Taxonomic and functional assessment of mesopredator diversity across an estuarine habitat mosaic

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Abstract. A long-standing rule in ecology is that structural complexity increases abundance and diversity of organisms, but this paradigm glosses over potential trait-specific benefits of habitat structure across different regional species pools. We tested this idea using multiple response variables emphasizing taxonomic and functional diversity in seagrass-vegetated, edge, and unvegetated habitats across three estuaries in Washington State (USA). We also used these variables in tandem to evaluate functional redundancy as a proxy for ecosystem resistance and resilience. The estuaries spanned a twofold range in richness of mesopredatory fishes and decapods. Increases in per-sample abundance with habitat structure were confined to three of seven functional groups, specifically those occupying the water column or directly associated with seagrass shoots. Consequently, seagrass reduced mesopredator diversity by reducing evenness. Habitats differed in mesopredator assemblages despite their spatial proximity (~3 m), supported by multivariate analyses performed at functional and taxonomic resolutions, but site differences were less apparent functionally than taxonomically. Functional redundancy did not differ by habitat, but increased with the richness of the regional species pool. Edge habitats were generally intermediate in community structure, per-sample abundance, and diversity between seagrass and unvegetated habitats. Structural complexity provided a trait-specific enhancement of abundance, and this pattern applied across species pools. Because seagrass benefits species with certain traits, management focused on the low-intertidal estuarine habitat mosaic, rather than a particular habitat type, and on places where redundancy is already low, best supports mesopredator diversity and function.

Key words: functional diversity; mesopredators; seagrass; structured habitat; *Zostera marina*.

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INTRODUCTION

An open question exists concerning the value of using taxonomic (species-level) vs. functional (trait-level) information to describe responses of species assemblages to environmental conditions and their effects in a food web context (Thrush et al. 2006, Lefcheck and Duffy 2015). Functional approaches are arising in ecology as ways to find broad patterns across idiosyncratic local assemblages, to understand functional redundancy and the risks associated with species losses across assemblages of different richnesses, and because functional diversity may augment ecosystem function (Hooper et al. 2005, Micheli and Halpern 2005, Mouillot et al. 2013a). A long-standing rule in ecology is that abundance and species richness increase with habitat structural complexity (MacArthur and MacArthur 1961), which makes habitat structure an ideal gradient for comparing assemblages using taxonomic and functional lenses. Here, we examine mesopredator community structure along

gradients of seagrass, an ecologically relevant biogenic structure widely acknowledged to underlie fisheries production (Heck et al. 2003, Blandon and Ermgassen 2014) and to harbor strong food web interactions (Duffy et al. 2005, 2015a, b).

Species assemblages are typically characterized in two basic ways to examine the influence of habitat characteristics on functional attributes of an assemblage: indices of functional diversity or functional groups. Rao's quadratic entropy (Q) is one of the most commonly used functional diversity indices and incorporates both trait richness and evenness. A decrease in Q may indicate dominance by a few traits conferring specialization to a particular habitat type, while an increase in Q may indicate greater niche availability, as in structured habitats (Botta-Dukat 2005). While diversity indices like Rao's are typically based on suites of traits that characterize species, species diversity indices may also be applied to functional groups to produce a related index (Micheli and Halpern 2005). Functional groups are often derived a priori based on gross morphology, feeding guild, reproductive mode, or habitat use (Nagelkerken and van der Velde 2004, Elliott et al. 2007, Villeger et al. 2008), but may also be derived a posteriori based on clusters in multivariate trait space (e.g., Aguilar-Medrano and Calderon-Aguilera 2016). Grouping species into functional groups, especially those based a posteriori on traits of interest, allows researchers to examine how particular habitat types may facilitate or exclude specific sets of traits (Verberk et al. 2013).

Through a multivariate lens, these functional perspectives are expected to give a more consistent test of community structure across environmental gradients than taxonomic perspectives (Nagelkerken and van der Velde 2004, Villeger et al. 2008, Wong and Dowd 2015, Aguilar-Medrano and Calderon-Aguilera 2016). Historical biogeographic and evolutionary processes determine the broad-scale distributions of species across sites, often comprising functionally identical but taxonomically distinct local assemblages, while the effects of habitat structure and species interactions tailor the traits in the species pool within a given habitat to produce the final assemblage (Pavoine and Bonsall 2011, Adler et al. 2013, Mouillot et al. 2013a, Kraft et al. 2015). Thus, by looking at species' functional traits across geographically distinct areas, one may be able to specifically pick out the role of structurally complex habitats like the interiors of seagrass beds in forming distinct communities.

Functional redundancy, defined as "a characteristic of species within an ecosystem where certain species contribute in equivalent ways to an ecosystem function such that one species may substitute for another" (Froese and Pauly 2015), has often been used as a measure of ecosystem resiliency and resistance to disturbance (Folke et al. 2004, Tilman et al. 2006, Downing et al. 2012); disturbances that remove particular species might have a smaller impact on an ecosystem function if the remaining species perform the ecosystem function in the same capacity as the extirpated species. The relationship between species and functional diversity determines the degree of functional overlap and redundancy and informs hypotheses about resilience and resistance to disturbance. At one extreme, a 1:1 relationship between functional and species diversity indicates that each species performs a unique function. At the other end, if functional diversity increases minimally with species diversity, species exhibit a high degree of overlap in functional traits. These relationships are expected to plateau as additional species have similar functional traits to those already present in the community (Micheli and Halpern 2005). Measures of ecosystem resiliency such as functional redundancy are useful in the context of resource management, in that they can help distinguish priority species, and guide species conservation plans and habitat protection policies (Micheli and Halpern 2005).

