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Anthropogenic disturbance homogenizes seagrass fish communities

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Running head: Biotic homogenization of coastal ecosystems

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Abstract

Anthropogenic activities have led to the biotic homogenization of many ecological communities, yet in coastal systems this phenomenon remains understudied. In particular, activities that locally affect marine habitat-forming foundation species may perturb habitat and promote species with generalist, opportunistic traits, in turn affecting spatial patterns of biodiversity. Here, we quantified fish diversity in seagrass communities across 89 sites spanning 6° latitude along the Pacific coast of Canada, to test the hypothesis that anthropogenic disturbances homogenize (i.e., lower beta-diversity) assemblages within coastal ecosystems. We test for patterns of biotic homogenization at sites within different anthropogenic disturbance categories (low, medium, high) at two spatial scales (within and across regions) using both abundance- and incidence-based beta-diversity metrics. Our models provide clear evidence that fish communities in high anthropogenic disturbance seagrass areas are homogenized relative to those in low disturbance areas. These results were consistent across within-region comparisons using abundance- and incidence-based measures of beta-diversity, and in across-region comparisons using incidence-based measures. Physical and biotic characteristics of seagrass meadows also influenced fish beta-diversity. Biotic habitat characteristics including seagrass biomass and shoot density were more differentiated amongst high disturbance sites, potentially indicative of a perturbed environment. Indicator species and trait analyses revealed fishes associated with low disturbance sites had characteristics including stenotopy, lower swimming ability, and egg guarding behaviour. Our study is the first to show biotic homogenization of fishes across seagrass

meadows within areas of relatively high human impact. These results support the importance of targeting conservation efforts in low anthropogenic disturbance areas across land- and seascapes, as well as managing anthropogenic impacts in high activity areas.

Introduction

Biotic homogenization, the loss of beta-diversity, has become a well-recognized signature of the Anthropocene. Anthropogenic disturbances, including the introduction of non-native species, intensive habitat modification (e.g., agriculture, deforestation), urbanization, and climate change, all have the potential to lead not only to altered species diversity within a community (i.e., alpha-diversity), but also to increased similarity in species composition amongst communities (i.e., beta-diversity) (Clavel *et al.*, 2011; Dornelas *et al.*, 2014; Magurran *et al.*, 2015; Socolar *et al.*, 2016).

Although biotic homogenization as a consequence of anthropogenic disturbances has been recognized for some time (Vitousek *et al.*, 1997; McKinney & Lockwood, 1999; Olden & Poff, 2003), interest in this particular component of diversity surged over the past decade (see review by Anderson *et al.*, 2011) as a means for detecting compositional changes that may not be detectable with local measures of alpha-diversity (McGill *et al.*, 2015). These new studies provide evidence that species assemblages are shifting in composition worldwide, and that beta-diversity indices capture these changes (Dornelas *et al.*, 2014; Magurran *et al.*, 2015; McGill *et al.*, 2015). Accordingly, beta-diversity has been proposed as a useful tool for evaluating biodiversity change across spatial scales (Socolar *et al.*, 2016).

Several anthropogenic drivers can cause biotic homogenization. Species assemblages may become less distinct when the same species are introduced across habitats (i.e., “additive homogenization”, Mechanism 1, “M1”); when habitat characteristics are homogenized such that the same species are promoted (additive, M2); when invasions or environmental degradation lead to the loss of rare or specialized species (with traits including low fecundity, stenotopy) (i.e., “subtractive homogenization”, M3); and through the propagation of generalist species able to tolerate a wide range

of environmental conditions (additive, M4; Socolar *et al.*, 2016). Homogenization of freshwater fish communities is largely caused by introductions of the same non-native species rather than losses of natives (M1; Villéger *et al.*, 2011), whereas introduced mammals have led to homogenization of avian fauna on islands by driving local endemic species extinct (M3; Steadman, 1995; Blackburn *et al.*, 2004). Bird communities in the homogenized habitat of agricultural land tend to be more similar among habitat patches than in forested areas (M2; Karp *et al.*, 2012), and coral reef assemblages have become homogenized over time owing to loss of species from environmental stress, and dominance of generalist species (M3-4; Burman *et al.*, 2012). Studies that attribute biotic homogenization to changes in habitat (M2-4) have often focused on community comparisons between highly modified habitat (e.g., agricultural land, cities) and natural, undisturbed habitat (e.g., forests, park reserves) (McKinney, 2006; Karp *et al.*, 2012; Mori *et al.*, 2015a). However, more nuanced localized human activities that degrade or perturb the environment may increase habitat heterogeneity across the disturbed area, thus making conditions unsuitable for specialist species. Biotic homogenization may then occur through loss of specialist species and gain of generalists reflecting environmental filtering (M3-4), an overall outcome predicted for the Anthropocene (reviews by McKinney & Lockwood, 1999; Clavel *et al.*, 2011).

Despite the recent increased focus on beta-diversity, there remains a need for further spatial and temporal comparisons of beta-diversity (McGill *et al.*, 2015), particularly in marine systems, and for drivers other than land conversion and invasions to broaden our understanding of changes to biodiversity (Socolar *et al.*, 2016). Beta-diversity has been found to be shifting over time across all biomes (Dornelas *et al.*, 2014), yet very few studies have assessed beta-diversity of coastal ecosystems in relation to anthropogenic impacts; one such study found biotic homogenization of benthic assemblages owing to an invasion (Piazzi & Balata, 2008), and another found within-site homogenization of invertebrates with coastal urbanization (Kelly *et al.* 2016). This is an important knowledge gap, as coastal ecosystems are simultaneously amongst the most valuable and threatened in the world (Agardy & Alder, 2005). Coastlines support a disproportionate amount of the human population, provisioning food resources, access to marine trade and transport, and fertile agricultural

land (Small & Nicholls, 2003; Hugo, 2011; Neumann *et al.*, 2015). Low-elevation coastal population densities are more than five times greater than the global mean (Neumann *et al.*, 2015), with coastal areas containing the majority of worldwide megacities (Brown *et al.*, 2013). Marine ecosystems supporting the highest human populations have been found to have the most depleted species abundances compared to historical baselines (Lotze *et al.*, 2006).

Here, using observed fish community composition spanning 6° latitude in coastal seagrass meadows, we test the hypothesis that anthropogenic disturbance homogenizes fish assemblages within coastal ecosystems. We predicted that coastal activities would have reduced specialist species with traits poorly adapted to anthropogenic disturbance, and increased species with more generalist, opportunistic traits within nearshore ecosystems, resulting in spatial biotic homogenization. Another objective was to determine whether physical and biotic habitat characteristics that mediate beta-diversity differed across disturbance levels in order to link beta-diversity trends with variation in the degree of similarity amongst habitat patches. We use seagrass meadows across the Pacific coast of Canada – a globally important nearshore habitat (Nordlund *et al.*, 2016) – as a model foundation species that can be highly responsive to perturbation and degradation (Short & Wyllie-Echeverria, 1996; Duarte, 2002; Unsworth *et al.*, 2015).

