Spatio-temporal species distribution models reveal dynamic indicators for ecosystem-based fisheries management

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Many economic sectors rely on marine ecosystem services, and holistic management is necessary to evaluate trade-offs between sectors and facilitate sustainable use. Integrated ecosystem assessments (IEA) integrate system components so that managers can evaluate pathways to achieve desired goals. Indicators are a central element of IEAs and capture the status and trend of individual components and should be sensitive to changes in the system; however, most indicators are aggregated over space and time as annual values, potentially leading to incomplete or inaccurate inferences about system change. Here, we demonstrate the utility of spatially and temporally explicit ecological indicators by fitting multivariate spatio-temporal models to survey data from the northeast US Shelf Ecosystem, encompassing three distinct ecoregions: Georges Bank, Gulf of Maine, and mid-Atlantic Bight. We evaluate three case studies to explore how these models can help assess ecosystem performance relative to management objectives, such as to: (1) identify dominant modes of variation in zooplankton communities; (2) quantify components of system stability; and (3) assess the density-dependent condition of groundfish over time. Collectively, these three examples demonstrate multiple interesting processes, but particularly highlight the rapid zooplankton changes and associated changes in benthivore condition and stability in the Gulf of Maine. Attributing changes in ecosystem indicators to localized processes is difficult using conventional "regionally aggregated" indicators, so this example highlights the benefits of spatio-temporal methods for integrated ecosystem analysis in this and other regions.

Keywords: ecosystem indicators, integrated ecosystem assessment, spatial indicators, vector autoregressive spatio-temporal (VAST).

Introduction

Marine ecosystems provide a myriad of services essential to human welfare, including provisioning (e.g. seafood), regulating (e.g. of climate, nutrient cycling), and cultural (e.g. recreation, spiritual value) goods and services. Concurrently, these ecosystems are increasingly exposed to a wide range of environmental and anthropogenic stressors, including climate change, habitat alterations, and fishing (Halpern *et al.*, 2012; Link and Watson, 2019). Many sectors overlap in ocean ecosystems, including energy production, shipping, commercial fishing, and recreational activities, and the spatial footprint and impact of these activities must be reconciled (NOAA, 2018).

Holistic ecosystem-based management approaches (EBM) attempt to integrate economic, social, biophysical, and cultural factors in the decision to more sustainably manage ocean resources (Slocombe, 1993; Link, 2002; Pikitch *et al.*, 2004; Arkema *et al.*, 2006; Curtin and Prellezo, 2010; Schultz *et al.*, 2012). The National Oceanic and Atmospheric Administration's (NOAA's) Integrated Ecosystem Assessment (IEA) is an example of EBM in which multiple components of an ecosystem are integrated into the decision-making process to articulate objectives and monitor progress towards goals (Levin *et al.*, 2008). In the northeast United States, the IEA programme produces annual reports that synthesize ecosystem information to allow fishery managers to better meet fishery management objectives (NEFSC, 2022). Ecosystem-level management objectives are largely derived from legal mandates (e.g. the Magnuson-Stevens Fishery Conservation and Management Act and the Marine Mammal Protection Act) and include objectives like stability and seafood production (see Table 1 in NEFSC, 2022). Indicators that capture the status and trend of key ecosystem components are a core component of the IEA approach and provide the basis for the assessment of ecosystem state and attributes of interest (Levin *et al.*, 2008; Levin *et al.*, 2009; deReynier *et al.*, 2010).

Marine ecosystems are complex, and a suite of representative and responsive indicators can be used to communicate changes in resources or ecosystem attributes relative to desired goals and objectives (Rice and Rochet, 2005). Accordingly, many indicators are routinely used in IEAs, such as physical indices, abundance of species or functional groups, or groups of species, sizes of individuals, the size structure of the community, biomass ratios, indices of diversity, and various metrics of ecosystem function derived from models (Link, 2005; Livingston *et al.*, 2005; Tam *et al.*, 2017). While there are many potential indicators, the value of each depends on its observability, reliability, and responsiveness to variation in processes that contribute to performance relative to management objectives (NEFSC, 2022; for a discussion on indicator properties, see Rice and Rochet, 2005).

Table 1. Species included in joint-dynamic species distribution model (JDSDM) to evaluate portfolio effects across feeding guilds in the northeast U.S. shelf ecosystem.

Feeding guild	Selected species	Aggregated species
Piscivores	Summer flounder (*Paralichthys dentatus*) Atlantic cod (*Gadus morhua*) Spiny dogfish (*Squalus acanthias*) Goosefish (*Lophius americanus*) Winter skate (*Leucoraja ocellata*)	Acadian redfish Atlantic halibut Bluefish Clearnose skate Fourspot flounder John dory Little skate Longfin squid Northern shortfin squid Offshore hake Pollock Red hake Sea raven Silver hake Smooth skate Summer flounder Striped bass Thorny skate Weakfish White hake Windowpane
Planktivores	Atlantic herring (*Clupea harengus*) Butterfish (*Peprilus triacanthus*) Atlantic mackerel (*Scomber scombrus*)	Alewife American shad Blackbelly rosefish Blueback herring Cusk Longhorn sculpin Lumpfish Menhaden Northern sandlance Northern searobin Sculpin, unclassified
Benthivores	Haddock (*Melanogrammus aeglefinus*) Winter flounder (*Pseudopleuronectes americanus*) Yellowtail flounder (*Pleuronectes ferruginea*) Black sea bass (*Centropristis striata*)	American plaice American lobster Atlantic wolffish Barndoor skate Blue crab Cancer crab, unclassified Chain dogfish Cunner Cuttlefish, unclassified Jonah crab Lady crab Ocean pout Octopod, unclassified Red deepsea crab Rosette skate Scup Smooth dogfish Spider crab, unclassified Striped searobin Squid, unclassified Tautog Tilefish Witch flounder

For each feeding guild modelled, species that expert opinion selected as representative of the guild were designated as separate categories, and all other species were aggregated into the last category.

Effectively monitoring indicators depends on adequate and reliable data collected and analysed at relevant spatio-temporal scales to make well-grounded inferences on ecosystem status (Heim *et al.*, 2021). Interpretations of many otherwise useful indicators may suffer from poor observation, e.g. from uneven, inconsistent, or opportunistic sampling; measurements occurring at too small or too large of a spatial scale to represent a management jurisdiction; mismatches between scale of measurements and the scale of the process being monitored; or spatial and temporal correlations in unexplained residuals that are not modelled or otherwise communicated (Rice and Rochet, 2005; Heim *et al.*, 2021). For any ecosystem, our understanding will depend both on the spatial and temporal scales at which dominant patterns of heterogeneity are expressed and on the rate at which correlations decay with distance and time (Stein *et al.*, 2001). For living marine

resources, habitat characteristics, environmental and anthropogenic stressors, and biotic interactions vary over space and time, and these changes will affect their distribution and dynamics. For example, Alaska pollock exhibits spatial variation in size, weight, and diet in their summer distribution in the eastern Bering Sea (Grüss *et al.*, 2020). As a result, developing indicators for individual subareas could misrepresent patterns occurring throughout the managed stock. In addition, climate-driven shifts in spatial distribution towards the northern Bering Sea will result in predictable changes in diet and demographic rates that are relevant to the ecology of that population. Accounting for changing spatio-temporal patterns will enable a better understanding of the status of marine species.