The purpose of this research was to test the paradigm that habitat structure fosters greater diversity and abundance by examining functional and taxonomic diversity in tandem, and using the relationships between these values to draw conclusions about community resilience. Our focal organisms were estuarine mesopredators, which represent a key trophic link, feeding on mesograzers (gastropods and crustaceans) that can limit algal blooms, and consumed by top predators of larger body size that are often exploited commercially (Heck et al. 2003, Hughes et al. 2014, Duffy et al. 2015a). We asked (1) "Do structurally complex habitats differentially benefit mesopredators with some functional

traits over others, and is this consistent across regional species pools?" and (2) "Are structurally complex and/or higher-richness sites or habitats more functionally redundant, predicting greater resiliency?"

Over the past 130 yr, an estimated >50,000 km^2 of seagrass meadow has been lost throughout the world (Waycott et al. 2009). Natural resource agencies are attempting to rectify this trend through conservation and restoration efforts. Understanding how structure and function of mesopredator communities change along a gradient of structural

complexity is particularly important for managers to design restoration projects and prioritize conservation sites that target specific species for protection.

METHODS

Study sites

Sampling for mesopredators was done at three sites spanning 186 km in Washington State, USA (Fig. 1; Appendix S1: Table S1). These sites differ in depth ranges and influence by freshwater, and
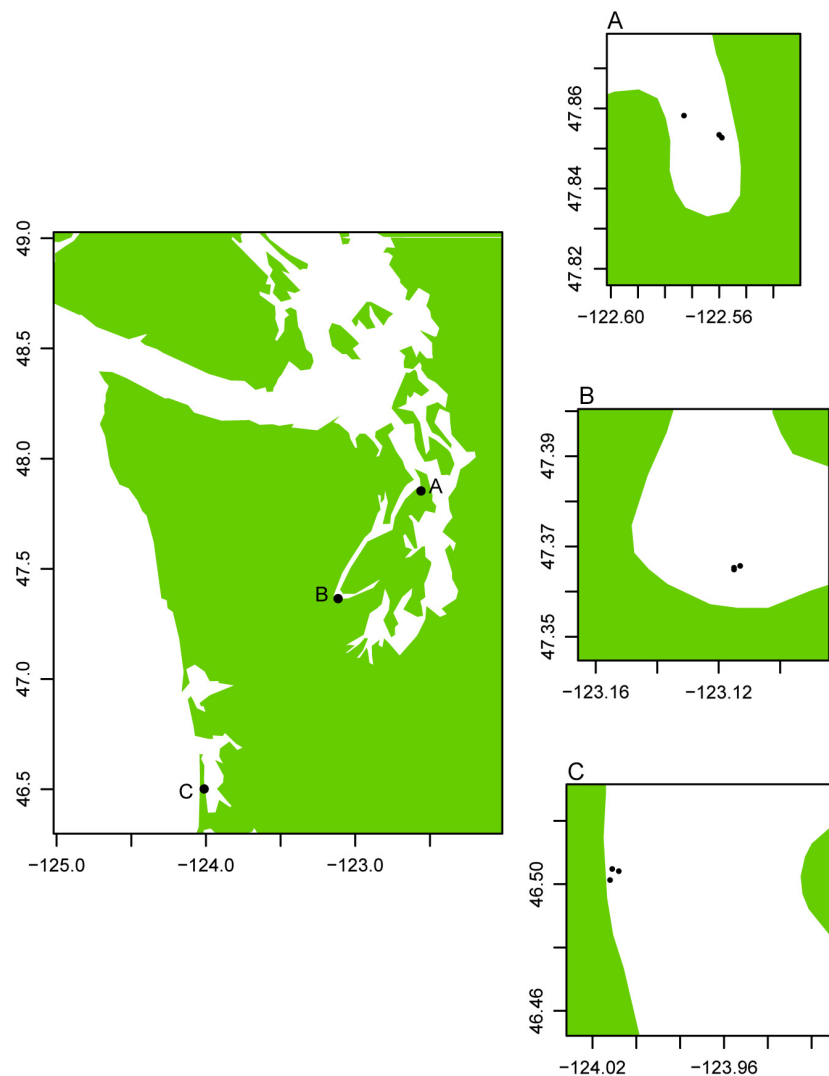

Fig. 1. Maps of sampling region and sampling sites. Points on the larger map represent sampling sites shown in the smaller maps at right; points on smaller maps represent sampling subsites, each containing unvegetated, edge, and eelgrass–vegetated habitats. (A) N fjord; (B) S fjord; (C) Coastal.

