# Understanding climate impacts on the Maine coastal fish and invertebrate community through synthesis of the Maine-New Hampshire Inshore Trawl Survey

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## Introduction

The Gulf of Maine is warming at an unprecedented rate and there is a critical need to understand the effects of climate change on Maine's marine resources. Changes in factors associated with climate change will influence the productivity of fishery resources through impacts on key life history processes, including recruitment, growth, and natural mortality (Kerr et al. 2009, Drinkwater et al. 2010, Pershing et al. 2015). Shifts in the distribution of species biomass have also been observed in response to gradual warming and extreme events (Nye et al. 2009, Pinsky et al. 2013, Mills et al. 2013). These changes have the potential to alter the composition and diversity of marine communities and to impact key predator-prey relationships. The effects of climate change can also act synergistically with fishing to drive ecosystem change in the Gulf of Maine, potentially rendering fished stocks less productive and less resilient to change. Evaluating how climate and fishing jointly affect community characteristics is central to understanding ecosystem change and anticipating future concerns as climate change progresses.

Long-term resource monitoring datasets are essential for quantifying fish-environment relationships. With a sufficient time-series, scientific surveys can provide information for investigating spatial and temporal changes in fish abundance, distribution, and community structure. The Maine-New Hampshire (ME-NH) Inshore Trawl Survey is recently established (starting in 2000) relative to other inshore surveys in the northeast, such as the Northeast Fisheries Science Center (NEFSC) Trawl Survey and Massachusetts Division of Marine Fisheries (MDMF) Trawl Survey. Information from these surveys provides a seasonal (spring and fall) time series of the distribution and abundance of a variety of fish and invertebrate species, including lobster, shrimp, herring, and groundfish. Presently, the ME-NH Inshore Trawl Survey time series extends back 21 years and is of sufficient length to capture changes in marine resource distribution and abundance relative to the rapid climate change experienced in our region during this period. Furthermore, other survey time series in the Gulf of Maine that extend over a broader spatial and temporal scale can offer the context to interpret our findings at the local scale in Maine coastal waters and the opportunity to compare and contrast trends.

The goal of this study was to synthesize data collected through the ME-NH Inshore Trawl Survey, and place it in the context of other surveys in the region (i.e., Northeast Science Center Bottom Trawl and Massachusetts Division of Marine Fisheries Trawl Surveys) , to understand how climate change and other drivers are impacting key fish and invertebrate communities in coastal Maine waters. We addressed four specific objectives:

1.) Analyze changes in biodiversity in space and time and evaluate associations with environmental factors and fishing

2.) Identify species groups and assess changes in habitat suitability of functional groups and communities in space and time

3.) Analyze joint distributions of key predator-prey species within the community, with a focus on lobster and cod

4.) Evaluate how ecosystem changes align with shifts in diversity and composition of fishery landings over time in ports along Maine's coastline.

## Methods

### *Data*

*Fisheries-independent survey data*

Long-term monitoring datasets of fisheries and environmental factors are essential for investigating spatial and temporal ecosystem change in the Gulf of Maine. Trawl surveys such as the ME-NH Inshore Trawl Survey, the Massachusetts Inshore Trawl Survey, and the Northeast Fisheries Science Center Trawl Survey can be used to encapsulate inshore and offshore fisheries communities in waters of the Northeast US. The ME-NH Inshore Trawl Survey is conducted by the Maine Department of Marine Resources along inshore waters (within 12 nautical miles of shore) from New Hampshire to Maine and occurs biannually in the fall and spring from 2000 to present. This survey collects information about the number and characteristics of fish and invertebrates as well as environmental data, such as temperature and salinity at each tow location. The survey follows a stratified random design with five regions and four depth strata (Figure 0.1, 0.2).

As part of this project, our team developed an ERDDAP website for distribution of the ME-NH Inshore Trawl Survey data to increase public access and accessibility to this data. The data included individual excel files broken out by sample year for: expanded catch (by species), expanded length frequency (by species), tow information, biological data (by species), and lobster length frequencies as well as metadata in MS Word documents. The files were converted to csv and txt before processing. Custom python scripts were developed to concatenate the individual yearly data files, append tow information (tow length, surface and bottom water temperature and salinity, start/end depth, tow length, gear condition, etc) to each dataset, and transform metadata to ingest and generate individual datasets on ERDDAP. The scripts were developed to make it easy to update the ERDDAP datasets as new yearly data became available. The code and documentation are available on GitHub (https://github.com/gulfofmaine/me-dmr-trawl-surveys). It should be noted that during the project, Maine DMR staff also developed online tools for public access to trawl survey data.

To put the ME-NH Inshore Trawl Survey into a broader context, we used the Northeast Fisheries Science Center (NEFSC) Bottom Trawl Survey and the Massachusetts Division of Marine Fisheries (MDMF) Inshore Trawl Survey. NEFSC Bottom Trawl Survey data includes spring (1968-2018) and fall (1963-2017) seasons and covers Cape Hatteras, NC to the Canadian border. Stations are randomly selected within geographic strata determined by depth and region. The survey follows a stratified random design and samples both inshore and offshore (3-200 nautical miles) waters collecting information on catch (abundance, biomass, and biological data) and environmental conditions (temperature and salinity). We extracted NEFSC tows that occurred offshore in the Gulf of Maine and Georges Bank (GOM/GB) for an intermediate comparison. The MDMF survey (fall 1978-spring 2018) is randomly stratified by five regions and six depth strata and covers fall and spring seasons. The MDMF survey also collects catch information and environmental data.

*Environmental data*

In addition to the observed environmental data collected from the trawl surveys, more finely resolved environmental data is needed to represent the full study area. For this purpose, we used two ocean data products. In objectives 1 and 2, we used the surface and bottom temperature as well as salinity from the Northeast Coastal Ocean Forecast System (NECOFS) which uses the Finite Volume Unstructured Grid Model (FVCOM) forced with surface fluxes from a meteorological model and assimilates available hydrographic data. The modeled data was compared to the observed environmental data collected at tow locations and demonstrated good agreement (Figure 0.3, 0.4, 0.5, 0.6). In objective 3, which focused on species distribution modeling, we used sea surface and bottom temperatures from the European Copernicus Marine Environment Monitoring Service GLORYs12v1 product (Lellouche et al. 2018). GLORYs is a global ocean reanalysis model, which continually assimilates new data from a suite of sources (e.g., satellites, in situ temperature and salinity vertical profiles) using a reduced-order Kalman filter approach. GLORYs provides daily ocean temperature and salinity data at a 1/12 degree (~ 8km) horizontal resolution from 1993 to present, with ocean temperatures modeled at 50 different vertical levels. Previous work suggests modeled sea surface and bottom temperatures from GLORYs align well with observations (see supplements in Chen et al. 2021).

*Fishery landings data*

Along with understanding how environmental factors influence fish distribution, abundance and community structure, we also wanted to evaluate how these patterns aligned with shifts in diversity and composition of fishery landings over time in ports along Maine's coastline. To do this, we extracted Maine landings data from the DMR landings portal. The modern data spans from 2006-2019 and includes landings by species by county, with some landings aggregated into "unknown" counties to make it non-confidential. Historical annual landings for species are available for 1950-2019.

***Objective 1: Analyze changes in community biodiversity in space and time and evaluate associations with environmental factors and fishing***

*Calculating biodiversity metrics*

We quantified changes in biodiversity in the Gulf of Maine and the broader Northeast US coast using state (Maine-New Hampshire and Massachusetts) and federal trawl survey data and investigated the relationship between biodiversity change and environmental factors as well as fishery landings. Biodiversity metrics calculated by haul included species richness, evenness, diversity, and taxonomic diversity. These indices were calculated for samples identified to the species level of classification. ME-NH samples that were not identified to the species level, recorded as a zero, or recorded without a total number observed were omitted from biodiversity calculations (~ 5% of samples). Observations from the NEFSC Trawl Survey and MDMF Trawl Survey that were not classified to the species level (~ 1%) were removed. Species richness by survey tow (*T*) was calculated:

$$S_T = s \qquad (1)$$

where *s* was number of species.

Species evenness by haul was calculated using the Simpson's Evenness Index (Simpson 1949):

$$E_T = \frac{1}{\Sigma_{i=1}^{s} p_i^2} \frac{1}{s} \quad (2)$$

where *s* was the number of species, and $p$ was the proportion of species *i* in each haul.

Species diversity was calculated using the Shannon-Weiner Index (*H*) (Shannon and Weaver 1949) and Simpson's Diversity Index (*D*) (Simpson 1949):

$$H_T = \Sigma_{i=1}^{s} p_i \, log \, p_i \quad (3)$$

$$D_T = \frac{1}{\Sigma_{i=1}^{s} p_i^2} \quad (4)$$

where *s* was number of species, and $p_i$ was the proportion of species *i* in each haul.

Taxonomic classifications of survey observations were expanded to kingdom, phylum, class, order, family, and genus level using the *taxize* package in R (Chamberlain and Szocs 2013). Taxonomic diversity (Warwick and Clarke 1995) was approximated:

$$\Delta = 2\frac{\Sigma\Sigma_{i<j} w_{ij} x_i x_j}{s(s-1)} \quad (5)$$

where $w_{ij}$ was the distinctness weight between species *i* and species *j* defined by Linnaean classification, $x_i$ was total number of species *i* per haul, $x_j$ was the total number of species *j* per haul, and *s* was number of species per haul.

Taxonomic distinctness (Warwick and Clarke 1995) was classified:

$$\Delta *= 2\frac{\Sigma\Sigma_{i<j} w_{ij} x_i x_j}{\Sigma\Sigma_{i<j} x_i x_j} \quad (6)$$

where $w_{ij}$ was the distinctness weight between species *i* and species *j* defined by Linnaean classification, $x_i$ was total number of species *i* per haul, $x_j$ was the total number of species *j* per haul, and *s* was number of species per haul.

Average taxonomic distinctness (Clarke and Warwick 1998) was defined:

$$\Delta += 2\frac{\Sigma\Sigma_{i<j} w_{ij}}{s(s-1)} \quad (7)$$

where $w_{ij}$ was the distinctness weight between species *i* and species *j* defined by Linnaean classification and *s* was the number of species per haul.

Variation in taxonomic distinctness (Clarke and Warwick 2001) was calculated:

$$\Lambda += 2\frac{\Sigma\Sigma_{i<j}(w_{ij}-\bar{w})^2}{s(s-1)} \tag{8}$$

where $w_{ij}$ was the distinctness weight between species *i* and species *j* defined by Linnaean classification, $\bar{w}$ was the average weight per haul, and *s* was the number of species per haul.

*Correlations between biodiversity metrics across surveys*

To determine if correlations between surveys for each biodiversity metric existed ($p > 0.05$), we constructed linear models and compared the slopes for each survey (i.e. ME-NH, MDMF, GOM/GB, and NEFSC). Yearly averages of each metric were calculated seasonally by survey. Comparisons were conducted over the entire time series and then over the years that all surveys had observations (2000-2017).

Regional maps were created for the ME-NH Inshore Trawl Survey area to identify areas of high diversity and how that has changed from 2000-2017.

*Influence of environmental factors on biodiversity metrics*

Changes in biodiversity metrics in relation to environmental factors and fishery landings were investigated using generalized additive mixed models (GAMMs). GAMMs for each biodiversity metric (*M*) in a season were generated for each survey using the *gamm4* package in R (Wood and Scheipl 2017) following the form:

$$M_{season} = s_1(surface\ temp) + s_2(bottom\ temp) + s_3(surface\ salinity) + s_4(bottom\ salinity) + s_4(bottom\ salinity) + s_5(landing) + s_6(depth) + s_7(lat, long) + b_{year} + \varepsilon,$$
$$\varepsilon \sim N(0, \sigma^2)$$

in which *s* was the default thin plate regression spline smoothing function, $b_{year}$ was the random effect for year, and ε was random error. ME-NH and GOM/GB temperature and salinity information from trawl hauls were used to inform the GAMMs. We also ran the GAMMs temperature and salinity estimates from Finite Volume Unstructured Grid Model (FVCOM; Chen et al. 2003) output from the closest spatial point via great-circle distance, and time (hourly averaged observations from the closest month) using the *sp* package in R (Pebesma and Bivand 2005). The MDMF trawl only records bottom temperature so GAMMs were informed using only FVCOM temperature and salinity values.

***Objective 2: Identify species groups and assess changes in habitat suitability of functional groups and communities in space and time***

We used multivariate ordination analyses to characterize changes in community and functional groups over space and time. Nonmetric multidimensional scaling (NMDS) was applied to the ME-NH trawl communities for taxonomic composition and functional groups for each season.

Functional groups were defined by feeding guilds based on the NOAA State of the Ecosystem report (https://noaa-edab.github.io/tech-doc/aggroups.html; based on Garrison and Link 2000), including benthivore, benthos, piscivore, planktivore and other. Communities were defined using either top 50 species found in the trawl by biomass or abundance, and functional groups by biomass or abundance.

For the NMDS, we used Bray-Curtis similarities and applied a square root transformation and Wisconsin double standardization. To visualize the ordination, we categorized regions as West of the Penobscot Bay (ME-NH Inshore Trawl Survey regions 1 and 2), Penobscot Bay (ME-NH Inshore Trawl Survey region 3), or East of the Penobscot Bay (ME-NH Inshore Trawl Survey regions 4 and 5), and years were grouped into 5-year blocks. The analysis was conducted using the *vegan* package in R (Oksanen et al. 2020) and functions are documented in parentheses when noteworthy. Analysis of similarity (*anosim*) and analysis of variance (*adonis*) were performed to look for statistical differences between communities by regions and year groups. Environmental factors were then added to the NMDS plots to show direction and strength of relationship using linear (*envfit*) and nonlinear (*ordisurf*) methods. These included bottom and surface salinity, bottom and surface temperature, depth, and location collected from the ME-NH Inshore Trawl Survey.

***Objective 3: Analyze joint distributions of key predator-prey species within the community, with a particular focus on lobster and cod***

After completing the biodiversity and community structure analyses in objectives 1 and 2, we focused on changes in the distribution and abundance of different species to evaluate potential changes in predator-prey dynamics, with particular attention placed on American lobster (*Homarus americanus)* and Atlantic cod (*Gadus morhua*). To do this, we used the 2000-2019 ME-NH Inshore Trawl Survey data and extracted all fall observations as previous work suggests our species distribution models tend to have higher predictive skill in the fall than the spring season (Allyn et al. 2020). We then analyzed the fall survey data using two different approaches to better understand changes in predator-prey dynamics.

In the first approach, we fit single species Poisson-link delta Vector Autoregressive Spatio-Temporal models (VAST, Thorson and Barnett 2017, Thorson 2019) to lobster and five of its historically important predator species: cod, little skate, winter skate, spiny dogfish, and sculpin. The VAST model structure can be broken down into three different parts. The first part of the model was a standard “environment-only” species distribution model, where we included depth, seasonal average bottom temperature and seasonal average sea surface temperature as smooth functions with two degrees of freedom. The second part of the model accounted for unmeasured, persistent spatial variability and unmeasured, ephemeral spatio-temporal variability. These two components were estimated as Guassian Markov random field random effects and try to soak up variability that can't be explained by the habitat covariates. The final part to the VAST model structure was including a random-walk temporal autoregressive structure for both the model intercepts (i.e., average probability of occurrence or positive biomass across the entire spatial domain) and the spatio-temporal model component. We validated fitted models using hold out testing data from 2017-2019 and then made predictions from the fitted models throughout the entire survey domain using gridded environmental data for each fall year from 2000 to 2019.

With species density predicted throughout the entire domain for lobster and the five predator species, we then assessed their spatial and temporal overlap using a suite of metrics developed to infer predator-prey relationships from distribution and abundance information (Carroll et al. 2019). Following recommendations by Carroll et al. given our data and specific research interests, we highlight the Schoener's D index (Schoener 1970) results that summarize similarity in the spatial niche occupied by a prey species and potential predator species and the AB ratio (Greer and Woodson 2016), which measures how much of a predator species' occurrence patterns could be attributed to the distribution and abundance of the prey species.

In the second approach, we progressed from our single species VAST models and modeled the entire suite of six species simultaneously within a joint modeling framework (Thorson et al. 2016). The main potential advantage to this joint species distribution modeling approach is that the model can pool information among species to estimate common spatial and spatio-temporal variability patterns, while identifying the influence of each species on these patterns, much like a Principal Component Analysis. After fitting the joint model to the community dataset, we summarized these shared patterns in a correlation matrix representing common distribution and abundance patterns between lobster and the five predator species across the entire survey time series. This effort is ongoing after receiving additional funding and we anticipate continuing this work by expanding the number of lobster predator species included and trying to develop a similar model for cod and its potential prey species. Though, many forage fish species important to cod can have extremely patchy distribution and create modeling challenges.

***Objective 4: Evaluate how ecosystem changes have aligned with shifts in diversity and composition of fishery landings over time by port***

Biodiversity of Maine landings were calculated using a subset of the diversity metrics in objective 1, which includes species richness (eq. 1), Simpson's Evenness (eq. 2), Shannon-Weiner Diversity (eq. 3), and Average Taxonomic Distinctness (eq. 7). Metrics were calculated annually and by county with the total weight of each species. Annual landings data was for a subset of select species from 1950-2019, while county specific was for all species 2006-2020. The county data included some generalized county or species records because of confidentiality. Confidential county data was about 28% of landings and confidential species was about 2% of landings. Maine landings data was also subset to only include species that were found in the ME-NH Inshore Trawl Survey for the most direct comparison. Landings data by county was also grouped into regions similar to the ME-NH Inshore Trawl Survey and diversity metrics were calculated for east of the Penobscot, west of the Penobscot, and Penobscot Bay. We also aggregated landings data into functional groups based on feeding guild, as shown in objective 2. Landings trends were compared to the ME-NH Inshore Trawl Survey.

We have created a github repository with code for all four objectives, https://github.com/jerellejesse/ME-NH-trawl-Seagrant, which is publicly accessible. There is also an associated website with a summary page as well as more in-depth analysis and any figures that did not make it into this report for the sake of brevity, https://jerellejesse.github.io/ME-NH-trawl-Seagrant/.

**Results**

***Objective 1***

ME-NH Inshore Trawl Survey average diversity indices all look mostly stable from 2000-2017 and similar for fall and spring. Specifically, species richness decreased from 2011-2014, Shannon-Weiner diversity and Simpon's diversity increased from 2010-2017, Simpson's evenness was generally decreasing then increasing over time (Figure 1.1). Taxonomic diversity and distinctness indices are also fairly stable with some spikes and valleys, but similar for both seasons. Taxonomic diversity had large outliers that makes trends hard to detect, taxonomic distinctness had a drop in 2005 and then generally increased with another dip in 2013-2015, average taxonomic distinctness was relatively constant over time, and variation in taxonomic diversity was increasing over time (Figure 1.2). The diversity indices broken down by region are mostly overlapping and there is not a general distinguishable pattern. Some spikes or valleys in these indices are from one region diverging from the average pattern. Shannon-Weiner diversity was consistently higher for region five and Simpson's diversity was higher in regions one and five (Figure 1.3, 1.4). By depth strata there are a few instances of strata having different trends, particularly the first strata behaving differently from the others. For fall species richness, the trend changes by depth with the first two depth strata decreasing, but strata three and four more even over time (Figure 1.5). Similarly for spring, taxonomic distinctness increased for depth strata one and two but decreased for strata three and four, average taxonomic distinctness dipped for strata two through four, but not for strata one, and variation in taxonomic distinctness was consistently lowest for strata one (Figure 1.6).

Diversity maps can show how the indices vary spatially across both regions and depth strata, as well as changes over time. In general, there are not large regional patterns in the spatial maps, similar to the regional trend plots (Figure 1.7-1.13). However, the spatial maps are useful for visualizing depth strata trends. For example, there is lower species richness inshore and higher offshore, while the opposite is seen for evenness in the fall (Figure 1.7, 1.10). Temporal changes are not easily visible with the maps over the short time frame of the survey (Figure 1.7-1.13). Only fall maps are shown for brevity ( spring available at https://jerellejesse.github.io/ME-NH-trawl-Seagrant/index.html).

Comparing the ME-NH Inshore Trawl Survey to the MADMF and NEFSC Trawl Surveys provides context with a longer time period and larger spatial coverage. Species richness is slightly higher for the ME-NH survey than the other surveys at first, then the NEFSC survey increases to be closer in magnitude in recent years while the MADMF looks to be increasing at a slower rate. Shannon-Weiner diversity and Simpson's diversity are very similar for all the surveys. Simpson's evenness is generally lower for the ME-NH survey, but in the longer time series trends indicate that it could be part of a larger decrease in evenness (Figure 1.14). The ME-NH Inshore Trawl Survey and MADMF Inshore Trawl Survey have the highest number of statistically significant relationships between non-taxonomic biodiversity indices (Species richness, Shannon-Wiener and Simpson's evenness) as determined by comparing their slopes from linear models (Table 1.1, Table 1.2). Taxonomic diversity is similar between the ME-NH and MADMF survey in the fall but is much higher than the other surveys in the spring. Taxonomic distinctness and average taxonomic distinctness for the ME-NH survey is similar to the other surveys, and the larger trend shows that it could be part of an increase over time. The variation in taxonomic distinctness is higher for the ME-NH survey, but the increasing trend is similar for all the surveys (Figure 1.15).

Evaluation of model results (i.e. GAMMs) provided insight on potential drivers of patterns of diversity. The depth and location (lat/long) of survey tows were highly significant predictor variables for almost every diversity index for the ME-NH Inshore Trawl Survey and the GOM NEFSC survey for both seasons (Table 1.3-1.6). For the fall ME-NH Inshore Trawl Survey, bottom temperature was significant across many of the diversity index models. Taxonomic distinctness and variation in taxonomic distinctness were influenced by multiple environmental effects (Table 1.3). In the spring, surface temperature was significant more frequently than the fall. Species richness was influenced by multiple environmental effects. Also, taxonomic distinctness and average taxonomic distinctness were significantly influenced by almost all environmental factors (Table 1.4). The NEFSC Trawl Survey was more affected by environmental effects than the ME-NH survey (Table 1.5 and 1.6). The fall was again highly influenced by bottom temperature, but surface temperature came up more often as significant than in the fall ME-NH survey. Surface salinity was the least frequent significant environmental factor (Table 1.5). In the spring NEFSC survey, bottom temperature was the most frequent significant factor, converse to the spring ME-NH survey. Surface salinity came up as significant more frequently in the spring GOM models. Simpson's evenness, species richness, Simpson's diversity, and variation in taxonomic distinctness all had significant relationships with all or most of the environmental factors (Table 1.6).

The ME-NH Inshore Trawl Survey GAMMs showed similar significant factors for the FVCOM and survey collected environmental data for both fall and spring (Table 1.7 and 1.8). Significant environmental factors also produced similar trends for both data types, so FVCOM plots are presented for brevity (all available at https://jerellejesse.github.io/ME-NH-trawl-Seagrant/index.html).

Trends across significant factors from the ME-NH models had some similarities for the various indices. Non-taxonomic diversity indices showed increases up to a certain depth and then a decrease for both seasons (Figure 1.16, 1.18, 1.19, 1.24, 1.25, 1.26). Fall non-taxonomic diversity indices increased with increasing bottom temperature, except for species richness which declined after the increase (Figure 1.16, 1.17, 1.19). Spring indices increased with increasing surface temperature instead for both non-taxonomic and taxonomic indices (Figure 1.24, 1.25, 1.26, 1.29, 1.30). Increasing bottom salinity for the spring resulted in decreasing non-taxonomic indices (Figure 1.24, 1.26) and a peak for taxonomic indices (Figures 1.29, 1.30). Landings increase with increasing indices (Figures 1.26, 1.27, 1.29).

For GOM models informed by the NEFSC Bottom Trawl Survey, non-taxonomic indices also showed increases to a peak and then a decrease for both seasons (Figure 1.32 1.,33, 1.34, 1.35, 1.40, 1.41, 1.42). Trends in bottom temperature impacted most non-taxonomic indices in both seasons (Figure 1.32, 1.33, 1.41, 1.42, 1.43). As bottom temperature increased taxonomic indices increased (Figure 1.37, 1.38, 1.45, 1.46, 1.47). Increasing surface temperature also had a positive relationship with non-taxonomic indices for spring (Figure 1.41, 1.42, 1.43). Spring non-taxonomic indices generally decreased with increasing surface salinity (Figure 1.40, 1.42, 1.43), while taxonomic indices generally increased (Figure 1.46, 1.47). As bottom salinity increased non-taxonomic indices tended to exhibit a similar pattern of a decrease then an increase (Figure 1.33, 1.34, 1.35). Species richness decreased with increasing bottom salinity for both seasons (Figure 1.32, 1.40).

***Objective 2:***

NMDS for the ME-NH Inshore Trawl Survey was plotted to visualize any changes in community structure in time and space. Functional group biomass structure changed over time. Although the center of the community ellipses were similar, the spread of the ellipses or variation in the community structure were more similar for 2000-2004 and 2005-2009 year groups, and 2010-2014 and 2015-2019 year groups, indicating a decadal shift in the functional group structure (Figure 2.1). The functional group community structure based on abundance does not show the same temporal changes, except that the 2005-2009 year block is different from the other year blocks (Figure 2.2). There is an indication of some regional differences east and west of Penobscot Bay over time based on biomass of functional groups over time, however these patterns are not as evident when based on abundance in which case data centers and ellipses are mostly overlapping (Figure 2.3, 2.4).

Community structure using the top 50 species had similar results to the functional groups structure. There were decadal shifts in community structure based on both biomass and abundance (Figure 2.5,  2.6). Similar to functional groups, there were not large regional differences in the top species community structure. Biomass and abundance community structure has slight differences east and west of Penobscot Bay (Figure 2.7, 2.8).

The community structure by season is very similar to the overall community structure with a few slight regional differences (all seasonal figures available at https://jerellejesse.github.io/ME-NH-trawl-Seagrant/index.html). For top species biomass in spring, the community structure east of Penobscot Bay seems to change more than to the west (Figure 2.9). The fall survey shows the ellipses for east and west overlapping more over time, indicating the community structure becoming more similar (Figure 2.10). Functional group biomass community structure exhibits similar patterns, but functional group and top species abundance does not.

Analysis of variance (*adonis*) indicates that region groups and year blocks both have statistically significant differences in community structure ($P<0.001$). The pairwise analysis for region groups and year blocks (Table 2.1, 2.2) signifies that there are statistically significant differences ($P <0.05$) for all community structure types analyzed and all region groups and year blocks, except functional group abundance east of the Penobscot versus west of the Penobscot ($P= 0.089$).

The environmental analysis showed that bottom temperature, surface temperature, and bottom salinity were consistently highly significant for linear relationships with community structure. Latitude and longitude were mostly highly significant, except for functional group abundance and depth had mixed statistical significance with community structure (Table 2.3, Figure 2.11-2.14). The nonlinear approach had similar significant environmental effects (Table 2.4, Figures 2.15- 2.18). Functional group biomass appeared to have increased bottom temperature, surface temperature, and bottom salinity correlated with the west region and more recent year blocks

(Figure 2.11, 2.15). Functional group abundance appeared to have increased bottom temperature, surface temperature, and bottom salinity in a direction away from the 2005-2009 year block (Figure 2.12, 2.16). Top species biomass appeared to have increased bottom temperature, surface temperature, and bottom salinity with more recent year blocks and slightly with the west region (Figure 2.13, 2.17). Top species abundance appeared to have increased bottom temperature, surface temperature, and bottom salinity slightly correlated with the west region and more recent year blocks (Figure 2.14, 2.18). Only bottom temperature nonlinear contour plots are shown for brevity (all available at https://jerellejesse.github.io/ME-NH-trawl-Seagrant/index.html).

***Objective 3:***

For the single species models, we were able to investigate overlap between lobster and its predators for both stages of the VAST model – the first stage and probability of presence or occurrence and then the second stage representing expected density (numbers per $km^2$). The overall occurrence overlap as measured by Schoener's D between lobster and its traditional predator species seems to have steadily declined over the survey years from 2000 to 2019 (Figure 3.1). This is likely caused by a large expansion in suitable lobster habitat and a contraction of suitable habitat for these traditional predator species, potentially best demonstrated with predicted density maps for lobster and cod (Figure 3.2 and 3.3). In response to these divergent trends, less of the lobster occurrence niche (i.e., distribution of probability of presence) can be explained by the occurrence of each of the predators.

Although occurrence results were very consistent among the different lobster predator species, overlap metrics based on predicted density showed more unique responses among predator species and more year-to-year variability. In particular, the Schoener's D index metric for predicted density showed relatively consistently low niche overlap between lobster and cod. However, density overlap with other predator species, particularly little skate, sculpin, and to a slightly lesser degree winter skate, was higher across the time series. Additionally, it seems there could be an increase in niche overlap during the most recent survey years (since ~2014) for little skate and sculpin (Fig 3.4). Plots of the AB ratio index suggest that in general, lobsters are actively avoiding high density aggregations of cod and spiny dogfish (negative AB ratio values), while index metrics for the other predators seem to be stabilizing (0 values of AB ratio). In combination with the Schoener's D results, this hints to a potential increase in distribution and abundance spatial overlap of lobster with other predators besides cod and spiny dogfish without a clear conclusion of if this is triggering a predator-avoidance response by lobster.

Joint species distribution modeling efforts using the community dataset provided more information to understand the potential changes in spatio-temporal overlap among lobster and its potential predator species. In particular, we focused on correlation plots, which summarize the collected overlap in spatio-temporal variability across the full time series (Fig 3.5). Agreeing with the single species results, overlap between lobster and cod has decreased over the years, while overlap while there has been a positive correlation in lobster density with little skate, and longhorn sculpin. Across the time series, the joint model did not show a conclusive relationship between lobster and winter skate or spiny dogfish. This lack of signal could be caused by high variability in the distribution and abundance of winter skate and spiny dogfish over time, which was also suggested by the single species results (Fig 3.4).

***Objective 4:***

Diversity metrics for landings data included species richness which increased at the beginning of the time series, but then remained mostly stable with a slight decrease between 40 and 35 species. Shannon-Weiner diversity decreased slightly until around 2016 when the diversity started to increase again. Simpson's evenness also decreased until a sharp increase in 2018. Average taxonomic distinctness increased slightly in the middle of the time series but started to decrease towards the end (Figure 4.1). For the landings data of selected species, the species richness was lower but followed a similar decreasing pattern. Shannon-Weiner diversity was also lower, and the trend was the same including the increase starting in 2016. Evenness was higher since there were less species included in the data but the decrease through the middle of the time series was the same as the county specified data. Average taxonomic distinctness was slightly lower for the selected species landings data and had increases and decreases but centered around a stable number (Figure 4.2).

Landings metrics that were subset to only include species also found in the trawl survey did not change much compared to the original metric including all species (Figure 4.2, 4.3). The landings metrics are similar to the metrics for the ME-NH Inshore Trawl Survey (Figure 4.3, 4.4). In particular, Shannon-Weiner diversity follows a very similar trend of decreasing in the middle of the time series. The other metrics align well with a general increasing, decreasing, or stable trend. Correlations between the trawl survey and landings are high for Simpson's evenness and average taxonomic distinctness (Table 4.1, Figure 4.5).

Diversity metrics had regional differences. Species richness was highest east of Penobscot Bay, but all regions were fairly stable. Shannon-Weiner diversity was also highest for the east region. At the beginning of the time series the east and west both had decreasing diversity, however, the east started to increase in 2015 while the west continued to decrease. Simpson's evenness was stable for the east and Penobscot Bay, but the west decreased. Average taxonomic distinctness trends were similar for east and Penobscot Bay with both decreasing around 2009 and then increasing to a stable point after, while the west region kept decreasing until 2013 when it began to increase again (Figures 4.6- 4.8).

The proportion of biomass for each functional group was very similar for the county specified and selected species landings data (Figure 4.9, 4.10). The largest group was benthivore and planktivore composed of mostly American lobster and Atlantic herring/ menhaden respectively. The ME-NH Inshore Trawl Survey had a higher proportion of the piscivore functional group which included hake species, spiny dogfish, and others in small amounts (Figure 4.11).

**Conclusions**

This study synthesized data from the ME-NH Inshore Trawl Survey in order to understand the effects of environmental change on marine communities over time. The ME-NH Inshore Trawl Survey extends back over 20 years and can be compared with other surveys in the area that have broader spatial and temporal scales which offers the context to interpret findings at the local level. Overall this analysis showed that marine communities in Maine coastal waters have changed over time.

Changes in biodiversity in coastal Maine waters were easier to interpret in the context of the longer time series of MDMF and NEFSC surveys. The trends in the ME-NH survey are part of a longer period increase in species richness, Shannon-Wiener diversity, and average taxonomic distinctness, and a decrease in Simpson's evenness. This means that more taxonomically distinct species were emerging in the survey and in a disproportionate way because of the decrease in evenness. Evaluating associations with environmental factors and fishing found that temperature was the most significant factor for the changes in biodiversity. As temperature increased, the indices either increased (evenness and average taxonomic distinctness) or had a bell shape with a decrease after a certain temperature (species richness and Shannon-Wiener diversity), indicating an ideal temperature for the peak of the index. This suggests that as temperatures continue to increase in Maine waters we will expect continued changes in biodiversity.

We identified changes in the community structure in Maine coastal waters over time. A decadal shift in the community structure at both the functional group and species scale was evident between 2000-2009 and 2010-2019. Environmental associations with temperature and bottom salinity were the most significant factors contributing to changes in community structure. Higher temperature seemed more tightly associated with the 2010-2019 years and partially with the west of Penobscot Bay region as well, implying that warming waters may continue to shift the community structure over time.

The diversity of Maine landings also changed over time. Species richness, diversity, and evenness all slightly decreased, but species diversity and evenness increased again at the end of the timeseries. Average taxonomic distinctness was mostly stable with a slight increase. Although there are many factors that influence the composition of landings beyond the availability of fish (e.g. regulations) we do see a general alignment between the patterns in Maine landings and the general trends in the ME-NH Inshore trawl survey. For example, similar to the trawl survey there is evidence of  taxonomically distinct species beginning to appear in the landings. When breaking down the landings into regions there were different trends in the indices. The east of the Penobscot Bay region was increasing in species richness and Shannon-Wiener diversity at the end of the time series and diverging from the other regions while west of the Penobscot Baywas decreasing in evenness. Both east and west were increasing in average taxonomic distinctness towards the latter half of the timeseries. This suggests that the east region is gaining more taxonomically distinct species while retaining its evenness, so must be also gaining proportional amounts of those new species. However, the west is losing evenness while retaining its total number of species, so must be gaining small amounts of new species at the same rate that it is losing other species.

The representation of functional groups over time were also compared between the ME-NH Inshore Trawl Survey and the landings. The ME-NH Inshore Trawl Survey had a much larger proportion of piscivores than was represented in the landings, but they both display an increase of benthivores, driven by increases in lobster landing and availability in the trawl survey. The landings comparison to the ME-NH Inshore Trawl Survey showed that landings also pick up community changes and, in part, reflect changes in the species availability in Maine waters.

Overall, communities in Maine coastal waters are changing over time and environmental factors are playing an important role in these changes. Temperature is a key contributing factor, which is a concern with the projected continued future warming of the Gulf of Maine. Trends identified in

Maine inshore waters aligned well with the offshore signal for biodiversity indices and environmental effects, and landings generally picked up changes in community structure.

