# Climate-induced habitat changes in commercial fish stocks

**Richard J. Bell** [1,*], **Brian Grieve**[1], **Marta Ribera**[2], **John Manderson**[3] **and Dave Richardson**[4]

[1]The Nature Conservancy, URI Bay Campus, South Ferry Road, Narragansett, RI 02882, USA
[2]The Nature Conservancy, 159 Waterman St, Providence, RI 02906, USA
[3]OpenOcean Research, Blue Hill Partners, Suite 101, 40 West Evergreen Avenue, PA 19118, USA
[4] Northeast Fisheries Science Center, National Marine Fisheries Service, 28 Tazwell Drive, Narragansett, RI 02882, USA

* Corresponding author: tel: +1-401-874-6511; e-mail: rich.bell@tnc.org

Climate change is altering the distribution and abundance of fish species in ways not anticipated by current management policy. We created spatially explicit, dynamic models of marine habitats that can inform stock assessments for 25 commercial species on the US Northeast Shelf. The habitat models integrated substrate and seabed features along with the dynamic properties of the ocean. Changes in climate-mediated habitat can affect the survey results by altering the availability component of catchability. Changes in availability were examined (1980–2014) by combining species distribution models with hindcast ocean models. Three patterns in availability were evident: (1) the availability for most species varied over time with no trend; (2) for a number of estuary-dependent species, availability varied with no trend and then dropped dramatically in 2009 when the federal trawl survey changed vessels; and (3) for a set of mid-depth, non-estuary dependent species, availability showed a continuous decline over time. There were few changes in dynamic habitat as the bottom water temperature did not exhibit a strong trend over the time-period studied, resulting in little climate-attributed changes in catchability. Changes in survey design can also have dramatic impacts on catchability, highlighting the method's ability to detect both climate driven and survey driven changes in catchability.

**Keywords:** catchability, climate change, habitat, species distribution models, stock assessments.

## Introduction

Marine ectotherms respond rapidly to changes in water temperature as temperature is one of the most important factors regulating metabolism and all subsequent vital rates (Magnuson *et al.*, 1979; Brown *et al.*, 2004). Water temperature, therefore, is a major factor in determining the broad-scale area marine organisms can occupy and is a fundamental component defining their habitat. Previous work has shown that distribution shifts in commercially and recreationally important species are directly related to changes in thermal habitat (Nye *et al.*, 2009; Pinsky *et al.*, 2013; Bell *et al.*, 2015). As water temperatures continue to increase with climate change (Saba *et al.*, 2016), species will continue to track thermal habitat poleward or into deeper water (Poloczanska *et al.*, 2013; Morley *et al.*, 2018). Thermal habitat is a powerful ecological factor but is only one dimension of a species' niche (Fry, 1971; McHenry *et al.*, 2019). For demersal fish, other factors such as depth, substrate or bathymetric features (e.g. peaks, valleys; Methratta and Link, 2006; Borland *et al.*, 2021) intersect with temperature to determine whether a species can occupy a given area in both time and space. Accounting for both the static and dynamic aspects of habitat provide a better picture of a species' niche requirements (Brodie *et al.*, 2018) and how the habitat changes on daily, seasonal, and decadal time scales. Accounting for dynamic habitat also represents a means to incorporate environmental drivers into the assessment and management process. Oceanographic conditions can vary on multiple temporal and spatial scales. Incorporating these environmental drivers into the assessment and management process can account for their seasonal and annual impacts on marine species and by extension, their longer-term impacts due to climate change.

Numerous studies have examined how shifts in dynamic habitat could impact the distribution of marine species with climate change (Pinsky *et al.*, 2013; Lam *et al.*, 2016; Morley *et al.*, 2018; McHenry *et al.*, 2019); however, these types of studies have rarely been explicitly developed to inform stock assessments. Changes in climate-mediated habitat can affect the index of abundance from fisheries independent trawl surveys by altering the catchability (*q*), the proportion of total biomass of a species caught in a trawl survey (Quinn and Deriso, 1999). Fisheries independent trawl survey data are the backbone of many stock assessments for species on the northeastern US Continental Shelf (Northeast Shelf) and around the world (Maureaud *et al.*, 2021). Therefore, any unaccounted for changes in catchability could have important impacts on model output.

Catchability (*q*) is one of the most important components of stock assessments (Arreguín-Sánchez, 1996) and scales total abundance (*N*) or biomass (*B*) to a relative index such as catch-per-unit-effort (CPUE; Quinn and Deriso, 1999).

$$\text{CPUE} = Nq.$$

Catchability is generally assumed to be static, but is known to vary over time for numerous reasons ranging from changes in gear and regulations to the impacts of the environment on the distribution and behaviour of marine species (Wilberg *et al.*, 2009; McGilliard *et al.*, 2019; Spies *et al.*, 2020). Incorporating time-varying catchability in assessment models has been done in multiple ways including estimating different *q*'s for discrete time blocks, making catchability a function of an environmental variable like bottom temperature, or by estimating catchability within a state-space model (Wilberg *et al.*,

2009). Here, we expand on previous studies (Kohut *et al.*, 2015; Manderson *et al.*, 2015) and directly estimate the availability component of species catchability to a fisheries independent trawl survey outside the assessment model.

Catchability is a function of availability—the proportion of total biomass within the space-time footprint of the trawl survey, and detectability—the proportion of biomass within the path of a survey that is caught in the survey gear (Godø *et al.*, 1999). The sample design for most surveys is stratified randomly over space, although they actually sample over time and space. Trawl surveys on the US Northeast Shelf sample in the spring and fall when water temperatures are changing rapidly, and species are migrating on or offshore. A single seasonal survey for the Northeast Fisheries Science Center (NEFSC) trawl survey can span two months, during which time there can be dramatic changes in the oceanographic conditions and the location of migrating organisms. Availability relates to the overlap between the trawl survey footprint and the area occupied by a given species. Should that overlap change over time, it would alter the catchability of the trawl survey and affect the survey index of abundance, even if abundance is not changing (Kotwicki *et al.*, 2009).

Climate-induced changes in habitat could alter the overlap between the survey and the area occupied by a species, impacting the timing of onshore and offshore migrations by affecting when water temperature changes (Henderson *et al.*, 2017; Langan *et al.*, 2021). It could restrict a species depth range, altering their distribution within a given area (Nye *et al.*, 2009; Pinsky *et al.*, 2013) and it could shift a species distribution out of a given area (Perry, 2005). Additionally, changes in the timing or design of the fisheries independent survey could also impact the spatial and temporal overlap between the survey footprint and the areas occupied by a species.

To determine if there have been changes in dynamic fish habitat, we developed species distribution models for a range of commercially important species. Species distribution models combine environmental data with species location information to develop the realized habitat of a species and determine the probability of occurrence over an area (Elith and Leathwick, 2009). They provide a means to identify the suitable habitat for a species and examine how that habitat changes spatially over different temporal scales from days, to seasons to decades. Areas of suitable habitat are used as a proxy for the areas occupied by a species and compared with the survey footprint to examine overlap. For marine species, water temperature is a major structuring component of their niche (Petitgas *et al.*, 2012; Sunday *et al.*, 2012), and the benthos is also an important niche dimension for demersal species (Borland *et al.*, 2021). We combined a thermal response model with a benthic habitat model to produce season-specific species distribution models.

Thermal response models have been developed for a range of organisms and provide a mechanistic link between the physiology of a species and their fundamental niche (Manderson *et al.*, 2015). Following Kohut *et al* (2015), the thermal habitat model was based on the Johnson and Lewin equation (Johnson and Lewin, 1946) which is a unimodal extension of the Bolzmann–Arrhenius function (Dell *et al.*, 2011). The Bolzmann–Arrhenius function is a mechanistic model explicitly relating the effect of temperature on a biological activity. Additionally, we included seven benthic characteristics to define the realized habitat. Components of the seafloor are frequently included in species distribution models, but are often

included as the measure of a variable at a single point where the tow occurred as opposed to including information about the larger area (Borland *et al.*, 2021). Fish exist within a larger seascape and are found in areas that may not be well described by a single point. A species may prefer valleys or troughs in the seafloor that are of a certain size and can be found in those types of bathymetric features as opposed to being present at every pixel on a map with a particular slope. We attempted to utilize this seascape approach and identified larger features of the seafloor for identifying the realized niche for each species.

The goal of this work was to identify changes in the availability component of catchability (*q*) for 25 commercially important species on the US Northeast Shelf commonly sampled with fishery independent surveys (Supplementary Table S1). In an attempt to provide a broader ecological perspective, the species distribution models combined a mechanistic thermal response curve with ecologically driven benthic features developed to better consider the relationship between fish and the sea floor.

## Methods

### Overview

The thermal-benthic habitat suitability index (HSI) was developed by combining an optimal species distribution model with daily hindcasted bottom temperature from an ocean model. The species distribution model was the combination of a mechanistic thermal habitat model and a benthic model developed with a generalized additive model based on data from ten inshore and offshore fisheries independent trawl surveys. Improving upon methods used in the 2014 Butterfish stock assessment (Adams *et al.*, 2015; Kohut *et al.*, 2015), we expanded the dimensions of habitat included in the species distribution models by integrating substrate and bathymetric features along with the dynamic properties of the water column that change on daily to decadal time scales. The HSI can be integrated into stock assessments by modifying the catchability parameter (*q*) of the fisheries independent trawl surveys. Catchability is a function of availability and detectability and the HSI can be used to produce an estimate of availability. The availability index is the ratio of the amount of suitable habitat sampled by the trawl survey to the total amount of suitable habitat calculated on a daily time step.

### Fisheries independent bottom trawl surveys

Fisheries independent bottom trawl surveys provided the species location data and water temperature data for the species distribution models. Ten surveys were compiled covering the entire Northeast US Shelf (Table 1). The NOAA NEFSC survey covered the entire offshore area of the shelf. The North East Area Monitoring Program (NEAMAP) sampled the nearshore waters from Virginia to Cape Cod, and state surveys covered the inshore waters from Cape Hatteras to Maine (Figure 1).

The NOAA NEFSC seasonal bottom trawl survey has been conducted since 1963. The survey methodology has been mostly consistent (Azarovitz, 1981; NMFS, 1988; Azarovitz *et al.*, 1997; Stauffer, 2004) up through 2008, but different vessels and survey gear have resulted in the need for correction factors.

In 2009, the R/V Albatross was replaced by the Henry Bigelow (Brown *et al.*, 2007). All NEFSC trawl survey capture

**Table 1.** The ten bottom trawl surveys included in this study.

| State | Department | Survey | Years available | Swept area (km²) |
|---|---|---|---|---|
| Federal | NOAA Northeast Fisheries Science Center | Seasonal Bottom Trawl Surveys | 1963–2018 | 0.037 |
| Massachusetts | Department of Marine Fisheries | Inshore Bottom Trawl Survey | 1978–2018 | 0.014 |
| Connecticut | Department of Energy and Environmental Protection | Long Island Sound Trawl Survey | 1984–2017 | 0.030 |
| New Jersey | Marine Fisheries Administration | Delaware Bay Juvenile Finfish Trawl Survey | 1991–2018 | 0.007 |
| | | Ocean Trawl Survey | 1988–2018 | 0.027 |
| Maine/New Hampshire | Department of Marine Resources | Inshore Trawl Survey | 2000–2018 | 0.014 |
| Delaware | Division Fish and Wildlife | Trawl Survey Program | 1990–2018 | 0.013 |
| Maryland | Department of Natural Resources | Coastal Bays Fisheries Investigation Trawl Survey | 1989–2018 | 0.002 |
| Virginia Institute of Marine Science | Northeast Area Monitoring and Assessment Program | Southern New England/Mid-Atlantic Nearshore Trawl Survey | 2007–2018 | 0.024 |
| Rhode Island | Division of Fish and Wildlife | Coastal Trawl Survey | 1980–2018 | 0.009 |

