

Identification of ecological structure and species relationships along an oceanographic gradient in the Gulf of Maine using multivariate analysis with bootstrapping

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Abstract: Ecosystem-based fisheries management requires a fundamental understanding of ecosystem boundaries and interspecies interactions. We report a delineation of fish and invertebrate data collected by trawl survey along the Maine, USA, coast. Principal components analysis (PCA) reduced the multidimensionality of the data and created new variables from correlations among species. Bootstrapped PCA was employed to assess PCA structure using eigenvalue variation and species associations using eigenvector variation. A general linear model related structure of fish community identified in PCA to depth, temperature, longitude, and interactions among these variables. Generally, alongshore and onshore–offshore assemblage patterns related to oceanographic gradients, with seasonal variation. PCA-created variables act as indicators of biodiversity and are related to the scale of observation, allowing for multiple scales to be integrated if data are available. Species targeted and gear used along with spatial extent and sampling density must be considered when management zonation is to be undertaken but would allow boundaries to follow biological and physical gradients rather than relying on the typical political and economic variables, avoiding ecologically deleterious spatial patterns in fishing pressure or other instances of *de facto* zoning. Regardless, this study describes some contributing factors causing division of species assemblages that should be considered.

Résumé : La gestion des pêches basée sur les écosystèmes nécessite une compréhension fondamentale des frontières entre les écosystèmes et des interactions entre les espèces. Nous présentons une délimitation des données sur les poissons et les invertébrés récoltés par inventaire au chalut le long de la côte du Maine, É.-U. Une analyse des composantes principales (PCA) a réduit la nature multidimensionnelle des données et a créé de nouvelles variables à partir des corrélations entre les espèces. Une PCA avec bootstrap a servi à estimer la structure de la PCA, ainsi que les associations d'espèces, d'après la variation des valeurs propres. Un modèle linéaire général a relié la structure de la communauté de poissons identifiée dans la PCA à la profondeur, à la température, à la longitude et aux interactions entre ces variables. En général, les patrons de regroupements le long de la côte et entre la côte et le large sont associés à des gradients océaniques avec une variation saisonnière. Les variables créées par la PCA servent d'indicateurs de la biodiversité et sont reliées à l'échelle d'observation, ce qui permet l'intégration de plusieurs échelles lorsque les données sont suffisantes. Il est nécessaire de tenir compte des espèces ciblées et des engins de pêche utilisés, de même que de l'étendue spatiale et de la densité d'échantillonnage, afin d'entreprendre un zonage de gestion; celui-ci doit permettre aux frontières de suivre les gradients biologiques et physiques plutôt que de se baser sur les variables politiques et économiques habituelles; ainsi, il est possible d'éviter les effets spatiaux néfastes de la pression de pêche et des autres circonstances du zonage *de facto*. Néanmoins, notre étude décrit certains facteurs à considérer qui contribuent à la division des regroupements d'espèces.

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Introduction

Biodiversity is a structural characteristic describing ecosystems that provides information on the state (Slocombe 1998) as well as the adaptive capacity and robustness of the ecosystem to external impacts including anthropogenic ac-

tivities and climate change (Levin and Lubchenco 2008). Detailing biodiversity with a spatial perspective and translating the results into a framework that allows for spatially specific management of human actions within ecological systems at the appropriate scale will minimize unintended deleterious impacts on ecosystem function (see Berkes et al.

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2006; Crowder et al. 2006). Commercial and recreational fishing as well as other anthropogenic disturbances such as aquaculture, oil and gas extraction/production, wind farms, and coastal development tend to cluster spatially by stakeholder preference for certain oceanographic conditions, benthic habitats, and location relative to human development (see Crowder et al. 2006). Thus, application of single-species and site-by-site management techniques has allowed *de facto* zoning, where political boundaries and stakeholder preferences dictate spatial organization of anthropogenic impacts, to be the rule. Comprehensive planning using spatial trends in biodiversity and abundance of species will help curtail *de facto* zoning whose case-by-case style of management results in spatially fragmented conservation efforts (Crowder et al. 2006). Such is the case when marine reserves shift fishing effort (Hilborn 2003) onto other fishing grounds that are important habitat (Hinrichsen et al. 2009; Suuronen et al. 2010). By considering spatial structure in species assemblages, we propose proxies for biodiversity as indicators in the application of zoning within ecosystem-based management strategies.

For fisheries management purposes, Northeastern US stocks are divided into two populations: one occupying shallow, productive, glacially derived Georges Bank and another the sheltered, but deeper, Gulf of Maine (Fig. 1). This simply recognizes the fundamental divergent physical and biological properties of the two environments and the resulting productivity differences between them (see Townsend et al. 2006). While ecosystem structure is often delineated along boundaries produced by gradients in the physical environment (Strayer et al. 2003), the designation ignored structure of organisms occurring at a larger scale (Frisk et al. 2008) and finer scale (Ames 2004), often with negative consequences such as extirpation of unrecognized subpopulations (see Ames 2004). Historic cod metapopulation dynamics along the coastal waters of the Gulf of Maine (Ames 2004) and an oceanographic gradient created by a coastal current system (Pettigrew et al. 2005; Townsend et al. 2006) both demonstrate the presence of finer-scale, biologically relevant gradients within the Gulf of Maine that were not recognized until recently. Ecosystem-based management policies support structuring basic units of management along ecological gradients as opposed to political ones (US Commission on Ocean Policy 2004), hence matching the spatial scales of management and ecological processes.

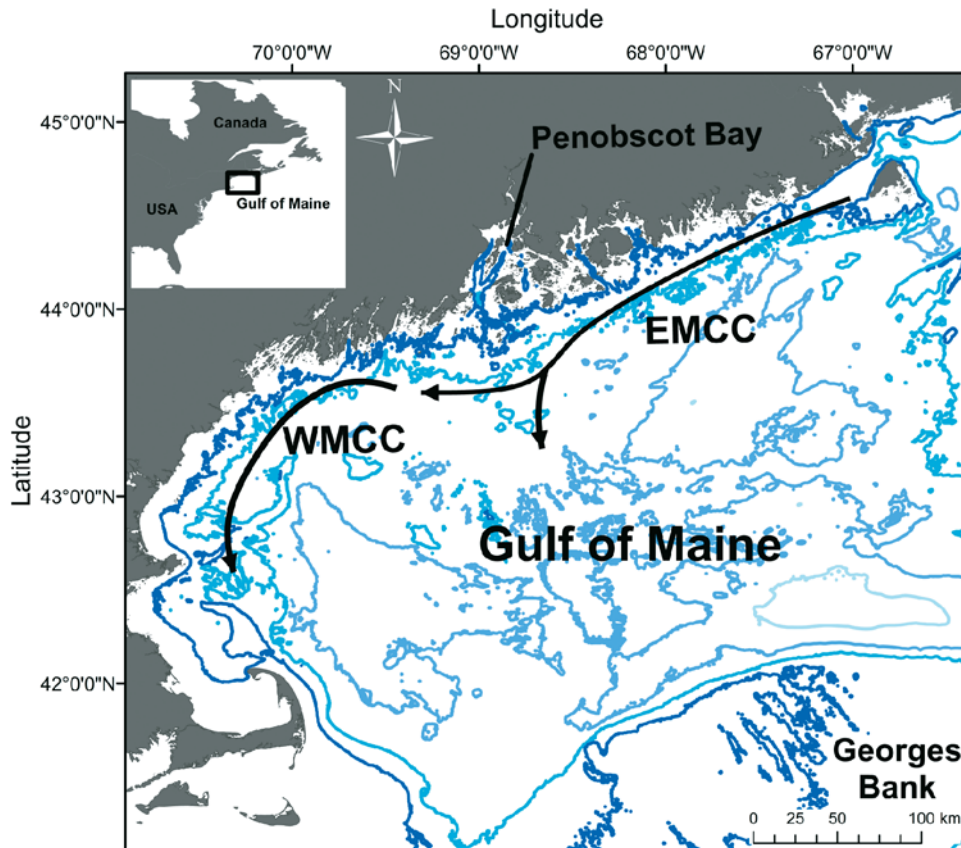
There has been substantial effort to classify areas of the ocean based on a variety of characteristics that consider spatial structure of biodiversity in support of geographically based management. First attempts used ordination techniques to demonstrate persistent biological structure along environmental discontinuities on the Northwest Atlantic continental shelf using trawl survey data (Overholtz and Tyler 1985; Gabriel 1992; Mahon et al. 1998). While the assemblage designations of Mahon et al. (1998) have been generally supported (Jørgensen et al. 2005), one valid critique of these techniques is the subjectivity with which cut-offs in eigenvalues and eigenvectors were made (Souissi et al. 2001). Bootstrapped and standard principal components analysis (PCA_{BTSP} and PCA, respectively) were employed to tackle analysis of a multivariable ecological data sets to address this very deficiency (Jackson 1993; Jackson 1995;

Pillar 1999). Despite criticism for allowing axis reversal among bootstrap runs (Mehlman et al. 1995), PCA_{BTSP}-based techniques have been shown, using both simulated and real data, to outperform other methods in determining the number of nontrivial components (Jackson 1993, 1995; Pillar 1999) and eigenvector loadings (Peres-Neto et al. 2003). As such, the PCA_{BTSP} provides a methodology for determining the cutoff (stopping rule) and determining relationships among species using a probability-based method. This method has significant advantage in that each new variable (principal component) is uncorrelated with others and can be statistically tested against physical variables. This is particularly helpful in dealing with multiple scales within data sets and the multifactor interacting influences of physical variables in determining species' distributions.

Other analyses exist that also have the same general characteristics, such as hierarchical clustering analyses (Souissi et al. 2001; Jørgensen et al. 2005). Jørgensen et al. (2005), for example, examined the fish assemblages of Davis Strait and southern Baffin Bay using two survey trips analyzed by cluster analysis and Bayesian multinomial logit models with assumed probability distribution functions to assign survey trawls to the clusters. Then, assemblages were mapped using a spherical variogram model and a kriging method. However, species in low numbers need to be excluded from the analyses to keep the model stable (Jørgensen et al. 2005). This is not the case with PCA_{BTSP}, which can handle rarer species as long as there are common trends in variation with other species. PCA_{BTSP} will exclude rarer species among bootstrap runs, thereby reducing their impact in determining assemblages probabilistically during evaluation of eigenvectors. Furthermore, PCA_{BTSP} does not depend on distributional assumptions.

Here, we attempt to discern multispecies structure along a small section of coastline within the Gulf of Maine, long assumed to constitute a single ecosystem. The existence of the Eastern and Western Maine Coastal Currents (EMCC and WMCC, respectively) creates strong physical gradients in temperature, salinity, stratification, and productivity. The EMCC is driven by tidal energy and to lesser degree wind stress that vertically mix the water column bringing deeper, nutrient-rich cold water to the surface and lower-salinity, warmer temperature to depth (Pettigrew et al. 2005). The mixed water then flows along the edge of the coastal shelf break as the EMCC (Pettigrew et al. 2005). The greater tidal mixing of the EMCC contrasts the increased stratification of the WMCC's and resulting warmer surface and colder benthos with a division between the two water masses roughly in midcoast Maine at Penobscot Bay (Fig. 1) (Pettigrew et al. 2005; Townsend et al. 2006). As such, a gradient in biodiversity and a discernable pattern in ecosystem structure are expected across the EMCC–WMCC boundary, although such an observation has never been evaluated quantitatively. To test whether fish species display common trends of variation such that biodiversity is structured along physical characteristics of the coastal waters of Maine, which is the objective of this study, a PCA_{BTSP}-based technique is used to characterize relative abundance data obtained from an in-shore trawl survey. Using new variables derived from the PCA, fish assemblages are identified and related to physical

Fig. 1. Gulf of Maine depth contours (50, 100, 200, and 300 m), idealized western and eastern Maine coastal current (WMCC and EMCC, respectively) pathways, and relative location of the region in North America (inset).



variables and plotted as biodiversity maps for use in geographically based management strategies.

Materials and methods

The Maine–New Hampshire inshore trawl survey has been conducted every fall and spring since fall 2000. It has a stratified random design modeled after the National Marine Fisheries Service bottom trawl surveys (Sherman et al. 2005) and includes four depth strata: 9–37, 37–64, 64–100, and >100 m (its outer boundary roughly delineated by the 12 mi. or 22 km limit; Chen et al. 2006). The fourth stratum was added in the spring of 2003. Additionally, five longitudinal strata were added based on oceanographic, geologic, and biological features, resulting in 20 separate strata. To randomize the survey area (~13 720 km²), each stratum is divided into 1 nautical mile (i.e., 1.85 km) sampling grids. A target of 100 stations in each survey results in a sampling density of about one station per 137 km² in comparison with the National Oceanic and Atmospheric Administration National Marine Fisheries Service surveys' one station per 892 km². Number of tows conducted per stratum was apportioned according to its total area.

