



# Spatial community structure of groundfish is conserved across the Gulf of Alaska

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**ABSTRACT:** The mechanisms structuring patterns of diversity and community composition can be difficult to identify in large, open ecological systems. However, it is important to understand what drives these patterns at larger scales, especially in the face of climate change and other perturbations. The Gulf of Alaska (GOA) is an ideal study system because it has complex topography, climate-driven variability, and an on-going groundfish community survey. We used groundfish community data to examine the ecological theory underlying spatial diversity and community composition across 10 study areas in the GOA. We created geostatistically modeled groundfish abundance and biomass from the Alaska Fisheries Science Center trawl survey data (1984 to 2015) to address inherent errors in trawl observations. We found that species richness and alpha, beta, and functional diversity varied little both within and between study areas. However, turnover in community composition was significant along a longitudinal gradient, with differences driven by lower-abundance species. Fishing pressure had non-linear effects only on species richness and local diversity, while productivity was linearly related to beta diversity. We conclude that spatial patterns of diversity were not driven by disturbance, but were largely driven by environmental heterogeneity, because of the longitudinal turnover in community composition and high beta diversity (and thus low saturation). In addition, the invariant functional diversity but varying community composition together indicate functional redundancy in this ecosystem. Finally, the spatially invariant alpha and functional diversity show that the underlying community structure of the GOA groundfish community was conserved across this large marine ecosystem.

**KEY WORDS:** Diversity · Community structure · Spatial invariance · Spatial insurance

## 1. INTRODUCTION

The mechanisms driving patterns of biodiversity, community structure, and ecosystem stability remain important topics of ecological study, as demonstrated by the substantial efforts dedicated to understanding diversity–stability relationships and the

processes underlying species co-existence (Hutchinson 1961, McCann 2000, Hart et al. 2017). However, our knowledge of these concepts stems mostly from the study of local ecological systems (systems defined at a finer spatial resolution than regional systems). Much less is known about what links local and regional spatial scales and what drives meta-

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community patterns of spatial diversity, stability, and structure.

Species richness is one of the most fundamental diversity metrics and measures the number of species in a given space (habitat, ecosystem, etc.). Similarly, functional diversity measures the number of traits or functions in a given space and is increasingly being used to assess ecological communities in many ways (Petchey & Gaston 2006, Cadotte et al. 2011). These diversity metrics can be used to describe ecological community structure (defined as an aggregate expression of traits and interactions that determine species coexistence) at any scale. In a spatial context, the effects of biodiversity can be examined within local communities ( $\alpha$  diversity), between local communities ( $\beta$  diversity), and within regional communities ( $\gamma$  diversity) (Legendre et al. 2005, Jost 2007). Ecological theory hypothesizes a few potential relationships between diversity at these two scales. The most common is a multiplicative relationship, where  $\gamma$  diversity is the product of  $\alpha$  and  $\beta$  diversity. Stability within local communities ( $\alpha$ ) occurs through asynchronous variation in species biomass, while stability among local communities ( $\beta$ ) occurs through asynchronous variation in local community biomass and composition (Jost 2007, Wang & Loreau 2014).

Spatial stability (hereafter invariance) can be dependent on patterns of biodiversity at several scales from organisms to ecosystems (Leibold et al. 2004, Gonzalez et al. 2009, Wang & Loreau 2014) and is summarized by the spatial insurance hypothesis (Loreau et al. 2003, Wang & Loreau 2016). This ecological meta-community theory states that biodiversity provides spatial insurance for ecosystem properties through spatial exchanges of materials or organisms among local communities in a heterogeneous landscape (Loreau et al. 2003, Gonzalez et al. 2009). This theory arises through 2 mechanisms that structure spatial patterns of diversity: (1) environmental heterogeneity, that drives compensation between species or functional groups, and (2) exchange of organisms among local habitats (hereafter dispersal), that increases biomass and buffers growth rates (Cadotte & Fukami 2005, Legendre et al. 2005, Declerck et al. 2011). Environmental heterogeneity links local and regional scales, and can underpin spatial patterns of diversity by creating local habitats suited to different suites of species (Tamme et al. 2010). Dispersal also links local and regional scales (Leibold et al. 2004, France & Duffy 2006) and supports invariance at the regional scale by enabling locally extirpated species to recolonize from neighboring local communities and permitting local spe-

cies coexistence (Hanski 1998, Vogwill et al. 2009, Mellin et al. 2014). Intermediate dispersal levels can maximize  $\alpha$  diversity and provide compensatory species dynamics, thus maximizing regional invariance (Loreau et al. 2003, Gonzalez et al. 2009). While the spatial insurance hypothesis has been documented among meta-populations, it has not been widely documented at the whole-community level (Mellin et al. 2014, Wang & Loreau 2014, Schindler et al. 2015).

Explaining ecosystem properties such as patterns of species coexistence and community composition (identity of community members) is difficult (Wilson 2011), but work in ecological meta-community theory in the last decade has shed some light on the mechanisms that create these ecosystem properties (Gonzalez et al. 2009). Patterns of species coexistence and composition can be generated by factors whose relative importance can vary among spatial scales (Leibold et al. 2004, Declerck et al. 2011). For example, local coexistence can be driven by dispersal via the spatial storage effect (Mouquet & Loreau 2002, Snyder & Chesson 2004), whereas regional coexistence can be promoted by regionally heterogeneous resource partitioning (Mouquet & Loreau 2002, Gonzalez et al. 2009). Both dispersal and heterogeneous environmental conditions can also influence the composition of meta-communities, resulting in suites of species that are locally diverse but regionally similar (Mouquet & Loreau 2002, Thompson & Gonzalez 2017).

Heterogeneous environmental conditions, such as those arising during disturbance, can structure biodiversity as outlined in the Intermediate Disturbance Hypothesis (hereafter IDH) (Connell 1978). In this framework, medium levels of disturbance increase  $\alpha$  diversity, while low or high levels of disturbance decrease local diversity. However, disturbance effects on diversity cannot be considered independently but must be considered together with productivity effects, which can also influence biodiversity (Huston 2014). In high-productivity areas, theory says that disturbance will increase  $\alpha$  diversity, but in low-productivity areas, disturbance will decrease  $\alpha$  diversity (Huston 2014). What has not been examined is how disturbance and productivity might also affect  $\beta$  diversity across communities within a large ecosystem.

While studies in terrestrial systems have examined mechanisms generating spatial patterns of community diversity, structure, composition, and co-existence (Leibold et al. 2004, Tamme et al. 2010, Yang et al. 2015), comparable studies in marine systems at larger scales are few and more difficult because of the open

nature of these ecosystems (Smith et al. 1993). Recent studies have supported the theory that community composition influences invariance of ecosystem functions in marine ecosystems through response redundancy, because compensation among species (or functional groups) leads to more consistent ecosystem properties (Schindler et al. 2010, 2015, Blake & Duffy 2010). Reviews also indicate that dispersal supports local coexistence of species via the spatial storage effect, where species disperse across an ecosystem to remain in optimal environmental conditions despite spatial variation in those conditions (Chesson et al. 2004, Snyder & Chesson 2004, Gonzalez et al. 2009). However, an examination of these mechanisms and how they influence diversity on a large scale ( $10^4$  km) across a large marine ecosystem is lacking.

An excellent study system to examine mechanisms governing ecosystem invariance, biodiversity, and community composition is the Gulf of Alaska (GOA). This high-latitude large marine ecosystem spans  $>1424493$  km<sup>2</sup> and  $>81281$  km of linear shoreline from Dixon Entrance in the east to the Alaska Peninsula in the west. It is subject to large seasonal, inter-annual (Stachura et al. 2014), decadal, and multi-decadal climate-driven environmental variability that can affect species and ecosystems (Anderson & Piatt 1999, Hare & Mantua 2000, Hollowed et al. 2001). Storm events, seasonal wind mixing, and longer-term shifts in climate forcing have been documented to be important factors governing this marine ecosystem, and can create heterogeneity (e.g. freshwater inputs and sea surface temperatures) (Di Lorenzo et al. 2008) or homogeneity (e.g. atmospheric forcing, Pacific Decadal Oscillation, Alaska Coastal Current [ACC], or Alaska Current [AC]) and affect communities at multiple spatial scales (Gargett 1997, Mantua & Hare 2002, Henson 2007). The ACC dominates the oceanography of the GOA, and promotes a productive ecosystem through supplying micronutrients from shelf sediment resuspension, while the AC contributes macronutrients from offshore via eddies and on-shelf surface flow (Stabeno et al. 2004). The submarine troughs and canyons and complex bathymetry which punctuate this continental shelf ecosystem steer currents and increase spatial heterogeneity, creating several relatively distinct areas of similar conditions that can be compared (Lagerloef 1983, Stabeno et al. 2004). Previous studies have utilized this complex topography for natural experiments based on comparing responses of selected fish species to natural or anthropogenic disturbance (Hollowed et al. 2007,

Logerwell et al. 2007, Walline et al. 2012). This spatial heterogeneity can also lead to spatial variation in environmental conditions that can influence ecosystem processes and properties.

