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Trends in Area of Occurrence and Biomass of Fish and Macroinvertebrates on the Northeast U.S. Shelf Ecosystem

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Abstract

Climate change can affect the habitat of marine species and hence their persistence and adaptation. Trends in area of occurrence and population biomass were examined for 177 fish and macroinvertebrates resident to the Northeast U.S. Continental Shelf ecosystem. Samples of these organisms were taken during a time series of research bottom trawl surveys conducted in the spring and autumn 1976–2019. The occurrence area of each taxon was modeled as the distribution of occurrence probability based on a random forest presence/absence classification model. Following, a population biomass of each taxon was modeled as a minimum swept area estimate, where the ecosystem was stratified biannually based on each taxon's spatial distribution. In both seasons, the sum of occurrence area and biomass across all modeled species increased over the study period. The summation of biomass is problematic since catchability is not known for most species; more importantly, most time series of individual species biomass trended higher. We found that the ratio of biomass to occurrence area, intended as a measure of productivity, showed no change in the autumn and had a weak increasing trend in spring. For the majority of taxa, the rate of change in biomass tracked changes in occurrence area (either positive or negative), but there were cases where the direction of change in biomass was opposite to the direction of change in occurrence area. Thermal conditions in surface waters appear to be a more important driver of occurrence area and biomass change than the change in thermal conditions near the bottom. These findings provide critical insights into the expected changes in ecosystem productivity transpiring with climate change.

Recognition of the main factors influencing biomass production of marine biota is among the crucial challenges to the implementation of sustainable development (Duffy et al. 2016). Complicating this task, climate change is modifying the distribution of species and the extent and quality of their habitats. Hence, understanding the underlying mechanisms and predicting future consequences of warming ocean conditions on marine organisms is essential in developing adaptive management strategies (Poloczanska et al. 2013). Temperature conditions and habitat availability have been identified as some of the fundamental predictors of patterns in marine biodiversity and abundance (Tittensor et al. 2010). The ongoing climate changes (IPCC 2019), in particular the changes in the ocean thermal environments, influence marine fishes and invertebrates directly through the modulation of metabolic processes (Carozza et al. 2019) and indirectly through the alteration of prey and predator distributions (Feng et al. 2018; Régnier et al. 2019). In addition, these changes affect the multidimensional aspects of habitats (Free et al. 2019), ultimately changing higher trophic level interactions (Record et al. 2019). These climate-related habitat modifications can strongly impact the persistence and adaptation of animal populations (Piou and Prévost 2013). Since the consequences of these changes in habitat may be taxon-specific (Stuart-Smith et al. 2017), there is an urgent need to investigate the relationships between habitat features and the distribution and abundance of marine organisms at the community level (Friedland et al. 2020a).

There has been considerable thought expended on the relationship between biota and the dimensions of habitat from both the perspective of cause and effect and resource limitation. A positive interspecific relationship between abundance and distribution has long been recognized as one of the most general patterns in ecology (Brown 1984;

Blackburn et al. 2006). Three main causes of the abundance–occupancy relationships listed by Faulks et al. (2015) include (1) niche differentiation in resources or environmental use, (2) population dynamics modulated by the migratory movements between sites, and (3) artifacts related to sampling methods. Despite this theoretical underpinning, previous studies have reported positive relationships between occupancy and abundance but rarely examined details of these relationships, which could increase understanding of the mechanisms driving these macroecological patterns (Gaston et al. 2000). Previous results suggest that climate-forced change in distribution may differentially affect the occurrence and biomass of marine taxa (Friedland et al. 2021c), which may result in the formation of novel communities rather than wholesale shifts of the current community structures (Hobbs et al. 2009; Pessarrodona et al. 2019). With the observed change in habitat distribution and concomitant phenological relationships we see at the individual species level, we should also expect to see complex responses at the community level (Staudinger et al. 2019; Friedland et al. 2020a).

Species that are declining in abundance are often characterized by simultaneous declines in the space (i.e., habitats) they occupy, while species increasing in abundance often show the opposite trend. These occupancy–biomass relationships are among the most commonly observed macroecological patterns in terrestrial and marine systems (Brown 1984; MacCall 1990; Blackburn et al. 2006). While the magnitude of these occupancy–biomass relationships is scale- and time-dependent, species occupancy is logistically easier to measure than abundance or biomass, and occupancy-based biomass estimates can potentially offer a cost-effective alternative to traditional sampling methods in data-limited regions (e.g., central Pacific

Ocean). In addition, occupancy–biomass relationships can provide insight into forecasts of species distributions. In order to effectively plan for and manage future changes, we need a better understanding of the ecological processes underlying positive abundance–occupancy patterns observed in nature.

Here, our objective was to examine the trends in the distribution of occurrence area, as a proxy measure of habitat, and biomass with respect to the significant environmental change occurring in the Northeast U.S. Continental Shelf (NES) ecosystem due to climate change. We based this objective on two factors. First, this ecosystem has experienced climate-induced warming trends at three times the global average (Saba et al. 2016), related to northerly shifts of the Gulf Stream (Gonçalves Neto et al. 2021). This warming has had cascading effects through trophic levels, and many marine species have shown northerly and/or offshore trends in their distributions in response (Walsh et al. 2015; Record et al. 2019). The high dynamicity of this region is not expected to halt soon, as many projections suggest continued warming through 2,100 (Saba et al. 2016; Grieve et al. 2017; Pershing et al. 2021). Exacerbating the problem, many species of the region have been labeled as highly vulnerable to the region's climate changes (Hare et al. 2016; Farr et al. 2021); thus, further shifts in species distributions are expected. Second, a long-term monitoring program has been conducted in this ecosystem to support fisheries management; data collected from fisheries-independent surveys that can be used to accurately measure the species distribution and biomass are critical to sustainable management of fishery resources (Krebs 1999). These surveys provide information to estimate the biomass for most macrofauna of the ecosystem and provide the basis to estimate distribution for these species in a quantitative frame of reference. The surveys have been running for six decades with spatial coverage from Cape Hatteras to Canada and have identified over 400 species (Friedland et al. 2020a). Furthermore, data on plankton, representing lower trophic levels, and environmental conditions, were concurrently collected.

The study system of the NES provides perhaps a unique opportunity to compare the relationship between the occurrence area and population biomass for a community of marine fishes and macroinvertebrates. Specifically, we sought to examine the trends in community cumulative biomass and occurrence area in the context of climate change, with a complimentary analysis of species trends to gauge the contribution of individual species to the cumulative time series. This study varies from a previous report addressing similar questions (Friedland et al. 2020a) in several important ways. It is based on a greatly expanded data set that now accounts for the majority of taxa sampled in the survey. The analysis introduces a novel

application of species distribution data to guide the expansion of swept area biomass estimates, which we consider superior to simple catch-per-unit-effort estimates used prior, and further, extensions include species-specific attribution of those taxa representing change in system biomass. Additionally, an examination of the relationship between occurrence area and species biomass was conducted by examining trends in the productivity per unit of occurrence area and the rate of change in biomass versus the rate of change in occurrence area. Finally, we evaluated trends in thermal conditions as a climate change driver affecting time series change in occurrence area and biomass.

METHODS

Species distribution models to estimate occurrence area.— The species distribution models presented here are an extension of those presented in a series of studies on the biology and ecology of the NES ecosystem (Friedland et al. 2020a, 2021b, 2021c). In those studies, random forest classification models of occurrence (presence/absence) and regression models of biomass catch per unit effort were used to estimate occurrence and biomass distributions and for simplicity called "occupancy and biomass habitats." In the current study, we limited the random forest modeling approach to occurrence models and will be referring to distributional output of these models as occurrence area and not habitat. The explanatory variables in these models provide an indication of where within the NES a species' physical habitat may be located. In brief, random forest models were developed for a suite of species based on captures made in the Northeast Fisheries Science Center bottom trawl survey (Despres-Patanjo et al. 1988), which is conducted in the spring and autumn seasons, yielding approximately 300 stations per season. This standardized survey started in 1963 in autumn and 1968 in spring. The survey covers areas off the coast of North Carolina to Nova Scotia and uses stratified random sampling. Location, sea surface temperature, and bottom water temperature, salinity, as well as number of individuals, total weight, and length frequencies of each species are recorded at each tow.