Materials and methods

Field surveys

Fish surveys were conducted in seagrass meadows (*Zostera marina*) at 89 sites covering 9 regions along the coast of British Columbia, Canada from June 19 to August 4, 2016 (Fig. 1). The regions span the Oregonian and Aleutian marine zoogeographic provinces, which transition near the northern tip of Vancouver Island around 50° N (Briggs & Bowen, 2012). Endemism of biota within the two provinces ranges from 2-24% (review by Briggs & Bowen, 2012), with fish distribution endpoints between California and Alaska peaking at 50° N (Peden & Wilson, 1976; Horn *et al.*, 2006). To accurately delineate species pools, we considered two of our sampled regions to be in the

Aleutian province, and the remaining seven regions to be part of the Oregonian province (see Appendix S1, “Study area” for list of regions).

Field methods were modeled after those of Parks Canada (Robinson *et al.*, 2011; Robinson & Yakimishyn, 2013), with sites separated by a minimum of 200 m and surveys conducted within two hours before or after morning low tide using the round-haul beach seine method, generally with the aid of a boat. Beach seining is the most efficient method for capturing seagrass fishes (Guest *et al.*, 2003), though certain species may be under-sampled based on swimming speeds and position over the seagrass (Nagelkerken *et al.*, 2001). All surveys were conducted with 10 x 3 m nets (¼ inch, 6.35 mm stretch mesh) to standardize catch efficiency; thus, we expect any under-sampling of species to be consistent across sites. Two seine sets were conducted at each site, separated by approximately 10 m, and fish were counted and identified to species after the second set. This was the maximum number of seine sets that could be achieved during low tide in order to survey two sites per day and conduct additional site characteristic sampling. Surveying two sites per day within the same low tide window enabled coordination of nine teams (4-5 people each) to finish the surveys within 6.5 weeks to minimize both tidal and seasonal shifts in community composition (Ribeiro *et al.*, 2006). Guest and colleagues (2003) found that two daytime beach seine sets sampling seagrass fishes across ten consecutive days were highly consistent in species presences and abundances, and were more precise than trawling methods.

At each site, seagrass meadow form, distribution (Durance, 2002), and tidal range was classified (Appendix S1, Table S1). Seagrass shoots were also collected from five quadrats (10 x 10 cm) placed haphazardly approximately 10 m apart along the nearshore edge of the area seined; quadrats that landed in a bare patch were re-placed in the next closest seagrass patch. Temperature and salinity were measured at each site 0.5 m below the water surface. Tidal constraints and some equipment malfunction resulted in 71 sites (8 missing from the Oregonian province and 10 Aleutian) with data on seagrass biotic characteristics and 68 sites with salinity measures (10 missing from Oregonian, 11 Aleutian); all other measures were complete for the 89 sites.

Additional biotic and abiotic measures

Seagrass quadrat samples were used to further characterize meadow habitat for each site, including measures of average seagrass dry biomass, shoot density, and epiphyte load (Appendix S1, “Lab measures”, Fig. S1). The following additional physical and spatial measures were also made from online geospatial data sources: mean July and annual sea surface temperatures, tidal current speed, shoreline type, wave exposure, freshwater influence, and shortest path overwater distance between sites within regions (Appendix S1, “Physical and spatial measures”, Table S1).

Anthropogenic disturbance

The level of anthropogenic disturbance at each site was estimated as a compilation of three indices that represent potential direct and indirect impacts to seagrass habitat and the resident fish community: (1) watershed human population size, (2) overwater structures, and (3) shoreline modification. Human population size has been previously used as a large-scale predictor of impacts to marine ecosystems (Halpern *et al.*, 2008, Drew *et al.*, 2015). Watershed population size was selected to encompass landscape activities of industry and agriculture that can lead to higher levels of pollution and nutrient inputs (Tewfik *et al.*, 2007, Bricker *et al.* 2008), as well as denoting hubs for marine transportation activities such as ferries, commercial shipping, and float planes which can modify flow dynamics and add to pollution. The relevant scale for assessing impacts to seagrass meadows is suggested to be within 1-3 km of shoreline (Shelton *et al.*, 2017). Watershed population counts (Center for International Earth Science Information Network, 2005) were obtained for all watersheds (Freshwater Atlas Assessment Watersheds, www.geobc.gov.bc.ca) that had any overlap within a 5 km buffer of each site; 5 km was selected in order to capture land from all site locations. Overwater structures represent shading and a centralization of recreational and industrial boating activities (i.e., marinas, ferry terminals, coal ports) that can lead to benthic perturbation, patchy habitat loss, noise pollution, and sewage effluent (Burgin & Hardiman, 2011). Overwater structures were measured as the proportion of overwater structure area / water surface area within a 2 km radius of each site using

Google Earth. Finally, shoreline modification was used as a localized measure of nearby development that indicates water accessibility, run-off, and altered wave refraction dynamics; this was measured as the percent of developed land within 100 m in either direction of the site, parallel to the shore, using Google Earth (Appendix S1, “Anthropogenic disturbance measures”).

Only a few fish species that use seagrass meadow habitat as juveniles are targeted for fishing as adults in British Columbia (<http://www.dfo-mpo.gc.ca/fisheries-peches/pac-yukon-eng.html>) as the majority of the seagrass community comprises non-targeted, small-bodied fishes (e.g., sculpins, pipefish, gunnels). The species that are targeted for fisheries were generally caught infrequently during our sampling (Pacific salmon *Oncorhynchus* spp., n = 14; lingcod *Ophiodon elongatus*, n = 37; walleye pollock *Gadus chalcogrammus*, n = 1; rock sole *Lepidopsetta bilineata*, n = 8), in part because our sampling period was after the outmigration of juvenile Pacific salmon. Rockfish *Sebastes* spp. (n = 2848) and English sole *Parophrys vetulus* (n = 1000) were caught in high numbers in comparison, but only made up 6% of the total catch. Rockfish were historically overfished in British Columbia, though conservation strategies implemented since 2001 have greatly reduced rockfish fishing mortality (Yamanaka and Logan, 2010). In addition, commercial and sport fishing intensities generally exhibit differences at much larger geographic scales than our site disturbance measures (e.g., “Commercial Fisheries – Groundfish Trawl” and “Sport Fishing – Groundfish” from British Columbia Marine Conservation Atlas, www.bcmca.ca). As a result, we did not include fishing intensity in our disturbance measures. Our selected measures of watershed human population size, overwater structures, and shoreline modification can have both localized (e.g., anchoring) and dispersed effects (e.g., pollution) on seagrass meadows, and could collectively lead to degraded habitat conditions for fishes that are characterized by reduced visibility, reduced oxygen, noise stress (Simpson *et al.*, 2016), high or rapidly changing current speeds, and loss of continuous refuge (review by Burgin & Hardiman, 2011).

