THEMED ISSUE: OFFSHORE WIND INTERACTIONS WITH FISH AND FISHERIES

Forage Fish Species Prefer Habitat within Designated Offshore Wind Energy Areas in the U.S. Northeast Shelf Ecosystem

Kevin D. Friedland* (iD)
National Marine Fisheries Service, Narragansett, Rhode Island 02882, USA

Evan M. Adams (iD) **Chandra Goetsch** (iD)**, and Julia Gulka** (iD)
Biodiversity Research Institute, Portland, Maine 04103, USA

Damian C. Brady (iD) **and Everett Rzeszowski** (iD)
Darling Marine Center, University of Maine, 193 Clark Cove Road, Walpole, Maine 04573, USA

Daniel P. Crear (iD)
ECS Federal, in support of National Marine Fisheries Service, Atlantic Highly Migratory Species Management Division, Silver Spring, Maryland 20910, USA

Sarah Gaichas (iD)
National Marine Fisheries Service, Woods Hole, Massachusetts 02543, USA

Andrew B. Gill (iD)
Centre for Environment, Fisheries and Aquaculture Science, Lowestoft, Suffolk NR33 0HT, UK

M. Conor McManus (iD)
Rhode Island Department of Environmental Management, Division of Marine Fisheries, Jamestown, Rhode Island 02835, USA

Elizabeth T. Methratta (iD)
IBSS Corporation, in support of National Marine Fisheries Service, Narragansett, Rhode Island 02882, USA

Janelle L. Morano (iD)
Department of Natural Resources and the Environment, Cornell University, Ithaca, New York 14853, USA

Michelle D. Staudinger (iD)
U.S. Geological Survey, Department of the Interior Northeast Climate Adaptation Science Center, Amherst, Massachusetts 01003, USA

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*Corresponding author: kevin.friedland@noaa.gov

Abstract

As the world develops sources of renewable energy, there is an intensifying interest in offshore wind energy production. The Northeast U.S. Continental Shelf (NES) ecosystem has favorable wind dynamics, with active development of wind energy. In this study, we present species distribution models that consider both occupancy and biomass responses for a broad spectrum of fish and macroinvertebrate taxa ($n = 177$). Building upon prior analyses, habitat was differentiated into overall and core habitats based on statistical distributions of habitat scores. Overall habitat was used to show each species' regional distribution based on fishery-independent survey captures between 1976 and 2019, whereas core habitat represented where the focus of the species' abundance was located as a subset of overall habitat. Wind energy developments may modify the water column in ways that impact lower-trophic-level productivity; therefore, added attention was given to the response of forage species. Over 20% of species showed preferential use of putative and potential wind development areas, including a disproportionate number of forage taxa. Principal usage varied by season, with forage species like Atlantic Menhaden *Brevoortia tyrannus* and Atlantic Mackerel *Scomber scombrus* preferentially using the lease areas in spring and Round Herring *Etrumeus teres* and longfin inshore squid *Doryteuthis pealeii* using lease areas in autumn. For species with relatively low usage of the lease areas, there was a tendency for the usage related to overall habitat to be lower than usage for core habitat; in contrast, for species with high usage of the lease areas, that usage was higher for overall habitat than for core habitat. The area of habitat tended to have positive trends across species, with these positive trends being disproportionately higher among forage taxa. These results frame the importance of wind lease areas for species in the NES, particularly forage taxa that fulfill many important ecological functions.

Continental shelf seas provide a range of resources and services to human populations but are also increasingly identified as regions with the potential to produce renewable energy through the utilization of wind. The long-standing provision of ecosystem services of these seas could now be in conflict with the requirements of renewable energy production, forcing jurisdictions and stakeholders to make challenging decisions that consider multi-use trade-offs, which often require negotiation and compromise. Continental shelf seas are areas of enhanced primary production (Friedland et al. 2021c), thus making them the focus of most of the world's seafood harvest (Watson and Tidd 2018). However, the installation of wind energy infrastructure imposes restrictions on the safe operation of many harvesting methods (Stelzenmüller et al. 2021) and is also predicted to alter the habitats of these ecosystems, thereby causing a change in resident species composition and abundance (Raoux et al. 2018). Additionally, shelf seas provide corridors for large container vessels, supporting global trade; however, wind energy installations have placed limits on shipping access and maneuvering of these ships (Hasanspahić et al. 2021). Wind energy installations are under development worldwide, including a great deal of activity in the continental Americas, particularly the Northeast U.S. Continental Shelf (NES), and with nascent activity in the Gulf of Mexico and the Pacific Northwest (deCastro et al. 2019). Hence, the determination of ecosystem-level anthropogenic impacts associated with offshore wind (OSW) development (Boehlert and Gill 2010; Gill et al. 2020) and the application of the spatial approaches gained from studies in the NES (Friedland et al. 2021a, 2021b) and other similar continental shelf seas should have broad appeal and utility.

At the local scale associated with the footprint of the wind farms, current evidence suggests that direct effects of operational OSW developments on benthic habitats occur in close proximity to (within 200 m of) the generating substructure (Coates et al. 2014; Degraer et al. 2020). Turbine foundations, subsea cables, and their associated hard protections are often installed in sand or mud habitats and thus create novel hard-bottom habitat in an otherwise soft-bottom environment. Hard structures provide settlement and recruitment habitat for a wide diversity of sessile and mobile benthic organisms, resulting in an artificial reef community that attracts structure-oriented demersal finfish species seeking forage and predation refugia (Wilhelmsson et al. 2006; Reubens et al. 2011; van Hal et al. 2017). The presence of OSW structures has resulted in patterns of benthic community succession (De Mesel et al. 2015), recruitment of nonindigenous species (De Mesel et al. 2015; HDR 2020), nonnative range expansion via the stepping-stone effect (Coolen et al. 2020), and altered trophic dynamics (Mavraki et al. 2020a, 2020b; Wilber et al. 2022). Biogenic materials associated with temporal reef organisms fall from the turbines and are deposited in the surrounding environment, increasing the organic composition of the benthos and reducing the grain size of bottom sediments, thus modifying benthic community composition (Coates et al. 2016). In addition to benthic habitat modification, operational OSW developments can affect electromagnetic fields via emissions of electromagnetic fields from subsea interarray and export cables (Gill et al. 2012; Hutchison et al. 2020), the acoustic environment via operational sound (Tougaard et al. 2020), the bioavailability of chemical contaminants via emissions of anticorrosives (Kirchgeorg et al. 2018), and localized

changes in flow via alteration of current patterns (Dorrell et al. 2022). These changes occur over different spatial scales and could have implications for fisheries species in the coastal shelf waters.

Mesoscale effects of operational OSW developments may occur through the impact of wind wakes that result from the removal of kinetic energy from the wind field on the leeward side of rotating turbines (Carpenter et al. 2016; Dorrell et al. 2022). Although concerns have been raised about the ability to discern wake effects from the background of natural variability (van Berkel et al. 2020), coupled atmospheric–hydrodynamic models suggest that wind wakes may reduce mixing and enhance vertical stratification of temperature and salinity (Christiansen et al. 2022). A modified mixing regime could alter biological oceanographic processes through altered vertical and horizontal transport of macro- and micronutrients to primary producers and changes to the distribution of suspended particulates affecting the depth of the photic zone. Modeling conducted by Christiansen et al. (2022) found seasonal changes in the depth of the mixed layer driven by wind wake effects that could change the transport of nutrients to the surface, thus affecting primary production. Empirical evidence from an OSW farm in the southern North Sea showed that increased vertical mixing around OSW substructures locally domed the thermocline, transporting nutrients to the surface mixed layer, where they fueled phytoplankton growth in the photic zone (Floeter et al. 2017).

Altered primary production due to OSW developments could affect upper-trophic-level organisms. Recent species distribution modeling in the NES system found that physical drivers (e.g., depth, bottom temperature) and lower-trophic-level indicators (e.g., primary production variables) likely drive the habitat distribution of ecologically and commercially important finfish and invertebrate species in areas that are leased for OSW development (Friedland et al. 2021b). Thus, OSW-driven changes in hydrodynamic regime could have broadscale effects for these species. Furthermore, the effects of changes in water column properties (water temperature, dissolved oxygen, and suspended matter concentration) have also been linked to altered zooplankton community structure at OSW farms in China (Wang et al. 2018). Hence, the potential for community-level effects and trophic cascades should be considered during the OSW planning process. For example, bivalves and other macrobenthic suspension feeders represent a major component of the artificial reef communities that colonize turbine foundations (Slavik et al. 2019; Mavraki et al. 2020b) and may benefit from OSW-enhanced primary production, which in turn could affect their predators.

