Original Article

Environmental drivers and trends in forage fish occupancy of the Northeast US shelf

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The Northeast US shelf ecosystem is undergoing unprecedented changes due to long-term warming trends and shifts in regional hydrography leading to changes in community composition. However, it remains uncertain how shelf occupancy by the region's dominant, offshore small pelagic fishes, also known as forage fishes, has changed throughout the late 20th and early 21st centuries. Here, we use species distribution models to estimate the change in shelf occupancy, mean weighted latitude, and mean weighted depth of six forage fishes on the Northeast US shelf, and whether those trends were linked to coincident hydrographic conditions. Our results suggest that observed shelf occupancy is increasing or unchanging for most species in both spring and fall, linked both to gear shifts and increasing bottom temperature and salinity. Exceptions include decreases to observed shelf occupancy by sand lance and decreases to Atlantic herring's inferred habitat suitability in the fall. Our work shows that changes in shelf occupancy and inferred habitat suitability have varying coherence, indicating complex mechanisms behind observed shelf occupancy for many species. Future work and management can use these results to better isolate the aspects of forage fish life histories that are important for determining their occupancy of the Northeast US shelf.

Keywords: forage fish, range shift, species distribution modelling.

Introduction

Small pelagic fishes dominate the biomass of many productive coastal ecosystems, including upwelling systems and temperate shelves (Cury *et al.*, 2000; Pikitch *et al.*, 2014). These fishes represent both important local fisheries and serve as the focal prey of numerous top predators, giving these fishes the moniker of "forage fishes" in many regions (Pikitch *et al.*, 2014). The coastal Northwest Atlantic is one of these productive, forage fish rich ecosystems, particularly in northern regions such as the Gulf of Maine and Scotian Shelf. The Northeast US shelf occupies a large portion of the coastal Northwest Atlantic, spanning oceanographic and ecological gradients that are temporally dynamic (Chen *et al.*, 2020; Friedland *et al.*, 2020a). Accordingly, the composition of the forage fish community of the region has historically oscillated on both small and large spatio-temporal scales (Fogarty *et al.*, 1991; Richardson *et al.*, 2014). These oscillations include seasonal changes in shelf occupancy by forage fish taxa based on spawning migrations and drastic interannual variability in overall abundance of each species (Fogarty, 1989; Suca *et al.*, 2021). These oscillations have notable effects on both fisheries catches of small pelagic fishes and the diet and distribution of their predators (Overholtz, 2002; Overholtz and Link, 2007; Smith and Link, 2010; Richardson *et al.*, 2014).

The Northeast US shelf hosts a moderate diversity of small pelagic fishes from a variety of taxonomic families with differing life history strategies. Throughout much of the middle to late 20th century, the offshore forage fish complex of the Northeast US shelf was dominated in biomass by northern sand lance (*Ammodytes dubius*) and Atlantic herring (*Clupea harengus*; Richardson *et al.*, 2014; Suca *et al.*, 2021) with high abundances of Atlantic butterfish (*Peprilus triacanthus*) occupying the shelf in the fall (Adams *et al.*, 2015; Adams, 2017). Of these species, sand lance distribution is the only one with minimal seasonal variability. This is in large part due to their reliance on sandy substrates for burying (Nøttestad *et al.*, 1999; Staudinger *et al.*, 2020). Despite this obligate connection with substrate, sand lance presence is highly variable on small spatial scales and interannual scales (Staudinger *et al.*, 2020). The cause of broad scale interannual variability has been linked to drivers of recruitment and overwinter survival given the lack of fishery for this species (Suca *et al.*, 2021), yet the favourability of coincident environmental conditions (often referred to as habitat suitability) has not been explored for this species.

Unlike sand lance, fisheries target Atlantic herring and, thus, historical Atlantic herring abundance has been driven by both fishing, including heavy exploitation until the 1980s (Overholtz and Link, 2007), and environmental conditions, such as haddock predation on herring eggs (Richardson *et al.*, 2011). Atlantic herring exhibit seasonal migrations, moving to portions of the Mid-Atlantic Bight in the winter and spring (in addition to portions of the coastal Gulf of Maine) and more specific spawning locations such as Georges Bank in the fall (Sinclair and Iles, 1985; Overholtz, 2002). While Atlantic herring exhibit some predictable behaviours, such as spawning migrations, the pelagic and schooling behaviour of these fish lead to highly dynamic and variable distribution patterns in space (Overholtz, 2002). The degree to which coincident environmental conditions play a role in herring shelf occupancy has not been explored in depth. Recent work suggests that shelf occupancy for Atlantic herring might be increasing as part of a larger tropicalization of the Northeast US shelf (Friedland *et al.*, 2020b).

Alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*), collectively known as river herring, are other important clupeids in the offshore Northeast US shelf forage fish complex. These species are known to school with Atlantic herring during offshore foraging periods, leading to high bycatch despite lacking targeted fisheries for much of the 20th century (Turner *et al.*, 2015, 2017). A notable separation in life history from Atlantic herring is the anadromous spawning behaviour of river herring, with mature adults moving into rivers and lakes in the spring to spawn and post-spawn adults exiting these freshwater systems in the early to mid-summer to return to ocean-based foraging (Turner *et al.*, 2017). Of the two species, alewife is considered a more northerly species and constitute most of the river herring biomass throughout the offshore Northeast US shelf, in part due to the more coastal distribution of blueback herring (Lynch *et al.*, 2020). Despite their lower abundance, blueback also overlap with Atlantic herring in trawl survey catches, indicating potential for bycatch and mixed schools of forage species (Turner *et al.*, 2015). Previous studies have shown both species of river herring are sensitive to temperature that can drive increased overlap with Atlantic herring and Atlantic mackerel (Turner *et al.*, 2017).

Atlantic mackerel (*Scomber scombrus*), another forage species that often mixes with Atlantic herring, exhibit notable migratory behaviour throughout the Northeast US shelf with highly variable occupancy in spring and migration in the fall after spring spawning, largely in Canadian waters (Radlinski *et al.*, 2013). Atlantic mackerel populations on the Northeast US shelf are composed of two spawning contingents, a southern contingent that spawns in US waters throughout southern New England and the Gulf of Maine, and a northern contingent that spawns on the Scotian shelf and Gulf of St. Lawrence (Overholtz, 1976; McManus *et al.*, 2018). Atlantic mackerel are thought to be highly sensitive to temperature regimes that affect spawning, larval survival, and adult migration patterns (Radlinski *et al.*, 2013; McManus *et al.*, 2018). As planktivorous fishes, Atlantic mackerel larvae have been shown to correspond with areas of higher zooplankton abundance in both the Northwest and Northeast Atlantic, suggesting an important link between Atlantic mackerel distribution and prey fields (Macy *et al.*, 1998; McManus *et al.*, 2018). However, catch of Atlantic mackerel in surveys has been highly variable in the region, leading to efforts to better understand what drives Atlantic mackerel catchability and shelf occupancy through time (Radlinski *et al.*, 2013; Deroba *et al.*, 2010).

Atlantic butterfish (butterfish hereafter), the final members of the offshore Northeast US shelf forage fish complex studied here, are a more sub-tropical to temperate species than the temperate to subpolar sand lance and Atlantic herring (Adams *et al.*, 2015). They also have the distinction of primarily consuming gelatinous zooplankton (Smith and Link, 2010; Suca *et al.*, 2018). Butterfish fisheries on the Northeast US shelf have been historically inconsistent with the largest fishing pressure occurring in the 1980s and a recent implementation of a directed fishery in 2013 (Adams *et al.*, 2015). Like Atlantic herring, butterfish exhibit notable seasonal patterns in distribution due to spawning behaviour, with large butterfish largely moving to the Northeast US shelf edge in the winter and returning to more nearshore shelf waters in summer and fall during spawning, tightly linked to temperature regimes (Adams, 2017). These fish also exhibit age-specific differences in shelf occupancy, particularly in the fall when young butterfish occupy more nearshore water while larger individuals remain offshore (Adams, 2017).

The Northeast US shelf is one of the most rapidly warming regions of the global oceans (Pershing *et al.*, 2015; Chen *et al.*, 2020). This warming has led to observed and predicted changes to the thermal habitat area available to the forage fishes of the region (Kleisner *et al.*, 2017; Friedland *et al.*, 2019). However, the description of a species' niche and habitat often goes beyond just thermal constraints (Friedland *et al.*, 2020b). Previous studies have used a broad suite of potential predictors to describe such habitat and indicated that occupiable habitat by the collective forage fish community of the Northeast US shelf is increasing (Friedland *et al.*, 2020b), though abundance trends do not always align (Friedland *et al.*, 2021). However, the explicit relationships and mechanisms underlying these changes on individual species levels is less clear. Additionally, it is uncertain to what degree coincident environmental conditions are the drivers of this change in occupancy or if external factors, such as recruitment variability, contribute to the observed changes.

Here, we use species distribution models to estimate the change in observed shelf occupancy, mean weighted latitude, and mean weighted bottom depth of six forage fishes of the Northeast US shelf. We further explore the extent to which coincident measures of hydrographic and hydrodynamic conditions control the observed interannual patterns in shelf occupancy (termed inferred habitat suitability) compared to changes in external factors such as

overall abundance and gear selectivity. We hypothesize that observed shelf occupancy in the Northeast US shelf will vary markedly by season but is generally decreasing for the historically abundant, colder-water species (northern sand lance, Atlantic herring, and alewife), increasing for the more sub-tropical species (butterfish and blueback herring), and variable for the migratory Atlantic mackerel. We also hypothesize that each species will likely be changing their mean weighted depth and moving northward with time, depending on temperature sensitivity. We believe this will be particularly notable in fall due to warming trends both constraining northerly species habitat to higher latitudes and deeper waters while expanding the northern range and depth of occupiable shelf for southerly species. Finally, we assess the degree to which patterns in shelf occupancy are connected to changes in inferred habitat suitability, or if they are linked to external factors such as gear selectivity, recruitment, or other parameters that covary with year.

Material and methods
Survey collections
Catches of forage fishes on the Northeast US shelf came from the spring and fall Northeast Fisheries Science Center (NEFSC) bottom trawl surveys, spanning 1968 to present for the spring survey and 1963 to present for the fall survey. During each survey, 300–400 stations are sampled in a random stratified design, ranging from the Western Scotian Shelf to Cape Hatteras. At each station, catches of each species are weighed and individuals are measured, with subsampling occurring when catches were large. Further details of the survey and sampling gear are found within Politis *et al.* (2014). We note that this survey employs a bottom trawl and, thus, does not fully or perfectly capture the habitat of pelagic and schooling fishes. However, this survey is used to attain indices of abundance for the purpose of stock assessment of these fishes and is reliable for understanding their distribution (Deroba 2018; NEFSC, 2018). The one possible exception to this is Atlantic mackerel, for which the survey is used but considered less reliable (see Discussion; Deroba *et al.* 2010).

The survey has changed gears on multiple occasions, including a change in survey vessel. In 1985, during the tenure of the first vessel, *Albatross IV*, the trawl doors were changed, which resulted in a notable change in Atlantic herring catches in the survey (NEFSC, 2018). Given noted mixed school behaviour of river herring (alewife and blueback herring) with Atlantic herring, we assumed this change also affected catches of river herring (Turner *et al.*, 2015). The change in doors was not considered to have as large an effect on the catch of the other forage fishes included in this study and is thus only considered for the clupeids. In 2009, the survey switched from the NOAA Ship *Albatross IV* to the NOAA Ship *Henry Bigelow* resulting in notable changes in catches for all species in this study (Miller *et al.*, 2010). This change in ship was coupled with a change in cod-end liner for collections, widening the mesh from 1/2" to 1" and rendering sand lance catchability unreliable after 2009 (Richardson *et al.*, 2014). A suite of inshore strata was also lost in the transition from the NOAA Ship *Albatross IV* to the NOAA Ship *Henry Bigelow*. We decided to retain inshore strata from the NOAA Ship *Albatross IV* because these strata represent important habitat for some taxa and an exploratory analysis indicated that models using only offshore strata did not influence the predictive capability of predominantly offshore species.