The presence/absence of a taxon was modeled with a putative group of 91 explanatory variables that were first tested for collinearity, providing the criteria to eliminate correlated variables ("multi.collinear" command from R package rfUtilities version 2.1-5; https://cran.r-project.org/web/packages/rfUtilities/index.html). From the reduced set of variables, a model was optimized using the method described in Murphy et al. (2010), which determined the final set of variables included in a species model ("rf.modelSel" command from R package rfUtilities). The candidate explanatory predictor set included variables

representing the physical oceanography, the distribution of lower trophic levels (i.e., zooplankton as a measure of prey availability), and the benthic terrain (see Supporting Information available separately online for covariate details). The current study's approach differs from the most recent reporting (Friedland et al. 2021b) concerning the preprocessing of zooplankton data. First, the data were combined over a 7-year time step instead of the 5 years for each seasonal period used previously. Second, seasonal periods were expanded for the zooplankton data, using February to May for the spring (previously February–April) and August–November for the autumn (previously September–November). The training data extends from 1976 to 2019 and were used to evaluate the potential to fit models for 223 species based on a criterion of at least 50 occurrences in at least one of the seasonal surveys (i.e., spring or autumn). A species seasonal model was accepted if it had an area under the receiver-operator characteristic curve score (Fielding and Bell 1997) of at least 0.7, resulting in satisfactory model fits for 177 species (Table 1). Of these satisfactory models, there were 121 species with spring models, 169 species with autumn models, and 113 species with models in both seasons. A range of variable performance statistics have been reported for these models (Friedland et al. 2021a); here we provide a summary of the frequency of variables appearing as a top 10 variable in species models (Table 2). There is a high reliance on variables that reflect gradients of primary and secondary production and on physical variables, such as depth and temperature. For each species seasonal model, estimates of occurrence probability were made over the NES extent represented by a 0.1° grid (Figure 1) over the period 1976–2019.

Biomass estimates.— To estimate the minimum population biomass of each species by season, we restratified the NES each year depending on the distribution of occurrence areas. For an annual estimate, the NES was partitioned into 10 strata based on the probability of occurrence from the respective species distribution model. The partitions were based on equal intervals of occurrence probability; hence, the size of each occurrence probability strata could vary. The trawl catch-per-unit-effort (CPUE) values were assigned to the appropriate probability strata based on the probability score associated with the location of the trawl haul. Tows from different vessels and gear configurations were standardized to a mean swept area of about $0.038\,\mathrm{km^2}$ per tow (NEFSC Vessel Calibration Working Group 2007) and reconciled with calibration factors applied to the total catch at each sampling station for each species (Miller et al. 2010). Once the requisite trawl hauls associated with a probability stratum were identified, a mean CPUE was determined and raised to a total minimum population estimate for that stratum assuming a constant trawl path area of standard tow. The total population was the sum of the estimates for the 10 strata.

$$\text{Total biomass} = \sum_{1}^{10} \frac{\text{strata area}}{\text{trawl path area}} \times \text{mean CPUE}$$

These estimates were conditioned by interpolating over probability strata by applying a smoother across the mean CPUE estimates in each stratum. A loess smoother (span = 0.75) was applied to generate the smoothed catch rates; the procedure also had the benefit of interpolating and extrapolating a rate to a probability stratum that may not have had catch samples associated with it. The biomass associated with the species that had distribution models accounted for on average 98% and 99% of the total biomass sampled by the trawl survey in spring and autumn, respectively, over the study period.

Analysis strategy.— The quantities were calculated by summing the biomass (kg) associated with each species modeled by season and the amount of occurrence area $(\mathrm{km^2})$ for each species according to the criterion of space associated with an occurrence probability >0.25. We tested for the monotonic trend in biomass and occurrence area and for relationships between these variables and time series of water temperature as an indicator of climate change across the ecosystem. Temperature was extracted from the surface and bottom water temperature fields used to describe trends in thermal regimes of this ecosystem (Friedland et al. 2020b). Mean annual temperature was extracted from the extent of the NES represented by a 0.1° grid that matches the grid used for distribution estimates. First, we tested whether there were trends in the seasonal bottom and surface water temperatures. Trends were tested with an autocorrelation corrected Mann–Kendall test (Yue et al. 2002) that also provided Theil–Sen slope estimates ("zyp.trend.vector" command from R package zyp version 0.10-1.1; https://cran.r-project.org/web/packages/zyp/). Trends were also evaluated in total biomass of the ecosystem and total occurrence area across all species. Owing to the differences in body size and catchability among species, interpretation of ecosystem biomass is problematic. We simply have no way of testing whether the index is an accurate portrayal of ecosystem biomass and must exercise caution in its use. Of more relevance to the central theme of the study is whether with the expansion of occurrence area, has there also been an expansion of biomass among a majority of species? This is less problematic to test since we can analyze the time series of species-specific biomass and determine if the majority have increasing or decreasing trends. We examined this in two ways. First, we calculated the Theil–Sen slopes and associated Mann–Kendall tests for each seasonal, species time series of biomass. We then scored the number of increasing and decreasing

TABLE 1. List of species, including fish and macroinvertebrates, modeled for occurrence probability and biomass in the Northeast U.S. Continental Shelf ecosystem. Abbreviation is a six-letter code used elsewhere, and seasonal models included in the analysis are indicated ("S" is for spring and "A" is for autumn).

Common and scientific names	Seasonal models	Abbreviation
Acadian Redfish *Sebastes fasciatus*	S, A	ACARED
Aesop shrimp *Pandalus montagui*	S, A	ASHRIM
Alewife *Alosa pseudoharengus*	S, A	ALEWIF
Alligatorfish *Aspidophoroides monopterygius*	S, A	ALLFSH
American lobster *Homarus americanus*	S, A	AMLOBS
American Plaice *Hippoglossoides platessoides*	S, A	AMEPLA
American Shad *Alosa sapidissima*	A	AMESHA
Armored Searobin *Peristedion miniatum*	S, A	ARMSEA
Atlantic Angel Shark *Squatina dumeril*	S, A	ANGSHR
Atlantic Argentine *Argentina silus*	S, A	ATLARG
Atlantic brief squid *Lolliguncula brevis*	A	ABSQUI
Atlantic Cod *Gadus morhua*	S, A	ATLCOD
Atlantic Croaker *Micropogonias undulatus*	S, A	ATLCRO
Atlantic Cutlassfish *Trichiurus lepturus*	A	ATLCUT
Atlantic Hagfish *Myxine glutinosa*	S, A	HAGFIS
Atlantic Halibut *Hippoglossus hippoglossus*	S, A	ATLHAL
Atlantic Herring *Clupea harengus*	S, A	ATLHER
Atlantic Mackerel *Scomber scombrus*	S, A	ATLMAC
Atlantic Menhaden *Brevoortia tyrannus*	S, A	ATLMEN
Atlantic Moonfish *Selene setapinnis*	A	ATMOON
Atlantic rock crab *Cancer irroratus*	S, A	RCKCRA
Atlantic Saury *Scomberesox saurus*	A	ATSAUR
Atlantic Seasnail *Liparis atlanticus*	S, A	ATSEAS
Atlantic Sharpnose Shark *Rhizoprionodon terraenovae*	A	ASSHAR
Atlantic Silverside *Menidia menidia*	S	ATLSIL
Atlantic Soft Pout *Melanostigma atlanticum*	S, A	ATLPOU
Atlantic Spadefish *Chaetodipterus faber*	A	ATSPAD
Atlantic Sturgeon *Acipenser oxyrhynchus*	S	ASSTUR
Atlantic Thread Herring *Opisthonema oglinum*	A	ATHERR
Atlantic Torpedo *Torpedo nobiliana*	S	ATTORP
Atlantic Wolffish *Anarhichas lupus*	S, A	ATLWOL
Banded Drum *Larimus fasciatus*	A	BADRUM
Banded Rudderfish *Seriola zonata*	A	BRRUDD
Barndoor Skate *Dipturus laevis*	S, A	BARSKA
Bathyal swimming crab *Bathynectes longispina*	S, A	BSCRAB
Bay Anchovy *Anchoa mitchilli*	S, A	BAYANC
Beardfish *Polymixia lowei*	S, A	BEARDF
Bigeye Scad *Selar crumenophthalmus*	A	BESCAD
Black Drum *Pogonias cromis*	A	BDDRUM
Black Sea Bass *Centropristis striata*	S, A	BLABAS
Blackbelly Rosefish *Helicolenus dactylopterus*	S, A	BLAROS
Blackcheek Tonguefish *Symphurus plagiusa*	S	BCTONG
Blackmouth Bass *Synagrops bellus*	A	BBBASS
Blotched Cusk-eel *Ophidion grayi*	A	BLCUSK
Blue crab *Callinectes sapidus*	S, A	BLUCRA
Blue Runner *Caranx crysos*	A	BLURUN
Blueback Herring *Alosa aestivalis*	S, A	BLUHER