Human community–OSW relationships can be viewed from the perspective of the two spatial scales of habitat modification mentioned above. Localized effects are associated with the OSW structures themselves, and mesoscale effects are associated with perturbations of wind and tidal mixing of the water column. Localized effects have been studied to a degree and related to alterations in the reproduction and abundance of key resource species. Offshore wind structures serve to enhance recruitment of the brown crab *Cancer pagurus* by increasing critical nursery habitat (Krone et al. 2017). There is evidence of neutral effects on the abundance of common lobster *Homarus gammarus* in wind fields versus control areas (Roach et al. 2022). There is also evidence of enhanced abundance of demersal species within wind fields related to a number of localized factors (Methratta and Dardick 2019; Wright et al. 2020). It is important to note that OSW areas become no-take fishing zones to varying degrees, as not all gears can be safely operated within them (Gill et al. 2020). In contrast, mesoscale effects have been less well studied. Many species have critical habitats that overlap OSW planning areas, including those associated with larval dispersal and early life history events, which are known to be subject to variability in mixing, transport, and lower-trophic-level productivity (Barbut et al. 2020). Mesoscale changes in lower-trophic-level productivity may affect the growth and productivity of adult forms, particularly forage taxa, which often have closer food web associations with primary producers.

Forage fish provide a range of ecosystem services (Pikitch et al. 2014), and from a fisheries perspective, there is intense interest in the management of forage fish as it relates to the yields of higher-trophic-level species (Free et al. 2021). Analyses of the cumulative ecosystem impacts of OSW fields that consider the potential of mesoscale effects on the oceanography and productivity of the surrounding areas are needed to determine whether and how forage taxa may be impacted. Such analyses can inform planners on how OSW development may interfere with protected resources and species with specific ecological functions so that these effects can be accounted for in the design and modification of ongoing and future projects (Lloret et al. 2022).

In this study, the potential impact of wind energy development on the NES was evaluated by using species distribution models to estimate the amount of functional habitat inside and outside of the lease areas. Building upon recent work (Friedland et al. 2021b), we employed a novel approach that differentiates overall and core habitats relevant for each species through estimations of occurrence probability and the distribution of species biomass. The anticipated footprint for wind lease areas is expected to continue to change, thus affecting the range of habitats and species that are likely to be impacted by development. This analysis uses a contemporary depiction of the anticipated footprint while recognizing that the spatial extent of

wind energy development in the NES is not settled. We do not consider where mesoscale effects due to water column perturbations and other factors exceed the lease area boundaries (Akhtar et al. 2022). In prior analyses, a more conservative standard was taken to determine the taxa included in the species group (Friedland et al. 2021b); however, for the present study, this standard was adjusted to include more taxa, thereby increasing the total number of species analyzed from 93 to 177.

METHODS

Study system.— The NES is a well-studied marine ecosystem that is routinely monitored with a bottom trawl survey for fisheries management and ecological studies supporting ecosystem-based management approaches (Figure 1). The map in Figure 1 shows the extent of the study area used to estimate fish and macroinvertebrate habitat denoted by a 0.1° resolution grid. Further, the map depicts putative and potential wind development areas (including lease areas, call areas, and planning areas) that occurred inside and outside of the study area grid as of

May 2022. The wind energy areas under development will likely change over time, but there are two features associated with these areas that vary from previous characterizations (Friedland et al. 2021b). The present characterization includes energy areas that encompass the shelf break segments of the mid-Atlantic region; this is important because many taxa have offshore distributions that are limited to the shelf break. Furthermore, the present characterization also includes a speculative area for the Gulf of Maine region, which is important since many species have a discontinuous distribution between the Gulf of Maine and the Middle Atlantic Bight.

Species distribution models.— The species distribution models presented here are an extension of those presented in a series of studies on the ecology of the NES ecosystem (Friedland et al. 2020, 2021a, 2021b, 2021d). In those studies, random forest classification models of presence/absence and regression models of biomass CPUE were used to estimate occupancy and biomass habitats. In brief, random forest models were developed for a suite of species based on captures made in the Northeast Fisheries Science Center's bottom trawl survey (Despres-Patanjo et al.
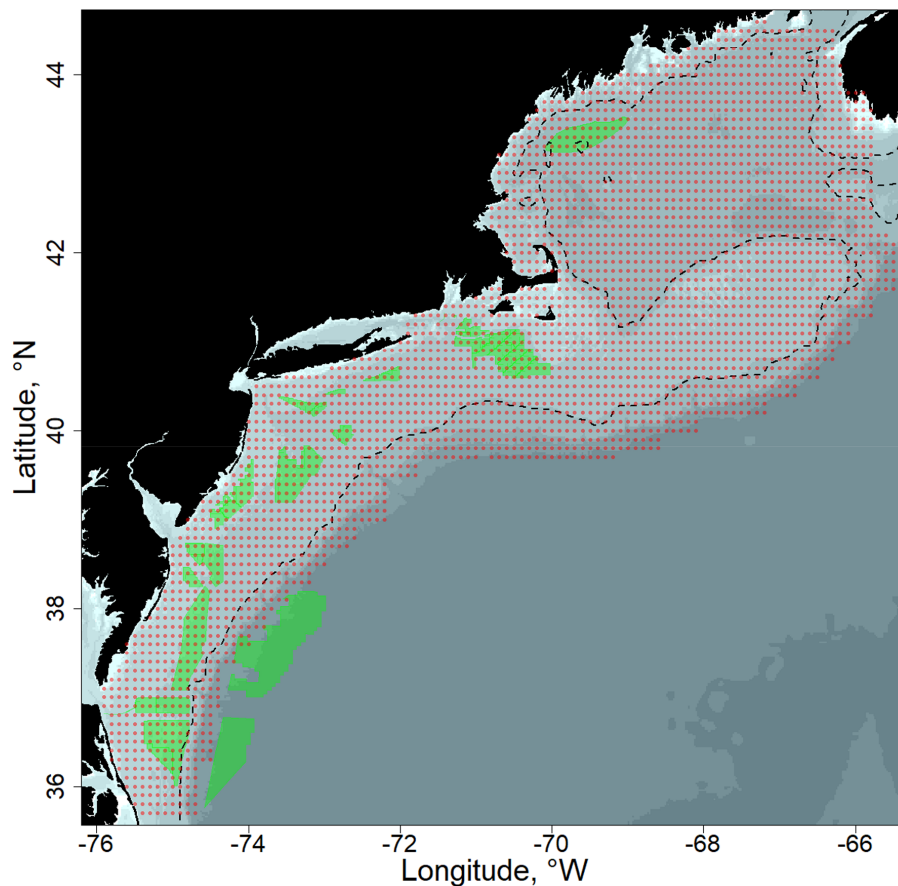

FIGURE 1. Map of the Northeast U.S. Continental Shelf ecosystem, with red dots marking the extent of the study domain for the estimation of habitat. Green regions mark the putative and potential wind development areas. The dashed line marks the 100-m depth contour.

1988), which is conducted in the spring and autumn seasons, equating to approximately 300 stations sampled per season. This random stratified survey started in 1963 for autumn sampling and in 1968 for spring sampling and covers areas off the coast of North Carolina to Nova Scotia. Location, sea surface temperature, bottom water temperature, and salinity, as well as the number of individuals, total weight, and length frequencies of each species, are collected at each tow. Hence, models were developed to reflect spring and autumn conditions based on these surveys.

The presence/absence for a taxon was modeled with a starting group of 91 explanatory variables that were first tested for collinearity, which provided 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, each model was optimized using the method described by Murphy et al. (2010), which determined the final set of variables included in a species' model ("rf.modelSel" command from 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 for covariate details). The current study's approach differs from recent reporting (Friedland et al. 2021b) concerning the preprocessing of zooplankton data in order to address issues with sample coverage in the later part of the time series. First, the data were combined over a 7-year time step instead of the 5 years used previously for each seasonal period. Second, seasonal periods were expanded for the zooplankton data, using February–May for the spring (previously February–April) and August–November for the autumn (previously September–November). The training data extended from 1976 to 2019 and were used to evaluate the potential model fits 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 a score of at least 0.7 for the area under the receiver operating characteristic curve (Fielding and Bell 1997; "auc" command from the R package Metrics version 0.1.4; https://cran.r-project.org/web/packages/Metrics/) based on out-of-sample test data; this criterion resulted 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 for both seasons (Table 1). In addition, we placed an added focus on taxa that can be considered principal forage species of NES predators; these taxa appear in the diets of a wide range of species and play an important role in food web energy transfer. For each species' seasonal model, estimates of occupancy habitat in the form of occurrence probability

were made over the NES extent, represented by a 0.1° grid (Figure 1), annually over the period 1976–2019.

For each species with a seasonal occupancy model, a biomass model was also fitted with essentially the same model selection approach used in the occurrence modeling; the only difference was that instead of fitting a classification random forest model, a random forest regression model was fitted on log-transformed biomass catch (kg) per tow: $\log_{10}[(\text{kg/tow}) + 1]$. Likewise, for each species' seasonal model, estimates of biomass habitat in the form of transformed catch per tow were made over the NES 0.1° grid over the period 1976–2019. Each species that met the satisfactory criteria was represented by four models: an occupancy model and a biomass model for each of the two seasonal periods (spring and autumn).