Observing the spatial and temporal dynamics of indicators is fundamental to managing shifts in ecosystem state (Clements and Ozgul, 2018). However, many ecosystem indicators are aggregated over space into a single temporal index. Even for multidecadal and ecosystem-wide surveys integral to many monitoring programmes, scientific communications typically report only regional time series of aggregate biomass (NEFSC, 2022). Spatial indicators remain underdeveloped, as accessible tools to analyse large dimensional datasets have only recently become available for researchers (e.g. INLA, Rue *et al.*, 2009; Lindgren *et al.*, 2011; ; VAST, Thorson, 2019; TMB, Kristensen *et al.*, 2016). These recent advances in computing and spatio-temporal modelling allow researchers to estimate variation across space and over time for multivariate ecosystem variables (representing numerical abundance and/or biological condition), thereby developing more informative and effective indicators of ecosystem status. Inference from spatially explicit models will enable more effective management and reduce the potential for suboptimal or incorrect management decision-making.

Climate change, and other large-scale disturbances, affect all biological levels, either directly (e.g. by affecting physiological thresholds) and/or indirectly (e.g. by modifying food resources), resulting in spatio-temporal changes in the density of living marine resources such as fish and plankton. Spatiotemporal models are increasingly capable of providing useful input to assessments in an effort to understand these dynamics to implement effective management strategies. Our aim is to highlight examples of management objectives and associated indicators that could be evaluated with spatio-temporal analyses, including:

(1) *Ecosystem stability*: Dominant modes of variation in zooplankton abundance may be used as an indicator of trophic structure, physical ocean conditions, early warning for regime shifts, and feeding potential for assessments, due to their sensitivity to environmental change and integrative role as a link between trophic levels (Litzow and Mueter, 2014; Litzow and Hunsicker, 2016).

(2) *Fish community stability*: Similarly, feeding guild biomass stability has been proposed as an indicator of ecosystem state, particularly as an early warning indicator (Garrison and Link, 2000). Variation in community abundance may be reduced through asynchronous fluctuations in population densities among community members that serve similar ecosystem functions. This phenomenon is called a portfolio effect and may mitigate the impact of variable resource densities on stakeholders (Sullaway *et al.*, 2021).

(3) *Fish productivity*: Physiological body condition is an important indicator of population productivity (Eero *et al.*, 2015) and is relevant to EBM through both ecosystem functioning and fisheries yield as a potential reference point, but is highly unlikely to trend uniformly across a species' range. So aggregating calculations over space will mask processes driving changes in condition, e.g. areas where habitat suitability is declining.

Here, we demonstrate the utility of spatio-temporal models to evaluate these potential indicators relevant to IEAs used for EBM by analysing long-term zooplankton and fish community data across the northeast US shelf large marine ecosystem (NES).

Methods

Study area

The NES is a highly productive region that encompasses an area of ~260000 km² from Cape Hatteras in the south to the Gulf of Maine in the north. The NES supports a number of important economic sectors, including commercial and recreational fishing, offshore energy development, and shipping. Numerous environmental drivers contribute to structural changes throughout the system (NEFSC, 2009). Ecosystem status and trends are regularly monitored and evaluated relative to fisheries management objectives (NEFSC, 2022).

The NES can be divided into four ecological production units (EPUs)—the Gulf of Maine (GOM), Georges Bank (GB), the Mid-Atlantic Bight (MAB), and the Scotian Shelf—that align on a southwest-northeast axis up the northeastern US coastline (Lucey and Fogarty, 2013; Figure 1). Due to variation in data availability and survey efforts, in the following analysis we focus on GOM, GB, and the MAB.

Data collection

The Northeast Fisheries Science Center (NEFSC) of the National Marine Fisheries Service (NMFS) has a longstanding monitoring programme covering most of the northeast US continental shelf (Brodziak and Link, 2002). Data used in this study were compiled from NEFSC surveys that monitor trends in abundance and distribution of marine species, and subsequently corrected for vessel effects (Miller *et al.*, 2010).

Zooplankton community data

The NEFSC Ecosystem Monitoring (EcoMon) sampling protocol collects hydrographic and tow data using a randomized spatial sampling technique that samples ~30 stations per EPU per two-month period (Figure 1). During these surveys, plankton are collected using a bongo net (333 μm mesh) towed obliquely from 200 m (or near the bottom in shallower depths) to the surface (Kane 2007, 2011).

Zooplankton abundance data used in this analysis includes samples limited to 2000–2017 to ensure adequate data coverage. Samples taken prior to 2000 were subject to less consistent sampling protocols. We filtered this dataset to five abundant copepod taxa considered ecologically relevant in previous analyses, discussions with experts, and ecosystem reports: *Calanus finmarchicus*, *Centropages typicus*, *Centropages hamatus, Temora longicornus*, and *Oithona* spp., hereafter referred to as *cfin*, *ctyp*, *cham*, *tlong*, and *oith*, respectively (Morse *et al.*, 2017, NEFSC, 2021). To control for the substantial variation in zooplankton abundance among seasons, this analysis was limited to samples taken in the spring (February–April, Morse *et al.*, 2017).
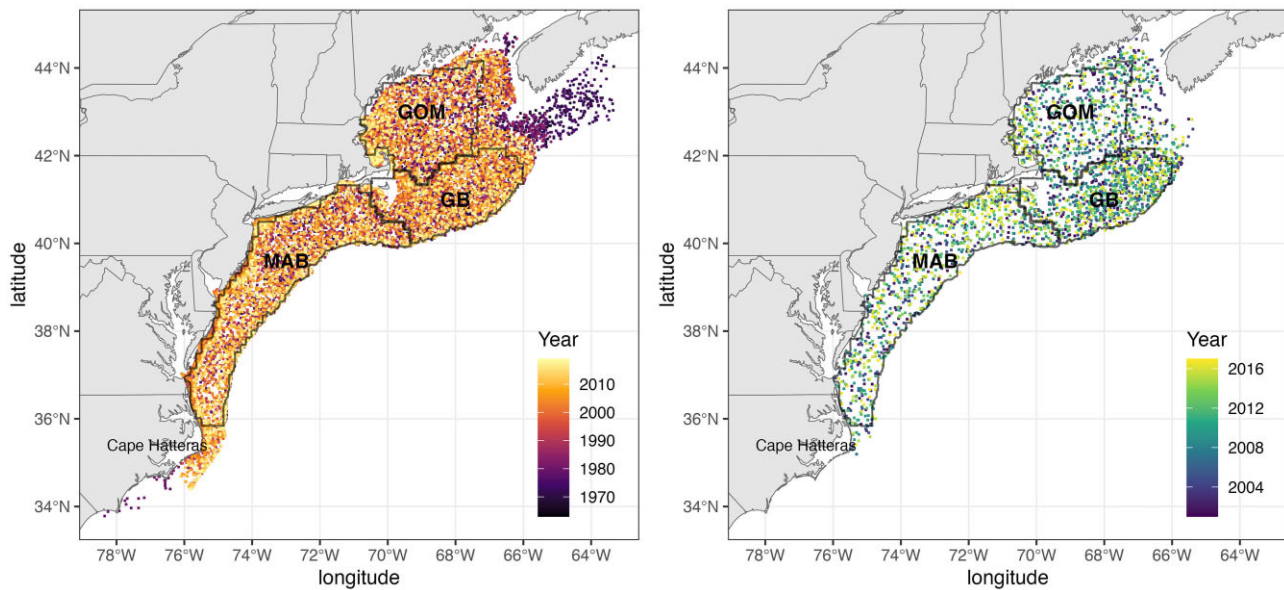
Figure 1. Data from two monitoring efforts in the Northeast Shelf Large Marine Ecosystem are used in this analysis. Dot colour represents the year that location was surveyed in the GOM, on the GB, and in the MAB ecoregions. Left panel: locations of bottom trawl surveys conducted in the fall from 1963 to 2019. Right panel: ecosystem monitoring surveys conducted springs of 2000–2017.

Fish community data

The NEFSC has been conducting standardized bottom trawl surveys in the fall since 1963 (Brodziak and Link, 2002). This scientific monitoring programme has sampled 350–400 stations every spring and fall from Cape Hatteras (North Carolina, USA) to Nova Scotia (Canada) using a random stratified design (Figure 1).