TABLE 1. Continued.

Common and scientific names	Seasonal models	Abbreviation
Bluefish *Pomatomus saltatrix*	S, A	BLUEFI
Bluntnose Stingray *Dasyatis say*	A	BLUNRA
Bristled longbeak *Dichelopandalus leptocerus*	S, A	BLONGB
Brown rock shrimp *Sicyonia brevirostris*	A	BRSHRI
Buckler Dory *Zenopsis conchifera*	S, A	BUCDOR
Bullnose Ray *Myliobatis freminvillei*	A	BULLRA
Butterfish *Peprilus triacanthus*	S, A	BUTTER
Chain Dogfish *Scyliorhinus retifer*	S, A	CHADOG
Chub Mackerel *Scomber colias*	S, A	CHUBMA
Clearnose Skate *Raja eglanteria*	S, A	CLESKA
Coarsehand lady crab *Ovalipes stephensoni*	S, A	CLCRAB
Cobia *Rachycentron canadum*	A	COBIAZ
Common octopus *Octopus vulgaris*	S, A	COOCTO
Conger Eel *Conger oceanicus*	S, A	CONGEL
Cownose Ray *Rhinoptera bonasus*	A	CONRAY
Crevalle Jack *Caranx hippos*	A	CJJACK
Cunner *Tautogolabrus adspersus*	S, A	CUNNER
Cusk *Brosme brosme*	S, A	CUSKZZ
Daubed Shanny *Lumpenus maculatus*	S	SHANNY
Deepbody Boarfish *Antigonia capros*	S, A	DBBOAR
Deepwater Flounder *Monolene sessilicauda*	S, A	DFFLOU
Dusky Shark *Carcharhinus obscurus*	A	DSSHAR
Fawn Cusk-eel *Lepophidium profundorum*	S, A	FAWMEL
Fourbeard Rockling *Enchelyopus cimbrius*	S, A	FRBERO
Fourspot Flounder *Paralichthys oblongus*	S, A	FOUFLO
Friendly blade shrimp *Spirontocaris liljeborgii*	S, A	FBSHRI
Gladiator box crab *Acanthocarpus alexandri*	S, A	GBCRAB
Golden Tilefish *Lopholatilus chamaeleonticeps*	S, A	TILEFI
Goosefish *Lophius americanus*	S, A	MONKFH
Gray Triggerfish *Balistes capriscus*	A	GRTRIG
Grubby *Myoxocephalus aenaeus*	S, A	GRUBBY
Gulf Stream Flounder *Citharichthys arctifrons*	S, A	GULFLO
Haddock *Melanogrammus aeglefinus*	S, A	HADDOC
Harvestfish *Peprilus alepidotus*	A	HARFIS
Hogchoker *Trinectes maculatus*	S, A	HOGCHO
Horseshoe crab *Limulus polyphemus*	S, A	HSCRAB
Inshore Lizardfish *Synodus foetens*	A	INLIZA
Jonah crab *Cancer borealis*	S, A	JONCRA
King Mackerel *Scomberomorus cavalla*	A	KMMACK
Lady crab *Ovalipes ocellatus*	S, A	LADCRA
Little Skate *Leucoraja erinacea*	S, A	LITSKA
Loggerhead seaturtle *Caretta caretta*	A	LSSEAT
Longfin Hake *Urophycis chesteri*	S, A	LGFINH
Longfin squid *Doryteuthis pealeii*	S, A	LONSQD
Longhorn Sculpin *Myoxocephalus octodecemspinosus*	S, A	LONSCU
Longnose Greeneye *Parasudis truculenta*	S, A	LGGREE
Longspine Snipefish *Macrorhamphosus scolopax*	S, A	LSSNIP
Lumpfish *Cyclopterus lumpus*	S, A	LUMPFI
Mackerel Scad *Decapterus macarellus*	A	MACSCA

TABLE 1. Continued.

Common and scientific names	Seasonal models	Abbreviation
Marlin-spike *Nezumia bairdi*	S	MARLSP
Moustache Sculpin *Triglops murrayi*	S, A	MOUSCL
Northern Kingfish *Menticirrhus saxatilis*	A	NKINGF
Northern Pipefish *Syngnathus fuscus*	S	NPIPEF
Northern Puffer *Sphoeroides maculatus*	S, A	NPUFFR
Northern Sand Lance *Ammodytes dubius*	S, A	SANDLA
Northern Searobin *Prionotus carolinus*	S, A	NORSEA
Northern Sennet *Sphyraena borealis*	A	NSENNE
Northern shortfin squid *Illex illecebrosus*	S, A	SHTSQD
Northern shrimp *Pandalus borealis*	S, A	NSHRIM
Northern Stargazer *Astroscopus guttatus*	A	NSSTAR
Northern stone crab *Lithodes maja*	S, A	NSCRAB
Norwegian shrimp *Pontophilus norvegicus*	S, A	NORSHR
Ocean Pout *Macrozoarces americanus*	S, A	OCPOUT
Offshore Hake *Merluccius albidus*	S, A	OFFHAK
Pigfish *Orthopristis chrysoptera*	A	PIGFIS
Pinfish *Lagodon rhomboides*	A	PINFIS
Pink glass shrimp *Pasiphaea multidentata*	S, A	PINKGS
Planehead Filefish *Monacanthus hispidus*	A	FILEFS
Polar lebbeid *Lebbeus polaris*	S, A	POLARL
Pollock *Pollachius virens*	S, A	POLLOC
Rainbow Smelt *Osmerus mordax*	S	RSSMEL
Red deepsea crab *Geryon quinquedens*	S, A	REDCRA
Red Goatfish *Mullus auratus*	A	RGGOAT
Red Hake *Urophycis chuss*	S, A	REDHAK
Rosette Skate *Leucoraja garmani*	S, A	ROSSKA
Rough Scad *Trachurus lathami*	S, A	ROSCAD
Roughtail Stingray *Dasyatis centroura*	A	RTSTIG
Round Herring *Etrumeus teres*	A	RHERRI
Round Scad *Decapterus punctatus*	A	RDSCAD
Sand Tiger *Carcharias taurus*	A	STTIGE
Sandbar Shark *Carcharhinus plumbeus*	A	SBSHAR
Longspine Porgy *Stenotomus caprinus*	A	SCUPSC
Scup *Stenotomus chrysops*	S, A	SCUPZZ
Sea Raven *Hemitripterus americanus*	S, A	SEARAV
Sea scallop *Placopecten magellanicus*	S, A	SEASCA
Sevenspine bay shrimp *Crangon septemspinosa*	S, A	SSBSHR
Shield Bobtail *Stoloteuthis leucoptera*	S, A	SBBOBT
Shortnose Greeneye *Chlorophthalmus agassizi*	S, A	SHORTP
Silver Anchovy *Engraulis eurystole*	A	SILANC
Silver Hake *Merluccius bilinearis*	S, A	SILHAK
Silver Perch *Bairdiella chrysoura*	A	SELPER
Silver Rag *Ariomma bondi*	A	SLERAG
Silver Seatrout *Cynoscion nothus*	A	SSSEAT
Slender Snipe Eel *Nemichthys scolopaceus*	A	SLENSE
Smallmouth Flounder *Etropus microstomus*	S, A	SMAFLO
Smooth Butterfly ray *Gymnura micrura*	A	SMBRAY
Smooth Dogfish *Mustelus canis*	S, A	SMODOG
Smooth Skate *Malacoraja senta*	S, A	SMOSKA

TABLE 1. Continued.

