

Changes in higher trophic level productivity, diversity and niche space in a rapidly warming continental shelf ecosystem

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ABSTRACT

There is long-standing ecological and socioeconomic interest in what controls the diversity and productivity of ecosystems. That focus has intensified with shifting environmental conditions associated with accelerating climate change. The U.S. Northeast Shelf (NES) is a well-studied continental shelf marine ecosystem that is among the more rapidly warming marine systems worldwide. Furthermore, many constituent species have experienced significant distributional shifts. However, the system response of the NES to climate change goes beyond simple shifts in species distribution. The fish and macroinvertebrate communities of the NES have increased in species diversity and overall productivity in recent decades, despite no significant decline in fishing pressure. Species distribution models constructed using random forest classification and regression trees were fit for the dominant species in the system. Over time, the areal distribution of occupancy habitat has increased for approximately 80% of the modeled taxa, suggesting most species have significantly increased their range and niche space. These niche spaces were analyzed to determine the area of niche overlap between species pairs. For the vast majority of species pairs, interaction has increased over time suggesting greater niche overlap and the increased probability for more intense species interactions, such as between competitors or predators and prey. Furthermore, the species taxonomic composition and size structure indicate a potential tropicalization of the fish community. The system and community changes are consistent with the view that the NES may be transitioning from a cold temperate or boreal ecoregion to one more consistent with the composition of a warm temperate or Carolinian system.

Keywords: species interactions, niche overlap, biodiversity, habitat, species distribution model

1. Introduction

On a global scale, production capacity associated with marine fish stocks has declined while accounting for the increase in temperature attributed to climate change (Free et al., 2019). The productivity of the global ocean is essential to supporting current and projected human needs (Watson et al., 2015) and even temporary reductions and interruptions of this productivity can result in dangerous food shocks (Cottrell et al., 2019). The ability of a socioeconomic system to resist shocks depends on the biodiversity of its dependent ecosystem; underscoring the importance of biodiversity to maintaining the resilience of ocean systems and their ability to provide vital services (Worm et al., 2006). Global patterns of biodiversity are largely attributed to temperature as a main driver (Tittensor et al., 2010); however, community restructuring may have more complex proximate causes often related to the requirements of specific taxa and habitats (Stuart-Smith et al., 2018; Teichert et al., 2018). The rapid pace of change in what are mostly continental shelf ecosystems (Belkin, 2009) underscores the interest in shifts that have occurred, or are likely to occur in the future, in the structure of exploited fish and invertebrate communities in response to temperature and other ecosystem parameters (Henson et al., 2017).

Continental shelf ecosystems are of particular importance since they are situated in areas of enhanced upwelling and primary production and their benthic habitats are readily accessible to a range of fishing gears. The majority of global fisheries landings can be attributed to capture fisheries executed on continental shelves (Amoroso et al., 2018). These fisheries continue to expand in the amount of effort applied and are negatively affected by declining biomass and catch-per-unit-effort (Anticamara et al., 2011; Rousseau et al., 2019). As noted, these ecosystems are warming rapidly and many of them have been characterized as hotspots or foci of exceptional warming, and thus on the vanguard of what we can expect in terms of a general ecosystem response (Hobday and Pecl, 2014). Where data support such analyses, continental shelf fish communities have reorganized in response to regional warming and changing abundance patterns (Kortsch et al., 2015; Simpson et al., 2011). Despite evidence of global reduction in species richness, regional analyses focusing on fish populations show dominant patterns of increasing species richness and range size for colonizing species (Batt et al., 2017). The Northeast Shelf ecosystem, the subject of this paper, is a member of this study group for which analyses have suggested species richness is increasing. These examples of change in community structure indicate, without a great deal of extrapolation, that shifting species distributions may stress dependent fishing communities as important target species move to new areas, thus requiring greater transit time and expense to fishermen (Dubik et al., 2019; Kleisner et al., 2017). In the extreme case, species may shift distribution across national boundaries and management jurisdictions (Jensen et al., 2015), increasing the potential for conflict (Pinsky et al., 2018).

The response of fish and macroinvertebrate communities to changing climate conditions has evolved from a focus on center of gravity measures of distributional change to more holistic approaches. Contemporary change in climate, often at rapid pace, coupled with comprehensive resource surveys have yielded a series of studies from individual systems (Mueter and Litzow, 2008; Nye et al., 2009; Perry et al., 2005) that support the view that poleward shifts in distribution occurred. These movements are often nuanced to include accommodations in habitats achieved through movement to new depth strata (Kleisner et al., 2016) and meta-analysis approaches have shown a high degree of coherence in these distributional changes across systems (Pinsky et al., 2013). The complexity of community response to climate change is revealed in different ways when other factors are included beyond center of distribution results. In the North Sea, fish communities have a high degree of stability in species composition despite dramatic localized shifts in distribution, which, when considered in context of changing fishing pressure and abundance, suggest regional change in productivity is of central importance (Simpson et al., 2011). In an Arctic system, the Barents Sea, climate change has aggressively transformed an Arctic fish community to one more typical of a boreal system (Fossheim et al., 2015); the

Arctic taxa were driven to depth refugia. There is an expectation that continued climate change will actuate even more movement among species beyond what has been demonstrated by historical example (Morley et al., 2018) and begin to impact warm water systems through the tropicalization of fish communities (Cheung et al., 2012). Though already widespread (Verges et al., 2014; Wernberg et al., 2016), we expect the pace of tropicalization may accelerate as the differential in global warming between high and low latitudes shifts and we experience rapid warming at lower latitudes (Francis and Vavrus, 2015).

The U.S. Northeast Shelf (NES) continental shelf marine ecosystem has in recent decades exhibited one of the strongest warming trends among the global oceans (Pershing et al., 2015; Saba et al., 2016) exacerbated by the occurrence of episodic marine heatwaves (Pershing et al., 2018; Scannell et al., 2016). In addition to climate change, temperatures in this region are strongly linked to large-scale circulation patterns (Greene et al., 2013; Thomas et al., 2017). The combination of these climatic processes has been observed to have profound effects on the marine community. Changes in phytoplankton bloom dynamics (Borkman and Smayda, 2009; Saba et al., 2015) and zooplankton abundance (Bi et al., 2014) have each been tied to fluctuations in regional circulation. Along- and cross-shelf vertebrate and invertebrate species distribution shifts have occurred in response to long-term warming (Friedland et al., 2018a), circulation patterns (Nye et al., 2011), and inter-annual temperature variation (Henderson et al., 2017). Patterns of temperature change acting across a similar range of temporal scales have also been implicated for alterations in the productivity of various fish species (Fogarty et al., 2008; O'Gorman et al., 2016). Combined with the effects of exploitation, long-term warming has caused significant changes in species assemblages along the NES (Bell et al., 2015; Lucey and Nye, 2010), with sub-regions now resembling the past assemblages of areas further south, and the initiation of regional regime shifts (Shackell et al., 2012; Steneck and Wahle, 2013). Such disruptions, however, have been difficult to anticipate, perhaps due to the apparent heightened vulnerability of species to the combined effects of bottom-up and top-down forcing at the edges of their thermal ranges (Boudreau et al., 2015). This unpredictability has pronounced consequences for the management of this marine ecosystem, as changes in catchability (Rolim and Avila-da-Silva, 2018) and conflict between harvest regulations and shifting species distributions (Dubik et al., 2019) have produced novel challenges.

We examined aspects of the fish and macroinvertebrate community structure of the NES, which generally matches the extent of the U.S. Northeast Continental Shelf Large Marine Ecosystem. We developed time series of total fishery removals, species diversity and richness, higher trophic level productivity, and individual size in the context of rapid change to the thermal regime of the system. Furthermore, we considered an ensemble of habitat or species distribution models to examine change in occupancy habitat by species and changes in species interaction space and interaction strength. We evaluated these parameters for the whole community and by functional groups based on feeding type.

2. Methods

2.1 Study System

This analysis focused on the NES ecosystem, which is a well-studied continental shelf marine system along the western boundary of the North Atlantic Ocean. Temperature, diversity measures, productivity in the form of fishery-independent biomass catch-per-unit-effort (CPUE), and occupancy habitat estimates were all made relevant to the extent of the ecosystem as shown by the estimation grid in Fig. 1. Catch estimates were made in respect to the Large Marine Ecosystem (LME) global habitat classification scheme (Sherman and Duda, 1999) for the U.S. Northeast Continental Shelf LME (see Fig. 1 map insert). We restricted the analysis to the years 1992-2016 even though many of the datasets had

longer time series. The restriction was imposed to match the years of the habitat model estimates, which was in turn limited by the period that salinity measurements have been made with electronic instrumentation.

2.2 Thermal Conditions

Thermal conditions in the ecosystem were characterized by temperature observations from both shipboard and satellite sensors. The shipboard data were seasonal interpolations of spring (April 3) and autumn (October 11) surface and bottom temperature using the methods described in Friedland et al. (2018a). These data provide complete temperature fields on the estimation grid; the mean temperatures by season and depth were based on all the values over the grid. The remote sensing data were sourced from the NOAA Optimum Interpolation $\frac{1}{4}$ Degree Daily Sea Surface Temperature Analysis (OISST) dataset, which provides high resolution sea surface temperature (SST) with a spatial grid resolution of 0.25° and temporal resolution of 1 day (Reynolds et al., 2007). The temperatures matching the dates of the observational data were extracted for comparative purposes. In addition, the mean and standard deviation of temperatures throughout the year were also extracted from this dataset. We evaluated the time series changes in temperature using Mann-Kendall non-parametric trend analysis. We calculated Kendall's tau test for the significance (two-tailed test) of a monotonic time series trend (Mann, 1945) for the observational and satellite data. We also calculated Theil-Sen slopes of trend, which is the median slope joining all pairs of observations (R package wql, version 4.9). The same trend tests were applied to the other time series data in the study.