Survey tows are conducted as consistently as possible in a straight line at 2.5 kn for 20 min duration (range 2.3–2.8 kn over the entire survey of 80–100 tows; tow speeds are adjusted slightly due to tidal currents to keep net fishing properly). The 20 min duration runs from the time the brakes are set on the winches until the brakes are released to start haul-

back. Tows of shorter or longer durations that are deemed representative standardize the numbers of fish caught to 20 min. Tows not deemed representative are rejected and repeated.

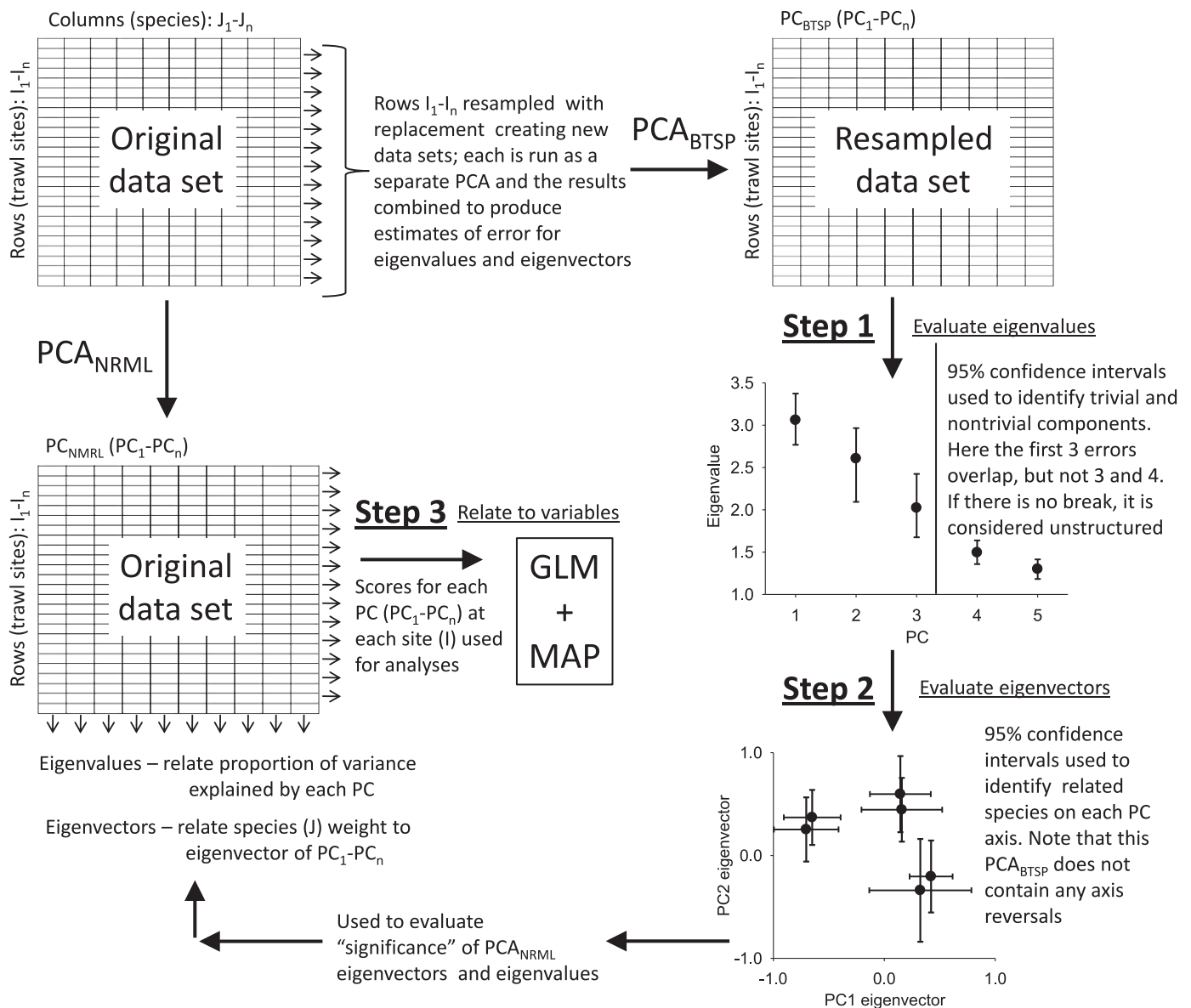
The net is a modified version of the shrimp net design used in Maine waters designed to fish for a variety of near-bottom-dwelling species without targeting any specific species. The net is constructed of 5 cm No. 24 polyethylene mesh with a 2.5 cm (stretched measure) mesh liner in the cod end. The 2003 survey, which we isolated for this analysis, included 101 sites sampled in the spring and 78 in the fall sample period (Sherman et al. 2005).

Principal components analysis with bootstrapping

The data set was divided into three different groups, benthic vertebrates, benthic invertebrates, and pelagic species (both vertebrate and invertebrate), since each represents generally divergent behavioural tendencies related directly to habitat use. Benthic vertebrates are generally more mobile, benthic invertebrates are sessile or slow moving, and pelagic species use the water column as primary habitat. Species that only occurred once in the data set were removed. PCA was applied to each of the three categories. The resultant principal components (PCs) were interpreted with respect to the original data. We used the following three-step procedure (Fig. 2) for analyzing the results of the PCA_{BTSP} and a “normal” PCA (PCA_{NRML}).

Step 1. Evaluate PCA_{BTSP} eigenvalues and establish stopping rules. Derive eigenvalues and confidence intervals and

Fig. 2. Flowchart of PCA used in study. The difference between PCA_{BTSP} and PCA_{NRML} simply revolves around the resampling of rows with replacement, hence developing a measure of variation in the former.



determine which PCs provide a meaningful dissection of the data and which are equivalent to random noise. PCs are judged based on 95% confidence limits (95% CLs). Once the 95% CLs for successive PCs overlap, they are judged to no longer produce a meaningful dissection of the data (Jackson 1993). Only PCs identified as unique for each group (benthic vertebrates, benthic invertebrates, and pelagic species) by the PCA_{BTSP} for both the spring and fall surveys were used in further analysis.

Step 2. Evaluate PCA_{BTSP} eigenvectors and species dependence. Derive distribution of eigenvector scores and evaluate for understanding of species contributing to meaningful components. Determine which species have statistically overlapping distributions and hence are correlated in abundance (i.e., form assemblages). Again, 95% CLs are used to determine overlapping eigenvector scores and hence which (groups of) species are driving the patterns for PCs

identified as relevant in step 1. There has not been adequate work to determine which method of assessing and correcting axis reversals—reflections in bootstrapped PCA is best (Jackson 1995); hence, we do not try to correct for this, but rather acknowledge the phenomena and treat the bimodality of eigenvectors within the analyses and interpretation. The bootstrap eigenvector loading distributions were compared with one another for species with similar distributions using Kolmogorov–Smirnov (KS) two-sample tests (SYSTAT version 10.2) (SYSTAT, Chicago, Illinois). Groupings of fish were designated based on the KS test, which determines statistically whether two sampled frequency distributions are from the same population. Additionally, the two species with each of the highest and lowest component loading scores were compared for trends in species correlations against the full group of species using the mean bootstrapped Pearson correlation coefficients and 95% CLs.

Step 3. Relate to variables and test structure. Relate relevant PC scores at each site to potential independent variables and use spatial data to map biodiversity indices. Once PCs that are relevant are determined (step 1) and the species that drive patterns are identified (step 2), the PC scores calculated for each site are tested against physical data using a general linear model (GLM) and mapped using the ending latitude and longitude. The scores generated in PCA_{NRML} for each site were compared for differences in relation to longitude, depth, and temperature (and interactions) using the GLM analysis. Furthermore, natural neighbor interpolation (Sibson 1981) using ArcMap ArcToolbox spatial analysis software (ESRI, Redlands, California), which interpolates a surface from points, was employed to demonstrate spatial patterns of PC scores. Natural neighbor interpolation is based on the Thiessen polygon network created from the Delaunay triangulation of the data points and uses a weighted average of the neighboring data points to calculate the interpolation point (Sibson 1981).

Steps 1 and 2 use the PCA_{BTSP} technique, while step 3 uses results from PCA_{NRML}, since each bootstrap run resamples (with replacement) the trawl stations. The PCA_{BTSP} was implemented using SAS version 9.1 (SAS Institute Inc., Cary, North Carolina) and 1000 bootstrap runs were completed. The analyses included 29 species of benthic vertebrates (Table 1), 24 species of benthic invertebrates (Table 2), and 10 pelagic species in the spring survey and 11 in the fall (Table 3).

Results

Evaluating eigenvalues and stopping rules (step 1)

The eigenvalues indicate that the first PC of each species group explained 16%–23% of the total variance in the spring survey and 17%–24% in the fall survey (Table 4). The eigenvalue scores were higher for PCA_{BTSP} than for PCA_{NRML} in all but one case (Table 4), although not significantly, since PCA_{NRML} scores were within the PCA_{BTSP} 95% CLs. The analysis of benthic vertebrate data demonstrated that the eigenvalues scores for PC1, PC2, and PC3 were all different from one another and those for PC4 onwards were similar for both the spring and fall surveys. An analysis of the pelagic data identified PC1 and PC2 as unique eigenvalues. Neither benthic invertebrate data set (spring or fall) provided unique values, suggesting a lack of structure in the data. As a result, benthic invertebrates were not considered further in the results.

Evaluating eigenvectors and species correlations (step 2)

Eigenvectors generated by PCA_{BTSP} and PCA_{NRML} demonstrated agreement in the division of species, but with dampened PCA_{BTSP} values compared with PCA_{NRML}-generated loadings (Figs. 3, 4, 5, and 6). Component eigenvector loadings alternated between negative and positive scores in different bootstrap runs; however, where individual species toggle between positive and negative eigenvectors in different bootstrap runs, the distances (vector) among species are conserved (Jackson 1993, 1995; Mehlman et al. 1995). The flip-flop highlights the arbitrary nature of assigning positive and negative values, also demonstrated by two other examples. First, for benthic vertebrates in the fall sample period,

Table 1. Species list for the benthic vertebrate group.

Species	Common name
<i>Aspidophoroides monopterygius</i>	Alligatorfish
<i>Cryptacanthodes maculatus</i>	Wrymouth
<i>Cyclopterus lumpus</i>	Lumpfish
<i>Enchelyopus cimbrius</i>	Fourbeard rockling
<i>Gadus morhua</i>	Atlantic cod
<i>Glyptocephalus cynoglossus</i>	Witch flounder
<i>Hemitripterus americanus</i>	Sea raven
<i>Hippoglossus hippoglossus</i>	Atlantic halibut
<i>Hippoglossoides platessoides</i>	American plaice
<i>Limanda ferruginea</i>	Yellowtail flounder
<i>Lophius americanus</i>	Goosefish/monkfish
<i>Lumpenus lumpretaeformis</i>	Snakeblenny
<i>Macrozoarces americanus</i>	Ocean pout
<i>Melanogrammus aeglefinus</i>	Haddock
<i>Merluccius bilinearis</i>	Silver hake
<i>Myoxocephalus octodecemspinosus</i>	Longhorn sculpin
<i>Myoxocephalus scorpius</i>	Shorthorn sculpin
<i>Paralichthys oblongus</i>	Fourspot flounder
<i>Pollachius virens</i>	Pollock
<i>Pseudopleuronectes americanus</i>	Winter flounder
<i>Raja erinacea</i>	Little skate
<i>Raja radiata</i>	Thorny skate
<i>Raja senta</i>	Smooth skate
<i>Reinhardtius hippoglossoides</i>	Greenland halibut
<i>Scophthalmus aquosus</i>	Windowpane flounder
<i>Sebastes fasciatus</i>	Acadian redfish
<i>Tautoglabrus adspersus</i>	Cunner
<i>Urophycis chuss</i>	Red hake
<i>Urophycis tenuis</i>	White hake

PCA_{NRML} scores were opposite to scores given by PCA_{BTSP} but identified the same pattern in species loadings (Fig. 6). Second, PCA_{NRML} has opposite eigenvector loadings in the spring (Fig. 4) and fall (Fig. 6) as evidenced by the species *Lophius americanus*.

In the spring sampling, patterns in pelagic species were generally driven by positive loadings (Fig. 3a) among the highly correlated (Fig. 3b) *Alosa aestivalis*, *Alosa pseudoharengus*, and *Clupea harengus*, although the species were not identified as similar KS groups (KS test determined groupings, center of Fig. 3). The particularly strong agreement among the species with positive loadings was weaker with *Osmerus mordax* and *Alosa sapidissima*. The negative loading species *Euphausid* spp. and *Mauroliscus muelleri* had little correlation with one another (Fig. 3b).