**Tables and Figures**

**Objective 1**

**Table 1.1.** Comparison of overlapping time series. Direction of the relationship between each survey as positive (+) or negative (-) and whether it is significant (*) as determined from comparing slopes from linear models.

| | Fall | | | | Spring | | | |
|---|---|---|---|---|---|---|---|---|
| | **Species richness** | **Shannon-Weiner** | **Simpson's diversity** | **Simpson's evenness** | **Species richness** | **Shannon-Weiner** | **Simpson's diversity** | **Simpson's evenness** |
| **ME-MA** | + | +* | +* | -* | -* | - | - | -* |
| **MA-NEFSC** | - | - | -* | + | - | - | -* | + |
| **MA- GOM** | - | +* | + | + | - | +* | + | + |
| **ME-NEFSC** | - | - | -* | + | - | +* | +* | + |
| **ME-GOM** | - | +* | + | + | - | + | + | + |
| **NEFSC-GOM** | + | + | + | + | + | - | - | - |

**Table 1.2.** Linear models slopes for each survey.

| | Fall | | | | Spring | | | |
|---|---|---|---|---|---|---|---|---|
| | **Species richness** | **Shannon-Weiner** | **Simpson's diversity** | **Simpson's evenness** | **Species richness** | **Shannon-Weiner** | **Simpson's diversity** | **Simpson's evenness** |
| **ME** | -0.11 | 0.002 | 0.006 | 0 | 0.05 | 0.008 | 0.02 | 0 |
| **MA** | 0.04 | 0.002 | 0.02 | 0 | 0.03 | -0.005 | -0.01 | -0.001 |
| **GOM** | 0.42 | -0.006 | -0.03 | -0.006 | 0.50 | -0.01 | -0.05 | -0.01 |
| **NEFSC** | 0.34 | 0.01 | 0.02 | -0.003 | 0.43 | 0.005 | 0.003 | -0.007 |

**Table 1.3.** Fall ME-NH Inshore Trawl Survey GAMMs with FVCOM data. Highlighted P values are statistically significant

| | Bottom temperature | Surface temperature | Bottom salinity | Surface salinity | Landings | Start depth | Start lat/long |
|---|---|---|---|---|---|---|---|
| **Species richness** | $P < 0.001$ | $P = 0.379$ | $P = 0.173$ | $P = 0.168$ | $P = 0.0045$ | $P < 0.001$ | $P < 0.001$ |
| **Shannon-Weiner** | $P = 0.002$ | $P = 0.085$ | $P = 0.038$ | $P = 0.059$ | $P = 0.996$ | $P < 0.001$ | $P < 0.001$ |
| **Simpson's diversity** | $P = 0.060$ | $P = 0.051$ | $P = 0.118$ | $P = 0.222$ | $P = 0.676$ | $P < 0.001$ | $P < 0.001$ |
| **Simpson's evenness** | $P = 0.002$ | $P = 0.206$ | $P = 0.166$ | $P = 0.134$ | $P =0.217$ | $P < 0.001$ | $P < 0.001$ |
| **Taxonomic diversity** | $P = 0.025$ | $P = 0.876$ | $P = 0.279$ | $P = 0.394$ | $P = 0.005$ | $P = 0.013$ | $P < 0.001$ |
| **Taxonomic distinctness** | $P < 0.001$ | $P = 0.031$ | $P < 0.001$ | $P =0.390$ | $P = 0.148$ | $P < 0.001$ | $P < 0.001$ |
| **Average taxonomic distinctness** | $P = 0.502$ | $P =0.111$ | $P = 0.133$ | $P < 0.001$ | $P < 0.001$ | $P < 0.001$ | $P < 0.001$ |
| **Variation taxonomic distinctness** | $P = 0.250$ | $P = 0.027$ | $P = 0.030$ | $P = 0.014$ | $P = 0.325$ | $P < 0.001$ | $P < 0.001$ |

**Table 1.4.** Spring ME-NH Inshore Trawl Survey GAMMs with FVCOM data. Highlighted P values are statistically significant

| | Bottom temperature | Surface temperature | Bottom salinity | Surface salinity | Landings | Start depth | Start lat/long |
|---|---|---|---|---|---|---|---|
| **Species richness** | P = 0.571 | P < 0.001 | P = 0.001 | P = 0.004 | P = 0.147 | P < 0.001 | P < 0.001 |
| **Shannon-Weiner** | P = 0.062 | P = 0.022 | P = 0.090 | P = 0.570 | P = 0.070 | P < 0.001 | P < 0.001 |
| **Simpson's diversity** | P = 0.077 | P = 0.025 | P = 0.020 | P = 0.329 | P = 0.048 | P < 0.001 | P < 0.001 |
| **Simpson's evenness** | P = 0.165 | P = 0.656 | P =0.055 | P = 0.346 | P = 0.013 | P < 0.001 | P < 0.001 |
| **Taxonomic diversity** | P = 0.254 | P =0.454 | P = 0.562 | P = 0.932 | P = 0.125 | P = 0.023 | P < 0.001 |
| **Taxonomic distinctness** | P = 0.010 | P = 0.010 | P < 0.001 | P = 0.125 | P < 0.001 | P < 0.001 | P < 0.001 |
| **Average taxonomic distinctness** | P = 0.032 | P = 0.037 | P = 0.028 | P = 0.022 | P = 0.235 | P < 0.001 | P < 0.001 |
| **Variation taxonomic distinctness** | P = 0.014 | P = 0.425 | P = 0.863 | P = 0.058 | P = 0.298 | P < 0.001 | P < 0.001 |

**Table 1.5.** Fall NEFSC Trawl Survey for the GOM region GAMMs with FVCOM data. Highlighted P values are statistically significant

| | Bottom temperature | Surface temperature | Bottom salinity | Surface salinity | Start depth | Start lat/long |
|---|---|---|---|---|---|---|
| **Species richness** | P < 0.001 | P < 0.001 | P = 0.003 | P = 0.057 | P < 0.001 | P < 0.001 |
| **Shannon-Weiner** | P < 0.001 | P =0.243 | P < 0.001 | P = 0.025 | P < 0.001 | P < 0.001 |
| **Simpson's diversity** | P < 0.001 | P = 0.416 | P = 0.001 | P = 0.176 | P < 0.001 | P < 0.001 |
| **Simpson's evenness** | P = 0.008 | P < 0.001 | P = 0.006 | P = 0.810 | P < 0.001 | P < 0.001 |
| **Taxonomic diversity** | P = 0.220 | P = 0.027 | P = 0.059 | P = 0.167 | P = 0.105 | P = 0.012 |
| **Taxonomic distinctness** | P < 0.001 | P = 0.256 | P = 0.042 | P = 0.002 | P < 0.001 | P < 0.001 |
| **Average taxonomic distinctness** | P < 0.001 | P < 0.001 | P = 0.122 | P = 0.647 | P < 0.001 | P < 0.001 |
| **Variation taxonomic distinctness** | P = 0.178 | P = 0.013 | P =0.090 | P = 0.027 | P < 0.001 | P < 0.001 |

**Table 1.6.** Spring NEFSC Trawl Survey for the GOM region GAMMs with FVCOM data. Highlighted P values are statistically significant

| | Bottom temperature | Surface temperature | Bottom salinity | Surface salinity | Start depth | Start lat/long |
|---|---|---|---|---|---|---|
| **Species richness** | P < 0.001 | P = 0.448 | P < 0.001 | P = 0.008 | P < 0.001 | P < 0.001 |
| **Shannon-Weiner** | P < 0.001 | P = 0.001 | P = 0.590 | P = 0.083 | P < 0.001 | P < 0.001 |
| **Simpson's diversity** | P < 0.001 | P =0.010 | P = 0.342 | P = 0.026 | P < 0.001 | P < 0.001 |
| **Simpson's evenness** | P < 0.001 | P = 0.012 | P = 0.038 | P = 0.035 | P < 0.001 | P < 0.001 |
| **Taxonomic diversity** | P = 0.083 | P = 0.622 | P < 0.001 | P = 0.400 | P = 0.243 | P = 0.060 |
| **Taxonomic distinctness** | P < 0.001 | P = 0.133 | P = 0.166 | P = 0.059 | P < 0.001 | P < 0.001 |
| **Average taxonomic distinctness** | P < 0.001 | P = 0.215 | P = 0.073 | P < 0.001 | P < 0.001 | P < 0.001 |
| **Variation taxonomic distinctness** | P = 0.002 | P = 0.002 | P = 0.396 | P < 0.001 | P < 0.001 | P < 0.001 |

**Table 1.7.** Fall ME-NH Inshore Trawl Survey with trawl environmental measurements. Highlighted P values are statistically significant

| | Bottom temperature | Surface temperature | Bottom salinity | Surface salinity | Depth | Lat/long | Landings |
|---|---|---|---|---|---|---|---|
| **Species richness** | P < 0.001 | P = 0.793 | P = 0.059 | P = 0.314 | P < 0.001 | P < 0.001 | P = 0.003 |
| **Shannon-Wiener** | P = 0.003 | P = 0.809 | P = 0.561 | P = 0.229 | P < 0.001 | P < 0.001 | P = 0.674 |
| **Simpson's diversity** | P = 0.003 | P = 0.795 | P = 0.868 | P = 0.472 | P < 0.001 | P < 0.001 | P = 0.482 |
| **Simpson's evenness** | P <0.001 | P = 0.983 | P = 0.299 | P = 0.958 | P = 0.009 | P <0.001 | P = 0.245 |
| **Taxonomic diversity** | P = 0.465 | P = 0.964 | P = 0.996 | P = 0.570 | P = 0.051 | P < 0.001 | P <0.001 |
| **Taxonomic distinctness** | P = 0.013 | P = 0.067 | P= 0.168 | P = 0.101 | P < 0.001 | P < 0.001 | P = 0.467 |
| **Average taxonomic distinctness** | P = 0.372 | P = 0.783 | P = 0.055 | P = 0.264 | P < 0.001 | P < 0.001 | P = 0.254 |
| **Variation taxonomic distinctness** | P < 0.001 | P = 0.044 | P = 0.537 | P < 0.001 | P < 0.001 | P < 0.001 | P = 0.147 |

**Table 1.8.** Spring ME-NH Inshore Trawl Survey with trawl environmental measurements. Highlighted P values are statistically significant

| | Bottom temperature | Surface temperature | Bottom salinity | Surface salinity | Depth | Lat/long | Landings |
|---|---|---|---|---|---|---|---|
| **Species richness** | P = 0.022 | P = 0.363 | P = 0.365 | P = 0.212 | P < 0.001 | P < 0.001 | P = 0.173 |
| **Shannon-Weiner** | P = 0.964 | P = 0.840 | P = 0.011 | P = 0.260 | P < 0.001 | P <0.001 | P = 0.190 |
| **Simpson's diversity** | P = 0.456 | P = 0.254 | P = 0.011 | P = 0.925 | P < 0.001 | P < 0.001 | P = 0.123 |
| **Simpson's evenness** | P = 0.110 | P = 0.190 | P = 0.047 | P = 0.048 | P < 0.001 | P < 0.001 | P = 0.030 |
| **Taxonomic diversity** | P = 0.865 | P = 0.027 | P = 0.419 | P = 0.042 | P = 0.127 | P < 0.001 | P = 0.081 |
| **Taxonomic distinctness** | P = 0.775 | P = 0.051 | P = 0.209 | P = 0.005 | P < 0.001 | P < 0.001 | P < 0.001 |
| **Average taxonomic distinctness** | P = 0.452 | P = 0.015 | P = 0.754 | P = 0.002 | P < 0.001 | P < 0.001 | P = 0.096 |
| **Variation taxonomic distinctness** | P = 0.006 | P = 0.001 | P = 0.110 | P = 0.120 | P < 0.001 | P < 0.001 | P = 0.169 |

**Objective 2**

**Table 2.1.** Pairwise analysis of variance (*adonis*) results for ME-NH Inshore Trawl Survey region groups from each community structure. Regions 1 and 2 are West of Penobscot Bay, region 3 is Penobscot Bay, and regions 4 and 5 are East of Penobscot Bay.

| | West vs. Pen Bay | East vs. Pen Bay | East vs West |
|---|---|---|---|
| **Functional group biomass** | P = 0.015 | P = 0.0063 | P < 0.001 |
| **Functional group abundance** | P = 0.001 | P <0.001 | P = 0.089 |
| **Top 50 biomass** | P < 0.001 | P <0.001 | P <0.001 |
| **Top 50 abundance** | P < 0.001 | P < 0.001 | P < 0.001 |

**Table 2.2.** Pairwise analysis of variance (adonis) results for ME-NH Inshore Trawl Survey year groups from each community structure

| | 2000-2004 vs. 2005-2009 | 2000-2004 vs. 2010-2014 | 2000-2004 vs. 2015-2019 | 2005-2009 vs. 2010-2014 | 2005-2009 vs. 2015-2019 | 2010-2014 vs. 2015-2019 |
|---|---|---|---|---|---|---|
| **Functional group biomass** | P = 0.0019 | P < 0.001 | P < 0.001 | P <0.001 | P <0.001 | P = 0.001 |
| **Functional group abundance** | P < 0.001 | P = 0.009 | P = 0.023 | P < 0.001 | P <0.001 | P < 0.001 |
| **Top 50 biomass** | P =0.003 | P <0.001 | P <0.001 | P <0.001 | P <0.001 | P <0.001 |
| **Top 50 abundance** | P = 0.009 | P = 0.016 | P < 0.001 | P <0.001 | P < 0.001 | P = 0.005 |

**Table 2.3.** Linear environmental effects (*envfit*) for ME-NH Inshore Trawl Survey

| | Start latitude | Start longitude | End latitude | End longitude | Start depth | End depth | Bottom temperature | Bottom salinity | Surface temperature | Surface salinity |
|---|---|---|---|---|---|---|---|---|---|---|
| **Functional group biomass** | P=0.001 | P= 0.001 | P=0.001 | P=0.001 | P=0.028 | P=0.058 | P=0.001 | P=0.001 | P=0.001 | P=0.927 |
| **Functional group abundance** | P=0.750 | P=0.861 | P=0.748 | P=0.859 | P=0.035 | P=0.045 | P=0.001 | P=0.001 | P=0.001 | P=0.970 |
| **Top 50 biomass** | P=0.001 | P=0.001 | P=0.001 | P=0.001 | P=0.005 | P=0.007 | P=0.001 | P=0.001 | P=0.001 | P=0.370 |
| **Top 50 abundance** | P=0.001 | P=0.001 | P=0.001 | P=0.001 | P=0.032 | P=0.096 | P=0.001 | P=0.001 | P=0.001 | P=0.986 |

**Table 2.4.** Nonlinear environmental effects (*ordisurf*) for ME-NH Inshore Trawl Survey

| | Start latitude | Start longitude | Start depth | Bottom temperature | Bottom salinity | Surface temperature | Surface salinity |
|---|---|---|---|---|---|---|---|
| **Functional group biomass** | P < 0.001 | P < 0.001 | P = 0.0027 | P < 0.001 | P < 0.001 | P < 0.001 | P = 0.947 |
| **Functional group abundance** | P < 0.001 | P < 0.001 | P = 0.015 | P < 0.001 | P < 0.001 | P <0.001 | P = 0.627 |
| **Top 50 biomass** | P < 0.001 | P < 0.001 | P < 0.001 | P < 0.001 | P < 0.001 | P < 0.001 | P = 0.13 |
| **Top 50 abundance** | P < 0.001 | P < 0.001 | P = 0.007 | P < 0.001 | P < 0.001 | P < 0.001 | P = 0.544 |

**Objective 4.**

**Table 4.1.** Correlation between Maine landings and ME-NH Inshore Trawl Survey biodiversity indices

| | |
|---|---|
| **Species richness** | **0.40** |
| **Shannon-Weiner** | **0.84** |
| **Simpson's evenness** | **0.87** |
| **Average taxonomic diversity** | **0.22** |

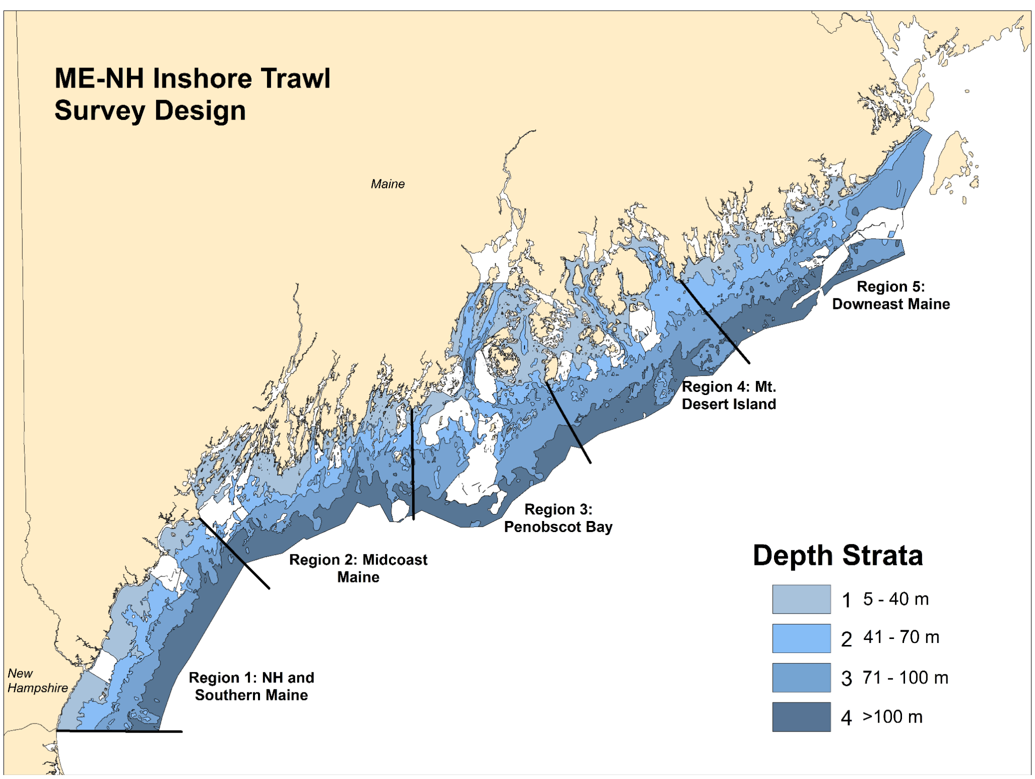


**Figure 0.1.** ME-NH Inshore Trawl Survey design with 5 regions and 4 depth strata. From Data Portal (**https://mainedmr.shinyapps.io/MaineDMR_Trawl_Survey_Portal/**).

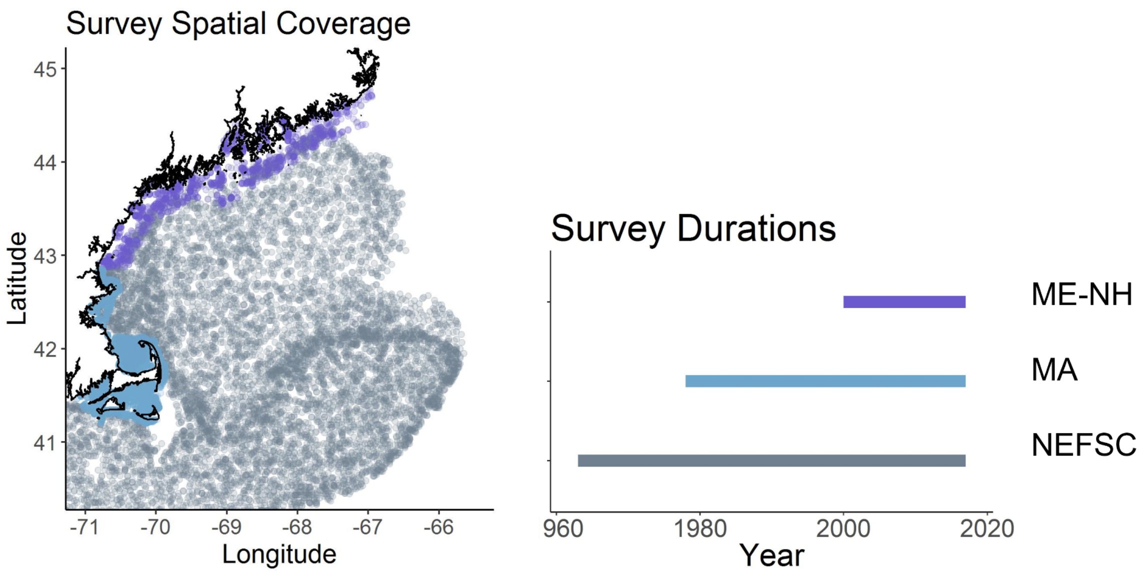


**Figure 0.2.** Spatial coverage and duration for ME-NH Inshore Trawl Survey, MA DMF Inshore Trawl Survey, and NEFSC Bottom Trawl Survey GOM region.

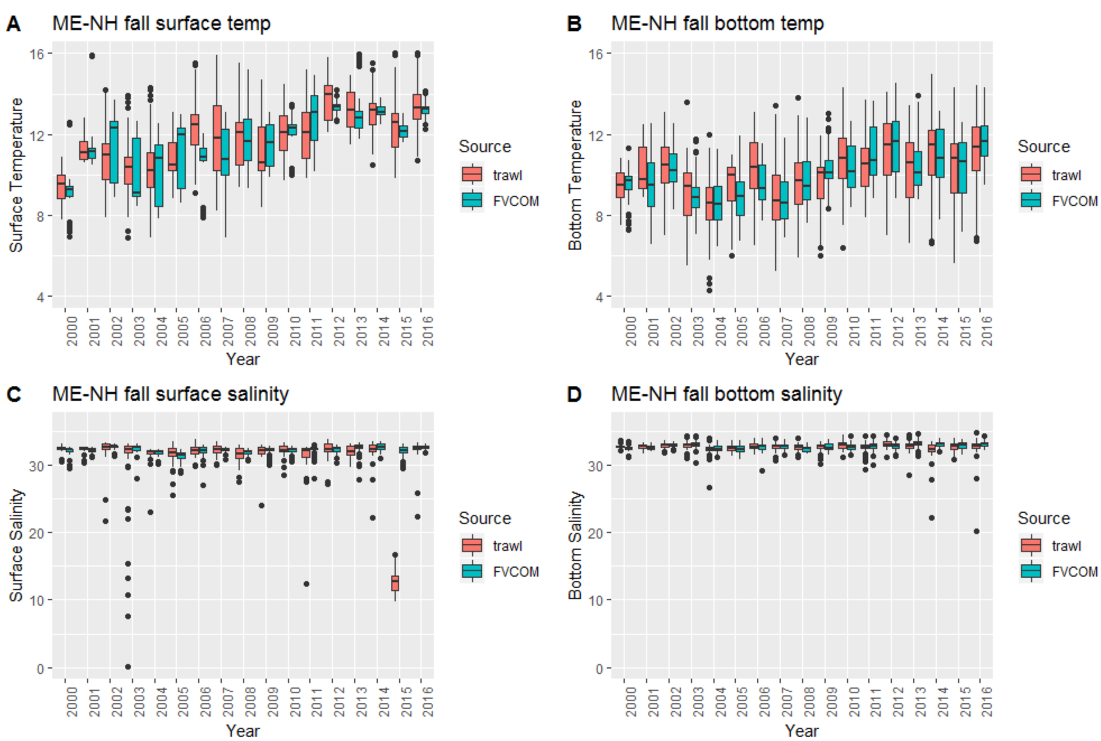


**Figure 0.3.** ME-NH Inshore Trawl Survey fall environmental data compared to FVCOM for surface temperature (A), bottom temperature (B), surface salinity (C), and bottom salinity (D).

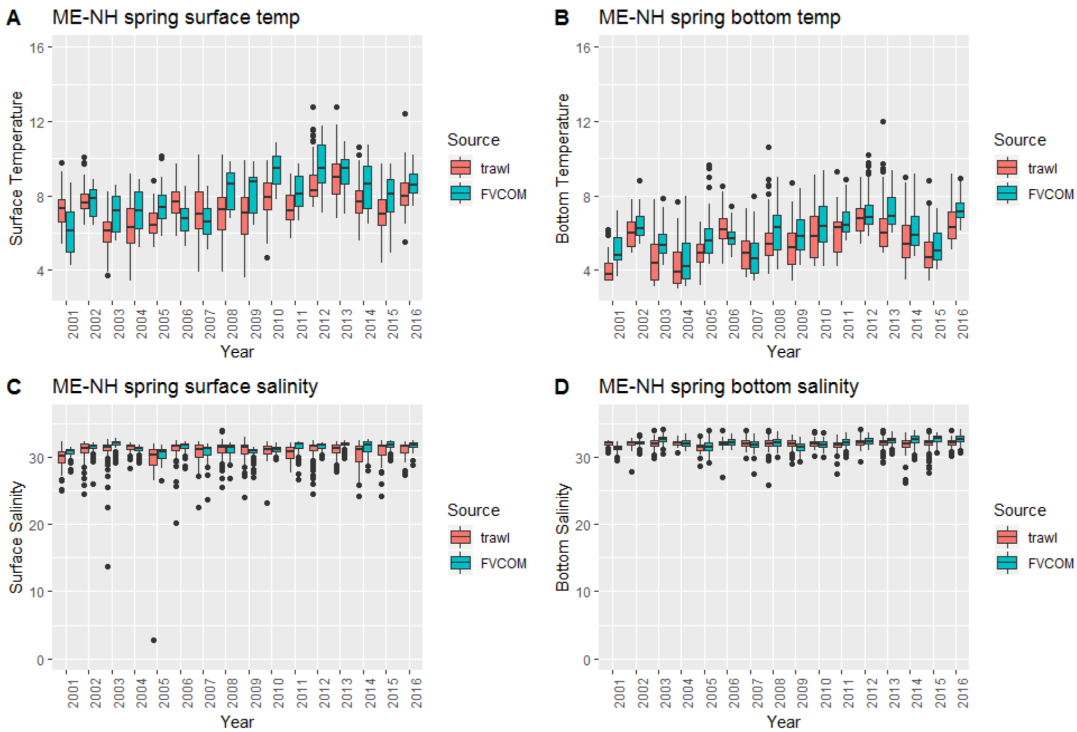


**Figure 0.4.** ME-NH Inshore Trawl Survey spring environmental data compared to FVCOM for surface temperature (A), bottom temperature (B), surface salinity (C), and bottom salinity (D).

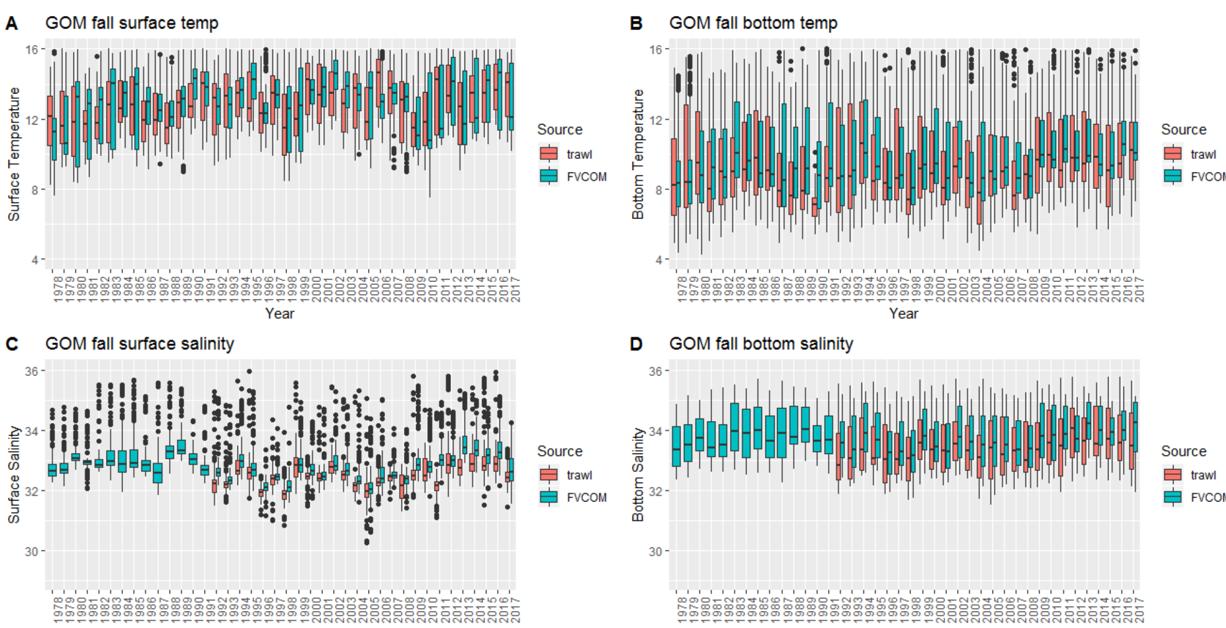


**Figure 0.5.** NEFSC Trawl Survey GOM region fall environmental data compared to FVCOM for surface temperature (A), bottom temperature (B), surface salinity (C), and bottom salinity (D).

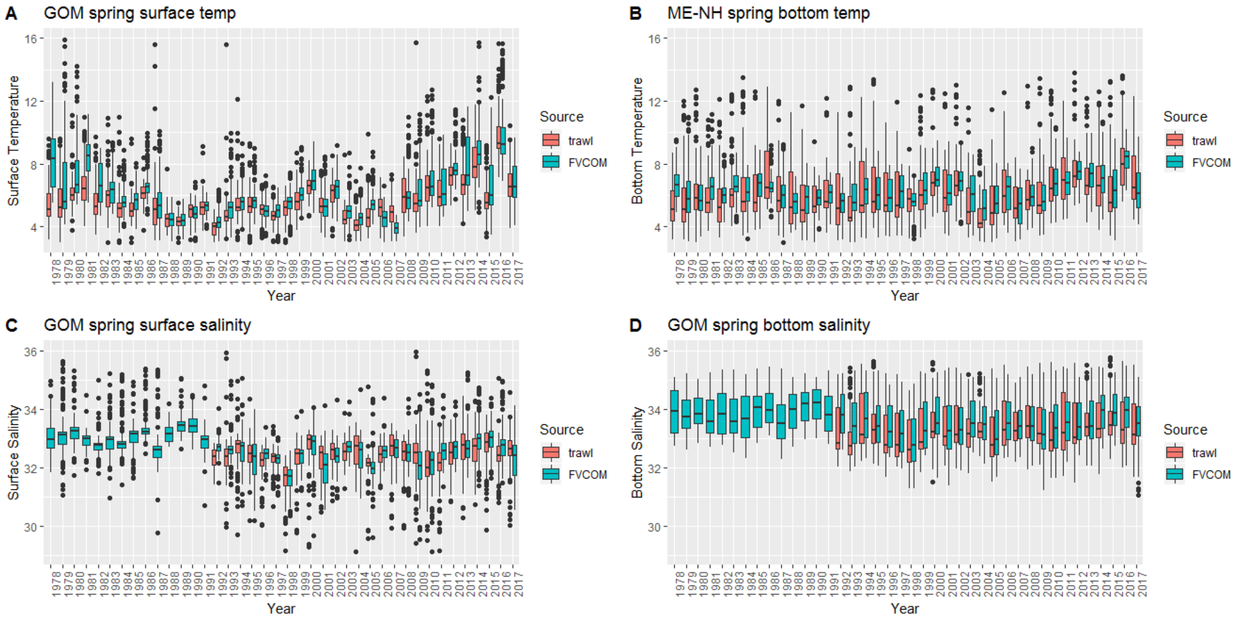


**Figure 0.6.** NEFSC Trawl Survey GOM region spring environmental data compared to FVCOM for surface temperature (A), bottom temperature (B), surface salinity (C), and bottom salinity (D).

**Objective 1:**

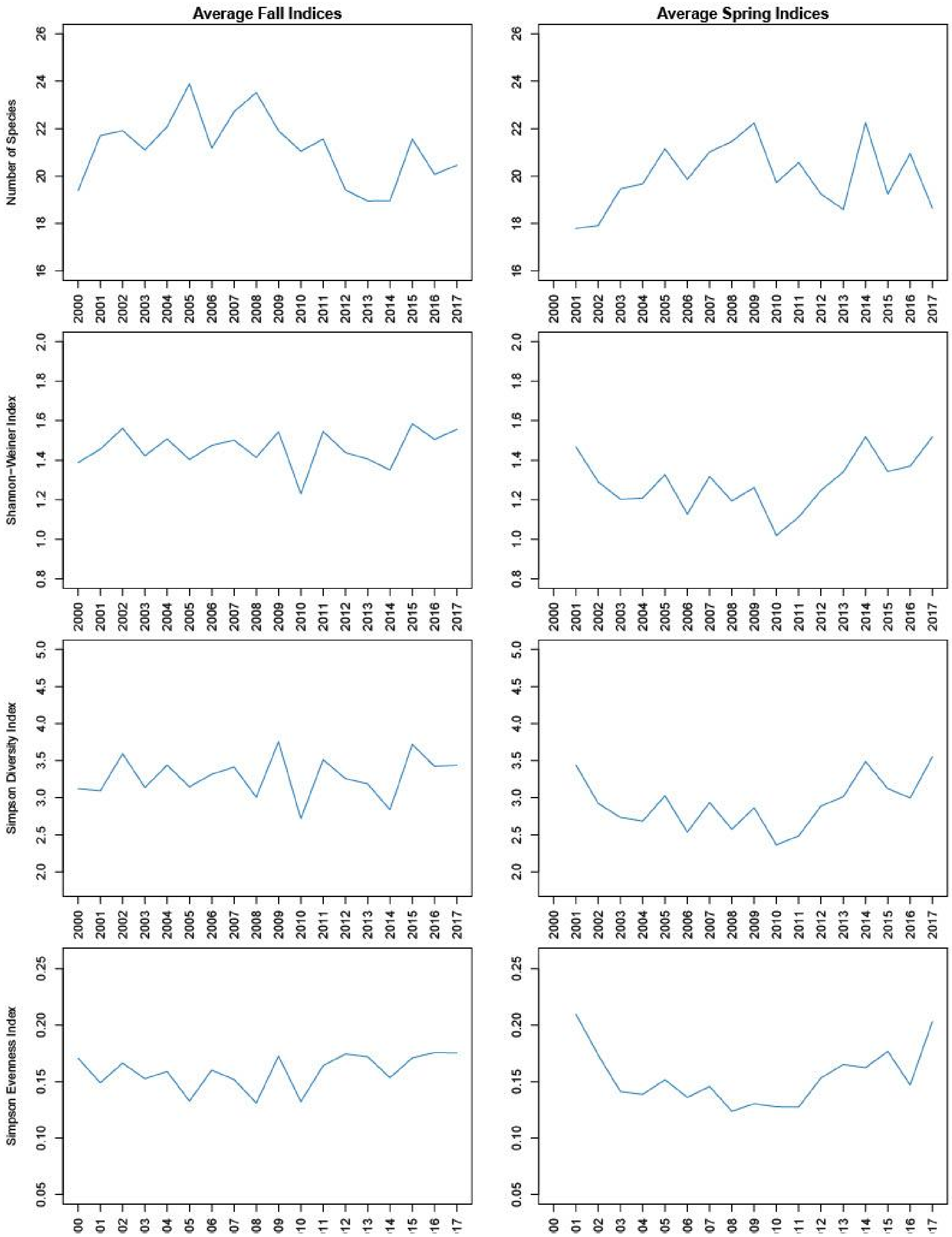


**Figure 1.1.** ME-NH Inshore Trawl Survey average fall and spring biodiversity indices (2000-2017), including species richness, Shannon-Weiner diversity, Simpson's diversity, and Simpson's evenness.

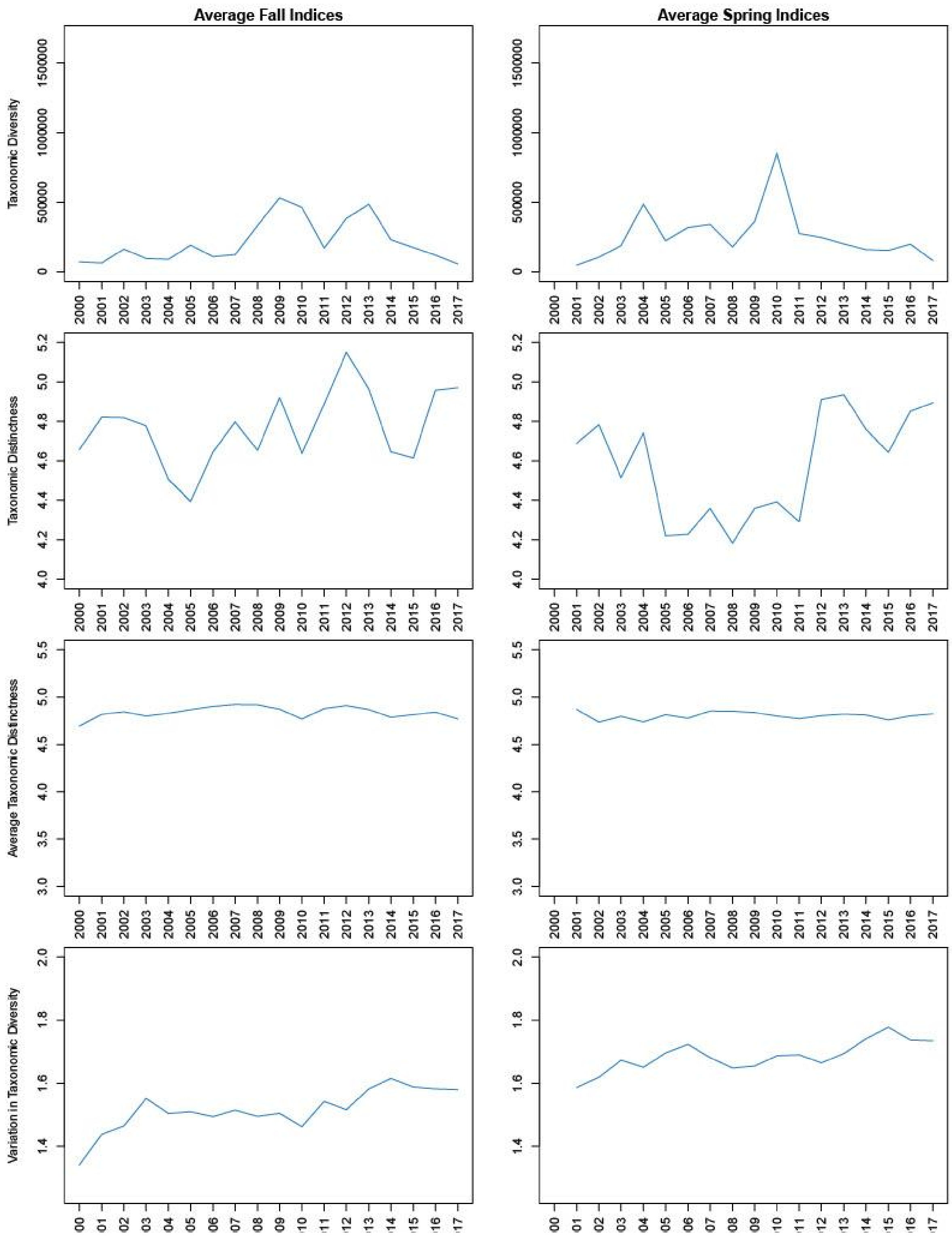


**Figure 1.2.** ME-NH Inshore Trawl Survey average fall and spring biodiversity indices (2000-2017), including taxonomic diversity, taxonomic distinctness, average taxonomic distinctness, and variation in taxonomic distinctness.

