1b); 3) There

436    was a low contribution of spatial autocorrelation to variance in species abundance (Fig. 2a); and

437    4) Hierarchical cluster analysis did not group meadows according to spatial regions (black

438    symbols in Fig. 3d), all suggest that distance between meadows likely does not confer dispersal

439    limitation preventing populations at distant sites from exchanging individuals. It is however

440    likely that meadows that are physically near each other likely experience higher rates of

21

441 exchange in individuals than distant ones, given our observation that dissimilarity increases

442 logarithmically with increased spatial distance. The six taxa that were present at all meadows and

443 an additional ten taxa that were present in all regions had representation from across phyla and

444 life history traits (including rare taxa), suggesting that no single taxonomic group or dispersal

445 strategy had a consistently larger spatial distribution than others. Many meadows were small (< 1

446 ha), and epifaunal abundances can vary substantially within meadows from year to year (Nelson

447 1997, Douglass et al. 2010) such that local extinctions followed by rescue from nearby

448 populations are likely (Thom et al. 1995). However, the specific pathway that dispersing

449 organisms travelled to arrive at these meadows remains unknown. We used Euclidean distances

450 in our analysis, which preserved the rank order of distances between meadows, but actual

451 distances are likely greater due to oceanographic circulation patterns (Kinlan and Gaines 2003,

452 Mitarai et al. 2008).

453       It is unclear whether distant meadows share taxa because they: 1) Are linked by direct

454 dispersal via oceanographic processes (currents); 2) Are indirectly linked by dispersal via

455 unsampled "stepping-stone" meadows or other habitat types; or 3) Were colonized by

456 populations of the same species in a historical dispersal event, but have not seen the exchange of

457 individuals since (Lefcheck et al. 2016). Seagrass-associated epifauna generally disperse

458 passively between meadows, either through larval transport in currents or by "rafting" on

459 floating pieces of seagrass or macroalgae. Rafts have been observed dispersing benthic and

460 epifaunal invertebrates across phyla (echinoderms, peracarids, molluscs, annelids), and facilitate

461 connectivity between coastal ecosystems across 100s of kilometres (Wichmann et al. 2012).

462       Our inferences are based on an analysis that necessarily emphasized common taxa –

463 either numerically dominant or present in most meadows, or both. We observed seventeen rare

464    taxa that were found in fewer than 5% of our samples, often at extremely low abundances (1-2

465    individuals per meadow, or per 6 quadrats) in our survey of over 50 000 individuals. The spatial

466    extent of their range could be dispersal-limited for reasons other than prohibitively long travel

467    distances. Populations with low abundances may not disperse in appreciable numbers, and

468    therefore cannot establish populations as readily as abundant species; this is supported by our

469    observation of a positive relationship between range size (the number of meadows a species was

470    observed at) and abundance (Appendix 1: Fig. S4). This highlights a potential bias in studies like

471    ours against detecting dispersal limitation if it is most severe for rare taxa. Increasing the sample

472    size might reduce the risk of this type of bias, but would cost a substantial amount of time

473    associated with invertebrate identification. More efficient biodiversity sampling methods (e.g.

474    eDNA) could overcome this time cost.

475         Theory predicts that intermediate dispersal ('dispersal sufficiency', Leibold and Chase

476    2017) allows species to colonize sites where local environmental conditions are optimal for

477    growth and reproduction, whereas high dispersal ('dispersal surplus') overrides this, allowing

478    species to persist in habitats that cannot sustain positive population growth without substantial

479    immigration ('mass effects', Mouquet and Loreau 2013). A subset of species was present at all

480    meadows, but their abundances varied (Fig 3d); this pattern may suggest weak mass effects,

481    where dispersal rates are high enough for several taxa to occur at most meadows even if local

482    conditions are suboptimal, but not so high as to completely overwhelm the signature of

483    environmental conditions (Schmida and Wilson 1985, Mouquet and Loreau 2003).

484    Metacommunity theory predicts that such weak mass effects are likely whenever dispersal rates

485    are not limiting (Thompson et al. 2017), particularly in organisms that cannot control their own

486    dispersal (Leibold and Chase 2017) such as seagrass-associated invertebrates. This may explain

23

487    the poor model fit in some ubiquitous taxa such as *Amphissa columbiana* ($R^2$ = 0.05, Appendix

488    1: Table S2). The poor model fit may suggest that these taxa either 1) persist at several meadows

489    even if local environmental conditions are not optimal, due to sufficient immigration, or 2) have

490    broader environmental niches, and thus the environmental gradient observed across the study

491    region is not sufficient to observe clear responses (lower or higher abundances) in these taxa.

