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Spatial heterogeneity contributes more to portfolio effects than species variability in bottom-associated marine fishes

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Variance of community abundance will be reduced relative to its theoretical maximum whenever population densities fluctuate asynchronously. Fishing communities and mobile predators can switch among fish species and/or fishing locations with asynchronous dynamics, thereby buffering against variable resource densities (termed ‘portfolio effects’, PEs). However, whether variation among species or locations represent the dominant contributor to PE remains relatively unexplored. Here, we apply a spatio-temporal model to multidecadal time series (1982–2015) for 20 bottom-associated fishes in seven marine ecosystems. For each ecosystem, we compute the reduction in variance over time in total biomass relative to its theoretical maximum if species and locations were perfectly correlated (total PE). We also compute the reduction in variance due to asynchrony among species at each location (species PE) or the reduction due to asynchrony among locations for each species (spatial PE). We specifically compute total, species and spatial PE in 10-year moving windows to detect changes over time. Our analyses revealed that spatial PE are stronger than species PE in six of seven ecosystems, and that ecosystems where species PE is constant over time can exhibit shifts in locations that strongly contribute to PE. We therefore recommend that spatial and total PE be monitored as ecosystem indicators representing risk exposure for human and natural consumers.

1. Introduction

Human impacts on ecosystems around the world are mounting, with implications for ecological functioning and stability [1]. Uncertainties in predicting consequences of human activities continue to challenge the management of natural resources and the maintenance of ecosystem services [2,3]. This challenge has prompted on-going research to identify biological characteristics that buffer resource users (e.g. extractive human activities or natural predators) against a wide range of potential impacts.

Decades of research suggest that biological complexity can reduce the variance over time of an ecosystem service relative to the variance of each individual component [4]. This is often termed the ‘portfolio effect’ (PE), analogous to how a portfolio of financial investments can be used to decrease variance in economic performance in a collection of assets for a given expected rate of return [5,6]. The PE is strongest when the ecological ‘assets’ are negatively correlated over time, termed ‘asynchrony’, and the PE decreases as the assets become more positively correlated with one another, termed ‘synchrony’ [7,8]. For example, maintaining PE via preserving different components of populations or communities can improve economic outcomes in fishing communities by decreasing resource variability [9,10] and allowing top consumers

stable access to food [11]. This represents a feasible step towards ecosystem-based resource management [12].

Portfolio effects can arise from asynchronous variation at multiple levels of organization within an ecosystem, including genotypes within a cohort, cohorts within a deme, demes within a population, populations within a species and species within a guild [13]. Thus, an emergent property of many ecosystems is that their dynamics have a lower coefficient of variation than each individual component [14]. However, measurements of biological rates or biomass are often unavailable for lower levels of organization. For example, biological surveys of fishes routinely sample biomass for individual species, but less often collect information to assign samples to a given cohort, population or genotype. Therefore, fish survey data are available to estimate synchrony among species, but generally not among genotypes and demes. Populations or demes, however, will often partition available habitats spatially [10,15], so the spatial location of sampling may, in some cases, be a proxy for identifying different populations within a given species' range. Asynchrony could, in theory, emerge so that total abundance or biomass has no variance over time (where increases for one component are always perfectly compensated by decreases in others). Similarly, ecosystem variance can never be higher than a limit defined by the temporal variance of each ecosystem component. Therefore, Loreau & de Mazancourt [16] developed an index of synchrony, and we use one minus their index such that one indicates perfect buffering from asynchronous fluctuations and zero indicates a complete absence of community buffering. Importantly, this index relaxes the simplifying assumptions in early calculations of PE (e.g. [7]), although increases/decreases in this index can be caused either by increased/decreased variance in aggregate abundance (the numerator) or a decrease/increase in variance for each individual component (the denominator).

With growing interest in PE, ecologists seek to better understand how abundance and ecosystem rates vary among locations within a given ecosystem, motivated by the recognition that species coexistence depends critically upon spatial covariation in resource availability and species productivity [17,18]. Spatio-temporal models are increasingly capable of simultaneously estimating random variation in density among different ecosystem components, locations and times [19], and can also be used to predict outcomes from a continuum of neutral and niche models of community dynamics [20]. Although prior research has addressed both the impact of PE on ecosystem-level variance [21] and spatial heterogeneity on ecosystem stability and persistence [22], much less is known about the relative contribution of synchrony among species versus among sites to spatially aggregated PE. For example, PE has been analysed using time-series methods focused on variation in total abundance for multiple species [16,23], spatio-temporal variation in abundance for a single species [24,25] or spatial (without temporal) variation in abundance for multiple species [26]. However, previous studies have not generally attributed PE to spatial heterogeneity and species differences when simultaneously analysing density for multiple species at multiple locations. The relative contribution of spatial heterogeneity and species variability to PE is important to understand, for example, because central place foragers and local fisheries can only exploit PE arising from species variability at a given

location, while specialized mobile predators and fisheries only exploit PE arising from spatial heterogeneity.

In this paper, we demonstrate a pragmatic approach to measuring portfolio effects that involves estimating synchrony arising from two separate mechanisms: asynchronous fluctuations in density of multiple species at a given location and fluctuations of a single species across multiple locations. Although both sources of ecosystem heterogeneity have the potential to contribute to PE, the influence of these two dimensions of complexity on emergent ecosystem stability has not previously been quantified for marine ecosystems. We therefore estimate PE arising from dynamics of multiple species at a given location (species PE), multiple locations for a given species (spatial PE) or both mechanisms simultaneously (total PE). We estimate all three aspects of PE for 20 numerically dominant bottom-associated fishes using biomass-sampling data from the last three decades within each of seven major marine ecosystems (while also testing sensitivity to analysing fewer species). For each ecosystem, we estimate species, spatial and total PE over 10-year moving windows, to detect whether the strength of PE has changed over time (while also testing sensitivity to 6-year or 15-year moving windows). We analyse PE for community biomass (rather than abundance in numbers) because biomass determines the value of fishery catch available for human exploitation. The average number of samples per year for each region was 320 (s.d. 169), thereby providing a remarkable opportunity to estimate the magnitude of (and changes in) spatial PE, species PE and total PE. In particular, we (i) compare the magnitude of spatial and species PE relative to total PE across species and locations, (ii) identify decadal-scale changes in species, spatial and total PE, and (iii) identify geographical locations within each ecosystem that have stronger or weaker species PE than the spatial average for that ecosystem.