The spring sampled benthic vertebrate eigenvector loadings were strongly driven by the species group of *Lophius americanus*, *Sebastes fasciatus*, and *Hippoglossoides platessoides* and to a lesser degree the other species that are correlated (Fig. 4). Weak correlation coefficients amongst these species did not impact the KS groupings (Fig. 4b). KS group A were often more highly correlated (correlation coefficient > 0.5) with species with lesser eigenvectors such as *Lophius americanus* and *Merluccius bilinearis* (Fig. 4b). *Myoxocephalus scorpius* had a correlation coefficient $-1 <$ correlation coefficient < 1 with large error bars (Fig. 4b), which results from being sampled inconsistently among bootstrap runs. If a species, by not being contained in the

Table 2. Species list for the benthic invertebrate group.

Species	Common name
<i>Arctica islandica</i>	Ocean quahog
<i>Astarte undata</i>	Waved astarte
<i>Cancer borealis</i>	Jonah crab
<i>Cancer irroratus</i>	Rock crab
<i>Caudina arenata</i>	Rat-tail cucumber
Cephalopoda spp.	Octopus (unclassified)
<i>Chionectes opilio</i>	Snow crab
<i>Crangon septemspinosa</i>	Sevenspine Bay shrimp, sandshrimp
<i>Cucumaria frondosa</i>	Sea cucumber
<i>Dichelopandalus leptocerus</i>	Bristled longbeak
Echinoidae sp.	Sand dollar
<i>Geryon quinquedens</i>	Red crab
<i>Homarus americanus</i>	American lobster
<i>Hyas araneus</i>	Toad crab
<i>Lithodes</i> sp.	Northern stone crab
<i>Mytilus edulis</i>	Blue mussel
<i>Pandalus borealis</i>	Northern shrimp
<i>Pandalus montagui</i>	Aesop shrimp
<i>Pasiphaea multidentata</i>	Pink glass shrimp
<i>Placopecten magellanicus</i>	Sea scallop
Stomatopod sp.	Mantis shrimp
<i>Stronglyocentrotus droebachiensis</i>	Sea urchin
<i>Venercardia borealis</i>	Northern cardita
<i>Yoldia thraciaeformis</i>	Ax head clam

Table 3. Species list for the pelagic group.

Species	Common name
<i>Alosa aestivalis</i>	Blueback herring
<i>Alosa pseudoharengus</i>	Alewife
<i>Alosa sapidissima</i>	American shad
<i>Brevoortia tyrannus</i>	Atlantic menhaden
<i>Clupea harengus</i>	Atlantic herring
Euphausiid spp.	Krill
<i>Loligo pealei</i>	Longfin squid
<i>Maurollicus muelleri</i>	Pearlsides
<i>Osmerus mordax</i>	Rainbow smelt
<i>Scomber scombrus</i>	Atlantic mackerel
<i>Squalus acanthias</i>	Spiny dogfish

bootstrap subsample, receives a coefficient of 0 when excluded in bootstrap runs, 95%CL error bars will relate the frequency of absence. This is also reflected in eigenvector frequencies (Fig. 4a).

In the analysis of pelagic species from the fall sampling, using PCA_{NRML} separated *Osmerus mordax* and *Brevoortia tyrannus* from each other and the rest of the species, although they maintain high correlations with *Clupea harengus* and *Alosa pseudoharengus* (Fig. 5b). The species with the most negative eigenvectors, *Squalus acanthias* and *Maurollicus muelleri*, had only a weak relationship with each other, and *Maurollicus muelleri* had a number of 0 scores, indicating infrequency in capture (Fig. 5a), and in fact was only captured in two tows. There was significant variation in eigenvector loadings, with most species showing

uniform or wide distributions, with the uniformly distributed species grouping together in KS tests (Fig. 5).

The PCA_{BTSP} of fall-sampled benthic vertebrate species demonstrates a more polarized pattern with negative and positive eigenvectors (Fig. 6a). Furthermore, both positive and negative species sets show significant correlations with one another and negative correlations with species of the opposing sign (Fig. 6b). A bimodal distribution in eigenvector loadings, due to axis reversals, occurs (Fig. 6a), but the magnitude of vectors among species is conserved (Jordaan 2006). The species group *Lophius americanus*, *Glyptocephalus cynoglossus*, *Hippoglossoides platessoides*, *Enchelyopus cimbrius*, and *Urophycis chuss* are all highly correlated with one another and negatively correlated with the group consisting of *Pseudopleuronectes americanus*, *Myoxocephalus octodecemspinosus*, *Raja erinacea*, and *Scophthalmus aquosus* (Fig. 6).

Relate to variables, spatial biological structure, and physical correlates (step 3)

The results of the GLM demonstrate that there were differences in the structure of the data sets associated with longitude, temperature, depth, and their interactions. For the spring pelagics, PC1 produced a significant model with longitude, depth, and the depth–longitude interaction all significant factors and with temperature and all other interactions not significant (Table 5). For the spring pelagics, PC2 also produced a significant model with all factors and interactions significantly contributing to the model, except for temperature and the temperature–longitude interaction (Table 5). For the spring benthic vertebrates, PC1 produced a significant model with longitude, temperature, and the temperature–longitude interaction as significant contributors to the model with depth and all other interactions not significant (Table 5). PC2 and PC3 produced a significant model but with no significant contributory factors (Table 5).

For the fall benthic vertebrates, PC1 produced a significant model; only longitude was near significance (Table 6). By removing all depth-associated factors (none had $P < 0.68$), the model remains significant ($F_{[3,66]} = 28.6$, $P < 0.001$, $r^2 = 0.55$) with longitude ($T = -3.1$, $P = 0.003$), temperature ($T = -2.6$, $P = 0.013$), and the temperature–longitude interaction ($T = 2.7$, $P = 0.01$) as significant factors. The benthic vertebrate PC2 was also significantly explained by the model (Table 6). Only the depth–temperature interaction and longitude–depth–temperature interactions (Table 6) were significant, but depth and the longitude–depth interaction were marginal. Depth and the longitude–depth interaction were significant for the PC3 benthic vertebrate GLM (Table 6). The GLM for the pelagic PC1 analysis produced a significant model ($F_{[7,66]} = 20.0$, $P < 0.001$, $r^2 = 0.68$) with all factors and interactions being significant ($P < 0.001$).

The spatial distribution of species assemblages, using the scores for each site generated by PCA_{NRML}, suggests a complex mosaic with general onshore–offshore and east–west gradients (Figs. 7, 8, 9, and 10). The spring pelagic species PC1 follows a general onshore–offshore gradient and has similar assemblages in eastern and western Maine, with separation in the Penobscot region (Fig. 7a). PC2 also demonstrates an onshore–offshore gradient and some east–west

Table 4. Eigenvalues (EV) and percent explained variance (%) for the first three PCs generated for the three species groupings benthic vertebrates (VERT), benthic invertebrates (INV), and pelagic species (PEL) for the spring and fall surveys.

		Spring						Fall					
		PC1		PC2		PC3		PC1		PC2		PC3	
		EV	%	EV	%	EV	%	EV	%	EV	%	EV	%
PCA _{NRML}	VERT	4.7	16	3.2	11	2.3	8	5.5	19	3.3	11	2.7	9
	INV	4.3	18	2.9	12	2.5	11	4.2	17	3.0	12	2.5	10
	PEL	2.3	23	1.6	16	1.2	12	2.7	24	2.2	20	1.3	12
PCA _{BTSP}	VERT	5.1	18	3.4	12	2.5	9	5.9	20	3.6	12	2.8	10
	INV	4.5	19	3.0	12	2.3	10	4.5	19	3.2	13	2.5	10
	PEL	2.4	24	1.7	17	1.2	12	2.9	26	2.2	20	1.4	12

Note: Both the SYSTAT generated and SAS bootstrap generated values are given.

Fig. 3. (a) Species eigenvectors and (b) Pearson correlation coefficients for spring pelagic species generated by PCA_{BTSP} for PC1 only. The species list located in the middle is ordered by increasing loading frequencies. The loading calculated by PCA_{NRML} and grouping based on KS tests of eigenvector probability frequency distributions are also given (U, unique distribution; letters indicate like distributions). Pearson correlation coefficients include mean and standard deviation for two species at the top and bottom of the list; see legend for species and symbols.

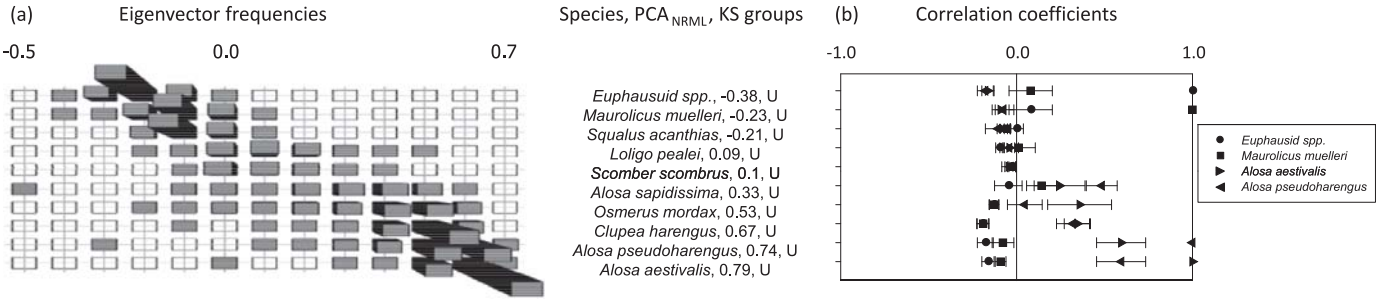


Fig. 4. (a) Species eigenvectors and (b) Pearson correlation coefficients for spring benthic vertebrate species generated by PCA_{BTSP} for PC1 only. The species list located in the middle is ordered by increasing loading frequencies. The loading calculated by PCA_{NRML} and grouping based on KS tests of eigenvector probability frequency distributions are also given (U, unique distribution; letters indicate like distributions). Pearson correlation coefficients include mean and standard deviation for two species at the top and bottom of the list; see legend for species and symbols.

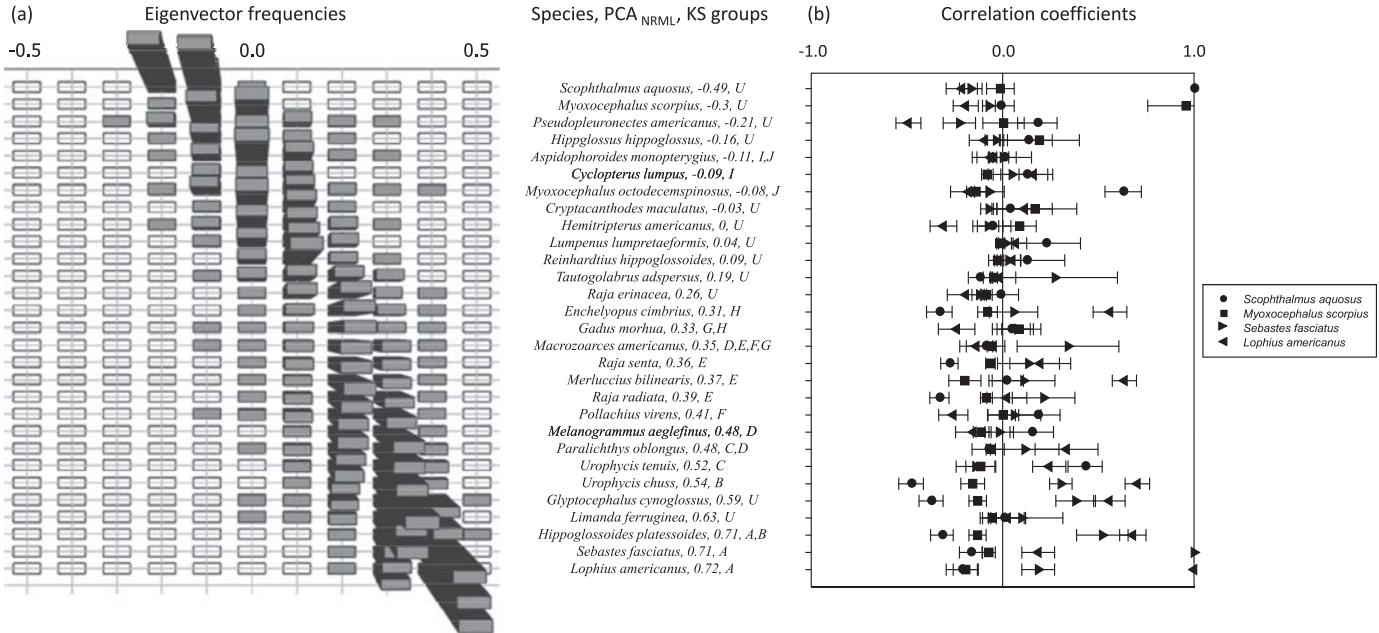


Fig. 5. (a) Species eigenvectors and (b) Pearson correlation coefficients for fall pelagic species generated by PCA_{BTSP} for PC1 only. The species list located in the middle is ordered by increasing loading frequencies. The loading calculated by PCA_{NRML} and grouping based on KS tests of eigenvector probability frequency distributions are also given (U, unique distribution; letters indicate like distributions). Pearson correlation coefficients include mean and standard deviation for two species at the top and bottom of the list; see legend for species and symbols.