consequently in their complement of mesopredator species. Willapa Bay (hereafter referred to as Coastal; 46.52° N, 123.99° W) is a coastal estuary formed at a drowned river mouth, with an average depth of 3.2 m (Hickey and Banas 2003). Several rivers fed by winter rains influence its salinity, which rarely exceeds 27 psu at the study site. Port Gamble Bay (N fjord, 47.84° N, 122.58° W) and the Skokomish River delta (S fjord, 47.36° N, 123.13° W) are at the north and south, respectively, of Hood Canal, an estuarine fjord that is long (100 km), deep (54 m), and narrow, usually <2 km wide (Williams 2001). These fjord sites occur at two distinct positions along a strong gradient in environmental conditions, with salinity and dissolved oxygen lower at the S fjord than at the N fjord site, and temperature higher (Kawase and Bang 2013, Keister and Tuttle 2013). All study sites have a mesotidal regime, given a mean diurnal tidal range of 2.8–3.5 m, which exposes intertidal eelgrass beds (*Zostera marina*) on extreme low tides. Replication occurred within each site, where we selected three subsites, each containing three intertidal habitat types (eelgrass, edge, and unvegetated tideflat). These habitats represent a gradient of structural complexity; eelgrass shoot density was roughly half as dense on edges as inside patches (Appendix S1: Table S2, Fig. S1). Aboveground biomass of eelgrass was similar across sites (63 g DW/m^2; Appendix S1: Table S2, Fig. S2).

Sampling of fishes and decapods

Samples were collected in July and August 2015 in a custom beach seine when the water level on the target habitat patches was below 1 m deep. The seine sampled a circular area of 11 m^2 (Appendix S1: Fig. S3). Animals were counted, identified to the lowest possible taxonomic level (typically species), and released. Of these, 10 individuals per species were measured to the nearest 0.5 cm (total length for fish and shrimp, carapace width for crabs) to be incorporated into functional trait analyses. Two seines were carried out in each habitat patch.

Functional traits and functional groups

Each mesopredator was evaluated for a suite of nine functional traits based on published literature including FishBase (Froese and Pauly 2000, 2015). These traits included Estuarine Use, Reproductive Mode, and Feeding Mode Functional Groups (EUFG, RMFG, and FMFG, Elliott et al. 2007), and others emphasizing morphology, feeding habits, and body size (Table 1), that could be broadly applied across fishes and decapods. Additional references for trait data are provided in Appendix S2. We used similarities based on the nine functional traits to arrange species into a functional dendrogram based on Gower distances and cut the dendrogram at a Gower height of 0.475 to produce seven discrete species clusters as functional groups (Fig. 2).

Table 1. Traits used for quadratic entropy (*Q*) analyses and functional group designation.

Trait	Type	Values/Range
Trophic level	Continuous numerical	2.99–4.40
Vertical distribution	Categorical	Benthic, epifaunal/eelgrass associate, pelagic
Morphology	Categorical	Anguilliform, shrimp, compressed, fusiform, majoid, cottoid, depressed, cancroid
Median size	Continuous numerical	Total length for fishes and shrimps, carapace width for crabs; 0.5–33 cm
Maximum size	Continuous numerical	Total length for fishes and shrimps, carapace width for crabs; 0.5–33 cm
Prey phyla	Discrete numerical	1–6
Estuarine Use Functional Group	Categorical	Semi-anadromous (SA), marine straggler (MS), estuarine resident (ER), estuarine-dependent marine migrant (MMD), opportunist marine migrant (MMO), freshwater migrant (FM), estuarine migrant (EM), anadromous (AN)
Reproductive Mode Functional Group	Categorical	Viviparous (V), egg-guarder (Og), egg-brooder (Os), unguarded benthic eggs (Ob), unguarded eggs attached to structure (Ov), pelagic eggs (Op)
Feeding Mode Functional Group	Categorical	Opportunistic feeder (OP), epibenthivore (ZB-E), generalist zoobenthivore (ZB), detritivore (DV), zooplanktivore (ZP), hyperbenthivore (ZB-H), omnivore (OV), infaunal feeder (ZB-I)