Fall butterfish catches were split into two size classes based on age and known differences in distribution (Adams, 2017). Small butterfish, known to inhabit more nearshore waters in fall, were classified as those ≤11 cm, while large butterfish were all fish >11 cm. This was only done for the fall survey as the spring survey primarily catches large individuals (Adams, 2017).

Environmental data
Conductivity, temperature, and depth sensors (CTDs) became commonplace on the bottom trawl surveys in 1992, and this *in situ* data was used for sea surface temperature (SST), sea surface salinity (SSS), bottom temperature (BT), and bottom salinity (BS) when available. To fill in data from years prior to 1992, hindcast estimates of hourly surface and BT and salinity were used from the third generation Gulf of Maine Finite Volume Community Ocean Model (FVCOM-GOM3; Chen *et al.*, 2011; Li *et al.*, 2017). Horizontal resolution ranges from 0.3 to 10 km, with finer horizontal resolution in coastal regions and tidal mixing fronts (e.g. Georges Bank, Supplementary Figure S1) and coarser resolution at the boundaries near the shelf break (Chen *et al.*, 2011; Xue *et al.*, 2014; Ji *et al.*, 2017). GOM-FVCOM is nested within the FVCOM-Global model to ensure water property conservation at its boundaries (Chen *et al.*, 2011). Previous studies have confirmed that GOM-FVCOM accurately recreates hourly to interannual variability in currents (Sun *et al.*, 2016; Li *et al.*, 2017), including a comparison with observed drifters (Sun *et al.*, 2016). GOM-FVCOM assimilates satellite SST and CTD data from surveys and a buoy array, leading to accurate representations of temperature and salinity throughout much of the survey domain (Xue *et al.*, 2014).

To ensure FVCOM accurately represented temperature and salinity fields during the trawl surveys, hourly estimates from GOM-FVCOM were matched to every station from 1992 to 2016 for salinity and every station with available temperature data from 1979 to 2016 from *in situ* CTD casts or expendable bathythermographs. Overall trends show good agreement with surface temperature (spring $R^2 = 0.81$, fall $R^2 = 0.95$) and moderately good agreement for surface salinity (spring $R^2 = 0.79$, fall $R^2 = 0.72$), BT (spring $R^2 = 0.71$, fall $R^2 = 0.79$), and BS (spring $R^2 = 0.77$, fall $R^2 = 0.80$). The residuals from these trends were grouped by stratum, and any stratum that had an average residual $> 2°C$ for spring and $> 3°C$ for fall for temperature, or >1 for salinity, was excluded from analyses in all years (Figure 1). The more relaxed threshold for fall was to ensure there were sufficient strata to represent the habitat of the fishes in the study due to FVCOM's poorer performance of recreating BTs in the summer and early fall (Li *et al.*, 2017). This strategy of removing entire strata across years was to retain the random stratified nature of the survey so that interannual differences were not driven by spatial biases. We note that the error within these thresholds may be significant for biological function, but more restrictive thresholds did not affect model performance. This led to the exclusion of 17 strata in the fall (4.9% of the cumulative area) and 35 strata in the spring (10.1% of cumulative area; Figure 1). In the case of the spring survey, many slope strata, which represent known habitat for Atlantic mackerel and butterfish (Overholtz *et al.*, 2011; Adams, 2017), were excluded. It is thus important to acknowledge that our metrics represent shelf occupancy within the strata included in each model and do not always represent the full shelf occupancy for each species, namely spring Atlantic mackerel and butterfish.
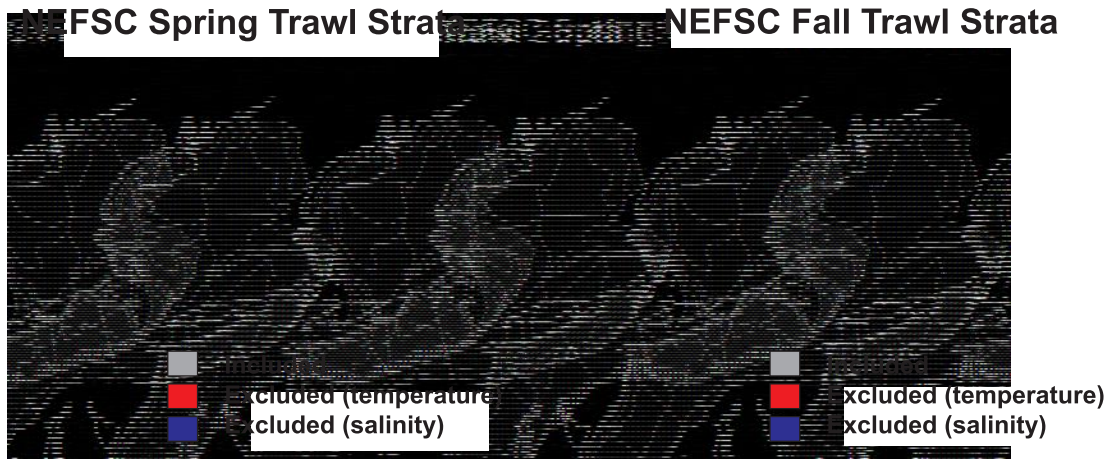
Figure 1. Map of Northeast US shelf and strata from the NEFSC spring and fall bottom trawl survey. Strata are colour coded by whether they were used for modelling for the given season based on accuracy of FVCOM temperature or salinity estimates.

Daily mean total kinetic energy (TKE) was used to incorporate kinetic energy generated from tidal dynamics along many shallow banks on the Northeast US shelf that represent zooplankton aggregations and feeding hotspots (Lough and Manning, 2001; Wishner *et al.*, 2006). Use of daily current averages negates tidal effects due to the multiple shifts in direction throughout the course of the day. We, thus, calculated an estimate of daily mean kinetic energy based on hourly data with the following equation:

$$TKE_{Daily} = \frac{\sum_{i=1}^{24} \frac{1}{2} \left(u^2_i + v^2_i \right)}{24} \, ,$$

where u_i and v_i represent vertically averaged hourly zonal and meridional velocities at a given location. u_i and v_i estimates originated from FVCOM-GOM3.

Sediment grain size data were estimated based on point observations in the US Geological Survey East Coast Sediment Texture Database (http://pubs.usgs.gov/of/2005/1001/data/surficial_sediments/ecstdb2005.zip). Sediment grain size were interpolated to each collection location using inverse distance weighting in the *gstat* package in R (Pebesma and Graeler 2021).

Bathymetric slope estimates were calculated from NOAA NCEI bathymetry data. A 2-km slope was used as the metric to represent local scale slope that is less likely to be associated with the offshore slope of the Northeast US shelf, where strong correlations exist between bottom hydrography and slope (Mountain, 2012).

Species distribution model formation

Species distribution models were formed using generalized additive models (Wood, 2017). Generalized additive models are non-parametric extensions of generalized linear models, with the assumption that variables are additive. GAMs can represent complex, nonlinear relationships between predictor and response variables, a common occurrence with ecological data (Guisan and Thuiller, 2005).

For each taxon, the full suite of hydrographic and benthic variables were included. Year was included as a random intercept for each species and season to account for changes in overall presence of each taxon driven by dynamics other than localized habitat availability (Brodie *et al.*, 2015; Thorson, 2019). These year effects were

coupled with a fixed-gear effect, reflecting a change in intercept based on catchability by the gear changes described above. This resulted in the following general equation:

$$\log \left(\frac{pr}{1 - pr} \right) = \beta + Gear + s \left(Env_1, \ k \ = \ 6 \right)$$
$$+ s \left(Env_2, k \ = \ 6 \right) \ldots + \ s \left(Env_n, k \ = \ 6 \right)$$
$$+ te \left(Longitude, \ Latitude \right) + s \left(Year, \ ``re" \right),$$

where *pr* represents the probability of occurrence of a given species, *s* represents a thin-plate regression spline, *k* represents the number knots for the basis functions of the spline, *Env* represents an environmental predictor (e.g. temperature), *te* represents a tensor product, *re* represents a random effect, and β represents the model intercept. The number of knots were capped at six to prevent overfitting of data, ensuring the relationships between the predictor variables and the response are ecologically feasible (Rooker *et al.*, 2012). Models were fit to all but the final 3 years of the usable time series for each taxon (1979–2013 Atlantic herring, alewife, blueback herring, Atlantic mackerel, and butterfish; 1979–2005 for sand lance).

We used the information theory approach to model selection and fitting (DeLeeuw, 1973). Variance inflation factors (VIF) were used for determination of which variables to drop from consideration before model selection. These values were determined using the vif.gam function in the *mgcv.helper* package (Clifford, 2019). Variables with a VIF > 10 were removed from consideration. While this value is fairy relaxed, we chose this value to include as many possible predictors in model selection as reasonably possible. If multiple variables resulted in VIF > 10, single variable GAMs (including year effects and longitude, latitude tensor product) were fit to the data for each variable and the model containing the variable with the lowest AIC was retained. This process was repeated until the largest possible suite of variables with VIFs < 10 remained.

Model selection and averaging

After predictors resulting in high VIF values were removed, all possible combinations of predictors for each taxon and season were compared using Akaike Information Criterion (AIC) *via* the dredge

Table 1. Sum of Akaike weights for variables for spring models. Variables with no value were not included in the model because of variance inflation (see methods). AUC represents the area under the receiver operating curve for predictions of the test set of data for each model.

Variable	Spring					
	Sand lance	**Butterfish**	**Atl. herring**	**Alewife**	**Blueback herring**	**Atl. mackerel**
Bottom temperature	–	1	–	1	–	1
Bottom salinity	0.999	–	1	–	–	–
Surface temperature	0.716	–	1	1	1	1
Surface salinity	–	–	0.142	0.999	0.895	1
TKE	1	–	0.962	1	–	0.999
Bathymetric slope	–	–	–	0.987	–	–
Grain Size	0.962	–	0.786	0.379	0.999	0.891
AUC	**0.822**	**0.888**	**0.724**	**0.762**	**0.713**	**0.610**

function within the *MuMIn* package in R (Barton, 2010). In all cases, gear, year random intercepts and the tensor product of longitude, latitude were included to reduce run time. Models with AIC values <4 from the best fit model were averaged to account for uncertainty in model selection given the exploratory nature of our analyses and information theory-based approach. These model averages for each taxon and season were used for all subsequent analyses and predictions.

Model validation

Predictive capability of models was tested using receiver operating characteristic curves (ROC). ROC curves measure true positive rate (specificity) against false positive rate (sensitivity) at different thresholds. The area under this curve (AUC) can be used as a metric of predictive strength of presence/absence models, with values close to 1 representing high predictive capability and values close to 0.5 representing capability approaching random chance. AUC values were calculated for model predictions over the final 3 years of each time series. In these predictions, year intercepts were set to the year within the final gear type that had the closest mean stratified catch to the catch in the predicted year due to the close relationship between the year intercept value and abundance (see results; Supplementary Figures S2 and S3). Gear type was set to the final gear type used in the survey for a given species.