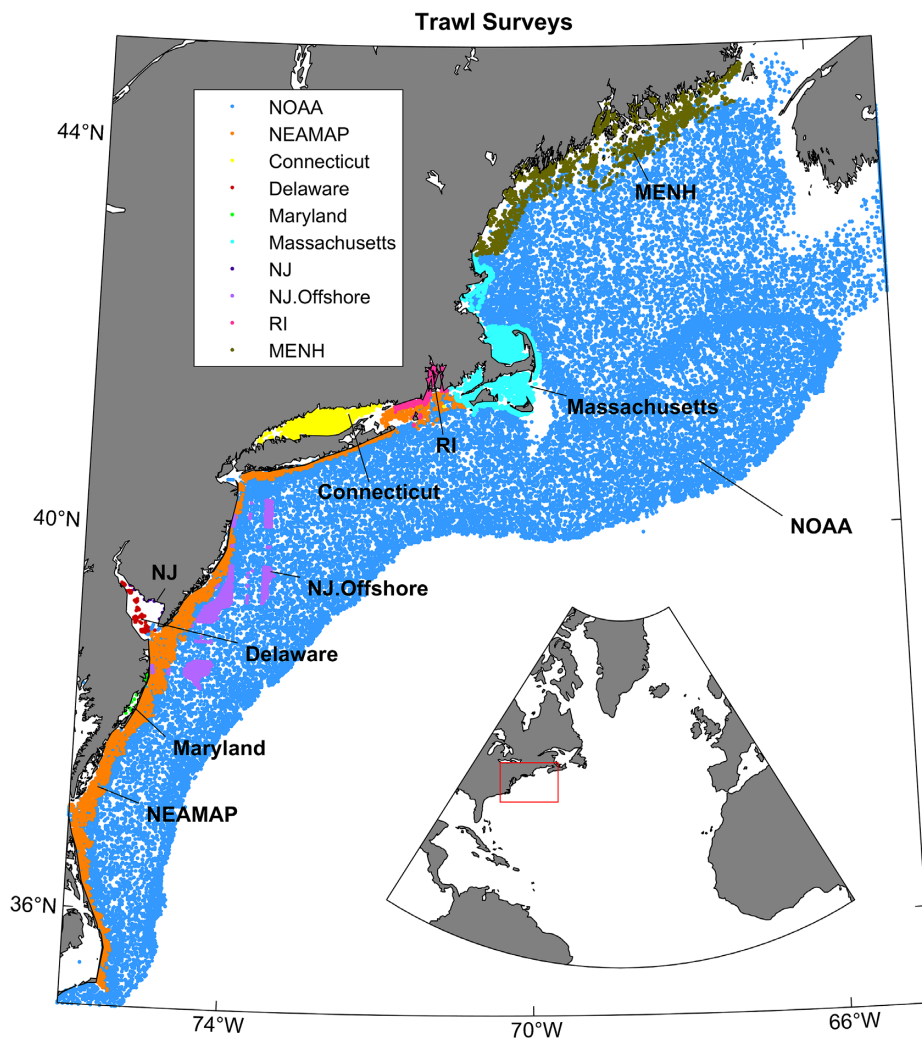Availability predictions only go through 2014 due to the availability of ocean model data.

**Figure 1.** Location of surveys on the Northeast Shelf.

data were converted into R/V Albatross units to be consistent with the vessel used for most surveys (Reid *et al.*, 1999) as is done for most NEFSC stock assessments (NEFSC, 2019). During the Albatross era, most trawls used a #36 Yankee net, except for 1973–1981 when a #41 Yankee was used. Trawl doors were BMV until replaced by Polyvalent doors in spring 1985 (Azarovitz *et al.*, 1997). Not all changes required a correction. Species-specific conversions were used for the Henry Bigelow surveys (Miller *et al.*, 2010). Final conversion factors were calculated by multiplying conversion factors for door, vessel, and the inverse of gear (Miller *et al.*, 2010).

The NEAMAP surveys the inshore waters from Cape Hatteras, NC to Cape Cod, MA, USA. The NEAMAP bottom trawl survey began in 2007 and overlaps both the federal survey and many state surveys (Bonzek *et al.*, 2017). Eight bottom trawl surveys from seven states covered the coastal and inshore waters along the entire Northeast Shelf (Figure 1). To standardize these surveys, all capture data were corrected by swept area. For surveys where this was not calculated for each individual tow, such as most state surveys, swept area was calculated as the product of intended tow duration, tow speed, and net size. For the NEFSC bottom trawl survey, tow duration for all samples was 30 min until the vessel switched to the Henry Bigelow in 2009, when it was reduced to 20 min (Politis *et al.*, 2014). Tows were conducted at 3.8 m s$^{-1}$ (Stauffer, 2004; Jech and Sullivan, 2014) prior to the Henry Bigelow, and then switched to 3.0 m s$^{-1}$ for the Henry Bigelow (Politis *et al.*, 2014). Various nets were used during the pre-Bigelow era, the sizes of which are documented in Azarovitz (1981). Swept area correction was applied as a ratio of the survey swept area to the swept area of the Albatross, keeping the Albatross unit format applied earlier.

Following the swept area correction, a nighttime correction was applied to all surveys conducted during non-daylight hours to account for day and night differences in catch of species. NOAA conducts day and night surveys while most state surveys do not. A few individual tows from state surveys occurred during non-daylight hours and were also corrected. Following NEFSC procedures, corrections were calculated based on the solar zenith angle which accounted for the time, date, and location of the tow (Jacobson *et al.*, 2011, 2015).

## Species distribution model
### Thermal habitat
The thermal niche model defines the potential thermal habitat available for each species on the Northeast Shelf. The number of fish caught at a given temperature in the trawl surveys is assumed to be a proxy for the suitable thermal habitat for each species (Brown *et al.*, 2004). The thermal niche model produces a temperature response, range, and optima that can be mapped onto historical temperature fields of the Northeast Shelf to define the dynamic available thermal habitat on a given day, season, and year. The model is based on the Johnson and Lewin (1946) equation which is a unimodal extension of the Bolzmann–Arrhenius function. The Bolzmann–Arrhenius function is a mechanistic model explicitly relating the effect of temperature on a biological activity.

The Johnson–Lewin equation is

$$h\left(T\right) = ce^{-\frac{E_R}{k_b T}} \Big/ 1 + e^{-\frac{1}{k_b T}\left(E_D - \left(\frac{E_D}{T_{opt}} + k_b \ln\left(\frac{E_R}{E_D - E_R}\right)\right)T\right)},$$

where $h(T)$ is the predicted catch at a given temperature (K), $T_{opt}$ is the optimal temperature for the species, $c$ is a scaling constant, $k_b$ is Boltzmann's constant (8.62E-5 eV K$^{-1}$), and $E_R$ and $E_D$ are the activation energy for increasing and decreasing the response with temperature, respectively. $E_R$ and $E_D$ allowed for an asymmetric response of how quickly $h$ declined at temperature values increasingly far away from $T_{opt}$. Template Model Builder (Kristensen *et al.*, 2016) was used to determine $T_{opt}$, $c$, $E_R$, and $E_D$. The resulting equation predicts abundance for each species and season for the range of bottom temperatures.

## Benthic habitat
### Benthic data
To examine the relationship to benthic habitat, we divided the entire Northeast Shelf into habitat patches based on substrate, including hard bottom, depth, and bathymetric features. Moving beyond simple calculations of slope at the specific location of the survey tow, the habitat patches were first formed by dividing the entire shelf into one of three bathymetric features: valleys, peaks, and flats based on the Benthic Position Index (BPI). These three features were then subdivided based on depth zones and then further partitioned based on substrate. The resulting habitat patches provide an approach for examining the abundance of fish in each tow in relation to the larger patch as opposed to simply the exact depth or slope at the location of the tow. The habitat patch size and shape (compactness) were also considered within the model. Since patch area and perimeter are correlated, only one of the metrics was used in the benthic models based on model diagnostics. Depth ranges were included as a categorical variable instead of the exact depth of the tow to account for the variability in the bathymetry for a tow and to ensure that species moving deeper over time could still remain within a depth zone. All points in the trawl survey were matched to the nearest Euclidian neighbour in the benthic data to label the bathymetric feature for each observation. The model was fit with five benthic variables in addition to polygon shape information.

The Bathymetry layer was created by estimating the average depth within each 100 m$^2$. It was created by interpolating the most recent bottom sounding for the region to ensure a continuous surface. The majority of soundings originate from multibeam bathymetry and single beam maps acquired by NOAA, the National Ocean Service (NOS), and other organizations (see sources at NOAA NCEI, 2021). In locations where multibeam bathymetry was not available, gaps were filled by using the digital bathymetry database from the US Naval Oceanographic Office (NAVO DBDBV, 2021). All available soundings were merged into a single layer using ArcPro (ESRI, 2019) and interpolated to a raster surface using the Empirical Bayesian Kriging Tool from the Geostatistical Toolbox. Bathymetry values were then reclassified into five categories based on their percentiles.

The bathymetric features (peak, valley, and flat) were created from the BPI. BPI is a measure that compares the depth at one location with the depths of the surrounding cells. This index is based on the Topographic Position Index developed by Weiss (2001). It is often used to locate features across the

seafloor. We used the NOAA's Benthic Terrain Modeler to calculate BPI values using our bathymetry layer (Walbridge *et al.*, 2018). BPI is a scale-dependent measure, so its values depend on the number of cells used to calculate it. We calculated BPI at two different scales: broad scale (inner radius: 9 cells, outer radius: 90 cells) and fine scale (inner radius: 3 cells, outer radius: 25 cells). Both layers were then standardized and reclassified into different features (valleys, flats, and peaks) depending on their values.

The sediment layer estimated the percentage of each type of main soft sediment (sand, gravel, and mud) within each 100 m cell. This was created by interpolating the most recent sediment estimates across the region. Multiple sources of sediment information were combined to produce the layer: Woods Hole Sediment texture database (McMullen *et al.*, 2014), USGS usSEABED database (Reid *et al.*, 2005), the University of Massachusetts Dartmouth School of Marine Science and Technology video survey data (Harris and Stokesbury, 2010), and data from selected NOS bathymetric surveys (NOAA NCEI, 2021). All these samples were cleaned to remove erroneous values (e.g. over land), and compared to eliminate duplicates. We also removed samples where percentages could not be easily derived. All the points were merged using ArcGIS Pro (ESRI, 2019), and interpolated using the EBK regression prediction tool from ArcGIS' Geostatistical Analyst, with bathymetry and BPI at two different scales as covariates. We interpolated three different surfaces: percentage of sand, percentage of mud, and percentage of gravel. We reclassified each surface depending on the percentages. For example, for sand, the classes were (1) absence of sand (<25%), sand combined with others (25–75%), and majority sand (>75%). We finally combined all three reclassified rasters into one single layer with the following classes:

- o dominant sand (>75% sand).
- o dominant mud (>75% mud).
- o dominant gravel (>50% gravel).
- o sand and gravel mixed.
- o sand and mud mixed.
- o mud and gravel mixed.
- o other (three type mixes in different quantities).

The probability of hard bottom was also included as a variable within the benthic habitat model.

To include a measure of the shape and area of the seafloor features, we made a layer consisting of the unique permutations of bathymetric features, depth, and sediment. This was converted to polygons using ArcPro (ESRI, 2019). We simplified polygons to make sure that the shape did not include any artifacts from the original raster data. We also removed any features that were smaller than 21000 m$^2$ (less than 3 by 3 cells in size). For each of the resulting polygons, we calculated their total area, perimeter, and a compactness score. For compactness, we used the Polsby–Popper index, a measure of compactness of a shape that is often used in gerrymandering studies (Polsby and Popper, 1991), and it is calculated as

$$\frac{4\pi \, \text{area}}{\text{perimeter}^2}.$$

## Benthic model

The different benthic habitat components were then integrated into a logistic generalized additive model (GAM; Wood, 2006). GAMs provide the flexibility to both determine if a particular parameter is an important component of the benthic habitat relationship and determine its functional form.

The GAM formula for all variables was

$$\begin{aligned} Presence \sim\ & BPI_{broadclasses} + BPI_{fineclasses} \\ & + sedclasses + depthclasses \\ & + HB + s\left(\ln\left(patch\right)\right) + s\left(compact\right), \end{aligned}$$

where presence is a binary presence/absence label for each species, each benthic class is as described above, *HB* is a binary hard bottom label, patch is either the area or perimeter of the defined patch where the pixel is located, and compact is the Polsby–Popper index of the patch. Smoother splines (s) were set to have a maximum of four degrees of freedom to avoid overfitting and inferring a relationship that may not be biologically relevant. All variable combinations were considered, with the lowest Akaike's Information Criterion (AIC; Akaike, 1974) score determining the best model. A five-fold cross validation was performed for each species and season. The final model for each species was calculated using all available data for that season, utilizing the variable selection from the partitioned model with the lowest AIC. Benthic probability was predicted across the entire model domain, resulting in separate habitat projections for each species and season. Since benthic probability for low-prevalence species was not necessarily on the same scale as thermal suitability and normalization is sensitive to outliers, benthic projections were capped at and normalized to the value where the Z score of the geographic model domain equaled 2.

## Ocean model

The thermal-benthic HSI was calculated from 1980 to 2014 at a daily time step for the spring and fall seasons (mean 40 d per season) across the entire US Northeast Shelf for each species. The HSI was produced by combining the species distribution model for each species with daily hindcast bottom temperature data derived from the ROMS-COBALT-NWA ocean model (Kang and Curchitser, 2013, 2015), developed by Rutgers University and NOAA Geophysical Fluid Dynamics Laboratory (shortened to "ROMS" hereafter). The ocean model uses the Regional Ocean Modeling System framework (Shchepetkin and McWilliams, 2005) and consists of curvilinear 7 km cells with 40 terrain-following depth layers. The spatial domain covers most of the Northwest Atlantic Ocean from the Caribbean Sea through the Gulf of St. Lawrence. SODA v2.1.6 (Carton and Giese, 2008) provides the boundary conditions, and surface components are derived from the CORE.v2 data sets (Large and Yeager, 2009). Ocean model output was available from 1980 to 2014. More information regarding the physical components can be found in Kang and Curchitser (2013, 2015).

