



Delineating ecological regions in marine systems: Integrating physical structure and community composition to inform spatial management in the eastern Bering Sea



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ABSTRACT

Characterizing spatial structure and delineating meaningful spatial boundaries have useful applications to understanding regional dynamics in marine systems, and are integral to ecosystem approaches to fisheries management. Physical structure and drivers combine with biological responses and interactions to organize marine systems in unique ways at multiple scales. We apply multivariate statistical methods to define spatially coherent ecological units or ecoregions in the eastern Bering Sea. We also illustrate a practical approach to integrate data on species distribution, habitat structure and physical forcing mechanisms to distinguish areas with distinct biogeography as one means to define management units in large marine ecosystems. We use random forests to quantify the relative importance of habitat and environmental variables to the distribution of individual species, and to quantify shifts in multispecies assemblages or community composition along environmental gradients. Threshold shifts in community composition are used to identify regions with distinct physical and biological attributes, and to evaluate the relative importance of predictor variables to determining regional boundaries. Depth, bottom temperature and frontal boundaries were dominant factors delineating distinct biological communities in this system, with a latitudinal divide at approximately 60°N. Our results indicate that distinct climatic periods will shift habitat gradients and that dynamic physical variables such as temperature and stratification are important to understanding temporal stability of ecoregion boundaries. We note distinct distribution patterns among functional guilds and also evidence for resource partitioning among individual species within each guild. By integrating physical and biological data to determine spatial patterns in community composition, we partition ecosystems along ecologically significant gradients. This may provide a basis for defining spatial management units or serve as a baseline index for analyses of structural shifts in the physical environment, species abundance and distribution, and community dynamics over time.

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1. Introduction

Spatial classification of patterns in biogeography provide a practical approach to understand ecosystem dynamics. This has useful application to conservation (Lourie and Vincent, 2004; Spalding et al., 2007) and resource management (Marasco et al., 2007; Levin et al., 2009; Livingston et al., 2011; Link and Auster, 2011). Oceanographic processes, bathymetric structure and environmental conditions regulate

system organization and productivity (Speckman et al., 2005) and influence competitive and predatory interactions (Kildaw et al., 2005). By recognizing and explicitly characterizing spatial heterogeneity in marine systems, we are able to define and better explain distinct regional patterns (Bailey, 1998).

There is an extensive history of classifying biogeographic patterns in the marine environment (Forbes, 1856; Ekman, 1953; Hedgpeth, 1957a,b). Hierarchical approaches are often used, scaling from geographical realms (continental or oceanic scales), to provinces (seas or basins), ecosystems (self-contained systems), and regional-scale processes. To distinguish boundaries, classification systems have employed species endemism (Briggs, 1974), bathymetry (Allen and Smith, 1988), biogeochemical processes (Longhurst, 1998), oceanic production (Bailey, 1998), thermogeography (Adey and Steneck, 2001)

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and physiographic and oceanographic patterns (Piatt and Springer, 2007). Such classification systems have also used functional considerations such as utility and parsimony (Spalding et al., 2007). As part of this process, the concept of large marine ecosystems (LME) was established to define the continental margins according to ecological criteria (e.g. bathymetry, hydrography, productivity, and trophic relationships) and to facilitate transboundary and ecosystem-based management (Morgan, 1987; Sherman and Alexander, 1989; Sherman, 1991). LMEs are also widely used as distinct units of analysis in comparisons of marine systems (Branch et al., 2010; Pinsky et al., 2011). Due in part to the emphasis on Ecosystem-Based Fishery Management (EBFM) in the reauthorization of the Magnuson-Stevens Act, LMEs were also adopted by the US National Oceanic and Atmospheric Administration (<http://www.lme.noaa.gov>) and currently provide the basis for assessing and managing discrete fish stocks. While LMEs provide a robust and useful designation of distinct marine areas, there is increased interest in higher resolution understanding of ecosystem processes and regional phenomena relevant to both conservation (Dinerstein and Olson, 1997; Ford, 1998; Banks et al., 1999; Spalding et al., 2007) and natural resource management (Fogarty and Murawski, 1998; Fogarty and Keith, 2009; <http://bsierp.nprb.org>). This is recognized by international (UN FAO, 2003) and national authorities (Ecosystem Principles Panel, 1996; National Marine Fisheries Service, 1999; US Commission on Ocean Policy, 2004). As distinct units within LMEs, ecoregions serve this purpose. We define an ecoregion as an ecologically and geographically defined area characterized by distinct assemblages of biological communities and environmental conditions.

1.1. Purpose and intent

Both spatial and multispecies management approaches require robust methods to synthesize physical and biological data to identify regional structure within ecosystems, and determine the relative impacts of various environmental and biological drivers. We illustrate an approach to integrate data on species distribution with data on

environmental variables and physical structure to distinguish regions with distinct biogeography and ecology (i.e. ecoregions).

1.2. Regional Delineation

LMEs are defined using broad-scale patterns of biodiversity, productivity and hydrographical features (Hempel and Sherman, 2003; Murawski, 2007). These boundaries distinguish ecosystem processes, food web and trophic interactions, and commercially exploited stocks. The criteria distinguishing ecoregions is less clear. Most approaches have been synthetic (consensus and expert opinion) and largely qualitative (Piatt and Springer, 2007; Ortiz, 2012). Past efforts to apply quantitative methods have typically focused on physical variables alone (Allen and Smith, 1988), used aggregate biomass without consideration of the composition of the ecological communities represented (Fogarty and Keith, 2009; Livingston et al., 1999; Pepin et al., 2010; Zwanenburg et al., 2010) or included anthropogenic and political considerations (Spalding et al., 2007).

Hard boundaries rarely exist in marine systems (Murawski, 2007). Ecological processes and species distributions fluctuate along gradients, often dictated by a relatively limited group of covariates (e.g. temperature, depth, salinity, stratification, nutrient availability, substrate type, productivity). Identifying how distinct biological communities organize across environmental gradients offers one means to differentiate ecoregions.

1.3. Study system: eastern Bering Sea

Our analyses focus on the eastern Bering Sea (EBS), a highly productive system that generates roughly half of US fish and shellfish landings and supports important populations of seabirds and marine mammals (National Research Council, 1996). It is characterized by a broad coastal shelf and a deep-sea basin, extending from the Alaska Peninsula to the Bering Strait. The Bering Sea shelf extends 800 km from Norton Sound to the

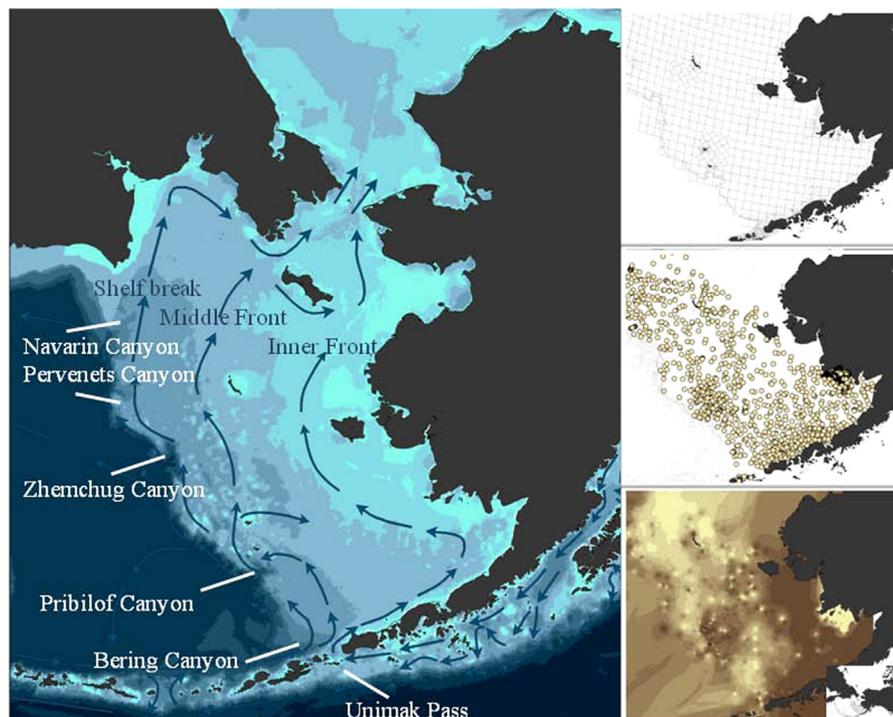


Fig. 1. Eastern Bering Sea shelf. Main panel displays depth, predominant currents, fronts and canyons. Side panels display fixed grid survey stations for survey biomass (top right), sampling locations for sediment (middle right) and inverse distance weighting of surficial sediments (darker shades indicate coarser substrates, bottom right).

continental slope and the Shelf Break extends 1200 km from Unimak Pass to Cape Navarin (Fig. 1). Patterns in productivity and energy flow are influenced by temperature, currents, annual cycles of sea ice formation (Napp and Hunt, 2001; Hunt et al., 2011, 2002) and multi-year climate regimes (Mantua and Hare, 2002; Bond et al., 2003). Temperature and hydrographic structure are dynamic, driven by terrestrial inputs, insolation, ice melt, tidal currents and wind events and are characterized by high inter-annual and spatial variability (Overland et al., 1999). These physical conditions influence localized production (Coyle and Cooney, 1993) and the distributions and interactions of commercially and ecologically important species (Coyle and Pinchuk, 2002; Ciannelli et al., 2004).

Depth gradients are often used to differentiate three bathymetric domains within the EBS: the coastal or inner domain (0–50 m), the middle domain (50–100 m) and the outer shelf (100–200 m) (Smith and Bakkala, 1982; Coachman, 1986) (Fig. 1). These domains are separated by hydrographic fronts, with inner, middle, and outer fronts located along the 50, 100 and 170-m isobaths, respectively (Coachman, 1986; Schumacher and Stabeno, 1998). In summer, the coastal domain is well mixed to weakly stratified, the middle domain is a strongly stratified two-layer system with a relatively warm wind-mixed surface layer overlaying a cold bottom layer, and the outer shelf has well mixed upper and lower layers separated by a zone of gradually increasing density. Profiles in all domains have high variability within and among years (Buckley et al., 2009). Despite strong structural fronts, cross-shelf transport does occur. Wind-driven circulation has important effects on nutrient flux and advection processes related to biological production and distribution (Stabeno et al., 2001; Danielson et al., 2012; Gibson et al., 2013). Canyon systems along the Shelf Break (Bering, Pribilof, Zhemchug, Pervenets, and Navarin) also play an important role in shelf/basin exchange (Stabeno et al., 1999; Kinney et al., 2009).

An extensive cold pool, defined as bottom temperatures $\leq 2^\circ\text{C}$, forms as a legacy of sea ice melt (Wyllie-Echeverria and Wooster, 1998; Stabeno et al., 2012a,b) and persists until storm-induced

mixing occurs in the fall (Ladd and Stabeno, 2012) (Fig. 2). The intensity and spatial extent of this cold pool is a dominant physical driver in the system, limiting nutrient transport and species distribution (National Research Council, 1996; Mueter and Litzow, 2008; Stabeno et al., 2012a,2012b). Stratification also influences nutrient transport and availability, primary and secondary production, larval survival and species interactions (National Research Council, 1996, Kachel et al., 2002). In concert, these oceanographic features influence inter-annual variability in species distribution (Lauth, 2012; Kotwicki and Lauth, 2013) and early life stage survival (Mueter et al., 2006, 2007), and constrain species overlap, predatory interactions, and cross-shelf distribution (Kotwicki et al., 2005; Ciannelli and Bailey, 2005, Spencer, 2008). Extensive research in this system, including the joint National Science Foundation Bering Sea Ecosystem Study (BEST) and North Pacific Research Board Bering Sea Integrated Ecosystem Research Program (BSIERP), suggests that depth, sediment type, prey distribution and spatial distribution of the cold pool define distinct core distributions for forage fish and flat fish species and structure distinct marine communities (Ciannelli and Bailey, 2005; Hollowed et al., 2012).

1.4. Previous regional classifications of the eastern Bering Sea

Several expert-based classification schemes have been applied to the EBS (Ford, 1998; Banks et al., 1999; Piatt and Springer, 2007; Sigler, 2011; Ortiz, 2012). While expert-derived qualitative divisions based large-scale oceanographic characteristics or published species–environment relationships are useful, environmental variables should be weighted proportional to their relative influence on biological patterns (Pitcher et al., 2012). Our analyses build on existing schemes to define biogeographical domains (ecoregions) that explicitly link environmental and biological data and identify statistically relevant breakpoints in biological community composition along distinct environmental gradients. We also highlight a method to project spatial shifts in these ecoregions as a function of dynamic physical variables, which fluctuate over time.

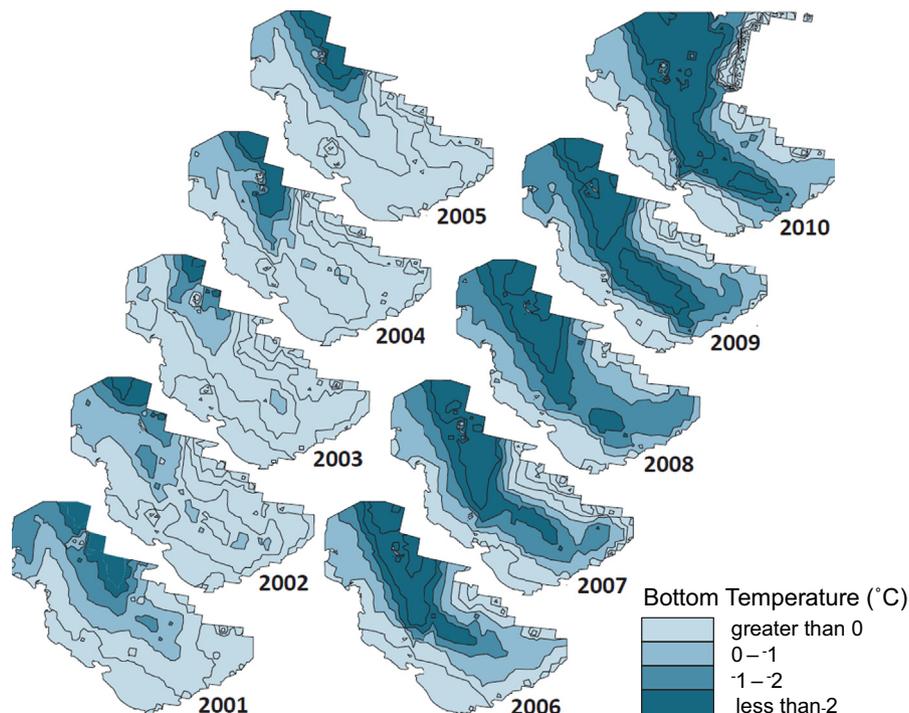


Fig. 2. Recent cold versus warm temperature regimes in the eastern Bering Sea. Maps of the cold pool extent (bottom temperature $< 2^\circ\text{C}$) are displayed for warm (2001–2005) and cold (2006–2010) years.