2. Material and methods

We calculate three measurements of the strength of PEs arising from asynchronous biomass dynamics among species, sites or both simultaneously. To do so, we estimate density for multiple species, sites and years using a recently developed joint dynamic species density model (JDSDM). This JDSDM estimates density $n(s, c, t)$ (number of individuals per area) for each year t , site s and species c , the average mass for individuals of each species (biomass per individual) $m(c)$ and predicts density (biomass per area) $d(s, c, t)$ as the product of these two components, $d(s, c, t) = n(s, c, t) \times m(c)$. We calculate PE using estimates of density from the JDSDM (rather than raw data) for three reasons: (i) results using a JDSDM are less sensitive to ad hoc decisions about how to post-stratify available data when calculating spatial variation in PE; (ii) research suggests that spatio-temporal models like JDSDM will be statistically efficient in extracting signal from noisy biological data [27,28]; and (iii) the JDSDM can estimate the uncertainty of resulting PE estimates, allowing us to evaluate whether changes are greater than those arising from chance alone. To improve computational efficiency, we divide the spatial domain for each ecosystem into 100 partitions (each with approximately equal size) and track density $d(s, c, t)$ at each of 100 'knots' (i.e. $s \in \{1, 2, \dots, 100\}$), where we assume that density for a given sample is equal to density at the nearest knot. This computational approach is conceptually similar to a predictive process model used in spatial statistics [29], and we further improve computational efficiency by using a combination of the Laplace approximation [30], a sparse approximation to

spatial variation [31] and a factor model for co-regionalization [32]. This model is fitted to bottom trawl data, where each bottom trawl sample i yields biomass \mathbf{b}_i that includes biomass $b_i(c)$ for every modelled species c at the location s_i and year t_i of that sample. All datasets used obtain biomass samples using bottom trawl gear following a fixed-station, random or stratified-random design. Bottom trawl samples in each year are conducted without replication; therefore, 'detectability' cannot be estimated and we follow common practice in assuming that expected trawl biomass $\mathbb{E}_i[b(c)]$ is proportional to local density $d(s, c, t)$.

(a) Spatial, species and total portfolio effects

PE measures the degree to which the variance over time in an ecosystem service (e.g. biomass potentially available for human harvest) is decreased by asynchronous variation in different components of an ecosystem [21,22]. We use a standardized measure of PE that ranges from zero (no PE) to one (strongest possible PE). To calculate PE, we first convert predicted density $d(s, c, t)$ to biomass $b(s, c, t)$:

$$b(s, c, t) = a(s) \times d(s, c, t),$$

where $a(s)$ is the area associated with location s (the following derivation assumes that $a(s) > 0$ for all locations, but equations can also be derived when allowing $a(s) = 0$ for some modelled location s). We then calculate PE as one minus a standardized measure of synchrony [16], which is, in turn, calculated as the ratio of observed variance in aggregate biomass (the numerator) and the maximum possible variance for aggregate biomass that would arise if all components were perfectly correlated (the denominator):

$$PE = 1 - \frac{\text{Var}(\sum b^*)}{\sum \text{Var}(b^*)},$$

where $\text{Var}(\sum b^*) / \sum \text{Var}(b^*)$ is the measure of synchrony, b^* is the biomass for a given species, location and time, the numerator $\text{Var}(\sum b^*)$ is the variance across years of biomass summed across sites, species or both (depending upon the PE calculation being used) and the denominator $\sum \text{Var}(b^*)$ is the sum of variances across sites, species or both (again depending upon the PE calculation). PE equals one whenever variance of aggregate biomass (the numerator) is zero and is zero whenever aggregate variance (the numerator) is equal to its theoretical maximum (the denominator). The variance of aggregate biomass is itself a nonlinear function of the correlation in log-density between species (estimated by \mathbf{L}_ω and \mathbf{L}_ε) as well as other model parameters (see the section 'Joint dynamic species distribution model' for details).

We calculate three measures of aggregate biomass when summing across (i) all species at a given location (community biomass), (ii) all locations for a given species (domain-wide biomass) or (iii) both species and locations simultaneously (total biomass). We then calculate the mean and variance of community, domain-wide and total biomass over different 10-year moving windows (where the calculation of biomass and PE includes all years with available sampling data within a given 10-year window). We use the mean and variance of aggregate biomass to calculate PE attributable to variation among species at a given site (species PE), among sites for a given species (spatial PE) or due to variation among species and sites simultaneously (total PE). Further details and notation regarding these calculations are provided in electronic supplementary material S1.

Species PE measures the degree to which variance in community-level biomass at a given location is reduced due to asynchronous variation among species at that location. We calculate species asynchrony $\varphi_c(s)$ for each location s , where species PE

for location s is defined as $1 - \varphi_c(s)$. We also calculate the weighted average of species asynchrony across locations, with weights equal to the proportion of domain-wide community biomass that is at site s on average across years. For comparison, we also calculate average variance for community biomass, where this variance indicates whether changes in species synchrony are concurrent with changes in the observed variance (the numerator) or the maximum theoretical variance (the denominator).

