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Trait-based and phylogenetic approaches to understanding community assembly processes in
eelgrass beds

by

COLLIN PATRICK GROSS
DISSERTATION

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ABSTRACT

The field of community ecology is fundamentally concerned with the assembly and maintenance of diversity across space and time. Two of the most fundamental questions in the field, then, are 1) why do we see variation in composition and diversity across space and time, and 2) how are diversity and assemblage structures maintained? A common model for beginning to understand these questions is the idea of ecological “filters” that restrict species from a regional pool. Different kinds of filters apply different kinds of selective pressures, and because species’ traits are what allow them to pass through filters, studying the distributions and dispersion of traits within the community can help us understand how these filters act on the species pool. A variety of factors may cause communities to have traits that are overdispersed – more disparate than expected by chance – or underdispersed or clustered – more similar than expected by chance.

My dissertation attempts to address these fundamental questions in communities associated with eelgrass (*Zostera marina*) – an herbaceous marine angiosperm (seagrass) that forms monospecific beds across nearly 40° of latitude in the northern hemisphere. Eelgrass is home to a diversity of epifaunal invertebrate mesograzers – animals that live on the leaves of the plant and feed on fouling microalgal epiphytes, as well as macroalgae and fresh and decaying eelgrass tissue. Peracarid crustaceans are one of the most abundant and diverse of the mesograzers. These crustaceans – amphipods, isopods, and their relatives – are found worldwide and are especially susceptible to predation by the diverse suite of resident and juvenile fishes that also call eelgrass beds home.

My first chapter draws on data from a global experimental network to examine how the functional structure of eelgrass peracarid communities varies across space and with different ecological filters. I found that dispersion strongly increased with increasing predation and decreasing latitude – communities at low-latitude sites and those that experienced high predation intensity were more overdispersed than those at high latitudes and with low predation intensity. Ocean and epiphyte load appeared as secondary predictors; Pacific communities were more overdispersed while Atlantic communities were more clustered, and increasing epiphytes were associated with increased clustering. Together these results point to the importance of both biotic interactions and the historical legacies of distinct species pools in structuring communities.

My second chapter narrows in on eelgrass beds in Northern California to investigate the role of diverse suites of predator (fish) community traits as ecological filters that drive patterns of dispersion in prey (peracarid) communities. Fish traits related to prey detection and capture selected for more overdispersed peracarid communities, particularly with respect to body size and activity level, suggesting that prey may be pushed to disparate areas of trait space to avoid consistent detection by predators across the community. I also found correlations between the trait dispersions of predator and prey communities that strengthened after accounting for the effects of habitat filters on predator dispersion, suggesting that habitat filtering effects on predator species pools may hinder their ability to affect prey community assembly. Specific predator traits may have measurable impacts on the community assembly of prey, inviting experimental tests of predator trait means on community assembly, and explicit comparisons of how the relative effects of habitat filters and intraguild competition on predators impact their ability to affect prey community assembly.

Finally, my third chapter returns to the global experimental network from the first chapter to address more coarse-scale patterns of community structure beyond peracarids. This time, I examined in epifauna communities dominated by peracarids and gastropods. The abundance of these two taxa exhibited a strong latitudinal cline in turnover, with gastropods abundant at high-latitude sites, and peracarids abundant at low-latitude sites, especially in the Atlantic. This pattern appeared to be driven by greater eelgrass genetic diversity at lower latitudes, which strongly influenced both the richness and abundance of peracarids, but less so for gastropods. The two taxa exhibited functional complementarity, and so global variation in genetic diversity led to geographic variation in the distribution of functional traits across the range of eelgrass. These results add to a growing body of literature that suggests that variation in traits underlain by genetic differences within species has important bottom-up consequences for assemblage variation and ecosystem function across broad spatial scales.

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TABLE OF CONTENTS

ABSTRACT.....	ii
ACKNOWLEDGMENTS.....	iv
TABLE OF CONTENTS.....	vii
CHAPTER 1: The biogeography of community assembly: latitude and predation drive variation in community trait distribution in a guild of epifaunal crustaceans.....	1
CHAPTER 2: Extending trait dispersion across trophic levels: functionally diverse predator assemblages act as top-down filters on prey community traits.....	24
CHAPTER 3: Eelgrass genetic diversity is strongly associated with a novel latitudinal cline in taxonomic turnover.....	51
APPENDIX 1: Supplementary material for Chapter 1.....	74
APPENDIX 2: References for peracarid trait data used in global analyses of trait dispersion.....	84
APPENDIX 3: Methods and Results – post-hoc modeling of individual peracarid trait dispersion (SES) against environmental predictors in global eelgrass beds.....	90
APPENDIX 4: Species and trait data for fish and peracarid communities in Tomales Bay and Bodega Harbor, California.....	102
APPENDIX 5: Supplementary material for Chapter 2	120
APPENDIX 6: Supplementary material for Chapter 3.....	160

CHAPTER 1: The biogeography of community assembly: latitude and predation drive variation in community trait distribution in a guild of epifaunal crustaceans¹

ABSTRACT

While considerable evidence exists of biogeographic patterns in the intensity of species interactions, the influence of these patterns on variation in community structure is less clear. Studying how the distributions of traits in communities vary along global gradients can inform how variation in interactions and other factors contribute to the process of community assembly. Using a model selection approach on measures of trait dispersion in crustaceans associated with eelgrass (*Zostera marina*) spanning 30° of latitude in two oceans, we found that dispersion strongly increased with increasing predation and decreasing latitude. Ocean and epiphyte load appeared as secondary predictors; Pacific communities were more overdispersed while Atlantic communities were more clustered, and increasing epiphytes were associated with increased clustering. By examining how species interactions and environmental filters influence community structure across biogeographic regions, we demonstrate how both latitudinal variation in species interactions and historical contingency shape these responses. Community trait distributions have implications for ecosystem stability and functioning, and integrating large-scale observations of environmental filters, species interactions, and traits can help us predict how communities may respond to environmental change.

INTRODUCTION

Community ecology is fundamentally concerned with the assembly and maintenance of diversity across space and time. Key to this endeavor is the idea that the composition of a local community is the result of multiple ecological filters selecting species from a regional pool (Poff 1997; Thompson *et al.* 2020). Different kinds of filters apply different kinds of selective pressures on the species pool, and because species' traits are what allow them to pass through filters, studying the distribution of traits within the community can help us understand how these filters act on the species pool as a whole. Strong environmental filters (i.e., abiotic filters *sensu* Kraft *et al.* 2015) such as climate are thought to act on large spatial scales to constrain trait diversity such that species are more alike (clustered) in traits that respond to these factors than

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we would expect under a purely random assembly process (Webb *et al.* 2002; Cavender-Bares *et al.* 2009; Starko *et al.* 2020; Thompson *et al.* 2020). Biotic filters, such as competition, then act at smaller spatial scales to enhance or reduce trait diversity among species with broadly similar abiotic tolerances, depending on which traits are affected (Mayfield & Levine 2010). When traits related to the acquisition of distinct resources are considered, competition for these resources drives the distribution of traits to be wider than expected by chance (overdispersed) as there are multiple resource niche optima that can be occupied (Webb *et al.* 2002; Cavender-Bares *et al.* 2009; Pavoine & Bonsall 2011). In contrast, competition for a single, dominant limiting resource can also act as a filter, selecting for traits related to acquiring this resource to converge around an optimal value, because species deviating from the optimum are otherwise competitively excluded. All else being equal, as richness increases, an increase in trait dispersion may point to stronger stabilizing mechanisms and limiting similarity, while a decrease in trait dispersion can suggest stronger equalising mechanisms promoting unstable coexistence. (Chesson 2000; Mayfield & Levine 2010).

Despite well-known geographic patterns in the strength of both biotic interactions and environmental filters (Schemske *et al.* 2009; Reynolds *et al.* 2018; Longo *et al.* 2019; Zvereva & Kozlov 2021), few studies have examined the global-scale consequences of geographic variation in these filters for community trait distributions (Ford & Roberts 2018, Skeels *et al.* 2020). In particular, intense predation, competition, and mutualistic interactions at lower latitudes (Freestone & Osman 2011; Longo *et al.* 2019; Zvereva & Kozlov 2021), may lead to the predominance of biotic interactions over environmental filters in structuring low-latitude communities. This may cause stronger trait clustering near the poles that shifts towards more overdispersed communities at lower latitudes. On the other hand, selection for tolerance of extreme heat conditions could also cause trait clustering at low latitudes. Finally, patterns in community structure along latitudinal gradients could be dominated by idiosyncratic and historically-contingent effects of predators, prey, competitors, and mutualists that vary among biogeographic provinces (Sanford & Bertness 2009; Mittelbach & Schemske 2015; Ford & Roberts 2019; Whalen *et al.* 2020). Local abiotic factors, habitat complexity, assemblage composition, and adaptation to these local factors could further obscure broader geographic patterns of community assembly (Sanford & Bertness 2009; Lavender *et al.* 2017), stressing the importance of assessing patterns across multiple independent species pools. For example, the

effects of regional gradients in predation may be overshadowed by local increases in habitat complexity, which can decrease predation pressure (Reynolds *et al.* 2018) and increase trait dispersion as species assort into disparate microhabitat niches (Best & Stachowicz 2014). Understanding trait distributions and their drivers should provide insight into the likely responses of communities to environmental fluctuations or perturbations in the same way that understanding the diversity of traits within a population can inform us on its evolutionary potential (Cadotte *et al.* 2011; Rumm *et al.* 2018).

Here we examine geographic patterns in the trait distribution of epifaunal invertebrates living on eelgrass throughout the northern hemisphere to assess the extent and causes of geographic variation in the drivers of the assembly of these communities. Eelgrass (*Zostera marina*) is the world's most widespread species of temperate seagrass, a marine angiosperm found throughout the Northern Hemisphere from 30° to 67° N latitude in both the Atlantic and Pacific Oceans (den Hartog 1970; Green & Short 2003). Much of the animal community in eelgrass beds is made up of invertebrate mesograzers that primarily feed on the epiphytic microalgae fouling the seagrass blades (Valentine & Duffy 2006). Competition for food and microhabitat space occurs among mesograzers, and can significantly affect community composition (Edgar 1990; Best *et al.* 2013; Best & Stachowicz 2014; Amundrud *et al.* 2015). Peracarid crustaceans (amphipods, isopods, and tanaids) are the most widespread, abundant, and species-rich mesograzer taxon in these eelgrass beds, and they experience elevated predation in low-latitude eelgrass beds (Reynolds *et al.* 2018) which could either cause clustering of communities around traits that increase resistance or tolerance to predation, or cause dispersion of communities due to competition for enemy-free space. *Z. marina*'s wide range across latitudes provides an opportunity to assess the role of gradients of ecological filters on global scales without the confounding influence of changing habitat type. We predicted: (1) that trait dispersion would increase with decreasing latitude as species interactions become more intense and (2) that abiotic filters would be strongest and result in clustering at higher latitudes and where biotic interactions are weak. While marine systems often show non-linear variation in species diversity and interaction strength with latitude (peaking at mid-latitudes; Chaudhary *et al.* 2017; Whalen *et al.* 2020), our predictions are reasonable within the range of latitudes occupied by eelgrass (~30-70°N). We test these predictions in separate ocean basins with largely unique fauna, allowing us to assess whether the unique histories of these zoogeographic

provinces result in different patterns and drivers of trait distribution in each ocean basin (Roy *et al.* 2009; Dyer & Forister 2019).

METHODS

Study design and sample collection. Between May and September 2014, we sampled 42 sites across the range of *Z. marina*, spanning 30 degrees of latitude along both coasts of Eurasia and North America (30.4°N to 60.1°N; Fig. 1.1) to characterize the biological and physical structure of eelgrass beds using standardized measurements. We implemented a hierarchical sampling design consisting of two oceans (Atlantic and Pacific), each with two coasts (east and west), each with 6-14 sites, each with 20 plots, for a total of 840 plots in 42 sites sampled as part of the *Zostera* Experimental Network (ZEN; Fig. A1.1). Plots were 1 m² and spaced 2 m apart at each site. Along each coastline, sites were separated by 4.9 km (Virginia, USA) to 485.4 km (Washington State, USA) of water.

Assessing eelgrass habitat characteristics. We sampled eelgrass biomass by haphazardly placing and pushing a 20-cm diameter core tube 20 cm into the sediment within each plot. We gathered all shoots rooted within the core bottom area into the core tube to ensure that no shoots were cut off during sampling. We then removed the shoots from the sediment, transferred the core contents into a mesh bag. In the lab, we rinsed the core contents, removed fouling algae and sediment from the eelgrass tissue, and separated above- and belowground biomass by cutting the plant above the rhizome. In addition to eelgrass, we also removed all of the macroalgae from the plot. All eelgrass and macroalgal tissue was dried to a constant weight at 60°C and weighed. From five haphazardly collected eelgrass shoots per plot, we also collected 3-cm lengths of tissue from a healthy, unfouled inner leaf and processed these samples for tissue nitrogen using a CHN analyser (Thermo Fisher Scientific Inc., Waltham, MA, USA).

We quantified eelgrass habitat structure at the plot level by measuring shoot density and canopy height. We estimated shoot density by counting the number of shoots emerging within a 20-cm diameter ring placed haphazardly in the plot. In plots where density was particularly low (less than 50 shoots m⁻², about 5% of plots), we counted all of the shoots in the plot. We measured canopy height by haphazardly collecting five shoots from each plot and measuring their length from the tip of the longest leaf to the leaf sheath.

We sampled epiphyte load on the eelgrass blades by selecting four shoots from each plot and removing them from the substrate either by gently uprooting or clipping at the meristem and

placing them in a plastic bag on ice for transport. In the lab, we scraped both sides of all the leaves with a glass slide to remove fouling material, which was then filtered, transferred to an aluminium pan, dried to a constant weight at 60°C, and weighed.

Measuring predation intensity. Predation intensity was quantified by tethering locally-collected prey (“gammarid” amphipods) in each plot for 24 hours. These data and methods are reported in detail in Reynolds et al. (2018). Briefly, each individual amphipod was glued to a 10-cm piece of monofilament line 0.133 mm in diameter (Berkley Fireline™, Spirit Lake, IA, USA) tied to a transparent acrylic stake anchored in the sediment, so that it could swim freely in the water column and cling to adjacent eelgrass blades. After 24 hours, we removed the stakes and scored prey as present (uneaten) or absent (eaten); partially-consumed prey were considered eaten, and moulted prey were excluded from analyses. Site-level predation was calculated by averaging scores across plots.

Abiotic environmental variables. To characterize the abiotic environment experienced by epifauna across the range of eelgrass, we measured in-situ temperature and salinity at each site at the time of sampling. To characterize the overall abiotic environment of each site, we also retrieved estimates of annual mean sea surface temperature (SST), photosynthetically active radiation (PAR), and surface chlorophyll A (Chl a) from the surrounding region, available in the Bio-ORACLE data set (Tyberghein *et al.* 2012). These data were taken from monthly readings of the Aqua-MODIS and SeaWiFS satellites at a 9.6 km² spatial resolution from 2002 to 2009. We used the raster package in R v. 3.6.3 (Hijmans & Etten 2020; R Development Core Team 2021) to extract the annual mean SST, SST range, PAR, and Chl a from all cells within 10 km of each site, and averaged these cell-level estimates to generate site-level predictors. Other water quality parameters, including dissolved nitrate and other nutrients, were spatially interpolated based on surface measurements in the World Ocean Database 2009 (Garcia *et al.* 2010).

Epifaunal community composition. To sample the macrofauna associated with the eelgrass blades, we carefully placed an open-mouthed fine-mesh drawstring bag (500 µm mesh, 18 cm diameter) over a clump of shoots in the centre of the plot so that the mouth of the bag was flush with the sediment surface. We then cut the shoots where they emerged from the sediment and quickly closed the drawstring to capture the shoots and associated animals. The shoots were transferred to the lab on ice, rinsed and hand-inspected to dislodge the epifauna, which were then passed through a 1-mm sieve and ultimately transferred into 70% ethanol. Epifauna were then

identified to the lowest possible taxonomic level (typically species). Epifaunal abundance was standardized by the aboveground biomass of the eelgrass sample from which they were collected.

We scored all peracarids (amphipods, isopods, and tanaids) for a series of traits based on information available in the literature, including body size, fecundity, body shape, living habit, motility, bioturbation, and diet components (Table 1.1, Appendix 2 for literature). Due to a paucity of data on intraspecific trait variation for most species, literature values were assumed to be representative for all individuals in our study. For subsequent analyses, we categorized each of these traits as related to microhabitat or dietary niche; we also performed analyses with all traits ungrouped. While we acknowledge that these broad categories may overlap, we elected to sort traits into these categories because they represent two potential components of trait dispersion exhibited by peracarids in field studies and laboratory experiments (Best *et al.* 2013; Best & Stachowicz 2014). Correlations among traits were generally weak, save for strong positive relationships between eating live seagrass tissue and macroalgae, detritivory and consuming seagrass detritus, and suspension feeding and bioturbation (Fig. A1.2).

Characterizing community dispersion. For all the peracarid species observed in our dataset, we used the trait dataset to generate three matrices of Gower distances between species: one of all traits, one for diet traits, and one for microhabitat traits using the FD package in R (Laliberté *et al.* 2014). Using subsets of these matrices for communities at the site level (summed across 20 plots at each site, $n = 42$), we measured the trait distance between species as the Mean Pairwise Distance (MPD) and Mean Nearest Taxon Distance (MNTD) for each set of traits (Webb *et al.* 2002; Sessa *et al.* 2018). MPD is the average of the trait distances between all pairs of species found within a given sample unit (site), while MNTD is the average minimum distance between species pairs in a site. Both are independent of species richness, but the two metrics can behave differently depending on the clustering of species in trait space within a sample (Sessa *et al.* 2018).

To determine whether the observed species traits in each community differed from those expected by chance, we standardized MPD and MNTD against null distributions generated according to two permutation algorithms. The first, independent swap, is a semi-constrained model that randomly re-assembles the sample-by-species community matrix while maintaining the species richness of each sample and the presence/absence of each species across samples.

The second, tip shuffle, is a more constrained model that directly shuffles the traits of the species in the community while maintaining richness, occurrence, and trait distances between community members, effectively moving the tip labels on a trait dendrogram. Imposing more constraints on permutation controls for patterns in the data that are not directly relevant to the question at hand, such as species richness, occurrence, or identity, ultimately reducing type I error rates (Swenson 2014). Because of the relatively low overlap in species pools across the range of our study, comparing the results relative to both types of models can be informative of the importance of species identity in these types of permutations, and also facilitate comparison with other studies in which the independent swap algorithm has been used together with less constrained permutations (e.g., Best and Stachowicz 2014). These permutations were each completed 999 times for each community, and null distributions of MPD and MNTD were generated based on values calculated from randomized communities.

We examined the effect of the species pool on community dispersion, using varying degrees of constraint on the matrix and trait dendrogram used to generate null distributions. To make comparisons among sites, we permuted within the global species pool (all sites) and ocean-level Atlantic and Pacific species pools. Using a global pool in our permutations is appropriate because while all species were not present in all regions, there were no traits that were exclusive to any region (Fig. A1.2).

Each observed value of community trait distance was then compared to the corresponding null distribution by calculating the standard effect size (SES_{MPD} or SES_{MNTD}). A positive value of SES indicates that the observed community trait distance (as measured by MPD or MNTD) is greater than the null mean, meaning that community members are more dissimilar than expected under a random draw (overdispersion), while a negative SES indicates that trait distance is less than the null mean, meaning that community members are more similar to each other than expected under a random draw (clustering). MPD, MNTD, null distributions and SES values were calculated using the picante package in R (Kembel *et al.* 2010).

Data analysis. Two distance metrics (MPD and MNTD), two permutation algorithms (independent swap and tip shuffle), three species pools (global, Pacific, and Atlantic), and three trait sets (all, diet, and microhabitat) totalled 36 sets of SES values. However due to missing diet data for some species, we were unable to calculate diet SES_{MNTD} with the tip shuffle algorithm, leaving us with a total of 33 sets. For each distance metric, algorithm, species pool, and trait set,

SES values were used as response variables in a set of 16 linear models incorporating latitude, ocean, continental margin (east vs. west), in-situ temperature and salinity, annual mean and range of SST, total crustacean abundance and median crustacean size, epifaunal and peracarid richness, macroalgal biomass, average predation intensity, epiphyte load, Chl a, PAR, water column nitrate, mean leaf nitrogen content, and two axes of eelgrass habitat structure as derived from a principal component analysis incorporating shoot density, leaf sheath width and length, longest leaf length, and aboveground biomass (PC1 and 2, Fig. A1.4) as predictor variables, as well as select interactions between them (Table 1.2). Predictors were log-, square-root-, or arcsin-transformed where appropriate to conform to a normal distribution based on Shapiro-Wilk normality tests and visual examinations of histograms. Collinearity of predictors was accounted for using variance inflation factors (VIF) for variables in composite models using the car package in R (Fox & Weisberg 2019). Predictors with a VIF greater than five were removed from composite models. We also examined the effects of predictors on the SES of individual traits to understand what traits may drive the patterns we see across environmental gradients (Appendix 2).

We ranked these initial hypothesis-driven models of SES using AICc scores (MuMIn package; Bartoń 2020), and then incorporated predictors from the three lowest-scoring models of each set into a set of composite models to examine the combined effects of multiple predictor types. We then used backwards elimination to select the lowest-scoring model from these composite models. Where two models had a ΔAICc less than 3 units, we selected the model with the fewest parameters for interpretation.

RESULTS

Peracarid assemblages at Pacific sites had greater trait dispersion than Atlantic sites, and dispersion increased with increasing predation and decreasing latitude, though there were some differences among the two oceans that we outline below. Across our sites, we found a total of 105 species, 55 of which were found in the Atlantic, and 60 of which were found in the Pacific, with 10 species found in both oceans. There were 15 species in the Northwest Pacific, 48 species in the Northeast Pacific, 36 species in the Northwest Atlantic, and 24 species in the Northeast Atlantic (Fig. A1.3). The patterns and predictors of trait dispersion were robust across SES metrics and permutation algorithms (Fig. A1.5); here we present and interpret the results of

model selection on SES_{MNTD} calculated using the tip shuffle algorithm, with exceptions presented where relevant.

Dispersion of traits by ocean basin. Of the set of all traits examined, communities at Atlantic sites were on average clustered ($SES < 0$) relative to the global null, particularly for body size and living habit (Fig. A3.2) – species clustered around a mean body size of 14.09 mm (47.5% smaller than the mean Pacific body size), and most were free-living. Communities at Pacific sites were overdispersed ($SES > 0$) on average relative to the global null (Fig. 1.2, Table A1.1). This pattern held for both metrics and null models but was significant only for SES_{MPD} (SES_{MPD} independent swap $t_{38.097} = 2.43$, $p = 0.020$; SES_{MPD} tip shuffle $t_{38.242} = 2.31$, $p = 0.027$; two-sample t tests). Within the global pool, the separate calculations of SES using microhabitat and feeding traits showed a similar pattern; for microhabitat traits, Pacific communities were more overdispersed and Atlantic communities more clustered (SES_{MNTD} tip shuffle $t_{35.654} = 3.64$, $p = 0.00086$; Fig. 1.2).

Correlates of among-site variation in trait dispersion. Predation intensity, latitude, epiphyte load, and ocean basin (within the global species pool) were the strongest and most consistent predictors of SES across all species pools and all trait sets (Fig. A1.5). In-situ temperature, bed characteristics, epifaunal richness, continental margin, nitrate, and salinity also appeared occasionally (less than 30% of models) across the best models of SES. Mean annual sea surface temperature, epifaunal richness, salinity, nitrate, in-situ temperature, and crustacean abundance also varied significantly with latitude (Fig. A1.8).

In all of the best models, peracarid communities at sites with higher predation intensity had more overdispersed traits, whereas those with less intense predation had more clustered traits relative to a random draw from the species pool (Fig. 1.3a, Fig. A1.5a-c). Predation (removal of amphipod baits) varied from 20% in Quebec to 100% in Sweden, San Francisco Bay, Ireland, Korea, and British Columbia; the average predation rate was significantly greater in the Pacific than in the Atlantic Ocean (Table A1.2, Fig. A1.7, A1.8), but this did not translate to a difference in the effect of predation on dispersion across the two basins when permuting within the global pool ($p = 0.48$; Fig. 1.3a). Across the three species pools, the predation effect was stronger on average when permuting within the Pacific than the Atlantic or global pools, (Fig. A1.5a), and strongest in models of the dispersion of all traits together (Fig. A1.5b).

As predicted, trait dispersion decreased with increasing latitude in the best models (global species pool, microhabitat traits); communities became more clustered at higher latitude, while communities toward the equatorward edge of *Z. marina*'s range were more overdispersed (Fig. 1.3b, Fig. A1.5d-f). These latitude effects were stronger in the Pacific Ocean than in the Atlantic ($F_{1,38} = 7.95$, $p = 0.0076$; Fig. 1.3b) although they did not appear in the top models when permuting within the Pacific species pool (Fig. A1.5d); the best model including latitude was 1.3 AICc units better than the top model, but it was not selected as the top model because of the small difference in AICc score and greater number of parameters. Like predation, the latitude effect was strongest in models including all traits together (Fig. A1.5e).

Communities were more clustered (more negative SES) at sites with high epiphyte loads, but this effect was most obvious in the Atlantic species pool when only microhabitat traits were considered (Fig. 1.3c; Fig. A1.5g-h). There was rarely an effect of epiphyte load on SES when using other species pools (Fig. A1.5g) and never for diet traits (Fig. A1.5h).

DISCUSSION

Using a global dataset of eelgrass-associated peracarid crustaceans, we found a strong increase in community trait dispersion with decreasing latitude and increasing predation (Fig. 1.3a, b). Latitudinal clines in different ecological filters have been well-characterized in a wide variety of systems (Schemske *et al.* 2009; Reynolds *et al.* 2018; Zvereva & Kozlov 2021), particularly temperature and the strength of species interactions (Schemske *et al.* 2009; Longo *et al.* 2019; Zvereva & Kozlov 2021), both of which decrease at high latitudes. Stronger biotic interactions, in particular stabilizing interactions (*sensu* Chesson 2000), at lower latitudes may select for an overdispersed community (Webb *et al.* 2002; Mayfield & Levine 2010; Pavoine & Bonsall 2011), while stronger abiotic filters (or relatively weaker biotic filters) at either end of range (e.g. cold at the poleward edge or hot at the equatorward edge) could select for a clustered community (Webb *et al.* 2002; Cavender-Bares *et al.* 2009; Kraft *et al.* 2015). We found similar total numbers of species in the two oceans (Fig. A1.3) given similar sampling effort, and all traits were found in both oceans, so the differences we observe among oceans are not simply the result of different diversities in the underlying species pool.

Several lines of evidence point to the relatively greater effect of biotic interactions over temperature in structuring our communities. First, temperature rarely appeared as a significant factor in our best models (Fig. 1.3d). Second, latitudinal clines in dispersion were more

dependent on ocean basin than continental margins, which differ significantly in their temperature gradients (western side of oceans are warmer at an equivalent latitude; Fig. 1.3b; Reynolds *et al.* 2018). Third, predation in this system decreases with latitude, as it does in many others (Reynolds *et al.* 2018; Longo *et al.* 2019; Zvereva & Kozlov 2021). Fourth, we observed greater dispersion in living habit, motility, and macroalgae consumption at lower latitudes (Fig. A3.1b-d), all of which can be reasonably linked to stabilizing competition for food or enemy-free space. Finally, for some traits (body size, fecundity), we would expect clustering at both ends of a thermal gradient, but around different optima: large-bodied and highly fecund peracarids at cool sites, and small-bodied peracarids that produce fewer eggs at warm sites (Sainte-Marie 1991; Jaramillo *et al.* 2017). However, in ectotherms like peracarids, decreases in temperature at higher latitudes are less likely to be strong drivers of community structure than increases in temperature at lower latitudes as a result of asymmetrical performance curves (Martin & Huey 2008; Vasseur *et al.* 2014). While we saw that high-latitude sites tended to have species with high fecundity (65 to <135 eggs per brood; part of a general trend for clustered sites to have high or very high fecundity; Fig. A3.1a), we saw no similar trend towards clustering at low latitudes around low fecundity values or any other traits.

The decline in trait dispersion with latitude was significantly greater in the Pacific than the Atlantic. This difference in latitudinal clines and trait dispersion more generally between the two ocean basins (Fig. 1.2, Fig. 1.3b) may be in part due to differences in these assemblages' biogeographic and evolutionary histories (Mittelbach & Schemske 2015). First, glaciation in the north Atlantic during the last Ice Age means that many of the areas in which eelgrass now occurs would have been colonized after glaciers retreated (Vermeij 1991; Olsen *et al.* 2004), leaving less time for in-situ adaptation and specialization that might lead to increased trait dispersion (Cavender-Bares *et al.* 2009). Similarly, given *Z. marina*'s origin in the Pacific and more recent Pleistocene expansion into the Atlantic (Olsen *et al.* 2004), we might also generally expect Atlantic species to have colonized eelgrass from other Atlantic-native habitats, perhaps predisposing them to be less overdispersed in their traits as they cluster around a single mean. Consistent with this, we found that species in Atlantic sites were clustered around a smaller mean body size, which may be selected for by the denser eelgrass habitat in the Atlantic (Fig. A1.4, Fig. A3.2a; Bartholomew *et al.* 2000). Finally, gastropod relative abundance increases with latitude, and gastropods are a more abundant and speciose component of the epifaunal

community in the north Atlantic than in the Pacific (See Chapter 3). Competition with gastropods for epiphytes or other shared resources may push the peracarids there into a more constrained area of trait space, leading to the clustering we observed.

The precise impacts of these and other historical factors are difficult to quantify but may be further investigated with analyses of phylogenetic dispersion or more detailed studies of trait distributions in the regional species pool (Denelle *et al.* 2019; Skeels *et al.* 2020). However, we currently lack a phylogeny of peracarids with sufficient resolution and taxon sampling with which to evaluate underlying differences in phylogenetic diversity between the two ocean basins. We do note that richness of species, genera and families did not vary substantially between the ocean basins (Fig. A1.3).

One of the most striking results of our study was the positive effect of predation intensity on community dispersion among sites that was consistent in both oceans (Fig. 1.3a); peracarid species were more dissimilar in their traits than expected by chance in sites with high predation intensity. This effect appeared across trait sets, species pools, dispersion metrics and methods, although we rarely saw this signal at the level of individual traits (Table A3.1, Fig. A3.3). Changes in predator community structure, predation intensity, or both could lead to an increase in competition for predator-free space, an ecological selective filter that may result in overdispersion, particularly with respect to microhabitat and predator avoidance traits (Best & Stachowicz 2014). Herbivorous arthropods in both marine and terrestrial systems are known to select their microhabitat niches based largely on their effectiveness as shelter from predators rather than the availability or quality of food (Bernays & Graham 1988; Duffy & Hay 1991; Lasley-Rasher *et al.* 2011). Consequently, competition for enemy-free space can be an important factor structuring communities. Alternatively, predation could affect trait dispersion by reducing competition (Pianka 1966; Amundrud *et al.* 2015), but we would expect this to lead to an increase in dispersion from strongly clustered ($SES < 0$) to random communities ($SES = 0$) as stabilizing competition lessened, rather than the observed shift from clustered to overdispersed ($SES > 0$, Fig. 1.3a, Fig. A1.5b).

Latitudinal patterns of species interactions are now broadly appreciated (Schemske *et al.* 2009; Freestone & Osman 2011; Reynolds *et al.* 2018; Longo *et al.* 2019; Whalen *et al.* 2020; Zvereva & Kozlov 2021), but rarely are these results explicitly connected to variation in the structure of communities. By examining both how species interactions and environmental drivers

vary within a single habitat type across a broad geographic gradient, we demonstrate an important role for latitudinal variation in species interactions in driving patterns of community assembly. Diversity in important traits can increase the completeness with which epiphytes are removed, leading to increased seagrass growth (Duffy *et al.* 2003), an effect that is strongest in the presence of predators (Duffy *et al.* 2005). More generally, trait clustering and dispersion have implications for redundancy, stability, and ecosystem functioning (Cavender-Bares *et al.* 2009; Cadotte *et al.* 2011; Leibold *et al.* 2017). For instance, communities may be less resilient to environmental change if they are clustered by environmental filters (Cadotte *et al.* 2011, Rumm *et al.* 2018). Clustering that occurs as a result of equalizing mechanisms (*sensu* Chesson 2000) can weaken the relationship between diversity and ecosystem functioning, or certain ecosystem functions may be enhanced in communities with overdispersed effect traits, especially if diversity-function relationships arise through complementarity (Leibold *et al.* 2017; Thompson *et al.* 2020). Thus, historical contingency and broad-scale ecological drivers may play an important role in constraining not only the assembly of local communities, but the resulting trait diversity can affect the functioning of the entire ecosystem. This approach, if applied broadly, offers the potential for developing a predictive understanding of how entire communities respond to environmental change.

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CHAPTER 1: The biogeography of community assembly

Table 1.1. Traits used in analyses of ZEN peracarid communities. Full citations, as well as sources for individual species traits, are listed in Appendix 2.

Trait	Type	Values	Category	Interpretation	Citations
Maximum fecundity (number of eggs)	Ordered categorical	Very low (0 to <18), Low (18 to <31), Medium (31 to <65), High (65 to <135), Very high (>135)	Neither	Competitive ability, population resilience, population density	Sainte-Marie 1991, Best and Stachowicz 2013, Lefcheck and Duffy 2015, Ashford <i>et al.</i> 2018
Maximum adult length	Continuous	2-50 mm	Microhabitat	Susceptibility to predators, ability to occupy physical space	Sainte-Marie 1991, Best and Stachowicz 2013, Lefcheck and Duffy 2015, Ashford <i>et al.</i> 2018
Body shape	Categorical	Laterally compressed, Dorsoventrally compressed, Vermiform	Microhabitat	Ability to occupy physical space, palatability	Lefcheck and Duffy 2015
Living habit	Categorical	Free, Parasite/direct commensal, Tube/burrow dweller	Microhabitat	Degree of substrate association, substrate type, population density	Best and Stachowicz 2013, Ashford <i>et al.</i> 2018
Motility	Categorical	Swimmer, Crawler	Microhabitat	Susceptibility to predators, dispersal ability, degree of substrate association	Lefcheck and Duffy 2015, Ashford <i>et al.</i> 2018
Bioturbator?	Binary		Microhabitat	Degree of substrate association, substrate type	Ashford <i>et al.</i> 2018
Microalgae feeding	Binary		Diet		
Macroalgae feeding	Binary		Diet		
Seagrass feeding	Binary		Diet		
Seagrass detritus feeding	Binary		Diet	Dietary niche partitioning	Duffy and Harvilicz 2001, Best and Stachowicz 2012, 2013
Suspension feeding	Binary		Diet		
Detritivory, deposit feeding	Binary		Diet		

CHAPTER 1: The biogeography of community assembly

Carnivory,
parasitism,
scavenging

Binary

Diet

Table 1.2. A priori models used to analyse site-level SES values. These 16 models were separately applied to 33 sets of SES values for different trait distance metrics, permutation algorithms, species pools, and trait sets, for a total of 528 models.

Model name	Predictors				
Biogeography 1	Latitude				
Biogeography 2	Latitude	Continental Margin	Ocean		
Biogeography 3	Latitude	Continental Margin	Latitude × Continental Margin		
Biogeography 4	Latitude	Continental Margin	Ocean	Latitude × Continental Margin	
Biogeography 5	Latitude	Continental Margin	Ocean	Latitude × Continental Margin	Latitude × Ocean
Abiotic Environment	in-situ Temperature	in-situ Salinity	Mean Leaf % N		
Temperature Regime 1	Mean SST				
Temperature Regime 2	SST Range				
Temperature Regime 3	Mean SST	SST Range	Mean SST × SST Range		
Community	log(Mean Standard Total Crustacean Abundance)	Median Crustacean Size			
Total Biodiversity	log(Site Epifaunal Richness)				
Peracarid Biodiversity	log(Site Peracarid Richness)				
Habitat	PC1	PC2	log(Macroalgal Biomass + 1)		
Predation	arcsin(Mean Amphipod Predation)				
Resource 1	log(Mean Epiphyte load)	log(Mean Chl a)			
Resource 2	$\sqrt{\text{NO}_2}$	Mean PAR			

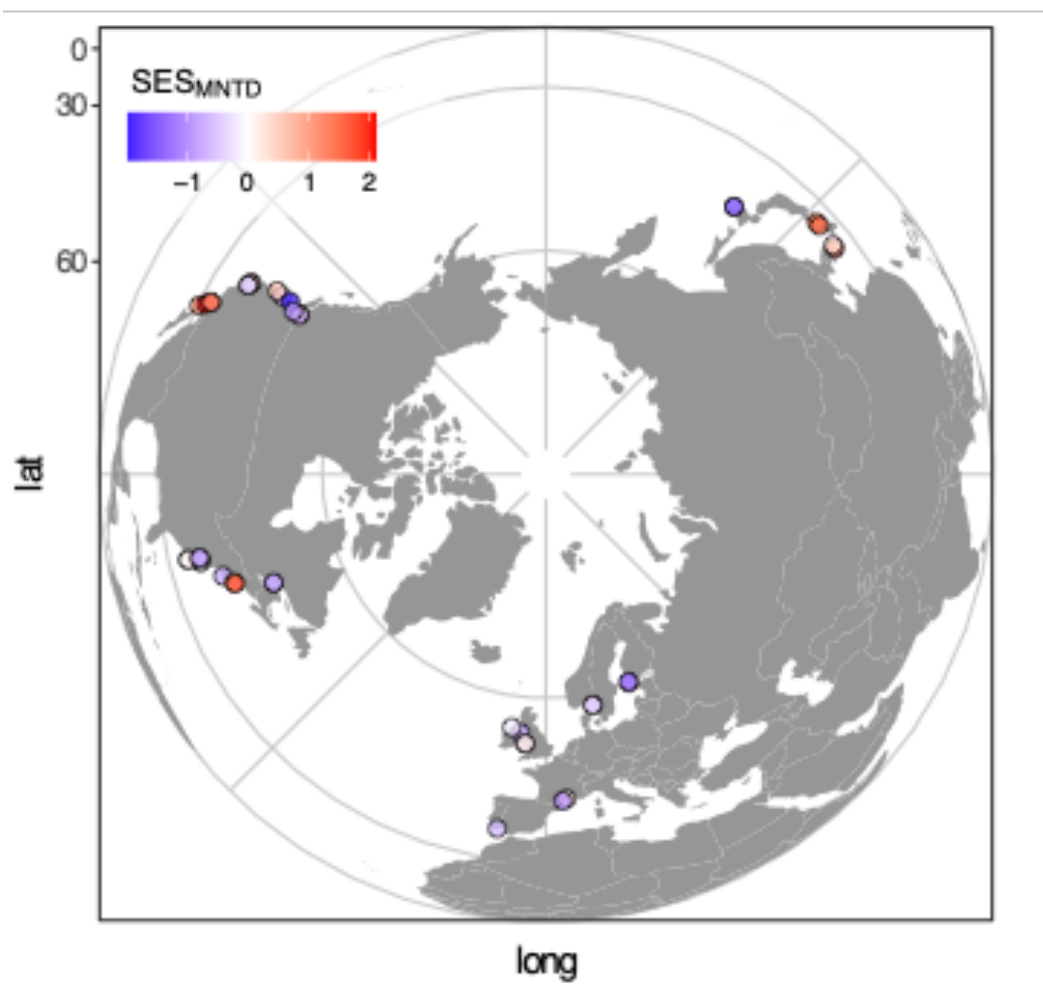


Figure 1.1. *Zostera* Experimental Network (ZEN) sites used in our analyses. Sites spanned 30° of latitude on the Pacific and Atlantic coasts of North America and Eurasia, including the Baltic and Mediterranean seas, covering most of the range of *Zostera marina* (eelgrass). Colors indicate trait dispersion (SES_{MNTD} calculated using the tip shuffle algorithm); positive values of SES_{MNTD} indicate greater dispersion in traits than expected from a random draw from the global species pool, whereas negative values of SES_{MNTD} indicate clustering in traits relative to a random draw. See Fig. A1.1 for more detailed information about site locations.

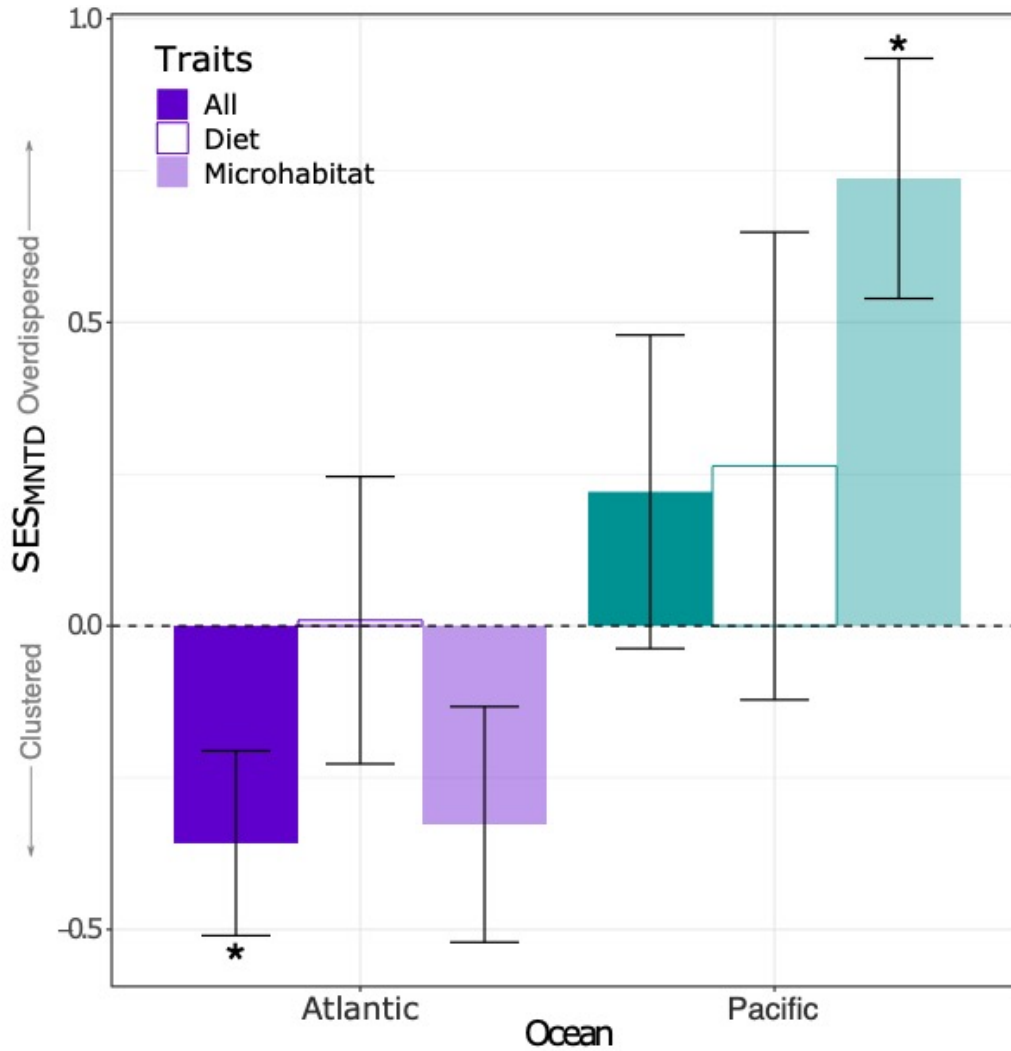


Figure 1.2. Trait dispersion (SES_{MNTD}) in eelgrass-associated peracarid crustacean communities across trait sets. In general, communities at sites in the Pacific Ocean were more overdispersed, while communities at Atlantic sites were less dispersed than expected. The dashed horizontal line represents an SES_{MNTD} value of 0, indicating random assembly. Asterisks indicate means significantly different from zero (two-tailed one-sample t tests; see table A1.1); error bars represent standard errors. Figure shows SES_{MNTD} calculated according to the Tip Shuffle permutation algorithm; results were comparable across permutation algorithms and SES values.

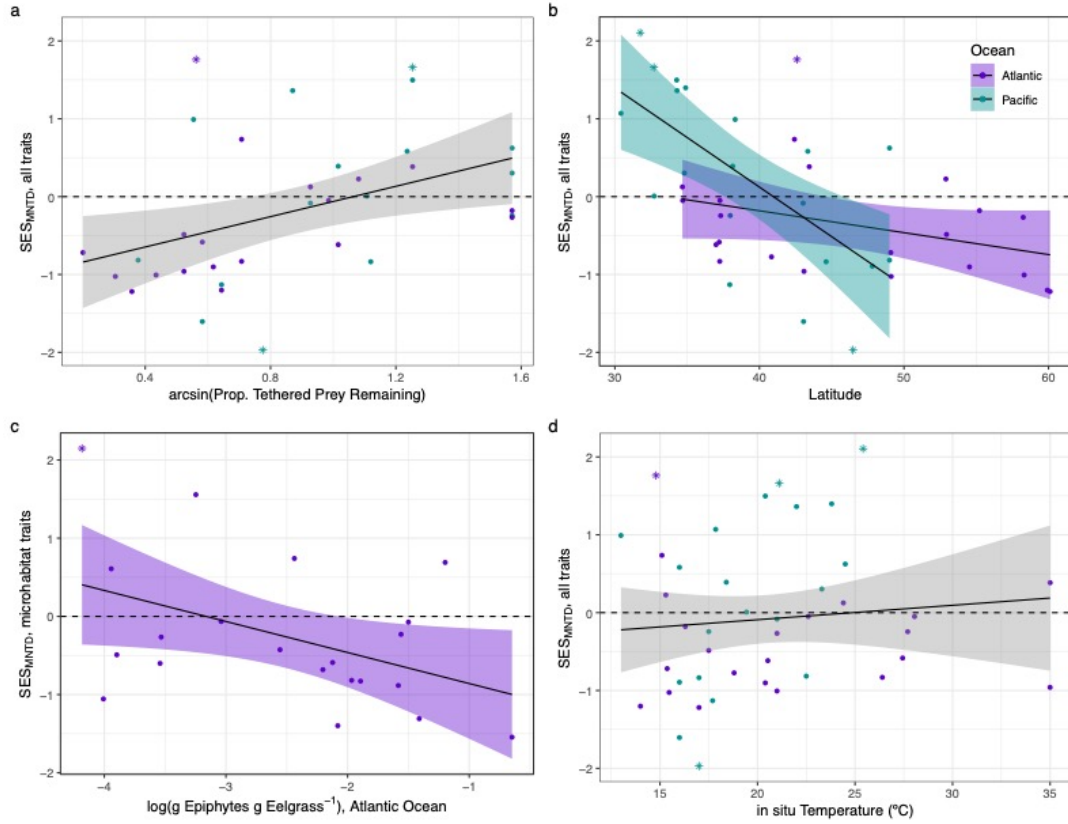


Figure 1.3. The effects of predation (a), latitude (b), epiphyte load (c), and in-situ temperature (d) on trait dispersion (SES_{MNTD} using the tip shuffle algorithm) in univariate analyses. In all of the best models of dispersion, sites with higher predation intensity had more overdispersed communities, while those with lower predation intensity had more clustered communities (a; $R^2 = 0.15$, $p = 0.012$). In the best models that had a non-zero latitude effect, sites at lower latitudes had more overdispersed communities, while those at higher latitudes had more clustered communities. This effect was stronger in the Pacific than the Atlantic species pool (b; $R^2 = 0.36$, interaction $p = 0.0076$). In the best models with a non-zero epiphyte effect, sites where eelgrass had lower epiphyte density had more overdispersed communities, while sites with more heavily fouled blades had clustered communities (c; plot shows SES_{MNTD} for microhabitat traits in the Atlantic species pool; $R^2 = 0.15$, $p = 0.046$). In-situ temperature appeared only sporadically across permutations and dispersion metrics, and was not significant for total trait dispersion ($R^2 = 0.0094$, $p = 0.54$). The dashed horizontal line represents an SES value of 0, indicating random assembly; sites in bold italics are those for which SES is significantly different from 0 at $\alpha = 0.05$.

CHAPTER 2: Extending trait dispersion across trophic levels: functionally diverse predator assemblages act as top-down filters on prey community traits

ABSTRACT

Studies of community assembly typically focus on the effects of abiotic environmental filters and stabilizing competition on functional trait dispersion within single trophic levels. Predation is a well-known driver of trait distributions within communities, but the role of functionally diverse predator communities in filtering prey community traits has received less attention. We examined functionally diverse communities of predators (fishes) and prey (epifaunal crustaceans) in eelgrass (*Zostera marina*) beds in two Northern California estuaries to evaluate the filtering effects of predator traits on community assembly, and how filters acting on predators influence their ability to mediate prey community assembly. Fish traits related to prey detection and capture selected for more overdispersed epifauna communities, particularly with respect to body size and activity level, suggesting that prey may be pushed to disparate areas of trait space to avoid consistent detection by predators across the community. We also found correlations between the trait dispersions of predator and prey communities that strengthened after accounting for the effects of habitat filters on predator dispersion, suggesting that habitat filtering effects on predator species pools may hinder their ability to affect prey community assembly. Our results present compelling observational evidence that specific predator traits have measurable impacts on the community assembly of prey, inviting experimental tests of predator trait means on community assembly, and explicit comparisons of how the relative effects of habitat filters and intraguild competition on predators impact their ability to affect prey community assembly. Integrating our understanding of traits at multiple trophic levels can help us better predict the impacts of community composition on food web dynamics as regional species pools shift with climate change and anthropogenic introductions.

INTRODUCTION

One of the key goals of community ecology is to understand the mechanisms by which communities assemble from a regional species pool (Poff 1997, Thompson et al. 2020). Ecological filters such as temperature, habitat structure, and interspecific competition exert selective pressures in multiple different directions on the species pool. Because species' traits are what allow them to pass through these filters, studying the distribution of traits within the community provides insight into how filters have acted on the species pool. Strong

environmental filters (i.e., abiotic filters *sensu* Kraft *et al.* 2015) such as climate are thought to act on large spatial scales to constrain trait diversity such that species are more alike (clustered) in traits that respond to these factors than would be expected under a purely random assembly process (Webb *et al.* 2002, Cavender-Bares *et al.* 2009, Starko *et al.* 2020, Thompson *et al.* 2020). Biotic filters, such as competition, act at smaller spatial scales to enhance or reduce trait diversity among species with broadly similar abiotic tolerances, depending on which traits are affected (Mayfield and Levine 2010). When traits related to the acquisition of distinct resources are considered, competition for these resources drives the distribution of traits to be wider than expected by chance (overdispersed) as there are multiple resource niche optima that can be occupied (Webb *et al.* 2002, Cavender-Bares *et al.* 2009, Pavoine and Bonsall 2011). In contrast, competition for a single limiting resource can also act as a filter, selecting for traits related to resource acquisition to converge around an optimal value as species deviating from the optimum are competitively excluded (Mayfield and Levine 2010).