The groundfish assemblage in the GOA is widely distributed, well-studied (Mueter & Norcross 2000, 2002), readily identified to species, and supports important fisheries (Hollowed et al. 2001), and most species are mobile and known to respond to perturbations (Anderson & Piatt 1999, Hollowed et al. 2007). These species also exhibit relatively long life spans, which could preserve reproductive potential over time, but also have different life history strategies. Strategies include broadcast spawning (e.g. walleye pollock *Gadus chalcogrammus*), protracted pelagic larval stages (e.g. dover sole *Solea solea*), and larval parturition in regions of high larval retention (e.g. rockfish species). While generally mobile, adults do exhibit differences, with some species having broad feeding migrations (e.g. Pacific cod *Gadus macrocephalus*), and others showing territorial behavior (e.g. rockfish *Sebastes* species). In addition, food webs in the GOA are usually dominated by short interaction chains with a select group of species, suggesting that shifts in environmental conditions (that affect these species) could be detected relatively quickly (Gaichas & Francis 2008). The life history and community structure of groundfish species, the high environmental variability, and the propensity for disturbance in this large marine ecosystem led us to select this system to empirically investigate the ecological theory underlying patterns of biodiversity, spatial invariance, and community composition.

We took an ecological approach to applying the meta-community and biodiversity theory outlined above to our examination of patterns of biodiversity, community composition, and ecosystem invariance. We used existing public data from the GOA high-latitude large marine ecosystem and focused on the 55 most common groundfish species across 10 study areas in the GOA over a period of large natural (e.g. climate regime shifts) and anthropogenic (e.g. fishing disturbance) environmental perturbations. Specifically, we considered whether we could identify the underlying mechanisms behind spatial patterns of biodiversity and community composition. We asked: (1) Does diversity (both taxonomic and functional) and community composition differ across this large ecosystem? (2) Is there evidence that environmental heterogeneity or dispersal drive diversity or community composition? (3) Is there evidence that disturbance and productivity are influencing diversity in this ecosystem?

## 2. MATERIALS AND METHODS

### 2.1. Data

To examine the questions we pose in this study empirically, we needed to use data with good spatial resolution collected over a long time period. Since 1984, the Alaska Fisheries Science Center (AFSC) has conducted comprehensive bottom trawl surveys in the GOA to monitor trends in the distribution and abundance of groundfish populations. Because species exhibit different vulnerability to the survey trawl, these data reflect the demersal fish community on the continental shelf. The surveys were run triennially from 1984 to 1999 and biennially between 1999 and 2015 (14 yr total). The full survey area includes the continental shelf and upper continental slope (to 1000 m depth) in the GOA, and extends from the Islands of Four Mountains (170°W) 2300 km east to Dixon Entrance (54°N). The AFSC contracts 3 commercial trawlers from May through August, and samples the 320 000 km<sup>2</sup> survey area with ~820 survey stations (Alaska Fisheries Science Center). The catch data result in observations of catch-per-unit-effort (CPUE) which are then averaged and expanded by survey area to estimate the relative abundance of important groundfish species. This multi-species survey is based upon a stratified-random design and the area-swept method of estimating abundance (von Szalay et al. 2010). The net used in this survey is a 4-seam, high-opening Poly Nor'Eastern trawl featuring a 27.2 m headrope and a 36.7 m footrope equipped with rubber bobbin roller gear. The net is deployed from the vessel while the vessel steams ahead at 3 knots. Once on the seafloor, the net is towed for 30 min (prior to 1992) or 15 min (1992 to present). In most years, the net was equipped with a bottom contact sensor on the footrope and a Seabird SBE-39 bathythermograph on the headrope. The catch was processed by the scientific crew who identified all living organisms and weighed and counted the catch of each species.

We used smoothed estimates of AFSC survey data generated by a geostatistical model developed by Shelton and colleagues (Shelton et al. 2014, 2018, Ono et al. 2016) for several reasons, as follows. These geostatistical models accounted for imprecision in the data (expressly because the raw survey data is variable), environmental covariates (e.g. depth), and the effect of changing effort (tow duration) across the study period. For this study, we constructed separate spatio-temporal statistical models for 55 groundfish species groups (hereafter species) to identify their patterns of occurrence and density (conditioned on

the species presence) in the GOA. However, it is critical to note that we present only spatial analyses here. Species correlations are included implicitly, in that species that are strongly correlated in the raw data will necessarily correlate in their statistically modeled spatial fields. These 55 species represent taxa that were observed in  $\geq 3\%$  of the survey tows (>230 tows). Because most species were absent from a large number of observed trawls, we modeled the presence and distribution of species density separately, using a delta-GLMM approach with 2 sub-models (Pennington 1983, Maunder & Punt 2004, Shelton et al. 2014). The first sub-model ('occurrence model') described the probability of occurrence of individual species in a given year and at each given location; the second sub-model ('positive model') described the CPUE (kg hectare<sup>-1</sup>) of species in a given year and at each location conditional on the occurrence of at least 1 individual (please see specific equations in Shelton et al. 2017, 2018). Both sub-models included spatial random effects that follow a first-order autoregressive process and account for variation not explicitly included in the model (e.g. environmental variation, population processes, or the triennial [1984–1999] and biennial [1999–2015] nature of the trawl data). Because most groundfish exhibit spatial patterns related to depth, we used CPUE observed in each trawl as the response variable, and the explanatory variables included both linear and quadratic terms for log(bottom depth) at each trawl location (Perry & Smith 1994, Tolimieri 2007, Shelton et al. 2014).

Once the sub-models were estimated, we used them to project densities for each species for the GOA. We projected model estimates to the centroid of 2 × 2 km grid cells covering the entire GOA from 1000 Markov Chain Monte Carlo (MCMC) samples generated from the joint (both sub-models) approximate posterior density for each species (Shelton et al. 2018). We calculated unconditional expectations for CPUE (kg hectare<sup>-1</sup>) of each species in each year and at each location by multiplying each MCMC sample from the occurrence and positive model (Shelton et al. 2018). We properly accounted for the uncertainty in these estimates by sampling from the joint posterior distribution. These predicted CPUEs for each 2 × 2 km grid cell were combined to generate mean estimates (and standard deviations) of CPUE for each species in each year within discrete study areas (see Section 2.2) (Shelton et al. 2014, 2018, Ward et al. 2015). Further information on model structures, formulations, and projections can be found in Shelton et al. (2018) and in the code from that publication (Shelton et al. 2017).

We then combined the independently estimated spatio-temporal models for each species to generate a suite of multi-species metrics to assess spatial diversity across the GOA. To assess functional diversity, we selected functional traits representing orthogonal components of community structure, including body size, longevity, trophic structure, use of benthic vs pelagic resources, and habitat (see Table S2 in Supplement 1 at [www.int-res.com/articles/suppl/m626p145\\_supp1.xlsx](http://www.int-res.com/articles/suppl/m626p145_supp1.xlsx)). We selected 44 of the 55 GOA groundfish species used in this study because trait and diet data were available for these species, they represent the majority of total community abundance, and the subset was not biased towards any particular functional groups or traits. We used existing, publicly available data sources. First, we assembled functional trait data from the AFSC's life history database (NOAA AFSC 2016a), FishBase (Froese & Pauly 2016), and 2015 Stock Assessment reports (NOAA AFSC 2015). We then added diet information from the AFSC's Resource Ecology and Ecosystem Monitoring diet database (NOAA AFSC 2016b), and estimates of trophic position based on Aydin et al. (2007). Where possible, we used trait data from the Gulf of Alaska; however, when these were not available, we used all available data from other regions. Our assembled functional trait data used in this study is publicly available on the Knowledge Network for Biocomplexity repository (Ward & Blake 2016).

We used catch data from the Commercial Fisheries Entry Commission (CFEC; [www.cfec.state.ak.us](http://www.cfec.state.ak.us), accessed 5 May 2017) to represent the disturbance from fishing pressure across our study areas. In this case, we defined disturbance as the removal of fish biomass (aside from natural mortality) from the ecosystem, rather than habitat destruction from fishing methods and gear (Hiddink et al. 2017). Because fisheries catches are reported differently by species and jurisdictional areas, we grouped our study areas into 4 broader regions defined by the statistical catch areas for longline and trawl fisheries. While other datasets such as vessel monitoring system data with geographically referenced locations might provide higher resolution, these data do not exist for the entire time period of this study and so were not used. Instead, using the CFEC catch data, we calculated the total groundfish mass sold (sum) from trawl and longline fisheries to get a catch value (metric tons km<sup>-2</sup>) representing fisheries removals for each broad region and study year (1985–2014) (Shelton et al. 2018). For some analyses, we then took the average across years or sites within a catch area for each year.

Finally, we used publicly available remotely-sensed chlorophyll *a* data as a proxy for primary productivity. The SeaWiFS and MODIS Ocean Color datasets (Hu et al. 2012, NASA Goddard Space Flight Center 1997–2010, 2003–2015) are frequently used as an indicator of primary productivity in the literature (Witman et al. 2008, Lander et al. 2009, Wood et al. 2015, Rueda et al. 2015). In addition, in this region, there are no other publicly available sources for ocean productivity data. Data were available for the years 1997–1998 and 2003–2016. After downloading, we selected only the data from grid points that overlapped with each of our 10 study areas (grid data are at 4 km resolution). We then calculated annual mean chlorophyll *a* values for each study area, again, as a proxy for primary productivity.

## 2.2. Study areas

We mapped the extent of the trawl survey data over the shelf region of the central GOA. We then selected study areas on the shelf based on bottom depth: 10 contiguous areas of depth 50 to 150 m (Fig. 1). Choosing sites in this depth range kept our study areas on the continental shelf (not the slope) and generally within similar habitat conditions. Study areas were located between 145° W and 159° W, were separated by canyons or areas of shallower depth, and ranged in size from 1352 to 8364 km<sup>2</sup> (see Table S1 for more information on study areas). Though study areas were discrete, a feature of the spatio-temporal statistical model is that some information may be shared between study areas due to the spatial range of correlations. However, in most cases in this project, the distances between the study areas exceeded the species range model parameter (Shelton et al. 2017, 2018).