Spatial PE measures the degree to which the variance of domain-wide biomass for each individual species is reduced relative to its theoretical maximum due to asynchronous variation among different spatial locations for that individual species. We calculate spatial asynchrony $\varphi_s(c)$ for each species c , where spatial PE for species c is defined as $1 - \varphi_s(c)$. We also calculate the average spatial asynchrony across species, with weights equal to the proportion of domain-wide community biomass belonging to species c on average across years. We calculate variance for domain-wide biomass averaged across species for comparison with spatial synchrony, where this variance indicates whether changes in PE are primarily due to changes in observed or theoretical maximum variance.

Finally, we calculate asynchrony $\varphi_{s,c}$ arising from asynchronous dynamics for each species at each location where total PE is defined as $1 - \varphi_{s,c}$. For comparison, we again calculate the variance of total biomass (the numerator in this calculation).

(b) Joint dynamic species distribution model

The JDSDM specifically uses a Poisson-link delta model [33] where the distribution for biomass b_i is:

$$\Pr(b_i(c) = B) = \begin{cases} 1 - p_i(c) & \text{if } B = 0 \\ p_i(c) \times g\{B|r_i(c), \sigma_m^2(c)\} & \text{if } B > 0 \end{cases}$$

where $p_i(c)$ is the probability that species c is encountered, r_i is the expected biomass given that the species is encountered in sample i and $\sigma_m^2(c)$ is the residual variance in catch rates when species c is encountered. The encounter probability $p_i(c)$ is derived from numbers-density $n(s_i, c, t_i)$ for each species c , location s_i and year t_i for sample i , given the assumption that individuals are randomly distributed in the vicinity of sampling $p_i(c) = 1 - \exp(-w_i n(s_i, c, t_i))$, where w_i is the area-swept by survey sample i . The definition of expected biomass given that the species is encountered then follows directly, $r_i(c) = w_i n(s_i, c, t_i) m(c) / p_i(c)$. This specification assumes that density $d(s, c, t) > 0$ and therefore encounter probability $p(s, c, t) > 0$ for all sampled locations, but encounter probabilities can still be vanishingly small for some combinations of species, location and year.

Numbers-density $n(s, c, t)$ is predicted using a spatial dynamic factor analysis (SDFA). SDFA approximates variation in population density among species, sites and times using one or more latent factor, where each factor represents the aggregate effect of many unobserved processes driving variation. This approach avoids pre-specifying important environmental covariates and instead reconstructs factors based on observed covariance in density:

$$\log(n(s, c, t)) = \alpha(c) + \sum_{f=1}^{n_f} (L_\omega(c, f) \times \omega(s, f)) + \sum_{f=1}^{n_f} (L_\varepsilon(c, f) \times \varepsilon(s, f, t)),$$

where $\omega(f) = (\omega(1, f), \dots, \omega(S, f))$ is a vector representing spatial variation for factor f and $\mathbf{E}(f) = \begin{bmatrix} \varepsilon(1, f, 1) & \dots & \varepsilon(1, f, T) \\ \vdots & \ddots & \vdots \\ \varepsilon(S, f, 1) & \dots & \varepsilon(S, f, T) \end{bmatrix}$ is a matrix representing spatio-temporal variation for factor f . \mathbf{L}_ω is

a loadings matrix that represents correlated spatial variation where $L_{\omega}(c, f)$ represents the impact of estimated factor $\omega(f)$ on density for species c and therefore has one row for every species and one column for every factor, L_e is a loadings matrix representing spatio-temporal covariation (with the same interpretation and dimensions as L_{ω}) and $\alpha(c)$ is a constant intercept for each species c . Parameters in loadings matrices (L_e and L_{ω}), intercepts ($\alpha(c)$), average masses ($w(c)$) and variance parameters for spatial and spatio-temporal factors are estimated as fixed effects, while spatio-temporal factors ($\omega(f)$ and $E(f)$) are estimated as random effects (see [34] for details). Covariance in density among species represented by factors $\omega(f)$ and $E(f)$ arises from the net effect of biological processes that are not explicitly modelled, including responses to changing water temperature, interannual variability in primary productivity and predator–prey relationships (among others).

We then predict density $d(s, c, t)$ for each site s , species c and year t , conditional on maximum-likelihood estimates of all model parameters and empirical Bayes predictions of factors. Predicted density is used to calculate PE and variance for aggregate density when aggregating across species, locations or both. For calculations of PE and aggregate variance, we use the generalized delta method to calculate standard errors for these calculations given the estimated standard error for model parameters. Parameter estimation is accomplished using TEMPLATE MODEL BUILDER [30] within the R statistical environment [35], and all calculations can be replicated or applied to new datasets using release number 1.6.0 of R-package VAST [34], publicly available online (<https://github.com/James-Thorson/VAST>). In this study, we specifically estimate factors $\omega(s, f)$ and $\epsilon(s, f, t)$, and predict $d(s, c, t)$, at each of 100 knots ($S = 100$), where each knot s is associated with a spatial area $a(s)$ that is similar for all knots S in a given region, and assume that density at any location s^* is equal to its value at the nearest knot. We also estimate five factors for spatial and spatio-temporal variation ($n_f = 5$) and confirm that results are qualitatively similar when increasing the number of knots or factors. This factor model is able to estimate fine-scale variation in density for poorly sampled species and does so by shrinking estimated dynamics for poorly informed species towards patterns for well-informed species [34].

(c) Empirical examples: decadal changes in synchrony in bottom-associated marine fishes

We seek to determine for bottom-associated marine fishes whether (i) asynchronous variation among species or locations contributes more to PE, (ii) changes in spatial-, species- and total PE are likely to occur at decadal time-scales for marine ecosystems, and (iii) certain areas within each region have relatively stronger or weaker species PE. We accomplished this by assembling a database of bottom trawl sampling data for bottom-associated fishes occurring at large spatial scales, over multiple decades and following a consistent sampling design. We restrict analysis to regions with publicly available data spanning at least 15 years, with at least 4 years of sampling data in each 10-year period between the first and last year of data. These restrictions yielded seven regions with suitable data, and for each, we analyse data for the 20 fish species with greatest total biomass across all years (see electronic supplementary material S1 for visualization of regions and annual sample sizes, and electronic supplementary material S2 for a list of species).