To ensure accuracy of the ocean model, we compared bottom water temperatures simulated by the ROMS model with *in situ* temperature observations from the state and federal trawl surveys. We separated 55976 trawl survey locations by geography, season, and year to determine where biases may be impacting the bottom temperature output of the ROMS model. Because bias was only detected spatially and not temporally, a correction factor was calculated by subtracting the average seasonal modelled temperature from the average observed temperature for the seasonal trawl time series for each

point in the ROMS model and applied to the daily bottom water temperature for the availability calculation. In areas on the shelf where there were no trawl survey data to compare the model to, bias was linearly interpolated from surrounding points. This process debiased the model while still allowing for the nuances and variation provided by the higher resolution model to be identified.

### Habitat suitability index and availability

The thermal habitat model and the benthic habitat model were equally weighted and combined to produce an overall thermal-benthic HSI. The square root of the normalized thermal abundance and the Z-normalized probabilistic benthic habitat model were used for each component of the HSI equation. This combination optimized the predictive model fit of the testing data for most species.

$$HSI_{j,T} = sqrt\left(\frac{h_T}{h_{Topt}}\right) \times \left(\frac{b_j}{Zmax\,(b)}\right),$$

where $h$ is the thermal abundance projected by the Johnson–Lewin equation at bottom water temperature $T$ located at point $j$. $T_{opt}$ is the optimum temperature for the species, $b$ is the benthic probability, and $Zmax$ is the $Z = 2$-normalized benthic probability of the model domain. The resulting HSI is a value between 0 and 1 indicating the overall habitat suitability for a species at a single point in space and time.

Seasonal availability ($\rho$) is a measure of the overlap between the trawl survey and the area the species occupied (Supplementary Figure S1). The HSI was used as a proxy for the area the species occupied. Availability was calculated as the cumulative percentage of the available species habitat (determined by HSI values) the NOAA bottom trawl survey covered in a particular season using the formula

$$\rho_H = \sum_{k=1}^{o} \frac{HSI_{k,j,i} \times \frac{area\,of\,survey\,strata_k}{p}}{\sum_{j=1}^{n} HSI_{j,i} \times Area_j},$$

where $HSI_{k,j,i}$ is the HSI of sample $k$ at location, $j$ on day $i$. The $p$ is the number of times the strata containing sample $k$ was surveyed, $n$ is all pixels in the model domain, and the average area of each pixel $j$ is 0.0169 km$^2$.

The annual availability index and the annual thermal-benthic HSI for each species were evaluated for linear trends over time in each season. Trends were examined with standard linear regression (Index = m × year + $\beta_0$ + e). All linear models were tested with the Durbin–Watson statistic (Durbin and Watson, 1950) to evaluate autocorrelation. Linear models with autocorrelation were rerun within a generalized least squares linear model that included autocorrelation. An $\alpha$ of 0.05 was used to determine significance.

### Model evaluation metrics

In addition to the validation for each separate component, the combined thermal-benthic HSI models for each species and season were validated with a five-fold cross validation. For each partition, the model was trained on 80% of the data and tested on the other 20% with each cross validation pulling randomly to select the training and test data sets. The partitions were the same as used in the initial GAM CV. HSI was treated as a probability of occurrence so it could be validated against observations in the test set. Model predictions were

evaluated using the True Skill Statistic (TSS) where

$$TSS = sensitivity + specificity - 1.$$

TSS balances the true positive rate (sensitivity) and the true negative rate (specificity) while punishing the model for heavily prioritizing one metric over the other, as may be the case with unbalanced data with fewer observed positives (Allouche et al., 2006). It ranges from -1 to 1 with 0 indicating random classification. Models with a TSS > 0.40 are considered adequate (e.g. Zhang et al., 2015). Area under the curve (AUC) is a threshold-independent metric measuring the tradeoff between sensitivity and specificity and was also considered in evaluation. Here, 0.70 was a minimum acceptable score (e.g. Zhang et al., 2015).

### Dynamic factor analysis

Common patterns across the time-series of species availability were evaluated with DFA. DFA is a state-space technique for identifying common patterns or trends across numerous, short, non-stationary time-series making it well suited for fisheries data (Zuur et al 2013). The method uses both a process equation and an observation equation. Selection of the most appropriate number of common trends is done through AIC after examining a user supplied number of common trends. The process equation is a random walk with multivariate normal error (MVN). The $Q$ matrix is set to the identity matrix. The number of random walks contained within the process equation denotes the number of common trends.

$$x_t = x_{t-1} + w_{t-1},$$

where $w_{t-1} \sim MVN(0,Q)$. The observation equation linearly combines the random walks and the $Z$ matrix resulting in the availability indices (ys).

$$y_t = Z_{Xt} + V_t,$$

where $v_t \sim MVN(0,R)$. The factor loading variable $Z$ is a matrix that accounts for the degree to which an individual time series of availability is represented by the common trend. The measurement error $v_t$ is MVN.

### Software

All GAMs were created in R (version 4.0.2; R Core Team, 2021) using the "mgcv" package (Wood, 2006). Thermal abundance was calculated using Template Model Builder (Kristensen et al., 2016). Fit statistics and threshold determination used the "PresenceAbsence" R package (Freeman and Moisen, 2008). The DFA was run in the R package MARSS (Holmes et al. 2012). Figures were created in R and MATLAB (version 2020b; Mathworks Inc, 2020) using the open-source m_map software package (https://www.eoas.ubc.ca/~rich/map.html) for all MATLAB mapping.

## Results

### Species distribution models

The species distribution model defined the suitable habitat for each species for the dimensions of the niche included in the model. Species generally had different optimal temperature ranges between the spring and fall seasons (Figure 2), but less seasonal variability in depth range, substrate, and bathymetric features. Depth and bathymetric features were relatively consistent between seasons, but substrate could be variable
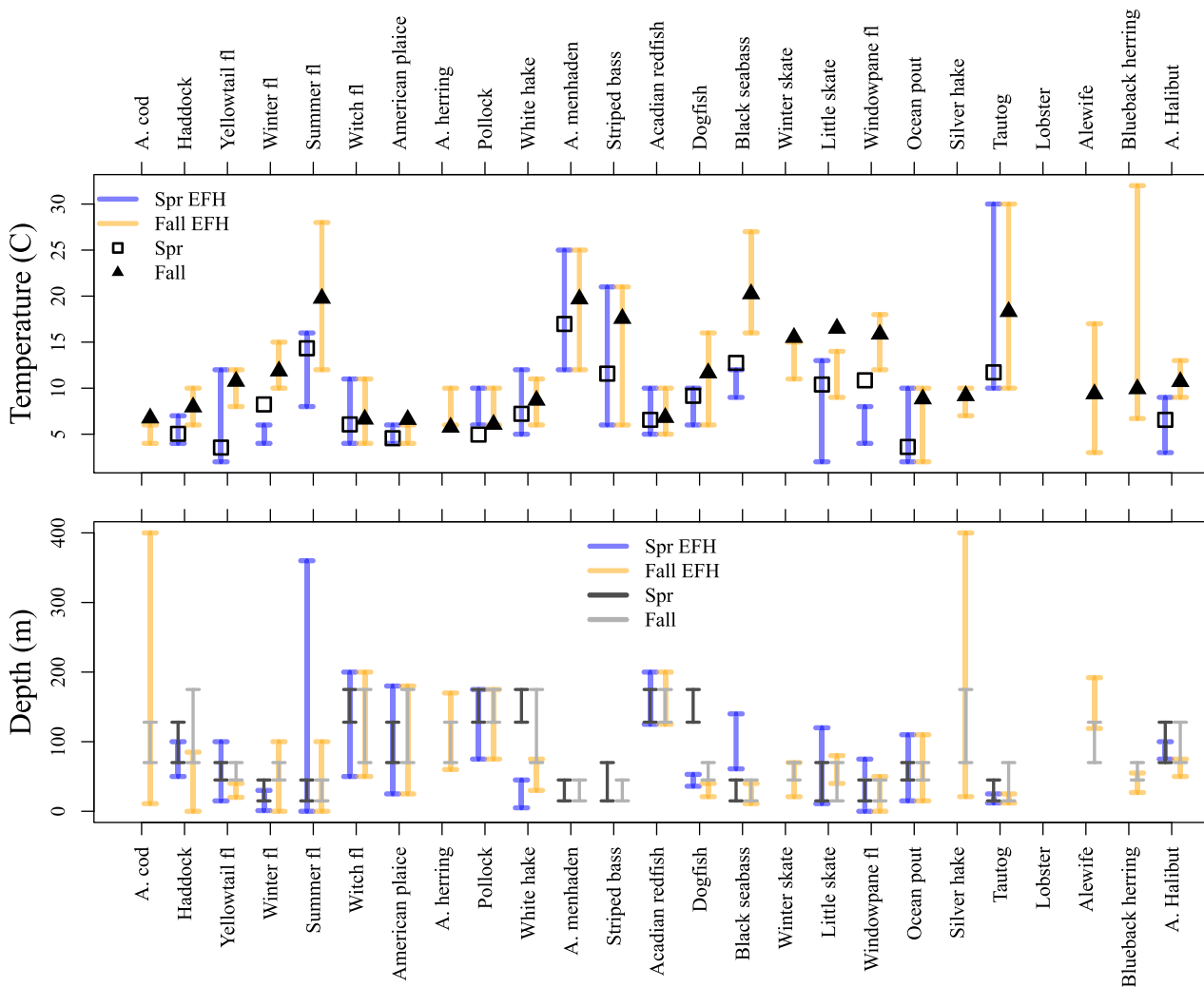
**Figure 2.** The temperature and depth range for each species from their essential fish habitat (EFH) reports and the output of the species distribution models. Information is displayed for species and seasons with an acceptable species distribution model. EFH information was not available for every species.

in some species. The final models for each season and species utilized bathymetric classes, sediment classes, and patch size. Most models used all of the other variables, with some exceptions (Supplementary Tables S2 and S3). Classifying peaks and valleys with BPI was useful in most models, and generally had more impact on broader scales rather than finer scales. Offshore species such as Acadian redfish and pollock exhibited very little difference in suitable habitat between the spring and fall, while species with seasonal estuary use tended to have more variability in their habitat components between seasons.

Specific species distribution models were generated for each species in each season. As an example, the species distribution model for summer flounder in the fall is presented and compared to the National Marine Fisheries Service essential fish habitat (EFH) documentation that is a legally required description of habitat for all federally managed species (Packer, 1999). Summer flounder are found over a wide depth range, however, this study found the flatfish most prominent in shallow water with abundance decreasing with depth (Figure 3). EFH and the species distribution model both indicated similar temperature ranges and similar substrate characteristics. Summer flounder are found predominantly in temperatures

ranging from 12–15 C, on sandy substrates or sand mixed with mud or gravel or both. As expected, the species was not found on hard bottom (No HB). One of the focuses of this study was to also include the type of features where species are likely to be found. Summer flounder are most commonly found on areas that are peaked or mounded along with flat areas. They are generally not found in valleys.