2. Materials and methods

2.1. Approach

Species distribution, abundance, and spatial patterns in community composition (or species turnover) are driven by multiple biological and physical factors, including threshold environmental tolerances and resource preferences, system connectivity, recruitment, climate shifts, and species interactions (McGlenn and Hurlbert, 2012). We apply the concept of turnover functions to delineate distinct ecoregions using random forest methods, specifically we: (1) quantify the extent to which environmental drivers (physical predictor variables) predict distribution patterns (biological abundance) for individual species; (2) assess the relative importance of predictor variables to species distributions; and (3) determine threshold values along the gradient of the predictor variable where species abundance shifts. To extend these methods to biological community assemblages, we then apply gradient forests to: (1) characterize the magnitude of change in the composition of biological communities along environmental predictor gradients and (2) identify critical values along the predictor gradients that correspond to threshold shifts in composition. A schematic of our overall approach is presented as a conceptual diagram in the appendix (Fig. A1)

We use random forest methods to recursively partition on species abundance, where splits are made at discrete values for a set of environmental predictor variables. The extent to which abundance shifts across partitions represents a metric for turnover in species abundance. By aggregating over species, weighting for relative predictor importance and goodness-of-fit for each species distribution model, we identify important environmental thresholds and produce functions that represent turnover in biological communities along each predictor gradient. Centroid-based clustering methods are then applied to partition the ecosystem into coherent spatial units (e.g. ecoregions) on the basis of distinct breakpoints in community composition. Finally, the persistence and inter-annual stability of ecoregion boundaries is evaluated. We use data across a time series of available bottom trawl surveys (1982–2012) to delineate ecoregions within the EBS LME and compare distinct temperature regimes within the time series (2000–2005, 2006–2011; Fig. 2).

2.2. Data

We used data collected by the Resource Assessment and Conservation Engineering (RACE) Division of the Alaska Fisheries Science Center, NOAA, which has conducted annual, standardized bottom trawl surveys since 1982 (Lauth, 2012). Each June–August, the EBS shelf (approximately 488,000 km²) is systematically surveyed at depths ranging from 20 to 200 m. An 83–112 eastern otter trawl is deployed from chartered vessels at 376 standard stations in a sampling grid with 20 × 20 nautical mile cells (Fig. 1, top right). Species abundance data for each station were standardized to an index of catch per unit effort (CPUE), by dividing catch weight (kg) by area swept (ha), estimated as mean net width multiplied by distance towed (Alverson and Pereyra, 1969).

Depth, bottom temperature and surface temperature data were available for each tow and used to develop mean values per station across years. To further characterize temperature and hydrographic structure, we used data compiled from depth-temperature traces and digital bathythermograph recorders (BTR) attached to the headrope of the trawl net deployed in bottom trawl surveys (Buckley et al., 2009) to determine surface mixing and stratification within each depth-temperature profile. In the area of the shelf south of 60° N, temperature is the primary determinant of density

(Stabeno et al., 1999; Stabeno et al., 2012a,b) and the most complete representation of physical structure of the water column (Kachel et al., 2002). Top layer depth (m) was calculated as the deepest of contiguous points within 1 °C of surface temperature. Bottom layer depth (m) was calculated as the shallowest of contiguous points within 1 °C of bottom temperature. Transition layer extent (m) was the difference between bottom layer and top layer depth. Mean, maximum, and minimum temperatures were calculated using data from all tows at a particular station. Thermocline depth was calculated as the depth of the maximum rate of decrease in temperature (as a function of increasing depth). The areal extent of the cold pool was calculated as the area (km²) of bottom temperatures < 2 °C within the sampled shelf. The cold pool index is a standardized estimate of the fraction of the survey area covered by bottom water < 2 °C.

Sediments were assessed using the NOAA EBSSD database of surface sediments (Smith and McConnaughey, 1999), a compilation of historical (1934–1997) point-sample data ($N=2587$) from all available sources (Fig. 1, middle right). Data were used to develop standardized statistics characterizing grain size (phi, negative log₂ diameter in mm), variation in grain size (sorting coefficient), percent composition by weight of various size grades (e.g. gravel, sand, mud, silt, clay), and a relative index of coarseness (percent sand and/or gravel). To link sediment type data to standardized trawl survey stations, we interpolated values using inverse distance weighting methods (Fig. 1, bottom right). We then related raster fields on sediment type to trawl stations via zonal statistics (ArcGIS v9.3).

2.3. Analytical methods

2.3.1. Assignment of species to functional group

Species were classified to functional groups on the basis of mean percent total weight of prey in the diet (<http://access.afsc.noaa.gov/REEM/WebDietData/DietTableIntro.php>). As per Garrison and Link (2000), we categorized fish as pelagic planktivores, benthivores, demersal piscivores, and pelagic piscivores based on pathway and content in the diet. Invertebrates were categorized by their use of habitat (Table 1). As per Mueter and Litzow (2008) arctic species were distinguished as those with > 50 percent total biomass in areas < 2 °C.

2.3.2. Criteria for inclusion of species in analyses

In most long-term bottom trawl surveys, there are discrepancies in precision of species identification over time. Some species aggregated to genus or family early in the time series are identified to species in later years. To ensure consistency over time we aggregated species to groups where necessary to ensure a common level of identification over time. To prevent errors in over-representing rare or inadequately sampled species, persistence plots were used to determine whether to include a given species or aggregated group in our analyses (Genner et al., 2004). The species ($n=126$) and aggregate groups ($n=57$) included in our analyses account for 99.89% of surveyed biomass in the EBS.

2.3.3. Contour plots of temperature and depth

To visualize how temperature and depth might shape the ecosystem, contour plots were developed. Contour plots of selected individual species were developed using mean weighted biomass (1982–2012).

2.3.4. Random forests

To assess importance of physical variables on individual species distributions, we applied random forest methods (package

Table 1
Functional guilds.**Planktivores**

Pacific herring (*Clupea pallasii*), Arctic cod (*Boreogadus saida*), Saffron cod (*Eleginus gracilis*), Walleye pollock (*Gadus chalcogramma*), Eulachon (*Thaleichthys pacificus*), Capelin (*Mallotus villosus*), Rainbow smelt (*Osmerus mordax*), Prowfish (*Zaprora silenus*), Pacific ocean perch (*Sebastes alutus*), Dusky/dark rockfish (*Sebastes* spp.), Northern rockfish (*Sebastes polyspinis*), Yellow Irish lord (*Hemilepidotus jordani*), Butterfly sculpin (*Hemilepidotus papilio*)

Benthivores

Flathead sole (*Hippoglossoides elassodon*), Bering flounder (*Hippoglossoides robustus*), Rex sole (*Glyptocephalus zachirus*), Yellowfin sole (*Limanda aspera*), Longhead dab (*Limanda proboscidea*), Sakhalin sole (*Limanda sakhalinensis*), Starry flounder (*Platichthys stellatus*), Rock sole (*Lepidopsetta* spp.), Buttersole (*Isopsetta pleuronectes*), Alaska plaice (*Pleuronectes quadrituberculatus*), Sawback poacher (*Leptagonus frenatus*), Sturgeon poacher (*Podothecus accipenserinus*), Bering poacher (*Ocella dodecaedron*), Searcher (*Bathymaster signatus*), *Gymnocanthus* sp., Threaded sculpin (*Gymnocanthus pistilliger*), Armorhead sculpin (*Gymnocanthus galeatus*), Spectacled sculpin (*Triglops septicus*), Ribbed sculpin (*Triglops pingeli*), Spinyhead sculpin (*Dasycottus setiger*), Thorny sculpin (*Icelus spiniger*), Icelus species (*Icelus* spp.), Snailfish unident. (*Liparidae* spp.), Variegated snailfish (*Liparis gibbus*), Salmon snailfish (*Careproctus rastrinus*), Eelpout unident. (*Zoarcidae* spp.), Marbled eelpout (*Lycodes raridens*), Wattled eelpout (*Lycodes palearis*), Polar eelpout (*Lycodes turneri*), Shortfin eelpout (*Lycodes brevipes*)

Pelagic piscivores

Arrowtooth flounder (*Atheresthes stomias*), Kamchatka flounder (*Atheresthes evermanni*), Greenland turbot (*Reinhardtius hippoglossoides*), Pacific sleeper shark (*Somniosus pacificus*), Sablefish (*Anoplopoma fimbria*), Pacific sandfish (*Trichodon trichodon*), Chum salmon (*Oncorhynchus keta*)

Demersal piscivores

Pacific cod (*Gadus macrocephalus*), Alaska skate (*Bathyraja parmifera*), Pacific halibut (*Hippoglossus stenolepis*), Whitespotted greenling (*Hexagrammos stelleri*), Rougheye/Blackspotted rockfish, Bigmouth sculpin (*Hemitripterus bolini*), Bering wolffish (*Anarhichas orientalis*), Warty sculpin (*Myoxocephalus verrucosus*), Great sculpin (*Myoxocephalus polyacanthocephalus*), Plain sculpin (*Myoxocephalus jaok*)

Crab

Red King crab (*Paralithodes camtschaticus*), Blue king crab (*Paralithodes platypus*), Graceful decorator crab (*Oregonia gracilis*), Tanner crab (*Chionoecetes bairdi*), Circumboreal toad crab (*Hyas coarctatus*), Pacific lyre crab (*Hyas lyratus*), Snow crab (*Chionoecetes opilio*), Hybrid Tanner crab (*Chionoecetes hybrid*), Helmet crab (*Telmessus cheiragonus*), Hermit crab unident. (*Paguridae*), Sponge hermit (*Pagurus brandti*), Aleutian hermit (*Pagurus aleuticus*), Splendid hermit (*Labidochirus splendescens*), Knobbyhermit hermit (*Pagurus confragosus*), Fuzzy hermit crab (*Pagurus trigonocheirus*), Alaskan hermit (*Pagurus ochotensis*), Longfinger hermit (*Pagurus rathbuni*), Hairy hermit crab (*Pagurus capillatus*)

Motile invertebrates

Seastars (15), Basket Star (*Gorgonocephalus eucnemis*), Brittlestars (3), Urchins (3), Common sand dollar (*Echinarachnus parma*), Sea cucumbers (2), Gastropods (26), Scyphozoa (5)

Benthic infauna

Clams (5), Blue mussel (*Mytilus trossulus*), Weathervane scallop (*Patinopecten caurinus*), Shrimp (4), Worms (6)

Sessile invertebrates

Anemones (9), Ascidians (9), Bryozoans (2), Corals (4), Sea Whips (2), Sponges (2)

randomForest, R Development Core Team 2011) to data on abundance (species biomass) at discrete sites (survey stations). Random forests (Breiman, 2001) are comprised of regression trees, where sample sites are partitioned into two groups such that species abundances at sites within each partition are as homogeneous as possible. Partitioning occurs at a specific split value v for each predictor p (e.g. 0.2 °C for temperature), and at each partition, the split is selected to minimize impurity or the sum of squared deviations about the group mean. Partitions are recursively split until a partition becomes a terminal node. At each node in the tree, the importance of a split is measured as the reduction in impurity or the amount of variation explained by the partition.

A random forest aggregates results from an ensemble of regression trees to develop synthesized output with high classification accuracy, accounting for interactions among predictor variables (Liaw and Wiener, 2002; Cutler et al., 2007). Each tree is fit to an independent bootstrap sample of the data (resampling with replacement) and each partition within a tree is split on the best of a random subsample of the predictor variables. For each tree, data not selected in the bootstrap sample are termed the out-of-bag (OOB) data and used to provide a cross-validated estimate of generalization error. Random forests provide three relevant metrics: the goodness-of-fit R_s^2 for species s , the importance I_{sp} of each predictor p , and the raw importance value I_{spvt} for that predictor at each split value v in each tree t . Predictor importance I_{sp} quantifies the contribution of a predictor to the model goodness-of-fit by computing the prediction error of the model without the predictor and comparing it to the prediction error of the full model. Specifically, I_{sp} is estimated as the increase in OOB mean square prediction error when the predictor is randomly permuted while other variables in the model remain constant, effectively removing the predictor signal.

The goodness-of-fit R_s^2 (proportion of variance explained in a random forest) for species s is defined as

$$R_s^2 = 1 - \sum_i (X_{si} - \hat{X}_{si})^2 / (X_{si} - \bar{X}_s)^2 \quad (1)$$

where X_{si} is the i th abundance observation, \hat{X}_{si} is the OOB prediction, and \bar{X}_s is the mean abundance.

The goodness-of-fit R_s^2 for each random forest is partitioned among predictor variables in proportion to their importance I_{sp} , such that R_{sp}^2 (predictor p for species s) is calculated as

$$R_{sp}^2 = \frac{R_s^2 I_{sp}}{\sum_p I_{sp}} \quad (2)$$

The importance of a predictor variable for the entire biological community (R_p^2) is estimated by averaging R_{sp}^2 across all species, such that

$$R_p^2 = \frac{1}{N} \sum_s R_{sp}^2 \quad (3)$$

Correlation matrices were developed to examine multi-collinearity among environmental predictor variables (Figs. A2–A4). On this basis we removed minimum and maximum temperatures, as these closely mirrored top and bottom temperatures. To address correlations between remaining predictor variables, we applied a conditional permutation approach developed by Strobl et al. (2008), where values for each predictor were permuted only within data defined by splits on any other predictors that were correlated above a threshold of $r=0.5$ (Ellis et al., 2012).

2.3.5. Gradient forests

To establish where community composition changes occur along a given environmental gradient, we applied gradient forest

methods, which integrate results from individual random forest analyses over a suite of species. While random forest methods quantify the extent to which environmental variables predict species distribution patterns and the relative importance of each variable to the predictions, gradient forests quantify shifts in the composition of the aggregate biological community along environmental gradients and identify threshold values where important breakpoints occur. These methods develop flexible, non-parametric functions to quantify species turnover or threshold shifts in abundance for multiple species in response to physical predictors (R Package gradientForest, Ellis et al., 2012).

We developed a physical data matrix (sites-by-environment) and a log transformed biological abundance matrix (sites-by-species):

$$\log(y + \min(y, y > 0)) \quad (4)$$

where y is the abundance at the 334 survey stations and $\min(y, y > 0)$ is the minimum positive abundance at each station.

Estimates of turnover in community composition along the gradient of each physical predictor p were generated by distributing R^2 values from all species among predictors in proportion to predictor importance I_{sp} and along the gradient of values for each predictor according to the density of raw importance values I_{spvt} . In random forests, the importance associated with a split value along a predictor gradient indicates the relative change in species abundance. Therefore, species turnover is reflected in split importance. For each predictor p , the split values v and importance values at each split I_{spvt} were assembled from every tree in random forests for each species s . For each species, importance values I_{spvt} were standardized by the density of observed values for each predictor p and normalized to sum to R_{sp}^2 . Individual species turnover $F_{sp}(x)$ along a predictor gradient was defined as a monotonic function with minimum 0 and maximum R_{sp}^2 , proportional to the importance of splits. This allowed us to depict cumulative shifts in species abundance along each predictor gradient and estimate the importance for any given predictor value x . Community composition turnover $F_p(x)$ or shifts in the assemblage of aggregate biological communities along each predictor variable was estimated as mean $F_{sp}(x)$ over all species (Pitcher et al., 2012). The derivative $f_p(x)$ of $F_p(x)$ is the compositional turnover rate at any given predictor value (Ellis et al., 2012). F_p provides a means to transform each physical predictor to

biological units reflecting turnover in community composition. By applying this function to each predictor in sequence, we developed a spatial map of inferred biological community composition on the basis of multi-dimensional environmental data.

