Office of National Marine Sanctuaries
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NATIONAL MARINE SANCTUARIES CONSERVATION SCIENCE SERIES

TIME-SERIES PATTERNS OF SPECIES RICHNESS, DIVERSITY, AND COMMUNITY COMPOSITION OF FISHES AT STELLWAGEN BANK NATIONAL MARINE SANCTUARY (1970-2017)

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Cover Photo:
A diversity of fish species are found at Stellwagen Bank National Marine Sanctuary. Photos: NOAA

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Report Availability

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Abstract

Here we present analyses conducted in support of the most recent Stellwagen Bank National Marine Sanctuary (SBNMS) Condition Report for 2008-2017. Our focus was on patterns and trends in species richness, diversity, and community composition of fishes in SBNMS and surrounding waters over a nearly 50-year period. These analyses of the larger Gulf of Maine, in which SBNMS is nested, are used to compare regional and local scale patterns and trends. The NOAA Northeast Fisheries Science Center bottom trawl survey data, based on a stratified random sampling design, was used to represent the fish fauna of SBNMS (sampling stratum 26) along with 19 additional strata (*i.e.*, 21-40) for the larger Gulf of Maine. Our results demonstrate that fish communities in SBNMS have changed substantially during the past decade. Following a long period of slowly rising species richness through 2006, richness rose rapidly over the last decade. This change coincided with changes in composition and patterns of numerical dominance for both local (i.e., SBNMS) and large-scale (i.e., Gulf of Maine) fish communities as well. Depth was the most significant correlate of fish community structure, but the threshold between shallow and deep communities has moved from 52.5 to 75.5 m over time. Further, composition and distribution of communities were influenced by temperature. For example, Acadian redfish were more common when bottom temperature was <5.7°C while American plaice, longhorn sculpin, yellowtail and witch flounder, and silver and white hake were associated with warmer bottom conditions. Over the past decade, shallow communities south of 42°N were characterized by higher abundances of warm-tolerant species, like Atlantic mackerel and little skate, while the cold-associated species like haddock are much more abundant north of this latitude. Based on related studies, these community scale changes are attributed to changes in fisheries management, changes in species interactions mediated by changes in species and trophic guild abundance, and shifts in the distributions and abundances of fish species due to climate change as a direct or indirect driver. While maintaining and enhancing diversity is a central mission of the sanctuary, the structural changes to its communities is concerning and deserves additional investigation. Identifying the drivers of these changes is important and may provide some insight on what policies might mitigate adverse changes while not sacrificing the benefits of diversity.

Key Words

Trawl survey, catch per unit effort, multivariate, multidimensional scaling, regression tree, condition report

Introduction

Stellwagen Bank National Marine Sanctuary (SBNMS) is set at the eastern edge of Massachusetts Bay between Cape Ann and Cape Cod in the western Gulf of Maine (northwest Atlantic), a sub-region of the Northeast United States Large Marine Ecosystem (Sherman et al. 1996, Cook and Auster 2007). SBNMS bounds an area of 1281 km^2 (638 nm^2) with diverse seafloor topography including Stellwagen Bank, Tillies Bank, the southern portion of Jeffreys Ledge, Stellwagen Basin, and numerous smaller topographic rises and basins (ONMS 2010). The seafloor habitats and overlying waters that produce a complex marine seascape support a diversity of fish species that are broadly representative of the Gulf of Maine region (Auster 2002, Auster et al. 1998, 2006). Designated in 1992 under the National Marine Sanctuaries Act (NMSA 1992, 2000) as the 12th such sanctuary, SBNMS was established as a means for conservation, protection, and enhancement of this productive natural system (ONMS 1993).

National marine sanctuary management plans are reviewed periodically to assess whether management policies adequately meet the goals and serve the stated mission of the sanctuary. This review process is meant to assess whether management plans and their implementation have supported conservation objectives, to identify areas where changes to policies could improve conservation, and to identify where additional research is needed (Battista et al. 2006). These reviews are both mandated by law (NMSA 2000) and are a requisite aspect of adaptive management, which is a key component of effective conservation in marine protected areas (Edgar et al. 2014, McCook et al. 2010).

The management plan review process relies on evaluating the state and dynamics of sanctuary resources in the context of both the past and the wider region. Here we present analyses conducted as part of the most recent sanctuary condition report (ONMS in press). Our focus was on patterns and trends in species richness, diversity, and community composition of fishes in SBNMS and surrounding waters over a nearly 50-year period. These analyses of the larger Gulf of Maine, in which SBNMS is nested, are used to compare regional and local scale patterns and trends. In the decade since the last such report was published (see NMSP 2007) there have been substantial changes in and around the sanctuary and in the greater region (e.g., patterns of fishing, vessel traffic, and associated noise; ONMS in press), and particularly as the rate of ocean warming has climbed steeply (Saba et al. 2016). Both natural and anthropogenic drivers influence fish population structure and distribution, spatial patterns of fish diversity, and components of community structure (e.g., Auster et al. 2006, Auster and Link 2009, Hare et al. 2012). The current condition review process facilitated the opportunity to investigate the current state of SBNMS's living resources given these changes.

Methods

We used multiple approaches to compare the present and past status of demersal fish assemblages within SBNMS and throughout the Gulf of Maine. Since one of the central missions of the sanctuary is to “conserve, protect and enhance the biological diversity [and] ecological integrity” of SBNMS (ONMS 2010), we attempted to thoroughly characterize diversity and community composition. To these ends, we used community scale metrics to provide easily interpretable, univariate measures of diversity, followed by multivariate analyses of community composition (i.e., the species that were identified during sampling and their abundances; species listed in table 1) to investigate observed diversity. When combined, these approaches can provide an overall picture of demersal fish biodiversity, how diversity has changed through time, what drivers may have contributed to these changes, and what individual species may typify observed changes. Fishery independent sampling datasets provide an excellent source of abundance data for use in characterizing fish diversity at the larger geographic scales in this study (Auster 2002). Northeast Fisheries Science Center (NEFSC) bottom trawl survey data collected between 1970 and 2017 were used in these analyses, with each individual tow being treated as a community sample (Politis et al. 2014).

Northeast Fisheries Science Center bottom trawl survey data

The NEFSC bottom trawl survey maintains the stratified random sampling design established in 1963 to sample the U.S. continental shelf from North Carolina through Maine. Randomly selected trawl stations within depth- and latitude-based strata are sampled during the spring and fall of each year (Grosslein 1969). We used data collected in stratum 26 to represent SBNMS and data collected in strata 21-40 for the larger Gulf of Maine (figure 1a). Despite the limited number of tows conducted within each stratum during any given survey season and year, the geographic scope of the stratum is represented over a period of multiple and consecutive years (figure 1b). Similar geographic and temporal delineations were used in fish diversity analyses that contributed to the 2007 sanctuary condition report (Auster et al. 2006, NMSP 2007).

The bottom trawl survey samples a wide range of demersal and benthic species, including both vertebrate and invertebrate fauna. We were interested in vertebrate diversity, therefore we limited our analyses to finfish, skates, rays, and sharks. Although survey scientists collect a large amount of information during sample processing, including sex and stage for some species, we limited our analysis to catch enumerated as number of individuals by species. Individual abundance indices were produced for each finfish species and tow. However, it is important to note that these indices are not measures of raw abundance or density due to variations in catchability by the sampling gear (Politis et al. 2014). Abundance indices were log-transformed, ln(x+1), to reduce the influence of rare outliers (i.e., large abundances) on results for multivariate procedures (McConnaughey and Conquest 1993). Patterns of abundance for individual species, based on catch-per-unit effort (CPUE; catch-per-tow), are reported as untransformed abundances. Additional data recorded for each tow include time, location, depth, duration, and temperature. We excluded from our analyses tows that were less than 15 minutes in duration; short tows sample less bottom area than standard duration tows, which would inevitably influence species abundance indices. For all analyses seasonal variation was addressed by parsing the data set into spring (February – June) and fall (July – December) periods and decadal variation by parsing tows as 1970s (i.e., 1970-1979), 1980s, 1990s, 2000s, and 2010s. Overall sample size for Stellwagen Bank National Marine Sanctuary and adjacent waters (stratum 26) was 488 tows, while region wide samples across the Gulf of Maine consisted of 7624 tows. Over the course of the time series several vessels and trawl designs were used to collect data. We used raw count data from across time as catch by species was positively and significantly correlated for most taxa (e.g., Miller et al. 2010).

Diversity metrics

We used five commonly employed metrics (species richness, Shannon, Simpson, Chao 1, and Uniques) to characterize diversity in SBNMS (stratum 26) over the 50-year period. Species richness (S), and both Shannon (H’ log *e*) and Simpson (1-lambda’) diversity indices were computed for each tow using PRIMER software (v.7.0.13; Clarke and Gorely 2015). Species richness is simply a tally of the distinct species (or taxa) identified within a sample. The Shannon and Simpson indices use the relative proportion of individuals belonging to a species within a sample to characterize diversity. Despite their similarity, these indices differ in their relative sensitivity to species rarity, as Shannon index values increase with species richness regardless of evenness (i.e., relative proportion of species within a sample) and Simpson index values increase with increasing evenness. We used linear regression models to identify trends in diversity indices through time using the R statistical program (v.3.4.2; R Core Team 2017). During this process, we used the approach developed by Muggeo (2008) to identify “breakpoints,” locations of changes in regression slopes. Breakpoints were confirmed by comparing regression coefficients before and after an identified break via tests to detect non-zero changes in slope (Davies 1987). We interpreted breakpoints in these models as changes in diversity trends and associated 95% confidence intervals of breakpoints as measures of how quickly trends changed.

For each decade in the time series, species richness “S (est)” as an estimate of the expected number of species in *t* pooled samples, was calculated based on the Chao 1 richness estimator with 100 random restarts using Estimate S software (v.9.1.0; Colwell 2013). The Chao 1 estimator relies on the relative rate of rare species in sampling to estimate total diversity asymptotically. The number of unique species “Uniques mean (Q1)” as the number of unique species that occur in only one sample over *t* pooled samples was also calculated using Estimate S, along with 95% confidence intervals and standard deviations for both values. Minitab (v.14; Minitab, Inc. 2000) was used to produce boxplots for visualizing annual trends within seasonal samples as well as patterns in seasonal abundance, based on CPUE, of select species. The R statistical program (R Core Team 2017) was used to plot rarefication curves, with associated confidence intervals (S and Chao 1) or standard deviation (Q1). Curves were compared visually.

The breadth of these approaches belies the difficulty of defining diversity in a meaningful way, even in the specific case of demersal fish diversity within a geographically limited sanctuary. However, a more complete representation of diversity is possible by combining these different indices and estimates, which accounts for the influence of both rare and dominant species (Magurran 2004, Morris et al. 2014). By using multiple measures to characterize diversity of this time series dataset, we provide a more comprehensive accounting of how fish assemblages within SBNMS have changed over time relative to those of the region as a whole.

Community composition

We investigated the composition of communities sampled in SBNMS using multivariate analyses and data visualization approaches. Multivariate comparisons of species composition by season and decade at SBNMS (stratum 26) were calculated using PRIMER software (Clarke and Gorely 2015). Non-metric multidimensional scaling (nMDS) was used to visualize the similarity in species composition in 2D and 3D plots, with calculated stress level indicating the most parsimonious approach for interpreting relationships. A Bray-Curtis similarity matrix was calculated to implement the multivariate comparisons. Analysis of Similarities (ANOSIM) routines were calculated to contrast the significance of differences in community composition over time and Similarity-Percentage (SIMPER) routines were used to identify the dominant species driving differences.

The influences of potential drivers on observed changes in demersal fish assemblages both within SBNMS and throughout the larger Gulf of Maine were investigated via a multivariate extension of decision tree analysis (multivariate regression trees, MRT; De’ath 2002). MRT models are created by recursively splitting the response variables, in this case species, into two groups based on the associated values of predictor variables, which were geographic location (decimal degrees latitude) and depth (m) at the start of a tow, bottom temperature (°C), as well as the date, time, and season when sampling occurred. Which predictor variable is the basis of the split and the value at which partitioning takes place must maximize the homogeneity of the resulting groups (Breiman et al. 1984). The final models are readily interpretable in an ecological context based on the limited number of predictor variable thresholds (“partitions” or “splits”) that define groups of responses (“terminal nodes” or “leaves”; De’ath and Fabricius 2000, Breiman 2001). Since temperature, depth, or latitude was missing from some trawl records, we employed Breiman et al.’s (1984) majority direction approach for assigning those records featuring missing data to nodes, which allowed us to retain all trawl records throughout the analysis. Following model construction, we focused on species that drove each partition; species were considered “drivers” if they contributed ≥5 percent of the total variance explained by the partition. These analyses were conducted using the R statistical program (R Core Team 2017).

Results

Diversity of demersal fishes within SBNMS has varied substantially year to year (figure 2). Our direct measures of diversity, based on annual mean values of species richness (14.17 ±0.19se), Shannon index (1.58 ±0.02se), and Simpson index (0.68 ±0.01se) all fluctuated substantially, as evidenced by their relatively high coefficient of variation values of 35.6, 33.1, and 29.1 percent, respectively. Despite this observed variance, species richness per tow during both spring and fall periods increased significantly throughout the time series (figure 3a). Richness slowly increased over the earlier part of the time series (1970 to ca. 2006; $\beta_1 = 0.11$, $F = 150.8$, $p = 2.2 \cdot 10^{-16}$), but increased rapidly over the past decade ($\beta_1 = 0.75$, $F = 53.1$, $p = 8.7 \cdot 10^{-13}$). However, neither of the diversity metrics incorporating relative abundance, Shannon and Simpson indices, followed clear trends of increasing or decreasing diversity (figure 3b). Unsurprisingly, neither linear models of Shannon ($F = 0.40$, $p = 0.75$) or Simpson ($F = 0.26$, $p = 0.85$) detected clear trends and no breakpoints were identified in the time series. This recent rise in species richness was also apparent in decadal rarefaction curves (figure 4); noteworthy is that the 95% confidence interval (CI) around the 2010s curve for estimated species was outside the range of CIs for earlier decades. Although the Chao 1 richness estimate for the current decade was highest, estimates were similar across the decades. That the number of uniques (Q1) is lowest in the 2010s decade suggests that abundance of species that nonetheless are rare may have increased in number and distribution over time and appeared in multiple tows.

Analyses of community composition in the SBNMS region (stratum 26) from both spring and fall surveys across decades indicate significant shifts over time. Composition during the spring survey period was significantly different when comparing the 1980s and 1990s with the current decade (2010s; figure 5; table 2). SIMPER analysis indicated increased abundance of multiple species with haddock, silver hake, and Acadian redfish contributing most to observed changes in spring fish communities (tables 3 and 4). For fall surveys, the community composition from the 1970s, 1990s, and 2000s were all significantly different from the 2010s; figure 6; table 5) with haddock and silver hake becoming increasingly common (tables 6-8).

The final MRT model of Stellwagen Bank consisted of seven partitions and eight terminal nodes, explaining 26.7 percent of the variance in species abundances observed in trawls conducted within stratum 26 (figure7). The 2010s decade marked a shift in the composition of fish communities sampled in the trawl survey, driven by growing numbers of several species, most notably haddock, silver hake, and spiny dogfish (figure 8). Prior to 2010, assemblages within SBNMS were largely correlated with depth and season. Shallow communities (<52.5 m, figure 9) were characterized by large abundances of sand lance, largely absent at depth, and a shift in species starting in September (figure 10), as longhorn sculpin and American plaice decreased and silver and red hake as well as yellowtail and winter flounder increased. Deeper areas exhibited (figure 11) increases in Atlantic herring, spiny dogfish, and silver and red hake during the early summer period. In recent years, depth is still an important factor influencing fish communities, but season appears less important than temperature and geography. Depth remains the most significant correlate of fish community structure, but the apparent threshold between shallow and deep has moved to 75.5 m (*i.e.*, from 52.5 m prior to 2010 as above), below which spiny dogfish and silver hake are more numerous (figure 12). These deeper communities are further influenced by temperature, as Acadian redfish are more common when bottom temperature is <5.7° C (figure 13); American plaice, longhorn sculpin, yellowtail and witch flounder, and silver and white hake are associated with warmer bottom conditions. Over the past decade, shallow communities south of 42° N are characterized by higher abundances of warm-tolerant species, like Atlantic mackerel and little skate, while the cold-associated species haddock is much more abundant north of this latitude (figure 14).

When extended to the entire Gulf of Maine, the final MRT model consisted of five partitions and six terminal nodes, explaining 19.3% of the variance in species abundance and remarkably similar to the model for SBNMS that is smaller in spatial extent (figure 15). As within SBNMS, the year 2010 marked a significant change in the Gulf of Maine, as abundances of several species, including silver hake, haddock, and red hake, increased in the most recent years (figure 16). Across the region, fish assemblages have been consistently correlated with depth (figures 17 and 18). Silver hake, haddock, and Acadian redfish remained more abundant in deeper waters, as they had been prior to 2010. Although species were also influenced by season and geography prior to 2010 (figures 19 and 20), variations in species abundances were not correlated with these factors after 2010 (figure 15).

Temporal dynamics in the abundance of select species illustrates the patterns of decline and recovery of ecologically and economically important taxa. Atlantic cod, while at low numbers overall, appears to be marginally increasing in abundance during the spring period (figure 21, top). Atlantic wolffish and cusk, both Species of Concern under the Endangered Species Act (ESA) for the northeast region, remain at low abundance based on the trawl survey (figure 21, middle, bottom), especially during the fall, while the abundance of longhorn sculpin has increased over the time series (figure 22, top). Alligatorfish (figure 22, middle), thorny skate (figure 23, top), and barndoor skate (figure 23, bottom) have experienced a more recent, and moderate, rise in abundance. For alligatorfish and barndoor skate, this follows a prolonged period of low abundance. Atlantic herring generally trended upward over the time series but year to year variation in the sanctuary is high (figure 22, bottom).

In addition to these temporal trends in abundance, the vertical distributions of some species have changed appreciably. Of the 38 fish species collected within the sanctuary in at least 5% of tows over the past two decades, nearly half (45%) have experienced a change in mean depth of capture greater than 5 m since 2010 (table 9). Among the species that shifted deeper were butterfish, winter flounder, ocean pout, and yellowtail flounder; these species also experienced substantial increases in abundance over the same period. Similar patterns were also observed for those species, except yellowtail founder, across the Gulf of Maine.