## 2.3. Statistical analysis

To examine spatial patterns in biodiversity, we calculated several diversity metrics for the GOA groundfish community: species richness, alpha, beta, and gamma diversity, and functional diversity. In this study, alpha diversity ( $expH\alpha$ , hereafter  $\alpha$ ) quantifies the effective number of distinct species in each study area, beta diversity ( $expH\beta$ , hereafter  $\beta$ ) quantifies the effective number of distinct communities and represents differences in species diversity among the study areas, and gamma diversity ( $expH\gamma$ , hereafter  $\gamma$ ) is the effective number of distinct species across all study areas. These values of effective number of spe-



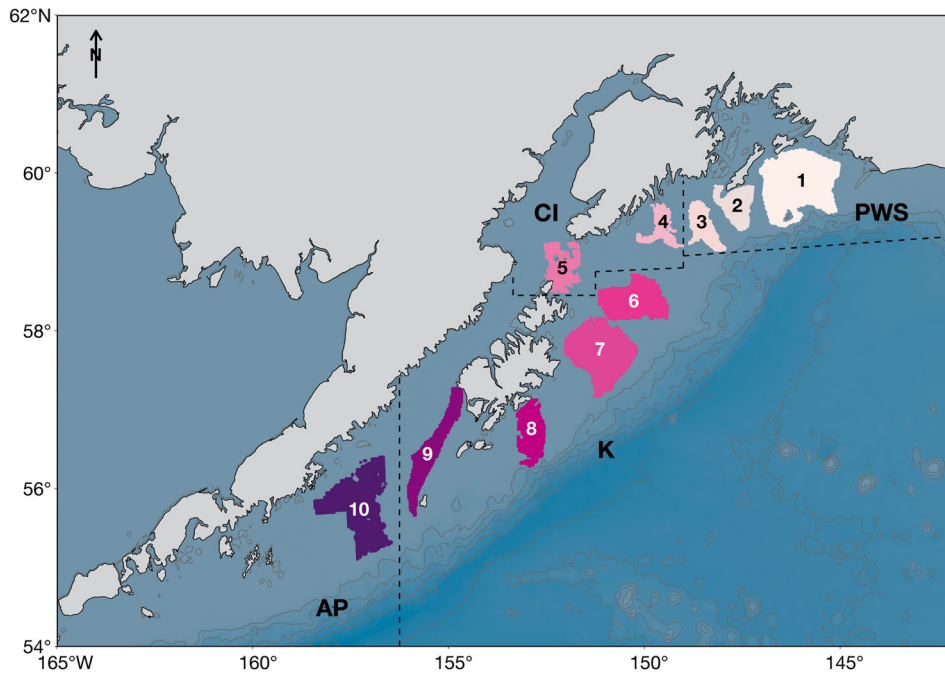


Fig. 1. Study areas along the central GOA continental shelf. Dashed lines demarcate fishing catch statistical areas. AP: Alaska Peninsula, K: Kodiak, CI: Cook Inlet, PWS: Prince William Sound

cies represent the diversity of a community with equally common species, and allowed us to compare between study area communities.

We began by identifying uncertainty in the model predictions used to estimate species diversity metrics by resampling the predicted distributions of species occurrence and densities within each study area 1000 times using bootstrap methods, then calculating the mean and variance of the diversity metrics. We then estimated species richness by summing the predicted occurrence (generated by the occurrence model) of all species within each study area in each year (Dorazio et al. 2006). To calculate  $\alpha$  (within study area) and  $\gamma$  (within region) diversity, we took the exponent of the Shannon-Wiener diversity ( $\exp H$ ) to calculate the effective number of species. We then used the values of  $\alpha$  and  $\gamma$  to solve the multiplicative relationship ( $\alpha \times \beta = \gamma$ ) for  $\beta$  (between study area) diversity (Shannon 1948, Jost 2007). This multiplicative relationship also allowed us to discuss saturation (proportion of species in local communities as compared to those in the regional meta-community) and how it relates to  $\beta$ . Diversity metrics were calculated for each study area in each year using the vegan package in R (Oksanen et al. 2016).

We also examined functional diversity in the 10 study areas using Rao's index of quadratic entropy (henceforth Rao's  $Q$ ) (Rao 1982, Mouchet et al. 2010). This measure of functional diversity is widely

used in ecological literature, is especially useful in examining functional diversity when several traits are used (Botta-Dukát 2005, Maynard et al. 2017), and incorporates both functional richness and functional divergence (Weigelt et al. 2008, Stuart-Smith et al. 2013, Robroek et al. 2017). Rao's  $Q$  is also particularly well-suited to understanding the mechanisms driving the turnover of diversity and composition along environmental gradients (De Bello et al. 2010). We used a square-root corrected species-by-species Gower distance matrix for functional traits and mean densities from the spatio-temporal model for the species-by-species abundance matrix. Continuous traits were log-transformed prior to analysis, and we used only uncorrelated traits (Botta-Dukát 2005). We calculated Rao's  $Q$  for each study area in each year but did not correct Rao's  $Q$  for the effect of species richness because richness did not vary significantly between local areas (Mouchet et al. 2008). To test for differences in Rao's  $Q$  between study areas, we used a 1-way ANOVA followed by a Tukey post-hoc test. Functional diversity analyses were conducted using the FD package in R (Laliberte et al. 2014).

To assess spatial variation in community composition between local study areas, we used non-metric multidimensional scaling (NMDS) with Bray-Curtis dissimilarities. This common method of examining community composition (Mueter & Norcross 2000,

Blake & Duffy 2012) is a statistical technique that has been used widely in ecological studies (Smith et al. 2014, Tolkkinen et al. 2015, Moore & Duffy 2016). The modeled mean abundance of individual species varied by 8 orders of magnitude between local study areas and years. Therefore, we employed the Hellinger transformation (Legendre & Gallagher 2001), which allowed us to examine results driven predominantly by abundant species. Then, to account for differences in relative abundance, we conducted an additional analysis that used a Wisconsin-style double standardization of square-root transformed data (Bray & Curtis 1957). This allowed the result to be driven equally by rare and abundant species. We used permutational multivariate analysis of variance (PERMANOVA) to evaluate the significance of between-area differences in community composition (Anderson 2001). To evaluate whether PERMANOVA results were driven by between- or within-area differences in replicates, we evaluated the homogeneity of within-ecoregion dispersions (Anderson 2006). Multivariate analyses were conducted using the *vegan* package in R (Oksanen et al. 2016).

To test the influence of disturbance and primary productivity in structuring diversity across this large marine ecosystem, we fit both linear models and generalized additive models (hereafter GAMs) for each diversity metric to either fishing catch data or chlorophyll *a* data. Diversity metrics (response variables) included species richness,  $\alpha$  diversity,  $\beta$  diversity, and functional diversity. Due to the limited overlap of all our datasets (chlorophyll *a*, fishing pressure, and trawl survey), we could include 12 years of data in these analyses (1987, 1990, 1993, 1996, 1999, 2001, 2003, 2005, 2007, 2009, 2011, and 2013). GAMs were fit using the *mgcv* package in R (Wood 2011). We evaluated candidate models using the *gam.check()* and *plot()* functions to examine residuals and other metrics for potential correlations that would invalidate this analysis (none found). The best model for each diversity metric was then selected based on adjusted  $R^2$  values and AIC comparison.

#### 2.4. Data and code availability

All data used in this study are publicly available. Derived and processed data, geostatistical model code and output, bootstrapping code, and code used to generate statistical results are publicly available in the data package for this publication on the Knowledge Network for Biocomplexity repository at <https://knb.ecoinformatics.org/> (Blake et al. 2019).

### 3. RESULTS

#### 3.1. Diversity

We examined 4 diversity metrics (species richness,  $\alpha$ ,  $\beta$ , and functional diversity) within each of the 10 study areas in the GOA to understand how diversity varied spatially across this large marine ecosystem. Species richness in each study area was relatively low (across the 31 yr), and ranged from approximately 9 to 13, with the largest difference between any 2 study areas being just 4 and the average difference just 2 (Fig. 2b). The western-most study areas (8 to 10) had higher species richness (on average 2 more species), and those areas to the east had lower richness (on average 2 fewer species) (Fig. 2b).  $\alpha$  diversity (within area diversity) varied little between study areas and averaged  $\sim 9$  species across areas (Fig. 2a).  $\beta$  diversity (between area diversity) was also remarkably similar across study areas and also averaged  $\sim 9$  (Fig. 2c). Because  $\beta$  diversity is multiplicative ( $\beta = \gamma/\alpha$ ), local diversity was on average  $1/9^{\text{th}}$  of regional diversity, indicating low saturation in local communities.

Given the spatial invariance of taxonomic diversity metrics both within and between study areas, we examined functional diversity (Rao's  $Q$ ) to better understand the structure of this groundfish community. Rao's  $Q$  also showed little variation across local communities with few exceptions (Fig. 2d): local study area 6 differed significantly from local areas 1, 2, and 4, and local areas 2 and 10 also differed significantly from each other (Tukey test,  $p < 0.05$ ). Despite these statistical differences, the overall variation in functional diversity was low across local communities. Taken together with the taxonomic diversity metrics, these results point towards the conservation of groundfish community structure across the central GOA during this period.