Analysis strategy.— Our purpose in this study was to compare the use of the wind lease areas by species to the use of the NES habitat as a whole. Given that there is less information available on the responses of forage taxa to OSW development in comparison with information on benthic species' responses, we also structured the analysis with a particular focus on the forage taxa of the NES. In previous analyses, demarcations to illustrate the quality of habitat based on arbitrary threshold values were used to calculate the areal extent of habitat. For example, the occupancy habitat for a species was taken as the area (km^2) having an occurrence probability above a certain value (e.g., 0.5 or greater). For species with habitat modeled using predicted occurrence probabilities that range from 0 to 1, this approach is quite satisfactory. However, for species' models that are well estimated but with predicted occurrence probability over a narrow range of values, such as from 0.1 to 0.4, cross-species comparisons are less useful. An alternative approach, applied here, was to estimate the occurrence probability associated with each 10% quantile of probabilities for each species by season (Crear et al. 2021). Hence, the lower percentage quantiles and probabilities define the threshold delineating the overall habitat area. Conversely, the higher percentage quantiles and probabilities define the threshold of the core habitats for the species. The biomass habitat was treated in the same way. The trends in occupancy and biomass habitat by quantile across all species and by season were calculated; the overall habitat was visualized using the second quantile (20%), whereas the core habitat was represented with the eighth quantile (80%). It should be noted that other threshold combinations were considered, and they yielded similar results.

For the first representation of lease area utilization, we constructed ratios of the quantity of habitat in the lease area (km^2) to the quantity of habitat in the NES ecosystem (km^2). We examined the scatterplots between the ratio associated with the overall habitat (20% level) and the core habitat (80% level) for each of the occupancy and

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TABLE 1. List of fish and macroinvertebrate taxa modeled for occupancy and biomass habitat on the Northeast U.S. Continental Shelf. The common and scientific names of each taxon are presented along with the taxon's six-letter abbreviation (Code). Availability of spring (s) and autumn (a) models is indicated in parentheses for each taxon. Forage species are designated in bold.

Taxon (models)	Code	Taxon (models)	Code	Taxon (models)	Code
Atlantic brief squid *Lolliguncula brevis* (a)	ABSQUI	Cownose Ray *Rhinoptera bonasus* (a)	CONRAY	Rough Scad *Trachurus lathami* (s, a)	ROSCAD
Acadian Redfish *Sebastes fasciatus* (s, a)	ACARED	Common octopus *Octopus vulgaris* (s, a)	COOCTO	Rosette Skate *Leucoraja garmani* (s, a)	ROSSKA
Alewife *Alosa pseudoharengus* (s, a)	**ALEWIF**	Cunner *Tautogolabrus adspersus* (s, a)	CUNNER	Rainbow Smelt *Osmerus mordax* (s)	RSSMEL
Alligatorfish *Aspidophoroides monopterygius* (s, a)	ALLFSH	Cusk *Brosme brosme* (s, a)	CUSKZZ	Roughtail Stingray *Dasyatis centroura* (a)	RTSTIG
American Plaice *Hippoglossoides platessoides* (s, a)	AMEPLA	Deepbody Boarfish *Antigonia capros* (s, a)	DBBOAR	Striated Argentine *Argentina striata* (s, a)	SAARGE
American Shad *Alosa sapidissima* (a)	AMESHA	Deepwater Flounder *Monolene sessilicauda* (s, a)	DFFLOU	**Northern Sand Lance *Ammodytes dubius* (s, a)**	**SANDLA**
American lobster *Homarus americanus* (s, a)	AMLOBS	Dusky Shark *Carcharhinus obscurus* (a)	DSSHAR	Butterfly bobtail squid *Stoloteuthis leucoptera* (s, a)	SBBOBT
Atlantic Angel Shark *Squatina dumeril* (s, a)	ANGSHR	Fawn Cusk-eel *Lepophidium profundorum* (s, a)	FAWMEL	Striped Burrfish *Chilomycterus schoepfi* (a)	SBBURR
Armored Searobin *Peristedion miniatum* (s, a)	ARMSEA	Friendly blade shrimp *Spirontocaris liljeborgii* (s, a)	FBSHRI	Sandbar Shark *Carcharhinus plumbeus* (a)	SBSHAR
Aesop shrimp *Pandalus montagui* (s, a)	ASHRIM	Planehead Filefish *Stephanolepis hispidus* (a)	FILEFS	Spiny Butterfly Ray *Gymnura altavela* (a)	SBURAY
Atlantic Sharpnose Shark *Rhizoprionodon terraenovae* (a)	ASSHAR	Fourspot Flounder *Paralichthys oblongus* (s, a)	FOUFLO	Longspine Porgy *Stenotomus caprinus* (a)	SCUPSC
Atlantic Sturgeon *Acipenser oxyrinchus* (s)	ASSTUR	Fourbeard Rockling *Enchelyopus cimbrius* (s, a)	FRBERO	Scup *Stenotomus chrysops* (s, a)	SCUPZZ
Atlantic Thread Herring *Opisthonema oglinum* (a)	**ATHERR**	Gladiator box crab *Acanthocarpus alexandri* (s, a)	GBCRAB	Spotfin Dragonet *Foetorepus agassizi* (s, a)	SDDRAG
Atlantic Argentine *Argentina silus* (s, a)	ATLARG	Gray Triggerfish *Balistes capriscus* (a)	GRTRIG	Sea Raven *Hemitripterus americanus* (s, a)	SEARAV
Atlantic Cod *Gadus morhua* (s, a)	ATLCOD	Grubby *Myoxocephalus aenaeus* (a)	GRUBBY	Atlantic sea scallop *Placopecten magellanicus* (s, a)	SEASCA
Atlantic Croaker *Micropogonias undulatus* (s, a)	ATLCRO	Gulf Stream Flounder *Citharichthys arctifrons* (s, a)	GULFLO	Silver Perch *Bairdiella chrysoura* (a)	SELPER

TABLE 1. Continued.

Taxon (models)	Code	Taxon (models)	Code	Taxon (models)	Code
Atlantic Cutlassfish *Trichiurus lepturus* (a)	ATLCUT	Haddock *Melanogrammus aeglefinus* (s, a)	HADDOC	Daubed Shanny *Leptoclinus maculatus* (s)	SHANNY
Atlantic Halibut *Hippoglossus hippoglossus* (s, a)	ATLHAL	Atlantic Hagfish *Myxine glutinosa* (s, a)	HAGFIS	Shortnose Greeneye *Chlorophthalmus agassizi* (s, a)	SHORTP
Atlantic Herring *Clupea harengus* (s, a)	**ATLHER**	Harvestfish *Peprilus alepidotus* (a)	HARFIS	Northern shortfin squid *Illex illecebrosus* (s, a)	SHTSQD
Atlantic Mackerel *Scomber scombrus* (s, a)	**ATLMAC**	Hogchoker *Trinectes maculatus* (s, a)	HOGCHO	**Silver Anchovy *Engraulis eurystole* (a)**	**SILANC**
Atlantic Menhaden *Brevoortia tyrannus* (s, a)	**ATLMEN**	Atlantic horseshoe crab *Limulus polyphemus* (s, a)	HSCRAB	Silver Hake *Merluccius bilinearis* (s, a)	SILHAK
Atlantic Soft Pout *Melanostigma atlanticum* (s, a)	ATLPOU	Inshore Lizardfish *Synodus foetens* (a)	INLIZA	Southern Kingfish *Menticirrhus americanus* (a)	SKINGF
Atlantic Silverside *Menidia menidia* (s)	**ATLSIL**	Jonah crab *Cancer borealis* (s, a)	JONCRA	Slender Snipe Eel *Nemichthys scolopaceus* (a)	SLENSE
Atlantic Wolffish *Anarhichas lupus* (s, a)	ATLWOL	King Mackerel *Scomberomorus cavalla* (a)	KMMACK	Silver-rag *Ariomma bondi* (a)	SLERAG
Atlantic Moonfish *Selene setapinnis* (a)	ATMOON	Lady crab *Ovalipes ocellatus* (s, a)	LADCRA	Smallmouth Flounder *Etropus microstomus* (s, a)	SMAFLO
Atlantic Saury *Scomberesox saurus* (a)	**ATSAUR**	Longfin Hake *Phycis chesteri* (s, a)	LGFINH	Smooth Butterfly Ray *Gymnura micrura* (a)	SMBRAY
Atlantic Seasnail *Liparis atlanticus* (s, a)	ATSEAS	Longnose Greeneye *Parasudis truculenta* (s, a)	LGGREE	Smooth Dogfish *Mustelus canis* (s, a)	SMODOG
Atlantic Spadefish *Chaetodipterus faber* (a)	ATSPAD	Little Skate *Leucoraja erinacea* (s, a)	LITSKA	Smooth Skate *Malacoraja senta* (s, a)	SMOSKA
Atlantic Torpedo *Torpedo nobiliana* (s)	ATTORP	Longhorn Sculpin *Myoxocephalus octodecemspinosus* (s, a)	LONSCU	Snakeblenny *Lumpenus lampretaeformis* (s, a)	SNAKEB
Banded Drum *Larimus fasciatus* (a)	BADRUM	**Longfin inshore squid *Doryteuthis pealeii* (s, a)**	**LONSQD**	Snow crab *Chionoecetes opilio* (s, a)	SNOWCR
Barndoor Skate *Dipturus laevis* (s, a)	BARSKA	Loggerhead sea turtle *Caretta caretta* (a)	LSSEAT	Spanish Mackerel *Scomberomorus maculatus* (a)	SPAMAC
Bay Anchovy *Anchoa mitchilli* (s, a)	**BAYANC**	Longspine Snipefish *Macroramphosus scolopax* (s, a)	LSSNIP	Spider crabs (family Majidae) (a)	SPICRA
Blackmouth Bass *Synagrops bellus* (a)	BBBASS	Lumpfish *Cyclopterus lumpus* (s, a)	LUMPFI	Spiny Dogfish *Squalus acanthias* (s, a)	SPIDOG
Blackcheek Tonguefish *Symphurus plagiusa* (s)	BCTONG	Mackerel Scad *Decapterus macarellus* (a)	MACSCA	Spotted Hake *Urophycis regia* (s, a)	SPOHAK

TABLE 1. Continued.