Discussion

Fish communities in Stellwagen Bank National Marine Sanctuary have changed substantially during the past decade. Following a long period of fluctuating diversity and slowly rising species richness, the number of taxa observed in the sanctuary began to increase rapidly. This coincided with changes in composition and patterns of numerical dominance at both local (SBNMS) and large spatial scales (Gulf of Maine) . Underlying these community scale shifts are changes in fisheries management, variations in species interactions mediated by transitions in species and trophic guild abundance, and shifts in the distributions and abundances of fish species due to climate change as a direct or indirect driver (Auster and Link 2009, NEFSC 2012, Link and Auster 2013, Hare et al. 2016).

The potential drivers of shifts in species richness become clearer when viewed in the context of recent changes in ocean conditions. The early 1980s began a 20-year period of steadily rising sea surface temperatures during which waters across the entire northeast U.S. continental shelf warmed at a rate three times the global average (Pershing et al. 2015). Within the sanctuary, Massachusetts state water temperature records document increases in both surface and bottom water temperature (ONMS in press). Diversity, as measured by the number of fish species observed in survey trawls, slowly increased. Rising variance in local taxa is a characteristic response of communities to shifting conditions in cold climates, driven directly by temperature variation or indirectly by changing species interactions (Currie 2001, Hawkins et al. 2003). Interestingly, the rise in species richness accelerated in the mid-2000s, around the time when ocean warming in the Gulf of Maine sped up by nearly an order of magnitude (Mills et al. 2013).

Several distinct mechanisms might underlie the observed increase in species richness. Increasing fish species richness in response to warming in the North Sea was ascribed to poleward shifts in the distribution of fish assemblages (Hiddink et al. 2008). Essentially, diverse fish assemblages shifted north into the region, replacing fish assemblages moving north out of the region that were relatively taxa-poor. Shifts in fish distributions have been observed in the western North Atlantic but these have not always been in the expected northerly direction (Nye et al. 2009). In a terrestrial example of responses to increased temperature, butterflies in the United Kingdom exhibited a climate-associated rise in species richness largely driven by the arrival of generalist species that were tolerant of wider temperature ranges and less selective of specific habitat features, rather than the wholesale shift of entire communities (Menéndez et al. 2006). Recently, the National Marine Fisheries Service conducted a vulnerability assessment of species along the northeast U.S. continental shelf, predicting their sensitivity to changing ocean conditions (Hare et al. 2016). Most of the fish species we identified in this study as driving shifts in community composition through their increased abundance were identified by Hare et al. as either likely to benefit as a result of changing ocean climate, like butterfish, or less sensitive to changing conditions, such as spiny dogfish, silver and red hake, American plaice, yellowtail and winter flounder, haddock, and Atlantic herring. These assessments were based, in part, on habitat selectivity and temperature tolerance. Noteworthy is that cold-adapted taxa like cusk are predicted to contract their range in the Gulf of Maine due to the interaction of both thermal tolerance limits and restricted habitat specific distributions (Hare et al. 2012).

Changes due to warming conditions are taxa specific, complicating any interpretation of community-scale diversity measures. These relationships also can be impacted by the non-uniformity of climate change, local and regional geography (e.g., habitat and landscape variability) and bathymetry, and species biogeography. Species distributions follow local changes in temperature, and for many species bottom sea water temperature is a larger influence than corresponding sea surface temperature (e.g., silver hake; Nye et al. 2011). Although local changes in climate tend to track larger regional and global trends, this is not always the case, and the rate of change differs substantially within larger regions (Burrows et al. 2011). Climate velocity, the rate and direction of these changes, has provided consistent correlations with marine species distributions (Pinsky et al. 2013). These responses rely not only on climate, but also geography. Pinsky et al. identified fish assemblages within the Gulf of Alaska and Gulf of Mexico as examples of fish assemblages reacting to local changes in climate by shifting west or deeper, respectively. Likewise, Nye et al. (2009) notes the role of geography within the Gulf of Maine, which limits poleward advancement in distribution, and the varied responses of species, including deeper "centers of mass" as well as range contractions apparent in sampling over time. Regional sea surface temperatures have been rising at a rapid rate over the past decade, which has driven large shifts in the availability of thermal habitats within the Gulf of Maine (Friedland et al. 2013, Mills et al. 2013). As warm surface water has expanded deeper, many species within the Gulf of Maine have moved to greater depths (Nye et al. 2009). These shifts in vertical distribution are detectable within the relatively shallow SBNMS, as the mean depth at capture since 2010 was at least 5 m deeper than the previous 10 years for more than 10 percent of fish taxa collected within the sanctuary. However, for some species deeper habitats may not contain the attributes of habitat necessary for survival and growth. For example, sand lance relies on sandy or fine gravel well-oxygenated sediments which comprise most of sediments on the peak of Stellwagen Bank, while deeper areas tend to be composed of finer cohesive sediments (Meyer et al. 1979, Poppe et al. 2003). The relatively minimal number of sand lance collected in the trawl survey since 2010 may reflect, in part, the results of this squeeze between warming waters and preferred habitat.

By no means is climate considered the sole driver of change, as other factors have inevitably influenced diversity and patterns of community composition. Fishing, especially those forms that physically contact the seafloor, can have significant effects on habitat and contribute to variation in patterns of habitat use by fishes (Auster 2015, Auster and Langton 1999, Auster and Lindholm 2005, Auster et al. 1996, Tamsett et al. 2010). Repeated fishing effort over time in the same area can lead to reduced species richness, but the greatest decreases are found where fishing expands to previously unexploited areas (Hiddink et al. 2006).

Atlantic cod, an iconic marine species for the Gulf of Maine-Georges Bank region including SBNMS, was once a dominant piscivore in this large marine ecosystem. Now the Gulf of Maine cod population is at historical lows for both spawning stock biomass and recruitment within the current 2010s decade (to 2016), continuing a decline from the low population status in the 2000s decade (NEFSC 2017). The distribution of cod also has shifted. While once distributed throughout the Gulf of Maine region, occurrences now are primarily in the western Gulf of Maine region, with declining population status resulting in spatially limited hyper-aggregations that possibly influences the diversity and abundance of co-occurring species through predation and competition (Auster and Link 2009, Link and Auster 2013, Richardson et al. 2014). Notable is that within SBNMS, mean cod abundance per survey tow across decadal time periods has increased during spring periods from the 1970s-2000s, reflecting the general trend in concentration of cod in the western Gulf of Maine, while abundance declined between the 2000s and 2010s (this study).

Changes in the abundance of other species can reflect changing mortality rates or shifts in spatial distributions with larger consequences for fish communities within the sanctuary. Alligatorfish, once common in visual surveys of gravel habitats, had since the mid-1990s declined in abundance (Auster, unpublished data), suggesting some degree of local endangerment in the sanctuary. Rises in catch rates of this small poacher suggest a moderate recovery of the local population may be underway. Similarly, thorny skate and barndoor skate appear to be recovering within SBNMS (Figure 23), after extremely low abundances and consideration for listing under the ESA. Increasing numbers of longhorn sculpin, an important ambush predator, could have significant effects on the recruitment of other fish, especially within the gravel habitats where this species occurred most frequently (Auster et al. 2013). Rising abundances of Atlantic herring, an important prey species for a number of medium to large predators, could improve forage conditions for a range of other species within the sanctuary. Isolated instances of large catches against the background of increasing abundance are indicative of patchy spatial distributions and the potential for variation in the functional role of this species as prey. In contrast, while abundances of Atlantic wolffish and cusk have been consistently low, supporting their designation as Species of Concern under the ESA, the return of high density patches of these species to the sanctuary (suggested by similarly rare instances of large catches) could be viewed as an early indication of recovery. However, persistently low abundances of these species during the fall are just as likely to reflect seasonal movements to deeper waters in response to warm bottom temperatures in the summer or mortality due to greater fishing effort over the mid-months of the year. Both of these would be more persistent issues that would greatly impede population recovery. Overall, local changes in ocean climate have coincided with substantial shifts in fish community dynamics that are still ongoing. It is likely that in another decade, species assemblages may look as different from the present as today does from a decade ago.

Despite the substantial bottom trawling effort that has been focused on the sanctuary throughout the past half century, species richness of fishes has grown steadily. Exploited for centuries, with instances of local depletions dating to the early 19th century (Goode

1887), Gulf of Maine fish assemblages, and marine faunal communities in general, have not been in an undisturbed state within the survey's history (Jackson et al. 2001, Steneck et al. 2013). While trends in species richness cannot be ascribed to exploitation generally, specific changes in fishing activities have likely had some effect on composition. Reductions in fishing effort since the 1990s have likely led to the recent surge in abundance of haddock (NEFSC 2017), which was one of the species that drove the compositional shifts in fish assemblages around 2010 detected within our analyses. The type and direction of species interactions that resulted in this response remains to be determined.

While maintaining and enhancing diversity is a central mission of the sanctuary, the structural changes to its communities is concerning and deserves additional investigation. Understanding the effects of local versus regional drivers on species diversity and community composition can provide critical insight on what policies might mitigate adverse changes while not sacrificing the benefits of diversity (Auster 2002). Well-designed studies in an adaptive management context can provide such insight while involving the stakeholder community in the urgent work to link conservation and sustainable use in a world of rapidly changing climate.

Tables

Table 1. Fish species collected in all Gulf of Maine strata during the trawl survey from 1970-2017. Those that also occurred in SBNMS (stratum 26) are denoted by an asterisk.

common name	**scientific name**	**stratum 26**
slickhead species	*Alepocephalid spp.*	
blueback herring	*Alosa aestivalis*	*
hickory shad	*Alosa mediocris*	
Alewife	*Alosa pseudoharengus*	*
American shad	*Alosa sapidissima*	*
American sand lance	*Ammodytes americanus*	*
northern sand lance	*Ammodytes dubius*	*
Atlantic wolfish	*Anarhichas lupus*	*
striped anchovy	*Anchoa hepsetus*	
bay anchovy	*Anchoa mitchilli*	
American eel	*Anguilla rostrata*	
deepbody boarfish	*Antigonia capros*	
Atlantic argentine	*Argentina silus*	*
striated argentine	*Argentina striata*	*
silver hatchetfish	*Argyropelecus aculeatus*	
silver rag	*Ariomma bondi*	*
hookear sculpin uncl	*Artediellus spp.*	*
Alligatorfish	*Aspidophoroides monopterygius*	*
gray triggerfish	*Balistes capriscus*	
Frostfish	*Benthodesmus simonyi*	
Atlantic menhaden	*Brevoortia tyrannus*	*
Cusk	*Brosme brosme*	*
boarfish uncl	*Caproidae spp.*	
blue runner	*Caranx crysos*	

Table 1 (cont'd). Fish species collected in all Gulf of Maine strata during the trawl survey from 1970-2017. Those that also occurred in SBNMS (stratum 26) are denoted by an asterisk.

common name	scientific name	stratum 26
black sea bass	*Centropristis striata*	*
viperfish	*Chauliodus sloani*	
greeneye uncl	*Chlorophthalmid spp.*	
shortnose greeneye	*Chlorophthalmus agassizi*	
Gulf Stream flounder	*Citharichthys arctifrons*	*
Atlantic herring	*Clupea harengus*	*
herring uncl	*Clupeidae spp.*	
conger eel	*Conger oceanicus*	
conger eel uncl	*Congridae spp.*	
sculpin uncl	*Cottidae uncl*	
wrymouth	*Cryptacanthodes maculatus*	*
lumpfish snailfish uncl	*Cyclopteridae spp.*	
lumpfish	*Cyclopterus lumpus*	*
red dory	*Cyttopsis roseus*	
round scad	*Decapterus punctatus*	
fourbeard rockling	*Enchelyopus cimbrius*	*
silver anchovy	*Engraulis eurystole*	
epigonus pandionis	*Epigonus pandionis*	
smallmouth flounder	*Etropus microstomus*	
round herring	*Etrumeus teres*	
Atlantic spiny lumpsucker	*Eumicrotremus spp.inosus*	
Atlantic cod	*Gadus morhua*	*
threespine stickleback	*Gasterosteus aculeatus*	*
snake mackerel uncl	*Gempylidae spp.*	
witch flounder	*Glyptocephalus cynoglossus*	*
lightfish uncl	*Gonostomatidae spp.*	
blackbelly rosefish	*Helicolenus dactylopterus*	*
sea raven	*Hemitripterus americanus*	*
American plaice	*Hippoglossoides platessoides*	*

Table 1 (cont'd). Fish species collected in all Gulf of Maine strata during the trawl survey from 1970-2017. Those that also occurred in SBNMS (stratum 26) are denoted by an asterisk.

common name	scientific name	stratum 26
Atlantic halibut	*Hippoglossus hippoglossus*	*
halfbeak	*Hyporhamphus unifasciatus*	
honeycomb cowfish	*Lactophrys polygonia*	
smooth puffer	*Lagocephalus laevigatus*	
porbeagle	*Lamna nasus*	
fawn cusk-eel	*Lepophidium cervinum*	*
yellowtail flounder	*Limanda ferruginea*	*
seasnail	*Liparis atlanticus*	*
striped seasnail	*Liparis liparis*	
goosefish	*Lophius americanus*	*
snakeblenny	*Lumpenus lumpretaeformis*	*
daubed shanny	*Lumpenus maculatus*	*
wolf eelpout	*Lycenchelys verrillii*	*
grenadier uncl	*Macrouridae uncl*	
ocean pout	*Macrozoarces americanus*	*
capelin	*Mallotus villosus*	
pearlsides	*Maurolicus muelleri*	*
pearlsides	*Maurolicus pennanti*	
haddock	*Melanogrammus aeglefinus*	*
Atlantic soft pout	*Melanostigma atlanticum*	*
Atlantic silverside	*Menidia menidia*	*
offshore hake	*Merluccius albidus*	*
silver hake	*Merluccius bilinearis*	*
planehead filefish	*Monacanthus hispidus*	
deepwater flounder	*Monolene sessilicauda*	
mora uncl	*Moridae spp.*	
striped bass	*Morone saxatilis*	*
smooth dogfish	*Mustelus canis*	
lanternfish uncl	*Myctophid spp.*	*

Table 1 (cont'd). Fish species collected in all Gulf of Maine strata during the trawl survey from 1970-2017. Those that also occurred in SBNMS (stratum 26) are denoted by an asterisk.

common name	scientific name	stratum 26
grubby	*Myoxocephalus aenaeus*	*
longhorn sculpin	*Myoxocephalus octodecemspinosus*	*
shorthorn sculpin	*Myoxocephalus scorpius*	*
Atlantic hagfish	*Myxine glutinosa*	*
slender snipe eel	*Nemichthys scolopaceus*	
marlin-spike	*Nezumia bairdi*	
white barracudina	*Notolepis rissoi*	
snake eel uncl	*Ophichthyidae spp.*	
cusk-eel uncl	*Ophidiidae spp.*	
rainbow smelt	*Osmerus mordax*	*
barracudina uncl	*Paralepidae spp.*	
paralepis coregonoides	*Paralepis coregonoides*	
summer flounder	*Paralichthys dentatus*	*
fourspot flounder	*Paralichthys oblongus*	*
longnose greeneye	*Parasudis truculenta*	*
butterfish	*Peprilus triacanthus*	*
sea lamprey	*Petromyzon marinus*	*
rock gunnel	*Pholis gunnellus*	
longfin hake	*Phycis chesteri*	
snake eel	*Pisoodonophis cruentifer*	*
righteye flounder uncl	*Pleuronectidae spp.*	*
pollock	*Pollachius virens*	*
hatchetfish	*Polyipnus asteroides*	
polymetme corytheola	*Polymetme corytheola*	
beardfish	*Polymixia lowei*	
bluefish	*Pomatomus saltatrix*	*
bigeye	*Priacanthus arenatus*	
northern searobin	*Prionotus carolinus*	*
striped searobin	*Prionotus evolans*	*

Table 1 (cont'd). Fish species collected in all Gulf of Maine strata during the trawl survey from 1970-2017. Those that also occurred in SBNMS (stratum 26) are denoted by an asterisk.

common name	scientific name	stratum 26
winter flounder	*Pseudopleuronectes americanus*	*
clearnose skate	*Raja eglanteria*	
little skate	*Raja erinacea*	*
rosette skate	*Raja garmani*	
barndoor skate	*Raja laevis*	*
winter skate	*Raja ocellata*	*
thorny skate	*Raja radiata*	*
smooth skate	*Raja senta*	*
skate uncl	*Raja spp.*	
Greenland halibut	*Reinhardtius hippoglossoides*	*
chub mackerel	*Scomber japonicus*	
Atlantic mackerel	*Scomber scombrus*	*
Atlantic saury	*Scomberesox saurus*	*
windowpane	*Scophthalmus aquosus*	*
scorpionfish uncl	*Scorpaenidae spp.*	
Acadian redfish	*Sebastes fasciatus*	*
lookdown	*Selene vomer*	
slime eel	*Simenchelys parasiticus*	
northern puffer	*Sphoeroides maculatus*	
blunthead puffer	*Sphoeroides pachygaster*	
northern sennet	*Sphyraena borealis*	
barracuda uncl	*Sphyraenidae spp.*	
spiny dogfish	*Squalus acanthias*	*
scup	*Stenotomus chrysops*	*
hatchetfish uncl	*Sternoptychidae spp.*	
boa dragonfish	*Stomias ferox*	
scaly dragonfish uncl	*Stomiatidae spp.*	
tonguefish uncl	*Symphurus spp.*	
pipefish seahorse uncl	*Syngnathidae spp.*	*

Table 1 (cont'd). Fish species collected in all Gulf of Maine strata during the trawl survey from 1970-2017. Those that also occurred in SBNMS (stratum 26) are denoted by an asterisk.

common name	scientific name	stratum 26
northern pipefish	*Syngnathus fuscus*	*
cunner	*Tautogolabrus adspersus*	*
Atlantic torpedo	*Torpedo nobiliana*	*
rough scad	*Trachurus lathami*	
Atlantic cutlassfish	*Trichiurus lepturus*	
moustache sculpin	*Triglops murrayi*	*
radiated shanny	*Ulvaria subbifurcata*	*
eel uncl	*unknown eel*	
hake uncl	*unknown hate*	
red hake	*Urophycis chuss*	*
Carolina hake	*Urophycis earlli*	
spotted hake	*Urophycis regius*	*
ling uncl	*Urophycis spp.*	*
white hake	*Urophycis tenuis*	*
American straptail grenadier	*Ventrifossa occidentalis*	
Atlantic moonfish	*Vomer setapinnis*	
spotted tinselfish	*Xenolepidichthys dalgleishi*	
buckler dory	*Zenopsis conchifera*	
eelpout uncl	*Zoarcidae spp.*	

Table 2. Results of ANOSIM procedure comparing differences in decadal groups for spring season tows in SBNMS (Global R = 0.115, significant at 0.1%). An asterisk denotes significantly high R value (closer to 1 and above background values).