Notes: Estuarine Use, Reproductive Mode, and Feeding Mode Functional Groups are based on Elliott et al. (2007). Species for which trait values were not available were assigned values based on species with similar diets, taxonomic position, and/or size.
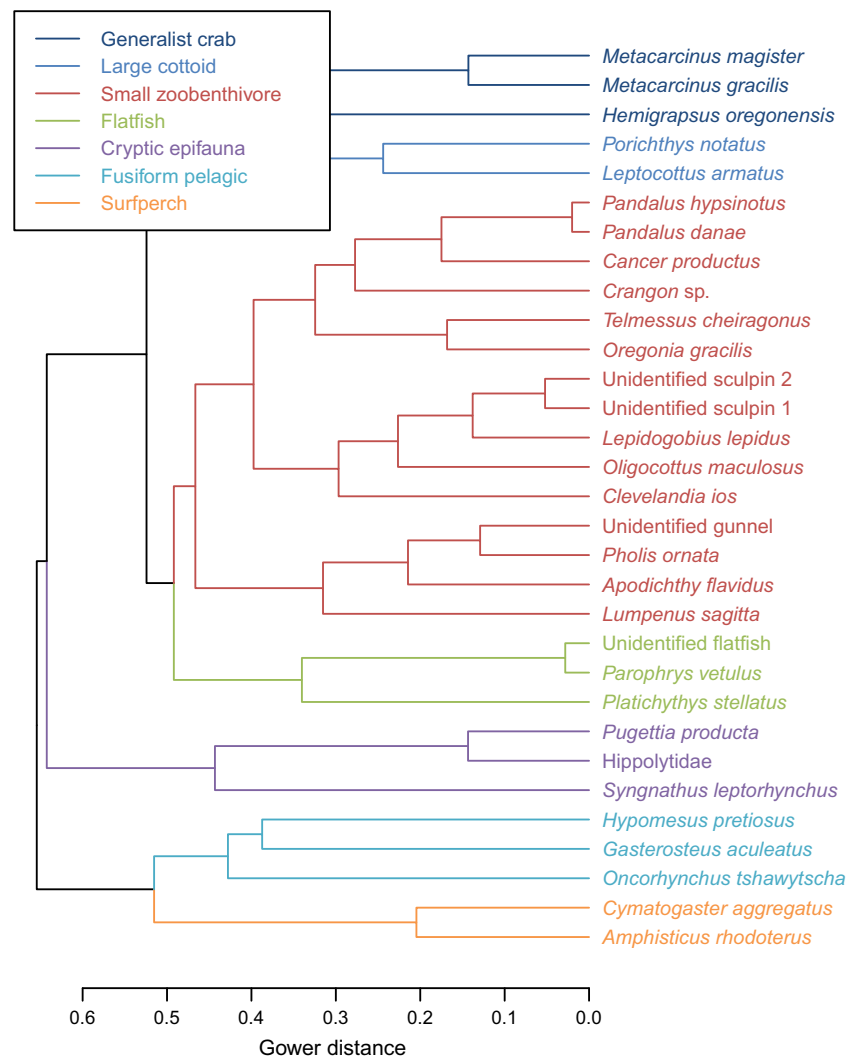
Fig. 2. Functional dendrogram of mesopredators observed in seines, clustered by Gower distance. The dendrogram was cut at an arbitrary distance of 0.475 to form seven functional groups.

Mesopredator analyses—abundance

Mesopredator abundance per seine was analyzed in aggregate, including all fishes and decapods, and as the number in each functional group. Abundance per seine (total and subdivided by functional group) was the response variable in linear mixed-effects models including site, habitat, and their interaction as fixed effects and subsite as a random effect to account for two seines in each replicate and the spatial juxtaposition of habitat types within subsites. To meet normality assumptions, abundance was log-transformed. Due to the linear mixed-effects structure, significance of fixed effects was determined by likelihood ratio tests comparing models with and without each main effect and the interaction. Post hoc comparisons of habitats were made using Tukey's tests on models including fixed effects only.

Univariate analyses of taxonomic and trait diversity

Diversity was initially calculated for each seine as the Shannon-Weiner diversity index (H'), applied both at the species level and to functional groups. Further, we calculated functional trait diversity as Rao's quadratic entropy (Q, Botta-Dukat 2005).

A linear mixed-effects model was applied to each diversity index (species, functional group, trait), with habitat, site, and their interaction as fixed effects and subsite as a random effect. Significance was determined using likelihood ratio tests to compare more vs. less complex models.

Functional redundancy analyses

We measured functional redundancy by using ANCOVAs to evaluate the relationships between functionally derived and taxonomically derived Shannon-Weiner indices, using each seine as a sample. Separate analyses were carried out to test for differences in these relationships within groups of seines grouped by habitat and by site. Model intercepts were fixed at zero. We also compared the slopes of these relationships to a slope of 1 (zero functional redundancy) using one-tailed *t* tests for each habitat and site. These analyses were conducted under the assumption that the relationships between diversity indices were in their linear phases, below the plateau predicted by Micheli and Halpern (2005).

Multivariate analyses of mesopredators

Non-metric multidimensional scaling (NMDS) analyses were conducted on Bray-Curtis dissimilarities to describe and visualize community variation. Because certain samples exhibited high dominance of one or two species, we log($n + 1$)-transformed the species abundance data per seine to downweight the most abundant species and allow rare species to exert more influence on distance calculation (Clarke and Warwick 2001). A permutational multivariate ANOVA (PERMANOVA, maximum permutations = 9999) was carried out on the sample-by-species abundance matrix (each seine as a sample) to test whether mesopredator communities differed according to habitat, site, and their interaction. Subsites were treated as strata within sites to ensure that randomizations occurred only within habitat patches per subsite.

In addition to the above analyses based on taxonomy, trait-based approaches were taken by performing similar NMDS analyses using data as (1) log($n + 1$)-transformed per-seine abundance by functional group and (2) log($n + 1$)-transformed per-seine abundance by trait (Table 1; Hewitt et al. 2016). We expected that the PERMANOVAs for traits and functional groups would show an increased amount of variation attributed to habitat, and reduced amount of variation attributed to site, relative to the species-based analyses. All analyses were carried out using the lme4, FD, and vegan packages in R (Bates et al. 2014, Laliberté et al. 2014, Oksanen et al. 2015, R Core Development Team 2015).