2.3.6. Ordination and projection of survey stations according to biological composition

Using cumulative functions to transform grid data layers of environmental data into a common biological scale, we applied F_p to quantify community responses along predictors. By taking the principle components of the transformed data we used ordination to represent the data as a biplot of survey stations where coordinate position represents different patterns in species composition, as associated with the predictors. The environmental variables were superimposed on this plot as vectors indicating the direction and magnitude of the most important environmental predictors.

2.3.7. Cluster analyses of sampling sites to delineate distinct ecoregions

We applied centroid-based approaches (partitioning around medoids, PAM, R package cluster; Kaufman and Rousseeau, 1990) to identify survey stations that exhibited similar patterns in biological community composition on the basis of gradient forest output. We clustered stations in a manner that minimized the sum of dissimilarities. These clusters were used to define distinct ecoregions.

3. Results

3.1. Contour plots of species distribution by temperature and depth

The influence of the cold pool in the middle domain (50–100 m) is clearly evident in contour plot of the surveyed area (Fig. 3). Contour plots of select individual species also suggest the cold pool shapes and constrains species distributions (Fig. 3). Certain species (e.g. demersal piscivores, Pacific cod, Pacific halibut) appear to range across temperature and depth gradients, whereas other (e.g. pelagic piscivores, arrowtooth flounder, Greenland turbot) appear largely constrained by depth and temperature gradients. There are also important differences by age and life stage as demonstrated by walleye pollock (*Gadus chalcogramma*).

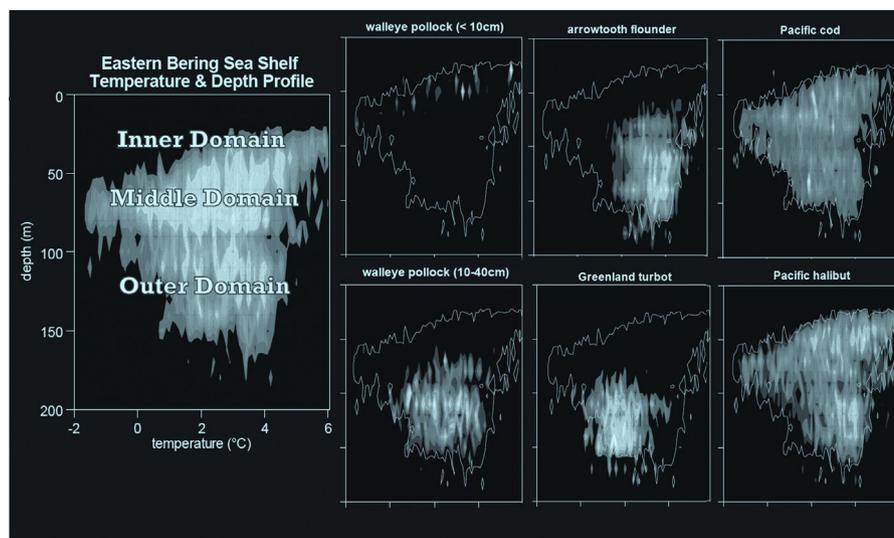


Fig. 3. Contour plots of relative species density (biomass) according to bottom temperature and depth (lighter areas indicate higher densities). A contour plot of the entire system outlines the three main domains of the eastern Bering Sea shelf (left). Distributions for select individual species are shown with an outline of the system-wide footprint superimposed on each species graph for reference.

Table 2
Model performance by species, R_s^2 .

Functional guild	No. species	Mean R_s^2 (range)
Pelagic piscivore	7	0.77 (0.68–0.92)
Benthivore	34	0.70 (0.27–0.91)
Crab	18	0.69 (0.19–0.88)
Planktivore	13	0.68 (0.23–0.87)
Demersal piscivore	10	0.65 (0.44–0.85)
Motile invertebrates	56	0.55 (0.08–0.93)
Benthic infauna	17	0.49 (0.14–0.80)

3.2. Overall model performance and relative fit for individual species

Random forests tended to provide a better fit (Table 2) to species that had a strong response to dynamic predictor variables such as temperature. The most prevalent species also tended to drive observed patterns, such that the relationship between log species abundance and R_s^2 was significant ($R^2=0.27$, $P=0.024$). Overall, performance of random forests (R_s^2) was higher for upper trophic level species (fish, $R^2=0.68 \pm 0.20$ SE, $N=55$; in contrast to invertebrates, $R^2=0.55 \pm 0.21$, $N=135$). Distributions for pelagic piscivores ($R^2=0.82 \pm 0.04$, $N=5$) and benthic flat fish ($R^2=0.81 \pm 0.15$, $N=10$) were particularly well fit, reflecting relatively defined distributions that shift in extent and range over time in response to dynamic environmental variables, such as temperature. Demersal piscivores ($R^2=0.65 \pm 0.04$, $N=11$) and planktivorous forage fish ($R^2=0.56 \pm 0.08$, $N=13$) were not fit as well, reflecting broad habitat ranges, use of diverse prey resources, and relative insensitivity to dynamic environmental variables in the former, and highly variable patterns and poor sampling efficiency in the latter. As expected, the fit to distributions of motile invertebrates (crabs, $R^2=0.69 \pm 0.04$, $N=22$; gastropods, $R^2=0.59 \pm 0.03$, $N=27$; seastars and sea cucumbers, $R^2=0.55 \pm 0.06$, $N=20$; urchins, $R^2=0.48 \pm 0.06$, $N=3$; brittle and basket stars, $R^2=0.43 \pm 0.10$, $N=4$) reflected higher sensitivity to dynamic environmental variables than sessile invertebrates and benthic infauna (ascidians, $R^2=0.56 \pm 0.09$, $N=10$; corals and sea whips, $R^2=0.48 \pm 0.12$, $N=5$; bryozoans, $R^2=0.46 \pm 0.04$, $N=2$; anemones, $R^2=0.42 \pm 0.05$, $N=9$; sponges, $R^2=0.36 \pm 0.18$, $N=2$; worms, $R^2=0.58 \pm 0.08$, $N=5$; bivalves, $R^2=0.44 \pm 0.08$, $N=7$), suggesting sessile invertebrates may provide a good proxy for static habitat attributes, such as depth and substrate.

3.3. Cumulative importance of predictor variables for species and functional guilds

Cumulative plots display thresholds in species abundance and distribution to environmental factors (Fig. 4). Among benthivores, the ranges of individual species are distinguished from others in the guild by depth gradients (with a notable breakpoint at 100m) and by bottom temperatures (with notable breakpoints at -1°C , 2°C , 4°C , and 6°C). Rock sole species (*Lepidopsetta polyxystra*, *Lepidopsetta bilineata*) are also distinguished in associating with coarser substrates. Most demersal piscivores are generalists, ranging widely across depth gradients, temperatures and substrates, though Pacific halibut (*Hippoglossus stenolepis*) and skates (*Rajidae* spp.) demonstrate sensitivity to substrate coarseness and sculpins (*Myoxocephalus* spp.) to bottom temperature and depth. Among pelagic piscivores, individual species are largely distinguished by temperature gradients. Among planktivores, individual species are largely distinguished by bottom depth and mid-layer extent stratification, though most species are also sensitive to temperature.

3.4. Relative importance of predictor variables and important breakpoints along predictor gradients

Binned outputs from random forests on the location and importance of regression tree splits for species abundance on each environmental predictor gradient are depicted (Fig. 5). Breakpoints in biological communities and threshold shifts in the abundance of multiple species along a given physical gradients are identified at peak values (ratios > 1) in the density plot of the splits standardized by the observations (Fig. 5). For kernel density plots of the splits and observations separately, see Figs. A5 and A6. Important breakpoints in aggregate community composition are noted at latitude (57°N , 60.5°N), longitude (-164°W , -168°W , -173°W), surface temperature (5.5°C , 7.4°C , 8.4°C), bottom temperature ($-1-0^\circ\text{C}$, $1-2^\circ\text{C}$, 3.5°C), depth (40 m, 80 m, 100 m), and at four separate grades of substrate coarseness. Based on the eigenvalue or latent root, depth was the strongest explanatory physical predictor, followed sequentially by latitude, bottom temperature, longitude, range of temperature within the water column, bottom layer depth, surface temperature, mid-layer extent, and substrate coarseness and composition (R_p^2 , Fig. 6, left).

3.5. Biplot of species distribution and orientation of biological communities according to environmental predictors

Shifts in biological community composition along predictor gradients via cumulative functions were used to transform environmental data layers into biological scales. We present the transformed multi-dimensional biological space as a product of ordination (Table A1) presenting the first two dimensions (principle components) as a biplot (Fig. 6). The first two principle components account for 63% of total variance. Coordinate position represents inferred biological community compositions, as associated with the physical predictors variables (represented as vectors). To examine how individual species distribute across the system, we superimpose the weighted mean location of select species (Fig. 7). Planktivore species (Fig. 7, panel 1) range mostly in shallow areas; individual species within the guild vary by surface temperature, bottom temperature, temperature range and stratification. Pelagic piscivores (Fig. 7, panel 2) are generally found at depth and vary within the guild by temperature. Demersal piscivores (Fig. 7, panel 3) are relatively evenly spread across various physical predictor gradients. Benthivores (Fig. 7, panel 4) also range over most physical variables, but distinctions between species within the guild are noted according to depth, bottom temperature, and substrate coarseness. Snow (*Chionoecetes opilio*) and Tanner (*Chionoecetes bairdi*) crab distributions contrast by bottom temperature (Fig. 7, panel 5), whereas blue (*Paralithodes platypus*) and red (*P. camtschaticus*) king crab, as well as echinoderm taxa (Fig. 7, panels 6 and 7, plot 6) are distinguished by a combination of bottom temperature, substrate and depth. Sessile invertebrates (Fig. 7, panels 8 and 9), benthic infauna (Fig. 7, panel 9, plots 4 and 5), and bivalves (Fig. 7, panel 7, plots 1–3) are almost exclusively distinguished by substrate coarseness, sediment type, and depth and may therefore serve as viable proxies for static habitat features.

3.6. Delineation of EBS ecoregions

Using clustering (PAM) to aggregate survey stations based on similar community composition (Fig. 8), we define six distinct ecoregions within the EBS shelf (Table 3 and Fig. 9). We noted distinct trends moving from the inner to outer shelf and distinctions between latitudes at $\sim 60^\circ\text{N}$. Across the time series, the inner shelf represents a consistent ecological region and a distinct region

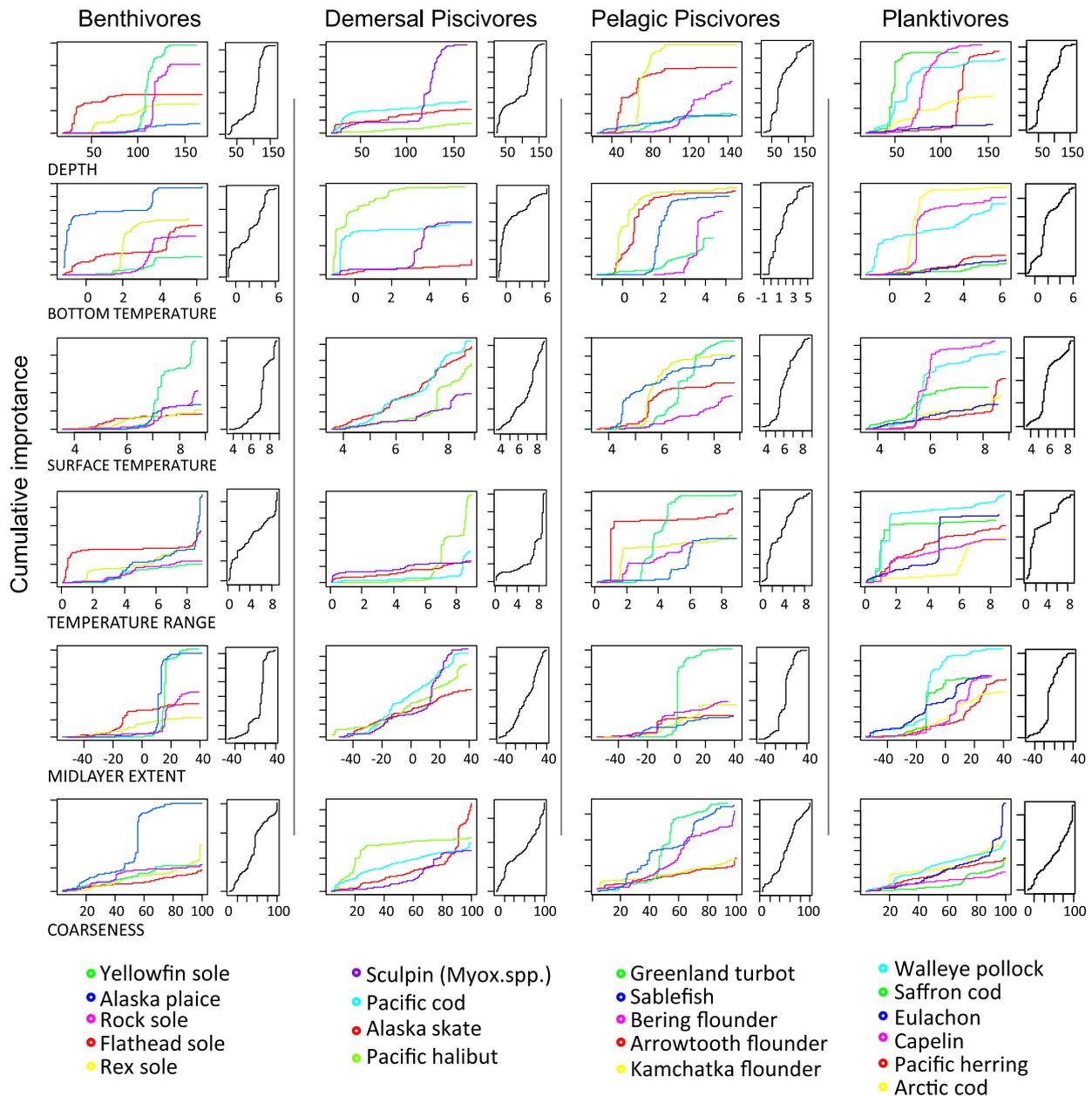


Fig. 4. Cumulative importance plots display cumulative shift (in R^2 units) of species abundance across the gradient of select environmental predictors. The common scale allows for the direct comparison of multiple species within each functional guild. Plots (colored, left) display prominent species from benthivore, pelagic planktivore, demersal piscivore and pelagic piscivore guilds. Plots (grayscale, right) display the aggregate response for each functional guild to a given environmental predictor. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this paper.)

is also identified along the outer shelf or slope. Within the middle domain and at island complexes, complex dynamics are observed, reflecting the dynamic nature of the environmental conditions and complex cross-shelf processes within these areas.