Pairwise Tests Groups	R Statistic	Significance Level %	Possible Permutations	Actual Permutations	Number ≥ Observed
1970s, 1980s	0.112	0.1	Very large	999	0
1970s, 1990s	0.100	0.1	Very large	999	0
1970s, 2000s	0.093	0.1	Very large	999	0
1970s, 2010s	0.193	0.1	Very large	999	0
1980s, 1990s	0.026	12.2	Very large	999	121
1980s, 2000s	0.081	0.1	Very large	999	0
1980s, 2010s	*0.220	0.1	Very large	999	0
1990s, 2000s	0.052	0.5	Very large	999	4
1990s, 2010s	*0.239	0.1	Very large	999	0
2000s, 2010s	0.105	0.1	Very large	999	0

Table 3. Results of SIMPER procedure identifying principal species driving dissimilarity of spring season tows from 1980s and 2010s decades in SBNMS. Species are in descending order of percent contribution to decadal differences (average dissimilarity = 62.21). Analytical results are group average abundance (Avg Abund), average dissimilarity (Avg Diss), standard deviation of dissimilarity (SD Diss), percent contribution of species x to dissimilarity (Contrib%), and cumulative percent dissimilarity in descending order of species contribution (Cum%).

Species	**Group 1980s Avg Abund**	**Group 2010s Avg Abund**	**Avg Diss**	**SD Diss**	**Contrib%**	**Cum%**
haddock	0.97	3.42	4.44	1.40	7.13	7.13
silver hake	1.19	3.40	3.95	1.38	6.35	13.49
Acadian redfish	0.46	2.71	3.86	1.14	6.21	19.70
yellowtail flounder	1.39	2.92	3.44	1.34	5.53	25.22
Atlantic herring	0.92	2.39	3.29	1.09	5.28	30.51
longhorn sculpin	2.05	3.16	3.21	1.18	5.16	35.66
winter flounder	0.67	2.31	3.09	1.33	4.96	40.62
American plaice	2.88	2.99	3.05	1.38	4.90	45.52
Atlantic cod	1.78	2.63	2.68	1.28	4.31	49.83
ocean pout	1.68	2.18	2.29	1.30	3.68	53.51
spiny dogfish	0.10	1.36	2.17	0.76	3.48	57.00
alewife	0.52	1.47	2.15	0.99	3.45	60.45
red hake	0.52	1.52	2.05	1.10	3.30	63.75
thorny skate	0.96	1.42	1.80	1.29	2.89	66.64
pollock	0.58	0.83	1.62	0.84	2.60	69.23
sea raven	1.00	1.12	1.48	1.26	2.38	71.62

Table 4. Results of SIMPER procedure identifying principal species driving dissimilarity of spring season tows from 1990s and 2010s decades in SBNMS. Species are in descending order of percent contribution to decadal differences (average dissimilarity = 60.12). Analytical results are group average abundance (Avg Abund), average dissimilarity (Avg Diss), standard deviation of dissimilarity (SD Diss), percent contribution of species x to dissimilarity (Contrib%), and cumulative percent dissimilarity in descending order of species contribution (Cum%).

Species	Group 1990s Avg Abund	Group 2010s Avg Abund	Avg Diss	SD Diss	Contrib%	Cum%
haddock	0.67	3.42	4.64	1.37	7.73	7.73
silver hake	1.28	3.40	3.99	1.38	6.64	14.36
Acadian redfish	1.38	2.71	3.70	1.21	6.16	20.52
Atlantic herring	1.67	2.39	3.43	1.15	5.70	26.22
yellowtail flounder	1.26	2.92	3.39	1.30	5.63	31.85
longhorn sculpin	2.51	3.16	2.96	1.15	4.92	36.77
American plaice	2.94	2.99	2.86	1.35	4.76	41.53
winter flounder	1.03	2.31	2.84	1.26	4.72	46.25
Atlantic cod	1.93	2.63	2.67	1.15	4.45	50.70
ocean pout	1.64	2.18	2.36	1.28	3.93	54.63
alewife	0.78	1.47	2.15	1.05	3.58	58.21
spiny dogfish	0.26	1.36	2.12	0.78	3.53	61.73
red hake	0.80	1.52	2.04	1.14	3.40	65.13
thorny skate	0.80	1.42	1.80	1.27	2.99	68.12
pollock	0.72	0.83	1.62	0.90	2.69	70.81

Table 5. Results of ANOSIM procedure comparing differences in decadal groups for fall season tows in SBNMS (Global R = 0.154, significant at 0.1%). An asterisk denotes significantly high R value (closer to 1 and above background values).

Pairwise Tests Groups	R Statistic	Significance Level %	Possible Permutations	Actual Permutations	Number ≥ Observed
1970s, 1980s	0.134	0.1	Very large	999	0
1970s, 1990s	0.133	0.1	Very large	999	0
1970s, 2000s	0.121	0.1	Very large	999	0
1970s, 2010s	*0.310	0.1	Very large	999	0
1980s, 1990s	0.090	0.1	Very large	999	0
1980s, 2000s	0.088	0.2	Very large	999	1
1980s, 2010s	0.149	0.1	Very large	999	0
1990s, 2000s	0.140	0.1	Very large	999	0
1990s, 2010s	*0.351	0.1	Very large	999	0
2000s, 2010s	*0.248	0.1	Very large	999	0

Table 6. Results of SIMPER procedure identifying principal species driving dissimilarity of fall season tows from 1970s and 2010s decades in SBNMS. Species are in descending order of percent contribution to decadal differences (average dissimilarity = 65.77). Analytical results are group average abundance (Avg Abund), average dissimilarity (Avg Diss), standard deviation of dissimilarity (SD Diss), percent contribution of species x to dissimilarity (Contrib%), and cumulative percent dissimilarity in descending order of species contribution (Cum%).

Species	**Group 1970s Avg Abund**	**Group 2010s Avg Abund**	**Avg Diss**	**SD Diss**	**Contrib%**	**Cum%**
silver hake	2.44	4.92	3.81	1.49	5.80	5.80
spiny dogfish	1.44	3.86	3.71	1.19	5.64	11.43
haddock	2.15	3.79	3.50	1.51	5.33	16.76
Atlantic herring	0.37	3.07	3.48	1.32	5.29	22.05
butterfish	0.13	2.52	2.94	1.43	4.46	26.51
American plaice	2.64	2.66	2.92	1.35	4.44	30.95
red hake	1.56	3.18	2.91	1.45	4.42	35.38
longhorn sculpin	0.97	2.69	2.75	1.31	4.19	39.57
winter flounder	0.30	2.36	2.75	1.46	4.18	43.75
alewife	0.57	2.45	2.68	1.26	4.08	47.83
yellowtail flounder	0.79	2.18	2.57	1.15	3.90	51.73
Acadian redfish	0.99	2.06	2.49	1.05	3.78	55.51
Atlantic mackerel	0.19	1.67	2.11	0.80	3.20	58.71
Atlantic cod	2.41	1.92	1.94	1.36	2.96	61.66
fourspot flounder	0.15	1.60	1.79	1.46	2.72	64.39
pollock	0.86	1.02	1.75	0.81	2.65	67.04
ocean pout	0.77	1.30	1.51	1.17	2.29	69.33
witch flounder	0.86	0.84	1.47	0.93	2.24	71.57

Table 7. Results of SIMPER procedure identifying principal species driving dissimilarity of fall season tows from 1990s and 2010s decades in SBNMS. Species are in descending order of percent contribution to decadal differences (average dissimilarity = 58.64). Analytical results are group average abundance (Avg Abund), average dissimilarity (Avg Diss), standard deviation of dissimilarity (SD Diss), percent contribution of species x to dissimilarity (Contrib%), and cumulative percent dissimilarity in descending order of species contribution (Cum%).

Species	**Group 1990s Avg Abund**	**Group 2010s Avg Abund**	**Avg Diss**	**SD Diss**	**Contrib%**	**Cum%**
haddock	0.90	3.79	3.80	1.48	6.47	6.47
spiny dogfish	1.77	3.86	3.28	1.18	5.60	12.07
silver hake	2.87	4.92	3.09	1.51	5.27	17.34
American plaice	3.66	2.66	2.83	1.37	4.83	22.17
Atlantic herring	3.14	3.07	2.83	1.32	4.83	27.00
butterfish	0.30	2.52	2.54	1.36	4.33	31.33
alewife	0.35	2.45	2.48	1.25	4.23	35.55
Acadian redfish	1.82	2.06	2.39	1.17	4.08	39.64
yellowtail flounder	1.06	2.18	2.35	1.17	4.00	43.64
winter flounder	0.74	2.36	2.34	1.40	3.99	47.63
red hake	2.48	3.18	2.28	1.29	3.89	51.52
longhorn sculpin	2.53	2.69	2.15	1.31	3.67	55.19
Atlantic mackerel	0.26	1.67	1.94	0.82	3.31	58.50
Atlantic cod	2.00	1.92	1.83	1.31	3.12	61.62
pollock	0.99	1.02	1.71	0.84	2.92	64.54
fourspot flounder	0.20	1.60	1.62	1.46	2.76	67.30
thorny skate	0.96	1.37	1.36	1.31	2.31	69.61
ocean pout	1.06	1.30	1.35	1.21	2.30	71.92

Table 8. Results of SIMPER procedure identifying principal species driving dissimilarity of fall season tows from 2000s and 2010s decades in SBNMS. Species are in descending order of percent contribution to decadal differences (average dissimilarity = 56.99). Analytical results are group average abundance (Avg Abund), average dissimilarity (Avg Diss), standard deviation of dissimilarity (SD Diss), percent contribution of species x to dissimilarity (Contrib%), and cumulative percent dissimilarity in descending order of species contribution (Cum%).

Species	**Group 2000s Avg Abund**	**Group 2010s AvgAbund**	**Avg Diss**	**SD Diss**	**Contrib%**	**Cum%**
silver hake	2.54	4.92	3.33	1.50	5.85	5.850
haddock	2.29	3.79	3.03	1.52	5.32	11.17
American plaice	2.40	2.66	2.67	1.31	4.68	15.85
spiny dogfish	3.87	3.86	2.65	1.16	4.65	20.50
Atlantic herring	3.05	3.07	2.55	1.34	4.48	24.98
red hake	1.87	3.18	2.51	1.43	4.41	29.40
Acadian redfish	2.06	2.06	2.48	1.21	4.36	33.75
butterfish	0.73	2.52	2.44	1.38	4.28	38.04
alewife	0.86	2.45	2.32	1.28	4.07	42.11
longhorn sculpin	2.17	2.69	2.32	1.35	4.07	46.17
yellowtail flounder	0.97	2.18	2.30	1.16	4.03	50.21
winter flounder	1.25	2.36	2.26	1.40	3.97	54.18
Atlantic cod	2.85	1.92	1.87	1.40	3.27	57.46
Atlantic mackerel	0.22	1.67	1.85	0.81	3.25	60.70
pollock	1.24	1.02	1.82	0.88	3.20	63.90
fourspot flounder	0.28	1.60	1.53	1.46	2.69	66.60
thorny skate	0.50	1.37	1.34	1.27	2.36	68.95
ocean pout	0.48	1.30	1.29	1.12	2.26	71.21

Table 9. Change in mean depth of capture comparing the 2000s with 2010s decade for both SBNMS and larger Gulf of Maine regions (as defined in text). Negative value in “Δ mean depth” columns indicates deeper mean depth in 2010s than previous decade while positive value indicates shallower depth. Arrows (↘ and ↗) are limited to changes in mean depth that exceed SE for both 2000 and 2010 depths. Continued on next page.

species	tows in Stellwagen Bank NMS (stratum 26)			tows throughout Gulf of Maine (strata 21-40)		
	mean ±SE depth (m)		Δ mean depth	mean ±SE depth (m)		Δ mean depth
	2000	2010	2000 to 2010	2000	2010	2000 to 2010
butterfish	60.0 ± 5.99	77.5 ± 3.84	-17.5 ↘	128.7 ± 3.75	150.1 ± 2.54	-21.4 ↘
winter skate	50.9 ± 6.67	68.2 ± 4.24	-17.3 ↘	112.3 ± 3.50	119.5 ± 3.43	-7.2 ↘
American shad	76.3 ± 6.57	88.3 ± 4.86	-12.0 ↘	159.8 ± 3.06	159.7 ± 2.29	0.1
Atlantic hagfish	84.8 ± 6.10	95.2 ± 7.97	-10.4 ↘	181.7 ± 3.11	181.6 ± 3.20	0.1
Atlantic mackerel	64.1 ± 9.53	72.3 ± 4.07	-8.2	133.7 ± 4.12	152.9 ± 2.61	-19.2 ↘
little skate	49.9 ± 5.10	56.9 ± 3.90	-7.0 ↘	92.5 ± 2.54	108.6 ± 3.59	-16.1 ↘
cunner	63.3 ± 2.63	69.5 ± 3.33	-6.2 ↘	68.0 ± 3.16	69.9 ± 2.53	-1.8
winter flounder	65.4 ± 3.00	71.1 ± 2.49	-5.7 ↘	88.7 ± 1.79	97.8 ± 2.00	-9.2 ↘
ocean pout	73.2 ± 3.14	78.4 ± 2.87	-5.2 ↘	122.7 ± 2.37	130.2 ± 2.08	-7.5 ↘
hookear sculpin	84.9 ± 3.21	90.0 ± 5.20	-5.1	125.8 ± 6.62	150.4 ± 12.12	-24.6 ↘
yellowtail flounder	68.4 ± 3.43	72.7 ± 2.74	-4.3 ↘	88.8 ± 1.96	87.4 ± 1.88	1.4
spiny dogfish	73.8 ± 3.49	77.6 ± 2.96	-3.8 ↘	165.4 ± 1.91	164.4 ± 1.99	1.1
moustache sculpin	68.8 ± 3.78	72.2 ± 3.06	-3.4	109.4 ± 6.72	104.9 ± 6.37	4.5
alligatorfish	83.8 ± 6.17	86.7 ± 2.89	-2.9	120.7 ± 3.72	123.8 ± 2.68	-3.1
haddock	76.4 ± 2.87	79.2 ± 2.64	-2.8	152.2 ± 1.96	158.9 ± 1.87	-6.7 ↘
fourspot flounder	80.5 ± 6.01	83.2 ± 3.25	-2.7	130.2 ± 3.39	127.3 ± 2.86	2.8
red hake	80.7 ± 3.43	83.2 ± 2.96	-2.5	162.0 ± 1.48	164.0 ± 1.62	-1.9 ↘
Atlantic herring	77.0 ± 3.17	78.7 ± 2.92	-1.7	156.3 ± 1.68	160.3 ± 1.68	-4.0 ↘
longhorn sculpin	72.9 ± 2.57	73.6 ± 2.52	-0.7	99.9 ± 1.44	104.0 ± 1.73	-4.1 ↘

Table 9 (cont'd). Change in mean depth of capture comparing the 2000s with 2010s decade for both SBNMS and larger Gulf of Maine regions (as defined in text). Negative value in "Δ mean depth" columns indicates deeper mean depth in 2010s than previous decade while positive value indicates shallower depth. Arrows (↘ and ↗) are limited to changes in mean depth that exceed SE for both 2000 and 2010 depths.

species	**tows in Stellwagen Bank NMS (stratum 26)**			**tows throughout Gulf of Maine (strata 21-40)**		
	mean ±SE depth (m)		Δ mean depth	mean ±SE depth (m)		Δ mean depth
	2000	2010	2000 to 2010	2000	2010	2000 to 2010
Atlantic wolffish	80.3 ± 4.05	81.0 ± 3.51	-0.7	115.8 ± 4.20	109.5 ± 4.12	6.4 ↗
sea raven	76.2 ± 3.20	76.8 ± 2.85	-0.6	107.6 ± 1.77	111.4 ± 2.35	-3.8 ↘
thorny skate	82.4 ± 3.39	82.7 ± 2.44	-0.3	160.9 ± 2.35	155.3 ± 2.52	5.5 ↗
alewife	83.5 ± 3.56	83.0 ± 3.20	0.5	155.4 ± 1.87	162.1 ± 1.71	-6.7 ↘
blueback herring	83.4 ± 6.62	82.6 ± 4.57	0.8	148.5 ± 2.73	146.2 ± 2.09	2.3
witch flounder	98.2 ± 4.79	96.1 ± 3.31	2.1	176.0 ± 1.41	174.6 ± 1.54	1.4
Acadian redfish	88.3 ± 2.89	85.3 ± 2.66	3.0 ↗	172.8 ± 1.50	173.0 ± 1.56	-0.2
silver hake	81.3 ± 3.03	78.3 ± 2.65	3.0	165.5 ± 1.44	161.7 ± 1.66	3.9 ↗
American plaice	82.7 ± 2.79	79.5 ± 2.67	3.2 ↗	161.2 ± 1.41	161.4 ± 1.67	-0.2
windowpane	70.5 ± 11.58	67.2 ± 5.57	3.3	85.4 ± 2.44	88.6 ± 2.81	-3.2 ↘
Atlantic cod	77.1 ± 2.83	73.3 ± 2.49	3.8 ↗	132.5 ± 1.89	139.7 ± 2.34	-7.2 ↘
snakeblenny	92.4 ± 5.07	88.5 ± 7.04	3.9	109.8 ± 4.95	100.9 ± 6.44	8.9 ↗
white hake	93.6 ± 5.03	88.0 ± 3.18	5.6 ↗	181.6 ± 1.57	176.5 ± 1.69	5.1 ↗
fourbeard rockling	100.6 ± 7.50	93.5 ± 4.23	7.1	158.7 ± 2.53	166.7 ± 1.76	-8.0 ↘
pollock	81.6 ± 3.60	72.4 ± 3.51	9.2 ↗	165.8 ± 2.23	160.0 ± 2.74	5.7 ↗
cusk	99.9 ± 9.23	90.0 ± 6.86	9.9 ↗	187.4 ± 4.52	184.1 ± 6.97	3.3
goosefish	103.0 ± 5.67	85.9 ± 3.52	17.1 ↗	173.2 ± 1.68	170.4 ± 1.78	2.8 ↗
smooth skate	112.5 ± 10.92	92.8 ± 3.56	19.7 ↗	185.3 ± 2.00	180.0 ± 1.79	5.4 ↗
wrymouth	119.7 ± 13.09	97.7 ± 8.86	22.0 ↗	144.7 ± 5.21	149.1 ± 3.39	-4.4