To the extent that traits are phylogenetically conserved, phylogenetic diversity may provide an integrated picture of functional distinctiveness across many traits, and might thus provide a proxy for ecological differences between species (Webb *et al.* 2002, Swenson *et al.* 2006, Cavender-Bares *et al.* 2009, Cadotte *et al.* 2017). However, the extent to which this assumption holds depends on the degree of trait convergence between distantly related taxa, intraspecific trait variation due to plasticity or adaptation, the species used to build the reference phylogeny, and other factors (Cadotte *et al.* 2017, Tucker *et al.* 2018). Nevertheless, the distribution of phylogenetic and functional trait distances among species in a community may reveal patterns in community functional or phylogenetic structure that allow us to draw inferences about the processes that determine community composition in nature.

The assumption that limiting similarity and environmental filters are the two main opposing forces in community assembly that lead to either overdispersion or clustering, respectively (Kraft *et al.* 2015, Cadotte *et al.* 2017) is pervasive, despite nuances in the effects of different filters on the functional (and phylogenetic) structure of communities. Less attention has been paid to other possible selective filters, such as predation. Yet predators are widely known to govern community structure, species coexistence, and even adaptive divergence among prey species (McPeck 1995, Vamosi 2005) by both consumptive and nonconsumptive effects (Paine 1966, Sommers and Chesson 2019, Dellinger *et al.* 2022). For example, predators affect prey

behavior and habitat use, and may determine which prey traits are important for facilitating prey coexistence. In the presence of predators, competition for enemy-free space may drive community assembly and promote divergence in microhabitat use (Best and Stachowicz 2014, Lürig et al. 2016, Gross et al. 2022), while in predator-free environments, prey may compete more for food (Best et al. 2013, Beermann et al. 2018). Predator traits may influence prey coexistence and community assembly by selecting for prey with traits that aid in predator evasion (McPeck 1995, Schmid et al. 2019), or by reducing the abundance of a dominant competitor (Paine 1966).

Despite the wealth of knowledge of how predators influence prey community structure, studies of functional and phylogenetic diversity and community assembly rarely examine the potential role of speciose predator communities in producing these patterns, both in terms of their traits and how those traits are distributed among predator species in the community. Instead, studies typically focus on one or two predator species or morphotypes (Post et al. 2008, Holdridge et al. 2017, Schmid et al. 2019) or coarse measures of community-level predation intensity without directly investigating the predator community itself (Palkovacs et al. 2009, Gross et al. 2022). Yet predators and their prey are affected by broader ecological filters, and the influences of predator selection on prey communities may carry the fingerprints of environmental filters, competition, or other factors that limit the suite of predator traits that can act to filter prey (Chang et al. 2021; Fig. 2.1a).

Looking specifically at the role that community-wide predator trait distributions might play in structuring prey communities, four general patterns of dispersion can be considered between guilds (Fig. 2.1b). First, an overdispersed predator community may lead to an overdispersed prey community, as a wide range of predator feeding modes may prevent the dominance of a single set of prey traits. Second, an overdispersed predator community may lead to a clustered prey community if diffuse pressure from predator traits in all directions pushes prey into a single refuge in trait space (Sih et al. 1998). Third, a clustered predator community might be associated with a clustered prey community, either because they respond to the same environmental filters, or because prey are forced into a single trait space that reduces their predation risk outside the range of predator traits. Finally, a clustered predator community might be associated with an overdispersed prey community if prey reduce their competition for enemy-free space by moving into different niches that are inaccessible to predators.

We investigated patterns of clustering and overdispersion in communities of mesopredatory fishes and their epifaunal invertebrate mesograzers found in eelgrass (*Zostera marina*) beds of northern California, USA. We addressed two major questions: (1) Does the trait composition of fish communities act as a selective filter to affect epifaunal community assembly? and (2) How do ecological filters acting on fishes affect the direction and magnitude of their selective pressure on the epifaunal species pool? We specifically chose to focus on peracarid crustaceans (amphipods, isopods, and tanaids), because they are the most widespread, abundant, and speciose mesograzers in these eelgrass beds (Ha and Williams 2018, Gross et al. 2022), are monophyletic, and are more susceptible to predation than other taxa such as gastropods (Reynolds et al. 2018), increasing the likelihood that predation and predators will act as filters. Understanding the effect of fish traits and trait distributions on peracarid traits and trait distributions is particularly interesting in seagrass beds, unique among marine benthic habitats in that mesograzers typically feed on fouling epiphytic algae, rather than on the seagrass tissue itself (Jernakoff et al. 1996, Valentine and Duffy 2006). The “mutualistic mesograzers model” (Reynolds et al. 2014) predicts that increased secondary consumption by mesopredators will indirectly harm the seagrass by decreasing the numbers of epiphyte-removing mesograzers, increasing competition between seagrass and epiphytes for light (Jackson et al. 2001, Estes et al. 2011). However, in communities of epiphyte grazers, relative abundances, interspecific variation in epiphyte feeding rates, and differences in mesopredator susceptibility due to predator-prey trait matching or mismatching may lead to idiosyncratic outcomes from experimental trophic cascades (Best and Stachowicz 2012). In light of these studies and others in which variation in predator traits leads to differences in prey community structure and alters trophic cascades (Post et al. 2008, Schmid et al. 2019), it is likely that the traits of both mesograzers and the predators that feed on them can have dramatic impacts on the strength and outcome of trophic cascades in eelgrass.

METHODS

Study sites and sampling. In the summers of 2019 and 2021, we sampled three eelgrass beds each in Bodega Harbor (38°19'N 123°03'W) and Tomales Bay (38°09'N 122°54'W), for a total of 12 site-by-year samples across both estuaries. Bodega Harbor is a small (approximately 5 km²) shallow bar-enclosed embayment characterized by extensive mudflats (Abbott et al. 2018), while Tomales Bay is a long (16 km) and narrow (2 km) drowned river estuary characterized by

strong environmental gradients (Cheng and Grosholz 2016, DuBois et al. 2022). We chose eelgrass beds across gradients of temperature and water residence time in each estuary.

We sampled fishes in 6 sets of a custom beach seine net when the water level was at or below 1 m above the seafloor. The seine sampled a circular area of 11 m². We counted, identified to the lowest possible taxonomic level (typically species), and released animals retained in the seine. We additionally grouped some species into discrete size classes (large or small, Table A4.2) based on earlier seining efforts (C.P. Gross, unpublished), keeping in mind that allometric growth may lead to ontogenetic differences in morphometric traits (Karachle et al. 2012). We retained two individuals of each species and size class from each estuary (in 2019) or each site (in 2021) to be euthanized for morphometric analyses. To get our final list of fish species and size classes, we removed singletons, species that only occurred in a single site-year combination, and species with 4 or fewer individuals across the entire dataset (Table A4.1).

At each site, we collected peracarid crustaceans and other epifauna along six 20-meter transects. Three transects were parallel to the shoreline at shallow subtidal elevations in the eelgrass, while three were parallel to these at a higher intertidal elevation in the same grass bed. At 4 and 16 meters along each transect, we collected each epifaunal sample by everting an open-mouth drawstring mesh bag (500 μ m mesh size) over a clump of shoots in the eelgrass bed so that the mouth of the bag was flush with the sediment surface. We then severed the shoots where they emerged from the sediment and closed the drawstring to capture shoots, macroalgae, and associated animals. We transferred the shoots to the laboratory on ice, rinsed and hand-inspected them to dislodge the epifauna, which we then passed through a 500 μ m sieve and ultimately transferred into 70% ethanol. We then identified epifauna to the lowest possible taxonomic level (typically species), and removed singletons and species that only occurred in one site-year combination. We standardized epifaunal abundance by the total aboveground biomass of macrophytes in the sample from which they were collected (Appendix Table A4.5).

In addition to sampling fishes and epifauna, we also collected data on total eelgrass shoot density m⁻², flowering shoot density m⁻², percent cover, canopy height, and epiphyte dry weight mm⁻² eelgrass as described by Aoki et al. (2022). We also measured mean in-situ summer temperatures by averaging hourly temperatures at the upper (intertidal) transect level between June and August as recorded by HOBO MX 2201 pendant temperature loggers (Onset). We also

quantified macroalgal abundance in each site-by-year sample as the total macroalgal wet mass collected in epifaunal grab samples.

Traits and phylogeny. For the 23 most abundant species of peracarids in our surveys, we assigned values for 11 traits putatively related to predator avoidance and microhabitat niche. We collected three of these traits (maximum body size, shape, and living habit) from the literature. We determined the tube fidelity for each species according to observations of living and preserved specimens along a four-point ordered scale as follows: none (species lacks silk glands to build tubes), low (species has silk glands but was never observed in a tube alive or preserved in ethanol), medium (species has silk glands and was observed in tubes when alive but readily flees tube when exposed to ethanol), and high (species has silk glands, is tubicolous when alive, and is regularly found inside tubes after preservation in ethanol). We measured mean body size (length from rostrum to telson), relative eye diameter, and relative antenna lengths from 10-20 preserved individuals collected across sites and years. We measured activity levels as fractions of time spent swimming, walking, and still (unmoving) from one-minute video recordings of 10-20 live individuals per species across sites and years. We log-transformed peracarid traits where appropriate to conform to a normal distribution. A more detailed discussion of peracarid traits including how we defined and measured each, any transformations prior to analysis, and mean values for each species is included in Appendix 4 (Table A4.6, Table A4.7, Fig. A4.3).

We assigned two categorical (vertical position and foraging mode) and one continuous trait (trophic level) to the 16 most abundant fishes based on the literature. We fuzzy-coded vertical position and foraging mode among 5 and 3 levels, respectively, to accommodate species that could be classified among multiple levels (Ashford et al. 2018). We collected linear morphometric measurements of fishes (body and head dimensions, fin lengths, eye size and position, and mouth height and protrusion) from 2-26 specimens per species and size class collected from seines as described above, and standardized them for ease of comparison across species. We log-transformed fish traits where appropriate to conform to a normal distribution. We also used principal component analysis (PCA) to condense variation among fish species' linear morphometric traits into 16 axes, the first three of which explained 66% of variation among species (Fig. A4.2). Detailed discussion of fish traits, including how each was defined and measured, any transformations prior to analysis, and mean values for each species, is included in Appendix 4 (Table A4.3, Table A4.4, Fig. A4.1).

To address the potential effects of evolutionary history on peracarid community responses to predators, we built a phylogeny of our species by subsetting from the peracarid supertree published by Ashford et al. (2018). Species in our dataset that were not included in the supertree were substituted in for congeners or closely-related confamilials.

Community dispersion. Hereafter, “community” refers to the sum of individual fishes from 6 seines or peracarids from 12 grab samples for each of the 12 site-by-year combinations. For peracarids, we used the trait dataset to create a matrix of weighted Gower distances, which incorporate both continuous and categorical variables, between species using the *gawdis* package in R (de Bello et al. 2021). This method iteratively assigns weights to traits that ensure the equal contribution of each trait to the mean Gower distances between taxa, and accounts for correlations between traits by grouping them so that the group as a whole contributes equally to the mean Gower distances rather than the individual elements of the group. We grouped tube fidelity and living habit a priori, because species for which living habit was anything other than “tubicolous” automatically was assigned a tube fidelity of “none.” We also calculated Gower distances between species for their individual traits to pinpoint which community trait distributions may be subject to top-down control by the predator community.

For fishes, we calculated overall Gower distances by averaging weighted Gower distances based on fuzzy-coded traits (foraging mode and vertical position) and continuous traits (linear morphometric measurements and trophic level, with correlated modules grouped based on Pearson correlation coefficients greater than 0.6) calculated separately. Correlated continuous trait modules were dorsal fin length, anal fin length, and caudal peduncle length; eye diameter and body depth; and mouth height, pectoral fin length, and caudal fin length. To examine how specific fish traits in the community might exert differential selective pressures on peracarid communities, we also calculated the community-weighted mean value of each fish trait and PC axis for each community.

We measured the trait distance between species within peracarids and within fishes as the Mean Pairwise Distance (MPD) and Mean Nearest Taxon Distance (MNTD; Webb et al. 2002, Sessa et al. 2018). MPD is the average of the trait distances between all pairs of species found within a given community, while MNTD is the average minimum distance between species pairs in a community. Both are independent of species richness, but the two metrics can behave differently depending on the clustering of species in trait space within a community (Sessa et al.

2018). For peracarids, we also calculated MPD and MNTD for phylogenetic distances within each community, based on total branch length within the subset of the phylogeny contained in each community.

To determine whether the traits of observed species in each community differed from those expected by chance (fishes and peracarids) or phylogenetic relationships (peracarids), we standardized MPD and MNTD against null distributions generated according to two permutation algorithms. The first, independent swap, is a semi-constrained model that randomly re-assembles the community-by-species matrix while maintaining the species richness of each community and the presence/absence of each species across communities. The second, tip shuffle, is a more constrained model that directly shuffles the traits of the species in the community while maintaining richness, occurrence, and trait distances between community members, effectively moving the tip labels on a trait dendrogram or phylogeny. Imposing more constraints on permutation controls for patterns in the data that are not directly relevant to the question at hand, such as species richness, occurrence, or identity, which ultimately reduces type I error rates (Swenson 2014). We completed each permutation 999 times for each community, and generated null distributions of MPD and MNTD based on values calculated from randomized communities.

We then compared each observed value of community trait distance to the corresponding null distribution by calculating the standard effect size (SES_{MPD} or SES_{MNTD}). A positive value of SES indicates that the observed community trait distance (as measured by MPD or MNTD) is greater than the null mean, meaning that community members are more dissimilar than expected under a random draw (overdispersion), while a negative SES indicates that trait distance is less than the null mean, meaning that community members are more similar to each other than expected under a random draw (clustering). We calculated MPD, MNTD, null distributions and SES values using the *picante* package in R (Kembel et al. 2010).

Data analyses. To estimate the overall influence of multivariate habitat and fish community structure on peracarid traits and phylogenetic relationships, we used Mantel tests. Using matrices of habitat differences between communities and fish trait differences between communities, we modeled peracarid trait and phylogenetic distances between communities. We also conducted partial Mantel tests, which accounted for variation in habitat distances between communities when modeling the relationship between fish community trait distances and peracarid community trait and phylogenetic distances.

To account for the background effects of habitat filters that may mask the direct filtering effects of fishes on peracarid communities, we focused on the residuals of overall peracarid trait and phylogenetic dispersion from multiple regression against our habitat variables as response variables in linear models with community-weighted mean fish trait values as predictors. Aware of the possibility of temporal autocorrelation between years within sites, we examined correlations between site-level dispersion in both years, but found no significant correlations. We thus continued our analyses using each community as an independent observation. We conducted these analyses twice: once using community-weighted mean PC scores as predictors (16 tests), and once more using individual fish trait means (19 tests). We felt it important to examine all PC axes as predictors in order to capture potential “keystone” traits that explain a small percentage of morphological variation in the species pool but disproportionately affect prey community composition. To account for multiple comparisons, we applied Bonferroni corrections and compared our statistical results to α levels of 0.00313 (PC scores) and 0.00263 (individual traits). Based on these initial analyses, we performed post-hoc tests of relationships between residual SES for individual peracarid traits and fish mean PC8 scores (positively associated with anal fin length, eye position, and mouth protrusion), PC16 scores (positively associated with eye diameter, eye position, and pectoral fin length; hereafter “eye index”), and body depth below midline (BDBM) values. To account for multiple comparisons across 11 peracarid traits we applied a Bonferroni correction and compared our statistical results to an α level of 0.00455. We then measured the phylogenetic signal of peracarid traits that exhibited significant responses to fish traits as Blomberg’s K and Pagel’s λ to understand how individual traits might drive the response of peracarid phylogenetic dispersion to fish traits (Best and Stachowicz 2013).

To examine the indirect effects of filters on peracarids mediated through fish traits, we modeled residual peracarid SES as a function of fish SES. This time we focused on total fish trait dispersion, PC8 dispersion, eye index dispersion, and BDBM dispersion as predictors; and total peracarid trait dispersion, phylogenetic dispersion, maximum body size dispersion, antenna length 1 and 2 dispersion, and activity level dispersion (measured as percent still) as response variables based on results from our first set of analyses. We repeated these analyses twice: once with unaltered values of fish trait dispersion to accommodate habitat variables that might be affecting fish dispersion, and once more using residual values of fish dispersion regressed against habitat variables to focus on intraguild competition or other filtering processes acting on fish

communities. Statistical results were compared to an α level of 0.0083 to account for 6 types of peracarid dispersion as response variables. All statistical analyses were conducted in R v.4.2.2 (R Development Core Team 2022).

RESULTS

Across both years and all six sites, we found a total of 35 fish species and 28 peracarid species, of which 16 and 23 species were retained in our analyses, respectively. The epifaunal community overall was dominated by peracarids, making up 87% of individual epifauna across both estuaries and years. The most speciose peracarid community in our dataset had 18 species, while the most speciose fish community had 13 species. Four fish species (*Cymatogaster aggregata*, *Gasterosteus aculeatus*, *Porichthys notatus*, and *Sebastes carnatus*) were present in two discrete size cohorts; we considered each of these cohorts as a different predator type.

Habitat differences across communities explained variation in peracarid trait structure (Mantel $r = 0.270$, $p = 0.044$), but did not explain phylogenetic structure across communities. Fish taxonomic and trait structure did not have any significant effects on any aspect of peracarid community structure both when accounting for habitat variation and not.

However, dispersion in the trait and phylogenetic distribution of peracarid communities was strongly correlated with both mean state and dispersion in the traits of the fish assemblage. Patterns and predictors of peracarid trait and phylogenetic dispersion were robust across SES metrics and permutation algorithms; here we present and interpret the results of modeling fish trait effects on SES_{MNTD} calculated using the tip shuffle algorithm, with exceptions presented where relevant. Detailed results using other metrics and permutation algorithms are presented in Tables A4.1-A4.3. Of the community-weighted mean predator traits that we modeled as predictors of residual prey community dispersion, only one – PC axis 16 of fish morphology (eye index) – emerged as a strong predictor of both trait ($R^2 = 0.657$, $p < 0.001$; Fig. 2.2a) and phylogenetic dispersion ($R^2 = 0.826$, $p < 0.001$; Fig. 2.2b). This axis ranges from fishes with relatively large eyes located high up on the head (positive values) to fishes with small eyes located relatively low on the head (negative values). This index was positively correlated with peracarid trait dispersion; fish communities with larger average eye indices co-occurred with more overdispersed peracarid communities. For phylogenetic dispersion, we additionally observed a strong positive correlation between community-weighted fish PC8 score and dispersion (longer anal fins, higher eye position, and less protrusive jaws; $R^2 = 0.590$, $p =$

0.0022; Fig. 2.3a), and a strong negative correlation between community weighted fish body depth below midline (BDBM) and dispersion ($R^2 = 0.671$, $p < 0.001$; Fig. 2.3b).

No individual peracarid trait showed a significant response to these mean predator traits, but we did observe trends towards increased dispersion of maximum body size ($R^2 = 0.381$, $p = 0.019$), antenna 1 length ($R^2 = 0.419$, $p = 0.0136$), and activity level (measured as % still; $R^2 = 0.300$, $p = 0.0380$) with increasing mean eye index (Fig. 2.2c, d, f), and decreased dispersion of antenna 2 length with increasing mean eye index ($R^2 = 0.361$, $p = 0.0228$; Fig. 2e). Dispersion of antenna 1 length also increased with increasing mean PC8 score ($R^2 = 0.307$, $p = 0.0359$; Fig. 2.3c); decreased dispersion of maximum body size ($R^2 = 0.308$, $p = 0.0356$; Fig. 2.3d) and antenna 1 length ($R^2 = 0.352$, $p = 0.0247$; Fig. 2.3e) with mean BDBM; and increased dispersion of antenna 2 length with mean BDBM ($R^2 = 0.303$, $p = 0.0372$; Fig. 2.3f). Where peracarids were clustered for particular traits, there was no apparent consistency in the mean trait value across communities (Fig. 2.2c-f, Fig. 2.3c-f). Both antenna lengths showed significant phylogenetic signal (antenna 1: $K = 1.88$, $p = 0.001$; $\lambda = 0.946$, $p < 0.001$; antenna 2: $K = 0.960$, $p = 0.024$; $\lambda = 1.00$, $p = 0.0493$).

To examine the potential indirect effects of habitat filters on peracarid communities via fishes, we used fish community dispersion – due to habitat filters and other factors – as predictors of peracarid community dispersion. Surprisingly, total fish trait dispersion and dispersion along PC8 and eye index had no significant relationships with peracarid residual trait dispersion, phylogenetic dispersion, or the dispersion of any one trait in the community. In contrast, dispersion of fish BDBM was strongly negatively correlated with peracarid trait dispersion (Fig. 2.4a; $R^2 = 0.549$, $p = 0.00355$), phylogenetic (Fig. 2.4c; $R^2 = 0.726$, $p < 0.001$), maximum body size (Fig. 2.4d; $R^2 = 0.463$, $p = 0.00889$), and antenna 1 length dispersion (Fig. 2.4g; $R^2 = 0.0107$, $p = 0.0107$). We also saw negative relationships between fish BDBM dispersion and dispersion of peracarid activity level (% still), but only when peracarid dispersion was measured as SES_{MPD} (Table A5.2). In other words, fish communities that were more clustered, particularly with less body depth below midline (Fig. 2.4), co-occurred with peracarid communities that were more overdispersed.

Examining the residual dispersion of fish communities as a predictor of peracarid dispersion allowed us to focus on potential fish-mediated indirect effects on peracarid communities. Controlling for habitat filtering of fish communities strengthened the relationships

between fish BDBM dispersion and peracarid dispersion for all traits (Fig. 2.4b; $R^2 = 0.732$, $p < 0.001$), phylogeny (Fig. 2.4d; $R^2 = 0.960$, $p < 0.001$), body size (Fig. 2.4f; $R^2 = 0.622$, $p = 0.0014$), and antenna 1 length (Fig. 2.4h; $R^2 = 0.598$, $p = 0.00194$). These analyses also revealed positive effects of fish trait dispersion on peracarid phylogenetic dispersion (Fig. 2.5c; Fig. $R^2 = 0.537$, $p = 0.00406$), maximum body size dispersion (Fig. 2.5e; $R^2 = 0.603$, $p = 0.0018$), and antenna 1 length dispersion (Fig. 2.5g; $R^2 = 0.883$, $p < 0.001$), and a nonsignificant but notable positive effect of fish trait dispersion on peracarid trait dispersion (Fig. 2.5a; $R^2 = 0.302$, $p = 0.0374$). That is, fish communities that were more overdispersed in their traits co-occurred with peracarid communities that were more overdispersed with respect to traits and phylogeny, even after accounting for habitat effects. Residual fish PC8 dispersion exhibited strong negative relationships with residual trait (Fig. 2.5b; $R^2 = 0.570$, $p = 0.00274$), phylogenetic (Fig. 2.5d; $R^2 = 0.927$, $p < 0.001$) and body size dispersion (Fig. 2.5f; $R^2 = 0.712$, $p < 0.001$), and a nonsignificant but notable negative relationship with antenna 1 length dispersion (Fig. 2.5h; $R^2 = 0.336$, $p = 0.0283$) that was significant when other methods of calculating fish and peracarid dispersion were applied (Table A5.3). In particular, fish communities clustered around higher average PC8 scores tended to select for more overdispersed peracarid communities. The effect of eye index dispersion was largely dependent on the method used to calculate it. Eye index SES_{MNTD} had no significant effect when calculated with the tip shuffle algorithm, but had strong positive effects when we used the independent swap algorithm to randomize communities; and we saw no significant effect of eye index SES_{MPD} when calculated with the independent swap algorithm, but strong negative effects when we used the tip shuffle algorithm to randomize (Table A5.3).

DISCUSSION

In our examination of peracarid community assembly in Northern California eelgrass beds, we found that the dispersion of traits in the peracarid community responded strongly to a particular set of community-weighted mean fish traits. Peracarid communities were more overdispersed when exposed to fish communities with larger eyes high up on the head (high PC16 score), a pattern that held for all traits combined and for phylogenetic dispersion (Fig 2.2). While PC16 (eye index) accounts for only 0.028% of the morphological variation in the fish species pool, our analyses focus on local fish communities that have already undergone filtering from the regional pool, and the explanatory power of individual PC axes on species pool

variability is not relevant to our study. In this sense, eye index acts as a “keystone trait” that has a disproportionate effect on prey communities despite its encompassing a small part of predator morphospace. The strong effect of eye index on peracarid community dispersion is particularly noteworthy because of its correlation with traits including eye size, which is strongly related to fish visual acuity (Myrberg and Fuiman 2002, Caves et al. 2017, Lisney et al. 2020).

Correspondingly, prey activity level and body size both contribute to detectability by and susceptibility to gape-limited predators like fishes (McPeck 1990, Urban 2007), and we found that higher mean eye index lead to increased dispersion of both maximum prey body size and the amount of time prey spent not moving, which may hinder the ability of visually oriented predators to detect or form a consistent search image for prey.

In contrast, mean fish body depth below midline (BDBM) was strongly negatively correlated with peracarid phylogenetic dispersion. By itself, BDBM may serve as a proxy for bottom orientation (Pease et al. 2012); in our dataset, it is highest in benthically-oriented fishes with low gape limitation such as sculpins (Cottidae) or midshipmen (*Porichthys notatus*) and lowest in laterally compressed fishes that occupy the water column such as surfperches (Embiotocidae) and rockfishes (*Sebastes* spp.; Fig. 2.3b). This suggests that large-mouthed benthic fishes, many of which are sit-and wait-predators, select for a narrow range of phylogenetically-conserved traits such as body size and antenna length. While maximum body size of peracarids as defined in this study showed no significant phylogenetic signal, biomass has shown to be phylogenetically conserved in other studies of these peracarid communities (Best and Stachowicz 2013).

In all cases where we observed correlations between clustered peracarid communities and particular mean fish traits, we saw few apparent consistencies in the direction to which peracarids are clustered for specific response traits (Fig. 2.2c-f, Fig. 2.3c-f). For example, although low average eye indices were associated with clustered prey communities, these clustered communities did not have consistently low body sizes or activity levels, despite the fact that these could minimize detection by small-eyed fishes (Fig. 2.2c, f; Myrberg and Fuiman 2002, Caves et al. 2017, Lisney et al. 2020). This suggests three non-mutually exclusive possibilities. First, that these fish traits may be exerting strong selection on unmeasured phylogenetically conserved peracarid traits that exhibited strong genetic correlations with traits like body size, antenna length, and activity level. Second, only fish traits at one extreme may

drive overdispersion, while those at the other extreme have minimal effects on clustering, and the clustering we observed may be driven by other forces. Finally, the direction of fish traits' effects on peracarid trait clustering in the summer may be contingent on processes occurring earlier in the year when predation was lower and other factors were more important in community assembly. Broader factors such as dispersal limitation, competition for resources, and stochasticity in community composition may be important in determining how specific traits are distributed early on in the community assembly process before the predator community exerts any selective pressure (Hein and Gillooly 2011, Pelinson et al. 2022). Of note here is the fact that many of these fishes are juveniles of outer rocky reef species that recruit to estuarine habitats such as eelgrass every year to use as nursery habitats (McDevitt-Irwin et al. 2016, Beheshti et al. 2022, Obaza et al. 2022), and that predation rates in eelgrass are seasonally variable (Ruesink et al. 2019, C.E. Murphy, unpublished).

The trait dispersion of predator communities was a strong predictor of prey community dispersion; additionally, accounting for habitat filters on predator community assembly strengthened these relationships. Overall, these results suggest that habitat filtering on the fish species pool tended to diminish or antagonize selection acting on peracarids by fishes. In other words, habitat filtering on fishes tended to select for trait values that were weaker drivers of peracarid dispersion. To some degree, both predator and prey communities are assembled according to the same set of habitat filters, which may act in the same or opposite direction as filters such as predation or competition that act on smaller spatial scales (Kraft et al. 2015). These different selective pressures may act concurrently on the same or different sets of traits to produce the emergent pattern (Grime 2006, Ingram and Shurin 2009, Fitzgerald et al. 2017), and traits that respond differentially to selective pressures in one trophic level could produce different responses in another (Daniel and Rooney 2022).

On one hand, we found negative correlations between PC8 and BDBM dispersion and peracarid trait dispersion (Fig. 2.4), suggesting that prey may reduce competition for enemy-free space by moving into multiple niche optima that reduce their susceptibility to predation when predators are clustered, while pressure from overdispersed predator traits push prey into a single refuge in trait space, potentially reflecting equalizing competition (Fig. 2.1b, quadrants i and iii). On the other hand, we observed a positive correlation between total fish trait dispersion and peracarid dispersion (Fig. 2.5). In this case, a wide range of predation strategies across traits in

overdispersed predator communities may have prevented the dominance of a single predator avoidance strategy, leading to stabilizing competition for enemy-free space, while clustered predator communities forced prey to a single niche optimum that avoids the similarly small range of predator traits in the community (Fig. 2.1b, quadrants ii and iv). However, the lack of consistent trait means we observed in clustered peracarid communities suggests that the single trait optimum for evading clustered predators varies from community to community according to either idiosyncratic factors including the specific clustering pattern of the predator community or external environmental filters that lead to clustering at both trophic levels. In some cases, selection appeared to have no effect whatsoever on fish communities' strength as filters on the peracarid species pool – mean fish eye index had strong effects on peracarid dispersion, but the distribution of this trait and its response to ecological filters had no consistent predictive power (Table A5.2, A4.3). For traits like eye index that show little variation in the species pool, ecological selection may not be able to further constrain communities beyond the mean value of the species pool and thus have a negligible top-down effect.

Throughout this study we have operated under the assumption that the relationships we observed between predator and prey communities are the result of top-down control. While a bottom-up interpretation (prey traits filtering predator traits) is a valid approach to understanding these communities, we lack the means to apply this interpretation confidently with our trait dataset, as we focused on prey traits thought to be important for predator avoidance and microhabitat niche, and predator traits that were more broadly associated with feeding, movement, and habitat use. Additionally, predation is already known as an important driver of peracarid community structure in eelgrass beds, even for traits that are not necessarily directly affected by predators *a priori* (Gross et al. 2022). Furthermore, we saw no significant relationships between the mean or distribution of fish gape sizes and prey body sizes, or any other trait-trait relationships that might be reasonably expected under bottom-up control by prey communities.

Although the roles of predators in affecting prey community assembly through both predation and non-consumptive effects are now well-appreciated, much of this work focuses on species-depauperate predator assemblages (Post et al. 2008, Holdridge et al. 2017, Schmid et al. 2019), and rarely considers the potential top-down effects of community assembly of predators on the community assembly of their prey. We present compelling observational evidence that

specific predator traits have measurable impacts on the community assembly of prey, and that habitat filtering effects on predator species pools may hinder their ability to affect prey community assembly. While these results are not conclusive, they invite experimental tests of predator mean trait values on community assembly, and explicit comparisons of how the relative effects of habitat filters and intraguild competition on predators impact their ability to affect prey community assembly, especially in systems that exhibit strong top-down control. Integrating our understanding of traits at multiple trophic levels can help us better predict the impacts of community composition on food web dynamics, especially as regional species pools shift with climate change and anthropogenic introductions.

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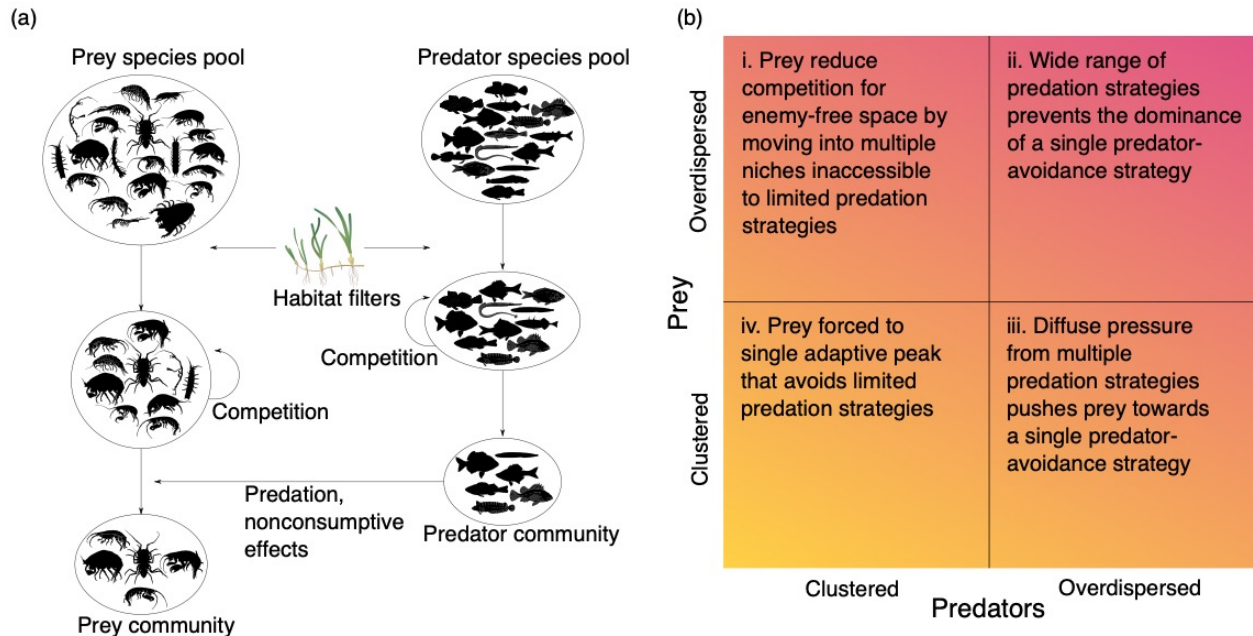


Figure 2.1. a) Species pools of both predators and prey are subject to abiotic and habitat filters as well as competition within trophic guilds, all of which exert selective pressure to restrict species from the local community. The local predator community, shaped by selection from other ecological filters, can act on the prey species pool to shape the final prey community. b) To the extent that predators act as filters on the prey species pool, predator trait dispersion patterns may exert selective pressure in directions that cause prey communities to mirror or oppose predator communities in terms of trait dispersion. Animal silhouettes by CPG; *Zostera* image by C. Collier, James Cook University (ian.umces.edu/media-library).

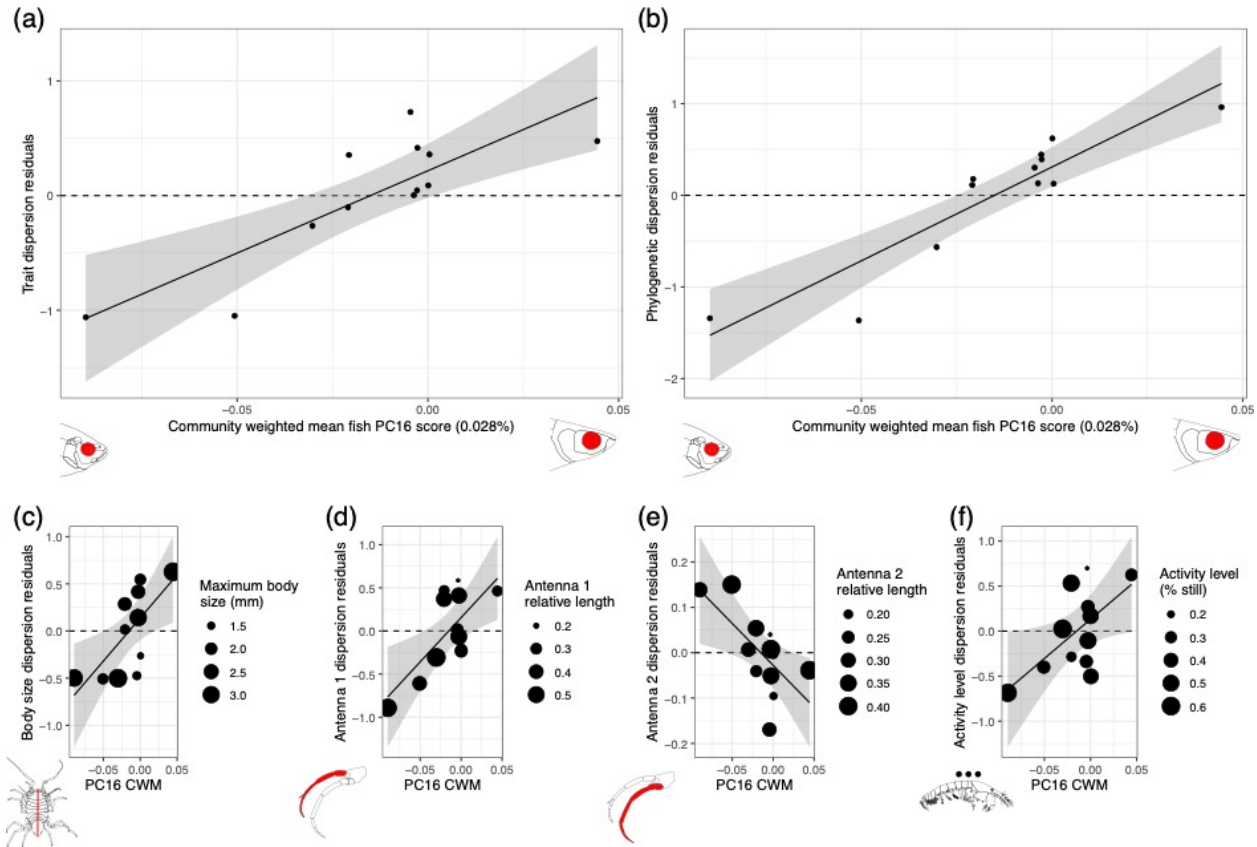


Figure 2.2. Responses of residual peracarid trait (a; $R^2 = 0.656$, $p < 0.001$) and phylogenetic (b; $R^2 = 0.826$, $p < 0.001$) dispersion to community-weighted mean (CWM) fish PC16 scores. Four traits showed noteworthy responses in their residual dispersion to PC16, although none were significant at $\alpha = 0.0045$: maximum body size (c; $R^2 = 0.381$, $p = 0.019$), antenna 1 length (d; $R^2 = 0.419$, $p = 0.0136$), antenna 2 length (e; $R^2 = 0.361$, $p = 0.0228$), and activity level measured as % still (f; $R^2 = 0.300$, $p = 0.0380$). In panels c-f, point size varies with CWM values for each individual trait examined. The dashed horizontal line represents a randomly assembled peracarid community ($SES_{MNTD} = 0$; calculated using the tip shuffle algorithm). Drawings by CPG.

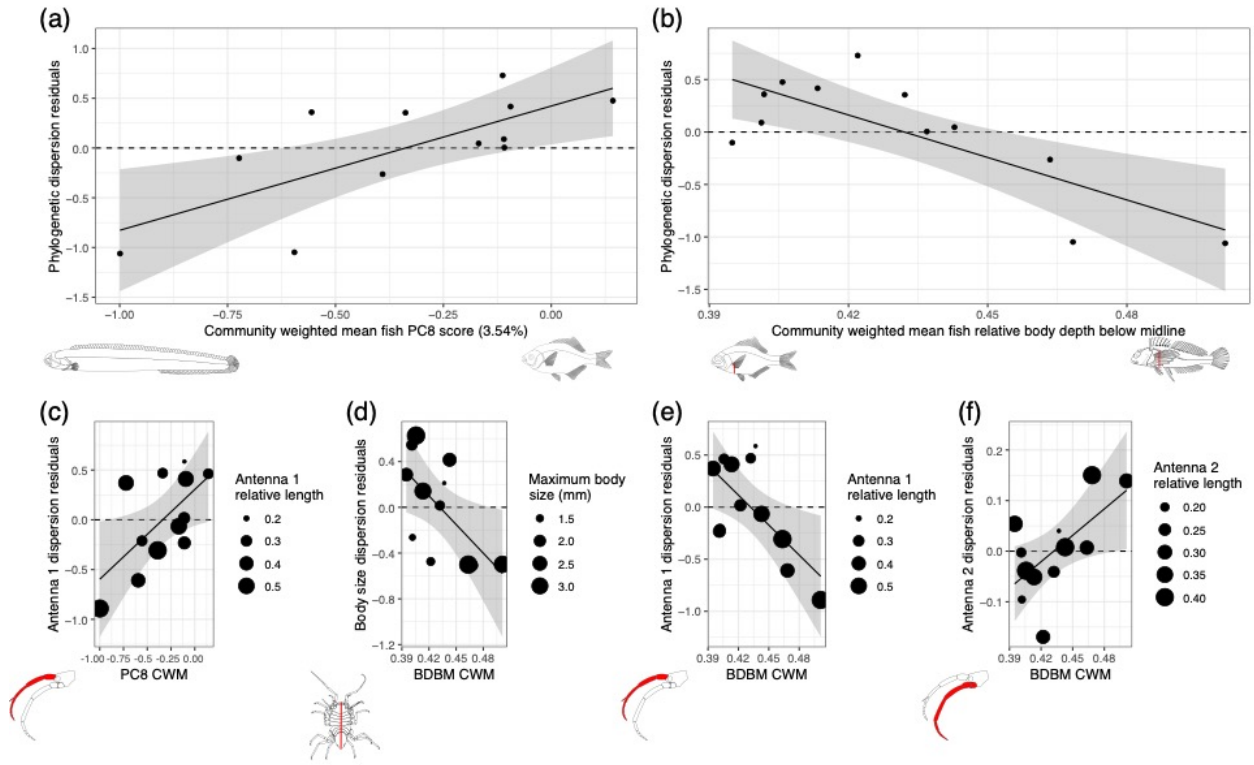


Figure 2.3. Responses of residual peracarid phylogenetic dispersion to community-weighted mean (CWM) fish PC8 scores (a; $R^2 = 0.590$, $p = 0.00215$) and body depth below midline (BDBM; b; $R^2 = 0.671$, $p < 0.001$). Antenna 1 length showed a noteworthy albeit nonsignificant positive correlation with community weighted mean PC8 score (c; $R^2 = 0.307$, $p = 0.0359$). Residual dispersion of maximum body size, antenna 1 length, and antenna 2 length were all correlated with community weighted mean BDBM (d: $R^2 = 0.308$, $p = 0.0356$; e: $R^2 = 0.352$, $p = 0.0247$; f: $R^2 = 0.303$, $p = 0.0372$), although none of these were significant at $\alpha = 0.0045$. In panels c-f, point size varies with community weighted mean values for each individual trait examined. The dashed horizontal line represents a randomly assembled peracarid community ($SES_{MNTD} = 0$; calculated using the tip shuffle algorithm). Drawings by CPG.

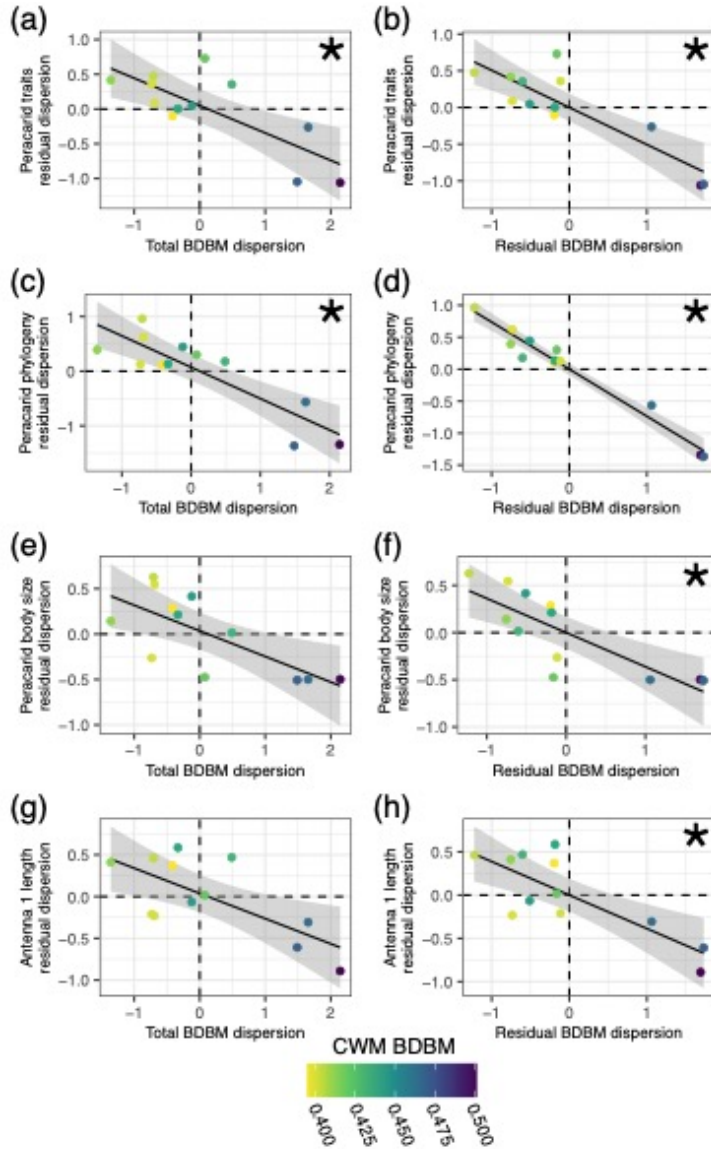


Figure 2.4. Responses of residual peracarid community dispersion to fish body depth below midline (BDBM) dispersion. Fish communities clustered around smaller BDBMs co-occur with peracarid communities that are more overdispersed when including (a, c, e, g) and controlling for the influence of habitat filters (b, d, f, h) for all traits (a, $R^2 = 0.549$, $p = 0.00355$; b, $R^2 = 0.732$, $p < 0.001$), phylogenetic distance (c, $R^2 = 0.726$, $p < 0.001$; d, $R^2 = 0.960$, $p < 0.001$), maximum body size (e, $R^2 = 0.463$, $p = 0.00889$; f, $R^2 = 0.622$, $p = 0.0014$), and antenna 1 length (g, $R^2 = 0.444$, $p = 0.0107$; h, $R^2 = 0.598$, $p = 0.00194$). Colors indicate the community weighted mean BDBM of each fish community. The dashed horizontal and vertical lines represent randomly assembled peracarid and fish communities, respectively ($SES_{MNTD} = 0$; calculated using the tip shuffle algorithm). Asterisks indicate a significant relationship at $\alpha = 0.0083$

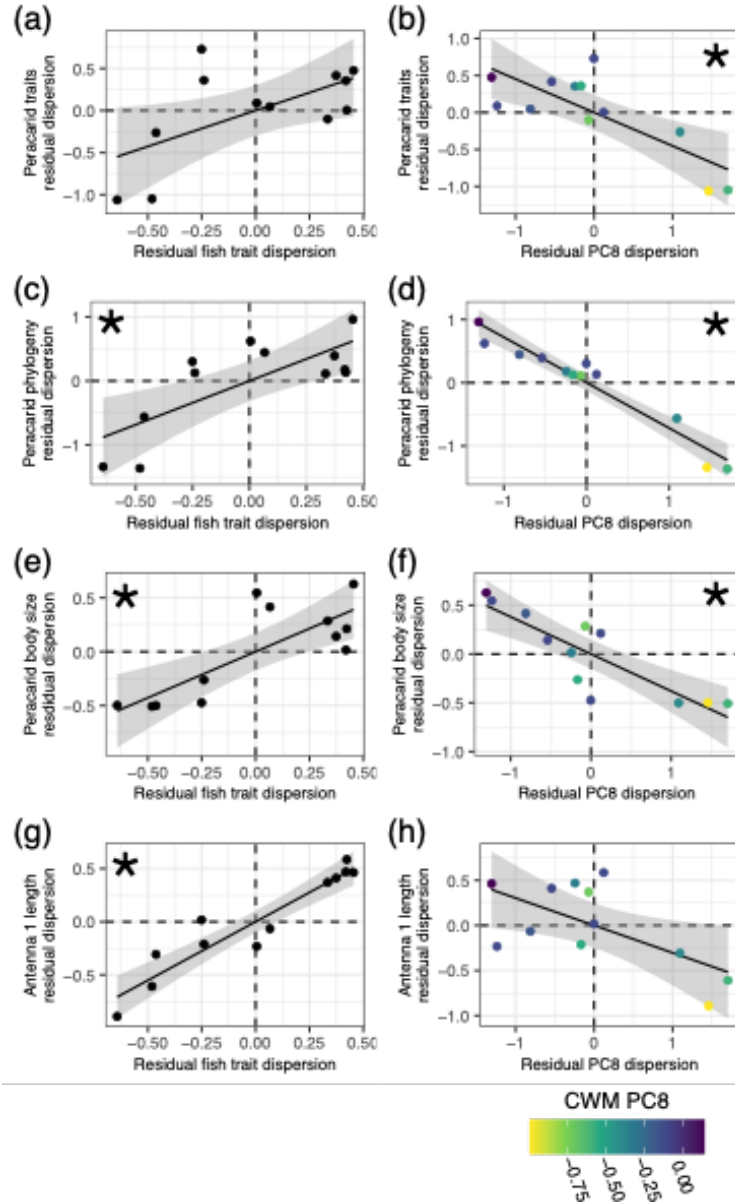


Figure 2.5. Residual fish trait dispersion (a, c, e, g) and PC8 dispersion (b, d, f, h) as predictors of residual peracarid trait dispersion (a, $R^2 = 0.302$, $p = 0.0374$; b, $R^2 = 0.570$, $p = 0.00274$), phylogenetic dispersion (c, $R^2 = 0.537$, $p = 0.00406$; d, $R^2 = 0.927$, $p < 0.001$), body size dispersion (e, $R^2 = 0.603$, $p = 0.0018$; f, $R^2 = 0.712$, $p < 0.001$), and antenna 1 length dispersion (g, $R^2 = 0.883$, $p < 0.001$; h, $R^2 = 0.336$, $p = 0.0283$). The dashed horizontal and vertical lines represent randomly assembled peracarid and fish communities, respectively ($SES_{MNTD} = 0$; calculated using the tip shuffle algorithm). In panels b, d, f, and h, colors indicate fish community-weighted mean scores of PC8. Asterisks indicate a significant relationship at $\alpha = 0.0083$.