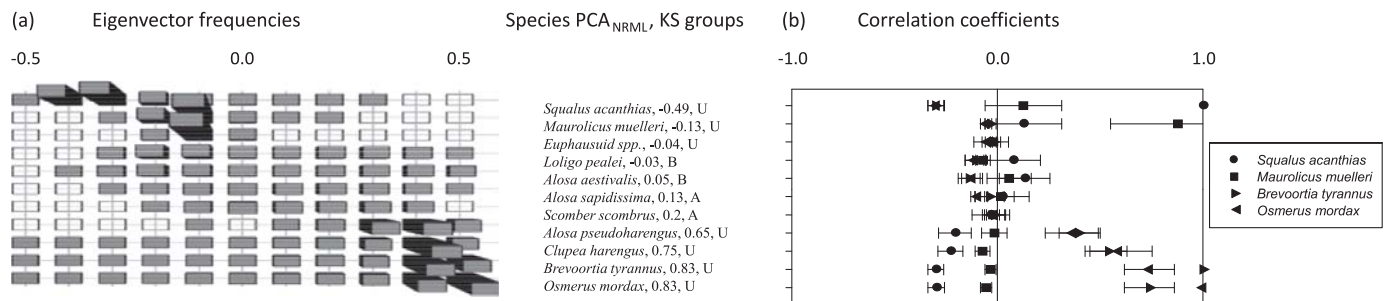
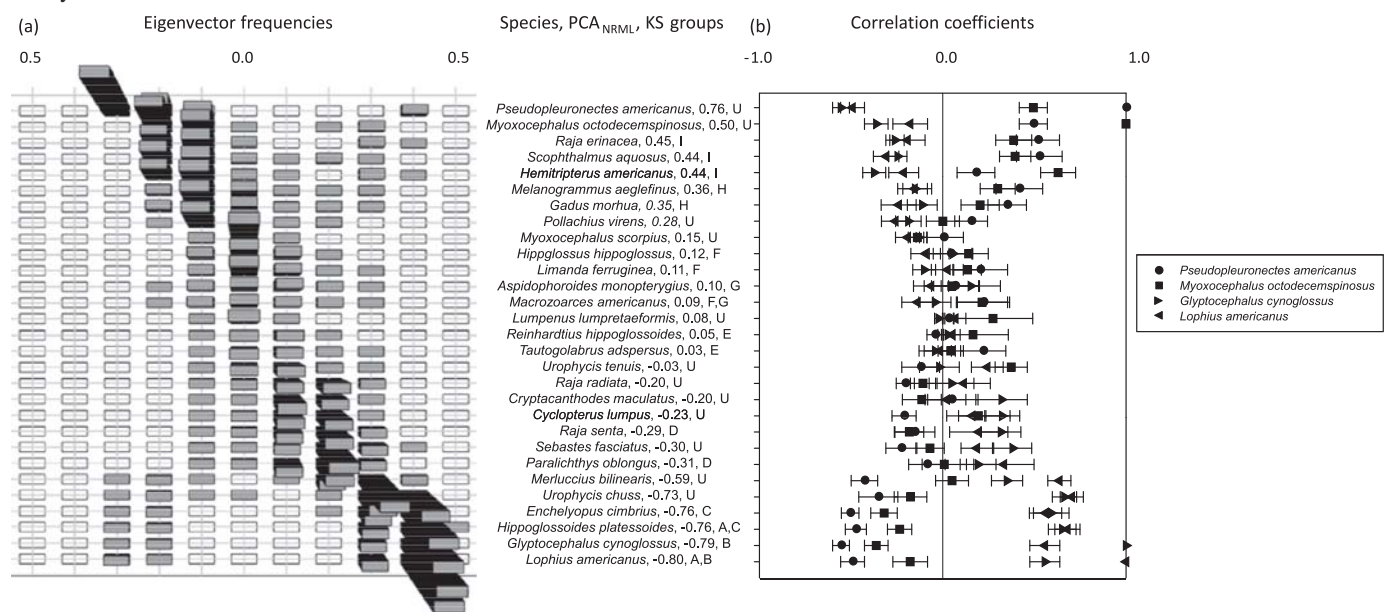


Fig. 6. (a) Species eigenvectors and (b) Pearson correlation coefficients for fall benthic vertebrate species generated by PCA_{BTSP} for PC1 only. The species list located in the middle is ordered by increasing loading frequencies. The loading calculated by PCA_{NRML} and grouping based on KS tests of eigenvector probability frequency distributions are also given (U, unique distribution; letters indicate like distributions). Pearson correlation coefficients include mean and standard deviation for two species at the top and bottom of the list; see legend for species and symbols.



similarity (Fig. 7b). The spatial distribution of spring benthic vertebrate scores demonstrates a primary onshore–offshore and east–west gradient (Fig. 8a). PC2 and PC3 each contrast an area in the eastern survey region with patches of habitat throughout the rest of the survey area (Figs. 8b and 8c).

The spatial distribution of the fall pelagic species suggests a divergence in the assemblages of eastern and western Maine across the Penobscot region boundary with the maintenance of some similarities within the coastal zone in PC1 (Fig. 9a). PC1 and PC2 appear to represent the east and west coastline, respectively (Fig. 9). The spatial distribution of fall benthic vertebrate scores demonstrates a general onshore–offshore and east–west gradient as well as some uniqueness about the Penobscot region (Fig. 10a). PC1 contrasts a coastal and offshore plume in the east that becomes coastally bound in the west, with an offshore region in the west. PC2 contrasts the far eastern and western areas with

the center of the survey region (Fig. 10b). PC3 demonstrates an onshore–offshore gradient focused along the eastern Maine coast (Fig. 10c).

Discussion

This study presents a previously unidentified division of species assemblages along a regional oceanographic gradient within the inshore Gulf of Maine. Individual and sets of species are organized in a nonuniform manner across a physical environment resulting in concordance between biological structuring and physical gradients. This provides an opportunity to account for trends in biodiversity in developing area-based management strategies.

Oceanographic processes associated with two water masses, the WMCC and EMCC, along coastal Maine exert primary control over ecological patterns, demonstrated by

Table 5. Spring 2003 general linear model results for each relevant PC for benthic vertebrates and pelagic species and the associated df, *F* ratio, *p* value, and *r*² for each test.

	Benthic vertebrates			Pelagic species	
	PC1	PC2	PC3	PC1	PC2
df	100	100	100	100	100
<i>F</i>	29.9	3.92	13.10	11.78	3.38
<i>p</i>	<0.0001	0.0009	<0.0001	<0.0001	0.0029
<i>r</i> ²	0.69	0.23	0.49	0.49	0.20
Longitude	0.0035	0.4782	0.5515	0.0277	0.0163
Temperature	0.0153	0.7963	0.6733	0.0997	0.0698
Depth	0.9766	0.6975	0.3112	0.0363	0.0061
Longitude × temperature	0.0158	0.8030	0.6917	0.0998	0.0702
Longitude × depth	0.9545	0.7040	0.3338	0.0350	0.0064
Temperature × depth	0.9919	0.7895	0.9968	0.1111	0.0328
Longitude × depth × temperature	0.9905	0.7727	0.9766	0.1148	0.0343

Note: The independent variables and *p* values with bolded values significant at the $\alpha < 0.05$ value are listed.

Table 6. Fall 2003 general linear model results for each relevant PC for benthic vertebrates and pelagic species and the associated df, *F* ratio, *p* value, and *r*² for each test.

	Benthic vertebrates			Pelagic species	
	PC1	PC2	PC3	PC1	PC2
df	73	73	73	73	73
<i>F</i>	23.91	3.82	6.87	20.03	14.92
<i>p</i>	<0.0001	0.0015	<0.0001	<0.0001	<0.0001
<i>r</i> ²	0.72	0.29	0.42	0.68	0.61
Longitude	0.0807	0.6182	0.1418	<0.0001	0.8019
Temperature	0.7475	0.0720	0.0300	0.0003	0.2931
Depth	0.1491	0.2651	0.1586	<0.0001	0.0663
Longitude × temperature	0.1425	0.2765	0.1693	<0.0001	0.0726
Longitude × depth	0.7581	0.0709	0.0333	0.0003	0.3064
Temperature × depth	0.6918	0.0162	0.0622	0.0002	0.0716
Longitude × depth × temperature	0.6897	0.0154	0.0704	0.0003	0.0738

Note: The independent variables and *p* values with bolded values significant at the $\alpha < 0.05$ value are listed.

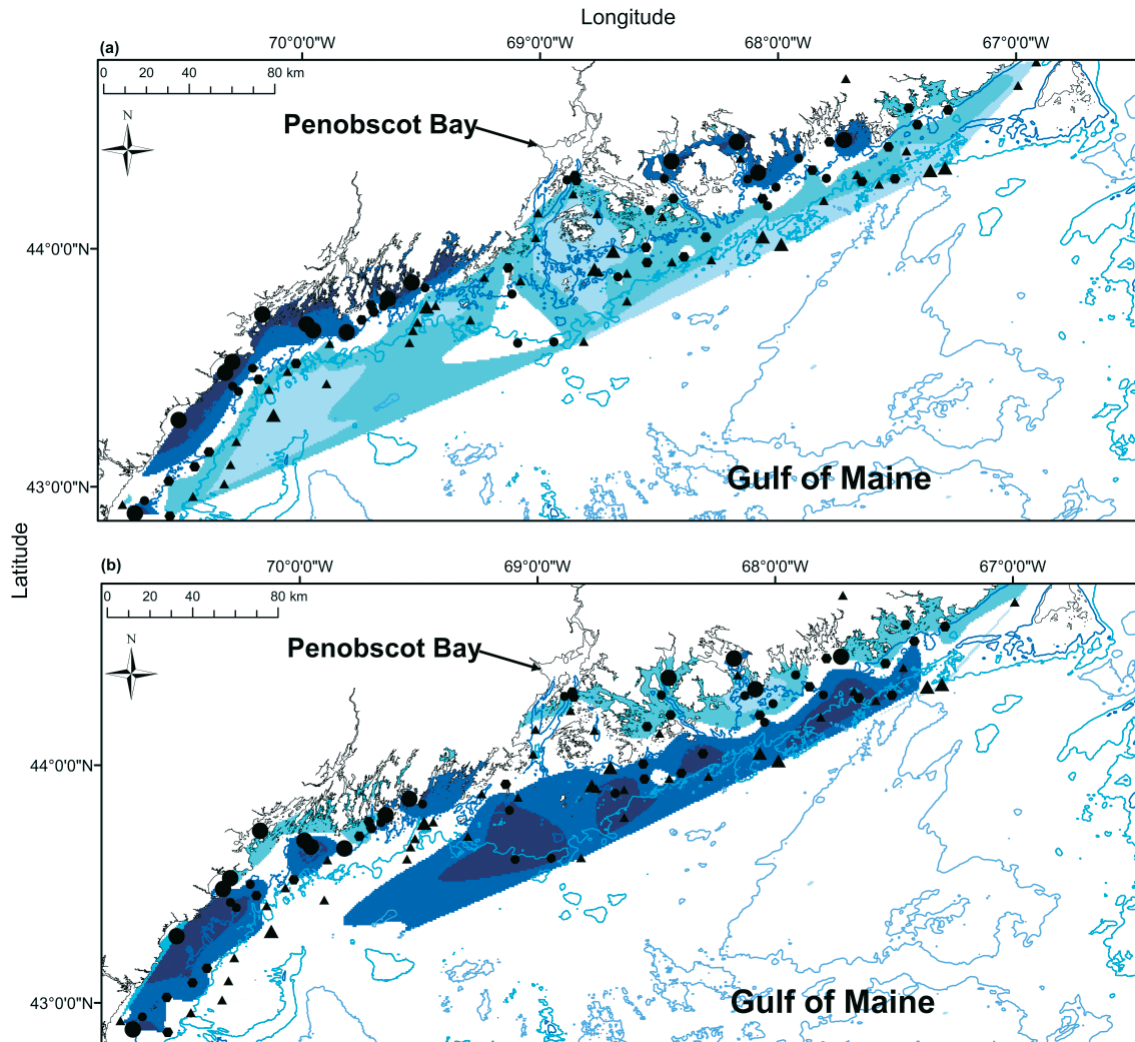
the consistency with which temperature, longitude, and their interaction were significant in the GLM analyses. Water temperatures are highly correlated with species abundances and fluctuation in fisheries landings regionally along the Maine coast (Dow 1981) and locally influence fish presence and absence in Maine tidal coves and embayments (Targett and McCleave 1974; Jordaan 2010). Thermal tolerance of a species, particularly during planktonic early life stages, is a critical component in development, growth, and survival (Jordaan and Kling 2003). It is not clear what component(s) of the water mass accounts for differences in the species assemblage structure, in particular because of large numbers of interacting variables. For example, cooler bottom temperatures occur beneath the vertically stratified WMCC, as opposed to warmer bottom water in the EMCC where the tidal currents effectively mix heating from solar energy throughout the water column and nutrients from depth to the surface (Townsend 1991). Differences in dissolved inorganic nutrient loads between the two coastal current systems, being highest in the east, result in lower overall primary productivity with a greater fraction of that productivity being recycled in the WMCC (Townsend 1991). Productivity varies substantially along the northeast US continental shelf due to variation in physical forces and inputs from different water

masses; continental shelf waters of southern New England and Georges Bank generally have higher primary productivity than Gulf of Maine waters and substantial differences exist along the Gulf of Maine coastline (Townsend et al. 2006). Thus, it is not surprising that bottom-up processes driving recruitment of New England groundfish stocks also appear to differ by region (Brodziak et al. 2001).