Weight and length of fish and invertebrates were measured at randomly sampled stations within each depth-region stratum since 1992. These data were used to estimate population density-weighted average condition, "condition" being defined as the relative weight of an individual fish given its body length (i.e. Le Cren's condition factor; Le Cren, 1951), described in more detail in the statistical analysis below (Thorson, 2015).

Statistical analysis

We use the same Vector Autoregressive Spatio-Temporal (VAST) modelling platform to maintain consistency across these three applications (Thorson and Barnett, 2017; Thorson, 2019). VAST implements a delta-generalized linear mixed model including two linear predictors, where these linear predictors are then transformed using inverse-link functions to predict the probability that measurement b_i for sample i is zero, $Pr\ (b_i = 0)$, as well as the expected value for a nonzero measurement, $E\ (b_i|b_i)0)$. Each linear predictor includes the additive effect of several components:

(1) Temporal main effect ("intercept") that typically varies for every variable c_i and year t_i;

(2) Spatial main effect ("spatial component") that represents the average spatial distribution for a given variable c_i;

(3) Interaction of space and time ("spatio-temporal component") that represents variation in spatial distribution among modelled times t_i;

(4) Density covariates, representing the impact on predicted local densities of either local environmental conditions or a spatially varying response to regional conditions, where the latter represent "ecological teleconnections";

(5) Catchability covariates, representing the impact of environmental or sampling conditions on expected responses, but are not reflective of local densities and therefore are "partialled out" prior to predicting densities across space and time.

Various applications include estimating or dropping these components.

Spatial (#2), spatio-temporal (#3), and spatially varying responses to covariates (#4–5) involve estimating latent variables that vary spatially. For computational efficiency, we specify a Gaussian Markov random field (GMRF) for these spatial variables, and each GMRF isthen treated as a random effect during parameter estimation within the R statistical environment (R Core Team, 2020). These and other random effects are integrated across when calculating the likelihood of fixed effects, and we use maximum likelihood implemented using Template Model Builder (Kristensen et al., 2016) to estimate fixed effects parameters. We specifically estimate the value of GMRFs at a fixed number of "knots", where knots are distributed evenly across space as vertices of a triangulated mesh that covers the spatial domain of interest (Thorson et al., 2021). The value of a GMRF at a given location is then calculated using bilinear interpolation based on its value at the three vertices surrounding it within this mesh, where the bilinear interpolation is accomplished using projection matrices computed by R-INLA (Rue et al., 2009; Lindgren et al., 2011; Lindgren, 2012).

Importantly, all five components included in each linear predictor can be implemented either for univariate (e.g. single-species) or multivariate (multispecies and/or multimodal) contexts. For example, to estimate spatial variation $w_1(s, c)$ for each location s and category c for the first linear predictor, we define a factor-model decomposition:

$$w_1\ (s, c) = \sum_{f=1}^{n_{w_1}} L_{w_1}\ (c, f)\, w_1\ (s, f)\,.$$

Where $w_1(s, f)$ is the estimate of spatial variation for each factor f and L_{w_1} is a loadings matrix that represents the estimated association of each category (e.g. species) c with each estimated factor f. The loadings matrix then represents co-variation among categories, where covariance is calculated as the loading matrix times its transpose. For identifiability, we specify that the loading matrix is lower-triangle. In the following, we sometimes rotate the loadings matrix and factors using a principal components analysis (PCA) rotation to improve interpretability; this rotation ensures that the first factor explains as much variation as possible and therefore summarizes dominant spatio-temporal patterns in model residuals.

We note that the model defines a predicted density at the location and time for each sample, and also a predicted density at a set of "extrapolation-grid" locations. Summing across these extrapolation-grid density estimates then yields an area-expanded calculation of the total across a specified spatial domain, and can also be used to visualize the model results. Further details can be found in the VAST User Manual (https://github.com/James-Thorson-NOAA/VAST/tree/main/manual). For the following analyses, we use VAST release version 3.7.0 and R version 4.0.1 (R Core Team, 2020).

Ecosystem stability: dominant modes of zooplankton community dynamics

Empirical orthogonal functions (EOFs) are in the same multivariate data-reduction family as principal component analysis (PCA) and factor analysis (FA), where the variability in multivariate data consisting of replicated spatial measurements of one or more variable(s) over time is reduced to a small number of dominant temporal axes and spatial response maps that explain a large portion of the variance in the original process (Lorenz, 1956). While EOFs have almost exclusively been used to analyse modes of spatio-temporal variability in physical climate data such as sea surface temperature or pressure (Hurrell *et al.*, 2003), recently Thorson *et al.* (2020) generalized the EOF analysis to fit noisy and zero-inflated samples of biomass/abundance for multiple species simultaneously in a spatio-temporal distribution model. In this configuration, indices of variation and associated spatial maps could represent ecological community dynamics while accounting for variation due to space and time. These axes can be rotated to allow interpretation similar to PCA's principal components, where the first axis explains the most variation, the second axis the second most, and so on. Here, we use this statistical generalization of the EOF to identify axes of variability in community zooplankton data in the NES using VAST.

EOFs ordinate on years, providing an annual index for modes of spatio-temporal variability as well as spatial maps for each species depicting the deviation in abundance associated with a positive mode value. The EOF uses a Poisson-link delta model (Thorson *et al.*, 2020), where encounter probability is the complementary log-log link of number density and the expected abundance of a given species is proportional to their number density at a specific location (knots). Number density is modelled as a function of intercepts for each species and year (to isolate spatio-temporal shifts rather than abundance) and the net effect of temporal indices and their species-specific spatial patterns. We fit an EOF with two factors (i.e. indices, spatial and spatio-temporal variation) over 100 knots for each EPU separately, as zooplankton dynam-

ics are expected to differ significantly in each EPU (Morse *et al.*, 2017). These two factors are zero-summed such that the spatial component (omega) represents the distribution in an "average" year.

Fish community stability: portfolio effects

To estimate feeding guild biomass stability, we calculate a measure of the strength of the portfolio effects arising from asynchronous biomass dynamics among species and locations in each guild over time. We estimated density for multiple species in each guild using a joint dynamic species distribution model (JDSDM, Thorson *et al.*, 2016) that simultaneously analyses the correlated distribution of multiple species while incorporating spatio-temporal variation. JDSDM models have been commonly implemented for species ordination, for example, demonstrating that the distributions of species of the same genus are more highly correlated than for species of differing genera (Thorson *et al.*, 2016). The JDSDM predicts density (biomass per area) for each year, location, and species.

Portfolio effects (PE) measure the degree to which the variance over time in one ecosystem component is decreased by asynchronous variation in different components of an ecosystem (Schindler *et al.*, 2015). Here, PE were calculated with JDSDM-estimated density as one minus a standardized Loreau measure of synchrony (Loreau and Manzacort, 2008), following Thorson *et al.* (2018). For our purposes, the Loreau metric is calculated as the ratio of observed variance in aggregate biomass (biomass summed across years for a given species and location), and the maximum possible variance for aggregate biomass that would arise if all components were perfectly correlated (the sum of the variances across sites and species).

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

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. This metric can be calculated locally (i.e. calculating variance for each location), or regionally (by summing across locations, and then calculating variance), where visualizing local portfolio effects can show spatial patterns that underlie regional portfolio effects. The numerator is the variance across years of biomass summed across sites and species, and the denominator is the sum of variances across sites and species. Then, PE equals 1 whenever the variance of aggregate biomass (the numerator) is zero and is 0 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 as well as other model parameters. So, our measure of PE ranges from 0 (no PE) to 1 (strongest possible PE), calculated using a moving window of 10 years, which results in 47 total calculations that cover the time series from 1963 to 2019. For a more detailed discussion on JDSDMs and calculation of portfolio effects, see Thorson *et al.* (2018).