Statistical analyses

Data preparation

Anthropogenic disturbance measures were standardized as z-scores (e.g., centered and divided by the standard deviation) separately and then summed to obtain a cumulative score. Site scores were then pooled into disturbance categories of low, medium, and high to enable within-category beta-diversity comparisons. Categorizing sites by disturbance level allowed us to address the question of whether beta-diversity was lower for high disturbance meadows compared to medium and low disturbance areas (similar to biotic homogenization studies comparing beta-diversity among habitat categories; e.g., McKinney, 2006, Karp *et al.* 2012, Mori *et al.*, 2015a, Karp *et al.* 2017). Further comparisons across the disturbance gradient (see dbRDA and trait analysis below) were made to assess how community dissimilarity among sites is influenced by a suite of factors (i.e., do site characteristics explain community composition differences among sites?) and how species traits are associated with anthropogenic disturbance (respectively). Many sites had similarly low disturbance scores (38 ranged from -1.43 to -1.42), whereas the southern mainland had some sites with notably high scores (4 sites ranged from 6.23 to 10.25). Divisions made between categories were based on visible breaks between scores and grouping of sites so that each site could be compared to at least one other within the same region and anthropogenic disturbance category. By selecting three categories we were able to retain a high number of site comparisons within regions and disturbance categories (i.e., further division would lead to some sites having no within-region comparative site, and thus could not be included in the within-region analysis). In addition, we verified our use of a cumulative z-score and classification of sites into categories using a principal components analysis on the three disturbance measures (cumulative proportion of variance explained by PC1 and PC2 = 0.92) (“vegan” in R; Oksanen *et al.*, 2016). Graphical visualization of the distance biplot showed site separations corroborated the site categorization (Appendix S2, Fig. S1); though watershed population size and overwater structures did not contribute independently, we retained the use of all scores in our cumulative measure as removing either of the former measures from the summation did not appreciably alter the site classifications (Appendix S2, Fig. S2). The final categorization led to a total

of 45 low anthropogenic disturbance sites (28 Oregonian, 17 Aleutian; score range = -1.43 to -1.38), 25 medium disturbance sites (19 Oregonian, 6 Aleutian; -1.35 to 1.07), and 19 high disturbance sites (all Oregonian; 1.53 to 10.25).

Fish counts from the two seine sets at each site were combined for a total count per species and site. Certain juvenile rockfish species (e.g., *Sebastes melanops* and *S. flavidus*) and greenlings (e.g., *Hexagrammos decagrammus* and *H. lagocephalus*) were particularly challenging to identify to species, so these were grouped by genus for all regions. Some sculpins, larval flatfish, and one goby were not identified to species, but this was uncommon (unidentified/total count, sculpin: 24/672, flatfish: 16/562, goby: 1/50) so these counts were removed for the analysis.

Beta-diversity measures

Beta-diversity of fishes was calculated within anthropogenic disturbance categories for sites within (e.g., Region 1 Site 1 vs. Region 1 Site 2) and across regions within the same province (e.g., Region 1 Site 1 vs. Region 2 Site 3) using two metrics with different null model constraints to examine the consistency of the results at two spatial scales (for workflow diagram of all subsequent analysis, see Appendix S1, Fig. S2). Both metrics used, Bray-Curtis and Raup-Crick, are common in the beta-diversity literature (e.g., Cao & Epifanio, 2010; Anderson *et al.* 2011; Chase *et al.*, 2011; Catano *et al.* 2016; Tucker *et al.*, 2016). Furthermore, the use of null models aims to disentangle beta-diversity driven by ecological processes from the component of beta-diversity that is expected owing to random sampling and stochastic spatial aggregation of species (i.e., effects based on gamma-diversity; Kraft *et al.*, 2011; Stegen *et al.*, 2013), and sampling effects caused by differences in species richness (i.e., effects based on alpha-diversity; Vellend *et al.*, 2007; Chase *et al.*, 2011). Specifically, more of the species pool is expected to be represented at each site based on random placement if gamma-diversity is low, leading to low beta-diversity (Stegen *et al.*, 2013). Conversely, sites with low alpha-diversity are expected to be more dissimilar from other sites because the number of possible shared species is lower (Vellend *et al.*, 2007). Our focus on deviation of beta-diversity

from the null expectation should improve our ability to distinguish the influences of anthropogenic and environmental factors on different aspects of community assembly apart from stochastic effects (Myers *et al.*, 2013; Tucker *et al.*, 2016).

First, we calculated Bray-Curtis (BC) dissimilarity on $\ln(x+1)$ transformed abundance data (Anderson & Willis, 2003) using a null model to account for stochastic sampling and spatial aggregation of species (Kraft *et al.*, 2011; Stegen *et al.*, 2013; Tucker *et al.*, 2016). Null models were made with 999 randomizations of our species counts that allowed site abundance and richness to vary, but species abundance to remain constant (i.e., rare species remained rare). This was achieved by randomly placing each observed individual into a site until all individuals in the metacommunity (i.e., the province) had been placed into a site, effectively randomizing the location of individuals (R code from Tucker *et al.*, 2016). The Oregonian and Aleutian provinces were treated as separate metacommunity pools for all null model assembly (Marchetti *et al.*, 2006). BC beta-deviation is a standardized effect size calculated as observed dissimilarity – mean (null model dissimilarities) / standard deviation (null model dissimilarities) (Mori *et al.*, 2015b; “vegan” in R; Oksanen *et al.*, 2016).

Second, we calculated Raup-Crick (RC) dissimilarity on incidence data using null models to control for differences in alpha-diversity amongst sites (Raup & Crick, 1979; Vellend *et al.*, 2007; Chase *et al.*, 2011). We chose RC over other incidence-based metrics, such as Jaccard’s index, because many of these metrics are not independent of alpha-diversity (i.e., sites with lower values of alpha-diversity may appear less similar) (Raup & Crick, 1979; Vellend *et al.*, 2007; Chase *et al.*, 2011). RC measures the probability that two sites share fewer species than expected under a null model (Vellend *et al.*, 2007; Chase *et al.*, 2011). RC dissimilarity was calculated with 999 null model randomizations while setting each species’ representation in the provincial pool to the mean of its frequency across anthropogenic disturbance categories (Vellend *et al.*, 2007; modified R code from Chase *et al.*, 2011). This controlled for a potential bias of sample size differences that would make low disturbance sites appear more similar to each other because they make up more of the provincial pool.