Individual variable importance for the final, averaged models were determined through the sum of Akaike weights. Akaike weights were calculated as follows:

$$w_i = \frac{\exp\left[-\frac{1}{2}\Delta_i\right]}{\sum_{i=0}^{n}\exp\left[-\frac{1}{2}\Delta_i\right]},$$

where Δ_i represents the difference in AIC of a particular model from the lowest AIC for any model iteration for a given species and season. The Akaike weight for each model in which a variable was included was then summed to reach the sum of Akaike weights for the variable. Values close to 1 represent high variable importance, with values close to 0 representing low importance (Giam and Olden, 2016).

Proportion of suitable habitat

Environmental covariates for each year of the survey (1979–2016 for all species but sand lance; 1979–2008 for sand lance) were averaged over 0.1° x 0.1° bins across "usable" strata for each season.

For FVCOM-sourced data (temperature, salinity, and mean kinetic energy), these values were averaged over March–April for the spring surveys and September–October for the fall survey, corresponding to the primary months of each survey. In each case, a small portion of grid cells (∼3%) did not contain an FVCOM node and thus did not have temperature, salinity, or kinetic energy estimates. Values for these cells were estimated using inverse distance weighting with the *gstat* package in R (Pebesma and Graeler, 2021).

For each year, the final, averaged model for each taxon and season was used to predict probability of occurrence within each grid cell. If a grid cell had a probability of occurrence greater than the mean prevalence for a given species and season, it was deemed suitable. Mean prevalence was used instead of a threshold such as 0.5 as using prevalence has been identified as minimizing the discrepancy between specificity and sensitivity (Jiminez-Valverde and Lobo, 2007). Annual proportion of suitable habitat for each season was calculated as the proportion of grid cells exceeding this threshold.

We performed predictions and calculations of shelf occupancy in two ways: (i) using models that included the random year intercepts and gear effects, thus, including a proxy for likelihood of occurrence due to factors other than coincident environmental covariates; and (ii) using models where the random year intercepts were set to 0 and the gear effect was set to that of the NOAA Ship *Albatross IV* after the door change (1985–2008; representing the gear type with an intermediate catchability and smallest standard error of the three gear types). These methods allow for comparison of trends in observed shelf occupancy that incorporate interannual differences due to factors like recruitment or catchability, which are not explicitly measured by the model (inclusion of random year intercepts and gear effects, i.e. terms *Gear + s(Year, "re")* in equation), to trends that solely assess changes to shelf occupancy due to changes in the environmental predictors (no random intercepts and fixed gear, i.e. terms $\beta + Gear_B + s(Env_1, k = 6) + s(Env_2, k = 6) \ldots + s(Env_n, k = 6)$ in equation). We term the latter metric, which controls gear and excludes year effects, "inferred habitat suitability" owing to the removal of effects that are not tied to the local hydrography and bathymetry (though some aspects of habitat may be implicitly associated with random effect terms). Given that environmental covariates represent coinciding measurements (matching in space and time), they do not well-represent lagged effects of hydrography on things like recruitment or interannual population growth. These effects would be captured within the year effects and further analysis of the drivers of year effects requires a careful examination of each species' life history and is beyond the scope of this study. The "inferred habitat suitability" metric allows
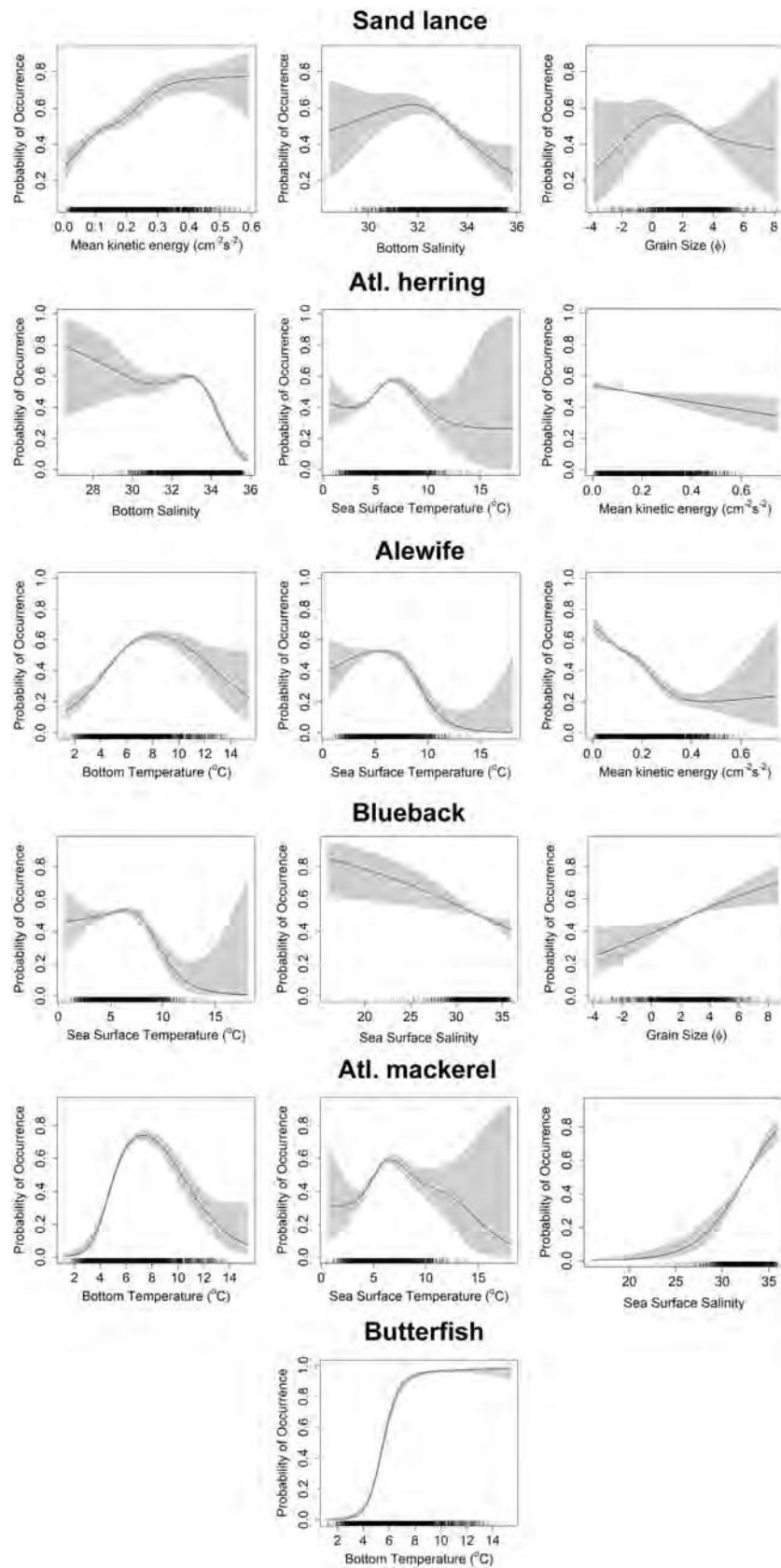
Figure 2. Response curves for variables with the three highest sum of Akaike weights per species for spring models.

Table 2. Sum of Akaike weights for variables for fall models. Variables with no value were not included in the model because of variance inflation (see methods). AUC represents the area under the receiver operating curve for predictions of the test set of data for each model.

Variable	Fall						
	Sand lance	Butterfish (<11 cm)	Butterfish (>11cm)	Atl. herring	Alewife	Blueback herring	Atl. mackerel
Bottom temperature	–	1	1	1	1	1	1
Bottom salinity	–	–	–	–	–	–	–
Surface temperature	–	–	0.995	–	–	–	–
Surface salinity	–	0.999	0.672	–	–	–	–
TKE	1	0.451	0.998	–	–	–	–
Bathymetric slope	–	–	1	–	–	–	–
Grain Size	–	0.461	0.965	–	–	–	–
AUC	**0.826**	**0.615**	**0.687**	**0.977**	**0.973**	**0.971**	**0.936**

us to garner insight on how hydrographic conditions drive spatial preferences and associations of these fishes that affect availability and catchability of these fishes to the surveys, fishers, and top predators. However, we recognize that we are using the term "habitat suitability" loosely, as the nature of our study is correlative (though not linear) and we are using an approximation of habitat characteristics of these forage fishes.

To estimate how much year intercepts and gear were related to total abundance of a given species caught in a given season, we calculated the correlation between year- and gear-specific intercept values and log stratified area-weighted mean abundance of a given taxon in a given season throughout the shelf. These models were fit as a simple linear regression (although note the log transform of the abundance metric).

Temporal trends in proportion of shelf occupancy for both fixed (inferred habitat suitability) and random intercept predictions (observed shelf occupancy) were tested with beta regression using the R package *betar*, with annual proportion of suitable habitat as the response variable and year as the predictor.

We illustrated spatio-temporal differences in occurrence for each species and season through estimating the change in mean occurrence of each species and group in the final 5 years of the survey minus the mean estimated occurrence in the first 5 years of the survey. This value was computed for each $0.1°$ by $0.1°$ grid cell and the value named "difference in occurrence." We only computed these values for the inferred habitat suitability metric (i.e. removing gear- and year-specific intercepts) due to gear effects obscuring inference from these maps for shelf occupancy.

We also calculated mean weighted latitude and depth of occurrence for each taxon and season. Depth values were assigned to each grid cell from $0.1°$ by $0.1°$ spatial averages. Weighted mean values were calculated using the following equation:

$$MW_{Var} = \frac{\sum_{i=1}^{n} \Pr(1)_i * Var_i}{\sum_{i=1}^{n} \Pr(1)_i},$$

where MW_{Var} represents the mean weighted value for variable *Var* (either depth or latitude), $\Pr(1)_i$ is the predicted probability of a species occurrence in grid cell i, and Var_i is the mean value for *Var* in grid cell i. Temporal trends in mean weighted latitude and depth were calculated for both shelf occupancy estimates with and without year- and gear-specific intercepts. Using model predictions has the advantage over direct survey observations both by allowing the calculation of these metrics over a fixed grid each year, removing any potential for subtle biases from changes in trawl locations

within each stratum by year that may confound these calculations, and allowing for the near removal of gear biases when fixing intercept values (Maureaud *et al.*, 2021).

Results

Predictor importance and predictive capability

Predictor importance, as determined by sum of Akaike weights, varied notably by forage fish species in spring (Table 1). SST and eddy kinetic energy were the environmental predictors with the most consistently high sum of Akaike weights, with both having a sum of Akaike weights > 0.9 for four of the six species (Figure 2). Temperature and/or salinity were important predictors for all species in the spring. Daily mean kinetic energy had high sum of Akaike weights values for sand lance, Atlantic mackerel, alewife, and Atlantic mackerel. Sediment grain size had high sum of Akaike weights values for sand lance and blueback herring and bathymetric slope only had a sum of Akaike weights > 0.9 for alewife.

Fall models were less complex, often including only one environmental predictor. BT was overwhelmingly important in fall models, being included in all species models except sand lance (Table 2 and Figure 3). BT was the only predictor included for Atlantic herring, alewife, blueback herring, and Atlantic mackerel due to its high predictive capability leading to high VIFs with other predictors. Both large and small butterfish fall models included more predictors, such as mean kinetic energy and grain size.

Variance estimates of the random year effects varied notably among species in both seasons, with the highest values for sand lance in both seasons. Blueback herring and alewife generally had low variance estimates compared to the other forage species (Supplementary Tables S1 and S2). Atlantic herring and Atlantic mackerel had moderate variance estimates in both seasons. Gear effects varied notably by species, with minimal effects for butterfish and mackerel for both seasons, while gear effects were strongest for Atlantic herring.