CHAPTER 3: Eelgrass genetic diversity is strongly associated with a novel latitudinal cline in taxonomic turnover

ABSTRACT

Structural complexity within and among populations of habitat-forming foundation species is important for facilitating mobile animal diversity and abundance. Yet not all animal taxa respond equally to different axes of structural complexity and microhabitat space provided by foundation species, and because of functional differences among these taxa, variation in structural complexity may cascade upwards to affect ecosystem function. We examined global patterns in communities of epifaunal mesograzers dominated by peracarid crustaceans and gastropod molluscs in eelgrass (*Zostera marina*) beds, where variation in shoot morphology is underlain by intraspecific genetic diversity. The abundance of peracarids and gastropods exhibited a strong latitudinal cline in turnover, with gastropods abundant at high-latitude sites, and peracarids abundant at low-latitude sites, especially in the Atlantic. This pattern appeared to be driven by greater eelgrass genetic diversity at lower latitudes, which strongly influenced both the richness and abundance of peracarids, but less so for gastropods. The two taxa exhibited functional complementarity, and so variation in eelgrass genetic diversity across latitudes and between ocean basins led to geographic variation in the distribution of functional traits across the range of eelgrass. Our results add to a growing body of literature that suggests that variation in traits underlain by genetic differences within species has important consequences for assemblage variation and ecosystem function across broad spatial scales.

INTRODUCTION

The variety of microhabitats created by structurally complex foundation species can be an important driver of diversity in animal communities in both marine and terrestrial systems (MacArthur and MacArthur 1961, Hughes et al. 2002, Loke and Chisholm 2022). Different taxa may coexist by physically partitioning niche space in these habitats, based on the utility of microhabitats for feeding, avoiding predators, or optimizing physiological performance (Schmitz and Suttle 2001, Lindo and Winchester 2013, Lürig et al. 2016). In habitats composed of monospecific stands of foundation species, intraspecific trait variation, whether as a result of plasticity or standing genetic variation, can influence foundation species' suitability as habitat for numerous organisms.

Yet not all taxa may respond equally to the same aspects of structural complexity that may be underlaid by inter- or intraspecific variation in genetic architecture. Diverse trophic guilds across ecosystems are often composed of distinct lineages of taxa that have converged upon similar niches, despite separate origins (Scheltema 1997, Lefcheck and Duffy 2015). Despite their functional similarity, these lineages' may have distinct morphologies or other traits that may be favored by different aspects of structural complexity (e.g., Montalbetti et al. 2022), imposing a separate set of filters on the parts of a habitat they can occupy or the types of foundation species that may facilitate them. For taxa that are especially deeply diverged in time, these filters play out on a background of differences in biogeographic or phylogenetic history, differential responses to abiotic environmental filters, and other factors that can influence how they are distributed across broad spatial scales. Understanding the drivers behind differences in distributions among otherwise functionally similar taxa is key to generalizing how functional and phylogenetic differences affect species distributions, abundance, and community composition.

Worldwide, habitats formed by submerged marine angiosperms (seagrasses) are often composed of clonal individuals of just one or a few species (Hughes et al. 2009, Serra et al. 2010, Leopardas et al. 2014, Duffy et al. 2022). In these species-depauperate systems, plasticity within beds and genetic differences between individual clones are responsible for variation in shoot density, numbers of leaves, canopy height, and other aspects of structural complexity that make these habitats suitable for diverse communities of epifaunal macroinvertebrates (Hughes et al. 2009, Abbott et al. 2017, 2018). Gastropod molluscs and peracarid crustaceans form an important component of these epifaunal communities around the world (Jernakoff and Nielsen 1997, Lefcheck and Duffy 2015, Ha and Williams 2018). Both are typically included in the herbivorous “mesograzer” guild, feeding on epiphytic microalgae that foul seagrass blades, as well as detritus, macroalgae, and live seagrass tissue itself. Yet these taxa are phylogenetically distinct, separated by more than 550 million years of evolutionary history. In some seagrass systems, they are also differentially susceptible to predation, with peracarids being much more vulnerable to consumption than gastropods at the same sites (Reynolds et al. 2018). Direct development is common to all peracarids and when coupled with short generation times can lead to rapid population increases compared to gastropods which have slower individual growth and more diverse developmental modes. Whether global seagrass communities dominated by gastropods or peracarids are functionally distinct in other ways, including their responses to the

structural complexity provided by seagrasses, can have major implications for understanding their broader patterns of distribution and the ability of whole epifaunal communities to promote seagrass growth by suppressing algae (Hughes et al. 2004).

Here, using a global dataset of epifaunal invertebrate communities associated with the world's most widespread seagrass species (eelgrass, *Zostera marina*), we describe how epifaunal community composition and functional trait distributions vary with environmental parameters including aspects of eelgrass habitat structure on broad biogeographic scales, including between ocean basins and across latitudes. We were specifically interested in documenting any patterns of turnover exhibited between higher taxonomic groups, particularly peracarid crustaceans and gastropod molluscs, across space, with the goal of uncovering the likely drivers underlying spatial turnover in taxonomic dominance as well as its consequences for ecosystem function in these imperiled habitats.

METHODS

Study design and sample collection. Between May and September 2014, we sampled 49 sites across the range of *Z. marina*, spanning 37 degrees of latitude along both coasts of Eurasia and North America (30.4°N to 67.3°N; Fig. 3.1; Table A4.1, Fig. A4.1) to characterize the biological and physical structure of eelgrass beds using standardized measurements. Each site had 20 plots, for a total of 980 plots sampled as part of the *Zostera* Experimental Network (ZEN). Plots were 1 m² and spaced 2 m apart at each site. We sampled eelgrass biomass and quantified eelgrass habitat structure at the plot level as described by Gross et al. (2022) – briefly, we quantified eelgrass aboveground biomass, shoot density, canopy height, and leaf nitrogen, as well as macroalgal biomass from 20-cm diameter cores in each plot. We quantified epiphyte load by scraping fouling microalgae from four eelgrass shoots per plot and drying to a constant weight. We additionally quantified eelgrass genotypic richness as the average site-level genetic dissimilarity (Rozenfeld distance) between individual shoots based on 24 microsatellite loci, and allelic richness as the average number of alleles per locus, normalized to 7 genets (Duffy et al. 2022).

Abiotic environmental variables. To characterize the abiotic environment experienced by epifauna across the range of eelgrass, we measured in-situ temperature and salinity at each site at the time of sampling. To characterize the overall abiotic environment of each site, we also retrieved estimates of annual mean sea surface temperature (SST), photosynthetically active

radiation (PAR), surface chlorophyll a (Chl a), salinity, and pH from the surrounding region, available in the Bio-ORACLE data set (Tyberghein et al. 2012). These data were taken from monthly readings of the Aqua-MODIS and SeaWiFS satellites at a 9.6 km² spatial resolution from 2002 to 2009. We used the raster package in R v. 3.6.3 (Hijmans and Etten 2020, R Development Core Team 2022) to extract the annual mean SST, SST range, PAR, and Chl a from all cells within 10 km of each site, and averaged these cell-level estimates to generate site-level predictors. Other water quality parameters, including dissolved nitrate and other nutrients, were spatially interpolated based on surface measurements in the World Ocean Database 2009 (Garcia et al. 2010).

Measuring predation intensity. Predation intensity was quantified with prey tethering units (PTUs) – locally-collected prey (shelled gastropods and “gammarid” amphipods) as well as standardized prey types (dried squid and kale) were tethered in each plot for 24 hours. Data and methods for amphipod and gastropod prey are reported in detail in Reynolds et al. (2018). Standardized squid prey were 1 cm² pieces of dried squid attached by monofilament line to one acrylic rod in each plot (Duffy et al. 2015, Whalen et al. 2020). Pieces of organic curly-leaf green kale measuring approximately 5 x 3 cm were wrapped around acrylic rods to measure macroherbivory pressure at each site. Each PTU type was deployed in each of the four corners of each plot. After 24 hours, we removed the stakes and scored prey as present (uneaten) or absent (eaten); partially-consumed prey were considered eaten, and molted prey were excluded from analyses. Site-level predation was calculated by averaging scores across plots. We calculated site-level consumption of each prey type by averaging scores across plots.

Epifaunal community composition. To sample the macrofauna associated with the eelgrass blades, we carefully placed an open-mouthed fine-mesh drawstring bag (500 µm mesh, 18 cm diameter) over a clump of shoots in the centre of the plot so that the mouth of the bag was flush with the sediment surface. We then cut the shoots where they emerged from the sediment and quickly closed the drawstring to capture the shoots and associated animals. We transferred shoots to the lab on ice and rinsed and hand-inspected them to dislodge the epifauna. We preserved all epifauna that remained on a 1-mm sieve in 70% ethanol and then identified them to the lowest possible taxonomic level (typically species). We standardized epifaunal abundance by the aboveground biomass of the eelgrass sample from which they were collected. We separated epifaunal species into 7 coarse taxonomic groups, including peracarid crustaceans (amphipods,

isopods, tanaids, and mysids), gastropod molluscs, polychaete annelids, bivalve molluscs, decapod crustaceans, anemones, and others (including but not limited to barnacles, nemertean worms, echinoderms, ostracods, and chironomid midge larvae). Peracarids and gastropods were by far the most abundant and speciose groups in these global epifaunal communities (comprising 21.6% and 39.9% of individuals and 116 and 91 species, respectively), and have known functional roles as grazers of eelgrass and associated epiphytes, so we chose to focus subsequent analyses on these taxa.

We scored all peracarid and gastropods for a common series of traits based on information available in the literature, including maximum body size, parental care, developmental mode, tolerance of brackish and fresh water, grazer diet components (fresh eelgrass tissue, eelgrass detritus, macroalgae, microalgae), and alternate non-grazing feeding modes (suspension feeder, carnivore/parasite/scavenger). We also used a series of nested sieves to group individual epifauna into size classes, and used these to approximate mean, mode, medium, and maximum observed sizes for each species. We additionally estimated each species' latitudinal range as the difference between the two most extreme point observations regardless of hemisphere (to account for introduced species and others that span the equator), and latitudinal mean as the mean latitude absolute latitude value of point observations, available online from the Ocean Biodiversity Information System (OBIS) and the Global Biodiversity Information Facility (GBIF) (UNESCO 2023, GBIF 2023). A more detailed discussion of traits including how we defined and measured each, and any transformations we applied prior to analysis is included in Table A4.2.

Functional trait ordination and clustering. To examine how communities dominated by peracarids and gastropods varied across trait space, we calculated continuous community weighted mean trait values for each site. For binary and discrete categorical traits, this translated to average relative abundances of each trait level, while for continuous traits it was the average value. We then calculated Bray-Curtis distances among sites based on their community-weighted trait means, and visualized sites in trait space using an NMDS ordination.

To examine any geographic signal in the trait composition of these communities, we hierarchically clustered communities in trait space based on average Bray-Curtis distances, separating clusters into discrete groups based on a maximum average distance of 0.1. We then

recalculated group-level community-weighted means for our trait values by considering individuals from all sites within a group to be part of one community.

Data analyses. We first examined how species richness and Shannon-Weiner diversity varied across latitude, both for the entire epifaunal community and separately for gastropods and peracarids. We additionally examined how the relative abundance of each of these two groups varied across latitudes and ocean basins. For both sets of analyses we used generalized linear models, assuming Poisson-distributed species richness and binomially-distributed relative abundance of gastropods and peracarids.

To identify candidate predictors of the relative abundance of peracarids and gastropods across sites, we used the log-transformed ratio of peracarid relative abundance to gastropod relative abundance (hereafter log-ratio) as the response variable in a random forest model that incorporated both abiotic and environmental predictor variables, including the first two principle components of eelgrass morphology (including sheath length, sheath width, longest leaf length, shoot density, and aboveground biomass; Fig. A4.4), and species richness of the entire epifaunal community as well as the gastropod and peracarid components. We transformed predictor variables (Table A4.2) where appropriate to conform to expectations of normality. Variables that showed a pairwise Kendall's τ value of greater than 0.6 were not included in the predictor pool. We tuned each forest model by visually inspecting out-of-bag error rates across all trees in the model, and adjusted the number of trees to the smallest number for which error was consistently low. We identified the top 10 predictors of relative abundance from each forest by the degree to which they increased MSE when removed from the model and the total increase in node impurities when removed from the model.

We then performed a model selection procedure to determine the best predictor of each taxon's relative abundance. First, we created a set of 30 a priori generalized linear models of relative abundance: one set based on the top 10 predictors alone, another set based on the top 10 predictors with an interaction term for ocean basin (Atlantic vs. Pacific; to address differences in historical processes that may affect local species pools), and another set based on the top 10 predictors with an interaction term for continental margin (Eastern vs. Western; to address differences in the slope of abiotic latitudinal gradients that may affect communities). We ranked these initial models using AICc scores (MuMIn package; Bartoń 2020), and then incorporated predictors from the three lowest-scoring models of each set into a set of composite models to

examine the combined effects of multiple predictor types. We then used backwards elimination to select the lowest-scoring model from these composite models. Where two models had a $\Delta AICc$ less than 3 units, we selected the model with the fewest parameters for interpretation. To specifically examine the responses of these two taxa to aspects of eelgrass habitat composition and structural complexity, we modelled the richness and total abundance of gastropods and peracarids as a function of eelgrass allelic richness, genotypic richness, and the first two principle components of eelgrass morphology. The significance of model predictors was assessed using the `Anova()` function in the `car` package in R.

To test whether gastropods and peracarids contributed distinct, non-overlapping suites of traits to epifaunal communities, we asked whether the log-ratio determined the clustering of sites in trait space. We performed a permutational multivariate ANOVA (PERMANOVA) on the Bray-Curtis distances of community-weighted means between sites, using 9,999 permutations. We also investigated whether the volume of trait space occupied by gastropod-dominated (negative log-ratio) or peracarid-dominated (positive log-ratio) sites differed significantly from each other by measuring the average dissimilarity from individual sites to their group centroid (Anderson et al. 2006). Because this procedure requires discrete categories across which to compare variances, we assigned sites with positive and negative log-ratios to separate groups and compared between them. All statistical analyses were conducted in R v.4.2.2 (R Development Core Team 2022).

RESULTS

As is typical for many marine and terrestrial systems, total epifaunal species richness and Shannon-Weiner diversity declined with increasing latitude, and this was true for both Atlantic and Pacific oceans ($\chi^2_1 = 67.999$, $p < 0.001$; Fig. 3.1A). For peracarids, species richness showed opposite latitudinal clines between ocean basins – in the Pacific, richness tended to increase with increasing latitude, while it declined significantly with increasing latitude in the Atlantic ($\chi^2_1 = 22.331$, $p < 0.001$; Fig. 3.1B). Gastropods showed no significant latitudinal clines in species richness, even after removing Porth Dinllaen, Wales, where the species richness was an anomalously high 17 species (Fig. 3.1C). Shannon-Weiner diversity for peracarids and gastropods did not show any significant latitudinal trends. Species richness increased with total abundance for peracarids, but not for gastropods (Fig. A4.2).

We found striking clines in the relative abundance of both peracarids and gastropods across the 37° of latitude surveyed in our study – at high latitudes, gastropods dominated (up to 99.55% in Seldianaya, Russia; $\chi^2_1 = 58295$, $p < 0.001$), while at lower latitudes, peracarids dominated ($\chi^2_1 = 11284.0$, $p < 0.001$; Fig. 3.2). These patterns also differed by ocean basin – in the Pacific, peracarids dominated (up to 98.54% in Willapa Bay, WA, USA) and declined more slowly with increasing latitude than in the Atlantic ($\chi^2_1 = 3524.8$, $p < 0.001$; Fig. 3.2A), where gastropods dominated and increased more steeply with increasing latitude ($\chi^2_1 = 1722$, $p < 0.001$; Fig. 3.2B). There were few sites dominated by other epifaunal taxa, including anemones, mussels, and polychaete worms, but this dominance of other taxa did not vary significantly by latitude or ocean basin (Fig. 3.2C).

Our random forest model employed to predict the log-ratio of peracarids to gastropods across sites used 4,000 trees with an average of 12.327 nodes per tree and explained 33.83% of the variance in log-ratios. Top predictors in this model included coast, ocean basin, in-situ temperature, eelgrass morphology PC1 (positively correlated with shorter leaf lengths and narrower sheath widths), eelgrass allelic richness, eelgrass leaf carbon content, site peracarid richness, eelgrass genotypic richness, mean water column Chl a, and water column silicate (Table 3.1). The log-ratio of peracarids to gastropods was best explained by an additive model including only 3 variables: peracarid richness, eelgrass allelic richness, and ocean basin ($F_{3,43} = 20.42$, $p < 0.001$). Log-ratios increased (more peracarids than gastropods) with peracarid richness and eelgrass allelic richness (Fig. 3.3A, B), and were greater in the Pacific than in the Atlantic Ocean (Fig. 3.3C). Eelgrass allelic richness declined with increasing latitude in the Atlantic, but not in the Pacific; eelgrass allelic richness and morphological variation were also greater on average in the Pacific than in the Atlantic (Fig A5.4).

Peracarid abundance and richness showed consistently significant responses to eelgrass allelic richness, genotypic richness, and the first two principle components of eelgrass morphology – sites with more genetically diverse eelgrass, eelgrass with wider, longer blades (negative PC1 scores), and more dense shoots and greater aboveground biomass (positive PC2) scores, had more peracarid species and individuals (Table A4.4, Table A4.5). Gastropod species richness showed a significant positive response to PC1 and genotypic richness (Table A4.4), while abundance responded positively only to PC1 (Table A4.5).

Gastropod-dominated epifaunal communities (those with a negative log-ratio) occupied a distinctive area of ordination space from peracarid-dominated communities (positive log-ratio; pseudo $F_{1,45} = 11.918$, $p < 0.001$; Fig. 3.4A). Gastropod and peracarid species also occupied complementary regions of trait space (Fig. A4.3). The proportion of other epifaunal taxa did not significantly affect a community's trait assemblage (pseudo $F_{1,48} = 0.33$, $p = 0.784$). The log-ratio did not significantly affect functional beta diversity among sites with similar proportions of these focal taxa ($F_{1,47} = 0.7606$, $p = 0.3876$). Community-weighted trait means explained 62.48% of the variation in log-ratio, according to a random forest model. Traits that drove the functional distinction between gastropod- and peracarid-dominated communities predictably included those related to parental care and developmental mode – Peracarid-dominance was significantly correlated with more brooding, less egg-case-laying, more direct development, and less broadcast spawning – but communities with more peracarids also had more suspension feeders, carnivores, parasites, and scavengers. Species' average latitudinal ranges and mean latitudes were also smaller in peracarid-dominated communities (Table 3.2).

Our hierarchical clustering scheme produced 5 distinct groups of sites with different mean trait values for both peracarids and gastropods (Fig. 3.4B). The first group (“cold Pacific”) consisted of cool-temperate Northeast Pacific sites in British Columbia, the outer coast of Washington State (Willapa Bay), Oregon, and Northern California, as well as sites in Japan (Hokkaido), South Korea, Portugal, and Mediterranean France. The second group consisted only of one site in Croatia, where we only found the snail *Bittium reticulatum*. The third group (“warm sites”) consisted of warm-temperate to subtropical sites in Southern California, Mexico (Baja California), Virginia, and North Carolina, as well as one site in the Salish Sea (Dabob Bay). The fourth group (“cold Atlantic”) consisted of cold temperate sites on both sides of the Atlantic, including Long Island, Massachusetts, Quebec, Ireland, Wales, Sweden, Finland, Norway, and Russia (White Sea). The fifth group (“Asia”) included sites in Japan and South Korea as well as one site in Southern California (San Diego Bay). Groups varied mostly by mean maximum body length (from the literature; group 1: 23.43 mm; group 5: 11.65 mm), latitudinal range (group 2: 68.47°; group 5: 21.79°), and mean latitude (group 4: 52.58°; group 5: 37.78°), while all groups were dominated by microalgal grazers and marine species (Table 3.3).

DISCUSSION

We found a prominent latitudinal gradient in epifaunal species richness, with greater richness at lower latitudes (Fig. 3.1A). At Atlantic sites, peracarids followed this same trend (Fig. 3.1B), but the pattern was not recapitulated by peracarids at Pacific sites or gastropods worldwide (Fig. 3.1C). While the negative correlation between species richness and latitude is typical for many terrestrial systems and some marine systems (Pianka 1966, Gaston 2000), evidence increasingly shows that for most marine taxa, richness peaks at mid-latitudes, with a dip near the equator (Chaudhary et al. 2016, Arfianti and Costello 2020, Thyrring and Peck 2021). Furthermore, previously published analyses place peaks in gastropod species richness between 25-30°N and peracarid (amphipod) richness between 50-60°N in the northern hemisphere (Chaudhary et al. 2016, Arfianti and Costello 2020), in direct contrast with our results. However, these analyses pooled species across multiple nearshore habitat types, including seagrasses, coral reefs, rocky shores, and soft sediments, and our observed peaks in richness at lower latitudes for total epifauna and Atlantic peracarids may reflect the responses of these taxa specifically to unique characteristics of eelgrass habitat that obscure broader patterns of species richness.

The composition of epifaunal communities shifts from being peracarid-dominated to gastropod-dominated at high latitudes, especially in the Atlantic (Fig. 3.2A, B). As far as we are aware, this latitudinal gradient in taxonomic turnover has not been documented elsewhere in the literature, although there is some limited evidence that gastropods may be more abundant in high-latitude seagrass beds than in low-latitude beds (Barnes and Ellwood 2011). This gradient in turnover mirrors the pattern we observed for peracarid species richness (Fig. 3.1B), but appears to be independent of any broader patterns in gastropod diversity (Fig. 3.1C). Despite superficially recovering some expected latitudinal patterns, the variation in taxa and relationship with eelgrass genetic diversity suggest these are not likely to be driven directly by the processes that might generate a latitudinal diversity gradient, such as temperature. Instead, the results of our analyses suggest a set of plausible explanations for this pattern that may hinge on the historical legacy created by eelgrass range expansion across the Pacific from Japan to North America and then through the Arctic to the Atlantic (Duffy et al. 2022, Yu et al. in revision).

Despite differences in the relative abundances of peracarids and gastropods between the Pacific and Atlantic (Fig. 3.3C), we still observe significant increases in gastropod dominance and decreases in peracarid dominance with increasing latitude in Pacific sites, suggesting

additional mechanisms acting within ocean basins to drive the latitudinal pattern. Notably, log-ratios increase with eelgrass allelic richness (Fig. 3.3A). Eelgrass genetic diversity and variation in morphology are both greater in the Pacific than the Atlantic, the result of bottlenecks that occurred during its colonization of the Atlantic via the Arctic starting 3.5 million years ago (Olsen et al. 2004, Duffy et al. 2022, Yu et al. in revision; Fig. A4.4A). Within the Atlantic, allelic richness also declines significantly with latitude (Fig. A4.4A). The response of epifaunal communities to structural complexity in eelgrass is well-characterized (Orth 1992, Carr et al. 2011, Lürig et al. 2016), particularly as refuge from predators. Experimental evidence has shown that eelgrass genetic diversity affects the abundance of epifaunal mesograzers, and that genetic diversity is associated with eelgrass trait diversity (Hughes et al. 2009, Abbott et al. 2017, 2018; Fig. A4.4B,C). We found similar associations between genetic diversity and abundance and richness for peracarids (Table A4.4, A5.5). Differences in numbers of leaves, shoot widths, and shoot length as a result of genetic differentiation may potentially create a greater variety of microhabitats that support more peracarid species and individuals – for example, longer leaves create horizontal “canopies” that are distinct from vertical “stem” habitats (Lürig et al. 2016). PC1’s place in the top predictors from our random forest model corroborates this result and indicate that aspects of eelgrass morphology, notably leaf length and sheath width, are also important determiners of epifaunal log-ratios (Table 3.2).

Our best model predicting epifaunal log-ratios shows a significant positive relationship with site-level peracarid species richness (Fig. 3.3B), suggesting that greater abundance and richness of peracarids (perhaps facilitated by greater eelgrass structural complexity; Table A4.4) at lower latitudes may occupy more niches and competitively exclude gastropods. Yet our ordinations (Fig. 3.4, Fig. A4.3) point to complementarity in the traits of gastropods and peracarids, rather than overlap or redundancy. However, the limited number of comparable traits we were able to assemble for both gastropods and peracarids may be biased more towards niche differences that promote stabilizing coexistence rather than fitness differences (*sensu* Mayfield and Levine 2010), obscuring potential interactions between these two taxa that may lead to competitive exclusion. For example, in many cases gastropods and peracarids differ in their feeding rates on microalgae, macroalgae, or detritus (Graça et al. 2000, Aberle et al. 2005, Sampaio et al. 2017), which may lead to competitive exclusion if multiple species are focusing on the same food source. Peracarids tend to be more selective grazers than gastropods, and

greater richnesses of species with complementary diets may contribute to the exclusion of gastropods (Jernakoff and Nielsen 1997, Duffy and Harvilicz 2001). Peracarids may also dislodge or even prey upon small molluscs (Lefcheck et al. 2014). It seems unlikely that these behaviors would have a major effect on global distributions of the two taxa, but this remains to be tested.

Our experimental network is notably biased in its sampling of eelgrass epifauna in the Atlantic and Pacific Oceans. Our 29 Atlantic sites span nearly 33° of latitude – nearly the full latitudinal range of eelgrass in the Atlantic (den Hartog 1970, Green and Short 2003) – and include 14 of our highest-latitude sites (Fig. 3.2C). In the Pacific, the remaining 20 sites span only 18.6° of latitude, excluding both higher-latitude sites in Alaska, British Columbia, and the Sea of Okhotsk as well as lower-latitude sites in Mexico. Our latitudinal pattern thus seems to be in part driven by high-latitude gastropod-dominated Atlantic sites at one extreme, and low-latitude peracarid-dominated Pacific sites at the other (Fig. 3.3C). However, the latitudinal pattern of taxonomic turnover is highly significant across our Atlantic sites, and the trend, while weaker, is still observable in the limited latitudinal range of our Pacific sites (Fig. 3.3A, 3.3B).

Regardless of the proximate mechanisms behind the patterns of taxonomic turnover we observed, they ultimately contribute to significant differences in the functional structure of global eelgrass communities. Gastropod-dominated sites were not only geographically distinct, but also occupied a distinct area of niche space from communities dominated by peracarids (Fig. 3.4A). Functionally similar groups of sites appeared to group according to similar latitudes within ocean basins (Fig. 3.4B), emphasizing the role of distinct ocean basins as well as correlated aspects of eelgrass habitat structure in affecting the structure and functioning of epifaunal communities (Fig. 3.3A, C). Epifaunal mesograzers in seagrass beds play a critical role in linking the primary production of algae and seagrass to populations of larger predators, including juveniles of economically important fishery species (Heck et al. 2003, Blandon and zu Ermgassen 2014, McDevitt-Irwin et al. 2016). Because epifauna vary in their ability to consume fouling epiphytes, feed directly on seagrass tissue, and their palatability to predators (Jernakoff and Nielsen 1997, Lewis and Anderson 2012, Reynolds et al. 2018), understanding the functional consequences of variation in taxonomic structure across broad biogeographic regions may help us begin to predict the idiosyncratic and geographically variable dynamics of seagrass ecosystem function (Duffy et al. 2014).

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Table 3.1. Top 10 predictors in a random forest model that explained 56.5% of variation in the log-ratio of peracarid relative abundance to gastropod relative abundance across global eelgrass sites. Bolded rows indicate predictors included in the best model of log-ratio.

Predictor	Transformation	% Increase in MSE	% Increase in Node Impurity
Coast	None	23.469200	31.201383
Ocean Basin	None	21.772421	29.091206
In-situ Temperature (°C)	None	14.963883	11.001778
Eelgrass Morphology PC1 (62.09%)	None	14.214091	30.976627
Eelgrass Allelic Richness (avg. number of alleles per locus, normalized to 7 genets)	Squared	12.844151	21.280422
Mean Eelgrass Leaf % C	None	10.997176	13.525104
Site Peracarid Richness	log + 1	9.401629	11.836563
Genotypic Richness (mean Rozenfeld distance)	None	6.845336	3.603339
Mean Water Column Chl a	log	6.779512	6.117515
Mean Water Column Silicate	log	6.455153	4.595070

Table 3.2. Top 10 candidate traits (continuous) and trait states (categorical) associated with increases in log-ratio peracarid relative abundance to gastropod relative abundance across sites, as output from a random forest model explaining 62.48% of variation in log-ratios. Bolded rows indicate trait states unique to gastropods.

Trait value	% Increase in MSE	Increase in Node Impurity	Spearman ρ	p
Brooder	14.792646	85.317146	0.8086603	6.188e-12
Mean Latitude	14.093822	72.964589	-0.6279949	2.298e-06
Lays Egg Case	8.811130	36.860245	-0.7153161	1.607e-08
Direct Developer	6.700999	19.853744	0.56727	3.214e-05
Latitudinal Range	5.559044	21.833437	-0.5122888	0.0002322
Suspension Feeder	5.396012	23.410392	0.5174202	0.0001958
Non-Suspension Feeder	4.523542	13.447565	-0.517311	0.0001965
Non-carnivore/parasite/scavenger	3.554432	10.720121	-0.471435	0.0008231
Broadcast Spawner	3.516959	4.040270	-0.1846305	0.2141
Microalgal Grazer	3.066659	5.222737	-0.3014138	0.0395

Table 3.3. Mean trait values of the peracarid and gastropod community in 5 a posteriori groups of eelgrass sites created by hierarchical clustering based on similarities in site-level community-weighted mean trait values. Dominant values for binary and categorical traits are shown, while group-level community-weighted means are supplied for continuous traits. Observed sizes are derived from sieved epifaunal samples. Latitudinal range and mean latitude are derived from observations gathered from GBIF and OBIS.

Group	Diet	Parental Care	Developmental mode	Mode Obs. Size (mm)	Max Obs. Size (mm)
1 - "Cold Pacific"	Microalgal grazer	Brooder	Direct development	2.585	5.556
2 - Croatia	Microalgal grazer, detritivore	Broadcast spawner	Lecithotrophic	2.800	8.000
3 - "Warm Sites"	Microalgal grazer	Brooder	Direct development	1.443	5.042
4 - "Cold Atlantic"	Microalgal grazer, macroalgal grazer	Lays egg case	Direct development	1.440	4.139
5 - "Asia"	Microalgal grazer, detritivore	Brooder	Direct development	1.578	4.959

Table 3.3, continued.

Group	Mean Obs. Size (mm)	Max Lit. Size (mm)	Lat. Range	Lat. Mean	Salinity
1 - "Cold Pacific"	2.473	23.428	32.574°	46.735°	Marine
2 - Croatia	2.364	15.000	68.471°	52.156°	Marine, Brackish, Freshwater
3 - "Warm Sites"	1.669	15.000	38.205°	36.942°	Marine
4 - "Cold Atlantic"	1.474	14.141	45.610°	52.584°	Marine
5 - "Asia"	1.713	11.646	21.788°	37.782°	Marine

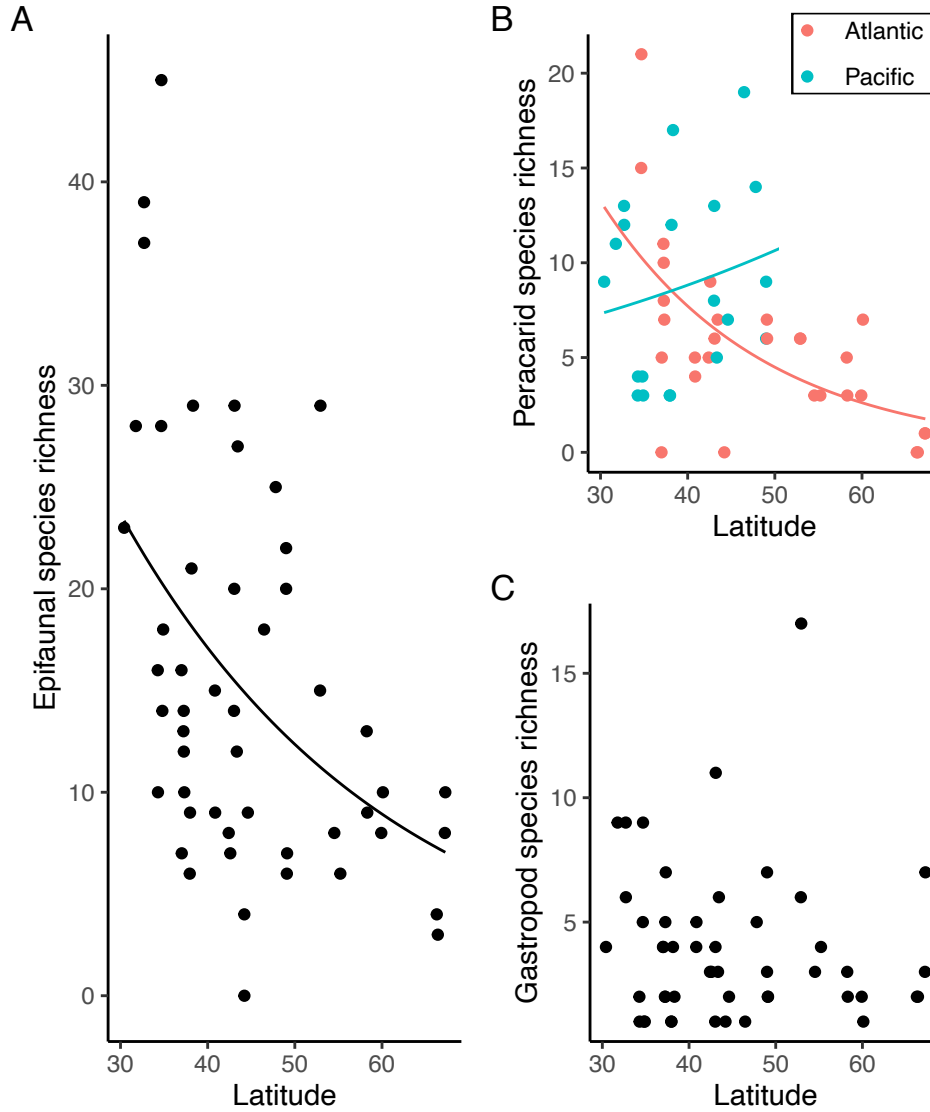


Figure 3.1. Latitudinal clines in species richness for all epifauna (A), peracarids (B), and gastropods (C) across global eelgrass sites. There was a significant relationship between latitude and total epifaunal species richness in both the Atlantic and Pacific oceans ($\chi^2_1 = 67.999$, $p < 0.001$). Peracarids showed opposite patterns of richness with latitude in the Pacific and Atlantic ($\chi^2_1 = 22.331$, $p < 0.001$), while gastropods showed no significant latitudinal richness gradient.

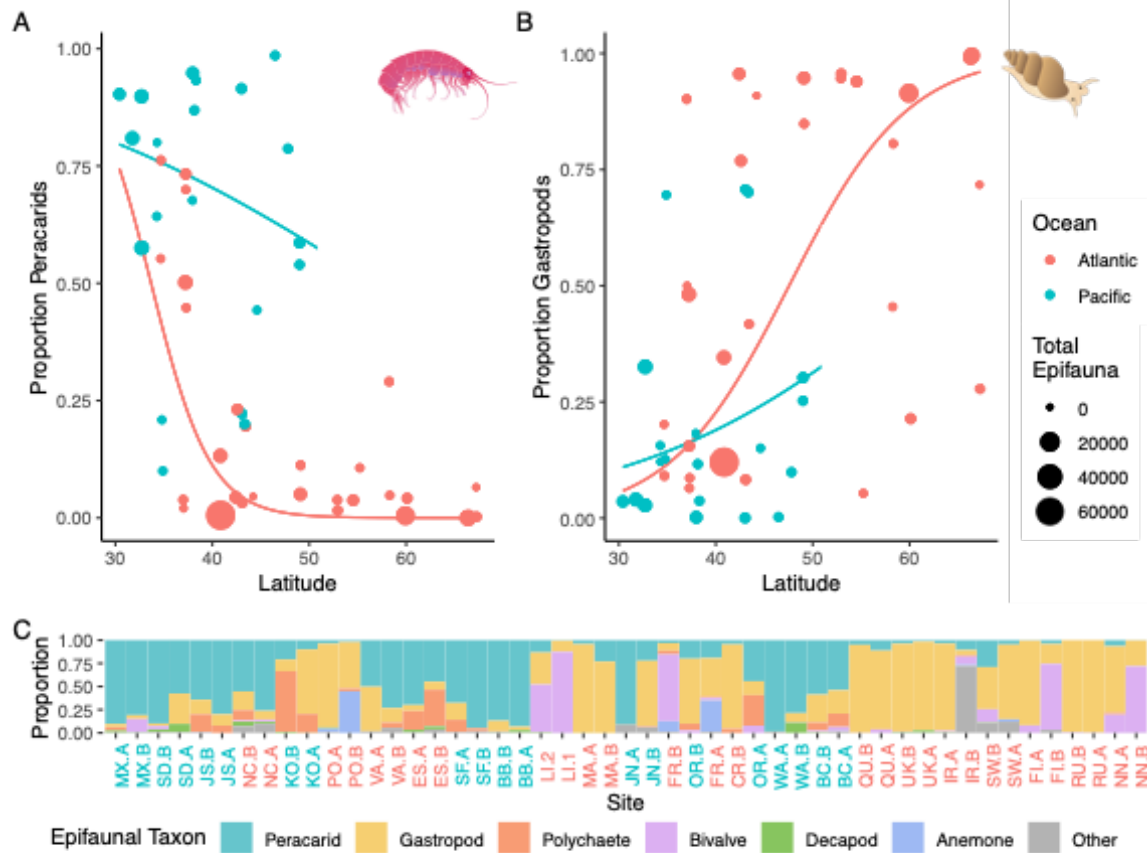


Figure 3.2. Latitudinal clines in the dominance of peracarid crustaceans (A) and gastropods (B) across global epifaunal communities (C). The relative abundance of each taxon changed significantly with latitude (peracarids $\chi^2_1 = 11284.0$, $p < 0.001$; gastropods $\chi^2_1 = 58295$, $p < 0.001$). For both taxa, the latitudinal clines varied significantly between ocean basins (peracarids $\chi^2_1 = 3524.8$, $p < 0.001$; gastropods $\chi^2_1 = 1722$, $p < 0.001$). Site labels in C are colored according to ocean basin as in panels A and B, and arranged from lowest (on the left) to highest latitude (on the right); site locations are shown in Fig. A4.1 and Table A4.1.

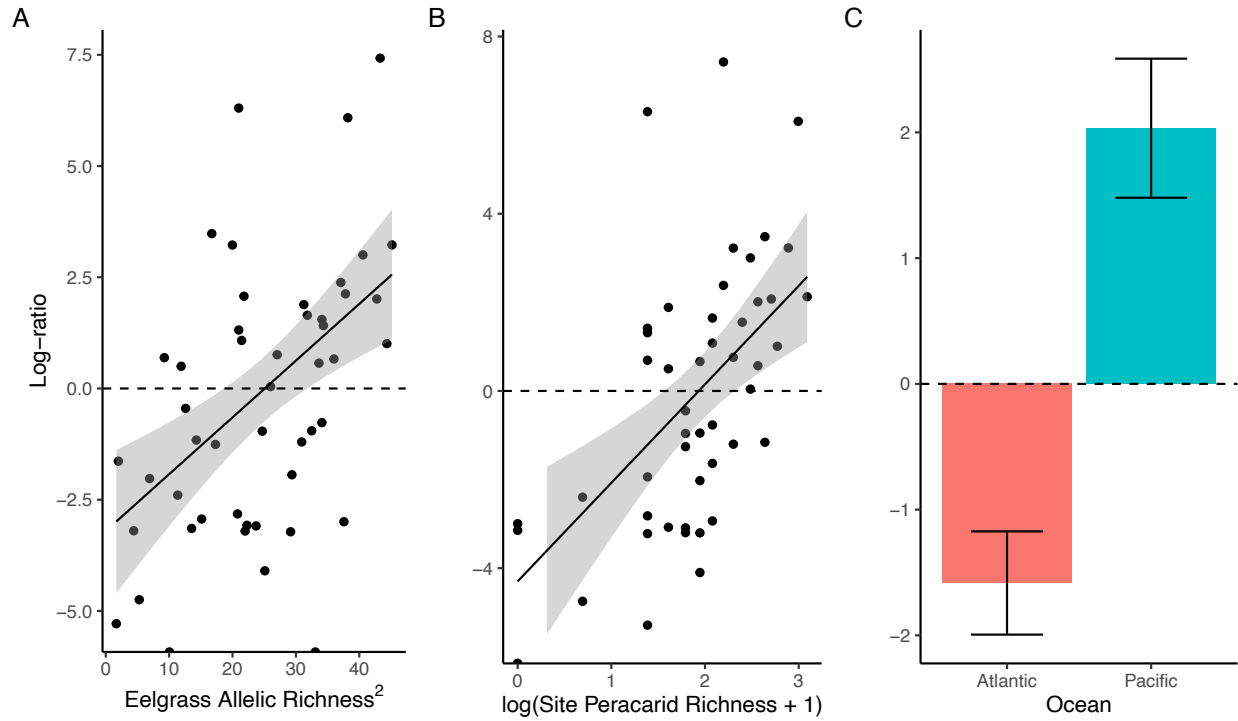


Figure 3.1. The best predictors of the log-transformed ratio of peracarid relative abundance to gastropod relative abundance in epifaunal communities across sites. Log-ratios were best explained by an additive model including eelgrass allelic richness, peracarid species richness, and ocean basin ($F_{3,43} = 20.42$, $p < 0.001$). The horizontal dashed line indicates a 1:1 ratio of gastropods to peracarids.

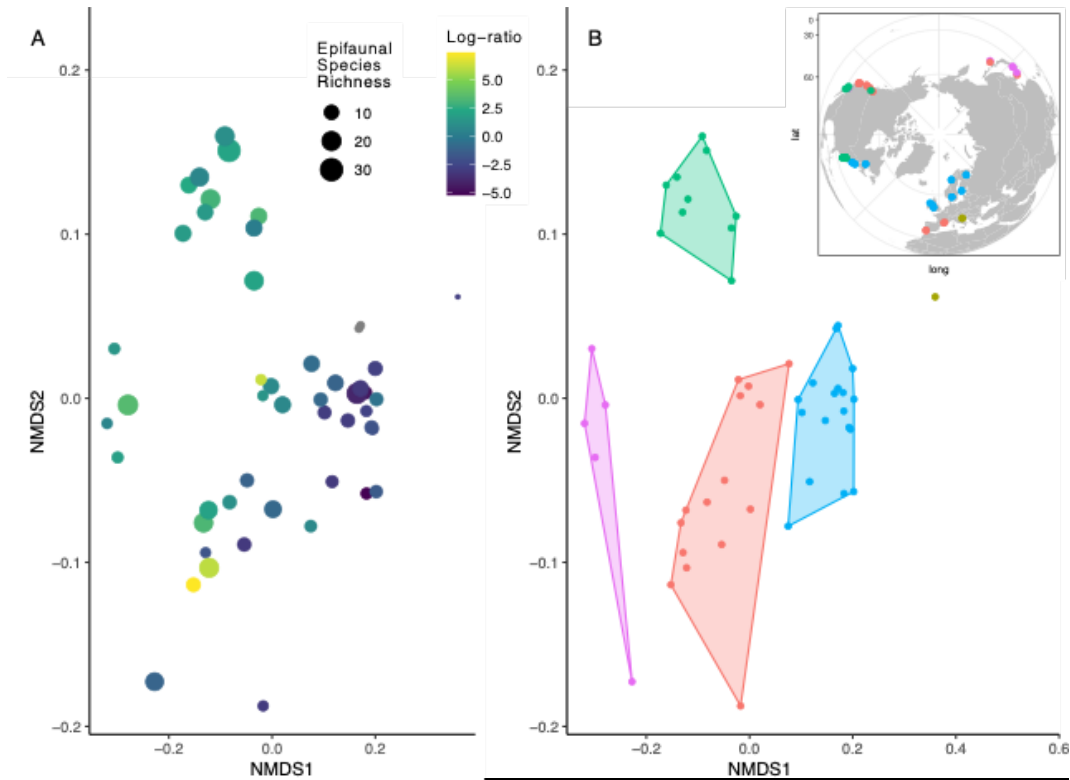


Figure 3.2. NMDS ordinations of eelgrass epifaunal communities in trait space. Points represent individual sites, and points that fall more closely together are more similar in community-weighted mean trait values. In (A), sites are colored by the log-ratio of the relative abundance of peracarids and gastropods; positive log-ratios indicate more peracarids than gastropods, while negative log-ratios indicate more gastropods than peracarids. Log-ratios significantly predicted sites' positions in trait space (pseudo $F_{1,45} = 11.918$, $p < 0.001$). In (B), the same sites are colored according to membership to one of 5 groups created by hierarchical clustering based on similarities in community-weighted mean trait values; inset map shows the geographic location of groups.

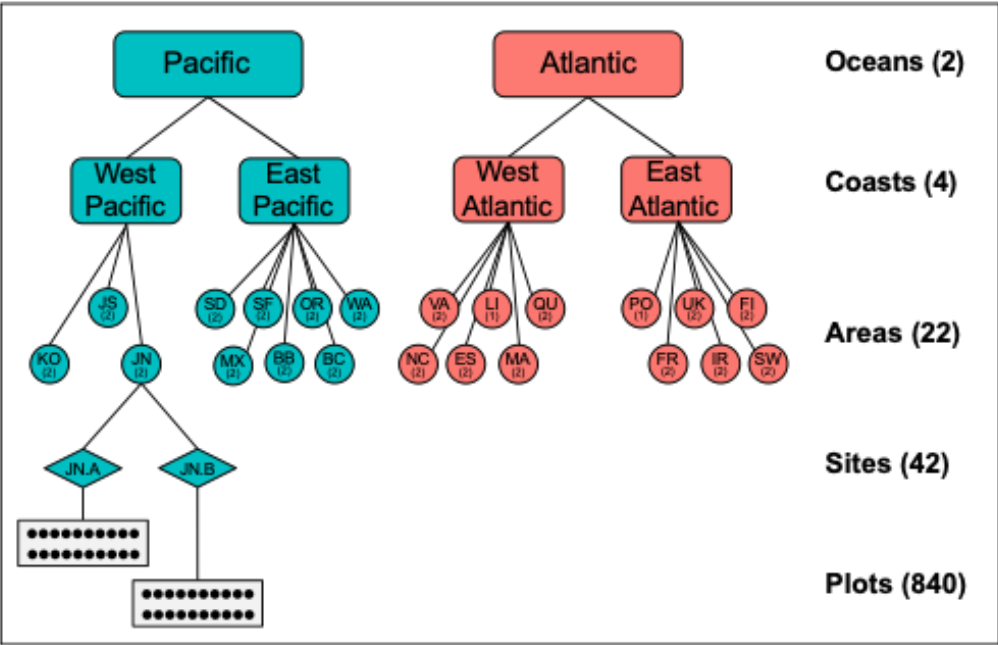
APPENDIX 1: Supplementary material for Chapter 1

Table A1.1. Results of t-tests comparing average SES values within ocean basins to zero. SES values are calculated relative to the global species pool; p values in bold represent significance at an a level of 0.05.

Ocean	Metric	Permutation Algorithm	Trait Set	Mean SES	t	df	p
Pacific	MPD	Independent Swap	All	0.393	2.27	19	0.0352
			Microhabitat	0.404	2.41	19	0.0261
			Diet	0.415	1.66	19	0.114
		Tip Shuffle	All	0.363	2.12	19	0.0479
			Microhabitat	0.412	2.86	19	0.0101
			Diet	0.381	1.56	19	0.135
	MNTD	Independent Swap	All	0.155	0.589	19	0.563
			Microhabitat	0.686	3.48	19	0.00254
			Diet	-0.0449	-0.155	17	0.879
		Tip Shuffle	All	0.221	0.855	19	0.403
			Microhabitat	0.737	3.73	19	0.00143
			Diet	0.263	0.684	14	0.505
Atlantic	MPD	Independent Swap	All	-0.156	-1.07	21	0.295
			Microhabitat	-0.0959	-0.518	21	0.61
			Diet	-0.0998	-0.532	20	0.601
		Tip Shuffle	All	-0.699	-4.23	21	0.000375
			Microhabitat	-0.505	-2.55	21	0.0185
			Diet	-0.382	-2.06	20	0.0531
	MNTD	Independent Swap	All	-0.364	-2.4	21	0.026
			Microhabitat	-0.314	-1.74	21	0.0974
			Diet	-0.272	-1.77	19	0.0935
		Tip Shuffle	All	-0.358	-2.35	21	0.0285
			Microhabitat	-0.3327	-1.69	21	0.011
			Diet	0.00933	0.0394	14	0.9691

Table A1.2. Average predation rate and epiphyte load across ocean basins. Values in the first two rows are mean $\pm$ standard deviation. Values in the third row represent the results of two-sample t-tests on untransformed (predation) and log-transformed (epiphytes) data across oceans.

Ocean	Prop. Tethered Prey Removed		g Epiphytes g Eelgrass ⁻¹	
Pacific	0.80 $\pm$ 0.20		0.30 $\pm$ 0.31	
Atlantic	0.64 $\pm$ 0.24		0.13 $\pm$ 0.12	
Difference	t = 2.18	p = 0.037	t = 1.13	p = 0.27



APPENDIX 1

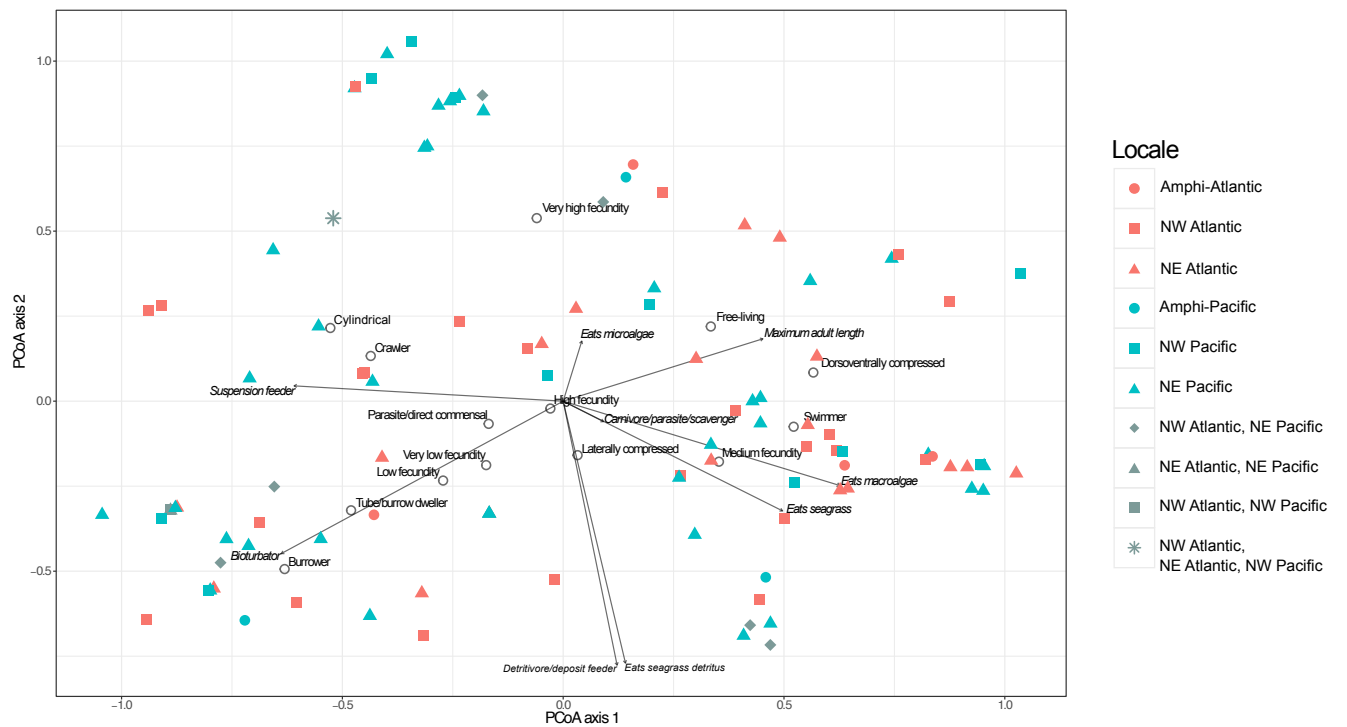


Figure A1.2. Principal coordinates analysis (PCoA) biplot of peracarid species in our global species pool, based on Gower distances. Solid symbols represent species in trait space, with symbol shape and colour corresponding to where they were found in our samples; hollow symbols represent centroids for categorical traits. Traits were fairly independent, and few were strongly correlated. Additionally, locale was not a significant predictor of where a given species fell in trait space (PERMANOVA; pseudo $F_{9,95} = 0.98$, $p = 0.51$). In other words, there were no traits that were particularly distinct to regions. Amphi-Pacific and Amphi-Atlantic distributions refer to species that occur in both the western and eastern margins of the Pacific and Atlantic Oceans, respectively.