3.7. Attributes of EBS ecoregions: physical structure and biological community

Attributes of the individual ecoregions are summarized (Table 4). The inner shelf has an extensive spread along coastal areas with relatively warm and stable water temperatures and coarse substrates. The biological community in this ecoregion has relatively high concentrations of forage fishes, sessile invertebrates, and red king crab, with the notable absence of arctic species and pelagic piscivores (Fig. A7i and ii). A middle–inner domain spans relatively shallow depths between 40 and 70 m

with relatively cold water temperatures and a broad range of species in the system with the notable exception of deepwater species (Fig. A7i and ii). A Southern domain spans the lower latitudes with moderate temperatures, fluctuating stratification patterns, and high substrate coarseness. This area has a relatively diverse assemblage of species (Fig. A7i and ii). A Northern domain occupies higher latitudes with the coldest water temperatures. This is the primary area for arctic species and capelin, corals, and blue king crab (Fig. A7i and ii); deep and warm water species are largely absent. A middle–outer domain encompasses consistently deep waters along an extensive latitudinal gradient with high variation in water temperatures and low substrate coarseness. This region contains high concentrations of both pelagic and demersal piscivores, echinoderms, and crab, but low abundance of sessile invertebrates (Fig. A7i and ii). The Shelf Break spans the entire shelf-slope interface and contains the

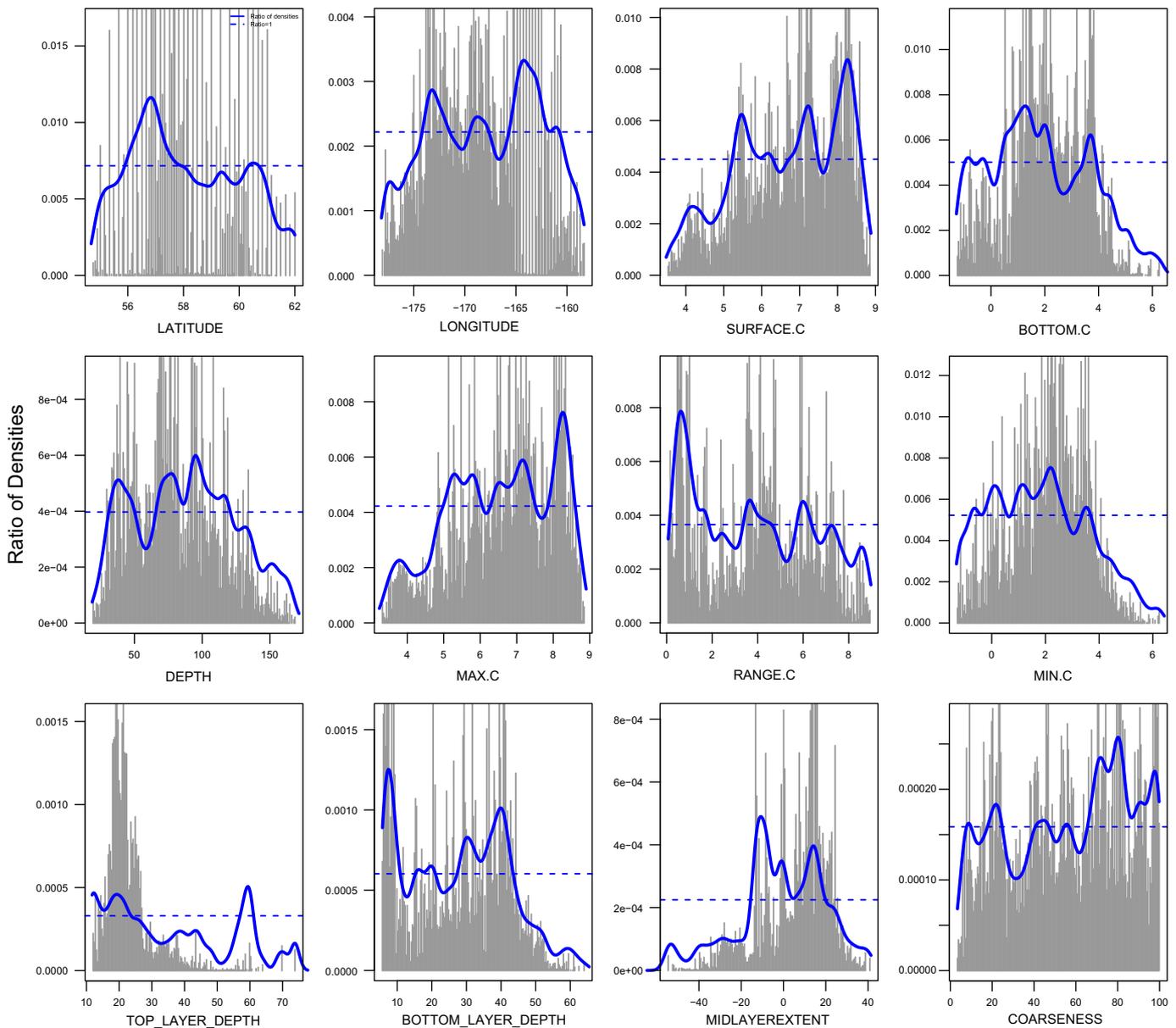


Fig. 5. Plots indicate threshold shifts in the abundance of multiple species along the gradient of a given environmental predictor, reflecting a rate of change in composition of the aggregate biological community. The gray histograms display the binned raw importance of splits from random forests for individual species relative to the environmental predictor variable on the horizontal axis. Density plots (lines) illustrate the estimated importance $f_p(x)$ or community turnover rate at any given predictor value, which is estimated as the ratio of the density of split importance (density of split values weighted by importance) to the density of observed predictor values along the predictor gradient. The horizontal dashed line indicates where the ratio is 1. Ratios > 1 indicate locations of relatively greater change in community composition, such that peaks in the density plot indicate threshold values for each environmental predictor where community composition is expected to shift.

deepest areas as well as the widest range of depths in the system; temperatures are relatively stable. The Shelf Break is the exclusive habitat for some deepwater species and supports relatively high abundance of pelagic piscivore species. There is a notable absence of arctic species and low abundance of forage fishes and benthic flatfishes (Fig. A7i and ii).

3.8. Climate fluctuations: evaluating the stability of ecoregion boundaries

Results from gradient forests analyses of warm (2001–2005) and cold (2006–2010) periods were similar to each other (Figs. 9 and 10) and to results that integrated over the entire time series (Fig. 6). This suggests relatively stable structuring of the system over time. Still, there were important differences, mainly that the Northern domain extends southward in cold years and retracts

northward in warm years. The expansion of the Northern domain seems to represent a constraint to subarctic species, but not an explicit benefit to arctic species, given the relationship between species abundance and cold pool extent (Fig. A8). Similar though non-significant trends were noted in indices for mean water column temperature, thermocline, and cold pool index (Fig. A8).

4. Discussion

We present a detailed overview of selected physical drivers influencing individual species distributions within the EBS and illustrate an approach to integrate biological and physical data to delineate ecoregions using statistical and geospatial analyses of biological community composition and physical habitat. Identifying ecologically significant units within LMEs is a necessary

and important step in defining units for spatial management and ecosystem approaches to management. Community ecology (which focuses on species diversity) and ecosystem ecology (which focuses on the physical processes that structure interactions) both offer insight into the ordering of complex ecosystems. Merging these perspectives is critical to holistic understanding of ecosystem functioning (Loreau, 2010).

4.1. Delineation and application of ecoregions

One element identified as an essential component of ecosystem-based approaches to fishery management is spatial resolution (National Marine Fisheries Service, 2000). This requires understanding population dynamic processes, species movement over time and space, stock structure, and habitat within a spatial

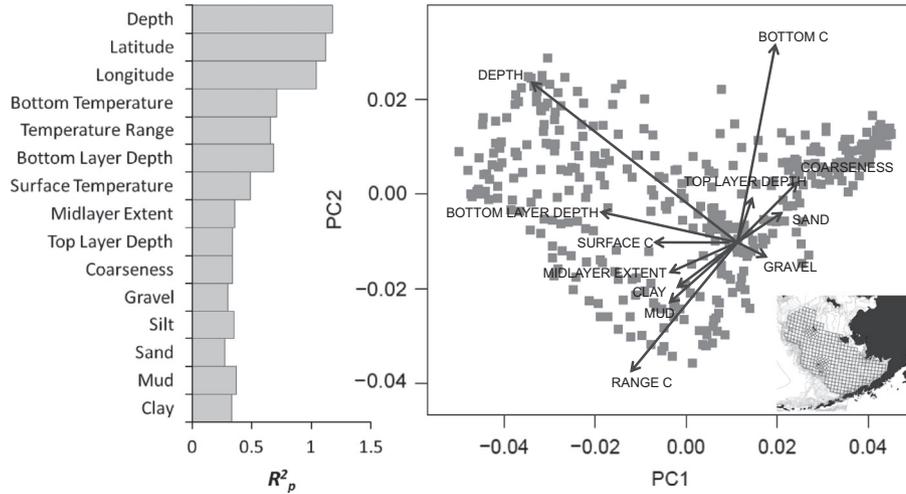


Fig. 6. Bar plot (left) of relative importance of environmental predictor variables weighted across species outputs (R^2_p), where temperature is indicated as °C. Biplot of survey stations (right), where each individual point represents a sample station in the standard EBS bottom trawl survey. Coordinate position represents inferred community composition patterns, displayed as a biplot of the two principle components with all environmental variables used in the analysis displayed as vectors. Map of survey stations is provided as a reference (inset).

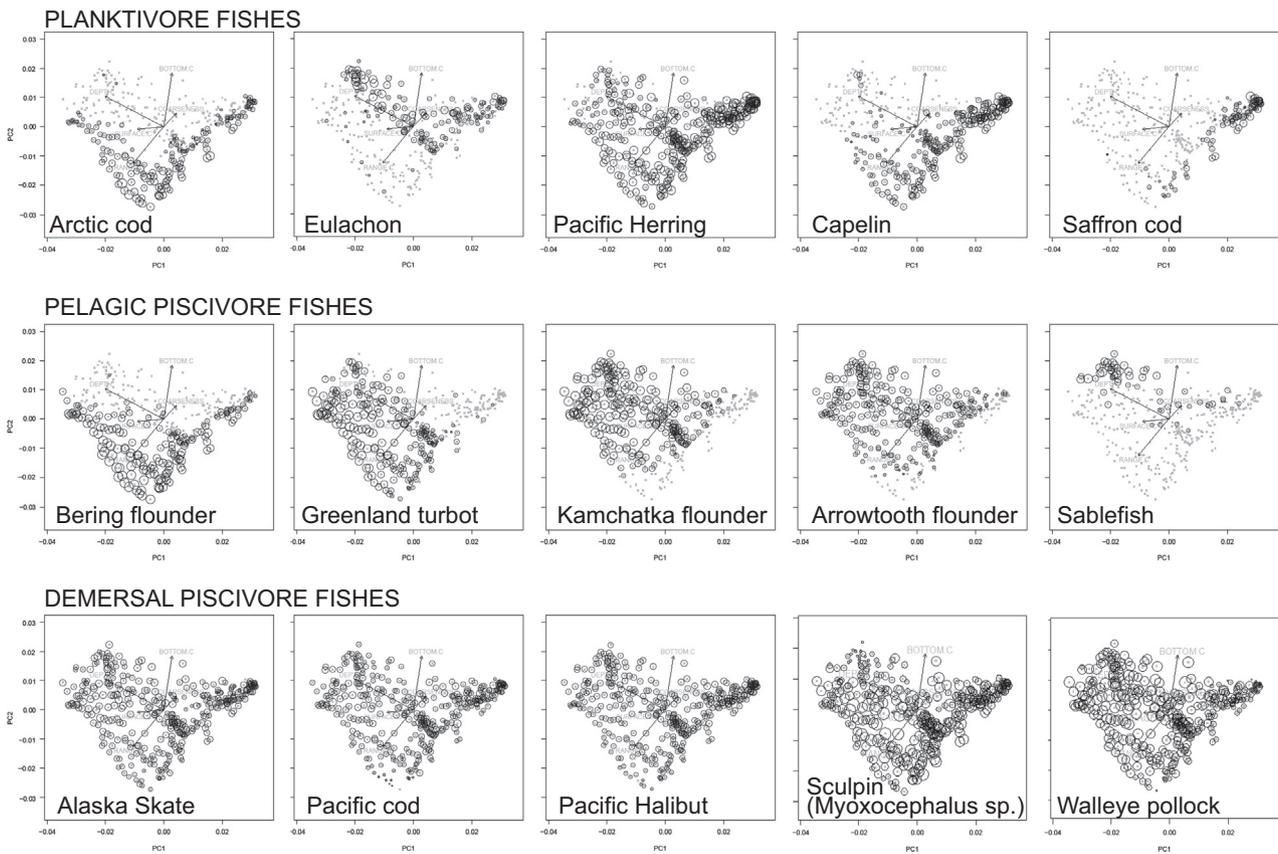


Fig. 7. Biplot of survey stations and environmental predictor vectors overlaid with weighted species abundance per station. Results demonstrate how individual species respond to multiple environmental variables and how individual species distributions compare to the system as a whole. Species are organized by function guild according to row. Note that invertebrates are integrated in random and gradient forest analyses as individual species, but aggregated in this figure to generalize trends. Trends for individual species within an aggregate group may differ.