2.3 Fishery Removals

Fishery removals or total catch was assembled from multiple catch databases. The system data were summarized using catch from Watson and Tidd (2018) for the LME boundaries from the description of the study system. This study harmonized publicly available data and mapped to 30-minute spatial cells guided by the ranges of the reported taxa, inshore fishing arrangements and satellite data where appropriate. Their data, however, did not specifically provide estimates of recreational catch. This catch component was estimated from the Marine Recreational Information Program, or MRIP database (www.fisheries.noaa.gov/topic/recreational-fishing-data).

2.4 Community Measures

The principal fishery-independent survey on the NES is the bottom trawl survey conducted by the Northeast Fisheries Science Center, which provides both spatial and temporal depictions of fish and macroinvertebrate abundances (Grosslein, 1969). Surveys conducted in the spring and autumn are based on a stratified random design. Most animals caught in the survey tows are identified to species; however, some are only identified to genus or family, and in rare instances assigned to an unidentified category. Since 1968, the survey has encountered 437 taxa, 303 species during the spring survey and 409 during the fall. These should be viewed as minimum estimates owing to identification issues mentioned, but also because the survey has also been conducted outside the study time frame (see appendix A for list of species). On average, an annual survey encounters 120 taxa in spring and 170 in fall reflecting the fact that many taxa are rare to the system. We restricted this analysis to catch identified to species since most of the catch is identified to this level and it provides the most reliable information on change in fish and macroinvertebrate distribution. Catches were standardized for various correction factors related to vessels and gears used in the time series (Miller et al., 2010). The survey data are publicly available at <https://inport.nmfs.noaa.gov/inport/>. Trends in community organization were represented

with a series of indices calculated using the software package “Past” (<https://folk.uio.no/ohammer/past/>, version 3.14). The indices were: the Shannon H diversity index, Simpson’s 1-D evenness index, and Taxa S species richness index. These indices represent different aspects of the organization of the fish and invertebrate community. The indices are presented as Z-scores (observation minus the time series mean and divided by the standard deviation) for plotting purposes. Finally, we inspected species occurrence data to test in part whether the NES may be undergoing tropicalization. In this analysis, we used the full time series of the bottom trawl data to detect species that occurred more frequently in the last two decades of the times series (1997-2016) than in the first two (1968-1987). If the difference in occurrences was ten or more, we considered the species had potentially established residence in the NES. For these species, we qualitatively evaluated distribution information to classify whether the species appeared to originate from lower latitudes and thus represent tropicalization.

2.5 Fish and Invertebrate Biomass Trends

Time series trends in biota were represented by the CPUE for biomass of all taxa from the bottom trawl survey dataset, which we consider a proxy productivity index. Whereas in the diversity calculations only taxa identified to species were used, all taxa, regardless of level of identification, contributed to the total biomass captured per trawl haul. To assess broader ecosystem changes, species were also assigned to functional groups based on their adult prey preferences and vertical distribution: benthivores, demersal piscivores, pelagic piscivores, or planktivores. These assignments were used to subdivide the productivity index into indices by functional group. Seasonal mean individual weights were calculated by dividing the total biomass CPUE by the total numbers CPUE.

2.6 Modelled Occupancy Habitat

Occupancy habitat or absence presence distribution models for the more consistently abundant taxa from the bottom trawl survey were constructed using random forest methods (Breiman, 2001). The model training set for a taxon consisted of absence or presence of the species in a trawl sample and an initial candidate list of 91 independent variables, organized into four categories including physical environment variables, habitat descriptors, zooplankton variables, and remote sensing variables (Table 1). The independent variables were either static variables, which were parameters that did not change annually or dynamic variables, which were allowed to change from year to year.

The physical environment variables included station data observations made contemporaneously to survey bottom trawl stations. Depth of the station (meters) was used as a static variable in the analysis. Surface and bottom water temperature and salinity were used as dynamic variables. These parameters were measured using Conductivity/Temperature/Depth (CTD) instruments.

Habitat descriptors were a series of static variables that reflect the shape and complexity of the benthos. Most of the variables were based on depth measurements, for example, vector ruggedness measure, rugosity, and slope variables (see Table B1 in Appendix B for a complete listing). Other variables were based on parameters such as benthic sediment grain size and the vorticity of benthic currents.

Zooplankton abundance variables were dynamic variables that reflected change in species abundance and biomass. The Ecosystem Monitoring Program (EcoMon), which conducted shelf-wide bimonthly surveys of the Northeast U.S. Shelf ecosystem over the study period (Kane, 2007), provided the abundance data. Zooplankton were collected throughout the water column to a maximum depth of 200 m using paired 61-cm Bongo samplers equipped with 333-micron mesh nets. Sample location in this

survey was based on a randomized strata design, with strata defined by bathymetry and along-shelf location. Plankton taxa were sorted and identified. We used the density (number per 100 m³) of the 18 most abundant taxonomic categories and a biomass indicator (settled bio-volume) as potential predictor variables (see Table B2 in Appendix B). The zooplankton sample time series had some missing values, which were ameliorated by summing data over five-year time steps for each seasonal period and interpolating a complete field using ordinary kriging. For example, the data for spring 2000 included the available data from tows made during the spring period 1998-2002.

Remote sensing variables were developed from chlorophyll concentration and SST data from remote sensing data sources. The chlorophyll concentration data included measurements made with the Sea-viewing Wide Field of View Sensor (SeaWiFS), Moderate Resolution Imaging Spectroradiometer on the Aqua satellite (MODIS), Medium Resolution Imaging Spectrometer (MERIS), and Visible and Infrared Imaging/Radiometer Suite (VIIRS) sensors during the period 1997-2016. The data were a merged product using the Garver, Siegel, Maritorena Model (GSM) algorithm (Maritorena et al., 2010) obtained from the Hermes GlobColour website (hermes.acri.fr/index.php). Monthly SST fields were based on data from the MODIS Terra sensor available from the Ocean Color Website (<http://oceancolor.gsfc.nasa.gov/cms/>). The data were summarized as monthly means with their associated gradient magnitude or frontal fields and applied in the habitat models as static variables. Many methods have been used to identify fronts (Belkin and O'Reilly, 2009) in oceanographic data and these usually apply some focal filter to reduce noise and then identify gradient magnitude with a Sobel filter. We did these calculations in R using the raster package (version 2.6-7) by applying a three by three mean focal filter and a Sobel filter to generate x and y derivatives, which are then used to calculate gradient magnitude.

Random forest occupancy models were fit using the randomForest R package (version 4.6-14). Prior to fitting the model, the independent variable set was tested for multi-collinearity among the predictors, and correlated variables were eliminated (R package rfUtilities, version 2.1-3). From this reduced set of predictors, the final model variables were selected utilizing the model selection criteria of (Murphy et al., 2010) as implemented in rfUtilities. The habitat models were evaluated for fit based on out-of-bag classification accuracy using the AUC or Area Under the ROC Curve index (irr package in R, version 0.84). Occupancy habitat was predicted for each species, by season, onto the estimation grid. The occupancy habitat area (km²) was the area of the NES associated with the grid locations with an occurrence probability > 0.5 for that species and is intended to represent the realized niche space. The species interaction area was estimated by finding the grid locations (and area in km²) in common between the habitat areas of two species. We also computed an index of interaction strength (Selden et al., 2018), which was the size of the interaction area for a species pair divided by the occupancy area for each species. This yielded two indices per pairing reflecting the potential asymmetry in the resulting effect of the interaction on each member of the species pair. We sorted this index into the minimum and maximum of the pairing, with the maximum representing the stronger pairwise interaction.

3. Results

3.1 Thermal Conditions

The Northeast Shelf ecosystem warmed over recent decades; however, the changes in thermal conditions have not been equivalent across seasons or depth. Bottom temperature increased in both spring and autumn over a range of approximately 0.5 and 1.25°C, respectively (Figs. 2a&b). However, only the autumn increasing trend was significant (Table 2). Similarly, data from both station and remote sensing sources suggest SST increased during spring and autumn over a range of approximately 0.5 and 2.25°C, respectively (Figs. 2c&d). As with the bottom temperature, only the autumn data trends were

significant. The remote sensing annual temperature index suggests a rate of warming of approximately 0.8°C per decade for the ecosystem (Fig. 2e), which is less than the peak rate associated with autumn surface temperature of approximately 1.2°C per decade. These differences in the rate of temperature change between seasons appear to affect the overall variability in thermal conditions in the ecosystem; variability in temperature based on the standard deviation in SST from the remote sensing data has significantly increased (Fig. 2f).

3.2 Fishery Removals

The composite catch estimate of the NES ecosystem suggests the total fisheries removals did not significantly change over the study period. Estimates based on marine ecoregion and the large marine ecosystem boundaries indicate catches have averaged approximately 1.65 to 1.5 million MT, respectively (Fig. 3). The trend analysis suggests a modest decline in catch of approximately 0.1 million MT in these time series, noting that neither trend was significant (Table 2).

3.3 Community Measures

The indicators reflecting change in the NES fish and macroinvertebrate community structure increased over recent decades; however, the changes in community have not been equivalent across seasons. The Shannon diversity index was without trend during the spring period, but significantly increased during the autumn of the year (Figs. 4a&b; Table 2). Similarly, evenness indices lacked trend during spring and trended significantly upwards in the autumn (Figs. 4c&d). Species richness indices trended upwards in both spring and autumn (Figs 4e&f); however, the probabilities associated with these trends were significant in spring and non-significant in fall.

Vertebrate and invertebrate taxa representing fish and shrimp, crab, and squid species, respectively, have apparently established residency in the NES in recent years. A group of species have met the difference in occurrences criteria in both spring and fall (Table 3). Slightly more than half these taxa were invertebrates, the majority of which appear to be sourced from higher latitudes. All the fish species would appear to be sourced from lower latitudes with the exception of *Reinhardtius hippoglossoides*. A second group of species met the criteria in the fall only and was comprised of mostly fish species, nearly all of which appeared to be sourced from lower latitudes. The only exception was the shrimp species *Pandalus borealis*, which could be classified as a cold-water species. Overall, most new residents appear to have been sourced from lower latitude habitats.