Figures

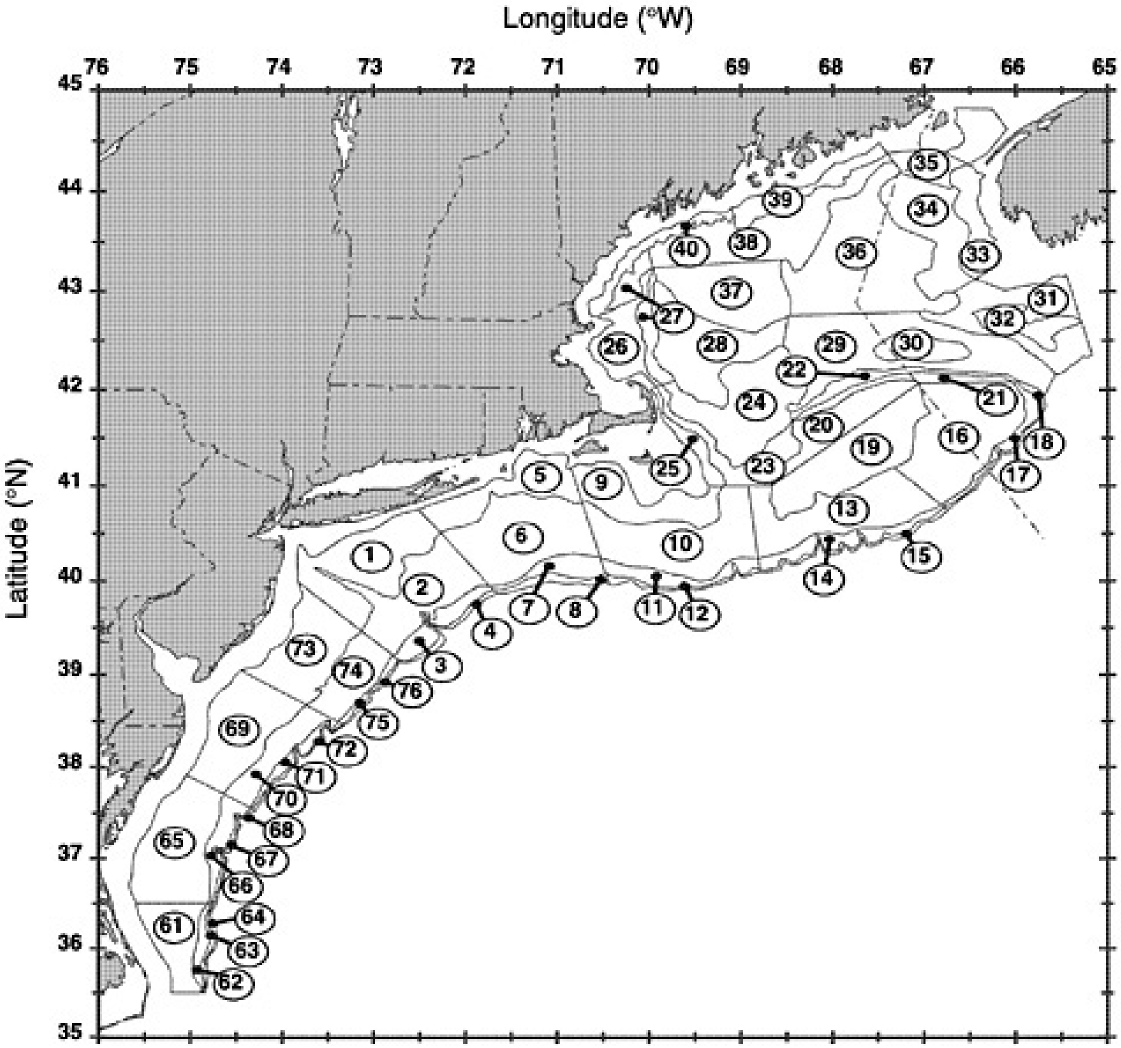


Figure 1a. Survey strata for National Marine Fisheries Service bottom trawl survey (above). SBNMS is contained in stratum 26. The Gulf of Maine region, for the purposes of this study, was delineated as strata 21-40.

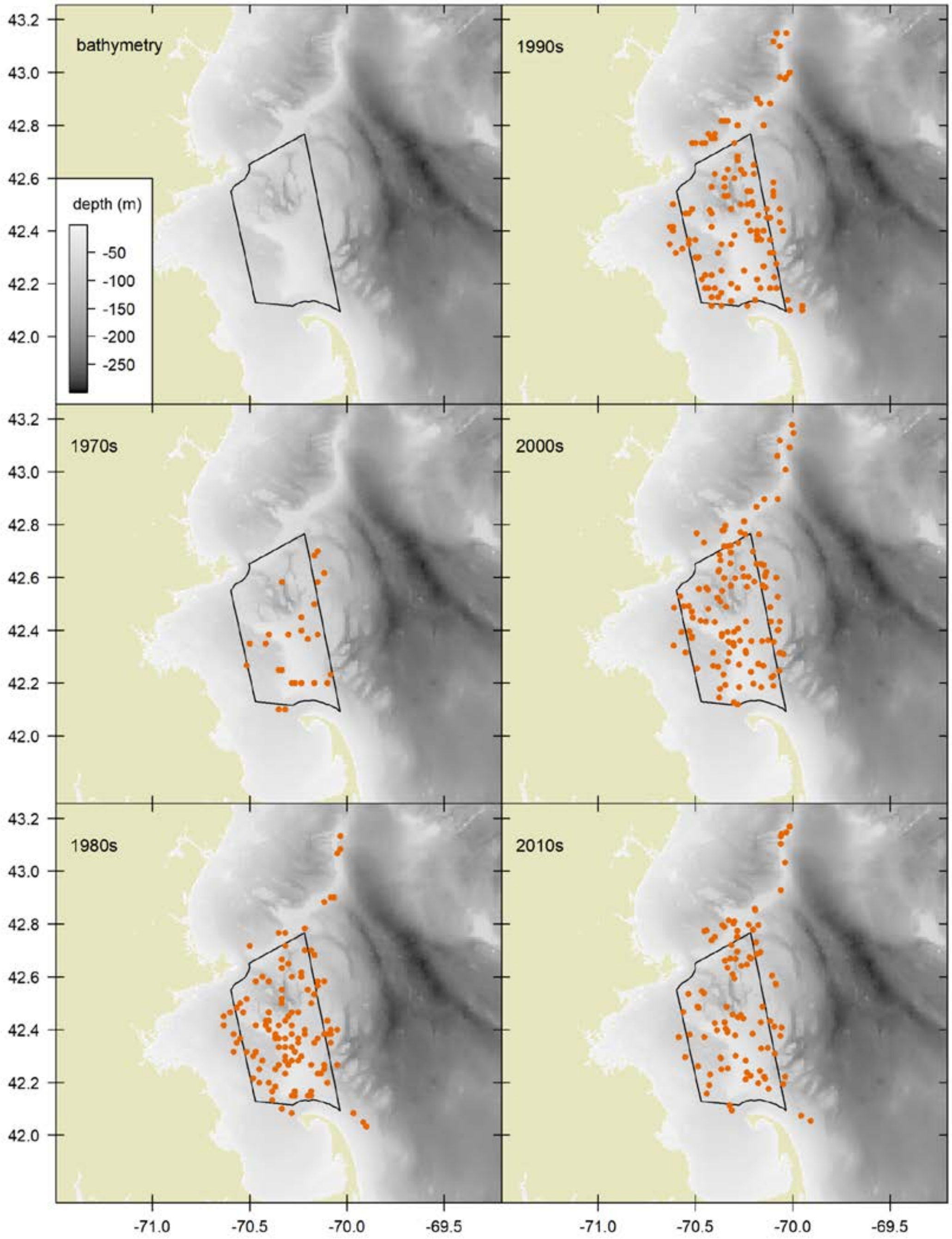


Figure 1b. Bathymetry and distribution of survey tows by decade within the SBNMS survey stratum.

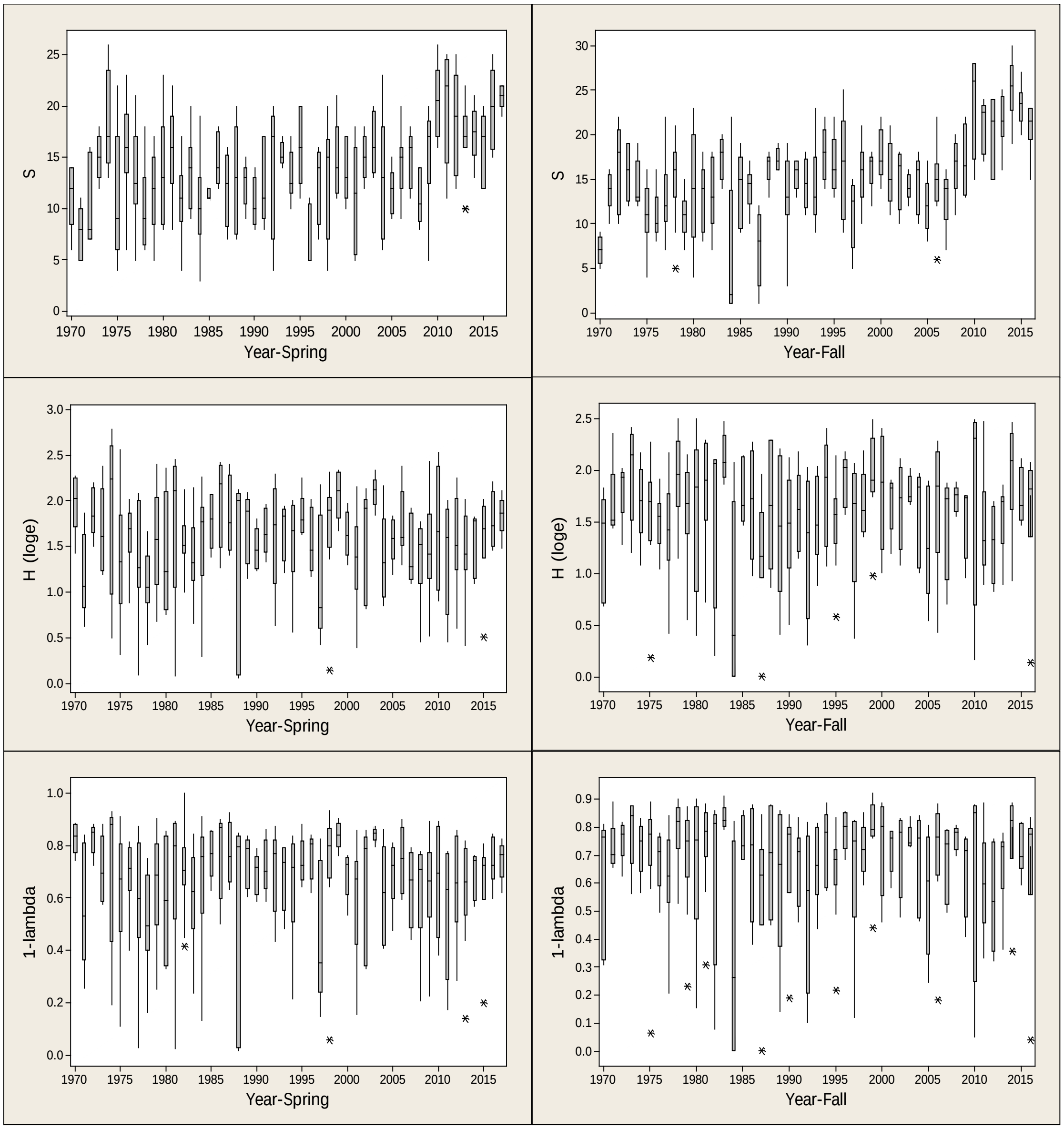


Figure 2. Box-and-whisker plots to compare distributions by tow for S (top) and Shannon (middle) and Simpson diversity (bottom), by year and season (spring left and fall right). Note upward trends in S in recent years while no clear trend is observed for Shannon and Simpson diversity indices that take both diversity and abundance into account. The central line in each box denotes the median value. The top of each box is the upper value of the third quartile (75% of data less than or equal to this value) and bottom is the upper value of the first quartile (25% of the data are less than or equal to this value). The tip of the upper whisker is the highest data value within the limit of Q3 + 1.5 (Q3 - Q1) while the tip of the lower whisker is the lowest value within the limit of Q1- 1.5 (Q3 - Q1). Stars represent outliers of unusually high or low values outside the limits of the whiskers.

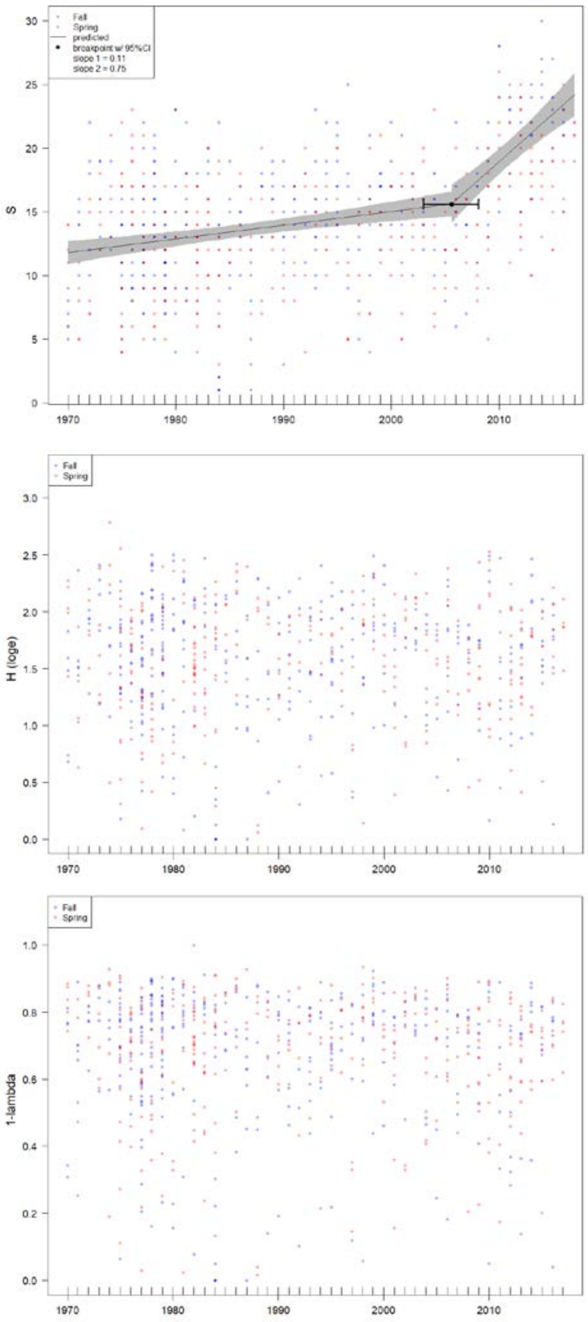


Figure 3. Segmented regression of species richness per tow over time with both spring and fall periods combined (top). Richness exhibited an increase over the earlier part of the time series (i.e., 1970 to ca. 2006) but over the past decade there has been a marked acceleration. However, neither Shannon (middle) and Simpson indices (bottom) exhibited such trends. (See text for details.)

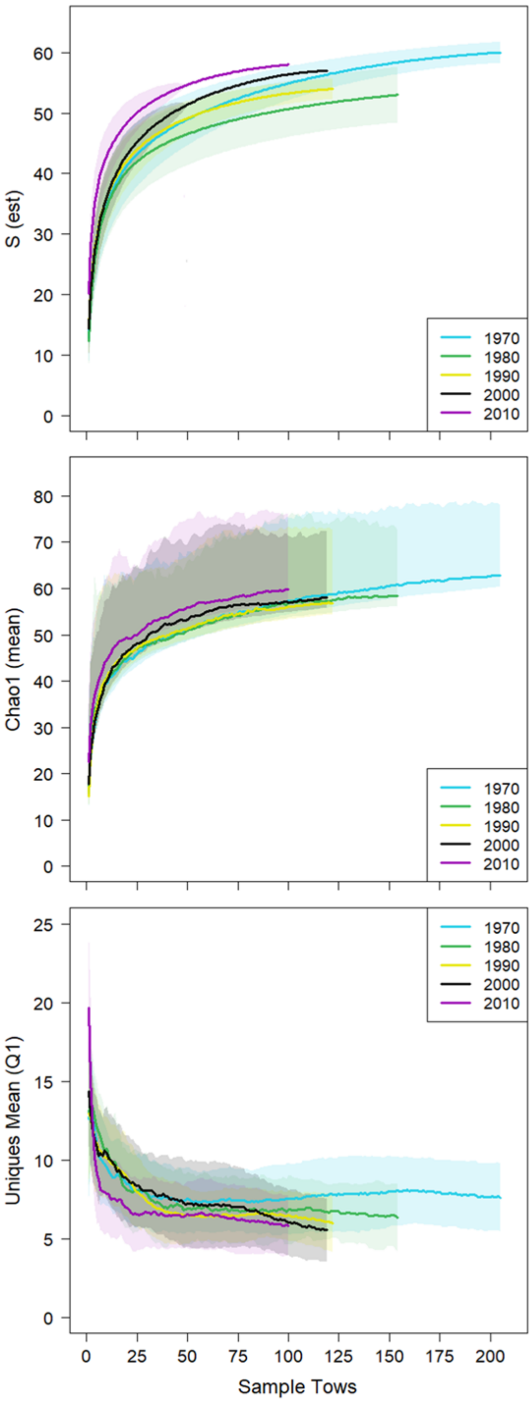


Figure 4. Rarefication curves by decade for S (est), Chao 1, and Uniques Mean (top to bottom, respectively). Shaded areas are 95% Confidence Interval bands for S(est) and mean Chao 1, and 1 Standard Deviation for Uniques Mean.