Sites within the same province were directly compared to each other for estimates of beta-diversity, and all beta-diversity values within each disturbance level were combined separately for within- and across-region comparisons, respectively, to compare overall beta-diversity across anthropogenic disturbance categories and geographic scales. BC beta-deviation and RC beta-diversity measures were compared across anthropogenic disturbance categories by generating bootstrapped estimates ($n = 2000$) of the mean dissimilarity (including all beta-diversity values for both provinces) and 95% confidence intervals (CIs) for each disturbance level (Karp *et al.*, 2012). Gower distances for physical and biotic characteristics of all sites, including only variables retained from the forward-model selection process (across all models, from dbRDA below [see Table 1]), were also calculated for each anthropogenic disturbance category using the same pairwise site comparisons as for the beta-diversity comparisons. These were similarly compared using bootstrapped CIs, and those that did not overlap were considered significantly different. Sensitivity analyses were conducted to determine any influence of alpha-diversity on beta-diversity, as low species richness can lead to high beta-diversity values unless accounted for by null models such as those constructed by RC beta-diversity (Raup & Crick, 1979; Vellend *et al.*, 2007; Chase *et al.*, 2011). This included analysis of species richness using sample-based rarefaction curves and the contribution of turnover versus nestedness to differences in beta-diversity between anthropogenic disturbance categories using Sorensen dissimilarities (Appendix S1, “Sensitivity analyses”).

Beta-diversity analyses

We visualized clustering of beta-diversity values for anthropogenic disturbance categories within and across regions of the Oregonian province using non-metric multidimensional scaling (NMDS) and tested for differences amongst disturbance level centroids using permutational multivariate analysis of variance (PERMANOVA) (“vegan” in R; Oksanen *et al.*, 2016). The Aleutian province sites were not used for NMDS, nor distance-based redundancy analysis (dbRDA) and *post-hoc* variance partitioning (see below), as these analyses require different metacommunity (i.e.,

provincial) pools to be tested separately, but the Aleutian province did not contain any high disturbance sites for the disturbance level comparison; however, all sites with relevant data were used for all other analyses.

Additional sensitivity analyses for fish beta-diversity were conducted using bootstrapped means and CIs to test the consistency of the comparisons across anthropogenic disturbance categories. Some regions were surveyed by the same field team, while others were surveyed by independent teams. A comparison was made of BC observed values between sites surveyed within Barkley Sound (considered one region for all other analyses) by two separate teams, one team that has been part of an annual monitoring program ongoing for 12 years (10 sites), and another that was conducting their first fish surveys (8 sites). This represented the largest field experience difference across all survey teams. In addition, spatial autocorrelation is an important determinant of beta-diversity that should be considered in analyses of biotic homogenization (e.g., Leprieur *et al.*, 2008; Karp *et al.*, 2012; Ferenc *et al.*, 2013; Karp *et al.*, 2017), and we conducted two within-region sensitivity analyses to verify beta-diversity comparisons after controlling for spatial autocorrelation. One analysis removed average geographic distance differences between anthropogenic disturbance levels and another fixed the relationship between geographic distance and beta-diversity values to be the same across disturbance categories (Karp *et al.*, 2012) (Appendix S1, “Sensitivity analyses”).

The importance of each anthropogenic disturbance metric as well as other physical and biotic variables (Appendix S1, Table S1) was tested using dbRDA for both BC beta-deviation and RC beta-diversity measures within the Oregonian province (“vegan” in R; Oksanen *et al.*, 2016). Distance-based RDA takes the provided dissimilarity matrix (i.e., BC or RC) and uses principal coordinate analysis to produce corresponding Euclidean coordinates for each site (Legendre and Anderson, 1999). This is followed by redundancy analysis, a direct gradient analysis that uses multiple linear regression to regress the Euclidean coordinates against the explanatory variables. Distance-based RDA tests the null hypothesis that there is no significant relationship between variation in the species data and a linear combination of environmental variables (Legendre and Anderson, 1999).

Full dbRDA models were assembled separately for anthropogenic disturbance, physical, and biotic components in order to then determine the proportion of variance explained by these components through variance partitioning. Continuous variables were standardized using the relevant data subset for each full model, and overall correlations were checked using all Oregonian sites (Appendix S1, “dbRDA model preparation”). Separate full models were then tested for significance (999 permutations) and adjusted R^2 for anthropogenic disturbance, physical, and biotic components for all sites; physical and biotic components were also tested separately for sites within each anthropogenic disturbance category (total of 9 full models each for the two beta-diversity metrics). Variables with a variance inflation factor (VIF) > 4 were removed one at a time, beginning with the highest VIF, before determining full model significance. Forward selection was performed on all significant full models (Borcard *et al.*, 2011). The best-fit variables retained did not exceed the adjusted R^2 of the full model by more than 0.003, with the exception of one best-fit model that exceeded the full model adjusted R^2 by 0.02. We chose to retain this best-fit model as the next best-fit model reduced the variance explained by half (17%).

We were interested in the proportion of variance explained by these best-fit variable components for all pairwise site dissimilarities, and separately for each anthropogenic disturbance category. Variance partitioning was conducted for BC beta-deviation to determine the proportion of variance explained by each variable component using the best-fit models (i.e., only variables that were retained in model selection) (“vegan” in R; Oksanen *et al.*, 2016); not enough variance was explained for RC beta-diversity to warrant partitioning. In addition, each retained continuous variable was separately compared across anthropogenic disturbance levels (including sites from both zoogeographic provinces) using restricted maximum likelihood linear mixed-effects models (LMMs), with spatial grouping of sites by region as a random effect (“lme4” in R; Bates *et al.*, 2015). Non-overlapping 95% CIs were used to determine significant differences.

Indicator species analysis was conducted for each anthropogenic disturbance category to determine which fish species were most associated with these disturbance levels (Dufrêne & Legendre, 1997). This was done for abundance- and incidence-based data across both zoogeographic provinces combined. The importance of individual species was tested by excluding very rare species, i.e., those counted less than 10 times, and/or at fewer than 5 sites (retaining 36 out of 64 species). Indicator value components “A” and “B” were generated (999 permutations) to determine the probability that a site belongs to an anthropogenic disturbance category given that the species was found at the site (i.e., specificity, A), and the probability of finding the species amongst sites within the disturbance category (i.e., fidelity, B) (Dufrêne & Legendre, 1997; “indicspecies” in R; De Cáceres and Legendre, 2009).