The suitable habitat defined by the species distribution models was generally similar to the habitat as defined by the NOAA EFH documents (Figure 2 and see Supplementary Material). There were some major discrepancies such as large differences in the optimal temperature range for windowpane and winter flounder compared to EFH ranges, but overall the ranges overlapped for most variables. Differences were likely related to time of year and location of samples. EFH does not include bathymetric features as a habitat dimension and so there was no comparison available. The bathymetric features variables were highly significant in the GAMs for every species and produced a single optimal feature (peak, valley, or flat) for almost every species in both seasons. In the spring, ocean pout, dogfish, and yellowtail flounder were the only species that were most common on flat areas. No species in the spring
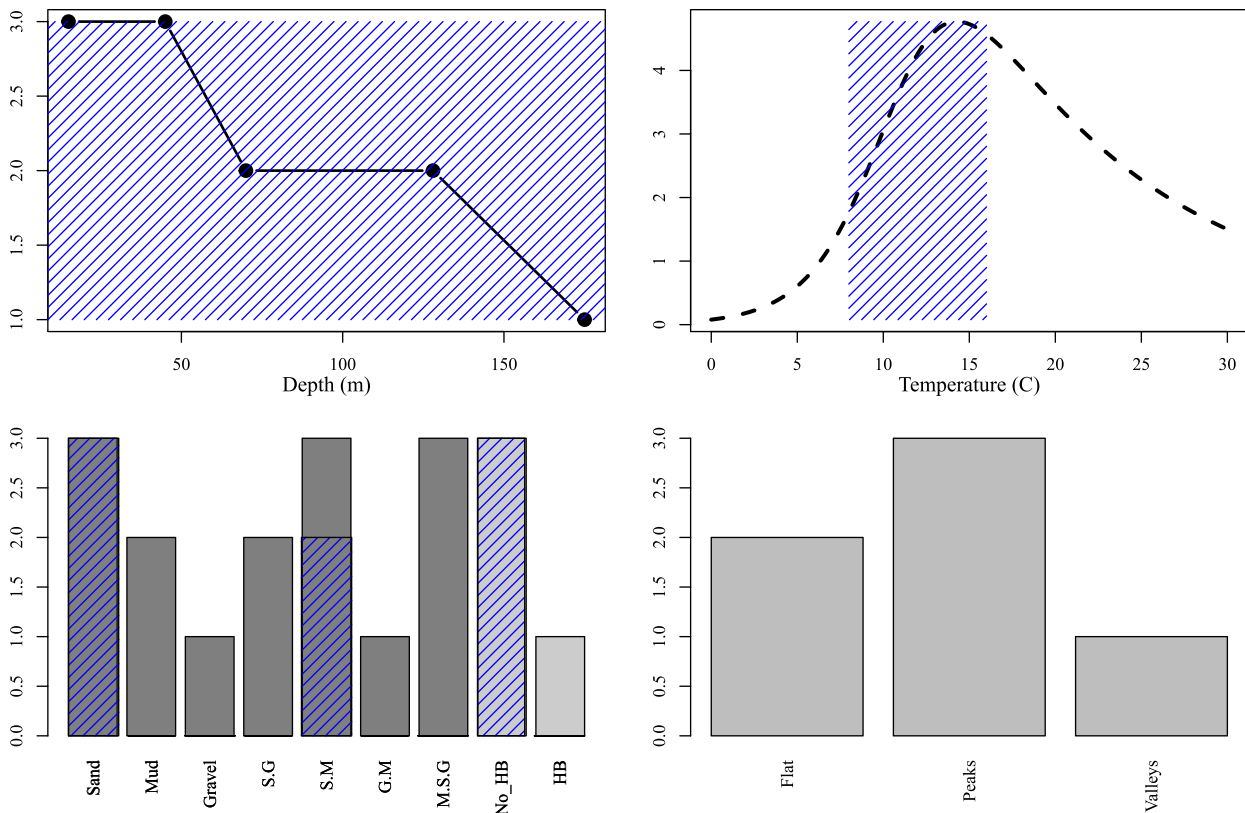
## Summer flounder − Spr



**Figure 3.** Plots of habitat characteristics of Summer Flounder in the spring from the species distribution model (SDM) (grey, black) overlaid with information from the Essential Fish Habitat documents (EFH) (blue hash marks). To visually compare descriptive EFH text to the species distribution models, SMD parameter estimates were scaled to low (1), medium (2), and high (3) occupancy. SDM parameter estimates can be found in the supplementary material. Depth is plotted from 0 to 175 m with 175 m representing all depths 175 m and greater. Sediments include Sand (S), Mud (M), Gravel (G), and combinations of these (e.g. S.G = Sand and Gravel mix). Sediment also displays whether the species was found on Hard Bottom (HB) or not on Hard Bottom (No_HB).

were common on both peaks and valleys. In the fall, winter flounder, dogfish, little skate, tautog, yellowtail flounder, and ocean pout were the only species that were most common on flat areas. For the few species in either season that were common on two features, they were found on peak and flat areas or valley and flat areas. White hake in the fall was the only instance across all species and seasons to be commonly caught on both peaks and valleys.

The size of the habitat patch and the compactness of the habitat patch (long and thin versus round) were significant and included in the distribution models for almost every species in both seasons. The distribution of patch size for most species was domed shape with an optimal range that varied by species. The distribution was not particularly peaked indicating that most species could be found on a range of patch sizes, but were more commonly found within a particular range. A few species such as striped bass, silver hake, and summer flounder were more commonly found on larger habitat patches with only blueback herring being more common on smaller patch sizes. The compactness variable, the measure of the shape of a habitat patch exhibited a similar pattern across a number of species in both seasons. The most common pattern was a slight peak at both end members (long and thin, tightly compacted) often with a small amount of wavi-

ness. Occurring much less frequently, a few species were more commonly found on habitat patches that were more compact (more cohesive as opposed to long and thin). Similar to the patch size, the majority of species could be found on a range of patch shapes, with only a slight increase within a particular shape suggesting generalist species.

### Regional ocean modeling system

The predicted bottom water temperature from the ROMS ocean model matched the seasonally averaged observed temperatures fairly well (Supplementary Figure S2). The ROMS model exhibited the expected geographic patterns of bottom water temperature and seasonal variability. However, the model generally overestimated water temperature in the southern Mid-Atlantic Bight, southern New England, and the western Gulf of Maine, while underestimating water temperature near the shoreline, shelf break, and eastern Gulf of Maine and Georges Bank (Supplementary Figure S2). Overall, the ROMS model and the trawl survey bottom water temperatures had a Pearson correlation coefficient of 0.905. The spatial pattern was consistent through time so no temporal correction was needed, but a spatial correction by season was required. After the spatial-seasonal correction factor was ap-

plied and the geographic biases in the uncorrected model were accounted for, the correlation coefficient between the ROMS model and the observations rose to 0.949.

### Species distribution model validation

The models produced useful (TSS > 0.4) HSIs for 18 of 25 species in the spring and 24 of 25 species in the fall. TSS ranged from 0.28 for Alewife in the spring to 0.79 for American plaice in the fall (Supplementary Tables S4 and S5). All models for all species except Lobster in the spring passed the AUC limit. Generally, models in the fall scored better than the spring models. Most of the models had a higher sensitivity than specificity, prioritizing true positives instead of true negatives. The TSS scores for each of the five cross validations were relatively close as indicated by the small standard deviation values for each species and season, indicating that the models produced a consistent level of fit regardless of the data selected to train the models. The standard deviation of performance metrics among individual fits in the cross validation was also unrelated to the overall quality of the model for either TSS or AUC.

### Habitat suitability index

The suitable habitat for each species as represented by the HSI varied both seasonally and annually in both the spring and fall (Figure 4). Deeper water species, such as Acadian redfish tended to exhibit smaller seasonal changes in HSI, while species that utilize estuaries and make strong onshore/offshore migrations typically had the largest changes in HSI. The HSI for species that prefer colder waters such as yellowtail flounder declined over the course of the spring season and increased over the fall season (Figure 5), while warmer water species exhibited the opposite pattern.

The cumulative HSI (sum of the bi-monthly HSI values of the model domain during the months the trawl survey typically operates) varied over the time series in both spring and fall with most species having no long-term trends. Over the time period of the study, suitable habitat varied for most species, but did not increase or decrease. The HSI for three species in the spring significantly increased and the HSI for five species in the fall had significant trends (Supplementary Table S6 and Figure 4). Two species had positive trends and three species had negative trends. Changes in the phenology of the dynamic habitat were examined by looking at changes in HSI at the beginning and end of the trawl seasons (Supplementary Tables S7 and S8). The HSI for the same three species in the spring indicated a significant increasing trend in suitable habitat at the beginning of the season (mean of the first two weeks of March), and only white hake exhibited an increasing trend in suitable habitat at the end of the spring season (mean of the last two weeks in May). In the fall, the HSI at the beginning of the season had significant trends for seven species and the HSI for six species at the end of the fall season were significantly trending. There was more change in the fall than in the spring.

### Availability

Based on the HSI, availability indices for the federal trawl survey were developed for 18 of 25 species in the spring and 24 of 25 species in the fall. Across the different species, availability was generally variable without a trend (Figure 6). This indicates that the federal trawl survey is, on average, sampling the same amount of the potential habitat each year and season. In both seasons, the availability indices for some of the species showed a drop toward the end of the time series (∼2009). The fall exhibited larger variability over time than the spring. Six species in the spring and seven species in the fall exhibited significant negative trends in their availability indices, and none of the species had significant positive trends (Table 2 and S9). Haddock, yellowtail flounder, and dogfish had significant negative trends in both seasons. The other species only exhibited the trend in one season.

### Dynamic factor analysis

DFA was run on the availability indices to examine overall patterns or trends in the time series (Zuur *et al.*, 2003). The analysis fit two common trends for the spring and four common trends in the fall (Supplementary Figures S3–S5). In the spring, the first trend declined through the initial part of the time series before becoming variable without a trend. The second common trend had three peaks (early 1980s, late 1990s, and mid 2000s) before declining sharply at the end of the time series. The species loadings, the amount of variability in the individual species availability indices that was accounted for by the trend, varied across the species. The availability indices for species with large positive loadings tracked the trend well, while those with large negative trends exhibited the opposite pattern. Species with small magnitude loadings did not track the trend well. Witch flounder, haddock, and American plaice loaded most strongly on trend one. Tautog, little skate, striped bass, and menhaden were the most closely aligned with the second common trend.

In the fall, the first common DFA trend was variable with no linear trend. Atlantic herring, pollock, and American plaice loaded strongly on this trend indicating their availability indices tracked with the trend. The magnitude of the factor loadings was large, suggesting a number of species exhibited components of this trend. DFA trend two was variable with a decline and/or potentially three declining periods. Loadings had large magnitude and yellowtail flounder loaded the strongest along with several other species that had significant declining availability indices. There were no species with large magnitude negative loadings that would suggest increasing availability. DFA trend three varied about a mean until the late 2000s and then jumped up. A number of species loaded negatively for this trend indicating that their availability indices exhibited the opposite pattern. DFA trend four was again variable without a linear trend. Similar to trend three, a number of species loaded negatively for this trend. Most species only loaded strongly on a single trend and had low magnitude loadings on the other trends indicating that they generally followed one of the four trends the most closely. Windowpane flounder was one of the few species that loaded strongly on two trends (three and four) resulting in an availability index that was variable with a sudden decrease in the late 2000s.

Trend two in the spring and trend three in the fall both exhibited substantial changes around 2009. In 2009, the federal trawl survey changed vessels and stopped sampling some of the inshore strata. In both seasons, the number of inshore tows dropped from a mean of 90 before the switch to a mean of ∼70 after the switch (Figure 7). Species that loaded strongly for these two trends were commonly found in inshore waters and exhibited a substantial drop in their availability index after 2009. Species like menhaden, tautog, and striped bass
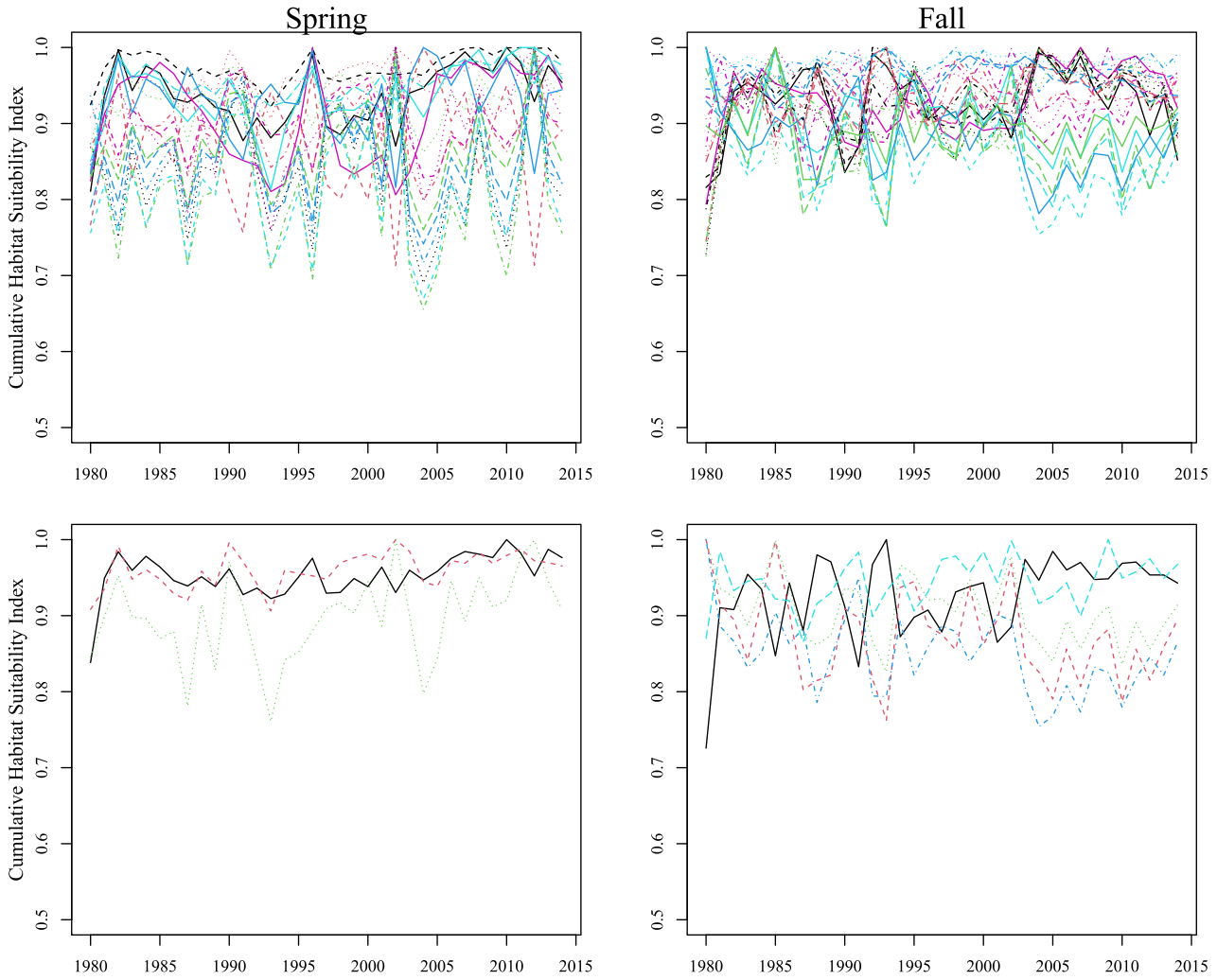
**Figure 4.** Annual HSI value for each species in the spring and fall. Lower plots display HSI with significant trends.
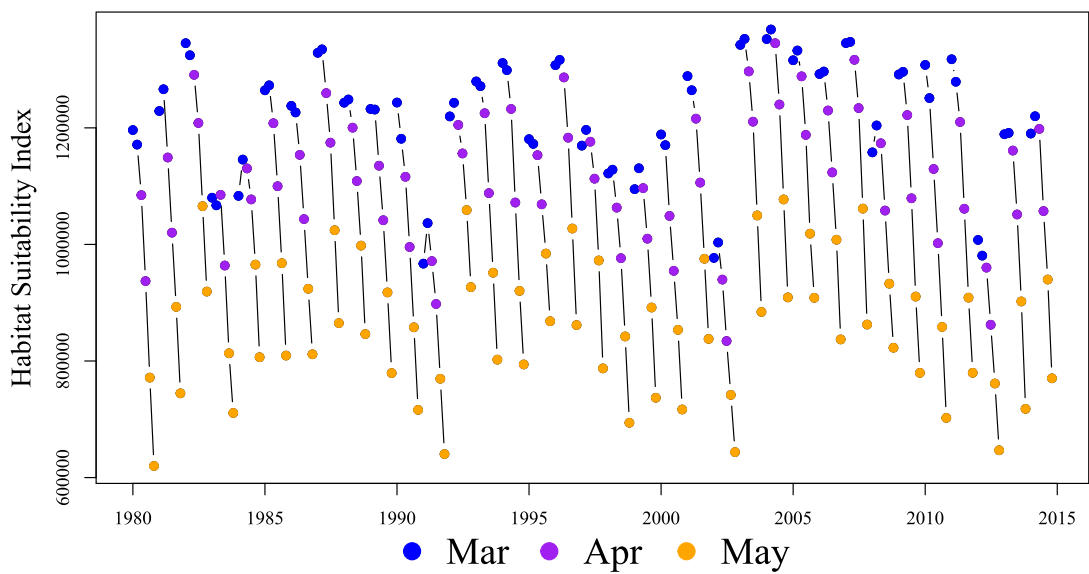