Common and scientific names	Seasonal models	Abbreviation
Snakeblenny *Lumpenus lumpretaeformis*	S, A	SNAKEB
Snow crab *Chionoecetes opilio*	S, A	SNOWCR
Southern Kingfish *Menticirrhus americanus*	A	SKINGF
Southern Stingray *Dasyatis americana*	A	SSSTIN
Spanish Mackerel *Scomberomorus maculatus*	A	SPAMAC
Spanish Sardine *Sardinella aurita*	A	SPSARD
Spider crab (family *Majidae*)	A	SPICRA
Spiny Butterfly ray *Gymnura altavela*	A	SBURAY
Spiny Dogfish *Squalus acanthias*	S, A	SPIDOG
Spiny Searobin *Prionotus alatus*	S, A	SSSEAR
Spoonarm octopus *Bathypolypus arcticus*	S, A	SPOONO
Spot *Leiostomus xanthurus*	S, A	SPOTZZ
Spotfin Dragonet *Foetorepus agassizi*	S, A	SDDRAG
Spotted Hake *Urophycis regia*	S, A	SPOHAK
Striated Argentine *Argentina striata*	S, A	SAARGE
Striped Anchovy *Anchoa hepsetus*	A	STRANC
Striped Bass *Morone saxatilis*	S, A	STRBAS
Striped Burrfish *Chilomycterus schoepfi*	A	SBBURR
Striped Cusk-eel *Ophidion marginatum*	S, A	STCUSK
Striped Searobin *Prionotus evolans*	S, A	STRSEA
Summer Flounder *Paralichthys dentatus*	S, A	SUMFLO
Tautog *Tautoga onitis*	A	TAUTOG
Thorny Skate *Amblyraja radiata*	S, A	THOSKA
Weakfish *Cynoscion regalis*	S, A	WEAKFI
Weitzmans Pearlsides *Maurolicus weitzmani*	S, A	WEITZP
White Hake *Urophycis tenuis*	S, A	WHIHAK
Windowpane *Scophthalmus aquosus*	S, A	WINDOW
Winter Flounder *Pseudopleuronectes americanus*	S, A	WINFLO
Winter Skate *Leucoraja ocellata*	S, A	WINSKA
Witch Flounder *Glyptocephalus cynoglossus*	S, A	WITFLO
Wrymouth *Cryptacanthodes maculatus*	S, A	WRYMOU
Yellowtail Flounder *Limanda ferruginea*	S, A	YELFLO

trends among the time series with significant Mann–Kendall tests. Second, for each species biomass time series, we divided the data into early and late periods (early = 1976–1997 and late = 1998–2019) and tested for differences between the periods with a *t*-test. For those species with significant differences, we used the difference in the mean biomasses of the early and later periods as another index of change in biomass. These trend and difference indicator data are presented as Treemaps, with positive and negative trend data presented as subgroups. Finally, we examined the productivity of NES occurrence area by examining the trend in the ratio of biomass and occurrence area and tested this for trends.

The biomass and occurrence area time series were tested for the synchronicity of trends with temperature time series using the method described in Lyubchich and Gel (2016). The method tests whether two or more observed time series exhibit the same trend as a prespecified form ("sync_test" command from R package funtimes version 8.2; https://cran.r-project.org/web/packages/funtimes/). The biomass and occurrence area variables and the ratio of biomass to occurrence area were tested for synchronicity with the temperature data for both the spring and autumn seasons.

Finally, we tested the nature of the relationship between biomass and occurrence area trend by species. The rate of change in biomass (as Theil–Sen slopes) was compared with the change in occurrence area in order to test whether biomass can be independent of occurrence area size. The relationship between these rates was described with linear regression. However, owing to the appearance of outlier coordinates, the occurrence area and

TABLE 2. The top 15 variables in spring and autumn random forest occurrence models sorted by the rank based on the proportion of species models the variable was among the top 10 variables. Dynamic and static variables are designated with (d) and (s), respectively. CHL, chlorophyll concentration; SST, sea surface temperature.

Variable	Proportion
Spring	
Depth (s)	0.620
Paracalanus parvus (d)	0.537
Centropages typicus (d)	0.529
July CHL (s)	0.421
March CHL (s)	0.413
October CHL (s)	0.380
March CHL (s)	0.364
June CHL (s)	0.347
Surface temperature (d)	0.347
September CHL (s)	0.339
Bottom temperature (d)	0.322
December SST fronts (s)	0.306
Chaetognatha (d)	0.298
November SST fronts (s)	0.289
Centropages hamatus (d)	0.248
Autumn	
Depth (s)	0.651
Bottom temperature (d)	0.592
Metridia lucens (d)	0.527
February CHL (s)	0.462
Salpa (d)	0.462
March CHL (s)	0.367
Appendicularians (d)	0.367
August CHL fronts (s)	0.343
December SST fronts (s)	0.314
September CHL fronts (s)	0.296
Penilia spp. (d)	0.296
September CHL (s)	0.284
Pseudocalanus spp. (d)	0.272
July CHL (s)	0.254
August CHL (s)	0.254

biomass data were screened and extreme values were removed (using the "boxplot" command from R package graphics version 4.0.5) and the regression was refit.

RESULTS

Trends in Water Temperature

The NES ecosystem experienced varied patterns of seasonal warming over the recent decades. The water column of the ecosystem is generally not stratified in the spring; hence, bottom and surface water temperatures were of a similar scale (Figure 2A). The trends in spring
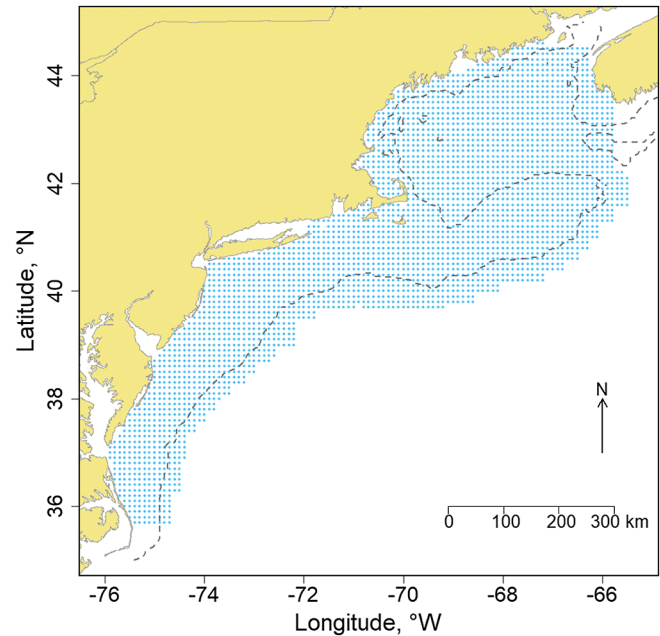

FIGURE 1. Map of the Northeast U.S. Continental Shelf study system showing the estimation grid (blue dots) for distribution models. The dashed line is the 100-m depth contour.

temperatures in both bottom and surface waters were positive; however, the surface water temperature trend was not significant at a rate of 0.016°C per year, whereas the trend in spring bottom water of 0.027°C per year was significant (Table 3). Autumn bottom and surface water temperatures diverged in scale, reflecting the tendency for water column stratification over much of the ecosystem (Figure 2B). The trends in autumn bottom and surface waters were both significant at rates of 0.037 and 0.045°C per year, respectively.