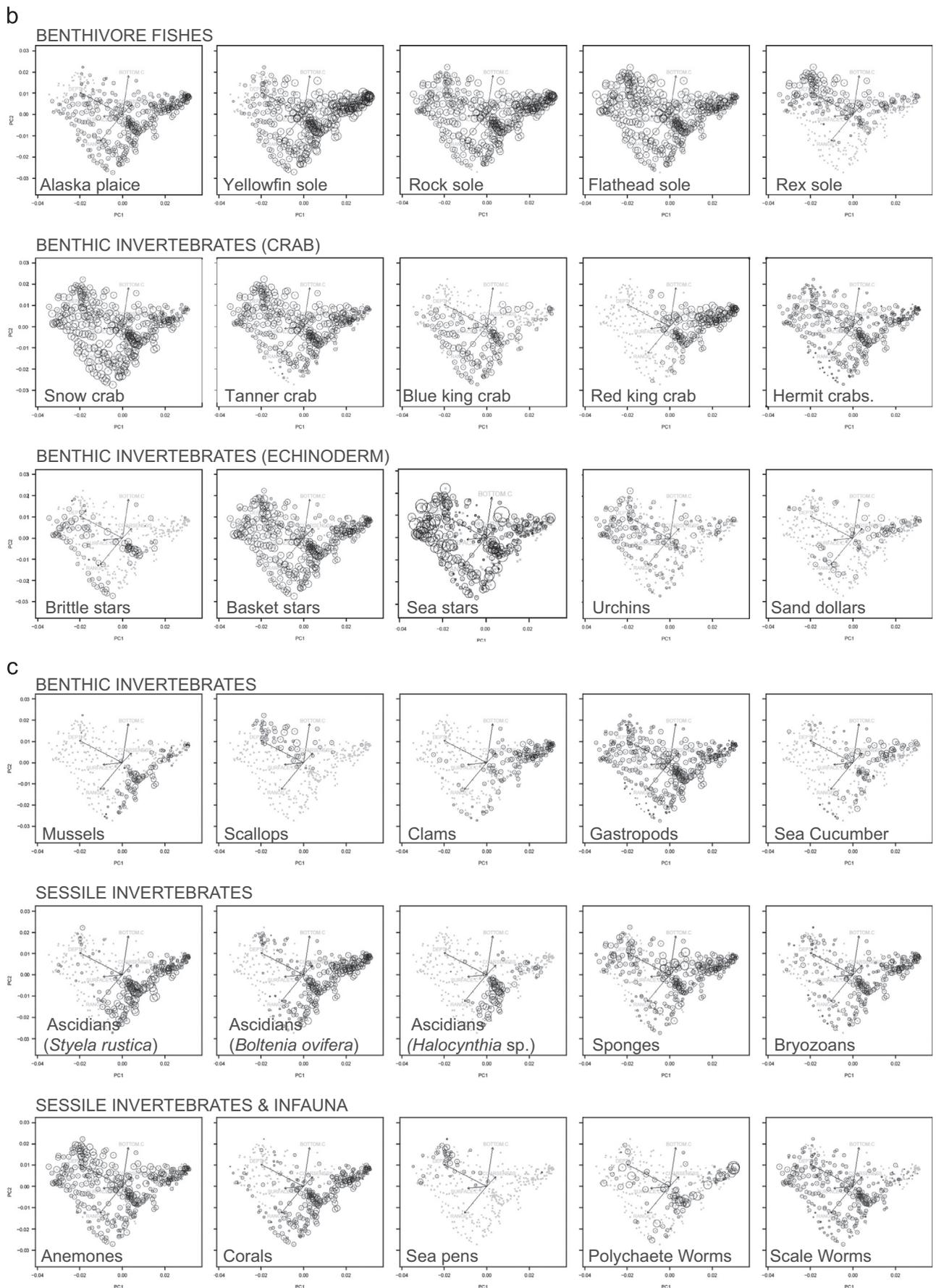


Fig. 7. (continued)

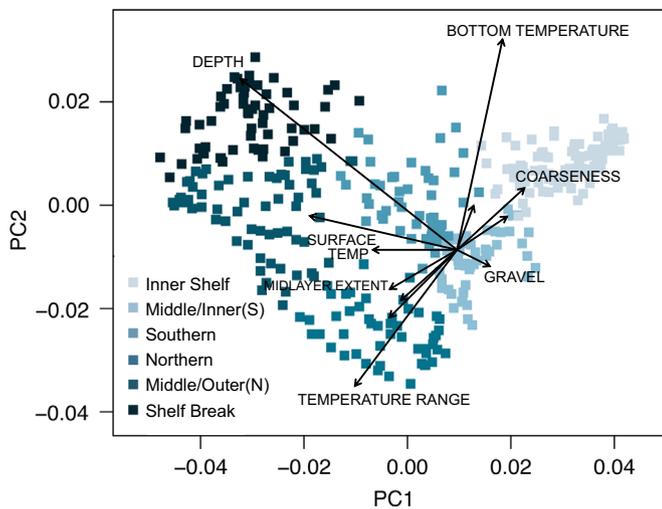


Fig. 8. Biplot of inferred community composition displays the results of the clustering (PAM) of survey stations, such that individual stations are grouped according to similarity in physical attributes (according to their relative position along the suite of environmental predictor vectors) and inferred species assemblages (species weighting associated with those vectors).

Table 3

Dissimilarity index for separation of survey stations into ecoregions. Isolation indicates relative distinctness between regions (the Northern region is most distinct).

Ecoregion	No. stations	Maximum dissimilarity	Mean dissimilarity	Isolation
(1) Inner shelf	101	0.023	0.010	0.900
(2) Middle/inner (south)	48	0.019	0.009	0.965
(3) Southern	59	0.022	0.010	1.155
(4) Northern	50	0.027	0.011	2.057
(5) Middle/outer (north)	64	0.020	0.012	1.035
(6) Shelf break	54	0.018	0.009	0.949

context. The concept of ecoregions is useful in identifying key biological features and ecological processes that define unique areas and govern their dynamics (Piatt and Springer, 2007). Our results delineate regional habitats within the EBS LME on the basis of distinct ecological attributes. These outputs are intended to inform habitat assessment and valuation, inform analyses of potential interactions in multispecies models, and set the framework to better integrate spatially discrete environmental effects and species interactions into stock assessments.

4.2. Physical drivers and cross-shelf transport via wind advection

Several key drivers and forcing mechanisms structure the EBS shelf. Depth is a critical defining feature. While not necessarily the primary driver of species distributions, depth is often a convenient predictor (Levin and Dayton, 2009). Temperature is another critical predictor of species distribution in the EBS. Critical processes regulated by temperature control and thermal tolerance include survival and reproduction (Hutchins, 1947). Stratification within the water column also creates distinct environmental conditions and barriers to movement and was an important factor in our analysis. There is less consensus on the relative importance of physical features such as sediment (Levin and Dayton, 2009). While our analysis found sediment to have low relative influence on species distributions, in a broad shallow shelf system dominated by benthic and demersal pathways, sediment data may be informative; properties such as hardness, porosity, permeability,

and displacement (none of which were examined here) influence the presence of fixed benthic invertebrates, prey availability, and predatory interactions.

Results of our analysis identified unique dynamics at island groups and distinct breakpoints between ecoregions along frontal boundaries. This suggests patterns consistent with studies of oceanographic processes that have revealed complex geostrophic currents at the Pribilof Islands and St Matthews Island (Stabeno et al., 2008) and the importance of frontal regions in concentrating prey resources (Lang et al., 2000; Coyle and Pinchuk, 2002; Stabeno et al., 2012a,b). We also noted cross-shelf patterns in the middle domain, possibly explained by wind-forced vectors that drive advection of nutrients and recruitment in this dynamic area. Circulation patterns in shelf flow alternate largely on the basis of wind direction, with westerly winds promoting off-shore transport and less frequent southeasterly winds associated with on-shelf transport across the shelf break (Danielson et al., 2012). Incorporating salinity data into future analyses (where available) may be instructive. In contrast to temperature gradients, which are predominantly along-isobath, salinity gradients are generally oriented cross-isobath (Danielson et al., 2011). Cross-isobath exchange has implications for both macronutrient (Whiteledge and Luchin, 1999) and micronutrient (Aguilar-Islas et al., 2007) transport and availability (Wespestad et al., 2000).

4.3. Comparison of EBS ecoregions to past biogeographic analyses of the system

Piatt and Springer (2007) define an ecoregion as an area distinguished from adjacent areas according to physiographic attributes (e.g. coastal, continental shelf, slope, basin) and bounded according to oceanographic processes (e.g. frontal boundaries and currents). Our results (arrived at through alternate means) reflect these attributes. Our delineation of ecoregions correspond to patterns recognized by previous classification schemes, which have divided the EBS along depth domains and latitudinal gradients. As in the previous studies (Stabeno et al., 2008; Hollowed et al., 2011; Ortiz, 2012), we also note unique patterns at canyons and island groups, related to recirculation patterns and topographic irregularities that create persistent oceanographic features and environments that support distinct fauna.

Integrating expert knowledge and previously established survey strata and ecological domains, Ortiz (2012) used the overarching structure of the conventional domains and applied regularly-spaced divisions along a North-South axis, designating several latitudinal divisions. Our analyses distinguishes only one (at approximately 60°N), which marks the approximate location of March minimum ice extent and corresponds to patterns in cross-shelf flow noted by Kinney et al. (2009) and Hollowed et al. (2012). Our analysis of discrete warm and cold phases, demonstrates how this boundary may shift based on climate and ice extent, such that the expansion of a Northern ecoregion is roughly associated with the extent of the cold pool. A workshop convened by the Nature Conservancy and World Wildlife Federation to distinguish biological features and ecological processes in the Bering Sea (Banks et al., 1999) identified four unique areas: (i) Bristol Bay; (ii) the Yukon-Kuskokwim Delta and Nunivak Island; (iii) the Golden Triangle (bounded by Bogoslof Island, the Pribilof Islands, and Izembek Lagoon); and (iv) the Bering Sea Shelf Break. The Inner, Southern and Shelf Break ecoregions defined in our analysis closely match the Bristol Bay, Golden Triangle and Bering Sea Shelf Break, respectively. Our Southern ecoregion is distinguished by physical processes such as tidal mixing, eddies and currents, which contribute to high levels of primary and secondary production. Our Shelf Break ecoregion is defined by the Bering Slope

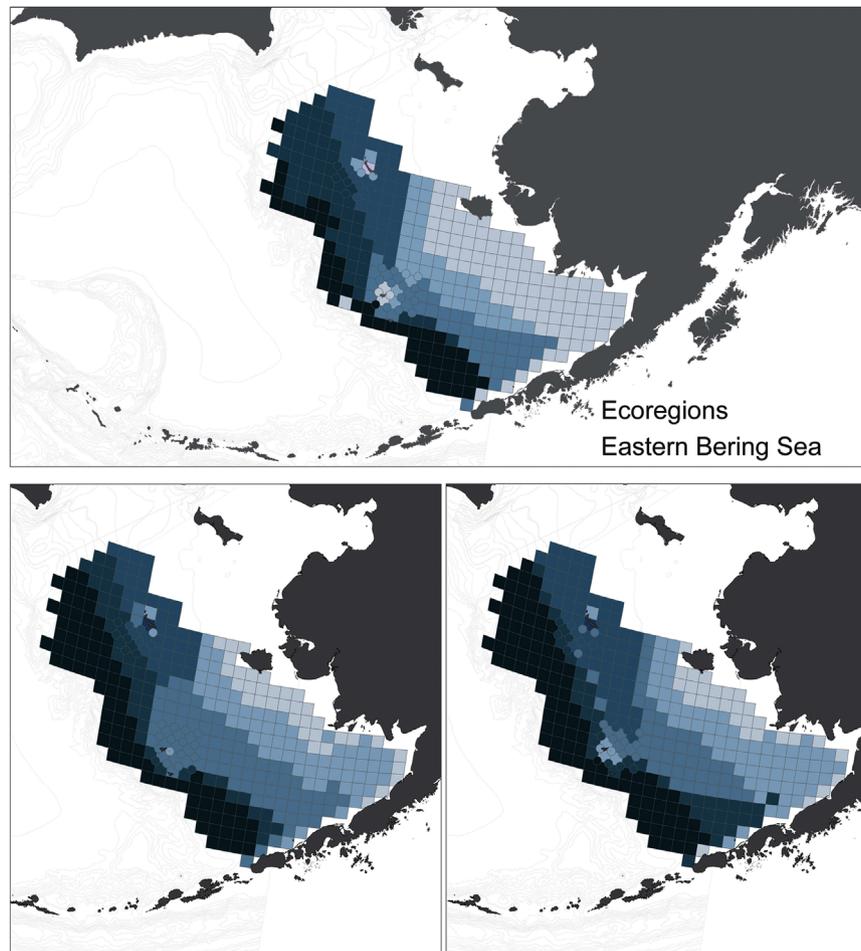


Fig. 9. Delineation of ecoregions based on the clustering of survey stations to represent distinct biological communities. Ecoregions are displayed for the entire time series (top graph) as well as for recent warm (2001–2005, bottom left) and cold (2006–2010, bottom right) years.

Current and marks the transition between basin and shelf dynamics, serving as a thermal refuge and area of enhanced biological productivity.

In general, our results support the conventional separation of the shelf according to major oceanographic boundaries, such as fronts associated with the 50 m and 100 m isobaths (Coachman, 1986), the Alaska Coastal Current, Bering Slope current, and circulation patterns in the southwestern Bering Sea (Stabeno et al., 1999). These domains are defined by relatively persistent bottom topography and current flow. However, we also recognize complex patterns in the inner and middle shelf, driven by a combination of substrate, temperature, and cross-shelf wind and geostrophic velocity vectors representing thermohaline circulation. While flow is generally along traditional frontal boundaries, advective corridors can transect the 100 m outer front and disrupt middle domain coherence, such that flow crosses from the outer to middle domain north of the Pribilof Islands and continues towards northeast towards St. Matthew Island (Hollowed et al., 2012). This cross-shelf flow corresponds with the proximate outline of our latitudinal divide between northern and southern ecoregions and may explain shifting patterns in ecoregion boundaries in the middle domains between distinct time periods (Fig. 9). On the inner shelf, south of the Pribilofs and landward of the 50 m isobaths, thermohaline flow is weak with areas of recirculation (Hollowed et al., 2012). This may explain the results of our composite analysis (across all years), which characterize the Inner Shelf as one large ecoregion. Conversely, shifts in the strength of thermohaline dynamics and recirculation patterns in distinct cold

and warm periods may explain why our analyses on shorter time frames (cold and warm phases) characterize this area as two distinct ecoregions (Fig. 9).

4.4. Strength of approach

Recent species-specific analyses of how environmentally driven shifts (Spencer, 2008; Kotwicki and Lauth, 2013) and bioclimatic windows (Cheung et al., 2008) drive patterns in spatial distribution have provided important insights to marine ecology in the context of climate variability and change. Comprehensive analyses examining broad-scale community metrics, particularly in the Northwest Atlantic (Fogarty and Keith, 2009; Zwanenburg et al., 2010; Pepin et al., 2010) have also better informed our understanding of marine systems. Pepin et al. (2010) note that the use of variables such as biomass, diversity, and richness often aggregate areas that differ fundamentally in taxonomic diversity and in the functional communities represented in these areas. Our analyses address this by incorporating community composition within our approach to regional partitioning. With regard to the EBS, Piatt and Springer (2007) note that cross-shelf boundaries are conspicuous and defined by persistent fronts or topographic gradients, whereas along shelf boundaries are more subtle and may be better resolved by patterns in biological characteristics. By integrating biological and physical data, we provide a more nuanced view of regional scale patterns.

Although we are able to integrate across a relatively extensive time series of data, we only have a snapshot of spring/summer

Table 4
Ecoregion characteristics.