3.4 Fish and Invertebrate Biomass Trends

Fish and macroinvertebrate community productivity appears to have increased over the study period as suggested by trends in total biomass CPUE. Aggregated CPUE increased from approximately 100 kg tow⁻¹ to in excess of 200 kg tow⁻¹ in nearly identical, significant trends in both spring and autumn (Fig. 5a, Table 4). Individual weight showed mixed trends declining in the spring and increasing in the autumn (Fig. 5b); only the autumn weight trend was significant. When we disaggregated the biomass trends by functional group, we found nearly identical trends in spring and autumn CPUE for benthivores, demersal piscivores, and planktivores (Figs. 6a,b&d), all of which were significant. The exceptions were the trends for spring and autumn pelagic piscivore biomass, which varied seasonally and were non-significant (Fig. 6c). Spring biomass of pelagic piscivores was much lower than autumn biomass, which can be attributed to four species including *Pomatomus saltatrix*, *Cynoscion regalis*, *Illex illecebrosus*, and *Loligo pealeii*, two seasonal migrating finfish taxa and the most abundant squid species occurring on the NES, which overwinter off the shelf break. When individual weights were disaggregated by functional group, we see

that average weight has declined for benthic species (Figs. 7a&b) and in both seasons, with mixed patterns of trend significance. However, average weight increased in planktivores and was without trend in fall pelagic piscivores; collectively this mix of trends among the functional group changes the perception of seasonal average weight suggested by the aggregate estimate. In both seasons, average weight has declined among benthically oriented species, however, average weight has increased among most pelagically oriented species, more so in the fall than in the spring.

3.5 Modelled Occupancy Habitat

Occupancy models were fit for an overlapped set of spring and autumn taxa of the NES ecosystem. Of the 78 candidate spring taxa, 49 were found to have sufficiently high model diagnostics to consider their model output in further analyses (Table 5, see Appendix C). The species list was composed of mostly finfish, but there were also benthic and pelagic macroinvertebrates in this group. Of the 89 candidate autumn taxa, 58 were found to have sufficiently high model diagnostics to consider their model output in further analyses (Table 6, see Appendix D). The intersection between the seasonal species sets included 48 taxa that were modeled in both seasons. The models for most taxa included depth and bottom temperature variables; however, variables associated with lower trophic levels played a prominent role (Table 7). Among the top 15 variables in the occupancy models that were selected as a top ten variable in at least one species model, the majority of variables were either zooplankton or chlorophyll variables in both seasons.

The majority of species modeled had increasing trends in occupancy area and as a consequence increased areas of niche overlap with other species. Of the 49 modeled taxa in the spring, 42 species had positive habitat trends, representing 86% of the taxa (Fig. 8a). The species with the highest rate of habitat increase was haddock (*Melanogrammus aeglefinus*), which had an annual rate of habitat size increase of 2,879 km² yr⁻¹. At the other end of the spectrum, the taxa showing the greatest loss of habitat was sea raven (*Hemitripterus americanus*) with a rate of habitat loss of 649 km² yr⁻¹. In the autumn, of the 58 modeled taxa, 45 species had positive habitat trends, representing 78% of the taxa (Fig. 8b). The greatest loss in habitat, -1,878 km² yr⁻¹, was experienced by Atlantic cod (*Gadus morhua*), which also experienced the second highest loss rate in the spring. However, the ordering of species with increased habitat in the autumn was dramatically different than the spring species, with the greatest increase of habitat, 3,834 km² yr⁻¹, observed with Gulf Stream flounder (*Citharichthys arctifrons*).

Occupancy habitat has increased among the species representing functional groups; however, the amount of habitat varied between seasons for some groups. The sum of spring and autumn benthivore and demersal piscivore habitats all increased, all within a similar range of 3-4 million km² yr⁻¹ of habitat (Figs. 9a&b). However, the seasonal sums of pelagic piscivore and planktivore habitats differed (Figs. 9c&d). Spring pelagic piscivore habitat totaled around 300,000 km² yr⁻¹, whereas autumn habitat totaled in excess of 1 million km² yr⁻¹. Though less of a pronounced difference, spring planktivore habitat totaled around 1.8 million km² yr⁻¹ while autumn habitat totaled in excess of 1.5 million km² yr⁻¹. All of these habitat trends were significant (Table 8).

The trends in interaction areas between species niches tended to be positive, increasing in absolute value regardless of sign with the time series mean interaction area. The vast majority of species-to-species interaction areas had positive trends- only 3% of these trends were negative in sign during spring (Fig. 10a) and only 8% during autumn (Fig. 10d). Mean interaction areas were larger in spring than autumn for most functional species groups pairings (Fig. 11a). There was a gradation of interaction area size associated with piscivore versus planktivore groups, with the smaller areas associated with benthically-oriented, planktivore taxa. The disparity between seasons was even more acute for interaction area trends (Fig. 11b); however, the ordering of rates did not strictly follow the pattern in the mean area data.

The effect of the increase in interaction area between species was not uniform across both members of the species pairs. The trend in the interaction area strength index for the weaker link (minimum index) (Fig. 10b&e) included more negative trends, approximately 23%, then that for the stronger link (maximum index), approximately 4% of which were negative (Fig. 10c&f). These data show that for the most part, at least one of the species in an interaction pair had a positive trend in the strength of interaction over the study period. Further, interaction strength had a greater increase for the member of the pair for which the interaction had a stronger potential effect. The data also show that the most dramatic change in interaction strength was associated with the smallest interaction areas.

When we contrast spring and autumn interaction strength by functional groups, as with the interaction area data, the means and trends in the spring data suggest greater interactions than in the autumn. Trends in interaction strength for both the weak and strong links of the species pairing tended to be higher in spring than in autumn (Fig. 12a&b). Trends in interaction strength for the weaker of the links amongst the demersal piscivore and pelagic piscivore interactions were negative in both seasons. In contrast, trends in interaction strength for the stronger of the links were all positive in both seasons and were lowest for the pelagic piscivore and planktivore interactions. The mean interaction strength for both members of the species pair tended to be higher in spring than in autumn, as also seen in the trends for these data. However, the contrast between seasons is less pronounced (Fig. 12c&d). In fact, with the exception of pelagic piscivore interactions, most coordinates lie very near the 1:1 reference line suggesting more parity between seasons. Unlike the trend data, the interaction indices tended to be smallest among pairings that involved benthivores.

4. Discussion

The combined stressors of overfishing and climate change are perceived as a threat to global marine biodiversity (Gattuso et al., 2015; Pitcher and Cheung, 2013; Poloczanska et al., 2013) and an existential threat to humanity in many ways (Cardinale et al., 2012; Naeem et al., 2016). Biodiversity is limited by the available niche space for species (Beaugrand et al., 2018), where habitats are formed and removed from an ecosystem as conditions shift. The same process of habitat change also has the capacity to affect productivity, as habitats limit within and between species' abundances (McCauley et al., 2015). Furthermore, thermal events have become more episodic, thus posing short-term, extreme challenges to many organisms (Smale et al., 2019). The NES has experienced significant change in thermal regime and extreme thermal events, which should affect habitats, yet our main finding is that the ecosystem appears to have increased in diversity and productivity. This agrees with global scale observations and predictions since they include the suggestion that change in diversity will likely have latitudinal patterns, with higher diversity realized at higher latitudes over time (Jones and Cheung, 2015).

With this change in diversity and productivity, we also observed a change in the spatial dynamics of species, with most species experiencing an increase in the extent of modelled occurrence, accompanied by an increase in the spatial overlap for the vast majority of species interactions. Marine species have a greater capacity for adaptation and display plasticity in the way they expand and shift their niche space than other faunal groupings (Donelson et al., 2019); hence, the change in thermal regime on the NES has likely expanded the extent of the ecosystem within the respective thermal ranges of individual species. The change in productivity of the system presents significant problems of interpretation since our data suggest that competition has likely increased with the increase in niche space overlap. Despite these changes, we observed an increase in productivity, and the only evidence of competition was the decline in body size principally among benthic species. Finally, there was little evidence that the change in productivity could be attributed to a change in fishing pressure. At most, fishing pressure appears to have declined about 20% whereas productivity appears to have increased by

a factor of two. We suspect that that energy flow has changed in respect to the segment of the food web represented by the fish and invertebrates captured in the bottom trawl survey.

The change in organization of the ecosystem did not appear to be uniform over seasons. In spring, diversity did not increase; yet spatial interactions did, suggesting that resident species increased their range or footprint with increasing temperature. This sort of response is well established in pelagic species where temperature regulates the extent of niche distribution, fundamentally through the response and activity of the species (Payne et al., 2018). However, for most species, the thermal niche space appears to be limited by the range of temperatures associated with cold tolerance (Stuart-Smith et al., 2017), which raises the possibility that mortality associated with overwintering conditions may be key (Morley et al., 2017). The annual thermal experience of spring residents, though they experienced slower change in spring thermal conditions, was also conditioned by rapidly increasing temperatures in summer and autumn. The decline in spring mean size suggests that despite increased productivity, there is also increased competition. In the autumn, diversity increased, but it would appear this was driven by seasonal species, most notably for pelagic piscivores. These seasonal increases in diversity or species richness can be episodic and appear to have little impact on the community structure of the resident taxa as seen in the Bering Sea (Siddon et al., 2018). However, unlike in spring, mean size of organisms on the NES increased in autumn with the increase in productivity, which we attributed to the contribution of the pelagic piscivores. If the increase in autumn mean size was at the expense of spring residents, we would have expected to see a decline in spring productivity in addition to the decline in spring mean size. Since that is not what we observed, we suspect autumn residents are accessing other resources.