Because fish assemblages are related to temperature, it will be important to consider decadal cycles in coupled ocean–atmosphere systems. The North Atlantic Oscillation (NAO), which is related to anthropogenic-driven climate change (Hoerling et al. 2001), influences the makeup of source waters entering the Gulf of Maine with low NAO years correlated with colder, fresher, and nutrient-depleted water compared with warmer, high-nutrient waters during positive NAO events (Thomas et al. 2003; Townsend et al. 2006; Townsend and Ellis 2010). Thus, shifts due to climate and NAO impacts are expected through changes in sources waters and their related physical properties.

Species assemblage structure shifted from a temperature–depth–longitude-based relationship during spring to a temperature–longitude-related ecological pattern in the fall. Seasonal shifts are not uncommon, for example, Georges Bank cod and haddock tend to occupy shifting temperature and

Fig. 7. Spring pelagic species biodiversity maps from (a) PC1 and (b) PC2 scores. Symbols represent PC scores classified into five categories from negative scores (triangles) to positive scores (circles) with larger symbols indicating larger absolute values. Contour plots are results of natural neighbor interpolation reflecting the spatial variation in scores with dark shading representing positive scores and light shading negative scores. Neutral scores are given by hexagons and lack of any shading.



depth preferences while maintaining preference for coarse sand or gravel bottom sediments (Sundermeyer et al. 2005) or by remaining within temperature ranges from winter through summer by altering depth, as shown for haddock (Perry and Smith 1994). As a result, many species movement patterns and observed distributions may demonstrate a relationship among depth, temperature, and season (Methratta and Link 2007). Discordance among species between spring and fall surveys (see cod and haddock, Table 7) may be due to seasonal shifts of habitat choice. It is precisely these relationships that become important in designing a geographically based management scheme.

While some species showed shifts, others did not. Both spring and fall structure of benthic vertebrates was strongly driven by monkfish, with this monkfish species group distribution matching that of monkfish caught by the shrimp survey in the Gulf of Maine (Northeast Data Poor Stocks Working Group 2007). During the spring survey, there were two pockets of the monkfish species group located in the deeper basins along with Acadian redfish, a deepwater fish

found inshore in colder months (Collette and Klein-MacPhee 2002), as a correlated species. The monkfish group contrasted a coastal species group with a spatial distribution that resembles the trajectory of the eastern Maine coastal current (see Pettigrew et al. 2005). The fall survey demonstrates reinforcement of the pattern seen in the spring with a larger number of species, including American plaice, witch flounder, fourbeard rockling, and red hake, becoming significantly correlated with monkfish. The strength of species–species relationships implies a connection to the seasonal pattern in the coastal currents and robustness of structure in communities around them. Secondly, over this mesoscale structure is a mosaic of habitats that appear to be important in the structuring of fish populations with a uniqueness of areas near the Bay of Fundy (benthics) and the mouth of the Penobscot River (pelagics). Historically and presently, the coastal Maine fishery focuses effort on a select few species, of which a number figured prominently in the results, including monkfish, redfish, gadids, flatfish, herring, and alewife (Table 7). While pelagic species are not caught with

Fig. 8. Spring benthic vertebrate species biodiversity maps from (a) PC1, (b) PC2, and (c) PC3 scores. Symbols represent PC scores classified into five categories from negative scores (triangles) to positive scores (circles) with larger symbols indicating larger absolute values. Contour plots are results of natural neighbor interpolation reflecting the spatial variation in scores with dark shading representing positive scores and light shading negative scores. Neutral scores are given by hexagons and lack of any shading.

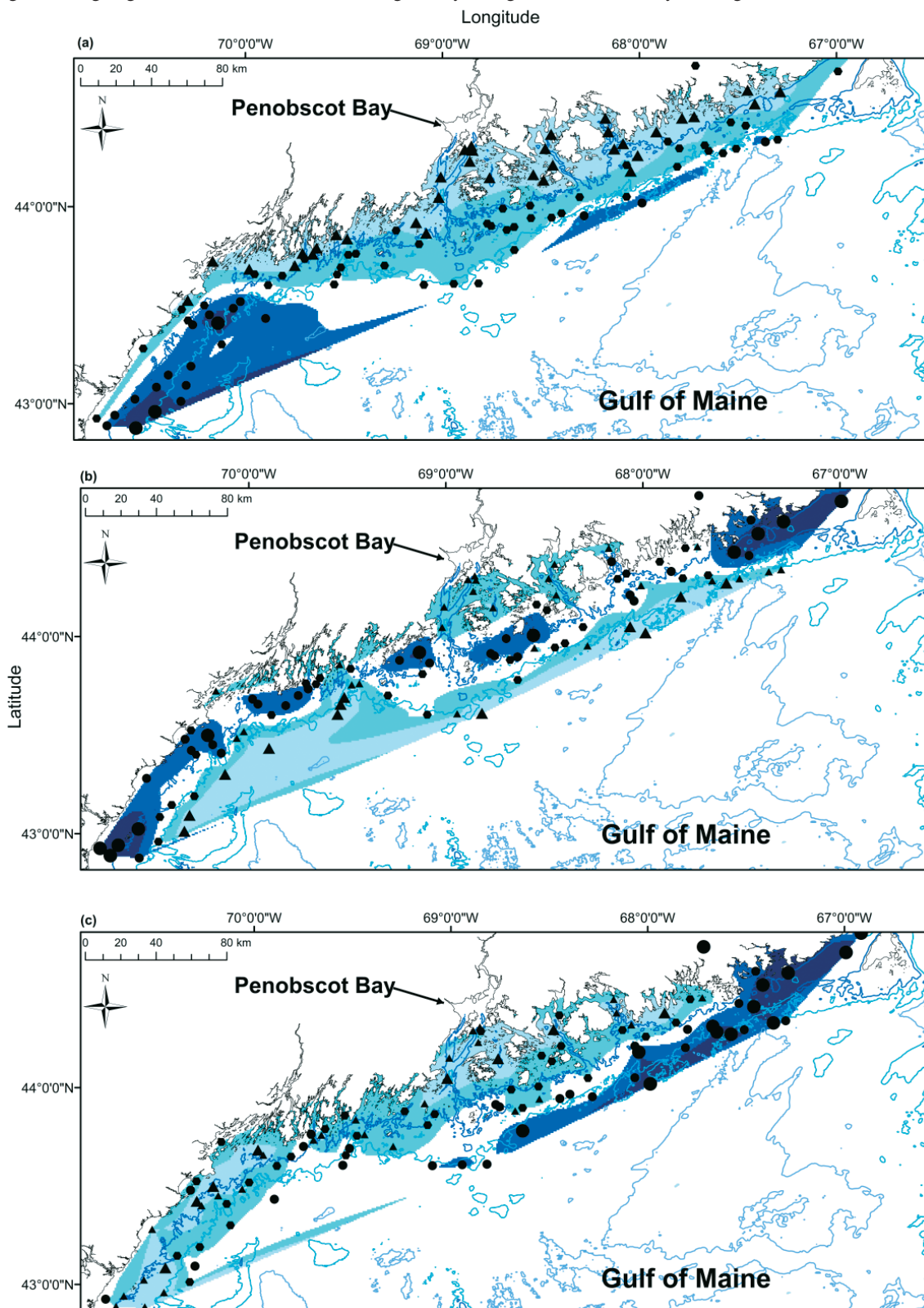
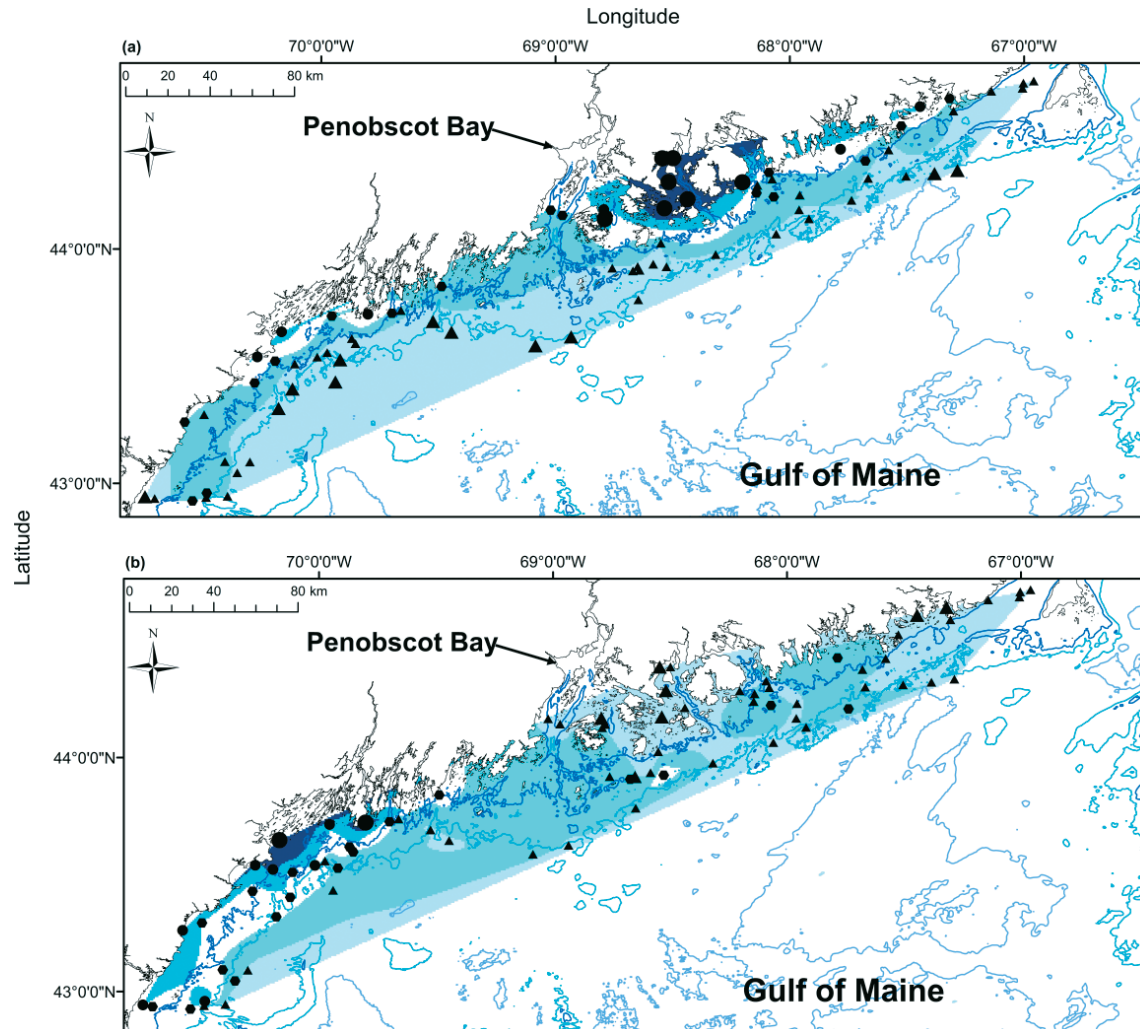


Fig. 9. Fall pelagic species biodiversity maps from (a) PC1 and (b) PC2 scores. Symbols represent PC scores classified into five categories from negative scores (triangles) to positive scores (circles) with larger symbols indicating larger absolute values. Contour plots are results of natural neighbor interpolation reflecting the spatial variation in scores with dark shading representing positive scores and light shading negative scores. Neutral scores are given by hexagons and lack of any shading.



high efficiency in bottom trawls, their abundance, frequency of capture, and structured data set identified by PCA_{BTSP} were such that we felt impelled to include them. Presently, herring fisheries have the largest landings by weight along coastal Maine. Pelagic and primarily anadromous nearshore herring-like forage fish (alewife, blueback herring, and Atlantic herring) spatially contrasted an offshore euphausiids and pearl-side group in the spring survey. Pearlsides are a deepwater bathypelagic fish and euphausiids are common large-bodied invertebrates that are an important predator of copepods (Baumgartner et al. 2003). There is little broadscale distribution information regarding euphausiids, although they are known to exhibit vertical migration and surface swarming behavior in response to internal waves interacting with banks (Stevick et al. 2008). In the fall, Atlantic herring remained an important nearshore species with menhaden and smelt and to a lesser degree the anadromous alosids. The nearshore pelagic group appeared to be focused just east of Penobscot Bay and contrasted an offshore predatory dogfish distribution. Timing and routes of migration by alewife, Atlantic herring, menhaden, and dogfish likely contribute to the observed assemblage

patterns, with species that overwinter in the mid Atlantic bight arriving in the western Gulf of Maine earliest (Collette and Klein-MacPhee 2002). The pelagic species schooling behavior (Collette and Klein-MacPhee 2002), complex patterns in behavior such as diel vertical distributions, and the resulting patchy distributions are likely responsible for the poor ability of any one variable to describe assemblage patterns. As a result, a large number of interacting variables appear to be responsible. Thus, interpretation of pelagic species assemblages should be approached with caution at finer scales but does demonstrate broad assemblage differences between inshore–offshore regions and along the coast. The distribution of forage fish has an inverse relationship to the mobile pelagic predatory spiny dogfish. A high degree of structure of assemblages is corroborated by the ability to create feeding guilds using dendrogram analysis of stomach contents from fishes in the Gulf of Maine (Garrison and Link 2000). These results suggest that predator–prey relationships are also captured to some degree by measures of assemblage structure. The relationship between diet-based grouping of fish and assemblage structure should be further studied.