492

493    *Regional species abundance patterns suggest weak environmental filtering*

494         We found that differences in local-scale environmental factors account for some

495    differences in invertebrate presence and abundance (H2), however there remains a great degree

496    of unexplained variation given the imperfect model fit (mean $R^2$ = 0.27). Abiotic environmental

497    variables had a greater influence on invertebrate distribution and abundance than biotic variables

498    (Fig. 2a). The estimated $\beta$ parameters suggest that, generally speaking, environments that are

499    saltier, have a higher seagrass surface area, smaller annual temperature range, and higher

500    dissolved oxygen levels have higher abundances of many taxa in this study (Fig. 2b). However,

501    there were several exceptions to this trend, highlighting the importance of understanding

502    individual species responses to the environment as opposed to the community as a whole.

503    Overall, we conclude that, at least in taxa for whom the model that had a higher fit (e.g.

504    *Leptochelia* sp., $R^2$ = 0.52), environmental filtering influences regional patterns in abundance

505    and distribution.

506         Differences in environmental conditions may influence distribution and abundance across

507    the region in one of three ways. First, abiotic variables such as temperature and nutrient

508    availability may influence food availability through primary productivity. This is possible despite

509    the fact that biometric variables (seagrass LAI, biomass) explained a relatively low proportion of

24

510    variance in abundance; while these measurements were taken at a single time point during field

511    sampling, the abiotic variables represented annual averages (Assis et al. 2018) and therefore

512    better represent long-term productivity. Second, temperature and salinity may affect species'

513    abundances via environmental tolerance ranges; for example, the isopod *Idotea baltica* (a

514    relative of *P. resecata* and *P. montereyensis* in our study) experiences significantly lower

515    survival in prolonged exposure to higher temperatures and lower salinities than those in their

516    home habitat (Rugiu et al. 2018). Third, temperature may influence invertebrate metabolic

517    demands, thereby influencing consumption rates and available primary biomass (O'Connor

518    2009). Reduced food availability may increase competition, thus altering the number of

519    individuals a seagrass patch can host.

520         Environmental conditions in temperate seagrass meadows fluctuate seasonally, driving

521    changes in epifaunal community structure throughout the year (Nelson et al. 1979, Wlodarska-

522    Kowalczuk et al. 2014, Whippo et al. 2018).  Sampling meadows several times within a year to

523    capture these temporal changes would clarify the importance of the environment if invertebrate

524    assemblages shift with changes in environmental variables following the linear relationships

525    uncovered in our analysis.

526

527    *Species co-occurrence patterns may suggest the importance of interspecific interactions*

528         We did not observe strong between-region co-occurrence patterns, suggesting that there

529    do not appear to be clear regional assemblages corresponding with the five subregions in our

530    analysis (Figs. 3c, black symbols in 3d). We also did not observe strong co-occurrence patterns

531    between quadrats, however we did observe strong co-occurrence patterns at the meadow-level

532    spatial scale. The explanation is that meadows had distinct assemblages, and these assemblages

25

533  tended to be homogenized within meadows; if two taxa co-occurred in a given meadow (Fig.

534  3b), then they likely co-occurred in all quadrats within the meadow (Fig. 3a). This is consistent

535  with previous findings that epifaunal diversity patterns do not differ from random patterns within

536  meadows (between quadrats) (Whippo et al. 2018).

537  At the meadow-level, two main co-occurrence groupings showed antagonistic abundance

538  patterns across meadows that could not be explained by spatial structure or shared responses to

539  the environment (Fig. 3d). These co-occurrence groups have not, to our knowledge, been

540  explicitly documented before in this region. While there are multiple possible explanations for

541  non-random species co-occurrence patterns (Connor and Simberloff 1979), we ruled out distance

542  between meadows and measured environmental variables, because co-occurrence values were

543  extracted from residual variation unexplained by the environment or space (Ovaskainen et al.

544  2017). This residual variation therefore likely can be explained by a combination of unmeasured

545  environmental variables, stochasticity, and biotic interactions.

546  Several interaction types may influence abundance and diversity. The majority of species

547  in our survey are herbivores or detritivores, and thus may compete for primary (mostly epiphytic

548  algae) biomass. Laboratory experiments have shown that grazing rate and habitat selection in

549  amphipods are altered in the presence of morphologically and functionally similar interspecific

550  competitors (Howard 1985, Brooks and Bell 2001, Beermann et al. 2018). Other species in our

551  study are suspension feeders, and thus may not compete for food but possibly predator-free space

552  or substrate on eelgrass blades.