Trends in Occurrence Area and Biomass

The NES ecosystem fish and macroinvertebrate biomass and occurrence areas have increased over recent decades. Based on the results of modeling species captured during the spring, the trend associated with the time series of occurrence area had a Theil–Sen slope of 46.12×10^3 km^2/year, representing an increase in the total occurrence area over the study period of about 2.03×10^6 km^2 (Figure 2C). The trend associated with the cumulative sum of occurrence area for autumn species was similar at 45.60×10^3 km^2/year and represents a similar increase in occurrence area (Figure 2D). The tracking of greater autumn occurrence area over the time series was a product of the larger number of species modeled compared with the spring. The cumulative biomass in the spring increased at a rate of 1.84×10^6 kg/year compared with the autumn
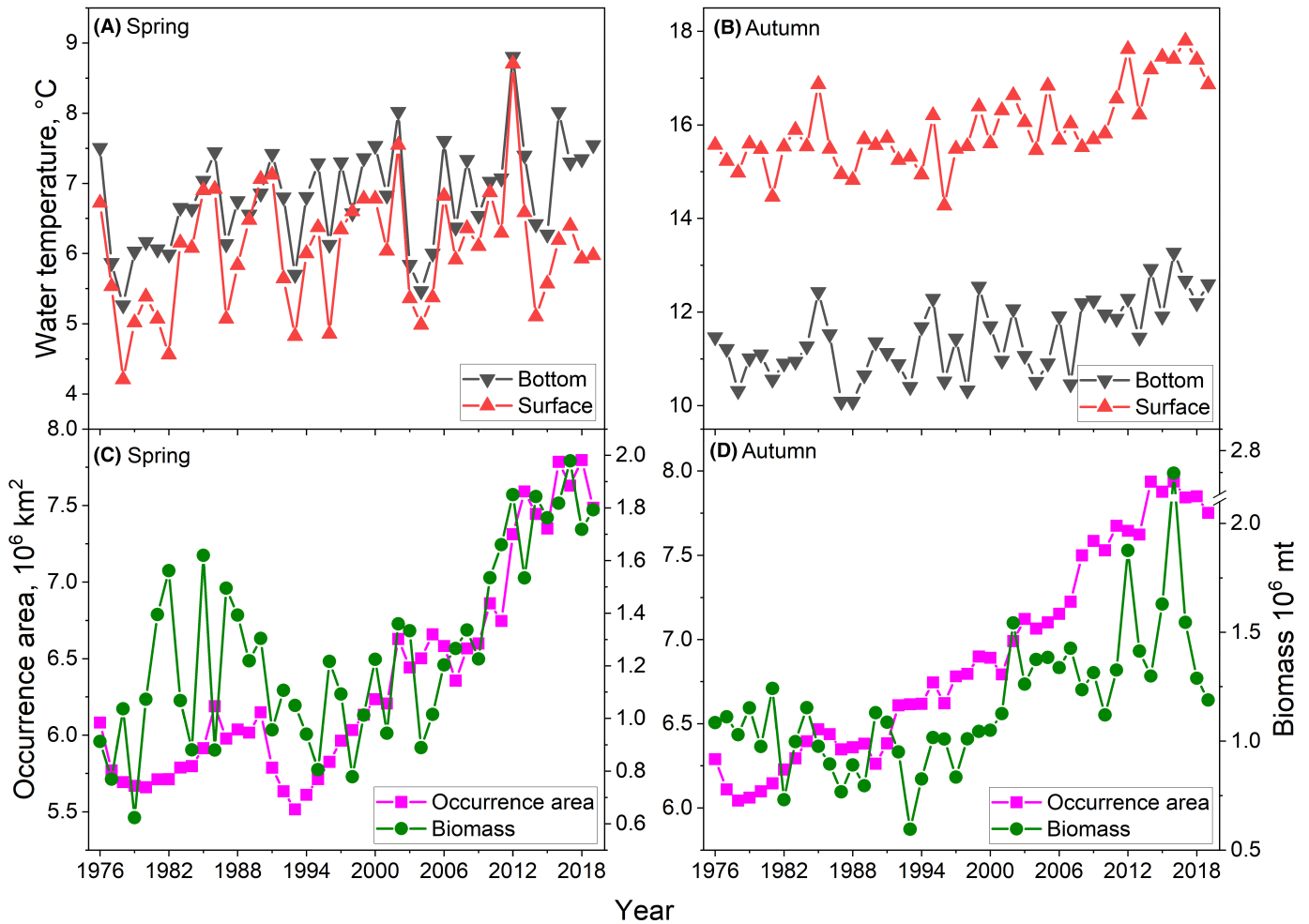
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FIGURE 2. Graphs of **(A)** spring and **(B)** autumn mean bottom and surface water temperature in the Northeast U.S. Continental Shelf ecosystem and total occurrence area and biomass across all species modeled in the **(C)** spring and **(D)** autumn.

rate of 1.32×10^6 kg/year, suggesting a slightly greater increase in spring biomass despite the smaller number of species included (Figure 2C,D). These Theil–Sen slopes suggest an increase in spring biomass of 80.96×10^6 kg compared with a fall increase of 58.08×10^6 kg. All the seasonal trends in occurrence area and biomass were significant (Table 3). It bears repeating that the trends in cumulative biomass across species must be interpreted with caution since the catchability among species is unknown.

In examining trends among species-specific biomass time series, most species with significant trends were characterized by increasing biomass over the study period. In spring, 68% of the significant trends ($P = 0.05$ for both trend tests and t-tests) were increasing trends and 67% of the significant difference indicators were increasing (Table 4). The mean increasing trend was 629×10^3 kg/year, which was nearly twofold greater than the decreasing

trend mean; the mean of increasing and decreasing difference indicators were similar. However, for both indicators, the standard deviation associated with the increasing indicator was greater than the decreasing indicator standard deviation. The largest spring trend was associated with Spiny Dogfish *Squalus acanthias* (Figure 3A). However, it is interesting to note that the difference indicator for Spiny Dogfish in spring was nonsignificant. Hence, it does not contribute to the spring difference indices (Figure 3B). The opposite was the case with Haddock *Melanogrammus aeglefinus*, which had a nonsignificant trend in the spring but a significant difference indicator. In the fall, 76% and 75% of the significant trend and difference indicators were increasing, respectively, a similar pattern to the spring data with greater increasing mean values compared with the decreasing means. Autumn Spiny Dogfish represent the largest single trend and difference indicator (Figure 3C,D), and again, the Haddock trends, though of

TABLE 3. Trend as Theil–Sen slopes of spring and autumn occurrence area, biomass, biomass to occurrence area ratio, and water temperature with statistic P-value and units. A probability of <0.05 is highlighted in bold italics.

Season	Variable	Trend	P	Units
Spring	Area	46.12	***<0.001***	$10^3\,km^2$
	Biomass	1.84	***0.001***	$10^6\,kg$
	Biomass/area	1.416	***0.042***	kg/km^2
	Bottom temperature	0.027	***0.002***	°C
	Surface temperature	0.016	0.225	°C
Autumn	Area	45.6	***<0.001***	$10^3\,km^2$
	Biomass	1.32	***0.001***	$10^6\,kg$
	Biomass/area	0.84	0.233	kg/km^2
	Bottom temperature	0.037	***<0.001***	°C
	Surface temperature	0.045	***<0.001***	°C

high value, were nonsignificant, whereas the Haddock difference indicator was significant.

Change between Habitat and Biomass

The annual ratio of biomass and occurrence area was calculated as an indicator of habitat productivity. The ratio averaged 197 and 169 kg/km in the spring and autumn, respectively (Figure 4). The trend in the ratio was significant and positive in the spring and nonsignificant and positive in the autumn (Table 3).