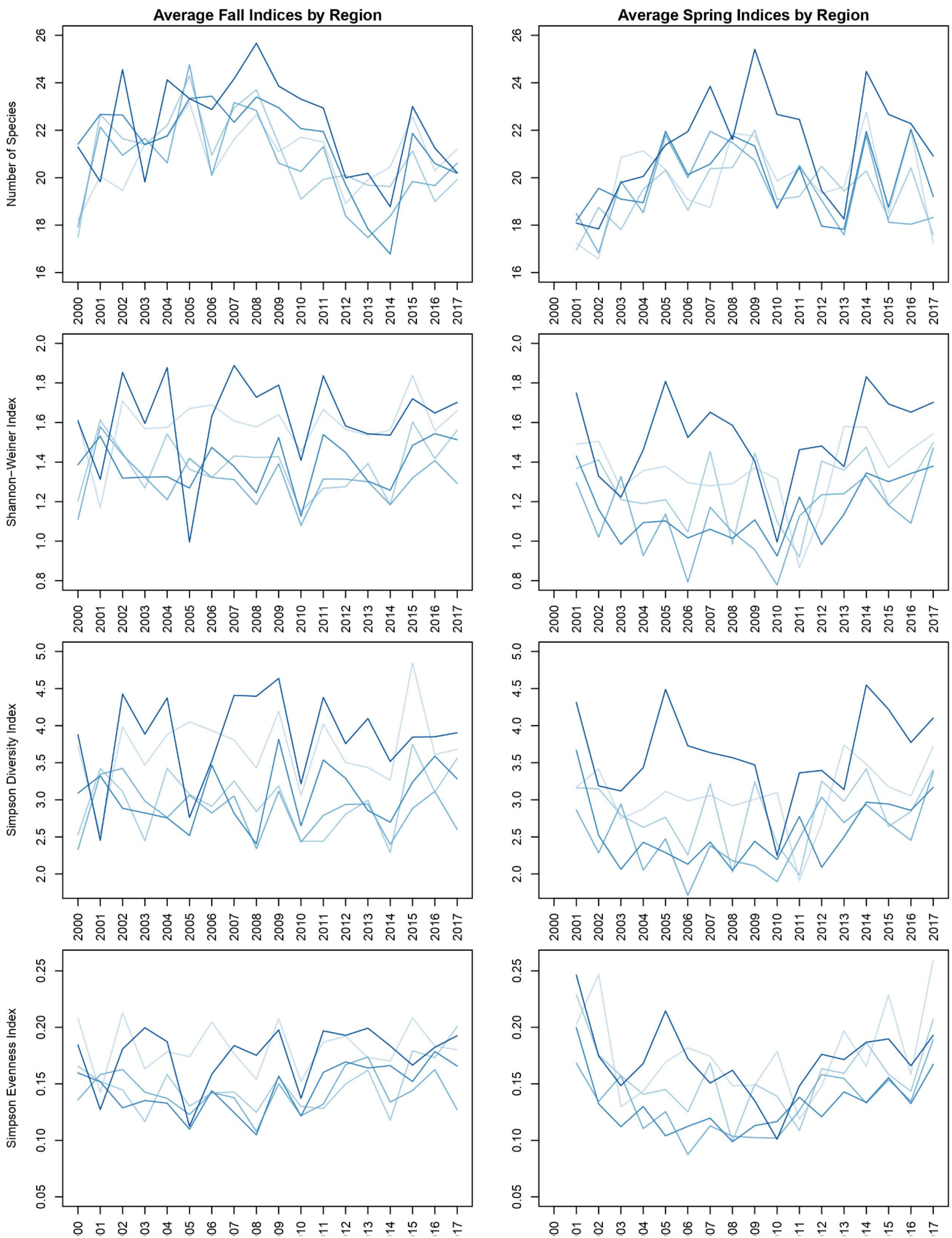


**Figure 1.3.** ME-NH Inshore Trawl Survey average fall and spring biodiversity indices by region (2000-2017), including species richness, Shannon-Weiner diversity, Simpson's diversity, and Simpson's evenness.

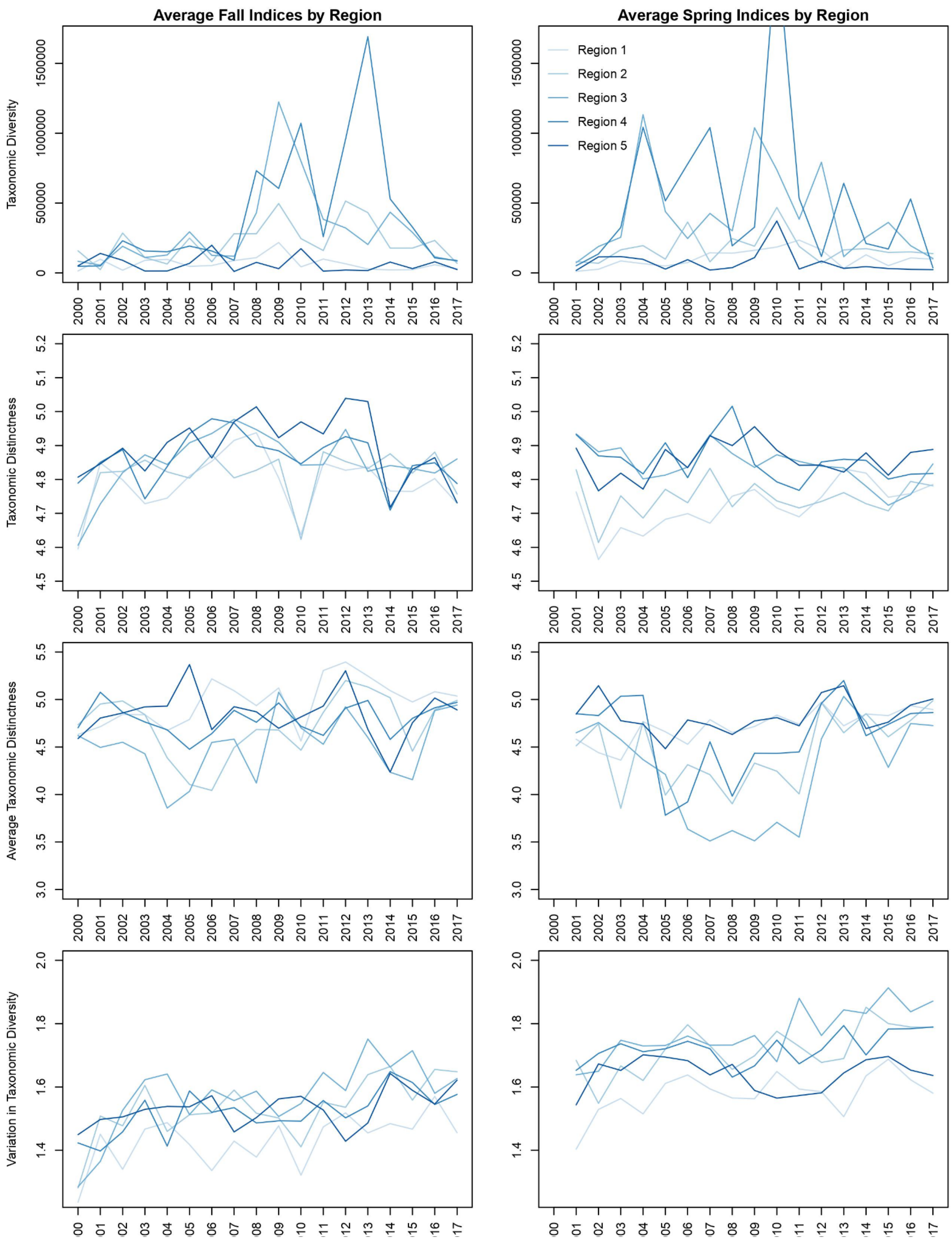


**Figure 1.4.** ME-NH Inshore Trawl Survey average fall and spring biodiversity indices by region (2000-2017), including taxonomic diversity, taxonomic distinctness, average taxonomic distinctness, and variation in taxonomic distinctness.

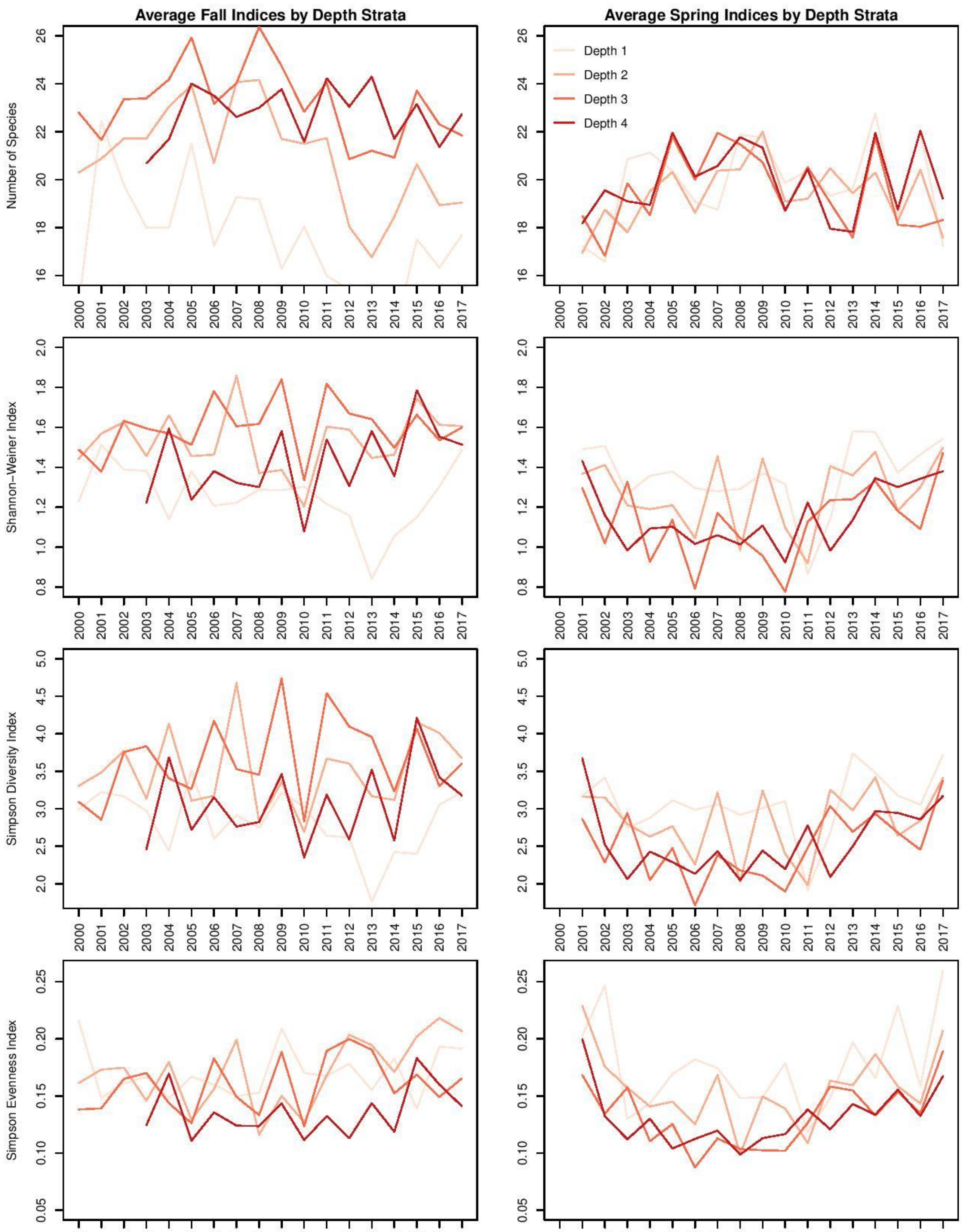


**Figure 1.5.** ME-NH Inshore Trawl Survey average fall and spring biodiversity indices by depth strata (2000-2017), including species richness, Shannon-Weiner diversity, Simpson's diversity, and Simpson's evenness.

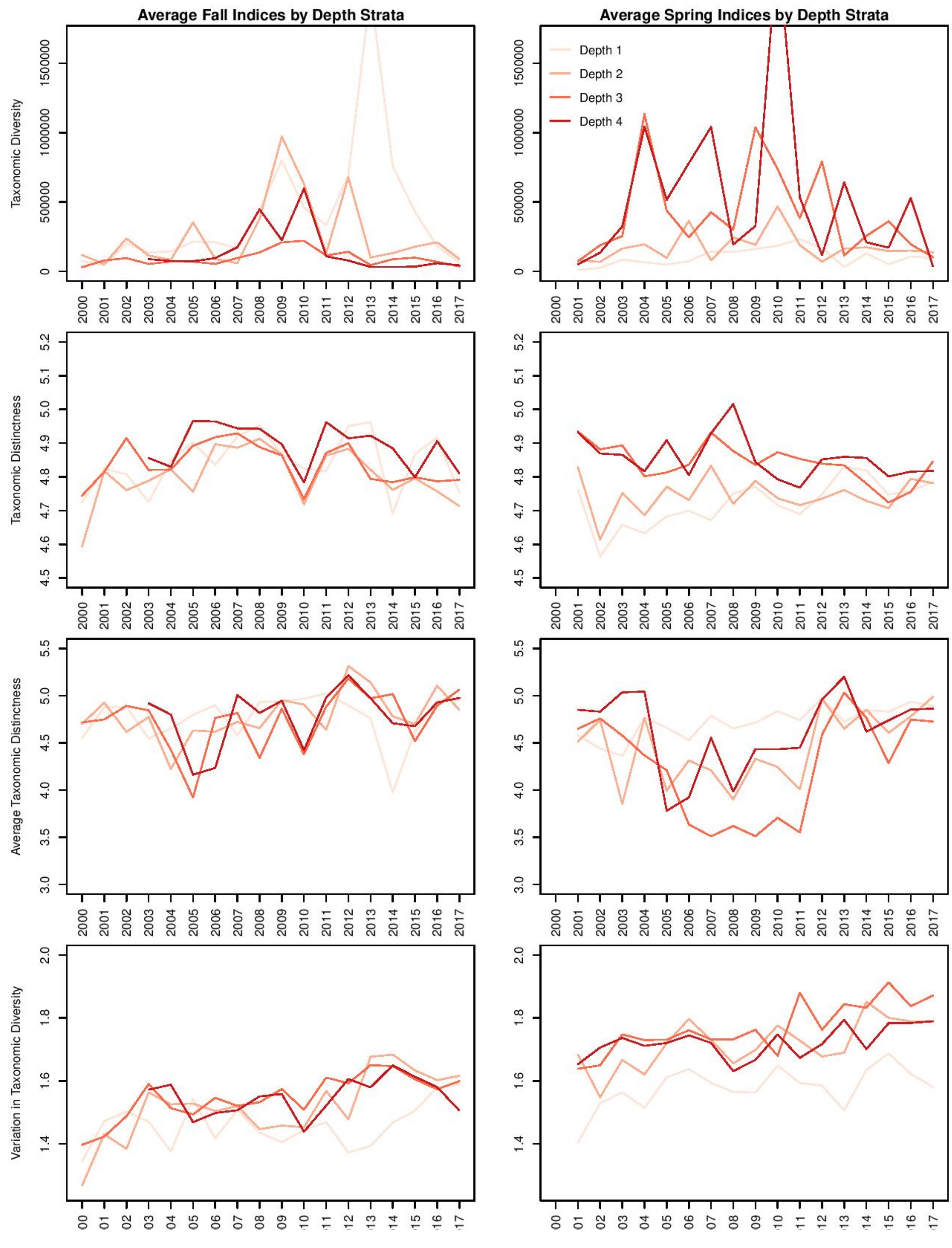


**Figure 1.6.** ME-NH Inshore Trawl Survey average fall and spring biodiversity indices by depth strata (2000-2017), including taxonomic diversity, taxonomic distinctness, average taxonomic distinctness, and variation in taxonomic distinctness.