The Eastern Bering Sea bottom trawl survey (EBSBTS) follows a fixed-station design using standardized gear from 1982 to 2016 (35 years), with an average 370 samples per year occurring over a spatial domain of 496 000 km² [36]. The Northwest Atlantic bottom trawl survey (NWABTS) follows a stratified-random design, and we restrict analysis to sampling during the autumn in years using the vessel *Albatross IV* and polyvalent

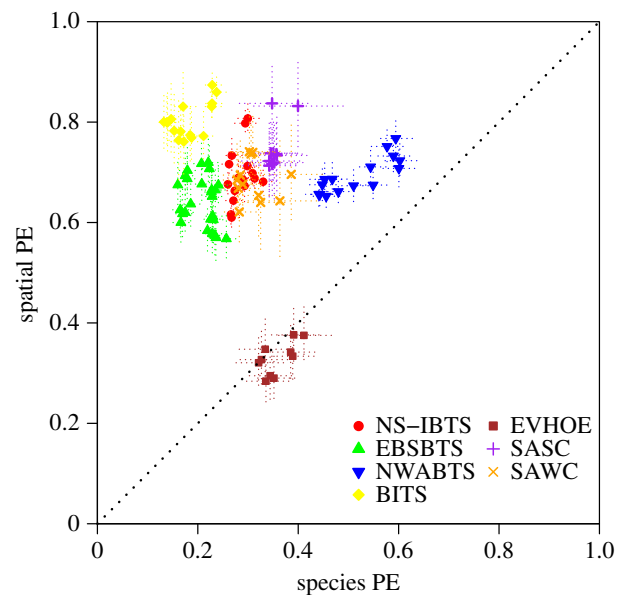


Figure 1. Comparison of average species PE (x-axis) and average spatial PE (y-axis) for each year (bullet: predicted value; dotted lines: ± 1 s.e.) and region (see bottom-right for colour code). The one-to-one line (dotted line) indicates equal spatial and species PE. (Online version in colour.)

trawl doors, which yields an average of 637 samples per year over 19 years occurring over a spatial domain of 318 000 km². The North Sea international bottom trawl survey (NS-IBTS) follows a randomized design, and we restrict analysis to winter sampling from 1991 to 2015 using the standardized ‘Gov’ gear, while converting sampling in numbers to biomass by expanding length subsamples and converting to biomass using average weight-at-length relationships for each species [37]. This yields an average 389 samples per year over 25 years and 589 000 km². The Baltic Sea international bottom trawl survey (BITS) follows a randomized design, and we use identical restrictions and conversions as the NS-IBTS survey (324 samples per year over 25 years and 232 000 km²). The Celtic Sea and Bay of Biscay bottom trawl survey (EVHOE) follows a randomized design and is operated by the French Research Institute for Exploitation of the Sea (IFREMER) [36]; we restrict analysis to autumn sampling from 1997 to 2015 while using identical conversion as the NS-IBTS survey (139 samples per year over 19 years and 267 000 km²). The South Africa South Coast (SASC) and South Africa West Coast (SAWC) bottom trawl surveys are conducted in the summer and autumn, respectively, and we restrict analysis to surveys using the ‘old’ gear type employed by the FRS Africana [38]. This yields 85 samples per year over 13 years and 101 000 km² for the South Coast and 97 samples per year over 14 years and 132 000 km² for the West Coast.

For each region, we fit the JDSDM to data for all species and years. We then calculate aggregate biomass, variance and synchrony for each 10-year interval between the first and last year of sampling data. Variance and synchrony calculations, however, are restricted to years with available sampling data within a given 10-year interval.

3. Results

Spatial PE generated by asynchronous variation among sites for each individual species caused a greater reduction in variance than the species PE generated by asynchronous variation among species at each location in six of seven regions (figure 1). The exception was for the Celtic Sea (EVHOE) where both spatial and species PE were relatively weak (spatial and species PE < 0.42 for all years). Total PE

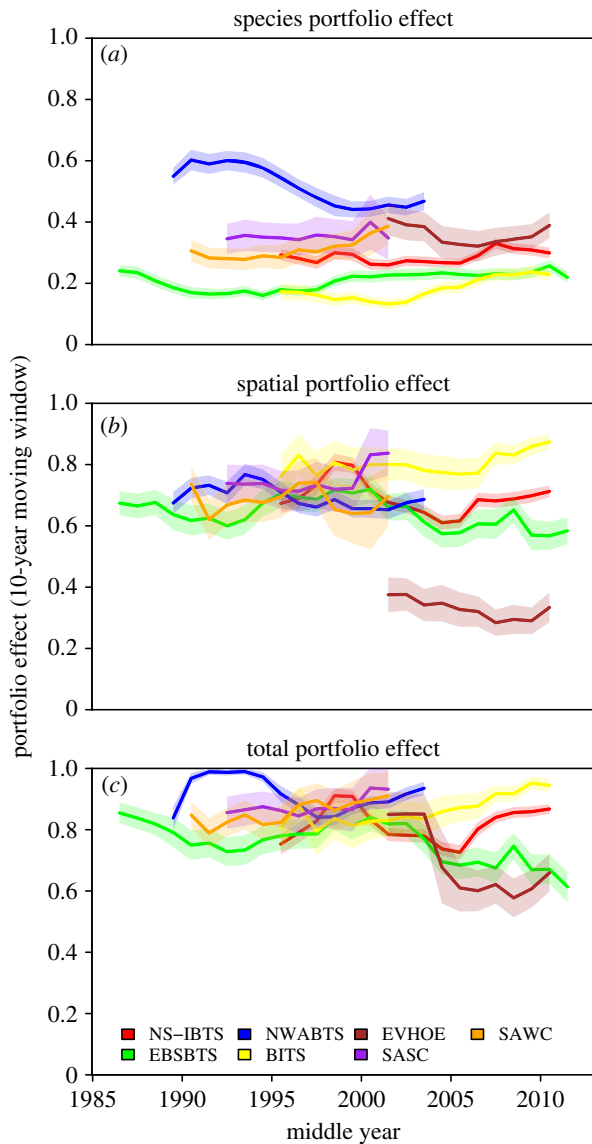


Figure 2. (a) Species PE averaged across sites, (b) spatial PE averaged across species and (c) total PE for each region and each 10-year moving window. A high value in each panel is associated with strong portfolio effects (weak synchrony) for the demersal community (line: maximum-likelihood estimate; shaded area: ± 1 s.e.).