The change in fish and macroinvertebrate productivity is beyond what can be explained with reliance on a single factor and is of a dimension that suggests a significant change to biogeochemical cycling of this ecosystem. With the net result of an increase in the macro-fauna, we need to ask if the energy inputs to the Northeast shelf have increased or whether the energy sinks or exports have diminished. Shelf seas can be important conduits of carbon cycling (Diesing et al., 2017) and this ecosystem, along with its dependent systems, has been intensely studied (Najjar et al., 2018). The NES depends on estuarine and atmospheric inputs of carbon and provides direct sequestration to the sediments and loss of carbon seaward to the open ocean. There is little to suggest that atmospheric inputs via primary production have increased to a similar scale as the increased faunal biomass. The Northwest Atlantic is not a region associated with any coherent trends in chlorophyll concentration (Gregg et al., 2017), though marked trends are seen elsewhere (Roxy et al., 2016). Similarly, results can be taken from bloom analyses, which suggest that this region has a mixed pattern of trends in bloom dimensions (Friedland et al., 2018b). However, the horizontal transport of carbon from estuaries is worth further consideration given the increase in precipitation in the region over recent decades (Karmalkar and Bradley, 2017). If this precipitation has increased flow or flow events, there may have been an increase in particulate transport and carbon input to the shelf ecosystem. Change in carbon exports rates, with the net effect of greater biomass among the macro-fauna, would seem to be a natural extension of a change in species distribution and niche space. With the increase in temperature, resident species increased their niche space and their capacity to utilize more of the energy resources of the ecosystem. This suggests that resources found their way into energy pathways that would have been underutilized prior, thus intercepting carbon and associated energy before it could be sequestered or transported horizontally off the shelf.

Our approach estimated habitat using a range of factors beyond thermal variables. Specifically, we included variables that reflected the influence of lower trophic levels represented by chlorophyll and zooplankton. Increasingly, species distribution model fits include primary production variables, which are contributing at an equal or higher value than the thermal variables to the overall model fit (Dell'Apa et al., 2018; Wang et al., 2018). Our understanding of shifting diversity is hampered by a lack of knowledge about other factors beyond thermal ecology that define these patterns. The connections

between lower trophic levels and resource and upper trophic level species is not well-studied (Poloczanska et al., 2016). Thermal regimes can define habitats for fish over large spatial scales, and when applied over finer spatial scales, differences in the feeding opportunities of the habitat may be the deciding factor (Genner, 2016). We think it is essential for practitioners attempting to model niche or habitat to consider the definition of niche in the context of potential food or energy resource and to go beyond simple thermal habitat.

The NES may be undergoing tropicalization of its fish community, the hallmarks of which include change to community structure and responses among individuals. With tropicalization, we can expect more diverse communities, increased occurrence of taxa once associated with lower latitudes, and a change in how energy is recycled, with overall less free energy available (Costa et al., 2014; Verges et al., 2016). The response among individuals includes a shift to smaller individual sizes, smaller sizes at maturity, more tightly coupled species interactions, and an increase in production and utilization of that production. We saw evidence for most of these signs of tropicalization in the NES. However, many of these hallmarks are beyond the scope of this analysis and may be difficult to address without significant investment in new data collection. Certainly, many more warm water species have taken up seasonal residency, which was followed by a seasonal reset over winter to more temperate taxa. As NES waters warm, niche space has clearly continued to expand to something much more akin to a tropical fish community. We suspect that over time, the overwintering reset may weaken, such that the community begins to resemble a more Carolinian system (Colburn et al., 2016). We also note that although generally there are overarching signs of tropicalization, not all segments of the NES ecosystem have changed in the same manner. For instance, the Gulf of Maine appears to be responding in a similar way to what has been observed in the North Sea. The North Sea fish distribution response to warming has been a widening of distribution limits to the north, suggestive of increased niche size (Punzon et al., 2016). Conversely, the Middle Atlantic Bight appears to be responding in a similar fashion to some Arctic systems, with a major introduction of new species and resultant shift in underlying food web structure, diversity, energy pathways and ecosystem functioning (Frainer et al., 2017). In the Middle Atlantic Bight and Arctic instances, niche space and distributions of existing taxa are expanding; however, the expansion of niche space is less prominent than for the novel taxa entering the system. Regardless of the specific mechanism, it is clear the NES is changing in its productivity, diversity and niche space, all indicative of a shift towards a more tropically-aligned system than the historical temperate one.

The systemic shift of diversity and productivity of the NES is a composite of the changes occurring at the species level, where individual fish taxa have experienced changing population dynamics and effective niches. This implies that there are economic, cultural and social implications from these changes to species dominance structure over time (Moyes and Magurran, 2019). For instance, as cod niche space has declined, there are ramifications for the groundfish fishery that has been historically dependent on that species. Essentially, as the suitable habitat for cod has shrunk, the fishing pressure has remained constant, and the effective observable production of this species has declined (Pershing et al., 2015). The options for improving cod productivity, and hence fishing opportunities, are increasingly limited. Conversely, there are opposite and more positive ramifications for fisheries that target taxa with expanded niche space. A co-occurring species in the groundfish fishery is the Atlantic haddock, whose population dynamics has been favored and has experienced expanded niche space (Friedland et al., 2015). Identifying both the limits and opportunities presented by changing species productivity is a major obligation for the research community in this, and likely most, continental shelf ecosystems.

There is an expectation that climate change will continue to reshape the organization of marine ecosystems and likely change the distribution of fish biodiversity (Molinos et al., 2016). We take this as a call for proactive action in the sense that there should be no impediments for fisheries management to

adapt to shifting patterns of productivity and species availability, thus offsetting many of the negative effects of climate change (Gaines et al., 2018). To achieve success in this context, management processes will need to be more flexible and anticipatory, which also means reaffirming a commitment to developing information for informed decision-making (Mumby et al., 2017). In many instances, change in a species' role will depend on its autecology, but we can also anticipate the exchange of system roles among species (Selden et al., 2018), which would likely pose challenges to decision makers in the absence of an ecosystem context.

Conflict of interest

The authors declare no competing financial interest.

Acknowledgements

We thank Z. Friedland for productive comments on the manuscript.

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Table 1. Summary of predictor variables used in the development of spring and autumn occupancy habitat models. Number refers to number of variables.

Predictor variable categories	Description	Number
Physical environment variables	Physical data including depth, surface and bottom temperature, and surface and bottom salinity.	5
Habitat descriptors	A series of variables that reflect the structure of benthic habitats, most of which are based on bathymetry data. See Appendix B, Table A1 for detail.	19
Zooplankton variables	Abundance of zooplankton taxa and a zooplankton biomass index (settled bio-volume) composed mostly of copepod species. Some taxa only identified to family or other general category. See Appendix B, Table A2 for detail.	19
Remote sensing variables	Remote-sensed measurements of monthly mean SST and chlorophyll concentration; and, the gradient magnitude or frontal data for the same fields.	48

Table 2. Theil–Sen slope estimates (slope) and Mann-Kendall trends test probabilities (p) for time series of temperature ($^{\circ}\text{C}$), catch (MT), and community indices Temperature includes station (STA) and remote sensing (RS) data; catch data is from the Large Marine Ecosystem (LME) area designation; significant tests shown in bold.

Data	Season	Type	slope	p
Temperature	Spring	STA Bottom	0.024	0.338
	Fall	STA Bottom	0.062	0.021
	Spring	STA Surface	0.017	0.528
	Fall	STA Surface	0.075	0.001
	Spring	RS Surface	0.037	0.129
	Fall	RS Surface	0.115	0.000
	Annual	RS Surface	0.076	0.000
	Annual	RS Surface Standard Deviation	0.014	0.030
Catch	Annual	LME	-4883	0.385
Community	Spring	Diversity	0.013	0.575
		Evenness	0.007	0.852
		Richness	0.072	0.017
	Fall	Diversity	0.075	0.006
		Evenness	0.043	0.016
		Richness	0.055	0.190

Table 3. Species more frequently encountered during the last two decades of the bottom trawl survey time series than in the first two decades. Spring and Fall column contains taxa that meet the criteria in both seasonal surveys where Fall only contains taxa in the fall survey only. Vertebrate (v) and invertebrate (i) taxa noted.

Spring and Fall	Fall only
<i>Argentina striata</i> (v)	<i>Fistularia petimba</i> (v)
<i>Morone saxatilis</i> (v)	<i>Chilomycterus schoepfi</i> (v)
<i>Reinhardtius hippoglossoides</i> (v)	<i>Gymnura micrura</i> (v)
<i>Antigonia capros</i> (v)	<i>Engraulis eurystole</i> (v)
<i>Foetorepus agassizi</i> (v)	<i>Astroscopus guttatus</i> (v)
<i>Prionotus alatus</i> (v)	<i>Sardinella aurita</i> (v)
<i>Lophius gastrophysus</i> (v)	<i>Upeneus parvus</i> (v)
<i>Pasiphaea multidentata</i> (i)	<i>Parasudis truculenta</i> (v)
<i>Dichelopandalus leptocerus</i> (i)	<i>Rhizoprionodon terraenovae</i> (v)
<i>Pandalus montagui</i> (i)	<i>Cookeolus japonicus</i> (v)
<i>Pandalus propinquus</i> (i)	<i>Larimus fasciatus</i> (v)
<i>Bathypolypus arcticus</i> (i)	<i>Opisthonema oglinum</i> (v)
<i>Acanthocarpus alexandri</i> (i)	<i>Cynoscion nothus</i> (v)
<i>Chionoectes opilio</i> (i)	<i>Pandalus borealis</i> (i)
<i>Crangon septemspinosa</i> (i)	<i>Sicyonia brevirostris</i> (i)
<i>Lithodes maja</i> (i)	
<i>Lebbeus polaris</i> (i)	
<i>Spirontocaris liljeborgii</i> (i)	
<i>Pontophilus norvegicus</i> (i)	
<i>Stoloteuthis leucoptera</i> (i)	

Table 4. Theil–Sen slope estimates (slope) and Mann-Kendall trends test probabilities (p) for time series of biomass catch-per-unit-effort (CPUE, kg tow⁻¹) and mean size in weight (kg). CPUE and weight are disaggregated by functional group; significant tests shown in bold.