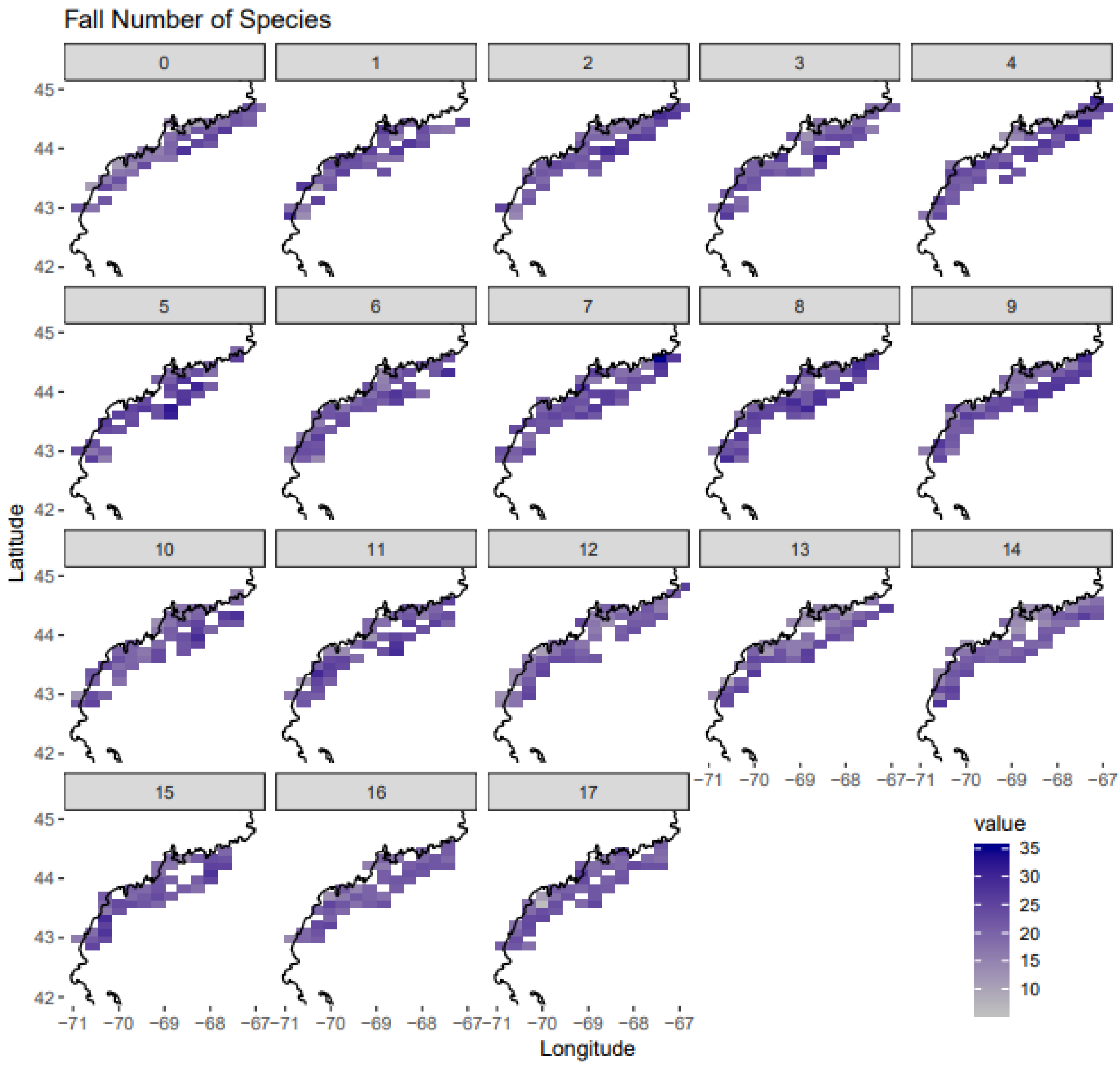


**Figure 1.7.** Annual fall ME-NH Inshore Trawl Survey species richness spatial maps (2000-2017).

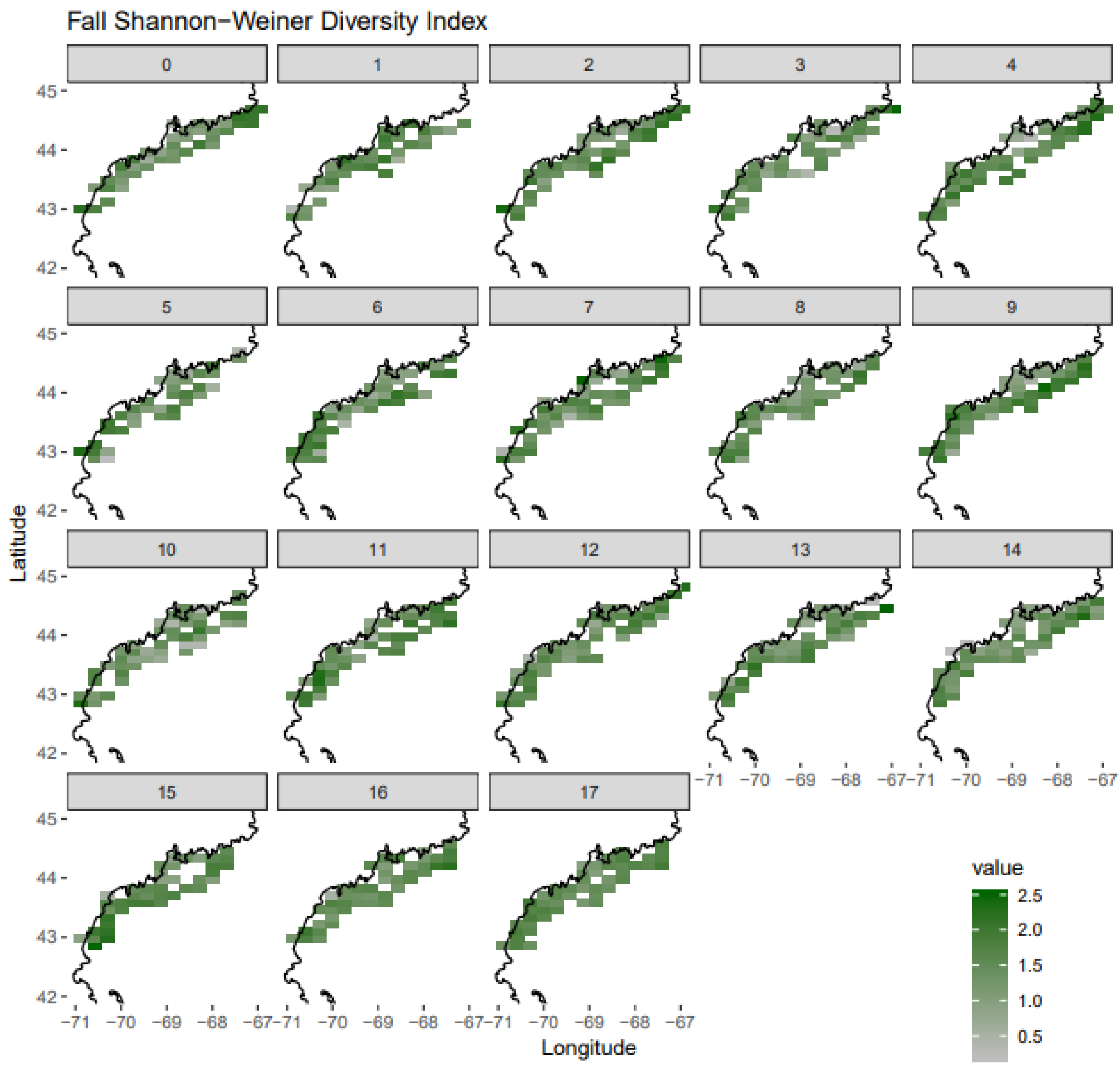


**Figure 1.8.** Annual fall ME-NH Inshore Trawl Survey Shannon-Weiner diveristy spatial maps (2000-2017).

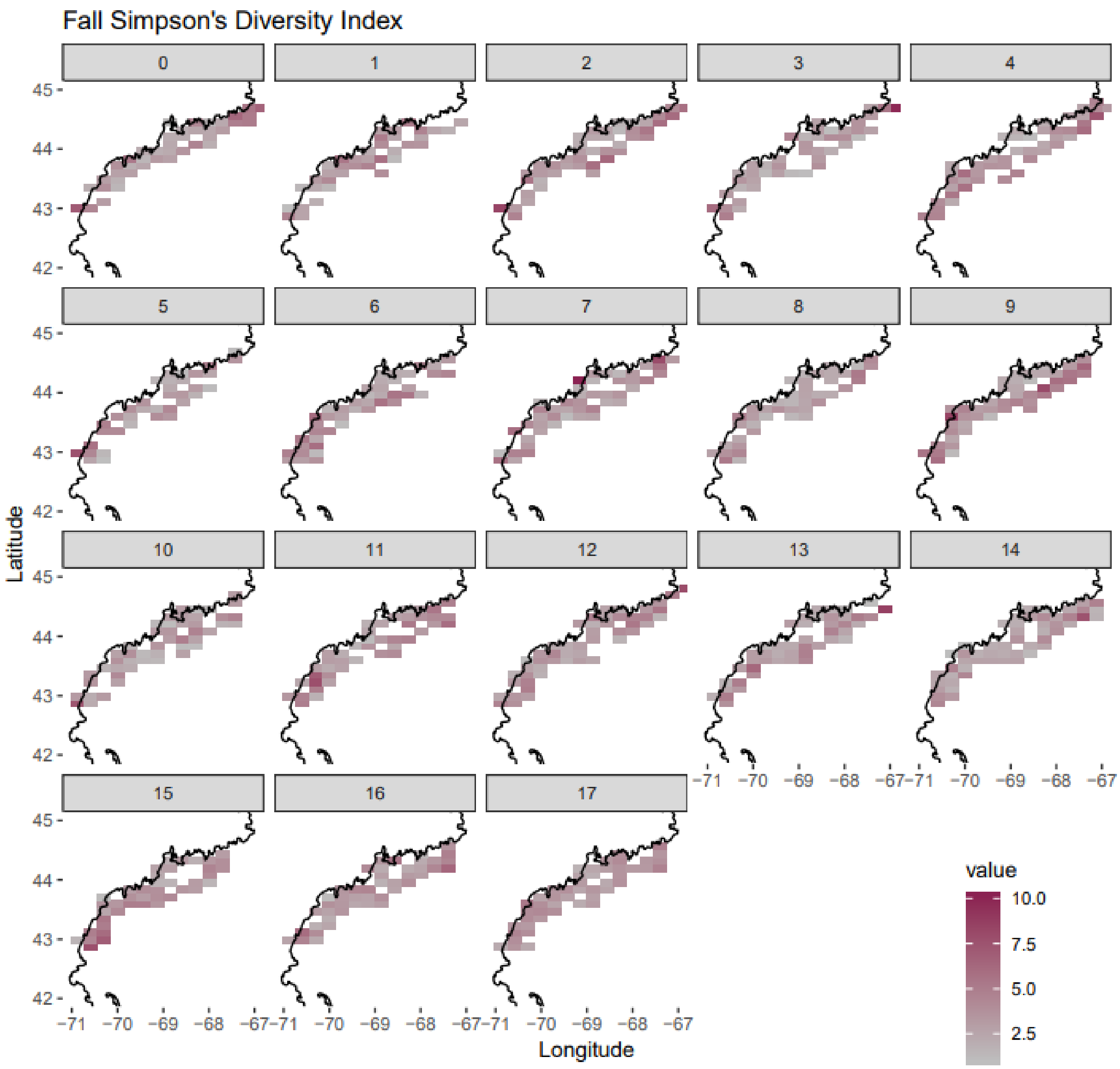


**Figure 1.9.** Annual fall ME-NH Inshore Trawl Survey Simpson's diversity spatial maps (2000-2017).

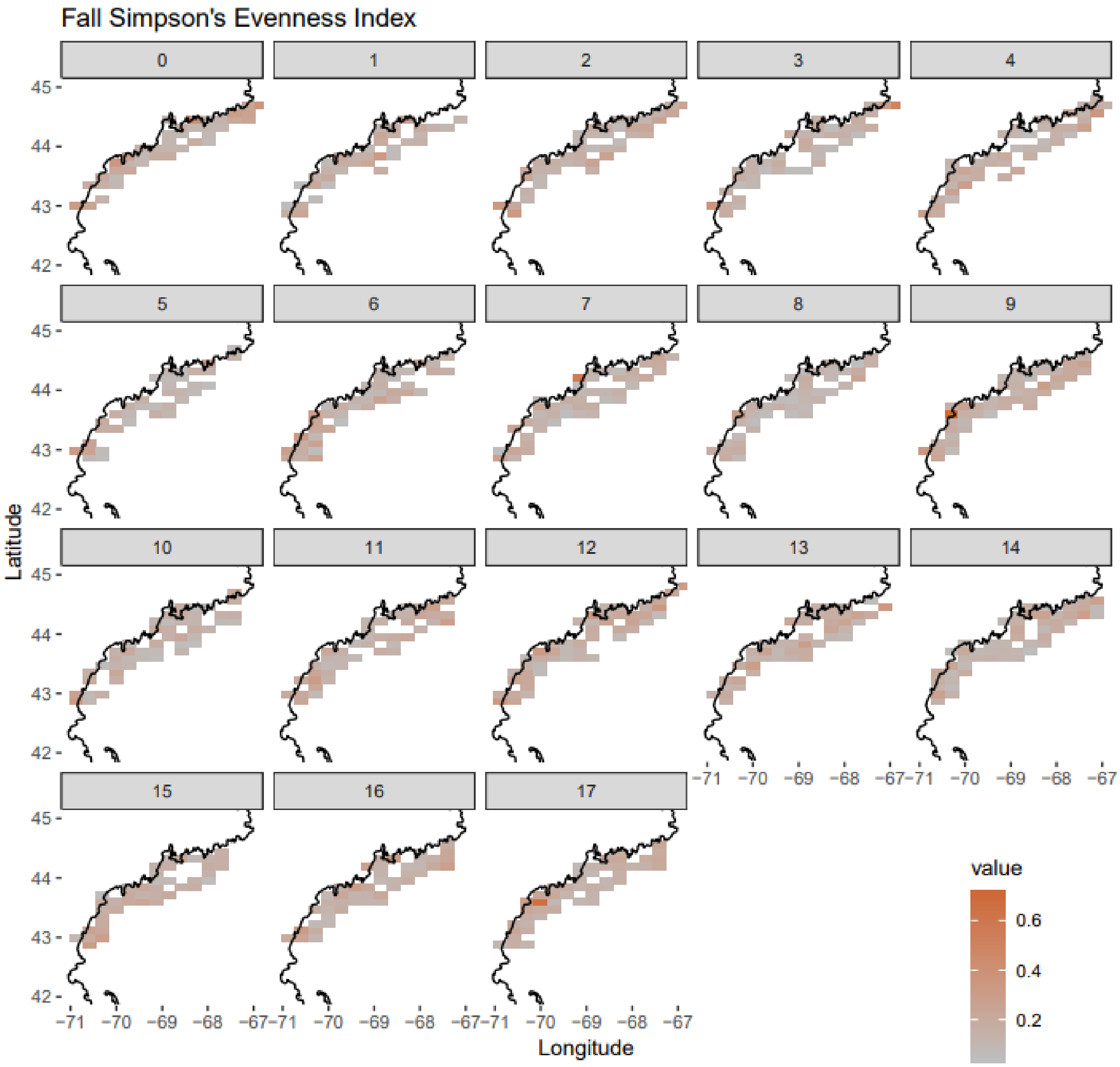


**Figure 1.10.** Annual fall ME-NH Inshore Trawl Survey Simpson's evenness spatial maps (2000-2017).

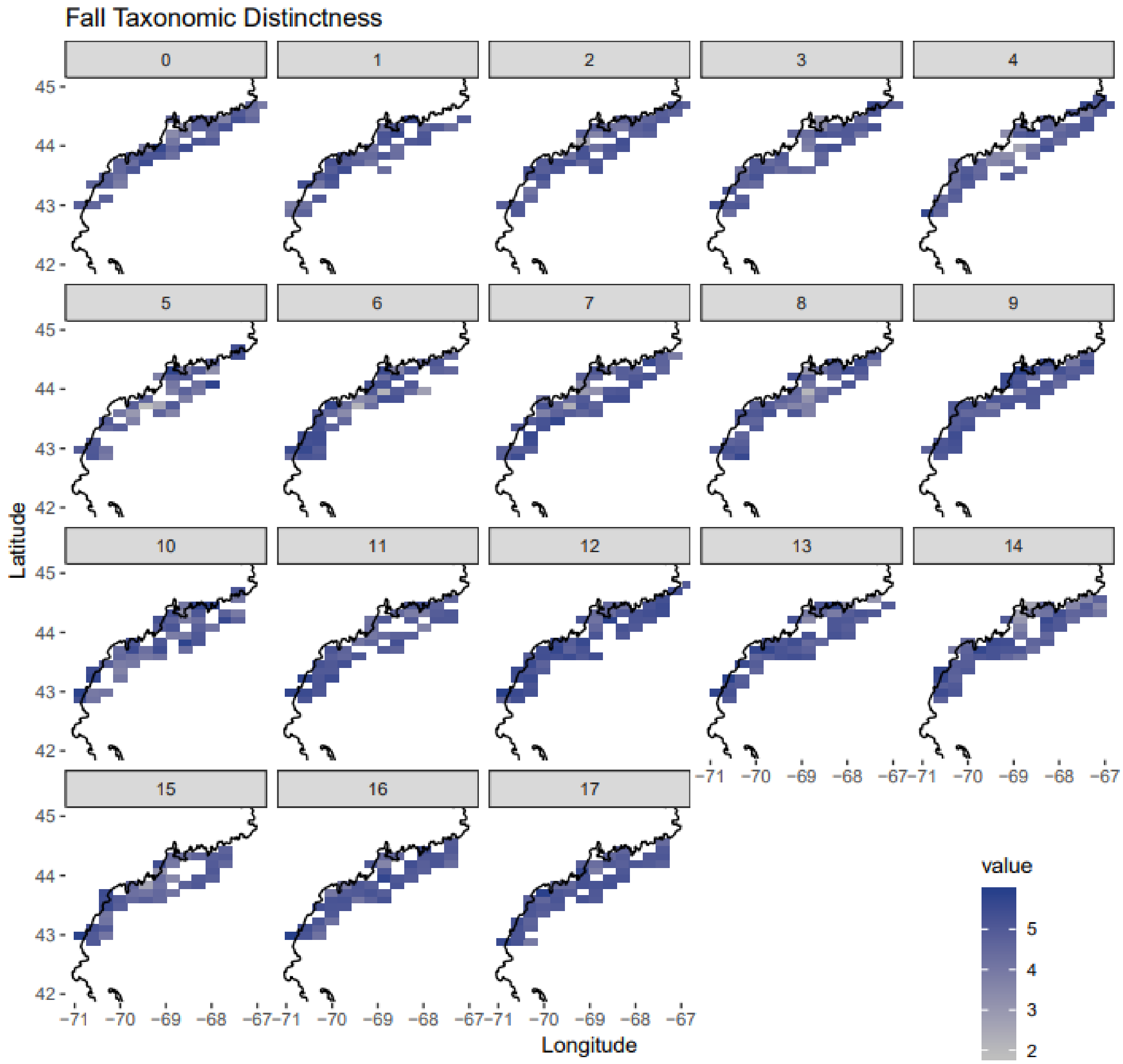


**Figure 1.11.** Annual fall ME-NH Inshore Trawl Survey taxonomic distinctness spatial maps (2000-2017).

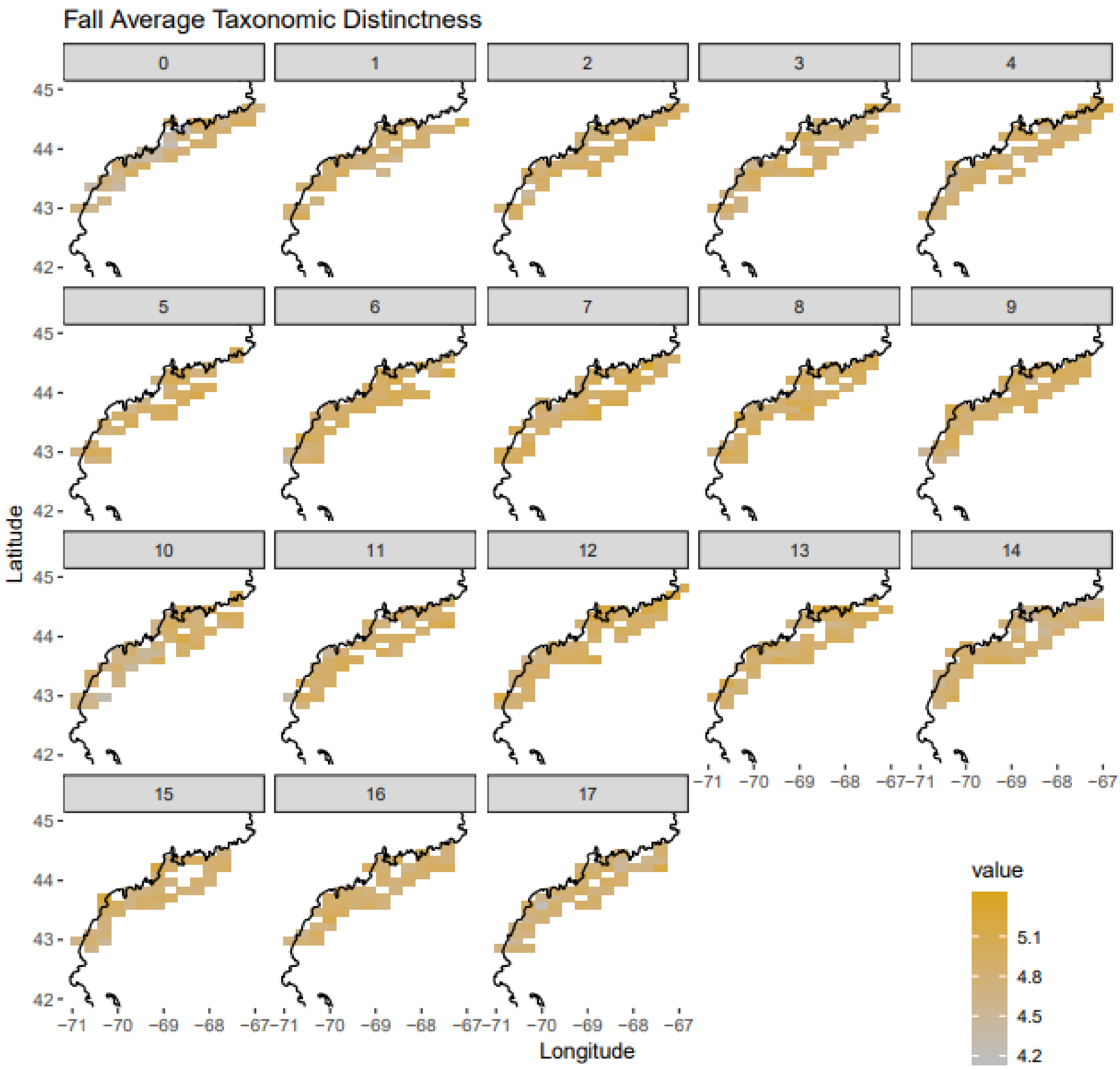


**Figure 1.12.** Annual fall ME-NH Inshore Trawl Survey average taxonomic distinctness spatial maps (2000-2017).

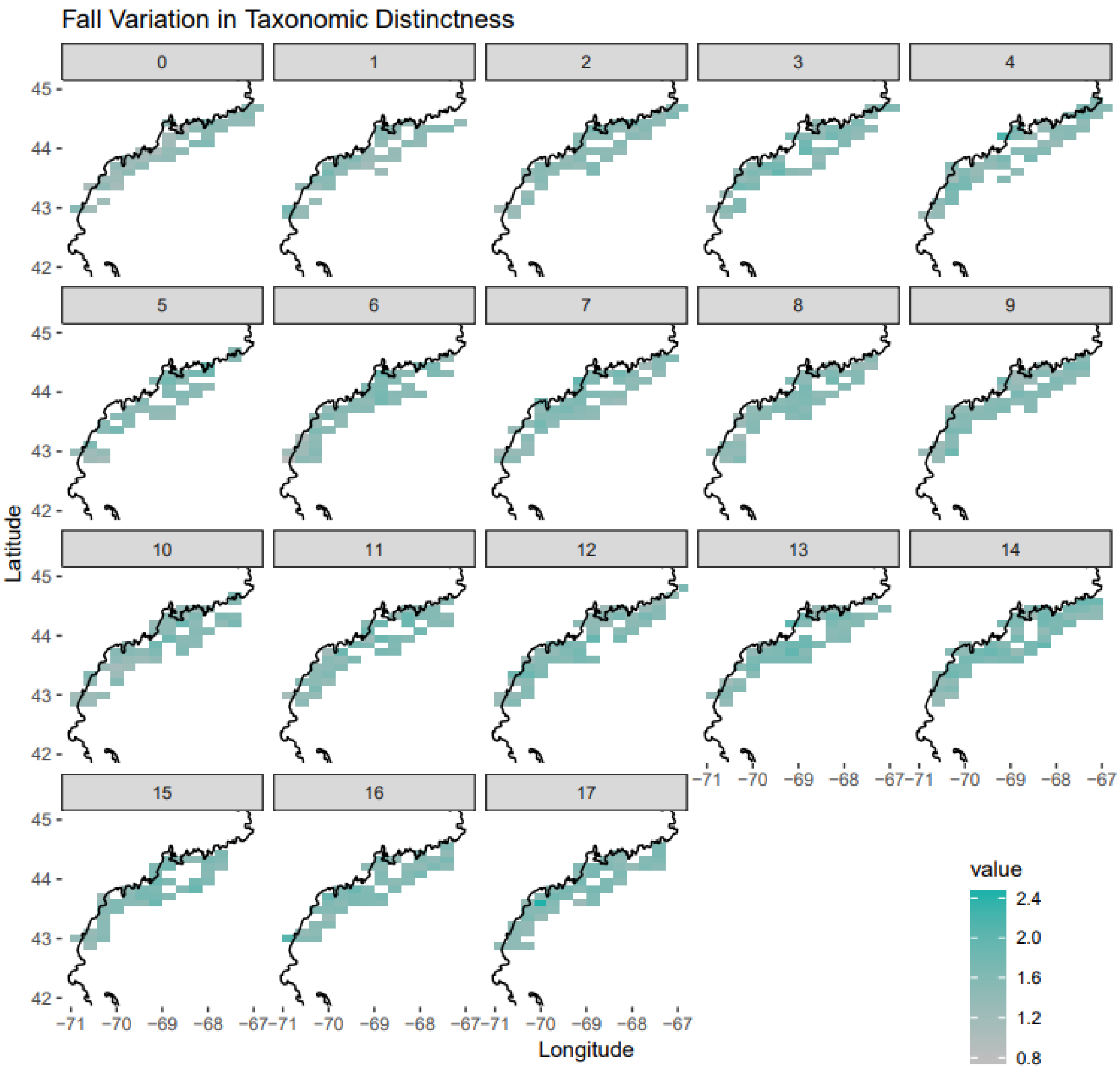


**Figure 1.13.** Annual fall ME-NH Inshore Trawl Survey variation in taxonomic distinctness spatial maps (2000-2017).

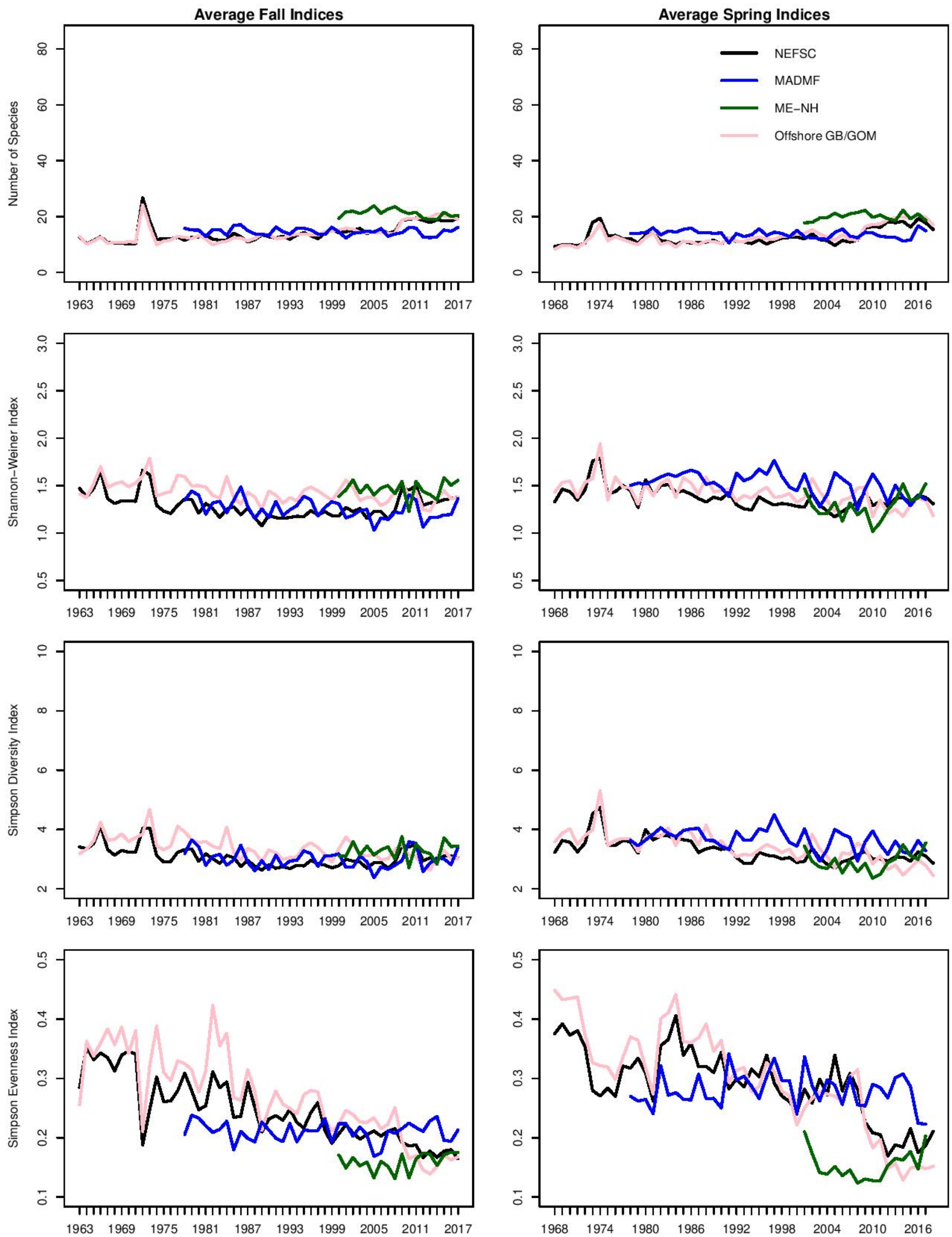


**Figure 1.14.** Average fall and spring biodiversity indices for NEFSC Trawl Survey (1963-2017), MADMF Inshore Trawl Survey (1978-2017), ME-NH Inshore Trawl Survey (2000-2017), and NEFSC Trawl Survey GOM region (1963-2017).

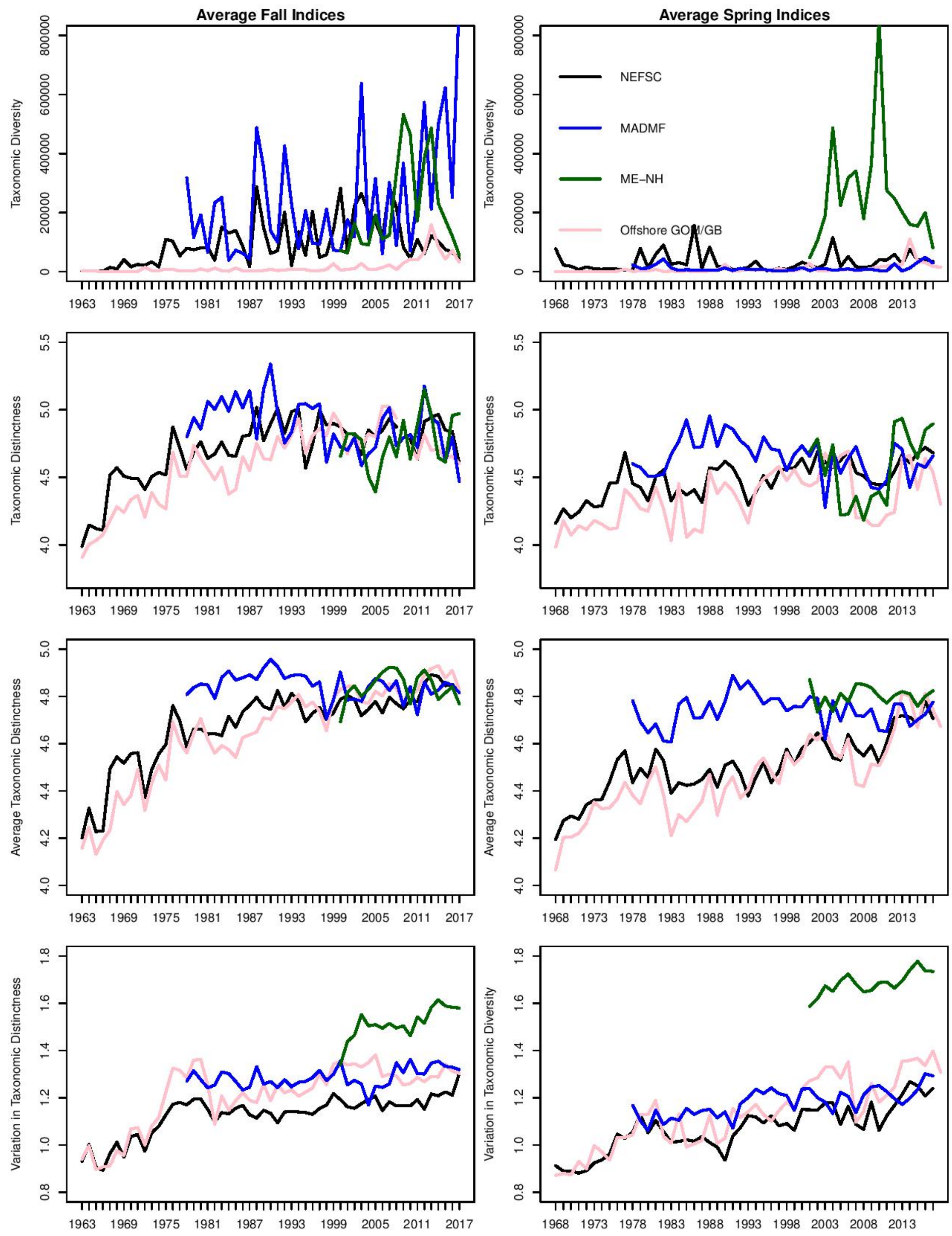


**Figure 1.15.** Average fall and spring biodiversity indices for NEFSC Trawl Survey (1963-2017), MADMF Inshore Trawl Survey (1978-2017), ME-NH Inshore Trawl Survey (2000-2017), and NEFSC Trawl Survey GOM region (1963-2017).

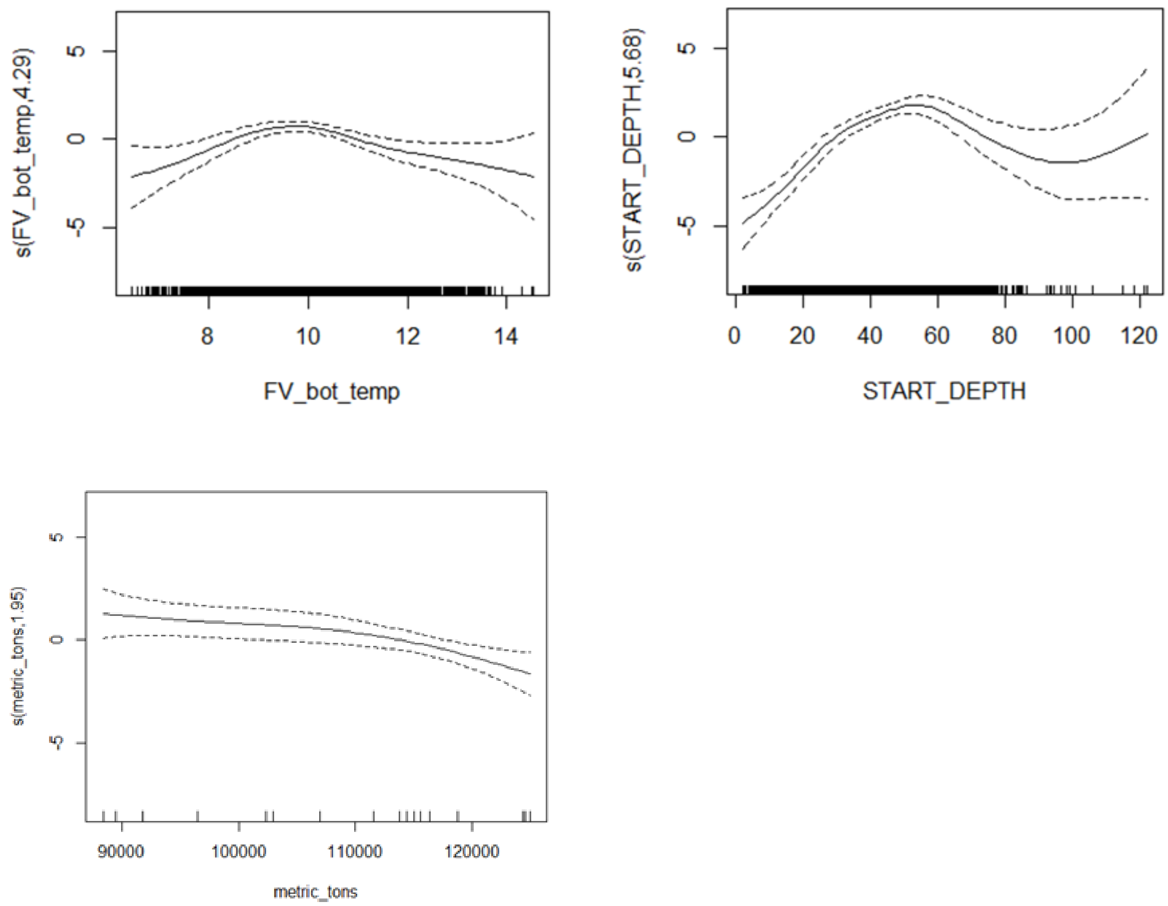


**Figure 1.16.** Fall ME-NH Inshore Trawl Survey significant factors for species richness GAMMs using FVCOM environmental data.

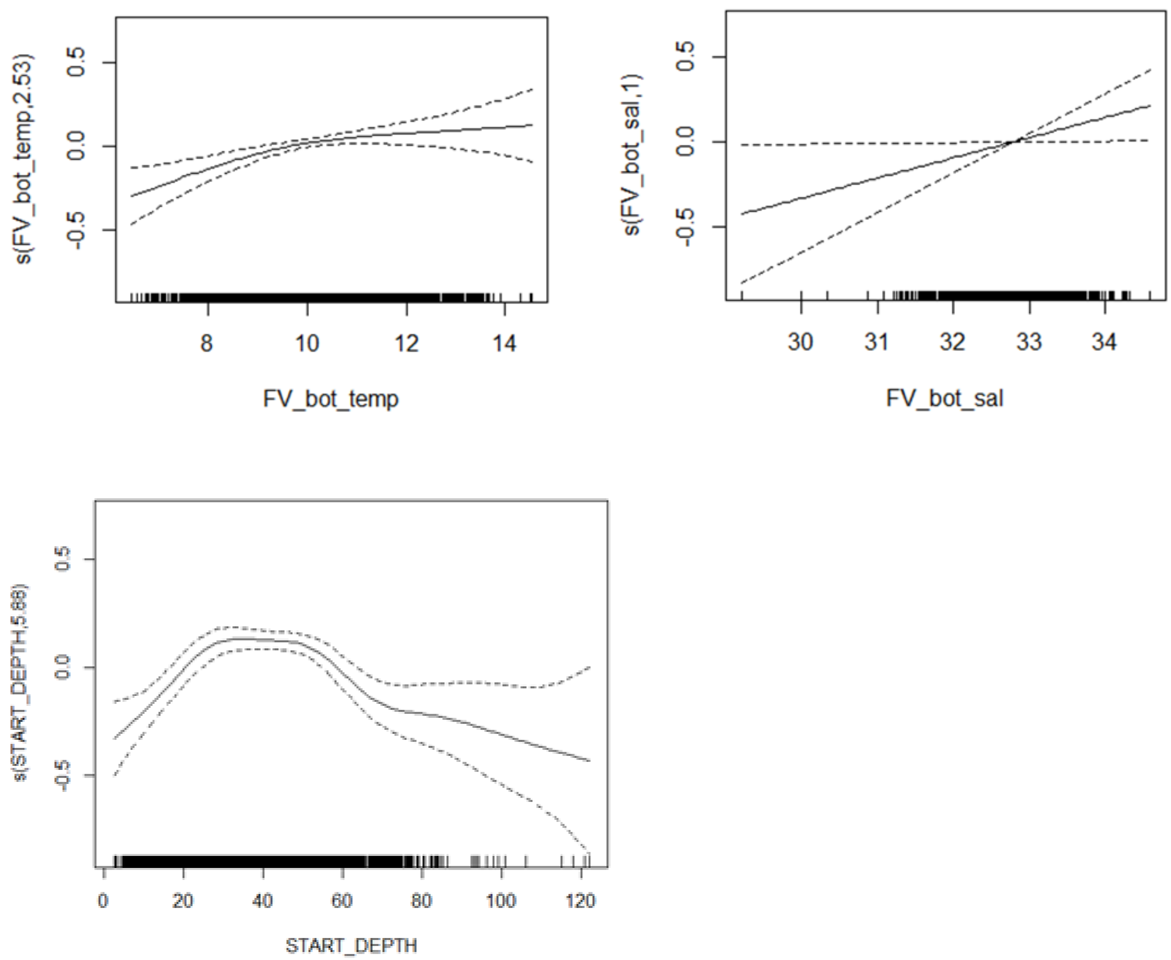


**Figure 1.17.** Fall ME-NH Inshore Trawl Survey significant factors for Shannon-Weiner diversity GAMMs using FVCOM environmental data.

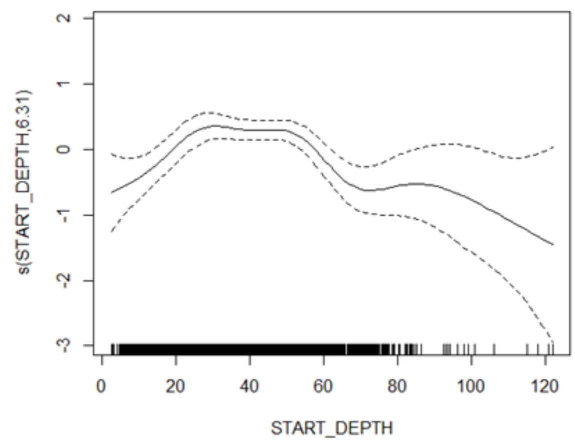


**Figure 1.18.** Fall ME-NH Inshore Trawl Survey significant factors for Simpson's diversity GAMMs using FVCOM environmental data.

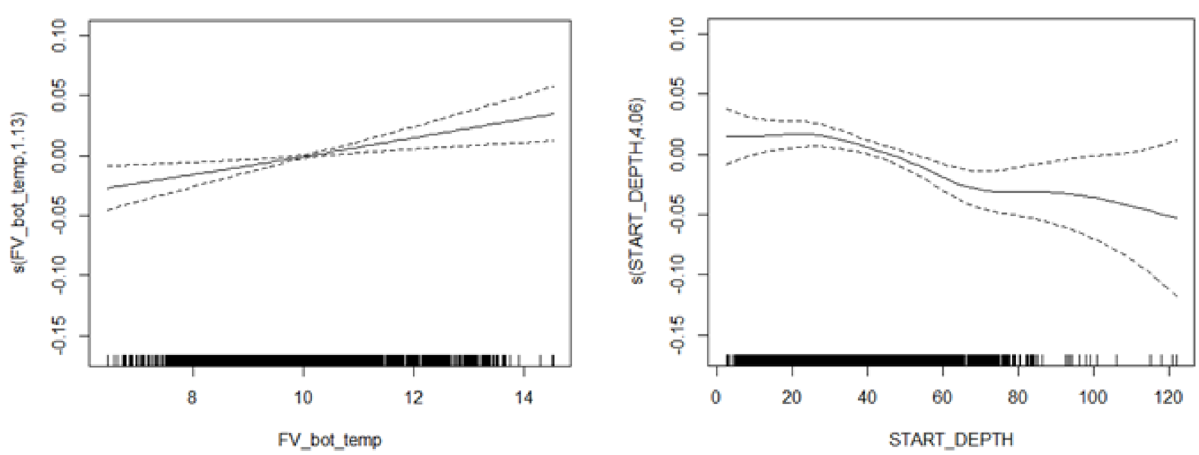


**Figure 1.19.** Fall ME-NH Inshore Trawl Survey significant factors for Simpson's evenness GAMMs using FVCOM environmental data.

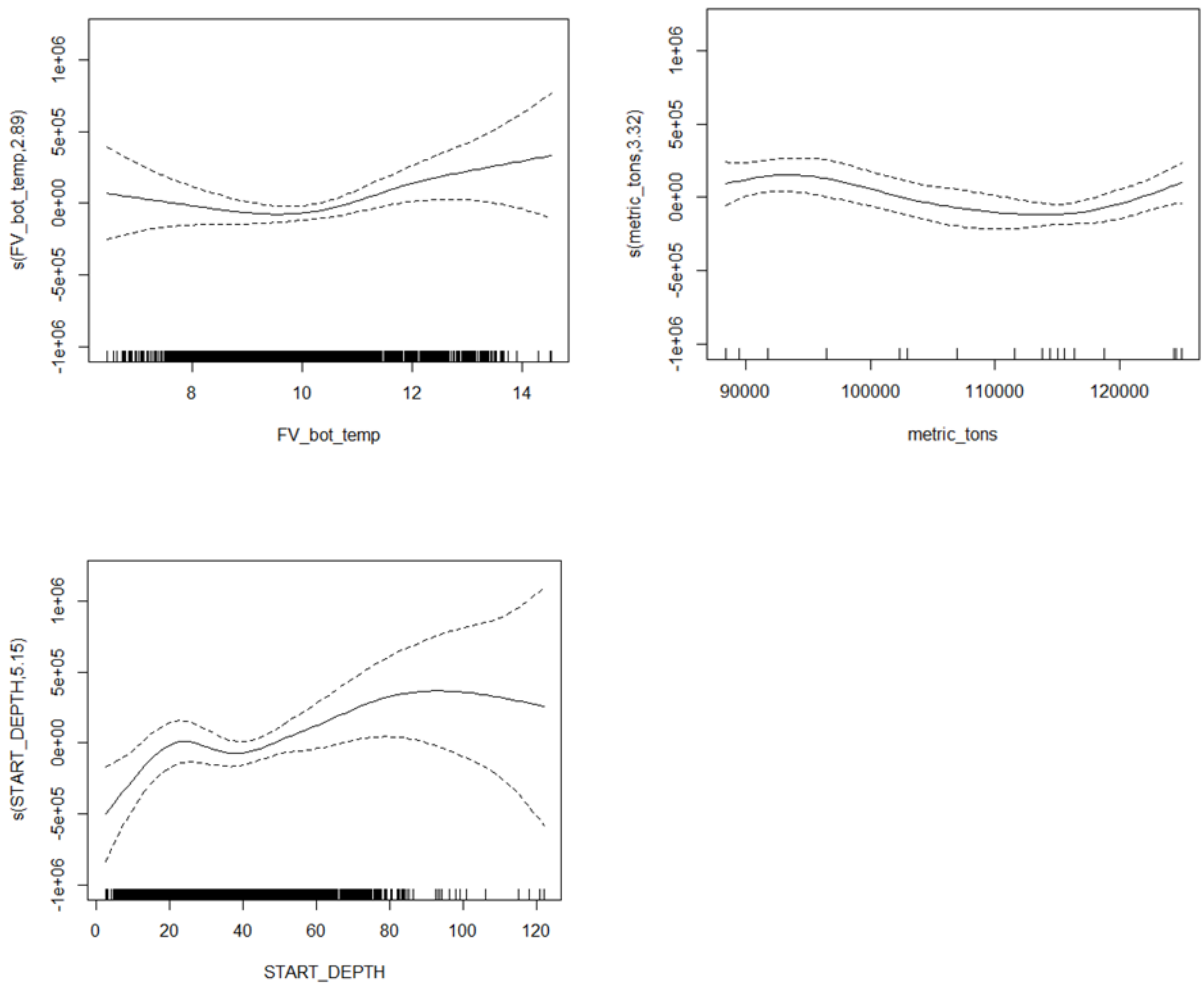


**Figure 1.20.** Fall ME-NH Inshore Trawl Survey significant factors for taxonomic diversity GAMMs using FVCOM environmental data.

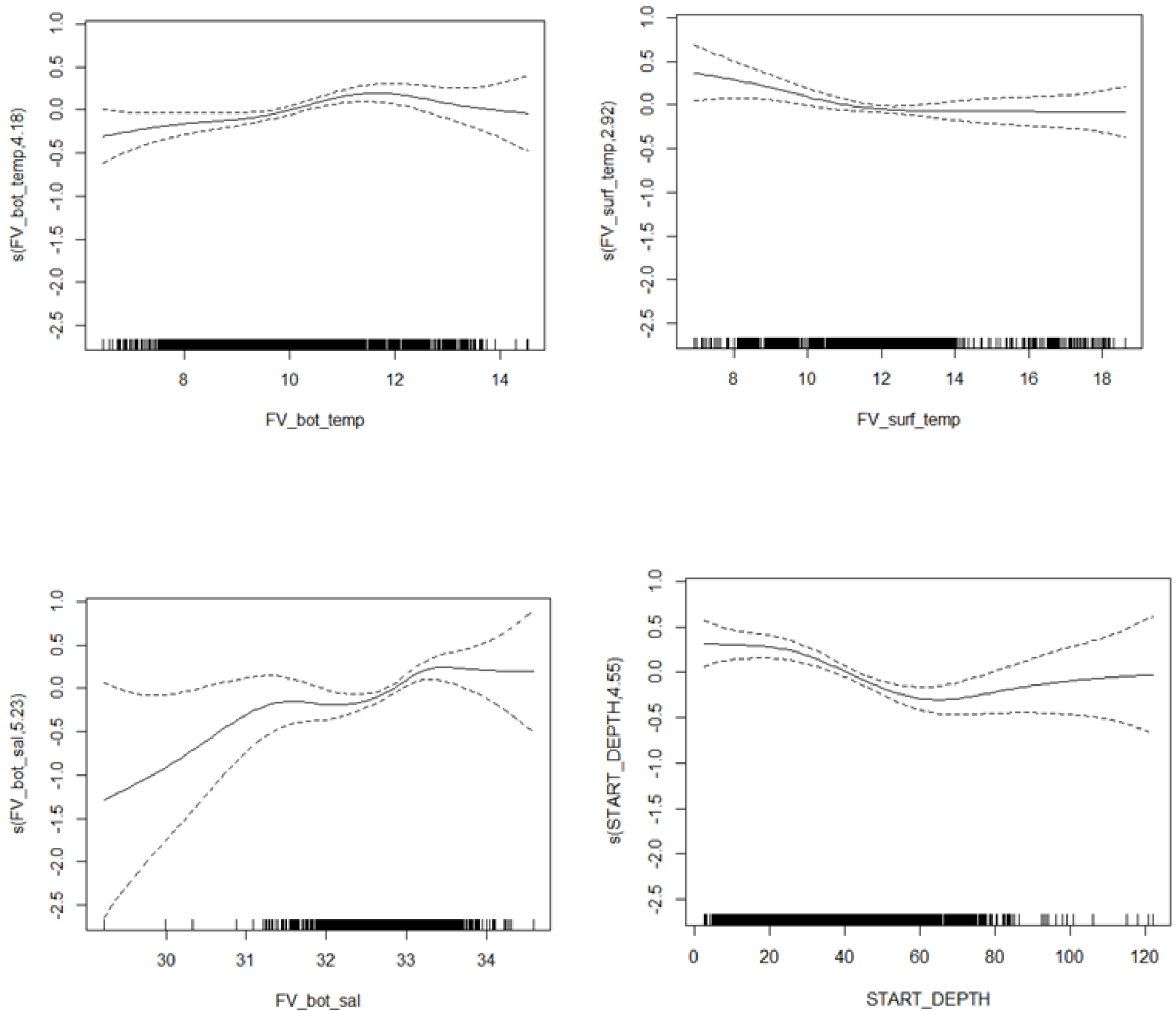


**Figure 1.21.** Fall ME-NH Inshore Trawl Survey significant factors for taxonomic distinctness GAMMs using FVCOM environmental data.

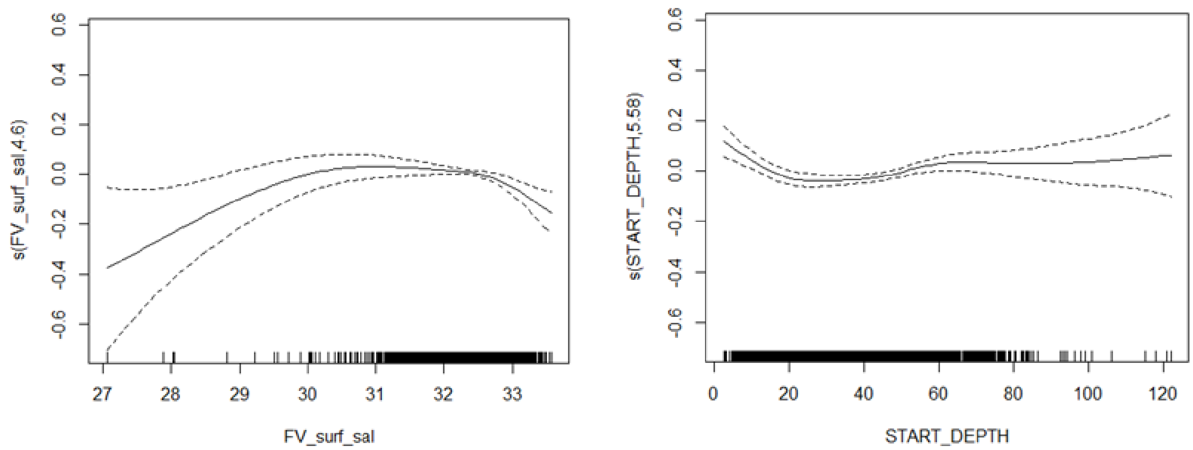


**Figure 1.22.** Fall ME-NH Inshore Trawl Survey significant factors for average taxonomic distinctness GAMMs using FVCOM environmental data.

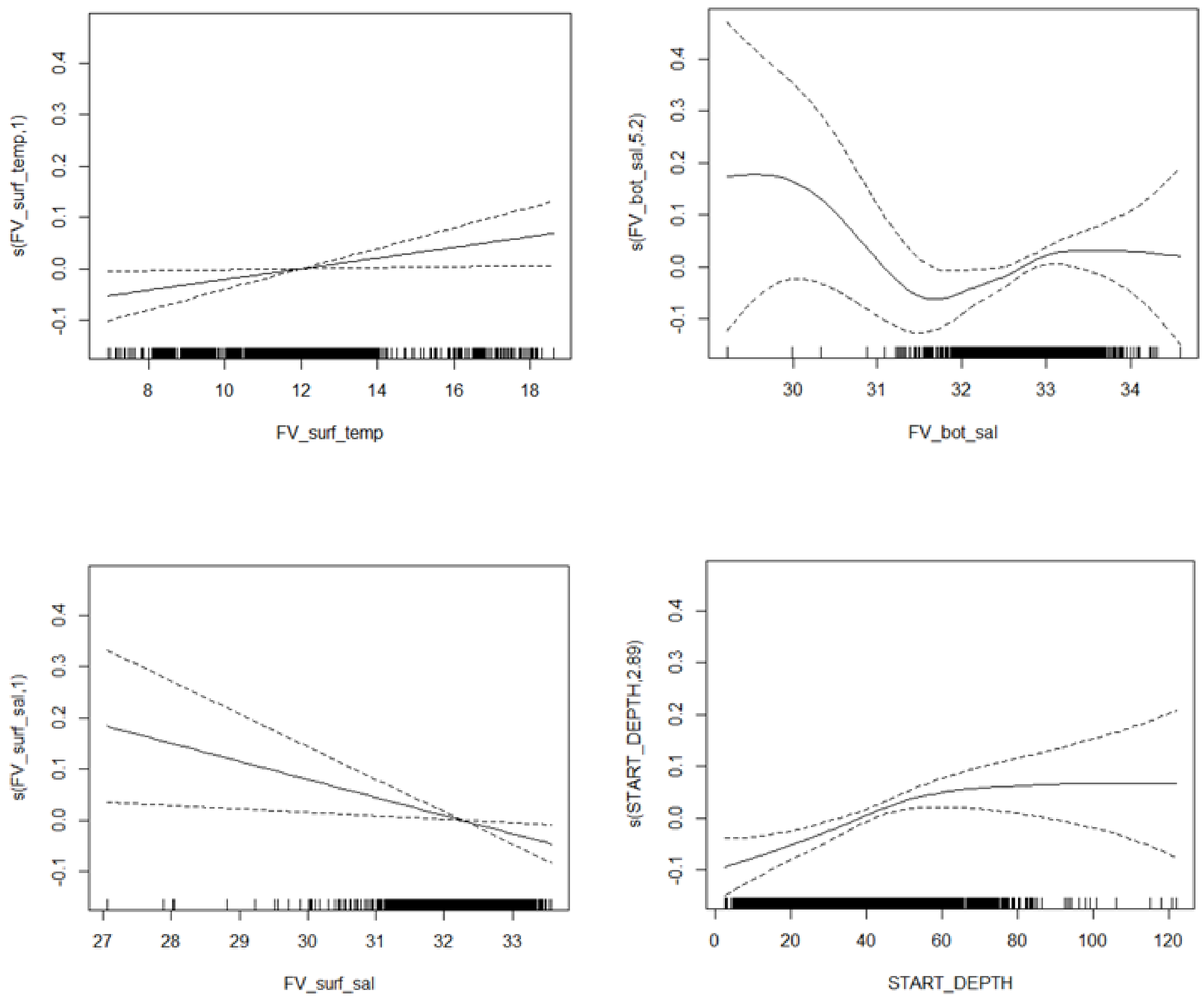


**Figure 1.23.**Fall ME-NH Inshore Trawl Survey significant factors for variation in taxonomic distinctness GAMMs using FVCOM environmental data.

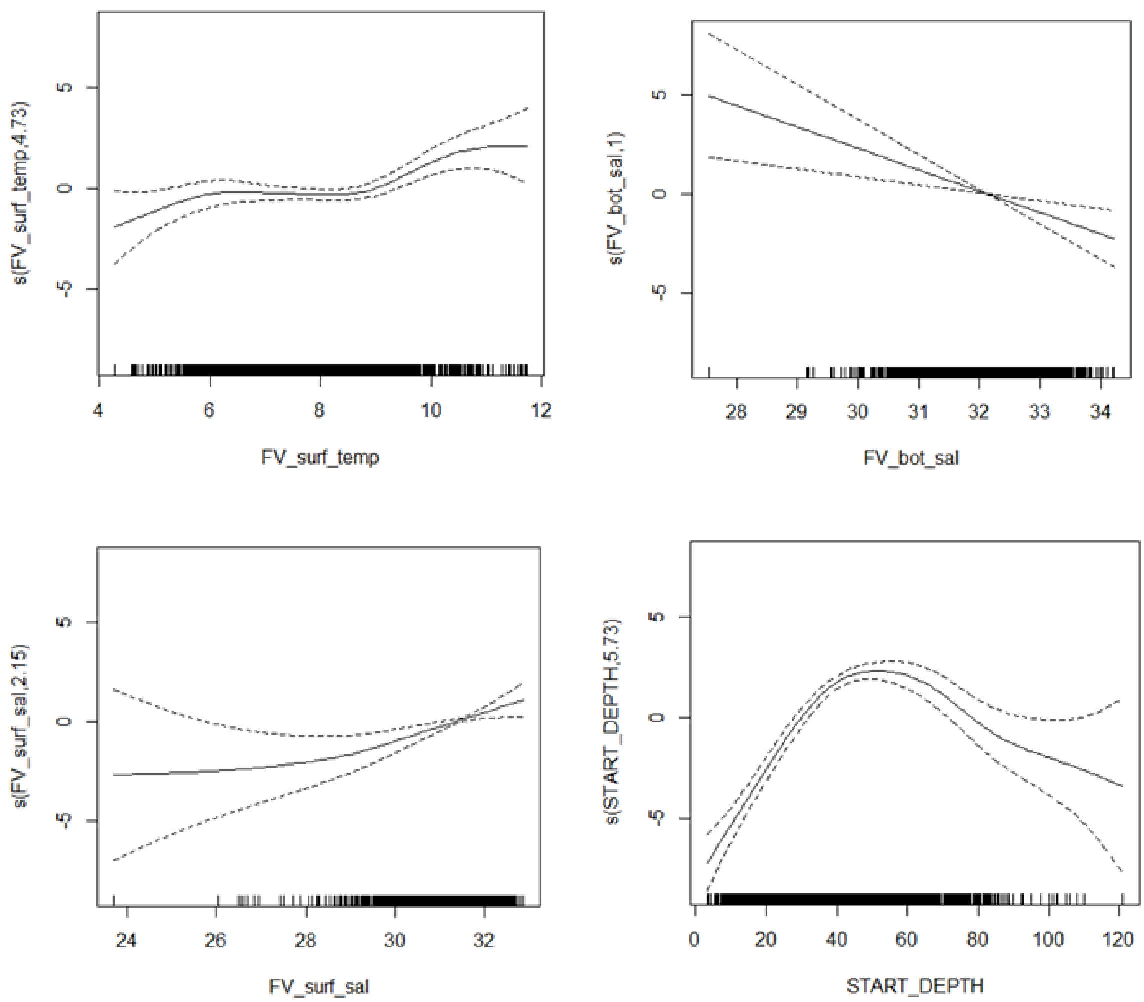


**Figure 1.24.** Spring ME-NH Inshore Trawl Survey significant factors for species richness GAMMs using FVCOM environmental data.