is never weaker than both species and spatial PE, so results suggest that spatial PE represents a lower boundary on total PE in all of these ecosystems except the Celtic Sea. Interestingly, the Celtic Sea had relatively high total PE prior to 2000, and total PE then rapidly decreased starting in the 2000–2009 period (figure 2). This decline in total PE was the most pronounced for any single region, although total PE also declined gradually in the Eastern Bering Sea and approached the level of spatial PE during recent periods (e.g. total PE = 0.61, while spatial PE = 0.58 for the 2007–2016 period). Examination of model diagnostics and illustration of model residuals among all years, species and knots shows no evidence that the JSDM fails to capture the observed patterns in population density (electronic supplementary material, S4 and figures S2–S4).

The conclusion that spatial PE was stronger than species PE in six of seven regions was consistent using both shorter (6-year) and longer (15-year) moving windows (electronic supplementary material S5 and figure S5). This pattern was also invariant when restricting analysis to either the top 10 or top

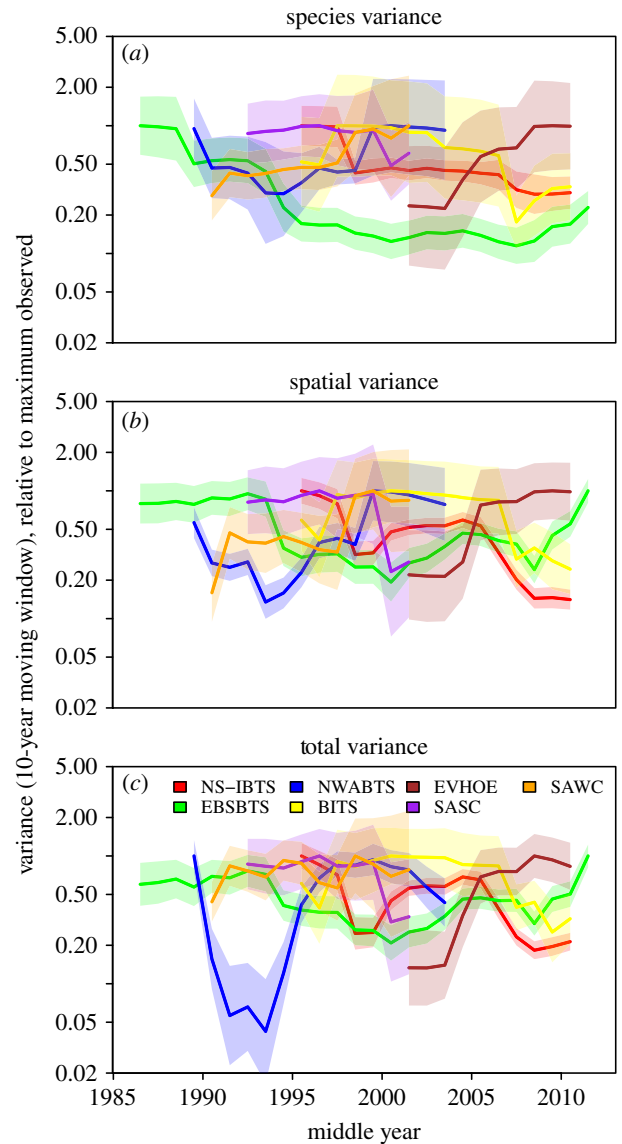


Figure 3. (a) Species variance averaged across sites, (b) spatial variance averaged across species and (c) total variance for each region and each 10-year moving window for the demersal community (line: maximum-likelihood estimate; shaded area: ± 1 s.e.).

15 numerically dominant species in each ecosystem (electronic supplementary material S6 and figure S6). This invariance likely arises because species with lower encounter rates have less information to estimate spatio-temporal patterns and are instead shrunk towards spatio-temporal patterns estimated for dominant species. Finally, this pattern does change somewhat when decreasing the spatial resolution (using 25 or 50 knots to approximate spatial variation in density; electronic supplementary material S7 and figure S7). For example, decreased spatial resolution causes spatial PE to decrease and species PE to increase for the Northwest Atlantic, Eastern Bering Sea and Celtic Sea regions such that spatial and species PE have comparable magnitude given this resolution.

We found that changes in synchrony were concurrent with changes in the observed variance in aggregate biomass rather than changes in its theoretical maximum (figure 3). For example, the increase and subsequent decrease in total PE for the Northwest Atlantic (NWABTS) showed a strong, inverse correlation with changes in variance for total community biomass. Similarly, variance for total community biomass increased recently in both Eastern Bering Sea (EBSBTS) and