**Figure 5.** Seasonal changes in the HSI for Yellowtail flounder on Georges Bank in the spring. In a given year, the HSI is generally largest in March (blue) and decreases as the water warms through April (purple) and May (Orange).
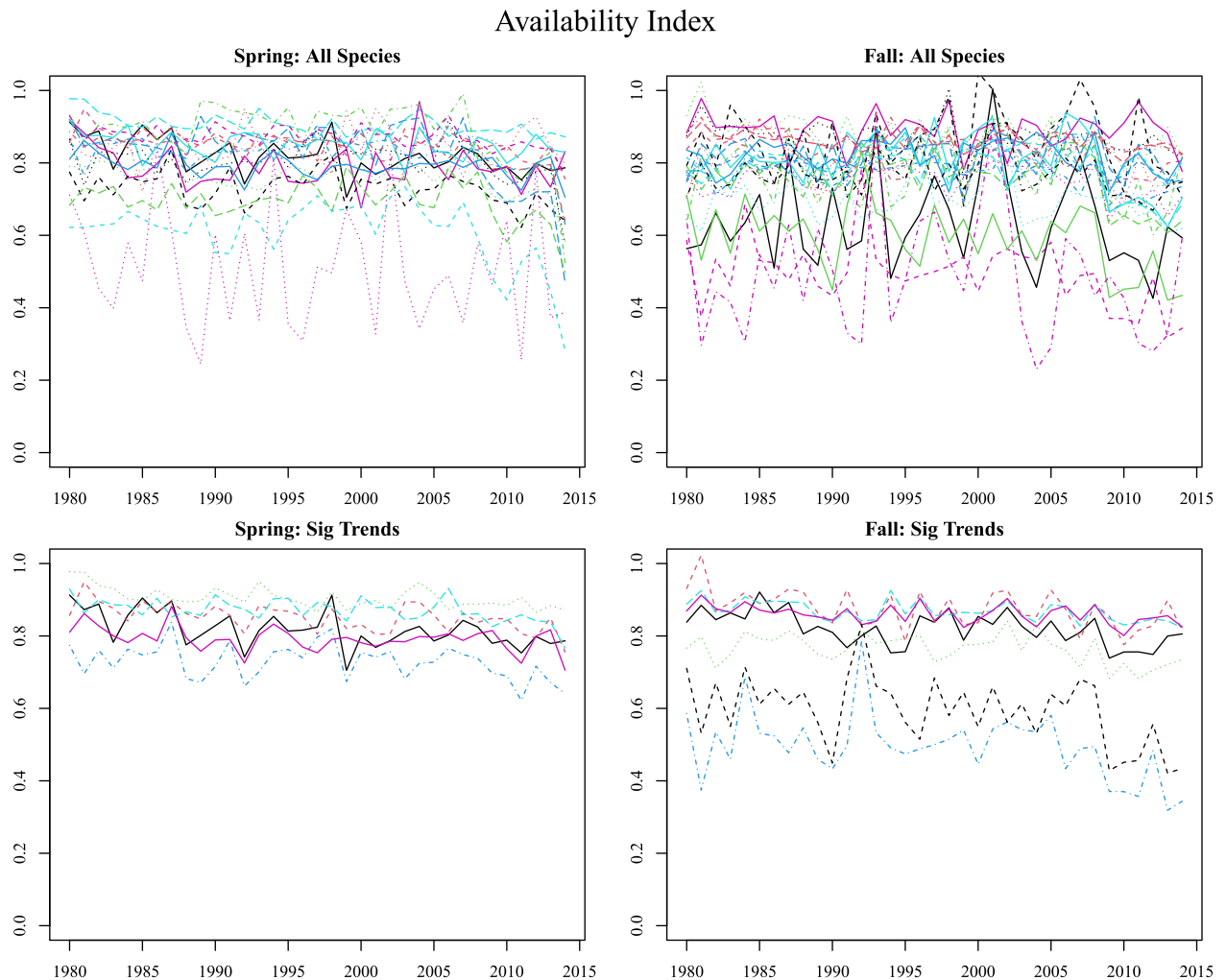
## Availability Index



**Figure 6.** Annual availability index for each species in the spring and fall. Lower plots display availability with significant trends.

**Table 2.** Species with significant trends in availability.

| Spring Species | Slope | P-value |
|---|---|---|
| Haddock | −0.003 | 0.001 |
| Yellowtail flounder | −0.002 | <0.001 |
| Witch flounder | −0.002 | 0.003 |
| Pollock | −0.002 | 0.036 |
| Dogfish | −0.002 | 0.002 |
| Ocean pout | −0.001 | 0.03 |
| | | |
| **Fall** | | |
| Haddock | −0.002 | 0.002 |
| Yellowtail flounder | −0.003 | 0.003 |
| Winter flounder | −0.002 | 0.019 |
| Striped bass | −0.004 | 0.011 |
| Dogfish | −0.001 | 0.001 |
| Silver hake | −0.001 | 0.014 |
| Tautog | −0.004 | 0.005 |

Trends were tested for autocorrelation and refit with an autocorrelation term if it was present.

are not particularly well sampled by the federal trawl survey, but had substantially higher catch rates in the inshore areas in both seasons. Species like black seabass, summer flounder, and winter flounder undergo seasonal onshore and offshore migrations. Black seabass and summer flounder exhibited sharp declines in their availability indices in the fall when they were inshore, but not in the spring when they are typically in offshore waters. Winter flounder undergoes an opposite seasonal migration pattern and had a drop in availability after 2009 only in the spring.

### NEFSC trawl survey

The timing of the trawl survey was variable without any strong trends from the mid-1980s through 2010s (Supplementary Figure S6). Prior to 1985 the survey generally occurred later in the year. During the time period of the study, there were some later surveys and shortened surveys, but they were typically intermittent. For example, the spring survey started several weeks later than normal in 1987, 2000, and 2014. The survey sampled the full Northeast Shelf almost every year providing similar spatial coverage, but the survey sometimes started in different locations and/or extended sampling south below Cape Hatteras changing the timing of when it sampled different sections of the shelf.
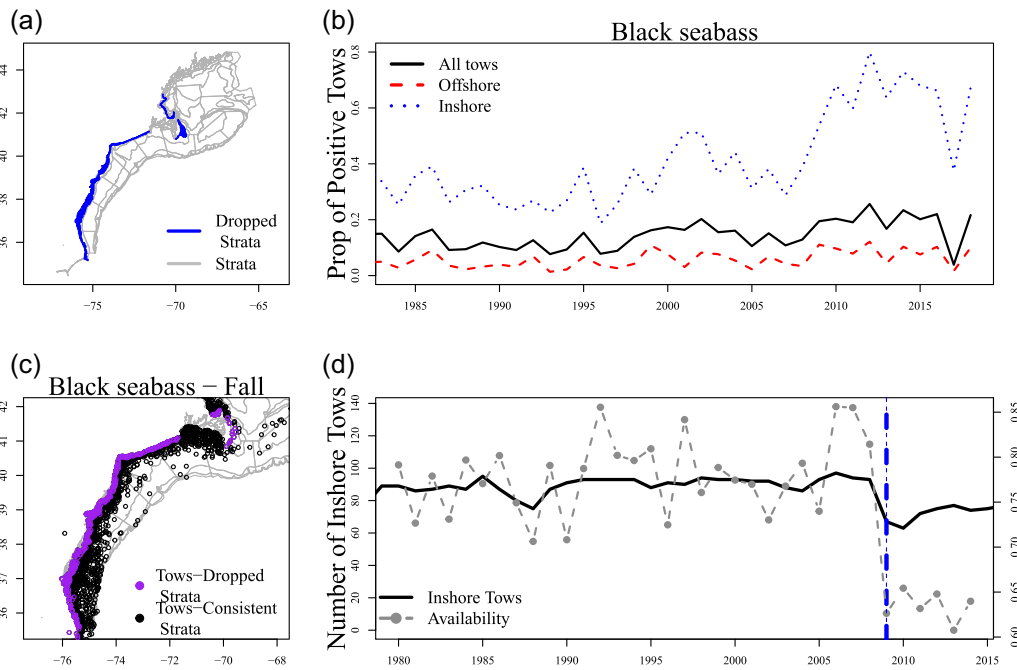
**Figure 7.** (a) The location of tows that were dropped from the survey in 2009. (b) Proportion of inshore and offshore survey tows that caught Black seabass in the fall. (c) Location of positive tows. Purple points are located in the dropped strata and black points are in strata that continue to be sampled. (d) The number of tows conducted in the inshore strata (mean pre-2009 = 90, mean post-2009 = 71) along with the annual availability index.

## Discussion

As climate varies and changes, it alters the suitable habitat available to natural marine resources, thus directly impacting the distribution and abundance of species. Changes in habitat drive shifts in distribution and influence abundance indices from fisheries surveys, potentially having major impacts on the management and stock assessments of species (O'Leary et al., 2021). On the US Northeast Shelf, warming conditions have increased the habitat available for species such as black seabass (Bell et al., 2015) and changed the seasonal timing of available habitat (Henderson et al., 2017; Langan et al., 2021). In addition to changing oceanographic conditions, the timing and location of sampling has not always been consistent by the fishery independent trawl surveys. Major changes in the spatial-temporal overlap between the trawl survey and location of the species can affect the index of abundance used in stock assessments and cause serious problems for specifying catch advice (O'Leary et al., 2021). Directly integrating a time-varying, habitat-mediated catchability coefficient into the assessment process, however, is one means to account for the changes in species and survey overlap (Wilberg et al., 2009).