RESULTS

Mesopredator abundance

Sites differed substantially in mesopredator species richness, with 14 species identified at the Coastal site, 15 at S fjord, and 27 at N fjord, but all seven functional groups occurred at all sites. Overall abundance per seine was 8.5 times greater in eelgrass than in unvegetated habitats at all three sites, but edges showed less consistency, sometimes grouping with eelgrass and at other sites containing mesopredators at intermediate abundance per seine. Overall, a significant site-by-habitat interaction highlighted differences in mesopredator response to edges across sites (Fig. 3; Appendix S1: Table S3). When examined by functional group, eelgrass contained more surfperches (40.3×), fusiform pelagic species (41.5×), and cryptic eelgrass climbers (4.4×) than unvegetated habitats, on average. Other functional groups showed no significant habitat associations (Fig. 3; Appendix S1: Table S4). Functional group representation also varied across sites, with the Coastal site relatively more represented by surfperches and generalist crabs, and the N fjord site containing relatively more small zoobenthivores and cryptic eelgrass climbers (Fig. 3; Appendix S1: Table S4).

Mesopredator diversity

Diversity metrics reflected that eelgrass harbored high abundance of one or a few dominant species per seine, which reduced *Q* and Shannon-Weiner indices. Consequently, these indices were lowest in eelgrass across taxonomic, functional group, and trait-based approaches to defining diversity. For species diversity, *H'* was significantly influenced by site, habitat, and their interaction (Appendix S1: Table S3). *H'* was highest in unvegetated, intermediate on edges, and lowest in eelgrass for Coastal and S fjord, while N fjord showed equal diversity in unvegetated and edge habitat and low diversity in eelgrass (Fig. 4A).
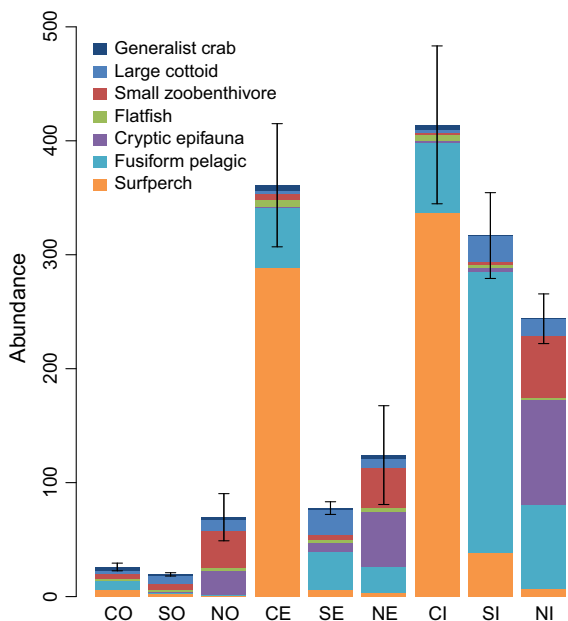
Fig. 3. Total abundance, subdivided into seven a posteriori functional groups. Bars represent site × habitat pairings, arranged from left to right by habitat. C = Coastal; S = S fjord; N = N fjord; O = unvegetated; E = edge; and I = vegetated. Error bars represent the standard error of total abundance (six seines per habitat at each site).

When calculated for functional groups, rather than species, diversity showed the same patterns (Fig. 4B; Appendix S1: Table S3).

Trait diversity (Q) was significantly related to habitat, site, and their interaction (Fig. 4C; Appendix S1: Table S3). Across habitats, Q was higher in unvegetated mudflat than in eelgrass or on edges, which were not significantly different. Q was significantly higher at N fjord than at the Coastal site.

Functional redundancy

The slope of the relationship between taxonomic and functional Shannon-Weiner diversity did not differ significantly among habitats, and averaged 0.85 ± 0.017. This slope was significantly less than 1 ($t_{0.05(1)53} = -9.28$, $P < 0.001$), indicating significant functional group overlap between species in all habitats. Sites differed significantly from each other in terms of the relationship between functional and taxonomic diversity indices ($F_{2,51} = 28.12$, $P < 0.001$; Fig. 5); at the

Coastal site, slope was 0.97 ± 0.025, S fjord 0.89 ± 0.021, and N fjord 0.76 ± 0.017. Only the fjord sites showed that slopes were significantly different from 1 (S fjord: $t_{0.05(1)17} = -5.054$, $P < 0.001$; N fjord: $t_{0.05(1)17} = -14.27$, $P < 0.001$), indicating significant functional redundancy.