Ecoregion	Latitude	Depth	Temperature	Stratification	Substrate
Physical characteristics					
Inner shelf	Extensive spread across latitude (55–60°N) and longitude (–158 to –170°W)	Shallow (range: 19–69 m) (mean=42 ± 12 m SD)	Stable temperatures Relatively cold surface (5 ± 1 °C) and warm bottom (3 ± 1 °C) temperatures. Narrow range in min/max values (2–7 °C) and low variation within the water column (1 °C)	Extensive top layer depth extending mostly to seafloor	Coarse (mean=80 ± 21%) Substrate entirely sand and gravel
Middle/inner (south)	Middle latitudes (57–61°N)	Relatively shallow Consistent depths (range: 41–69 m) (mean=61 ± 7 m SD)	Relatively cold surface 96 ± 1 °C and bottom (1 ± 0 °C) temperatures. Considerable range in min/max values (0–7 °C), and some variation within the water column (4 °C)	Extensive stratification (top layer depth 19 ± 3 m, bottom layer depth 22 ± 3 m) with minimal middle layer (3 ± 5 m)	Relatively coarse (mean=56 ± 16%). Substrate largely sand with areas of mud and silt
Southern	Low latitude (55–58°N)	Mid-range (range: 67–96 m) (mean=79 ± 8 m SD)	Moderate surface (7 ± 1 °C) and bottom (2 ± 1 °C) temperatures Moderate range in min/max values (2–8 °C), and some variation within the water column (4 °C)	Minimal, but variable middle layer (6 ± 12) (top layer depth 23 ± 8, bottom layer depth 29 ± 6)	Relatively coarse (mean=68 ± 19%). Sand with extensive areas of mud and silt
Northern	High latitude (58–62°N)	Mid-range (range: 58–94 m) (mean=75 ± 10 m SD)	Coldest bottom temperatures Warm surface (7+0 °C) and cold bottom (0+1 °C) temperatures Wide range in min/max values (0–9 °C), and extensive variation within the water column	Even partition of water column (top layer depth 17 ± 2 m, bottom layer depth 32 ± 5 m, middle layer 15 ± 4 m)	Low coarseness (mean=27 ± 15%). Substrate largely mud with areas of silt and clay
Middle/outer (north)	High latitude (56–62°N)	Consistently deep (range: 94–148 m) (mean=114 ± 15 m SD)	Moderate range temperatures (surface 8 ± 0 °C, bottom 2 ± 1 °C) Wide range in min/max values (–1–8 °C), and extensive variation within the water column (7 °C)	Highly stratified (top layer depth 21 ± 2 m, bottom layer depth 45 ± 5 m) with extensive middle layer 24 ± 6 m)	Low coarseness (mean=23 ± 15%). Substrate mud, silt, and clay
Shelf break	Extensive spread across latitude (51–61°N)	Deep Wide range of depth, including deepest and shallowest areas sampled (range: 12–171 m) (mean=131 ± 43 m SD)	Stable temperatures Relatively warm surface (8 °C) and bottom (4 °C) temperatures Moderate range in min/max values (1–9 °C), and some variation within the water (4 °C)	Highly variable water column (top layer depth 28 ± 10 m, mid-layer depth 19 ± 24 m, bottom layer depth 47 ± 19 m)	Moderately coarse (mean=48 ± 21) with high variation (3–100). Substrate equal mud, silt, sand
Biological characteristics					
Inner shelf	Relatively high concentrations of forage fish (saffron cod, capelin, eulachon, herring) and flat fish (yellowfin sole, Alaska plaice, rock sole). Arctic species (eelpout, snailfish) and pelagic piscivores (arrowtooth flounder, Kamchatka flounder, Greenland turbot) are absent. High abundance of fixed sessile invertebrates (e.g. ascidian, bryozoans, sponges, tube worms), sea cucumber and red king crab				
Middle/inner (south)	Relatively uniform representation of fish species, with lower relative abundance of warm and deepwater species (e.g. rex sole, eulachon, sablefish, Kamchatka and arrowtooth flounder, rockfish), demersal piscivore (e.g. Pacific halibut, Pacific cod, skates) and flat fish species (e.g. yellowfin sole, flathead sole, rock sole, Alaska plaice) and higher relative abundance of arctic species (e.g. arctic cod, snailfish, Bering flounder), fixed sessile invertebrates, and polychaetes				
Southern	Relatively low abundance of arctic species (e.g. arctic cod, snailfish, Bering flounder) and relatively high abundance of pelagic piscivores (e.g. Kamchatka and arrowtooth flounder), scallop, sand dollar, sea cucumber, and sponge				
Northern	Predominant area for arctic species (e.g. arctic cod, snailfish, eelpout, Bering flounder) and also for populations of Greenland turbot, capelin, coral and blue king crab. Deepwater (e.g. sablefish, rockfish), or warm water and southern ranging species (e.g. Kamchatka flounder, arrowtooth flounder, eulachon) species are largely absent				
Middle/outer (north)	Relatively high abundance of pelagic piscivore (e.g. Greenland turbot, Kamchatka and arrowtooth flounder) and arctic fish species (e.g. arctic cod, snailfish, Bering flounder, eelpout), echinoderm (e.g. brittle star, basket star, sea star, urchin), crab (e.g. blue king crab, hermit, Tanner, snow), gastropod, and octopus. Also characterized by relatively low abundance of fixed sessile invertebrates (e.g. coral, ascidian, bryozoans) and benthic infauna				
Shelf break	Exclusive habitat of deepwater species (e.g. sablefish, rockfish) and high abundance for pelagic piscivores (Kamchatka and arrowtooth flounder). Also characterized by the absence of arctic species and low relative abundance of forage fishes and benthic flatfishes				

temperatures. Important interactions occur in other seasons that have critical influences in determining distribution (see [Hunt et al., 2014](#)). Additionally, our analyses examine ecoregions as static

phenomena. It is clear, however, that as environmental gradients shift, climate regimes fluctuate, and relative species abundance vary within systems, boundaries may shift ([Wang et al., 2010](#)).

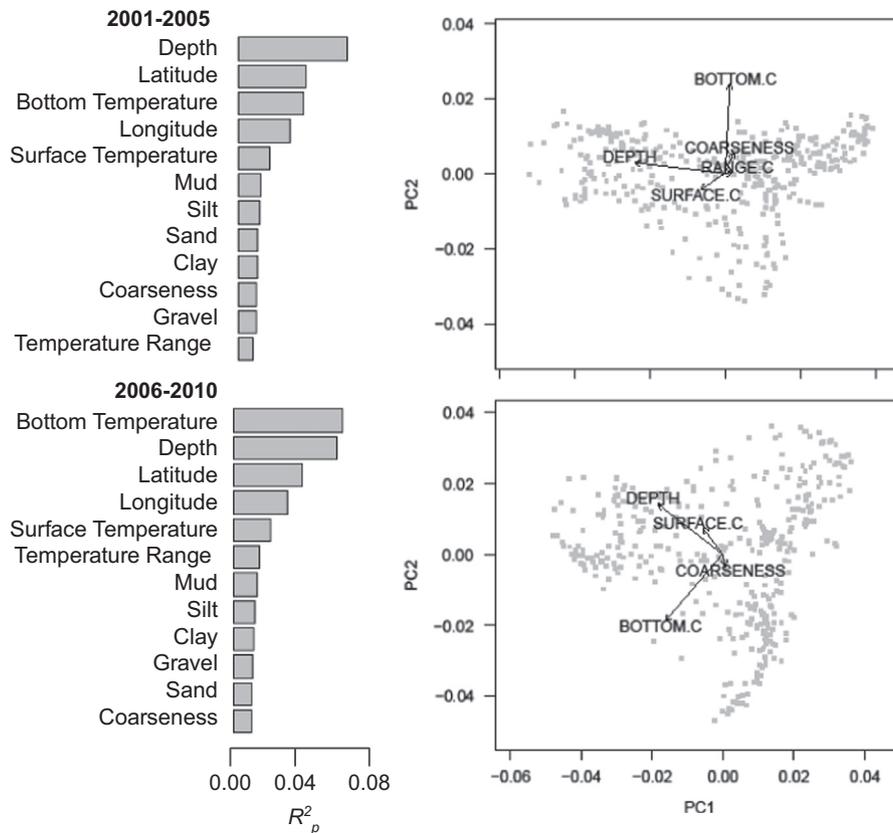


Fig. 10. Bar plot of relative predictor importance and projected biplots of survey stations according to predictor vectors for gradient forest outputs in warm (2001–2005) and cold (2006–2010) periods. Note that the relative importance of bottom temperature as a predictor variable differs across periods, ranking as the dominant variable in cold years, but third (behind depth and latitude) in warm years. Temperature range also ranks relatively higher as a predictor in cold years.

Climate variability and change will alter the volume of ecoregions within the EBS (Hollowed et al., 2012), resulting in shifts in interaction strength. We intend that our current results serve as a baseline against which to measure this phenomenon.

4.5. Practical applications

Our research approaches questions of broad-scale ecological interest in a manner that may inform practical understanding of species dynamics and their response to physical drivers. We highlight an analytical method that enables us to characterize unique regions on the basis of biological responses to physical processes and to project how the range and scope of such regions vary as a function of variables that shift in space over time. We use this method to delineate the EBS LME and to evaluate ecological dynamics at regional scales. We intend that our designation of ecoregions provide a framework for future analyses of the system, inform evaluations of ecological habitat, and serve as an important baseline for future analyses of the effects of climate change and fishing. Still, we note that ecosystem components overlap and interact at multiple scales (Levin et al., 2009); the appropriate scale of analysis will depend on the species, dynamics, and questions of interest. While our research investigates important drivers at relatively finite scales (20 nm × 20 nm scale of survey), processes that operate at broader ecosystem scales also drive patterns throughout the system. Moreover ecologically relevant boundaries may not correspond with boundaries appropriate to

policy, viable to management, or relevant to resource allocation or regulation. With that in mind, our results are designed to distinguish regional patterns nested within a hierarchical system of spatial management.

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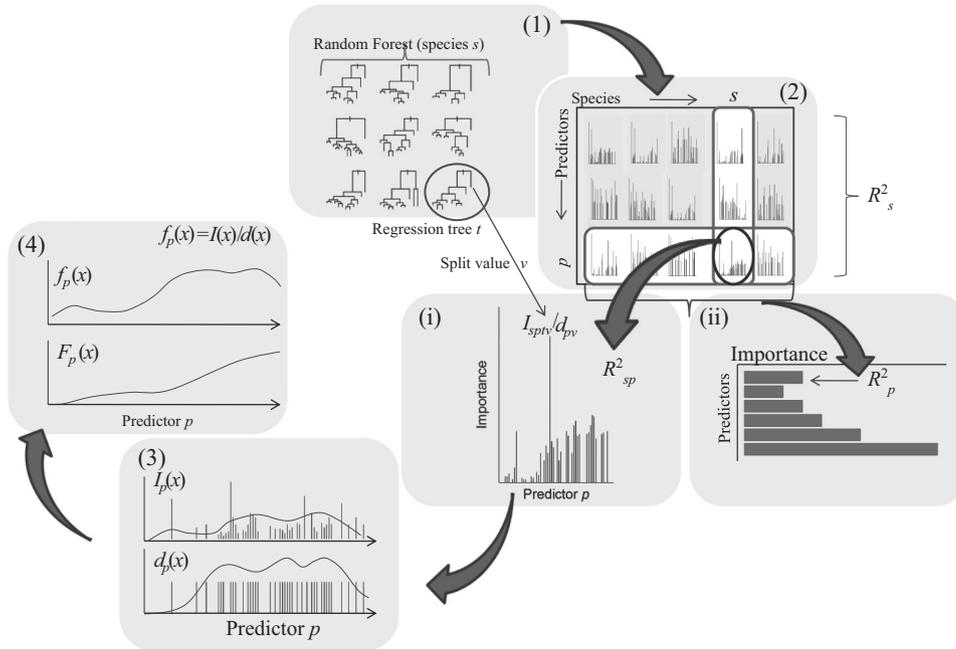


Fig. A1. Schematic of the analytical approach to random and gradient forest analyses. *Step I.* A random forest is generated for each species s , where the resulting model is a set of bifurcating trees (t) in which the nodes represent the predictor variables (environmental drivers) that split the response variable (species abundance) into partitions such that homogeneity within each partition is maximized (measured by the Gini index). Splitting continues until further partitioning does not reduce this index. The length of the branches following each partition indicates the relative importance of the partitioning variable as well as the predictor value at which the split occurs. Each random forest is an ensemble of regression trees, where bifurcations are selected from a set of best splits among a subset of environmental predictors. (Plot 1). *Step II.* The goodness of fit (R^2_s) of the random forest for each species is partitioned among the environmental predictors in proportion to their conditional importance (Plot 2, outlined column in Table 2). This provides an estimate of the relative importance (R^2_p) of each environmental predictor p for each species s (Plot 2, circled intersection of outlined row and column in Table 2). The overall importance (R^2_p) for an environmental predictor is determined as the mean across species (Plot 2, outlined row in table). *Step III.* For each predictor p in each random forest, the splits v and importances I_{spiv} are gathered from every tree t in the forest. The importances are standardized by the density of the predictor split values and normalized to sum to R^2_s (Plot 2i). *Step IV.* For each predictor p the normalized importances are gathered across species, and a combined importance density I_p is computed for each predictor value x along the gradient of the predictor (Plot 3). A combined estimate of the compositional turnover rate $f_p(x)$ is estimated as the ratio $I(x)/d(x)$ (Plot 4, top figure). A function for species turnover or shift in the composition of the biological community along the gradient of an environmental predictor variable $F_p(x)$ is estimated as the integral of $f_p(x)$ (Plot 4, bottom figure).

Modified from Ellis et al. (2012).

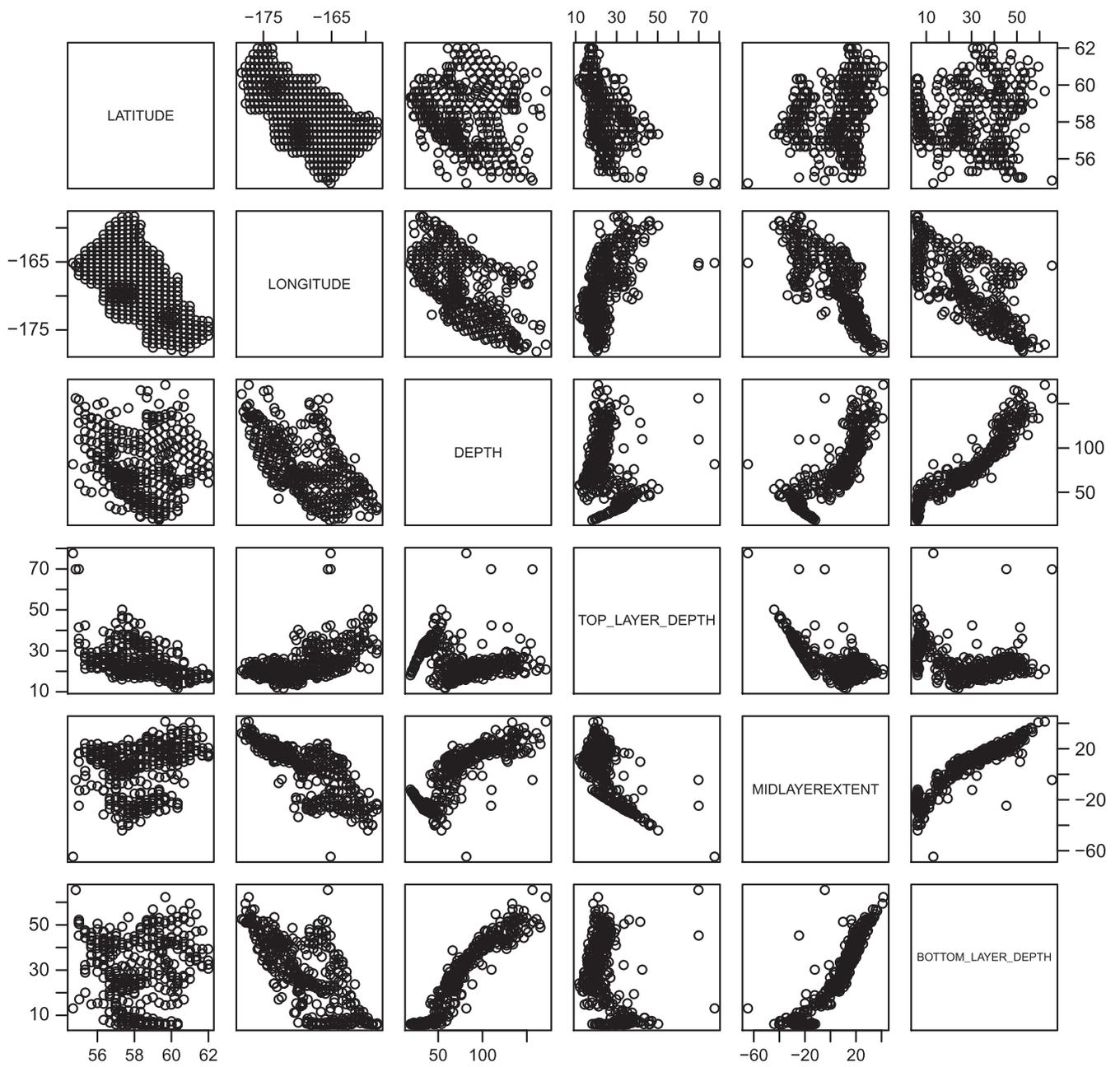


Fig. A2. Correlations between environmental predictor variables, including latitude, longitude, depth and stratification indices. Relationships between most predictor variables were significant (Pearson product-moment correlation, $P < 0.009$, Mean correlation, absolute value=0.59). Those without significant correlation were depth-latitude, depth-bottom temperature, and latitude-bottomlayer.