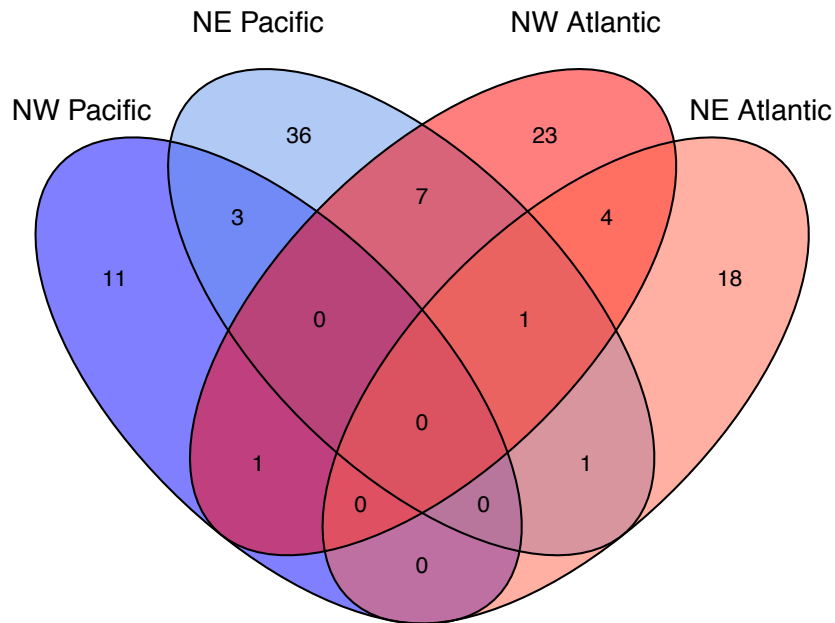


Figure A1.3. Peracarid species richnesses across the four coastlines observed in this study. 55 species were collected from Atlantic sites and 60 species were collected from Pacific sites. Of these, 15 species were collected from the Northwest Pacific, 48 species from the Northeast Pacific, 36 species from the Northwest Atlantic, and 24 species from the Northeast Atlantic. There were 37 genera in 24 families in the Pacific and 40 genera in 22 families in the Atlantic.

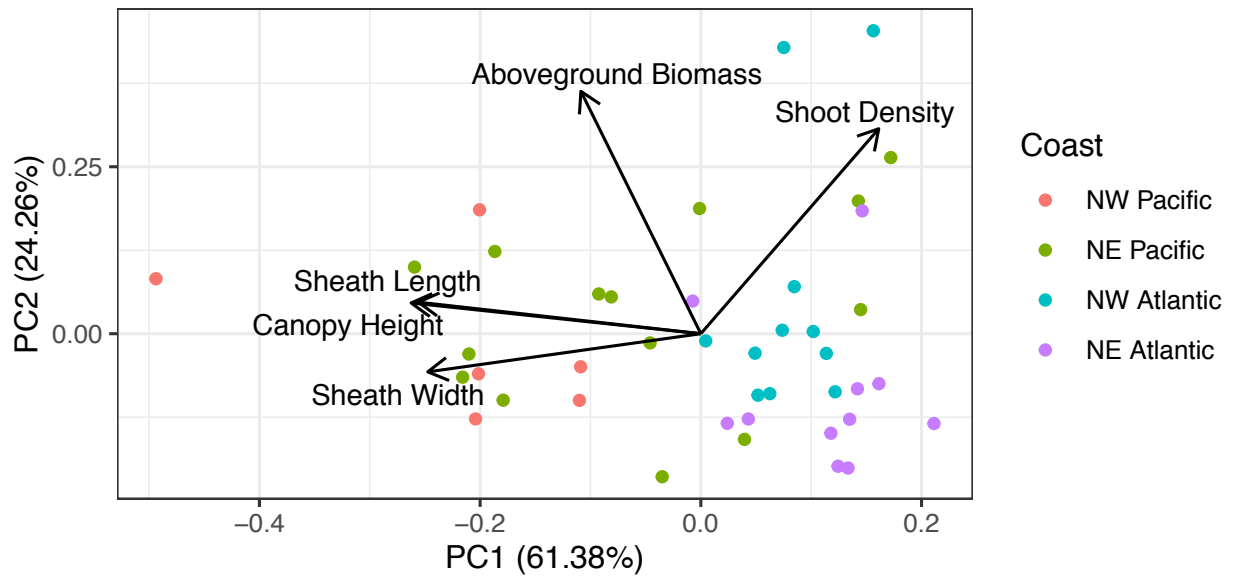


Figure A1.4. Principal component biplot for eelgrass habitat structure across sites. Most of the variation in eelgrass was between short canopies of dense shoots and taller canopies of sparser shoots. The first two principal components accounted for 85.64% of the total variation in habitat structure at the site level. Eelgrass beds in the Atlantic Ocean were mostly characterized by small, densely packed shoots, while those in the Northwest Pacific contained larger, sparser shoots. Northeast Pacific sites contained both of these bed types.

APPENDIX 1

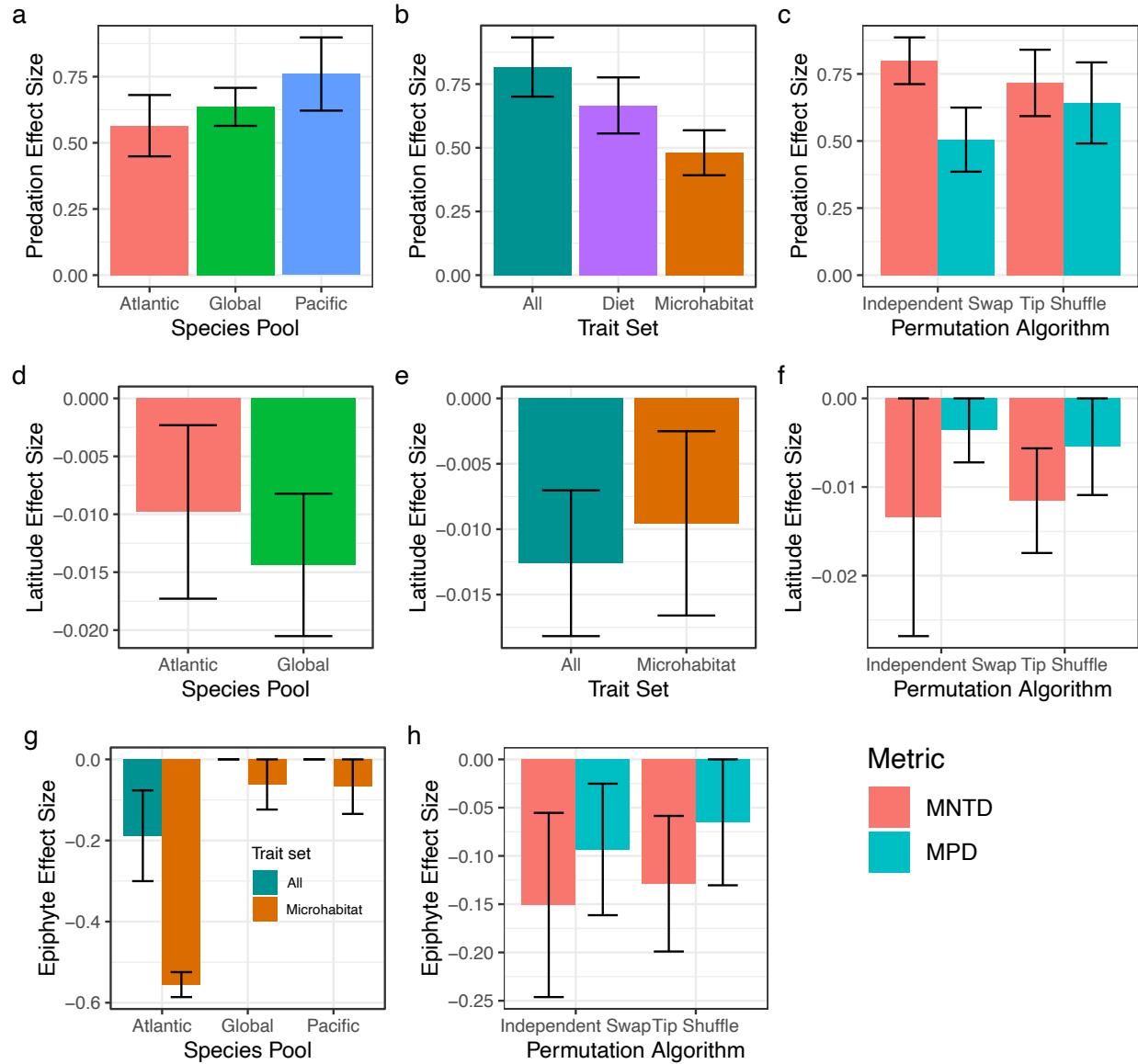


Figure A1.5. Effects of predation (a-c), latitude (d-f), and epiphyte load (g-h) in best models of site-level trait dispersion (SES values) across three species pools (a, d, g), 3 sets of traits (b, e, g), two permutation algorithms, and two dispersion metrics (c, f, h). Columns show mean effect sizes (across best models selected by AICc) averaged across species pools, trait sets, algorithms, and metrics where appropriate; error bars represent standard errors.

APPENDIX 1

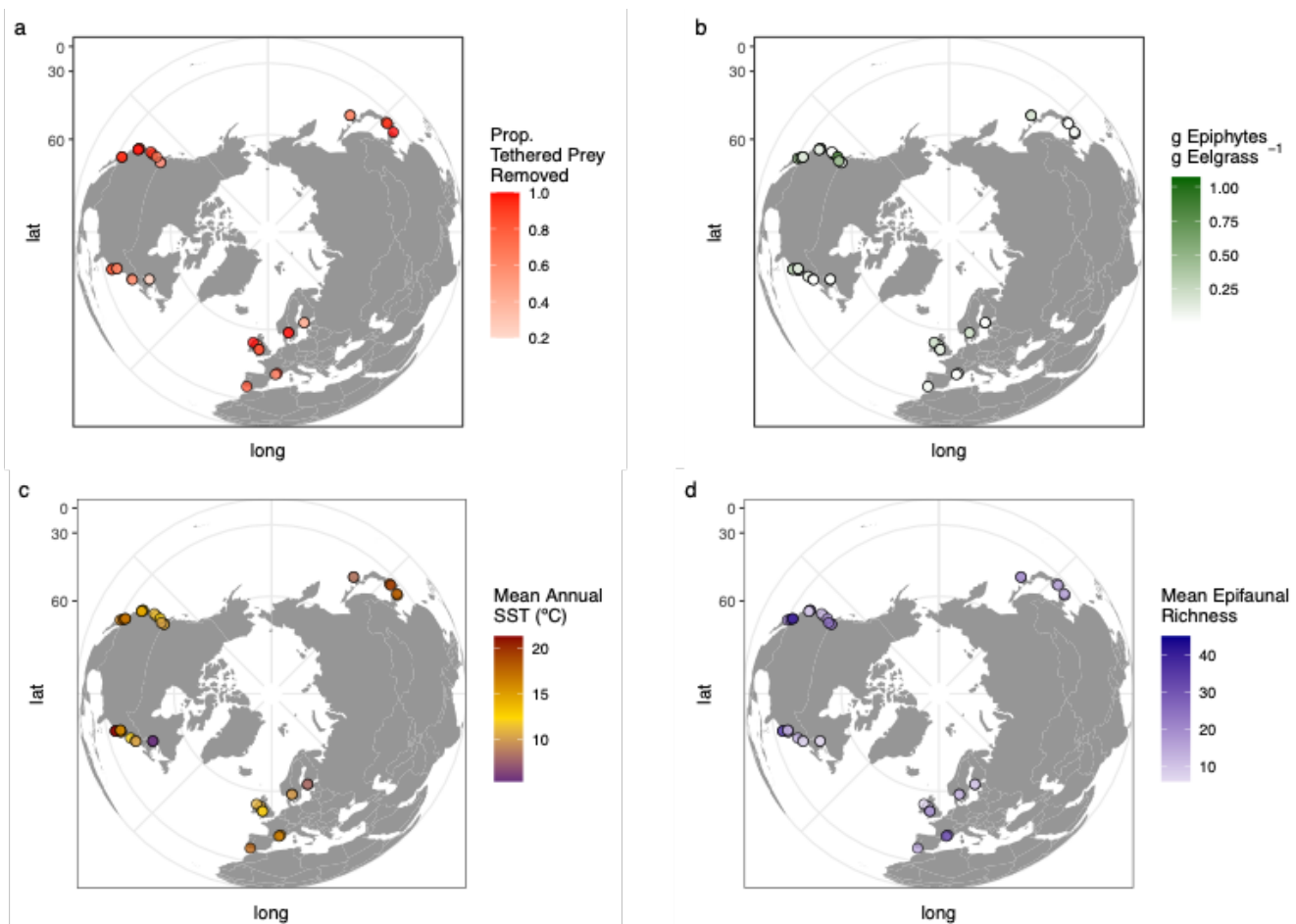


Figure A1.6. Maps of predation intensity (a), epiphyte load (b), mean annual sea surface temperature (c), and epifaunal species richness (d) across sites and ocean basins. None of these predictors varied significantly by ocean basin. See Fig. A1.1 for more detailed information about site locations.

APPENDIX 1

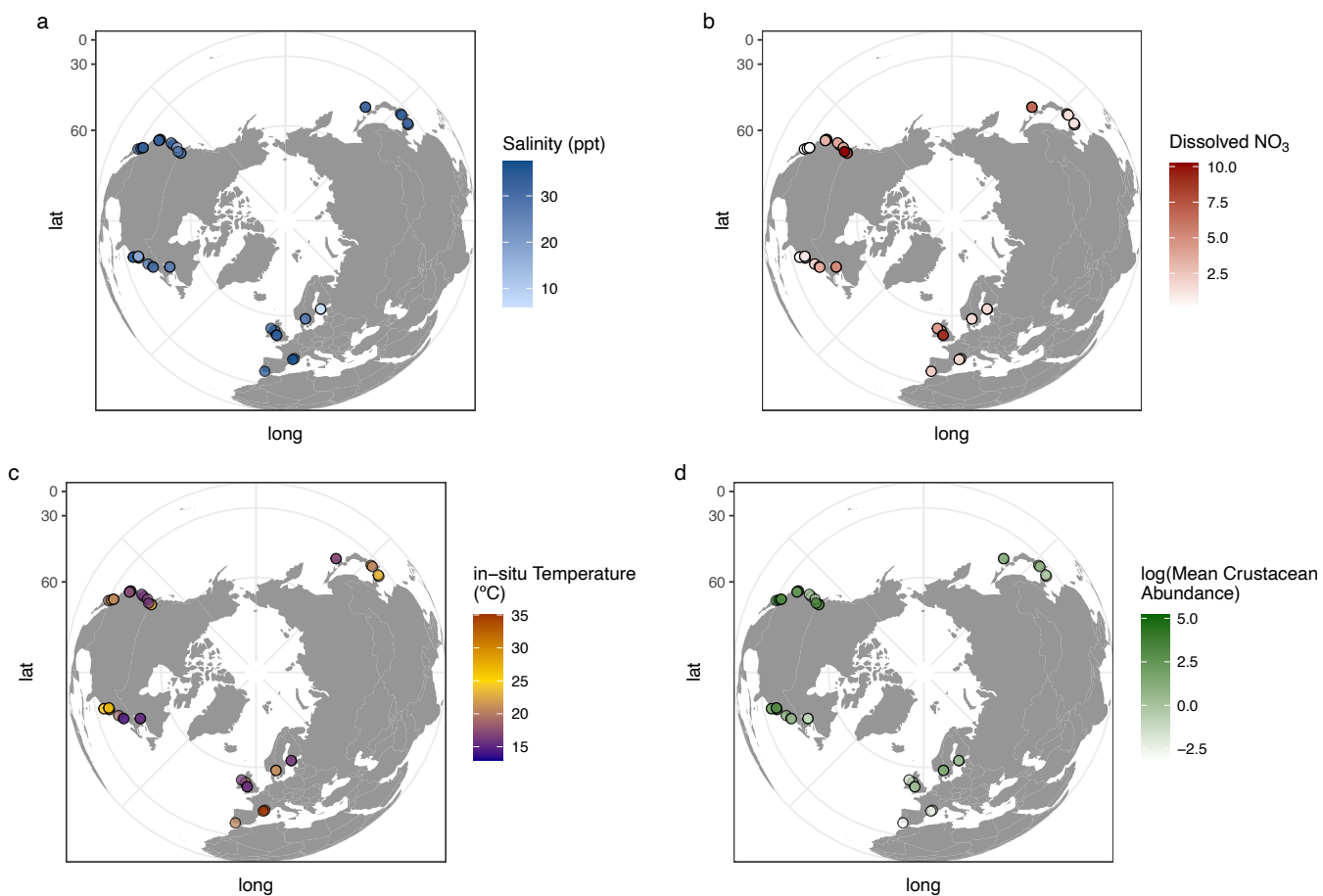
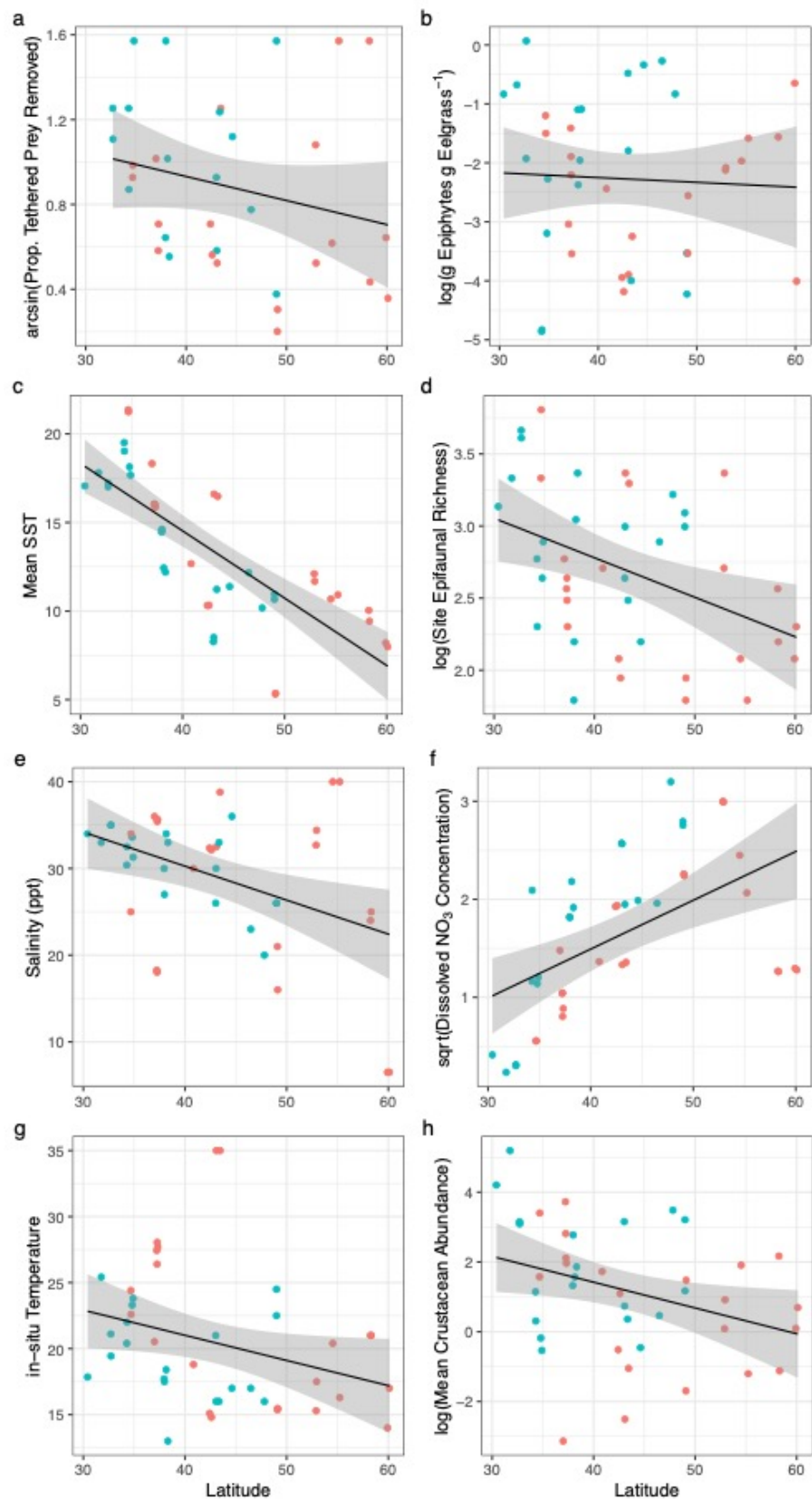


Figure A1.7. Maps of salinity (a), water column nitrate (b), in-situ temperature (c), and crustacean abundance (d) across sites and ocean basins. Of these predictor, only crustacean abundance was significantly greater in the Pacific ($R^2 = 0.076$, $p = 0.043$). See Fig. A1.1 for more detailed information about site locations.

APPENDIX 1



APPENDIX 1

Figure S8. Predictors used in models of dispersion, including predation intensity (a), epiphyte load (b), mean sea surface temperature (c), epifaunal richness (d), salinity (e), water column nitrate (f), in-situ temperature (g), and crustacean abundance (h), plotted against latitude.

Without accounting for other variables, latitude was a significant predictor of mean sea surface temperature ($R^2 = 0.58$, $p < 0.0001$), site epifaunal richness (log-transformed; $R^2 = 0.15$, $p = 0.0062$), salinity ($R^2 = 0.16$, $p = 0.0056$), nitrate (square root-transformed; $R^2 = 0.26$, $p = 0.00034$), in-situ temperature ($R^2 = 0.074$, $p = 0.046$), and crustacean abundance (log-transformed; $R^2 = 0.092$, $p = 0.029$). Points represent sites, color-coded by ocean; Atlantic sites are in red, Pacific sites are in blue.

APPENDIX 2: References for peracarid trait data used in global analyses of trait dispersion

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APPENDIX 2

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APPENDIX 3: Methods and Results – post-hoc modeling of individual peracarid trait dispersion (SES) against environmental predictors in global eelgrass beds

Data analysis. To assess how individual traits responded to ecological filters in our dataset, we built a series of simple post-hoc models with the subset of environmental variables that appeared most often in our best models of broader trait dispersion at the site level: latitude, ocean, epiphyte load, and predation on amphipods. For each of the traits in our dataset, we calculated the standard effect size of MPD and MNTD (SES_{MPD} and SES_{MNTD}) using the independent swap and tip shuffle algorithms across the global pool. We calculated SES_{MPD} for all 13 of our traits (Table 1.1), but because MNTD is sensitive to missing values, we were unable to calculate SES_{MNTD} for fecundity or any of the diet traits in our data.

SES values for each metric and permutation algorithm were used as continuous response variables in each of four models with the univariate predictors of latitude, ocean, epiphyte load, and predation. To account for multiple comparisons, we used a Bonferroni-corrected α -level of 0.0125 when evaluating the significance of the individual predictors. In total, we built 144 models: four predictors, two permutation algorithms, two diversity metrics, two sets of 13 traits, and two sets of five traits.

Results. The majority of trait SES values showed no significant response to any of the four predictors we examined (Table A3.1). However, we found that peracarid communities were more overdispersed in fecundity (SES_{MPD} independent swap and tip shuffle), living habit (SES_{MPD} independent swap and tip shuffle, SES_{MNTD} tip shuffle), motility (SES_{MPD} tip shuffle), and feeding on macroalgae (SES_{MPD} independent swap) at lower latitudes than at higher latitudes (Fig. A3.1). We also found that body size and living habit were significantly more dispersed in the Pacific than the Atlantic Ocean (SES_{MPD} independent swap and tip shuffle; Fig. A3.2), and that communities were increasingly dispersed in feeding on macroalgae as predation increased (SES_{MPD} tip shuffle; Fig. A3.3). These trait dispersion-environment patterns were consistent across other metrics and permutation algorithms for which they were calculated, albeit not significant in every case (Table A3.1).

APPENDIX 3

Table A3.1. Post-hoc models of individual trait dispersion (SES) as a function of latitude, ocean, predation on amphipods, and epiphyte load in eelgrass-associated peracarid crustaceans. Bolded rows indicate models that were significant according to a Bonferroni-corrected α -level of 0.0125.

Permutation Algorithm	Metric	Predictor	Trait	Intercept	Slope	AICc	Adj. R ²
Independent Swap	MPD	Latitude	Maximum adult body length	-0.373	0.012	133.647	-0.017
Independent Swap	MPD	Latitude	Maximum fecundity	2.565	-0.063	68.362	0.301
Independent Swap	MPD	Latitude	Body shape	0.954	-0.015	104.648	0.001
Independent Swap	MPD	Latitude	Living habit	2.734	-0.065	103.412	0.312
Independent Swap	MPD	Latitude	Motility	1.821	-0.041	122.781	0.088
Independent Swap	MPD	Latitude	Bioturbator	-0.691	0.017	126.783	-0.006
Independent Swap	MPD	Latitude	Eats microalgae	0.271	-0.006	117.443	-0.026
Independent Swap	MPD	Latitude	Eats macroalgae	2.465	-0.053	82.125	0.180
Independent Swap	MPD	Latitude	Eats seagrass	1.619	-0.028	76.790	0.026
Independent Swap	MPD	Latitude	Eats seagrass detritus	0.108	0.003	70.142	-0.044
Independent Swap	MPD	Latitude	Suspension feeder	-0.325	0.000	67.632	-0.045
Independent Swap	MPD	Latitude	Detritivore/deposit feeder	0.719	-0.015	75.792	-0.022
Independent Swap	MPD	Latitude	Carnivore/parasite/scavenger	0.800	-0.017	64.469	-0.016
Independent Swap	MPD	Pacific Ocean	Maximum adult body length	-0.329	0.969	124.989	0.173
Independent Swap	MPD	Pacific Ocean	Maximum fecundity	-0.625	0.608	75.889	0.085
Independent Swap	MPD	Pacific Ocean	Body shape	0.469	-0.333	103.797	0.021
Independent Swap	MPD	Pacific Ocean	Living habit	-0.472	0.914	108.725	0.219
Independent Swap	MPD	Pacific Ocean	Motility	0.040	0.059	127.646	-0.024

APPENDIX 3

Independent Swap	MPD	Pacific Ocean	Bioturbator	-0.048	0.140	127.353	-0.020
Independent Swap	MPD	Pacific Ocean	Eats microalgae	-0.053	0.106	117.439	-0.026
Independent Swap	MPD	Pacific Ocean	Eats macroalgae	-0.021	0.286	88.432	-0.012
Independent Swap	MPD	Pacific Ocean	Eats seagrass	0.444	-0.195	78.270	-0.031
Independent Swap	MPD	Pacific Ocean	Eats seagrass detritus	0.297	-0.085	70.116	-0.043
Independent Swap	MPD	Pacific Ocean	Suspension feeder	-0.485	0.434	66.125	0.018
Independent Swap	MPD	Pacific Ocean	Detritivore/ deposit feeder	-0.079	0.257	75.871	-0.025
Independent Swap	MPD	Pacific Ocean	Carnivore/ parasite/ scavenger	-0.012	0.210	64.982	-0.041
Independent Swap	MPD	arcsin(Mean Amphipod Predation)	Maximum adult body length	0.039	0.287	109.673	-0.018
Independent Swap	MPD	arcsin(Mean Amphipod Predation)	Maximum fecundity	-0.813	0.540	71.273	0.032
Independent Swap	MPD	arcsin(Mean Amphipod Predation)	Body shape	0.150	0.184	88.825	-0.021
Independent Swap	MPD	arcsin(Mean Amphipod Predation)	Living habit	-0.546	0.506	95.522	0.023
Independent Swap	MPD	arcsin(Mean Amphipod Predation)	Motility	-0.140	0.226	105.248	-0.022
Independent Swap	MPD	arcsin(Mean Amphipod Predation)	Bioturbator	0.063	0.099	105.528	-0.029
Independent Swap	MPD	arcsin(Mean Amphipod Predation)	Eats microalgae	-0.462	0.525	101.826	0.004
Independent Swap	MPD	arcsin(Mean Amphipod Predation)	Eats macroalgae	-1.040	1.112	70.734	0.194
Independent Swap	MPD	arcsin(Mean Amphipod Predation)	Eats seagrass	0.143	0.183	64.584	-0.045
Independent Swap	MPD	arcsin(Mean Amphipod Predation)	Eats seagrass detritus	-0.485	0.956	52.352	0.155
Independent Swap	MPD	arcsin(Mean Amphipod Predation)	Suspension feeder	-0.361	0.130	54.402	-0.055

APPENDIX 3

Independent Swap	MPD	arcsin(Mean Amphipod Predation)	Detritivore/ deposit feeder	-0.670	0.890	61.434	0.087
Independent Swap	MPD	arcsin(Mean Amphipod Predation)	Carnivore/ parasite/ scavenger	0.443	-0.700	47.083	0.016
Independent Swap	MPD	log(Mean Epiphyte Load)	Maximum adult body length	-0.189	-0.154	129.301	0.010
Independent Swap	MPD	log(Mean Epiphyte Load)	Maximum fecundity	-0.880	-0.207	74.635	0.065
Independent Swap	MPD	log(Mean Epiphyte Load)	Body shape	-0.172	-0.212	98.913	0.102
Independent Swap	MPD	log(Mean Epiphyte Load)	Living habit	-0.004	-0.001	116.137	-0.026
Independent Swap	MPD	log(Mean Epiphyte Load)	Motility	-0.471	-0.254	118.562	0.090
Independent Swap	MPD	log(Mean Epiphyte Load)	Bioturbator	-0.370	-0.156	121.828	0.018
Independent Swap	MPD	log(Mean Epiphyte Load)	Eats microalgae	-0.268	-0.122	114.464	-0.006
Independent Swap	MPD	log(Mean Epiphyte Load)	Eats macroalgae	-0.291	-0.157	85.502	0.015
Independent Swap	MPD	log(Mean Epiphyte Load)	Eats seagrass	-0.066	-0.191	71.932	0.045
Independent Swap	MPD	log(Mean Epiphyte Load)	Eats seagrass detritus	0.636	0.172	66.344	0.025
Independent Swap	MPD	log(Mean Epiphyte Load)	Suspension feeder	-0.715	-0.149	64.562	0.010
Independent Swap	MPD	log(Mean Epiphyte Load)	Detritivore/ deposit feeder	0.535	0.191	71.167	0.032
Independent Swap	MPD	log(Mean Epiphyte Load)	Carnivore/ parasite/ scavenger	0.620	0.215	59.953	0.050
Independent Swap	MNTD	Latitude	Maximum adult body length	0.078	0.001	125.763	-0.025
Independent Swap	MNTD	Latitude	Body shape	0.175	-0.006	97.761	-0.020

APPENDIX 3

Independent Swap	MNTD	Latitude	Living habit	0.578	-0.021	58.862	0.113
Independent Swap	MNTD	Latitude	Motility	-0.130	-0.003	86.032	-0.023
Independent Swap	MNTD	Latitude	Bioturbator	-0.807	0.017	101.258	0.011
Independent Swap	MNTD	Pacific Ocean	Maximum adult body length	-0.196	0.700	120.284	0.100
Independent Swap	MNTD	Pacific Ocean	Body shape	-0.120	0.083	97.822	-0.022
Independent Swap	MNTD	Pacific Ocean	Living habit	-0.442	0.212	62.895	0.024
Independent Swap	MNTD	Pacific Ocean	Motility	-0.249	-0.034	86.074	-0.024
Independent Swap	MNTD	Pacific Ocean	Bioturbator	-0.011	-0.118	102.525	-0.019
Independent Swap	MNTD	arcsin(Mean Amphipod Predation)	Maximum adult body length	-0.080	0.358	107.974	-0.011
Independent Swap	MNTD	arcsin(Mean Amphipod Predation)	Body shape	-0.225	0.135	83.174	-0.025
Independent Swap	MNTD	arcsin(Mean Amphipod Predation)	Living habit	-0.244	-0.126	56.605	-0.020
Independent Swap	MNTD	arcsin(Mean Amphipod Predation)	Motility	-0.018	-0.271	76.168	-0.003
Independent Swap	MNTD	arcsin(Mean Amphipod Predation)	Bioturbator	0.301	-0.409	86.409	0.015
Independent Swap	MNTD	log(Mean Epiphyte Load)	Maximum adult body length	0.007	-0.071	121.862	-0.016
Independent Swap	MNTD	log(Mean Epiphyte Load)	Body shape	-0.182	-0.048	96.288	-0.018
Independent Swap	MNTD	log(Mean Epiphyte Load)	Living habit	-0.320	0.002	62.545	-0.026
Independent Swap	MNTD	log(Mean Epiphyte Load)	Motility	-0.546	-0.132	80.162	0.057
Independent Swap	MNTD	log(Mean Epiphyte Load)	Bioturbator	-0.308	-0.088	95.046	0.001
Tip Shuffle	MPD	Latitude	Maximum adult body length	-0.059	0.011	148.536	-0.020

APPENDIX 3

Tip Shuffle	MPD	Latitude	Maximum fecundity	2.783	-0.067	77.612	0.254
Tip Shuffle	MPD	Latitude	Body shape	1.040	-0.018	94.983	0.022
Tip Shuffle	MPD	Latitude	Living habit	2.565	-0.064	103.586	0.310
Tip Shuffle	MPD	Latitude	Motility	1.958	-0.047	115.614	0.142
Tip Shuffle	MPD	Latitude	Bioturbator	-1.022	0.017	128.657	-0.007
Tip Shuffle	MPD	Latitude	Eats microalgae	0.219	-0.010	111.643	-0.021
Tip Shuffle	MPD	Latitude	Eats macroalgae	2.262	-0.052	90.555	0.132
Tip Shuffle	MPD	Latitude	Eats seagrass	1.575	-0.021	71.748	0.004
Tip Shuffle	MPD	Latitude	Eats seagrass detritus	-0.040	0.003	73.020	-0.045
Tip Shuffle	MPD	Latitude	Suspension feeder	-0.236	-0.005	68.924	-0.043
Tip Shuffle	MPD	Latitude	Detritivore/ deposit feeder	0.601	-0.016	77.781	-0.020
Tip Shuffle	MPD	Latitude	Carnivore/ parasite/ scavenger	0.728	-0.019	61.796	0.000
Tip Shuffle	MPD	Pacific Ocean	Maximum adult body length	-0.232	1.327	136.379	0.236
Tip Shuffle	MPD	Pacific Ocean	Maximum fecundity	-0.697	0.834	81.630	0.139
Tip Shuffle	MPD	Pacific Ocean	Body shape	0.307	-0.108	96.709	-0.019
Tip Shuffle	MPD	Pacific Ocean	Living habit	-0.695	1.038	104.831	0.290
Tip Shuffle	MPD	Pacific Ocean	Motility	-0.188	0.272	122.230	-0.005
Tip Shuffle	MPD	Pacific Ocean	Bioturbator	-0.415	0.236	128.873	-0.012
Tip Shuffle	MPD	Pacific Ocean	Eats microalgae	-0.369	0.290	111.125	-0.007
Tip Shuffle	MPD	Pacific Ocean	Eats macroalgae	-0.215	0.323	95.177	-0.012
Tip Shuffle	MPD	Pacific Ocean	Eats seagrass	0.694	-0.120	72.798	-0.037
Tip Shuffle	MPD	Pacific Ocean	Eats seagrass detritus	0.083	-0.004	73.037	-0.045
Tip Shuffle	MPD	Pacific Ocean	Suspension feeder	-0.675	0.589	66.299	0.065
Tip Shuffle	MPD	Pacific Ocean	Detritivore/ deposit feeder	-0.280	0.320	77.711	-0.017
Tip Shuffle	MPD	Pacific Ocean	Carnivore/ parasite/ scavenger	-0.223	0.328	62.245	-0.022

APPENDIX 3

Tip Shuffle	MPD	arcsin(Mean Amphipod Predation)	Maximum adult body length	0.240	0.391	123.622	-0.015
Tip Shuffle	MPD	arcsin(Mean Amphipod Predation)	Maximum fecundity	-0.919	0.701	78.825	0.049
Tip Shuffle	MPD	arcsin(Mean Amphipod Predation)	Body shape	0.031	0.255	83.991	-0.011
Tip Shuffle	MPD	arcsin(Mean Amphipod Predation)	Living habit	-0.805	0.611	96.893	0.043
Tip Shuffle	MPD	arcsin(Mean Amphipod Predation)	Motility	-0.438	0.409	104.419	-0.003
Tip Shuffle	MPD	arcsin(Mean Amphipod Predation)	Bioturbator	-0.317	0.144	108.902	-0.027
Tip Shuffle	MPD	arcsin(Mean Amphipod Predation)	Eats microalgae	-0.645	0.474	96.641	0.003
Tip Shuffle	MPD	arcsin(Mean Amphipod Predation)	Eats macroalgae	-1.457	1.357	75.901	0.231
Tip Shuffle	MPD	arcsin(Mean Amphipod Predation)	Eats seagrass	0.454	0.170	62.224	-0.046
Tip Shuffle	MPD	arcsin(Mean Amphipod Predation)	Eats seagrass detritus	-0.750	1.043	53.737	0.172
Tip Shuffle	MPD	arcsin(Mean Amphipod Predation)	Suspension feeder	-0.650	0.279	56.207	-0.042
Tip Shuffle	MPD	arcsin(Mean Amphipod Predation)	Detritivore/ deposit feeder	-0.916	0.960	62.376	0.100
Tip Shuffle	MPD	arcsin(Mean Amphipod Predation)	Carnivore/ parasite/ scavenger	0.139	-0.514	45.163	-0.018
Tip Shuffle	MPD	log(Mean Epiphyte Load)	Maximum adult body length	0.154	-0.124	144.474	-0.009
Tip Shuffle	MPD	log(Mean Epiphyte Load)	Maximum fecundity	-0.668	-0.143	83.871	-0.002
Tip Shuffle	MPD	log(Mean Epiphyte Load)	Body shape	-0.046	-0.133	93.252	0.036

APPENDIX 3

Tip Shuffle	MPD	log(Mean Epiphyte Load)	Living habit	-0.075	0.040	116.091	-0.022
Tip Shuffle	MPD	log(Mean Epiphyte Load)	Motility	-0.474	-0.201	115.002	0.056
Tip Shuffle	MPD	log(Mean Epiphyte Load)	Bioturbator	-0.636	-0.130	123.979	0.003
Tip Shuffle	MPD	log(Mean Epiphyte Load)	Eats microalgae	-0.407	-0.084	109.387	-0.016
Tip Shuffle	MPD	log(Mean Epiphyte Load)	Eats macroalgae	-0.446	-0.147	92.477	-0.001
Tip Shuffle	MPD	log(Mean Epiphyte Load)	Eats seagrass	0.354	-0.138	66.500	0.016
Tip Shuffle	MPD	log(Mean Epiphyte Load)	Eats seagrass detritus	0.585	0.225	68.210	0.063
Tip Shuffle	MPD	log(Mean Epiphyte Load)	Suspension feeder	-0.747	-0.109	66.520	-0.019
Tip Shuffle	MPD	log(Mean Epiphyte Load)	Detritivore/ deposit feeder	0.510	0.254	72.036	0.080
Tip Shuffle	MPD	log(Mean Epiphyte Load)	Carnivore/ parasite/ scavenger	0.453	0.218	57.386	0.066
Tip Shuffle	MNTD	Latitude	Maximum adult body length	0.210	0.005	150.228	-0.024
Tip Shuffle	MNTD	Latitude	Body shape	0.265	-0.008	105.847	-0.017
Tip Shuffle	MNTD	Latitude	Living habit	0.519	-0.022	56.049	0.130
Tip Shuffle	MNTD	Latitude	Motility	-0.063	-0.003	107.246	-0.024
Tip Shuffle	MNTD	Latitude	Bioturbator	-0.962	0.021	109.889	0.018
Tip Shuffle	MNTD	Pacific Ocean	Maximum adult body length	-0.033	0.939	144.753	0.101
Tip Shuffle	MNTD	Pacific Ocean	Body shape	-0.133	0.088	106.036	-0.022
Tip Shuffle	MNTD	Pacific Ocean	Living habit	-0.542	0.235	60.250	0.038
Tip Shuffle	MNTD	Pacific Ocean	Motility	-0.163	-0.085	107.177	-0.022
Tip Shuffle	MNTD	Pacific Ocean	Bioturbator	-0.006	-0.124	111.472	-0.019

APPENDIX 3

Tip Shuffle	MNTD	arcsin(Mean Amphipod Predation)	Maximum adult body length	0.090	0.518	128.226	-0.008
Tip Shuffle	MNTD	arcsin(Mean Amphipod Predation)	Body shape	-0.232	0.105	89.054	-0.027
Tip Shuffle	MNTD	arcsin(Mean Amphipod Predation)	Living habit	-0.371	-0.101	52.202	-0.023
Tip Shuffle	MNTD	arcsin(Mean Amphipod Predation)	Motility	0.117	-0.337	94.204	-0.005
Tip Shuffle	MNTD	arcsin(Mean Amphipod Predation)	Bioturbator	0.310	-0.403	93.942	0.006
Tip Shuffle	MNTD	log(Mean Epiphyte Load)	Maximum adult body length	0.193	-0.114	145.966	-0.012
Tip Shuffle	MNTD	log(Mean Epiphyte Load)	Body shape	-0.177	-0.041	104.488	-0.021
Tip Shuffle	MNTD	log(Mean Epiphyte Load)	Living habit	-0.397	0.007	60.495	-0.025
Tip Shuffle	MNTD	log(Mean Epiphyte Load)	Motility	-0.498	-0.140	102.387	0.029
Tip Shuffle	MNTD	log(Mean Epiphyte Load)	Bioturbator	-0.269	-0.071	105.115	-0.012

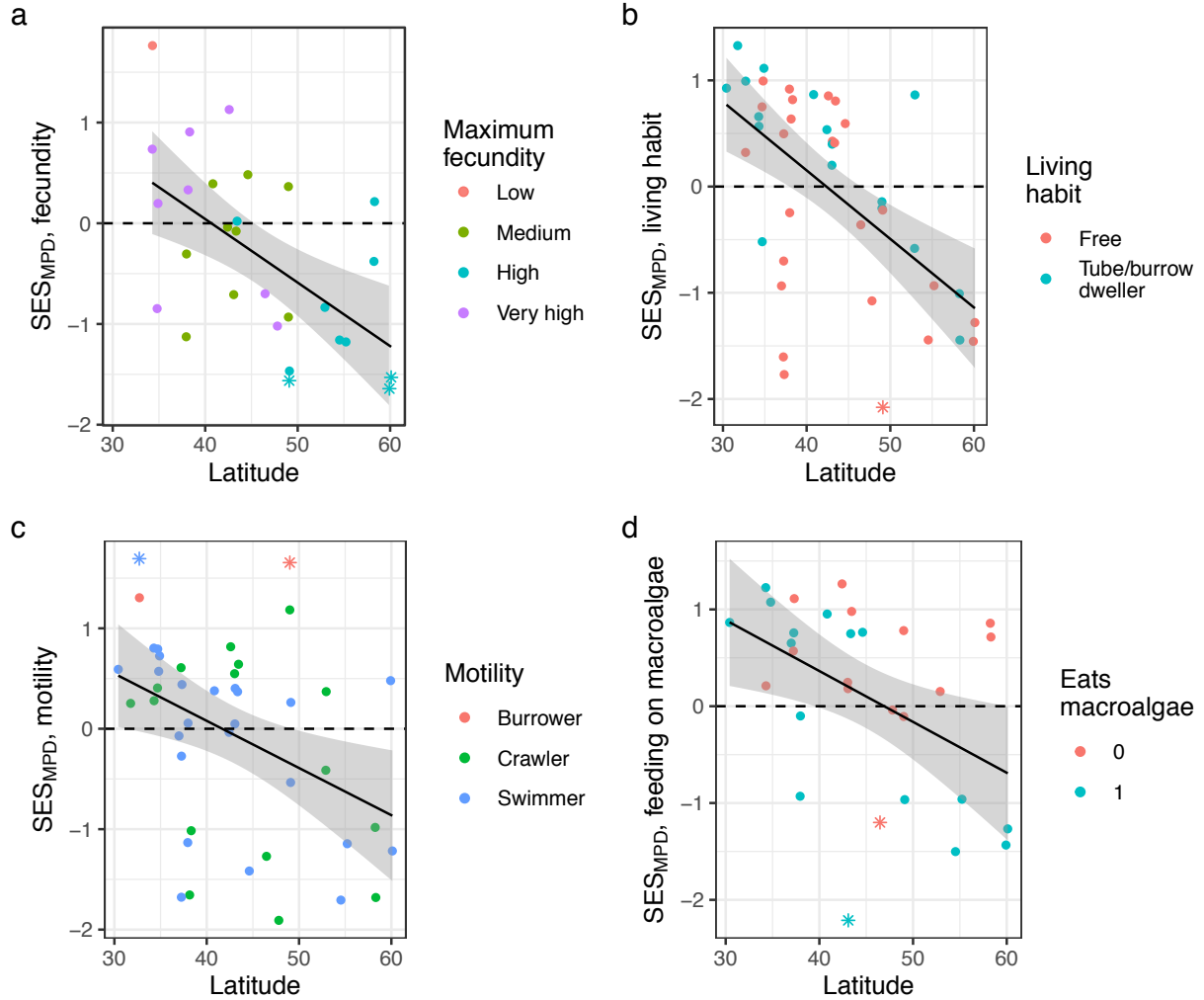


Figure A3.1. Effects of latitude on trait dispersion (measured by SES_{MPD} using the independent swap algorithm in panels A, B, and D and the tip shuffle algorithm in panel C). Permuting across the global species pool, SES_{MPD} declined with latitude for fecundity (A; $R^2 = 0.301$, $p = 0.002$), living habit (B; $R^2 = 0.312$, $p < 0.001$), motility (C; $R^2 = 0.142$, $p = 0.008$), and feeding on macroalgae (D; $R^2 = 0.180$, $p = 0.011$). The dashed horizontal line represents an SES value of 0, indicating an observed value of MPD indistinguishable from random assembly; points displayed as stars represent those for which SES is significantly different from 0 at $\alpha = 0.05$. Colors represent dominant trait values.

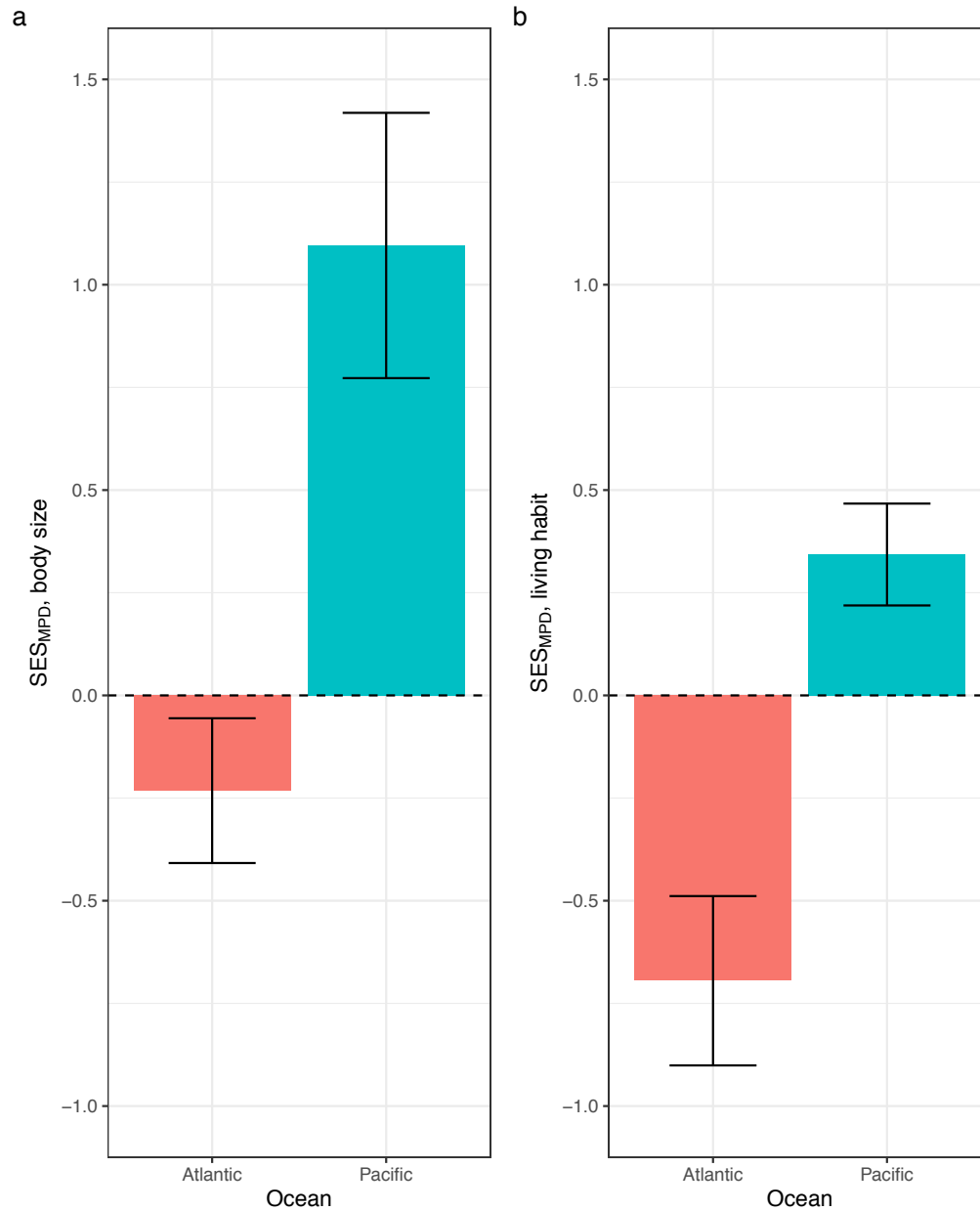


Figure A3.2. Trait dispersion across ocean basins (measured by SES_{MPD} using the tip shuffle algorithm). Permuting across the global species pool, SES_{MPD} was significantly greater in the Pacific than the Atlantic Ocean for maximum adult body length (A; $R^2 = 0.236$, $p < 0.001$) and living habit (B; $R^2 = 0.290$, $p < 0.001$). In the Atlantic, community-weighted mean body size was 14.09 mm; in the Pacific it was 20.79 mm. In both oceans, the majority of species were free-living. The dashed horizontal line represents an SES value of 0, indicating an observed value of MPD indistinguishable from random assembly.