Multivariate analyses of mesopredators

Across taxonomic-, functional group-, and trait-based assemblages, eelgrass and unvegetated habitats were distinct, while edge was intermediate (Fig. 6). Both habitat and site were significant factors influencing taxonomic structure in multivariate analyses, but site explained nearly twice as much of the variation in structure as habitat (habitat: $R^2 = 0.18$, pseudo-$F_{2,45} = 9.7$, $P < 0.001$; site: $R^2 = 0.35$, pseudo-$F_{2,45} = 18.6$, $P < 0.001$; Fig. 6A). Site and habitat remained significant in determining community structure at the level of functional groups, but contributed more equally to the variation in structure than they did at the species level (habitat: $R^2 = 0.21$, pseudo-$F_{2,45} = 10.23$, $P < 0.001$; site: $R^2 = 0.29$, pseudo-$F_{2,45} = 14.2$, $P < 0.001$; Fig. 6B). Similarly, at the functional trait level, site and habitat contributed equally to variation in community structure ($R^2 = 0.26$, pseudo-$F_{2,45} = 13.89$, $P < 0.001$, for both site and habitat; Fig. 6C). There was no significant site-by-habitat interaction for any of these multivariate analyses.

Discussion

Mesopredators share a set of functional traits within estuarine environments, which is evident by virtue of their being grouped together based on size and collective diet. Despite this, we distinguished seven functional groups within mesopredators that differed in traits related to feeding habits, life history, and morphology (Table 1, Fig. 2). Distinguishing functional groups revealed that the enhanced abundance of mesopredators per seine with habitat structure was primarily due to habitat selectivity of surfperches and pelagic fusiform fishes. Most other functional groups were found in statistically indistinguishable abundances per seine across the gradient of structural complexity. Because of differential enhancement of a few functional groups by eelgrass, functional and taxonomic diversity indices actually declined with structural complexity (Fig. 4), as assemblages in eelgrass contained similar numbers of
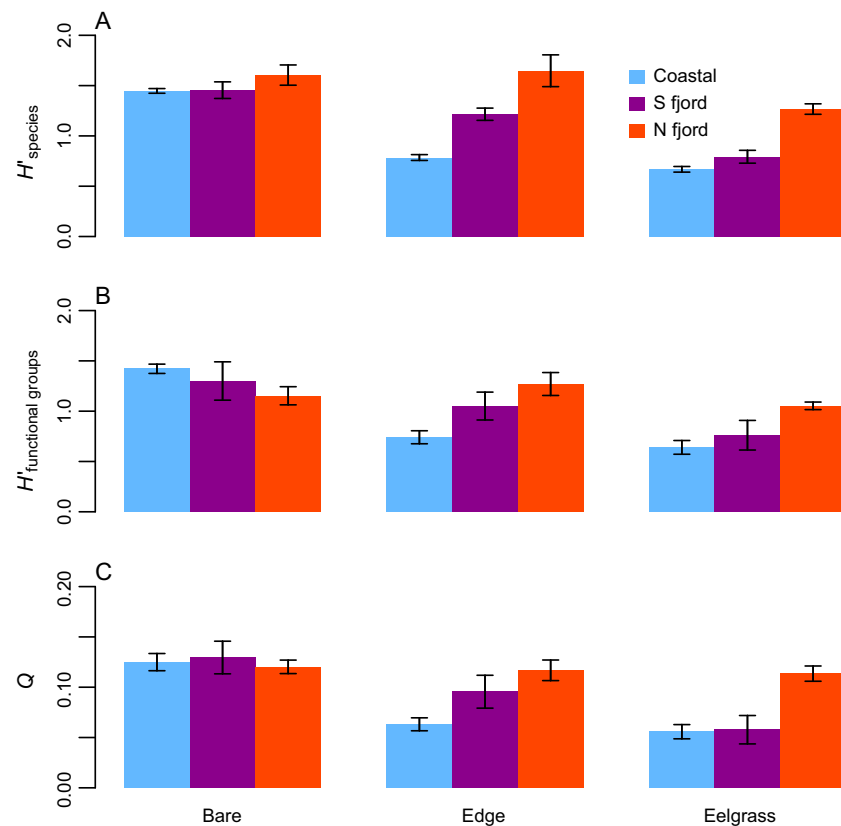
Fig. 4. Diversity metrics in seines. (A) Shannon-Weiner diversity in seines, based on individual species; (B) Shannon-Weiner diversity in seines, based on functional groups (Fig. 2); (C) Rao's quadratic entropy in seines, based on functional traits (Table 1). Quadratic entropy and species-based Shannon-Weiner responded significantly to site, habitat, and their interaction; functional group-based Shannon-Weiner responded significantly to habitat and a habitat-by-site interaction. Error bars represent standard error (six seines per habitat at each site).

species but with less evenness across species in comparison with mesopredators in bare areas (Fig. 3). Overall, in this study, functional traits provided novel insight into how organisms with different traits respond to eelgrass, relative to combining mesopredators as a whole. On the other hand, functional and species diversity showed similar patterns in their response to the structural complexity of lower intertidal habitats.

A broadly accepted paradigm is that seagrass harbors more fish and decapods than adjacent unvegetated habitats (Heck et al. 1989, Dean et al. 2000, Murphy et al. 2000, Hughes et al. 2002, Ferraro and Cole 2010, Boyer et al. 2015). Our results support this idea despite the close spatial proximity of habitats forming a gradient of structural complexity (Fig. 3). We found no additional benefit of habitat edge; in both multivariate and

univariate analyses, this habitat either grouped with fully vegetated, or was intermediate (Fig. 6). In contrast, our results in terms of diversity highlight that some mesopredators may benefit much more from structural complexity than others (Fig. 4). These tended to be cryptically colored species or those that inhabit the water column, for which floating aquatic vegetation would provide the most shelter from predators as well as easily accessible food in the form of canopy mesograzers.