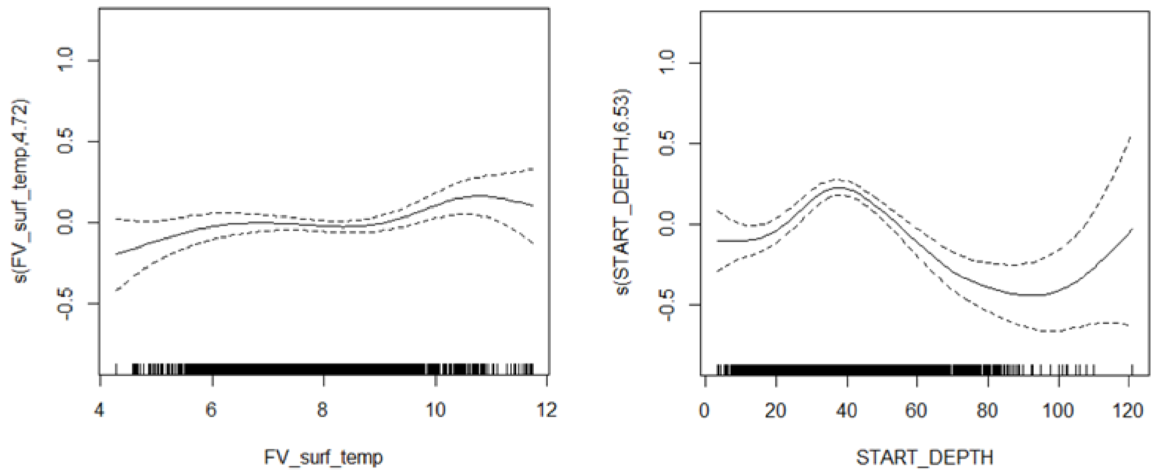


**Figure 1.25.** Spring ME-NH Inshore Trawl Survey significant factors for Shannon-Weiner diveristy GAMMs using FVCOM environmental data.

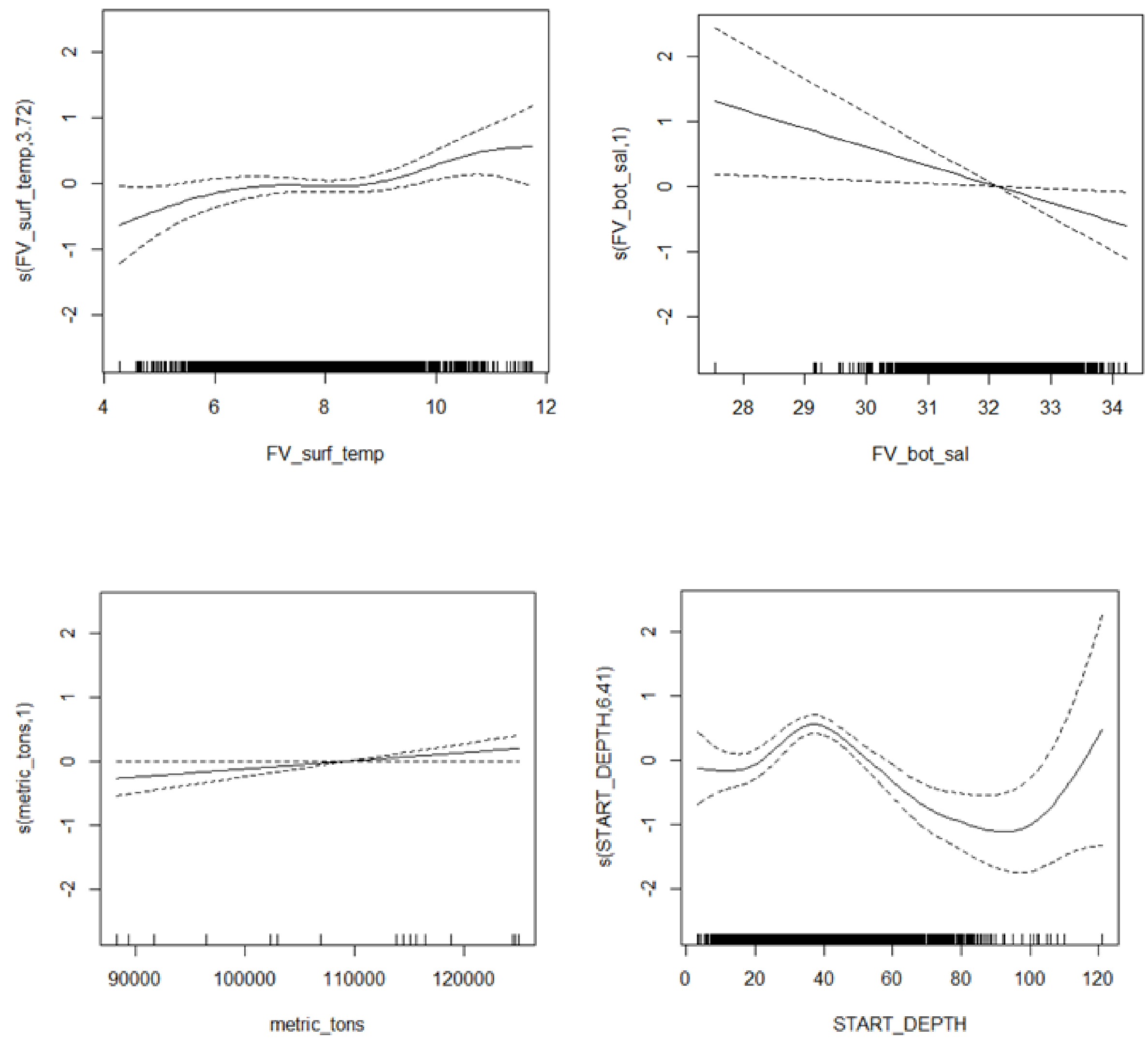


**Figure 1.26.** Spring ME-NH Inshore Trawl Survey significant factors for Simpson's diversity GAMMs using FVCOM environmental data.

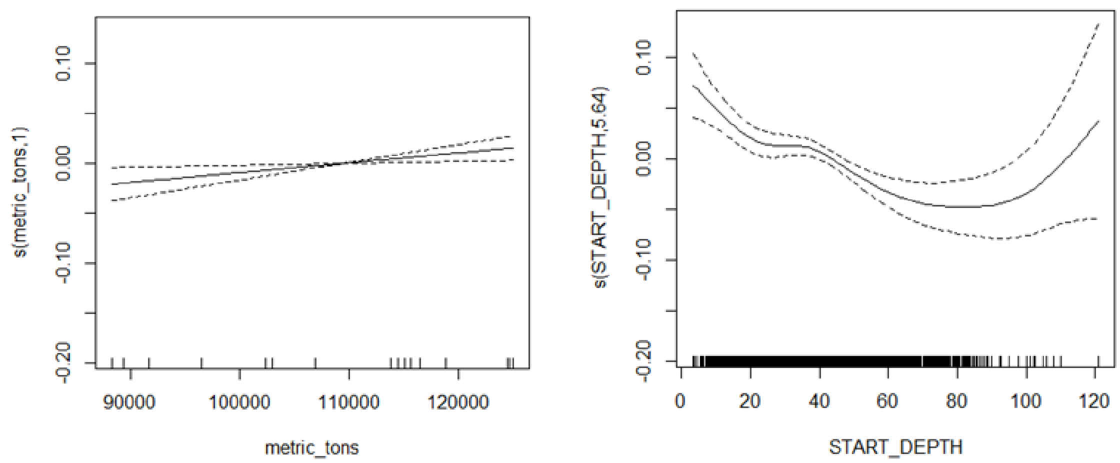


**Figure 1.27.** Spring ME-NH Inshore Trawl Survey significant factors for Simpson's evenness GAMMs using FVCOM environmental data.

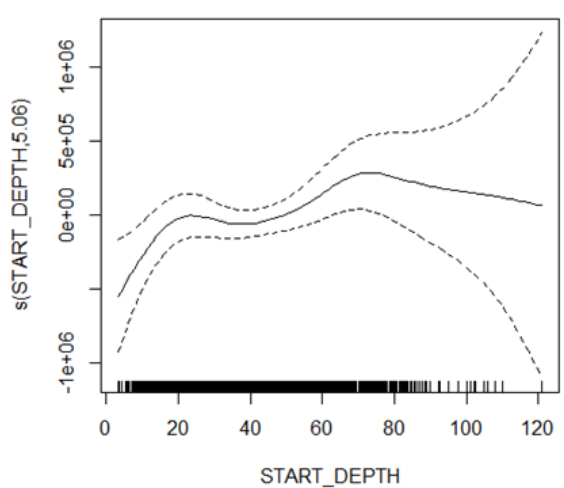


**Figure 1.28.** Spring ME-NH Inshore Trawl Survey significant factors for taxonomic diversity GAMMs using FVCOM environmental data.

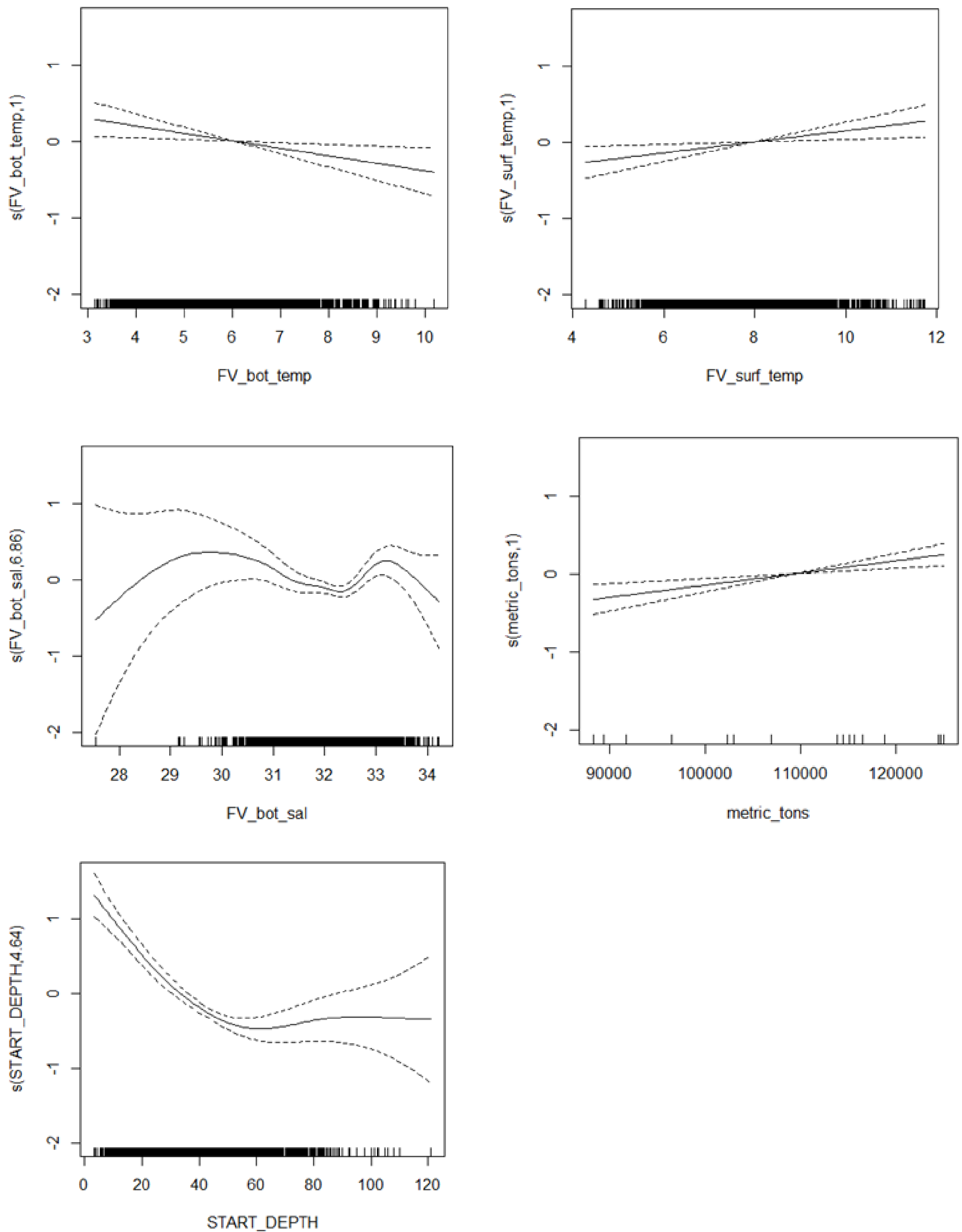


**Figure 1.29.** Spring ME-NH Inshore Trawl Survey significant factors for taxonomic distinctness GAMMs using FVCOM environmental data.

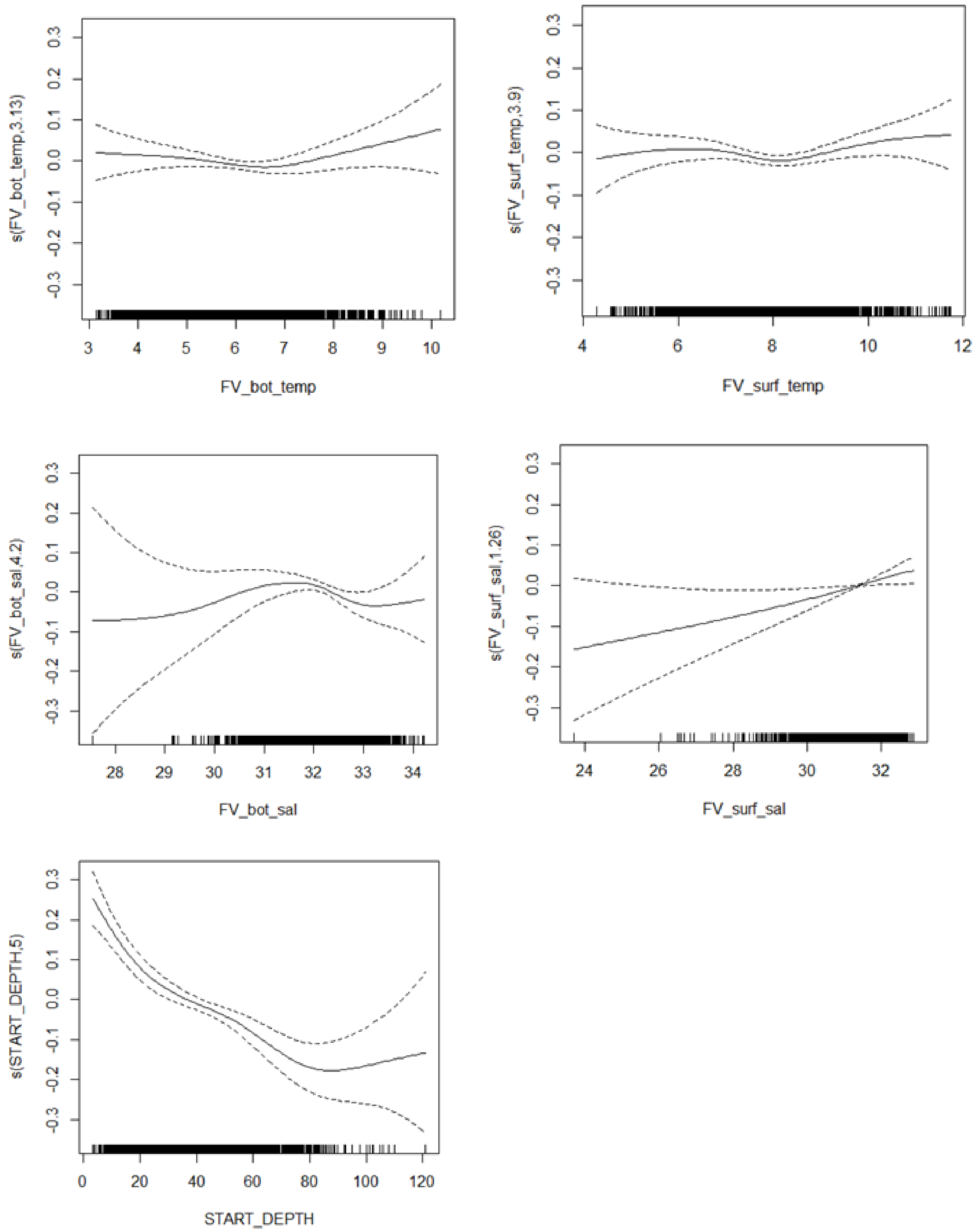


**Figure 1.30.** Spring ME-NH Inshore Trawl Survey significant factors for average taxonomic distinctness GAMMs using FVCOM environmental data.

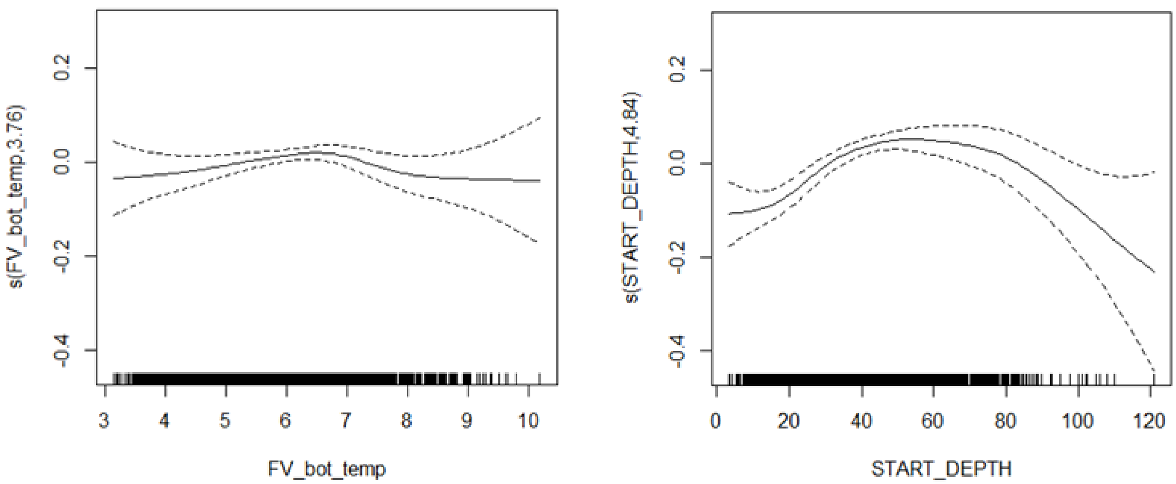


**Figure 1.31.** Spring ME-NH Inshore Trawl Survey significant factors for variation in taxonomic distinctness GAMMs using FVCOM environmental data.

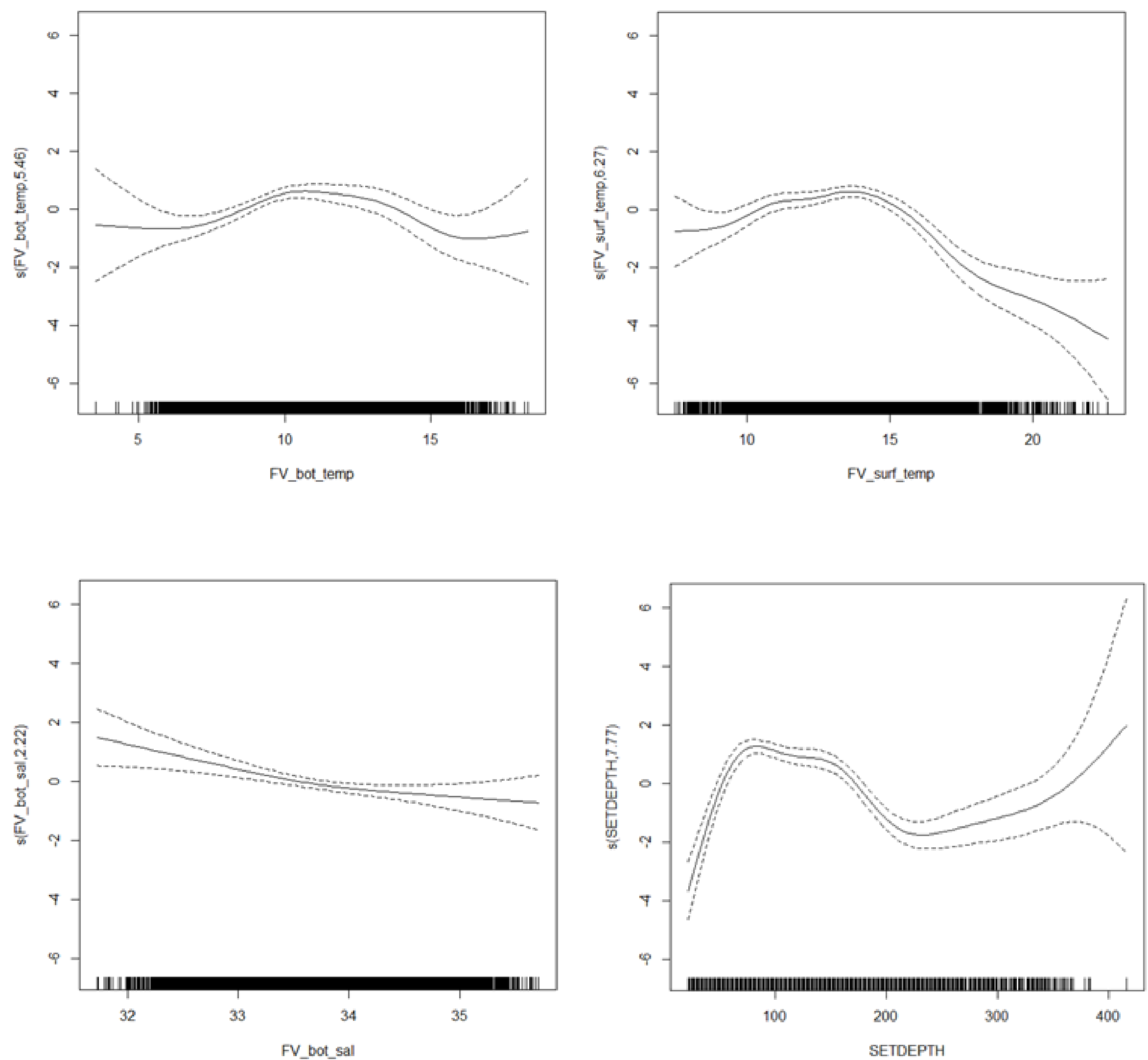


**Figure 1.32.** Fall NEFSC Trawl Survey GOM region significant factors for species richness GAMMs using FVCOM environmental data.

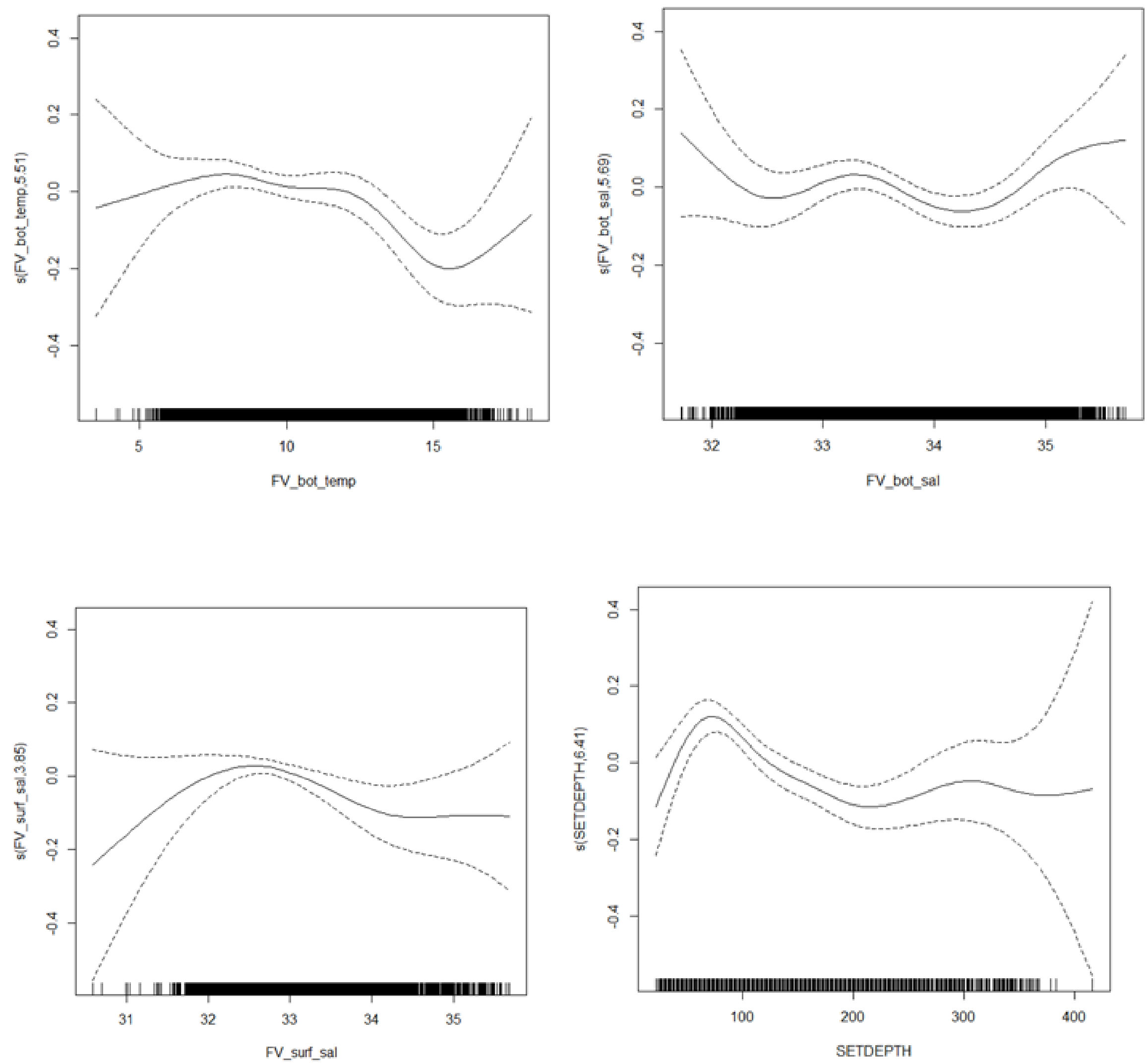


**Figure 1.33.** Fall NEFSC Trawl Survey GOM region significant factors for Shannon-Weiner diversity GAMMs using FVCOM environmental data.

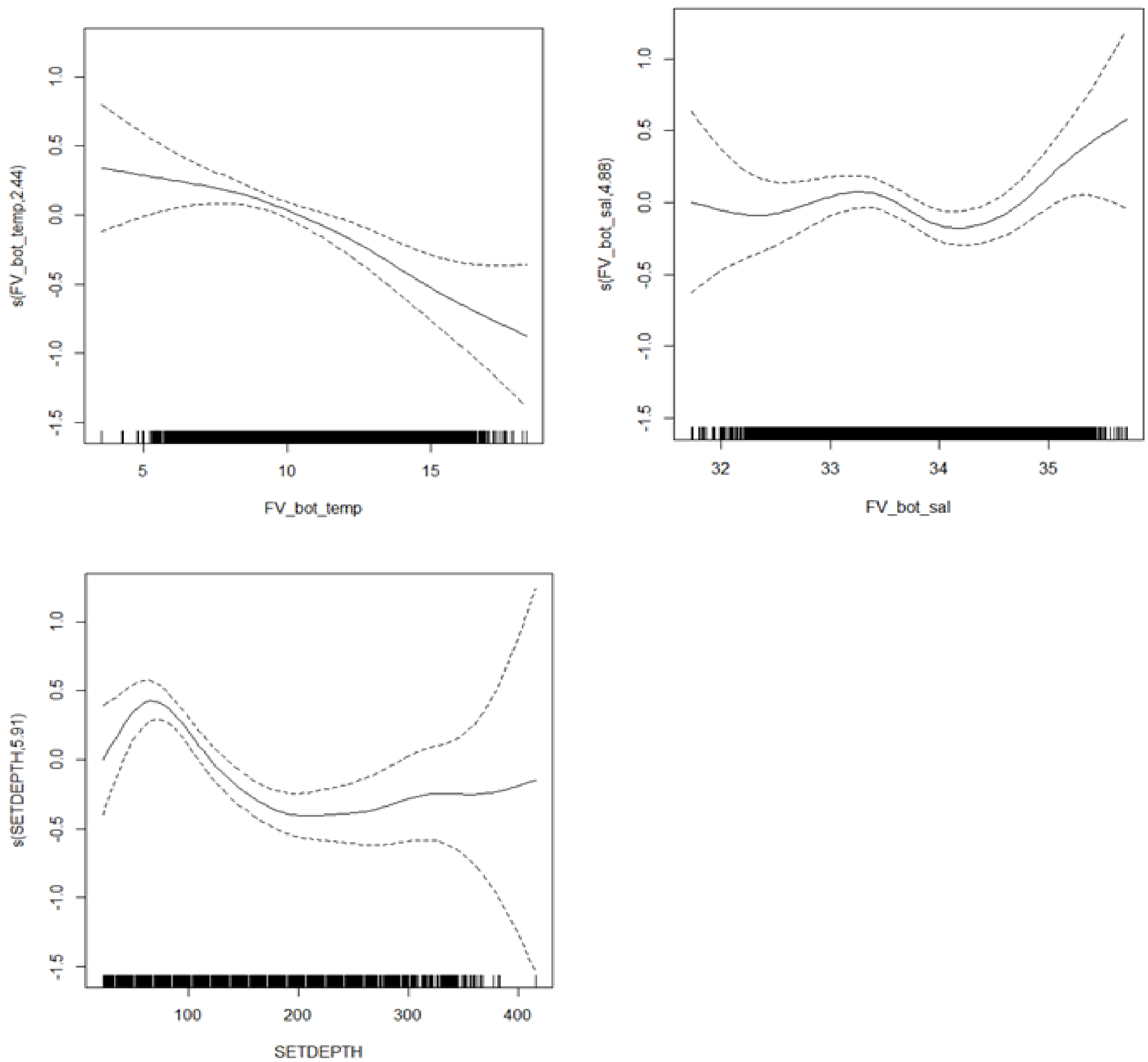


**Figure 1.34.** Fall NEFSC Trawl Survey GOM region significant factors for Simpson's diversity GAMMs using FVCOM environmental data.

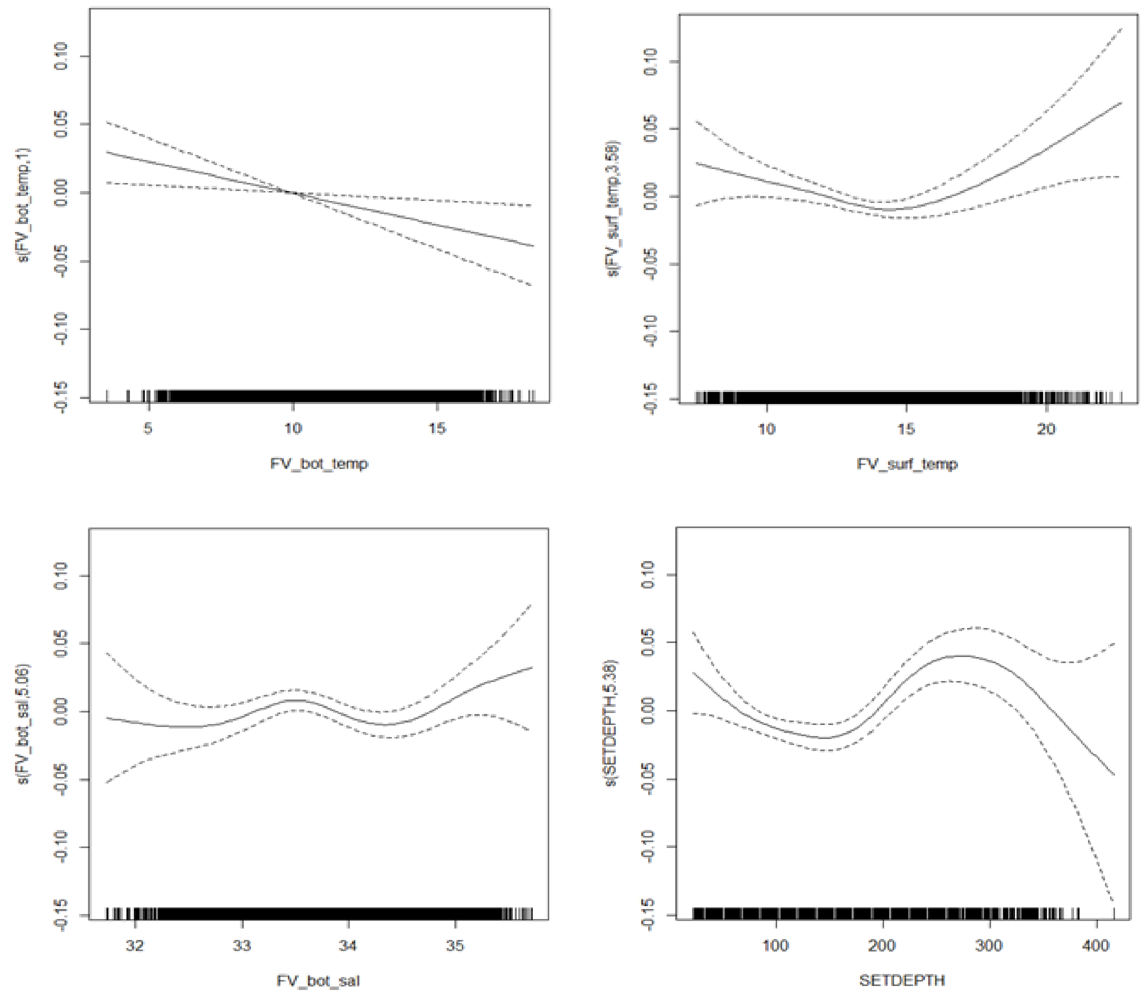


**Figure 1.35.** Fall NEFSC Trawl Survey GOM region significant factors for Simpson's evenness GAMMs using FVCOM environmental data.

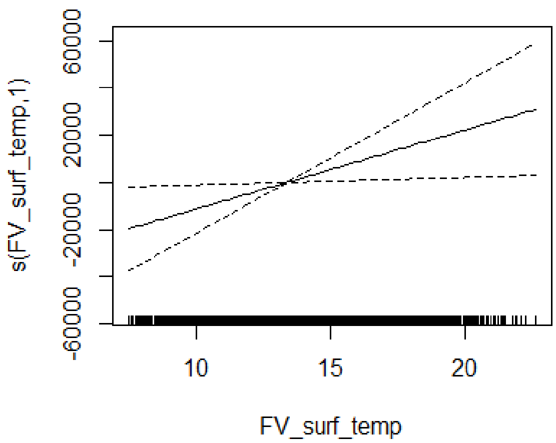


**Figure 1.36.** Fall NEFSC Trawl Survey GOM region significant factors for taxonomic diversity GAMMs using FVCOM environmental data.

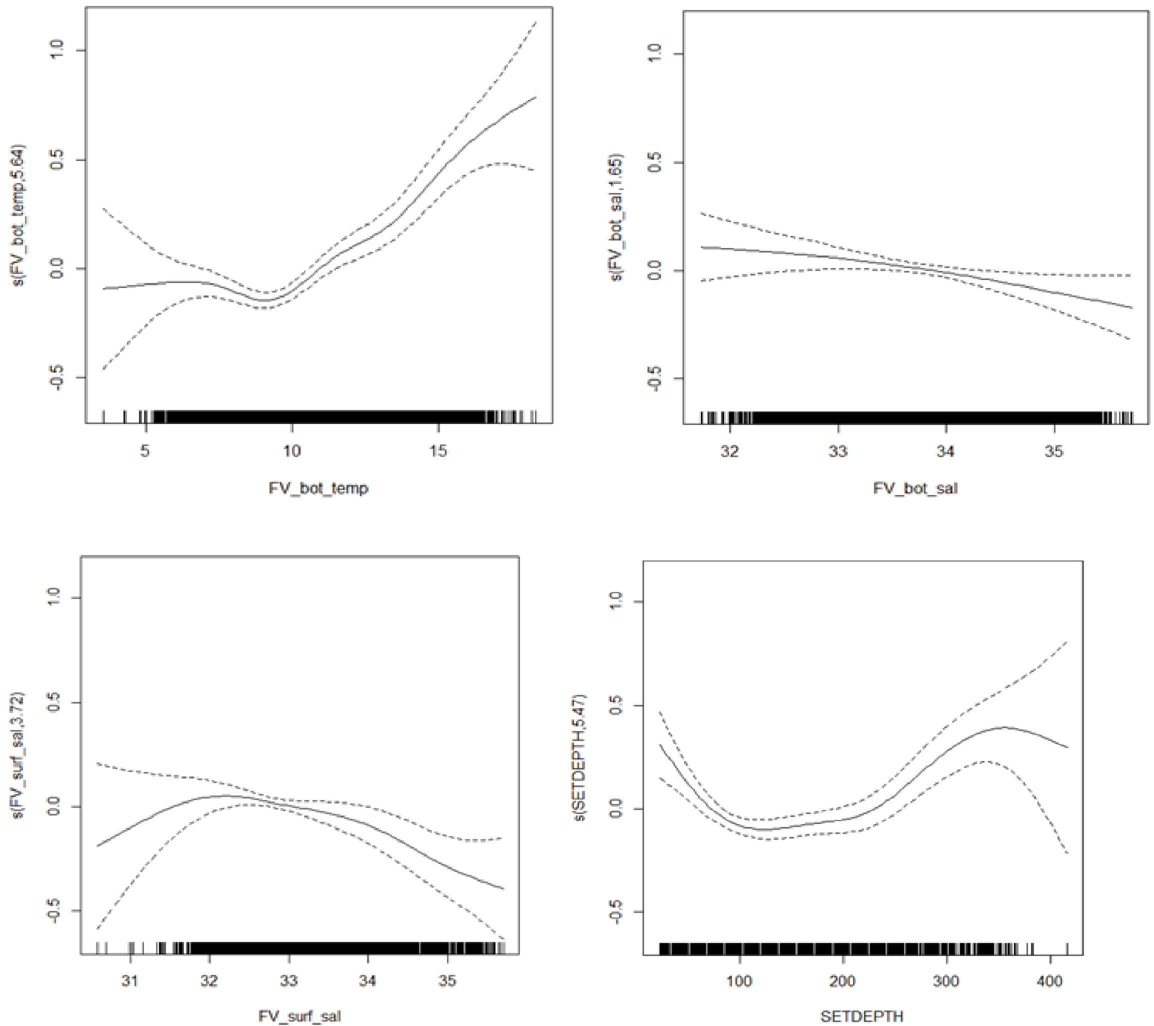


**Figure 1.37.** Fall NEFSC Trawl Survey GOM region significant factors for taxonomic distinctness GAMMs using FVCOM environmental data.