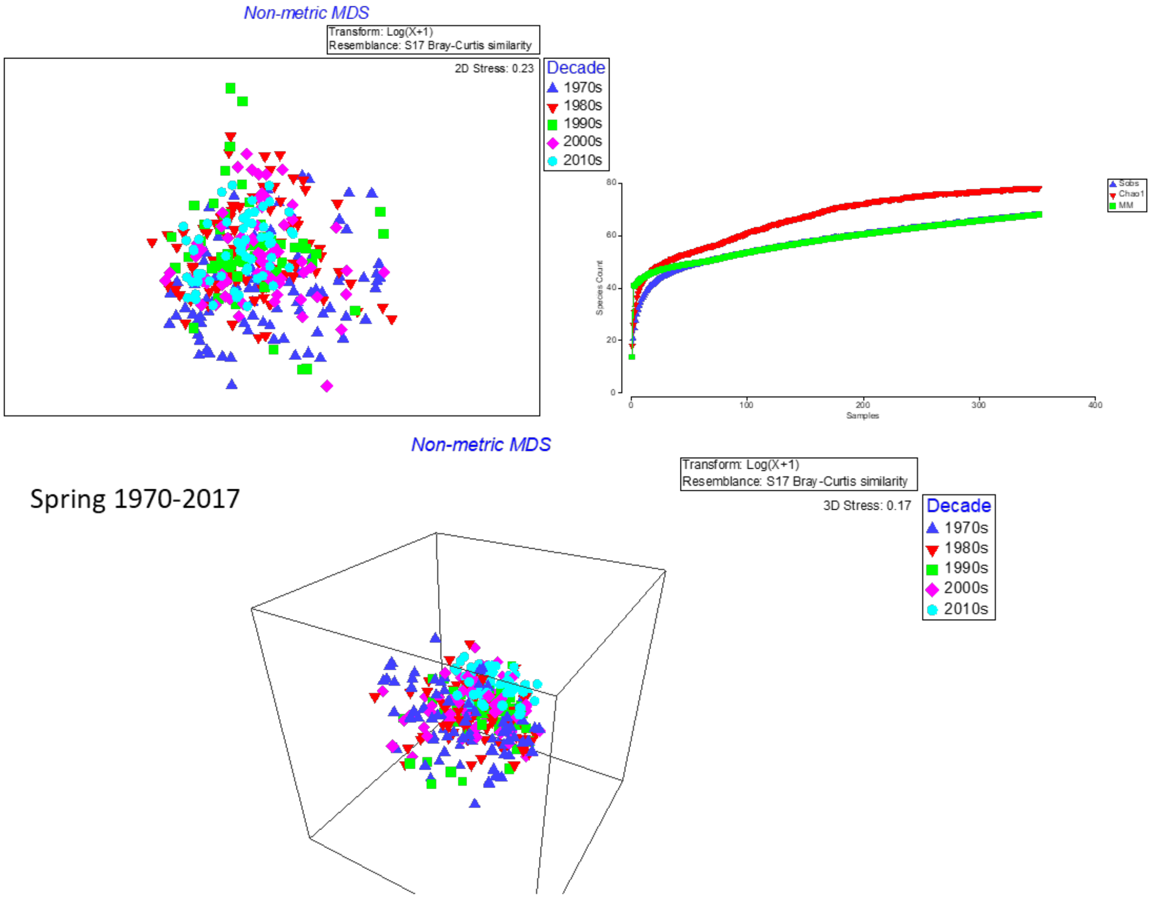


Figure 5. Strata 26 (SBNMS) spring period. NMDS as both 2D and 3D plots. Note stress levels above each visualization. Upper right is species accumulation curve for observed tows as well as Chao 1 and Michaelis-Menton diversity estimators.

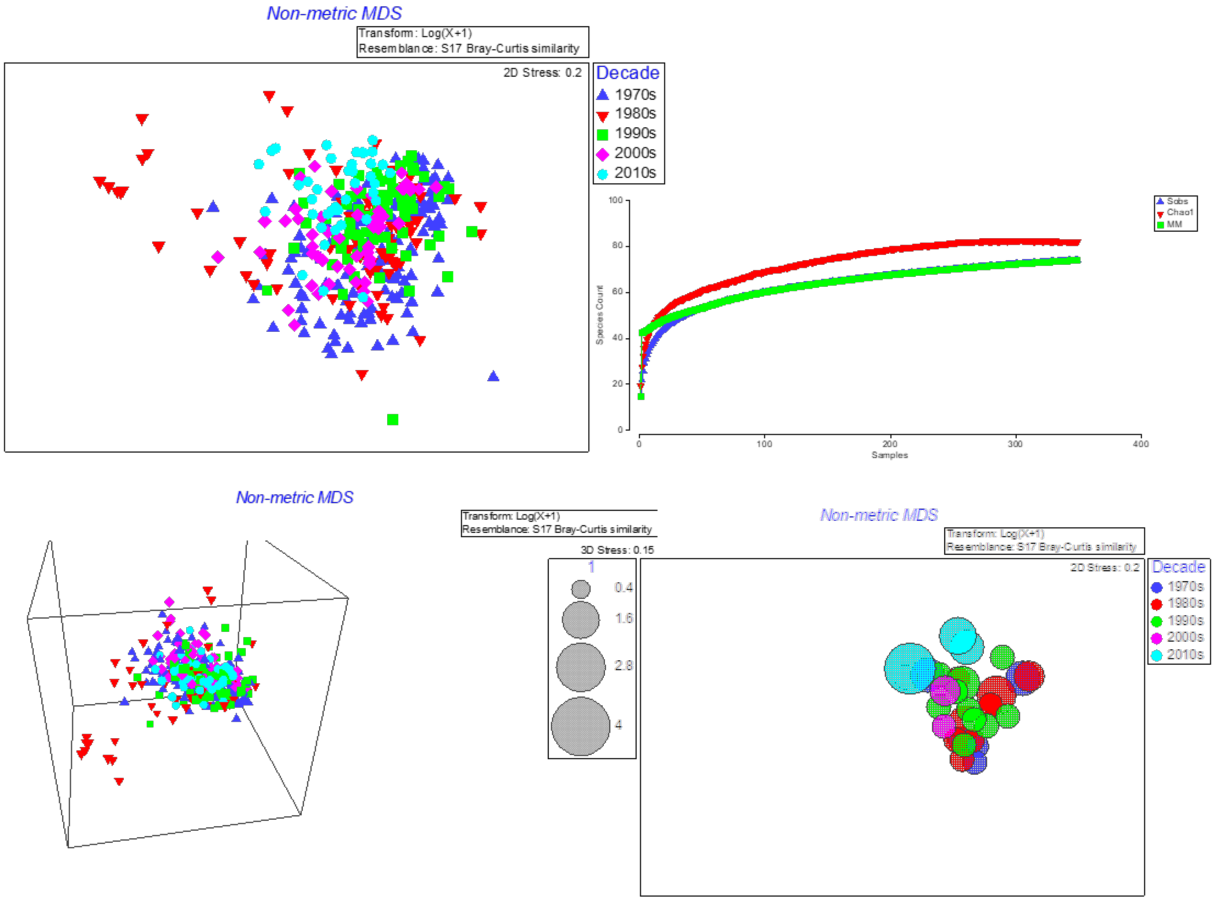
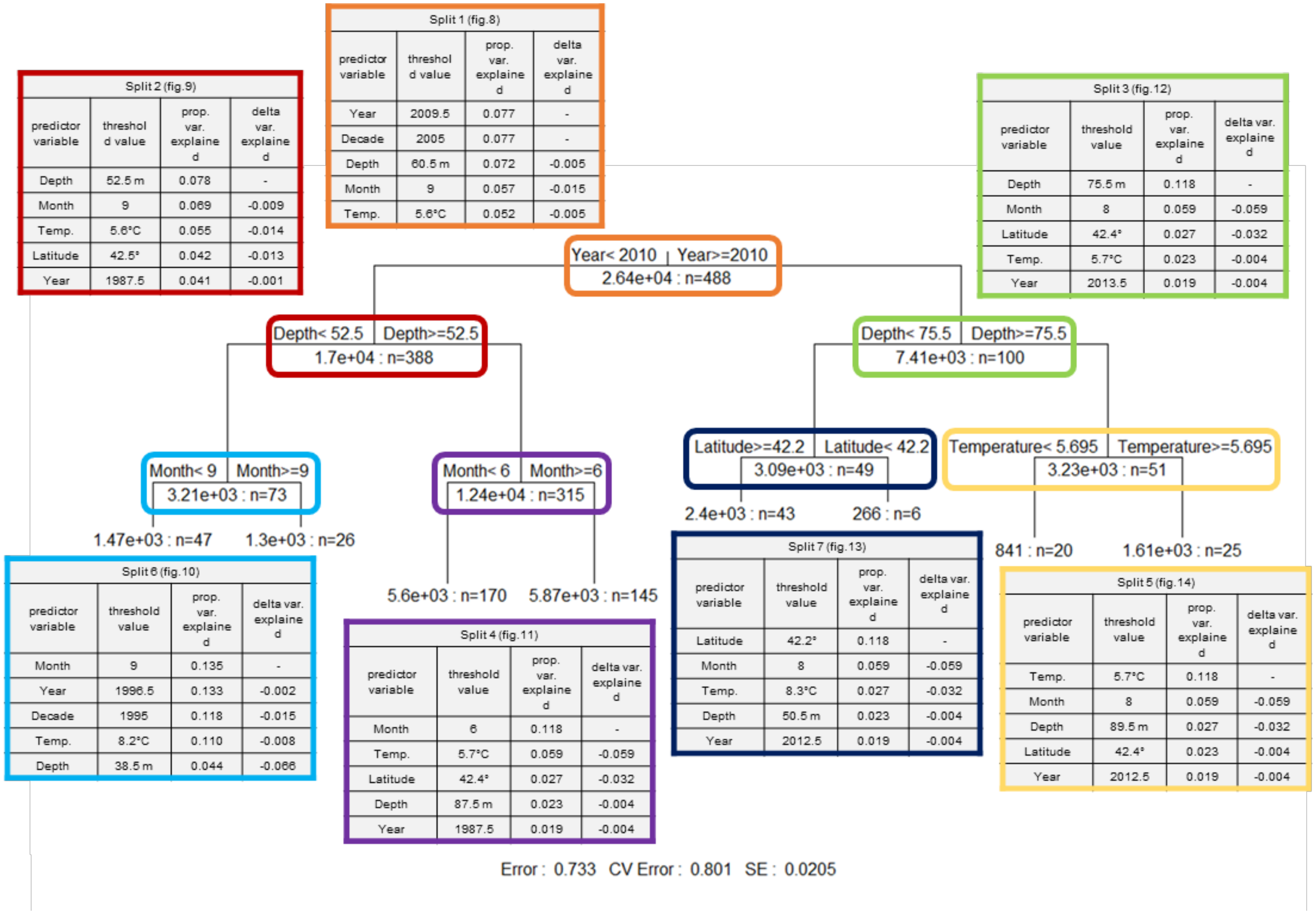


Figure 6. Strata 26 (SBNMS) fall period. NMDS as both 2D (tows and bubble centroids) and 3D plots. Note stress levels above each visualization. Upper right is species accumulation curve for observed tows as well as Chao 1 and Michaelis-Menton diversity estimators.



Split 2 (fig.9)

predictor variable	threshold value	prop. var. explained	delta var. explained
Depth	52.5 m	0.078	-
Month	9	0.069	-0.009
Temp.	5.6°C	0.055	-0.014
Latitude	42.5°	0.042	-0.013
Year	1987.5	0.041	-0.001

Split 1 (fig.8)

predictor variable	threshold value	prop. var. explained	delta var. explained
Year	2009.5	0.077	-
Decade	2005	0.077	-
Depth	60.5 m	0.072	-0.005
Month	9	0.057	-0.015
Temp.	5.6°C	0.052	-0.005

Split 3 (fig.12)

predictor variable	threshold value	prop. var. explained	delta var. explained
Depth	75.5 m	0.118	-
Month	8	0.059	-0.059
Latitude	42.4°	0.027	-0.032
Temp.	5.7°C	0.023	-0.004
Year	2013.5	0.019	-0.004

Split 6 (fig.10)

predictor variable	threshold value	prop. var. explained	delta var. explained
Month	9	0.135	-
Year	1996.5	0.133	-0.002
Decade	1995	0.118	-0.015
Temp.	8.2°C	0.110	-0.008
Depth	38.5 m	0.044	-0.066

Split 4 (fig.11)

predictor variable	threshold value	prop. var. explained	delta var. explained
Month	6	0.118	-
Temp.	5.7°C	0.059	-0.059
Latitude	42.4°	0.027	-0.032
Depth	87.5 m	0.023	-0.004
Year	1987.5	0.019	-0.004

Split 7 (fig.13)

predictor variable	threshold value	prop. var. explained	delta var. explained
Latitude	42.2°	0.118	-
Month	8	0.059	-0.059
Temp.	8.3°C	0.027	-0.032
Depth	50.5 m	0.023	-0.004
Year	2012.5	0.019	-0.004

Split 5 (fig.14)

predictor variable	threshold value	prop. var. explained	delta var. explained
Temp.	5.7°C	0.118	-
Month	8	0.059	-0.059
Depth	89.5 m	0.027	-0.032
Latitude	42.4°	0.023	-0.004
Year	2012.5	0.019	-0.004

Figure 7. Multiple regression tree for the SBNMS (stratum 26) region. Tables at each split indicate the proportion of variance explained by each factor in the analysis. Factor with greatest explanatory value (top of table at each split) was used for partitioning data.

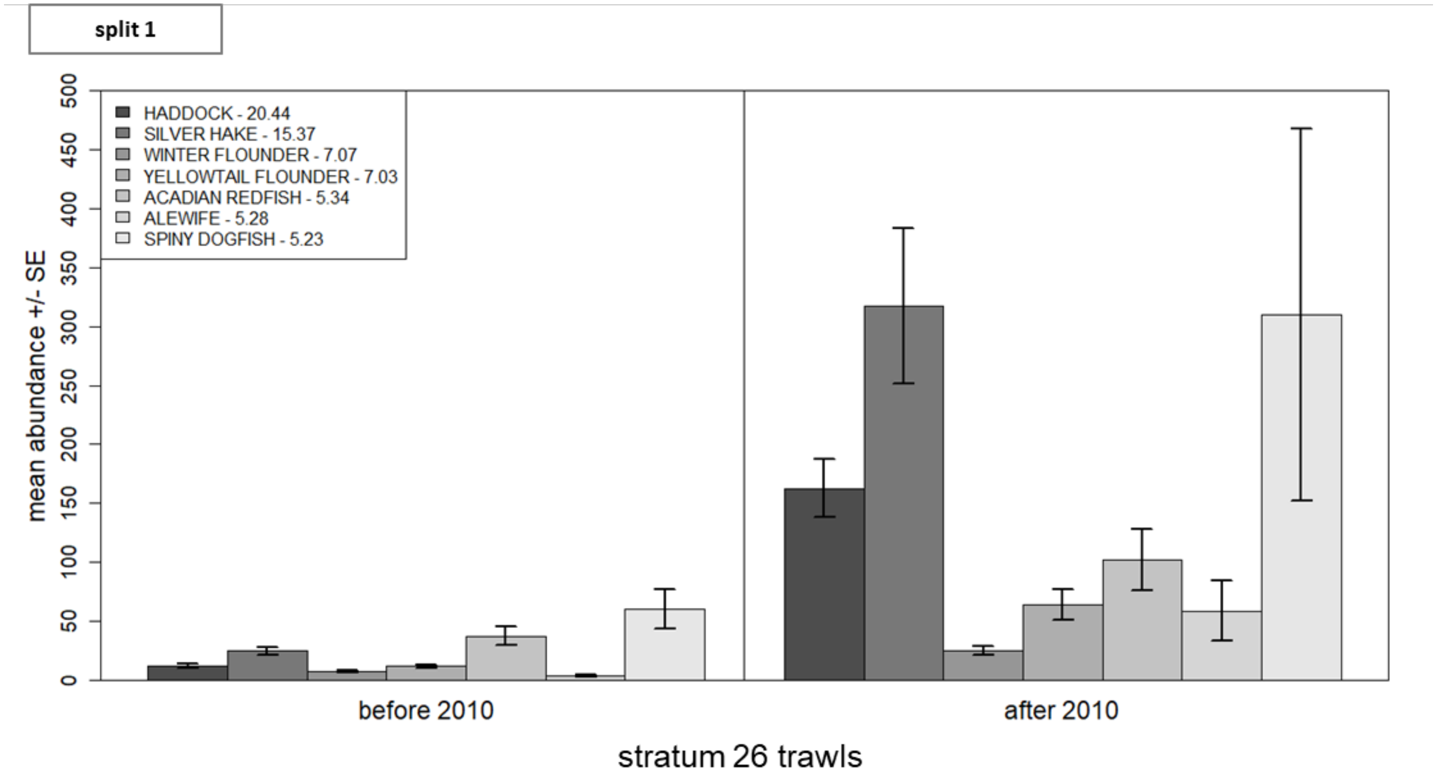


Figure 8. Barplot of principal species mean abundance at each side of split referenced above and in MRT. Error bars are standard error. Numbers in legend are the proportion of variance explained by each species.