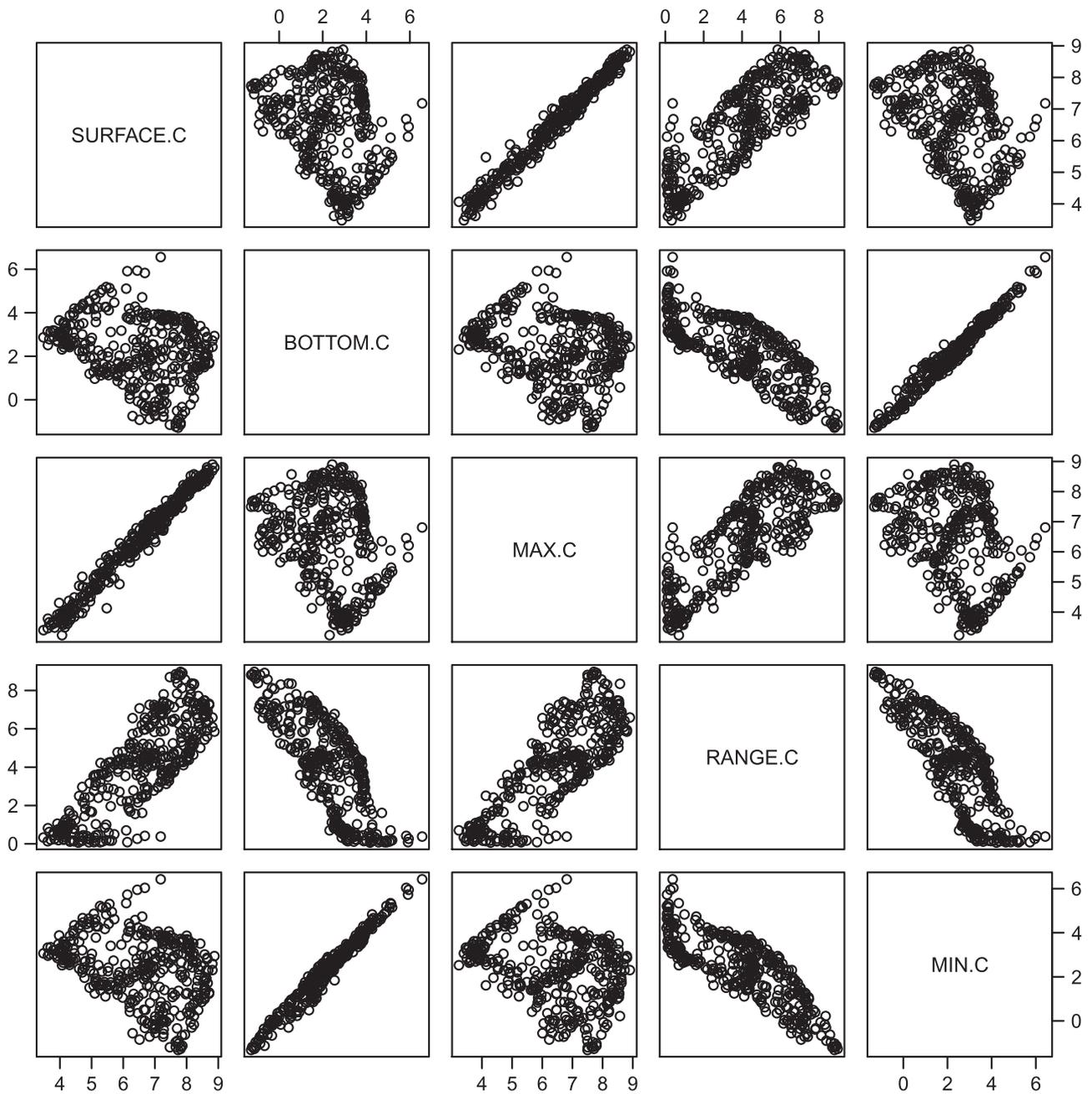


Fig. A3. Correlations between environmental predictor variables, including latitude, longitude, depth and water temperature indices. Relationships between most predictor variables were significant (Pearson product-moment correlation, $P < 0.009$, Mean correlation, absolute value=0.59). Those without significant correlation were depth-latitude, depth-bottom temperature, and latitude-bottomlayer.

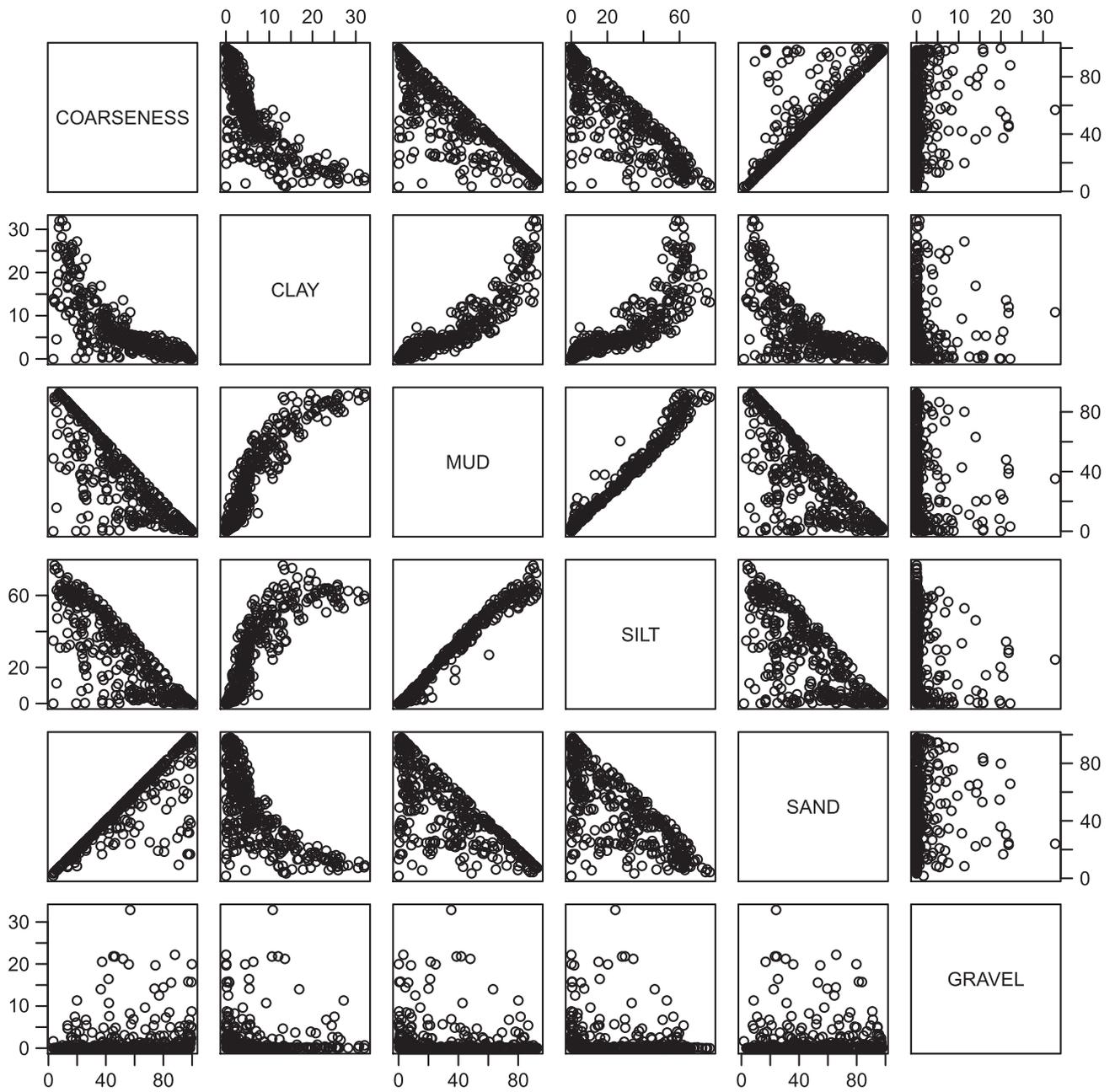


Fig. A4. Correlations between environmental predictor variables, including latitude, longitude, depth and sediment coarseness and substrate types. Relationships between most predictor variables were significant (Pearson product-moment correlation, $P < 0.009$, Mean correlation, absolute value=0.59). Those without significant correlation were depth-latitude, depth-bottom temperature, and latitude-bottomlayer.

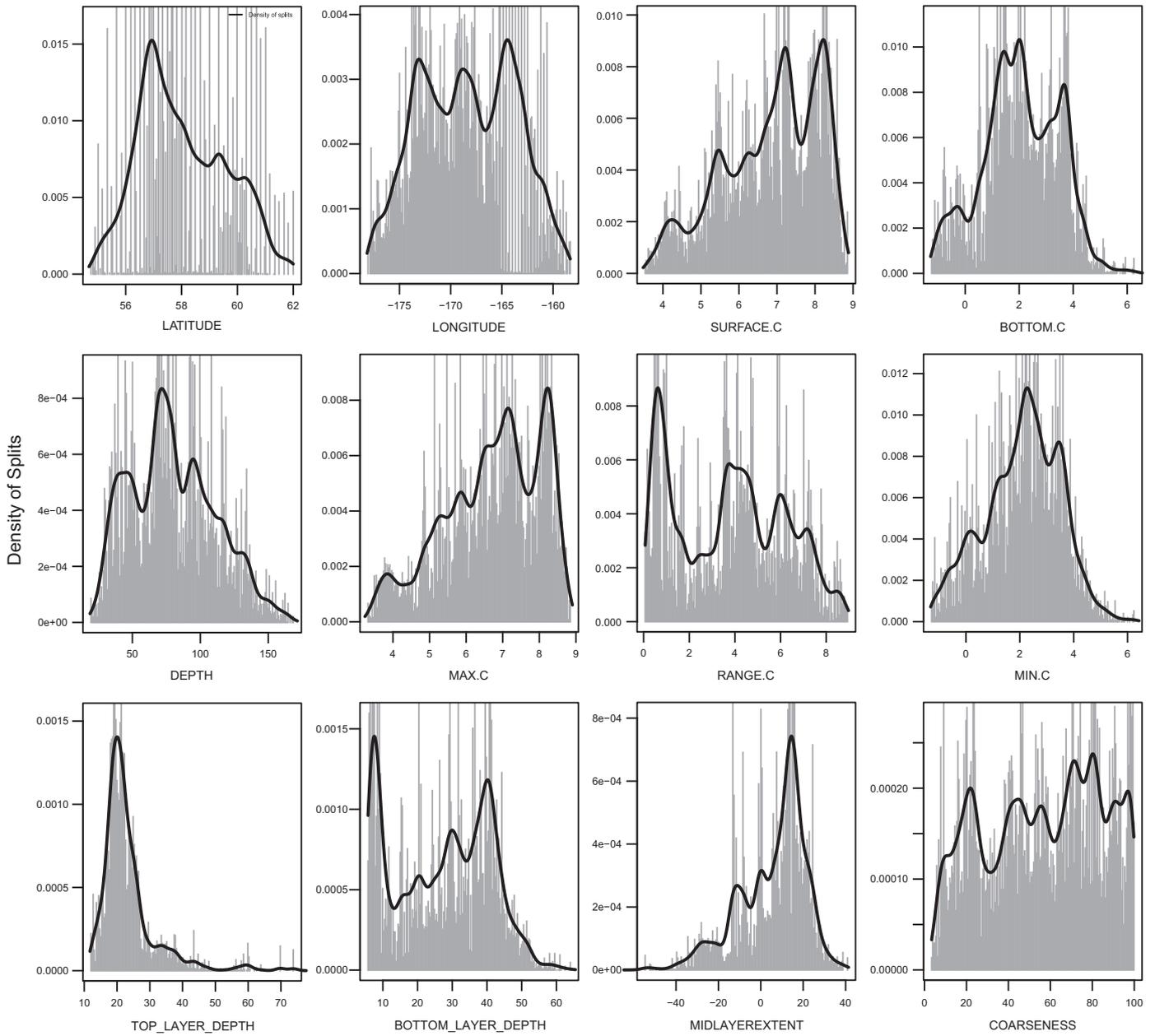


Fig. A5. Kernel density plot of the splits importance metrics from random forests of all species along each physical predictor gradient.