Taxon (models)	Code	Taxon (models)	Code	Taxon (models)	Code
Black Drum *Pogonias cromis* (a)	BDDRUM	Marlin-spike *Nezumia bairdii* (s)	MARLSP	Spoonarm octopus *Bathypolypus arcticus* (s, a)	SPOONO
Beardfish *Polymixia lowei* (s, a)	BEARDF	Goosefish (Monkfish) *Lophius americanus* (s, a)	MONKFH	Spot *Leiostomus xanthurus* (s, a)	SPOTZZ
Bigeye Scad *Selar crumenophthalmus* (a)	BESCAD	Mustache Sculpin *Triglops murrayi* (s, a)	MOUSCL	**Spanish Sardine *Sardinella aurita* (a)**	**SPSARD**
Black Sea Bass *Centropristis striata* (s, a)	BLABAS	Northern Kingfish *Menticirrhus saxatilis* (a)	NKINGF	Sevenspine bay shrimp *Crangon septemspinosa* (s, a)	SSBSHR
Blackbelly Rosefish *Helicolenus dactylopterus* (s, a)	BLAROS	Northern Searobin *Prionotus carolinus* (s, a)	NORSEA	Spiny Searobin *Prionotus alatus* (s, a)	SSSEAR
Blotched Cusk-eel *Ophidion grayi* (a)	BLCUSK	Norwegian shrimp *Pontophilus norvegicus* (s, a)	NORSHR	Silver Seatrout *Cynoscion nothus* (a)	SSSEAT
Bristled longbeak *Dichelopandalus leptocerus* (s, a)	BLONGB	Northern Pipefish *Syngnathus fuscus* (s)	NPIPEF	Southern Stingray *Dasyatis americana* (a)	SSSTIN
Blue crab *Callinectes sapidus* (s, a)	BLUCRA	Northern Puffer *Sphoeroides maculatus* (s, a)	NPUFFR	Striped Cusk-eel *Ophidion marginatum* (s, a)	STCUSK
Bluefish *Pomatomus saltatrix* (s, a)	BLUEFI	Northern stone crab *Lithodes maja* (s, a)	NSCRAB	**Striped Anchovy *Anchoa hepsetus* (a)**	**STRANC**
Blueback Herring *Alosa aestivalis* (s, a)	**BLUHER**	Sennet *Sphyraena borealis* (a)	NSENNE	Striped Bass *Morone saxatilis* (s, a)	STRBAS
Bluntnose Stingray *Dasyatis say* (a)	BLUNRA	Northern shrimp *Pandalus borealis* (s, a)	NSHRIM	Striped Searobin *Prionotus evolans* (s, a)	STRSEA
Blue Runner *Caranx crysos* (a)	BLURUN	Northern Stargazer *Astroscopus guttatus* (a)	NSSTAR	Sand Tiger *Carcharias taurus* (a)	STTIGE
Banded Rudderfish *Seriola zonata* (a)	BRRUDD	Ocean Pout *Zoarces americanus* (s, a)	OCPOUT	Summer Flounder *Paralichthys dentatus* (s, a)	SUMFLO
Brown rock shrimp *Sicyonia brevirostris* (a)	BRSHRI	Offshore Hake *Merluccius albidus* (s, a)	OFFHAK	Tautog *Tautoga onitis* (a)	TAUTOG
Bathyal swimming crab *Bathynectes longispina* (s, a)	BSCRAB	Pigfish *Orthopristis chrysoptera* (a)	PIGFIS	Thorny Skate *Amblyraja radiata* (s, a)	THOSKA
Buckler Dory *Zenopsis conchifera* (s, a)	BUCDOR	Pinfish *Lagodon rhomboides* (a)	PINFIS	Tilefish *Lopholatilus chamaeleonticeps* (s, a)	TILEFI
Bullnose Ray *Myliobatis freminvillei* (a)	BULLRA	Pink glass shrimp *Pasiphaea multidentata* (s, a)	PINKGS	Weakfish *Cynoscion regalis* (s, a)	WEAKFI
Butterfish *Peprilus triacanthus* (s, a)	**BUTTER**	Polar shrimp *Lebbeus polaris* (s, a)	POLARL	Atlantic Pearlside *Maurolicus weitzmani* (s, a)	WEITZP

TABLE 1. Continued.

Taxon (models)	Code	Taxon (models)	Code	Taxon (models)	Code
Chain Dogfish *Scyliorhinus retifer* (s, a)	CHADOG	Pollock *Pollachius virens* (s, a)	POLLOC	White Hake *Urophycis tenuis* (s, a)	WHIHAK
Atlantic Chub Mackerel *Scomber colias* (s, a)	**CHUBMA**	Atlantic rock crab *Cancer irroratus* (s, a)	RCKCRA	Windowpane *Scophthalmus aquosus* (s, a)	WINDOW
Crevalle Jack *Caranx hippos* (a)	CJJACK	Round Scad *Decapterus punctatus* (a)	RDSCAD	Winter Flounder *Pseudopleuronectes americanus* (s, a)	WINFLO
Coarsehand lady crab *Ovalipes stephensoni* (s, a)	CLCRAB	Red deep-sea crab *Geryon quinquedens* (s, a)	REDCRA	Winter Skate *Leucoraja ocellata* (s, a)	WINSKA
Clearnose Skate *Raja eglanteria* (s, a)	CLESKA	Red Hake *Urophycis chuss* (s, a)	REDHAK	Witch Flounder *Glyptocephalus cynoglossus* (s, a)	WITFLO
Cobia *Rachycentron canadum* (a)	COBIAZ	Red Goatfish *Mullus auratus* (a)	RGGOAT	Wrymouth *Cryptacanthodes maculatus* (s, a)	WRYMOU
Conger Eel *Conger oceanicus* (s, a)	CONGEL	**Round Herring *Etrumeus teres* (a)**	**RHERRI**	Yellowtail Flounder *Limanda ferruginea* (s, a)	YELFLO

biomass models by season. Ratios with higher values are indicative of a higher proportion of the habitat being contained within the lease areas. The relationship between ratio variables in these bivariate plots was presented via linear regression and segmented linear regression, with the coordinates for forage species highlighted. Our purpose here is not to suggest any specific underlying mechanisms represented by these relationships, but instead to provide visual guidance on how to interpret the relationship between the ratio variables.

For the second representation of lease area utilization, we constructed an overall index based on normalized ratios. As described above, for each modeled species by season, the ratio of habitat in the lease area (km^2) to the quantity of habitat in the ecosystem (km^2) was calculated. For each species, there were four ratios associated with seasonal data: ratios for overall and core habitats for both occupancy and biomass model outputs. Each of these ratios was normalized by dividing them by the ratio of the area (km^2) of the lease areas to the area of the study region. For this study, the lease areas totaled 20,261 km^2 and the ecosystem totaled 290,953 km^2, resulting in a ratio of 0.0696. If the normalized ratio exceeded 1.0, it indicated a preference for the lease areas since the normalized ratio exceeds the ratio based on total areas. Likewise, a normalized ratio of less than 1.0 indicated less preferential use of the lease areas compared to the overall ecosystem. For convenience, the normalized ratios were categorized

into five intervals arrayed by suggested preference level: maximum to 1.0, from 0.7 to 1.0, from 0.6 to 0.7, from 0.5 to 0.6, and less than 0.5. The four normalized indices were averaged to provide a single index per species. The position of forage species in the data table is noted. The data for the forage species were also plotted to provide a visual representation.

The trend in the size or area coverage of habitat for forage and nonforage species was examined over habitat types and seasons. For each species, time series of the quantity (km^2) of habitat were broken down by occupancy model versus biomass model, overall habitat versus core habitat, ecosystem-wide or within the lease areas, and finally by season. Trends in habitat (km^2/year) 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/). The data were summarized as box plots, with the relative data for nonforage and forage species paired for comparison.