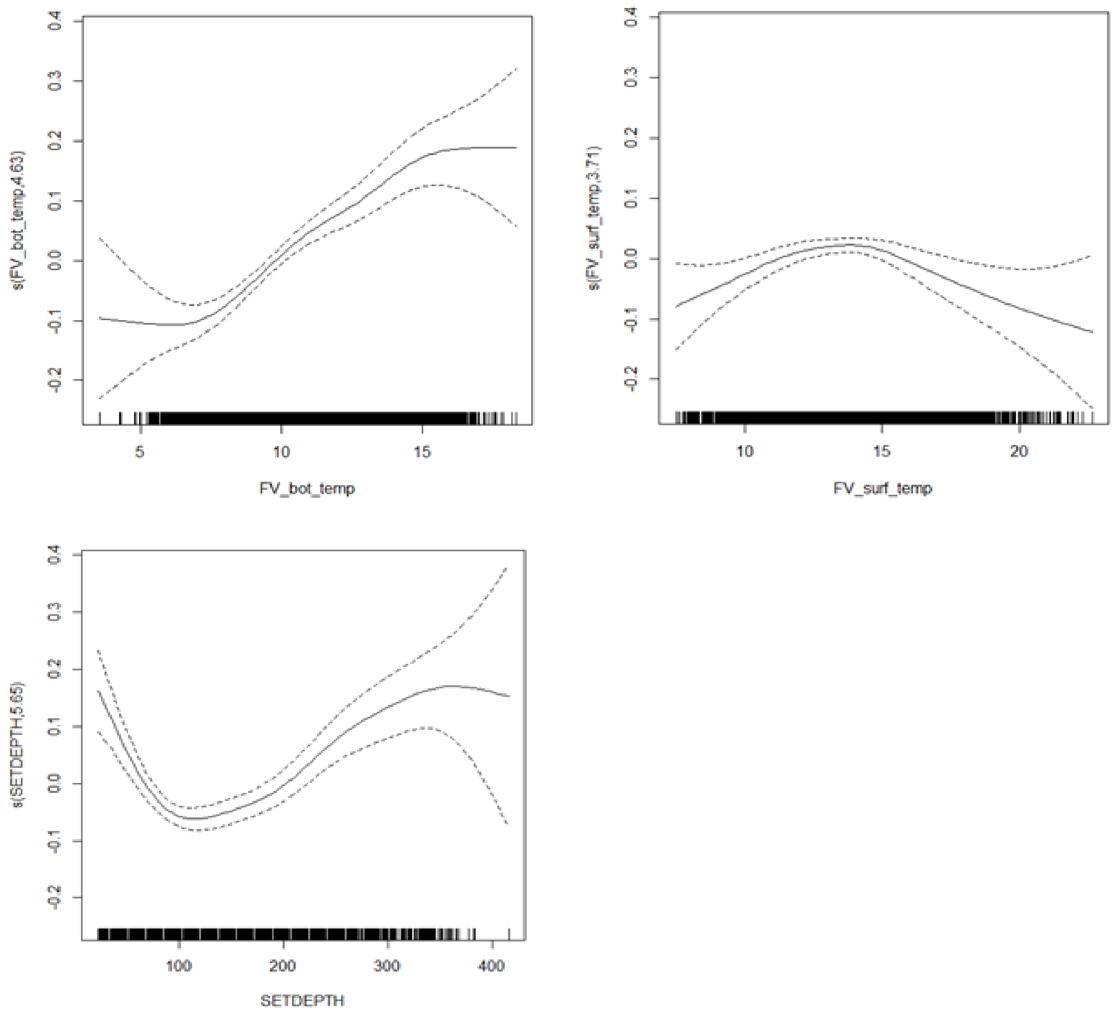


**Figure 1.38.** Fall NEFSC Trawl Survey GOM region significant factors for average taxonomic distinctness GAMMs using FVCOM environmental data.

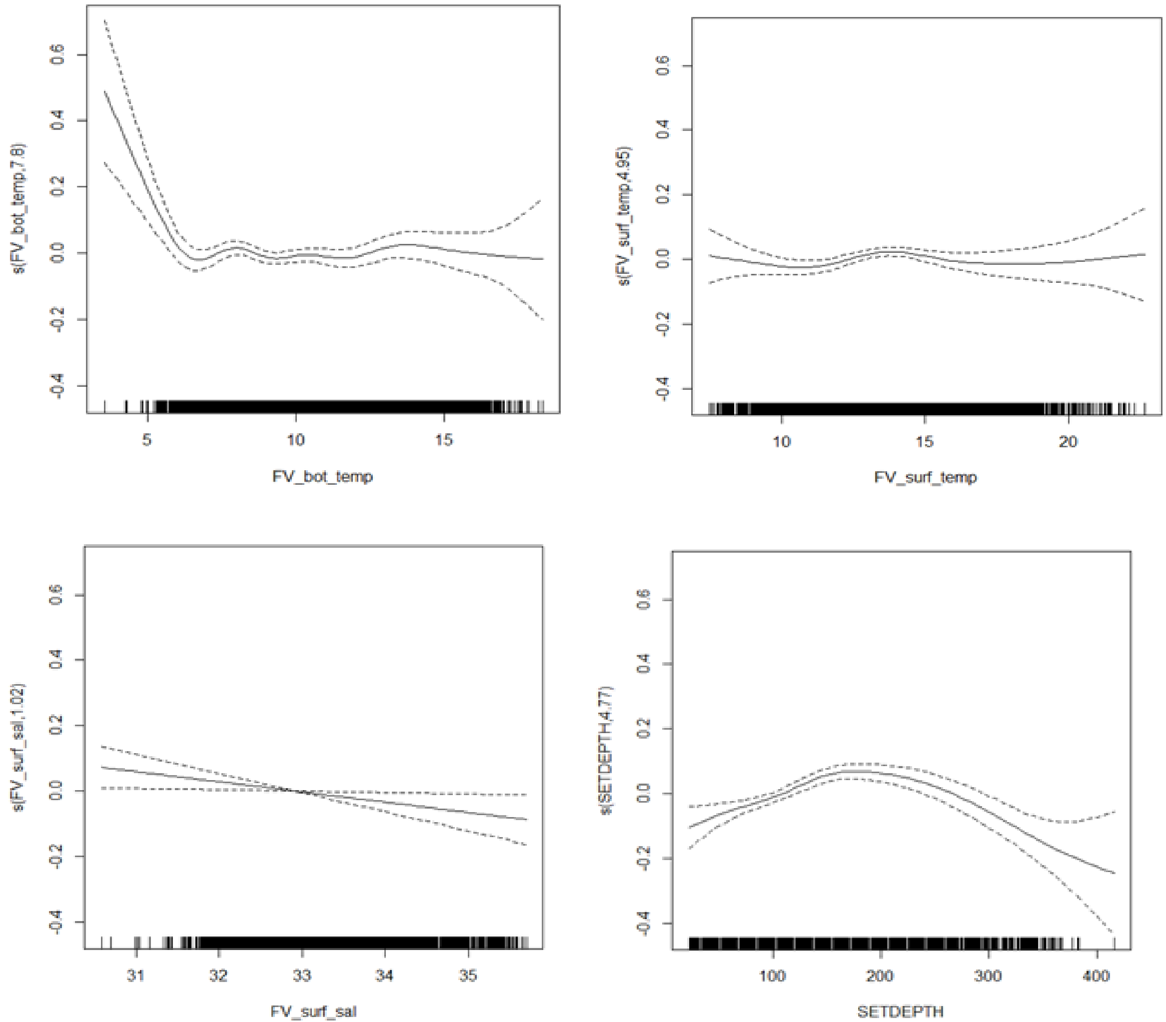


**Figure 1.39.** Fall NEFSC Trawl Survey GOM region significant factors for variation in taxonomic distinctness GAMMs using FVCOM environmental data.

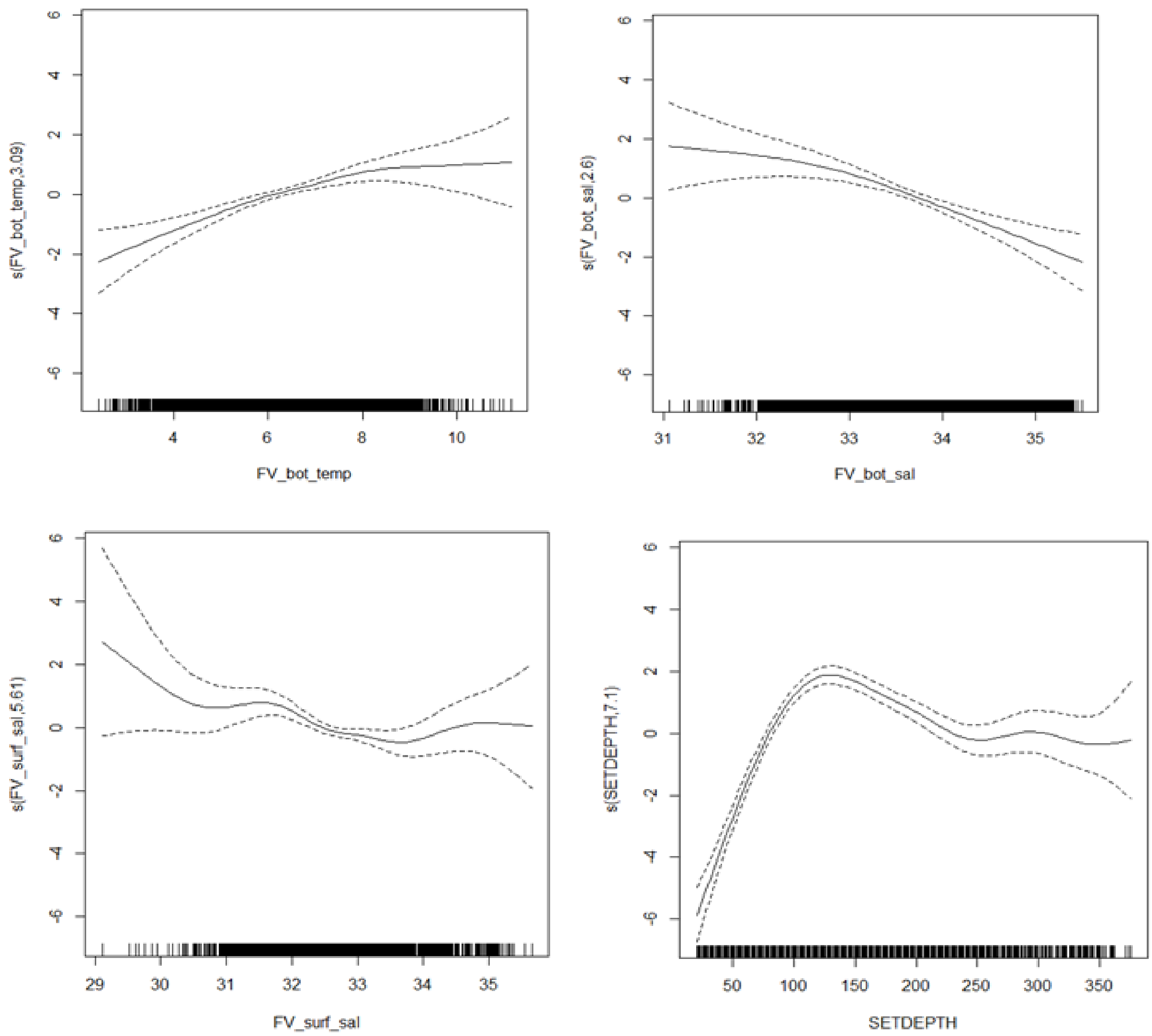


**Figure 1.40.** Spring NEFSC Trawl Survey GOM region significant factors for species richness GAMMs using FVCOM environmental data.

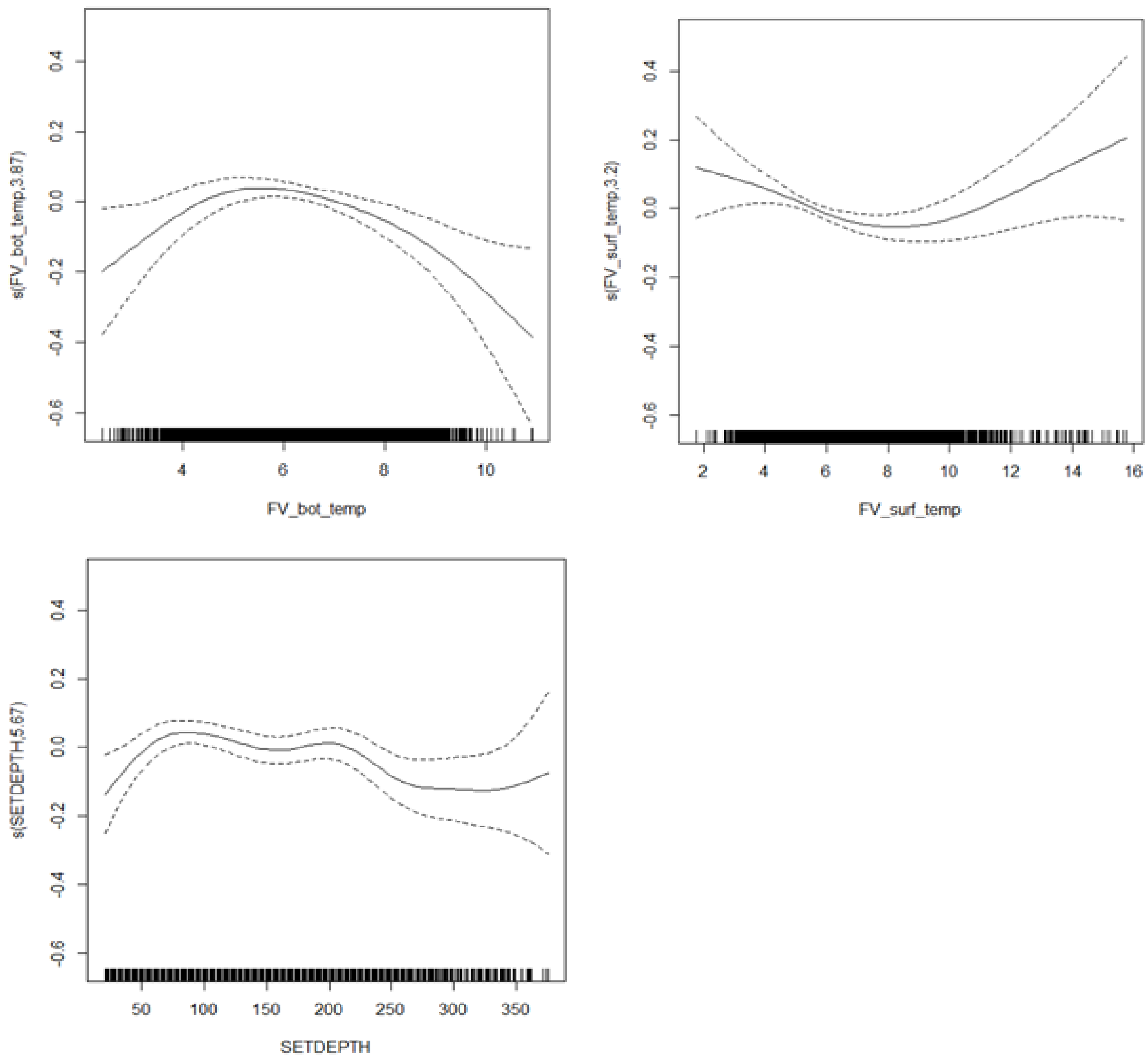


**Figure 1.41.** Spring NEFSC Trawl Survey GOM region significant factors for Shannon-Weiner diversity GAMMs using FVCOM environmental data.

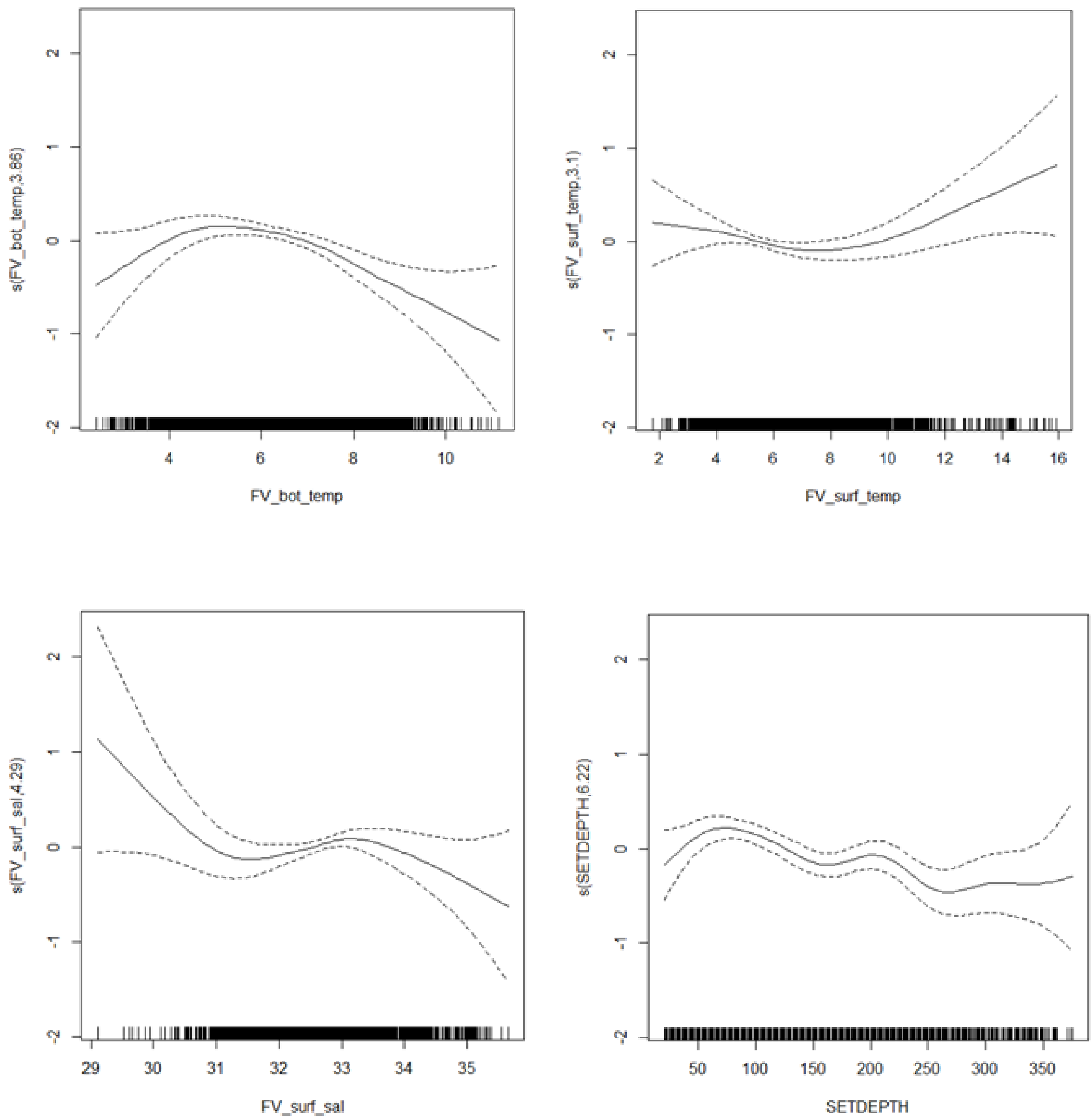


**Figure 1.42.** Spring NEFSC Trawl Survey GOM region significant factors for Simpson's diversity GAMMs using FVCOM environmental data.

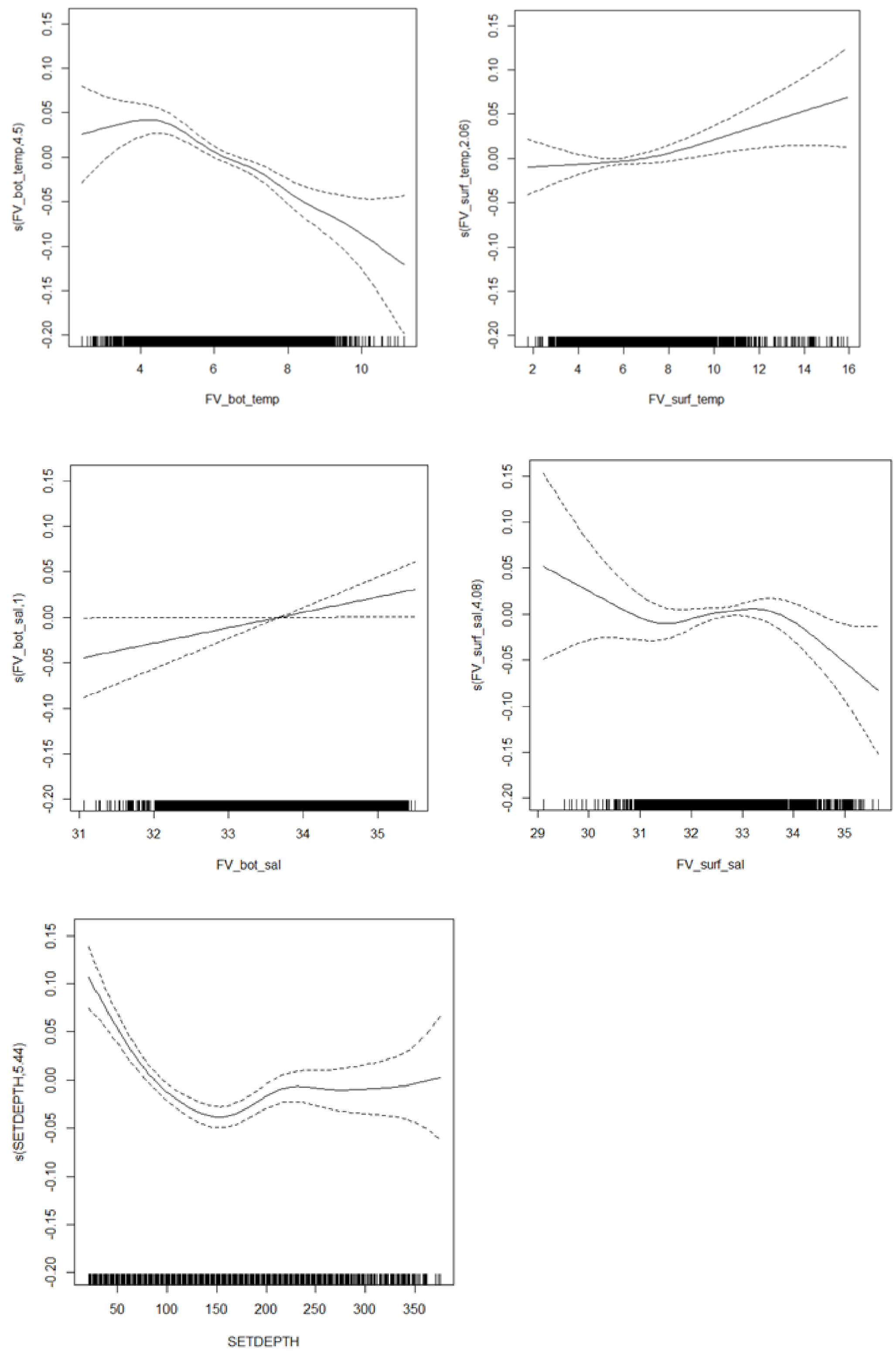


**Figure 1.43.** Spring NEFSC Trawl Survey GOM region significant factors for Simpson's evenness GAMMs using FVCOM environmental data.

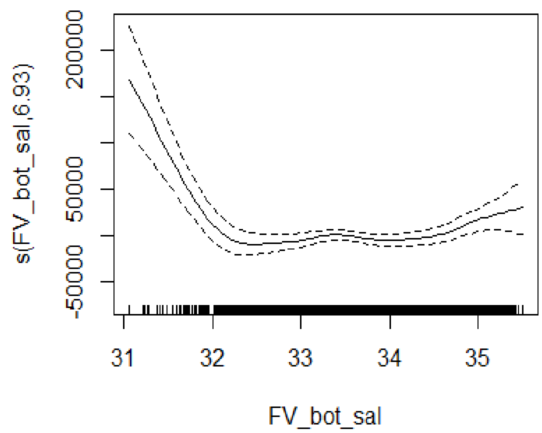


**Figure 1.44.** Spring NEFSC Trawl Survey GOM region significant factors for taxonomic diversity GAMMs using FVCOM environmental data.

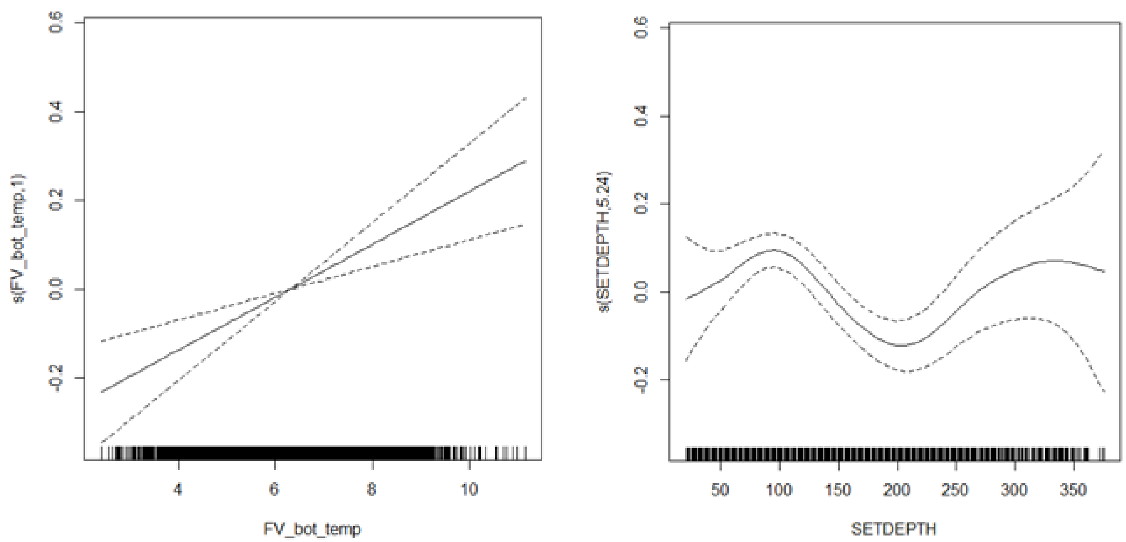


**Figure 1.45.** Spring NEFSC Trawl Survey GOM region significant factors for taxonomic distinctness GAMMs using FVCOM environmental data.

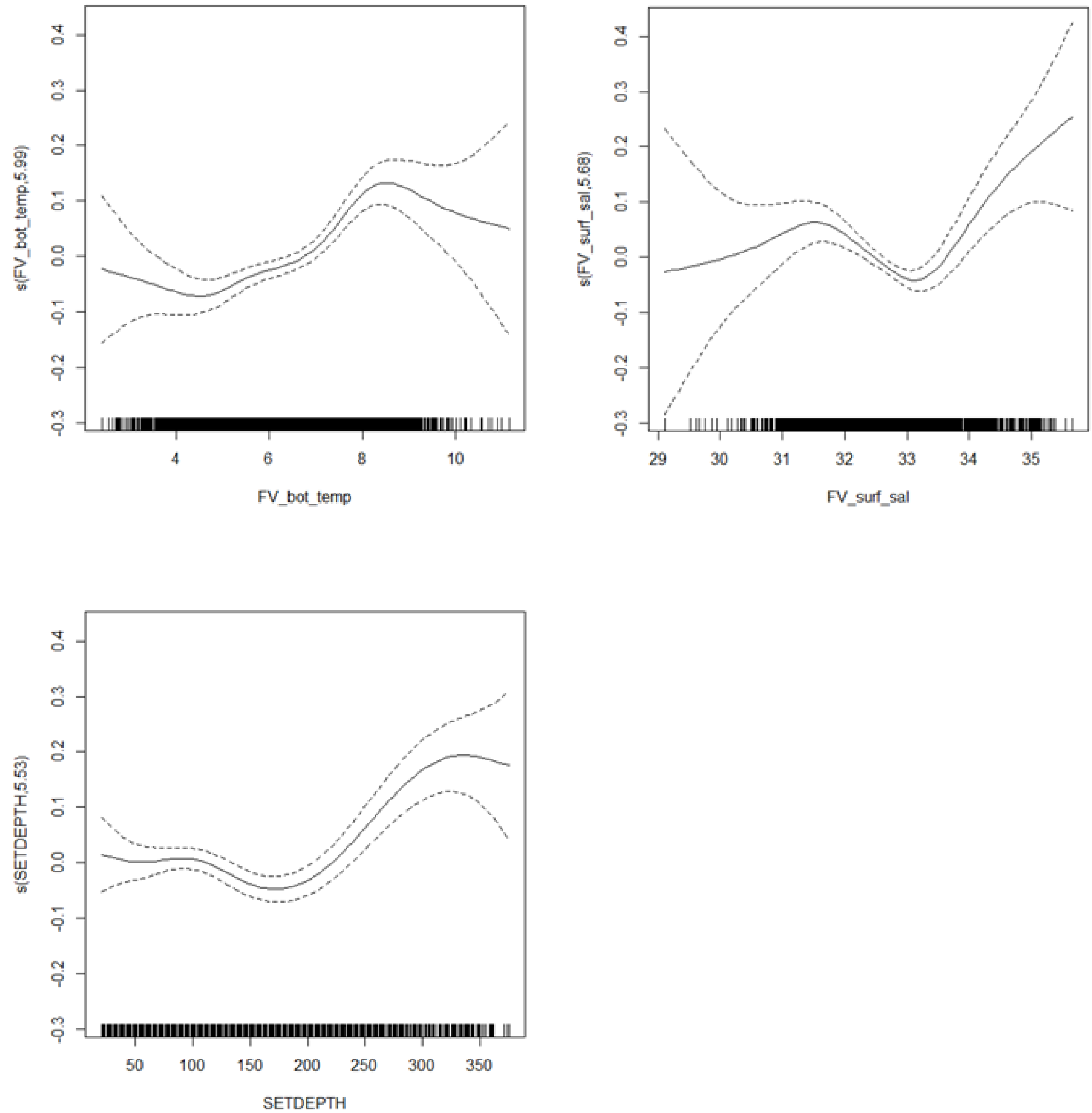


**Figure 1.46.** Spring NEFSC Trawl Survey GOM region significant factors for average taxonomic distinctness GAMMs using FVCOM environmental data.

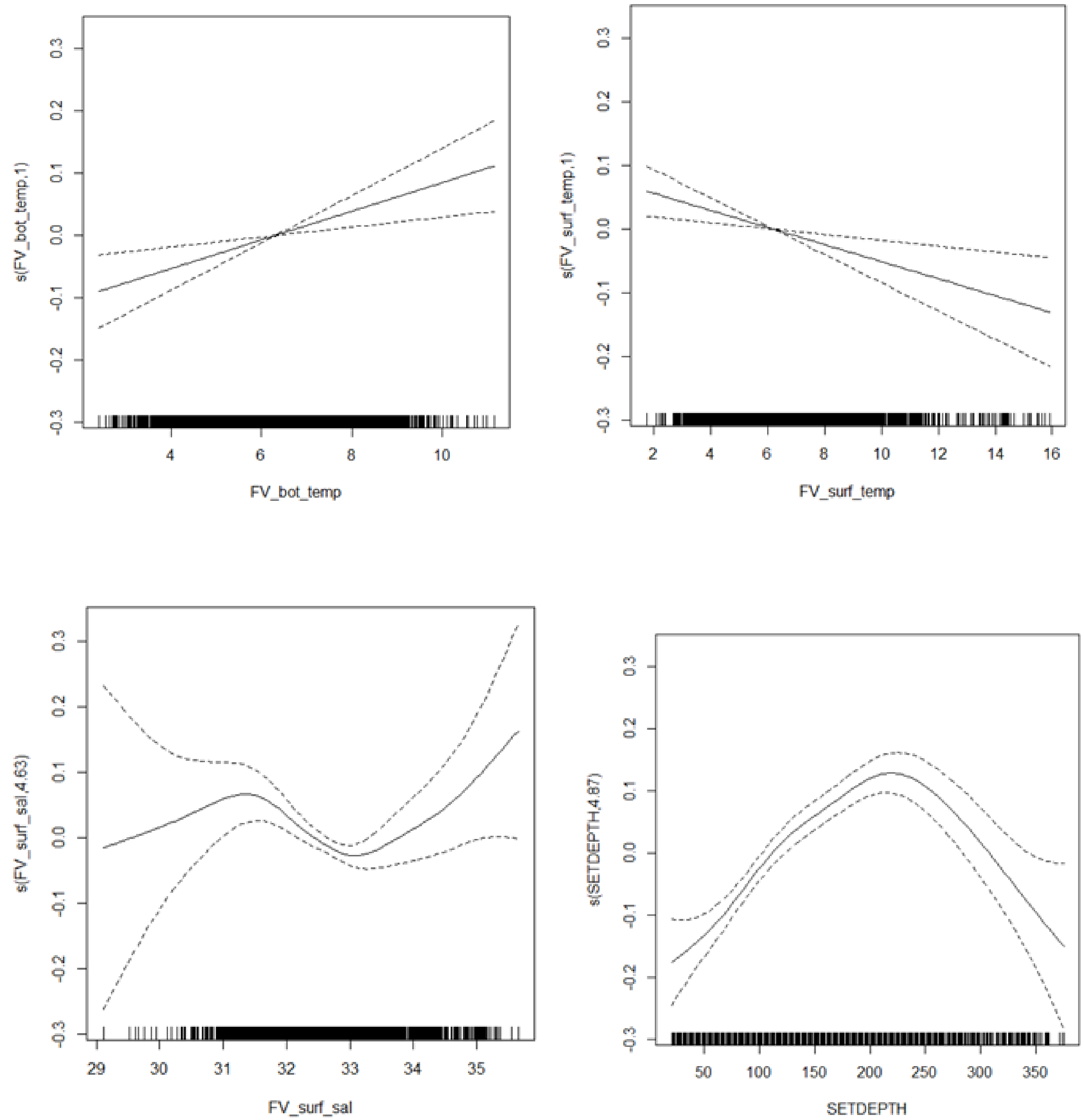


**Figure 1.47.** Spring NEFSC Trawl Survey GOM region significant factors for variation in taxonomic distinctness GAMMs using FVCOM environmental data.

**Objective 2:**

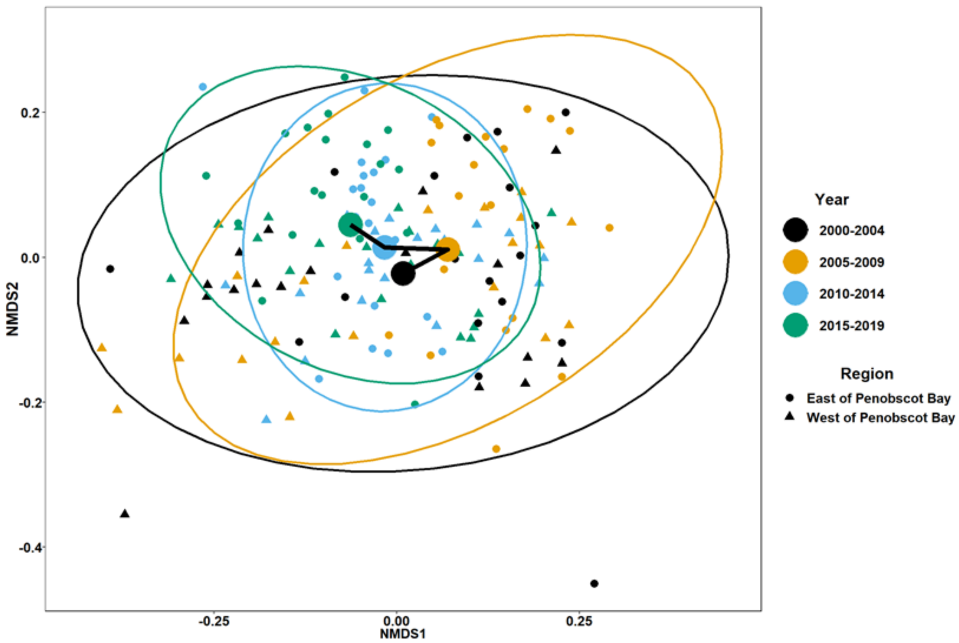


**Figure 2.1.** Functional group biomass NMDS for ME-NH Inshore Trawl Survey. Stress =0.174. Larger data points are the center of the data for each year group and ellipses are 95% confidence level.