#### 3.2. Community composition

We also examined community composition because functional diversity can be partially dependent on species identity. Community composition varied across a longitudinal gradient, with NMDS polygons for study areas 8–10 showing no overlap with the rest of the areas (Fig. 3). Despite areas 2 to 7 showing some overlap, all areas were significantly different in composition from each other (PERMANOVA,  $p = 0.005$ ,  $R^2 = 0.222$ ). These results were confirmed by a homogeneity test of within-area dispersions, which indicates the differences are attributed to real

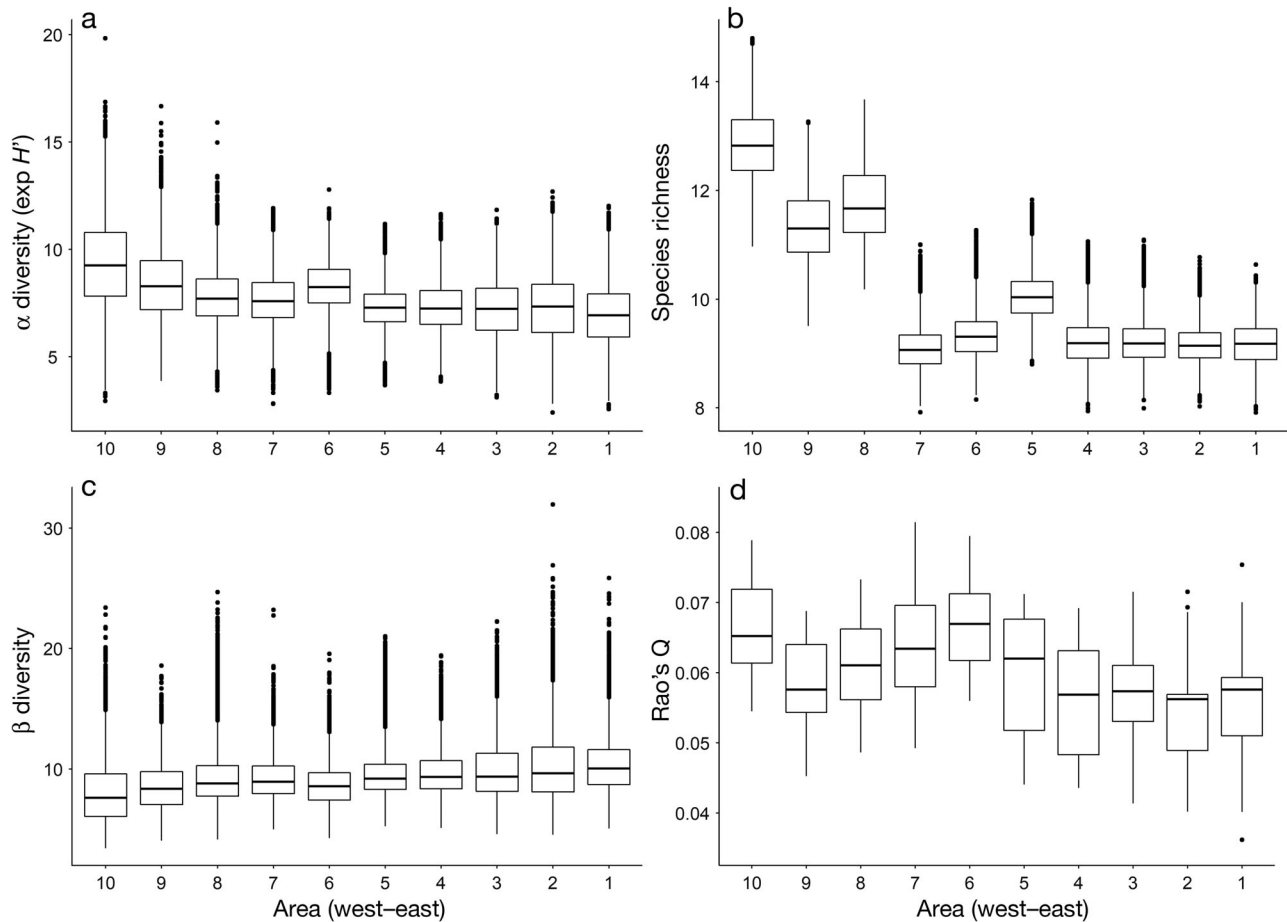


Fig. 2. Boxplots of (a)  $\alpha$  diversity, (b) species richness, (c)  $\beta$  diversity, and (d) functional diversity (Rao's Q) for local study areas 1 to 10. Tukey boxplots — horizontal lines: medians across the whole dataset for each local study area; box: 75<sup>th</sup> and 25<sup>th</sup> percentile; whiskers: values 1.5 times the interquartile range (75<sup>th</sup> percentile – 25<sup>th</sup> percentile); dots: values >1.5 times but <3 times the interquartile range

between-area differences in community composition ( $p = 0.94$ ). Therefore, the groundfish community composition varied across space with distinct groups of species in the individual study areas.

In the easternmost study areas 1 to 7, differences in community composition were driven by rare and intermediate-abundance species. Composition of the most abundant species did not show changes: transforming the data to emphasize the influence of the most abundant species resulted in non-significant differences in community composition between study areas (Hellinger transformation, Fig. S1 in Supplement 2, [www.int-res.com/articles/suppl/m626p145\\_supp2.pdf](http://www.int-res.com/articles/suppl/m626p145_supp2.pdf)). Instead, changes in community composition were only apparent when less-abundant species were allowed an equal chance of explaining community structure (Wisconsin-Square root transformation, Fig. 3).

### 3.3. Disturbance and productivity

We regressed each diversity metric (species richness,  $\alpha$ ,  $\beta$ , and functional diversity) against fisheries catch and chlorophyll *a* and found that non-linear and linear models best fit the catch and chlorophyll data respectively. Only 2 relationships (species richness and  $\alpha$  diversity on fishing pressure) followed the expected unimodal relationship supporting the intermediate disturbance hypothesis (Fig. 4a,b). Fishing pressure showed inverted unimodal and multi-modal relationships with  $\beta$  diversity and functional diversity, respectively (Fig. 4c,d). In contrast, primary productivity had a significant positive linear relationship with  $\beta$  diversity that did not follow the intermediate productivity hypothesis (Fig. 4e). Primary productivity had no other significant relationships with diversity metrics (Fig. S2).



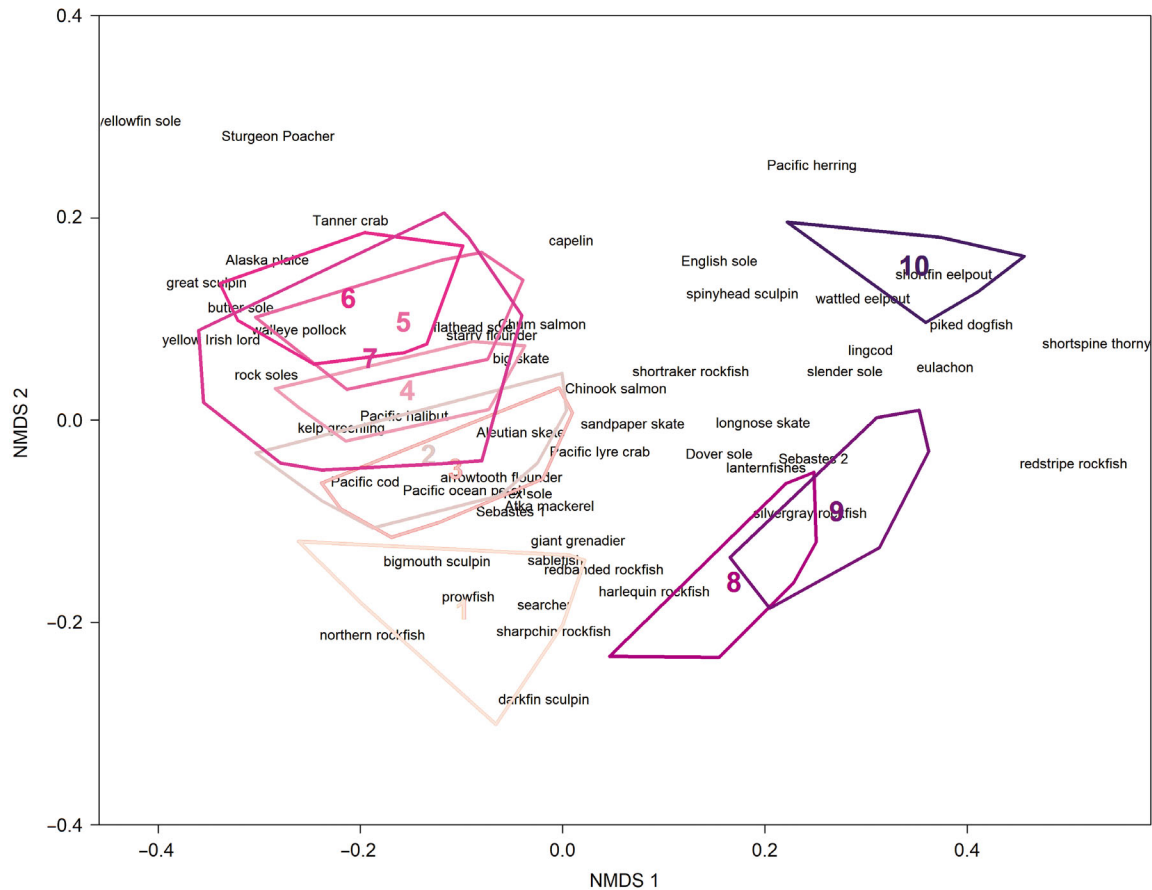


Fig. 3. NMDS plot of community composition for the 10 study areas. Hulls connect or encircle the community composition in each year for a given study area. This plot uses the Wisconsin-square root transformed data

#### 4. DISCUSSION

Overall, diversity and community structure were spatially invariant across the central GOA. Taxonomic and functional diversity varied little at either local or regional spatial scales. Species richness showed some variation longitudinally; while  $\alpha$  diversity was consistently low,  $\beta$  diversity was consistently high (and thus saturation was low), and functional diversity (Rao's  $Q$ ) showed no discernable pattern across the 10 study areas. Community composition varied longitudinally, driven by turnover of less-abundant species. However, only local diversity (species richness and  $\alpha$ ) varied unimodally with disturbance (fishing pressure). Despite these differences in species traits, disturbance, and community composition, community structure were invariant across this large marine ecosystem.