We implemented this process separately for three feeding guilds (Garrison and Link, 2000), piscivores, planktivores, and benthivores, using the fall NEFSC bottom trawl survey data from 1963 to 2019. For each guild, the JDSDM was fit to sampling data of 3–5 ecologically relevant species determined by experts, as well as an additional "other" group defined as the aggregated data from all other sampled species

in that guild (Table 1), where Thorson *et al.* (2020) confirm that changing this number of species typically has little impact once dominant species are included. The JDSDMs estimated density for each species at 200 knots across the NES for two factors (spatial and spatio-temporal variation). Unlike other sections of this manuscript, we did not use bilinear interpolation to project the GMRFs to more detail due to computational constraints. Because spatial densities are known to covary with bathymetry for many species of fish, we included a quadratic effect of bottom depth (i.e. survey station depth) as a density covariate, where this quadratic effect allows for a dome-shaped depth-response curve.

Fish productivity: condition of groundfish

Fish condition measures the bioenergetic status for individual fish beyond what is measured by size or age. A common measure of fish condition is the relative weight of an individual fish given its body length, which captures tissue accumulation (fat fish are heavier for a given size) and composition (muscle is heavier for a given animal volume), and stomach contents (where fish are weighted without explicitly removing the stomach) (Bolger and Connolly, 1989; Wuenshel *et al.*, 2019). This morphometric condition index is an integrated measure of physiology that accounts for fish behaviour and life history as well as environmental and species interactions. One of the most frequently employed condition indices is Le Cren's relative condition factor (Le Cren, 1951), which defines condition as the residuals of an allometric length–weight relationship. Thorson (2015) developed the first spatio-temporal model estimating spatio-temporal changes in fish condition proxied by the Le Cren condition factor, and Gruss *et al.* (2020) extended Thorson's approach to simultaneously estimate spatio-temporal variation in numerical density and condition (interpreting the correlations between the two as "apparent density dependence").

Here, we use this condition-and-density model in VAST to jointly estimate synchronous changes in population density (measured as numbers per area) and fish condition at fine spatial scales. The model is then used to predict abundance-weighted average condition by averaging over local condition, weighting by the product of population density and surface area. This abundance-weighted average condition corrects for biases that would arise when condition (weight-at-length) samples are not distributed proportional to population densities.

We estimate density-weighted fish condition for seven groundfish species: yellowtail flounder (*Pleuronectes ferruginea*), winter flounder (*Pseudopleuronectes americanus*), silver hake (*Merluccius bilinearis*), spiny dogfish (*Squalus acanthias*), haddock (*Melanogrammus aeglefinus*), pollock (*Pollachius virens*), and Atlantic cod (*Gadus morhua*). Condition was estimated at 200 knots across the NES using fall NEFSC bottom-trawl survey data from 1992 to 2019. Because groundfish distributions (and likely condition) are known to vary with bathymetry, we included bottom depth (i.e. survey station depth) as a quadratic density covariate.

Detection of temporal patterns in the time series

We fit a generalized additive model using the R package *mgcv* (Wood, 2011) to the time series of (1) EOF loadings for each factor, (2) portfolio effects for each feeding guild, and (3) conditions for each species to quantify significance of any temporal patterns, weighted by precision (reciprocal of standard error). A smooth term with a p-value > 0.05 was deemed non-significant.

Results

Ecosystem stability: dominant modes of zooplankton community dynamics

Dominant patterns of residual variation in zooplankton communities differed among EPUs. Spatio-temporal variation in spring zooplankton community abundance in the MAB displayed random year-to-year variation, but abundance on Georges Bank and in the Gulf of Maine followed a lower-frequency cycle (see Figure 2; Figures A1 and A2 in Appendix 1). The first spatio-temporal factor for Georges Bank after PCA rotation (proportion of explained variance = 79.3%) appears to be in a different zooplankton phase since 2010 (GAM estimated a significant smooth term, $p = 0.016$), when *cham* has lower density in the northern reaches, and *tlong* has higher density in the northeastern corner of the Georges Bank. In the Gulf of Maine, the first factor (proportion of explained variance = 78.7%) spiked in 2007–2009, with positive phases associated with an increase in concentration of *ctyp*, *cham*, and *oith* densities around the western Gulf of Maine and more widespread densities of *cfin* and *tlong* (Figures 2 and 3). However, the change in EOF loadings over time was not significant ($p > 0.05$), likely due to the high variance in 2007–2009 estimated loadings (Figure 2). The second index (proportion of explained variance = 21.3%) shifts phase ~2009, related to widespread oceanic densities of *tlong* and concentrated densities of *cfin* and *oith* in the coastal southwestern Gulf of Maine (Figures 2 and 3). This shift was estimated to be significant ($p = 0.005$). The first factor of the mid-Atlantic Bight (proportion of explained variance = 56.7%) was associated in positive phases with high densities of *ctyp* and *cham* in the southern and particularly coastal reaches, *tlong* and *oith* in coastal waters, and high densities and *cfin* concentrated to the outer shelf (Figure A1 in Appendix 1).

Portfolio effects and stability of feeding guilds

Spatial portfolio effects for fish feeding guilds were relatively large (~0.64, 0.86, and 0.88 for benthivores, piscivores, and planktivores, respectively), but each guild had distinct spatial and temporal dynamics (Figures 5, B1, B7, and B11 in Appendix 1).