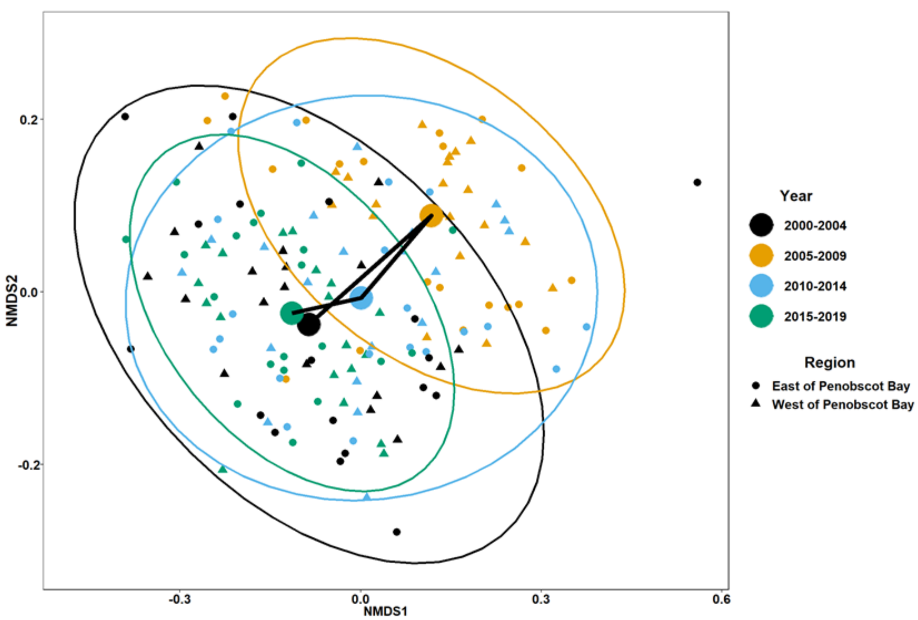


**Figure 2.2.** Functional group abundance NMDS for ME-NH Inshore Trawl Survey. Stress =0.140 Larger data points are the center of the data for each year group and ellipses are 95% confidence level.

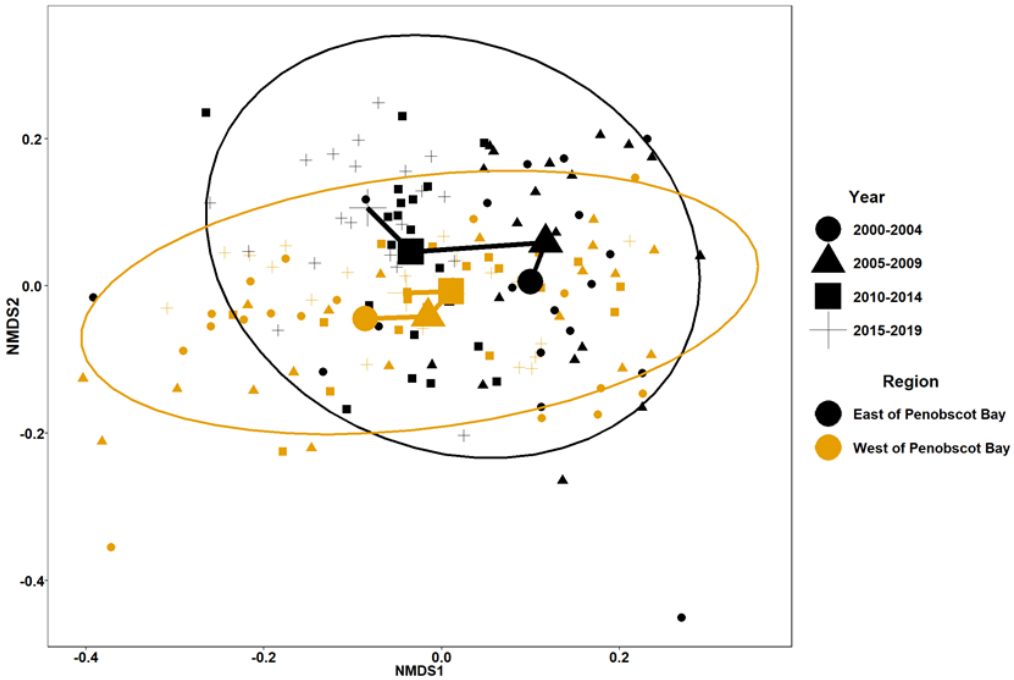


**Figure 2.3.** Functional group biomass NMDS for ME-NH Inshore Trawl Survey by region. Larger data points are the center of the data for each year group and ellipses are 95% confidence level.

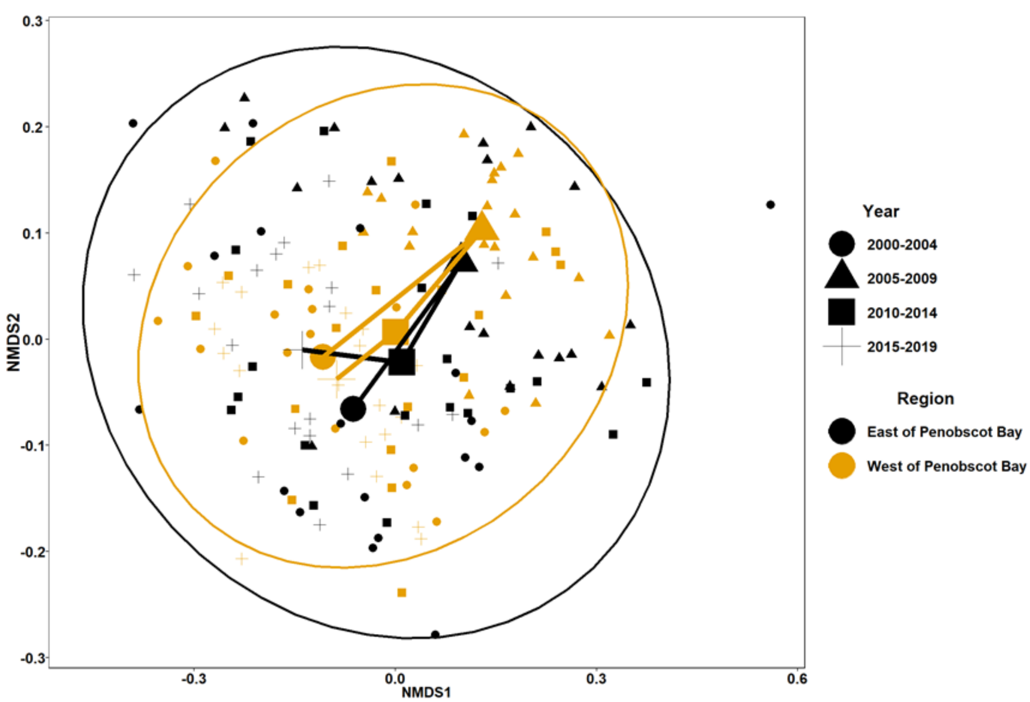


**Figure 2.4.** Functional group abundance NMDS for ME-NH Inshore Trawl Survey by region. Larger data points are the center of the data for each year group and ellipses are 95% confidence level.

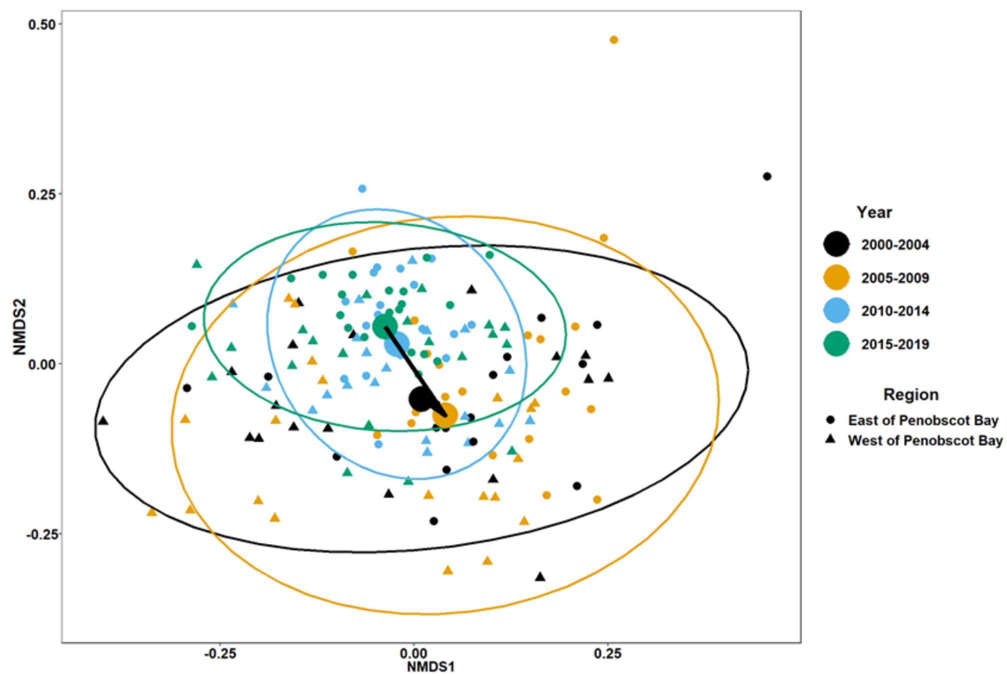


**Figure 2.5.** Top species biomass NMDS for ME-NH Inshore Trawl Survey. Stress= 0.205 Larger data points are the center of the data for each year group and ellipses are 95% confidence level.

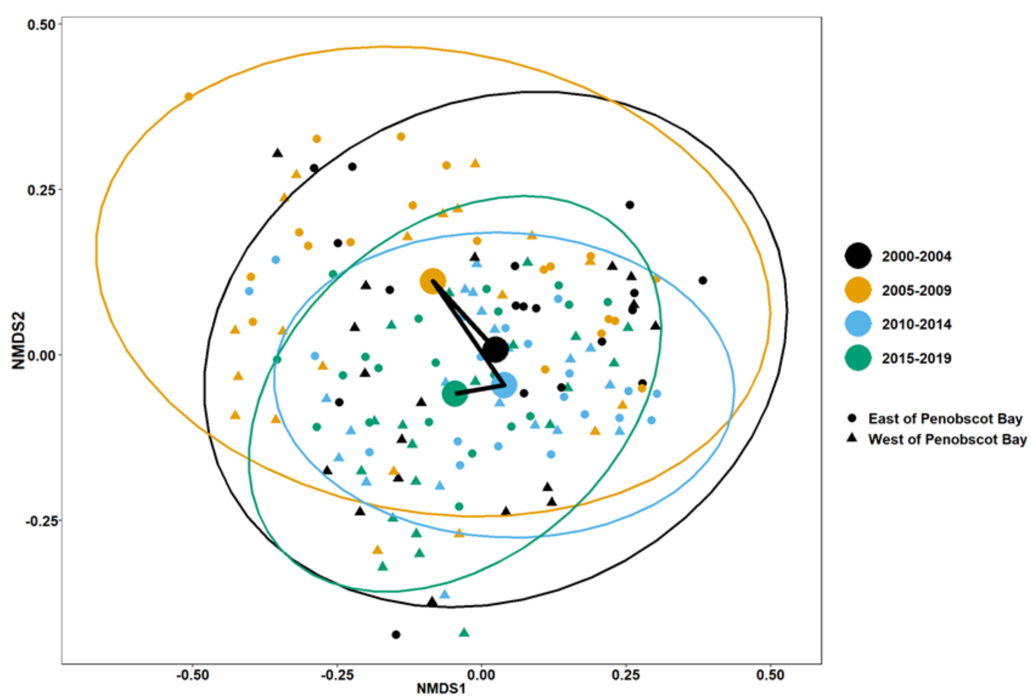


**Figure 2.6.** Top species abundance NMDS for ME-NH Inshore Trawl Survey. Stress = 0.162 Larger data points are the center of the data for each year group and ellipses are 95% confidence level.

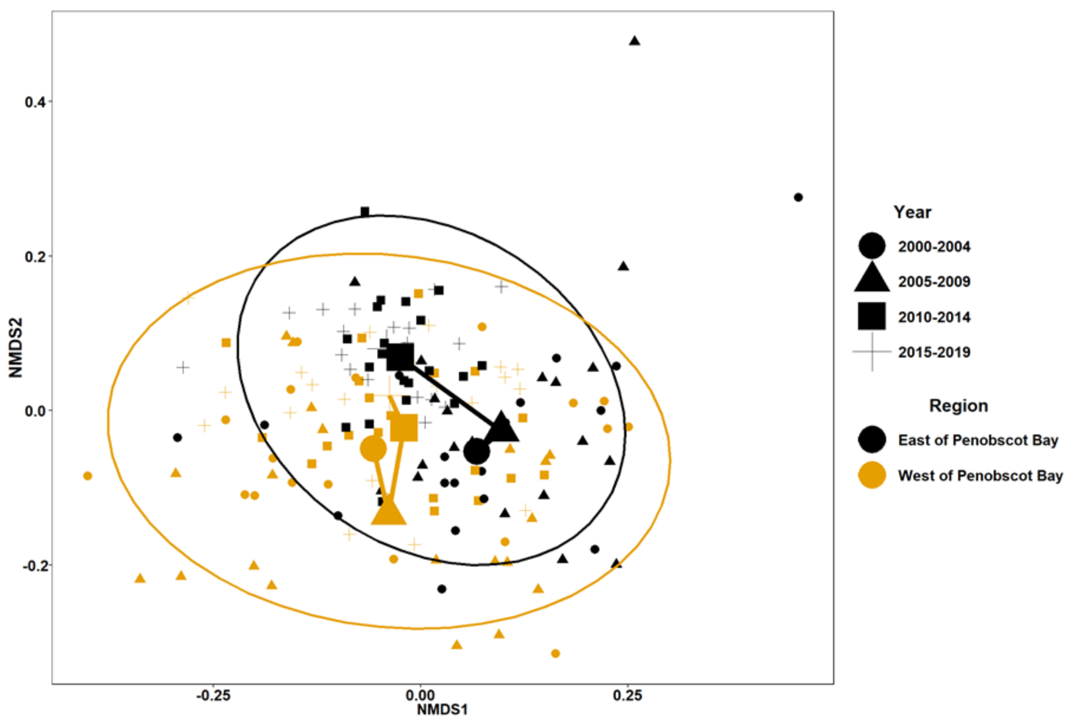


**Figure 2.7.** Top species biomass NMDS for ME-NH Inshore Trawl Survey by region. Stress =0.140 Larger data points are the center of the data for each year group and ellipses are 95% confidence level.

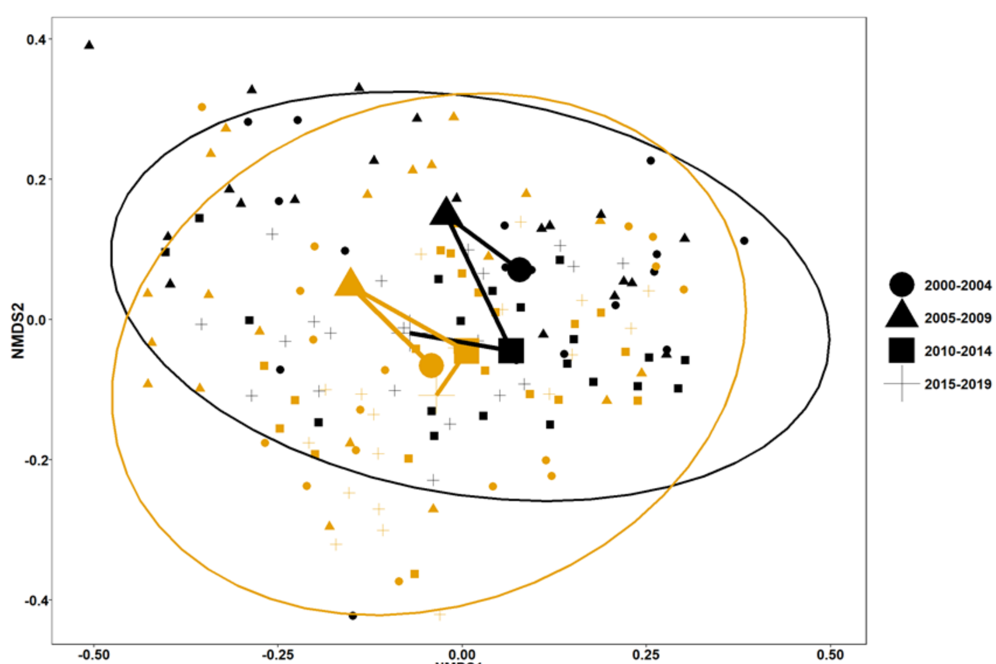


**Figure 2.8.** Top species abundance NMDS for ME-NH Inshore Trawl Survey. Larger data points are the center of the data for each year group and ellipses are 95% confidence level.

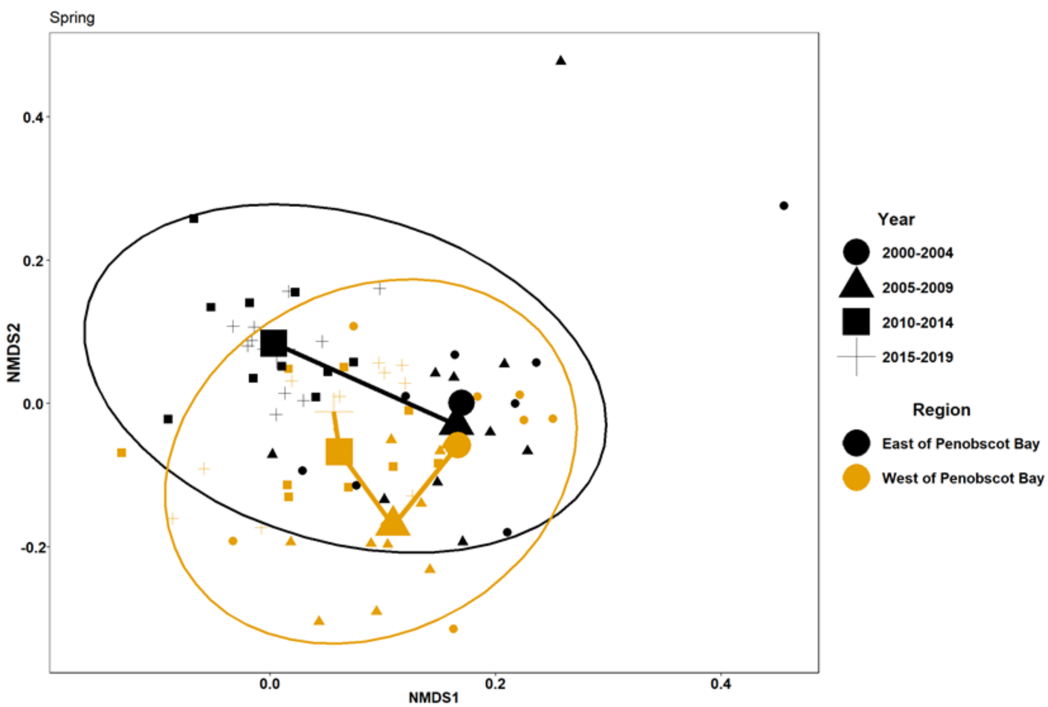


**Figure 2.9.** Spring top species biomass NMDS for ME-NH Inshore Trawl Survey by region. Larger data points are the center of the data for each year group and ellipses are 95% confidence level.

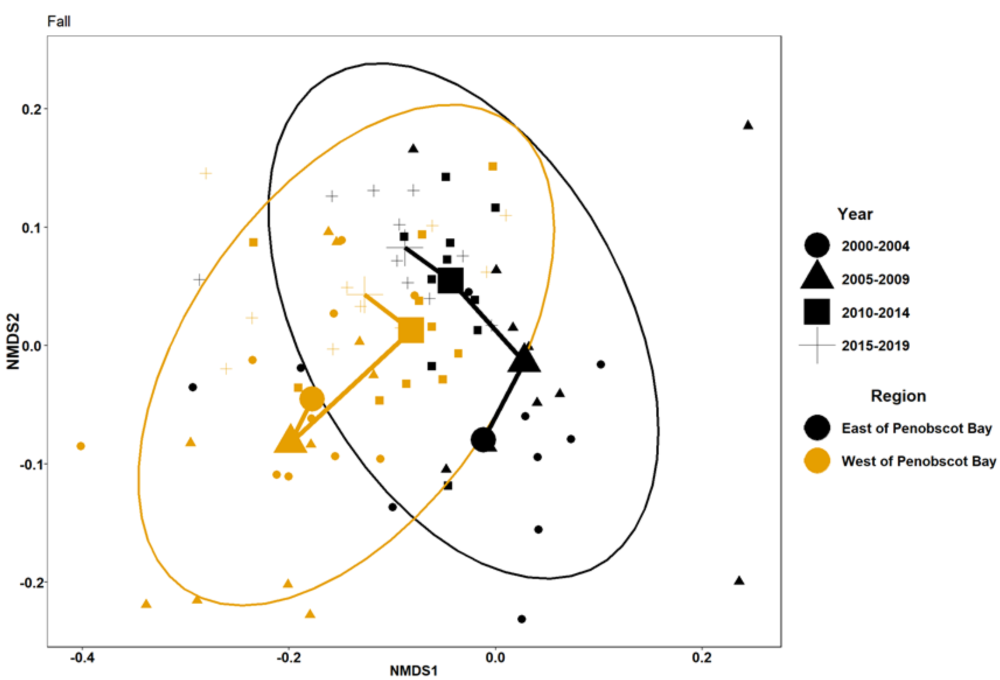


**Figure 2.10.** Fall top species biomass NMDS for ME-NH Inshore Trawl Survey by region. Stress =0.140 Larger data points are the center of the data for each year group and ellipses are 95% confidence level.

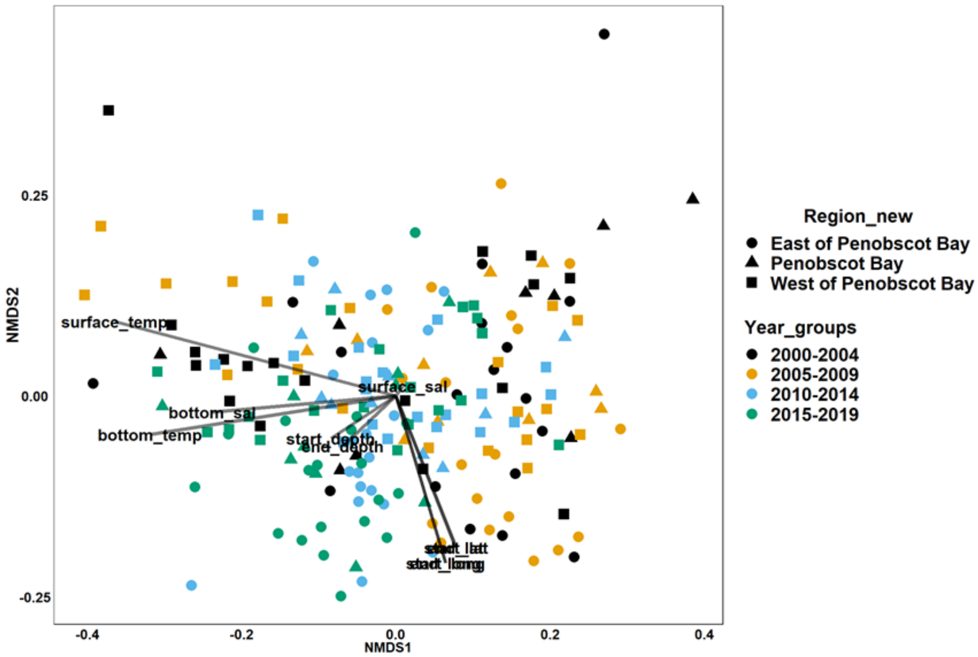


**Figure 2.11.** Functional group biomass NMDS for ME-NH Inshore Trawl Survey with linear correlated environmental factors.

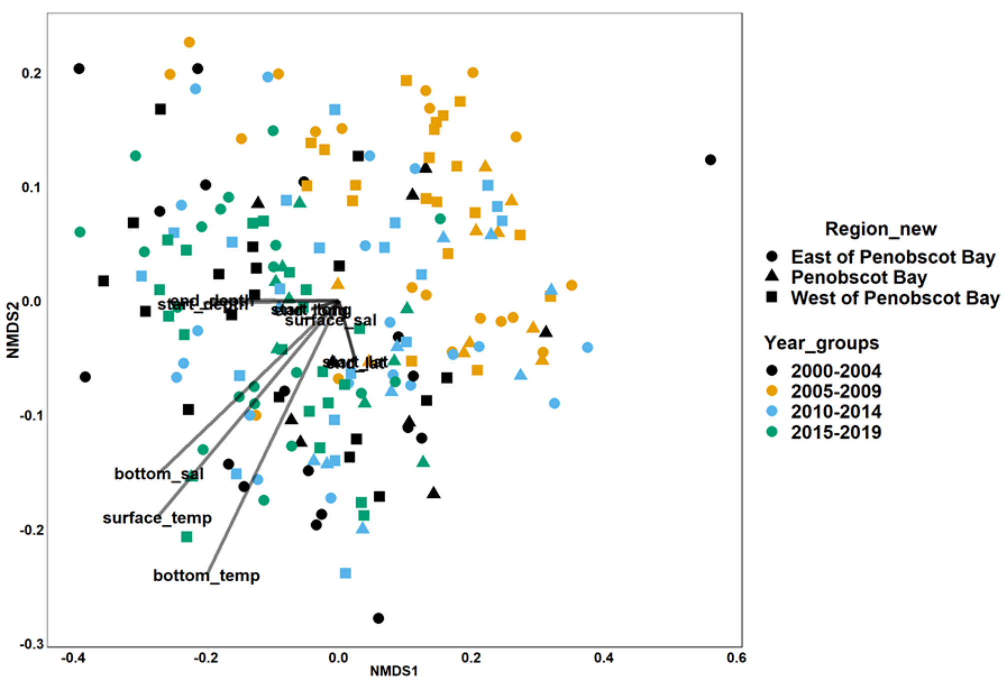


**Figure 2.12.** Functional group abundance NMDS for ME-NH Inshore Trawl Survey with linear correlated environmental factors.

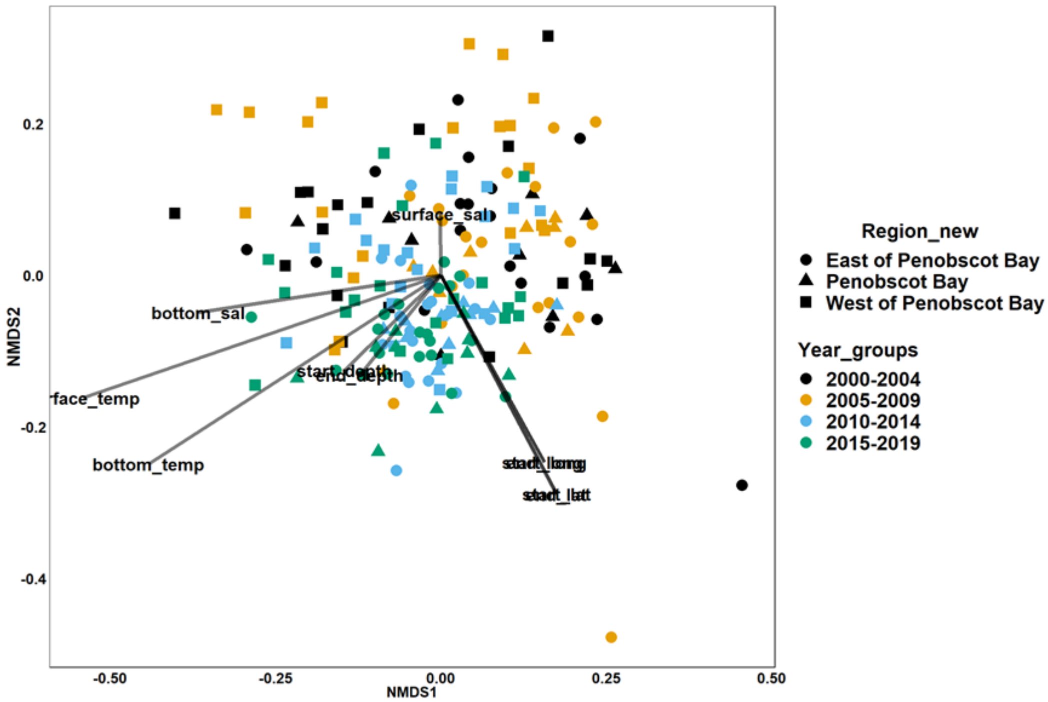


**Figure 2.13.** Top species biomass NMDS for ME-NH Inshore Trawl Survey with linear correlated environmental factors.

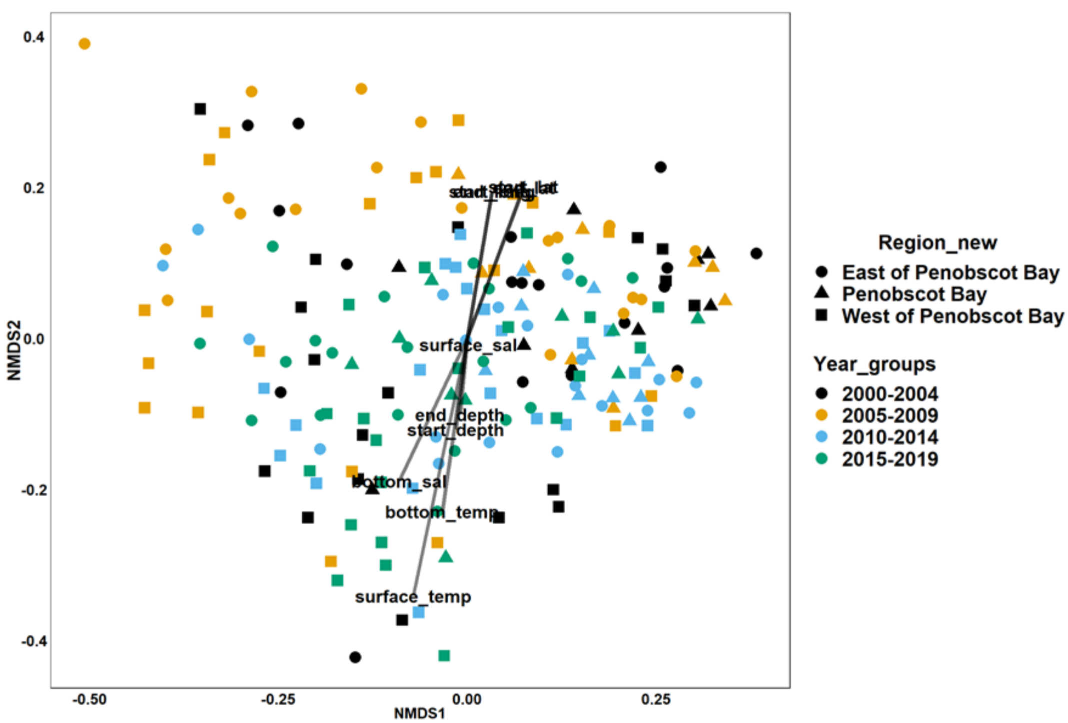


**Figure 2.14.** Top species abundance NMDS for ME-NH Inshore Trawl Survey with linear correlated environmental factors.

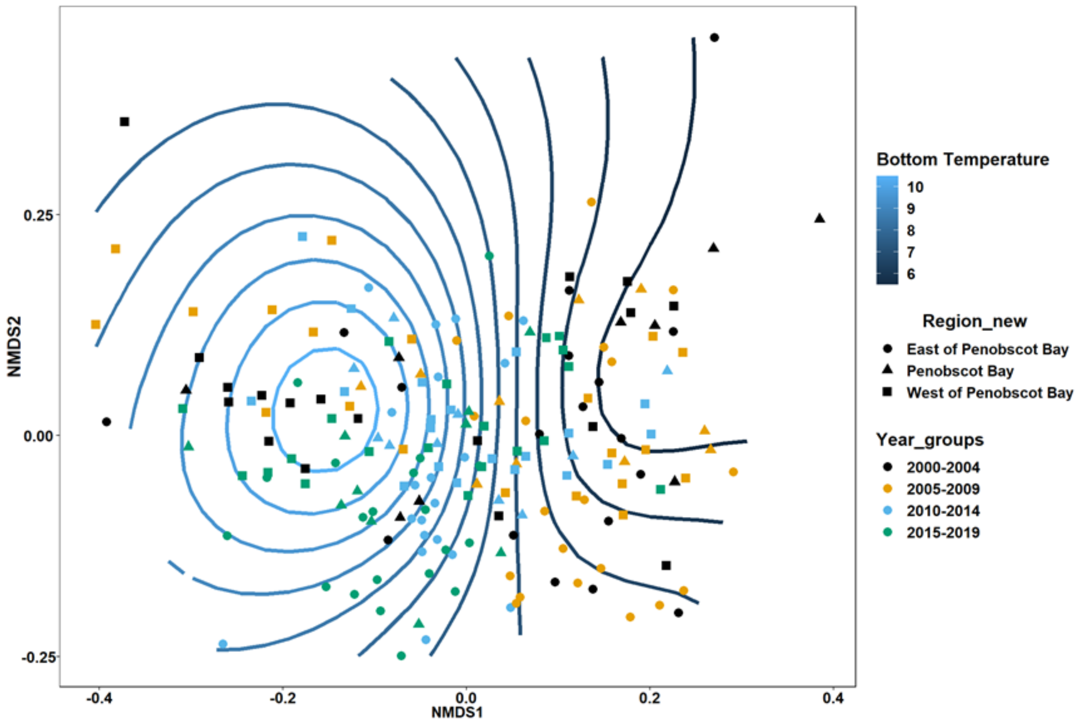


**Figure 2.15.** Functional group biomass NMDS for ME-NH Inshore Trawl Survey with generalized additive model effect of bottom temperature

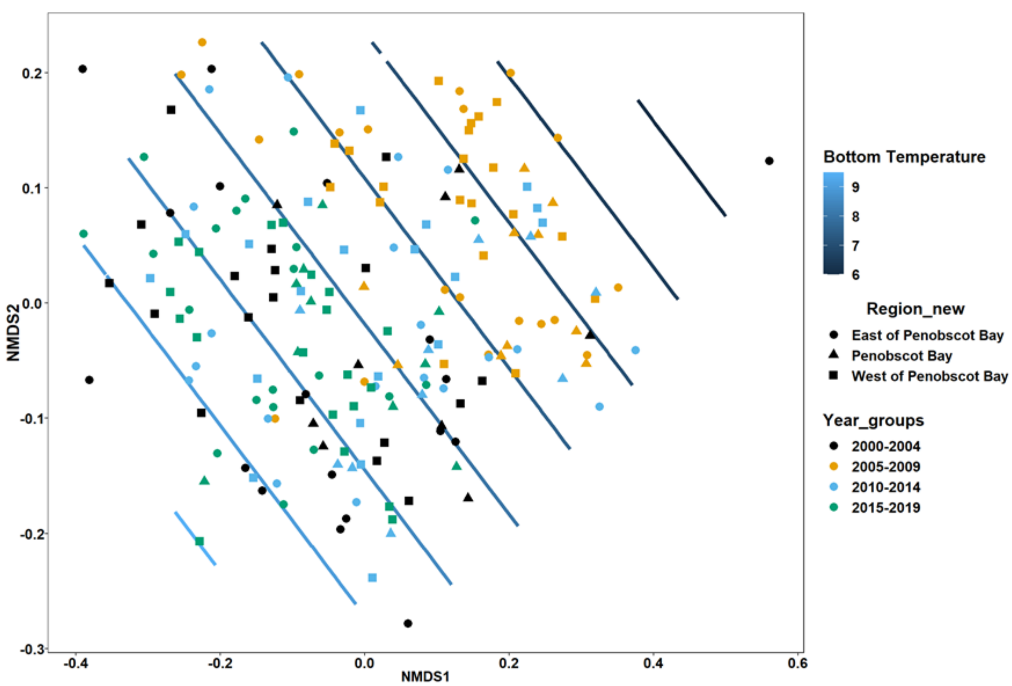


**Figure 2.16.** Functional group abundance NMDS for ME-NH Inshore Trawl Survey with generalized additive model effect of bottom temperature

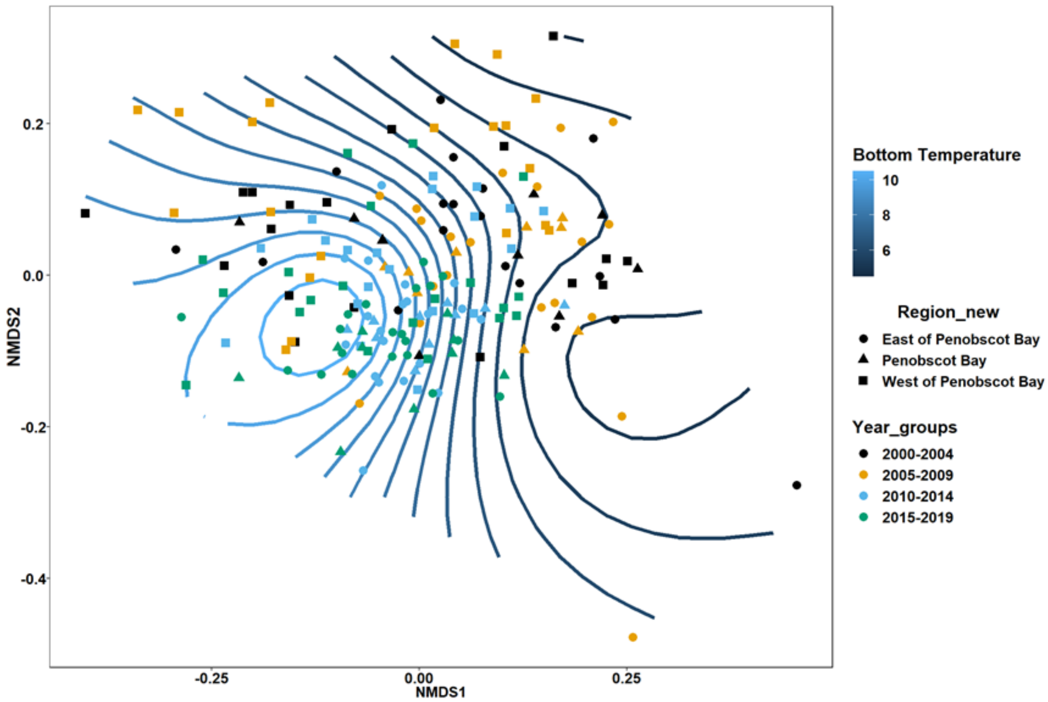


**Figure 2.17.** Top species biomass NMDS for ME-NH Inshore Trawl Survey with generalized additive model effect of bottom temperature

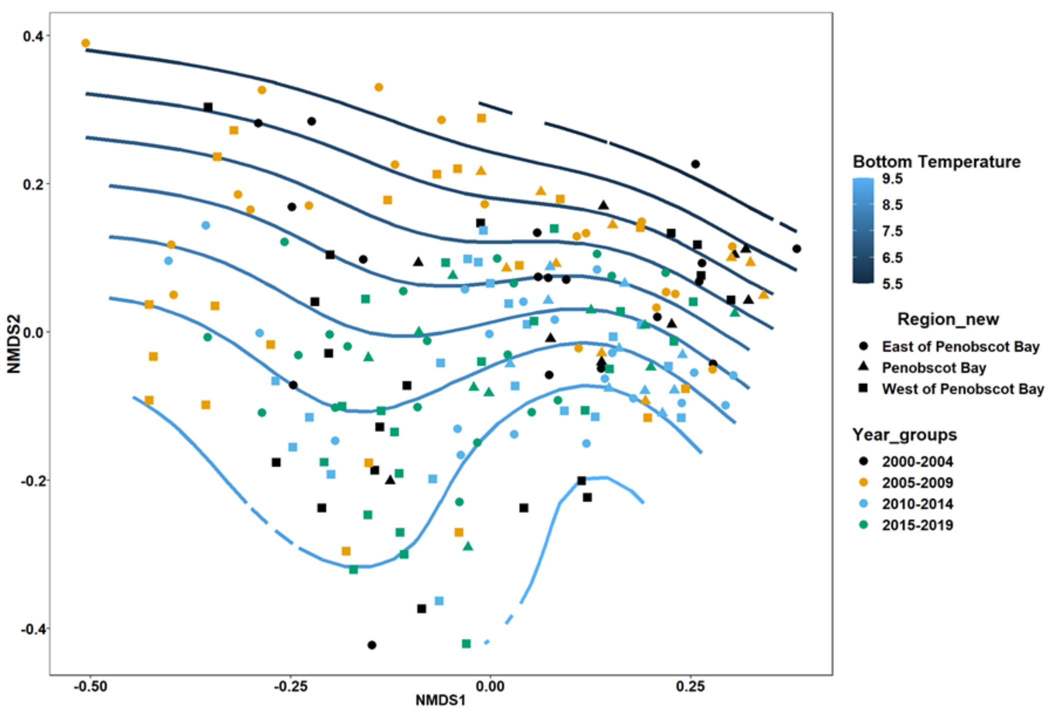


**Figure 2.18.** Top species abundance NMDS for ME-NH Inshore Trawl Survey with generalized additive model effect of bottom temperature

## Objective 3


**Figure 3.1.** Schoener's D overlap index for lobster and five predator species calculated from occurrence stage (i.e., probability of presence) predictions of single species Vector Autoregressive Spatio-Temporal models. Schoener's D is a measure of the similarity between a prey species niche and a predator species niche, with a value of 1 indicating complete overlap and a value of 0 indicating complete independence.