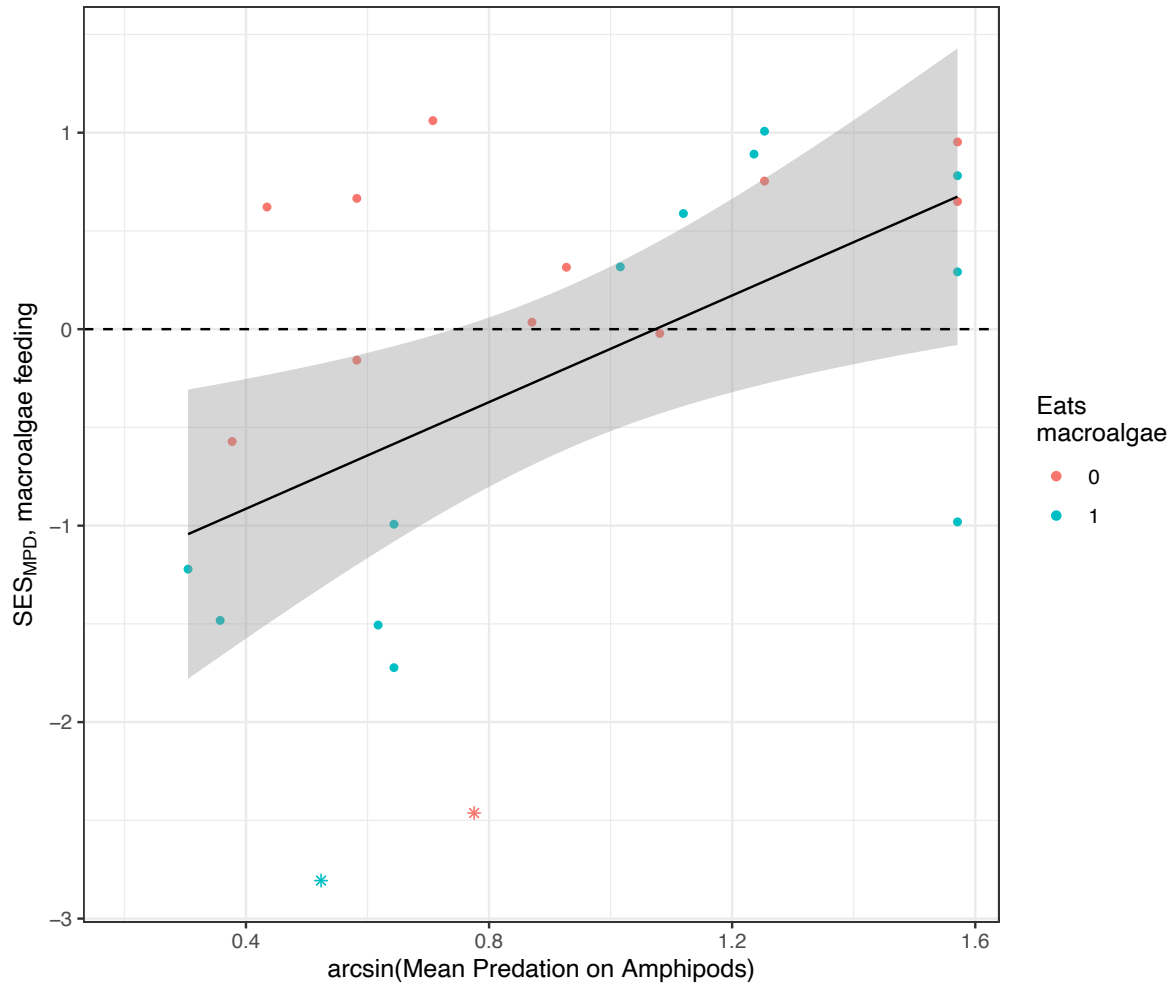


Figure A3.3. Effects of predation intensity on trait dispersion (measured by SES_{MPD} using the tip shuffle algorithm). Permuting across the global species pool, SES_{MPD} increased with increasing predation intensity for macroalgae consumption ($R^2 = 0.231$, $p = 0.009$). The dashed horizontal line represents an SES value of 0, indicating an observed value of MPD indistinguishable from random assembly; points displayed as stars represent those for which SES is significantly different from 0 at $\alpha = 0.05$. Colors represent dominant trait values.

APPENDIX 4: Species and trait data for fish and peracarid communities in Tomales Bay and Bodega Harbor, California

1. FISHES

Across both years and all six sites, we found a total of 35 fish species of which 16 species were retained in our analyses, after removing singletons, species that only occurred in one site-year combination, and species whose abundance totaled fewer than 4 individuals across samples (Table A4.1). The most speciose fish community had 13 species. Four fish species (*Cymatogaster aggregata*, *Gasterosteus aculeatus*, *Porichthys notatus*, and *Sebastes carnatus*) were present in discrete size cohorts and counted as separate groups for our analyses (Table A4.2).

We assigned two categorical (vertical position and foraging mode) and one continuous trait (trophic level) to fishes based on Fishbase (Froese & Pauly 2020) and Love (2011; Table A4.3). Vertical position, defined as the orientation of the fish in the water column, had three levels: 1) benthic – resting on the bottom, touching the substrate; 2) benthopelagic – suspended in the water column a short distance from the bottom; and 3) pelagic – suspended in the water column away from benthic structures, not bottom-associated aside from feeding. Foraging mode, defined as the suite of behaviors associated with feeding and foraging, had 5 levels: 1) pursuit predator – actively chases after fast-moving prey; 2) benthic browser – searches for and picks off bottom-associated prey items; 3) epifaunal browser – searches for and picks off prey items associated with eelgrass; 4) planktivore – feeds on suspended prey in the water column; and 5) sit-and-wait – ambush predators that feed on passing prey within reach. We fuzzy-coded vertical position and foraging mode among 5 and 3 levels, respectively, to accommodate species that occupied two or more levels (Ashford et al. 2018).

We collected linear morphometric measurements of fishes from 2-26 specimens of each species and size class collected from seines, and standardized them for ease of comparison across species (Fig. A4.1, Table A4.3). We log-transformed fish traits where appropriate to conform to a normal distribution. Species-level mean trait values are listed in Table A4.4. We also used principal component analysis (PCA) to condense variation among fish species' linear morphometric traits into 16 axes, the first three of which explained 66% of variation among species (Fig. A4.2).

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- Froese, R., and Pauly, D. (eds). 2023. Fishbase. World Wide Web electronic publication, ver. 01/2023
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Table A4.2. Total counts for all fish species observed across sites and years, including separate size classes for *G. aculeatus*, *C. aggregata*, *S. carnatus*, and *P. notatus*. Rows in bold indicate species and size classes that were retained for community analyses.

Species	Size class	Total count
<i>Gasterosteus aculeatus</i>	small	2468
<i>Cymatogaster aggregata</i>	small	729
<i>Syngnathus leptorhynchus</i>		563
<i>Gasterosteus aculeatus</i>	large	146
<i>Sebastes melanops</i>		143
<i>Leptocottus armatus</i>		51
<i>Embiotoca lateralis</i>		50
<i>Clevelandia ios</i>		43
<i>Gibbonsia metzi</i>		42
<i>Apodichthys flavidus</i>		37
<i>Brachyistius frenatus</i>		37
<i>Sebastes carnatus</i>	small	31
<i>Atherinops affinis</i>		19
<i>Sebastes carnatus</i>	large	18
<i>Oligocottus snyderi</i>		17
<i>Phanerodon vacca</i>		13
<i>Cymatogaster aggregata</i>	large	12
<i>Porichthys notatus</i>	large	10
<i>Pholis ornata</i>		9
<i>Porichthys notatus</i>	small	4
<i>Aulorhynchus flavidus</i>		5

APPENDIX 4

<i>Acanthogobius flavimanus</i>	4
<i>Citharichthys stigmaeus</i>	4
<i>Scorpaenichthys marmoratus</i>	4
<i>Sebastes caurinus</i>	4
<i>Xiphister mucosus</i>	4
<i>Hexagrammos stelleri</i>	3
<i>Embiotoca jacksoni</i>	2
<i>Oligocottus maculosus</i>	2
<i>Parophrys vetulus</i>	2
<i>Cebidichthys violaceus</i>	1
<i>Clupea pallasii</i>	1
<i>Lepidogobius lepidus</i>	1
<i>Ophiodon elongatus</i>	1
<i>Sebastes paucispinis</i>	1

Table A4.3. Size thresholds for delimiting large vs. small individuals of *G. aculeatus*, *C. aggregata*, *S. carnatus*, and *P. notatus*, based on preliminary seine surveys in the same sites as in our study. No individuals were collected of sizes in between the ranges listed.

Species	Size Class	Size threshold (standard length)
<i>Gasterosteus aculeatus</i>	Large	≥ 55 mm
<i>Gasterosteus aculeatus</i>	Small	≤ 45 mm
<i>Cymatogaster aggregata</i>	Large	≥ 60 mm
<i>Cymatogaster aggregata</i>	Small	≤ 56 mm
<i>Sebastes carnatus</i>	Large	≥ 50 mm
<i>Sebastes carnatus</i>	Small	≤ 48 mm
<i>Porichthys notatus</i>	Large	≥ 67 mm
<i>Porichthys notatus</i>	Small	≤ 25 mm

Table A4.4. Traits used to characterize fish communities. Cat = discrete categorical trait, Cont. = continuous trait

Trait	Type	Definition	Standardized	Transformed	Functional Category	Source
Vertical position	Cat.	The orientation of the fish in the water column. Levels: Benthic, Benthopelagic, Pelagic	N/A	N/A	Feeding	Love 2011
Foraging mode	Cat.	Suite of behaviors associated with	N/A	N/A	Feeding	Love 2011

APPENDIX 4

		feeding and foraging. Levels: pursuit predator, benthic browser, epifaunal browser, planktivore, sit-and-wait.				
Trophic level	Cont.	The average trophic level of the species, estimated from food items	N/A	N/A	Feeding	Fishbase
Standard length	Cont.	Body length from snout tip to the end of the caudal peduncle	N/A	N/A	Habitat use, feeding	Measured individuals
Mouth Height	Cont.	Distance from distal tip of the premaxilla to the distal tip of the dentary with the jaws fully extended	Height / Standard Length	N/A	Feeding	Measured individuals
Dorsal Fin Length	Cont.	Straight length from the anterior to posterior end of the dorsal fin; summed where dorsal fins were discontinuous	Length / Standard Length	N/A	Locomotion	Measured individuals
Anal Fin Length	Cont.	Straight length from the anterior to posterior end of the anal fin	Length / Standard Length	N/A	Locomotion	Measured individuals
Caudal Fin Length	Cont.	Straight distance from the end of the caudal peduncle to the distal tip of the longest caudal fin ray	Length / Standard Length	log	Locomotion	Measured individuals
Pectoral Fin Length	Cont.	Length from base to the tip of the longest pectoral ray	Length / Standard Length	N/A	Locomotion, habitat use	Measured individuals
Head Length	Cont.	Distance from posterior margin of the operculum to the distal tip of the premaxilla with the jaws closed	Length / Standard Length	N/A	Feeding	Measured individuals

APPENDIX 4

Body Depth	Cont.	Greatest vertical distance from the top of the fish to the bottom	Depth / Standard Length	N/A	Locomotion, habitat use	Measured individuals
Body Depth Below Midline	Cont.	Greatest vertical distance below a horizontal line drawn from the tip of the snout to the end of the caudal peduncle	Depth / Body Depth	log	Locomotion, habitat use	Measured individuals
Head Depth	Cont.	Vertical distance from the top of the head to the bottom of the head, passing through the eye pupil	Depth / Body Depth	N/A	Feeding	Measured individuals
Eye Position	Cont.	Vertical distance from the pupil to the bottom of the head	Position / Head Depth	N/A	Habitat use	Measured individuals
Eye Diameter	Cont.	Horizontal distance across the eye passing through the pupil	Diameter / Head Length	N/A	Feeding	Measured individuals
Mouth Protrusion	Cont.	Length from distal tip of the premaxilla to the eye pupil with the jaws fully extended	Protrusion / Head Length	log	Feeding	Measured individuals
Snout Length	Cont.	Distance from eye pupil to distal tip of the premaxilla, with the mouth closed	Length / Head Length	N/A	Feeding	Measured individuals
Caudal Peduncle Length	Cont.	Horizontal distance from the end of the caudal peduncle to the end of the anal fin	Length / Standard Length	log	Locomotion	Measured individuals
Caudal Peduncle Depth	Con.	Vertical distance across the narrowest portion of the caudal peduncle	Depth / Body Depth	log	Locomotion	Measured individuals

APPENDIX 4

Table A4.5. Mean trait values for each fish species and size class observed in seines. Continuous morphometric traits are standardized according to Table A4.3; sample size denotes the number of individuals used to collect morphometric measurements.

Species	Vertical position	Foraging mode	Trophic level	Standard length (mm)	Mouth Height	Dorsal Fin Length	Sample size
<i>Apodichthys flavidus</i>	Benthic	Benthic browser, epifaunal browser, sit-and-wait	3.55	94.0000	0.0428	0.8862	10
<i>Atherinops affinis</i>	Pelagic	Benthic browser, planktivore	2.76	42.1667	0.0760	0.1358	9
<i>Brachyistius frenatus</i>	Pelagic	Epifaunal browser, planktivore	3.5	56.0000	0.0860	0.3864	8
<i>Clevelandia ios</i>	Benthic	Benthic browser	3.12	35.4444	0.1299	0.1627	9
<i>Cymatogaster aggregata</i> large	Pelagic, Benthopelagic	Benthic browser, epifaunal browser	2.99	86.0000	0.1137	0.4869	7
<i>Cymatogaster aggregata</i> small	Pelagic	Planktivore	2.99	39.1731	0.1160	0.4282	26
<i>Embiotoca lateralis</i>	Pelagic, Benthopelagic	Benthic browser, epifaunal browser	3.33	64.0000	0.1353	0.4131	7
<i>Gasterosteus aculeatus</i> large	Pelagic, Benthopelagic	Benthic browser, epifaunal browser, planktivore	3.38	65.2500	0.1038	0.2646	12
<i>Gasterosteus aculeatus</i> small	Pelagic, Benthopelagic	Benthic browser, epifaunal browser, planktivore	3.38	25.7727	0.0756	0.2510	11
<i>Gibbonsia metzi</i>	Benthic	Sit-and-wait	3.06	48.5625	0.0911	0.7078	8
<i>Leptocottus armatus</i>	Benthic	Sit-and-wait	3.68	80.7143	0.1727	0.4446	21
<i>Oligocottus snyderi</i>	Benthic	Benthic browser, sit-and-wait	3.16	50.5625	0.1631	0.6191	8

APPENDIX 4

<i>Phanerodon vacca</i>	Pelagic, Benthopelagic	Benthic browser, epifaunal browser	3.38	67.0000	0.0848	0.4216	3
<i>Pholis ornata</i>	Benthic	Benthic browser, epifaunal browser, sit- and-wait	3.55	75.0000	0.0451	0.8854	6
<i>Porichthys notatus</i> large	Benthic, Benthopelagic	Pursuit predator, planktivore	4.04	77.0000	0.1634	0.5039	4
<i>Porichthys notatus</i> small	Benthic, Benthopelagic	Pursuit predator	4.04	24.5000	0.1824	0.5712	2
<i>Sebastes carnatus</i> large	Benthopelagic	Benthic browser, sit- and-wait	3.62	50.0000	0.2195	0.5128	4
<i>Sebastes carnatus</i> small	Benthopelagic	Benthic browser, planktivore	3.62	31.6250	0.2183	0.5078	7
<i>Sebastes melanops</i>	Pelagic, Benthopelagic	Pursuit predator, planktivore	3.9	45.5833	0.2171	0.5574	6
<i>Syngnathus leptorhynchus</i>	Pelagic, Benthopelagic	Epifaunal browser, planktivore	3.24	128.3400	0.0131	0.1129	25

Table A4.4, continued

Species	Anal Fin Length	log(Caudal Fin Length)	Pectoral Fin Length	Head Length	Body Depth	log(Body Depth Below Midline)	Head Depth	Sample size
<i>Apodichthys flavidus</i>	0.4127	-1.3213	0.0392	0.0956	0.1146	-0.2654	0.4688	10
<i>Atherinops affinis</i>	0.2217	-0.9279	0.1389	0.2090	0.1635	-0.2926	0.6175	9
<i>Brachyistius frenatus</i>	0.3220	-0.8215	0.2123	0.2900	0.3725	-0.3134	0.4749	8
<i>Clevelandia ios</i>	0.2122	-0.7990	0.1120	0.2263	0.1325	-0.2391	0.6821	9
<i>Cymatogaster aggregata</i> large	0.2541	-0.9175	0.2464	0.3073	0.3787	-0.3134	0.5063	7
<i>Cymatogaster aggregata</i> small	0.2477	-0.8154	0.2344	0.3133	0.3623	-0.3214	0.5587	26
<i>Embiotoca lateralis</i>	0.2883	-0.7982	0.2393	0.2989	0.4085	-0.3269	0.5133	7

APPENDIX 4

<i>Gasterosteus aculeatus</i> large	0.1817	-0.9132	0.1327	0.2742	0.1983	-0.1755	0.6826	12
<i>Gasterosteus aculeatus</i> small	0.1639	-0.9809	0.1539	0.2692	0.2364	-0.3194	0.5415	11
<i>Gibbonsia metzi</i>	0.3884	-0.8776	0.1601	0.2141	0.1785	-0.3089	0.5975	8
<i>Leptocottus armatus</i>	0.3112	-0.8138	0.2411	0.3130	0.1889	-0.2324	0.7066	21
<i>Oligocottus snyderi</i>	0.3959	-0.7076	0.2840	0.2572	0.2073	-0.1304	0.7178	8
<i>Phanerodon vacca</i>	0.2739	-0.7846	0.2354	0.3087	0.3868	-0.2999	0.5397	3
<i>Pholis ornata</i>	0.3927	-1.2525	0.0628	0.1150	0.1124	-0.2596	0.4975	6
<i>Porichthys notatus</i> large	0.4883	-0.9009	0.1751	0.2609	0.1774	-0.2417	0.6574	4
<i>Porichthys notatus</i> small	0.4978	-0.7547	0.1492	0.2123	0.1914	-0.2753	0.7659	2
<i>Sebastes carnatus</i> large	0.2023	-0.8042	0.2463	0.3261	0.3055	-0.2512	0.6436	4
<i>Sebastes carnatus</i> small	0.1925	-0.7509	0.2298	0.3681	0.2575	-0.2419	0.8601	7
<i>Sebastes melanops</i>	0.1869	-0.8116	0.2069	0.3322	0.2701	-0.3394	0.6755	6
<i>Syngnathus leptorhynchus</i>	0.0000	-1.5273	0.0203	0.1284	0.0309	-0.2518	0.7862	25

Table A4.4, continued

Species	Eye Position	Eye Diam.	log(Mouth Protrusion)	Snout Length	log(Caudal Peduncle Length + 1)	log(Caudal Peduncle Depth)	Sample size
<i>Apodichthys flavidus</i>	0.6797	0.2387	-0.3886	0.3662	0.0000	-0.4780	10
<i>Atherinops affinis</i>	0.4831	0.2531	-0.3137	0.3552	0.0708	-0.2898	9
<i>Brachyistius frenatus</i>	0.5510	0.2898	-0.2775	0.3960	0.0796	-0.3960	8
<i>Clevelandia ios</i>	0.8090	0.1153	-0.3887	0.3287	0.0675	-0.2702	9
<i>Cymatogaster aggregata</i> large	0.6484	0.2581	-0.2702	0.3950	0.0494	-0.5274	7
<i>Cymatogaster aggregata</i> small	0.5780	0.3552	-0.2315	0.4294	0.0560	1.2031	26
<i>Embiotoca lateralis</i>	0.5784	0.3287	-0.3805	0.3731	0.0630	-0.4818	7

APPENDIX 4

<i>Gasterosteus aculeatus</i> large	0.5319	0.2478	-0.3119	0.4166	0.0507	-0.5158	12
<i>Gasterosteus aculeatus</i> small	0.6582	0.2303	-0.2900	0.4224	0.0540	-0.5753	11
<i>Gibbonsia metzi</i>	0.6632	0.1998	-0.3606	0.3620	0.0313	-0.4292	8
<i>Leptocottus armatus</i>	0.8663	0.1219	-0.3504	0.3282	0.0436	-0.3910	21
<i>Oligocottus snyderi</i>	0.8195	0.2043	-0.3193	0.4333	0.0506	-0.3608	8
<i>Phanerodon vacca</i>	0.5659	0.2846	-0.2959	0.3782	0.0603	-0.4758	3
<i>Pholis ornata</i>	0.7278	0.1710	-0.5043	0.2323	0.0000	-0.4657	6
<i>Porichthys notatus</i> large	1.0048	0.1810	-0.5686	0.2525	0.0000	-0.5855	4
<i>Porichthys notatus</i> small	0.8781	0.1991	0.4096	0.4936	0.0000	-0.5794	2
<i>Sebastes carnatus</i> large	0.7764	0.2604	-0.2458	0.4105	0.0548	-0.4383	4
<i>Sebastes carnatus</i> small	0.6840	0.2753	-0.2326	0.3767	0.0603	-0.3827	7
<i>Sebastes melanops</i>	0.6204	0.2898	-0.2466	0.4023	0.0652	-0.3920	6
<i>Syngnathus leptorhynchus</i>	0.7109	0.0950	-0.2494	0.5647	0.1689	-0.6167	25

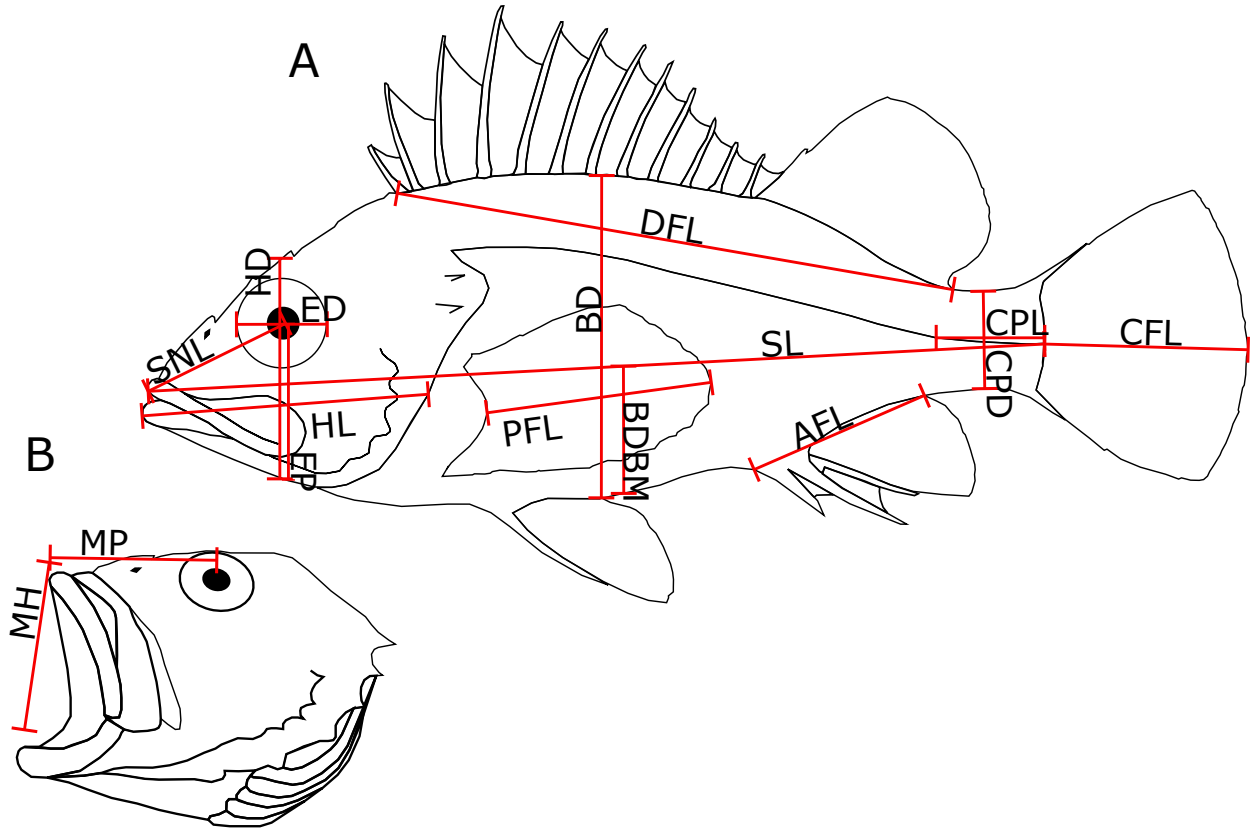


Figure A4.3. Fish morphometric traits used in functional analyses, here measured on a rockfish (*Sebastes* sp.) with its mouth closed (A) and open (B). SNL = snout length; HD = head depth; ED = eye diameter; HL = head length; EP = eye position; PFL = pectoral fin length; BD = body depth; BDBM = body depth below midline; SL = standard length; AFL = anal fin length; CPL = caudal peduncle length; CPD = caudal peduncle depth; CFL = caudal fin length; MP = mouth protrusion; MH = mouth height. Descriptions of individual traits are provided in Table A4.3.

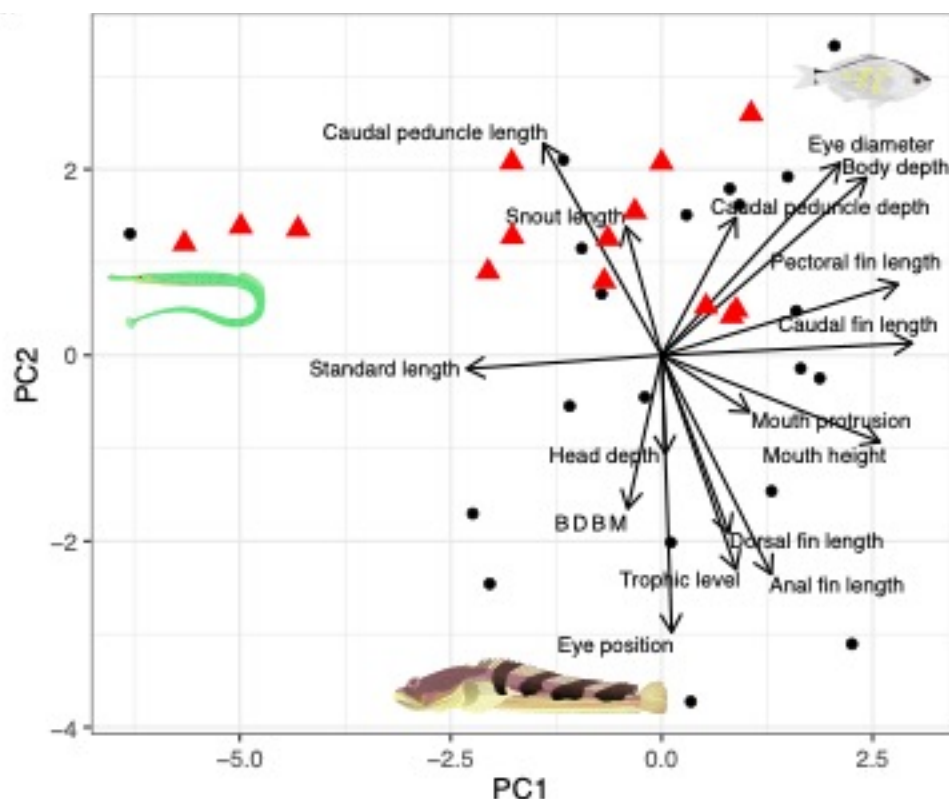


Figure A4.4. Principle coordinates axes of fish morphometric traits. PC1 explained 25.18% of the variation in fish morphology, while PC2 explained 23.10% of the variation. Black circular points represent mean values for species, while red triangles represent community weighted mean values. Species visually represented in morphospace include *Cymatogaster aggregata* (top right), *Syngnathus leptorhynchus* (middle left), and *Porichthys notatus* (bottom middle).

2. PERACARIDS

Across both years and all six sites, we found a total of 28 peracarid species of which 23 species were retained in our analyses, after removing singletons and species that only occurred in one site-year combination (Table A4.5). The most speciose peracarid community in our dataset had 18 species.

We assigned each two categorical traits (body shape and living habit) and one continuous trait (maximum body size) from the literature (Carlton 2007; Table A4.6). We determined tube fidelity for each species according to observations of living and preserved specimens and information in the literature about the presence or absence of silk glands. We ranked tube fidelity along a four-point ordered scale: none = lacks silk glands to build tubes; low = has silk glands but was never observed in tubes when alive or preserved in ethanol; medium = has silk glands

and was observed in tubes when alive but readily flees tube when exposed to ethanol, and high = has silk glands, is tubicolous when alive, and is regularly found inside tubes after preservation in ethanol. Living habit had 3 levels: tubicolous = has silk glands to build tubes, regardless of tube fidelity; clinging = lacks silk glands and typically remains stationary, clinging to eelgrass blades or other structure with well-developed dactyls; and swimming = lacks silk glands, readily swims among vertical structures, and lacks specialized dactyls for clinging. Body shape also had 3 levels: cylindrical = elongated or tube-shaped body, rounded in cross section; dorsoventrally compressed = body wider than it is tall; and laterally compressed = body taller than it is wide.

To measure activity level, we recorded videos of 9-20 individuals of each species, except for *Uromunna ubiquita*. After we started recording, we dropped each individual from a height of 6 centimeters into a cylindrical cup with 150 ml of seawater positioned over a grid on a dark background. We stopped recording 1 minute after the animal was first submerged in the seawater. After recording, we trimmed videos to a length of 1 minute to remove the initial seconds of dropping and splashing, and used FIJI (Schindelin et al. 2012) to record the number of frames during which the animal was not moving, walking, or swimming. We defined a lack of movement as a lack of sustained forward or backward locomotion facilitated by pereopods or pleopods. We defined walking as motion propelled primarily by the pereopod dactyls making contact with the bottom of the cup, while swimming was motion propelled primarily by beating the pleopods and freeing the pereopods from the substrate. We show the pleopods and pereopods of a typical amphipod in Fig. A4.3. We measured continuous morphometric traits from images of 9-22 individuals of each species in FIJI, and standardized and transformed them as described in Table A4.6 and shown in Fig. A4.3. We show species-level mean values for each trait in Table A4.7.

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Table A4.6. Total and standardized counts for all peracarid species observed across sites and years. Standardized abundances are obtained by dividing the number of individuals in a sample by the biomass of macrophytes in the sample Rows in bold indicate species and size classes that were retained for community analyses.

Species	Total count	Standardized total abundance (ind. g ⁻¹)
<i>Leptochelia</i> sp.	4468	7.92451204
<i>Photis brevipes</i>	2757	6.94097811
<i>Caprella californica</i>	3534	6.22669491
<i>Zeuxo normani</i>	2159	3.98439136
<i>Monocorophium insidiosum</i>	2012	3.30624947
<i>Paracorophium</i> sp.	1524	2.71298939
<i>Ampithoe valida</i>	1452	2.22806836
<i>Aoroides columbiae</i>	550	1.32119752
<i>Grandidierella japonica</i>	567	0.83671613
<i>Ampithoe lacertosa</i>	390	0.7393752
<i>Pentidotea resecata</i>	540	0.54697383
<i>Ericthonius brasiliensis</i>	170	0.35707027
<i>Ischyrocerus anguipes</i>	204	0.35049762
<i>Paranthura japonica</i>	96	0.17125917
<i>Uromunna ubiquita</i>	64	0.15066378
<i>Paracerceis cordata</i>	62	0.11774281
<i>Melita nitida</i>	67	0.11653687
<i>Paramicrodeutopus schmitti</i>	48	0.09474279
<i>Pontogeneia rostrata</i>	43	0.09220466
<i>Allorchestes angusta</i>	59	0.08527527
<i>Americorophium spinicorne</i>	34	0.05073408
<i>Apolochus barnardi</i>	26	0.03992121
<i>Gnorimosphaeroma</i> sp.	21	0.03192348
<i>Incisocalliope derzhavini</i>	6	0.00912099
<i>Ampithoe sectimanus</i>	2	0.00617033
<i>Hourstonius vilordes</i>	2	0.00384578
<i>Janiralata occidentalis</i>	1	0.0021857

APPENDIX 4

Megamoera subtener

2

0.00148796

Table A4.7. Traits used to characterize peracarid communities. Traits standardized by body length are standardized by the measured body length of the same individual. Cat = discrete categorical trait, Cont. = continuous trait.

Trait	Type	Definition	Standardized	Transformed	Functional category	Source
Body shape	Cat.	Overall body shape. Levels: Cylindrical, Dorsoventrally compressed, Laterally compressed Mode of contact with habitat substrate	N/A	N/A	Microhabitat use	Carlton 2007
Living habit	Cat.	(eelgrass). Levels: Tubicolous, Clinging, Swimming The degree of association with constructed silk tubes. Levels: None, Low, Medium, High	N/A	N/A	Microhabitat use	Carlton 2007
Tube fidelity	Ordered Cat.	Body length measured from the tip of the rostrum to the tip of the telson	N/A	N/A	Microhabitat use	Pers. obs.
Maximum body size	Cont.	Body length measured from the tip of the rostrum to the tip of the telson	N/A	log	Microhabitat use, predator susceptibility	Carlton 2007
Mean body size	Cont.	Percentage of total frames during which pleopod-driven locomotion occurred	N/A	log	Microhabitat use, predator susceptibility	Measured
% Swimming	Cont.	Percentage of total frames during which	N/A	log	Activity level, predator susceptibility	Measured
% Walking	Cont.		N/A	N/A	Activity level,	Measured

APPENDIX 4

		pereopod-driven locomotion in contact with the cup surface occurred			predator susceptibility	
% Still	Cont.	Percentage of total frames during which no forward locomotion occurred	N/A	N/A	Activity level, predator susceptibility	Measured
Eye diameter	Cont.	Diameter of a circle with an area equal to that of the eye (eyes are often irregularly-shaped)	Diameter / Body length	N/A	Sensory	Measured
Antenna length 1	Cont.	Distance from the base to the distal tip of antenna 1	Length / Body length	N/A	Sensory	Measured
Antenna length 2	Cont.	Distance from the base to the distal tip of antenna 2	Length / Body length	N/A	Sensory	Measured

Table A4.8. Mean trait values for each peracarid species observed in grab samples. Continuous morphometric traits are standardized according to Table A4.6; sample size denotes the number of individuals used to collect morphometric measurements, followed by the number of individuals used to collect movement data.

Species	Body shape	Living habit	Tube fidelity	log(Max. body size (mm))	log(Mean body size (mm))	Sample size
<i>Allorchestes angusta</i>	Laterally compressed	Swimming	None	1.0000	0.7656	10, 20
<i>Americorophium spinicorne</i>	Cylindrical	Tubicolous	Medium	0.8451	0.5573	20, 9
<i>Ampithoe lacertosa</i>	Laterally compressed	Tubicolous	Medium	1.3802	1.2241	20, 19
<i>Ampithoe valida</i>	Laterally compressed	Tubicolous	Medium	1.0969	0.8336	14, 19
<i>Aoroides columbiae</i>	Laterally compressed	Tubicolous	Low	0.7782	0.7108	22, 14
<i>Apolochus barnardi</i>	Laterally compressed	Clinging	None	0.3979	0.4465	18, 9

APPENDIX 4

<i>Caprella californica</i>	Cylindrical	Clinging	None	1.4771	1.2663	21, 20
<i>Erichthonius brasiliensis</i>	Cylindrical	Tubicolous	High	0.8129	0.7804	20, 15
<i>Gnorimosphaeroma</i> sp.	Dorsoventrally compressed	Clinging	None	1.0000	0.3656	10, 10
<i>Grandidierella japonica</i>	Laterally compressed	Tubicolous	Medium	1.1139	0.6055	12, 11
<i>Ischyrocerus anguipes</i>	Laterally compressed	Tubicolous	Low	1.0792	0.7205	22, 12
<i>Leptochelia</i> sp.	Cylindrical	Tubicolous	Medium	0.4771	0.5380	10, 10
<i>Melita nitida</i>	Laterally compressed	Swimming	None	1.0792	0.6598	14, 10
<i>Monocorophium insidiosum</i>	Cylindrical	Tubicolous	Medium	0.6532	0.4433	18, 15
<i>Paracerceis cordata</i>	Dorsoventrally compressed	Clinging	None	0.8513	0.5545	9, 14
<i>Paracorophium</i> sp.	Laterally compressed	Tubicolous	Low	0.6021	0.3888	16, 17
<i>Paramicrodeutopus schmitti</i>	Laterally compressed	Tubicolous	Low	0.6990	0.7730	10, 10
<i>Paranthura japonica</i>	Cylindrical	Tubicolous	Medium	0.9590	0.9129	10, 11
<i>Pentidotea resecata</i>	Dorsoventrally compressed	Clinging	None	1.6990	1.2320	10, 10
<i>Photis brevipes</i>	Laterally compressed	Tubicolous	High	0.8451	0.6721	21, 13
<i>Pontogeneia rostrata</i>	Laterally compressed	Swimming	None	0.8129	0.7542	22, 14
<i>Uromunna ubiquita</i>	Dorsoventrally compressed	Clinging	None	0.3010	0.0216	13, 0
<i>Zeuxo normani</i>	Cylindrical	Tubicolous	High	0.4771	0.5253	10, 10

Table A4.7, continued. A1 = antenna length 1, A2 = antenna length 2

Species	log(% Swimming)	% Walking	% Still	Eye diam.	A1	A2	Sample size
<i>Allorchestes angusta</i>	-0.2712	0.0560	0.4084	0.0334	0.2656	0.2451	10, 20
<i>Americorophium spinicorne</i>	-0.3674	0.3353	0.2355	0.0230	0.4270	0.5313	20, 9
<i>Ampithoe lacertosa</i>	-0.6914	0.2940	0.5025	0.0151	0.6798	0.4924	20, 19
<i>Ampithoe valida</i>	-0.3708	0.2619	0.3123	0.0200	0.5430	0.4249	14, 19
<i>Aoroides columbiae</i>	-0.9805	0.3705	0.5249	0.0191	0.5919	0.3128	22, 14
<i>Apolochus barnardi</i>	-1.4612	0.0205	0.9449	0.0433	0.2288	0.1896	18, 9
<i>Caprella californica</i>	-1.0288	0.2929	0.6135	0.0077	0.6116	0.2864	21, 20
<i>Erichthonius brasiliensis</i>	-0.9664	0.1314	0.7605	0.0244	0.4831	0.4838	20, 15

APPENDIX 4

<i>Gnorimosphaeroma</i> <i>sp.</i>	-0.8345	0.2346	0.6191	0.0667	0.2593	0.3793	10, 10
<i>Grandidierella</i> <i>japonica</i>	-0.3383	0.1971	0.3441	0.0228	0.5652	0.4371	12, 11
<i>Ischyrocerus</i> <i>anguipes</i>	-1.0569	0.4292	0.4831	0.0177	0.4416	0.4272	22, 12
<i>Leptochelia</i> <i>sp.</i>	-1.1577	0.5021	0.4283	0.0178	0.2144	0.1157	10, 10
<i>Melita nitida</i>	-0.4091	0.0615	0.5487	0.0245	0.5435	0.3654	14, 10
<i>Monocorophium</i> <i>insidiosum</i>	-0.2725	0.1974	0.2687	0.0246	0.3748	0.4900	18, 15
<i>Paracerceis</i> <i>cordata</i>	-1.8909	0.4669	0.5202	0.0739	0.2338	0.3244	9, 14
<i>Paracorophium</i> <i>sp.</i>	-0.6522	0.3501	0.4271	0.0240	0.3082	0.3156	16, 17
<i>Paramicrodeutopus</i> <i>schmitti</i>	-0.6657	0.0013	0.7828	0.0194	0.3932	0.2589	10, 10
<i>Paranthura</i> <i>japonica</i>	-1.1076	0.5976	0.3243	0.0155	0.0831	0.1013	10, 11
<i>Pentidotea resecata</i>	-0.4588	0.5181	0.1341	0.0186	0.0969	0.4472	10, 10
<i>Photis brevipes</i>	-1.6417	0.4967	0.4805	0.0202	0.3877	0.3628	21, 13
<i>Pontogeneia</i> <i>rostrata</i>	-0.2748	0.0401	0.4288	0.0594	0.4266	0.4973	22, 14
<i>Uromunna ubiquita</i>	NA	NA	NA	0.0393	0.2001	0.8503	13, 0
<i>Zeuxo normani</i>	-1.8539	0.8506	0.1354	0.0161	0.1411	0.1284	10, 10

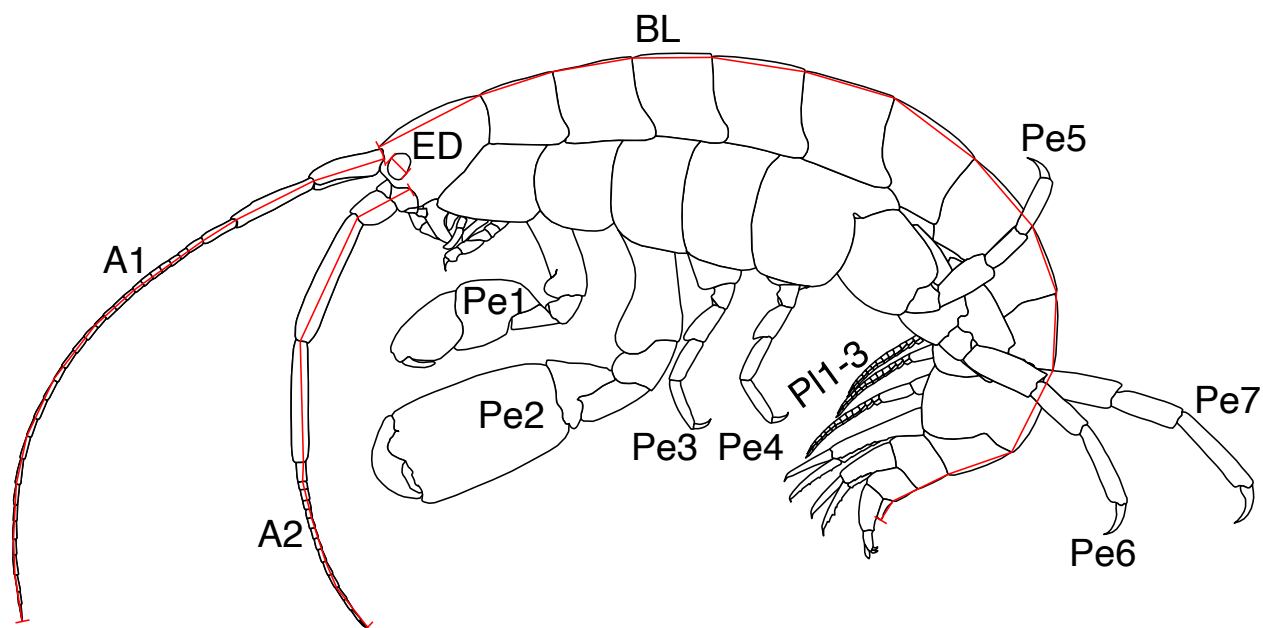


Figure A4.5. Peracarid morphometric traits used in functional analyses, here measured on an amphipod, *Ampithoe valida*. A1 = antenna length 1; A2 = antenna length 2; ED = eye diameter; BL = body length. Pe1-Pe7 denote individual pereopods (walking legs), while P11-P13 denote individual pleopods (swimming legs). Descriptions of individual traits are provided in Table A4.6.

APPENDIX 5: Supplementary material for Chapter 2.