RESULTS

Overall Habitat versus Core Habitat

The lease areas occur within variable proportions of both the overall and core habitats of species of the NES. Across seasons and model types, overall habitat (model

output at the 20% level) had an average ratio of 0.051 (SD = 0.042) for the area in lease areas relative to the ecosystem, whereas core habitat (model output at the 80% level) had an average ratio of 0.057 (SD = 0.019). These results suggest that for both types of habitats, approximately 5% of the area of the habitat was within lease areas compared to that over the entire NES. For spring occupancy models, the relationship between the ratio at the 20% level versus the ratio at the 80% level was best described with a segmented regression based on sum-of-squares error (Figure 2A). For species with lower ratios, there was a tendency for the ratio of the core habitat to exceed the ratio for the overall habitat, as apparent based on the location of most points below the 1:1 reference line. As the magnitude of the ratios increased, the ratios of the overall habitat tended to exceed the ratio of the core habitat, with most points being positioned above the reference line. For the ratios based on spring biomass models, the relationship was still present and supported by a lower sum-of-squares error for the segmented regression, but it was not as well developed as for the occupancy models (Figure 2B). A similar pattern emerged for autumn occupancy and biomass models (Figure 2C, D, respectively). In both cases, the segmented fits had the lower sum-of-

squares error, and there was a similar pivot around the reference line between low- and high-ratio species.

Habitat Use by Species

The normalized ratio index suggested that many species, including many forage taxa, made preferential use of the lease areas compared to the other parts of the ecosystem. For spring species, approximately 20% of the taxa had ratios exceeding 1.0, which suggested that the species made preferential use of the lease areas compared to the wider ecosystem (Table 2). Of those species, three were forage taxa, including Atlantic Mackerel, Atlantic Menhaden, and Atlantic Herring (Figure 3). The occupancy habitat for these species was also mapped to illustrate the distribution of mean locations for overall and core habitats (Figure 4A–C). Six of the remaining spring forage species were contained in the next index interval of 0.7–1.0, indicating a strong use of lease area habitats by Alewife, Bay Anchovy, Butterfish, Atlantic Chub Mackerel, longfin inshore squid, and Northern Sand Lance. The Atlantic Silverside was the only spring forage taxon that appeared in the lower-preference groups. For all species, the preferential and strong use intervals included 49 taxa, or approximately 40% of the modeled species. In autumn,
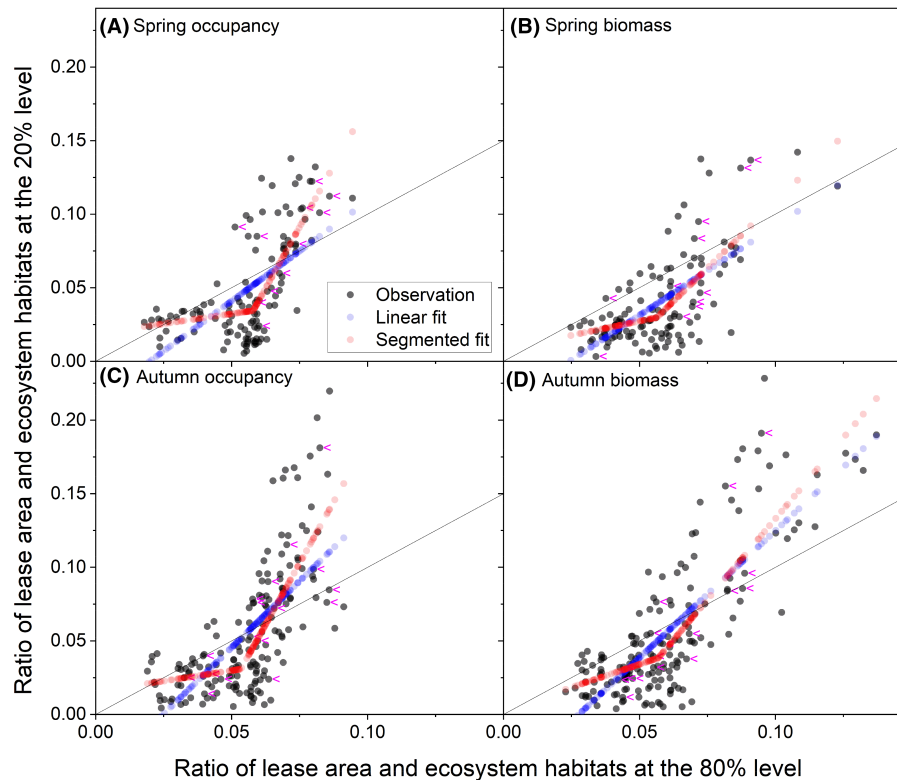

FIGURE 2. **(A)** Ratio of the quantity of spring occupancy habitat in wind lease areas to habitat in the ecosystem at the 20% quantile (representing overall habitat) versus the 80% quantile (representing core habitat) for modeled species; and, similarly, for **(B)** spring biomass habitat, **(C)** autumn occupancy habitat, and **(D)** autumn biomass habitat. Blue dots represent a linear regression fit to the data, whereas red dots represent a segmented linear fit. Coordinates for forage taxa are marked with a "<" symbol. The solid line is the 1:1 reference.

TABLE 2. Six-letter taxon codes (defined in Table 1) arrayed by season and the mean of four normalized ratios. The four ratios are between the area of habitat in the lease areas to the area of the ecosystem for occupancy and biomass habitat model output at the 20% and 80% quantiles; each ratio is normalized by the ratio of the area (km^2) of the lease areas to the area of the ecosystem (see Methods). Ratios closer to the 1.0 end of the range reflect relatively high or preferential habitat selection, whereas values closer to 0.5 reflect lower usage; ratios correspond with the results in Figure 3. Forage species are designated in bold.