In addition, we used fourth-corner analysis to evaluate the association of fish abundances with anthropogenic disturbance scores (continuous) and species traits. Fourth-corner models predict abundances based on environmental and species trait variables and their interaction; the fourth corner is the matrix of coefficients for the interaction between environmental and trait variables (Brown *et al.*, 2014). We defined the following set of traits for the same common species retained in the indicator analysis: standard length : body depth ratio (a measure of hydrodynamic ability, with a lower ratio indicating higher swimming ability; Mouillot *et al.*, 2007), reproductive guild (live bearer, egg guarder, egg scatterer, broadcast spawner), nearshore resident status based on individual life-history traits (transient – use nearshore habitat temporarily depending on life-history stage, seasonal resident – use nearshore habitat seasonally often depending on life-history stage, resident – remain in nearshore habitat throughout life-history stages; Nightingale & Simenstad, 2001), and trophic level (continuous measure). Species traits were collected from photos taken in the field (ave. of up to 5 photos), FishBase.com, Parks Canada’s “Field Guide to Eelgrass Fishes” (Yakimishyn, unpublished), and Nightingale and Simenstad (2001). We retained 32 species for which we were able to obtain complete trait information (Appendix S2, Table S1). Transient and seasonal resident status were combined as both types of species may leave nearshore habitats throughout their life-history, and only

one retained species was identified as transient. Fourth-corner coefficients were calculated using generalized linear models with LASSO penalties to minimize BIC, and the interaction between disturbance scores and traits was tested using analysis of deviance with 999 bootstrapped iterations (“mvabund” in R; Wang *et al.* 2017). All analyses were conducted in R (version 3.3.1) and code for all analysis is available on github – baumlab.

Results

We found evidence of biotic homogenization of seagrass fishes associated with high anthropogenic disturbance. Within-region comparisons of Bray-Curtis beta-deviation and Raup-Crick beta-diversity, as well as across-region comparisons of RC beta-diversity indicated lower beta-diversity amongst sites with high anthropogenic disturbance compared to sites with low disturbance (Fig. 2a-d). Beta-diversity of sites with medium anthropogenic disturbance levels varied in their similarity to high or low disturbance sites depending on the metric or within/across-region comparisons, but generally had intermediate beta-diversity values. Across-region comparisons of BC beta-deviation were the only inconsistent results, with higher beta-diversity between medium disturbance sites than low disturbance sites (Fig. 2b). Comparing fish beta-diversity trends to variation in similarity of physical and biotic characteristics amongst habitat patches revealed that lower beta-diversity in high disturbance areas corresponded with higher dissimilarity in biotic characteristics. Physical characteristics – including mean July and annual SST, salinity, and tidal current speed – had equivalent similarity amongst within-region meadows across disturbance levels, but were more dissimilar for high disturbance sites compared across regions (Gower distances, Fig. 2e, f). Biotic characteristics – including meadow tidal range, seagrass biomass, shoot density, and epiphyte load – of the sites within high disturbance levels were more differentiated within and across regions than for low disturbance sites (Fig. 2g, h). When meadow tidal range was excluded, the biotic characteristic that is unlikely to be influenced by anthropogenic activities, the same trends were found, and with a greater difference in within-region Gower distances between disturbance levels (Appendix S2, Fig. S3). Species richness tended to decrease successively from low to high anthropogenic

disturbance (Appendix S2, Fig. S4). However, spatial turnover – the replacement of species at a given site by different species at another site – within regions accounted for the difference in incidence-based beta-diversity across disturbance categories. Nestedness – the component of beta-diversity caused by differences in species richness – was similar across all disturbance levels (Sorensen dissimilarity, Appendix S2, Fig. S5). NMDS plots for the Oregonian province showed separation of low and high disturbance sites for both BC beta-deviation (PERMANOVA, partial $R^2 = 0.29$, $p < 0.001$) and RC beta-diversity (partial $R^2 = 0.39$, $p < 0.001$), with medium disturbance sites exhibiting spread between low and high levels (Fig. 3). Sensitivity analyses revealed no difference in observed BC beta-diversity between Barkley Sound sites that were sampled by teams with different levels of experience (95% CIs, Team A: 0.40-0.48, Team B: 0.40-0.49), nor a change in results when using a reduced dataset that removed differences in geographic distances, nor when using intercept values controlling for the relationship between geographic distance and BC beta-deviation (Appendix S2, Fig. S6-S7).

Anthropogenic disturbance, physical, and biotic variables generally explained more variation for BC beta-deviation than for RC beta-diversity of seagrass fishes within the Oregonian province (dbRDA, Table 1). Shoreline modification was retained as a significant explanatory variable for both beta-diversity metrics, whereas overwater structures was also an important predictor for BC beta-deviation; watershed human population size was not retained, but was correlated with overwater structure ($r = 0.7$) and shoreline modification measures ($r = 0.6$). Temperature (mean July and annual SST), salinity, and tidal current speed were generally important across all anthropogenic disturbance categories (Table 1). Best-fit biotic variables of BC beta-deviation across all sites included meadow tidal range, seagrass biomass, shoot density, and epiphyte load ($p < 0.001$). Different subsets of these variables were selected for low and high disturbance sites; however, no biotic variables were selected for medium disturbance sites (full model, $p > 0.05$). Full models of RC beta-diversity separated by disturbance categories were generally non-significant ($p > 0.05$) (Table 1).

Across all meadows, biotic variables explained the most independent variation in BC beta-deviation (variance partitioning, adj. $R^2 = 0.08$), followed by anthropogenic disturbance metrics (0.05) and physical variables (0.03; only considering those variables retained in the best-fit models) (Fig. 4, ‘All’). Physical variables were generally more important within separated anthropogenic disturbance categories, though there was a high amount of shared variance for physical and biotic variables for sites with high anthropogenic disturbance (adj. $R^2 = 0.21$) (Fig. 4, ‘P & B’). The most total variation explained (i.e., sum of all variance components) across anthropogenic disturbance categories was for BC beta-deviation of fishes within high disturbance areas (total adj. $R^2 = 0.41$ vs. all data: 0.21, low: 0.19, medium: 0.17) (Fig. 4). Epiphyte load was the only variable (of all retained physical and biotic variables) that significantly differed across anthropogenic disturbance levels (LMM, 95% CIs, high: 93.38-199.36, medium: 2.99-109.74, low: -21.79-62.37); loads increased with anthropogenic disturbance level (Fig. 4, inset), with three high disturbance sites with particularly high epiphyte loads (Appendix S1, “Lab measures”, Fig. S1). Salinity tended to be lower across high disturbance sites ($24.33\text{‰} \pm 4.88$) than medium ($26.94\text{‰} \pm 2.86$) or low ($28.78\text{‰} \pm 2.84$) disturbance sites, but did not differ significantly across disturbance levels (i.e., overlapping 95% CIs).