Most spring models showed reliable predictive capability for stations and years outside of the dataset (AUC > 0.70), while the Atlantic mackerel model had an AUC of 0.61 (Table 1). The butterfish model had the highest predictive capability (AUC = 0.89) and was the most parsimonious. Fall models only containing BTs had high predictive capability, with AUC > 0.9 for all four taxa. Similarly, daily mean kinetic energy was the only environmental predictor included in the sand lance model due to high VIFs when coupled
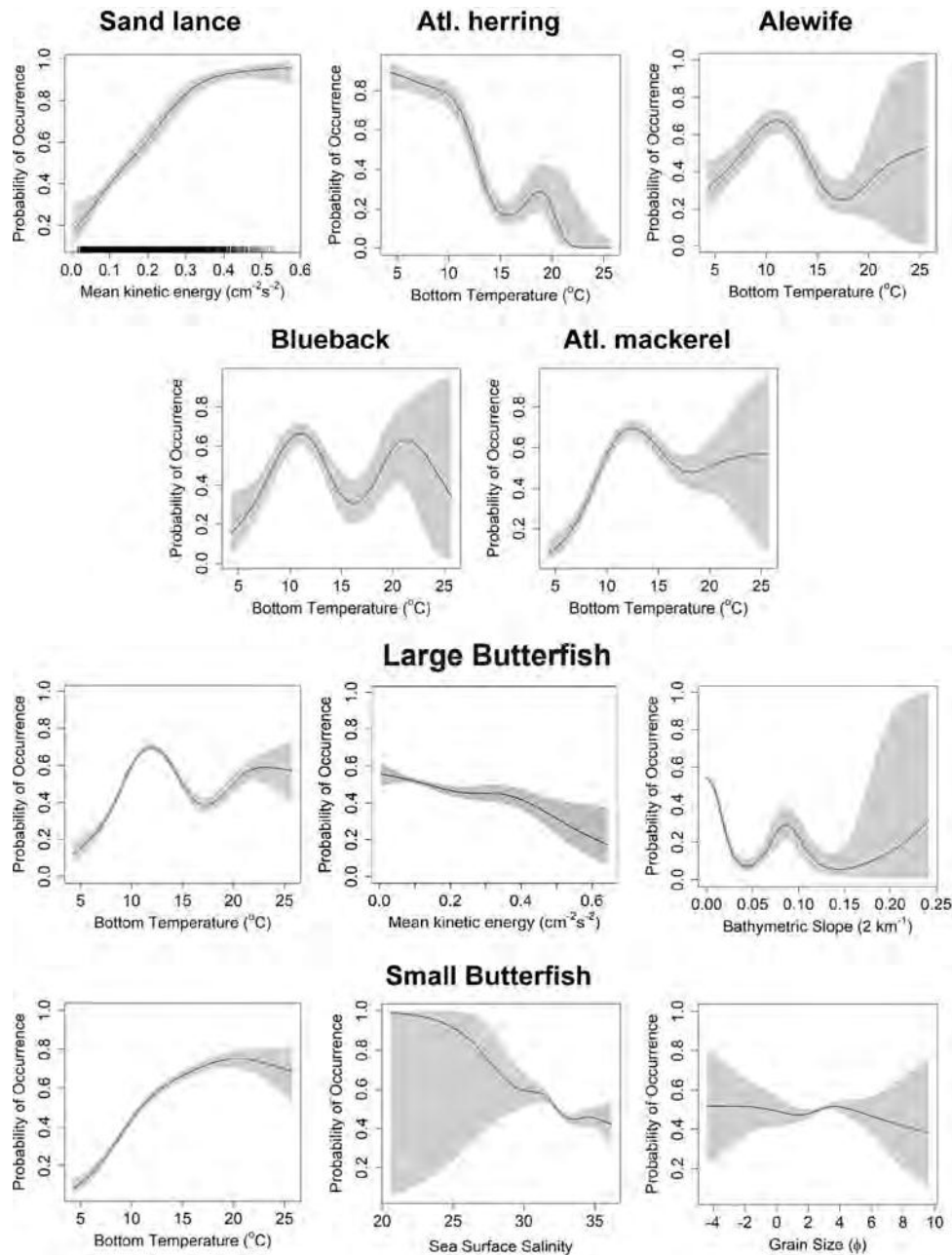
Figure 3. Response curves for variables with the three highest sum of Akaike weights per species for fall models.

with other predictors, though the predictive capability was lower (AUC = 0.83; Table 2). Unlike spring, both large and small butterfish models, which included multiple environmental predictors, had low AUC values (0.61 for small butterfish and 0.69 for large butterfish).

Year- and gear-specific intercepts and catch comparisons
Intercept estimates and stratified area-weighted mean abundance estimates from the survey were strongly correlated for most species in both seasons (Table 3; Supplementary Figures S2 and S3). Exceptions were alewife and blueback herring in the spring and blueback, Atlantic mackerel, and large butterfish in the fall. Sand lance and

Atlantic herring had the strongest correlations in both season between year- and gear-specific intercept estimates and log stratified area-weighted mean abundance.

Trends in occupiable habitat
Annual trends in spring occupiable habitat varied by species and by whether gear and year intercepts were incorporated (Table 3 and Figure 4). Using year-specific random intercepts Atlantic herring, blueback herring, Atlantic mackerel, and butterfish showed significant increases in spring proportion of shelf occupancy while sand lance showed a significant decrease in shelf occupancy with time. Using a fixed gear and removing year-specific intercepts, sand

Table 3. Correlation between year-specific intercepts and mean stratified area-weighted number of individuals per tow for spring and fall models.

Species	Season	Corr. coefficient	*p*-value
Sand lance	Spring	0.890	< 0.001
	Fall	0.653	< 0.001
Butterfish	Spring	0.447	0.007
	Fall—large	0.195	0.262
	Fall—small	0.487	0.00
Atl. herring	Spring	0.747	< 0.001
	Fall	0.929	< 0.001
Alewife	Spring	0.011	0.946
	Fall	0.511	0.001
Blueback	Spring	− 0.051	0.773
	Fall	0.242	0.160
Atl. mackerel	Spring	0.554	< 0.001
	Fall	0.207	0.232

lance showed a significant increase in inferred habitat suitability with time while all other species had non-significant trends. Slope estimates for alewife, blueback herring, and sand lance showed opposite signs between shelf occupancy and inferred habitat suitability.

Fall trends in shelf occupancy were stronger (greater slope estimates) and more frequently significant than in spring (Table 4 and Figure 5). Notably, Atlantic herring had a significant increase in occupiable shelf in year- and gear-specific model predictions, while having a significant negative trend in model predictions of inferred habitat suitability.

Spatio-temporal differences in occurrence

Atlantic mackerel and butterfish exhibited the largest spatio-temporal differences for spring models, with a near region-wide increase in probability of occurrence of butterfish while Atlantic mackerel had increases in probability of occurrence on Georges Bank and the inner Mid-Atlantic Bight with decreases on the outer shelf (Figure 6). Probability of occurrence declined along the
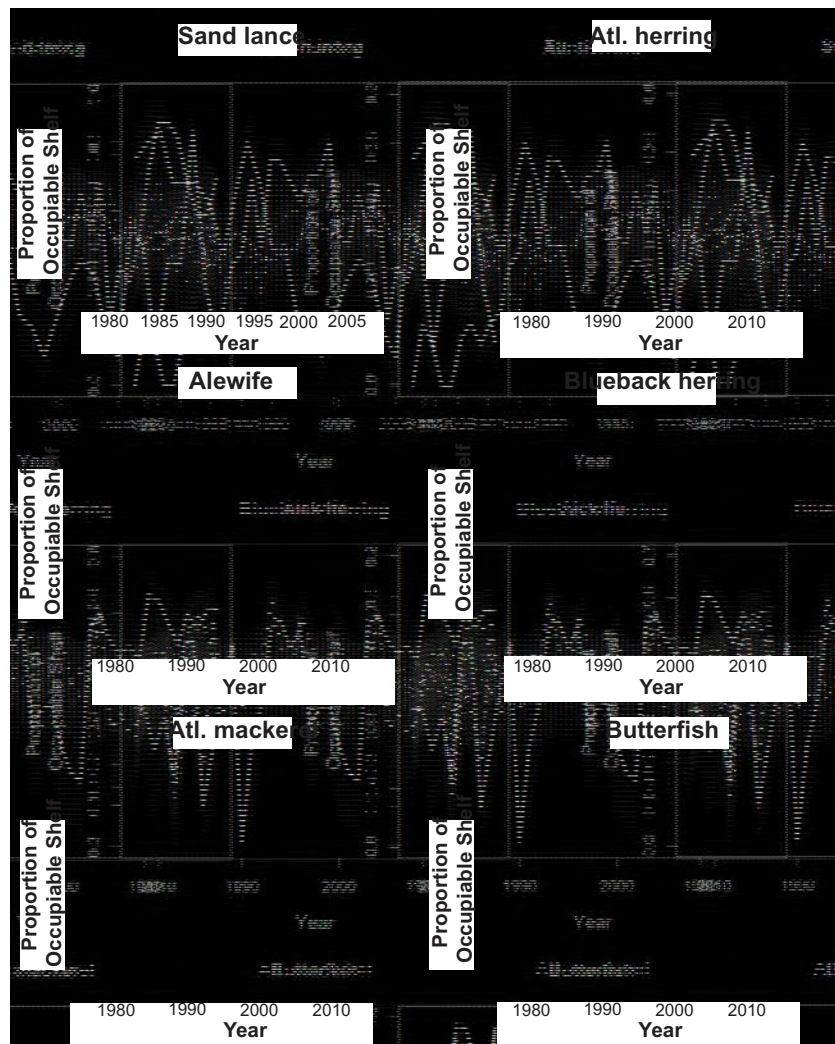

Figure 4. Trends in proportion of occupiable shelf including (shelf occupancy; black) and excluding year- and gear-specific intercepts (inferred habitat suitability; red) in spring. Significant trends are indicated by a solid line. Shading reflects 95% confidence intervals.

Table 4. Trends in shelf occupancy without year- and gear-specific intercepts (inferred habitat suitability) and with year- and gear-specific intercepts (shelf occupancy) with time as estimated through beta regression. Butterfish were only split into small and large groups for fall models.

Species	Season	Intercept	Slope estimate	Pseudo- R^2	*p*-value
Sand lance	Spring	Year-specific	− 0.053	0.300	< 0.001
		Fixed	0.010	0.294	< 0.001
	Fall	Year-specific	− 0.044	0.188	0.001
		Fixed	− 0.002	0.163	0.016
Butterfish	Spring	Year-specific	0.057	0.371	< 0.001
		Fixed	0.009	0.032	0.237
	Fall—large	Year-specific	0.041	0.282	< 0.001
		Fixed	0.002	0.084	0.060
	Fall—small	Year-specific	0.014	0.163	0.006
		Fixed	0.002	0.059	0.123
Atl. herring	Spring	Year-specific	0.101	0.266	< 0.001
		Fixed	0.006	0.020	0.374
	Fall	Year-specific	0.096	0.29	< 0.001
		Fixed	− 0.002	0.122	0.021
Alewife	Spring	Year-specific	0.008	0.067	0.096
		Fixed	− 0.002	0.029	0.287
	Fall	Year-specific	0.027	0.689	< 0.001
		Fixed	0.004	0.253	< 0.001
Blueback	Spring	Year-specific	0.035	0.215	< 0.001
		Fixed	− 0.003	0.016	0.415
	Fall	Year-specific	0.063	0.662	< 0.001
		Fixed	0.010	0.201	0.001
Atl. mackerel	Spring	Year-specific	0.078	0.613	< 0.001
		Fixed	0.001	0.001	0.843
	Fall	Year-specific	0.057	0.484	< 0.001
		Fixed	0.015	0.204	0.001

Mid-Atlantic Bight for Atlantic herring, alewife, and blueback herring, with only alewife having increases in expected occurrence in other regions. Sand lance had very weak increases in expected occurrence throughout the Mid-Atlantic Bight and the Gulf of Maine.