The spatial invariance of these ecosystem properties was a surprise, given the open, complex nature of this ecosystem. Because the environmental hetero-

geneity across the GOA creates local habitats suited to different suites of species, we expected to see large differences in species richness and  $\alpha$  diversity between study areas. While we did see some differences in species richness between areas, the higher and lower richness sites varied by only 2 species on average, and we did not observe variation in  $\alpha$  diversity. We also expected to see low values of  $\beta$  diversity (high saturation) because all species were expected to be able to colonize all local communities. On the contrary, local communities contained a spatially invariant number of species (spatially stable  $\alpha$  diversity), an invariant fraction of the regional species pool (spatially stable  $\beta$  diversity), and an invariant diversity of functions (spatially stable Rao's  $Q$ ). This invariance in diversity metrics occurred despite strong between-community differences in species composition (Fig. 3) and total community abundance (Shelton et al. 2018). Likewise, due to environmental conditions such as ecosystem openness, dispersal, and strong currents, we expected homogeneous commu-

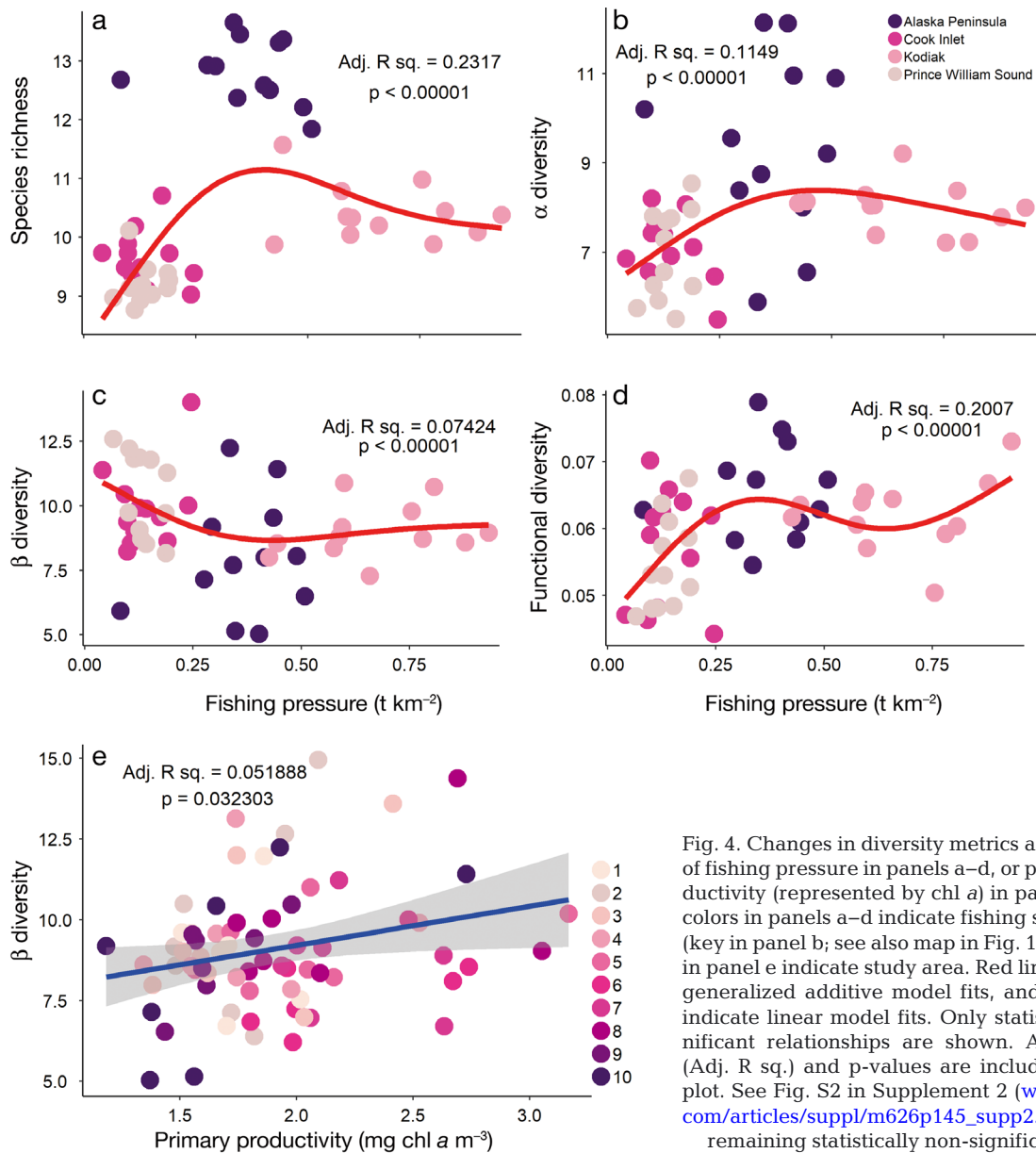


Fig. 4. Changes in diversity metrics as a function of fishing pressure in panels a–d, or primary productivity (represented by chl a) in panel (e). Dot colors in panels a–d indicate fishing sub-regions (key in panel b; see also map in Fig. 1); dot colors in panel e indicate study area. Red lines indicate generalized additive model fits, and blue lines indicate linear model fits. Only statistically significant relationships are shown. Adjusted  $R^2$  (Adj. R sq.) and p-values are included in each plot. See Fig. S2 in Supplement 2 ([www.int-res.com/articles/suppl/m626p145\\_supp2.pdf](http://www.int-res.com/articles/suppl/m626p145_supp2.pdf)) for the remaining statistically non-significant plots

nity composition across this large marine ecosystem. However, we were equally surprised to find variation (spatial turnover) in community composition across our study areas. Finally, despite generally high primary productivity across the GOA, we did not find an interaction between primary productivity and fishing disturbance, but only found the expected effect of intermediate fishing disturbance on local species richness and  $\alpha$  diversity. On the whole, our results differed from our expectations, which were formulated from ecological meta-community, species-coexistence, and biodiversity theory.

#### 4.1. Diversity

Despite small variations in species richness and functional diversity across local communities, our diversity metrics, taken all together, indicate that community structure was conserved across the GOA. Functional diversity, computed from traits representing multiple uncorrelated elements of community structure, was invariant. This suggests that local communities were structured similarly with respect to functional roles and contained species that were functionally redundant across the region. Previous work in

freshwater lake systems has also found conserved community structure via conserved zooplankton biomass size spectra between lakes (Sprules 2008). Additionally, we found invariant  $\alpha$  diversity, indicating that local communities had a similar distribution of relative abundance among those species present in the community. This result is corroborated by our previous examination of community structure, which indicated that local communities are consistently dominated by apex predators, with similar ratios of predator to prey abundance (Shelton et al. 2018). Additionally,  $\beta$  diversity was high in all local communities, and saturation was low (however, the terms high and low are only relevant within the context of this study). The multiplicative relationship between  $\alpha$  and  $\beta$  diversity ( $\beta = \gamma/\alpha$ ) indicates that if  $\beta$  diversity is invariant across space, then community saturation (inverse of  $\beta$ ) and  $\alpha$  diversity must be as well (Whittaker 1960, Jost 2007, Tuomisto 2010). Our results of spatially invariant  $\alpha$  diversity agree with this.

Local communities showed low saturation relative to the regional species pool, with low local ( $\alpha$ ) diversity relative to regional ( $\gamma$ ) diversity. In other words, local communities contained on average 1/7<sup>th</sup> to 1/10<sup>th</sup> of the regional species pool investigated (Fig. 2c). However, it is important to note that our determination of saturation used the effective number of species for both  $\alpha$  and calculated  $\gamma$  diversity, based on the multiplicative relationship between  $\alpha$  and  $\beta$  diversity. Therefore, our calculated  $\gamma$  diversity (effective number of species in the meta-community) was sometimes  $>55$  because it actually represented the number of equally abundant species that would provide the same diversity as the 55 species in this study. The low saturation of local communities is reflected in the relatively high  $\beta$  diversity we observed, which likely arose from high spatial turnover of community composition, which in turn likely arose from a longitudinal gradient in environmental conditions (environmental heterogeneity).

But why would local communities be equally saturated across a spatially expansive meta-community? It is first important to note that we were careful to standardize our data to biomass (as estimated by CPUE) or occurrence per unit area (as estimated from the occurrence model) to strongly reduce the chance our results could be confounded by the size of our local study areas (Shelton et al. 2018) because previous work shows there can be a relationship between saturation and the spatial scale of communities (Shurin et al. 2000). From theory, intense competition among species could drive saturation (constrained local richness) in local communities (Srivastava 1999), and if

that competition is relatively uniform across the meta-community, such competition could lead to equal saturation. Unsaturation (unconstrained local richness) in local communities is also likely to be driven by the number of species in the regional pool, higher immigrations than extinctions, and a dynamic, open community (Mateo et al. 2017). While we know that the central GOA is indeed a dynamic, open marine ecosystem, it would be pure speculation as to which of these mechanisms drove the patterns we observed across this large meta-community. We observed low saturation with high spatial turnover in community composition, but our data are not comprehensive enough to test these ecological theories.