Table A5.1. Effect sizes of community-weighted mean fish traits on peracarid community trait and phylogenetic dispersion. Bolded cells indicate values significant at the alpha level indicated; the first 103 rows are models for which results are presented in the main text. Italicized rows represent post-hoc tests of individual peracarid community response traits. Rows are colored according to the direction and magnitude of the effect size; red indicates a negative effect while blue indicates a positive effect, and color saturation is proportional to R^2 . TS = Tip Shuffle algorithm, IS = Independent Swap algorithm; BDBM = Body Depth Below Midline

Predictor trait	Response trait	Response metric	Response permutation algorithm	Effect size	R^2	alpha level
PC1	all	SES _{MNTD}	TS	0.04471	-0.07225	0.003125
PC2	all	SES _{MNTD}	TS	0.225	-0.01413	0.003125
PC3	all	SES _{MNTD}	TS	0.1713	0.001343	0.003125
PC4	all	SES _{MNTD}	TS	-1.07	0.2779	0.003125
PC5	all	SES _{MNTD}	TS	-0.25312	0.06352	0.003125
PC6	all	SES _{MNTD}	TS	0.2937	0.1789	0.003125
PC7	all	SES _{MNTD}	TS	-0.7743	0.2114	0.003125
PC8	all	SES _{MNTD}	TS	1.249	0.4769	0.003125
PC9	all	SES _{MNTD}	TS	0.9483	0.3428	0.003125
PC10	all	SES _{MNTD}	TS	-1.2957	0.03707	0.003125
PC11	all	SES _{MNTD}	TS	3.65107	0.03478	0.003125
PC12	all	SES _{MNTD}	TS	-3.24415	0.3404	0.003125
PC13	all	SES _{MNTD}	TS	2.48169	0.01732	0.003125
PC14	all	SES _{MNTD}	TS	-5.0352	0.3272	0.003125
PC15	all	SES _{MNTD}	TS	5.4195	0.03951	0.003125
PC16	all	SES _{MNTD}	TS	14.3565	0.6565	0.003125
Anal fin length	all	SES _{MNTD}	TS	1.4954	-0.06102	0.00263158
BDBM	all	SES _{MNTD}	TS	-13.492	0.5642	0.00263158
Body depth	all	SES _{MNTD}	TS	2.3018	0.004472	0.00263158
Caudal fin length	all	SES _{MNTD}	TS	2.3498	-0.08527	0.00263158
Caudal peduncle depth	all	SES _{MNTD}	TS	0.2568	-0.00711	0.00263158
Caudal peduncle length	all	SES _{MNTD}	TS	0.6436	-0.09203	0.00263158

APPENDIX 5

Dorsal fin length	all	SES _{MNTD}	TS	1.2216	-0.01383	0.00263158
Eye diameter	all	SES _{MNTD}	TS	1.4517	-0.0776	0.00263158
Eye position	all	SES _{MNTD}	TS	7.84	0.2658	0.00263158
Head depth	all	SES _{MNTD}	TS	-3.557	0.05329	0.00263158
Head length	all	SES _{MNTD}	TS	0.8822	-0.09438	0.00263158
Mouth height	all	SES _{MNTD}	TS	3.5411	-0.02024	0.00263158
Mouth protrusion	all	SES _{MNTD}	TS	4.283	0.06329	0.00263158
Pectoral fin length	all	SES _{MNTD}	TS	3.4599	0.007227	0.00263158
Standard length	all	SES _{MNTD}	TS	0.007442	0.005068	0.00263158
Snout length	all	SES _{MNTD}	TS	-0.2739	-0.09941	0.00263158
Trophic level	all	SES _{MNTD}	TS	-0.198	-0.09573	0.00263158
Foraging mode	all	SES _{MNTD}	TS	-0.4545	-0.04048	0.00263158
Vertical position	all	SES _{MNTD}	TS	-0.07623	-0.09513	0.00263158
PC1	phylogeny	SES _{MNTD}	TS	0.04383	-0.08396	0.003125
PC2	phylogeny	SES _{MNTD}	TS	0.3495	0.02462	0.003125
PC3	phylogeny	SES _{MNTD}	TS	0.2277	0.00781	0.003125
PC4	phylogeny	SES _{MNTD}	TS	-1.6731	0.456	0.003125
PC5	phylogeny	SES _{MNTD}	TS	-0.34585	0.08368	0.003125
PC6	phylogeny	SES _{MNTD}	TS	0.4308	0.2609	0.003125
PC7	phylogeny	SES _{MNTD}	TS	-1.0766	0.2622	0.003125
PC8	phylogeny	SES _{MNTD}	TS	1.7603	0.5895	0.003125
PC9	phylogeny	SES _{MNTD}	TS	1.253	0.3652	0.003125
PC10	phylogeny	SES _{MNTD}	TS	-1.83117	0.06472	0.003125
PC11	phylogeny	SES _{MNTD}	TS	4.9229	0.04743	0.003125
PC12	phylogeny	SES _{MNTD}	TS	-4.41861	0.3911	0.003125
PC13	phylogeny	SES _{MNTD}	TS	2.66958	-0.01832	0.003125
PC14	phylogeny	SES _{MNTD}	TS	-6.7443	0.3611	0.003125
PC15	phylogeny	SES _{MNTD}	TS	6.3838	0.01647	0.003125
PC16	phylogeny	SES _{MNTD}	TS	20.4799	0.8263	0.003125
Anal fin length	phylogeny	SES _{MNTD}	TS	1.6601	-0.0711	0.00263158
BDBM	phylogeny	SES _{MNTD}	TS	-18.736	0.6706	0.00263158
Body depth	phylogeny	SES _{MNTD}	TS	2.7896	-0.007678	0.00263158
Caudal fin length	phylogeny	SES _{MNTD}	TS	1.4752	-0.09651	0.00263158
Caudal peduncle depth	phylogeny	SES _{MNTD}	TS	0.3752	0.0193	0.00263158

APPENDIX 5

Caudal peduncle length	phylogeny	SES _{MNTD}	TS	1.237	-0.08227	0.00263158
Dorsal fin length	phylogeny	SES _{MNTD}	TS	1.476	-0.02431	0.00263158
Eye diameter	phylogeny	SES _{MNTD}	TS	1.5907	-0.08382	0.00263158
Eye position	phylogeny	SES _{MNTD}	TS	10.751	0.314	0.00263158
Head depth	phylogeny	SES _{MNTD}	TS	-4.946	0.07829	0.00263158
Head length	phylogeny	SES _{MNTD}	TS	0.36599	-0.09942	0.00263158
Mouth height	phylogeny	SES _{MNTD}	TS	3.799	-0.04477	0.00263158
Mouth protrusion	phylogeny	SES _{MNTD}	TS	6.184	0.1048	0.00263158
Pectoral fin length	phylogeny	SES _{MNTD}	TS	4.0482	-0.01168	0.00263158
Standard length	phylogeny	SES _{MNTD}	TS	0.01177	0.05813	0.00263158
Snout length	phylogeny	SES _{MNTD}	TS	0.4038	-0.09922	0.00263158
Trophic level	phylogeny	SES _{MNTD}	TS	-0.3671	-0.09117	0.00263158
Foraging mode	phylogeny	SES _{MNTD}	TS	-0.429	-0.0681	0.00263158
Vertical position	phylogeny	SES _{MNTD}	TS	-0.1518	-0.08838	0.00263158
<i>BDBM</i>	<i>activity level (% still)</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>-6.523</i>	<i>0.1309</i>	<i>0.0045455</i>
<i>PC16</i>	<i>activity level (% still)</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>8.7216</i>	<i>0.3152</i>	<i>0.0045455</i>
<i>PC8</i>	<i>activity level (% still)</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>0.7664</i>	<i>0.223</i>	<i>0.0045455</i>
<i>BDBM</i>	<i>activity level (% swimming)</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>-8.911</i>	<i>-0.008397</i>	<i>0.0045455</i>
<i>PC16</i>	<i>activity level (% swimming)</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>12.7537</i>	<i>0.08878</i>	<i>0.0045455</i>
<i>PC8</i>	<i>activity level (% swimming)</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>1.1776</i>	<i>0.06215</i>	<i>0.0045455</i>
<i>BDBM</i>	<i>activity level (% walking)</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>-10.302</i>	<i>-0.000527</i>	<i>0.0045455</i>
<i>PC16</i>	<i>activity level (% walking)</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>9.3668</i>	<i>-0.01727</i>	<i>0.0045455</i>
<i>PC8</i>	<i>activity level (% walking)</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>0.8837</i>	<i>-0.02581</i>	<i>0.0045455</i>
<i>BDBM</i>	<i>antenna 1 length</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>-9.596</i>	<i>0.3811</i>	<i>0.0045455</i>
<i>PC16</i>	<i>antenna 1 length</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>10.2606</i>	<i>0.4533</i>	<i>0.0045455</i>
<i>PC8</i>	<i>antenna 1 length</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>0.9024</i>	<i>0.3311</i>	<i>0.0045455</i>
<i>BDBM</i>	<i>antenna 2 length</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>1.7397</i>	<i>0.329</i>	<i>0.0045455</i>

APPENDIX 5

<i>PC16</i>	<i>antenna 2 length</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>-1.84729</i>	<i>0.3866</i>	<i>0.0045455</i>
<i>PC8</i>	<i>antenna 2 length</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>-0.16162</i>	<i>0.2753</i>	<i>0.0045455</i>
<i>BDBM</i>	<i>body shape</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>-1.4493</i>	<i>0.265</i>	<i>0.0045455</i>
<i>PC16</i>	<i>body shape</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>1.52118</i>	<i>0.3045</i>	<i>0.0045455</i>
<i>PC8</i>	<i>body shape</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>0.13093</i>	<i>0.2019</i>	<i>0.0045455</i>
<i>BDBM</i>	<i>eye diameter</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>2.5251</i>	<i>0.09542</i>	<i>0.0045455</i>
<i>PC16</i>	<i>eye diameter</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>-2.8551</i>	<i>0.1513</i>	<i>0.0045455</i>
<i>PC8</i>	<i>eye diameter</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>-0.26376</i>	<i>0.1161</i>	<i>0.0045455</i>
<i>BDBM</i>	<i>living habit</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>-1.0751</i>	<i>0.1289</i>	<i>0.0045455</i>
<i>PC16</i>	<i>living habit</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>1.05591</i>	<i>0.1221</i>	<i>0.0045455</i>
<i>PC8</i>	<i>living habit</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>0.0883</i>	<i>0.05653</i>	<i>0.0045455</i>
<i>BDBM</i>	<i>max body size</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>-8.346</i>	<i>0.3318</i>	<i>0.0045455</i>
<i>PC16</i>	<i>max body size</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>9.1473</i>	<i>0.4218</i>	<i>0.0045455</i>
<i>PC8</i>	<i>max body size</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>0.7703</i>	<i>0.2728</i>	<i>0.0045455</i>
<i>BDBM</i>	<i>mean body size</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>0.9199</i>	<i>-0.06737</i>	<i>0.0045455</i>
<i>PC16</i>	<i>mean body size</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>-</i>	<i>-0.08662</i>	<i>0.0045455</i>
<i>PC8</i>	<i>mean body size</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>-0.05646</i>	<i>-0.08754</i>	<i>0.0045455</i>
<i>BDBM</i>	<i>tube fidelity</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>0.2693</i>	<i>-0.09993</i>	<i>0.0045455</i>
<i>PC16</i>	<i>tube fidelity</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>-4.74418</i>	<i>-0.07704</i>	<i>0.0045455</i>
<i>PC8</i>	<i>tube fidelity</i>	<i>SES_{MNTD}</i>	<i>TS</i>	<i>-0.3953</i>	<i>-0.08394</i>	<i>0.0045455</i>
<i>PC1</i>	<i>all</i>	<i>SES_{MNTD}</i>	<i>IS</i>	<i>0.06359</i>	<i>-0.0628</i>	<i>0.003125</i>
<i>PC2</i>	<i>all</i>	<i>SES_{MNTD}</i>	<i>IS</i>	<i>0.2856</i>	<i>-0.008355</i>	<i>0.003125</i>
<i>PC3</i>	<i>all</i>	<i>SES_{MNTD}</i>	<i>IS</i>	<i>0.2031</i>	<i>-0.005549</i>	<i>0.003125</i>
<i>PC4</i>	<i>all</i>	<i>SES_{MNTD}</i>	<i>IS</i>	<i>-1.1039</i>	<i>0.1666</i>	<i>0.003125</i>
<i>PC5</i>	<i>all</i>	<i>SES_{MNTD}</i>	<i>IS</i>	<i>-0.25133</i>	<i>0.006855</i>	<i>0.003125</i>
<i>PC6</i>	<i>all</i>	<i>SES_{MNTD}</i>	<i>IS</i>	<i>0.3333</i>	<i>0.138</i>	<i>0.003125</i>
<i>PC7</i>	<i>all</i>	<i>SES_{MNTD}</i>	<i>IS</i>	<i>-0.9344</i>	<i>0.2005</i>	<i>0.003125</i>
<i>PC8</i>	<i>all</i>	<i>SES_{MNTD}</i>	<i>IS</i>	<i>1.3956</i>	<i>0.3774</i>	<i>0.003125</i>
<i>PC9</i>	<i>all</i>	<i>SES_{MNTD}</i>	<i>IS</i>	<i>1.0248</i>	<i>0.2427</i>	<i>0.003125</i>
<i>PC10</i>	<i>all</i>	<i>SES_{MNTD}</i>	<i>IS</i>	<i>-1.28943</i>	<i>-0.01003</i>	<i>0.003125</i>
<i>PC11</i>	<i>all</i>	<i>SES_{MNTD}</i>	<i>IS</i>	<i>3.53332</i>	<i>-0.01634</i>	<i>0.003125</i>
<i>PC12</i>	<i>all</i>	<i>SES_{MNTD}</i>	<i>IS</i>	<i>-3.49097</i>	<i>0.2377</i>	<i>0.003125</i>
<i>PC13</i>	<i>all</i>	<i>SES_{MNTD}</i>	<i>IS</i>	<i>2.98987</i>	<i>0.01287</i>	<i>0.003125</i>
<i>PC14</i>	<i>all</i>	<i>SES_{MNTD}</i>	<i>IS</i>	<i>-5.3802</i>	<i>0.2233</i>	<i>0.003125</i>
<i>PC15</i>	<i>all</i>	<i>SES_{MNTD}</i>	<i>IS</i>	<i>6.4034</i>	<i>0.02909</i>	<i>0.003125</i>
<i>PC16</i>	<i>all</i>	<i>SES_{MNTD}</i>	<i>IS</i>	<i>16.0453</i>	<i>0.5263</i>	<i>0.003125</i>
<i>Anal fin length</i>	<i>all</i>	<i>SES_{MNTD}</i>	<i>IS</i>	<i>1.8311</i>	<i>-0.06126</i>	<i>0.00263158</i>

APPENDIX 5

BDBM	all	SES _{MNTD}	IS	-15.136	0.4541	0.00263158
Body depth	all	SES _{MNTD}	IS	2.9529	0.01395	0.00263158
Caudal fin length	all	SES _{MNTD}	IS	3.7553	-0.07506	0.00263158
Caudal peduncle depth	all	SES _{MNTD}	IS	0.3279	0.0003347	0.00263158
Caudal peduncle length	all	SES _{MNTD}	IS	0.46255	-0.09727	0.00263158
Dorsal fin length	all	SES _{MNTD}	IS	1.367	-0.02848	0.00263158
Eye diameter	all	SES _{MNTD}	IS	2.1562	-0.06725	0.00263158
Eye position	all	SES _{MNTD}	IS	8.291	0.1712	0.00263158
Head depth	all	SES _{MNTD}	IS	-4.147	0.03808	0.00263158
Head length	all	SES _{MNTD}	IS	1.7281	-0.08571	0.00263158
Mouth height	all	SES _{MNTD}	IS	4.3921	-0.01868	0.00263158
Mouth protrusion	all	SES _{MNTD}	IS	4.868	0.03977	0.00263158
Pectoral fin length	all	SES _{MNTD}	IS	4.4111	0.01552	0.00263158
Standard length	all	SES _{MNTD}	IS	0.006985	-0.03865	0.00263158
Snout length	all	SES _{MNTD}	IS	-0.6682	-0.09765	0.00263158
Trophic level	all	SES _{MNTD}	IS	-0.3021	-0.09341	0.00263158
Foraging mode	all	SES _{MNTD}	IS	-0.483	-0.05545	0.00263158
Vertical position	all	SES _{MNTD}	IS	-	-0.09991	0.00263158
PC1	phylogeny	SES _{MNTD}	IS	0.05727	-0.06585	0.003125
PC2	phylogeny	SES _{MNTD}	IS	0.3166	0.0275	0.003125
PC3	phylogeny	SES _{MNTD}	IS	0.2281	0.03479	0.003125
PC4	phylogeny	SES _{MNTD}	IS	-1.3922	0.3798	0.003125
PC5	phylogeny	SES _{MNTD}	IS	-0.28792	0.05869	0.003125
PC6	phylogeny	SES _{MNTD}	IS	0.3784	0.2472	0.003125
PC7	phylogeny	SES _{MNTD}	IS	-0.9775	0.2722	0.003125
PC8	phylogeny	SES _{MNTD}	IS	1.5378	0.5559	0.003125
PC9	phylogeny	SES _{MNTD}	IS	1.1032	0.3495	0.003125
PC10	phylogeny	SES _{MNTD}	IS	-1.54419	0.04602	0.003125
PC11	phylogeny	SES _{MNTD}	IS	4.307	0.04067	0.003125
PC12	phylogeny	SES _{MNTD}	IS	-3.91788	0.3813	0.003125
PC13	phylogeny	SES _{MNTD}	IS	2.56861	-0.005734	0.003125
PC14	phylogeny	SES _{MNTD}	IS	-5.9804	0.352	0.003125
PC15	phylogeny	SES _{MNTD}	IS	5.8831	0.0233	0.003125

APPENDIX 5

PC16	phylogeny	SES _{MNTD}	IS	17.89997	0.7821	0.003125
Anal fin length	phylogeny	SES _{MNTD}	IS	1.9277	-0.05142	0.00263158
BDBM	phylogeny	SES _{MNTD}	IS	-16.773	0.6699	0.00263158
Body depth	phylogeny	SES _{MNTD}	IS	2.9711	0.03055	0.00263158
Caudal fin length	phylogeny	SES _{MNTD}	IS	2.7667	-0.08468	0.00263158
Caudal peduncle depth	phylogeny	SES _{MNTD}	IS	0.3562	0.03404	0.00263158
Caudal peduncle length	phylogeny	SES _{MNTD}	IS	0.6981	-0.09296	0.00263158
Dorsal fin length	phylogeny	SES _{MNTD}	IS	1.496	-0.003069	0.00263158
Eye diameter	phylogeny	SES _{MNTD}	IS	2.0708	-0.06581	0.00263158
Eye position	phylogeny	SES _{MNTD}	IS	9.082	0.2682	0.00263158
Head depth	phylogeny	SES _{MNTD}	IS	-4.762	0.106	0.00263158
Head length	phylogeny	SES _{MNTD}	IS	1.153	-0.0928	0.00263158
Mouth height	phylogeny	SES _{MNTD}	IS	4.0495	-0.02177	0.00263158
Mouth protrusion	phylogeny	SES _{MNTD}	IS	5.416	0.09584	0.00263158
Pectoral fin length	phylogeny	SES _{MNTD}	IS	4.3394	0.02651	0.00263158
Standard length	phylogeny	SES _{MNTD}	IS	0.00899	0.01499	0.00263158
Snout length	phylogeny	SES _{MNTD}	IS	-0.2454	-0.09964	0.00263158
Trophic level	phylogeny	SES _{MNTD}	IS	-0.3157	-0.09186	0.00263158
Foraging mode	phylogeny	SES _{MNTD}	IS	-0.4784	-0.05056	0.00263158
Vertical position	phylogeny	SES _{MNTD}	IS	-0.07682	-0.09629	0.00263158
BDBM	activity level (% still)	SES _{MNTD}	IS	-7.506	0.00504	0.0045455
PC16	activity level (% still)	SES _{MNTD}	IS	11.4922	0.1477	0.0045455
PC8	activity level (% still)	SES _{MNTD}	IS	1.0264	0.09906	0.0045455
BDBM	activity level (% swimming)	SES _{MNTD}	IS	-8.199	-0.005406	0.0045455
PC16	activity level (% swimming)	SES _{MNTD}	IS	11.5614	0.08922	0.0045455
PC8	activity level (% swimming)	SES _{MNTD}	IS	1.0714	0.06372	0.0045455
BDBM	activity level (% walking)	SES _{MNTD}	IS	-7.592	0.01645	0.0045455
PC16	activity level (% walking)	SES _{MNTD}	IS	7.207	0.005558	0.0045455

APPENDIX 5

PC8	activity level (% walking)	SES _{MNTD}	IS	0.6739	-0.007018	0.0045455
BDBM	antenna 1 length	SES _{MNTD}	IS	-10.835	0.3396	0.0045455
PC16	antenna 1 length	SES _{MNTD}	IS	11.5808	0.4052	0.0045455
PC8	antenna 1 length	SES _{MNTD}	IS	1.0178	0.2931	0.0045455
BDBM	antenna 2 length	SES _{MNTD}	IS	3.362	0.2894	0.0045455
PC16	antenna 2 length	SES _{MNTD}	IS	-3.92486	0.4338	0.0045455
PC8	antenna 2 length	SES _{MNTD}	IS	-0.34984	0.3273	0.0045455
BDBM	body shape	SES _{MNTD}	IS	-0.3067	-0.02747	0.0045455
PC16	body shape	SES _{MNTD}	IS	0.233292	-0.05778	0.0045455
PC8	body shape	SES _{MNTD}	IS	0.017372	-0.07641	0.0045455
BDBM	eye diameter	SES _{MNTD}	IS	8.208	0.2628	0.0045455
PC16	eye diameter	SES _{MNTD}	IS	-8.9757	0.3365	0.0045455
PC8	eye diameter	SES _{MNTD}	IS	-0.8018	0.251	0.0045455
BDBM	living habit	SES _{MNTD}	IS	-0.09085	-0.09906	0.0045455
PC16	living habit	SES _{MNTD}	IS	0.324136	-0.08793	0.0045455
PC8	living habit	SES _{MNTD}	IS	-0.04007	-0.08142	0.0045455
BDBM	max body size	SES _{MNTD}	IS	-10.955	0.2785	0.0045455
PC16	max body size	SES _{MNTD}	IS	11.9026	0.3494	0.0045455
PC8	max body size	SES _{MNTD}	IS	0.9915	0.2142	0.0045455
BDBM	mean body size	SES _{MNTD}	IS	3.816	0.02283	0.0045455
PC16	mean body size	SES _{MNTD}	IS	-3.78075	0.0213	0.0045455
PC8	mean body size	SES _{MNTD}	IS	-0.337	-0.002909	0.0045455
BDBM	tube fidelity	SES _{MNTD}	IS	-0.21395	-0.09994	0.0045455
PC16	tube fidelity	SES _{MNTD}	IS	-2.83726	-0.08982	0.0045455
PC8	tube fidelity	SES _{MNTD}	IS	-0.21927	-0.09388	0.0045455
PC1	all	SES _{MPD}	TS	0.02844	-0.08938	0.003125
PC2	all	SES _{MPD}	TS	0.1031	-0.08296	0.003125
PC3	all	SES _{MPD}	TS	0.1541	-0.02243	0.003125
PC4	all	SES _{MPD}	TS	-1.0746	0.2606	0.003125
PC5	all	SES _{MPD}	TS	-0.30594	0.126	0.003125
PC6	all	SES _{MPD}	TS	0.2437	0.08158	0.003125
PC7	all	SES _{MPD}	TS	-0.5432	0.04495	0.003125
PC8	all	SES _{MPD}	TS	1.1196	0.3385	0.003125
PC9	all	SES _{MPD}	TS	0.992	0.3584	0.003125

APPENDIX 5

PC10	all	SES _{MPD}	TS	-1.5469	0.0848	0.003125
PC11	all	SES _{MPD}	TS	4.8927	0.1289	0.003125
PC12	all	SES _{MPD}	TS	-3.40143	0.3575	0.003125
PC13	all	SES _{MPD}	TS	2.21331	-0.01173	0.003125
PC14	all	SES _{MPD}	TS	-5.4347	0.3708	0.003125
PC15	all	SES _{MPD}	TS	4.73924	0.000917	0.003125
PC16	all	SES _{MPD}	TS	12.7554	0.4649	0.003125
Anal fin length	all	SES _{MPD}	TS	1.5383	-0.06098	0.00263158
BDBM	all	SES _{MPD}	TS	-12.423	0.4327	0.00263158
Body depth	all	SES _{MPD}	TS	1.705	-0.04578	0.00263158
Caudal fin length	all	SES _{MPD}	TS	1.1645	-0.09658	0.00263158
Caudal peduncle depth	all	SES _{MPD}	TS	0.1372	-0.07493	0.00263158
Caudal peduncle length	all	SES _{MPD}	TS	0.7863	-0.08874	0.00263158
Dorsal fin length	all	SES _{MPD}	TS	1.3908	0.005655	0.00263158
Eye diameter	all	SES _{MPD}	TS	0.6543	-0.0957	0.00263158
Eye position	all	SES _{MPD}	TS	8.175	0.2763	0.00263158
Head depth	all	SES _{MPD}	TS	-3.15	0.01367	0.00263158
Head length	all	SES _{MPD}	TS	-0.10338	-0.09993	0.00263158
Mouth height	all	SES _{MPD}	TS	3.1774	-0.03926	0.00263158
Mouth protrusion	all	SES _{MPD}	TS	3.561	0.00674	0.00263158
Pectoral fin length	all	SES _{MPD}	TS	2.704	-0.03805	0.00263158
Standard length	all	SES _{MPD}	TS	0.008589	0.03239	0.00263158
Snout length	all	SES _{MPD}	TS	-0.1489	-0.09983	0.00263158
Trophic level	all	SES _{MPD}	TS	0.09102	-0.09915	0.00263158
Foraging mode	all	SES _{MPD}	TS	-0.6671	0.02129	0.00263158
Vertical position	all	SES _{MPD}	TS	-0.1976	-0.06905	0.00263158
PC1	phylogeny	SES _{MPD}	TS	0.05309	-0.07896	0.003125
PC2	phylogeny	SES _{MPD}	TS	0.3247	-0.003811	0.003125
PC3	phylogeny	SES _{MPD}	TS	0.1938	-0.03023	0.003125
PC4	phylogeny	SES _{MPD}	TS	-1.2883	0.1947	0.003125
PC5	phylogeny	SES _{MPD}	TS	-0.2897	0.01521	0.003125
PC6	phylogeny	SES _{MPD}	TS	0.377	0.1471	0.003125
PC7	phylogeny	SES _{MPD}	TS	-1.0497	0.2078	0.003125

APPENDIX 5

PC8	phylogeny	SES _{MPD}	TS	1.5874	0.4013	0.003125
PC9	phylogeny	SES _{MPD}	TS	1.1396	0.244	0.003125
PC10	phylogeny	SES _{MPD}	TS	-1.45346	-0.007229	0.003125
PC11	phylogeny	SES _{MPD}	TS	3.68702	-0.02607	0.003125
PC12	phylogeny	SES _{MPD}	TS	-3.81167	0.2267	0.003125
PC13	phylogeny	SES _{MPD}	TS	3.26063	0.008936	0.003125
PC14	phylogeny	SES _{MPD}	TS	-5.8638	0.2116	0.003125
PC15	phylogeny	SES _{MPD}	TS	7.1662	0.03121	0.003125
PC16	phylogeny	SES _{MPD}	TS	18.21	0.5547	0.003125
Anal fin length	phylogeny	SES _{MPD}	TS	1.4783	-0.07951	0.00263158
BDBM	phylogeny	SES _{MPD}	TS	-16.645	0.4437	0.00263158
Body depth	phylogeny	SES _{MPD}	TS	2.8054	-0.01652	0.00263158
Caudal fin length	phylogeny	SES _{MPD}	TS	2.8572	-0.08828	0.00263158
Caudal peduncle depth	phylogeny	SES _{MPD}	TS	0.3522	-0.006041	0.00263158
Caudal peduncle length	phylogeny	SES _{MPD}	TS	0.9322	-0.091	0.00263158
Dorsal fin length	phylogeny	SES _{MPD}	TS	1.2565	-0.05097	0.00263158
Eye diameter	phylogeny	SES _{MPD}	TS	1.7631	-0.08223	0.00263158
Eye position	phylogeny	SES _{MPD}	TS	9.66	0.1988	0.00263158
Head depth	phylogeny	SES _{MPD}	TS	-4.133	0.01128	0.00263158
Head length	phylogeny	SES _{MPD}	TS	1.2172	-0.09425	0.00263158
Mouth height	phylogeny	SES _{MPD}	TS	4.2515	-0.03816	0.00263158
Mouth protrusion	phylogeny	SES _{MPD}	TS	5.549	0.04739	0.00263158
Pectoral fin length	phylogeny	SES _{MPD}	TS	4.1853	-0.0156	0.00263158
Standard length	phylogeny	SES _{MPD}	TS	0.009002	-0.01731	0.00263158
Snout length	phylogeny	SES _{MPD}	TS	-0.1326	-0.09993	0.00263158
Trophic level	phylogeny	SES _{MPD}	TS	-0.3928	-0.09096	0.00263158
Foraging mode	phylogeny	SES _{MPD}	TS	-0.3937	-0.07598	0.00263158
Vertical position	phylogeny	SES _{MPD}	TS	-0.0519	-0.09879	0.00263158
<i>BDBM</i>	<i>activity level (% still)</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>-11.716</i>	<i>0.493</i>	<i>0.0045455</i>
<i>PC16</i>	<i>activity level (% still)</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>13.51323</i>	<i>0.6936</i>	<i>0.0045455</i>
<i>PC8</i>	<i>activity level (% still)</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>1.1939</i>	<i>0.5241</i>	<i>0.0045455</i>

APPENDIX 5

<i>BDBM</i>	<i>activity level (% swimming)</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>-12.082</i>	<i>0.05978</i>	<i>0.0045455</i>
<i>PC16</i>	<i>activity level (% swimming)</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>12.4202</i>	<i>0.06986</i>	<i>0.0045455</i>
<i>PC8</i>	<i>activity level (% swimming)</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>1.1517</i>	<i>0.04714</i>	<i>0.0045455</i>
<i>BDBM</i>	<i>activity level (% walking)</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>-13.287</i>	<i>0.116</i>	<i>0.0045455</i>
<i>PC16</i>	<i>activity level (% walking)</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>13.3525</i>	<i>0.1194</i>	<i>0.0045455</i>
<i>PC8</i>	<i>activity level (% walking)</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>1.2181</i>	<i>0.08399</i>	<i>0.0045455</i>
<i>BDBM</i>	<i>antenna 1 length</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>-15.248</i>	<i>0.5752</i>	<i>0.0045455</i>
<i>PC16</i>	<i>antenna 1 length</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>17.13355</i>	<i>0.7575</i>	<i>0.0045455</i>
<i>PC8</i>	<i>antenna 1 length</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>1.5025</i>	<i>0.5644</i>	<i>0.0045455</i>
<i>BDBM</i>	<i>antenna 2 length</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>0.18411</i>	<i>-0.07591</i>	<i>0.0045455</i>
<i>PC16</i>	<i>antenna 2 length</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>2.09415</i>	<i>-0.06906</i>	<i>0.0045455</i>
<i>PC8</i>	<i>antenna 2 length</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>0.18411</i>	<i>-0.07591</i>	<i>0.0045455</i>
<i>BDBM</i>	<i>body shape</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>6.29</i>	<i>0.137</i>	<i>0.0045455</i>
<i>PC16</i>	<i>body shape</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>-6.42637</i>	<i>0.1488</i>	<i>0.0045455</i>
<i>PC8</i>	<i>body shape</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>-0.5253</i>	<i>0.06753</i>	<i>0.0045455</i>
<i>BDBM</i>	<i>eye diameter</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>-0.4154</i>	<i>-0.09141</i>	<i>0.0045455</i>
<i>PC16</i>	<i>eye diameter</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>0.75786</i>	<i>-0.07125</i>	<i>0.0045455</i>
<i>PC8</i>	<i>eye diameter</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>0.05451</i>	<i>-0.08501</i>	<i>0.0045455</i>
<i>BDBM</i>	<i>living habit</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>-3.714</i>	<i>-0.05397</i>	<i>0.0045455</i>
<i>PC16</i>	<i>living habit</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>1.93645</i>	<i>-0.08741</i>	<i>0.0045455</i>
<i>PC8</i>	<i>living habit</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>0.09847</i>	<i>-0.09672</i>	<i>0.0045455</i>
<i>BDBM</i>	<i>max body size</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>-6.376</i>	<i>0.1635</i>	<i>0.0045455</i>
<i>PC16</i>	<i>max body size</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>5.10984</i>	<i>0.07023</i>	<i>0.0045455</i>
<i>PC8</i>	<i>max body size</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>0.4032</i>	<i>0.006777</i>	<i>0.0045455</i>
<i>BDBM</i>	<i>mean body size</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>-2.766</i>	<i>-0.03771</i>	<i>0.0045455</i>
<i>PC16</i>	<i>mean body size</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>1.52946</i>	<i>-0.08084</i>	<i>0.0045455</i>
<i>PC8</i>	<i>mean body size</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>0.09095</i>	<i>-0.09317</i>	<i>0.0045455</i>
<i>BDBM</i>	<i>tube fidelity</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>-11.093</i>	<i>0.1503</i>	<i>0.0045455</i>
<i>PC16</i>	<i>tube fidelity</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>9.1219</i>	<i>0.07026</i>	<i>0.0045455</i>
<i>PC8</i>	<i>tube fidelity</i>	<i>SES_{MPD}</i>	<i>TS</i>	<i>0.7595</i>	<i>0.01892</i>	<i>0.0045455</i>
<i>PC1</i>	<i>all</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>0.1312</i>	<i>0.05105</i>	<i>0.003125</i>

APPENDIX 5

PC2	all	SES _{MPD}	IS	0.2099	-0.05275	0.003125
PC3	all	SES _{MPD}	IS	0.34	0.1527	0.003125
PC4	all	SES _{MPD}	IS	-0.7953	0.03207	0.003125
PC5	all	SES _{MPD}	IS	-0.1668	-0.05508	0.003125
PC6	all	SES _{MPD}	IS	0.2603	0.0386	0.003125
PC7	all	SES _{MPD}	IS	-0.6837	0.05357	0.003125
PC8	all	SES _{MPD}	IS	0.9918	0.1301	0.003125
PC9	all	SES _{MPD}	IS	0.8282	0.1136	0.003125
PC10	all	SES _{MPD}	IS	-1.09532	-0.03804	0.003125
PC11	all	SES _{MPD}	IS	4.5731	0.03375	0.003125
PC12	all	SES _{MPD}	IS	-3.34981	0.1967	0.003125
PC13	all	SES _{MPD}	IS	2.08646	-0.04754	0.003125
PC14	all	SES _{MPD}	IS	-5.1499	0.1827	0.003125
PC15	all	SES _{MPD}	IS	3.93297	-0.05352	0.003125
PC16	all	SES _{MPD}	IS	11.8474	0.2259	0.003125
Anal fin length	all	SES _{MPD}	IS	4.3025	0.1041	0.00263158
BDBM	all	SES _{MPD}	IS	-13.779	0.3382	0.00263158
Body depth	all	SES _{MPD}	IS	4.6609	0.171	0.00263158
Caudal fin length	all	SES _{MPD}	IS	8.5411	0.02312	0.00263158
Caudal peduncle depth	all	SES _{MPD}	IS	0.3385	0.002095	0.00263158
Caudal peduncle length	all	SES _{MPD}	IS	-1.5693	-0.07001	0.00263158
Dorsal fin length	all	SES _{MPD}	IS	2.4794	0.1245	0.00263158
Eye diameter	all	SES _{MPD}	IS	4.7839	0.05387	0.00263158
Eye position	all	SES _{MPD}	IS	4.602	-0.02025	0.00263158
Head depth	all	SES _{MPD}	IS	-6.152	0.19	0.00263158
Head length	all	SES _{MPD}	IS	4.327	-0.01447	0.00263158
Mouth height	all	SES _{MPD}	IS	6.1171	0.05055	0.00263158
Mouth protrusion	all	SES _{MPD}	IS	3.466	-0.03238	0.00263158
Pectoral fin length	all	SES _{MPD}	IS	6.8813	0.1683	0.00263158
Standard length	all	SES _{MPD}	IS	0.0007999	-0.09923	0.00263158
Snout length	all	SES _{MPD}	IS	-3.188	-0.04901	0.00263158
Trophic level	all	SES _{MPD}	IS	0.04308	-0.09987	0.00263158
Foraging mode	all	SES _{MPD}	IS	-1.0744	0.1103	0.00263158

APPENDIX 5

Vertical position	all	SES _{MPD}	IS	0.12334	-0.09193	0.00263158
PC1	phylogeny	SES _{MPD}	IS	0.1347	0.1092	0.003125
PC2	phylogeny	SES _{MPD}	IS	0.2708	0.003273	0.003125
PC3	phylogeny	SES _{MPD}	IS	0.3124	0.1801	0.003125
PC4	phylogeny	SES _{MPD}	IS	-0.5609	-0.01375	0.003125
PC5	phylogeny	SES _{MPD}	IS	-0.07359	-0.08852	0.003125
PC6	phylogeny	SES _{MPD}	IS	0.245	0.06123	0.003125
PC7	phylogeny	SES _{MPD}	IS	-0.7439	0.1387	0.003125
PC8	phylogeny	SES _{MPD}	IS	0.8693	0.1321	0.003125
PC9	phylogeny	SES _{MPD}	IS	0.6145	0.05441	0.003125
PC10	phylogeny	SES _{MPD}	IS	-0.61088	-0.0747	0.003125
PC11	phylogeny	SES _{MPD}	IS	2.6675	-0.04025	0.003125
PC12	phylogeny	SES _{MPD}	IS	-2.55808	0.1272	0.003125
PC13	phylogeny	SES _{MPD}	IS	1.98236	-0.03782	0.003125
PC14	phylogeny	SES _{MPD}	IS	-3.8007	0.1022	0.003125
PC15	phylogeny	SES _{MPD}	IS	3.73891	-0.04485	0.003125
PC16	phylogeny	SES _{MPD}	IS	10.4749	0.2345	0.003125
Anal fin length	phylogeny	SES _{MPD}	IS	3.8571	0.1154	0.00263158
BDBM	phylogeny	SES _{MPD}	IS	-12.012	0.3373	0.00263158
Body depth	phylogeny	SES _{MPD}	IS	4.6634	0.2562	0.00263158
Caudal fin length	phylogeny	SES _{MPD}	IS	9.0636	0.08204	0.00263158
Caudal peduncle depth	phylogeny	SES _{MPD}	IS	0.388	0.07606	0.00263158
Caudal peduncle length	phylogeny	SES _{MPD}	IS	-1.7504	-0.05101	0.00263158
Dorsal fin length	phylogeny	SES _{MPD}	IS	2.0368	0.09897	0.00263158
Eye diameter	phylogeny	SES _{MPD}	IS	5.085	0.1283	0.00263158
Eye position	phylogeny	SES _{MPD}	IS	2.932	-0.05749	0.00263158
Head depth	phylogeny	SES _{MPD}	IS	-5.645	0.2206	0.00263158
Head length	phylogeny	SES _{MPD}	IS	4.98	0.04873	0.00263158
Mouth height	phylogeny	SES _{MPD}	IS	5.7597	0.07526	0.00263158
Mouth protrusion	phylogeny	SES _{MPD}	IS	3.272	-0.02085	0.00263158
Pectoral fin length	phylogeny	SES _{MPD}	IS	6.7875	0.2427	0.00263158
Standard length	phylogeny	SES _{MPD}	IS	-	-0.09606	0.00263158
Snout length	phylogeny	SES _{MPD}	IS	-3.197	-0.03268	0.00263158

APPENDIX 5

Trophic level	phylogeny	SES _{MPD}	IS	-0.1808	-0.09704	0.00263158
Foraging mode	phylogeny	SES _{MPD}	IS	-0.7833	0.0468	0.00263158
Vertical position	phylogeny	SES _{MPD}	IS	0.245	-0.05821	0.00263158
<i>BDBM</i>	<i>activity level (% still)</i>	<i>SES_{MPD}</i>	<i>IS</i>	-18.077	0.5759	0.0045455
<i>PC16</i>	<i>activity level (% still)</i>	<i>SES_{MPD}</i>	<i>IS</i>	17.8945	0.5662	0.0045455
<i>PC8</i>	<i>activity level (% still)</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>1.5369</i>	<i>0.3951</i>	<i>0.0045455</i>
<i>BDBM</i>	<i>activity level (% swimming)</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>-11.559</i>	<i>0.1032</i>	<i>0.0045455</i>
<i>PC16</i>	<i>activity level (% swimming)</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>10.6291</i>	<i>0.07286</i>	<i>0.0045455</i>
<i>PC8</i>	<i>activity level (% swimming)</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>0.9597</i>	<i>0.04197</i>	<i>0.0045455</i>
<i>BDBM</i>	<i>activity level (% walking)</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>-10.427</i>	<i>0.1532</i>	<i>0.0045455</i>
<i>PC16</i>	<i>activity level (% walking)</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>9.4573</i>	<i>0.1095</i>	<i>0.0045455</i>
<i>PC8</i>	<i>activity level (% walking)</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>0.8446</i>	<i>0.06836</i>	<i>0.0045455</i>
<i>BDBM</i>	<i>antenna 1 length</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>-14.464</i>	<i>0.4704</i>	<i>0.0045455</i>
<i>PC16</i>	<i>antenna 1 length</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>13.4336</i>	<i>0.395</i>	<i>0.0045455</i>
<i>PC8</i>	<i>antenna 1 length</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>1.1297</i>	<i>0.2527</i>	<i>0.0045455</i>
<i>BDBM</i>	<i>antenna 2 length</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>-7.51</i>	<i>0.08254</i>	<i>0.0045455</i>
<i>PC16</i>	<i>antenna 2 length</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>5.41524</i>	<i>-0.004533</i>	<i>0.0045455</i>
<i>PC8</i>	<i>antenna 2 length</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>0.4407</i>	<i>-0.03628</i>	<i>0.0045455</i>
<i>BDBM</i>	<i>body shape</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>2.328</i>	<i>-0.08247</i>	<i>0.0045455</i>
<i>PC16</i>	<i>body shape</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>-5.1407</i>	<i>-0.014</i>	<i>0.0045455</i>
<i>PC8</i>	<i>body shape</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>-0.4629</i>	<i>-0.02973</i>	<i>0.0045455</i>
<i>BDBM</i>	<i>eye diameter</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>-10.391</i>	<i>0.1864</i>	<i>0.0045455</i>
<i>PC16</i>	<i>eye diameter</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>8.836</i>	<i>0.1084</i>	<i>0.0045455</i>
<i>PC8</i>	<i>eye diameter</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>0.6975</i>	<i>0.03081</i>	<i>0.0045455</i>
<i>BDBM</i>	<i>living habit</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>-7.53</i>	<i>0.04946</i>	<i>0.0045455</i>
<i>PC16</i>	<i>living habit</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>5.137</i>	<i>-0.03002</i>	<i>0.0045455</i>
<i>PC8</i>	<i>living habit</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>0.3726</i>	<i>-0.0629</i>	<i>0.0045455</i>
<i>BDBM</i>	<i>max body size</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>-8.346</i>	<i>0.112</i>	<i>0.0045455</i>
<i>PC16</i>	<i>max body size</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>6.20164</i>	<i>0.01777</i>	<i>0.0045455</i>
<i>PC8</i>	<i>max body size</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>0.4755</i>	<i>-0.03024</i>	<i>0.0045455</i>

APPENDIX 5

<i>BDBM</i>	<i>mean body size</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>-5.872</i>	<i>0.02926</i>	<i>0.0045455</i>
<i>PC16</i>	<i>mean body size</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>4.06398</i>	<i>-0.03771</i>	<i>0.0045455</i>
<i>PC8</i>	<i>mean body size</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>0.29273</i>	<i>-0.06744</i>	<i>0.0045455</i>
<i>BDBM</i>	<i>tube fidelity</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>-10.087</i>	<i>0.1548</i>	<i>0.0045455</i>
<i>PC16</i>	<i>tube fidelity</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>8.1603</i>	<i>0.06775</i>	<i>0.0045455</i>
<i>PC8</i>	<i>tube fidelity</i>	<i>SES_{MPD}</i>	<i>IS</i>	<i>0.6825</i>	<i>0.01822</i>	<i>0.0045455</i>

Table A5.2. Effect sizes of fish community trait dispersion on residual peracarid community trait and phylogenetic dispersion, not accounting for the effects of habitat filters on fish dispersion. Bolded cells indicate values significant at $\alpha = 0.008333$; the first 24 rows are effects for which results are presented in the main text. Rows are colored according to the direction and magnitude of the effect size; red indicates a negative effect while blue indicates a positive effect, and color saturation is proportional to R^2 . TS = Tip Shuffle algorithm, IS = Independent Swap algorithm; BDBM = Body Depth Below Midline.

Predictor trait	Predictor metric	Predictor algorithm	Response trait	Response metric	Response algorithm	Effect size	R^2
all	SES _{MNTD}	TS	activity level (% still)	SES _{MNTD}	TS	0.1302	-0.01212
BDBM	SES _{MNTD}	TS	activity level (% still)	SES _{MNTD}	TS	-0.2055	0.1616
PC16	SES _{MNTD}	TS	activity level (% still)	SES _{MNTD}	TS	-0.07272	-0.09093
PC8	SES _{MNTD}	TS	activity level (% still)	SES _{MNTD}	TS	-0.13771	0.06993
all	SES _{MNTD}	TS	all	SES _{MNTD}	TS	0.13797	-0.03364
BDBM	SES _{MNTD}	TS	all	SES _{MNTD}	TS	-0.3945	0.5485
PC16	SES _{MNTD}	TS	all	SES _{MNTD}	TS	0.09154	-0.09034
PC8	SES _{MNTD}	TS	all	SES _{MNTD}	TS	-0.24802	0.2707
all	SES _{MNTD}	TS	antenna 1 length	SES _{MNTD}	TS	0.17849	0.059
BDBM	SES _{MNTD}	TS	antenna 1 length	SES _{MNTD}	TS	-0.30197	0.4439
PC16	SES _{MNTD}	TS	antenna 1 length	SES _{MNTD}	TS	-0.08891	-0.08695
PC8	SES _{MNTD}	TS	antenna 1 length	SES _{MNTD}	TS	-0.16647	0.1391
all	SES _{MNTD}	TS	antenna 2 length	SES _{MNTD}	TS	-0.010598	-0.08479

APPENDIX 5

BDBM	SES _{MNTD}	TS	antenna 2 length	SES _{MNTD}	TS	0.047625	0.2671
PC16	SES _{MNTD}	TS	antenna 2 length	SES _{MNTD}	TS	-0.02119	-0.07988
PC8	SES _{MNTD}	TS	antenna 2 length	SES _{MNTD}	TS	0.029647	0.1058
all	SES _{MNTD}	TS	max. body size	SES _{MNTD}	TS	0.13862	0.0138
BDBM	SES _{MNTD}	TS	max. body size	SES _{MNTD}	TS	-0.28207	0.4631
PC16	SES _{MNTD}	TS	max. body size	SES _{MNTD}	TS	0.03453	-0.09766
PC8	SES _{MNTD}	TS	max. body size	SES _{MNTD}	TS	-0.20856	0.3453
all	SES _{MNTD}	TS	phylogeny	SES _{MNTD}	TS	0.22165	0.003042
BDBM	SES _{MNTD}	TS	phylogeny	SES _{MNTD}	TS	-0.5742	0.7263
PC16	SES _{MNTD}	TS	phylogeny	SES _{MNTD}	TS	0.1332	-0.08769
PC8	SES _{MNTD}	TS	phylogeny	SES _{MNTD}	TS	-0.39414	0.4632
all	SES _{MNTD}	TS	activity level (% still)	SES _{MNTD}	IS	0.18328	-0.04017
BDBM	SES _{MNTD}	TS	activity level (% still)	SES _{MNTD}	IS	-0.23325	0.01581
PC16	SES _{MNTD}	TS	activity level (% still)	SES _{MNTD}	IS	-0.178	-0.08133
PC8	SES _{MNTD}	TS	activity level (% still)	SES _{MNTD}	IS	-0.15043	-0.03033
all	SES _{MNTD}	TS	all	SES _{MNTD}	IS	0.11902	-0.06727
BDBM	SES _{MNTD}	TS	all	SES _{MNTD}	IS	-0.43018	0.4109
PC16	SES _{MNTD}	TS	all	SES _{MNTD}	IS	0.1613	-0.08012
PC8	SES _{MNTD}	TS	all	SES _{MNTD}	IS	-0.27484	0.2017
all	SES _{MNTD}	TS	antenna 1 length	SES _{MNTD}	IS	0.21427	0.06424
BDBM	SES _{MNTD}	TS	antenna 1 length	SES _{MNTD}	IS	-0.34608	0.412
PC16	SES _{MNTD}	TS	antenna 1 length	SES _{MNTD}	IS	-0.11917	-0.08319
PC8	SES _{MNTD}	TS	antenna 1 length	SES _{MNTD}	IS	-0.19037	0.1241
all	SES _{MNTD}	TS	antenna 2 length	SES _{MNTD}	IS	-0.023894	0.686
BDBM	SES _{MNTD}	TS	antenna 2 length	SES _{MNTD}	IS	0.08781	0.2033
PC16	SES _{MNTD}	TS	antenna 2 length	SES _{MNTD}	IS	-0.01991	-0.09568
PC8	SES _{MNTD}	TS	antenna 2 length	SES _{MNTD}	IS	0.050719	0.04635
all	SES _{MNTD}	TS	max. body size	SES _{MNTD}	IS	0.17243	-0.01043

APPENDIX 5

BDBM	SES _{MNTD}	TS	max. body size	SES _{MNTD}	IS	-0.37488	0.406
PC16	SES _{MNTD}	TS	max. body size	SES _{MNTD}	IS	0.08646	-0.09255
PC8	SES _{MNTD}	TS	max. body size	SES _{MNTD}	IS	-0.29047	0.3394
all	SES _{MNTD}	TS	phylogeny	SES _{MNTD}	IS	0.18771	-0.00787
BDBM	SES _{MNTD}	TS	phylogeny	SES _{MNTD}	IS	-0.51094	0.7157
PC16	SES _{MNTD}	TS	phylogeny	SES _{MNTD}	IS	0.1362	-0.08396
PC8	SES _{MNTD}	TS	phylogeny	SES _{MNTD}	IS	-0.3461	0.4414
all	SES _{MNTD}	TS	activity level (% still)	SES _{MPD}	TS	0.15091	-0.006004
BDBM	SES _{MNTD}	TS	activity level (% still)	SES _{MPD}	TS	-0.33869	0.4658
PC16	SES _{MNTD}	TS	activity level (% still)	SES _{MPD}	TS	-0.01331	-0.09976
PC8	SES _{MNTD}	TS	activity level (% still)	SES _{MPD}	TS	-0.20024	0.1861
all	SES _{MNTD}	TS	all	SES _{MPD}	TS	0.20343	0.03646
BDBM	SES _{MNTD}	TS	all	SES _{MPD}	TS	-0.38374	0.4803
PC16	SES _{MNTD}	TS	all	SES _{MPD}	TS	-0.06502	-0.09539
PC8	SES _{MNTD}	TS	all	SES _{MPD}	TS	-0.2103	0.1521
all	SES _{MNTD}	TS	antenna 1 length	SES _{MPD}	TS	0.19853	0.00935
BDBM	SES _{MNTD}	TS	antenna 1 length	SES _{MPD}	TS	-0.4511	0.5746
PC16	SES _{MNTD}	TS	antenna 1 length	SES _{MPD}	TS	0.007573	-0.09995
PC8	SES _{MNTD}	TS	antenna 1 length	SES _{MPD}	TS	-0.27583	0.2648
all	SES _{MNTD}	TS	antenna 2 length	SES _{MPD}	TS	-0.030261	-0.09386
BDBM	SES _{MNTD}	TS	antenna 2 length	SES _{MPD}	TS	-0.059989	-0.07119
PC16	SES _{MNTD}	TS	antenna 2 length	SES _{MPD}	TS	0.10682	-0.07471
PC8	SES _{MNTD}	TS	antenna 2 length	SES _{MPD}	TS	-0.029769	-0.08974
all	SES _{MNTD}	TS	max. body size	SES _{MPD}	TS	0.11042	-0.02451
BDBM	SES _{MNTD}	TS	max. body size	SES _{MPD}	TS	-0.23592	0.3118
PC16	SES _{MNTD}	TS	max. body size	SES _{MPD}	TS	0.06831	-0.09044
PC8	SES _{MNTD}	TS	max. body size	SES _{MPD}	TS	-0.17195	0.2165
all	SES _{MNTD}	TS	phylogeny	SES _{MPD}	TS	0.1192	-0.07337
BDBM	SES _{MNTD}	TS	phylogeny	SES _{MPD}	TS	-0.46549	0.3855

APPENDIX 5

PC16	SES _{MNTD}	TS	phylogeny	SES _{MPD}	TS	0.189	-0.07784
PC8	SES _{MNTD}	TS	phylogeny	SES _{MPD}	TS	-0.30306	0.1977
all	SES _{MNTD}	TS	activity level (% still)	SES _{MPD}	IS	0.24903	0.02255
BDBM	SES _{MNTD}	TS	activity level (% still)	SES _{MPD}	IS	-0.56827	0.6626
PC16	SES _{MNTD}	TS	activity level (% still)	SES _{MPD}	IS	0.0647	-0.09726
PC8	SES _{MNTD}	TS	activity level (% still)	SES _{MPD}	IS	-0.35456	0.3294
all	SES _{MNTD}	TS	all	SES _{MPD}	IS	0.22319	0.009846
BDBM	SES _{MNTD}	TS	all	SES _{MPD}	IS	-0.46525	0.4704
PC16	SES _{MNTD}	TS	all	SES _{MPD}	IS	0.04955	-0.09821
PC8	SES _{MNTD}	TS	all	SES _{MPD}	IS	-0.29018	0.2209
all	SES _{MNTD}	TS	antenna 1 length	SES _{MPD}	IS	0.21298	0.01816
BDBM	SES _{MNTD}	TS	antenna 1 length	SES _{MPD}	IS	-0.47811	0.6116
PC16	SES _{MNTD}	TS	antenna 1 length	SES _{MPD}	IS	0.08451	-0.09385
PC8	SES _{MNTD}	TS	antenna 1 length	SES _{MPD}	IS	-0.31398	0.3439
all	SES _{MNTD}	TS	antenna 2 length	SES _{MPD}	IS	0.038464	-0.09543
BDBM	SES _{MNTD}	TS	antenna 2 length	SES _{MPD}	IS	-0.23202	0.0989
PC16	SES _{MNTD}	TS	antenna 2 length	SES _{MPD}	IS	0.1815	-0.06629
PC8	SES _{MNTD}	TS	antenna 2 length	SES _{MPD}	IS	-0.15222	0.02383
all	SES _{MNTD}	TS	max. body size	SES _{MPD}	IS	0.13779	-0.04479
BDBM	SES _{MNTD}	TS	max. body size	SES _{MPD}	IS	-0.31445	0.2436
PC16	SES _{MNTD}	TS	max. body size	SES _{MPD}	IS	0.1236	-0.08531
PC8	SES _{MNTD}	TS	max. body size	SES _{MPD}	IS	-0.23535	0.1784
all	SES _{MNTD}	TS	phylogeny	SES _{MPD}	IS	0.12528	-0.05456
BDBM	SES _{MNTD}	TS	phylogeny	SES _{MPD}	IS	-0.38672	0.4175
PC16	SES _{MNTD}	TS	phylogeny	SES _{MPD}	IS	0.1758	-0.0704
PC8	SES _{MNTD}	TS	phylogeny	SES _{MPD}	IS	-0.26378	0.2482
all	SES _{MNTD}	IS	activity level (% still)	SES _{MNTD}	TS	0.12006	0.01551
BDBM	SES _{MNTD}	IS	activity level (% still)	SES _{MNTD}	TS	-0.3024	0.2628
PC16	SES _{MNTD}	IS	activity level (% still)	SES _{MNTD}	TS	-0.013916	-0.09959