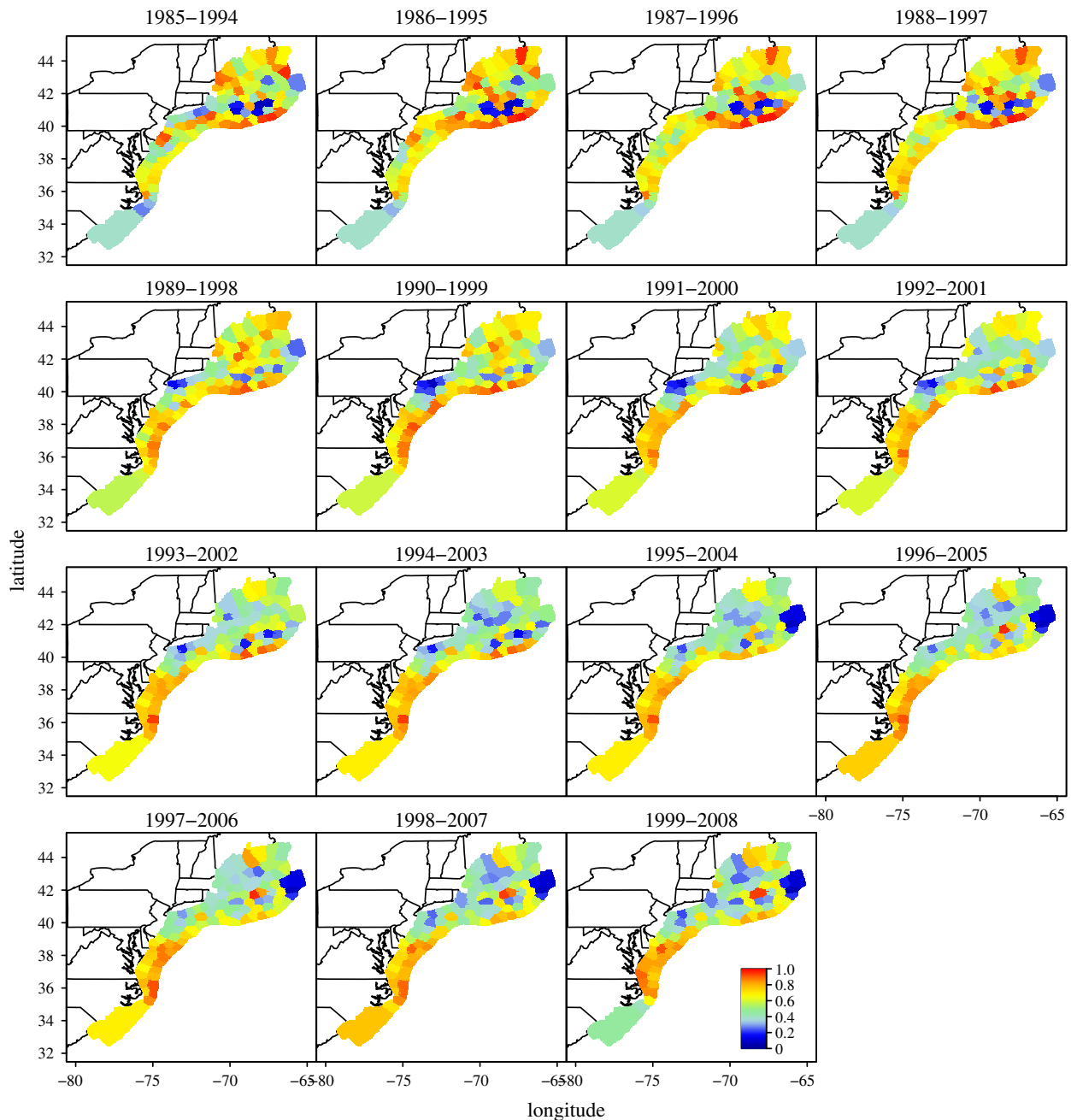


Figure 4. Species PE for each 10-year moving window at each site s in the bottom-associated fish community of the Northwest Atlantic. Blue indicates zero portfolio effect, where community biomass has the highest coefficient of variation possible for a given variance for each individual species; red indicates a maximum portfolio effect where the community biomass has a coefficient of variation approaching zero; see colour bar in the final panel.

Celtic Seas (EVHOE), concurrent with decreased total PE for these regions. Changes in synchrony were not well explained by changes in total community biomass (electronic supplementary material S8 and figure S9). Specifically, the two ecosystems with decreasing total PE have either decreasing (Eastern Bering Sea) or increasing (Celtic Sea) community biomass. However, the South Africa West Coast and North Sea also had increasing and decreasing total biomass, respectively, and neither had a clear trend in PE.

In addition to annual estimates of PE, we also revealed considerable spatial variation in species PE. Species PE in the Northwest Atlantic (NWABTS) decreased over time (figure 2a), and waters east of Cape Cod (i.e. near George's Bank) had much lower species PE than other areas during 1985–1994 (figure 4). By 1996–2005, however, species PE had decreased throughout much of the near-shore waters from New Jersey northwards, whereas deeper and southern

waters maintained a species PE of 0.6–1.0 during this transition. The decreased species PE is therefore explained by increased synchrony in near shore waters of New England. Similarly, the North Sea (NS-IBTS) had approximately stable species PE within our dataset (0.26–0.32) for all periods 1991–2015 (see figure 2a), although the total PE decreases and then recovers in the early to late 2000s mirroring a similar pattern in spatial PE. However, species PE was lowest in the northern portion of the North Sea in early years (1991–2000), and the location with lowest species PE then shifted to near shore southern waters in later years (e.g. 2003–2012; figure 5). In this case, a stable value for species PE masked a shift in the areas with strong and weak PE. Inspecting spatial variation in species PE also illustrates why results are sensitive to spatial resolution in the Northwest Atlantic (NWA) and Celtic Sea. For example, increasing species PE at coarse spatial resolution was seen