Changes in expected occurrence were lower for fall estimates of inferred habitat suitability (Figure 7). Small butterfish had nearly ubiquitous increases in expected occurrence, while most increases in occurrence of large butterfish occurred in the Gulf of Maine. Other species generally showed increases in expected occurrence in the Gulf of Maine, apart from Atlantic herring in which expected occurrence decreased throughout the Gulf of Maine. Atlantic mackerel had a more complex pattern, with decreases in expected occurrence on Georges Bank and Massachusetts Bay (southwestern Gulf of Maine) and increases in expected occurrence throughout the rest of the Gulf of Maine.

Mean weighted latitude and depth
Spring annual trends in mean weighted latitude and depth varied with species, but generally trended north and deeper with time (Table 5). Butterfish and Atlantic mackerel showed the most pronounced and significant northward shift in weighted mean latitude while Atlantic herring and alewife showed the least change in weighted mean latitude (Figure 8). Butterfish and Atlantic mackerel also showed the most pronounced and significant increase in mean weighted depth (Figure 9).

Fall annual trends in mean weighted latitude and depth varied more by species than in the spring (Table 6). Most species indicated no significant trend or a significant northward and deeper trend

with time. However, Atlantic herring and alewife showed significant decreases in mean weighted latitude with time (Figure 10). Atlantic herring in fall had opposite trends in mean weighted depth in model predictions with and without year- and gear-specific intercepts (Figure 11).

Discussion
Our work suggests that the shifting hydrography of the Northeast US shelf can be observed in and contribute to changes in the forage fish community's shelf occupancy. Clear effects include the movement of weighted mean bottom depth and weighted mean latitude to largely deeper and more northward locations for species in both seasons. However, our work also elucidates a distinction between changes in observed shelf occupancy by forage fish species throughout the time series as driven by the combination of year- and gear-specific effects vs. changes driven by coincident environmental conditions. The latter metric, "inferred habitat suitability," was largely stable with time for most species despite large variability in observed shelf occupancy. Identifying these differences is important for understanding the effects of climate change and variability on the life history of fishes as effects of fishing, recruitment, and local hydrographic conditions can represent compounding or compensatory effects on a species' occurrence.

Atlantic herring provide a clear example of the distinction between trends in shelf occupancy as driven by coincident environmental conditions compared to external (year- and gear-specific) factors. Atlantic herring had significant positive trends in shelf occupancy in both spring and fall through time, yet their inferred
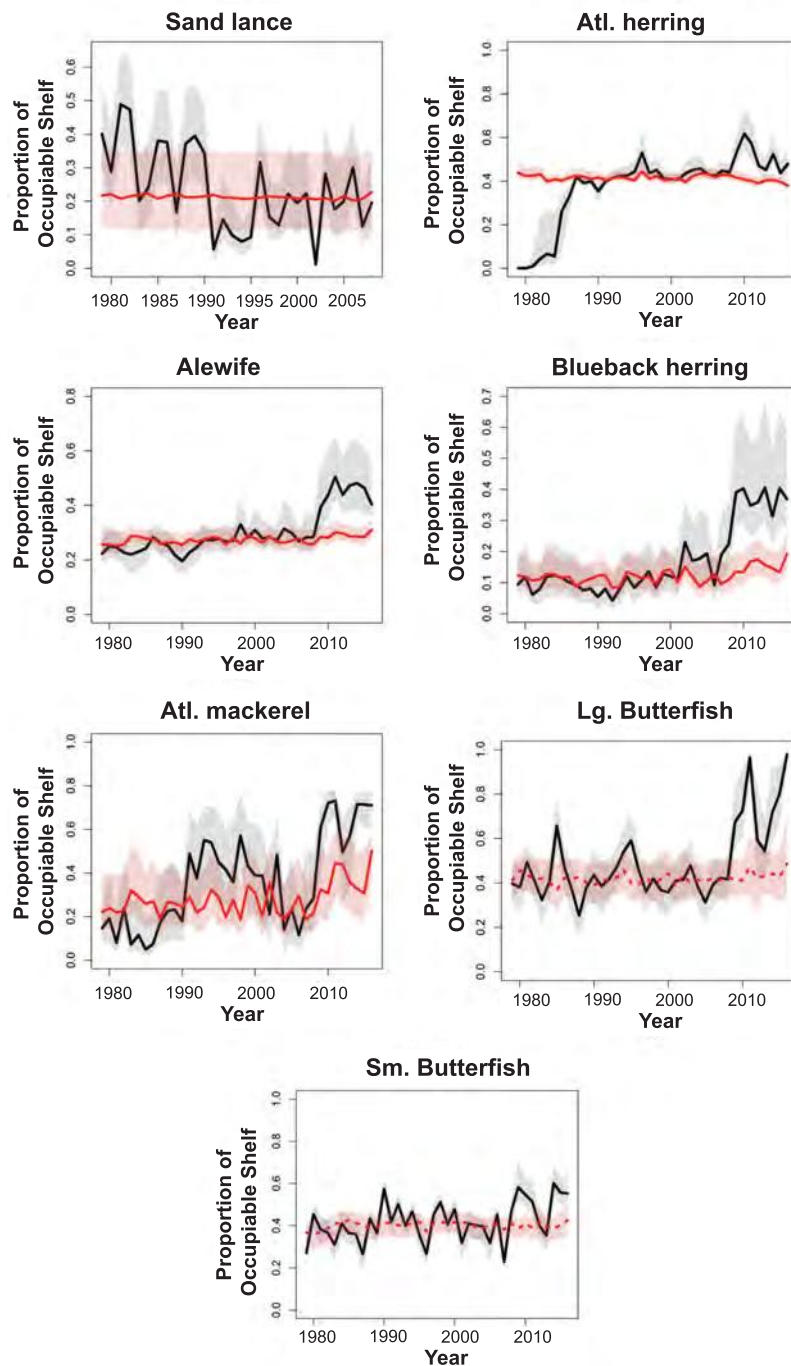
Figure 5. Trends in proportion of occupiable shelf including (shelf occupancy; black) and excluding year- and gear-specific intercepts (inferred habitat suitability; red) in fall. Significant trends are indicated by a solid line. Shading reflects 95% confidence intervals.

habitat suitability had no trend in spring and a significant decrease with time in the fall. These results reflect increasing catch of Atlantic herring throughout the trawl survey due to recovery from past fishing impacts as well as shifts in survey gear, while the trends based on environmental covariates suggest that the area of favorable habitat for Atlantic herring is decreasing with increasing mean temperatures and BS. This decrease in habitat suitability is intuitive given the more northerly distribution and reliance

on temperate to sub-polar zooplankton as food for Atlantic herring compared to other forage fishes in the region (Bowman *et al.*, 2000; Suca *et al.*, 2018). In the spring, this can be seen through decreases in inferred habitat suitability for Atlantic herring along the Mid-Atlantic Bight, while fall showed general decreases in inferred habitat suitability throughout much of the Gulf of Maine due to warming. Differences between trends in shelf occupancy and inferred habitat suitability were not striking for all species,
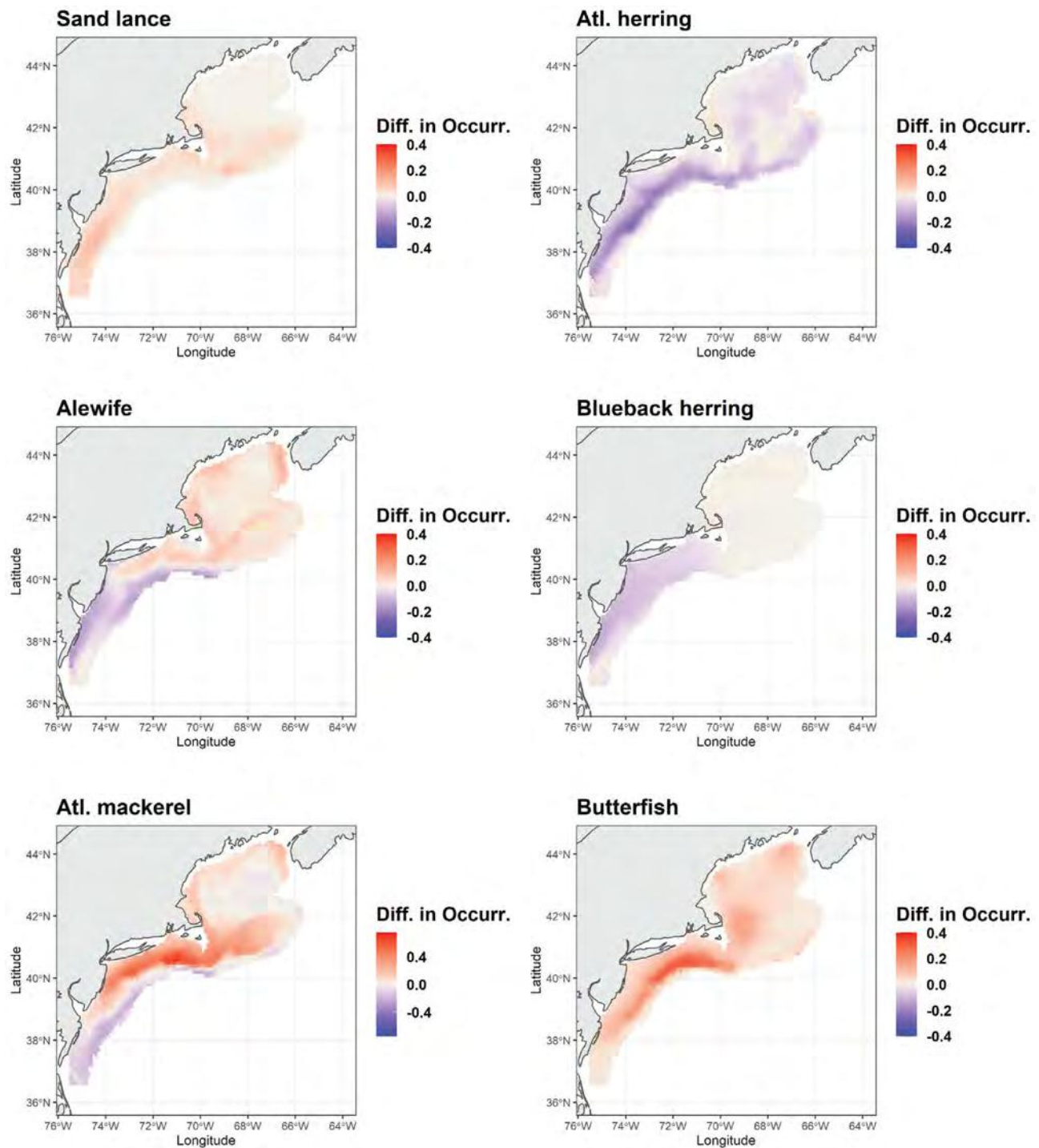
Figure 6. Difference in predicted probability of occurrence for each 0.1° by 0.1° grid cell for each species from the final 5 years of the survey compared to the first 5 years of the survey for spring models. Note that the scale is larger for Atlantic mackerel due to greater differences in occurrence compared to other species.