553  The invertebrate assemblage at a given meadow may have multiple possible

554  compositional states depending on the arrival order of species; this phenomenon is known as

555  priority effects (Fukami et al. 2016, Ke and Letten 2018) and has been documented in marine

556    fouling communities (Vieira et al. 2018). The antagonistic co-occurrence groupings in our

557    analysis could suggest priority effects at the meadow-level. It is possible that, following seasonal

558    declines in abundance or a disturbance event, the first few populations to increase in abundance

559    or colonize a meadow determine the success of others. Abundance patterns in the sessile

560    calcifying polychaete *Spirorbis* sp. might demonstrate an example of priority effects. *Spirorbis*

561    sp. dominated the HL meadow on Haida Gwaii; there were approximately 16 300 individuals,

562    several orders of magnitude higher than its abundance elsewhere. Meadow HL also had the

563    lowest taxonomic richness of all 17 meadows (9 species), and we observed fewer micro and

564    macro-epiphytes on eelgrass blades. Instead, the eelgrass was completely covered with *Spirorbis*

565    sp. This phenomenon has also been observed in *Z. marina* meadows in Akkeshi-Ko estuary,

566    Japan (Clark et al. 2018) and in *Thalassia testudinum* meadows in the Northwestern Gulf of

567    Mexico (Dirnberger 1990). Experimental evidence suggests that *Spirorbis* spp. larvae tend to

568    settle lower in the water column on newer seagrass growth, away from epiphytic algae and

569    previously settled conspecifics (Dirnberger 1990). Settlement rates were determined by

570    planktonic larval density rather than space availability on seagrass blades (Dirnberger 1990).

571    Given this, it is possible that *Spirorbis* sp. dominates HL from a combination of density-

572    dependent processes (high larval recruitment) and environmental conditions (high salinity, low

573    nitrates). The low epiphyte load on seagrass at HL, whether mostly driven by high *Spirorbis* sp.

574    densities or by the environment, may explain the low abundance and diversity of all other

575    invertebrate taxa. Overall, the importance of priority effects likely depends on the age,

576    colonization history, and disturbance regime of seagrass meadows.

577        Negative co-occurrence patterns in taxonomic distributions could also reflect the higher

578    abundance of predators at some meadows. Field experiments have shown that changes in

579 predation pressure by fish, shorebirds, and predatory invertebrates can shift seagrass-associated

580 epifaunal assemblages in a matter of weeks (Amundrud et al. 2015; Huang et al. 2015). Previous

581 studies involving some of the meadows in this analysis (Haida Gwaii, Clayoquot Sound, and

582 Barkley Sound) found high variation (beta diversity) in fish assemblages among meadows

583 (Robinson et al. 2011, Iacarella et al. 2018). A comprehensive survey of fish and bird predators

584 is required to determine the extent to which top-down trophic interactions structure these

585 invertebrate communities. Positive co-occurrence patterns may additionally be a result of

586 positive biotic interactions. An example is *Orchomenella recondita* - a gammarid amphipod that

587 lives in the gastrovascular cavity of the anemone *Anthopleura elegans* (Carlton 2007). This

588 species was only recorded at the SS meadow, and specifically only found in quadrats where *A.*

589 *elegans* was collected with the seagrass shoots.

590 While inferences from data taken at a single time point have limitations, our JDSM

591 approach suggests that there is more to learn about species interactions and the interplay between

592 interactions and dispersal in structuring these communities. The hypothesized processes driving

593 seagrass epifaunal diversity patterns that can be further tested with experiments to test for

594 priority effects or trophic interactions, with population genetics to test for demographic

595 connectivity, or with particle tracking models (e.g. Treml et al. 2008) to estimate dispersal

596 velocity.

597

598 **Conclusion**

599 Seagrasses are important coastal foundation species, valued throughout the world for

600 supporting diverse and productive food webs (Constanza et al. 1997, Williams and Heck 2001).

601 The extent of these ecosystems is declining at rates believed to exceed those of coral reef and

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602    rainforest habitat loss, suggesting major losses of associated biodiversity (Waycott et al. 2009).

603    Our finding that several seagrass-associated faunal taxa across functional groups are consistently

604    present across a fairly large spatial scale is consistent with notion that "the mobile, fast-

605    reproducing, and generally omnipresent animal community is keenly responsive to the presence

606    of habitat" (Lefcheck et al. 2016). Our study suggests that the management of seagrass for its

607    ecosystem services may be more effective if both local and regional processes are considered

608    explicitly in habitat protection plans (Economo 2011).

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