Portfolio effects among benthivores appear to be declining in the northeast U.S. shelf ecosystem across the time series, indicating that the spatio-temporal dynamics of distributions and densities of fish belonging to this guild are becoming more synchronous and therefore less stable (GAM estimated a significant smooth term, $p < 0.001$, Figure 4). Areas of most change in benthivore portfolio effects (i.e. greater trends) were concentrated to the outer reaches of Georges Bank, approaching the edge of the shelf (Figure 5). Examining single-species responses within the benthivore guild, black sea bass and haddock have consistently distinct spatial patterns, with black sea bass mainly found in the mid-Atlantic Bight and haddock, particularly in more recent years, only found on Georges Bank and in the Gulf of Maine (Figures B12 and B15 in Appendix 1). Haddock and black sea bass exhibited similar spatio-temporal dynamics, with ranges contracting in those areas over the time series. Yellowtail floun-
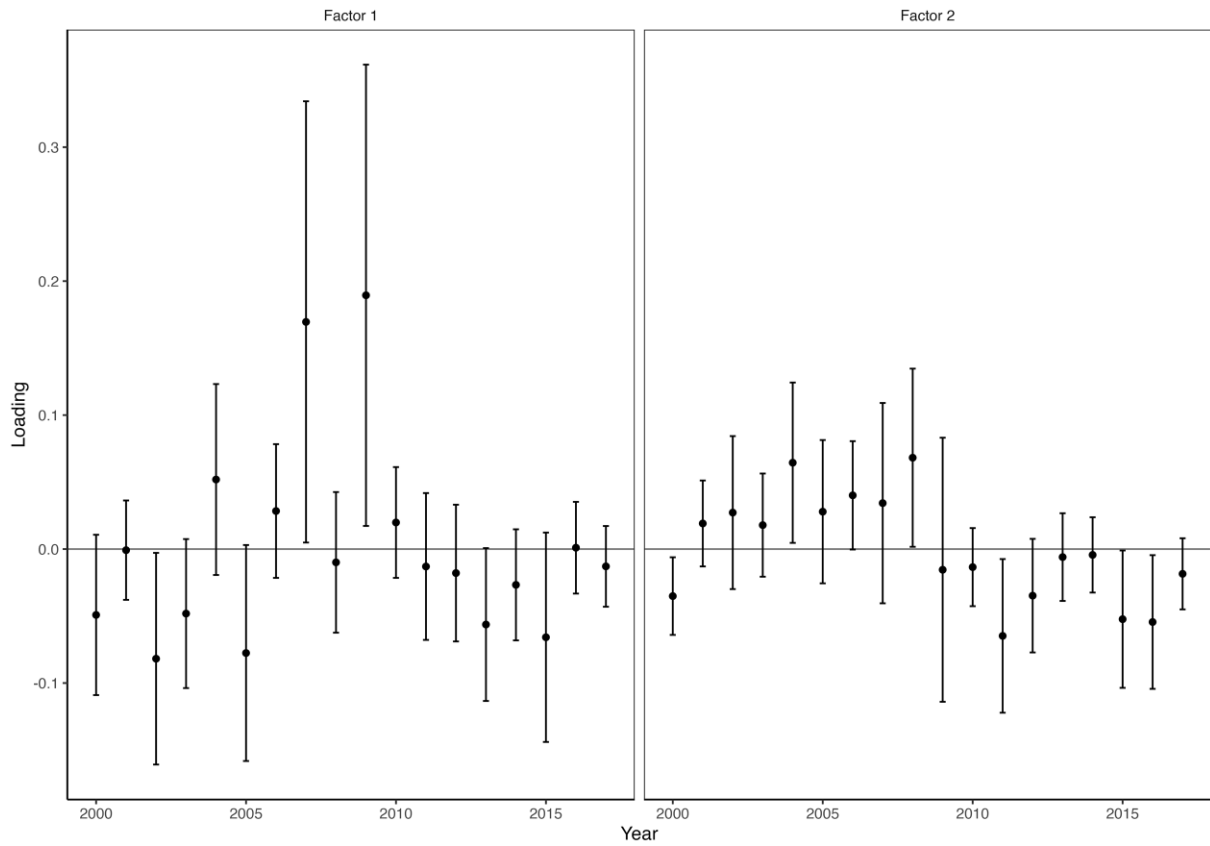
Figure 2. The first (proportion of variance explained = 78.7%) and second (proportion of variance explained = 21.3%) modes of spatio-temporal variation in spring zooplankton community abundance in the Gulf of Maine. Error bars represent 2 × SE for the loadings of each factor.
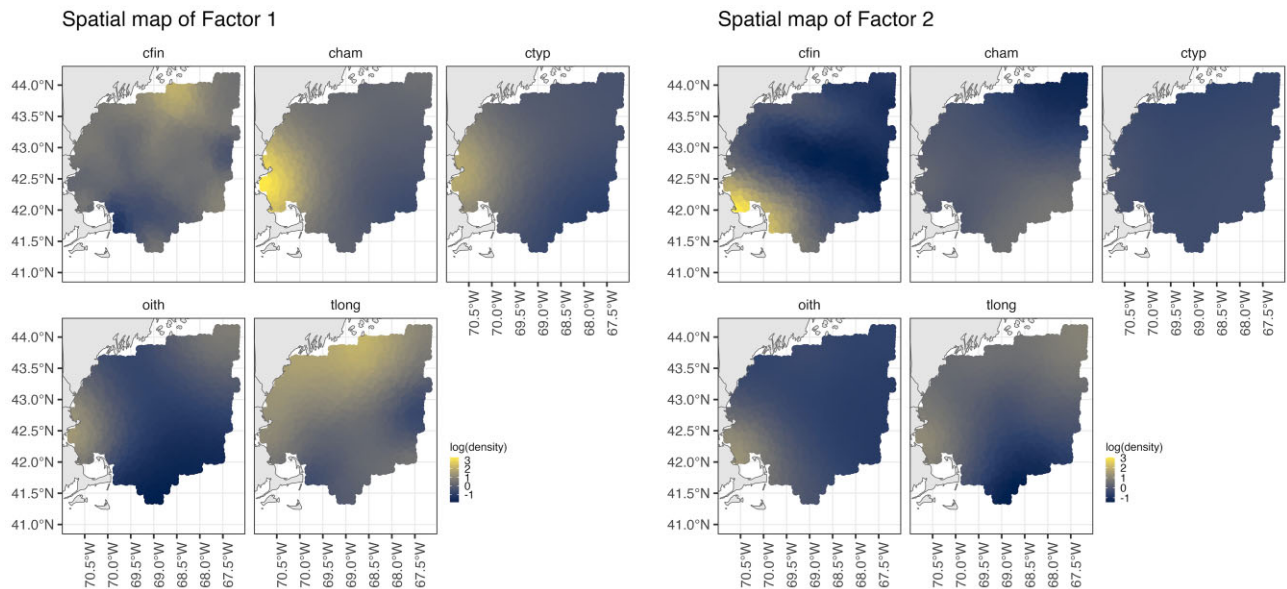

Figure 3. Spatial map of the first (proportion of variance explained = 78.7%) and second (proportion of variance explained = 21.3%) modes of spatio-temporal variation in the Gulf of Maine for zooplankton *Calanus finmarchicus* (cfin); *Centropages typicus* (ctyp); *Centropages hamatus* (cham); *Temora longicornus* (tlong); and *Oithona* spp. (oith) after bilinear interpolation.

der, while found in similar habitats as haddock, consistently declined over the time series (Figure B13 in Appendix 1). Distribution of winter flounder shifted out of the mid-Atlantic Bight and was mainly concentrated on Georges Bank, and ap-

peared to alternate between high and low abundance (Figure B14 in Appendix 1).

Portfolio effects among piscivores generally declined throughout the time series with a somewhat cyclical trend
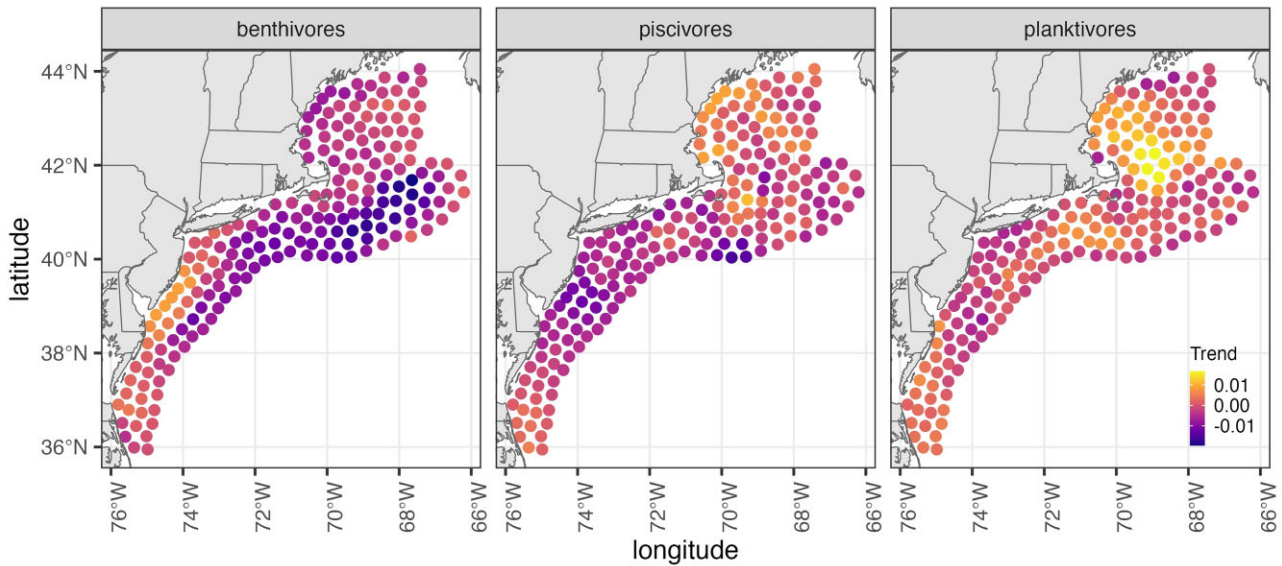
Figure 5. Trend in portfolio effects across time in the northeast U.S. shelf ecosystem for three feeding guilds from 1963 to 2019. Colour depicts the slope parameter from a linear regression fit to local portfolio effects estimates over the time series calculated for each knot.
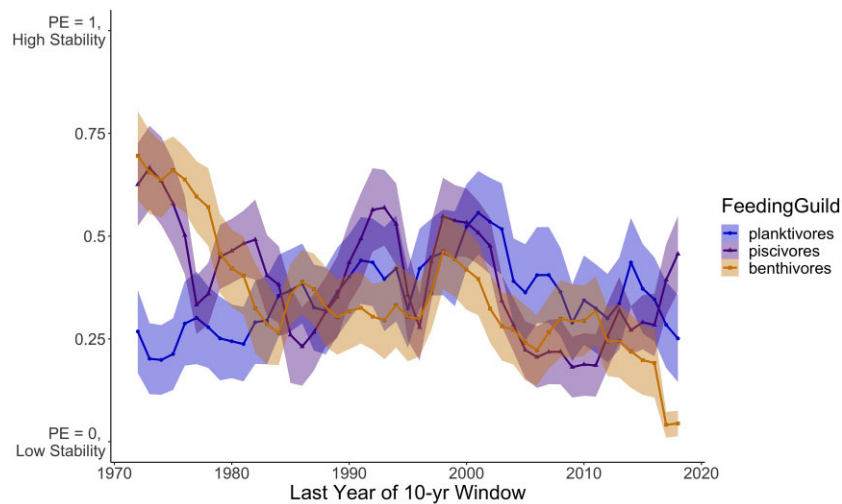