The top indicator species for low anthropogenic disturbance sites across the coast of British Columbia were rockfish (*Sebastes* spp.) and crescent gunnel (*Pholis laeta*; abundance metric) or cabezon (*Scorpaenichthys marmoratus*; incidence metric), whereas the indicator species for high disturbance sites were threespine stickleback (*Gasterosteus aculeatus*) and sharpnose sculpin (*Clinocottus acuticeps*; Table 2). For medium disturbance sites, the indicator species based on abundances were saddleback gunnel (*Pholis ornate*) and striped seaperch (*Embiotoca lateralis*), and Pacific staghorn sculpin (*Leptocottus armatus*) based on incidences (see Appendix S2, Table S1 for a list of all species identified). One or two significant indicator species were identified for medium and high disturbance areas, whereas low disturbance sites had several indicator species (only the top two are provided).

Species traits significantly interacted with anthropogenic disturbance scores (fourth-corner analysis of deviance, deviance statistic = 53.26, residual DF = 2808, $p = 0.002$) (Fig. 5). Seagrass meadows with high anthropogenic disturbance scores were most associated with fishes that have a lower standard length : body depth ratio (i.e., higher swimming ability; fourth-corner coefficient = -0.35) and are live bearers (e.g., perch; 0.19). Conversely, low disturbance meadows were most associated with fishes that have a higher standard length : body depth ratio (i.e., lower swimming ability; -0.35), and are egg guards (-0.31) (Fig. 5). Higher trophic levels were also somewhat associated with high disturbance meadows (0.08), but no correlation was found based on nearshore residency status.

Discussion

Our results provide evidence for biotic homogenization of fish communities in seagrass meadows characterized by high anthropogenic disturbance, both within and across regions spanning the extent of Canada's Pacific coast. We show that heterogeneity in the biotic characteristics of these more perturbed environments (Fig. 2g) contributes to low beta-diversity and the dominance of more adaptive, opportunistic species (i.e., threespine stickleback, Table 2) able to tolerate impacted systems (indicative of M3-4) (McKinney & Lockwood, 1999; Clavel *et al.*, 2011). Though our study does not determine the direct mechanisms of biotic homogenization of fishes, the heterogeneity of seagrass meadows within and across high disturbance regions may be related to human activities that have localized impacts (e.g., effects of boat propeller wash, overwater shading, and nutrient inputs on epiphyte load). Multiple stressors to seagrass meadows, though not well understood, are expected to have cumulative and synergistic effects (Unsworth *et al.*, 2015; Cullen-Unsworth & Unsworth, 2016). Past discoveries of biotic homogenization owing to anthropogenic impacts have compared novel landscapes to natural (i.e., not anthropogenically modified or created) habitats (Socolar *et al.*, 2016), whereas we have found biotic homogenization of communities within natural habitats that persist in seascapes influenced by localized human perturbations. Canada's Pacific coastline is less altered

relative to other global coastlines (UNEP, 2002), yet our results show that these globally-low levels of human activities and development correspond with lower beta-diversity in nearshore fish communities compared to less disturbed areas.

The positive BC beta-deviation and RC beta-diversity values we detected in our analysis indicate a departure from neutral or stochastic community assembly (Chase *et al.*, 2011; Tucker *et al.*, 2016). In particular, high BC beta-deviation values represent greater intraspecific aggregation within sites or less even abundance distributions than expected by chance (Tucker *et al.*, 2016). Low disturbance meadows were 5 standard deviations further from the null expectation of stochastic assemblage than high disturbance meadows compared within-regions. The higher level of intraspecific aggregation or unevenness may indicate greater ecological differentiation between species in the low disturbance meadows (i.e., niche-based structuring; Stegen *et al.*, 2013; Tucker *et al.*, 2016). At a larger geographic scale, the degree of species aggregation or evenness between sites across regions was similar for low and high disturbance meadows. However, RC beta-diversity revealed that low disturbance meadows were 2.1 and 1.7 times more likely to share fewer species than expected by chance than high disturbance meadows for within- and across-region comparisons, respectively. Deviation values from both null models depend on the accuracy of the provided metacommunity pool (Chase *et al.*, 2011; Tucker *et al.*, 2016). For instance, niche-structured metacommunities show an increase in BC beta-deviation from the null expectation when undersampled (Tucker *et al.*, 2016). Our highest BC beta-deviation values were, however, for low disturbance meadows for which we had more sampled sites. Furthermore, comparisons of deviation from stochastic assembly must generally be constrained within habitats and biogeographic zones, as done here (Chase *et al.*, 2011; Tucker *et al.*, 2016).

Factors that influence beta-diversity

Loss of beta-diversity amongst communities often coincides with loss of species richness within communities, and these two components are frequently not differentiated (Baiser *et al.*, 2012). We found that both beta-diversity and species richness were higher for low anthropogenic disturbance

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sites. Differences in beta-diversity across disturbance categories were shown to be attributed to the degree of difference in species composition between meadows (i.e., turnover), rather than differences in species richness (i.e., nestedness), through beta-diversity partitioning within regions (Baiser *et al.*, 2012; Magurran *et al.*, 2015) and by controlling for effects of species richness on beta-diversity calculations via null models (i.e., Raup-Crick beta-diversity; Chase *et al.*, 2011). Magurran and colleagues (2015) similarly showed that marine fish communities were differentiated across a climate gradient by changes in species composition, not species richness. Loss of species richness indicates a locally degraded environment, whereas biotic homogenization reveals greater similarity between communities that may reduce their ability to respond to further environmental change (Hooper *et al.*, 2005). In light of independently lower levels of beta-diversity and species richness associated with anthropogenic activities, conservation efforts may benefit from focusing protection measures on maintaining land- and seascape scale biodiversity – such as preserving low disturbance areas that harbour communities with different species compositions, maintaining connectivity, and managing human activities across high disturbance areas (Socolar *et al.*, 2016).