Some studies from Washington State have presented exceptions to the paradigm of greater mesopredator abundance inside eelgrass than outside. Two studies from Willapa Bay reported no difference in fish and decapod multivariate structure among habitats differing in above-ground structure (Hosack et al. 2006, Dumbauld et al. 2015), one of which also showed no
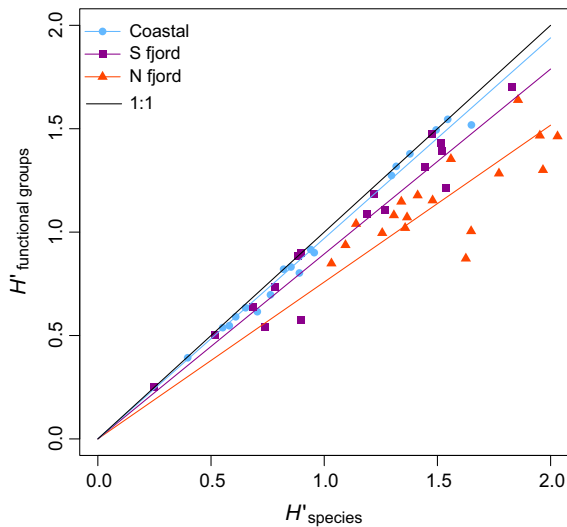
Fig. 5. Plot of relationships between species-based and functional group-based Shannon-Weiner diversity indices across sites. The slopes of these lines represent the degree of functional overlap among species, and are compared to a solid 1:1 line representing zero functional redundancy. Sites differed significantly from each other, although only S and N fjord differed significantly from the 1:1 line.

difference in abundance (Hosack et al. 2006). These studies used methods that sampled larger areas of the tideflat (freestanding fyke net and tow net, respectively), and they did not specifically sample across the vegetated–unvegetated ecotone. Sampling over large areas of patchy habitat might have obscured finer-scale differences in assemblage structure across habitats.

The functional approach of our study helped disentangle the use of habitat types by specific functional groups, and we were able to determine that while the pattern of no difference in abundance per seine holds for some groups, others were significantly more abundant in eelgrass seines than in seines in unvegetated habitats. Overall, our study forms an important contribution to the understanding of mesopredator usage of eelgrass in the Pacific Northwest, which is poorly known relative to other regions (Dean et al. 2000, Murphy et al. 2000, Ferraro and Cole 2010).

Functional redundancy and mesopredator resilience

A common finding in structurally complex habitats is that functional and taxonomic diversity

are highly correlated (Jackson et al. 2001, Micheli and Halpern 2005, Bustamante et al. 2014) and that functional redundancy is correspondingly low. These relationships make sense in light of the idea that structural complexity increases species richness by increasing available niches and thereby reducing competition, and that rare species that contribute significantly to species richness are often functionally distinct (MacArthur and MacArthur 1961, Mouillot et al. 2013b). In contrast, unstructured habitats or habitats in which structure has been removed might be populated by more generalist species with broad overlap in traits, conferring functional redundancy to the community (Thrush et al. 2006, Handley et al.
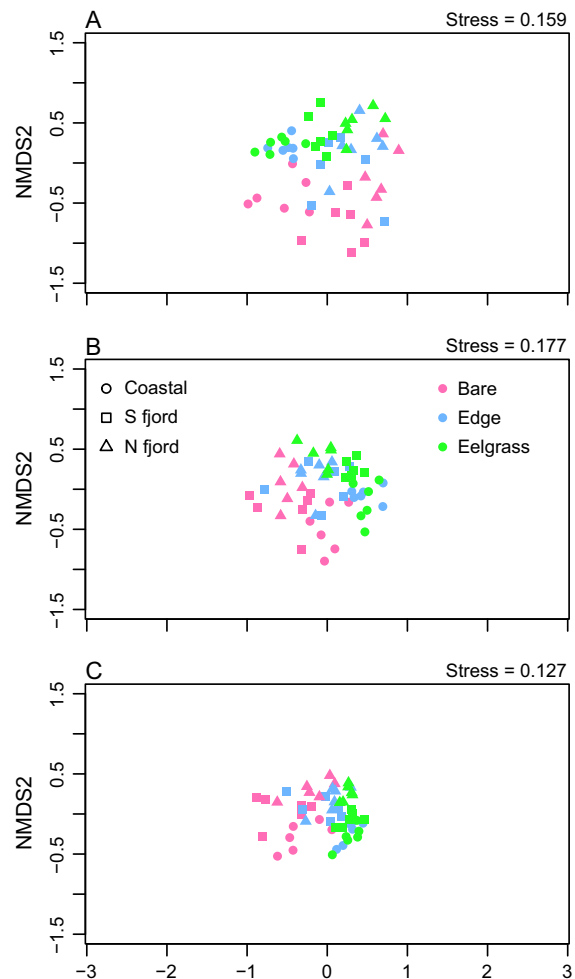

Fig. 6. Non-metric multidimensional scaling (NMDS) plots of species (A), functional groups (B), and functional traits (C) in seines.