however, with spring butterfish catches showing strong coherence between interannual variability in these two metrics. This pattern in butterfish is consistent with existing literature tying their distribution and trawl survey catch to temperature, although we observe the strongest pattern being with BT as opposed to surface temperature (Adams, 2017). These notable differences in coherence

between the two habitat metrics can provide direction to future studies of climate impacts on the forage fishes of the Northeast US shelf, with coincident environmental conditions being important for species such as butterfish and Atlantic mackerel, while external factors strongly outweigh these environmental covariates for Atlantic herring and sand lance during the time window of this study.
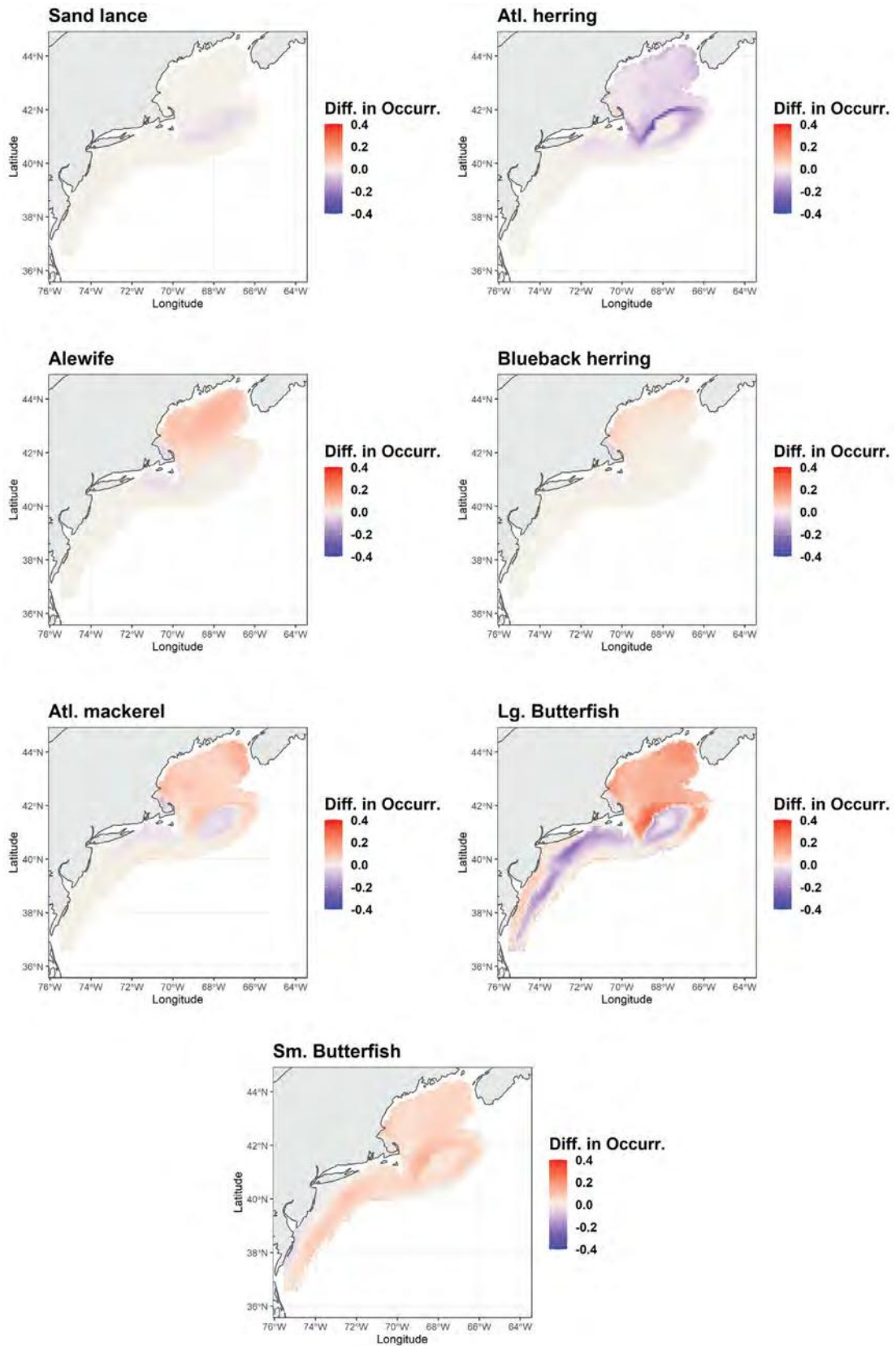
Figure 7. Difference in predicted probability of occurrence for each 0.1° by 0.1° grid cell for each species from the final 5 years of the survey compared to the first 5 years of the survey for fall models. Note that the scale is larger for large butterfish due to greater differences in occurrence compared to other species.

Table 5. Trends in annual mean weighted latitude and depth of shelf occupancy based on intercept condition for spring models.

Species	Predictor	Intercept	Slope estimate	R^2	p-value
Sand lance	Latitude	Year-specific	− 0.003	0.194	0.015
		Fixed	− 0.003	0.133	0.048
	Depth	Year-specific	0.170	0.269	0.003
		Fixed	− 0.040	0.168	0.024
Butterfish	Latitude	Year-specific	0.027	0.529	< 0.001
		Fixed	0.012	0.313	< 0.001
	Depth	Year-specific	− 0.551	0.320	< 0.001
		Fixed	− 0.319	0.141	0.020
Atl. herring	Latitude	Year-specific	0.001	0.022	0.378
		Fixed	0.001	0.009	0.571
	Depth	Year-specific	− 0.260	0.419	< 0.001
		Fixed	− 0.085	0.095	0.059
Alewife	Latitude	Year-specific	0.001	0.010	0.534
		Fixed	0.002	0.109	0.051
	Depth	Year-specific	− 0.002	<0.001	0.958
		Fixed	− 0.050	0.066	0.118
Blueback	Latitude	Year-specific	0.004	0.091	0.066
		Fixed	0.003	0.034	0.266
	Depth	Year-specific	− 0.178	0.237	0.002
		Fixed	− 0.093	0.062	0.130
Atl. mackerel	Latitude	Year-specific	0.014	0.295	< 0.001
		Fixed	0.001	0.001	0.842
	Depth	Year-specific	− 0.351	0.498	< 0.001
		Fixed	0.011	0.001	0.840

Coherence between shelf occupancy and inferred habitat suitability was also quite disparate in the fall. BT was an important variable for all species except sand lance in the fall, indicating that fall shelf occupancy may be more tightly linked to thermal niche availability than it is for spring (with the exception of butterfish). Trends were often intuitive for both seasons, with Atlantic herring's inferred habitat suitability decreasing with time (linked to increasing BT), while all others increased, largely following our hypotheses. However, patterns in alewife observed shelf occupancy did not follow our expectations, with shelf occupancy not changing with time in spring and increasing in the fall. This is notably opposite of the trends observed in previous work modelling presence/absence data of alewife, though it is consistent with trends observed when modelling abundance of alewife (Lynch *et al.*, 2020). In the case of fall models, the increased observed shelf occupancy for alewife was linked to the shift in survey vessel, increasing alewife catchability. In the spring, however, the gear change was not apparent in estimates of observed shelf occupancy by alewife and it appears that the environment did not transition to unfavorable conditions for alewife, despite the species generally being considered temperate. Response curves for presence and temperature conditions often indicated season-specific thermal windows of occurrence for fishes, supporting a strong role for thermal habitat availability in species occurrence (Kleisner *et al.*, 2017; Morley *et al.*, 2018). Notable exceptions were clear positive relationships between temperature and butterfish occurrence, and large uncertain probabilities of occurrence of alewife at high temperatures in the fall. These uncertain tails are likely due to high occurrence of these fishes in regions of the coastal Gulf of Maine, where north to south advection dominates in the form of the Gulf of Maine Coastal Current (Townsend *et al.*, 2015; Supplementary Figure S4). The coastal current represents a pathway for transport of *Calanus finmarchicus*, an important

prey item for many forage fish species, particularly alewife (Ji *et al.*, 2017; Suca *et al.*, 2018).

Contrary to the largely parsimonious BT-driven models for the fall, spring models often included other predictors, including SST and mean kinetic energy. This may be linked with the spring representing an important time of feeding for these species and thus their distribution may be more variable due to following food at small scales (Smith and Link 2010; Suca *et al.* 2018). We originally explored using zooplankton taxa as predictor variables, but the large loss of data caused by their inclusion (tows only occur at every third trawl and even these collections tend to be inconsistent) precluded many years from being included in model formation with often <100 stations remaining per year. The incorporation of prey as predictor variables will likely become more practical in coming decades as the EcoMon survey zooplankton collections became more consistent with trawls later in the time series. However, whether forage fishes even follow zooplankton aggregations remains an open question and it is likely that this prey following behaviour, if it occurs at all, does so at scales too small for the NEFSC trawl survey to observe (Holland *et al.*, 2021).

Another possible cause of more complex and less accurate spring models is the more subtle and complex gradients in temperature and salinity properties in the spring compared to fall. In the early fall, during much of the survey, the region is highly stratified leading to decoupling of surface and BTs while both still follow known gradients by latitude and cross-shelf distance (Townsend *et al.*, 2015). In spring, waters are largely well-mixed and, thus, there is greater coherence between surface and BTs and salinities, making identifying the mechanisms driving shelf occupancy more difficult to elucidate. The only exceptions to this are regions of high BTs and bottom salinities in the deeper regions that contain Gulf Stream influenced slope water and elevated surface salinity from Gulf Stream
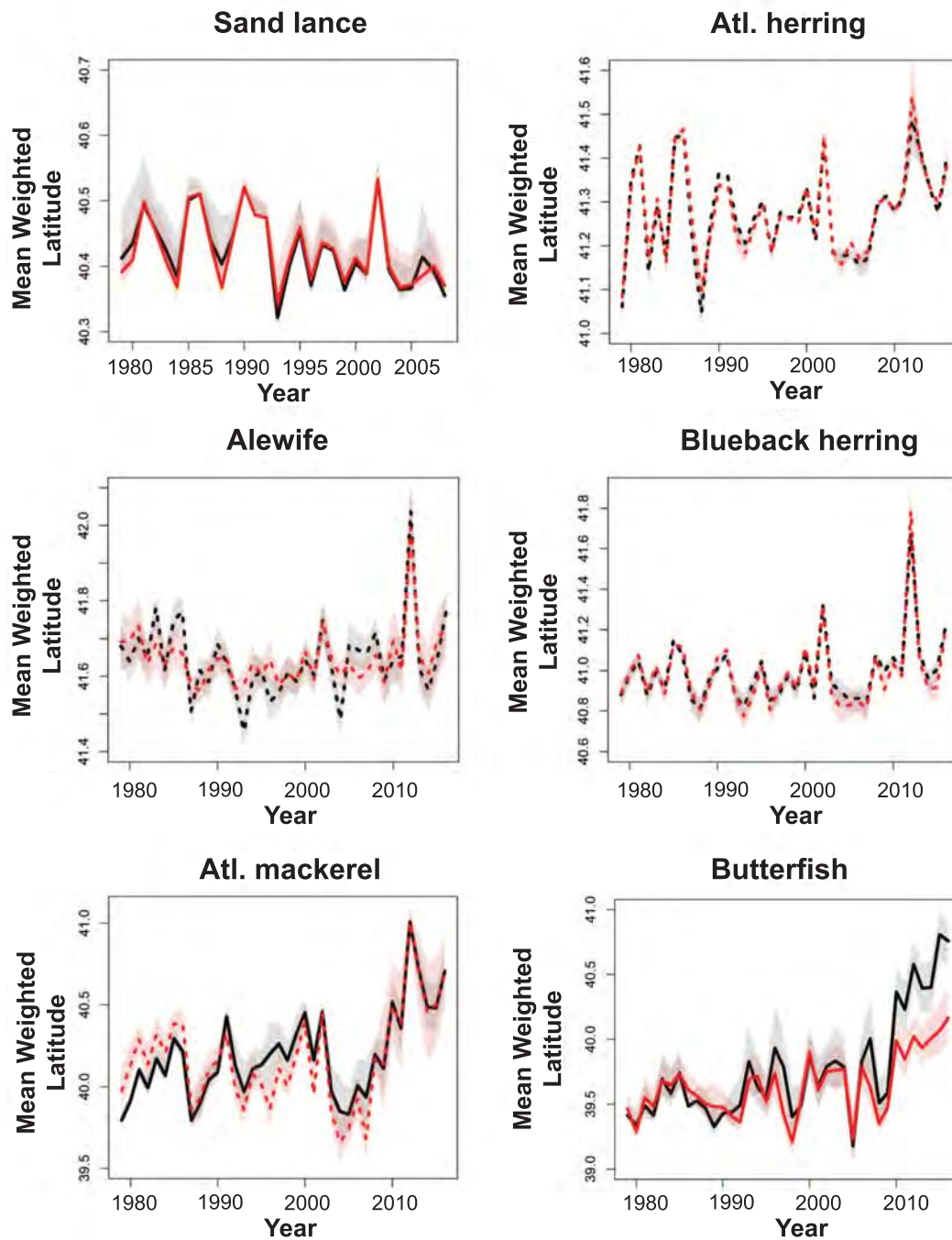
Figure 8. Trends in spring weighted mean latitude based on including (shelf occupancy; black) and excluding year- and gear-specific intercepts (inferred habitat suitability; red) in spring. Significant trends are indicated by a solid line. Shading reflects 95% confidence intervals.