APPENDIX 5

PC8	SES _{MNTD}	IS	activity level (% still)	SES _{MNTD}	TS	-0.199	0.09933
all	SES _{MNTD}	IS	all	SES _{MNTD}	TS	0.16135	0.04027
BDBM	SES _{MNTD}	IS	all	SES _{MNTD}	TS	-0.49631	0.5574
PC16	SES _{MNTD}	IS	all	SES _{MNTD}	TS	0.2819	0.01272
PC8	SES _{MNTD}	IS	all	SES _{MNTD}	TS	-0.29346	0.1915
all	SES _{MNTD}	IS	antenna 1 length	SES _{MNTD}	TS	0.17363	0.1326
BDBM	SES _{MNTD}	IS	antenna 1 length	SES _{MNTD}	TS	-0.38078	0.454
PC16	SES _{MNTD}	IS	antenna 1 length	SES _{MNTD}	TS	0.1119	-0.07458
PC8	SES _{MNTD}	IS	antenna 1 length	SES _{MNTD}	TS	-0.20403	0.1017
all	SES _{MNTD}	IS	antenna 2 length	SES _{MNTD}	TS	-0.015273	-0.05117
BDBM	SES _{MNTD}	IS	antenna 2 length	SES _{MNTD}	TS	0.059638	0.2688
PC16	SES _{MNTD}	IS	antenna 2 length	SES _{MNTD}	TS	-0.04693	0.02137
PC8	SES _{MNTD}	IS	antenna 2 length	SES _{MNTD}	TS	0.032959	0.04284
all	SES _{MNTD}	IS	max. body size	SES _{MNTD}	TS	0.14296	0.08709
BDBM	SES _{MNTD}	IS	max. body size	SES _{MNTD}	TS	-0.36485	0.5036
PC16	SES _{MNTD}	IS	max. body size	SES _{MNTD}	TS	0.05677	-0.09223
PC8	SES _{MNTD}	IS	max. body size	SES _{MNTD}	TS	-0.2825	0.3589
all	SES _{MNTD}	IS	phylogeny	SES _{MNTD}	TS	0.24844	0.1001
BDBM	SES _{MNTD}	IS	phylogeny	SES _{MNTD}	TS	-0.7385	0.7757
PC16	SES _{MNTD}	IS	phylogeny	SES _{MNTD}	TS	0.2965	-0.02499
PC8	SES _{MNTD}	IS	phylogeny	SES _{MNTD}	TS	-0.49931	0.4077
all	SES _{MNTD}	IS	activity level (% still)	SES _{MNTD}	IS	0.15697	-0.03216
BDBM	SES _{MNTD}	IS	activity level (% still)	SES _{MNTD}	IS	-0.37822	0.09508
PC16	SES _{MNTD}	IS	activity level (% still)	SES _{MNTD}	IS	-0.09835	-0.09299
PC8	SES _{MNTD}	IS	activity level (% still)	SES _{MNTD}	IS	-0.23597	-0.003703
all	SES _{MNTD}	IS	all	SES _{MNTD}	IS	0.15432	-0.01495
BDBM	SES _{MNTD}	IS	all	SES _{MNTD}	IS	-0.5393	0.4145
PC16	SES _{MNTD}	IS	all	SES _{MNTD}	IS	0.3636	0.02425
PC8	SES _{MNTD}	IS	all	SES _{MNTD}	IS	-0.31799	0.1268
all	SES _{MNTD}	IS	antenna 1 length	SES _{MNTD}	IS	0.20575	0.1341

APPENDIX 5

BDBM	SES _{MNTD}	IS	antenna 1 length	SES _{MNTD}	IS	-0.43648	0.4218
PC16	SES _{MNTD}	IS	antenna 1 length	SES _{MNTD}	IS	0.1094	-0.08258
PC8	SES _{MNTD}	IS	antenna 1 length	SES _{MNTD}	IS	-0.23605	0.09354
all	SES _{MNTD}	IS	antenna 2 length	SES _{MNTD}	IS	-0.030193	-0.05362
BDBM	SES _{MNTD}	IS	antenna 2 length	SES _{MNTD}	IS	0.11801	0.2509
PC16	SES _{MNTD}	IS	antenna 2 length	SES _{MNTD}	IS	-0.08006	-0.01418
PC8	SES _{MNTD}	IS	antenna 2 length	SES _{MNTD}	IS	0.057143	0.004347
all	SES _{MNTD}	IS	max. body size	SES _{MNTD}	IS	0.1823	0.05477
BDBM	SES _{MNTD}	IS	max. body size	SES _{MNTD}	IS	-0.4832	0.4386
PC16	SES _{MNTD}	IS	max. body size	SES _{MNTD}	IS	0.07557	-0.093
PC8	SES _{MNTD}	IS	max. body size	SES _{MNTD}	IS	-0.39588	0.3584
all	SES _{MNTD}	IS	phylogeny	SES _{MNTD}	IS	0.21551	0.0877
BDBM	SES _{MNTD}	IS	phylogeny	SES _{MNTD}	IS	-0.64641	0.7364
PC16	SES _{MNTD}	IS	phylogeny	SES _{MNTD}	IS	0.2984	-0.005307
PC8	SES _{MNTD}	IS	phylogeny	SES _{MNTD}	IS	-0.4298	0.3689
all	SES _{MNTD}	IS	activity level (% still)	SES _{MPD}	TS	0.15812	0.05951
BDBM	SES _{MNTD}	IS	activity level (% still)	SES _{MPD}	TS	-0.4502	0.5404
PC16	SES _{MNTD}	IS	activity level (% still)	SES _{MPD}	TS	0.1851	-0.0425
PC8	SES _{MNTD}	IS	activity level (% still)	SES _{MPD}	TS	-0.24541	0.1414
all	SES _{MNTD}	IS	all	SES _{MPD}	TS	0.20574	0.1158
BDBM	SES _{MNTD}	IS	all	SES _{MPD}	TS	-0.47088	0.4598
PC16	SES _{MNTD}	IS	all	SES _{MPD}	TS	0.1998	-0.04647
PC8	SES _{MNTD}	IS	all	SES _{MPD}	TS	-0.24609	0.0939
all	SES _{MNTD}	IS	antenna 1 length	SES _{MPD}	TS	0.21032	0.08968
BDBM	SES _{MNTD}	IS	antenna 1 length	SES _{MPD}	TS	-0.58901	0.6369
PC16	SES _{MNTD}	IS	antenna 1 length	SES _{MPD}	TS	0.2411	-0.03438
PC8	SES _{MNTD}	IS	antenna 1 length	SES _{MPD}	TS	-0.33989	0.2112
all	SES _{MNTD}	IS	antenna 2 length	SES _{MPD}	TS	-0.008941	-0.09917

APPENDIX 5

BDBM	SES _{MNTD}	IS	antenna 2 length	SES _{MPD}	TS	-0.053199	-0.08548
PC16	SES _{MNTD}	IS	antenna 2 length	SES _{MPD}	TS	0.1747	-0.01679
PC8	SES _{MNTD}	IS	antenna 2 length	SES _{MPD}	TS	-0.0079275	-0.09959
all	SES _{MNTD}	IS	max. body size	SES _{MPD}	TS	0.12066	0.03933
BDBM	SES _{MNTD}	IS	max. body size	SES _{MPD}	TS	-0.26045	0.2216
PC16	SES _{MNTD}	IS	max. body size	SES _{MPD}	TS	0.09129	-0.07901
PC8	SES _{MNTD}	IS	max. body size	SES _{MPD}	TS	-0.21713	0.1834
all	SES _{MNTD}	IS	phylogeny	SES _{MPD}	TS	0.15893	-0.02679
BDBM	SES _{MNTD}	IS	phylogeny	SES _{MPD}	TS	-0.59703	0.4117
PC16	SES _{MNTD}	IS	phylogeny	SES _{MPD}	TS	0.3938	0.01829
PC8	SES _{MNTD}	IS	phylogeny	SES _{MPD}	TS	-0.3555	0.1301
all	SES _{MNTD}	IS	activity level (% still)	SES _{MPD}	IS	0.27083	0.124
BDBM	SES _{MNTD}	IS	activity level (% still)	SES _{MPD}	IS	-0.68456	0.609
PC16	SES _{MNTD}	IS	activity level (% still)	SES _{MPD}	IS	0.3288	-0.01309
PC8	SES _{MNTD}	IS	activity level (% still)	SES _{MPD}	IS	-0.42436	0.2455
all	SES _{MNTD}	IS	all	SES _{MPD}	IS	0.23963	0.09572
BDBM	SES _{MNTD}	IS	all	SES _{MPD}	IS	-0.5208	0.3579
PC16	SES _{MNTD}	IS	all	SES _{MPD}	IS	0.2554	-0.04147
PC8	SES _{MNTD}	IS	all	SES _{MPD}	IS	-0.34169	0.15
all	SES _{MNTD}	IS	antenna 1 length	SES _{MPD}	IS	0.2327	0.118
BDBM	SES _{MNTD}	IS	antenna 1 length	SES _{MPD}	IS	-0.55807	0.5211
PC16	SES _{MNTD}	IS	antenna 1 length	SES _{MPD}	IS	0.2518	-0.03281
PC8	SES _{MNTD}	IS	antenna 1 length	SES _{MPD}	IS	-0.38184	0.2688
all	SES _{MNTD}	IS	antenna 2 length	SES _{MPD}	IS	0.07208	-0.07517
BDBM	SES _{MNTD}	IS	antenna 2 length	SES _{MPD}	IS	-0.23115	0.02647
PC16	SES _{MNTD}	IS	antenna 2 length	SES _{MPD}	IS	0.278	-0.002797
PC8	SES _{MNTD}	IS	antenna 2 length	SES _{MPD}	IS	-0.15378	-0.02901
all	SES _{MNTD}	IS	max. body size	SES _{MPD}	IS	0.15557	0.00879

APPENDIX 5

BDBM	SES _{MNTD}	IS	max. body size	SES _{MPD}	IS	-0.33702	0.1529
PC16	SES _{MNTD}	IS	max. body size	SES _{MPD}	IS	0.1355	-0.07828
PC8	SES _{MNTD}	IS	max. body size	SES _{MPD}	IS	-0.29496	0.1457
all	SES _{MNTD}	IS	phylogeny	SES _{MPD}	IS	0.15761	0.01117
BDBM	SES _{MNTD}	IS	phylogeny	SES _{MPD}	IS	-0.43416	0.3178
PC16	SES _{MNTD}	IS	phylogeny	SES _{MPD}	IS	0.2909	-0.0003524
PC8	SES _{MNTD}	IS	phylogeny	SES _{MPD}	IS	-0.30763	0.166
all	SES _{MPD}	TS	activity level (% still)	SES _{MNTD}	TS	0.033014	-0.0895
BDBM	SES _{MPD}	TS	activity level (% still)	SES _{MNTD}	TS	-0.26964	0.2573
PC16	SES _{MPD}	TS	activity level (% still)	SES _{MNTD}	TS	-0.09467	-0.04211
PC8	SES _{MPD}	TS	activity level (% still)	SES _{MNTD}	TS	-0.2855	0.1996
all	SES _{MPD}	TS	all	SES _{MNTD}	TS	0.013132	-0.09888
BDBM	SES _{MPD}	TS	all	SES _{MNTD}	TS	-0.3601	0.3285
PC16	SES _{MPD}	TS	all	SES _{MNTD}	TS	-0.14598	-0.007435
PC8	SES _{MPD}	TS	all	SES _{MNTD}	TS	-0.3422	0.1895
all	SES _{MPD}	TS	antenna 1 length	SES _{MNTD}	TS	0.029034	-0.09218
BDBM	SES _{MPD}	TS	antenna 1 length	SES _{MNTD}	TS	-0.30374	0.3364
PC16	SES _{MPD}	TS	antenna 1 length	SES _{MNTD}	TS	-0.14081	0.0233
PC8	SES _{MPD}	TS	antenna 1 length	SES _{MNTD}	TS	-0.3108	0.242
all	SES _{MPD}	TS	antenna 2 length	SES _{MNTD}	TS	0.001044	-0.09973
BDBM	SES _{MPD}	TS	antenna 2 length	SES _{MNTD}	TS	0.04179	0.1242
PC16	SES _{MPD}	TS	antenna 2 length	SES _{MNTD}	TS	0.015735	-0.05822
PC8	SES _{MPD}	TS	antenna 2 length	SES _{MNTD}	TS	0.03394	0.01065
all	SES _{MPD}	TS	max. body size	SES _{MNTD}	TS	0.040296	-0.08213
BDBM	SES _{MPD}	TS	max. body size	SES _{MNTD}	TS	-0.26935	0.3072
PC16	SES _{MPD}	TS	max. body size	SES _{MNTD}	TS	-0.1101	-0.01051
PC8	SES _{MPD}	TS	max. body size	SES _{MNTD}	TS	-0.3405	0.3869
all	SES _{MPD}	TS	phylogeny	SES _{MNTD}	TS	0.04277	-0.09287

APPENDIX 5

BDBM	SES _{MPD}	TS	phylogeny	SES _{MNTD}	TS	-0.5411	0.482
PC16	SES _{MPD}	TS	phylogeny	SES _{MNTD}	TS	-0.21187	0.01731
PC8	SES _{MPD}	TS	phylogeny	SES _{MNTD}	TS	-0.5795	0.3994
all	SES _{MPD}	TS	activity level (% still)	SES _{MNTD}	IS	0.9565	0.029
BDBM	SES _{MPD}	TS	activity level (% still)	SES _{MNTD}	IS	-0.6395	0.8058
PC16	SES _{MPD}	TS	activity level (% still)	SES _{MNTD}	IS	-1.083	0.6788
PC8	SES _{MPD}	TS	activity level (% still)	SES _{MNTD}	IS	-0.6478	0.523
all	SES _{MPD}	TS	all	SES _{MNTD}	IS	0.003516	-0.09995
BDBM	SES _{MPD}	TS	all	SES _{MNTD}	IS	-0.38064	0.2173
PC16	SES _{MPD}	TS	all	SES _{MNTD}	IS	-0.14793	-0.037
PC8	SES _{MPD}	TS	all	SES _{MNTD}	IS	-0.343	0.09281
all	SES _{MPD}	TS	antenna 1 length	SES _{MNTD}	IS	0.037087	-0.09086
BDBM	SES _{MPD}	TS	antenna 1 length	SES _{MNTD}	IS	-0.3506	0.3168
PC16	SES _{MPD}	TS	antenna 1 length	SES _{MNTD}	IS	-0.1646	0.02076
PC8	SES _{MPD}	TS	antenna 1 length	SES _{MNTD}	IS	-0.3666	0.2409
all	SES _{MPD}	TS	antenna 2 length	SES _{MNTD}	IS	0.0023632	-0.09966
BDBM	SES _{MPD}	TS	antenna 2 length	SES _{MNTD}	IS	0.09311	0.1705
PC16	SES _{MPD}	TS	antenna 2 length	SES _{MNTD}	IS	0.03172	-0.05874
PC8	SES _{MPD}	TS	antenna 2 length	SES _{MNTD}	IS	0.06735	0.005886
all	SES _{MPD}	TS	max. body size	SES _{MNTD}	IS	0.05506	-0.08302
BDBM	SES _{MPD}	TS	max. body size	SES _{MNTD}	IS	-0.34674	0.2433
PC16	SES _{MPD}	TS	max. body size	SES _{MNTD}	IS	-0.13929	-0.02717
PC8	SES _{MPD}	TS	max. body size	SES _{MNTD}	IS	-0.457	0.3463
all	SES _{MPD}	TS	phylogeny	SES _{MNTD}	IS	0.032402	-0.0949
BDBM	SES _{MPD}	TS	phylogeny	SES _{MNTD}	IS	-0.4636	0.4326
PC16	SES _{MPD}	TS	phylogeny	SES _{MNTD}	IS	-0.18612	0.01285
PC8	SES _{MPD}	TS	phylogeny	SES _{MNTD}	IS	-0.4911	0.3472
all	SES _{MPD}	TS	activity level (% still)	SES _{MPD}	TS	0.01758	-0.09763
BDBM	SES _{MPD}	TS	activity level (% still)	SES _{MPD}	TS	-0.36203	0.4128

APPENDIX 5

PC16	SES _{MPD}	TS	activity level (% still)	SES _{MPD}	TS	-0.1399	0.000615 2
PC8	SES _{MPD}	TS	activity level (% still)	SES _{MPD}	TS	-0.3286	0.216
all	SES _{MPD}	TS	all	SES _{MPD}	TS	0.027224	-0.09546
BDBM	SES _{MPD}	TS	all	SES _{MPD}	TS	-0.3597	0.3045
PC16	SES _{MPD}	TS	all	SES _{MPD}	TS	-0.17114	0.02035
PC8	SES _{MPD}	TS	all	SES _{MPD}	TS	-0.3582	0.2001
all	SES _{MPD}	TS	antenna 1 length	SES _{MPD}	TS	0.027213	-0.09618
BDBM	SES _{MPD}	TS	antenna 1 length	SES _{MPD}	TS	-0.4601	0.4566
PC16	SES _{MPD}	TS	antenna 1 length	SES _{MPD}	TS	-0.18283	0.01555
PC8	SES _{MPD}	TS	antenna 1 length	SES _{MPD}	TS	-0.4406	0.2819
all	SES _{MPD}	TS	antenna 2 length	SES _{MPD}	TS	-0.021943	-0.094
BDBM	SES _{MPD}	TS	antenna 2 length	SES _{MPD}	TS	-0.009834	-0.09939
PC16	SES _{MPD}	TS	antenna 2 length	SES _{MPD}	TS	-0.006666	-0.09963
PC8	SES _{MPD}	TS	antenna 2 length	SES _{MPD}	TS	0.03169	-0.09523
all	SES _{MPD}	TS	max. body size	SES _{MPD}	TS	0.032259	-0.08803
BDBM	SES _{MPD}	TS	max. body size	SES _{MPD}	TS	-0.15096	0.03375
PC16	SES _{MPD}	TS	max. body size	SES _{MPD}	TS	-0.08894	-0.03897
PC8	SES _{MPD}	TS	max. body size	SES _{MPD}	TS	-0.2445	0.1625
all	SES _{MPD}	TS	phylogeny	SES _{MPD}	TS	0.001917	-0.09999
BDBM	SES _{MPD}	TS	phylogeny	SES _{MPD}	TS	-0.4296	0.228
PC16	SES _{MPD}	TS	phylogeny	SES _{MPD}	TS	-0.1562	-0.04298
PC8	SES _{MPD}	TS	phylogeny	SES _{MPD}	TS	-0.3777	0.08969
all	SES _{MPD}	TS	activity level (% still)	SES _{MPD}	IS	0.039802	-0.09418
BDBM	SES _{MPD}	TS	activity level (% still)	SES _{MPD}	IS	-0.4809	0.3332
PC16	SES _{MPD}	TS	activity level (% still)	SES _{MPD}	IS	-0.22572	0.02544
PC8	SES _{MPD}	TS	activity level (% still)	SES _{MPD}	IS	-0.5246	0.2857
all	SES _{MPD}	TS	all	SES _{MPD}	IS	0.0423	-0.09267
BDBM	SES _{MPD}	TS	all	SES _{MPD}	IS	-0.33234	0.1309
PC16	SES _{MPD}	TS	all	SES _{MPD}	IS	-0.18925	-0.00159
PC8	SES _{MPD}	TS	all	SES _{MPD}	IS	-0.4238	0.1809

APPENDIX 5

all	SES _{MPD}	TS	antenna 1 length	SES _{MPD}	IS	0.04317	-0.09098
BDBM	SES _{MPD}	TS	antenna 1 length	SES _{MPD}	IS	-0.3688	0.2359
PC16	SES _{MPD}	TS	antenna 1 length	SES _{MPD}	IS	-0.18644	0.01282
PC8	SES _{MPD}	TS	antenna 1 length	SES _{MPD}	IS	-0.4552	0.2828
all	SES _{MPD}	TS	antenna 2 length	SES _{MPD}	IS	-0.004148	-0.0999
BDBM	SES _{MPD}	TS	antenna 2 length	SES _{MPD}	IS	-0.09871	-0.07144
PC16	SES _{MPD}	TS	antenna 2 length	SES _{MPD}	IS	-0.06791	-0.08223
PC8	SES _{MPD}	TS	antenna 2 length	SES _{MPD}	IS	-0.12109	-0.06785
all	SES _{MPD}	TS	max. body size	SES _{MPD}	IS	0.0425	-0.09024
BDBM	SES _{MPD}	TS	max. body size	SES _{MPD}	IS	-0.17961	-0.01107
PC16	SES _{MPD}	TS	max. body size	SES _{MPD}	IS	-0.1136	-0.05324
PC8	SES _{MPD}	TS	max. body size	SES _{MPD}	IS	-0.3172	0.1075
all	SES _{MPD}	TS	phylogeny	SES _{MPD}	IS	0.02093	-0.09764
BDBM	SES _{MPD}	TS	phylogeny	SES _{MPD}	IS	-0.25492	0.07834
PC16	SES _{MPD}	TS	phylogeny	SES _{MPD}	IS	-0.13258	-0.03658
PC8	SES _{MPD}	TS	phylogeny	SES _{MPD}	IS	-0.3178	0.1074
all	SES _{MPD}	IS	activity level (% still)	SES _{MNTD}	TS	0.08915	-0.06832
BDBM	SES _{MPD}	IS	activity level (% still)	SES _{MNTD}	TS	-0.15453	0.01039
PC16	SES _{MPD}	IS	activity level (% still)	SES _{MNTD}	TS	0.0127594	-0.09884
PC8	SES _{MPD}	IS	activity level (% still)	SES _{MNTD}	TS	-0.051485	-0.08262
all	SES _{MPD}	IS	all	SES _{MNTD}	TS	0.4155204	0.3628
BDBM	SES _{MPD}	IS	all	SES _{MNTD}	TS	-0.029272	-0.09734
PC16	SES _{MPD}	IS	all	SES _{MNTD}	TS	0.072724	-0.07469
PC8	SES _{MPD}	IS	all	SES _{MNTD}	TS	0.051274	-0.08841
all	SES _{MPD}	IS	antenna 1 length	SES _{MNTD}	TS	0.3505693	0.3717
BDBM	SES _{MPD}	IS	antenna 1 length	SES _{MNTD}	TS	-0.014731	-0.09903
PC16	SES _{MPD}	IS	antenna 1 length	SES _{MNTD}	TS	0.05012	-0.08279
PC8	SES _{MPD}	IS	antenna 1 length	SES _{MNTD}	TS	0.033471	-0.09293

APPENDIX 5

all	SES _{MPD}	IS	antenna 2 length	SES _{MNTD}	TS	-0.06274	0.3099
BDBM	SES _{MPD}	IS	antenna 2 length	SES _{MNTD}	TS	-0.006551	-0.09482
PC16	SES _{MPD}	IS	antenna 2 length	SES _{MNTD}	TS	-0.013763	-0.06478
PC8	SES _{MPD}	IS	antenna 2 length	SES _{MNTD}	TS	-0.01445	-0.0642
all	SES _{MPD}	IS	max. body size	SES _{MNTD}	TS	0.01788	-0.09854
BDBM	SES _{MPD}	IS	max. body size	SES _{MNTD}	TS	-0.23032	0.1802
PC16	SES _{MPD}	IS	max. body size	SES _{MNTD}	TS	-0.03551	-0.08974
PC8	SES _{MPD}	IS	max. body size	SES _{MNTD}	TS	-0.11715	0.002835
all	SES _{MPD}	IS	phylogeny	SES _{MNTD}	TS	0.3510316	0.09874
BDBM	SES _{MPD}	IS	phylogeny	SES _{MNTD}	TS	-0.2364	0.004544
PC16	SES _{MPD}	IS	phylogeny	SES _{MNTD}	TS	0.033958	-0.09668
PC8	SES _{MPD}	IS	phylogeny	SES _{MNTD}	TS	-0.059588	-0.09058
all	SES _{MPD}	IS	activity level (% still)	SES _{MNTD}	IS	0.107	-0.08431
BDBM	SES _{MPD}	IS	activity level (% still)	SES _{MNTD}	IS	-0.21041	-0.02968
PC16	SES _{MPD}	IS	activity level (% still)	SES _{MNTD}	IS	0.029508	-0.09787
PC8	SES _{MPD}	IS	activity level (% still)	SES _{MNTD}	IS	-0.062562	-0.09118
all	SES _{MPD}	IS	all	SES _{MNTD}	IS	0.4769437	0.3041
BDBM	SES _{MPD}	IS	all	SES _{MNTD}	IS	-0.0077435	-0.09988
PC16	SES _{MPD}	IS	all	SES _{MNTD}	IS	0.092329	-0.07296
PC8	SES _{MPD}	IS	all	SES _{MNTD}	IS	0.0776	-0.0824
all	SES _{MPD}	IS	antenna 1 length	SES _{MNTD}	IS	0.3874407	0.3129
BDBM	SES _{MPD}	IS	antenna 1 length	SES _{MNTD}	IS	-0.028704	-0.09737
PC16	SES _{MPD}	IS	antenna 1 length	SES _{MNTD}	IS	0.051007	-0.08722
PC8	SES _{MPD}	IS	antenna 1 length	SES _{MNTD}	IS	0.028051	-0.09644
all	SES _{MPD}	IS	antenna 2 length	SES _{MNTD}	IS	-0.1417	0.4085
BDBM	SES _{MPD}	IS	antenna 2 length	SES _{MNTD}	IS	-0.021817	-0.08603
PC16	SES _{MPD}	IS	antenna 2 length	SES _{MNTD}	IS	-0.037163	-0.03759
PC8	SES _{MPD}	IS	antenna 2 length	SES _{MNTD}	IS	-0.039501	-0.03503

APPENDIX 5

all	SES _{MPD}	IS	max. body size	SES _{MNTD}	IS	-0.04848	-0.09456
BDBM	SES _{MPD}	IS	max. body size	SES _{MNTD}	IS	-0.35215	0.2332
PC16	SES _{MPD}	IS	max. body size	SES _{MNTD}	IS	-0.067544	-0.08113
PC8	SES _{MPD}	IS	max. body size	SES _{MNTD}	IS	-0.18914	0.03635
all	SES _{MPD}	IS	phylogeny	SES _{MNTD}	IS	0.352747	0.1502
BDBM	SES _{MPD}	IS	phylogeny	SES _{MNTD}	IS	-0.17085	-0.03194
PC16	SES _{MPD}	IS	phylogeny	SES _{MNTD}	IS	0.038126	-0.09478
PC8	SES _{MPD}	IS	phylogeny	SES _{MNTD}	IS	-0.030648	-0.09689
all	SES _{MPD}	IS	activity level (% still)	SES _{MPD}	TS	0.4061137	0.4235
BDBM	SES _{MPD}	IS	activity level (% still)	SES _{MPD}	TS	-0.019472	-0.0986
PC16	SES _{MPD}	IS	activity level (% still)	SES _{MPD}	TS	0.084798	-0.05925
PC8	SES _{MPD}	IS	activity level (% still)	SES _{MPD}	TS	0.06188	-0.08
all	SES _{MPD}	IS	all	SES _{MPD}	TS	0.4852413	0.497
BDBM	SES _{MPD}	IS	all	SES _{MPD}	TS	0.025127	-0.09814
PC16	SES _{MPD}	IS	all	SES _{MPD}	TS	0.073079	-0.07582
PC8	SES _{MPD}	IS	all	SES _{MPD}	TS	0.068623	-0.08035
all	SES _{MPD}	IS	antenna 1 length	SES _{MPD}	TS	0.4735671	0.3784
BDBM	SES _{MPD}	IS	antenna 1 length	SES _{MPD}	TS	-0.062153	-0.09044
PC16	SES _{MPD}	IS	antenna 1 length	SES _{MPD}	TS	0.086683	-0.07138
PC8	SES _{MPD}	IS	antenna 1 length	SES _{MPD}	TS	0.047626	-0.09204
all	SES _{MPD}	IS	antenna 2 length	SES _{MPD}	TS	0.1912914	0.08853
BDBM	SES _{MPD}	IS	antenna 2 length	SES _{MPD}	TS	0.11418	-0.0221
PC16	SES _{MPD}	IS	antenna 2 length	SES _{MPD}	TS	0.047824	-0.07896
PC8	SES _{MPD}	IS	antenna 2 length	SES _{MPD}	TS	0.08659	-0.03644
all	SES _{MPD}	IS	max. body size	SES _{MPD}	TS	0.005722	-0.09984
BDBM	SES _{MPD}	IS	max. body size	SES _{MPD}	TS	-0.15679	0.03574
PC16	SES _{MPD}	IS	max. body size	SES _{MPD}	TS	-0.058124	-0.07128
PC8	SES _{MPD}	IS	max. body size	SES _{MPD}	TS	-0.1059	-0.01215

APPENDIX 5

all	SES _{MPD}	IS	phylogeny	SES _{MPD}	TS	0.5049448	0.2676
BDBM	SES _{MPD}	IS	phylogeny	SES _{MPD}	TS	-0.02663	-0.09881
PC16	SES _{MPD}	IS	phylogeny	SES _{MPD}	TS	0.106704	-0.07069
PC8	SES _{MPD}	IS	phylogeny	SES _{MPD}	TS	0.082716	-0.08377
all	SES _{MPD}	IS	activity level (% still)	SES _{MPD}	IS	0.5028334	0.2842
BDBM	SES _{MPD}	IS	activity level (% still)	SES _{MPD}	IS	-0.08985	-0.08577
PC16	SES _{MPD}	IS	activity level (% still)	SES _{MPD}	IS	0.046504	-0.09413
PC8	SES _{MPD}	IS	activity level (% still)	SES _{MPD}	IS	0.0061558	-0.09991
all	SES _{MPD}	IS	all	SES _{MPD}	IS	0.3459184	0.1029
BDBM	SES _{MPD}	IS	all	SES _{MPD}	IS	-0.0861	-0.08542
PC16	SES _{MPD}	IS	all	SES _{MPD}	IS	-0.0099042	-0.0997
PC8	SES _{MPD}	IS	all	SES _{MPD}	IS	-0.038843	-0.09579
all	SES _{MPD}	IS	antenna 1 length	SES _{MPD}	IS	0.2939826	0.07311
BDBM	SES _{MPD}	IS	antenna 1 length	SES _{MPD}	IS	-0.1488	-0.04857
PC16	SES _{MPD}	IS	antenna 1 length	SES _{MPD}	IS	-0.011551	-0.09952
PC8	SES _{MPD}	IS	antenna 1 length	SES _{MPD}	IS	-0.063766	-0.0866
all	SES _{MPD}	IS	antenna 2 length	SES _{MPD}	IS	0.2270953	0.02261
BDBM	SES _{MPD}	IS	antenna 2 length	SES _{MPD}	IS	0.034939	-0.09663
PC16	SES _{MPD}	IS	antenna 2 length	SES _{MPD}	IS	0.0104468	-0.09954
PC8	SES _{MPD}	IS	antenna 2 length	SES _{MPD}	IS	0.027849	-0.09697
all	SES _{MPD}	IS	max. body size	SES _{MPD}	IS	-0.0264231	-0.09844
BDBM	SES _{MPD}	IS	max. body size	SES _{MPD}	IS	-0.22135	0.02707
PC16	SES _{MPD}	IS	max. body size	SES _{MPD}	IS	-0.09183	-0.06633
PC8	SES _{MPD}	IS	max. body size	SES _{MPD}	IS	-0.15676	-0.009592
all	SES _{MPD}	IS	phylogeny	SES _{MPD}	IS	0.2396337	0.02785
BDBM	SES _{MPD}	IS	phylogeny	SES _{MPD}	IS	-0.09424	-0.07707
PC16	SES _{MPD}	IS	phylogeny	SES _{MPD}	IS	-0.008824	-0.09969
PC8	SES _{MPD}	IS	phylogeny	SES _{MPD}	IS	-0.038022	-0.0947

Table A5.3. Effect sizes of fish community trait dispersion on residual peracarid community trait and phylogenetic dispersion, controlling for the effects of habitat filters on fish dispersion.

APPENDIX 5

Bolded cells indicate values significant at $\alpha = 0.008333$; the first 24 rows are effects for which results are presented in the main text. Rows are colored according to the direction and magnitude of the effect size; red indicates a negative effect while blue indicates a positive effect, and color saturation is proportional to R^2 . TS = Tip Shuffle algorithm, IS = Independent Swap algorithm; BDBM = Body Depth Below Midline.

Predictor trait	Predictor metric	Predictor algorithm	Response trait	Response metric	Response algorithm	Effect size	R^2
all	SES _{MNTD}	TS	activity level (% still)	SES _{MNTD}	TS	0.8045	0.443
BDBM	SES _{MNTD}	TS	activity level (% still)	SES _{MNTD}	TS	-0.2636	0.2355
PC16	SES _{MNTD}	TS	activity level (% still)	SES _{MNTD}	TS	-0.7534	-0.006049
PC8	SES _{MNTD}	TS	activity level (% still)	SES _{MNTD}	TS	-0.251	0.2098
all	SES _{MNTD}	TS	all	SES _{MNTD}	TS	0.8525	0.3018
BDBM	SES _{MNTD}	TS	all	SES _{MNTD}	TS	-0.506	0.7316
PC16	SES _{MNTD}	TS	all	SES _{MNTD}	TS	0.9485	0.0001235
PC8	SES _{MNTD}	TS	all	SES _{MNTD}	TS	-0.4521	0.5757
all	SES _{MNTD}	TS	antenna 1 length	SES _{MNTD}	TS	1.103	0.8825
BDBM	SES _{MNTD}	TS	antenna 1 length	SES _{MNTD}	TS	-0.3873	0.5975
PC16	SES _{MNTD}	TS	antenna 1 length	SES _{MNTD}	TS	-0.9212	0.03522
PC8	SES _{MNTD}	TS	antenna 1 length	SES _{MNTD}	TS	-0.3035	0.3358
all	SES _{MNTD}	TS	antenna 2 length	SES _{MNTD}	TS	-0.06549	-0.006011
BDBM	SES _{MNTD}	TS	antenna 2 length	SES _{MNTD}	TS	0.06108	0.3708
PC16	SES _{MNTD}	TS	antenna 2 length	SES _{MNTD}	TS	-0.2196	0.1085
PC8	SES _{MNTD}	TS	antenna 2 length	SES _{MNTD}	TS	0.05404	0.2751
all	SES _{MNTD}	TS	max. body size	SES _{MNTD}	TS	0.8565	0.6032
BDBM	SES _{MNTD}	TS	max. body size	SES _{MNTD}	TS	-0.3617	0.6221
PC16	SES _{MNTD}	TS	max. body size	SES _{MNTD}	TS	0.3578	-0.07579
PC8	SES _{MNTD}	TS	max. body size	SES _{MNTD}	TS	-0.3802	0.7117
all	SES _{MNTD}	TS	phylogeny	SES _{MNTD}	TS	1.37	0.5367
BDBM	SES _{MNTD}	TS	phylogeny	SES _{MNTD}	TS	-0.7364	0.9597
PC16	SES _{MNTD}	TS	phylogeny	SES _{MNTD}	TS	1.38	0.02755

APPENDIX 5

PC8	SES _{MNTD}	TS	phylogeny	SES _{MNTD}	TS	-0.7185	0.9267
all	SES _{MNTD}	TS	activity level (% still)	SES _{MNTD}	IS	1.133	0.2697
BDBM	SES _{MNTD}	TS	activity level (% still)	SES _{MNTD}	IS	-0.2991	0.04852
PC16	SES _{MNTD}	TS	activity level (% still)	SES _{MNTD}	IS	-1.845	0.09348
PC8	SES _{MNTD}	TS	activity level (% still)	SES _{MNTD}	IS	-0.2742	0.027
all	SES _{MNTD}	TS	all	SES _{MNTD}	IS	0.7354	0.1022
BDBM	SES _{MNTD}	TS	all	SES _{MNTD}	IS	-0.5517	0.5553
PC16	SES _{MNTD}	TS	all	SES _{MNTD}	IS	1.671	0.106
PC8	SES _{MNTD}	TS	all	SES _{MNTD}	IS	-0.501	0.4499
all	SES _{MNTD}	TS	antenna 1 length	SES _{MNTD}	IS	1.324	0.9149
BDBM	SES _{MNTD}	TS	antenna 1 length	SES _{MNTD}	IS	-0.4438	0.5567
PC16	SES _{MNTD}	TS	antenna 1 length	SES _{MNTD}	IS	-1.235	0.07413
PC8	SES _{MNTD}	TS	antenna 1 length	SES _{MNTD}	IS	-0.347	0.3085
all	SES _{MNTD}	TS	antenna 2 length	SES _{MNTD}	IS	-0.1476	0.01612
BDBM	SES _{MNTD}	TS	antenna 2 length	SES _{MNTD}	IS	0.1126	0.289
PC16	SES _{MNTD}	TS	antenna 2 length	SES _{MNTD}	IS	-0.2063	-0.05528
PC8	SES _{MNTD}	TS	antenna 2 length	SES _{MNTD}	IS	0.09246	0.1668
all	SES _{MNTD}	TS	max. body size	SES _{MNTD}	IS	1.065	0.4535
BDBM	SES _{MNTD}	TS	max. body size	SES _{MNTD}	IS	-0.4808	0.5489
PC16	SES _{MNTD}	TS	max. body size	SES _{MNTD}	IS	0.8959	-0.0228
PC8	SES _{MNTD}	TS	max. body size	SES _{MNTD}	IS	-0.5295	0.701
all	SES _{MNTD}	TS	phylogeny	SES _{MNTD}	IS	1.16	0.4693
BDBM	SES _{MNTD}	TS	phylogeny	SES _{MNTD}	IS	-0.6553	0.9461
PC16	SES _{MNTD}	TS	phylogeny	SES _{MNTD}	IS	1.411	0.06622
PC8	SES _{MNTD}	TS	phylogeny	SES _{MNTD}	IS	-0.6309	0.8869
all	SES _{MNTD}	TS	activity level (% still)	SES _{MPD}	TS	0.9325	0.4808
BDBM	SES _{MNTD}	TS	activity level (% still)	SES _{MPD}	TS	-0.4344	0.6256
PC16	SES _{MNTD}	TS	activity level (% still)	SES _{MPD}	TS	-0.1379	-0.09749
PC8	SES _{MNTD}	TS	activity level (% still)	SES _{MPD}	TS	-0.365	0.4215
all	SES _{MNTD}	TS	all	SES _{MPD}	TS	1.257	0.7432
BDBM	SES _{MNTD}	TS	all	SES _{MPD}	TS	-0.4921	0.6442

APPENDIX 5

PC16	SES _{MNTD}	TS	all	SES _{MPD}	TS	-0.6736	-0.05222
PC8	SES _{MNTD}	TS	all	SES _{MPD}	TS	-0.3834	0.3596
all	SES _{MNTD}	TS	antenna 1 length	SES _{MPD}	TS	1.227	0.5757
BDBM	SES _{MNTD}	TS	antenna 1 length	SES _{MPD}	TS	-0.5785	0.7652
PC16	SES _{MNTD}	TS	antenna 1 length	SES _{MPD}	TS	0.07847	-0.09945
PC8	SES _{MNTD}	TS	antenna 1 length	SES _{MPD}	TS	-0.5028	0.5651
all	SES _{MNTD}	TS	antenna 2 length	SES _{MPD}	TS	-0.187	-0.06209
BDBM	SES _{MNTD}	TS	antenna 2 length	SES _{MPD}	TS	-0.07693	-0.06305
PC16	SES _{MNTD}	TS	antenna 2 length	SES _{MPD}	TS	1.107	0.1621
PC8	SES _{MNTD}	TS	antenna 2 length	SES _{MPD}	TS	-0.05427	-0.08129
all	SES _{MNTD}	TS	max. body size	SES _{MPD}	TS	0.6823	0.3665
BDBM	SES _{MNTD}	TS	max. body size	SES _{MPD}	TS	-0.3026	0.4281
PC16	SES _{MNTD}	TS	max. body size	SES _{MPD}	TS	0.7078	-0.000965
PC8	SES _{MNTD}	TS	max. body size	SES _{MPD}	TS	-0.3135	0.4769
all	SES _{MNTD}	TS	phylogeny	SES _{MPD}	TS	0.7364	0.06457
BDBM	SES _{MNTD}	TS	phylogeny	SES _{MPD}	TS	-0.597	0.5227
PC16	SES _{MNTD}	TS	phylogeny	SES _{MPD}	TS	1.958	0.1296
PC8	SES _{MNTD}	TS	phylogeny	SES _{MPD}	TS	-0.5525	0.4427
all	SES _{MNTD}	TS	activity level (% still)	SES _{MPD}	IS	1.539	0.6573
BDBM	SES _{MNTD}	TS	activity level (% still)	SES _{MPD}	IS	-0.7288	0.878
PC16	SES _{MNTD}	TS	activity level (% still)	SES _{MPD}	IS	0.6703	-0.07165
PC8	SES _{MNTD}	TS	activity level (% still)	SES _{MPD}	IS	-0.6463	0.6828
all	SES _{MNTD}	TS	all	SES _{MPD}	IS	1.379	0.5788
BDBM	SES _{MNTD}	TS	all	SES _{MPD}	IS	-0.5967	0.6315
PC16	SES _{MNTD}	TS	all	SES _{MPD}	IS	0.5134	-0.08145
PC8	SES _{MNTD}	TS	all	SES _{MPD}	IS	-0.529	0.4851
all	SES _{MNTD}	TS	antenna 1 length	SES _{MPD}	IS	1.316	0.6302
BDBM	SES _{MNTD}	TS	antenna 1 length	SES _{MPD}	IS	-0.6132	0.8126
PC16	SES _{MNTD}	TS	antenna 1 length	SES _{MPD}	IS	0.8756	-0.03623
PC8	SES _{MNTD}	TS	antenna 1 length	SES _{MPD}	IS	-0.5724	0.7092

APPENDIX 5

all	SES _{MNTD}	TS	antenna 2 length	SES _{MPD}	IS	0.2377	-0.07173
BDBM	SES _{MNTD}	TS	antenna 2 length	SES _{MPD}	IS	-0.2976	0.1551
PC16	SES _{MNTD}	TS	antenna 2 length	SES _{MPD}	IS	1.881	0.2493
PC8	SES _{MNTD}	TS	antenna 2 length	SES _{MPD}	IS	-0.2775	0.1257
all	SES _{MNTD}	TS	max. body size	SES _{MPD}	IS	0.8514	0.2412
BDBM	SES _{MNTD}	TS	max. body size	SES _{MPD}	IS	-0.4033	0.3407
PC16	SES _{MNTD}	TS	max. body size	SES _{MPD}	IS	1.28	0.05219
PC8	SES _{MNTD}	TS	max. body size	SES _{MPD}	IS	-0.429	0.4076
all	SES _{MNTD}	TS	phylogeny	SES _{MPD}	IS	0.7741	0.1808
BDBM	SES _{MNTD}	TS	phylogeny	SES _{MPD}	IS	-0.496	0.5636
PC16	SES _{MNTD}	TS	phylogeny	SES _{MPD}	IS	1.821	0.2067
PC8	SES _{MNTD}	TS	phylogeny	SES _{MPD}	IS	-0.4808	0.5348
all	SES _{MNTD}	IS	activity level (% still)	SES _{MNTD}	TS	0.4837	0.3654
BDBM	SES _{MNTD}	IS	activity level (% still)	SES _{MNTD}	TS	-0.3759	0.3511
PC16	SES _{MNTD}	IS	activity level (% still)	SES _{MNTD}	TS	-0.116	-0.09659
PC8	SES _{MNTD}	IS	activity level (% still)	SES _{MNTD}	TS	-0.3868	0.2875
all	SES _{MNTD}	IS	all	SES _{MNTD}	TS	0.65	0.4651
BDBM	SES _{MNTD}	IS	all	SES _{MNTD}	TS	-0.6171	0.7174
PC16	SES _{MNTD}	IS	all	SES _{MNTD}	TS	2.351	0.8399
PC8	SES _{MNTD}	IS	all	SES _{MNTD}	TS	-0.5705	0.4666
all	SES _{MNTD}	IS	antenna 1 length	SES _{MNTD}	TS	0.6995	0.8369
BDBM	SES _{MNTD}	IS	antenna 1 length	SES _{MNTD}	TS	-0.4734	0.5888
PC16	SES _{MNTD}	IS	antenna 1 length	SES _{MNTD}	TS	0.933	0.112
PC8	SES _{MNTD}	IS	antenna 1 length	SES _{MNTD}	TS	-0.3966	0.2921
all	SES _{MNTD}	IS	antenna 2 length	SES _{MNTD}	TS	-0.06153	0.09672
BDBM	SES _{MNTD}	IS	antenna 2 length	SES _{MNTD}	TS	0.07415	0.3585
PC16	SES _{MNTD}	IS	antenna 2 length	SES _{MNTD}	TS	-0.3913	0.912
PC8	SES _{MNTD}	IS	antenna 2 length	SES _{MNTD}	TS	0.06407	0.1777
all	SES _{MNTD}	IS	max. body size	SES _{MNTD}	TS	0.576	0.6537
BDBM	SES _{MNTD}	IS	max. body size	SES _{MNTD}	TS	-0.4536	0.6504
PC16	SES _{MNTD}	IS	max. body size	SES _{MNTD}	TS	0.4734	-0.03525

APPENDIX 5

PC8	SES _{MNTD}	IS	max. body size	SES _{MNTD}	TS	-5.492	0.792
all	SES _{MNTD}	IS	phylogeny	SES _{MNTD}	TS	1.001	0.7061
BDBM	SES _{MNTD}	IS	phylogeny	SES _{MNTD}	TS	-0.9181	0.9888
PC16	SES _{MNTD}	IS	phylogeny	SES _{MNTD}	TS	2.472	0.5354
PC8	SES _{MNTD}	IS	phylogeny	SES _{MNTD}	TS	-0.9706	0.8869
all	SES _{MNTD}	IS	activity level (% still)	SES _{MNTD}	IS	0.6324	0.1733
BDBM	SES _{MNTD}	IS	activity level (% still)	SES _{MNTD}	IS	-0.4703	0.1425
PC16	SES _{MNTD}	IS	activity level (% still)	SES _{MNTD}	IS	-0.82	-0.04156
PC8	SES _{MNTD}	IS	activity level (% still)	SES _{MNTD}	IS	-0.4587	0.08719
all	SES _{MNTD}	IS	all	SES _{MNTD}	IS	0.6217	0.2427
BDBM	SES _{MNTD}	IS	all	SES _{MNTD}	IS	-0.6705	0.5397
PC16	SES _{MNTD}	IS	all	SES _{MNTD}	IS	3.031	0.936
PC8	SES _{MNTD}	IS	all	SES _{MNTD}	IS	-0.6182	0.341
all	SES _{MNTD}	IS	antenna 1 length	SES _{MNTD}	IS	0.8289	0.843
BDBM	SES _{MNTD}	IS	antenna 1 length	SES _{MNTD}	IS	-0.5427	0.5488
PC16	SES _{MNTD}	IS	antenna 1 length	SES _{MNTD}	IS	0.9123	0.04528
PC8	SES _{MNTD}	IS	antenna 1 length	SES _{MNTD}	IS	-0.4589	0.2762
all	SES _{MNTD}	IS	antenna 2 length	SES _{MNTD}	IS	-0.1216	0.08684
BDBM	SES _{MNTD}	IS	antenna 2 length	SES _{MNTD}	IS	0.1467	0.3363
PC16	SES _{MNTD}	IS	antenna 2 length	SES _{MNTD}	IS	-0.6675	0.6155
PC8	SES _{MNTD}	IS	antenna 2 length	SES _{MNTD}	IS	0.1111	0.1028
all	SES _{MNTD}	IS	max. body size	SES _{MNTD}	IS	0.7345	0.5235
BDBM	SES _{MNTD}	IS	max. body size	SES _{MNTD}	IS	-6.008	0.5697
PC16	SES _{MNTD}	IS	max. body size	SES _{MNTD}	IS	0.6301	-0.04163
PC8	SES _{MNTD}	IS	max. body size	SES _{MNTD}	IS	-0.7695	0.7911
all	SES _{MNTD}	IS	phylogeny	SES _{MNTD}	IS	0.8682	0.6562
BDBM	SES _{MNTD}	IS	phylogeny	SES _{MNTD}	IS	-0.8037	0.94
PC16	SES _{MNTD}	IS	phylogeny	SES _{MNTD}	IS	2.488	0.6895
PC8	SES _{MNTD}	IS	phylogeny	SES _{MNTD}	IS	-0.8354	0.8115
all	SES _{MNTD}	IS	activity level (% still)	SES _{MPD}	TS	0.637	0.5426
BDBM	SES _{MNTD}	IS	activity level (% still)	SES _{MPD}	TS	-0.5597	0.6936