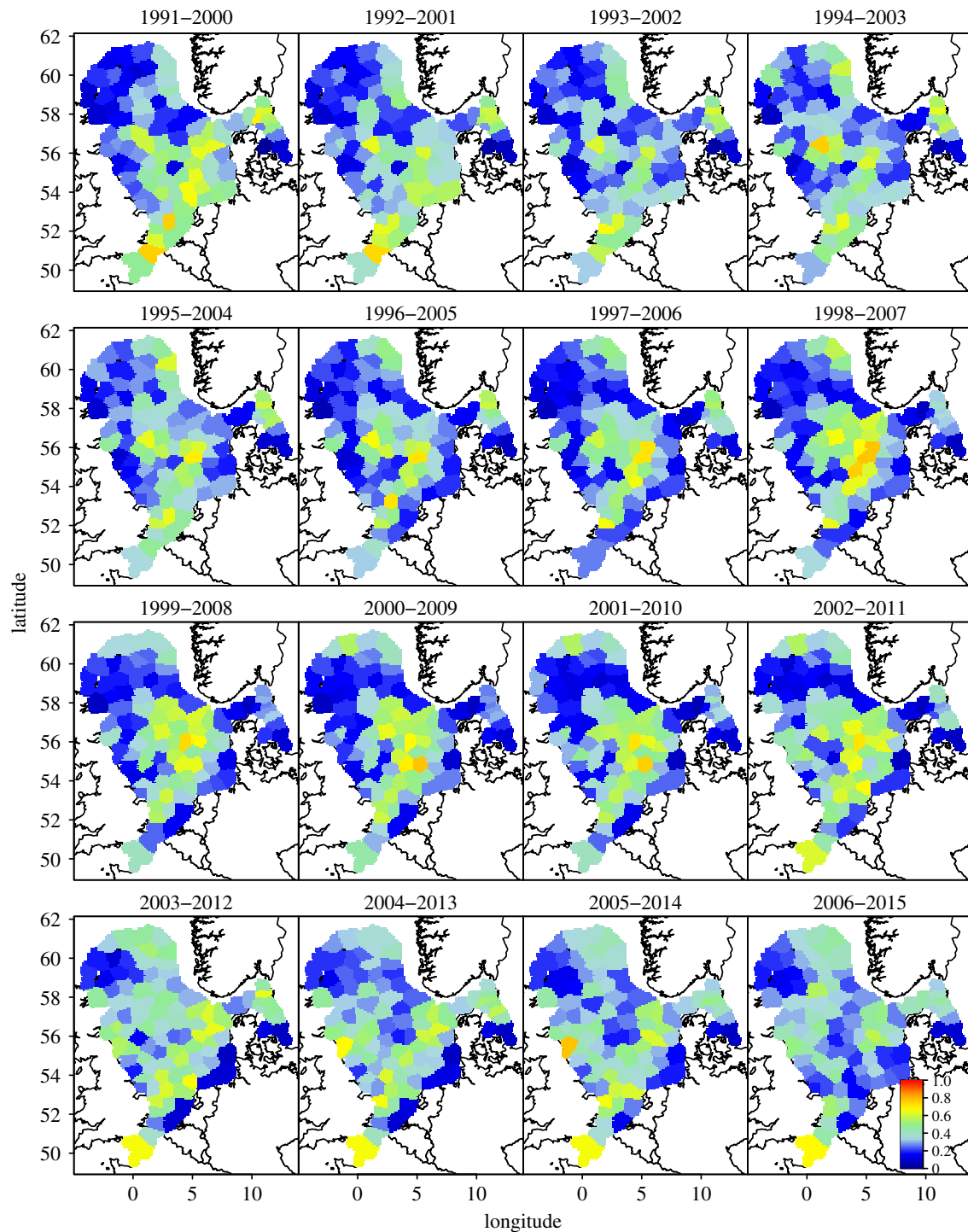


Figure 5. Species PE at each site for the bottom-associated fish community of the North Sea. Blue indicates zero portfolio effect; red indicates a maximum portfolio effect; see colour bar in the final panel.

for the Northwest Atlantic, where offshore areas with low species PE at fine spatial resolution (100 knots, figure 4) were estimated to have higher species PE at course resolution because inshore and offshore areas were being aggregated at this course resolution (electronic supplementary material S7 and figure S8). This highlights the need to model fine-scale variation to differentiate processes occurring in near shore versus offshore areas in marine ecosystems.

4. Discussion

Our study revealed that spatial PEs are substantially stronger than species PEs for the dominant bottom-associated fishes for six of seven marine ecosystems (figure 1). We therefore

recommend that spatial and total PE be monitored as dynamic ecosystem indicators, representing an integrated measure of risk for fishing communities and mobile predators, specifically measuring protection from variability in fishing and prey resources. However, we acknowledge that introducing a new ecosystem indicator requires addressing many additional considerations, including cost, ease of communication and sensitivity to potential management actions [39]. Fully exploring these necessitates subsequent research and collaborations among regional scientists and managers. We also showed that marine ecosystems where total PE appears to be stable may still exhibit shifts in the areas associated with strong or weak species PE (e.g. in the North Sea). Artisanal fishing fleets have growing importance worldwide

[40], but typically access a smaller geographical area than industrialized fleets that fish in different ecosystems during different seasons and can relocate when fishing opportunities shift. Therefore, artisanal fleets are more vulnerable to changes in economic risk arising from spatial shifts in species PE than industrialized fishing fleets. Consequently, we emphasize the importance of tracking spatial variation in species PE to anticipate changes in risk exposure associated with changing resource variability for local fishing communities and predators with limited spatial mobility, such as central place foragers.

Exploitation of natural communities can generate changes in species PE, spatial PE and total PE. Fisheries harvest affects the abundance and productivity of one or more species through changes in size and age distributions, and may also substantially modify species interactions and environmental sensitivities [41]. Knowing whether PE are generated by either temporal or spatial changes in species abundance could help inform managers which combination of spatial or seasonal closures is likely to minimize risks due to resource variation. For example, seasonal spatial closures and implementation of transferrable quotas can increase the productivity and profitability of multispecies fisheries that are spatially heterogeneous [42,43], but the benefits of such actions rapidly erode when managers are unaware of the underlying spatial dynamics [44]. Management strategies aimed at maximizing intra- and inter-species diversity (through selective closures or size limits that vary over space and time) could therefore be informed by PE estimates from spatio-temporal models. Importantly, the spatial extent of environmental forcing for PEs is unlikely to overlap perfectly with fisheries management jurisdictions. Management actions targeting the maintenance of PE will thus require cooperation among multiple (local, national and international) jurisdictions, depending critically on the spatial scales that define ecosystem PEs relative to the scales that define management jurisdictions.