Data	Season	Type	slope	p
CPUE	Spring	Total	5.750	0.000
		Benthivore	1.762	0.000
		Demersal Piscivore	2.071	0.027
		Pelagic Piscivore	0.001	0.981
		Planktivore	1.182	0.000
	Fall	Total	5.099	0.000
		Benthivore	1.875	0.000
		Demersal Piscivore	1.758	0.042
		Pelagic Piscivore	0.134	0.154
		Planktivore	0.694	0.000
Weight	Spring	Total	-0.002	0.088
		Benthivore	-0.005	0.059
		Demersal Piscivore	-0.016	0.016
		Pelagic Piscivore	-0.002	0.001
		Planktivore	0.002	0.010
	Fall	Total	0.002	0.006
		Benthivore	-0.007	0.000
		Demersal Piscivore	-0.007	0.216
		Pelagic Piscivore	0.000	0.907
		Planktivore	0.002	0.002

Table 5. Occupancy models for species captured the NEFSC spring bottom trawl survey for random forest models with an occupancy probability > 0.5. Abbr. is species abbreviation code; FG are the species functional groups benthivores (b), demersal piscivores (dp), pelagic piscivores (pp), and planktivores (p); AUC or area under the curve index; only those models with an AUC of at least 0.65 are included.

Species	Abbr.	FG	AUC	Species	Abbr.	FG	AUC
<i>Alosa aestivalis</i>	bluher	p	0.66	<i>Malacoraja senta</i>	smoska	b	0.77
<i>Alosa pseudoharengus</i>	alewif	p	0.79	<i>Melanogrammus aeglefinus</i>	haddoc	b	0.81
<i>Amblyraja radiata</i>	thoska	dp	0.66	<i>Menidia menidia</i>	atlsil	p	0.67
<i>Anchoa mitchilli</i>	bayanc	p	0.72	<i>Merluccius albidus</i>	offhak	dp	0.87
<i>Cancer irroratus</i>	rckcra	b	0.68	<i>Merluccius bilinearis</i>	silhak	dp	0.8
<i>Centropristis striata</i>	blabas	b	0.7	<i>Mustelus canis</i>	smodog	b	0.76
<i>Chlorophthalmus agassizi</i>	shortp	b	0.71	<i>Myoxocephalus octodecemspinosus</i>	lonscu	b	0.9
<i>Citharichthys arctifrons</i>	gulflo	b	0.8	<i>Paralichthys dentatus</i>	sumflo	dp	0.82
<i>Clupea harengus</i>	atlher	p	0.72	<i>Paralichthys oblongus</i>	fouflo	dp	0.84
<i>Dipturus laevis</i>	barska	b	0.71	<i>Peprilus triacanthus</i>	butter	p	0.84
<i>Enchelyopus cimbrius</i>	frbero	b	0.72	<i>Placopecten magellanicus</i>	seasca	b	0.8
<i>Gadus morhua</i>	atlcod	dp	0.76	<i>Prionotus carolinus</i>	norsea	b	0.75
<i>Glyptocephalus cynoglossus</i>	witflo	b	0.84	<i>Pseudopleuronectes americanus</i>	winflo	b	0.85
<i>Helicolenus dactylopterus</i>	blaros	p	0.79	<i>Raja eglanteria</i>	cleska	b	0.75
<i>Hemitripterus americanus</i>	searav	dp	0.75	<i>Scomber scombrus</i>	atlmac	p	0.69
<i>Hippoglossoides platessoides</i>	amepla	b	0.91	<i>Scophthalmus aquosus</i>	window	b	0.77
<i>Homarus americanus</i>	amlobs	b	0.81	<i>Scyliorhinus retifer</i>	chadog	b	0.84
<i>Illex illecebrosus</i>	shtsqd	pp	0.83	<i>Sebastes fasciatus</i>	acared	p	0.88
<i>Leucoraja erinacea</i>	litska	b	0.84	<i>Squalus acanthias</i>	spidog	dp	0.81
<i>Leucoraja garmani</i>	rosska	b	0.65	<i>Stenotomus chrysops</i>	scupzz	p	0.68
<i>Leucoraja ocellata</i>	winska	dp	0.77	<i>Urophycis chesteri</i>	lgfinh	dp	0.65
<i>Limanda ferruginea</i>	yelflo	b	0.82	<i>Urophycis chuss</i>	redhak	dp	0.81
<i>Loligo pealeii</i>	lonsqd	pp	0.87	<i>Urophycis regia</i>	spohak	dp	0.84
<i>Lophius americanus</i>	monkfh	dp	0.74	<i>Urophycis tenuis</i>	whihak	dp	0.86
<i>Macrozoarces americanus</i>	ocpout	b	0.72				

Table 6. Occupancy models for species captured the NEFSC autumn bottom trawl survey for random forest models with an occupancy probability > 0.5. Abbr. is species abbreviation code; FG are the species functional groups benthivores (b), demersal piscivores (dp), pelagic piscivores (pp), and planktivores (p); AUC or area under the curve index; only those models with an AUC of at least 0.65 are included.

Species	Abbr.	FG	AUC	Species	Abbr.	FG	AUC
<i>Alosa aestivalis</i>	bluher	p	0.72	<i>Malacoraja senta</i>	smoska	b	0.74
<i>Alosa pseudoharengus</i>	alewif	p	0.80	<i>Melanogrammus aeglefinus</i>	haddoc	b	0.82
<i>Amblyraja radiata</i>	thoska	dp	0.68	<i>Merluccius albidus</i>	offhak	dp	0.80
<i>Anchoa hepsetus</i>	stranc	p	0.81	<i>Merluccius bilinearis</i>	silhak	dp	0.80
<i>Anchoa mitchilli</i>	bayanc	p	0.80	<i>Micropogonias undulatus</i>	atlcro	b	0.87
<i>Cancer irroratus</i>	rckcra	b	0.68	<i>Mustelus canis</i>	smodog	b	0.82
<i>Centropristis striata</i>	blabas	b	0.74	<i>Myoxocephalus octodecemspinosus</i>	lonscu	b	0.86
<i>Chlorophthalmus agassizi</i>	shortp	b	0.73	<i>Ovalipes ocellatus</i>	ladcra	b	0.67
<i>Citharichthys arctifrons</i>	gulflo	b	0.79	<i>Paralichthys dentatus</i>	sumflo	dp	0.88
<i>Clupea harengus</i>	atther	p	0.90	<i>Paralichthys oblongus</i>	fouflo	dp	0.82
<i>Cynoscion regalis</i>	weakfi	pp	0.88	<i>Peprilus triacanthus</i>	butter	p	0.75
<i>Dipturus laevis</i>	barska	b	0.67	<i>Placopecten magellanicus</i>	seasca	b	0.84
<i>Enchelyopus cimbrius</i>	frbero	b	0.69	<i>Pollachius virens</i>	polloc	dp	0.65
<i>Gadus morhua</i>	atlcod	dp	0.79	<i>Pomatomus saltatrix</i>	bluefi	pp	0.75
<i>Glyptocephalus cynoglossus</i>	witflo	b	0.87	<i>Prionotus carolinus</i>	norsea	b	0.78
<i>Helicolenus dactylopterus</i>	blaros	p	0.77	<i>Prionotus evolans</i>	strsea	dp	0.78
<i>Hemitripterus americanus</i>	searav	dp	0.72	<i>Pseudopleuronectes americanus</i>	winflo	b	0.87
<i>Hippoglossoides platessoides</i>	amepla	b	0.91	<i>Raja eglanteria</i>	cleska	b	0.76
<i>Homarus americanus</i>	amlobs	b	0.77	<i>Scomber scombrus</i>	atlmac	p	0.65
<i>Illex illecebrosus</i>	shtsqd	pp	0.81	<i>Scophthalmus aquosus</i>	window	b	0.84
<i>Leiostomus xanthurus</i>	spotzz	b	0.86	<i>Scyliorhinus retifer</i>	chadog	b	0.82
<i>Lepophidium profundorum</i>	fawmel	b	0.72	<i>Sebastes fasciatus</i>	acared	p	0.93
<i>Leucoraja erinacea</i>	litska	b	0.85	<i>Squalus acanthias</i>	spidog	dp	0.81
<i>Leucoraja garmani</i>	rosska	b	0.77	<i>Stenotomus chrysops</i>	scupzz	p	0.87
<i>Leucoraja ocellata</i>	winska	dp	0.86	<i>Urophycis chesteri</i>	lgfinh	dp	0.70
<i>Limanda ferruginea</i>	yelflo	b	0.81	<i>Urophycis chuss</i>	redhak	dp	0.83
<i>Loligo pealeii</i>	lonsqd	pp	0.85	<i>Urophycis regia</i>	spohak	dp	0.83
<i>Lophius americanus</i>	monkfh	dp	0.75	<i>Urophycis tenuis</i>	whihak	dp	0.88
<i>Macrozoarces americanus</i>	ocpout	b	0.65	<i>Zenopsis conchifera</i>	bucdor	p	0.70

Table 7. The top fifteen variables in spring and autumn random forest occupancy models sorted by the rank based on the proportion of species models the variable was among the top ten variables. Dynamics and static variable designated with (d) and (s), respectively.