intrusions, which were important in identifying Atlantic herring and Atlantic mackerel spring occupancy, respectively (Mountain, 2012). The positive relationship between spring Atlantic mackerel presence and surface salinity is likely an indication of preference for Gulf Stream influenced water that enters the Northeast US shelf and may be related to feeding or migrations along the shelf (Churchill and Cornillon, 1991). This is illustrated by habitat maps showing the highest occurrence near the shelf edge in the Mid-Atlantic Bight (Supplementary Figure S5). Multiple changepoints in Gulf Stream

behaviour occurred in the 21st century, including a westward shift in the destabilization point (Andres, 2016) and near doubling in the production of warm core rings (Gangopadhyay *et al.*, 2019). These changes in Gulf Stream behaviour are also likely linked to changepoints observed in warm slope water entering the Gulf of Maine (Suca *et al.*, 2021) and the marked change in BTs around 2009 (Friedland *et al.*, 2020a). Collectively, these changes are likely to lead to increased BS throughout much of the shelf and increased intrusions of waters with high surface salinity. Our results suggest
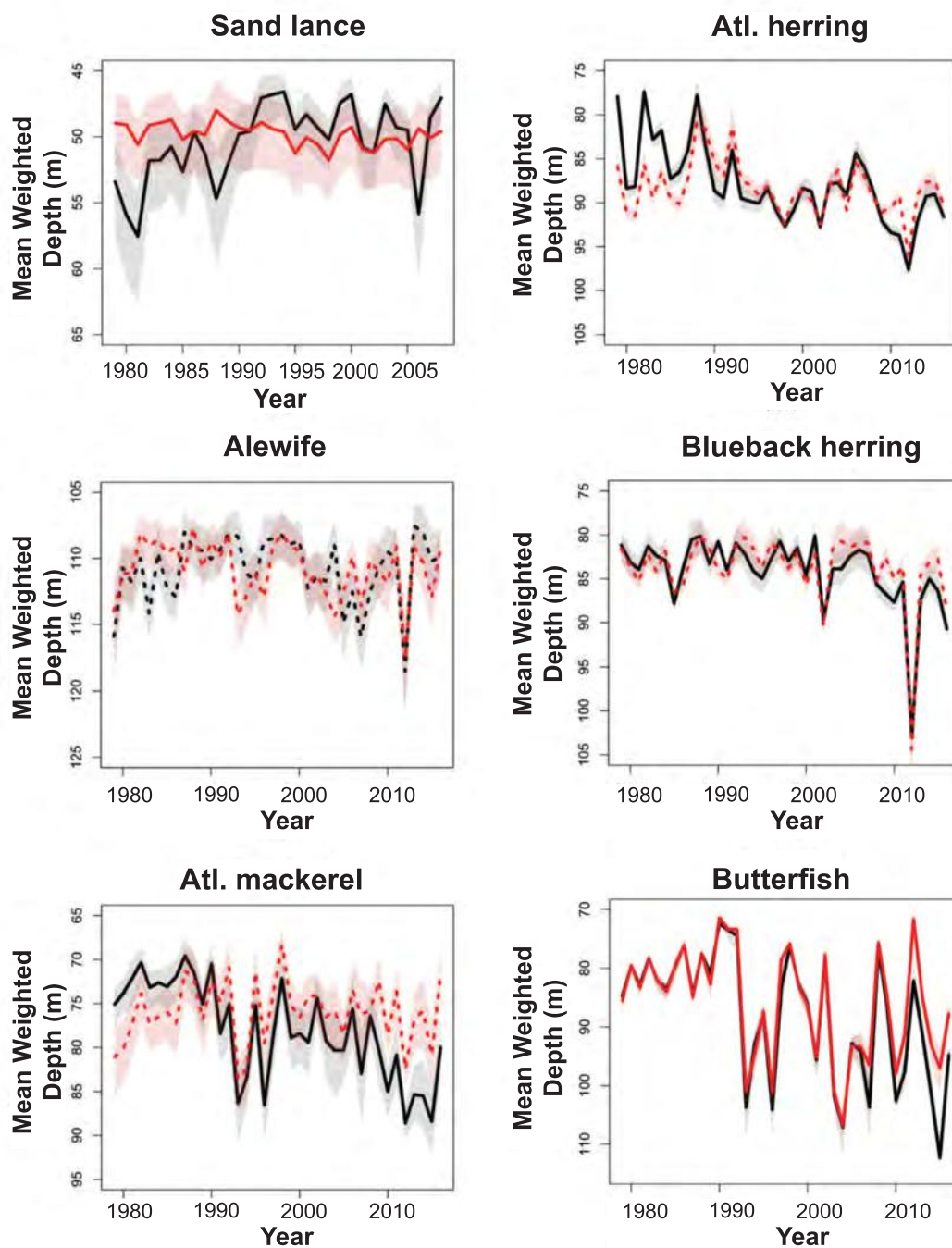
Figure 9. Trends in spring weighted mean depth based on including (shelf occupancy; black) and excluding year- and gear-specific intercepts (inferred habitat suitability; red) in spring. Significant trends are indicated by a solid line. Shading reflects 95% confidence intervals.

this may have negative consequences for Atlantic herring shelf occupancy in the spring, while increasing shelf occupancy for Atlantic mackerel in the spring. This can be seen in the increases to spring Atlantic mackerel expected occurrence throughout the Mid-Atlantic Bight and Georges Bank regions and the decreases in expected occurrence of Atlantic herring the Gulf of Maine during fall. Changes in the Gulf Stream behaviour is likely one of the largest factors driving the change of both hydrography and species composition observed in our study and others (Kleisner *et al.*, 2017;

Friedland *et al.*, 2020a, 2020b). Further, the change in Gulf Stream behaviour coincided with the shift from the NOAA Ship *Albatross IV* to the NOAA Ship *Henry Bigelow*, rendering it possible that the changes in observed shelf occupancy in 2009—which we largely attribute to gear effects in our models—may also be related to larger ecosystem changes from the shift in Gulf Stream behaviour. It is worth noting that Gulf Stream water is unlikely to influence small butterfish shelf occupancy in the fall. This is because the negative relationship between the occurrence of small butterfish and SSS is

Table 6. Trends in annual mean weighted latitude and depth of shelf occupancy based on intercept condition for fall models.

Species	Predictor	Intercept	Slope estimate	R^2	p-value
Sand lance	Latitude	Year-specific	0.002	0.070	0.157
		Fixed	− 0.002	0.283	0.002
	Depth	Year-specific	0.142	0.288	0.002
		Fixed	0.014	0.162	0.028
Lg. Butterfish	Latitude	Year-specific	0.009	0.347	< 0.001
		Fixed	0.007	0.299	< 0.001
	Depth	Year-specific	− 0.317	0.343	< 0.001
		Fixed	− 0.239	0.275	< 0.001
Sm. Butterfish	Latitude	Year-specific	0.008	0.331	< 0.001
		Fixed	0.004	0.354	< 0.001
	Depth	Year-specific	− 0.309	0.283	< 0.001
		Fixed	− 0.112	0.236	0.002
Atl. herring	Latitude	Year-specific	− 0.005	0.446	0.001
		Fixed	0.001	0.029	0.310
	Depth	Year-specific	0.388	0.600	< 0.001
		Fixed	− 0.072	0.128	0.028
Alewife	Latitude	Year-specific	− 0.006	0.507	< 0.001
		Fixed	0.001	0.053	0.163
	Depth	Year-specific	− 0.390	0.554	< 0.001
		Fixed	− 0.190	0.246	0.001
Blueback	Latitude	Year-specific	− 0.001	0.006	0.647
		Fixed	0.003	0.147	0.018
	Depth	Year-specific	0.511	0.481	< 0.001
		Fixed	− 0.278	0.275	< 0.001
Atl. mackerel	Latitude	Year-specific	0.003	0.059	0.141
		Fixed	0.006	0.193	0.006
	Depth	Year-specific	− 0.470	0.375	< 0.001
		Fixed	− 0.336	0.237	0.002

more likely due to a cross shelf effect rather than avoidance of Gulf Stream influenced water (see Supplementary Figure S4).

Collectively, our results corroborate trends of species distribution shifts throughout the Northeast US shelf, including changes in shelf occupancy, depth, and latitude of the forage fish complex. Most species had deeper mean weighted depth with time, particularly in the fall, which is consistent with past observations for species such as alewife (Nye *et al.*, 2009). However, unlike Nye *et al.* (2009), we noticed significant changes in depth for Atlantic herring in both seasons and a different trend for Atlantic mackerel in the fall (deeper instead of shallower). This latter case is linked to increased inferred habitat suitability for Atlantic mackerel in the deeper Gulf of Maine and decreased inferred habitat suitability on the relatively shallow Georges Bank in the fall. The northward shifts in our study for many species is also consistent with those seen for similar species from previous studies (Kleisner *et al.*, 2017; Friedland *et al.*, 2020b).

However, a limitation of our study is our inability to address the drivers of non *in situ* and coincident environmentally driven shelf occupancy for many species beyond abundance and survey gear, particularly Atlantic herring, sand lance, and river herring. For Atlantic herring and sand lance, observed shelf occupancy is tightly correlated with trawl abundance, suggesting shelf occupancy is primarily controlled by changes to collective biomass and gear catchability. The drivers of these inter-annual fluctuations in abundance have been studied for both species, providing hypotheses for the mechanisms behind these patterns (Richardson *et al.*, 2011; Suca *et al.*, 2021). River herring intercept values, however, did not

significantly correlate with abundance metrics in the spring (or for blueback herring in the fall), suggesting mechanisms other than environmental covariates used in this study and survey abundance drive interannual differences in shelf occupancy. This may be due to their spawning behaviour in the spring and coastal distributions (Lynch *et al.*, 2020), but further research is needed to refine hypotheses. This example highlights the limitation of the method used in this work and others—namely defining habitat through statistical models using survey or catch data—for describing habitat suitability. Using statistical relationships between catch and environmental variables is a rather coarse approximation of habitat suitability and a true understanding of habitat suitability for a species requires indepth study of how a species' behaviour and physiology changes in response to environmental conditions.