We further tested the relationship between biomass and occurrence area by comparing the rates of change in occurrence area and biomass among species. Among taxa with nonzero trends, occurrence area increased for 75% and 83% of spring and autumn species, respectively, and similarly, biomass increased in 60% and 62% of spring and autumn species, respectively. The bivariate relationships between the two rates suggest positive relationships in both the spring and autumn data (Figure 5A,B). This finding was reinforced by the regression excluding outlier data. However, an important extension of this finding is to consider the species in which the rates of change of

biomass and occurrence area have opposite signs. In spring, 16 of 84 (or 19%) species had opposite rates of change (positive biomass change paired with negative occurrence area change or vice versa) after excluding species with zero rates. In fall, it is 32 of 122 (or 26%) species with opposite rates of change.

Concordance between Occurrence Area, Biomass, and Temperature

There were seasonal differences in the synchronicity between occurrence area and biomass and temperature on the NES. Spring bottom temperature time series change was synchronous with spring biomass but was found to be nonsynchronous with habitat and biomass/occurrence area ratio (Table 5). Spring bottom water temperature was nonsynchronous with all the autumn occurrence area and biomass. However, spring surface water temperature was found to be synchronous with all spring and autumn occurrence area and biomass in both seasons. A similar pattern of synchronicity was observed with the autumn water temperatures. Autumn bottom water temperature was found to be nonsynchronous with all variables except spring biomass and biomass/occurrence area ratio, whereas autumn surface temperature was synchronous with occurrence area and biomass in both seasons.

DISCUSSION

Climate change has produced a patterned effect on marine ecosystems, resulting in a loss of productivity in lower-latitude ecosystems and an increase in higher-latitude ecosystems (Worm and Lotze 2021). These predictions are consistent with the changes in fish and macroinvertebrate occurrence area (referred therein as "occupancy habitats") seen in the NES ecosystem (Friedland et al. 2020a), which we extended by considering a larger number of taxa and examining the change in biomass in aggregate for the ecosystem and by species. The occurrence area for marine fish and macroinvertebrates in the NES has increased along with a concomitant change in the biomass

TABLE 4. The number of trend and difference indicators with increasing and decreasing time series patterns in species-specific biomass time series. Mean and standard deviation (SD) units are $10^3\,kg/year$ and $10^3\,kg$ for trend and difference indicators, respectively.

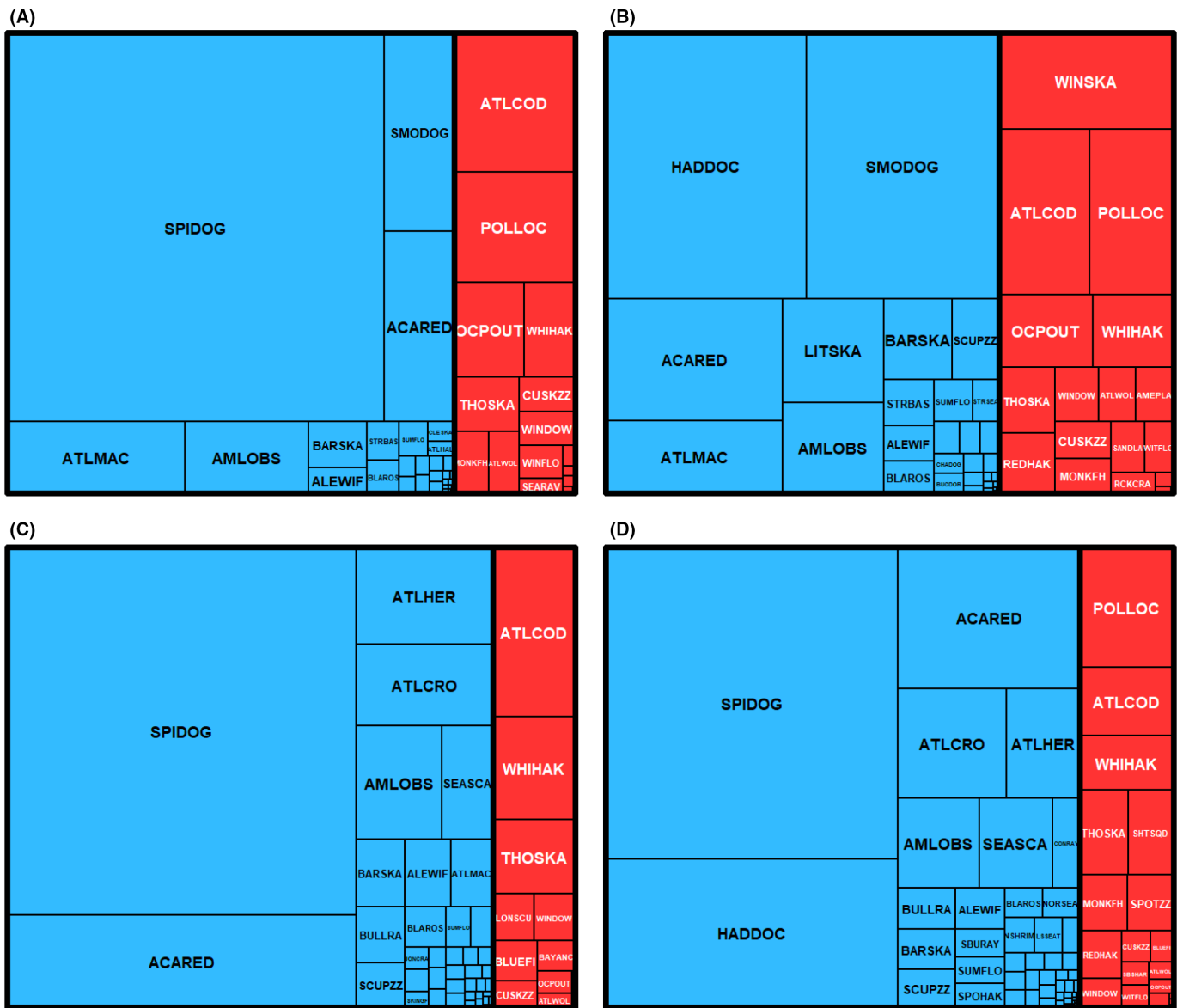| Season	Indicator	Direction	Number	Percent	Mean	SD
Spring	Trend	Increasing	38	68	629	2,767
	Trend	Decreasing	18	32	359	553
	Difference	Increasing	38	67	13,607	34,802
	Difference	Decreasing	19	33	12,051	14,908
Autumn	Trend	Increasing	44	76	498	1,941
	Trend	Decreasing	14	24	263	397
	Difference	Increasing	58	75	13,833	49,589
	Difference	Decreasing	19	25	8,315	10,554

FIGURE 3. Treemaps of trend indicators for **(A)** spring and **(C)** autumn and difference indicators for **(B)** spring and **(D)** autumn. The blue subgroup is a positive trend and difference value, while the red are negative. Species abbreviations appear in boxes of sufficient size for the text; abbreviations are defined in Table 1.