Figure 4. Time series of portfolio effects for each feeding guild. Portfolio effects range from 0 (no PE; species within guilds are more synchronous, low stability) to 1 (strongest possible PE; species within guilds are more asynchronous, high stability). Species included in each guild are listed in Table 1. Shading represents +/− 2 SE, as estimated using the delta method.

(GAM estimated a significant smooth term, $p < 0.001$)—asynchrony was high early in the time series, again in the late 1990s, and has increased in recent years (Figure 4). Trend in portfolio effects was generally spatially consistent, though areas in the GOM and southern MAB tended to increase while the most decline came from the central MAB (Figure 5). The largest portfolio effects were found mostly on Georges Bank and in the Gulf of Maine in the late 1970s to early 1980s (Figure 6). Examining single-species responses within the piscivore guild, summer flounder, Atlantic cod, and spiny dogfish exhibited similar spatial variation, particularly distinct from winter skate, whose densities were concentrated almost exclusively on Georges Bank (Appendix 1).

Planktivore portfolio effects rose to a peak ∼2000, and steadily declined thereafter (GAM estimated a significant smooth term, $p < 0.001$, Figure 4). The planktivore feeding guild had discrete areas of positive trends in portfolio effects

across the time series, such as on the central GB (Figure 5). The planktivores included in this sample had relatively similar habitat preferences, with the greatest difference in distribution from butterfish, which were generally absent from the Gulf of Maine later in the time series (Figure B9 in Appendix 1). Butterfish also exhibited different spatio-temporal dynamics than other planktivores, broadly distributed along the mid-Atlantic Bight and Georges Bank early in the time series and later concentrating to a small coastal area in the GOM (Figure B9 in Appendix 1).

Density-dependent groundfish condition

Differences among species in condition (weight per length) was generally greater than temporal variability in condition for a given species (Figure 7). Haddock and pollock experienced relatively little consistent spatial variation in their con-
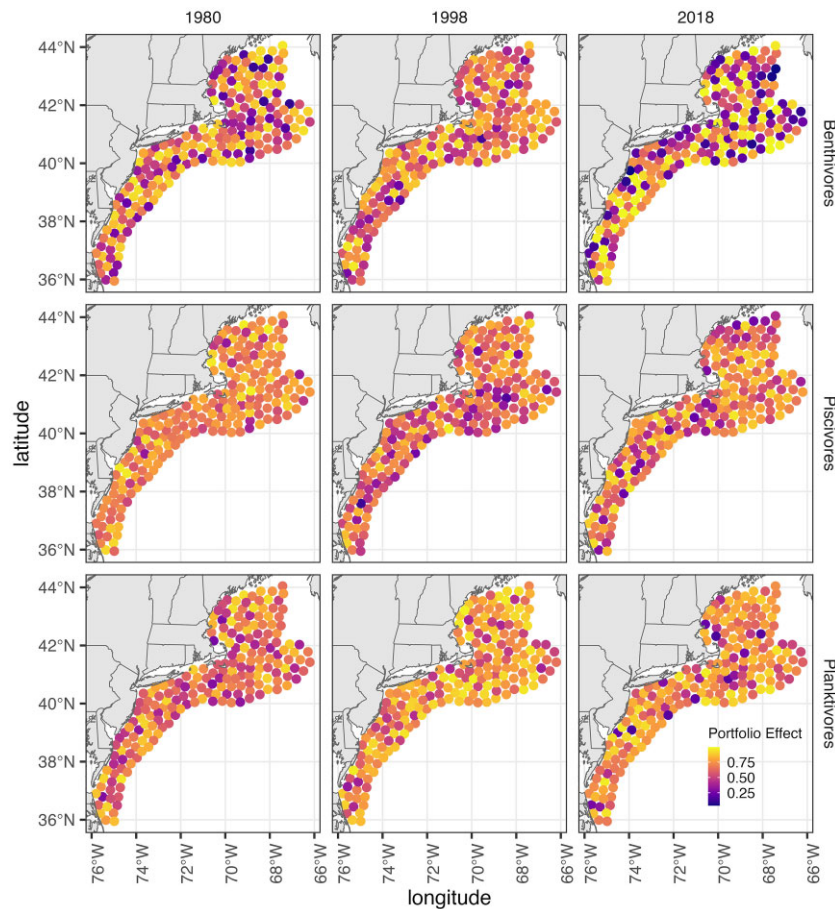
Figure 6. Spatial variation in portfolio effects in the beginning (1980), middle (1998), and end (2018) of the time series for three feeding guilds: benthivores (top), piscivores (middle), and planktivores (bottom). Portfolio effects range from 0 (no PE; species within guilds are more synchronous) to 1 (strongest possible PE; species within guilds are more asynchronous).

dition (Figures C3 and C4 in Appendix 1), whereas Atlantic cod and yellowtail flounder had hot spots of high variation in condition that persisted over the course of the study (Figures 9, C1, and C5 in Appendix 1). Though condition was relatively stable across the time series, a few species (haddock, silver hake, and winter flounder) appear to have experienced depressed average conditions over space in the early 2000s–2010. The species that experienced the greatest change was yellowtail flounder, which experienced an 8.2% decline in condition across the time series (Figure 8). We fit these condition estimates to a GAM weighted by precision and found this decline was statistically significant ($p < 0.001$, R package *mgcv*). Yellowtail condition was greatest in areas of either high or very low density, which was concentrated to a discrete coastal area at mid-latitudes (coastal Massachusetts) and on the outer reaches of the shelf.

Discussion

Here, we demonstrate how recent advances in spatio-temporal modelling can be used to develop dynamic ecological indicators to reflect ecosystem processes at multiple levels and linkages evaluated in IEAs. Shifts in zooplankton dynamics, distinct trends in portfolio effects among fish feeding guilds, and changes in groundfish condition that varied across the NES. In each of these examples, disentangling the spatial compo-

nents highlights that ecosystem processes are highly variable over both space and time and could be used to improve living marine resource management.