Fig. 10. Fall benthic vertebrate species biodiversity maps from (a) PC1, (b) PC2, and (c) PC3 scores. Symbols represent PC scores classified into five categories from negative scores (triangles) to positive scores (circles) with larger symbols indicating larger absolute values. Contour plots are results of natural neighbor interpolation reflecting the spatial variation in scores with dark shading representing positive scores and light shading negative scores. Neutral scores are given by hexagons and lack of any shading.

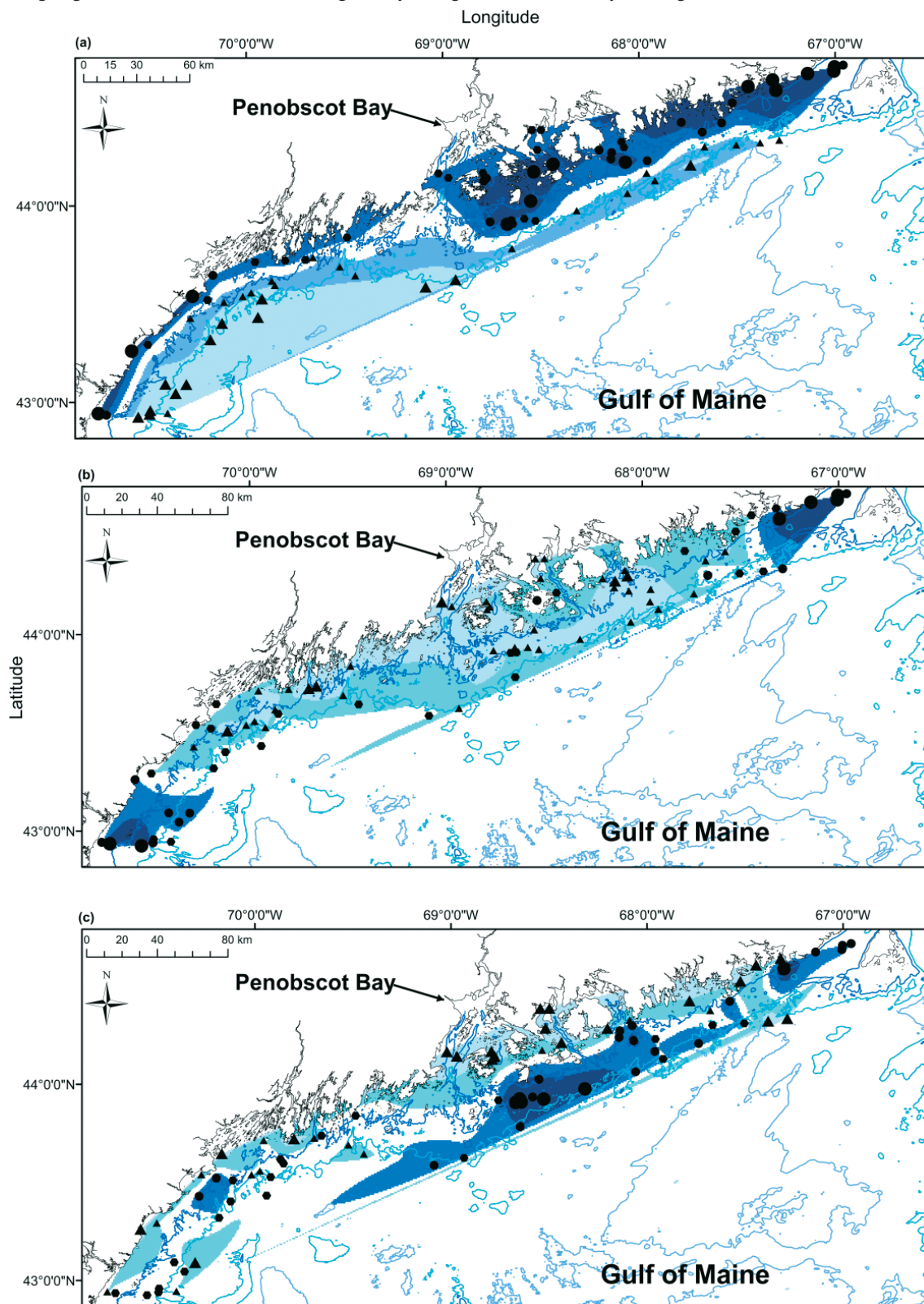


Table 7. Spring and fall species groupings for analyses of vertebrate and pelagic data.

	Positive loading	Negative loading
Spring		
Vertebrate	<i>Lophius americanus</i>	<i>Scophthalmus aquosus</i>
	<i>Sebastes fasciatus</i>	
	<i>Hippoglossoides platessoides</i>	<i>Myoxocephalus octodecemspinosus</i>
	<i>Urophycis chuss</i>	
		<i>Pseudopleuronectes americanus</i>
	<i>Limanda ferruginea</i>	
		<i>Hippoglossus hippoglossus</i>
	<i>Urophycis tenuis</i>	
	<i>Paralichthys oblongus</i>	
	<i>Melanogrammus aeglefinus</i>	
Pelagic	<i>Clupea harengus</i>	<i>Squalus acanthias</i>
	<i>Alosa pseudoharengus</i>	Euphausioid spp.
	<i>Alosa aestivalis</i>	
Fall		
Vertebrate	<i>Pseudopleuronectes americanus</i>	<i>Lophius americanus</i>
		<i>Glyptocephalus cynoglossus</i>
	<i>Myoxocephalus octodecemspinosus</i>	<i>Hippoglossoides platessoides</i>
		<i>Enchelyopus cimbrius</i>
	<i>Raja erinacea</i>	
	<i>Hemitripterus americanus</i>	<i>Urophycis chuss</i>
	<i>Scophthalmus aquosus</i>	
	<i>Gadus morhua</i>	
	<i>Melanogrammus aeglefinus</i>	
	<i>Osmerus mordax</i>	<i>Squalus acanthias</i>
Pelagic	<i>Brevoortia tyrannus</i>	
	<i>Clupea harengus</i>	
	<i>Alosa pseudoharengus</i>	

Note: Species are listed starting with the highest loadings with spaces in the list indicating weaker associations.

We found groups of co-occurring species distributed unevenly across spatial gradients in physical characteristics, including temperature. New PC variables showed primary east–west and onshore–offshore differences in community structure and a secondary mosaic of patches along the coast of Maine. Placing the results within the context of hierarchical patch dynamics (Wu and Loucks 1995) helps to elucidate key ecosystem boundaries. Concordance between the pattern in species assemblages and surface currents of the interior Gulf of Maine strengthen in the fall. The matching physical structure and species eigenvectors lead us to nominate ocean mixing regimes, generated by a gradient in tidal current and other forces (see Pettigrew et al. 2005), as the primary driver of community structure when viewed at the scale of the inshore waters of the Gulf of Maine. However, it should be remembered that this regional structuring is embedded within a broader division along the continental shelf (Mahon et al. 1998; Jordaan et al. 2007), among Georges Bank and the deeper basins and coastal areas of the Gulf of Maine (Overholtz and Tyler 1985; Gabriel 1992; A. Jordaan unpublished data) and overlooks finer-scale local patterns that occur within and among coastal embayments (Jordaan 2010).

Most benthic vertebrate and invertebrate species sampled possess typical broadcast spawning and pelagic egg and larval life history characteristics suggesting that responses to the environment should be similar between the two groups;

however, this was not the case. The lack of coherence by invertebrates, many of which are sessile or have limited potential for movement, suggests that differences between invertebrate and vertebrate analyses reflect differences in adult mobility as opposed to dispersal. It appears that patterns in sediment type and other static physical properties were not strong enough to create consistent patterns at the measurement scale employed in this study. The concordance between the EMCC and the benthic vertebrate structure strengthening over the summer suggests that more mobile species adjust their distributions. Structuring of invertebrates may occur at scales within or beyond the scope of this survey, for example, associated significantly with either benthic heterogeneity (Wahle and Steneck 1992; Poppe et al. 2003) or global distributions in fishing effort (Berkes et al. 2006). Further, low catchability of benthic invertebrates by sampling gear and lack of trawl coverage of more complex habitats, which may not be trawlable, may be playing an important role in observations of invertebrate and pelagic species assemblages. Different survey designs would be required to accomplish more comprehensive analysis.

Eastwood et al. (2006) mapped benthic assemblages to find only minor differences in top-down or bottom-up classification of assemblages and the resulting assemblage maps but indicated that bottom-up approaches seem to improve as more physical acoustic-derived data are made available. We did not include any acoustic data but rather focused on bio-

logical data only using what is a top-down division of the data set into new principal components, largely because fisheries survey data are collected frequently and reliably and thus will eventually allow for a strong time series analysis that can begin to parse out seasonal trends. With only a handful of years with consistent data available, there is no advantage to including a temporal component at this point but rather to introduce the spatial variation in assemblage structure in a single year. However, we must recognize the limitations of the analysis focusing on three factors and their interactions. Habitat types, and other data, would improve the detection of trends in assemblage structure.

The methods applied here depend on correlations among species to generate new variables. The addition of bootstrap-generated stopping rules and identification of significant species–species relationships have improved the application of PCA to this end; however it is not the only method available. We agree with Field et al. (1982) that patterns in species should be examined prior to determining important physical factors, which precludes the use of canonical correlation analysis. Current ecological classification has widely adopted nonparametric ranking of similarities to create a matrix that can identify geographically related divisions in assemblages and species that contribute to patterns (Field et al. 1982). Heavy computing loads were identified as a limitation in classification analysis and stopping rules (Field 1969; Field et al. 1982), a factor that no longer exists. The commonly employed Bray–Curtis measure of similarity and nonmetric multidimensional scaling ordination accommodate robustness and flexibility but sacrifice information by using rank data (Field et al. 1982). PCA_{BTSP}, on the other hand, will sacrifice some flexibility and robustness to gain a more quantitative edge. It is unfortunately not possible to identify the most appropriate techniques without a systematic evaluation of each combined with input from stakeholders who depend on the results being applied appropriately. This line of research should be examined, as should the refinement of postclassification analyses.