## 4.2. Community composition

Despite the presence of conditions which should facilitate strong dispersal in our study system (an open ecosystem, mobile fish species with pelagic eggs or larvae, and the ACC and AC), we observed turnover of composition between local communities along a longitudinal gradient. Changes in diversity and species identities (turnover in community composition) along a latitudinal gradient are expected from longstanding biogeography theory (Mittelbach et al. 2007). While compositional turnover has been observed in open marine systems spatially along latitudinal gradients (e.g. coral-associated fish [Mellin et al. 2014] and fish assemblages of the North Sea prior to warming [Magurran et al. 2015]), few examples exist documenting turnover along a longitudinal gradient (but see Conord et al. 2012, Smith et al. 2014, Blowes et al. 2017), and the mechanisms and processes underlying longitudinal diversity and turnover patterns are less well understood (Mueter & Norcross 2002, Smith et al. 2014). At the largest scale (global), a longitudinal gradient in diversity (commonly measured as species richness) is usually ascribed to historical biogeography, with indications that differences in community composition between sites underlie this gradient (Blowes et al. 2017). Recent work in the Barents Sea did document a longitudinal pattern of diversity in the demersal fish community, with eastern sites having lower diversity (Certain & Planque 2015). This agrees with our results showing lower species richness at our 7 eastern-most local communities and higher species richness at the 3 western-most local communities. Other recent work on Australasian reefs has shown a clear longitudinal gradient in species compositional turnover, which supports our NMDS results of longitudinal turnover in community

composition (Smith et al. 2014). What remains unclear are the underlying mechanisms driving these similar patterns in turnover.

Two ecological mechanisms that could structure spatial patterns of community composition include dispersal and environmental heterogeneity, which would lead to communities with the same composition or different composition, respectively (Ricklefs & Schluter 1994, Freestone & Inouye 2006). Because we found longitudinal turnover in composition, this suggests that species sorting along an environmental gradient is the mechanism underlying spatial turnover in community composition (Whittaker 1962, Leibold et al. 2004). In other words, environmental heterogeneity is more important than dispersal in structuring our local communities, despite the fact that this is a completely open system, linked by the ACC/AC, and these are generally mobile fish species.

Intriguingly, we found that spatial turnover in community composition along the longitudinal (environmental) gradient occurred among subdominant but not dominant species (Fig. 3, Fig. S1). Turnover in community composition was not apparent when data were transformed to emphasize the influence of the most abundant species (i.e. Hellinger transformation; Fig. S1); instead, it was only apparent when data were transformed to allow subdominant species an equal chance of explaining community structure (i.e. Wisconsin-Square root transformation; Fig. 3). The degree of turnover varied somewhat between our local study areas and was strongest in areas 1 to 7 and weaker towards areas 8 to 10 as evidenced by reduced distances between centroids following the Hellinger transformation (Fig. S1). This indicates that all the spatial turnover occurred in the less-abundant lower trophic-level species, while the more numerically dominant species (here, top predators) showed similar spatial composition. These results, in combination with the spatial invariance in functional diversity, indicates that numerically subdominant species were replaced along the longitudinal gradient in such a way that they filled the same functional role in each local community. Identity and community composition of numerically dominant species (arrowtooth flounder *Atheresthes stomias*, Pacific halibut *Hippoglossus stenolepis*, walleye pollock *Theragra chalcogramma*, Pacific cod *Gadus macrocephalus*; see also Table S3) was invariant among easternmost sites and less variable than subdominant species among westernmost sites. Our observation of functional redundancy (invariant functional diversity with high spatial turnover in species composition), together with

our result of low saturation (high  $\beta$  diversity) might indicate the presence of a spatial insurance effect.

### 4.3. Disturbance and productivity

Despite the integral nature of the intermediate disturbance and productivity hypotheses in ecological theory, we found no support for their interaction. This is potentially because the magnitude and sustained nature of fishing pressure across this ecosystem has larger effects than any effects of primary productivity, which following from our one analysis might play a less important role in structuring diversity in this region. We only found support for the intermediate disturbance effect of fishing on local species richness and  $\alpha$  diversity, with higher diversity values at intermediate levels of fishing pressure (Fig. 4). However, because we only had data from 12 yr in this particular analysis, we are cautious in drawing conclusions from this analysis.  $\beta$  diversity showed a relationship with fishing pressure that was the inverse of the relationship with  $\alpha$  diversity, as expected from the intrinsic relationship between these 2 components of diversity. However, functional diversity showed a more complex multi-modal relationship. Primary productivity had little significant effect, except for a significant positive relationship with  $\beta$  diversity, and a marginally negative effect on  $\alpha$  diversity (Fig. 3, Fig. S1). The significant effect on  $\beta$  diversity could stem from an increasingly patchy pattern as primary productivity increased, leading to larger differences in diversity between local communities across the landscape. Local, short-term responses to changes in primary productivity (chlorophyll *a*) have been demonstrated for walleye pollock *T. chalcogramma* and capelin *Mallotus villosus* (Hollowed et al. 2007, Logerwell et al. 2007).

Like other recent work (Adler et al. 2011, Grace et al. 2014), our results stand in contrast to longstanding theory, which predicts that species richness should exhibit a unimodal relationship (rise and then fall) with productivity (Connell 1978, Grime 1979). Recent theoretical work also refutes the IDH, to a large extent, because if the predicted unimodal relationship is observed, it is often due to other mechanisms (Fox 2013). While it is possible that fishing pressure in this large ecosystem is a strong-enough driver that we observed the IDH effect as originally proposed, it is also conceivable that we observed this unimodal relationship for other reasons, such as species having bounded growth or other non-linear factors that promote species coexistence and ecosystem invariance (Fox 2013).

The spatial insurance hypothesis describes how diversity can buffer communities against ecosystem perturbations, but empirical demonstrations of this effect are less abundant (Shanafelt et al. 2015). The importance of environmental heterogeneity (species sorting) and functional compensation mechanisms underlying spatial patterns of high  $\beta$  diversity and turnover in community composition in our study system may contribute to the spatial insurance effect and buffer the regional Gulf of Alaska groundfish community against perturbations.

#### 4.4. Summary

Across the central Gulf of Alaska during this study period, local communities held a spatially invariant number of species (stable  $\alpha$ ), an invariant fraction of the regional species pool (stable  $\beta$ ), and constant functional diversity, despite between-area differences in community composition, total community abundance, and some environmental variables (productivity and fishing disturbance). In this study, low  $\alpha$  diversity and low saturation of local communities (and relatedly high  $\beta$  diversity) in all probability arose from high spatial turnover of community composition, which in turn likely arose from a longitudinal gradient in environmental conditions (environmental heterogeneity). Collectively, our observations of varying species richness, varying community composition (spatial turnover), and high  $\beta$  diversity (low saturation) suggest that spatial patterns of diversity were largely driven by environmental heterogeneity, presumably via species sorting (Leibold et al. 2004). Additionally, functional redundancy likely arose from the high spatial turnover of community composition combined with invariant functional diversity, such that traits remained constant in local communities despite changing species identities across the longitudinal gradient. This suggests that functional redundancy was widespread in this large ecosystem, and implies conserved community structure. Finally, taken collectively, our observations of invariant  $\alpha$  and functional diversity and constant predator/prey ratios (Shelton et al. 2018) indicate that the underlying community structure was conserved across the GOA shelf ecosystem. Yet, with these analyses, we were not able to fully tease apart the components of diversity that are the underlying mechanisms structuring our observed patterns of diversity. Identifying how all the components of diversity discussed above build on each other in this large marine ecosystem to collectively create the spatial diversity-invariance results and the scaling of the spatial insurance

hypothesis at the large community level remain the next steps in better understanding how diversity is structured in this and other large marine ecosystems.

*Acknowledgements.* This work stems from a National Center for Ecological Analysis and Synthesis (NCEAS) working group funded by a grant from the Exxon Valdez Trustee Council to examine the evidence for the portfolio effect on ecosystem responses to natural and anthropogenic disturbances, including the Exxon Valdez oil spill. The Exxon Valdez Trustee Council had no part in the research idea, design, analysis, or preparation of this manuscript. The findings and conclusions presented by the authors are their own and do not necessarily reflect the views or position of the Exxon Valdez Oil Spill Trustee Council. We thank the scientists and crew who collected data on the AFSC trawl surveys, Jessica Couture, funding for NCEAS working group, funding for R.E.B. and C.L.W., and other working group members.