supported in this ecosystem. The previous assertion concerning the expansion of occurrence area was made with data from fully threefold less species, which raised concerns over the representativeness of the estimate (Friedland et al. 2020a). We believe that our current estimate is more robust and supports the assertion that occurrence area is increasing in this temperate ecosystem. A similar concern arose over the previously reported increase in biomass among modeled species; it would be reasonable to suspect that the trend in biomass is driven by a small number of high-biomass taxa, which it is. However, the more relevant question is whether most individual species

have increasing biomass. We now provide evidence directly addressing this, supporting the hypothesis that with the expansion of occurrence areas among species there has also been an expansion of biomass. This study provides a novel method to address this concern by identifying which species accounted for the changes in biomass. In the bottom trawl survey, catchability will vary due to differences in body size and vertical distribution in the water column among taxa; however, despite the biomass in total being disproportionately influenced by just a few taxa, the trend is influenced by many taxa. With these concerns about catchability, we cannot conclude that our
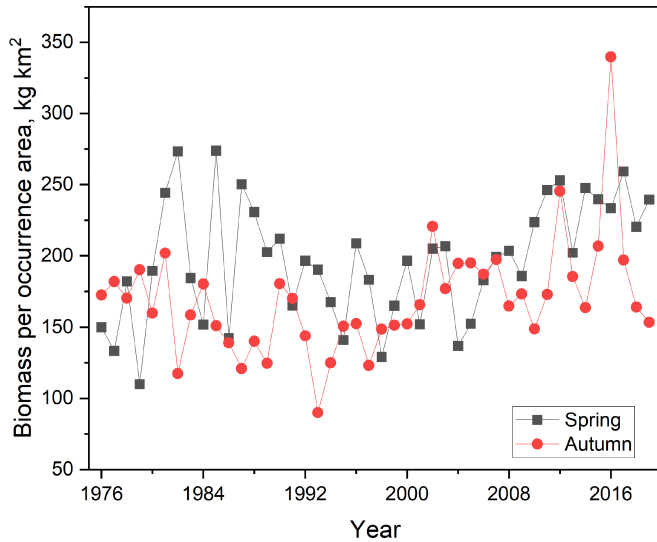
FIGURE 4. Ratio of biomass to occurrence area over time in spring and autumn.

aggregate biomass index is accurate, but we can assert that since most species contributing to the trend are trending upward, it would support the guarded use of the aggregate index as an indicator of overall ecosystem productivity. We feel confident in asserting that the occurrence areas for many species have increased in the NES

and that there has been an overall increase in the region's biomass, resulting from an increase in the biomass of many taxa.

Water temperature as a leading indicator of climate change would appear to be a driver of occurrence area expansion by increasing the spatial range of thermal tolerance for species and shifting and expanding zones of thermally optimal habitat. It is striking that surface temperature is more synchronous with occurrence area and biomass time series than bottom temperature, considering that the community of species tends to be demersal since the survey data are from a bottom-tending gear. Since both surface and bottom temperature have increased, it suggests that a patterned change in water column temperature may be more influential in defining occurrence area distribution than bottom temperature. A mechanistic connection may be formed with the change observed in lower-trophic-level species. For this ecosystem, latitudinal shifts in the distribution of fish species were associated with similar shifts in copepods, which would be associated with water column temperature (Friedland et al. 2019). From this reasoning, change in occurrence area thus controls the expansion or contraction of biomass; however, we recognize that there are other interpretations of these changes, with the alternate view that change in biomass intrinsic to a population controls the expansion or contraction of occurrence area.
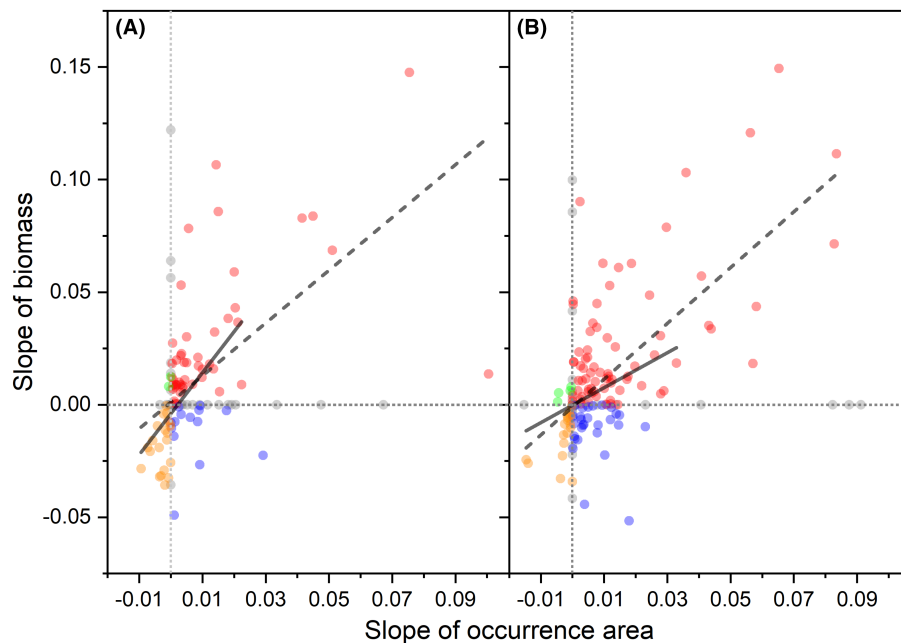

FIGURE 5. Theil–Sen slope of biomass and occurrence area for all (A) spring and (B) autumn species modeled. The dashed line is the linear regression using all the data, whereas the solid line is a linear regression after outlier removals. Red dots denote positive biomass and occurrence area slopes, yellow indicates negative biomass and occurrence, blue indicates negative biomass and positive occurrence, and green indicates positive biomass and negative occurrence. Gray dots are species with either or both slopes that have a value of zero.

TABLE 5. Test for synchronicity of time series trends between occurrence area and biomass variables and seasonal temperatures. Values with a probability of <0.05 are highlighted in bold italics.

Season	Variable	Spring		Autumn	
		Bottom temperature	Surface temperature	Bottom temperature	Surface temperature
Spring	Area	0.456	*0.044*	0.416	*0.004*
	Biomass	*0.020*	*<0.001*	*0.004*	*<0.001*
	Biomass/area	0.140	*0.032*	*0.028*	*<0.001*
Autumn	Area	0.332	*0.028*	0.384	*0.004*
	Biomass	0.132	*0.004*	0.156	*<0.001*
	Biomass/area	0.172	*0.024*	0.076	*<0.001*

The Alternate View that Biomass Controls Distribution

Though our main hypothesis is that occurrence area has increased for species as a result of changing environmental conditions, allowing for the expansion of populations, we are also cognizant of the alternate hypothesis that those same environmental changes may have actuated changes in populations that then modified their occurrence areas. We can find support for this alternate view in some studies that have found that occurrence area expands with an increase in biomass (Petitgas 1998; Anderson and Gregory 2000). The positive relationship we observed between the rate of change in occurrence area and biomass for many species would appear to be consistent with both the main and alternate hypotheses. Most species either had increasing or decreasing rates of change (same sign) for both occurrence area and biomass. However, the exceptions to this relationship (i.e., species that had a negative correlation between the change in occurrence area and biomass) lend more support to the main hypothesis. The majority of species with differing signs on their rates of change in occurrence area and biomass had positive slopes of area change and negative slopes in biomass. This would suggest that these species have increased their occurrence area but not as the result of a population increase. In other words, environmental change likely modified the extent of usable or tolerable habitat for these taxa and so the modeled occurrence area increased. There are only a few species with a positive rate of change in biomass and negative rate of change of occurrence area, and for these few species, the changes are relatively minor.

Our observations may expose weaknesses in applying existing theory on species spatial dynamics since much of existing theory is based on the assumption of constant environmental conditions. Density-dependent habitat selection is considered an important ecological mechanism in marine populations (Melo-Merino et al. 2020), and much of the thinking concerning density dependence stems from the basin model hypothesis of MacCall (1990). The basin hypothesis attributes large-scale patterns of habitat usage in marine environments to the "ideal free distribution" (Fretwell 1969), which assumes that populations occupy habitats to maximize their fitness (Morris 1987). In a practical sense, the theory predicts that habitats will change with the abundance of a taxon, with populations utilizing less well-suited habitats during expansion beyond the core favorable habitats used by most individuals (Simpson and Walsh 2004). We highlight that for density-dependence mechanisms to be at work, less well-suited and core habitats would need to be static. With the NES experiencing dramatic change in thermal conditions, and considering the importance of temperature in defining habitat for fishes (Free et al. 2019), the NES does not meet that underlying assumption of the basin hypothesis. Application of density-dependent habitat selection is also challenged when populations show varying rates of habitat–biomass relationships, suggesting some level of independence between biomass and habitat (Swain and Morin 1996). Several hypotheses were identified by Gaston et al. (1997) as drivers of positive habitat–biomass relationships, including the vital rate model (Holt et al. 1997) that attributes increase in habitat space to positive changes in birth, death, and growth rates due to the release from local competitors. Strong effects of interspecies interactions can result in mixed or inverse habitat–biomass relationships, where an increase in habitat space (i.e., high co-occurrence between predators and prey habitats) leads to negative correlations between predator and prey biomass (Barra et al. 2015; Mehner et al. 2021). This may play a role for the species identified in this study that have either positive or negative relationships among rates of occurrence area and biomass change.