Zooplankton provide crucial linkages between trophic levels in marine ecosystems, providing detritus to benthic consumers and a direct food source to juvenile fish and large megafauna (Friedland *et al.*, 2012; Tam *et al.*, 2017). Here, we found dominant modes of variation (Figures 2 and 3) that illustrate spatial patterns that persist for multiple years throughout the Gulf of Maine. Morse *et al.* (2017) found a similar temporal pattern, using constrained correspondence analysis to identify important variables; however, the analysis was not able to decipher between local areas of high concentration. Zooplankton dynamics are important in the NES, where recent declines in winter-spawning cod on the NES have been associated with a reduced abundance of the copepod *Pseudocalanus* spp. in spring, and *Calanus finmarchicus* are the preferred prey of the critically endangered North Atlantic right whale (Baumgartner and Mate, 2003). Changes in the spatial extent of *Calanus finmarchicus* may be related to phenology and persistence of right whale habitat use (Meyer-Gutbrod *et al.*, 2022) and could result in increased overlap between ocean-use sectors like offshore energy development or shipping. Therefore, understanding zooplankton variability over space and time is integral for effective ecosystem management. These patterns
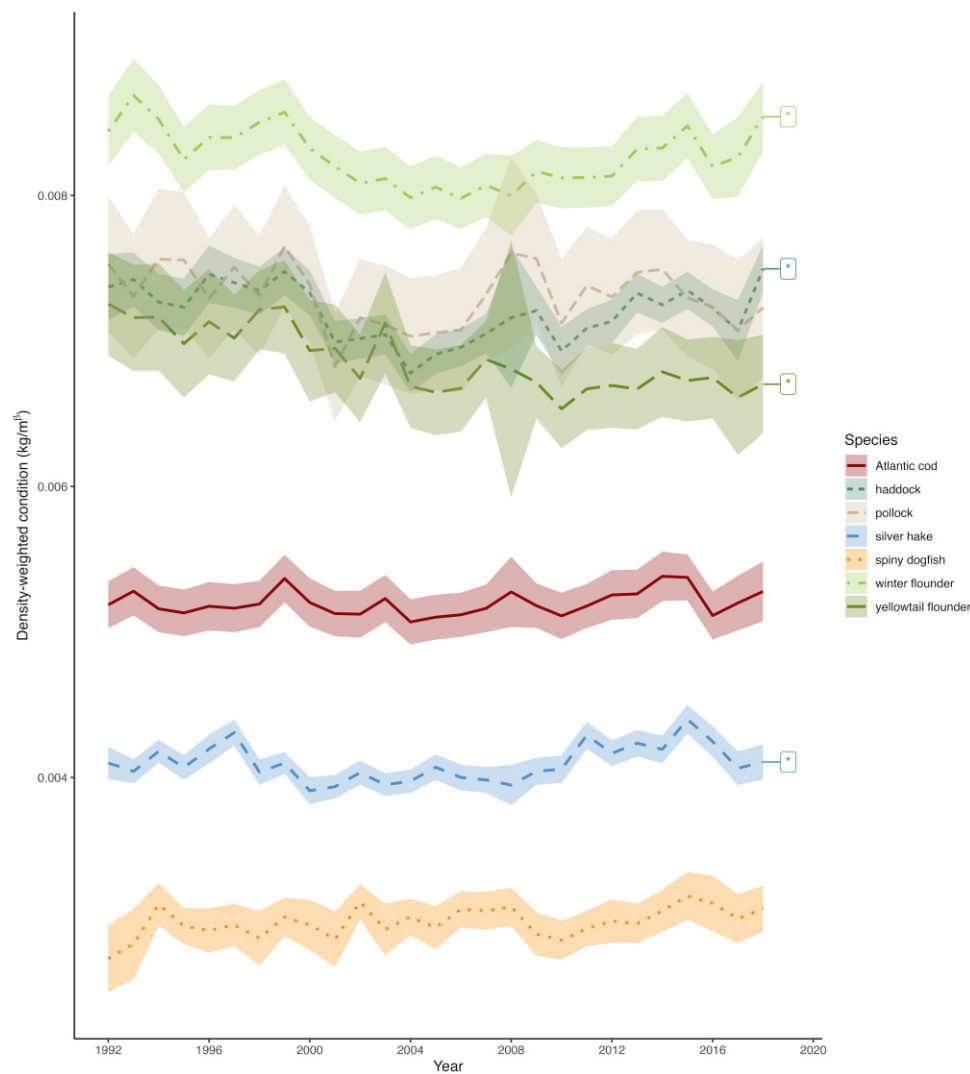
Figure 7. Time series of abundance-weighted condition α of all modelled species (left: haddock, pollock, winter flounder, yellowtail flounder; right: Atlantic cod, silver hake, spiny dogfish), specifically showing α in units kg/m^β from the allometric relationship $W = \alpha L^\beta$. An asterisk denotes statistical significance, estimated using GAMs.

of spatio-temporal variability may coincide with large-scale oceanographic changes. Grüss *et al.* (2021) and Thorson *et al.* (2020) used confirmatory analysis to evaluate potential causal linkages between EOF modes and physical factors. Further investigation into physical covariates that may be driving changes in zooplankton abundance will provide useful insight into the spatio-temporal dynamics of lower-trophic-level species and concomitant ecosystem responses that will likely require trade-offs between ocean-use sectors.

Portfolio effects (i.e. stability) of the benthivore feeding guild in the NES marine ecosystem, averaged over space, have decreased monotonically since the onset of the NEFSC bottom-trawl surveys, with the largest changes occurring in the mid-Atlantic Bight (Figure 4). Planktivore portfolio effects have also been declining over the last two decades, mainly on Georges Bank. These changes in feeding guild buffering influences ecosystem resilience to disturbance and climate variation and have important implications for EBFM. Using a different subset of the NEFSC bottom-trawl survey data along with similar data from six other marine ecosystems, Thorson *et al.* (2018) found that the spatial distribu-

tion of groundfish throughout the ecosystem was more influential to buffering than the diversity of the groundfish at any location. However, forces driving stability of guild-level biomass may vary depending on the strength of top-down and bottom-up processes. Importantly, fisheries rely on the buffering granted by spatial heterogeneity in species biomass. For example, the hundreds of spatially discrete populations of Bristol Bay sockeye salmon buffers stock returns, reducing interannual variation by a factor of 2.2—if it were a single homogeneous population, fisheries closures would theoretically be ten times more frequent (Schindler *et al.*, 2015). Ecosystem and fishery stability are important fishery management objectives for the NES (Gaichas *et al.*, 2018), and current indicators used for ecosystem reporting focus on a lack of temporal trends across aggregate functional groups (NEFSC, 2022). Evaluating feeding guild portfolio effects across space and time highlights that some areas might be less resilient to exploitation.