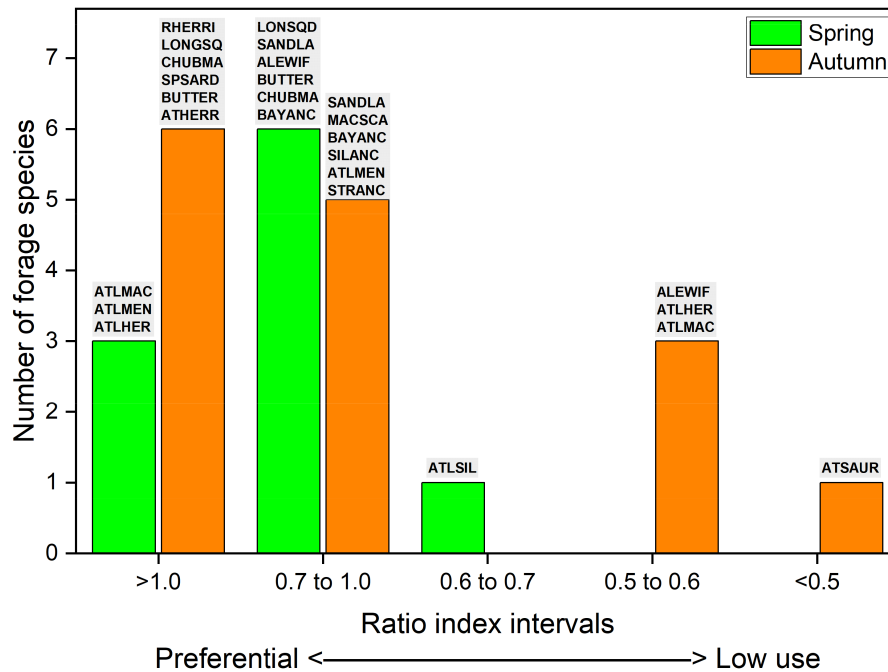| Spring					Autumn				
>1.0	0.7–1.0	0.6–0.7	0.5–0.6	<0.5	>1.0	0.7–1.0	0.6–0.7	0.5–0.6	<0.5
CLESKA	RCKCRA	CHADOG	ACARED	BLAROS	NORSEA	NSENNE	WEAKFI	ARMSEA	ATLARG
BLUHER	YELFLO	SNAKEB	COOCTO	BUCDOR	**RHERRI**	SEASCA	WINSKA	SDDRAG	BEARDF
SMAFLO	BLUEFI	SNOWCR	LGGREE	HAGFIS	RTSTIG	SPOTZZ	SNAKEB	BSCRAB	ATLCOD
SPIDOG	HOGCHO	WINFLO	SHTSQD	LUMPFI	CLESKA	CONGEL	BLUHER	DBBOAR	LUMPFI
ATLMAC	**LONSQD**	STCUSK	ARMSEA	WHIHAK	ANGSHR	BLUNRA	COOCTO	STRBAS	REDCRA
LITSKA	SCUPZZ	**ATLSIL**	BSCRAB	ATLCOD	BULLRA	INLIZA	SLENSE	TILEFI	SHORTP
SPOHAK	NORSEA	CONGEL	POLARL	GRUBBY	CLCRAB	BLUEFI	NSSTAR	WITFLO	DFFLOU
STRBAS	ROSSKA	DBBOAR	REDCRA	OFFHAK	SMODOG	BLURUN	RDSCAD	FBSHRI	BARSKA
ATLMEN	ATSEAS	NSHRIM	SILHAK	SAARGE	SUMFLO	BADRUM	CHADOG	FRBERO	CUSKZZ
ATLHER	SSSEAR	RSSMEL	TILEFI	ATLPOU	LSSEAT	BDDRUM	SILHAK	LGGREE	JONCRA
SUMFLO	SEASCA	SEARAV	BARSKA	ATLWOL	BLABAS	BLUCRA	SLERAG	MONKFH	SAARGE
WINDOW	**SANDLA**	AMEPLA	FRBERO	FOUFLO	STRSEA	COBIAZ	AMESHA	ATLPOU	SSBSHR
ATLCRO	SHANNY	ATTORP	NSCRAB	PINKGS	ATLCRO	PIGFIS	BUCDOR	**ALEWIF**	OCPOUT
NPIPEF	**ALEWIF**	DFFLOU	SDDRAG	REDHAK	ATSEAS	ABSQUI	HAGFIS	CONRAY	WHIHAK
HSCRAB	**BUTTER**	LONSCU	ATLARG	WEITZP	ROSCAD	SPAMAC	LSSNIP	HOGCHO	AMEPLA
SMODOG	GULFLO	WITFLO	BEARDF	FAWMEL	**LONSQD**	ASSHAR	WRYMOU	NSCRAB	AMLOBS
WEAKFI	GBCRAB		LADCRA	BLONGB	SMAFLO	ATMOON		REDHAK	ATLWOL
STRSEA	**CHUBMA**		LSSNIP	CUNNER	HSCRAB	**SANDLA**		SBBOBT	LONSCU
BCTONG	MARLSP		MONKFH	SHORTP	SCUPZZ	WINDOW		SNOWCR	NORSHR
OCPOUT	BLUCRA		SBBOBT	SPOONO	SPOHAK	HARFIS		ACARED	WEITZP
CLCRAB	**BAYANC**		SSBSHR	ALLFSH	SBSHAR	**MACSCA**		**ATLHER**	ALLFSH
NPUFFR	SPOTZZ		FBSHRI	AMLOBS	BLCUSK	NKINGF		**ATLMAC**	CUNNER
ANGSHR	ROSCAD		JONCRA	ATLHAL	ATSPAD	SMBRAY		BLONGB	SPOONO
BLABAS	WRYMOU		LGFINH	NORSHR	BRSHRI	**BAYANC**		FAWMEL	THOSKA
WINSKA			THOSKA	POLLOC	RCKCRA	SBURAY		GBCRAB	BLAROS
			ASSTUR	CUSKZZ	**CHUBMA**	**SILANC**		NSHRIM	**ATSAUR**
				ASHRIM	FILEFS	**ATLMEN**		POLARL	LGFINH
				SMOSKA	RGGOAT	DSSHAR		SEARAV	TAUTOG
				HADDOC	ATLCUT	ROSSKA		BBBASS	ASHRIM
				MOUSCL	PINFIS	SKINGF			POLLOC
					BESCAD	WINFLO			GRUBBY
					LADCRA	SBBURR			HADDOC
					KMMACK	SELPER			PINKGS
					LITSKA	SPIDOG			OFFHAK
					NPUFFR	SSSEAR			SMOSKA
					SPSARD	SSSEAT			SHTSQD
					GULFLO	**STRANC**			ATLHAL
					SCUPSC	BRRUDD			MOUSCL
					STTIGE	SPICRA			
					BUTTER	GRTRIG			
					ATHERR	STCUSK			
					FOUFLO	YELFLO			
					SSSTIN	CJJACK			

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FIGURE 3. Number of forage species within each ratio index interval for spring and autumn time frames. Ratios close to the 1.0 end of the range reflect relatively high or preferential habitat selection, whereas values closer to 0.5 reflect relatively low use; ratios correspond with the results in Table 2. Six-letter taxon codes (defined in Table 1) associated with each seasonal interval are listed above each column.

preferential and strong categorizations were found for many more taxa. Of all species, 86 taxa were in these groups, or approximately 51% of the autumn species. Of these taxa, 12 were forage species, with Atlantic Thread Herring, Butterfish, Atlantic Chub Mackerel, longfin inshore squid, Round Herring, and Spanish Sardine in the preferential grouping and Atlantic Menhaden, Bay Anchovy, Mackerel Scad, Northern Sand Lance, Silver Anchovy, and Striped Anchovy in the strong grouping. The five autumn taxa found in the high-preference categories were also plotted to illustrate their distributions (Figure 4D–G). Four forage taxa—Alewife, Atlantic Herring, Atlantic Mackerel, and Atlantic Saury—were found in the lower-preference groups.

Trends in Habitat Area

The area of habitats for fish and macroinvertebrates generally expanded over the study period, with the habitat for forage taxa expanding at a greater rate than that for nonforage species. For spring occupancy and biomass models, the trends in overall and core habitat areas across the ecosystem were mostly positive; interquartile and whisker ranges were mostly positive, as were the mean and median values (Figure 5A). When we examined rates for nonforage and forage pairs, the box plots for forage taxa indicated high trends based both on interquartile and whisker ranges and the distribution of means and medians. This

same pattern was repeated in the spring lease area data; most trend values were positive, particularly the rates associated with forage species as compared to the counterpart data among nonforage taxa (Figure 5B). Similar patterns can be seen in the autumn model data, with some exceptions. Trends across the ecosystem were mostly positive except for the overall biomass models for forage species, which tended to have negative trends (Figure 5C). Likewise, the only negative trends in the lease areas were observed for the biomass data for forage taxa (Figure 5D).

DISCUSSION

To reach national goals of renewable energy production, by necessity much of the new production capacity will need to come from OSW generation. Determination of the consequences for marine fisheries species' habitat associations and distributions is critical when considering the outcome of the complex interaction between OSW energy development and the environment. Incumbent to informed decision making is an understanding of the spatial utilization of wind energy areas by marine fisheries species and the means to consider the relative importance of the areas for the species in question. In our analysis, we comprehensively considered the portion of the ecosystem that is monitored by the principal fisheries-independent survey in the region and we found that the inclusion of new lease areas has
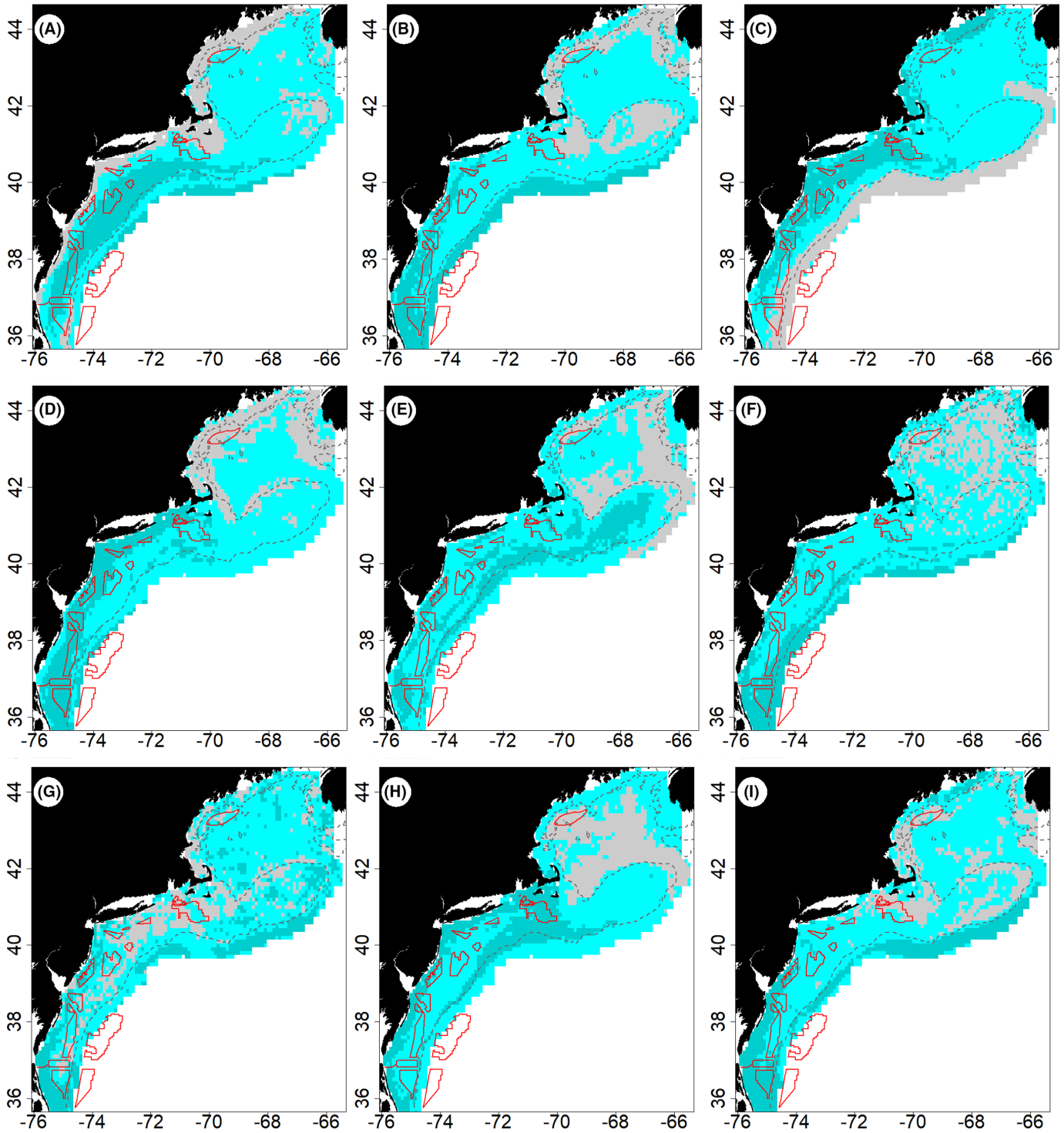
FIGURE 4. Mean occupancy habitats at the 20% (light blue) and 80% (dark blue) quantile thresholds across forage species; gray shows the model extent. Taxa with spring models include **(A)** Atlantic Mackerel, **(B)** Atlantic Menhaden, and **(C)** Atlantic Herring; taxa with autumn models include **(D)** Round Herring, **(E)** longfin inshore squid, **(F)** Atlantic Chub Mackerel, **(G)** Spanish Sardine, **(H)** Butterfish, and **(I)** Atlantic Thread Herring. Offshore wind lease areas are outlined in red. The dashed line marks the 100-m depth contour.