We feel that it is not possible to establish any universal governing principle here regarding which change, occurrence area or biomass, is preemptive or controlling. In the NES, Banded Drum *Larimus fasciatus* and Longnose Greeneye *Parasudis truculenta* were virtually absent from the early segments of the survey time series and only appear in substantial numbers in recent decades; we suspect species like these, which have foci of distributions at lower latitudes, found new occurrence areas as a

consequence of climate change. At the same time, we can point to other species like Haddock with recruitment events (Friedland 2021) that increased population size followed by a rapid expansion of their distribution, redefining the spatial extent of their occurrence area. In another example, Mazur et al. (2020) found that American lobster *Homarus americanus* moved into previously unoccupied areas offshore and hypothesized that the increase in biomass inshore may have contributed to the increase in habitat use. Perhaps the most defensible point of view is that the ordering of these processes differ for different species.

Biomass to Habitat Relationship

Many factors contribute to the biomass of a population, including the area of the physical environment occupied by the species. For salmonid fish taxa for example, this can be seen in the fundamental relationship between the amount of stream habitat and the size of resident populations (Bowlby and Roff 1986). Moreover, it is also seen in the response of pelagic species like sardine (family Clupeidae) and anchovy (family Engraulidae) to changes in the oceanographic parameters defining their pelagic habitats (Barange et al. 2009). The quantitative relationship between habitat area and biomass has been approached in a generalized fashion, where biomass is a simple linear scalar of habitat as reported for coral reef fish populations (McClanahan et al. 2019), whereas in this study, other productivity factors were explicitly modeled. In an analysis examining a similar species group to the one we examined, the biomass of North Sea benthic taxa was found to be principally influenced by species evenness and seasonal temperature (Maureaud et al. 2019). In our analysis, we encountered mixed results in that the biomass per unit occurrence area was without trend in autumn and had a weak positive trend in spring. The absence of a trend would suggest a linear relationship between biomass and occurrence area, whereas an increase in the biomass per unit occurrence area would suggest a nonlinear change in biomass with occurrence area across different taxa. This mixed result may reflect the different responses of biomass to occurrence area changes in different seasons. Predator biomass has been modeled as a function of both prey biomass and habitat size, suggesting that there are nonlinear properties between predator biomass and the combined effects of these factors (McIntosh et al. 2018). However, any nonlinear form of the relationship may be related to the underlying cubic scaling of weight to length, which we would expect to be evident if the cumulative population length of a taxon scaled with the extent of two-dimensional habitat, which in turn would translate into a cubic increase in biomass. This would be consistent with the simple morphological relationship of the weight scaling as the cube of the length of an individual.

Limitations

The results of this study are dependent upon the survey design and available data. The bottom trawl survey does not sample near rocky or ledge substrates (Smith and Tremblay 2003), which are important habitats for many species. The survey also samples offshore federal waters, so the results do not account for inshore and estuarine population dynamics. Additionally, survey gear length-based selectivity leans toward larger or smaller sizes for some species and may result in biased occurrence area and biomass estimates. Change in the size of fish over time, be it the consequence of fishing activities or ecosystem effects, introduces the issue of change in catchability with size. Since the size of fish in the NES are known to have changed in recent decades (Friedland et al. 2020c), shifting biomass may also be shaped by the change in size-specific catchability for a species. Additionally, species distributions could have shifted outside of the survey area, resulting in a change in catchability. This study was designed to quantify relationships between biomass and occurrence area with data from 1976 to 2019. However, these biomass–occurrence area relationships may change over time and with climate change, which can be examined in future studies with more data. Additionally, it is important to note that change in population biomass in this study may be impacted by human activity to varying degrees, especially for commercial fish species. The survey gear used to measure these populations has common properties to a range of fishing gears, so any commercial fish species caught in the survey may also be captured in fisheries as either target species or bycatch. Hence, patterns of temporal change in biomass may be influenced not only by habitat, but also by factors other than environmental effects alone, namely fishing effects (Jørgensen and Holt 2013). This becomes difficult to track since the abundances of species are responding to a range of factors. The contemporary increase in Spiny Dogfish was likely due to a relaxation of fishing pressure two decades ago (Sagarese et al. 2016). In contrast, Haddock has also increased in abundance, while fishery removals were unchanged; the expansion of the Haddock population was due to conditions favorable to large, episodic recruitment events (Friedland 2021). On the other hand, there are a range of species, including iconic species such as Atlantic Cod *Gadus morhua*, that have been under stock rebuilding regimes that limit fishing, yet the population has continued to decline (Pershing et al. 2021).

Management Implications

With change in habitats, there are also interactions between species and life stages that could have negative impacts on biomass (Orio et al. 2019) and distributional organization that likely reflects the differential utilization of geographically distributed resources (Turner et al. 2017).

For example, changing climate may adversely affect larval dispersal and spawning habitat and nursery connectivity (Petitgas et al. 2013), leading to declines in species biomass, while adult habitat area appears to expand. In addition, climate change can lead to phenological mismatches in predator–prey interactions that may adversely affect a species' ability to maintain or increase overall biomass as its habitat area shifts differentially to that of its prey (Donnelly et al. 2011). Long-term changes in biomass and habitat occupancy may also result in unexpected patterns in species biodiversity, manifest through the overlapping of species' core habitats. Present and future patterns in species diversity, while important for fisheries management, also provide vital information for the design of marine protected areas (Hodge et al. 2022), which will be increasingly important as pressure mounts to preserve 30% of well-connected coastal and marine areas of particular importance to biodiversity by 2030 (Visalli et al. 2020). These changes offer opportunities to apply climate-adaptive management, where increased fishery yields can be achieved if management systems track and understand changes in habitat and the concomitant changes in abundance that will likely follow environmental change (Free et al. 2020). Specifically, the incorporation of habitat in fisheries stock assessments allows for better estimations of population size changes (Bello et al. 2005), and as the interest in ecosystem-based fisheries management increases (Hall and Mainprize 2004; Hilborn 2011), these species–habitat interactions will become more imperative to the overall framework. However, it will require that specific and ordered actions be taken by individuals and institutions to adapt to the shifts in production centers of species, a set of actions that includes guidance from both the oceanographic and social sciences (Ojea et al. 2020). There is also a high likelihood that demersal fish habitats will continue to shift latitudinally for decades to come (Mason et al. 2021).

CONCLUSION

With climate change, the spatial distribution of many species and thus their habitats are changing, leading to both gradual and abrupt reorganization of marine ecosystems. The relationship between occurrence area and biomass provides insight into the productivity of the NES ecosystem under a changing climate. Our analysis will further aid scientists and planners in understanding how ecosystems arrayed over different parts of the world are displaying differing patterns of changing productivity among higher-trophic-level organisms. These ecosystem considerations can be incorporated into management advice frameworks to help guide the sustainable management of traditionally and nontraditionally utilized species. Additionally, an understanding of upper-trophic-level occurrence area and biomass dynamics emphasizes the importance of spatial management for small populations of threatened and endangered species and may help to identify optimal boundaries for marine protected areas that will promote high biodiversity. This study focused on the ecosystem level of biomass and occurrence area changes and their relationships. Future studies focused on some commercially or ecologically important species in this ecosystem separately would shed more light on climate change impact on biomass and occurrence area and the implication for fishery management (Hare et al. 2012).

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.