#### LITERATURE CITED

- ✦ Adler PB, Seabloom EW, Borer ET, Hillebrand H and others (2011) Productivity is a poor predictor of plant species richness. *Science* 333:1750–1753
- Alaska Fisheries Science Center (1984–2015) Gulf of Alaska continental shelf and slope survey. [www.afsc.noaa.gov/RACE/groundfish/goa.htm](http://www.afsc.noaa.gov/RACE/groundfish/goa.htm) (accessed February 2015)
- ✦ Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecol* 26:32–46
- ✦ Anderson MJ (2006) Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* 62:245–253
- ✦ Anderson PJ, Piatt JF (1999) Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Mar Ecol Prog Ser* 189:117–123
- Aydin KY, Gaichas SK, Ortiz I, Kinzey D, Friday N (2007) A comparison of the Bering Sea, Gulf of Alaska, and Aleutian Islands Large Marine Ecosystems through food web modeling. US Dept Comm, NOAA Tech Memo NMF-SAFSC-178
- ✦ Blake RE, Duffy JE (2010) Grazer diversity affects resistance to multiple stressors in an experimental seagrass ecosystem. *Oikos* 119:1625–1635
- ✦ Blake R, Duffy J (2012) Changes in biodiversity and environmental stressors influence community structure of an experimental eelgrass *Zostera marina* system. *Mar Ecol Prog Ser* 470:41–54
- ✦ Blake RE, Ward C, Hunsicker M, Shelton AO, Hollowed AB (2019) Code and data for biodiversity, spatial community structure, and spatial community composition of groundfish in the Gulf of Alaska. Knowl Netw Biocomplexity, doi:10.5063/F1V40SJ8
- ✦ Blowes SA, Armstrong JB, Chase JM (2017) Global reef fish richness gradients emerge from divergent and scale-dependent component changes. *Proc Biol Sci* 284: 20170947
- ✦ Botta-Dukát Z (2005) Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *J Veg Sci* 16:533–540
- ✦ Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecol Monogr* 27: 325–349



- Cadotte MW, Fukami T (2005) Dispersal, spatial scale, and species diversity in a hierarchically structured experimental landscape: Dispersal, scale and diversity. *Ecol Lett* 8:548–557
- Cadotte MW, Carscadden K, Mirotchnick N (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. *J Appl Ecol* 48:1079–1087
- Certain G, Planque B (2015) Biodiversity baseline for large marine ecosystems: an example from the Barents Sea. *ICES J Mar Sci* 72:1756–1768
- Chesson P, Gebauer RLE, Schwinning S, Huntly N and others (2004) Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia* 141:236–253
- Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310
- Conord C, Gurevitch J, Fady B (2012) Large-scale longitudinal gradients of genetic diversity: a meta-analysis across six phyla in the Mediterranean basin. *Ecol Evol* 2: 2600–2614
- De Bello F, Lavergne S, Meynard CN, Lepš J, Thuiller W (2010) The partitioning of diversity: showing Theseus a way out of the labyrinth. *J Veg Sci* 21:992–1000
- Declerck SAJ, Coronel JS, Legendre P, Brendonck L (2011) Scale dependency of processes structuring metacommunities of cladocerans in temporary pools of High-Andes wetlands. *Ecography* 34:296–305
- Di Lorenzo E, Schneider N, Cobb KM, Franks PJS and others (2008) North Pacific Gyre Oscillation links ocean climate and ecosystem change. *Geophys Res Lett* 35: L08607
- Dorazio RM, Royle JA, Söderström B, Glimskär A (2006) Estimating species richness and accumulation by modeling species occurrence and detectability. *Ecology* 87:842–854
- Fox JW (2013) The intermediate disturbance hypothesis should be abandoned. *Trends Ecol Evol* 28:86–92
- France KE, Duffy JE (2006) Diversity and dispersal interactively affect predictability of ecosystem function. *Nature* 441:1139–1143
- Freestone AL, Inouye BD (2006) Dispersal limitation and environmental heterogeneity shape scale-dependent diversity patterns in plant communities. *Ecology* 87: 2425–2432
- Froese R, Pauly D (2016) FishBase. [www.fishbase.org](http://www.fishbase.org) (accessed 22 February 2016)
- Gaichas SK, Francis RC (2008) Network models for ecosystem-based fishery analysis: a review of concepts and application to the Gulf of Alaska marine food web. *Can J Fish Aquat Sci* 65:1965–1982
- Gargett AE (1997) The optimal stability 'window': a mechanism underlying decadal fluctuations in North Pacific salmon stocks? *Fish Oceanogr* 6:109–117
- Gonzalez A, Mouquet N, Loreau M (2009) Biodiversity as spatial insurance: the effects of habitat fragmentation and dispersal on ecosystem functioning. In: Naeem S, Bunker DE, Hector A, Loreau M, Perrings C (eds) Biodiversity, ecosystem functioning and human wellbeing. Oxford University Press, Oxford, p 134–146
- Grace JB, Adler PB, Stanley Harpole W, Borer ET, Seabloom EW (2014) Causal networks clarify productivity–richness interrelations, bivariate plots do not. *Funct Ecol* 28: 787–798
- Grime JP (1979) Plant strategies and vegetation processes. John Wiley & Sons, New York, NY
- Hanski I (1998) Metapopulation dynamics. *Nature* 396:41–49
- Hare SR, Mantua NJ (2000) Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Prog Oceanogr* 47: 103–145
- Hart SP, Usinowicz J, Levine JM (2017) The spatial scales of species coexistence. *Nat Ecol Evol* 1:1066–1073
- Henson SA (2007) Water column stability and spring bloom dynamics in the Gulf of Alaska. *J Mar Res* 65:715–736
- Hiddink JG, Jennings S, Sciberras M, Szostek CL and others (2017) Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. *Proc Natl Acad Sci USA* 114:8301–8306
- Hollowed AB, Hare SR, Wooster WS (2001) Pacific Basin climate variability and patterns of Northeast Pacific marine fish production. *Prog Oceanogr* 49:257–282
- Hollowed AB, Wilson CD, Stabeno PJ, Salo SA (2007) Effect of ocean conditions on the cross-shelf distribution of walleye pollock (*Theragra chalcogramma*) and capelin (*Mallotus villosus*). *Fish Oceanogr* 16:142–154
- Hu C, Lee Z, Franz B (2012) Chlorophyll *a* algorithms for oligotrophic oceans: a novel approach based on three-band reflectance difference. *J Geophys Res Oceans* 117: C01011
- Huston MA (2014) Disturbance, productivity, and species diversity: empiricism vs. logic in ecological theory. *Ecology* 95:2382–2396
- Hutchinson GE (1961) The paradox of the plankton. *Am Nat* 95:137–145
- Jost L (2007) Partitioning diversity into independent alpha and beta components. *Ecology* 88:2427–2439
- Lagerloef G (1983) Topographically controlled flow around a deep trough transecting the shelf off Kodiak Island, Alaska. *J Phys Oceanogr* 13:139–146
- Laliberte E, Zemunik G, Turner BL (2014) Environmental filtering explains variation in plant diversity along resource gradients. *Science* 345:1602–1605
- Lander ME, Loughlin TR, Logsdon MG, VanBlaricom GR, Fadely BS, Fritz LW (2009) Regional differences in the spatial and temporal heterogeneity of oceanographic habitat used by Steller sea lions. *Ecol Appl* 19:1645–1659
- Legendre P, Gallagher E (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia* 129:271–280
- Legendre P, Borcard D, Peres-Neto PR (2005) Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecol Monogr* 75:435–450
- Leibold MA, Holyoak M, Mouquet N, Amarasekare P and others (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecol Lett* 7:601–613
- Logerwell EA, Stabeno PJ, Wilson CD, Hollowed AB (2007) The effect of oceanographic variability and interspecific competition on juvenile pollock (*Theragra chalcogramma*) and capelin (*Mallotus villosus*) distributions on the Gulf of Alaska shelf. *Deep Sea Res II* 54:2849–2868
- Loreau M, Mouquet N, Gonzalez A (2003) Biodiversity as spatial insurance in heterogeneous landscapes. *Proc Natl Acad Sci USA* 100:12765–12770
- Magurran AE, Dornelas M, Moyes F, Gotelli NJ, McGill B (2015) Rapid biotic homogenization of marine fish assemblages. *Nat Commun* 6:8405
- Mantua NJ, Hare SR (2002) The Pacific Decadal Oscillation. *J Oceanogr* 58:35–44
- Mateo RG, Mokany K, Guisan A (2017) Biodiversity models: What if unsaturation is the rule? *Trends Ecol Evol* 32: 556–566
- Maunder MN, Punt AE (2004) Standardizing catch and ef-