Rank	Spring Variable	Proportion	Autumn Variable	Proportion
1	Bottom temperature (d)	0.879	<i>Paracalanus parvus</i> (d)	0.776
2	Depth (s)	0.828	Depth (s)	0.755
3	<i>Metridia lucens</i> (d)	0.776	<i>Centropages typicus</i> (d)	0.510
4	March chlorophyll (s)	0.586	July chlorophyll (s)	0.449
5	<i>Pseudocalanus spp.</i> (d)	0.552	Surface temperature (d)	0.449
6	Appendicularians (d)	0.517	Bottom temperature (d)	0.408
7	Salpa (d)	0.466	June chlorophyll (s)	0.388
8	<i>Calanus finmarchicus</i> (d)	0.414	December SST fronts (s)	0.388
9	Echinodermata (d)	0.414	October chlorophyll (s)	0.367
10	December SST fronts (s)	0.379	March SST fronts (s)	0.367
11	Chaetognatha (d)	0.293	Chaetognatha (d)	0.367
12	June chlorophyll (s)	0.276	March chlorophyll (s)	0.347
13	July chlorophyll (s)	0.276	September chlorophyll (s)	0.347
14	September chlorophyll (s)	0.259	<i>Calanus finmarchicus</i> (d)	0.347
15	<i>Penilia spp.</i> (d)	0.241	April SST fronts (s)	0.286

Table 8. Theil–Sen slope estimates (slope) and Mann-Kendall trends test probabilities (ρ) for time series of the sum of spring and autumn occupancy habitat area (10^6 km^2) associated with an occupancy probability > 0.5 derived from random forest models for functional groups benthivores, demersal piscivores, pelagic piscivores, and planktivores. Only those models meeting the criterion of AUC scores > 0.65 were used in the analysis. Significant tests shown in bold.

Season	Functional group	slope	ρ
Spring	Benthivores	0.062	0.000
	Demersal piscivores	0.029	0.000
	Pelagic piscivores	0.004	0.003
	Planktivores	0.017	0.000
Autumn	Benthivores	0.055	0.000
	Demersal piscivores	0.014	0.000
	Pelagic piscivores	0.005	0.000
	Planktivores	0.014	0.000

Fig. 1. Map of the Northeast Shelf ecosystem with estimation grid (blue dots) showing the extent of the habitat used in developing occupancy models. Dashed line indicates 200 m depth contour. Gulf of Maine and Middle Atlantic Bight sub-regions marled. Insert labeled LME shows the extent of the U.S. Northeast Continental Shelf large marine ecosystem.

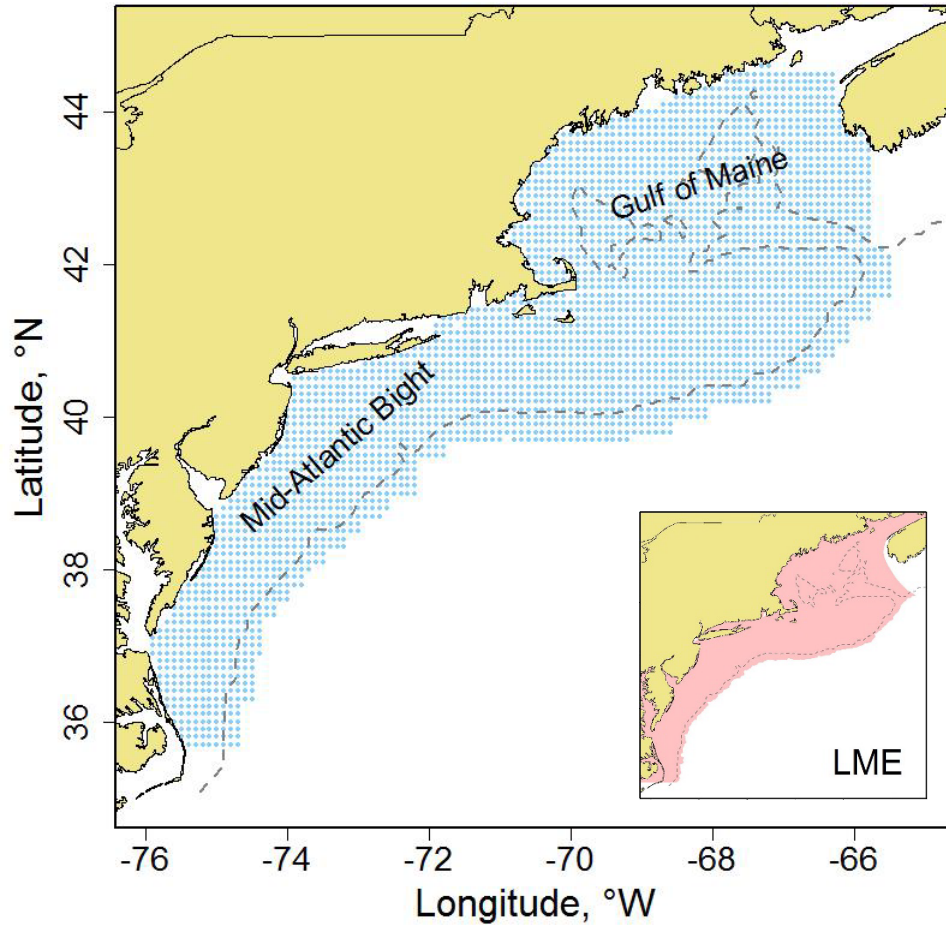


Fig. 2. NES ecosystem mean bottom temperature for spring (a) and autumn (b) from interpolated station data and surface temperature for spring (c) and autumn (d) from station (black circles) and remote sensing (red squares) data. Mean annual sea surface temperature for the ecosystem (e) and the standard deviation of daily temperature (f) from remote sensing data. Solid lines are linear trends.

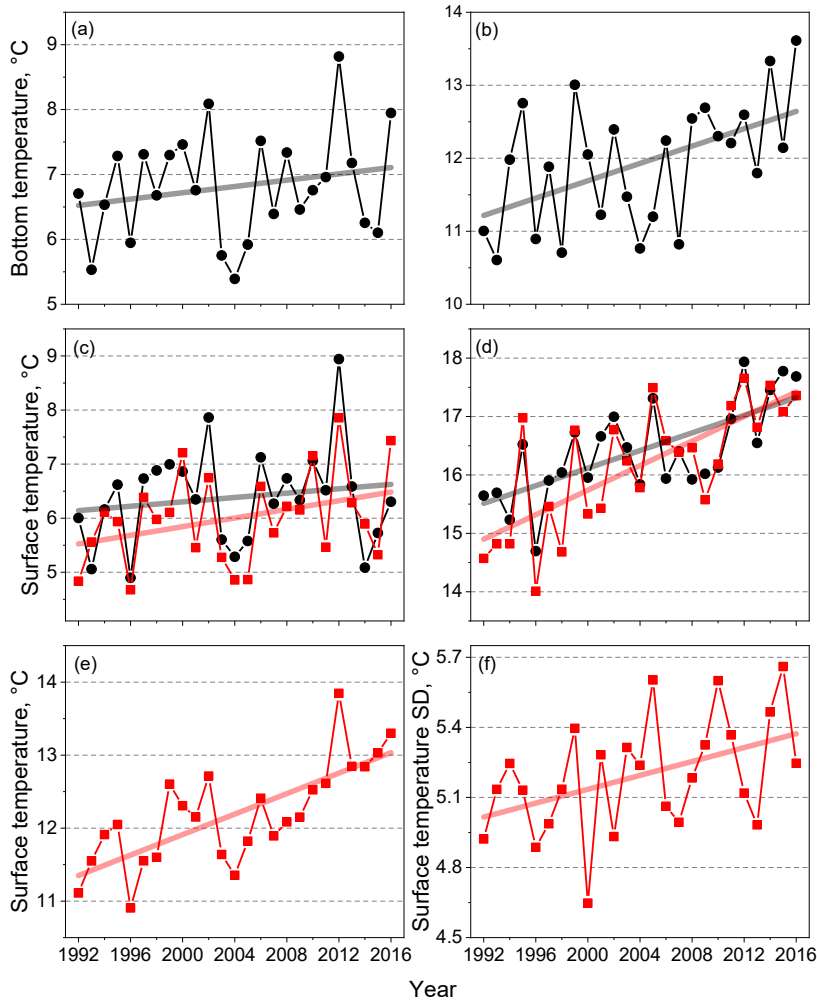


Fig. 3. Catch estimate for the NES by the large marine ecosystem designation. Solid line is a linear trend.

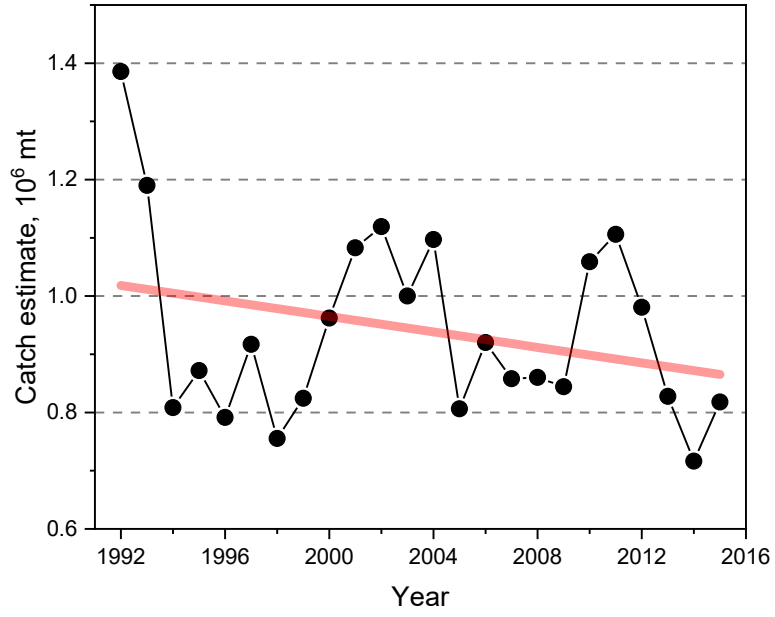


Fig. 4. NES ecosystem spring (a) and autumn (b) Shannon H diversity indices, Simpson index 1-D evenness indices (c and d, seasons respectively), and Number of taxa (Taxa_s) richness indices (e and f, seasons respectively). Red line marks linear trend of mean Z-score.