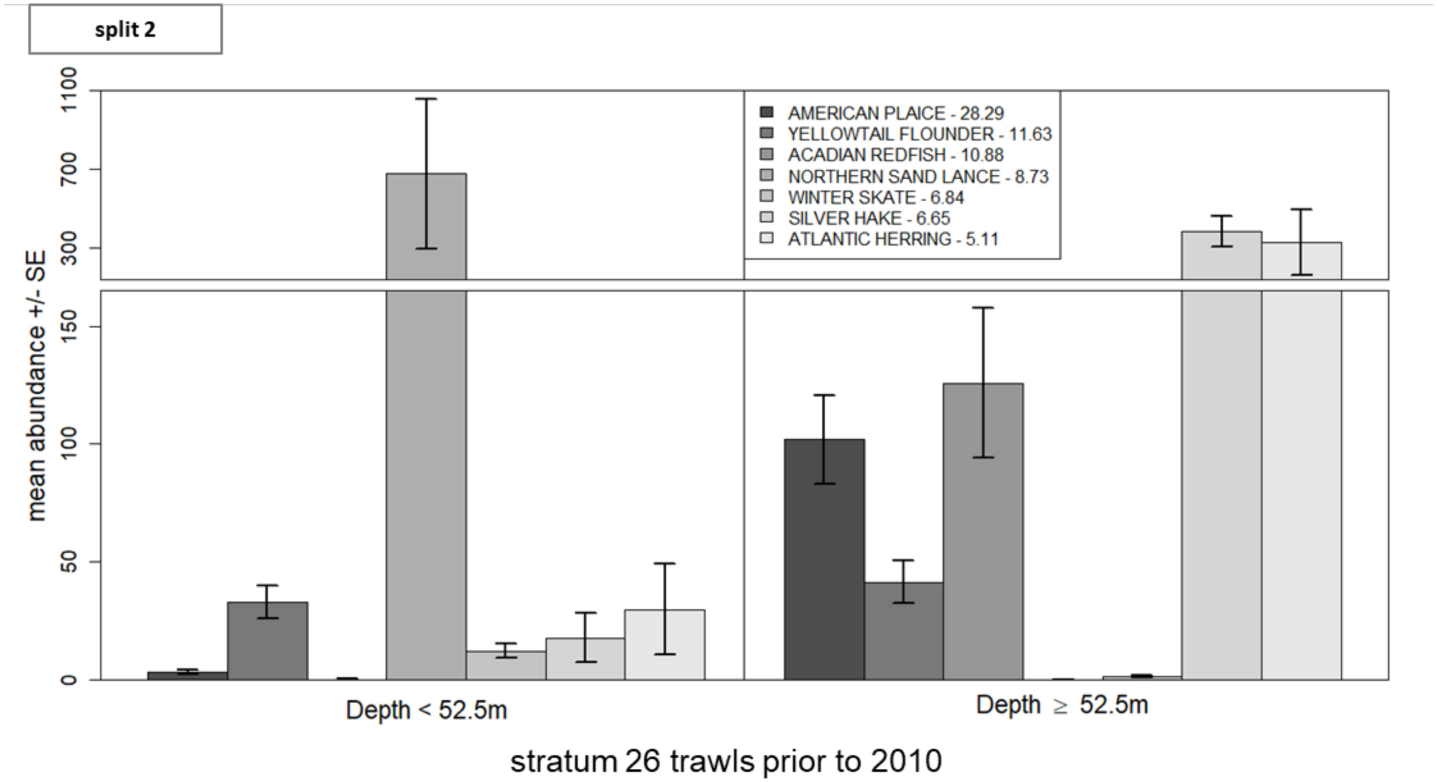


Figure 9. Barplot of principal species mean abundance at each side of split referenced above and in MRT. Error bars are standard error. Numbers in legend are the proportion of variance explained by each species.

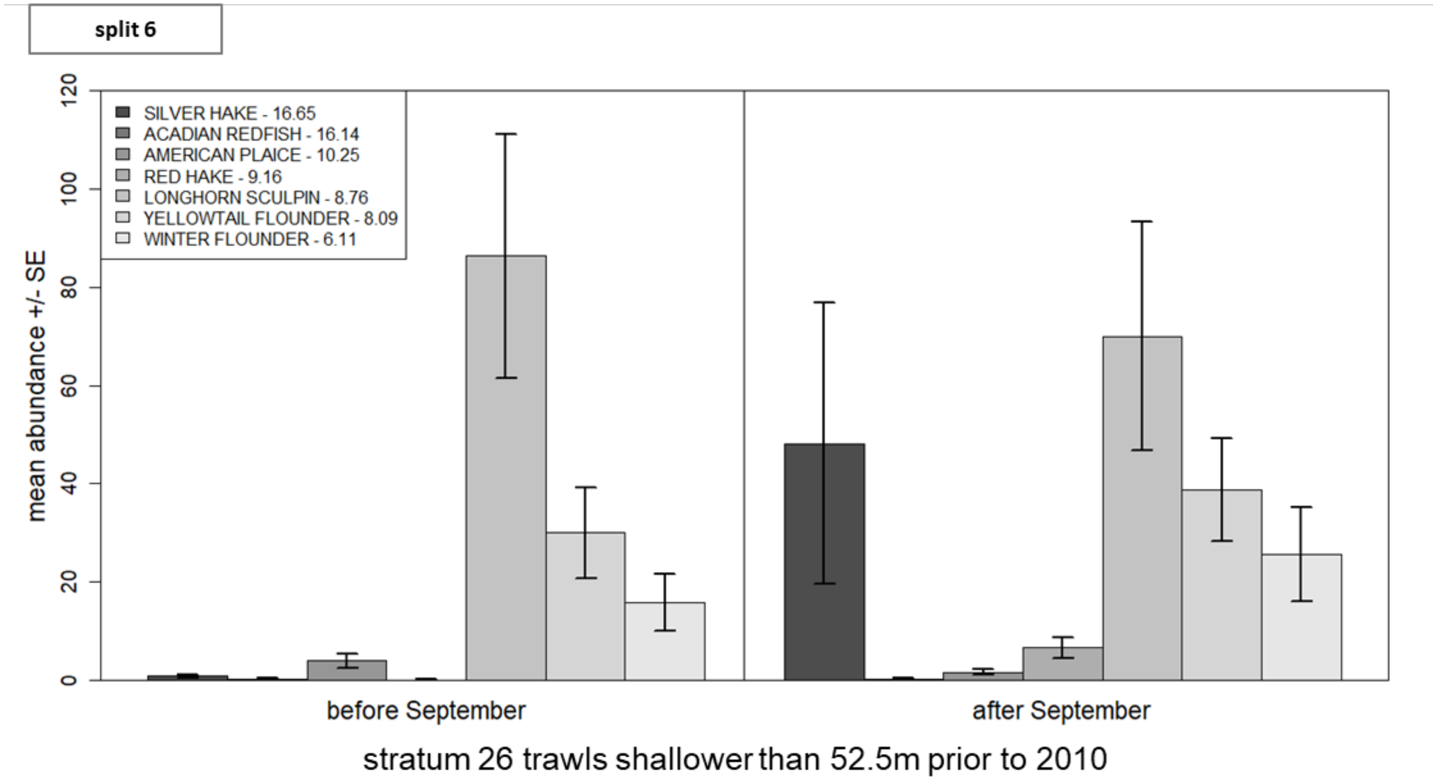


Figure 10. Barplot of principal species mean abundance at each side of split referenced above and in MRT. Error bars are standard error. Numbers in legend are the proportion of variance explained by each species.

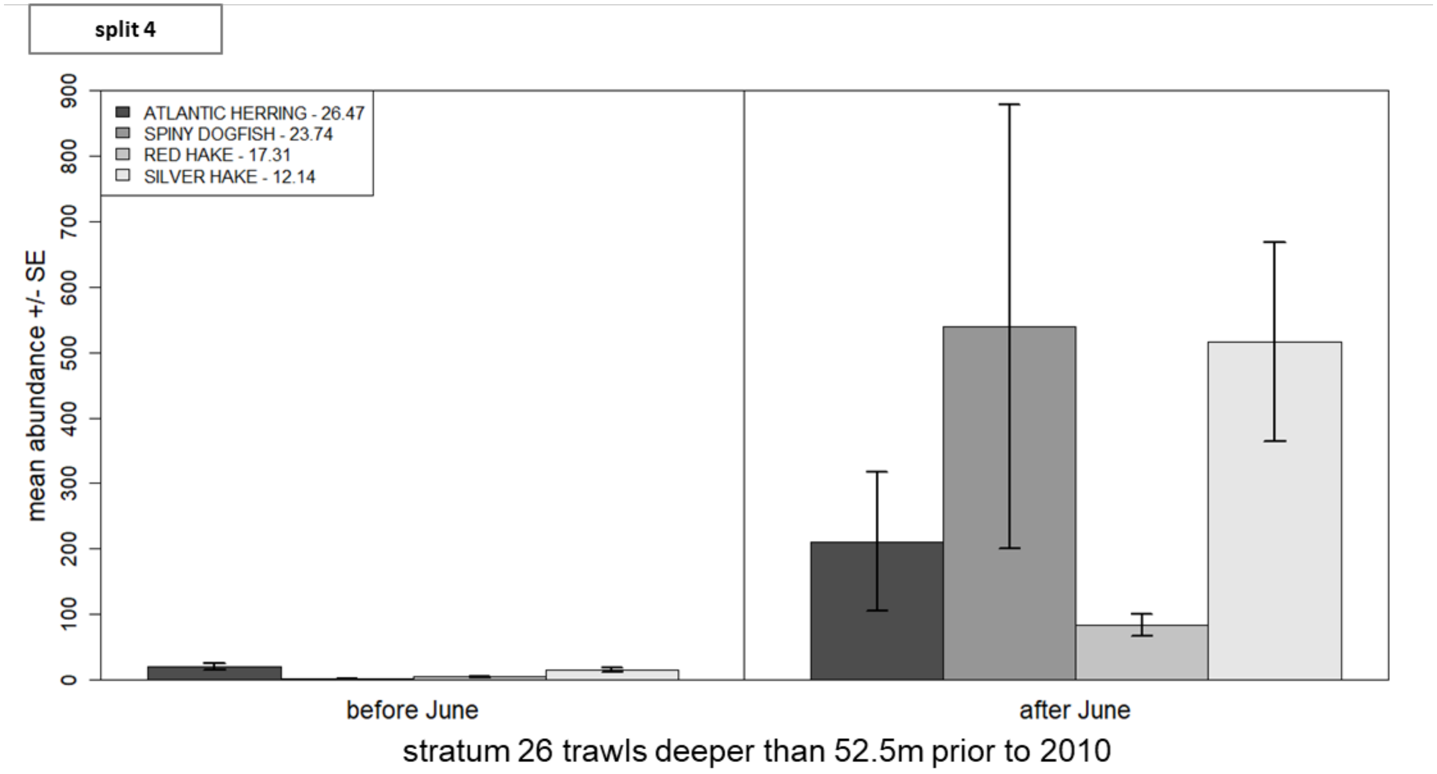


Figure 11. Barplot of principal species mean abundance at each side of split referenced above and in MRT. Error bars are standard error. Numbers in legend are the proportion of variance explained by each species.

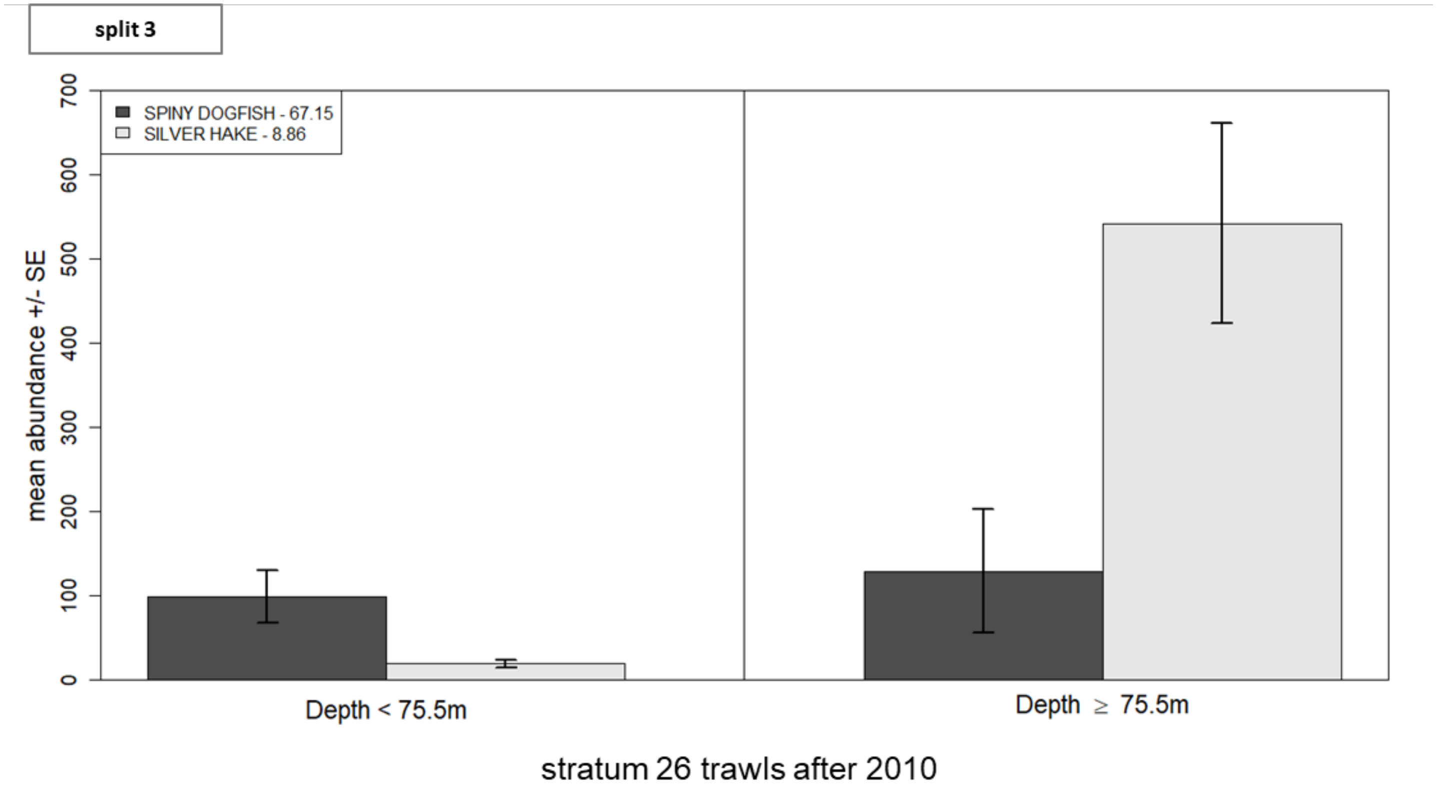


Figure 12. Barplot of principal species mean abundance at each side of split referenced above and in MRT. Error bars are standard error. Numbers in legend are the proportion of variance explained by each species.

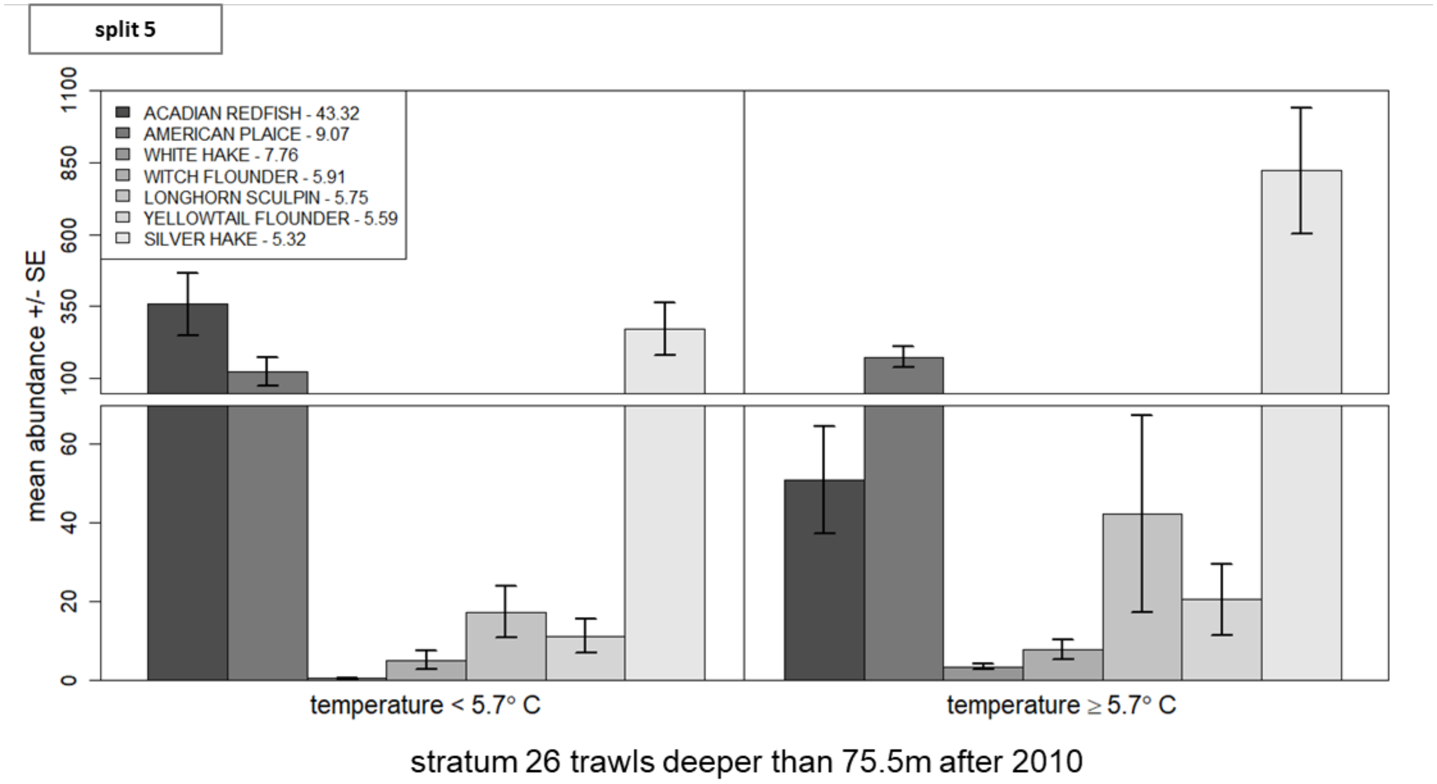


Figure 13. Barplot of principal species mean abundance at each side of split referenced above and in MRT. Error bars are standard error. Numbers in legend are the proportion of variance explained by each species.