Management implications

An important element to this work is the application to area- and ecosystem-based management in the Gulf of Maine. Due to dependence of species distributions on bottom type, Auster et al. (2001) suggested that trawl survey data can be used as proxies for distribution of seafloor habitats and used to infer habitat requirements of co-occurring species. Across the Gulf of Maine, Georges Bank, and Scotian Shelf, depth and temperature are related more strongly to species distributions than substrate type (Mahon and Smith 1989; Methratta and Link 2007), but thus, it is more helpful to recognize the sum total of “habitat” and not concentrate on one physical factor. Our results suggest a number of distributional relationships between species and physical variables and agree with the assertion that survey data can be used to infer patterns in habitat and biodiversity because correlation of species’ distributions provides a proxy for the physical environment. However, interpretations will be entirely dependent on the scale and effort of sampling. A more detailed investigation relating variability of temperatures, current patterns, and species abundances

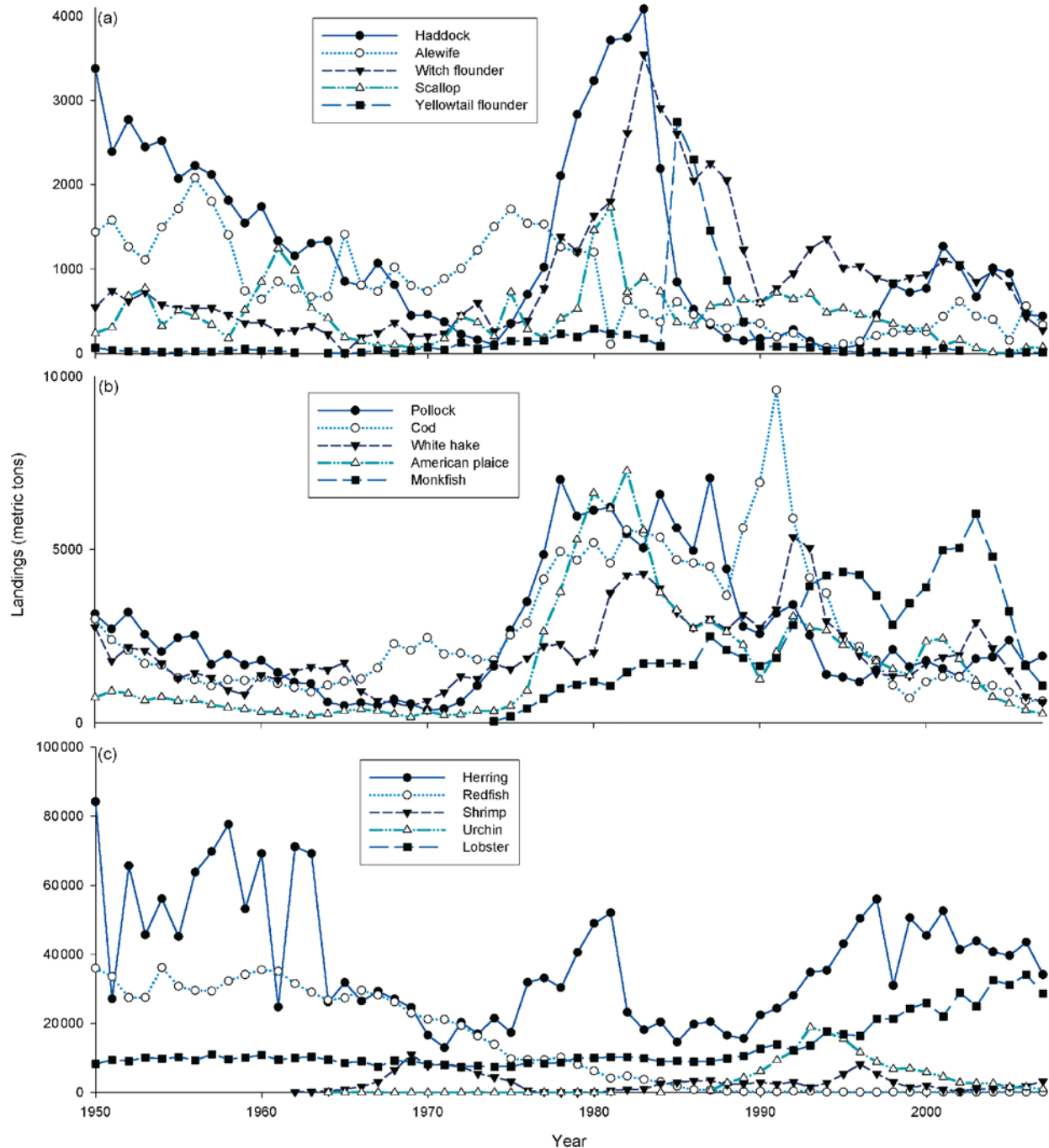
and assemblage distributions will be necessary to understand spatial structuring of ecosystems.

Fisheries in the past 50 years have been typified by boom–bust cycles, with effort shifting to new species after the completion of a cycle, reflected in the commercial landings (Fig. 11). It is thought that by matching the scales of management to those of ecological structure, management will be more effective. Part of this is the recognition that a large number of differing habitats will have to be included to provide for species year-to-year variation in movements and distributions. Species that were structured at scales that match the extent and sampling density of the data used in this analysis and were involved in driving patterns in assemblage structure along the Maine coastal area include monkfish (Table 7), the most recent Maine groundfish fishery (Fig. 11), and Acadian redfish (Table 7), one of the older fisheries (Fig. 11). Compared with historical conditions, cod are no longer playing any structuring role along the Maine coast largely due to managers ignoring and fishers targeting finer-scale metapopulations that removed the species from coastal Maine (Ames 2004), as is the case for a number of other species. The present analysis suggests that a spatially explicit management of benthic vertebrates is possible and that many commercially and ecologically relevant groundfish species can be spatially managed at far smaller scales than the two-stock paradigm of today.

It is important to consider the method of capture, in particular how interpretation differs between fisheries-dependent and fisheries-independent catches. If the analysis were performed on fisheries-dependent data, correlations among species and similar eigenvector loadings would indicate increasing likelihood of capture; therefore, the approach could also be used to identify bycatch risk. For example, the analysis of fisheries-independent data in this work suggests a high likelihood of bycatch of the anadromous river herrings (alewife and blueback herring) during hypothetical spring menhaden and smelt and fall herring fisheries. In contrast, the fall benthic vertebrates have a large number of species susceptible to catch as a nontargeted species if any one of the correlated species is targeted by a hypothetical fishery. Because fishing effort is unevenly distributed (Murawski et al. 2005; Mills et al. 2007) and impacts could be either amplified or diminished, there is opportunity for overfishing or a system of area-based management that satisfies ecosystem-based principals to develop.

The periodicity of sampling and selectivity of gear will always be a consideration in interpretation of results for directing management. This study used data collected from a fisheries-independent survey that employs the same sampling protocol over sampling seasons and years. The selectivity of sampling gear is different from species to species. Thus, the composition of fish species abundance observed in the survey data may differ from that of the actual fish community in the ecosystem. However, because the standard sampling protocol is used throughout the sampling program, the selectivity of each species is the same over time, which makes the correlations or covariance between species abundance indices consistent over time. The proposed approach used the correlations, which makes the results derived from this study robust with respect to differences in selectivity among species. The associations between the highest loading

Fig. 11. Fisheries landings for the State of Maine from 1950 to the present organized according to maximum historic peak landings: (a) <5000 metric tons, (b) 5000–10 000 metric tons, and (c) >10 000 metric tons. Landings data do not translate into a measure of abundance but rather show the progression of fisheries from redfish through a variety of other groundfish, flatfish, and invertebrates and ending with only herring and lobster making contributions in the final years. Herring is the only species that contributes substantial landings through the entire time period. Note that Maine fisheries only represent a fraction of total landings in the Gulf of Maine but are expected to reflect dynamics along the Maine coast. Data available at www.maine.gov/dmr/commercialfishing/historicaldata.htm (Maine Department of Marine Resources).



species and correlation coefficients were consistent, suggesting that groups of species are important in determining structure rather than any one species. O'Neill (2001) argued that ecosystems, by definition, include biases regarding spatial coverage by assuming a closed system. The analyses presented here constitute a methodology for determining

structure in populations of organisms. By doing so, biases imposed by prior assumptions of ecosystem boundaries are removed in favor of designating structure based on biological variables. No-take marine reserves or marine protected areas have been advocated as integral components of ecosystem-based zoning, but there has also been considerable

debate regarding their effectiveness in that capacity (Norse et al. 2003). Smith et al. (2008) found that the western Gulf of Maine closure was having no appreciable effect on monkfish population recovery. Since monkfish became the active groundfish fishery after the loss of coastal cod, managers should consider guarding against overcapitalized fleets shifting effort from failing fisheries. One mechanism to accomplish this is to restrict effort spatially. Our results indicate that the western Gulf of Maine closure is small compared with the region associated with the monkfish-dominated assemblage. To designate an effective plan that includes monkfish and other species, a larger, more comprehensive closure system is required.

To use the methods outlined in this paper as a mechanism for identifying appropriate management scales within a broad area-based management scheme will require further steps, including the establishment and management of a marine protected area network. The challenge that remains is achieving a shared vision in management that is adequately geographically based (Murawski 2007). It will be necessary to incorporate other ecological and socioeconomic indicators that consider such attributes as local (genetic) stocks, species dispersal potentials, size and age structure, and fleet dynamics. Furthermore, specific plans should be tested through multispecies modeling such as available in the Ecospace model (Walters et al. 1999). Still, the analysis presented here can determine expansion of species groups or shifts in interactions with other species and, when combined with process-oriented indicators that register changes in trophic interactions, can add valuable information to the management of fisheries. Developing plans without basing them on the underlying biodiversity could lead to potentially serious consequences of overfishing or otherwise impact certain specific or underrepresented species and habitats, a principal that is consistent for all forms of *de facto* zoning.

While devising species-specific plans is required to stave off extinction of species at critically low abundances (Bain et al. 2007), there are situations where the full life cycle or a critical prey resource is not adequately protected. For example, Baltic Sea marine protected areas have been criticized for shifting fishing effort onto smaller juvenile fishes, resulting in higher discard rates and other negative consequences (Hinrichsen et al. 2009; Suuronen et al. 2010). Thus, achieving a geographically based system will require all habitats to be represented under a flexible, but comprehensive, plan. A major step toward this is recognizing the gradients in biodiversity. The development of techniques for uncovering spatial structure in marine assemblages and defining the limitations and advantages of each will be critical to appropriately partitioning the marine environment.

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References

- Ames, E.P. 2004. Atlantic cod stock structure in the Gulf of Maine. *Fisheries*, **29**(1): 10–28. doi:10.1577/1548-8446(2004)29[10:ACSSIT]2.0.CO;2.
- Auster, P.J., Joy, K., and Valentine, P.C. 2001. Fish species and community distributions as proxies for seafloor habitat distributions: the Stellwagen Bank National Marine Sanctuary example (Northwest Atlantic, Gulf of Maine). *Environ. Biol. Fishes*, **60**(4): 331–346. doi:10.1023/A:1011022320818.
- Bain, M.B., Haley, N., Peterson, D.L., Arend, K.K., Mills, K.E., Sullivan, P.J., and Lusseau, D. 2007. Recovery of a US endangered fish. *PLoS One*, **2**(1): e168. doi:10.1371/journal.pone.0000168. PMID:17245444.
- Baumgartner, M.F., Cole, T.V.N., Campbell, R.G., Teegarden, G.J., and Durbin, E.G. 2003. Associations between North Atlantic right whales and their prey, *Calanus finmarchicus*, over diel and tidal time scales. *Mar. Ecol. Prog. Ser.* **264**: 155–166. doi:10.3354/meps264155.
- Berkes, F., Hughes, T.P., Steneck, R.S., Wilson, J.A., Bellwood, D.R., Crona, B., Folke, C., Gunderson, L.H., Leslie, H.M., Norberg, J., Nyström, M., Olsson, P., Osterblom, H., Scheffer, M., and Worm, B. 2006. Ecology. Globalization, roving bandits, and marine resources. *Science*, **311**(5767): 1557–1558. doi:10.1126/science.1122804. PMID:16543444.
- Brodziak, J.K., Overholtz, W.J., and Rago, P.J. 2001. Does spawning stock affect recruitment of New England groundfish? *Can. J. Fish. Aquat. Sci.* **58**(2): 306–318. doi:10.1139/cjfas-58-2-306.
- Chen, Y., Sherman, S., Wilson, C., Sowles, J., and Kanaiwa, M. 2006. A comparison of two fishery independent survey programs used to define the population structure of American lobster (*Homarus americanus*) in the Gulf of Maine. *Fish. Bull.* (Wash., D.C.), **104**: 247–255.
- Collette, B.B., and Klein-MacPhee, G. 2002 *Bigelow and Schroeder's Fishes of the Gulf of Maine*. 3rd ed. Smithsonian Institution Press, Washington, D.C.
- Crowder, L.B., Osherenko, G., Young, O.R., Aïramé, S., Norse, E.A., Baron, N., Day, J.C., Douvère, F., Ehler, C.N., Halpern, B.S., Langdon, S.J., McLeod, K.L., Ogden, J.C., Peach, R.E., Rosenberg, A.A., and Wilson, J.A. 2006. Sustainability. Resolving mismatches in U.S. ocean governance. *Science*, **313**(5787): 617–618. doi:10.1126/science.1129706. PMID:16888124.
- Dow, R.L. 1981. Influence of sea temperature cycles on the abundance and availability of marine and estuarine species of commerce. In *Proceedings of the Oceans 1981 Conference Record*, Boston, Massachusetts, 16–18 September 1981. The Ocean: An International Workplace. Vol. 2. IEEE, New York. pp. 775–779.
- Eastwood, P.D., Souissi, S., Rogers, S.I., Coggan, R.A., and Brown, C.J. 2006. Mapping seabed assemblages using comparative top-down and bottom-up classification approaches. *Can. J. Fish. Aquat. Sci.* **63**(7): 1536–1548. doi:10.1139/F06-058.
- Field, J.G. 1969. The use of the information statistic in the numerical classification of heterogeneous systems. *J. Ecol.* **57**(2): 565–569. doi:10.2307/2258400.
- Field, J.G., Clarke, K.R., and Warwick, R.M. 1982. A practical strategy for analysing multispecies distribution patterns. *Mar. Ecol. Prog. Ser.* **8**: 37–52. doi:10.3354/meps008037.
- Frisk, M.G., Miller, T.J., Martell, S.J.D., and Sosebee, K. 2008. New hypothesis helps explain elasmobranch “outburst” on