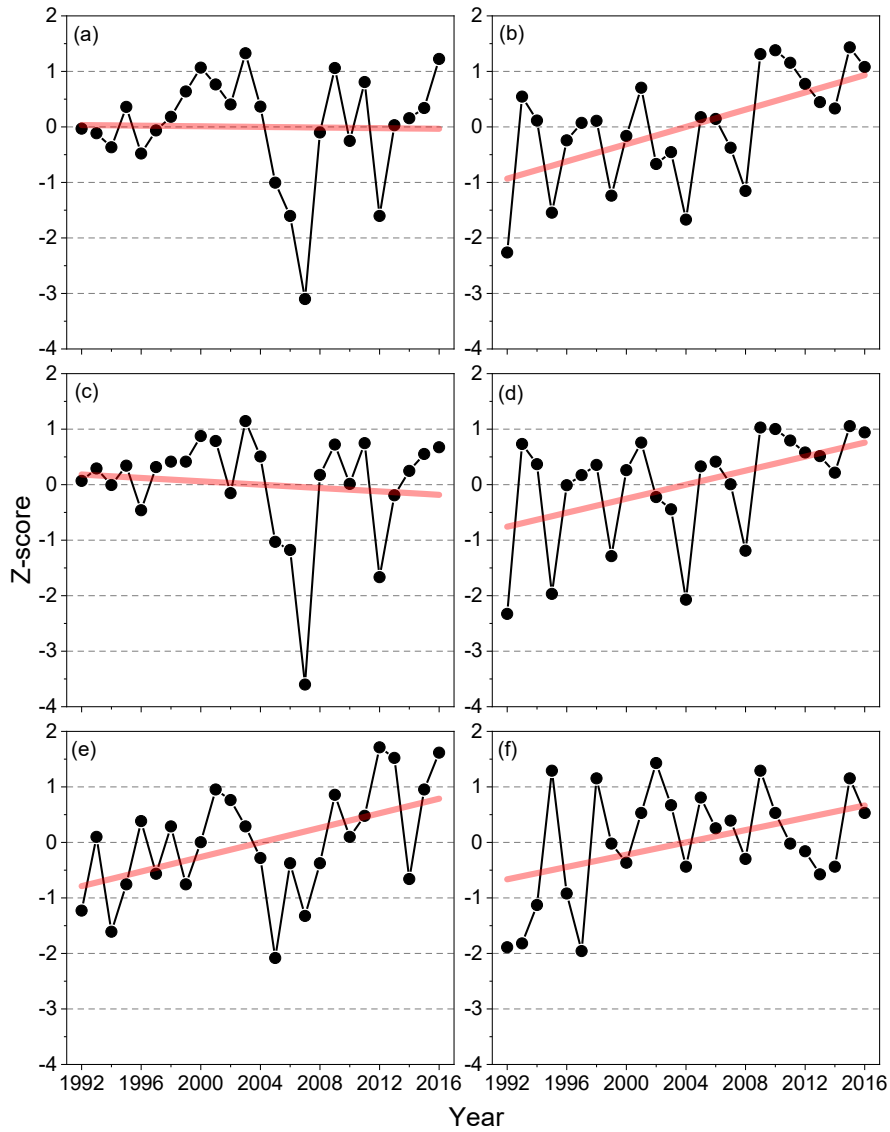


Fig. 5. NES total spring and autumn biomass catch per unit effort (a) and mean weight of individuals by season (b). Solid lines are linear trends.

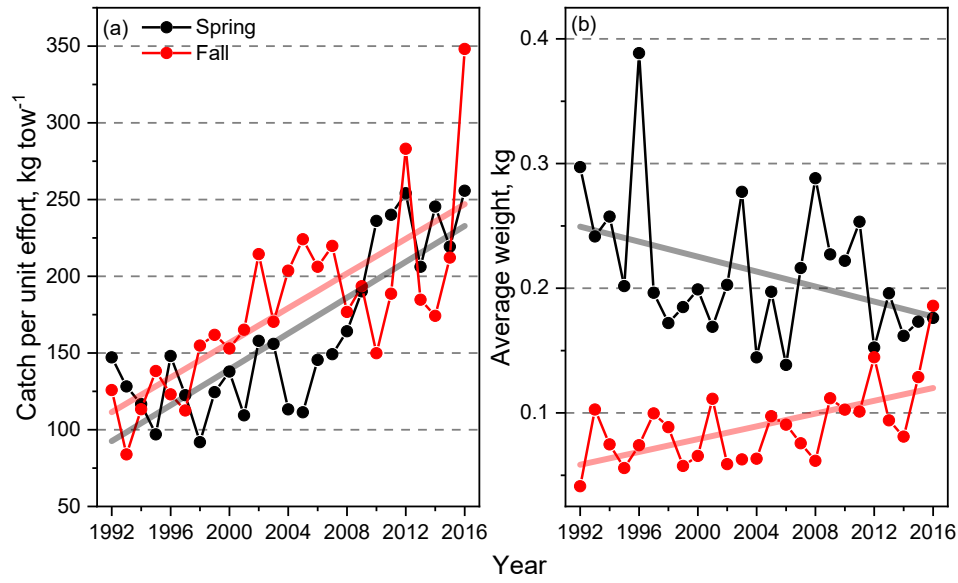


Fig. 6. NES ecosystem spring and autumn catch per unit effort (kg tow^{-1}) by functional group including benthivores (a), demersal piscivores (b), pelagic piscivores (c), and planktivores (d). Solid lines are linear trends.

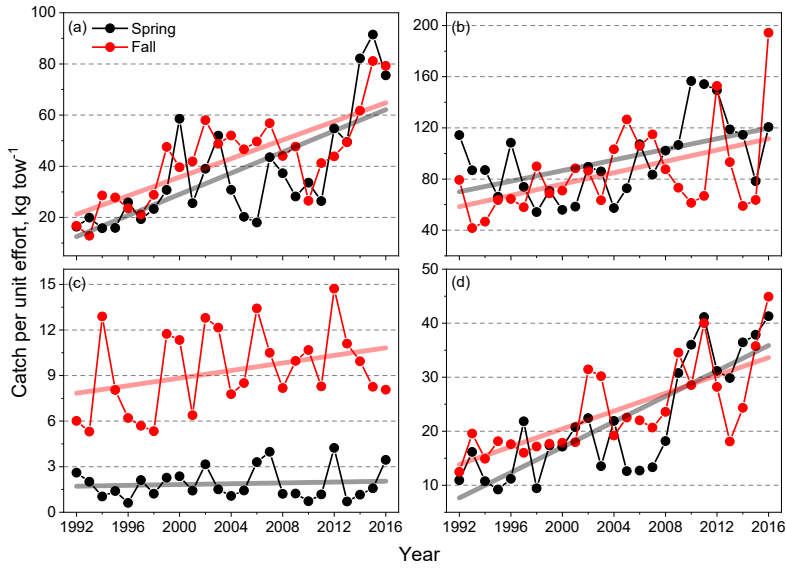


Figure 7. NES ecosystem spring and autumn average weight (kg) by functional group including benthivores (a), demersal piscivores (b), pelagic piscivores (c), and planktivores (d). Solid lines are linear trends.

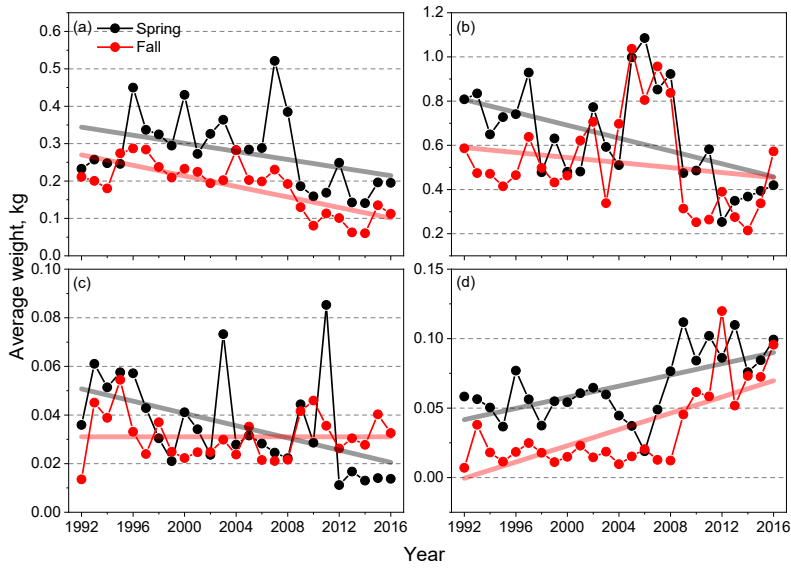


Fig. 8. Theil–Sen slope estimates for trends in spring (a) and autumn (b) occupancy habitat area associated with an occupancy probability > 0.5 derived from random forest models; only those models with an AUC of at least 0.65 are included.