The 2014 butterfish stock assessment demonstrated how integrating thermal habitat can improve survey estimates and provide better catch advice (Adams et al., 2015). Expanding on the 2014 method, we developed the thermal-benthic HSI. While thermal habitat is one of the main drivers determining where organisms can exist, not every location with optimal temperature is suitable habitat (McHenry et al., 2019; Borland et al., 2021). For marine taxa, particularly demersal species, additional niche dimensions such as the benthos are essential for defining suitable habitat (Methratta and Link, 2006; Borland et al., 2021). The habitat models provided good estimates of the probability of occupancy for most of the species examined in the study and when paired with a hind-

cast ocean model enabled us to track habitat over space and time.

In general, the suitable habitat for each species as defined by the species distribution models was very similar to the descriptions from the EFH materials. The optimal temperature ranges and depth distribution tended to match well, and the substrate specifications were similar. Many of the demersal species within the study are considered generalists and can be found on a number of substrates (Collette and Klein-MacPhee, 2002). Species like windowpane flounder can be found on sand, mud, or mixed substrates and previous work found that substrate alone was not a particularly good indicator of species abundance on the Northeast Shelf (Methratta and Link, 2006). Some patterns did emerge, however, indicating that while species can be found on a range of substrates, they do have a preference for certain sediments. Little skate and summer flounder were sampled on all substrate types, but were most commonly sampled on sand or sand mixed with other sediment types. Similarly, pollock was found on all substrate types, but was in highest abundance on gravel or gravel mixes, while silver hake could be found across the substrate types, but preferred mud or mixed mud substrates. Other species, such as dogfish, followed the generalist pattern with a preference, but the preference was different for the two different seasons. Dogfish were most commonly found on sand and mixed sand substrates in the spring, but switched to mud or mixed mud substrates in the fall.

Within the species distribution model, substrate was likely not well specified for species that prefer structured habitat like tautog and striped bass, as these species are not particularly well sampled by the trawl surveys. The trawl surveys do not sample the full habitat for these species, and only provide a limited view of their substrate preferences. The surveys do, however, provide good estimates of depth and temperature (Collette and Klein-MacPhee, 2002).

While substrate alone may not be a particularly good indicator of a species preferred habitat (Langton *et al.*, 1995), within the multilayered benthic habitat variables included in the models, substrate, and all the variables were highly significant. By combining the bathymetric features with depth and substrate, the models produced good estimates of benthic habitat. Species tended to have a strong preference for a single bathymetric feature (peak, valley, and flat) or a combination of one of the features with a flat area. Seafloor topology is rarely included in essential fish habitat determination, but the models indicate that like previous studies (Auster *et al.*, 1991, 1995) the species are responding to the shape of the seafloor itself. Including simple metrics such as peak, valley, and flat, as was done in this study could provide a better description and more accurate location of essential fish habitat.

The combination of the species distribution models with hindcast ocean model data enabled the examination of the changes in species habitat over the last 35 years. Suitable habitat for most species varied over time without a trend; however, some species exhibited changes in the amount and timing of suitable habitat over the time period. Compared to the voluminous literature on climate-induced changes for species on the Northeast Shelf (Hare *et al.*, 2016; Peck and Pinnegar, 2018, and references within both), the changes in suitable habitat are relatively minor.

There are at least four potential reasons for the small changes in suitable habitat. (1) While studies have made much of the rapid increase in sea surface temperature on parts of the Northeast Shelf (Pershing *et al.*, 2015), bottom temperature does not exhibit an increasing trend. Over the time span of the study, 1980–2014, the observed bottom temperature on the Northeast Shelf has generally varied with little to no trend (NEFSC, 2012). Bottom temperature, particularly in the northern part of the shelf, increased dramatically in the 2010s, however, such that the bottom temperature time series going from 1980 to 2020 does exhibit a significant increasing trend (NEFSC, 2021a, b). (2) The spring and fall seasons are important transitional periods for many species, but may not be the major thermal structuring time period. Other times of year—such as the peak of summer or the dead of winter, when temperatures are extreme are not part of the study— could have a more important climate impact. (3) Observed temperature data provides the true temperature from the federal trawl survey, but only for the locations and times sampled. For example, when the trawl survey measures the bottom temperature off Virginia, it cannot simultaneously measure the temperature in the Gulf of Maine and may not record the temperature in the Gulf of Maine until two months later. We used a synthetic data product in order to get location-specific, daily bottom temperature information over the entire Northeast Shelf. The observed trawl survey data cannot provide temperature information at that resolution and can only provide a shelf wide seasonal average of the bottom temperature. Thus, comparisons of the observed seasonal temperature with the seasonal synthetic data product are not exactly matched. (4) And, finally, the COBALT ocean model is a good model that captures the seasonal dynamics and long term changes well, but is still a model (Kang and Curchitser, 2013, 2015). It does not perfectly capture the observed data, but still provided the best estimate of daily hindcast bottom temperature over the longest time span. The observed and modelled data were highly correlated with no change in the correlation over time indicating that the model captured the dynamics of the

ocean well. The combination of these factors likely results in the relatively small changes in suitable habitat for the suite of species examined. It is anticipated that updated ocean models with hindcast bottom temperatures through to the current year would show changes in HSI.

While the suitable habitat for species exhibited some changes over time, there were also various degrees of changes to the timing and location of the NEFSC trawl survey over the same period. The combination of changes in suitable habitat and changes in the trawl survey timing and location resulted in three overarching patterns in the availability component of catchability.

The first pattern in availability was an index that varied over time without a trend and was the most common pattern, particularly in the fall. This pattern combines trend one and four from the DFA in the fall and those species not captured well by either trend in the spring. The majority of species that had this pattern were offshore or basin species such as white hake and Acadian redfish that generally do not exhibit large onshore/offshore seasonal migrations. The species are generally not estuary-dependent, are found in deeper water, and have similar thermal habitat needs in the spring and fall. Their suitable habitat does not change a great deal over the season, and they are predominantly found within the Gulf of Maine. Because the species do not make major changes to their location, if the trawl survey samples the full spatial extent of their suitable habitat within a season, the overlap between the species and the survey is relatively robust to the timing of the trawl survey.

The availability index of two estuary dependent fish, alewife and blueback herring followed pattern one (variable without a trend). These two species are not sampled particularly well by the NEFSC trawl survey and have a highly variable survey index. The overlap between the survey and the two species was never particularly good. It is likely that any changes in the survey or suitable habitat may have increased the noise in that relationship, but has not resulted in any significant changes. The lack of a trend in the availability indices for species following pattern one does not indicate anything about the potential changes in the quantity or location of suitable habitat for these species, simply that the trawl survey has sampled the same proportion of suitable habitat each year.

The second pattern in the availability indices resulted from a known change in the NEFSC trawl survey in 2009 (Miller *et al.*, 2010; Politis *et al.*, 2014). The indices are variable for the first few decades and then drop substantially in 2009. This pattern was captured by the DFA as trend two in the spring and trend three in the fall. In 2009, the NEFSC trawl changed vessels, gear, and survey design. Some of the inshore strata were dropped and the number of tows in inshore waters went from roughly 90 to about 70 each season. The change had almost no change on the availability of offshore species but was clearly visible for nearshore and estuary dependent species such as tautog, striped bass, and Atlantic menhaden. Unlike alewife and blueback herring that are also estuary-dependent, these three species are only caught in nearshore waters. In both seasons, almost all positive tows are inshore resulting in their availability indices changing dramatically with the change in the number of inshore tows. For other species that migrate on and offshore seasonally, there was a clear change in availability when they were inshore. Summer flounder and black seabass exhibited a drop in availability in the fall when

they were inshore during the warmer months, while winter flounder and little skate showed a drop in availability during the winter months (spring survey) when they were inshore. Summer flounder and black seabass are offshore during the cooler months, however, some individuals are still caught in the nearshore waters during the spring. The availability indices for both species in the spring did not show the large change it exhibited in the fall, but did show a small difference suggesting a change in availability.

A number of species also showed a substantial drop in availability in spring 2014 that was not related to the change in inshore strata coverage. The NEFSC trawl survey did not begin sampling until April of 2014, a few weeks later than its typical start in March. Furthermore, the survey started three degrees farther north than usual. The survey started at 38 N instead of 35 N and therefore did not cover the Northeast Shelf all the way down to Cape Hatteras (Figure 8). The change resulted in certain areas not being sampled, decreasing availability for species whose range extends further south. It also altered the timing of when the trawl survey sampled certain strata during the time of year that suitable habitat is changing rapidly across the shelf. Though most of the strata were sampled, the delayed start of the trawl survey caused a change in the spatial-temporal overlap between the trawl survey and the species location, resulting in a sharp drop in availability in spring 2014 for some species. All the species affected were fish that used nearshore waters and had a large presence in the Mid-Atlantic Bight–Southern New England area. The species not affected tended to be found farther north and in deeper water. Similar to pattern one, the species that were not affected tended to exhibit less seasonal movement so that as long as the trawl survey sampled their full spatial extent, the timing was not as critical.

Pattern three was a significant decline in availability over the course of the time series. It was identified by DFA trend one in the spring and trend two in the fall. The species in the spring that fit this pattern were all offshore species such as haddock, yellowtail flounder, and dogfish that were found in mid to deeper waters and were not estuary-dependent. In the fall, similar mid to deeper water species had significant negative trends along with one inshore species, tautog. When testing the availability indices for trends, every species had a negative trend, but only the trends for six species in the spring and seven species were statistically significant. The slopes of the significant and non-significant trends were similar and relatively small in magnitude suggesting there was not a tremendous amount of difference between species following pattern one and species following pattern three. What made the trends significant for these species is likely lower variability of the availability index. For a number of species, there is a small, but continual decline in the overlap between the trawl survey and suitable habitat.

While changes in long-term fisheries independent trawl surveys are typically not good, the change in 2009 represents a known test of the methods outlined in this study. The clear change in availability for numerous inshore species, but not offshore species demonstrates that the method is effective and can account for changes in the availability component of catchability. The Northeast US Shelf has a number of fisheries independent trawl surveys and fortunately an inshore survey, NEAMAP, that covers much of the strata dropped by the federal survey came online in 2007. NEAMAP has sampled much of the inshore strata through to the present, and

therefore captures much of the information with a similar methodology, though as a different survey index. In addition to maintaining the same sampling frame in order to provide a consistent index of abundance, most stock assessments on the Northeast Shelf pull information from a consistent set of sampling strata that defines the stock boundaries. When the inshore strata were dropped from the federal survey, the assessments for many inshore species changed the strata used in the model and only pulled data from the offshore strata. This removed the large change in catchability caused by the change in availability and is not a problem as long as the abundance signal for the inshore strata and the offshore strata are the same.

Like all modelling projects, the results of this study are contingent on decisions and assumptions made during the project. The spatial scope of the study was limited to the shelf break and areas covered by US fishery independent trawl surveys largely because of data. Continuous benthic data were available from mean low water to the shelf break and therefore suitable habitat could only be defined within that geographic area. Species such as dogfish that are often found beyond the shelf break likely have larger suitable habitat ranges than accounted for in this study. In addition, the dynamic components of suitable habitat were defined by bottom temperature information from an ocean model. The method required daily bottom temperature information and therefore could not use sea surface temperature or seasonally interpolated observations (Friedland et al., 2020). The ocean model output was only available from 1980 to 2014 and thus defined the time period of the study. Some species have more specific habitat requirements and may, for example, have a stronger affinity to the bottom than others. The method assumes some habitat specificity and therefore may not be as applicable for highly generalist species. The HSI specifies the suitability of a habitat, but fish may not occupy the full extent of their suitable habitat, particularly if their population has declined from historical biomass levels as the majority of these species have. In addition, the suitable habitat for different sizes/ages of a fish may shift as they go through ontogenetic changes. To keep the study tractable, species were not broken down by size class, but could be in future studies. Lastly, this analysis was focused on providing a broadly applicable framework for integrating dynamic habitat into the stock assessment process by modelling 25 different species. Future studies, focused on a single species, may want to improve this framework for those species by adding specific relevant variables, exploring potential spatio-temporal autocorrelation, examining other ocean models and evaluating the weighting of the thermal and benthic components of the model.