2014). These patterns may increase the vulnerability of structurally complex ecosystems to disturbance; redundancy of species within functional groups is often associated with increased ecosystem resilience, and greater numbers of rare, functionally distinct species in habitats like kelp forests and coral reefs decrease this resilience (Folke et al. 2004, Tilman et al. 2006, Downing et al. 2012).

In contrast to these assumptions, our data showed increased functional redundancy with increased species richness; richness and redundancy were dependent on site, and habitat complexity did not influence their relationship. A number of factors may contribute to this discrepancy. First, from a practical perspective, the degree of functional redundancy observed in a system is dependent on the scale at which functional groups are defined. Finer-scale functional resolution increases the number of functional groups and decreases the number of species within each group, thereby increasing the slope between taxonomic and functional group diversity; had we defined more functional groups, we would have observed less functional redundancy (Micheli and Halpern 2005). Second, assemblage connectivity may contribute to redundancy because species that are both functionally redundant and far ranging may contribute to richness at a site while increasing functional redundancy in a particular subsite or habitat (Auster and Link 2009). The habitats we sampled were patchy and had broad connections to the surrounding regions, and many of the species we observed are only part-time residents of these estuaries and are considered to use both eelgrass and unstructured tideflats at juvenile stages (Hughes et al. 2014). High mesopredator mobility and habitat connectivity might have contributed to the relatively high functional redundancy we observed at our most species-rich sites because these factors increase the likelihood that multiple species with similar functional traits or from different habitats will end up in the same sampling area. Although this was likely not the case in our study, a third explanation for high functional redundancy in species-rich areas is that these areas may have a greater number of rare species, which are often functionally distinct (Mouillot et al. 2013b), creating greater functional redundancy in these areas by sampling probability. In our study, rare species did not form distinct functional groups and thus had little influence on functional redundancy.

The different degrees of functional overlap between species observed in our study sites suggest differing levels of ecosystem resiliency (Auster and Link 2009; Fig. 5), potentially necessitating site-specific management plans for maintaining ecosystem function. It is also important that management decisions be based not only on potential ecosystem resiliency but also on the identities of specific community members, especially given the cultural and economic value of some community members compared to others that might be functionally equivalent. For example, *Metacarcinus magister* and *Hemigrapsus oregonensis* are both in the generalist crab functional group, but only *M. magister* is commercially valuable.

Species- and trait-based evaluation of habitat differences

Using different response variables at taxonomic and functional resolutions generally supported the notion that a trait-based perspective is more robust in explaining assemblage variation across sites varying in species pool. From a taxonomic perspective, site explained nearly twice as much of the multivariate variation in community structure as did habitat, but site and habitat were equally important in explaining the variation in community structure through a functional lens. The species in assemblages are constrained by stochastic, broad-scale historical processes like vicariance and dispersal leading to unique assemblages in particular geographic areas. Functional traits in assemblages, however, are more often determined by focused, smaller-scale processes, like environmental filters imposed by a particular habitat, or interspecific interactions (Pavoine and Bonsall 2011, Adler et al. 2013, Mouillot et al. 2013a, Kraft et al. 2015). In multivariate analyses, site explained less variation in functional group and trait composition than species composition, but notwithstanding, the role of habitat was relatively small. This may reflect that environmental filtering effects differed more among sites than among habitats within sites, that species were allocated to functional groups that did not accurately characterize their role in the ecosystem, or that the small spatial scale of the habitat mosaic makes it

more likely that all functional groups and traits are present in all habitats.

Seagrass beds and estuaries worldwide provide "nursery habitat" for juvenile fishes and decapods before moving to offshore waters. This nursery role is one of the most oft-cited services of eelgrass beds (Costanza 1997, Orth et al. 2006, Cullen-Unsworth and Unsworth 2013). A survey of estuaries on the west coast of the United States revealed eelgrass beds and unvegetated tideflats as the most commonly used estuarine nursery habitats among 15 ecologically and economically important species (Hughes et al. 2014). Twelve of these species are documented to use our focal estuaries as juveniles, and seven of them—sand shrimp (*Crangon* sp.), Dungeness crab (*M. magister*), Chinook salmon (*Oncorhynchus tshawytscha*), English sole (*Parophrys vetulus*), starry flounder (*Platichthys stellatus*), shiner perch (*Cymatogaster aggregata*), and staghorn sculpin (*Leptocottus armatus*)—were caught in seines. Two of these species—*C. aggregata* and *O. tshawytscha*—belong to functional groups with highest abundance observed in eelgrass patches. The data on these and other species collected in this study can be used to quantitatively assess the value and ecosystem services of eelgrass and other habitats in Washington's tideflats, and will ultimately help inform management and policy decisions. Because eelgrass benefits species with certain traits, management focused on the low-intertidal estuarine habitat mosaic, rather than a particular habitat type, and on places where redundancy is already low, best supports mesopredator diversity and function.

Acknowledgments

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