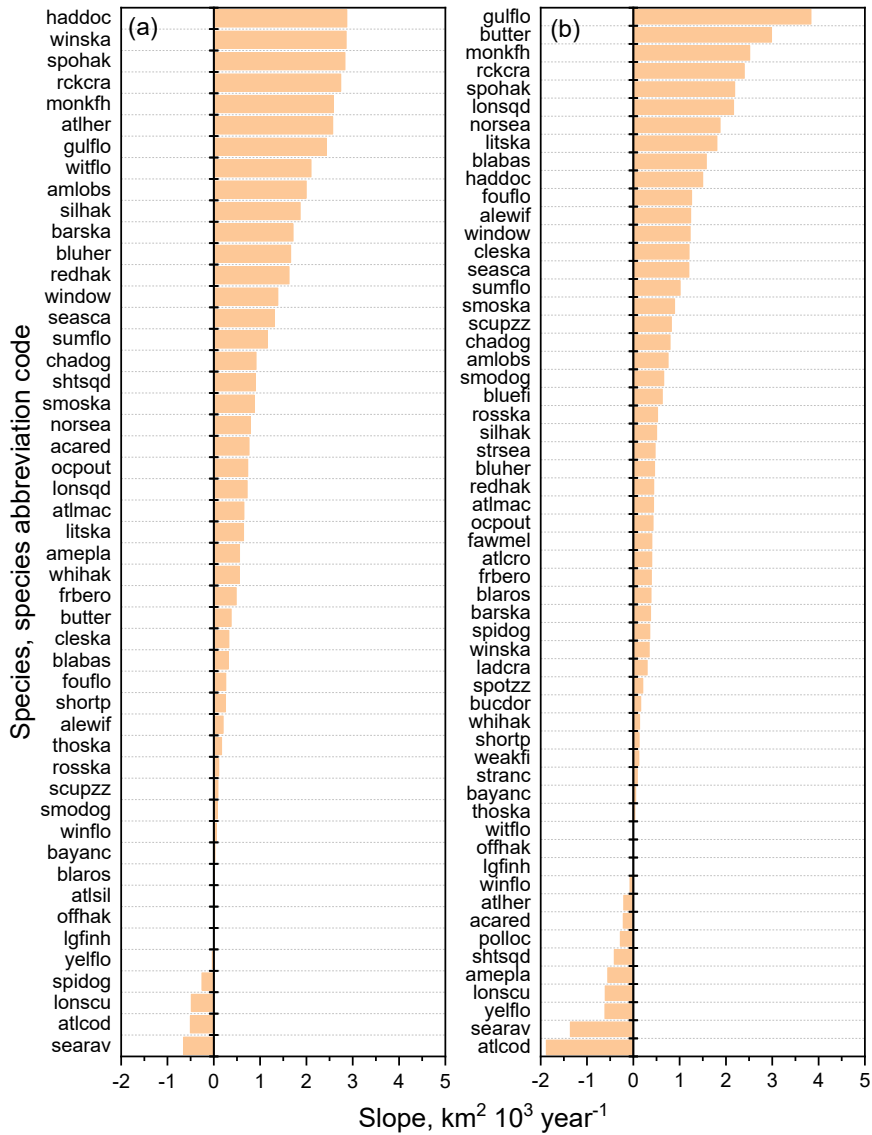


Fig. 9. Sum of spring and autumn occupancy habitat area associated with an occupancy probability > 0.5 derived from random forest models: benthivores (a), demersal piscivores (b), pelagic piscivores (c), and planktivores (d). Only those models with an AUC of at least 0.65 are included. Solid lines are linear trends.

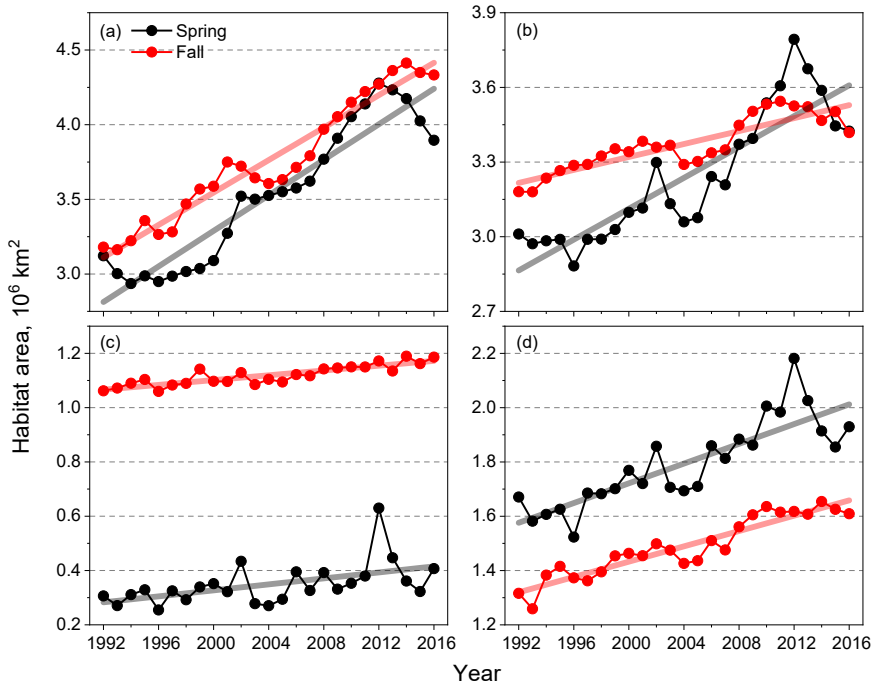


Fig. 10. Mean species interaction area versus the trend in interaction area (a and d, spring and autumn respectively) for species pairs; trend in minimum interaction strength index (b and e, spring and autumn respectively); and, trend in maximum interaction strength index (c and f, spring and autumn respectively). Point color denotes sign of the trend; only those models with an AUC of at least 0.65 are included.

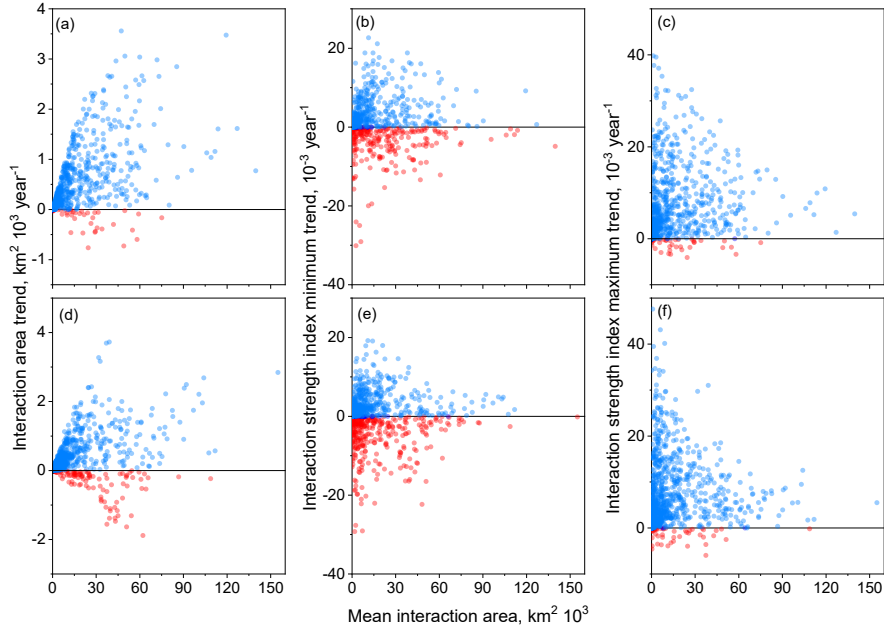


Fig. 11. Mean species interaction area versus the mean interaction area by functional group pairings, spring data plotted on the abscissa and autumn is on the ordinate (a). Mean species interaction area trend versus the mean trend by functional group pairings, spring data plotted on the abscissa and autumn is on the ordinate (b). Symbol labels as follows: Benthivore_Benthivore (B_B), Benthivore_Demersal Piscivore (B_DP), Benthivore_Pelagic Piscivore (B_PP), Benthivore_Planktivore (B_P), Demersal Piscivore_Demersal Piscivore (DP_DP), Demersal Piscivore_Pelagic Piscivore (DP_PP), Demersal Piscivore_Planktivore (DP_P), Pelagic Piscivore_Pelagic Piscivore (PP_PP), Pelagic Piscivore_Planktivore (PP_P), Planktivore_Planktivore (P_P). Only includes models with an AUC > 0.65. Dashed line marks 1:1.

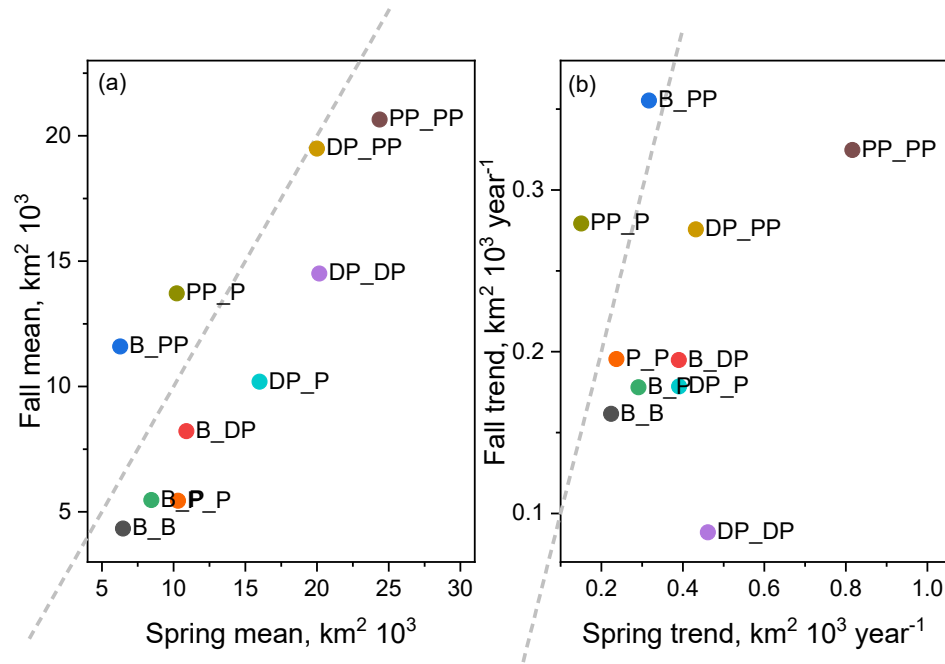


Fig. 12. Mean trend in interaction strength index by functional group pairings, spring versus autumn minimum (a) and maximum (b). Mean interaction strength index by functional group pairings, spring versus autumn minimum (c) and maximum (d). Symbol labels: Benthivore_Benthivore (B_B), Benthivore_Demersal Piscivore (B_DP), Benthivore_Pelagic Piscivore (B_PP), Benthivore_Planktivore (B_P), Demersal Piscivore_Demersal Piscivore (DP_DP), Demersal Piscivore_Pelagic Piscivore (DP_PP), Demersal Piscivore_Planktivore (DP_P), Pelagic Piscivore_Pelagic Piscivore (PP_PP), Pelagic Piscivore_Planktivore (PP_P), Planktivore_Planktivore (P_P). Only includes models with an AUC > 0.65. Dashed line marks 1:1.