In heavily exploited ecosystem like the Northeast Shelf, fishing is a major driver that can impact the abundance and distribution of species. It is challenging to disentangle the effects of fishing and the environment and there is no question that the density of fish is impacted by fishing. The methods laid out in the study do not eliminate the effects of fishing, but hope to reduce the impact of fishing on the ability to develop the measures of suitable habitat and thus, the availability index. Given that almost all the species in the study are commercially exploited species, it is certain that fishing reduced their numbers (in some cases greatly), but also that they are still present in sufficient numbers to support the industry. The fish that are present, therefore, are likely still found in their preferred habitat. The method assumes that fish follow Mac-
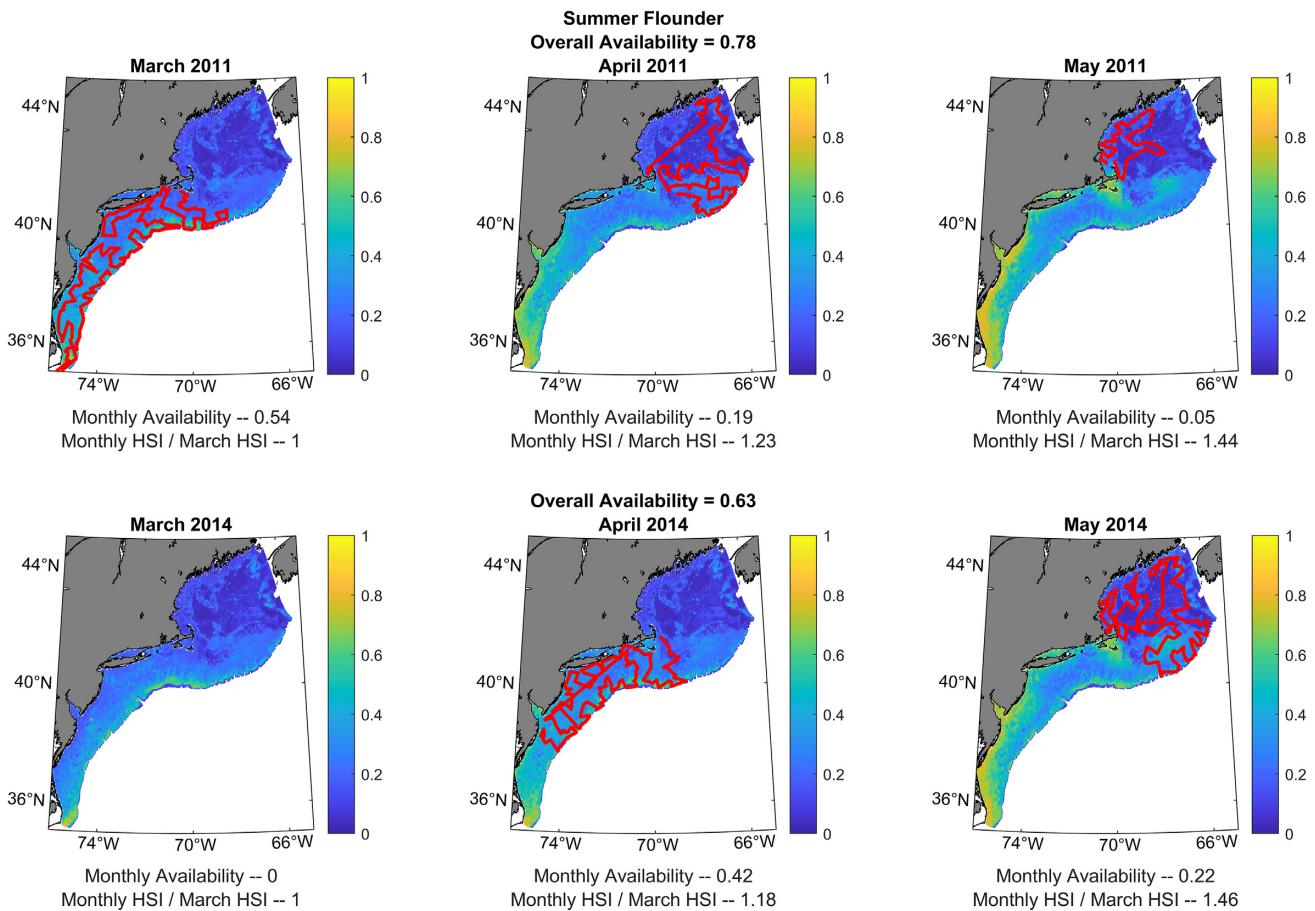
**Figure 8.** The HSI and availability for Summer Flounder in spring of 2011 and 2014. The cumulative availability index in each spring is in bold at the top of each year. Monthly availability and HSI are below each figure. HSI is given as the proportion of the HSI in March of each year. The red line is the path of the survey vessel each month. In 2014, the survey did not start until April.

Call's Basin model (MacCall, 1990) and that suitable habitat is roughly the same for all individuals of a species, throughout the range of the species, for the entire time series. Fishing can have a large impact on the abundance of fish (Worm et al., 2009); however, due to density dependence, the Basin model hypothesizes that the highest density of a species will occur where the habitat is the best. As density increases in the optimal habitat, the condition factor of individuals will decline because of competition for resources and individuals will expand to occupy suboptimal habitat, but habitat that provides an equal level of condition factor. In heavily fished species, the abundance is likely to be reduced from unfished populations, however, lower population numbers should not change the optimal habitat for a species, but simply change the density of individuals within the former distribution of the species. The highest density of individuals should still be located in the best habitat. The study estimates suitable habitats based on the differences in relative density between habitat types, and the effects of fishing are not eliminated, but hopefully are minimized. Despite the range of caveats listed, the models captured the major elements of suitable habitat and produced time-varying availability indices that could be directly integrated into the stock assessment process (Adams et al., 2015; Manderson et al., 2015).

Unaccounted for changes in catchability can cause major problems in the use of bottom trawl data (Hilborn and Wal-

ters, 1992; Quinn and Deriso, 1999; Wilberg et al., 2009). While hyperstability and hyperdepletion are often discussed (even for surveys), time-varying catchability can result in perceived changes in abundance when no changes have actually occurred. This creates biases in stock assessments and poor management advice as well as potentially biasing research studies that rely on fisheries independent trawl surveys (Kotwicki et al., 2009, 2014). An availability index that varies around a mean without a trend such as in pattern one is to be expected; however, long-term gradual changes can be of major concern and in need of correction. While the majority of species did not exhibit availability related changes in catchability, two patterns of change did emerge. The change in catchability due to the 2009 switch in survey methodology has largely been integrated into the assessment process by changing the survey strata from which the index of abundance is developed. The small, but significant decline in catchability over time for certain species, however, has the potential to impact assessment results. With the COBALT ocean model, we found limited evidence for major changes in suitable habitat that could change the species overlap with the trawl survey. Changes in the timing, location, and methodology of the survey, however, clearly emerged as impacting the catchability of the survey. Specifically, accounting for changes in availability integrates both changes in fisheries independent surveys as well as dynamic habitats that can capture short and long term environmental variability to potentially produce an index of

abundance that better represents a species abundance in the water.

## Supplementary data

Supplementary material is available at the *ICESJMS* online.

## Acknowledgements

## References

Adams, C. F., Miller, T. J., Manderson, J. P., Richardson, D. E., and Smith, B. E. 2015. Butterfish 2014 Stock Assessment. US Department of Commerce, Northeast Fisheries Science Center Reference Document 15-06: 110 p.

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control, 19: 716–723.

Allouche, O., Tsoar, A., and Kadmon, R. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS): assessing the accuracy of distribution models. Journal of Applied Ecology, 43: 1223–1232.

Arreguín-Sánchez, F. 1996. Catchability: a key parameter for fish stock assessment. Reviews in Fish Biology and Fisheries, 6: 221–242.

Auster, P., Malatesta, R., Larosa, S., Cooper, R., and Stewart, L. 1991. Microhabitat Utilization by the Megafaunal Assemblage at a Low Relief Outer Continental Shelf Site -Middle Atlantic Bight, USA. Journal of Northwest Atlantic Fishery Science, 11: 59–69.

Auster, P.J., Malatesta, R.J. and LaRosa, S.C. 1995. Patterns of microhabitat utilization by mobile megafauna on the southern New England (USA) continental shelf and slope. Marine Ecology Progress Series, 127: 77–85.

Azarovitz, T. 1981. Bottom trawl surveys a brief historical review of the woods hole laboratory trawl survey time series. Canadian Special Publication of Fisheries and Aquatic Sciences, 58: 62–81.

Azarovitz, T., Clark, S., Despres, L., and Byrne, C. 1997. The Northeast Fisheries Science Center Bottom Trawl Survey Program. ICES Document CM 1997/Y:33. 23 pp.

Bell, R. J., Richardson, D. E., Hare, J. A., Lynch, P. D., and Fratantoni, P. S. 2015. Disentangling the effects of climate, abundance, and size on the distribution of marine fish: an example based on four stocks from the Northeast US Shelf. ICES Journal of Marine Science, 72: 1311–1322.

Bonzek, C. F., Gartland, J., Gauthier, D. J., and Latour, R. J. 2017. Data collection and analysis in support of single and multispecies stock assessments in the Mid-Atlantic: Northeast Area Monitoring and Assessment Program near Shore Trawl Survey.

Borland, H. P., Gilby, B. L., Henderson, C. J., Leon, J. X., Schlacher, T. A., Connolly, R. M., Pittman, S. J. *et al.* 2021. The influence of seafloor terrain on fish and fisheries: a global synthesis. Fish and Fisheries, 22: 707–734.

Brodie, S., Jacox, M. G., Bograd, S. J., Welch, H., Dewar, H., Scales, K. L., Maxwell, S. M. *et al.* 2018. Integrating dynamic subsurface habitat metrics into species distribution models. Frontiers in Marine Science, 5: 219.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., and West, G. B. 2004. Toward a metabolic theory of ecology. Ecology, 85: 1771–1789.

Brown, R. W., Fogarty, M. J., Legault, C., Miller, T., Nordahl, V., Politis, P., and Rago, P. 2007. Survey transition and calibration of bottom trawl surveys along the northeastern continental shelf of the United States. ICES Document CM 2007/Q:20. 25 pp.

Carton, J. A., and Giese, B. S. 2008. A reanalysis of ocean climate using simple ocean data assimilation (SODA). Monthly Weather Review, 136: 2999–3017.

Collette, B. B., and Klein-MacPhee, G. 2002. Bigelow and Schroeder's Fishes of the Gulf of Maine. Smithsonian Institution, Washington, WA. 748pp.

Core Team, R. 2021. R: A language and environment for statistical computing. https://www.R-project.org.

Dell, A. I., Pawar, S., and Savage, V. M. 2011. Systematic variation in the temperature dependence of physiological and ecological traits. Proceedings of the National Academy of Sciences, 108: 10591–10596.

Durbin, J., and Watson, G. 1950. Testing for serial correlation in least squares regression: I. Biometrika, 37: 409–428.

Elith, J., and Leathwick, J. R. 2009. Species distribution models: ecological explanation and prediction across space and time. Annual Review of Ecology, Evolution, and Systematics, 40: 677–697.

ESRI. 2019. ArcGIS Pro. https://www.esri.com/en-us/home (last accessed January 2022).

Freeman, E. A., and Moisen, G. 2008. PresenceAbsence : an *R* package for presence absence analysis. Journal of Statistical Software, 23. http://www.jstatsoft.org/v23/i11/( last accessed 21 October 2021).

Friedland, K. D., Langan, J. A., Large, S. I., Selden, R. L., Link, J. S., Watson, R. A., and Collie, J. S. 2020. Changes in higher trophic level productivity, diversity and niche space in a rapidly warming continental shelf ecosystem. Science of the Total Environment, 704: 1–17.

Fry, F. E. J. 1971. The effect of environmental factors on the physiology of fish. *In* Fish Physiology. Ed. by W. S. Hoar, D. J. Randall, and D. J. Randall. Academic Press, New York, NY. 559pp.

Godø, O. R., Walsh, S. J., and Engås, A. 1999. Investigating density-dependent catchability in bottom-trawl surveys. ICES Journal of Marine Science, 56: 292–298.

Hare, J. A., Morrison, W. E., Nelson, M. W., Stachura, M. M., Teeters, E. J., Griffis, R. B., Alexander, M. A. *et al.* 2016. A vulnerability assessment of fish and invertebrates to climate change on the northeast U.S. continental shelf. PloS One, 11: e0146756.

Harris, B. P., and Stokesbury, K. D. E. 2010. The spatial structure of local surficial sediment characteristics on Georges Bank USA. Continental Shelf Research, 30: 1840–1853.

Henderson, M. E., Mills, K. E., Thomas, A. C., Pershing, A. J., and Nye, J. A. 2017. Effects of spring onset and summer duration on fish species distribution and biomass along the Northeast United States continental shelf. Reviews in Fish Biology and Fisheries, 27: 411–424.

Hilborn, R., and Walters, C. J. 1992. Quantitative Fisheries Stock Assessment. Chapman and Hall, New York, NY. 570pp.

Holmes, E., E., Ward, E., J., and Wills, K. 2012. MARSS: multivariate autoregressive state-space models for analyzing time-series data. The R Journal, 4: 11.

Jacobson, L., Seaver, A., and Tang, J. 2011. AstroCalc4R: Software to Calculate Solar Zenith Angle; Time at Sunrise, Local Noon and Sunset; and Photosynthetically Available Radiation based on Date, Time and Location. US Dept Commer, Northeast Fish Sci Cent Ref Doc. Woods Hole, MA. p. 11–14.

Jacobson, L. D., Hendrickson, L. C., and Tang, J. 2015. Solar zenith angles for biological research and an expected catch model for diel vertical migration patterns that affect stock size estimates for longfin inshore squid (*Doryteuthis pealeii*). Canadian Journal of Fisheries and Aquatic Sciences, 72: 1329–1338.