Body condition of groundfish (but yellowtail flounder) was generally stable over time, and though spatiotemporal variation was present, variation among species was greater than
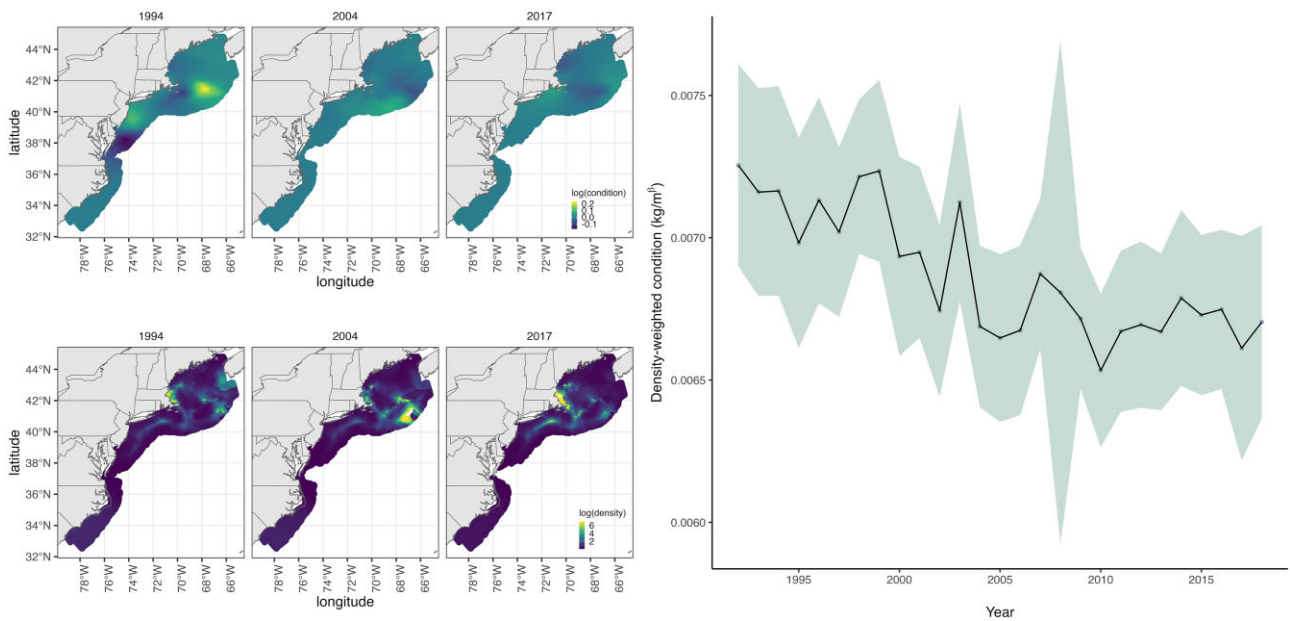
Figure 8. Yellowtail flounder condition (top left) and numerical density (bottom left) across the northeastern U.S. shelf during years of high (1994; density-weighted condition = 0.0071), medium (2004; density-weighted condition = 0.0067), and low (2017; density-weighted condition = 0.0065) condition, extrapolated using bilinear interpolation. Right panel shows time series of yellow-tail flounder density-weighted condition (units kg/m^β from the allometric relationship $W = \alpha L^\beta$). The shaded band represents ± 2 SE.

variation within species. A few species (winter flounder, haddock, and silver hake) experienced depressed condition in the period from 2000 to 2010 (Figure 7, $p < 0.001$), consistent with NEFSC's State of the Ecosystem Condition Trend Reports (NEFSC, 2022). Only one species, yellowtail flounder, showed substantial and statistically significant declines in average condition over the time series. These findings are especially relevant to socioeconomic users, such as commercial or artisanal fisheries and subsistence users, given that large-bodied fish often have higher value. How fishing excursions concentrate with high-condition "hot spots" of their catch could impact the efficiency of their efforts and variability in their haul. We therefore recommend combining these results with discrete-choice models of fishery locational choice to understand impacts on fishery catch and profit (e.g. Dépalle *et al.*, 2021).

Spatially explicit modelling allows researchers to provide holistic ecosystem advice that does not average across predefined zones or traditional boundaries. However, as many of these management processes currently stand, spatial definitions are an important consideration in ecosystem-based management. In our analyses, we used ecological production units (EPU) and the NES as spatial definitions, as these are used for reporting ecosystem information relative to fishery management objectives to the New England and mid-Atlantic Fishery Management Councils (see NEFSC, 2022; SOE), and indicators can be developed using VAST according to a range of spatial definitions. For example, ecological indicators can be developed according to single-species stock areas to provide context and improve the quality of advice (Skern-Mauritzen *et al.*, 2016). Spatio-temporal modelling can also be used to develop multiple species and ecosystem indicators that can be used to quantify the impact of other ocean-use sectors (e.g. offshore energy) at a spatial scale relevant to decision-makers.

While not formally explored in this analysis, the rapid changes of zooplankton in the Gulf of Maine coincide with changes in the stability and condition of groundfish in the region. These observations may be attributed to changes in source waters in the Gulf of Maine (Gonçalves Neto *et al.*, 2021). In 2019, the Gulf Stream was at its most northern position since 1993, which is associated with warmer ocean temperatures on the northeast U.S. shelf, a higher proportion of warm slope water in the Northeast Channel, and increased sea surface heights along the U.S. east coast (Gonçalves Neto*et al.*, 2021). Concurrently, the Labrador slope water entering the Gulf of Maine has been the lowest since 1978 (Gonçalves Neto *et al.*, 2021), which provides cooler and less saline water at depth. The changing proportions of source waters and their properties affect the temperature, salinity, and nutrient inputs to the ecosystem, impacting zooplankton communities through physiological responses or prey availability (Batchelder *et al.*, 2013).

Our results offer a broader picture of ecological processes underlying indicators than nonspatial analyses commonly used in IEAs. Previous reporting on trophic structure and guild stability using these data, aggregated biomass caught for each guild, suggested no major disturbances to guild stability (NEFSC, 2021, 2022). Diversity metrics used as indicators, including fishery fleet and catch diversity, were reported as stable over time, with current values near the long-term average, but with increasing adult fish diversity in the Gulf of Maine. Auster and Link (2009) found remarkable stability of seven feeding guilds in the NES ecosystem, though the proportion of species represented changed dramatically over the study. Previous condition analyses averaging over space were generally in agreement with our results, finding relatively good condition prior to 2000, followed by a period of generally poor condition from 2001 to 2010, followed by more variable condition until 2019 (NEFSC, 2021). Our results provide species-specific spatial context to these reports. As for zooplankton dynamics in the NES, previous analyses by Morse *et al.* (2017) highlight extensive shifts in zooplankton community dynamics that varied by EPU, and our results zoom into those areas to find hot spots of changing community structures.

Future research could explore multiple avenues to improve spatio-temporal methods for use in IEA. Specifically:

(1) *Quantitative network models*: IEA often begins by defining a conceptual model linking ecosystem components and services. These are often extended by formally specifying a quantitative network model (QNM), representing causal linkages within the conceptual model (Reum, 2015; Holsman *et al.*, 2017). The QNM, in turn, can be represented using a multivariate spatio-temporal model, wherein arrows (describing causal mechanisms) are estimated as parameters governing the covariance in spatio-temporal terms. By doing so, the QNM identifies a small number of parameters that must be estimated to generate a sparse parameterization for covariance in the spatio-temporal model. A similar "structural equation model" has been developed to estimate parameters in a multi-causal evolutionary context (Thorson *et al.*, 2023), so we are hopeful that developing a spatial QNM is a realistic goal (in terms of reasonable precision and runtimes). Combining QNMs and spatio-temporal models would allow relationships among ecosystem components to be explicitly specified and estimated.

(2) *Subarea thresholds*: Ongoing research seeks to define thresholds (targets or limits) for comparison with value of indicators within an IEA. In some cases, these thresholds can easily be developed for subareas, e.g. system-level yield (Link and Watson, 2019) and community size spectra (Daan *et al.*, 2005) can be calculated easily for an entire region or subareas of interest. Spatio-temporal methods automatically allow indicators to be developed for subareas, so we see corresponding value in developing thresholds for subareas, e.g. to understand ecosystem status for individual states, tribes, or marine sanctuaries.

Here we provide a demonstration of the potential benefits of spatio-temporal methods for IEA, and we hope this study motivates additional research to evaluate performance of spatio-temporal indicators. As climate change, anthropogenic stressors, and natural fluctuations induce broad and local-scale effects that vary in space and time, expanding and implementing spatio-temporal methods will allow us to most effectively monitor ecosystem components and evaluate trade-offs between ocean-use sectors.

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Supplementary material

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Author contributions

JJB, SIL, and JTT all contributed to the conceptualization of the study. JJB lead the analysis with substantial guidance from JTT (statistical methodology) and SIL (system expertise). Manuscript drafting was a fully collaborative effort, with sections contributed from all three authors.

Conflicts of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in the article.

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Data availability

Data used in the analysis of this manuscript can be accessed through the GitHub repository: https://github.com/jjbadger/SpatiotemporalIndicators.

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