Although habitat modelling, such as our work here, has limitations, future work can expand beyond our focus explicitly on presence/absence *via* using similar models to incorporate abundance. Previous research suggests opposite trends may occur in the relationships between a species' presence and abundance with a given environmental covariate (Lynch *et al.*, 2020; Friedland *et al.*, 2021), though the mechanisms behind this are likely complex and poorly understood. Abundance models for schooling small pelagic fishes often have poor fits and predictive capability when using trawl survey data (see methods; (Deroba, 2018), leading to presence/absence models driving hurdle model predictions (Deroba, 2018). This limitation is also related to issues with catching small pelagic fishes using bottom trawl survey gear. This survey is often used for forage fish studies, but catches may miss portions of these species'
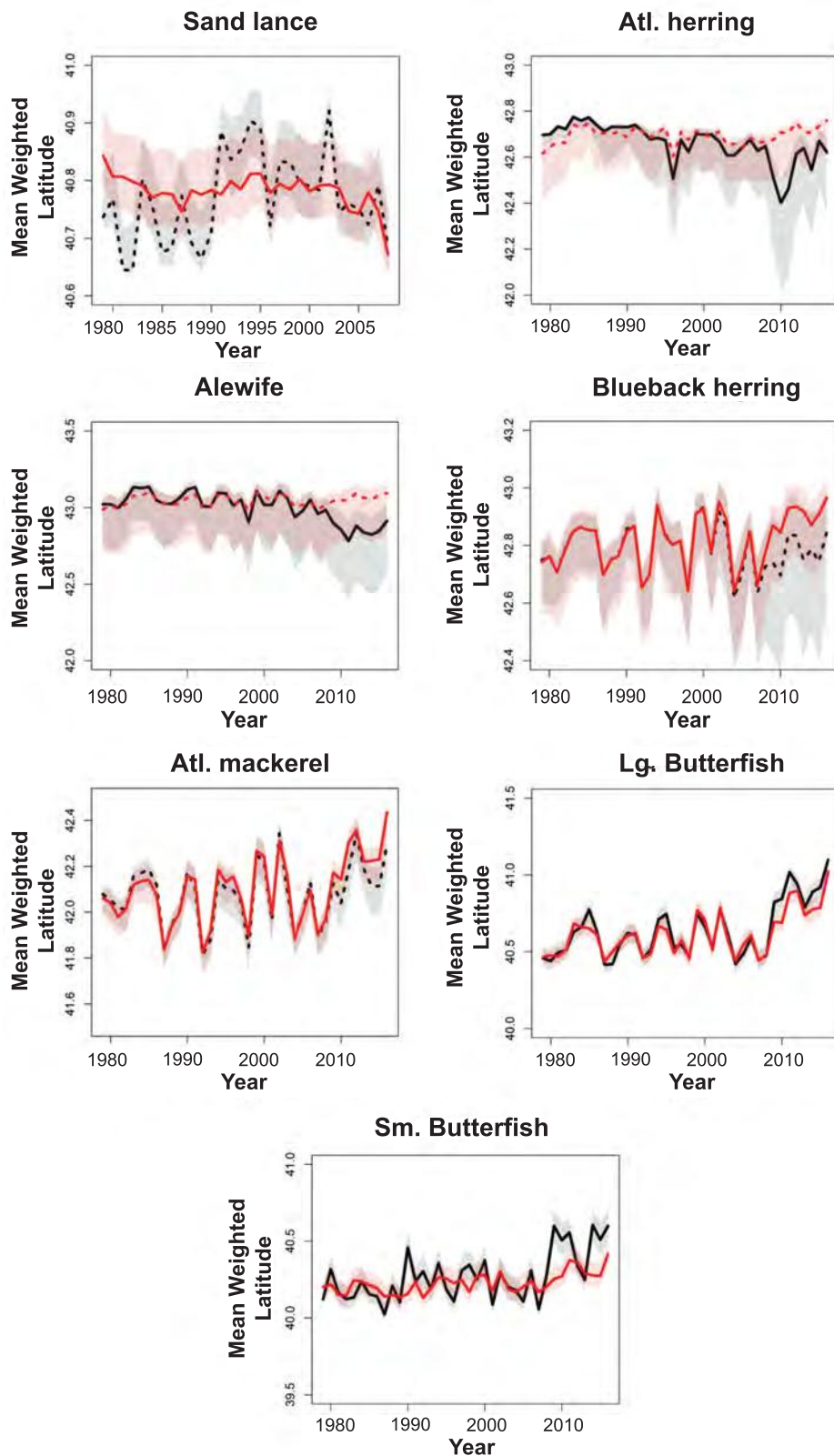
Figure 10. Trends in fall weighted mean latitude based on including (shelf occupancy; black) and excluding year- and gear-specific intercepts (inferred habitat suitability; red). Significant trends are indicated by a solid line. Shading reflects 95% confidence intervals.
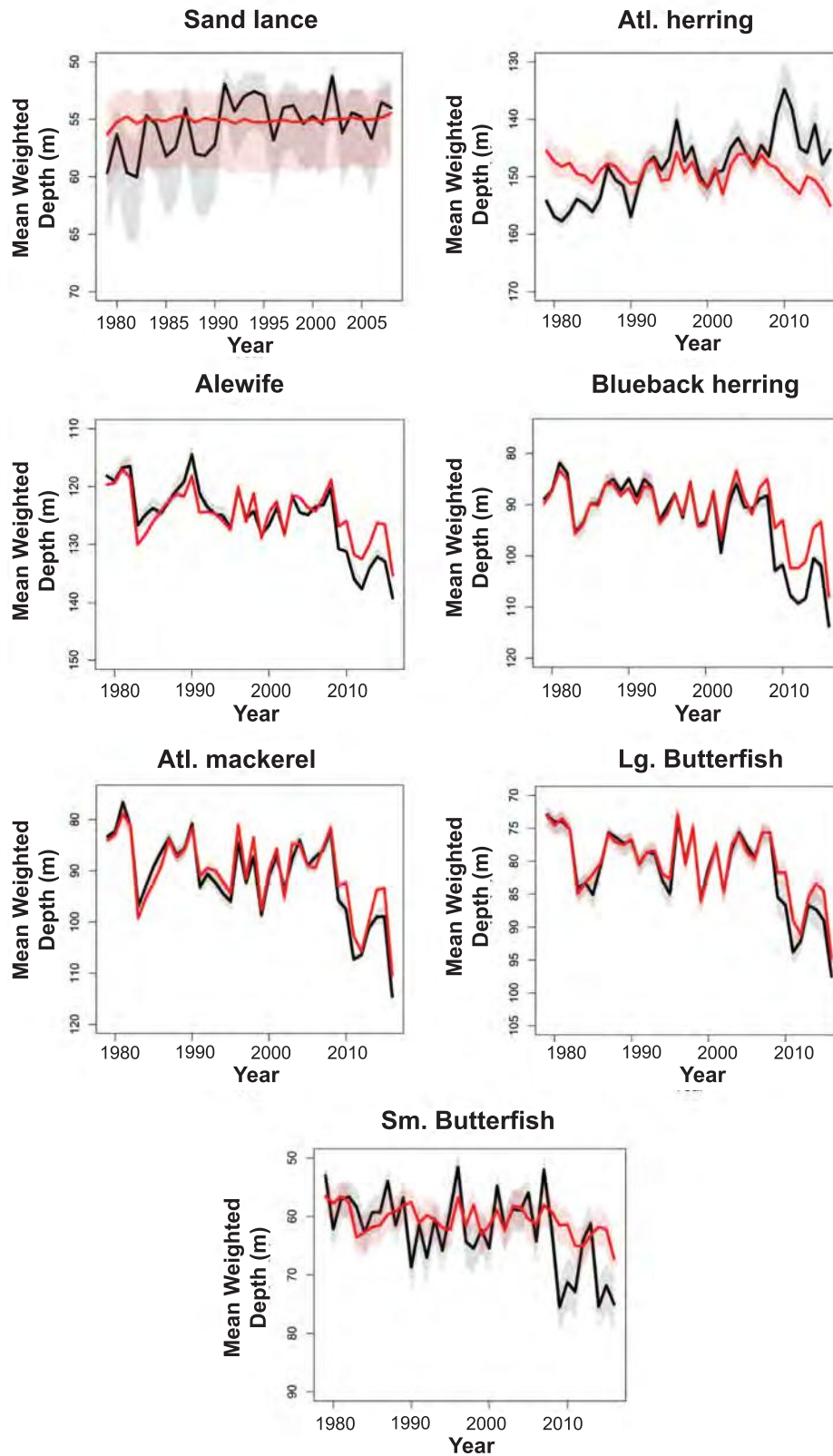
Figure 11. Trends in fall weighted mean depth based on including (shelf occupancy; black) and excluding year- and gear-specific intercepts (inferred habitat suitability; red). Significant trends are indicated by a solid line. Shading reflects 95% confidence intervals.

behaviours and niches by not sampling the full water column. An important example of this phenomenon is Atlantic mackerel, the species with the lowest spring predictive capability of our models. In this case, not only does the trawl survey have issues with capturing the vertical distribution of this species, but mackerel habitat may extend beyond the Northeast US shelf in the spring into the Slope Sea, though this hypothesis remains unconfirmed (Overholtz *et al.*, 2011). Additionally, due to issues with re-creation of accurate BTs, we excluded many of the slope strata for our spring models. This caused a loss of strata where both Atlantic mackerel and butterfish are often caught, possibly leading to the poorly constrained spring Atlantic mackerel models. Conversely, despite this loss of known habitat, spring butterfish models were the most accurate (as defined by AUC) of all spring models indicating we were able to accurately constrain the relationship between butterfish presence and BT for the non-slope strata of the Northeast US shelf. Incorporating alternative survey methods to accurately assess forage fish abundance in the vertical domain and expanding the horizontal sampling area for species that extend beyond the shelf will be essential in further research.

Shifts in shelf occupancy of forage species may have consequences on food web interactions and fisheries given the importance of forage fishes as prey for top predators on the Northeast US Shelf. This may be particularly true for predators that follow forage species in their distribution (Overholtz and Link, 2007; Richardson *et al.*, 2014). While total shelf occupancy is largely driven by abundance and recruitment for many forage fish species, environmental covariates linked to habitat suitability can provide insight into regions where they may occur frequently and can represent reliable feeding hotspots for predators (Silva *et al.*, 2021). Mean weighted depth and latitude of habitat suitability for many of the forage fishes trended deeper and northward with time, potentially shifting foraging grounds for predators as well. These changes may shift the distance traveled from port for fishing vessels targeting predators reliant on these forage species or even change which port lies closest to fishing hotspots (Kleisner *et al.*, 2017; Selden *et al.*, 2020).

Ultimately, it will be important to study the interactions between future forage fish survey catches (observed year- and gear-specific shelf occupancy) and environmental covariates associated with shelf occupancy (inferred habitat suitability). Our results show that these metrics do not always align, and may even show opposite trends, but future conditions may lead to coincident environmental covariates becoming a limiting factor in the life history of certain forage fishes. Understanding if or when this comes to fruition will be essential to our understanding of the future dynamics of the changing Northeast US shelf forage fish complex.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Funding

Data availability

Author contributions

Acknowledgements

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