Jech, J. M., and Sullivan, P. J. 2014. Distribution of Atlantic herring (*Clupea harengus*) in the Gulf of Maine from 1998 to 2012. Fisheries Research, 156: 26–33.

Johnson, F. H., and Lewin, I. 1946. The growth rate of *E. coli* in relation to temperature, quinine and coenzyme. Journal of Cellular and Comparative Physiology, 28: 47–75.

Kang, D., and Curchitser, E. N. 2013. Gulf Stream eddy characteristics in a high-resolution ocean model: Gulf Stream eddy characteristics. Journal of Geophysical Research: Oceans, 118: 4474–4487.

Kang, D., and Curchitser, E. N. 2015. Energetics of eddy—mean flow interactions in the Gulf Stream region. Journal of Physical Oceanography, 45: 1103–1120.

Kohut, J., Palamara, L., Curchitser, E., Manderson, J., and DiDomenico, G. 2015. Cooperative development of dynamic habitat models informed by the integrated ocean observing system (IOOS) informs fisheries management decision making in the coastal ocean. *In* OCEANS 2015 - MTS/IEEE Washington, p. 1–8. IEEE, Washington, WA. http://ieeexplore.ieee.org/document/7404436/( last accessed 8 February 2019).

Kotwicki, S., De Robertis, A., von Szalay, P., and Towler, R. 2009. The effect of light intensity on the availability of walleye pollock (*Theragra chalcogramma*) to bottom trawl and acoustic surveys. Canadian Journal of Fisheries and Aquatic Sciences, 66: 983–994.

Kotwicki, S., Ianelli, J. N., and Punt, A. E. 2014. Correcting density-dependent effects in abundance estimates from bottom-trawl surveys. ICES Journal of Marine Science, 71: 1107–1116.

Kristensen, K., Nielsen, A., Berg, C. W., Skaug, H., and Bell, B. M. 2016. TMB : automatic differentiation and laplace approximation. Journal of Statistical Software, 70: 51–21. http://www.jstatsoft.org/v70/i05/( last accessed 21 October 2021).

Lam, V. W. Y., Cheung, W. W. L., Reygondeau, G., and Sumaila, U. R. 2016. Projected change in global fisheries revenues under climate change. Scientific Reports, 6: 32607.

Langan, J. A., Puggioni, G., Oviatt, C. A., Henderson, M. E., and Collie, J. S. 2021. Climate alters the migration phenology of coastal marine species. Marine Ecology Progress Series, 660: 1–18.

Langton, R. W., Auster, P. J., and Schneider, D. C. 1995. A spatial and temporal perspective on research and management of groundfish in the northwest Atlantic. Reviews in Fisheries Science, 3: 201–229.

Large, W. G., and Yeager, S. G. 2009. The global climatology of an inter-annually varying air–sea flux data set. Climate Dynamics, 33: 341–364.

MacCall, A. D. 1990. Dynamic Geography of Marine Fish Populations. Washington Sea Grant Program, Seattle, WA.

McGilliard, C. R., Stockhausen, W., Nichol, D., and Palsson, W. 2019. Assessment of the flathead sole-bering flounder stock in the Bering Sea and Aleutian Islands. *In* Stock Assessment and Fishery Evaluation Report for the Groundfish Resources of the Bering Sea and Aleutian Islands region, North Pacific Fishery Management Council, Anchorage, AK. p. 1229–1318.

McHenry, J., Welch, H., Lester, S. E., and Saba, V. 2019. Projecting marine species range shifts from only temperature can mask climate vulnerability. Global Change Biology, 25: 4208–4221.

McMullen, K. Y., Paskevich, V. F., and Poppe, L. J. 2014. GIS data catalog (ver. 3.0, November 2014). *In* USGS East-Coast Sediment Analysis: Procedures, database, and GIS data. Ed. by L. J. Poppe, K. Y. McMullen, S. J. Williams, and V. F. Paskevich U.S. Geological Survey Open-File Report 2005-1001.

Magnuson, J. J., Crowder, L. B., and Medvick, P. A. 1979. Temperature as an ecological resource. American Zoologist, 19: 331–343.

Manderson, J. P., Schmidt, A., Palamara, L., Richardson, D., Kohut, J., and Bonzek, C. 2015. TOR 3: Describe the thermal habitat and its influence on the distribution and abundance of scup, and attempt to integrate the results into the stock assessment. 2015 SAW 60 Scup Working Group Working Paper A11. 52 pp.

Mathworks Inc. 2020. MATLAB and Statistics Toolbox Release 2020b. Mathworks Inc, Natick, MA.

Maureaud, A. A., Frelat, R., Pécuchet, L., Shackell, N., Mérigot, B., Pinsky, M. L., Amador, K. *et al*. 2021. Are we ready to track climate-driven shifts in marine species across international boundaries?—A global survey of scientific bottom trawl data. Global Change Biology, 27: 220–236.

Methratta, E. T., and Link, J. S. 2006. Seasonal variation in groundfish habitat associations in the Gulf of Maine–Georges Bank region. Marine Ecology Progress Series, 326: 245–256.

Miller, T. J., Das, C., Politis, P. J., Miller, A. S., Lucey, S. M., Legault, C. M., Brown, R. W. *et al*. 2010. Estimation of Albatross IV to Henry B. Bigelow calibration factors. Northeast Fishery Science Center Reference Document. 10-05: 233p.

Morley, J. W., Selden, R. L., Latour, R. J., Frölicher, T. L., Seagraves, R. J., and Pinsky, M. L. 2018. Projecting shifts in thermal habitat for 686 species on the North American continental shelf. PloS One, 13: e0196127.

NAVO DBDBV. 2021. DBDB2.https://www7320.nrlssc.navy.mil/DBDB2_WWW/NRLCOM_dbdb2.html( last accessed July 2021).

NEFSC. 2012. Ecosystem Assessment Program. 2012. Ecosystem Status Report for the Northeast Shelf Large Marine Ecosystem—2011. Northeast Fisheries Science Center, US Dept Commer, Northeast Fish Sci Cent Ref Doc. 12-07; 32pp. Available from: National Marine Fisheries Service, 166 Water Street, Woods Hole, MA 02543-1026, or online at http://www.nefsc.noaa.gov/nefsc/publications/

NEFSC, 2019. Operational Assessment of 14 Northeast Groundfish Stocks, Updated Through 2018. In: W.H. Northeast Fisheries Science Center, MA, US Dep Commer, NOAA Fisheries, Northeast Fish Sci Cent Ref Doc

NEFSC. 2021a. State of the Ecosystem 2021: New England. Northeast Fisheries Science Center. https://apps-nefsc.fisheries.noaa.gov/rcb/publications/SOE-NEFMC-2021-508-Final.pdf (last accessed January 2022).

NEFSC. 2021b. Northeast Fisheries Science Center. 2021. State of the Ecosystem 2021: Mid-Atlantic. Northeast Fisheries Science Center https://apps-nefsc.fisheries.noaa.gov/rcb/publications/soe/SOE_MAFMC_2021_Final-revised.pdf (last accessed January 2022).

NMFS. 1988. An Evaluation of the Bottom Trawl Survey Program of the Northeast Fisheries Center. NOAA Technical Memorandum, NMFS-F/NEC-52: 94.

NOAA NCEI. 2021. NOAA NCEI Bathymetric Data Viewer. https://www.ncei.noaa.gov/maps/bathymetry/ (last accessed July 2021).

Nye, J., Link, J., Hare, J., and Overholtz, W. 2009. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. Marine Ecology Progress Series, 393: 111–129.

O'Leary, C. A., Kotwicki, S., Hoff, G. R., Thorson, J. T., Kulik, V. V., Ianelli, J. N., Lauth, R. R. *et al*. 2021. Estimating spatiotemporal availability of transboundary fishes to fishery-independent surveys. Journal of Applied Ecology, 58: 2146–2157.

Packer, D. B. 1999. Essential fish habitat source document. Summer flounder, Paralichthys dentatus, life history and habitat characteristics. https://repository.library.noaa.gov/view/noaa/3149 (last accessed July 2021).

Peck, M., and Pinnegar, J. K. 2018. Chapter 5: Climate change impacts, vulnerabilities and adaptations: North Atlantic and Atlantic Arctic marine fisheries. *In* Impacts of Climate Change on Fisheries and Aquaculture: Synthesis of Current Knowledge, Adaptation and Mitigation Options. Ed. by M. Barange, T. Bahri, M. C. M. Beveridge, K. L. Cochrane, S. Funge-Smithand and F. Poulain.FAO Fisheries and Aquaculture, Rome. 628pp.

Perry, A. L. 2005. Climate change and distribution shifts in marine fishes. Science, 308: 1912–1915.

Pershing, A. J., Alexander, M. A., Hernandez, C. M., Kerr, L. A., Le Bris, A., Mills, K. E., Nye, J. A. *et al*. 2015. Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. Science, 350: 809–812.

Petitgas, P., Alheit, J., Peck, M., Raab, K., Irigoien, X., Huret, M., van der Kooij, J. *et al*. 2012. Anchovy population expansion in the North Sea. Marine Ecology Progress Series, 444: 1–13.

Pinsky, M. L., Worm, B., Fogarty, M. J., Sarmiento, J. L., and Levin, S. A. 2013. Marine taxa track local climate velocities. Science, 341: 1239–1242.

Politis, P. J., Galbraith, J. K., Kostovick, P., and Brown, R. W. 2014. Northeast Fisheries Science Center Bottom Trawl Survey protocols for the NOAA ship Henry B Bigelow. NEFSC Reference Document, 14-06: 138.

Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., Brander, K. *et al.* 2013. Global imprint of climate change on marine life. Nature Climate Change, 3: 919–925.

Polsby, D. D., and Popper, R. D. 1991. The third criterion: compactness as a procedural safeguard against partisan gerrymandering. Yale Law & Policy Review, 9: 301–353.

Quinn, T. J., and Deriso, R. B. 1999. Quantitative Fish Dynamics. Oxford University Press, New York, NY. 542pp.

Reid, R. N., Almeida, F. P., and Zetlin, C. A. 1999. Fishery-Independent Surveys, Data Sources, and Methods. NOAA Technical Memorandum NMFS-NE-122.

Reid, J. M., Reid, J. A., Jenkins, C. J., Hastings, M. E., Williams, S. J., and Poppe, L. J. 2005. usSEABED: Atlantic coast offshore surficial sediment data release. Report, Data Series, 118. http://pubs.er.usgs .gov/publication/ds118.

Saba, V. S., Griffies, S. M., Anderson, W. G., Winton, M., Alexander, M. A., Delworth, T. L., Hare, J. A. *et al.* 2016. Enhanced warming of the Northwest Atlantic Ocean under climate change. Journal of Geophysical Research: Oceans, 121: 118–132.

Shchepetkin, A. F., and McWilliams, J. C. 2005. The regional oceanic modeling system (ROMS): a split-explicit, free-surface, topography-following-coordinate oceanic model. Ocean Modelling, 9: 347–404.

Spies, I., Wilderbuer, T. K., Nichol, D. G., and Ianelli, J. 2020. Assessment of the yellowfin sole stock in the Bering Sea and Aleutian Islands. *In* Stock Assessment and Fishery Evaluation Report for the Groundfish Resources of the Bering Sea/Aleutian Islands Regions. NOAA Fisheries, Alaska, AK.

Stauffer, G. 2004. NOAA Protocols for Groundfish Bottom Trawl Surveys of the Nation's Fishery Resources. NOAA Technical Memorandum, NMFS-F/SPO-65: 205.

Sunday, J. M., Bates, A. E., and Dulvy, N. K. 2012. Thermal tolerance and the global redistribution of animals. Nature Climate Change, 2: 686–690.

Walbridge, S., Slocum, N., Pobuda, M., and Wright, D. 2018. Unified geomorphological analysis workflows with benthic terrain modeler. Geosciences, 8: 94.

Weiss, A. 2001. Topographic Position and Landforms Analysis. Geology, San Diego, CA.

Wilberg, M. J., Thorson, J. T., Linton, B. C., and Berkson, J. 2009. Incorporating time-varying catchability into population dynamic stock assessment models. Reviews in Fisheries Science, 18: 7–24.

Wood, S. 2006. Generalized Additive Models: An Introduction with R. CRC press, Boca Raton, FL.

Worm, B., Hilborn, R., Baum, J. K., Branch, T. A., Collie, J. S., Costello, C., Fogarty, M. J. *et al.* 2009. Rebuilding global fisheries. Science, 325: 578–585.

Zhang, L., Liu, S., Sun, P., Wang, T., Wang, G., Zhang, X., and Wang, L. 2015. Consensus forecasting of species distributions: the effects of niche model performance and niche properties. PloS One, 10: e0120056.

Zuur, A. F., Tuck, I. D., and Bailey, N. 2003. Dynamic factor analysis to estimate common trends in fisheries time series. Canadian Journal of Fisheries and Aquatic Sciences, 60: 542–552.

*Handling Editor: Howard Browman*