- fort data: a review of recent approaches. *Fish Res* 70: 141–159
- ✦ Maynard DS, Crowther TW, Bradford MA (2017) Competitive network determines the direction of the diversity–function relationship. *Proc Natl Acad Sci USA* 114: 11464–11469
- ✦ McCann KS (2000) The diversity–stability debate. *Nature* 405:228–233
- ✦ Mellin C, Bradshaw CJA, Fordham DA, Caley MJ (2014) Strong but opposing b-diversity-stability relationships in coral reef fish communities. *Proc Biol Sci* 281:20131993
- ✦ Mittelbach GG, Schemske DW, Cornell HV, Allen AP and others (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecol Lett* 10:315–331
- ✦ Moore AFP, Duffy JE (2016) Foundation species identity and trophic complexity affect experimental seagrass communities. *Mar Ecol Prog Ser* 556:105–121
- ✦ Mouchet M, Guilhaumon F, Villéger S, Mason NWH, Tomasini JA, Mouillot D (2008) Towards a consensus for calculating dendrogram-based functional diversity indices. *Oikos* 117:794–800
- ✦ Mouchet MA, Villéger S, Mason NWH, Mouillot D (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Funct Ecol* 24:867–876
- ✦ Mouquet N, Loreau M (2002) Coexistence in metacommunities: the regional similarity Hypothesis. *Am Nat* 159: 420–426
- ✦ Mueter FJ, Norcross BL (2000) Changes in species composition of the demersal fish community in nearshore waters of Kodiak Island, Alaska. *Can J Fish Aquat Sci* 57:1169–1180
- Mueter FJ, Norcross BL (2002) Spatial and temporal patterns in the demersal fish community on the shelf and upper slope regions of the Gulf of Alaska. *Fish Bull* 100:559–581
- NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group (1997–2010) SeaWiFS Ocean Color Data. NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group. <https://coastwatch.pfeg.noaa.gov/erddap/griddap/erdSW1chlamday.html> (accessed March 2017)
- NASA Goddard Space Flight Center, Ocean Biology Processing Group (2003–2015) MODIS Ocean Color Data. NASA Goddard Space Flight Center, Ocean Biology Processing Group. <https://coastwatch.pfeg.noaa.gov/erddap/griddap/erdMH1chlamday.html> (accessed March 2017)
- NOAA Alaska Fisheries Science Center (NOAA AFSC) (2015) North Pacific Groundfish Assessments. [www.afsc.noaa.gov/refm/stocks/2015\\_assessments.htm](http://www.afsc.noaa.gov/refm/stocks/2015_assessments.htm) (accessed 29 September 2015)
- NOAA Alaska Fisheries Science Center (NOAA AFSC) (2016a) Life History Database. <https://access.afsc.noaa.gov/reem/lhweb/Index.php> (accessed 29 September 2017)
- NOAA Alaska Fisheries Science Center (NOAA AFSC) (2016b) Resource ecology and ecosystem modeling fish food habits database. [www.afsc.noaa.gov/REFM/REEM/Data/Default.htm](http://www.afsc.noaa.gov/REFM/REEM/Data/Default.htm) (accessed 29 September 2016)
- Oksanen J, Blanchet FG, Friendly M, Kindt R and others (2016) Vegan: community ecology package. <https://CRAN.R-project.org/package=vegan>
- ✦ Ono K, Shelton AO, Ward EJ, Thorson JT, Feist BE, Hilborn R (2016) Space-time investigation of the effects of fishing on fish populations. *Ecol Appl* 26:392–406
- ✦ Pennington M (1983) Efficient estimators of abundance for fish and plankton surveys. *Biometrics* 39:281–286
- ✦ Perry RI, Smith SJ (1994) Identifying habitat associations of marine fishes using survey data: an application to the Northwest Atlantic. *Can J Fish Aquat Sci* 51:589–602
- ✦ Petchey OL, Gaston KJ (2006) Functional diversity: back to basics and looking forward. *Ecol Lett* 9:741–758
- ✦ Rao CR (1982) Diversity and dissimilarity coefficients: a unified approach. *Theor Popul Biol* 21:24–43
- Ricklefs RE, Schluter D (eds) (1994) *Species diversity in ecological communities*. University of Chicago Press, Chicago, IL
- ✦ Robroek BJM, Jassey VEJ, Payne RJ, Martí M and others (2017) Taxonomic and functional turnover are decoupled in European peat bogs. *Nat Commun* 8:1161
- ✦ Rueda L, Massutí E, Alvarez-Berastegui D, Hidalgo M (2015) Effect of intra-specific competition, surface chlorophyll and fishing on spatial variation of gadoid's body condition. *Ecosphere* 6:art175
- ✦ Schindler DE, Hilborn R, Chasco B, Boatright CP, Quinn TP, Rogers LA, Webster MS (2010) Population diversity and the portfolio effect in an exploited species. *Nature* 465: 609–612
- ✦ Schindler DE, Armstrong JB, Reed TE (2015) The portfolio concept in ecology and evolution. *Front Ecol Environ* 13: 257–263
- ✦ Shanafelt DW, Dieckmann U, Jonas M, Franklin O, Loreau M, Perrings C (2015) Biodiversity, productivity, and the spatial insurance hypothesis revisited. *J Theor Biol* 380: 426–435
- ✦ Shannon CE (1948) A mathematical theory of communication. *Bell Syst Tech J* 27:379–423
- ✦ Shelton AO, Thorson JT, Ward EJ, Feist BE (2014) Spatial semiparametric models improve estimates of species abundance and distribution. *Can J Fish Aquat Sci* 71: 1655–1666
- ✦ Shelton AO, Hunsicker ME, Ward EJ, Feist BE and others (2017) Data from: Spatio-temporal models reveal subtle changes to demersal communities following the Exxon Valdez oil spill. Dryad Digit Repos, doi:10.5061/dryad.j3t86
- ✦ Shelton AO, Hunsicker ME, Ward EJ, Feist BE and others (2018) Spatio-temporal models reveal subtle changes to demersal communities following the Exxon Valdez oil spill. *ICES J Mar Sci* 75:287–297
- ✦ Shurin JB, Havel JE, Leibold MA, Pinel-Alloul B (2000) Local and regional zooplankton species richness: a scale-independent test for saturation. *Ecology* 81:3062–3073
- ✦ Smith EP, Orvos DR, Cairns J Jr (1993) Impact assessment using the before-after-control-impact (BACI) model: concerns and comments. *Can J Fish Aquat Sci* 50:627–637
- ✦ Smith HL, Anderson MJ, Gillanders BM, Connell SD (2014) Longitudinal variation and effects of habitat on biodiversity of Australasian temperate reef fishes. *J Biogeogr* 41: 2128–2139
- ✦ Snyder RE, Chesson P (2004) How the spatial scales of dispersal, competition, and environmental heterogeneity interact to affect coexistence. *Am Nat* 164:633–650
- ✦ Sprules WG (2008) Ecological change in Great Lakes communities — a matter of perspective. *Can J Fish Aquat Sci* 65:1–9
- ✦ Srivastava DS (1999) Using local–regional richness plots to test for species saturation: pitfalls and potentials. *J Anim Ecol* 68:1–16
- ✦ Stabeno PJ, Bond NA, Hermann AJ, Kachel NB, Mordy CW, Overland JE (2004) Meteorology and oceanography of the Northern Gulf of Alaska. *Cont Shelf Res* 24:859–897
- ✦ Stachura MM, Essington TE, Mantua NJ, Hollowed AB and

- others (2014) Linking Northeast Pacific recruitment synchrony to environmental variability. *Fish Oceanogr* 23: 389–408
- ✦ Stuart-Smith RD, Bates AE, Lefcheck JS, Duffy JE and others (2013) Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature* 501: 539–542
- Tamme R, Hiiesalu I, Laanisto L, Szava-Kovats R, Pärtel M (2010) Environmental heterogeneity, species diversity and co-existence at different spatial scales. *J Veg Sci* 21: 796–801
- ✦ Thompson PL, Gonzalez A (2017) Dispersal governs the reorganization of ecological networks under environmental change. *Nat Ecol Evol* 1:0162
- ✦ Tolimieri N (2007) Patterns in species richness, species density, and evenness in groundfish assemblages on the continental slope of the U.S. Pacific coast. *Environ Biol Fishes* 78:241–256
- ✦ Tolkinen M, Mykrä H, Annala M, Markkola AM, Vuori KM, Muotka T (2015) Multi-stressor impacts on fungal diversity and ecosystem functions in streams: natural vs. anthropogenic stress. *Ecology* 96:672–683
- ✦ Tuomisto H (2010) A diversity of beta diversities: straightening up a concept gone awry. 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography* 33:2–22
- ✦ Vogwill T, Fenton A, Brockhurst MA (2009) Dispersal and natural enemies interact to drive spatial synchrony and decrease stability in patchy populations. *Ecol Lett* 12: 1194–1200
- von Szalay PG, Raring NW, Shaw FR, Wilkins ME, Martin MH (2010) 2010 data report: 2009 Gulf of Alaska bottom trawl survey. U.S. Dept Commerce, Seattle, WA
- ✦ Walline PD, Wilson CD, Hollowed AB, Stienessen SC (2012) Short-term effects of commercial fishing on the distribution and abundance of walleye pollock (*Theragra chalcogramma*). *Can J Fish Aquat Sci* 69:354–368
- ✦ Wang S, Loreau M (2014) Ecosystem stability in space:  $\alpha$ ,  $\beta$  and  $\gamma$  variability. *Ecol Lett* 17:891–901
- ✦ Wang S, Loreau M (2016) Biodiversity and ecosystem stability across scales in metacommunities. *Ecol Lett* 19:510–518
- ✦ Ward CL, Blake RE (2016) Gulf of Alaska portfolio effects: groundfish functional diversity traits dataset. doi:10.5063/F1MK6B5J
- ✦ Ward EJ, Jannot JE, Lee YW, Ono K, Shelton AO, Thorson JT (2015) Using spatiotemporal species distribution models to identify temporally evolving hotspots of species co-occurrence. *Ecol Appl* 25:2198–2209
- ✦ Weigelt A, Schumacher J, Roscher C, Schmid B (2008) Does biodiversity increase spatial stability in plant community biomass? *Ecol Lett* 11:338–347
- ✦ Whittaker RH (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol Monogr* 30:279–338
- ✦ Whittaker RH (1962) Classification of natural communities. *Bot Rev* 28:1–239
- ✦ Wilson JB (2011) The twelve theories of co-existence in plant communities: the doubtful, the important and the unexplored. *J Veg Sci* 22:184–195
- ✦ Witman JD, Cusson M, Archambault P, Pershing AJ, Miesz-kowska N (2008) The relation between productivity and species diversity in temperate-arctic marine ecosystems. *Ecology* 89:S66–S80
- ✦ Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J R Stat Soc B* 73:3–36
- ✦ Wood CL, Baum JK, Reddy SMW, Trebilco R and others (2015) Productivity and fishing pressure drive variability in fish parasite assemblages of the Line Islands, equatorial Pacific. *Ecology* 96:1383–1398
- ✦ Yang Z, Liu X, Zhou M, Ai D and others (2015) The effect of environmental heterogeneity on species richness depends on community position along the environmental gradient. *Sci Rep* 5:15723

Editorial responsibility: Franz Mueter,  
Juneau, Alaska, USA

Submitted: May 11, 2018; Accepted: July 2, 2019  
Proofs received from author(s): August 24, 2019