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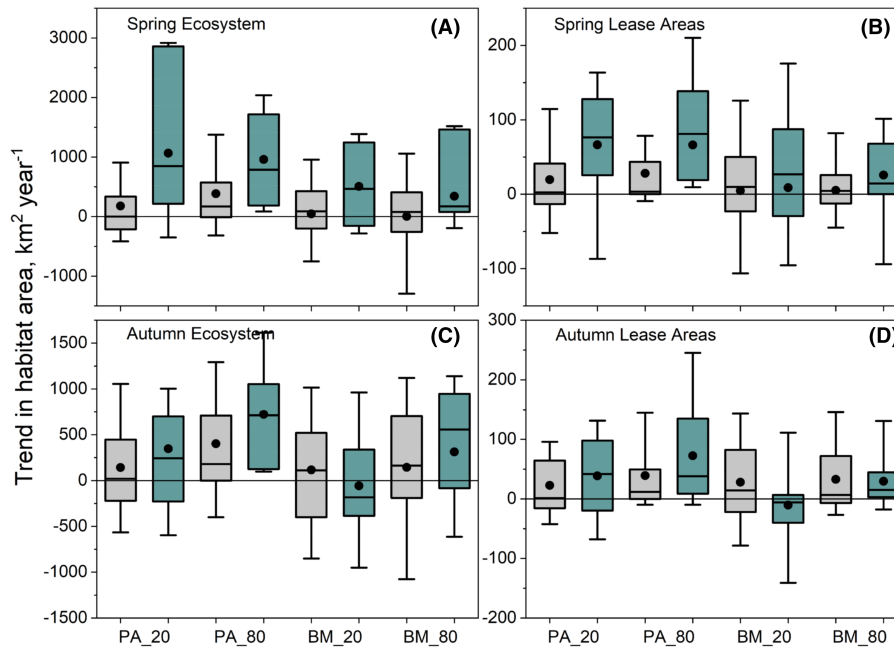
FIGURE 5. Box plots (box = 25–75%; whiskers = 10–90%; line = median; dot = mean) of trend (1976–2019) as Theil–Sen slope estimates in occupancy habitat at the 20% and 80% quantiles (PA_20 and PA_80, respectively, from the presence/absence [PA] models) and biomass habitat at the 20% and 80% quantiles (BM_20 and BM_80, respectively, from the biomass models [BM]). Plots for nonforage species are in gray; plots for forage species are in green. Results are depicted for **(A)** the spring ecosystem, **(B)** spring wind lease areas, **(C)** the autumn ecosystem, and **(D)** autumn wind lease areas.

increased the overlap between these areas and forage fish habitat. This departure from previous analyses (Friedland et al. 2021b) is primarily due to the inclusion of habitat along the shelf break of the NES and habitat in the Gulf of Maine—regions not previously part of the potential areas for development. In addition, the novel habitat scoring scheme presented here suggests that many taxa have distribution preferences for the habitat within the lease areas. Furthermore, by characterizing on the basis of whether the habitat within the lease areas was part of the overall (generalized use) habitat for a species or represented the core habitat associated with the most reliable occurrence and highest biomass distributions, we now have a more detailed characterization of the potential for interactions between OSW development and taxon-specific habitat.

Among the taxa with high use of lease area habitat were those that comprise the trophic grouping of forage species—the species we consider to be important energy conduits between lower-trophic-level productivity and higher-level consumers. These species are typically consumers of zooplankton biomass and, in turn, serve as prey for piscivorous teleost fish and sharks, seabirds, and marine mammals, although in some cases the forage species directly utilize phytoplankton (Ballón et al. 2011; Peck et al. 2021). Our interest with respect to OSW development is the anticipated effects of wind infrastructure on

mesoscale processes in the water column and their impacts on lower-trophic-level productivity (Cury et al. 2008). A net change in system productivity that would be actuated from the base of the food chain to species that are used as food resources could have both ecological and societal consequences. Even if there are no detectable changes in system productivity, more subtle changes in lower trophic levels related to distribution and patchiness may have consequences for the growth of higher-level consumers (Breck 1993). The development of OSW has the potential of changing the food web through either of these perturbations: mesoscale effects on overall productivity and local-scale species patchiness. The changes that we anticipate through mesoscale events are not limited to the marine food webs within the aquatic realm but also include connected wildlife communities, such as birds and mammals (Burke and Montevecchi 2008; Free et al. 2021). It should also be remembered that forage fish meet other human needs by serving as the basis of feeds that support aquaculture production of food fish and fish oil supplements; supporting these uses is the Atlantic Menhaden, which comprises the largest fishery by volume across the U.S. East Coast (Froehlich et al. 2018; Anstead et al. 2021).

The tendency for usage of the lease areas preferentially as core habitat among species and particularly among many of the forage taxa suggests that the centralized

location of lease areas may play an important ecological role. Although not well studied, where core habitats have been considered in relation to the life history and processes affecting species, it becomes clear that they support aspects of species productivity. For example, core habitat for Walleye Pollock *Gadus chalcogrammus* can be differentiated by thermal regime but more importantly by the different growth potential that these habitats provide (Spies et al. 2022). Furthermore, the differentiation of overall habitat versus core habitat reveals important differences in habitat use within the NES. Habitat estimates are shaped by many gradients within the ecosystem, but many of the most important gradients (e.g., depth and lower-trophic-level productivity) have cross-shelf properties that result in core habitat shapes occurring well within the boundaries of the NES. Further, not only do the OSW lease areas overlap much of the core habitat of species, but potential mesoscale effects of the lease areas could also affect core habitats just outside of and beyond the lease areas. We are also faced with the dilemma of considering the interaction of fixed areas (OSW) versus dynamically defined core habitats that are changeable as a consequence of climate change (Shields et al. 2018). When these mismatches in scale and permanency involve protected species, as has been observed for common bottlenose dolphins *Tursiops truncatus*, other regulatory issues take on increased importance (Bennington et al. 2021). The baleen whales of the NES, in particular the North Atlantic right whale *Eubalaena glacialis*, humpback whale *Megaptera novaeangliae*, and fin whale *Balaenoptera physalus*, have demonstrated climate-related changes in the phenology of their seasonal habitat use, which could increase their potential interactions with OSW development near critical foraging grounds in Cape Cod Bay and the broader Gulf of Maine (Pendleton et al. 2022). Piscivorous whales and dolphins as well as a range of colonial-nesting seabirds that use NES coastal areas as seasonal breeding and foraging grounds (Kress et al. 2017; Staudinger et al. 2020; Yakola et al. 2021) rely heavily on Atlantic Herring and sand lances *Ammodytes* spp. as prey; importantly, both of these forage taxa were found to have higher levels of habitat common to the location of the OSW fields. Large predatory fish that represent important fisheries, such as Atlantic Bluefin Tuna *Thunnus thynnus* and Cobia, are additional examples of species that are experiencing distribution and phenology shifts and that also prey heavily on many of the forage fish assessed in this study (Muhling et al. 2017; Crear et al. 2020).