An important limitation for management efforts to maintain or promote PE is understanding the degree to which spatio-temporal variance in resource density is produced by anthropogenic versus natural factors. For example, large-scale atmospheric forcing of the marine environment can cause some degree of synchronization of Pacific salmon over time, but climate linkages vary among coastal ecosystems [45] and these differences complicate efforts to disentangle human versus natural drivers of abundance changes. Similarly, the distribution of important marine fishes has shifted [46], having important implications for optimal risk management of coastal fishing communities [47], despite the exact mechanism for distribution shifts remaining unknown [48]. In cases where variable resource densities are driven primarily by natural forcing (rather than human actions), resource managers will presumably have few management options to protect PE beyond promoting species diversity via restoring or conserving critical habitats. By contrast, managers will presumably be capable of promoting PE through the spatial and temporal regulation on human activities in cases where variable densities are driven primarily by human impacts.

Regarding the trends in PE documented here, the decrease in species PE observed in the Northwest Atlantic occurs primarily in the Gulf of Maine, and this region has subsequently shown strong synchronous responses to large

temperature increases [49]. Similarly, the onset of declines in total PE during the early 2000s in the Eastern Bering Sea occurred when the region shifted from a regime of interannual variation in sea-ice extent to a regime with 5-year phases with large or small sea-ice extent [50]. Finally, spatial synchrony has decreased somewhat in the North Sea, probably due in part to fishing-induced truncation of age-structure. Based on these examples, we believe that changes in synchrony documented here could plausibly be explained by changes in oceanographic drivers within each ecosystem. However, there is little previous research regarding changes in PE for fish biomass in these regions, and the research that has been conducted is not expressed in units that are directly comparable with the PE measured here [51]. We therefore encourage further comparative research to measure changes in PE in units that are similar across regions and over time, and process-oriented research to attribute changes in PE to specific environmental or anthropogenic drivers (e.g. truncation of age-structure or changes in community evenness due to fishing).

Any measurement of PE (including the index developed by Loreau & de Mazancourt [16]) is affected by the spatial extent and grain over which aggregate ecosystem biomass is calculated [6,14,52]. For any ecosystem, the strength of PE will depend on both the spatial scales at which dominant patterns of ecosystem heterogeneity are expressed and the rate at which correlations decay with distance [52]. It is likely that marine ecosystems are produced by environmental variation at multiple spatial scales, such that the strength of PE continues to increase as the spatial extent of an ecosystem increases. However, it is also likely that spatial PE shows critical scale-dependencies, such that PE strength displays an irregular response to changes in spatial scale. In this case, the spatial scale of PE can be informative about the dominant processes structuring ecosystems and the spatial scales at which management should focus on achieving reliable resource flows to consumers. The scaling between PE and ecosystem extent remains an important topic for future research in fisheries and other natural resource systems. We have analysed marine ecosystems ranging in size from 100 000 to 600 000 km², and spatial heterogeneity will probably contribute less to total portfolio effects when dynamics are explored over a smaller spatial extent.

Ecosystem-based management plans could more explicitly consider the economic and political trade-offs involved with achieving reliable resource flows at increasingly broader spatial scales. Because the PEs expressed at broad spatial scales are generated by heterogeneity produced at finer spatial scale [14], ecosystem-based management should also strive to understand and maintain the processes that generate local heterogeneity. Although we are unlikely to fully understand the specific mechanisms that generate heterogeneity in marine ecosystems [2,3], management strategies that enable their expression may be critical for maintaining reliable resource flows to people and consumers that currently benefit from PE.

Developments in statistical modelling, such as the joint dynamic species distribution model used here, will undoubtedly better inform resource managers as to how PE manifests in resource systems besides marine fisheries. For example, agricultural systems often involve complex and multispecies dependencies upon shared nutrients [53,54]. Similarly, the impact of pests upon agricultural output is mediated by multiple biological control agents, such that agricultural yield

may depend upon asynchronous variation in biological control agents [55]. We therefore foresee that management of multispecies resources (e.g. fisheries, forestry and agricultural systems) will broadly benefit from monitoring the relative contribution of spatial and species PE to variance in resource availability.

Ethics. This paper does not include work with human subjects. It does involve work with animals, and sampling data analysed here were conducted exclusively by national and international agencies: the International Council for the Exploration of the Seas, ICES (NS-IBTS, BITS and EVHOE), the National Marine Fisheries Service, NMFS (EBSBTS and NWABTS) and the South African Department of Agriculture, Forestry and Fisheries, DAFF (SASC and SAWC). These data collections were reviewed and authorized by each national sampling authority.

Data accessibility. All data used are publicly available. Data for the Eastern Bering Sea are available at http://www.afsc.noaa.gov/RACE/groundfish/survey_data/data.htm. Data for the Northwest Atlantic are available at http://oceanadapt.rutgers.edu/regional_data/. Data for the Celtic Sea and Bay of Biscay, North Sea and Baltic Sea

are available at https://datras.ices.dk/Data_products/Download/Download_Data_public.aspx. Data for the South and West Coast of South Africa can be obtained by contacting South Africa's Department of Agriculture, Forestry and Fisheries directly. Online data analysed here were obtained on 22 December 2016 and were downloaded using package *FishData* (<https://github.com/James-Thorson/FishData>).

Authors' contributions. J.T.T. designed and implemented the analysis. All authors contributed to its interpretation. J.T.T., M.D.S. and D.E.S. contributed writing, and all authors contributed edits.

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