APPENDIX 5

PC16	SES _{MNTD}	IS	activity level (% still)	SES _{MPD}	TS	1.543	0.3795
PC8	SES _{MNTD}	IS	activity level (% still)	SES _{MPD}	TS	-0.4771	0.3692
all	SES _{MNTD}	IS	all	SES _{MPD}	TS	0.82889	0.7692
BDBM	SES _{MNTD}	IS	all	SES _{MPD}	TS	-0.5855	0.596
PC16	SES _{MNTD}	IS	all	SES _{MPD}	TS	1.666	0.3463
PC8	SES _{MNTD}	IS	all	SES _{MPD}	TS	-0.4784	0.2769
all	SES _{MNTD}	IS	antenna 1 length	SES _{MPD}	TS	0.8473	0.6642
BDBM	SES _{MNTD}	IS	antenna 1 length	SES _{MPD}	TS	-0.7323	0.8162
PC16	SES _{MNTD}	IS	antenna 1 length	SES _{MPD}	TS	2.011	0.4471
PC8	SES _{MNTD}	IS	antenna 1 length	SES _{MPD}	TS	-0.6607	0.5049
all	SES _{MNTD}	IS	antenna 2 length	SES _{MPD}	TS	-0.03602	-0.09666
BDBM	SES _{MNTD}	IS	antenna 2 length	SES _{MPD}	TS	-0.06614	-0.08195
PC16	SES _{MNTD}	IS	antenna 2 length	SES _{MPD}	TS	1.457	0.5938
PC8	SES _{MNTD}	IS	antenna 2 length	SES _{MPD}	TS	-0.01541	-0.09921
all	SES _{MNTD}	IS	max. body size	SES _{MPD}	TS	0.4861	0.4613
BDBM	SES _{MNTD}	IS	max. body size	SES _{MPD}	TS	-0.3238	0.2998
PC16	SES _{MNTD}	IS	max. body size	SES _{MPD}	TS	0.7611	0.07502
PC8	SES _{MNTD}	IS	max. body size	SES _{MPD}	TS	-0.4221	0.4509
all	SES _{MNTD}	IS	phylogeny	SES _{MPD}	TS	0.6403	0.1949
BDBM	SES _{MNTD}	IS	phylogeny	SES _{MPD}	TS	-0.7423	0.5362
PC16	SES _{MNTD}	IS	phylogeny	SES _{MPD}	TS	3.283	0.8863
PC8	SES _{MNTD}	IS	phylogeny	SES _{MPD}	TS	-0.691	0.3472
all	SES _{MNTD}	IS	activity level (% still)	SES _{MPD}	IS	1.091	0.8025
BDBM	SES _{MNTD}	IS	activity level (% still)	SES _{MPD}	IS	-0.8511	0.7815
PC16	SES _{MNTD}	IS	activity level (% still)	SES _{MPD}	IS	2.742	0.6247
PC8	SES _{MNTD}	IS	activity level (% still)	SES _{MPD}	IS	-0.8249	0.5716
all	SES _{MNTD}	IS	all	SES _{MPD}	IS	0.9654	0.6885
BDBM	SES _{MNTD}	IS	all	SES _{MPD}	IS	-0.6475	0.4694
PC16	SES _{MNTD}	IS	all	SES _{MPD}	IS	2.13	0.388
PC8	SES _{MNTD}	IS	all	SES _{MPD}	IS	-0.6642	0.3859
all	SES _{MNTD}	IS	antenna 1 length	SES _{MPD}	IS	0.9375	0.7783

APPENDIX 5

BDBM	SES _{MNTD}	IS	antenna 1 length	SES _{MPD}	IS	-0.6939	0.6723
PC16	SES _{MNTD}	IS	antenna 1 length	SES _{MPD}	IS	2.1	0.4602
PC8	SES _{MNTD}	IS	antenna 1 length	SES _{MPD}	IS	-0.7423	0.6168
all	SES _{MNTD}	IS	antenna 2 length	SES _{MPD}	IS	0.2904	0.00001889
BDBM	SES _{MNTD}	IS	antenna 2 length	SES _{MPD}	IS	-0.2874	0.05725
PC16	SES _{MNTD}	IS	antenna 2 length	SES _{MPD}	IS	2.318	0.7105
PC8	SES _{MNTD}	IS	antenna 2 length	SES _{MPD}	IS	-0.2989	0.038
all	SES _{MNTD}	IS	max. body size	SES _{MPD}	IS	0.6268	0.3383
BDBM	SES _{MNTD}	IS	max. body size	SES _{MPD}	IS	-0.419	0.2144
PC16	SES _{MNTD}	IS	max. body size	SES _{MPD}	IS	1.13	0.08112
PC8	SES _{MNTD}	IS	max. body size	SES _{MPD}	IS	-0.5734	0.3775
all	SES _{MNTD}	IS	phylogeny	SES _{MPD}	IS	0.635	0.3479
BDBM	SES _{MNTD}	IS	phylogeny	SES _{MPD}	IS	-0.5398	0.4195
PC16	SES _{MNTD}	IS	phylogeny	SES _{MPD}	IS	2.425	0.7309
PC8	SES _{MNTD}	IS	phylogeny	SES _{MPD}	IS	-0.598	0.4172
all	SES _{MPD}	TS	activity level (% still)	SES _{MNTD}	TS	1.796	0.4713
BDBM	SES _{MPD}	TS	activity level (% still)	SES _{MNTD}	TS	-0.4763	0.5311
PC16	SES _{MPD}	TS	activity level (% still)	SES _{MNTD}	TS	-0.7327	0.348
PC8	SES _{MPD}	TS	activity level (% still)	SES _{MNTD}	TS	-0.5628	0.4907
all	SES _{MPD}	TS	all	SES _{MNTD}	TS	0.7145	-0.03922
BDBM	SES _{MPD}	TS	all	SES _{MNTD}	TS	-0.6362	0.657
PC16	SES _{MPD}	TS	all	SES _{MNTD}	TS	-1.13	0.6164
PC8	SES _{MPD}	TS	all	SES _{MNTD}	TS	-0.6747	0.4708
all	SES _{MPD}	TS	antenna 1 length	SES _{MNTD}	TS	1.58	0.3254
BDBM	SES _{MPD}	TS	antenna 1 length	SES _{MNTD}	TS	-5.366	0.671
PC16	SES _{MPD}	TS	antenna 1 length	SES _{MNTD}	TS	-1.09	0.8543
PC8	SES _{MPD}	TS	antenna 1 length	SES _{MNTD}	TS	-0.6129	0.5743
all	SES _{MPD}	TS	antenna 2 length	SES _{MNTD}	TS	0.0568	-0.08507
BDBM	SES _{MPD}	TS	antenna 2 length	SES _{MNTD}	TS	0.07383	0.2961
PC16	SES _{MPD}	TS	antenna 2 length	SES _{MNTD}	TS	0.1218	0.2234

APPENDIX 5

PC8	SES _{MPD}	TS	antenna 2 length	SES _{MNTD}	TS	0.06692	0.1182
all	SES _{MPD}	TS	max. body size	SES _{MNTD}	TS	2.192	0.8723
BDBM	SES _{MPD}	TS	max. body size	SES _{MNTD}	TS	-0.4758	0.6194
PC16	SES _{MPD}	TS	max. body size	SES _{MNTD}	TS	-0.8523	0.5926
PC8	SES _{MPD}	TS	max. body size	SES _{MNTD}	TS	-0.6713	0.8599
all	SES _{MPD}	TS	phylogeny	SES _{MNTD}	TS	2.327	0.2879
BDBM	SES _{MPD}	TS	phylogeny	SES _{MNTD}	TS	-0.9558	0.9281
PC16	SES _{MPD}	TS	phylogeny	SES _{MNTD}	TS	-1.64	0.808
PC8	SES _{MPD}	TS	phylogeny	SES _{MNTD}	TS	-1.142	0.8847
all	SES _{MPD}	TS	activity level (% still)	SES _{MNTD}	IS	2.599	0.311
BDBM	SES _{MPD}	TS	activity level (% still)	SES _{MNTD}	IS	-0.662	0.3188
PC16	SES _{MPD}	TS	activity level (% still)	SES _{MNTD}	IS	-0.9429	0.1549
PC8	SES _{MPD}	TS	activity level (% still)	SES _{MNTD}	IS	-0.7479	0.2583
all	SES _{MPD}	TS	all	SES _{MNTD}	IS	0.1913	-0.09711
BDBM	SES _{MPD}	TS	all	SES _{MNTD}	IS	-0.6724	0.4605
PC16	SES _{MPD}	TS	all	SES _{MNTD}	IS	-1.145	0.3876
PC8	SES _{MPD}	TS	all	SES _{MNTD}	IS	-0.6763	0.2801
all	SES _{MPD}	TS	antenna 1 length	SES _{MNTD}	IS	2.018	0.3975
BDBM	SES _{MPD}	TS	antenna 1 length	SES _{MNTD}	IS	-0.6194	0.6363
PC16	SES _{MPD}	TS	antenna 1 length	SES _{MNTD}	IS	-1.274	0.8347
PC8	SES _{MPD}	TS	antenna 1 length	SES _{MNTD}	IS	-0.7228	0.5721
all	SES _{MPD}	TS	antenna 2 length	SES _{MNTD}	IS	0.1286	-0.08141
BDBM	SES _{MPD}	TS	antenna 2 length	SES _{MNTD}	IS	0.1645	0.3778
PC16	SES _{MPD}	TS	antenna 2 length	SES _{MNTD}	IS	0.2455	0.2194
PC8	SES _{MPD}	TS	antenna 2 length	SES _{MNTD}	IS	0.1328	0.1088
all	SES _{MPD}	TS	max. body size	SES _{MNTD}	IS	2.996	0.8236
BDBM	SES _{MPD}	TS	max. body size	SES _{MNTD}	IS	-0.6125	0.5065
PC16	SES _{MPD}	TS	max. body size	SES _{MNTD}	IS	-1.078	0.4637
PC8	SES _{MPD}	TS	max. body size	SES _{MNTD}	IS	-0.9011	0.7799
all	SES _{MPD}	TS	phylogeny	SES _{MNTD}	IS	1.763	0.1775
BDBM	SES _{MPD}	TS	phylogeny	SES _{MNTD}	IS	-0.8189	0.8409
PC16	SES _{MPD}	TS	phylogeny	SES _{MNTD}	IS	-1.441	0.7735

APPENDIX 5

PC8	SES _{MPD}	TS	phylogeny	SES _{MNTD}	IS	-0.9683	0.7817
all	SES _{MPD}	TS	activity level (% still)	SES _{MPD}	TS	0.9565	0.029
BDBM	SES _{MPD}	TS	activity level (% still)	SES _{MPD}	TS	-0.6395	0.8058
PC16	SES _{MPD}	TS	activity level (% still)	SES _{MPD}	TS	-1.083	0.6788
PC8	SES _{MPD}	TS	activity level (% still)	SES _{MPD}	TS	-0.6478	0.523
all	SES _{MPD}	TS	all	SES _{MPD}	TS	1.481	0.1471
BDBM	SES _{MPD}	TS	all	SES _{MPD}	TS	-0.6355	0.6145
PC16	SES _{MPD}	TS	all	SES _{MPD}	TS	-1.325	0.8315
PC8	SES _{MPD}	TS	all	SES _{MPD}	TS	-0.7063	0.4917
all	SES _{MPD}	TS	antenna 1 length	SES _{MPD}	TS	1.481	0.1077
BDBM	SES _{MPD}	TS	antenna 1 length	SES _{MPD}	TS	-0.8127	0.8832
PC16	SES _{MPD}	TS	antenna 1 length	SES _{MPD}	TS	-1.415	0.7944
PC8	SES _{MPD}	TS	antenna 1 length	SES _{MPD}	TS	-0.8687	0.653
all	SES _{MPD}	TS	antenna 2 length	SES _{MPD}	TS	-1.194	0.2262
BDBM	SES _{MPD}	TS	antenna 2 length	SES _{MPD}	TS	-0.01737	-0.09891
PC16	SES _{MPD}	TS	antenna 2 length	SES _{MPD}	TS	-0.05159	-0.09713
PC8	SES _{MPD}	TS	antenna 2 length	SES _{MPD}	TS	0.06248	-0.09059
all	SES _{MPD}	TS	max. body size	SES _{MPD}	TS	1.755	0.5515
BDBM	SES _{MPD}	TS	max. body size	SES _{MPD}	TS	-0.2667	0.1363
PC16	SES _{MPD}	TS	max. body size	SES _{MPD}	TS	-0.6884	0.3723
PC8	SES _{MPD}	TS	max. body size	SES _{MPD}	TS	-0.4821	0.4176
all	SES _{MPD}	TS	phylogeny	SES _{MPD}	TS	0.1043	-0.0993
BDBM	SES _{MPD}	TS	phylogeny	SES _{MPD}	TS	-0.7589	0.4794
PC16	SES _{MPD}	TS	phylogeny	SES _{MPD}	TS	-1.209	0.3414
PC8	SES _{MPD}	TS	phylogeny	SES _{MPD}	TS	-0.7447	0.274
all	SES _{MPD}	TS	activity level (% still)	SES _{MPD}	IS	2.166	0.2165
BDBM	SES _{MPD}	TS	activity level (% still)	SES _{MPD}	IS	-0.8495	0.6652
PC16	SES _{MPD}	TS	activity level (% still)	SES _{MPD}	IS	-1.747	0.8709
PC8	SES _{MPD}	TS	activity level (% still)	SES _{MPD}	IS	-1.034	0.6604
all	SES _{MPD}	TS	all	SES _{MPD}	IS	2.302	0.299
BDBM	SES _{MPD}	TS	all	SES _{MPD}	IS	-0.5871	0.3078

APPENDIX 5

PC16	SES _{MPD}	TS	all	SES _{MPD}	IS	-1.465	0.6617
PC8	SES _{MPD}	TS	all	SES _{MPD}	IS	-0.8356	0.4538
all	SES _{MPD}	TS	antenna 1 length	SES _{MPD}	IS	2.349	0.3908
BDBM	SES _{MPD}	TS	antenna 1 length	SES _{MPD}	IS	-0.6516	0.4934
PC16	SES _{MPD}	TS	antenna 1 length	SES _{MPD}	IS	-1.443	0.7732
PC8	SES _{MPD}	TS	antenna 1 length	SES _{MPD}	IS	-0.8976	0.6548
all	SES _{MPD}	TS	antenna 2 length	SES _{MPD}	IS	-0.2257	-0.09462
BDBM	SES _{MPD}	TS	antenna 2 length	SES _{MPD}	IS	-0.1744	-0.04955
PC16	SES _{MPD}	TS	antenna 2 length	SES _{MPD}	IS	-0.5256	0.03751
PC8	SES _{MPD}	TS	antenna 2 length	SES _{MPD}	IS	-0.2387	-0.03661
all	SES _{MPD}	TS	max. body size	SES _{MPD}	IS	2.312	0.4311
BDBM	SES _{MPD}	TS	max. body size	SES _{MPD}	IS	-0.3173	0.0571
PC16	SES _{MPD}	TS	max. body size	SES _{MPD}	IS	-0.8792	0.2619
PC8	SES _{MPD}	TS	max. body size	SES _{MPD}	IS	-0.6254	0.3092
all	SES _{MPD}	TS	phylogeny	SES _{MPD}	IS	1.139	0.02829
BDBM	SES _{MPD}	TS	phylogeny	SES _{MPD}	IS	-0.4503	0.215
PC16	SES _{MPD}	TS	phylogeny	SES _{MPD}	IS	-1.026	0.3908
PC8	SES _{MPD}	TS	phylogeny	SES _{MPD}	IS	-0.6267	0.309
all	SES _{MPD}	IS	activity level (% still)	SES _{MNTD}	TS	0.1259	-0.05524
BDBM	SES _{MPD}	IS	activity level (% still)	SES _{MNTD}	TS	-0.397	0.1836
PC16	SES _{MPD}	IS	activity level (% still)	SES _{MNTD}	TS	0.1423	-0.08708
PC8	SES _{MPD}	IS	activity level (% still)	SES _{MNTD}	TS	-0.2349	-0.02067
all	SES _{MPD}	IS	all	SES _{MNTD}	TS	0.587	0.5538
BDBM	SES _{MPD}	IS	all	SES _{MNTD}	TS	-0.0752	-0.09316
PC16	SES _{MPD}	IS	all	SES _{MNTD}	TS	0.8108	0.1822
PC8	SES _{MPD}	IS	all	SES _{MNTD}	TS	0.234	-0.04709
all	SES _{MPD}	IS	antenna 1 length	SES _{MNTD}	TS	0.4952	0.5663
BDBM	SES _{MPD}	IS	antenna 1 length	SES _{MNTD}	TS	-0.03784	-0.09752
PC16	SES _{MPD}	IS	antenna 1 length	SES _{MNTD}	TS	0.5588	0.0919
PC8	SES _{MPD}	IS	antenna 1 length	SES _{MNTD}	TS	0.1527	-0.06772

APPENDIX 5

all	SES _{MPD}	IS	antenna 2 length	SES _{MNTD}	TS	-0.08863	0.4791
BDBM	SES _{MPD}	IS	antenna 2 length	SES _{MNTD}	TS	-0.01683	-0.08669
PC16	SES _{MPD}	IS	antenna 2 length	SES _{MNTD}	TS	-0.1535	0.2927
PC8	SES _{MPD}	IS	antenna 2 length	SES _{MNTD}	TS	-0.06596	0.06334
all	SES _{MPD}	IS	max. body size	SES _{MNTD}	TS	0.02527	-0.09794
BDBM	SES _{MPD}	IS	max. body size	SES _{MNTD}	TS	-0.5917	0.6197
PC16	SES _{MPD}	IS	max. body size	SES _{MNTD}	TS	-0.396	0.01435
PC8	SES _{MPD}	IS	max. body size	SES _{MNTD}	TS	-0.5346	0.3692
all	SES _{MPD}	IS	phylogeny	SES _{MNTD}	TS	0.4959	0.1807
BDBM	SES _{MPD}	IS	phylogeny	SES _{MNTD}	TS	-0.6073	0.1686
PC16	SES _{MPD}	IS	phylogeny	SES _{MNTD}	TS	0.3786	-0.06298
PC8	SES _{MPD}	IS	phylogeny	SES _{MNTD}	TS	-0.2719	-0.05701
all	SES _{MPD}	IS	activity level (% still)	SES _{MNTD}	IS	0.1512	-0.07783
BDBM	SES _{MPD}	IS	activity level (% still)	SES _{MNTD}	IS	-0.5405	0.08066
PC16	SES _{MPD}	IS	activity level (% still)	SES _{MNTD}	IS	0.329	-0.07626
PC8	SES _{MPD}	IS	activity level (% still)	SES _{MNTD}	IS	-0.2855	-0.05975
all	SES _{MPD}	IS	all	SES _{MNTD}	IS	0.6738	0.4709
BDBM	SES _{MPD}	IS	all	SES _{MNTD}	IS	-0.01989	-0.09968
PC16	SES _{MPD}	IS	all	SES _{MNTD}	IS	1.029	0.2015
PC8	SES _{MPD}	IS	all	SES _{MNTD}	IS	0.3541	-0.01968
all	SES _{MPD}	IS	antenna 1 length	SES _{MNTD}	IS	0.5473	0.4833
BDBM	SES _{MPD}	IS	antenna 1 length	SES _{MNTD}	IS	-0.07374	-0.09325
PC16	SES _{MPD}	IS	antenna 1 length	SES _{MNTD}	IS	0.5687	0.04248
PC8	SES _{MPD}	IS	antenna 1 length	SES _{MNTD}	IS	0.128	-0.08375
all	SES _{MPD}	IS	antenna 2 length	SES _{MNTD}	IS	-0.2002	0.6184
BDBM	SES _{MPD}	IS	antenna 2 length	SES _{MNTD}	IS	-0.05604	-0.06411
PC16	SES _{MPD}	IS	antenna 2 length	SES _{MNTD}	IS	-0.4143	0.5958
PC8	SES _{MPD}	IS	antenna 2 length	SES _{MNTD}	IS	-0.1802	0.1965
all	SES _{MPD}	IS	max. body size	SES _{MNTD}	IS	-0.06848	-0.09231

APPENDIX 5

BDBM	SES _{MPD}	IS	max. body size	SES _{MNTD}	IS	-0.9046	0.7559
PC16	SES _{MPD}	IS	max. body size	SES _{MNTD}	IS	-0.7531	0.1104
PC8	SES _{MPD}	IS	max. body size	SES _{MNTD}	IS	-0.8631	0.5222
all	SES _{MPD}	IS	phylogeny	SES _{MNTD}	IS	0.4983	0.2534
BDBM	SES _{MPD}	IS	phylogeny	SES _{MNTD}	IS	-0.4389	0.07484
PC16	SES _{MPD}	IS	phylogeny	SES _{MNTD}	IS	0.4251	-0.04182
PC8	SES _{MPD}	IS	phylogeny	SES _{MNTD}	IS	-0.1398	-0.08582
all	SES _{MPD}	IS	activity level (% still)	SES _{MPD}	TS	0.5737	0.6395
BDBM	SES _{MPD}	IS	activity level (% still)	SES _{MPD}	TS	-0.05002	-0.09641
PC16	SES _{MPD}	IS	activity level (% still)	SES _{MPD}	TS	0.9455	0.3544
PC8	SES _{MPD}	IS	activity level (% still)	SES _{MPD}	TS	0.2824	-0.00876
all	SES _{MPD}	IS	all	SES _{MPD}	TS	0.6855	0.7434
BDBM	SES _{MPD}	IS	all	SES _{MPD}	TS	0.06455	-0.09523
PC16	SES _{MPD}	IS	all	SES _{MPD}	TS	0.8148	0.1696
PC8	SES _{MPD}	IS	all	SES _{MPD}	TS	0.3131	-0.01036
all	SES _{MPD}	IS	antenna 1 length	SES _{MPD}	TS	0.669	0.5758
BDBM	SES _{MPD}	IS	antenna 1 length	SES _{MPD}	TS	-0.1597	-0.07545
PC16	SES _{MPD}	IS	antenna 1 length	SES _{MPD}	TS	0.9665	0.2191
PC8	SES _{MPD}	IS	antenna 1 length	SES _{MPD}	TS	0.2173	-0.06367
all	SES _{MPD}	IS	antenna 2 length	SES _{MPD}	TS	0.2702	0.1663
BDBM	SES _{MPD}	IS	antenna 2 length	SES _{MPD}	TS	0.2933	0.1001
PC16	SES _{MPD}	IS	antenna 2 length	SES _{MPD}	TS	0.5332	0.1346
PC8	SES _{MPD}	IS	antenna 2 length	SES _{MPD}	TS	0.3951	0.19
all	SES _{MPD}	IS	max. body size	SES _{MPD}	TS	0.008083	-0.09978
BDBM	SES _{MPD}	IS	max. body size	SES _{MPD}	TS	-0.4028	0.2487
PC16	SES _{MPD}	IS	max. body size	SES _{MPD}	TS	-0.6481	0.2202
PC8	SES _{MPD}	IS	max. body size	SES _{MPD}	TS	-0.4832	0.3009
all	SES _{MPD}	IS	phylogeny	SES _{MPD}	TS	0.7133	0.4193
BDBM	SES _{MPD}	IS	phylogeny	SES _{MPD}	TS	-0.0684	-0.09695
PC16	SES _{MPD}	IS	phylogeny	SES _{MPD}	TS	1.19	0.2268
PC8	SES _{MPD}	IS	phylogeny	SES _{MPD}	TS	0.3774	-0.02594
all	SES _{MPD}	IS	activity level (% still)	SES _{MPD}	IS	0.7103	0.4427

APPENDIX 5

BDBM	SES _{MPD}	IS	activity level (% still)	SES _{MPD}	IS	-0.2308	-0.06346
PC16	SES _{MPD}	IS	activity level (% still)	SES _{MPD}	IS	0.5185	-0.03458
PC8	SES _{MPD}	IS	activity level (% still)	SES _{MPD}	IS	0.02809	-0.09957
all	SES _{MPD}	IS	all	SES _{MPD}	IS	0.4887	0.1866
BDBM	SES _{MPD}	IS	all	SES _{MPD}	IS	-0.2212	-0.06255
PC16	SES _{MPD}	IS	all	SES _{MPD}	IS	-0.1104	-0.09669
PC8	SES _{MPD}	IS	all	SES _{MPD}	IS	-0.1772	-0.08079
all	SES _{MPD}	IS	antenna 1 length	SES _{MPD}	IS	0.4153	0.1446
BDBM	SES _{MPD}	IS	antenna 1 length	SES _{MPD}	IS	-0.3823	0.03213
PC16	SES _{MPD}	IS	antenna 1 length	SES _{MPD}	IS	-0.1288	-0.09468
PC8	SES _{MPD}	IS	antenna 1 length	SES _{MPD}	IS	-0.291	-0.03885
all	SES _{MPD}	IS	antenna 2 length	SES _{MPD}	IS	0.3208	0.07321
BDBM	SES _{MPD}	IS	antenna 2 length	SES _{MPD}	IS	0.08975	-0.09135
PC16	SES _{MPD}	IS	antenna 2 length	SES _{MPD}	IS	0.1165	-0.09483
PC8	SES _{MPD}	IS	antenna 2 length	SES _{MPD}	IS	0.1271	-0.08616
all	SES _{MPD}	IS	max. body size	SES _{MPD}	IS	-0.03733	-0.09779
BDBM	SES _{MPD}	IS	max. body size	SES _{MPD}	IS	-0.5686	0.2264
PC16	SES _{MPD}	IS	max. body size	SES _{MPD}	IS	-1.024	0.2754
PC8	SES _{MPD}	IS	max. body size	SES _{MPD}	IS	-0.7153	0.3125
all	SES _{MPD}	IS	phylogeny	SES _{MPD}	IS	0.3385	0.08061
BDBM	SES _{MPD}	IS	phylogeny	SES _{MPD}	IS	-0.2421	-0.04109
PC16	SES _{MPD}	IS	phylogeny	SES _{MPD}	IS	-0.09838	-0.09655
PC8	SES _{MPD}	IS	phylogeny	SES _{MPD}	IS	-0.1735	-0.07584

APPENDIX 6: Supplementary material for Chapter 3

Table A6.9. ZEN sites. Site names, codes, and geospatial coordinates.

Site	Name	Ocean	Margin	Latitude	Longitude
BB.A	Westside Park, Bodega Bay, CA, USA	Pacific	East	38.319755	-123.05514
BB.B	Sacramento Landing, Tomales Bay, CA, USA	Pacific	East	38.1496437	-122.90638
BC.A	Tsawwassen, BC, Canada	Pacific	East	49	-123.1
BC.B	White Rock, BC, Canada	Pacific	East	49	-122.8
CR	Sveti Duh, Croatia	Atlantic	East	44.2055713	15.4777338
ES.A	South Bay, VA, USA	Atlantic	West	37.265686	-75.812668
ES.B	Cobb Bay, VA, USA	Atlantic	West	37.31855	-75.789076
FI.A	Fårö, Finland	Atlantic	East	59.92025	21.7961833
FI.B	Ängsö, Finland	Atlantic	East	60.10785	21.70995
FR.A	Bouzigues, Etang de Thau, France	Atlantic	East	43.446971	3.661503
FR.B	Peyrac sur mer, Etang de Bages-Sigean, France	Atlantic	East	43.082895	2.973231
IR.A	Greyabbey, Northern Island, UK	Atlantic	East	54.531944	-5.569167
IR.B	Donegal, Ireland	Atlantic	East	55.2225	-7.701944
JN.A	Akkeshi-ko estuary, Hokkaido, Japan	Pacific	West	43.021167	144.903217
JN.B	Akkeshi-bay, Hokkaido, Japan	Pacific	West	43.052222	144.842699
JS.A	Ikunoshima, Hiroshima, Japan	Pacific	West	34.297834	132.91631
JS.B	Onoura, Hiroshima, Japan	Pacific	West	34.274018	132.26617
KO.A	Dongdae Bay, South Korea	Pacific	West	34.8946611	128.020272
KO.B	Koje Bay, South Korea	Pacific	West	34.8009722	128.583694
LI.1	Landscape Lab, Long Island, NY, USA	Atlantic	West	40.85762	-72.45119
LI.2	Tiana Beach, Long Island, NY, USA	Atlantic	West	40.83158	-72.54082
MA.A	Dorothy Cove, MA, USA	Atlantic	West	42.42014	-70.91544
MA.B	Niles Beach, MA, USA	Atlantic	West	42.59697	-70.6556
MX.A	San Quintin Bay, Baja California, Mexico	Pacific	East	30.419675	-115.96419
MX.B	Punta Banda Estuary, Baja California, Mexico	Pacific	East	31.7584722	-116.62278
NC.A	Middle Marsh, NC, USA	Atlantic	West	34.692458	-76.622589
NC.B	Shackleford Island, NC, USA	Atlantic	West	34.670544	-76.574561
NN.A	Misvaerfjorden, Norway	Atlantic	East	67.2147	15.0083
NN.B	Rövika, Norway	Atlantic	East	67.2667233	15.2560633
OR.A	Yaquina Bay, OR, USA	Pacific	East	44.6127333	-124.01413
OR.B	Coos Bay, OR, USA	Pacific	East	43.34625	-124.31828
PO.A	Culatatra, Portugal	Atlantic	East	36.997057	-7.82849
PO.B	Marim, Portugal	Atlantic	East	37.027333	-7.810105

APPENDIX 6

QU.A	Pointe-Lebel, QU, Canada	Atlantic	West	49.11237	-68.17593
QU.B	Baie-St-Ludger, QU, Canada	Atlantic	West	49.08696	-68.32041
RU.A	Seldianaya, Russia	Atlantic	East	66.4061111	33.7230556
RU.B	Nicolskaya, Russia	Atlantic	East	66.2858333	34.0025
SD.A	Shelter Island, San Diego Bay, CA, USA	Pacific	East	32.713756	-117.22547
SD.B	Coronado, San Diego Bay, CA, USA	Pacific	East	32.700762	-117.17289
SF.A	Point Molate, San Francisco Bay, CA, USA	Pacific	East	37.946557	-122.4185
SF.B	Point San Pablo, San Francisco Bay, USA	Pacific	East	37.978118	-122.40594
SW.A	Torseröd, Sweden	Atlantic	East	58.3131	11.5488
SW.B	Bökevik, Sweden	Atlantic	East	58.2488	11.4536
UK.A	Porth Dinllaen, Wales, UK	Atlantic	East	52.942282	-4.565173
UK.B	Penn Y Chain, Wales, UK	Atlantic	East	52.89856	-4.321868
VA.A	Goodwin Islands, Chesapeake Bay, VA, USA	Atlantic	West	37.2204206	-76.401335
VA.B	Allen's Islands, Chesapeake Bay, VA, USA	Atlantic	West	37.2543093	-76.437447
WA.A	Willapa Bay, WA, USA	Pacific	East	46.474	-124.028
WA.B	Dabob Bay, WA, USA	Pacific	East	47.809	-122.815

Table A6.10. Traits used in functional analyses of epifaunal community structure. Traits were selected for their variation both within and among peracarids and gastropods; only parental care and developmental mode are invariant within peracarids (all peracarids are brooding direct developers). Observed sizes were measured by sieving epifauna through a series of 9 sieves with pore sizes of 0.5, 0.71, 1, 1.4, 2, 2.8, 4, 5.6, 8 mm. Latitudinal range was calculated as the range in absolute values of latitude from the combined set of observations from OBIS and GBIF for a given species after using the CoordinateCleaner package to remove inland observations, centroids, and identical latitude-longitude pairs.

Trait	Type	Values	Interpretation	Transformation	Source
Eats			Dietary niche		Gross et al.
Microalgae	Bin.		partitioning		2022, MRK
Eats			Dietary niche		Gross et al.
Macroalgae	Bin.		partitioning		2022, MRK
Eats Seagrass	Bin.		partitioning		Gross et al.
Suspension			Dietary niche		2022, MRK
Feeder	Bin.		partitioning		Gross et al.
Detritivore	Bin.		Dietary niche		2022, MRK
			partitioning		

APPENDIX 6

Carnivore, Parasite, Scavenger	Bin.		Dietary niche partitioning		Gross et al. 2022, MRK
Parental Care	Cat.	broadcast spawner, brooder, lays egg case	Dispersal ability		MRK
Developmental Mode	Cat.	lecithotrophic, planktotrophic, direct developer	Dispersal ability Susceptibility to predators, ability to occupy physical space, competitive ability		MRK
Mode Observed Size	Cont.	0.5 - 8 mm	Susceptibility to predators, ability to occupy physical space, competitive ability	log	Empirically measured
Maximum Observed Size	Cont.	0.5 - 8 mm	Susceptibility to predators, ability to occupy physical space, competitive ability	log	Empirically measured
Mean Observed Size	Cont.	0.5 - 8 mm	Susceptibility to predators, ability to occupy physical space, competitive ability	log	Empirically measured
Maximum Size (Literature) Latitudinal Range	Cont.	1 - 140 mm	Susceptibility to predators, ability to occupy physical space, competitive ability	log	Light & Smith, Gastropods. com, etc.
Mean Latitude	Cont.	0 - 72.569°	Thermal niche		OBIS, GBIF
Marine	Cont.	13.719 - 66.183°	Thermal niche		OBIS, GBIF
Brackish	Bin.		Salinity niche		WoRMS
Freshwater	Bin.		Salinity niche		WoRMS

Table A6.11. Predictors used in random forest model of the log-transformed ratio of peracarid relative abundance to gastropod relative abundance (log-ratio). Mean in-situ measurements are derived from averaging across measurements from 20 sites; measurements from Bio-ORACLE are yearly averages measured between 2002-2009 within a 10-km radius of each site; measurements from World Ocean Database (WOD) were spatially interpolated based on sea surface measurements in 2009.

Predictor	Values	Transformation	Source
Ocean	Pacific, Atlantic	None	

APPENDIX 6

Coast	West Pacific, East Pacific, West Atlantic, East Atlantic	None	
Margin	West, East	None	
In-Situ Temperature (°C)	8 - 35	None	In situ
Salinity (ppt)	6.5 - 40	None	In situ
Genotypic Richness (mean Rozenfeld distance)	0.11 - 1.0	None	In situ
Allelic Richness (avg. number of alleles per locus, normalized to 7 genets)	1.29 - 6.72	Squared	In situ
Epiphyte Load (g cm ⁻² eelgrass)	0.00554072 - 1.071013	log	In situ
Macroalgal Abundance (g m ⁻²)	0 - 4172.653	log + 1	In situ
Eelgrass morphology PC1 (62.09%)	-6.06524939 - 2.30096651	None	In situ
Eelgrass morphology PC2 (24.34%)	-1.48402338 - 3.59837339	None	In situ
Total Seagrass Biomass (g)	45.74725 - 1364.95000	log	In situ
Mean Leaf % N	1.092617 - 3.049590	None	In situ
Mean Leaf % C	31.59211 - 42.03824	None	In situ
Predation on Amphipods	0.2 - 1	arcsin	In situ
Predation on Gastropods	0 - 0.8	logit	In situ
Predation on Kale	0 - 0.9	None	In situ
Predation on Dried Squid	0 - 1	None	In situ
Mean Total Epifaunal Abundance	0.00 - 795.55	log	In situ
Site Epifaunal Richness	0 - 34	log	In situ
Calcite	0.00031100 - 0.02810775	log	WOD
Mean Chl A	0.613 - 24.016	log	Bio-Oracle
Nitrate	0.05533333 - 10.23499997	square root	WOD
Phosphate	0.034800 - 2.172433	log	WOD
Mean PAR	27.34367 - 42.52075	None	Bio-Oracle
pH	7.705167 - 8.311857	None	Bio-Oracle
Silicate	0.93350 - 39.64817	log	WOD
Maximum SST (°C)	12.6166 - 29.6965	log	Bio-Oracle
Mean SST (°C)	4.0669 - 21.3620	None	Bio-Oracle
SST Range (°C)	3.573667 - 22.870750	None	Bio-Oracle
Peracarid Richness	0 - 21	log + 1	In situ
Gastropod Richness	1 - 17	log	In situ

Table A6.4. Results of generalized linear models examining the effects of eelgrass genetic diversity and morphology on the species richness of peracarids and gastropods across global eelgrass beds. Allelic richness refers to the average number of alleles per locus normalized to 7 genets, while genotypic richness refers to the mean Rozenfeld distance between individuals in a site. PC1 is positively correlated with shorter, thinner shoots, while PC2 is positively correlated with more dense shoots and greater aboveground biomass. Bolded rows indicate significant predictors at $\alpha = 0.05$.

	Predictor	χ^2_1	p	Effect size	pseudo R^2
Peracarid richness	Allelic Richness	37.258	1.035e-09	0.028996	0.2076344
	Genotypic Richness	19.88	8.247e-06	1.125	0.1107829
	PC1	4.8839	0.02711	-0.0652	0.0271942
	PC2	17.978	2.235e-05	0.1907	0.100195
Gastropod richness	Allelic Richness	2.271	0.1318	0.009235	0.02300632
	Genotypic Richness	4.8883	0.02704	0.7009	0.04951779
	PC1	12.976	0.0003154	0.16457	0.1314531
	PC2	0.78951	0.3742	0.05649	0.00799295

Table A6.5. Results of linear models examining the effects of eelgrass genetic diversity and morphology on the log-transformed total site-level abundance of peracarids and gastropods across global eelgrass beds. Allelic richness refers to the average number of alleles per locus normalized to 7 genets, while genotypic richness refers to the mean Rozenfeld distance between individuals in a site. PC1 is positively correlated with shorter, thinner shoots, while PC2 is positively correlated with more dense shoots and greater aboveground biomass. Bolded rows indicate significant predictors at $\alpha = 0.05$.

	Predictor	F	p	Effect size	R^2
log(Peracarid abundance + 1)	Allelic Richness	8.968	0.00433	0.07691	0.1399
	Genotypic Richness	5.191	0.0272	2.921	0.07879
	PC1	4.722	0.0347	-0.3904	0.0706
	PC2	9.963	0.00276	0.8638	0.1546
log(Gastropod abundance + 1)	Allelic Richness	3.171	0.0813	-0.04703	0.04242
	Genotypic Richness	3.162	0.0817	-2.266	0.04226
	PC1	6.533	0.0138	0.4402	0.1015
	PC2	0.7402	0.394	0.2503	-0.005331

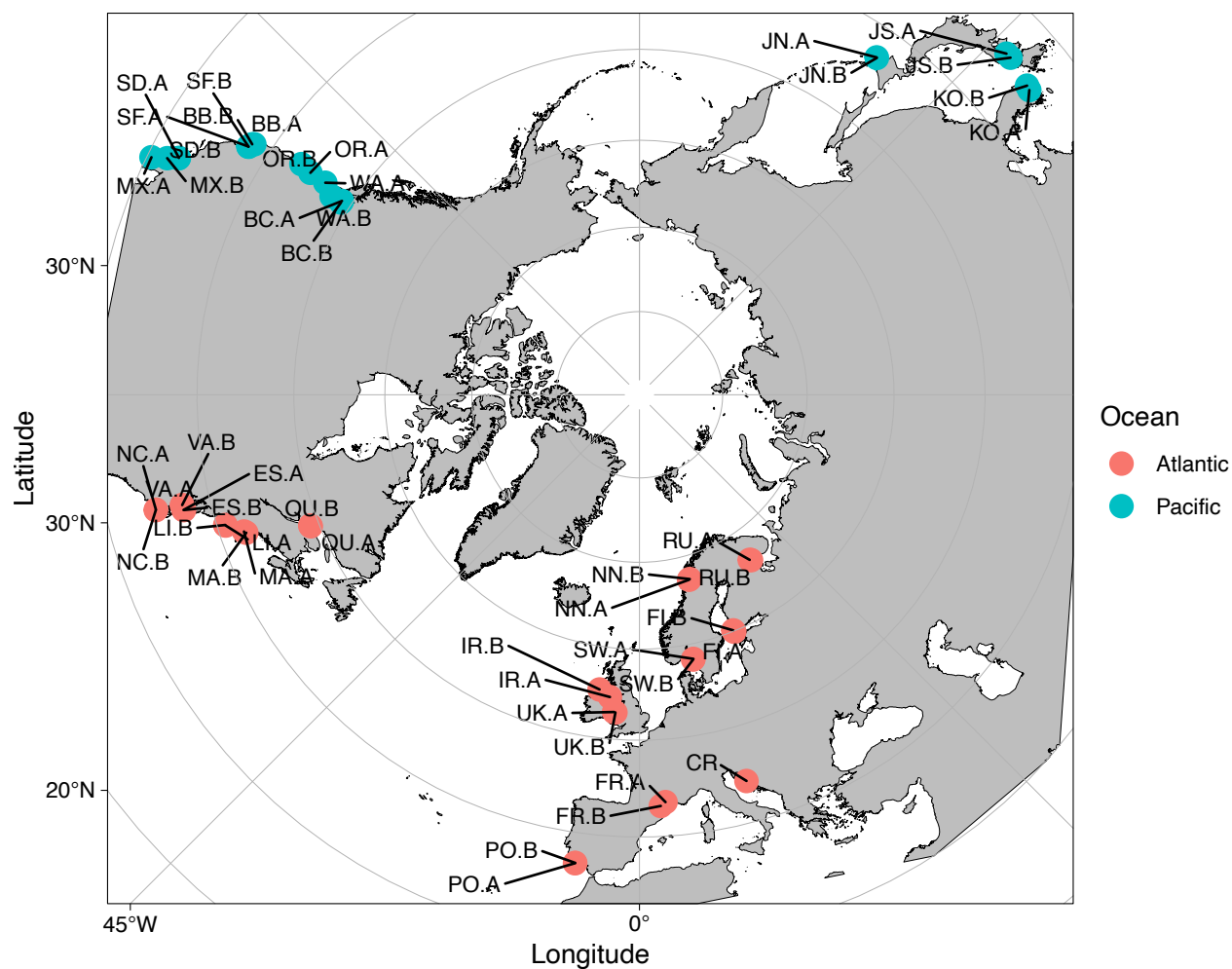


Figure A6.6. ZEN sites in the Atlantic (pink) and Pacific (blue) oceans. See Table A6.1 for site codes.

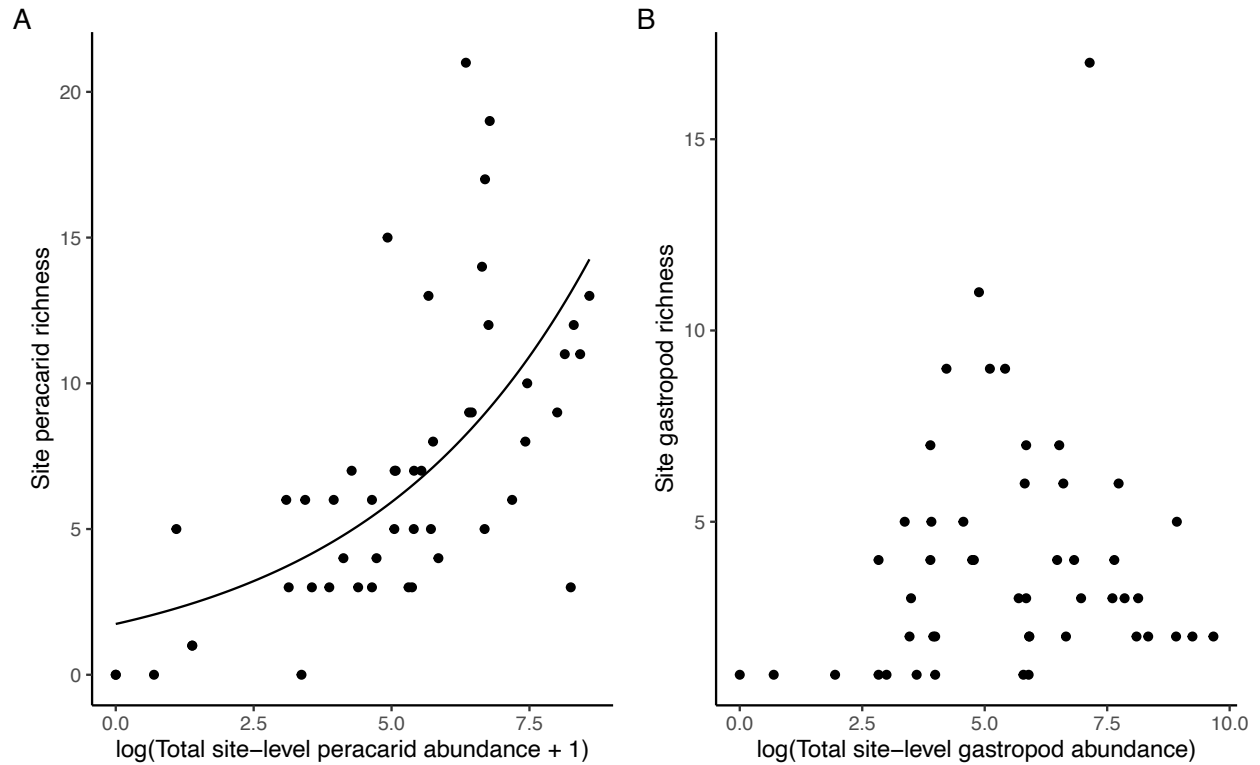


Figure A6.2. Relationships between total site-level abundance (calculated as the sum of plot-level abundances standardized by eelgrass biomass) and species richness for peracarids (A) and gastropods (B) in eelgrass epifaunal communities. Species richness only increased with increasing abundance for peracarids ($\chi^2_1 = 77.038$, $p < 0.001$); gastropods showed no significant trend.

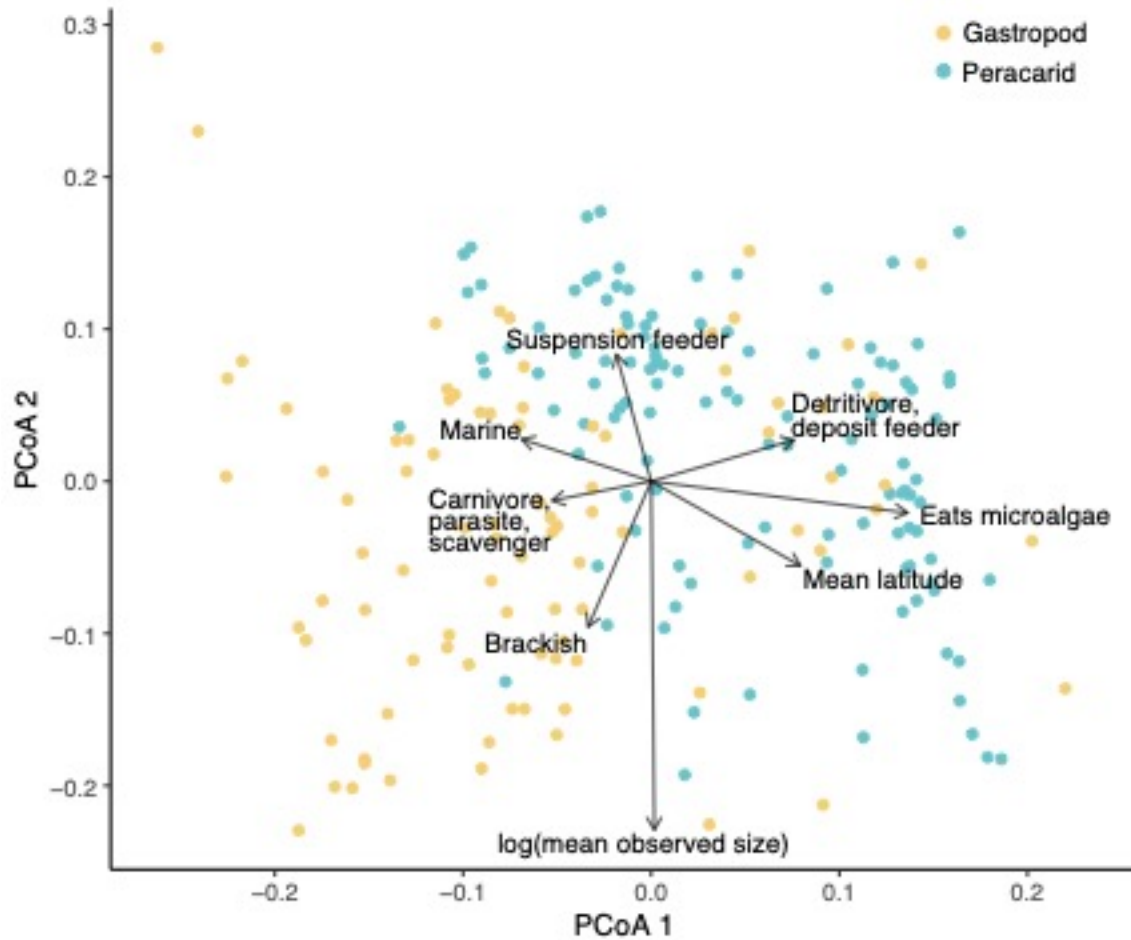


Figure A6.3. Principle components analysis (PCoA) biplot of gastropod and peracarid species in global eelgrass beds. Distances between points (species) are based on weighted Gower distances, which take into account among-species variation in continuous, binary, and categorical traits. For clarity, not all traits are included in this ordination.

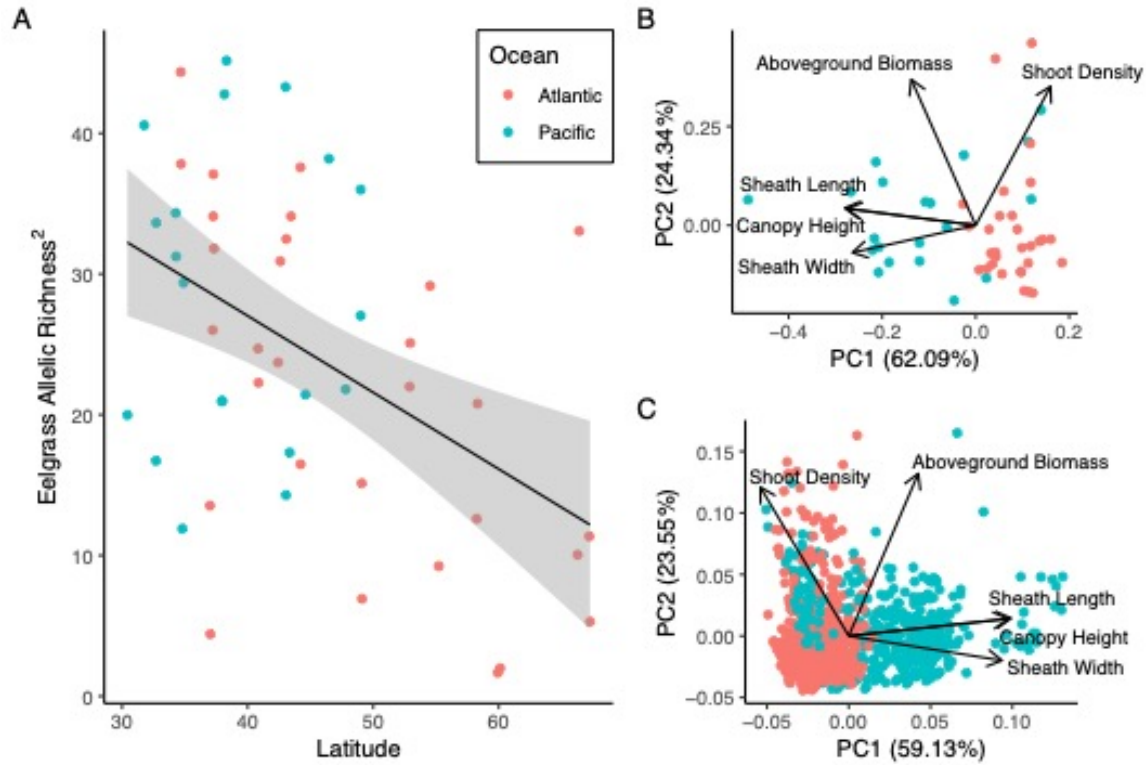


Figure S4. Variation in eelgrass allelic richness and morphology across ocean basins. Allelic richness declined with latitude across sites in both oceans (A; $F_{1,48} = 13.36$, $p = 0.0006375$), and was greater on average in the Pacific, although this was marginally nonsignificant ($F_{1,48} = 3.804$, $p = 0.05699$). Eelgrass morphological variation was greater in the Pacific than in the Atlantic when looking across sites (B) and across plots within sites (C).