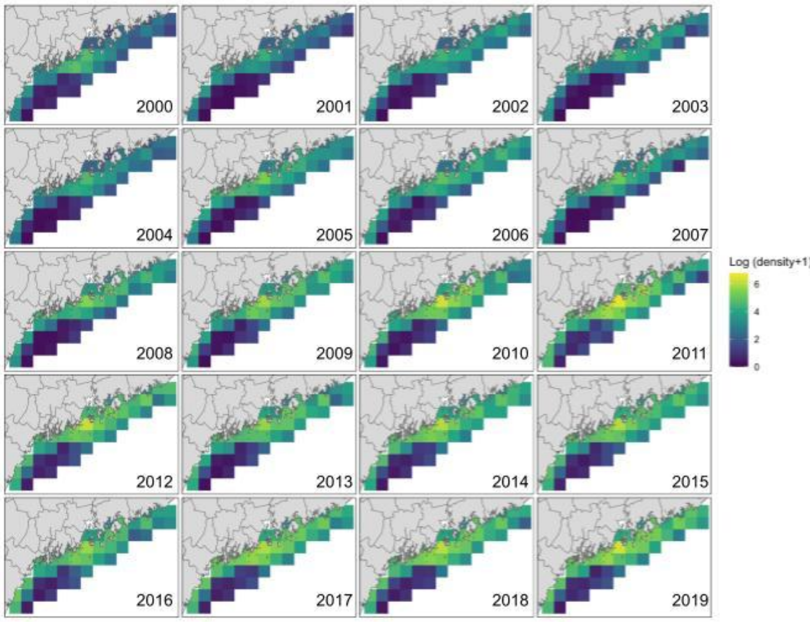


**Figure 3.2.** Predicted log density of lobster calculated using fitted single species Vector Autoregressive Spatio-Temporal model and gridded GLORYsv12.1 environmental data. Predictions were made for each fall from 2000 to 2019 within the general domain of the ME-NH Inshore Trawl Survey.

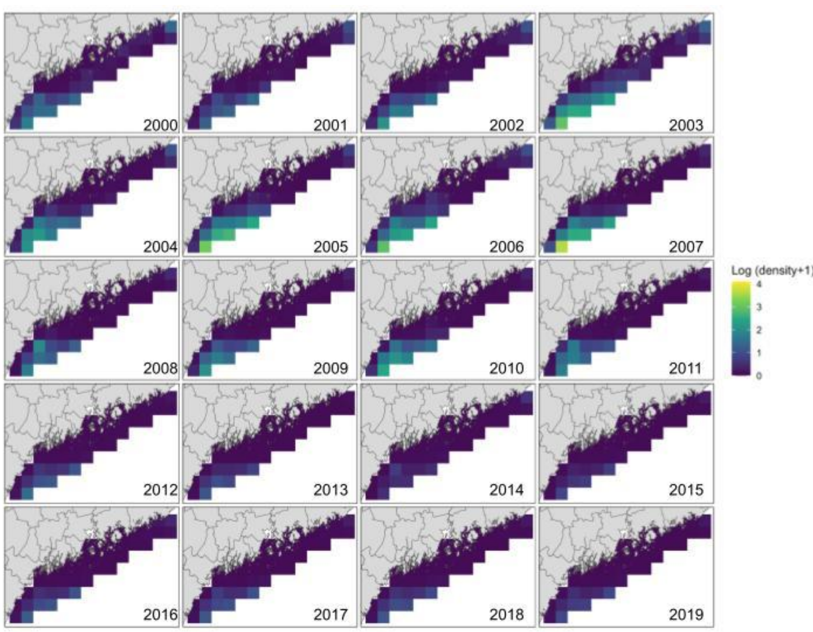


**Figure 3.3.** Predicted log density of cod calculated using fitted single species Vector Autoregressive Spatio-Temporal model and gridded GLORYsv12.1 environmental data. Predictions were made for each fall from 2000 to 2019 within the general domain of the ME-NH Inshore Trawl Survey.

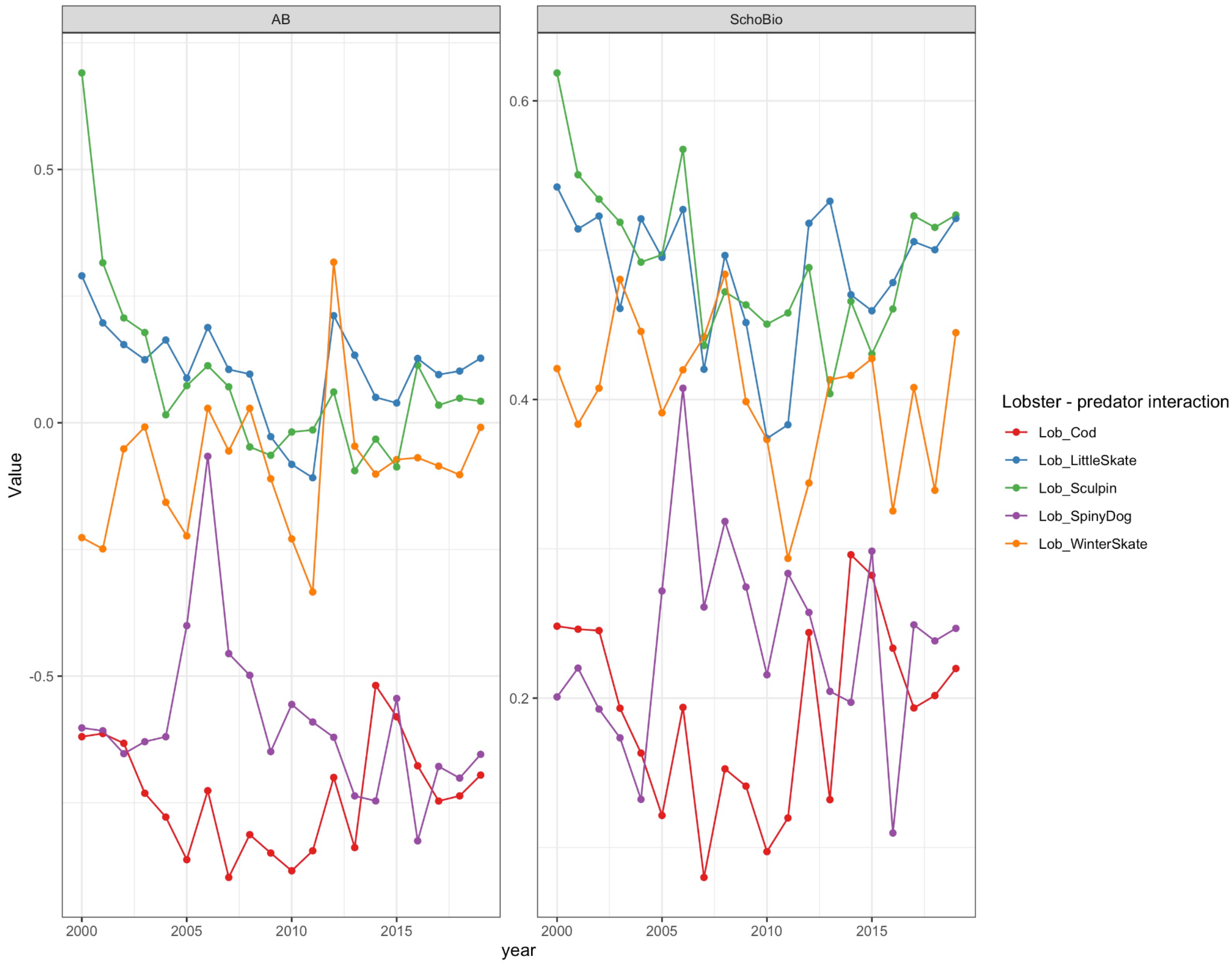


**Figure 3.4.** AB ratio (left panel) and Schoener's D (right panel) overlap index metrics for lobster and five predator species calculated from density predictions of single species Vector Autoregressive Spatio-Temporal models. AB ratio is a measure of potential trophic transfer, capturing how much predator density can be attributed to spatial overlap of prey with values less than 0 suggesting active predator avoidance. As with the occurrence stage of the model, Schoener's D is a measure of the similarity between a prey species niche and a predator species niche, with a value of 1 indicating complete overlap and a value of 0 indicating complete independence.

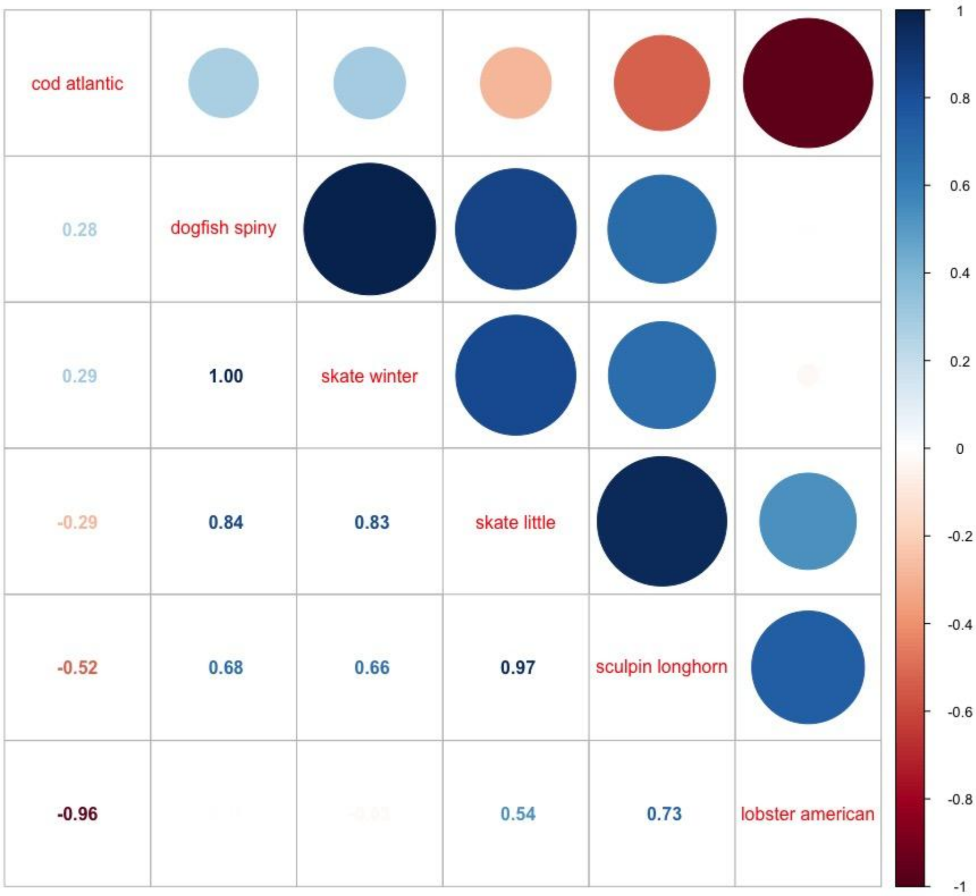


**Figure 3.5.** Spatio-temporal correlation between lobster and predator species occurrence estimated from the Vector Auto-regressive Spatio-Temporal joint species distribution model. Size of the circle indicates strength of the relationship and color indicates correlation direction, with blue colors suggesting positive correlations and red values suggesting negative correlations in occurrence patterns across the full survey time series.

**Objective 4:**

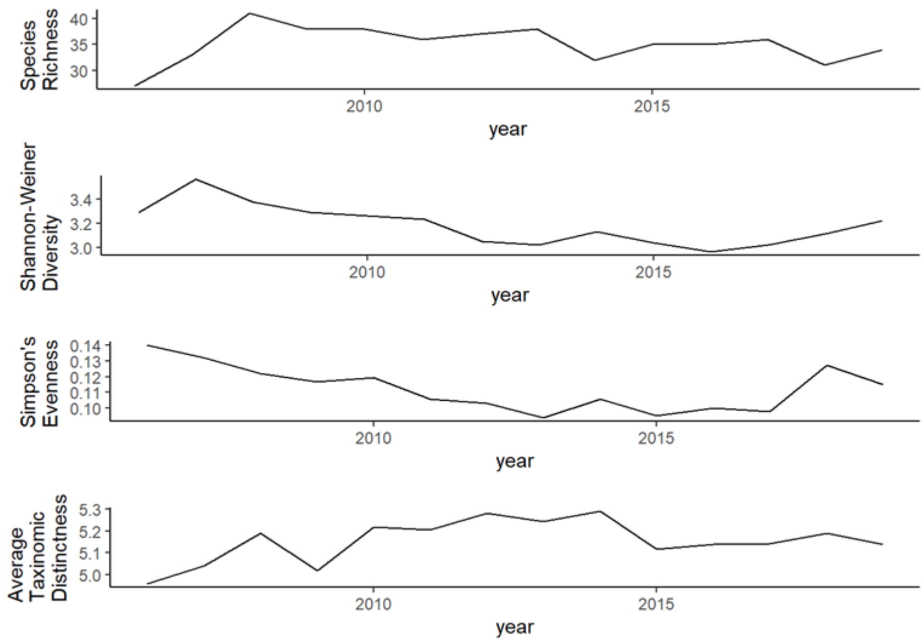


**Figure 4.1.** Maine landings specified by county average annual biodiversity indices (2006-2019), including species richness, Shannon-Weiner diversity, Simpson's evenness, and average taxonomic distinctness.

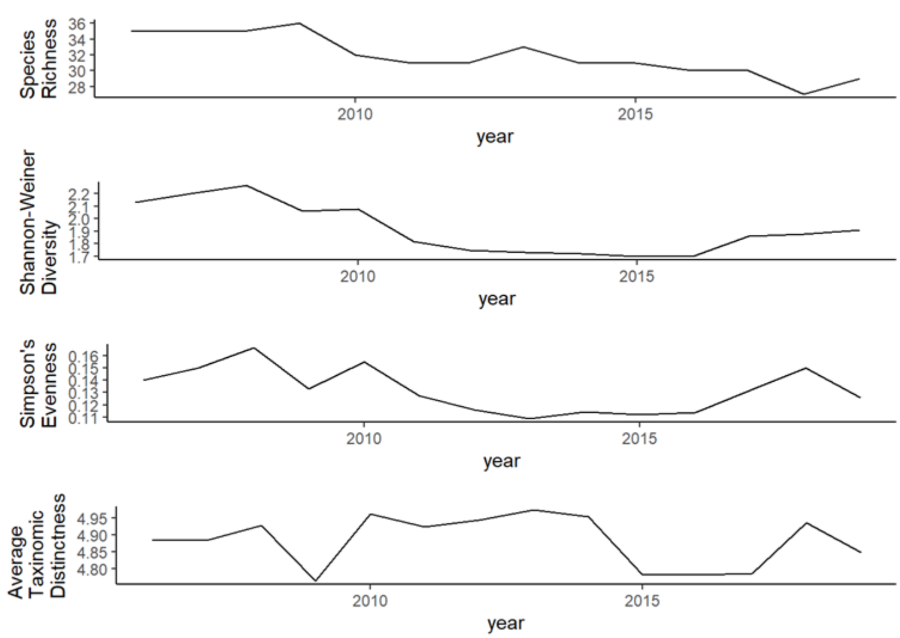


**Figure 4.2.** Maine landings for selected historical species annual biodiversity indices (2006-2019), including species richness, Shannon-Weiner diversity, Simpson's evenness, and average taxonomic distinctness.

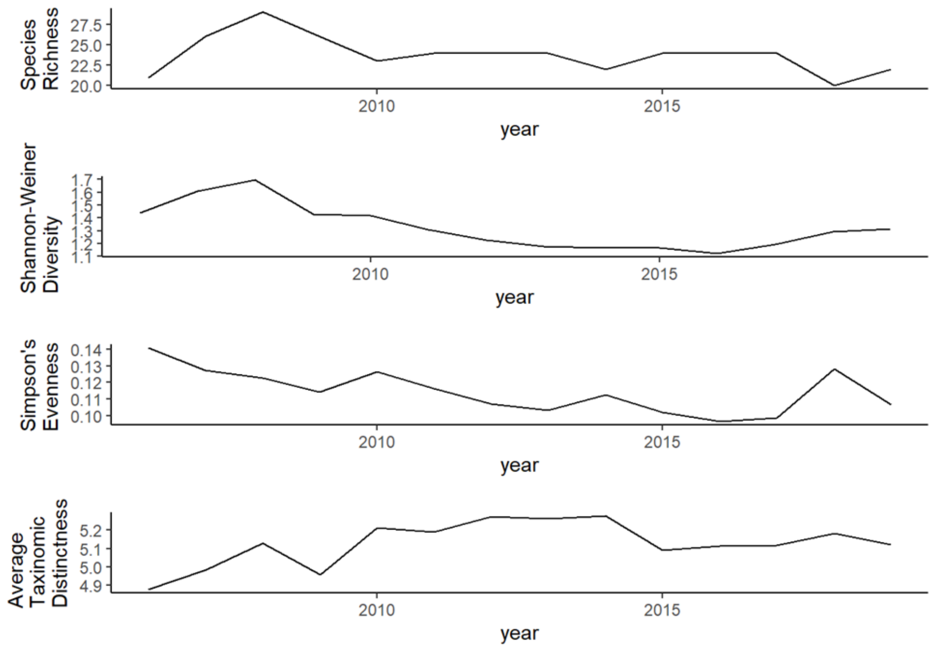


**Figure 4.3.** Maine landings specified by county and filtered to include species encountered in the ME-NH Inshore Trawl Survey average annual biodiversity indices (2006-2019), including species richness, Shannon-Weiner diversity, Simpson's evenness, and average taxonomic distinctness.

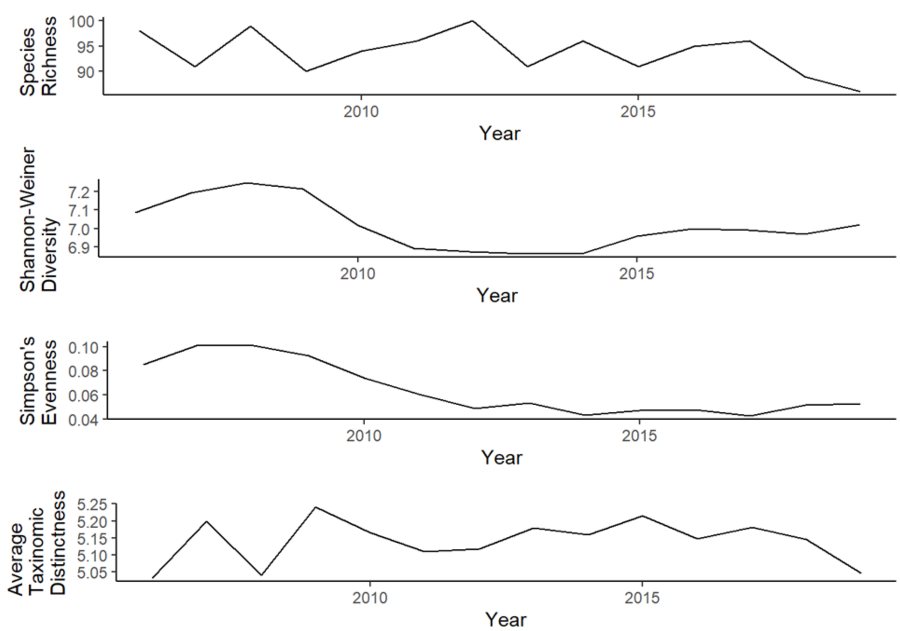


**Figure 4.4.** ME-NH Inshore Trawl Survey annual biodiversity indices (2006-2019), including species richness, Shannon-Weiner diversity, Simpson's evenness, and average taxonomic distinctness.

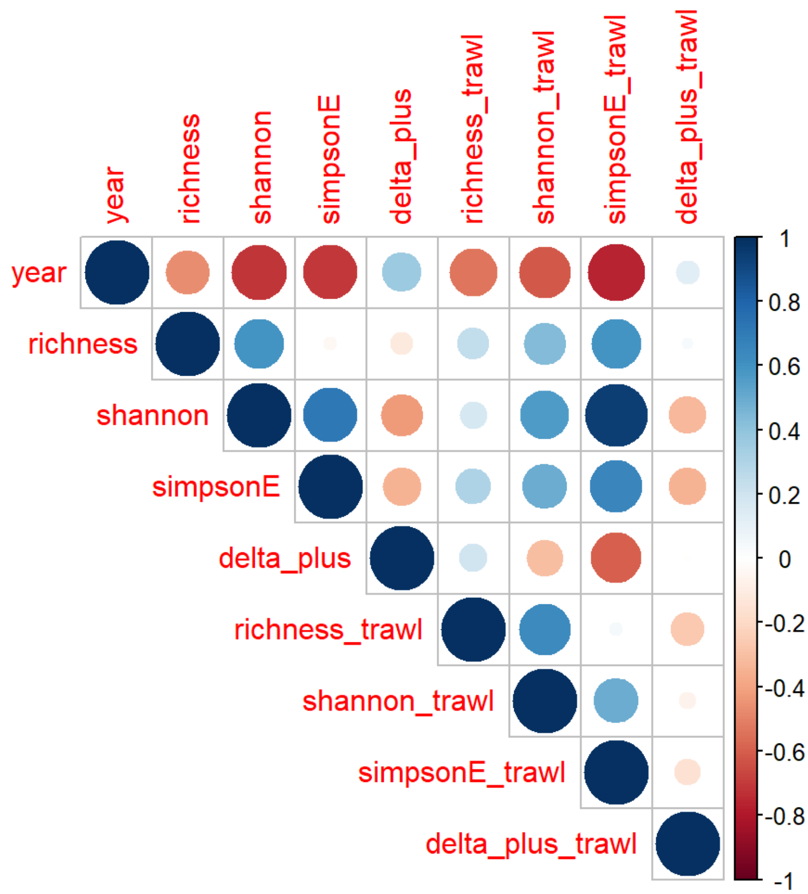


**Figure 4.5.** Correlation matrix comparing biodiversity indices for ME-NH Inshore Trawl Survey (metrics ending in _trawl) and Maine landings filtered to include species found in the ME-NH Inshore Trawl Survey

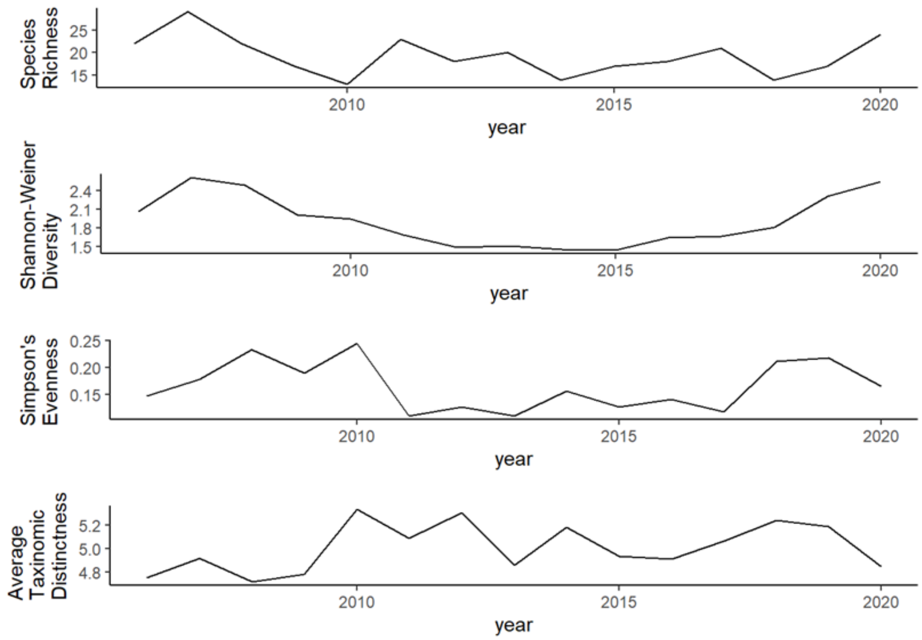


**Figure 4.6.** Maine landings for East of the Penobscot Bay specified by county average annual biodiversity indices (2006-2020), including species richness, Shannon-Weiner diversity, Simpson's evenness, and average taxonomic distinctness.

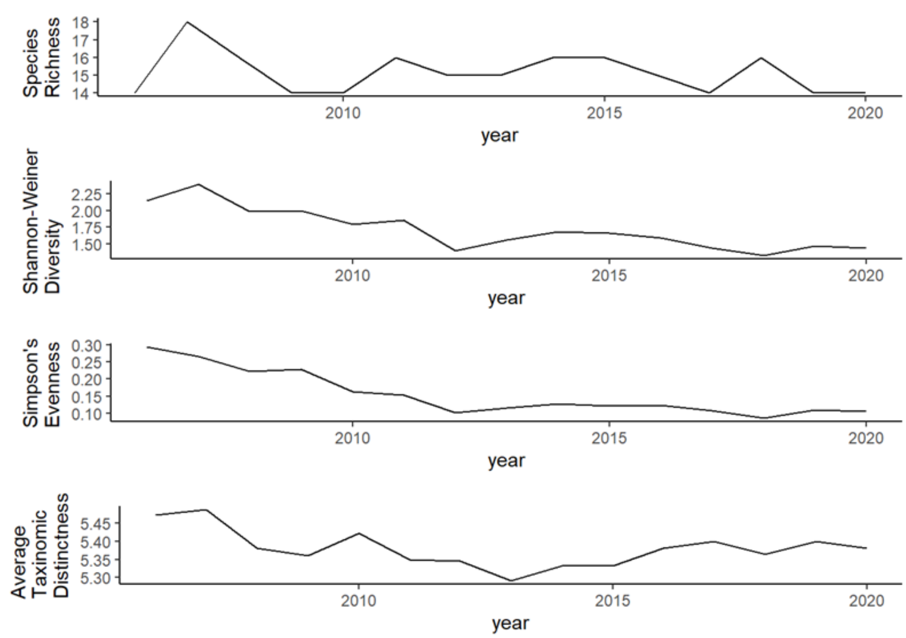


**Figure 4.7.** Maine landings for East of the Penobscot Bay specified by county average annual biodiversity indices (2006-2020), including species richness, Shannon-Weiner diversity, Simpson's evenness, and average taxonomic distinctness.

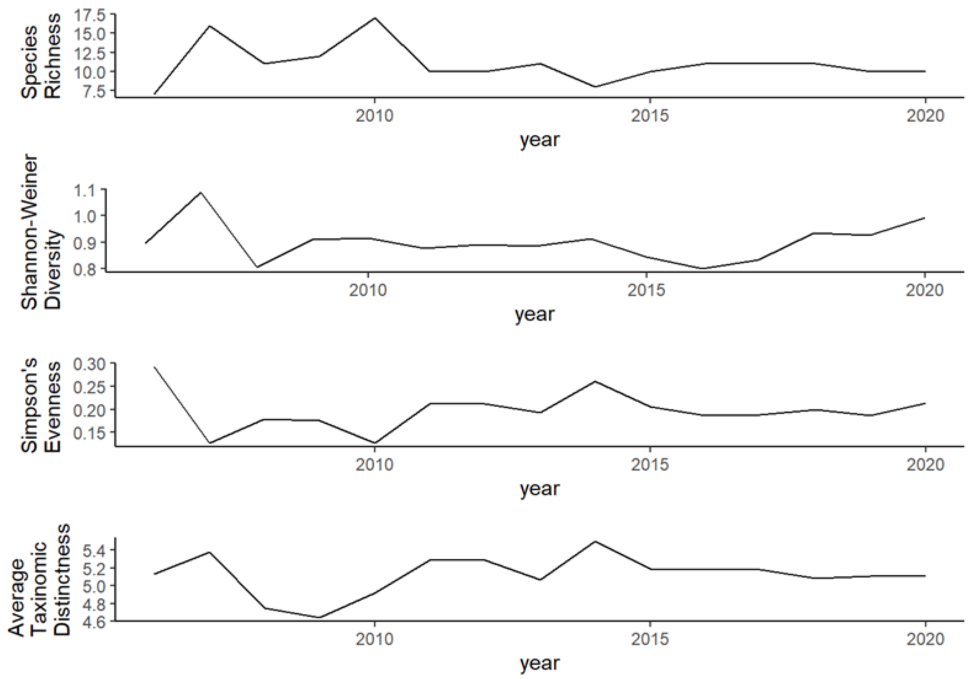


**Figure 4.8.** Maine landings for Penobscot Bay specified by county average annual biodiversity indices (2006-2020), including species richness, Shannon-Weiner diversity, Simpson's evenness, and average taxonomic distinctness.

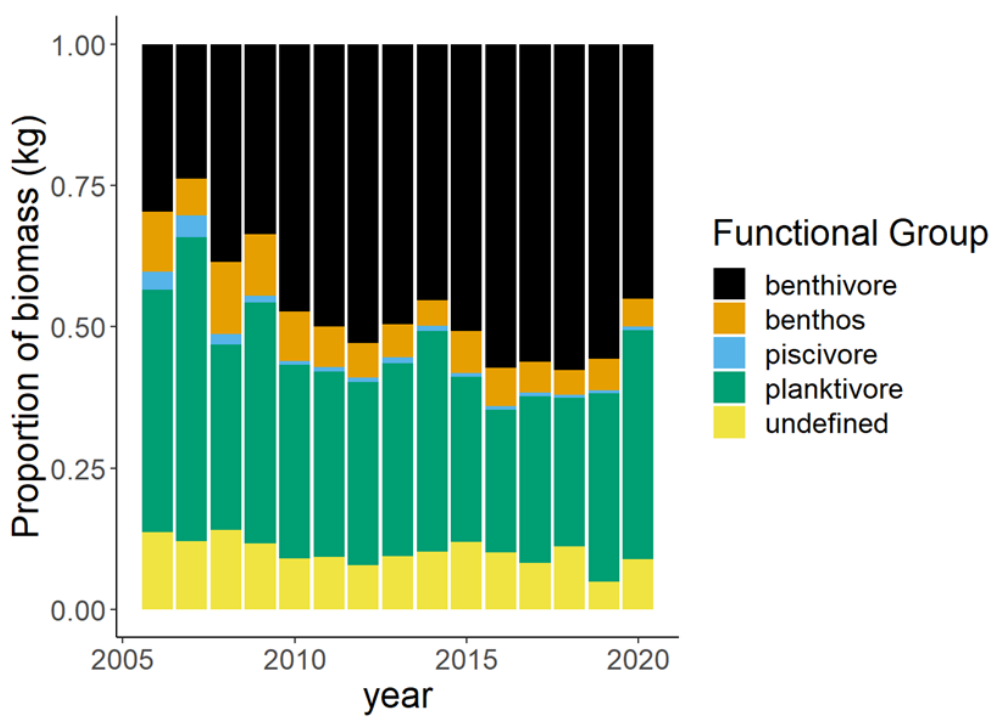


**Figure 4.9.** Maine landings specified by county proportion of biomass in each functional group (2006-2020).

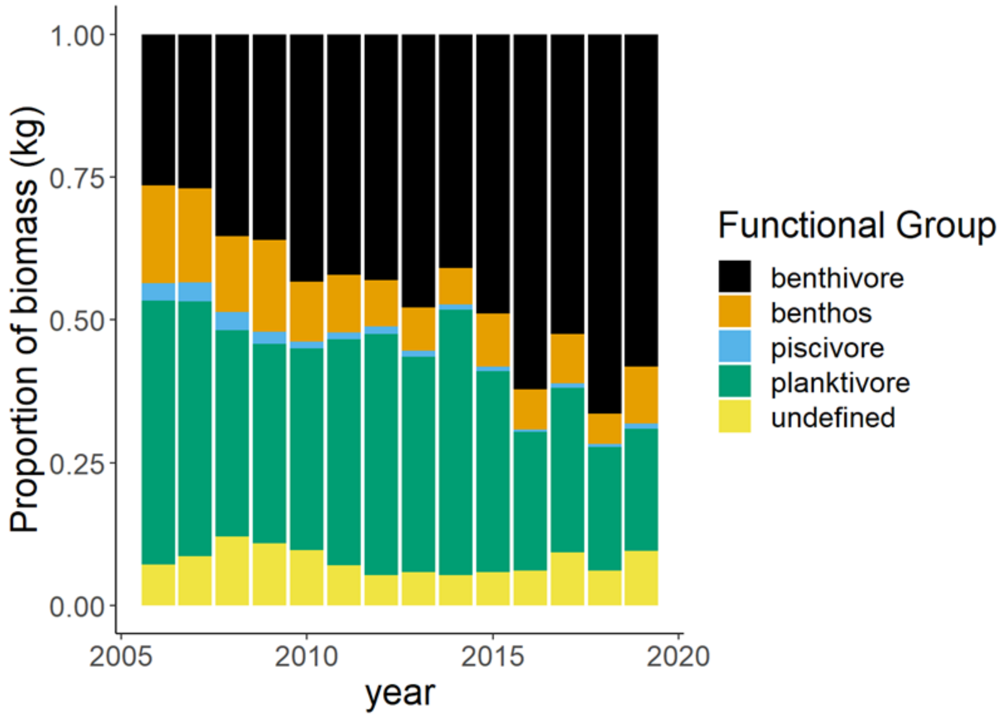


**Figure 4.10.** Maine landings for selected historical species proportion of biomass in each functional group (2006-2020).

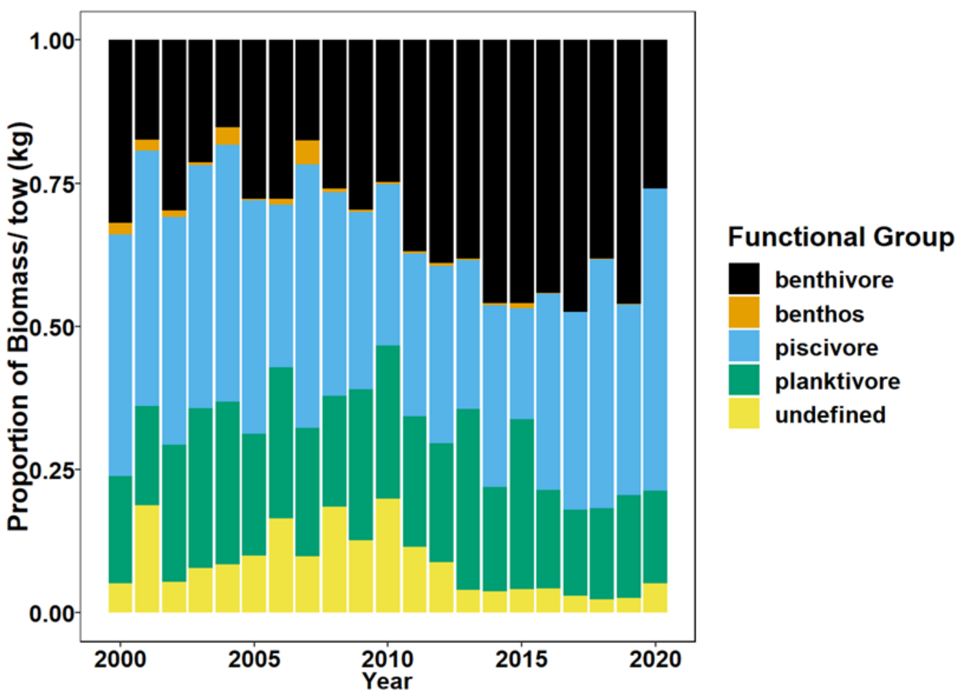


**Figure 4.11.** Maine-New Hampshire Inshore Trawl Survey proportion of biomass/ tow in each functional group (2000-2020).

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