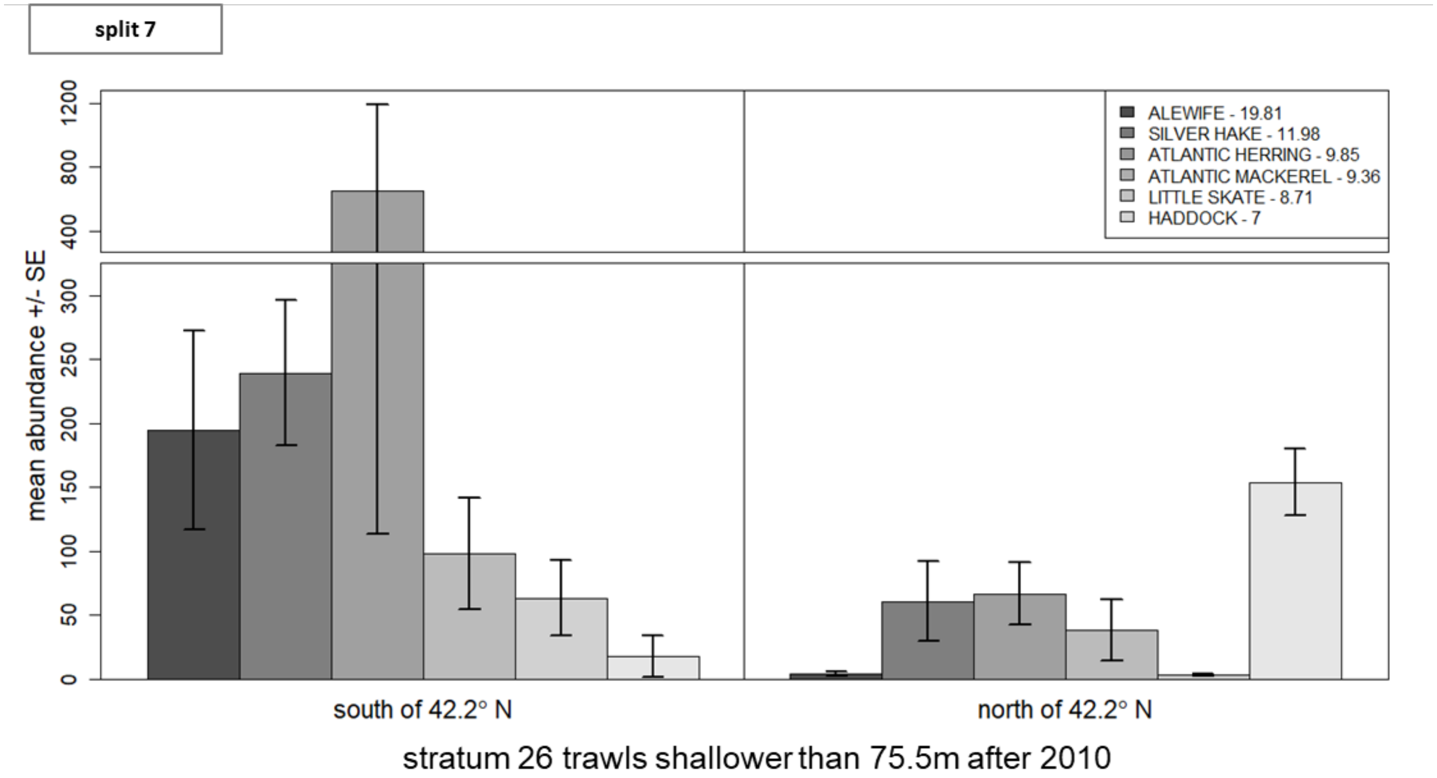
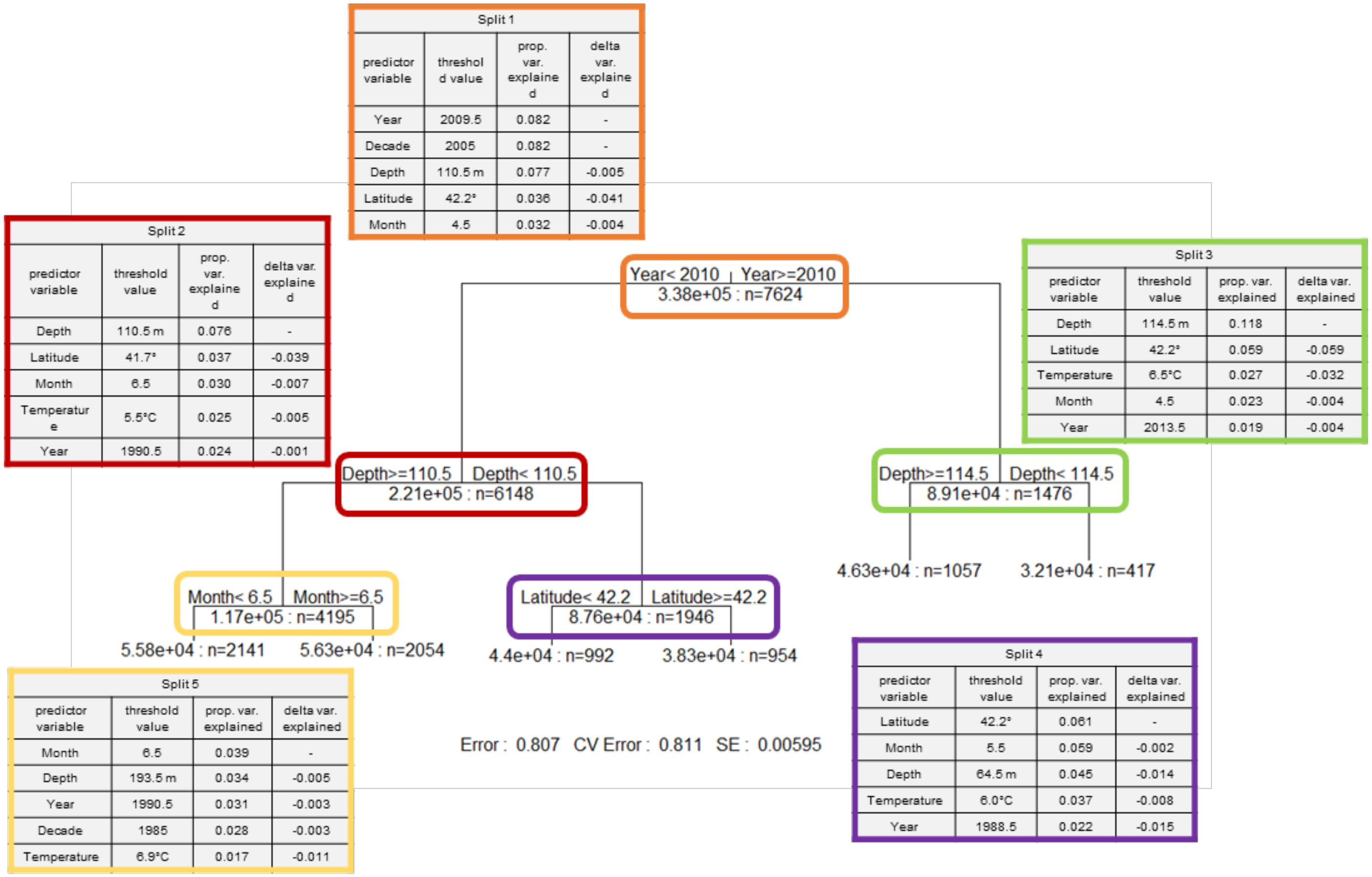


Figure 14. Barplot of principal species mean abundance at each side of split referenced above and in MRT. Error bars are standard error. Numbers in legend are the proportion of variance explained by each species.



Split 1

predictor variable	threshold value	prop. var. explained	delta var. explained
Year	2009.5	0.082	-
Decade	2005	0.082	-
Depth	110.5 m	0.077	-0.005
Latitude	42.2°	0.036	-0.041
Month	4.5	0.032	-0.004

Split 2

predictor variable	threshold value	prop. var. explained	delta var. explained
Depth	110.5 m	0.076	-
Latitude	41.7°	0.037	-0.039
Month	6.5	0.030	-0.007
Temperature	5.5°C	0.025	-0.005
Year	1990.5	0.024	-0.001

Split 3

predictor variable	threshold value	prop. var. explained	delta var. explained
Depth	114.5 m	0.118	-
Latitude	42.2°	0.059	-0.059
Temperature	6.5°C	0.027	-0.032
Month	4.5	0.023	-0.004
Year	2013.5	0.019	-0.004

Split 4

predictor variable	threshold value	prop. var. explained	delta var. explained
Latitude	42.2°	0.061	-
Month	5.5	0.059	-0.002
Depth	64.5 m	0.045	-0.014
Temperature	6.0°C	0.037	-0.008
Year	1988.5	0.022	-0.015

Split 5

predictor variable	threshold value	prop. var. explained	delta var. explained
Month	6.5	0.039	-
Depth	193.5 m	0.034	-0.005
Year	1990.5	0.031	-0.003
Decade	1985	0.028	-0.003
Temperature	6.9°C	0.017	-0.011

Figure 15. Results of multivariate regression tree for the Gulf of Maine region. Tables at each split indicate the proportion of variance explained by each factor in the analysis. Factor with greatest explanatory value (top of table at each split) was used for partitioning data.

split 1

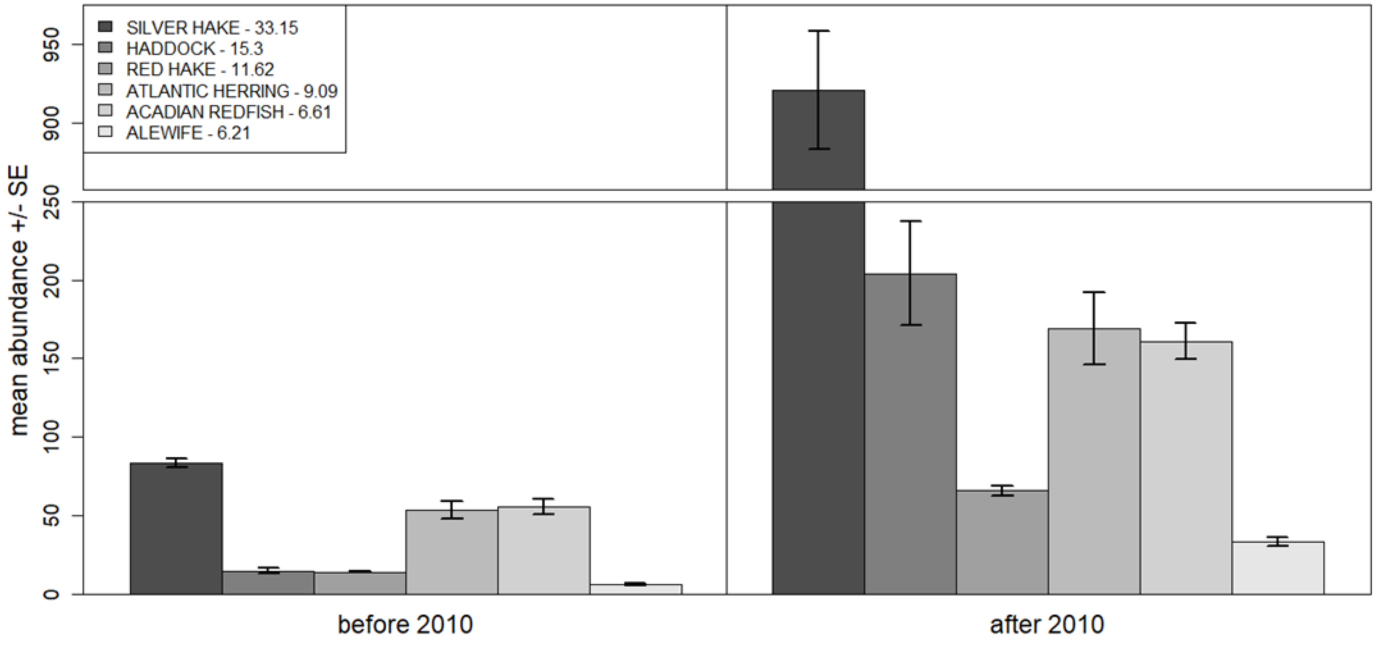


Figure 16. Barplot of principal species mean abundance at each side of split referenced above and in MRT. Error bars are standard error. Numbers in legend are the proportion of variance explained by each species.

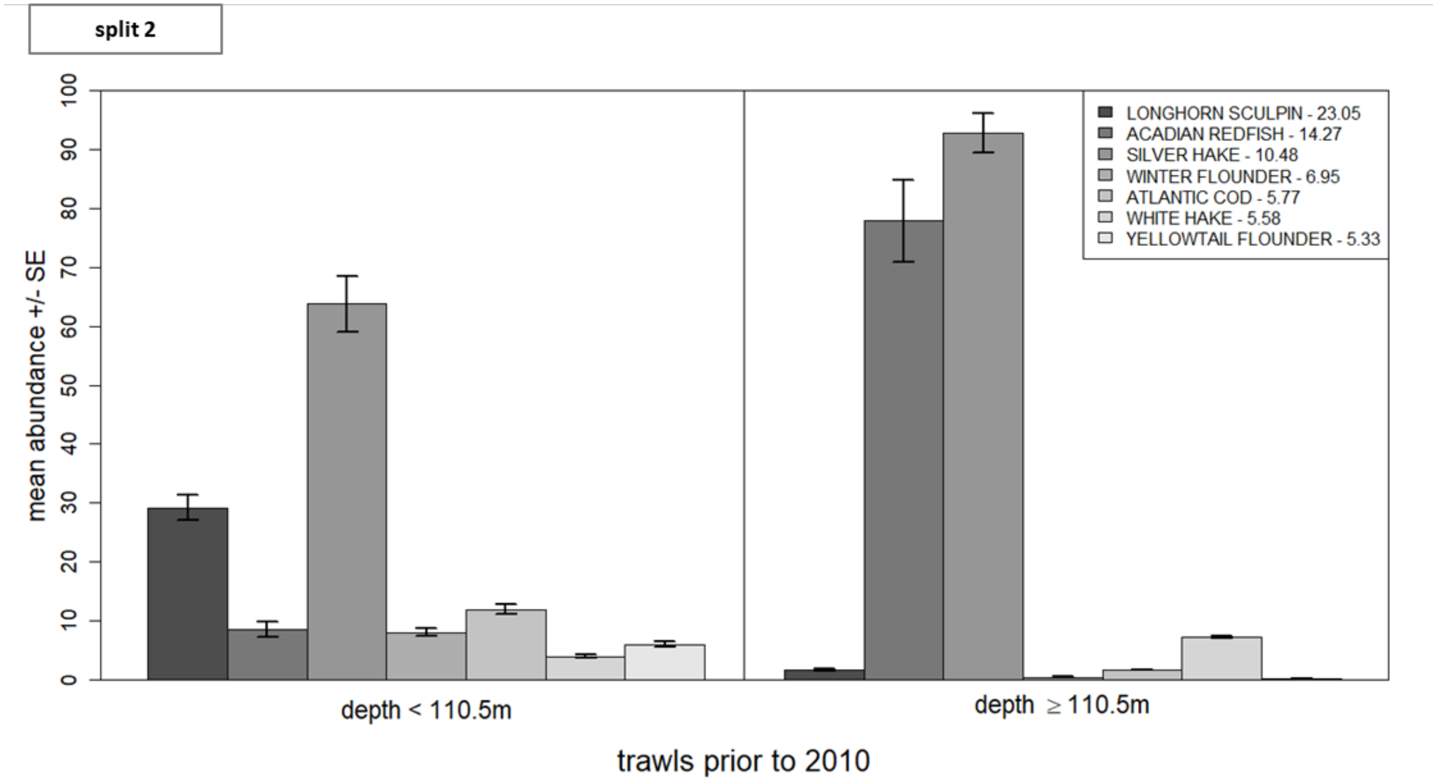


Figure 17. Barplot of principal species mean abundance at each side of split referenced above and in MRT. Error bars are standard error. Numbers in legend are the proportion of variance explained by each species.

split 3

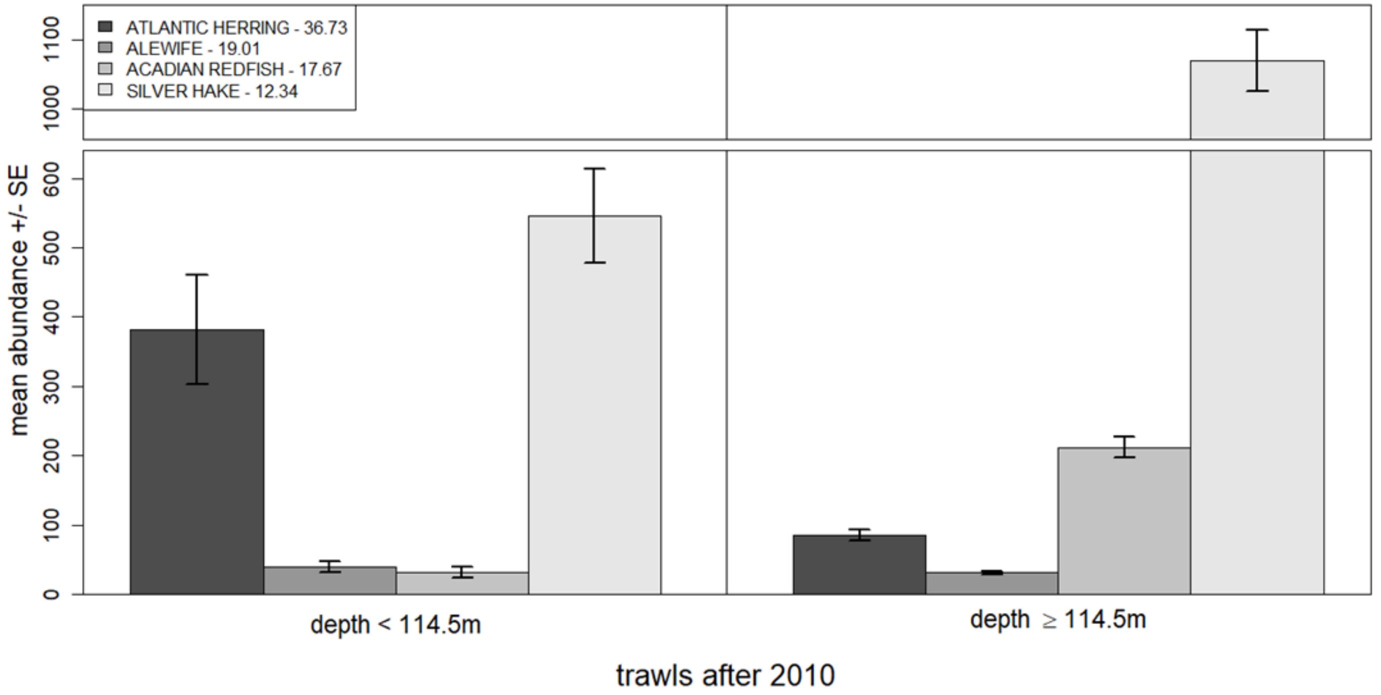


Figure 18. Barplot of principal species mean abundance at each side of split referenced above and in MRT. Error bars are standard error. Numbers in legend are the proportion of variance explained by each species.