The results presented here represent species abundance and distributions that were based on historical conditions of the NES. However, the NES is considered a hot spot of warming, with annual and seasonal coastal temperatures having already risen by 2°C, and projections show that these increases will continue in the coming decades due to shifting circulation patterns (Karmalkar and Horton 2021; Pershing et al. 2021). Therefore, the regional conditions and habitats currently occupied by the species modeled in this study are not expected to remain static in time and space. Indeed, many species in the NES, including forage species, have already shown distribution shifts northward and to deeper waters in response to warming ocean temperatures, as well as changes in the timing of habitat use and growth schedules (Pinsky et al. 2013; Walsh et al. 2015; Burrows et al. 2019; Fredston-Hermann et al. 2020; Lenoir et al. 2020). As warming continues, species are projected to experience gains and losses in suitable thermal habitat (Kleisner et al. 2017; Morley et al. 2018). Some species, such as Scup and Butterfish, are expected to gain suitable habitat area under future conditions, whereas many species, particularly coldwater-associated and subarctic species, are predicted to lose habitat and experience population declines (Kleisner et al. 2017; Pershing et al. 2021). Explicit consideration of how the placement of OSW areas overlaps with identified seasonal core habitats and changes in projected future habitats is needed to determine whether OSW development affects critical areas that support climate-vulnerable species (Hare et al. 2016) or changes the amount of fishing pressure these populations experience in the future. Precautionary approaches are especially important for forage species, such as sand lances, which support numerous commercially important fish species as well as species of conservation concern (Staudinger et al. 2020). For example, species-specific information on current distribution and abundance is poor for sand lances, and recent research has demonstrated that these species may be disproportionately sensitive to the combined impacts of warming and ocean acidification (Baumann et al. 2022). Although OSW development may have unfavorable consequences for fish species, there should also be appreciation of potential positive effects, such as how OSW structures create artificial reef effects—specifically, that constructed subsurface structures provide habitat for the settlement of sessile reef organisms and in turn attract prey species (Gill et al. 2020).

Spatial models of predator–prey interactions are needed to inform marine spatial planning. Marine predators migrate using large areas to search for food, but certain areas with high prey availability can attract and disproportionately support diverse assemblages of top predators (Silva et al. 2021). J. Gulka and colleagues (unpublished manuscript) showed significant correlations between seabird movements (habitat use) and many of the forage fish species described here. Moreover, higher-trophic-level species have complex interactions with OSW development: some species show significant and seemingly permanent displacement from these sites, while others are attracted to OSW areas (Vanermen et al. 2015). If OSW project sites provide refugia for pelagic forage fish, then predicting the

communities that form around these sites could be challenging and may represent a spatial mismatch between prey resources and predators. In addition, if OSW sites support higher production of forage fish and attract predators, then the increased use of OSW areas by forage fish could lead to increased interactions with seabirds and predators depending on their sensitivity to subsea noise, electromagnetic fields, and other factors associated with wind operations (Gill et al. 2012). In the Gulf of Mexico, oil structures act as artificial reefs, aggregating predatory fish. At early life stages, highly migratory species may alter their behavior to increase the time spent around these structures, which may increase their vulnerability to fishing (Snodgrass et al. 2020). Determining how the addition of new hard-bottom habitat will result in species-specific responses in local abundance, as observed at previous NES OSW projects, is additionally important to understanding the mesoscale impacts of large-scale development (Carey et al. 2020). The next step for understanding the potential impacts of OSW development would be to evaluate the amount of seasonal overlap in habitat use among trophically linked species and to determine areas where predators and prey are co-located or more reliant on one another. Combining these data with other sources of information on habitat use from a broad suite of predators could be key for expanding our understanding of which habitats are critical to species.

The potential disproportionate impact of OSW development on core habitat for these forage species is an important consideration in stock assessments and ecosystem-based fishery management. Fisheries for forage species within the NES region are currently managed by two federal fishery management councils and one interstate commission, as well as by individual states. The New England Fishery Management Council (NEFMC) manages Atlantic Herring; the Mid-Atlantic Fishery Management Council (MAFMC) manages Atlantic Mackerel, Atlantic Chub Mackerel, Butterfish, and longfin inshore squid; and the Atlantic States Marine Fisheries Commission (ASMFC) manages Atlantic Menhaden. Recently, these organizations have developed management approaches that consider the supporting ecosystem services provided by forage species. The NEFMC developed and implemented a harvest control rule for Atlantic Herring that was designed to simultaneously maintain fishery yield, herring population status, and predator population status (Deroba et al. 2019; Feeney et al. 2019). The MAFMC added the Atlantic Chub Mackerel as a managed species and implemented rules constraining harvest and requiring reporting for 16 unmanaged forage species to ensure that any new fishery development on this group occurs sustainably (www.mafmc.org/actions/unmanaged-forage). The MAFMC also reviews predator–prey interactions among its managed species as part of an annual ecosystem-level risk assessment (Gaichas

et al. 2018). The ASMFC developed and implemented ecological reference points for Atlantic Menhaden that constrain maximum fishing rates to levels maintaining adequate forage for the Striped Bass, a commercially and recreationally important predator (Chagaris et al. 2020; Drew et al. 2021; Howell et al. 2021). While some of these forage management measures have considered the spatial distribution of fishing effort (particularly for Atlantic Herring), to date none has specifically considered forage–habitat interactions with OSW development. Our results suggest that this potential habitat interaction with wind development should be evaluated in updates to forage assessments and ecosystem approaches to forage fishery management.

Our findings were made possible by utilizing long-term monitoring surveys of nekton and the oceanographic environment throughout the NES in a standardized, systematic fashion. With the development of OSW, it is possible that wind lease areas will no longer support sampling with the longstanding survey methods that have been used to inform the management of fish, macroinvertebrates, and their ecosystem (Methratta et al. 2020). For decades, these data sets have been vital in understanding ecosystem changes over time and in managing the marine resources of the NES. Given the potential for sampling to be discontinued in these areas using current monitoring tools, assessment of marine resources in these areas will rely on alternative sampling designs that will provide limited data before OSW construction and thus are unable to provide the historical context that is often needed as inputs for stock assessment models and for the evaluation of ecosystem changes. Long-term, fisheries-independent data sets are the lens through which we observe climate–fisheries interactions and habitat alterations of marine ecosystems and set quotas during stock assessments. Although we recognize that OSW development is a key strategic initiative for reducing greenhouse gas emissions, we contend that all due consideration must be given to also maintaining our long-term lens of observation on the NES.

Taking a more outward-looking perspective, we can ask whether lessons learned from the NES wind development area may be transferred to other potential areas in U.S. waters and perhaps further afield. A cautionary example emerges when considering the Gulf of Mexico call area for OSW development—an area that circumscribes most of the Gulf continental shelf to depths generally less than 100 m. Much of the inshore portion of the call area represents the fishing areas for Gulf Menhaden *Brevoortia patronus* and Gulf shrimp (three species of penaeid shrimp that comprise the bulk of the fishery); both are forage taxa, and both fisheries are prosecuted with mobile gear (Smith et al. 2002; Pickens et al. 2021). Perhaps even more problematic for the Gulf Menhaden fishery is that the fishing procedure is a pursuit fishery,

which may cause more interactions between gear and OSW structures. Shrimp fishing is a trawl fishery, in which these interactions can be avoided to a higher degree. These forage taxa, unlike most of the NES forage taxa, comprise important regional fisheries that may be spatially impacted by OSW structures. To further complicate the development of spatial planning to accommodate fishing interests, the distributions of both fisheries are impacted by the distribution of oxygen levels in the Gulf of Mexico (Langseth et al. 2014; Purcell et al. 2017). Without looking very hard, we see ample evidence that different regions will pose species-specific spatial planning challenges to ameliorate ecosystem and fisheries concerns with the installation of OSW structures. Although some parts of U.S. continental shelf waters, like the Bering Sea, may not be developed for OSW due to distance from power application and environmental risk, others, such as the California Current and the Hawaiian Islands, are likely to be developed.

ACKNOWLEDGMENTS

ORCID

Kevin D. Friedland https://orcid.org/0000-0003-3887-0186
Evan M. Adams https://orcid.org/0000-0002-4327-6926
Chandra Goetsch https://orcid.org/0000-0001-5247-5102
Julia Gulka https://orcid.org/0000-0002-5695-233X
Damian C. Brady https://orcid.org/0000-0001-9640-2968
Everett Rzeszowski https://orcid.org/0000-0003-3856-9924
Daniel P. Crear https://orcid.org/0000-0002-9045-3649
Sarah Gaichas https://orcid.org/0000-0002-5788-3073
Andrew B. Gill https://orcid.org/0000-0002-3379-6952
M. Conor McManus https://orcid.org/0000-0003-3504-0371
Elizabeth T. Methratta https://orcid.org/0000-0003-0109-913X
Janelle L. Morano https://orcid.org/0000-0001-5950-3313
Michelle D. Staudinger https://orcid.org/0000-0002-4535-2005

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SUPPORTING INFORMATION

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