Environmental factors of seagrass meadows were also important determinants of fish beta-diversity. Robinson and colleagues (2011) similarly found that salinity, temperature, seagrass biomass, and epiphyte load were important variables for explaining beta-diversity of seagrass fishes. Freshwater influence measured in our study was correlated with our anthropogenic disturbance measures, as coastal development often congregates around river mouths (Neumann *et al.*, 2015). Salinity frequently influences fish communities, but with varying effects; for example, in a tropical lagoon, richness was found to decline within increasing salinity (Sosa-López *et al.*, 2007), whereas in European estuaries, more species were found in higher salinity (> 18‰) (Nicolas *et al.*, 2010). All but two of our study sites had salinities higher than 18‰. Furthermore, the level of heterogeneity in physical variables (including salinity) between sites was relatively similar across anthropogenic disturbance categories, with the exception of dissimilarity being higher for high disturbance sites across regions. Thus, there was no apparent mechanism for salinity to have contributed to the lower beta-diversity found within high anthropogenic disturbance areas. Tidal current was also found to be

an important predictor of fish beta-diversity. Food and habitat availability likely differ across tidal current regimes, as low current meadows are a sink for organic material and are generally characterized by more continuous habitat structure (Fonseca *et al.*, 1983). In addition, the presence of intertidal meadow habitat, versus subtidal-only habitat, influenced fish communities; a greater variety of resources is likely available within meadows that cover both tidal ranges. Overall, the characteristics that were found to be important across sites were quite consistent across the different levels of anthropogenic disturbance, suggesting strong environmental filtering by these particular parameters, as well as the potential for indirect human impacts through their alteration.

Remaining unexplained variation indicated other important factors for seagrass fish community assembly processes (review by Boström *et al.*, 2011; Fig. 4) that may also have influenced the different pattern observed in abundance-based dissimilarity (BC beta-deviation) in communities across regions (Fig. 2b). In particular, seagrass meadows exist within a coastal mosaic of habitats, including kelp forests and salt marshes in temperate regions, and coral reefs and mangroves in tropical regions. These habitats combined provision resource subsidies and corridors for movement (Boström *et al.*, 2011). For instance, a transient fish species was found to move from interior seagrass meadows to edges as it grew larger, and finally to rocky reef habitat as adults (Espino *et al.*, 2015). Seagrass meadows adjacent to mangroves have also been found to have a higher richness of nursery fishes than meadows alone (Nagelkerken *et al.*, 2001). Metacommunity dynamics within seagrass and other coastal habitats are likely influenced by this larger scale seascape.

Anthropogenic impacts on communities and ecosystems

The meadows in high disturbance areas appear to be heterogeneous, perturbed environments which may favor species with traits that require less stable environments (Clavel *et al.*, 2011). The top indicator species found for low and high disturbance sites (Table 2) have characteristics that generally correspond with those that promote extinction or range expansion in impacted systems, respectively, including large size, low fecundity, stenotopy, and poorly adapted to human activities (i.e.,

‘specialist’) in the former, and small size, high fecundity, eurytopy, and human commensalism (i.e., ‘generalist’) in the latter (McKinney & Lockwood, 1999). Some species of rockfish, the top indicator species of meadows within low disturbance areas, are listed as endangered (e.g., *S. paucispinis*) for the Pacific coast of Canada owing to overfishing and slow reproduction (Yamanaka & Logan, 2010; COSEWIC, 2013). Though Rockfish Conservation Areas have been enforced across the coast of British Columbia since 2007, historical overfishing of rockfish, particularly in the waters between Vancouver Island and the mainland (coinciding with many of our high disturbance sites, Fig. 1), may have contributed to the higher association of rockfish in low disturbance areas (Yamanaka and Logan, 2010). Conversely, threespine stickleback, the top indicator species of meadows in high disturbance areas, is well-known for its evolutionary adaptability (Bell & Aguirre, 2013) and short generation time (Bell *et al.*, 2004). In addition, high disturbance meadows were associated with species traits including high swimming ability and live bearing reproduction, both characteristics of perch (Fig. 5). Traits of low swimming ability and egg guarding associated with low disturbance meadows characterize bay pipefish (*Syngnathus leptorhyncus*), tube-snout (*Aulorhynchus flavidus*), and penpoint gunnel (*Apodichthys flavidus*). Bay pipefish in particular may be considered keystone predators of *Z. marina* epifauna, and as such play an important functional role in seagrass ecosystems (Jorgensen *et al.*, 2007). These results indicate that coastal activities may lead to nearshore environments that are better suited for generalist, opportunistic species, whereas specialist species may require low disturbance habitats. Local diversity of seagrass invertebrate communities has also been found to decline across anthropogenic nutrient enrichment gradients, with a dominance of invertebrates with opportunistic diets in degraded meadows (Tewfik *et al.*, 2007). The widespread replacement of specialist species by generalists in impacted systems may ultimately lead to biotic homogenization at a global level (McKinney & Lockwood, 1999; Clavel *et al.*, 2011).

Our finding of higher epiphyte loads within high anthropogenic disturbance areas may be a signature of nutrients from anthropogenic inputs, terrestrial sources, or oceanographic mixing (Frankovich & Zieman, 2005; Fig. 4, inset), or possibly from mesopredator release of threespine sticklebacks (Eriksson *et al.*, 2011). Offshore fishing of large predatory fish has been found to

increase nearshore mesopredator populations including threespine stickleback, which can subsequently result in release of filamentous algae growth from heightened predation on invertebrate grazers (Eriksson *et al.*, 2011). Seagrass meadows have been found to host higher fish abundances than seaweeds that have replaced meadows (Tuya *et al.* 2014). To-date, there is no evidence of seagrass habitat replacement by algae occurring along the Pacific coast of Canada, though the higher epiphyte loads in high disturbance areas may be important to monitor.

Baseline data for the high disturbance meadows of our study region does not exist to track the change in beta-diversity as human impacts have varied over time. Anthropogenic impacts at high disturbance sites may in some cases have been historically higher than they are now (e.g., reduction in industrial practices in some estuaries), and may allow for a recovery of fish diversity over time. Seagrass fish communities appear to be relatively stable in areas representing low to medium disturbance levels in our study, with little change in beta-diversity over an eight year timespan (Robinson & Yakimishyn, 2013). *Zostera marina* has also been found to be largely persistent despite urbanization in Puget Sound across 40 years, with both increases and declines at a localized scale (≤ 1 km) (Shelton *et al.*, 2017). However, seagrass is a particularly important nursery habitat for marine fishes and invertebrates (Heck *et al.*, 2003; McDevitt-Irwin *et al.*, 2016) that remains a global conservation concern (Cullen-Unsworth & Unsworth, 2016).

Biotic homogenization appears to be developing as a widespread phenomenon of the Anthropocene (Baiser *et al.*, 2012; McGill *et al.*, 2015), particularly, thus far, in novel landscapes (Socolar *et al.*, 2016). Our study provides novel evidence of homogenization of communities that exist within disturbed parts of natural habitats. At the global level, knowledge of how biodiversity, and especially beta-diversity, is changing during the Anthropocene is emerging (McGill *et al.*, 2015). To-date, beta-diversity studies in the context of species homogenization have focused primarily on the impacts of farming and invasive species on plants and birds in terrestrial systems (Socolar *et al.* 2016), as well as on freshwater fishes (Baiser *et al.*, 2012). However, there is increasing emphasis on the conservation application of beta-diversity for detecting community shifts, in part because local species richness may remain constant at the same time as larger-scale community shifts are occurring

(McGill *et al.*, 2015; Socolar *et al.*, 2016). Conservation efforts are now challenged with the need to protect biodiversity across land- and seascapes so that communities may be resilient to further development, non-native species introductions, and ongoing climate change.