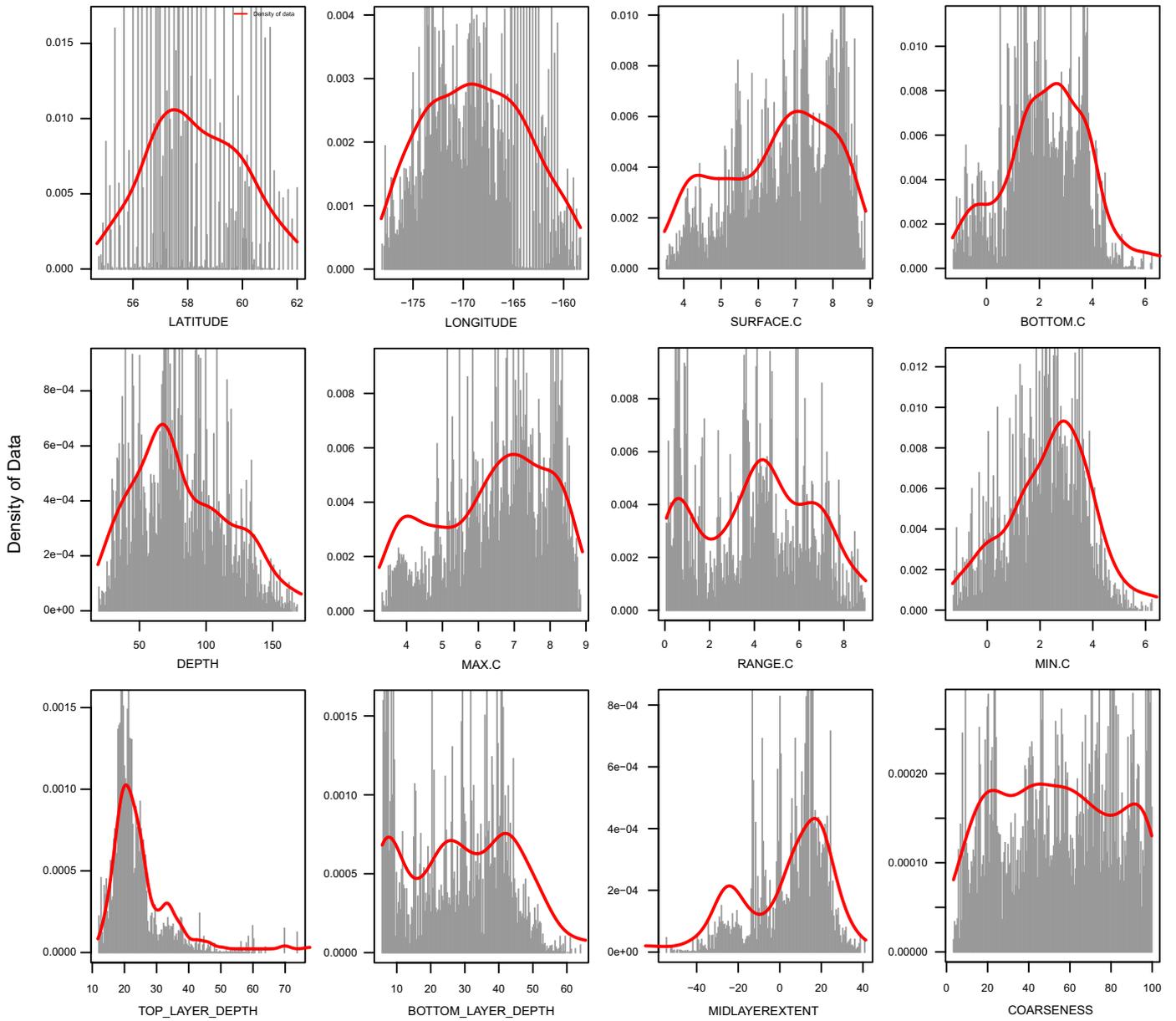


Fig. A6. Kernel density plot of the splits location from random forests of all species along each physical predictor gradient.

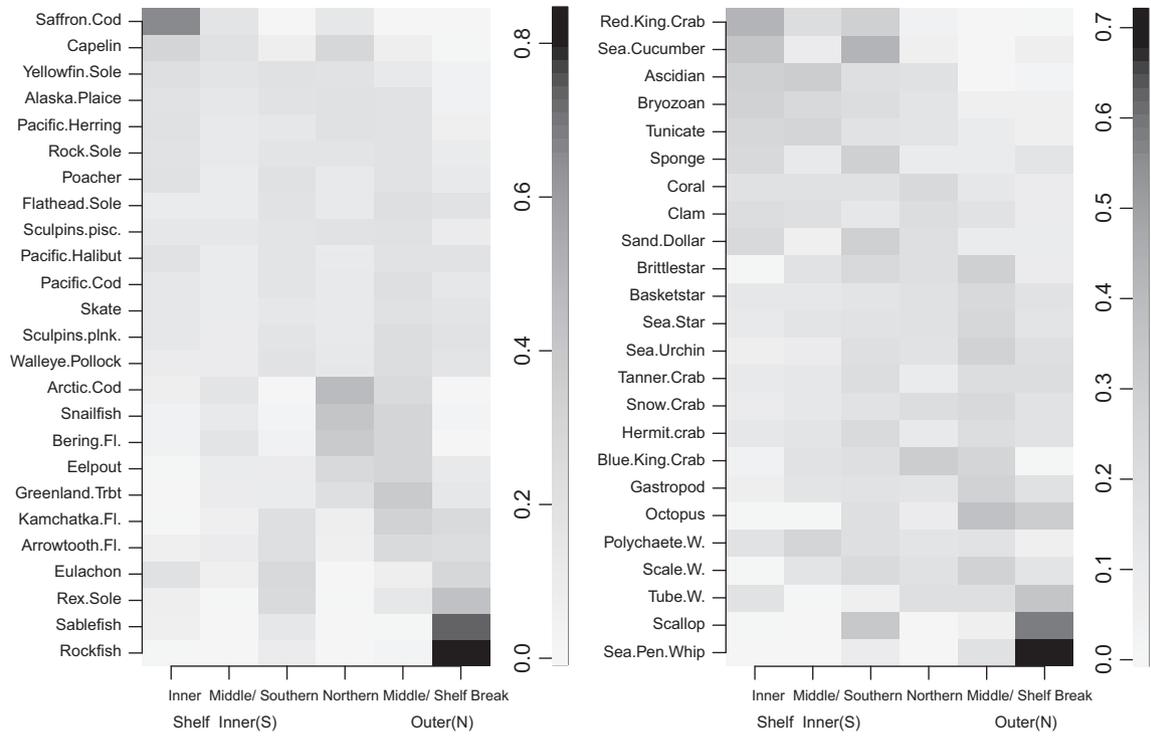


Fig. A7. Relative weighting of species abundance across ecoregions (vertebrates, i; invertebrates, ii). Darker colors indicate higher concentrations.

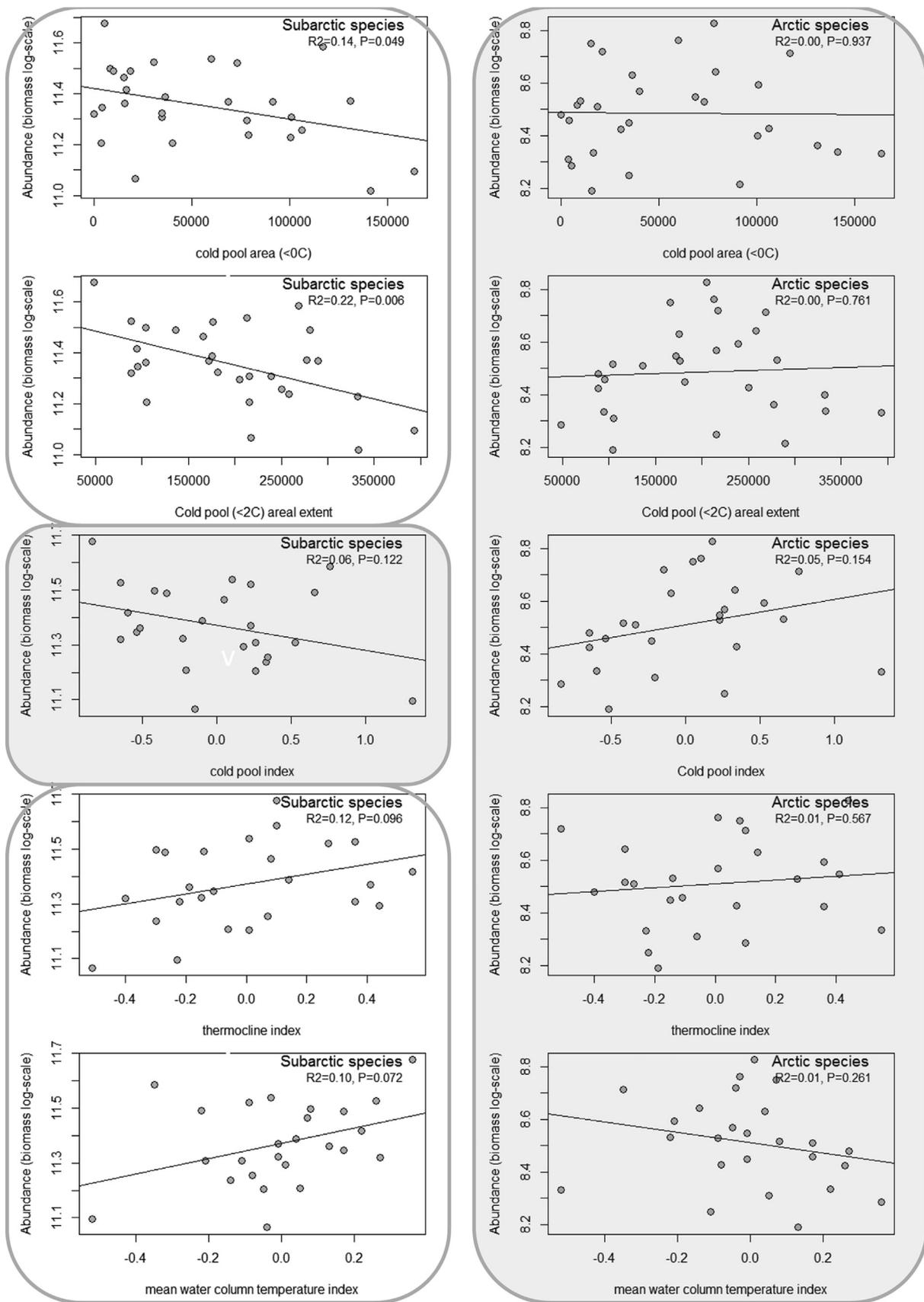


Fig. A8. Response of arctic species ($N=8$, right column) and subarctic species ($N=37$, left column) to the areal extent of the cold pool (0°C , 2°C), mean water column temperature, thermocline, and cold pool index. Plots with non-significant relationships are noted by shading. Note that subarctic species are negatively correlated with the areal extent of the cold pool and the cold pool index and positively correlated with thermocline and mean water column temperature indices. Arctic species demonstrate the reverse trends, though the relationships are not significant. These results extend analyses performed in Mueter and Litzow (2008) through recent years.

Table A1
Principle components output.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11	PC12	PC13
Variance explained (%)	42	21	8	6	6	6	4	4	2	2	2	0	0
Rotation													
Depth	-6.2E-1	5.0E-1	-1.4E-1	-3.7E-1	2.2E-1	9.6E-2	-1.4E-1	-2.4E-1	7.3E-2	-2.6E-1	1.2E-2	2.8E-2	2.0E-2
Surface temperature	-2.8E-1	8.7E-3	-8.0E-2	6.5E-1	-1.1E-1	1.3E-1	-4.4E-1	-2.1E-1	-1.3E-1	1.3E-1	-4.4E-1	2.9E-2	5.6E-2
Bottom temperature	1.1E-1	6.6E-1	3.1E-1	4.1E-1	-1.7E-1	-2.6E-2	2.2E-2	7.6E-2	-9.9E-2	-2.5E-2	4.8E-1	-6.9E-2	-8.1E-2
Temperature range	-3.5E-1	-4.1E-1	-3.6E-1	1.3E-1	-1.4E-2	1.4E-2	-1.2E-1	-1.8E-2	-2.4E-1	6.5E-2	6.8E-1	-9.9E-2	-1.3E-1
Top layer depth	3.8E-2	1.4E-1	6.4E-2	-2.3E-1	1.7E-1	4.3E-2	-1.4E-1	5.7E-2	-3.5E-1	5.4E-1	-1.2E-1	1.1E-1	-6.5E-1
Bottom layer depth	-4.5E-1	1.2E-1	-7.6E-2	4.4E-2	-9.2E-2	-1.8E-1	4.0E-1	4.9E-1	1.2E-2	4.8E-1	-1.2E-1	-8.2E-2	2.9E-1
Mid-layer extent	-2.3E-1	-6.9E-2	-9.1E-2	2.2E-1	-2.2E-1	-1.4E-1	3.2E-1	1.2E-1	3.6E-1	-3.3E-1	-1.4E-1	1.3E-1	-6.5E-1
Substrate coarseness	1.5E-1	1.7E-1	-4.3E-1	-1.4E-1	-4.1E-1	3.2E-1	3.0E-2	3.4E-1	-4.8E-1	-3.1E-1	-1.5E-1	7.0E-2	2.6E-2
Mud	-2.2E-1	-1.7E-1	4.3E-1	-1.1E-1	-3.2E-1	1.5E-1	9.5E-2	-1.3E-1	-1.4E-1	3.4E-2	1.1E-1	7.2E-1	1.3E-1
Silt	-2.1E-1	-1.5E-1	4.2E-1	-1.6E-1	-3.3E-1	3.9E-2	1.9E-1	-2.6E-1	-3.1E-1	-9.3E-2	-1.4E-1	-6.2E-1	-9.4E-2
Clay	-1.3E-1	-1.4E-1	3.4E-1	-1.0E-1	-2.8E-2	3.9E-1	-4.7E-1	5.8E-1	3.1E-1	-7.0E-2	5.4E-2	-1.5E-1	-5.8E-2
Gravel	1.7E-2	-1.4E-2	-2.6E-2	2.0E-1	3.0E-1	7.8E-1	4.7E-1	-1.3E-1	8.5E-2	1.1E-1	2.7E-2	-4.8E-2	-2.4E-2
Sand	1.1E-1	1.2E-1	-2.6E-1	-2.0E-1	-5.9E-1	1.7E-1	-1.1E-1	-2.9E-1	4.6E-1	4.0E-1	9.9E-2	-8.7E-2	-1.5E-2
Medoids													
(1) Inner shelf	-2.0E-2	1.4E-2	9.3E-4	7.5E-4	-1.3E-3	-7.8E-4	1.0E-3	-1.4E-3	1.7E-4	-8.4E-4	7.6E-4	-3.2E-4	-1.4E-4
(2) Middle/inner (south)	2.9E-2	3.6E-3	-3.2E-5	-2.2E-3	4.8E-4	-1.3E-5	-1.2E-3	3.6E-4	5.7E-4	6.6E-4	-3.9E-5	-2.4E-4	2.9E-4
(3) Southern	5.3E-3	-1.1E-3	-7.5E-3	2.3E-3	-3.0E-3	-4.0E-4	-1.1E-3	-1.4E-5	6.6E-4	3.5E-4	1.4E-3	-4.6E-4	-3.6E-4
(4) Northern	5.0E-3	-9.7E-3	1.2E-3	-1.1E-3	-2.0E-3	-1.4E-3	1.7E-3	-1.8E-3	-2.0E-4	-1.3E-3	8.3E-4	-3.3E-4	3.5E-4
(5) Middle/outer (north)	-1.2E-2	-1.8E-2	5.8E-4	-1.9E-3	-9.0E-4	1.7E-3	-1.2E-4	7.8E-4	1.8E-4	-2.0E-4	-2.9E-4	-1.6E-4	-3.2E-4
(6) Shelf break	-3.0E-2	-8.2E-4	5.5E-3	1.1E-3	-1.4E-5	1.6E-3	-3.1E-3	1.4E-3	-2.0E-4	-6.7E-5	5.8E-4	-3.3E-5	-9.4E-5

Notes: Output of principle components analysis. Environmental predictor variables that loaded heavily ($< -4.0E-1$ or $> 4.0E-1$) on principle components (PC) are highlighted (negative=dark, positive=light). Ecoregions most influenced by each PC are also highlighted.

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Appendix A

See Figs. A1–A8 and Table A1.

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