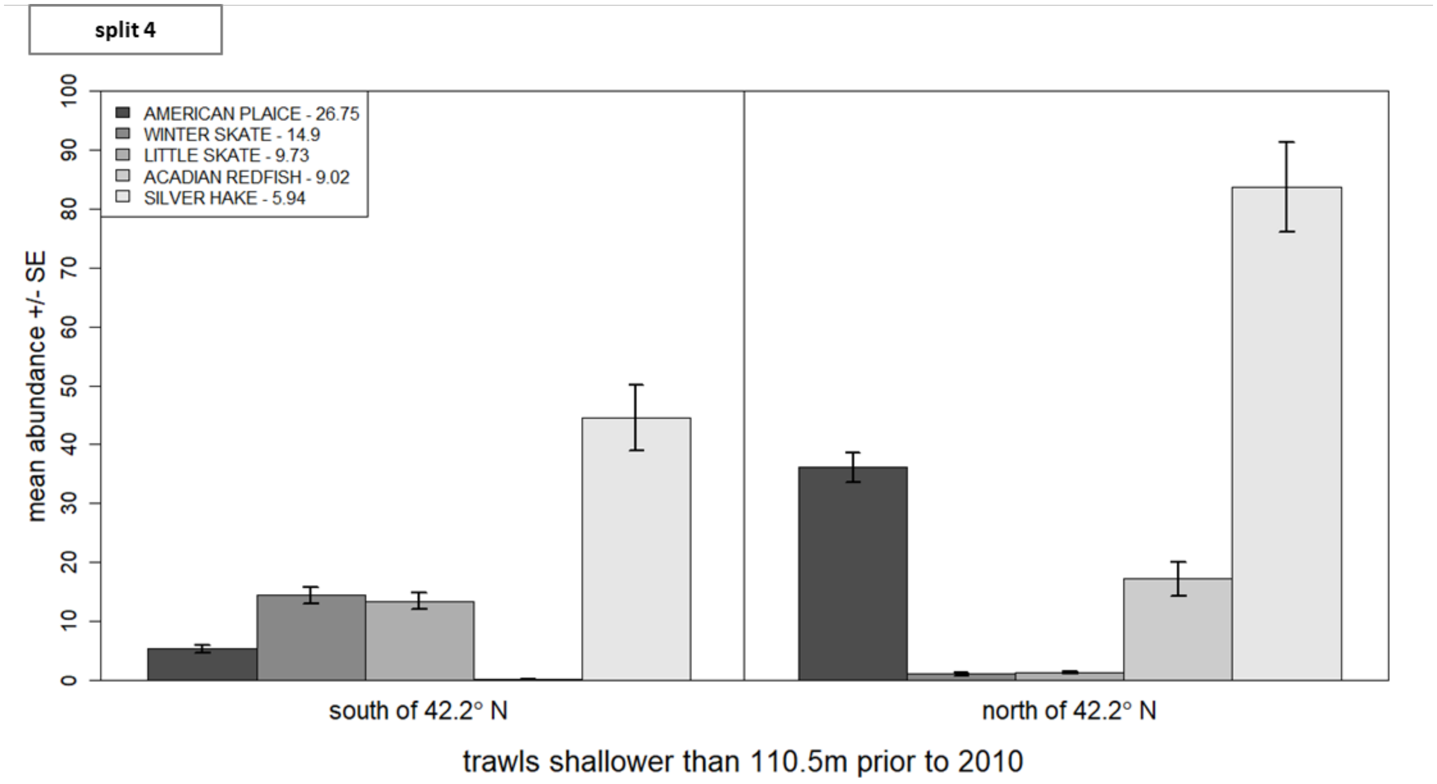


Figure 19. Barplot of principal species mean abundance at each side of split referenced above and in MRT. Error bars are standard error. Numbers in legend are the proportion of variance explained by each species.

split 5

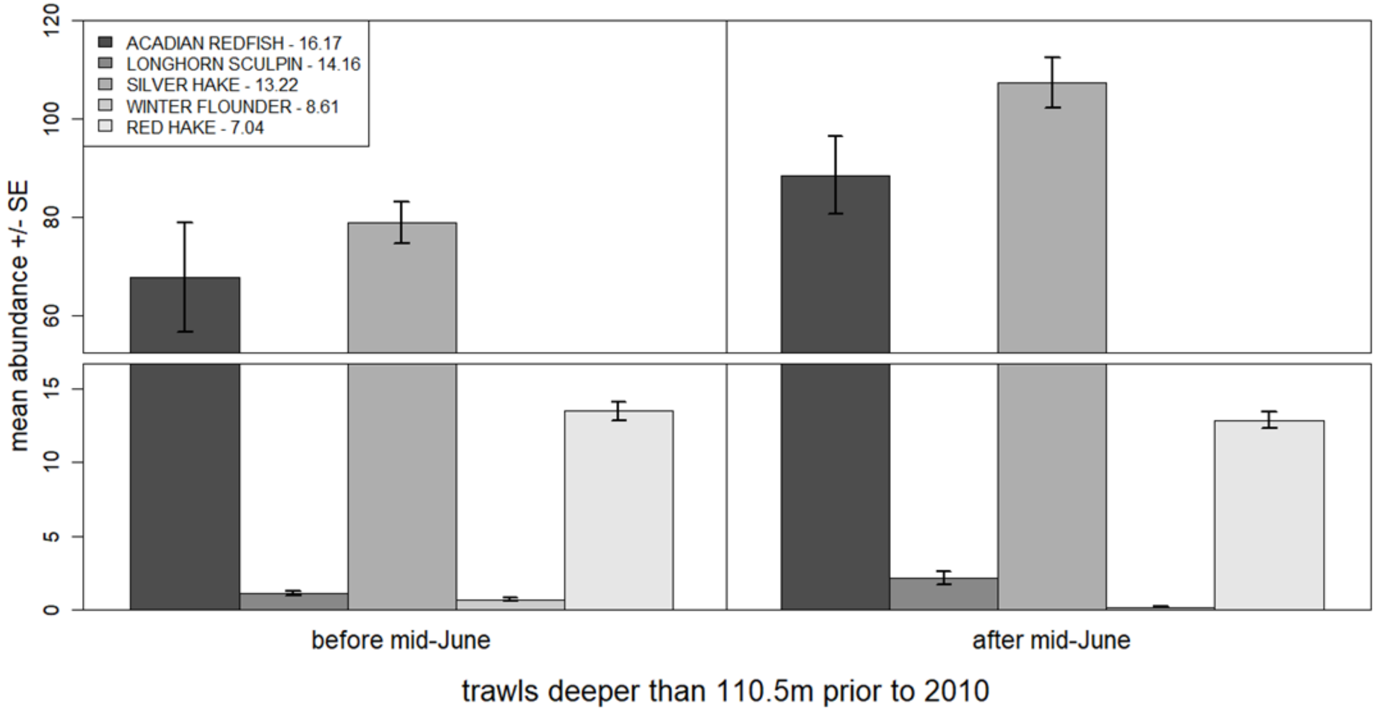


Figure 20. Barplot of principal species mean abundance at each side of split referenced above and in MRT. Error bars are standard error. Numbers in legend are the proportion of variance explained by each species.

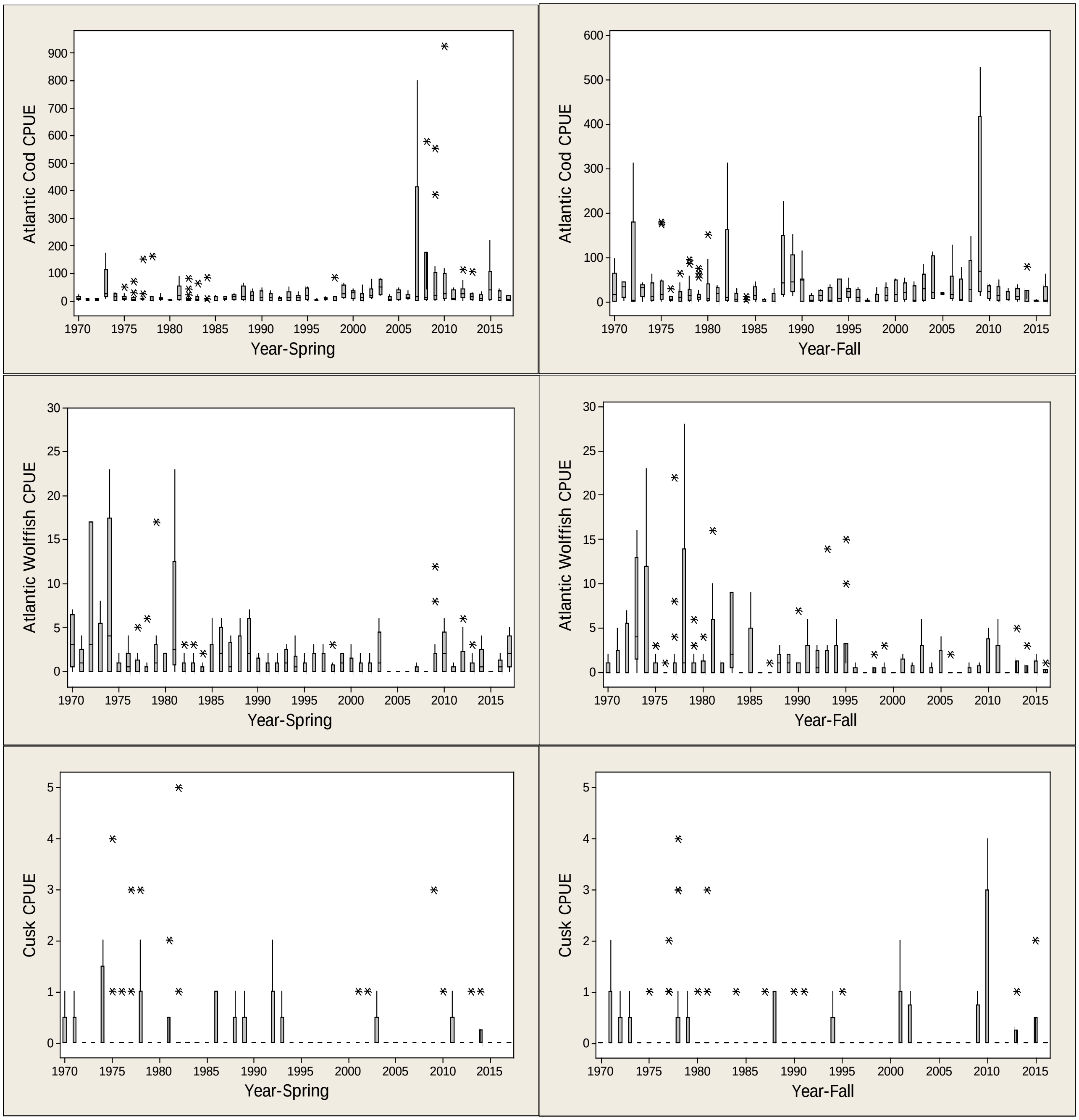


Figure 21. Spring (left) and fall (right) patterns of abundance for Atlantic cod, Atlantic wolfish, and cusk. Refer to Figure 2 regarding details of box-and-whisker plots.

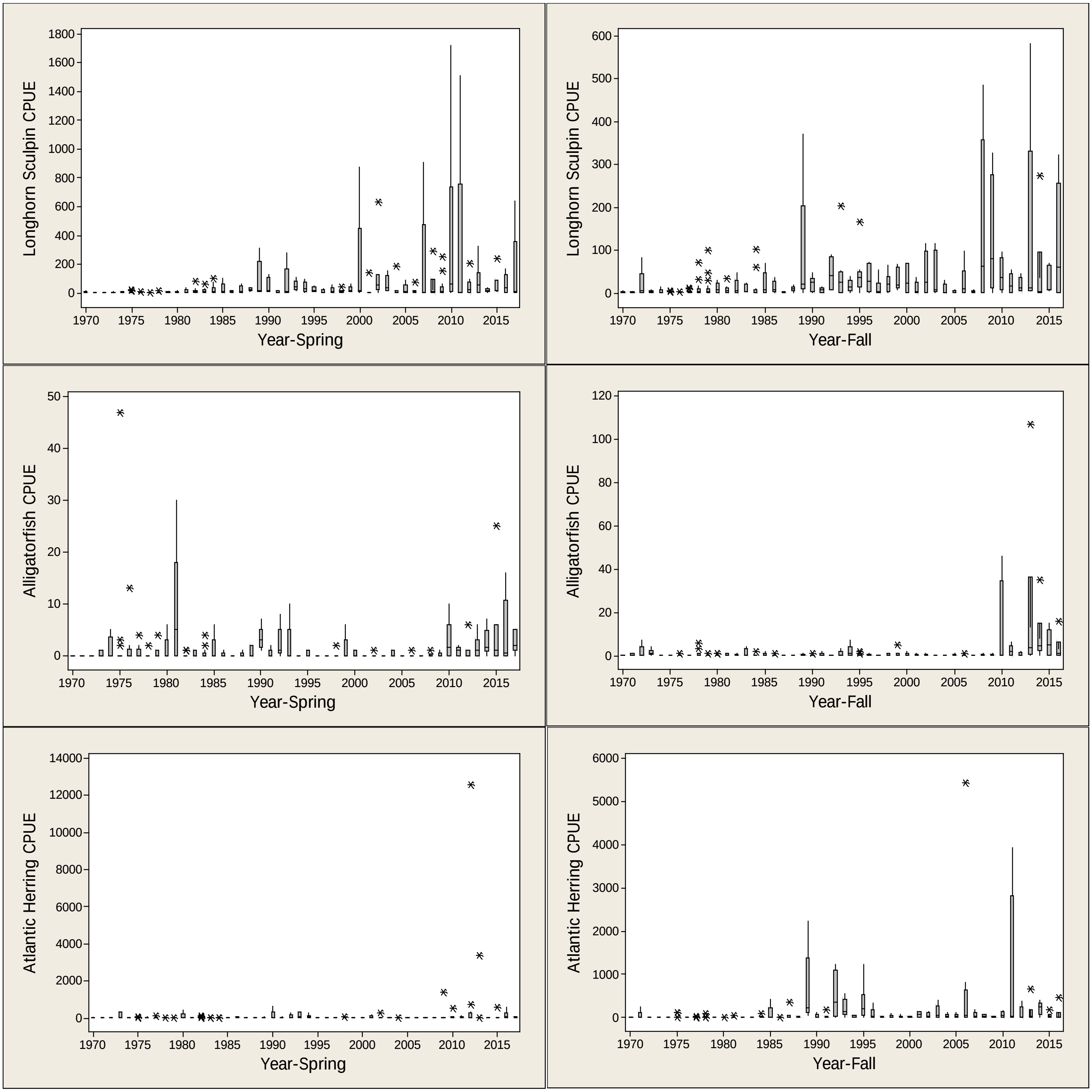


Figure 22. Spring (left) and fall (right) patterns of abundance for longhorn sculpin, alligatorfish, and Atlantic herring. Refer to Figure 2 regarding details of box-and-whisker plots.

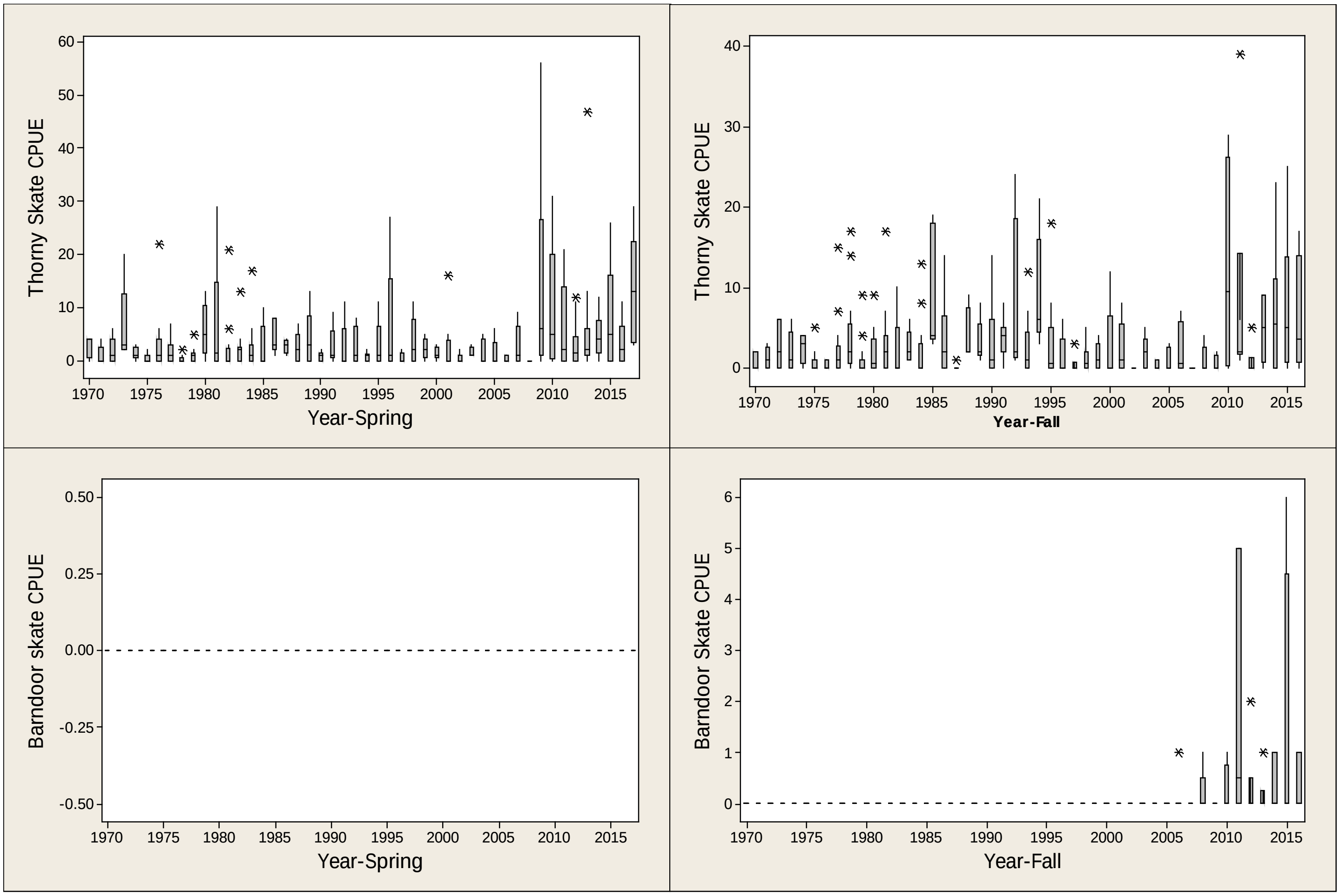


Figure 23. Spring (left) and fall (right) patterns of abundance for thorny skate and barndoor skate. Refer to Figure 2 regarding details of box-and-whisker plots.

Glossary of Acronyms

ANOSIM	Analysis of similaries
CI	Confidence interval
CPUE	Catch-per-unit effort
ESA	Endangered Species Act
MRT	Multivariate regression tree
NEFSC	NOAA Northeast Fisheries Science Center
nMDS	Non-metric multidimensional scaling
NMSA	National Marine Sanctuaries Act
NOAA	National Oceanic and Atmospheric Administration
ONMS	NOAA Office of National Marine Sanctuaries
SBNMS	Stellwagen Bank National Marine Sanctuary
SIMPER	Similarity-percentage

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