- Georges Bank in the 1980s. *Ecol. Appl.* **18**(1): 234–245. doi:10.1890/06-1392.1. PMID:18372569.
- Gabriel, W. 1992. Persistence of demersal fish assemblages between Cape Hatteras and Nova Scotia, Northwest Atlantic. *J. Northwest Atl. Fish. Sci.* **14**: 29–46.
- Garrison, L.P., and Link, J.S. 2000. Dietary guild structure of the fish community in the Northeast United States continental shelf ecosystem. *Mar. Ecol. Prog. Ser.* **202**: 231–240. doi:10.3354/meps202231.
- Hilborn, R. 2003. Forum. Marine reserves: the best option for our oceans? *Front. Ecol. Environ.* **1**(9): 497.
- Hinrichsen, H.H., Kraus, G., Böttcher, U., and Köster, F. 2009. Identifying eastern Baltic cod nursery grounds using hydrodynamic modelling: knowledge for the design of Marine Protected Areas. *ICES J. Mar. Sci.* **66**(1): 101–108. doi:10.1093/icesjms/fsn207.
- Hoerling, M.P., Hurrell, J.W., and Xu, T. 2001. Tropical origins for recent North Atlantic climate change. *Science*, **292**(5514): 90–92. doi:10.1126/science.1058582. PMID:11292869.
- Jackson, D.A. 1993. Stopping rules in principal components analysis: a comparison of heuristic and statistical approaches. *Ecology*, **74**(8): 2204–2214. doi:10.2307/1939574.
- Jackson, D.A. 1995. Bootstrapped principal component analysis — reply to Mehlman et al. *Ecology*, **76**(2): 644–645. doi:10.2307/1941220.
- Jordaán, A. 2006. Determining environmental drivers of fish community structure along the coast of Maine. Ph.D. thesis, University of Maine, Orono, Maine.
- Jordaán, A. 2010. Fish assemblages spatially structure along a multi-scale wave energy gradient. *Environ. Biol. Fishes*, **87**(1): 13–24. doi:10.1007/s10641-009-9537-9.
- Jordaán, A., and Kling, L.J. 2003. Determining the optimal temperature range for Atlantic cod (*Gadus morhua*) during early life. In *Proceedings of the 26th Annual Larval Fish Conference*, Oslo, Norway, 22–26 July 2002. The Big Fish Bang. Institute of Marine Research, Bergen, Norway. pp. 45–62. ISBN 82-7461-059-8. Available from www.fishlarvae.com/e/Book_Reader.asp?pg=/e/BigBang/Jordaán.pdf&pgid=223.
- Jordaán, A., Frisk, M.G., Wolff, N.H., Incze, L.S., Hamlin, L., and Chen, Y. 2007. Structure of fish assemblages along the north-eastern United States based on trawl survey data: indicators of biodiversity and a basis for ecosystem and area-based management. International Council for the Exploration of the Sea, Copenhagen, Denmark. CM 2007/A:05. Available from www.ices.dk/products/CMdocs/CM-2007/A/A0507.pdf
- Jørgensen, O.A., Hvingel, C., Møller, P.R., and Treble, M.A. 2005. Identification and mapping of bottom fish assemblages in Davis Strait and southern Baffin Bay. *Can. J. Fish. Aquat. Sci.* **62**(8): 1833–1852. doi:10.1139/f05-101.
- Levin, S.A., and Lubchenco, J. 2008. Resilience, robustness, and marine ecosystem-based management. *Bioscience*, **58**(1): 27–32. doi:10.1641/B580107.
- Mahon, R., and Smith, R.W. 1989. Demersal fish assemblages on the Scotian Shelf, northwest Atlantic: spatial distribution and persistence. *Can. J. Fish. Aquat. Sci.* **46**(Suppl. 1): s134–s152. doi:10.1139/f89-285.
- Mahon, R., Brown, S.K., Zwanenburg, K.C.T., Atkinson, D.B., Buja, K.R., Claffin, L., Howell, G.D., Monaco, M.E., O’Boyle, R.N., and Sinclair, M. 1998. Assemblages and biogeography of demersal fishes of the East Coast of North America. *Can. J. Fish. Aquat. Sci.* **55**(7): 1704–1738. doi:10.1139/cjfas-55-7-1704.
- Mehlman, D.W., Shepherd, U.L., and Kelt, D.A. 1995. Bootstrapping principal components analysis: a comment. *Ecology*, **76**(2): 640–643. doi:10.2307/1941219.
- Methratta, E.T., and Link, J.S. 2007. Ontogenetic variation in habitat association for four groundfish species in the Gulf of Maine—Georges Bank region. *Mar. Ecol. Prog. Ser.* **338**: 169–181. doi:10.3354/meps338169.
- Mills, C.M., Townsend, S.E., Jennings, S., Eastwood, P.D., and Houghton, C.A. 2007. Estimating high resolution trawl fishing effort from satellite-based vessel monitoring system data. *ICES J. Mar. Sci.* **64**(2): 248–255. doi:10.1093/icesjms/fsl026.
- Murawski, S.A. 2007. Ten myths concerning ecosystem approaches to marine resource management. *Mar. Policy*, **31**(6): 681–690. doi:10.1016/j.marpol.2007.03.011.
- Murawski, S.A., Wigley, S.E., Fogarty, M.J., Rago, P.J., and Mountain, D.G. 2005. Effort distribution and catch patterns adjacent to temperate MPAs. *ICES J. Mar. Sci.* **62**: 1150–1167.
- Norse, E.A., Grimes, C.B., Ralston, S., Hilborn, R., Castilla, J.C., Palumbi, S.R., Fraser, D., and Kareiva, P. 2003. Marine reserves: the best option for our oceans? *Front. Ecol. Environ.* **1**(9): 495–502. doi:10.2307/3868117.
- Northeast Data Poor Stocks Working Group. 2007. Monkfish assessment report for 2007. Reference Document 07-21. US Department of Commerce, Northeast Fish Science Center, Woods Hole, Mass.
- O’Neill, R.V. 2001. Is it time to bury the ecosystem concept? (with full military honors, of course!). *Ecology*, **82**(12): 3275–3284.
- Overholtz, W.J., and Tyler, A.V. 1985. Long-term responses of the demersal fish assemblages of Georges Bank. *Fish. Bull. (Wash., D.C.)*, **83**: 507–520.
- Peres-Neto, P.R., Jackson, D.A., and Somers, K.M. 2003. Giving meaningful interpretation to ordination axes: assessing loading significance in principal component analysis. *Ecology*, **84**(9): 2347–2363. doi:10.1890/00-0634.
- Perry, R.I., and Smith, S.J. 1994. Identifying habitat associations of marine fishes using survey data: an application to the Northwest Atlantic. *Can. J. Fish. Aquat. Sci.* **51**(3): 589–602. doi:10.1139/f94-061.
- Pettigrew, N.R., Churchill, J.H., Janzen, C.D., Mangum, L.J., Signell, R.P., Thomas, A.C., Townsend, D.W., Wallinga, J.P., and Xue, H. 2005. The kinematic and hydrographic structure of the Gulf of Maine Coastal Current. *Deep-Sea Res. II: Top. Stud. Oceanogr.* **52**(19–21): 2369–2391. doi:10.1016/j.dsr2.2005.06.033.
- Pillar, V.D. 1999. The bootstrapped ordination re-examined. *J. Veg. Sci.* **10**(6): 895–902. doi:10.2307/3237314.
- Poppe, L.J., Paskevich, V.F., Williams, S.J., Hastings, M.E., Kelley, J.T., Belknap, D.F., Ward, L.G., FitzGerald, D.M., and Larsen, P.F. 2003. Surficial sediment data from the Gulf of Maine, Georges Bank, and vicinity: a GIS compilation. U.S. Geol. Surv. Open-File Rep. 03-001. Available from <http://pubs.usgs.gov/of/2003/of03-001/index.htm>.
- Sherman, S.A., Stepanek, K., and Sowles, J. 2005. Maine—New Hampshire inshore groundfish trawl survey. Procedures and protocols. Res. Ref. Doc. 05/01. Maine Department of Marine Resources. Available from www.maine.gov/dmr/rm/trawl/reports/proceduresandprotocols.pdf.
- Sibson, R. 1981. Interpolating multivariate data. John Wiley & Sons, New York.
- Slocumbe, D.S. 1998. Defining goals and criteria for ecosystem-based management. *Environ. Manag.* **22**(4): 483–493. doi:10.1007/s002679900121. PMID:9582385.
- Smith, M.D., Grabowski, J.H., and Yund, P.O. 2008. The role of closed areas in rebuilding monkfish populations in the Gulf of Maine. *ICES J. Mar. Sci.* **65**(7): 1326–1333. doi:10.1093/icesjms/fsn137.
- Souissi, S., Ibanez, F., Hamadou, R.B., Boucher, J., Cathelineau,

- A.C., Blanchard, F., and Poulard, J.C. 2001. A new multivariate mapping method for studying species assemblages and their habitats: example using bottom trawl surveys in the Bay of Biscay (France). *Sarsia*, **86**: 527–542.
- Stevick, P.T., Incze, L.S., Kraus, S.D., Rosen, S., Wolff, N., and Baukus, A. 2008. Trophic relationships and oceanography on and around a small offshore bank. *Mar. Ecol. Prog. Ser.* **363**: 15–28. doi:10.3354/meps07475.
- Strayer, D.L., Power, M.E., Fagan, W.F., Pickett, S.T.A., and Belnap, J. 2003. A classification of ecological boundaries. *Bioscience*, **53**(8): 723–729. doi:10.1641/0006-3568(2003)053[0723:ACOE]2.0.CO;2.
- Sundermeyer, M.A., Rothschild, B.J., and Robinson, A.R. 2005. Using commercial landings data to identify environmental correlates with distributions of fish stocks. *Fish. Oceanogr.* **14**(1): 47–63. doi:10.1111/j.1365-2419.2004.00302.x.
- Suuronen, P., Jounela, P., and Tschernij, V. 2010. Fishermen responses on marine protected areas in the Baltic cod fishery. *Mar. Policy*, **34**(2): 237–243. doi:10.1016/j.marpol.2009.07.001.
- Targett, T.E., and McCleave, J.D. 1974. Summer abundance of fishes in a Maine tidal cove with special reference to temperature. *Trans. Am. Fish. Soc.* **103**(2): 325–330. doi:10.1577/1548-8659(1974)103<325:SAOFIA>2.0.CO;2.
- Thomas, A.C., Townsend, D.W., and Weatherbee, R. 2003. Satellite measured phytoplankton variability in the Gulf of Maine. *Cont. Shelf Res.* **23**(10): 971–989. doi:10.1016/S0278-4343(03)00086-4.
- Townsend, D.W. 1991. Influences of oceanographic processes on the biological productivity of the Gulf of Maine. *Rev. Aquat. Sci.* **5**: 211–230.
- Townsend, D.W., and Ellis, W.G. 2010. Primary production and nutrient cycling on the Northwest Atlantic continental shelf. In *Carbon and nutrient fluxes in continental margins: a global synthesis. Edited by K.-K. Liu, L. Atkinson, R. Quiñones, and L. Talaue-McManus. IGBP Book Series. Springer, Berlin.* pp. 234–248.
- Townsend, D.W., Thomas, A.C., Mayer, L.M., Thomas, M., and Quinlan, J. 2006. Oceanography of the Northwest Atlantic Continental Shelf. In *The sea. Vol. 14. Edited by A.R. Robinson and K.H. Brink. Harvard University Press, Boston, Mass.* pp. 119–168.
- U.S. Commission on Ocean Policy. 2004. An ocean blueprint for the 21st century. Final report. U.S. Commission on Ocean Policy, Washington, D.C.
- Wahle, R.A., and Steneck, R.S. 1992. Habitat restrictions in early benthic life: experiments on habitat selection and in situ predation with the American lobster. *J. Exp. Mar. Biol. Ecol.* **157**(1): 91–114. doi:10.1016/0022-0981(92)90077-N.
- Walters, C., Pauly, D., and Christensen, V. 1999. Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *Ecosystems* (N.Y., Print), **2**(6): 539–554. doi:10.1007/s100219900101.
- Wu, J., and Loucks, O.L. 1995. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. *Q. Rev. Biol.* **70**(4): 439–466. doi:10.1086/419172.