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Table 1. Best-fit models from distance-based redundancy analyses on (1) Bray-Curtis beta-deviation and (2) Raup-Crick beta-diversity metrics for fishes in seagrass meadows within the Oregonian province, using all sites (“All”), or sites separated by anthropogenic disturbance categories (“Low”, “Medium”, “High”). Variables were forward selected from separate full models containing anthropogenic disturbance (“All” data only), physical, or biotic parameters. Adjusted R^2 , F-values with residual degrees of freedom (“df”), and p-values are given for all models. Bold text indicates significant models.

Disturbance	Variable component	Best-fit models	Adj. R^2	F-value (df residual)	p-value
All	Anthropogenic disturbance measure	(1) Overwater structures,	(1) 0.09	(1) 3.77 (54)	(1) <0.001
		shoreline modification	(2) 0.02	(2) 1.89 (55)	(2) <0.001
		(2) Shoreline modification			
	Physical	(1) SST July, SST annual, salinity	(1) 0.09	(1) 2.95 (53)	(1) <0.001
		(2) SST July, salinity	(2) 0.02	(2) 1.57 (54)	(2) <0.001
	Biotic	(1) Meadow tidal range, seagrass biomass, shoot density, epiphyte load	(1) 0.11	(1) 2.67 (52)	(1) <0.001
			(2) 0.03	(2) 1.77 (54)	(2) <0.001
		(2) Meadow tidal range, epiphyte load			

Low	Physical	(1) Salinity, tidal current speed	(1) 0.13	(1) 2.47 (18)	(1) 0.002
		(2) Full model NS	(2) 0.05	(2) 1.19 (14)	(2) 0.067
	Biotic	(1) Shoot density, epiphyte load	(1) 0.10	(1) 2.11 (18)	(1) 0.002
		(2) Full model NS	(2) 0.06	(2) 1.18 (13)	(2) 0.052
Medium	Physical	(1) SST July, SST annual	(1) 0.17	(1) 2.63 (14)	(1) <0.001
		(2) Full model NS	(2) 0.07	(2) 1.18 (9)	(2) 0.103
	Biotic	(1) Full model NS	(1) 0.02	(1) 1.06 (10)	(1) 0.381
		(2) Full model NS	(2) -0.03	(2) 0.92 (10)	(2) 0.746
High	Physical	(1) SST July, tidal current speed	(1) 0.35	(1) 5.88 (16)	(1) <0.001
		(2) SST July, tidal current speed	(2) 0.08	(2) 1.85 (16)	(2) <0.001
	Biotic	(1) Meadow tidal range, seagrass biomass	(1) 0.26	(1) 4.24 (16)	(1) <0.001
		(2) Full model NS	(2) -0.01	(2) 0.97 (12)	(2) 0.600

Table 2. Top indicator species for seagrass meadows within anthropogenic disturbance categories of low, medium, and high using abundance- (1) and incidence-based (2) metrics. Top indicator species (up to two shown) have the highest overall permuted test statistic based on the probability that a site belongs to an anthropogenic disturbance category given that the species was found at the site (i.e., specificity, “A”) and the probability of finding the species amongst sites within the disturbance category (i.e., fidelity, “B”).

Disturbance	Indicator species	A	B	Test stat.	p-value
Low	(1) Rockfish spp., crescent gunnel	(1) 0.97, 0.58	(1) 0.76, 0.82	(1) 0.86, 0.70	(1) <0.001, 0.047
	(2) Rockfish spp., cabezon	(2) 0.74, 0.82	(2) 0.76, 0.56	(2) 0.75, 0.68	(2) <0.001, <0.001
Medium	(1) Saddleback gunnel, striped seaperch	(1) 0.72, 0.83	(1) 0.60, 0.44	(1) 0.66, 0.61	(1) 0.009, 0.003
	(2) Pacific staghorn sculpin	(2) 0.42	(2) 0.92	(2) 0.62	(2) 0.02
High	(1) Threespine stickleback, sharpnose sculpin	(1) 0.84, 0.80	(1) 0.95, 0.32	(1) 0.86, 0.50	(1) <0.001, 0.006
	(2) Same species	(2) 0.54, 0.66	(2) 0.95, 0.32	(2) 0.72, 0.46	(2) <0.001, 0.016

Figure captions

Figure 1. Map of the Pacific coast of Canada, British Columbia, showing 89 sampled seagrass meadows (circles with black outline), and the extent of documented *Zostera marina* (green points; British Columbia Marine Conservation Atlas, www.bcmca.ca). Anthropogenic disturbance scores are depicted from high (red) to low (blue) across sites, and the marine zoogeographic provinces are indicated (dashed line).

Figure 2. Bray-Curtis beta-deviation (**a-b**) and Raup-Crick beta-diversity (**c-d**) of seagrass fishes, and Gower distances of physical (**e-f**) and biotic (**g-h**) characteristics of meadows between sites within (**a, c, e, g**) and across regions (**b, d, f, h**) for low (square), medium (circle), and high (triangle) anthropogenic disturbance categories. Higher beta-diversity and Gower distance values indicate more dissimilarity between sites within the same disturbance category. Symbols show bootstrapped averages and error bars are 95% confidence intervals (CIs). Letters indicate significant differences, as determined by non-overlapping 95% CIs.

Figure 3. Non-metric multidimensional scaling (“NMDS”) plots for Bray-Curtis beta-deviation (**a**) and Raup-Crick beta-diversity (**b**) of fishes in seagrass meadows within the Oregonian province. Degree of clustering is shown for low (white square), medium (light gray circle), and high (dark gray triangle) anthropogenic disturbance categories.

Figure 4. Variation in Bray-Curtis beta-deviation of seagrass fishes within the Oregonian province explained (adj. R^2) by variable components of anthropogenic disturbance (“All” data only), physical, and biotic measures (including only variables retained by model selection), as well as shared variation between components. Inset plot shows epiphyte load (grams / m²) in seagrass meadows across anthropogenic disturbance levels. Error bars are mean \pm 1 SE. Letters indicate significant differences, as determined by non-overlapping 95% confidence intervals.

Figure 5. Fourth-corner coefficients for the interaction between anthropogenic disturbance scores and species traits that predict fish abundances in seagrass meadows. Darker colours show higher positive (red) or negative (blue) correlations with anthropogenic disturbance. “Sl : Bd” is the standard length : body length ratio.







