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Assessing individual movement, habitat use, and behavior of non-breeding marine birds in relation to prey availability in the US Atlantic

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ABSTRACT: Resource availability is a key factor driving marine bird movements and distributions, but direct information on prey availability is difficult to obtain at relevant scales. We present novel methods for describing multi-scale trophic associations, combining movement analyses of marine birds with estimates of forage fish surface aggregations from digital aerial survey data and species occupancy from bottom trawl survey data. We analyzed satellite telemetry data from northern gannets *Morus bassanus*, red-throated loons *Gavia stellata*, and long-tailed ducks *Clangula hyemalis* in the US Atlantic during the non-breeding period. Using discrete-time hidden Markov models to distinguish area-restricted (i.e. putative foraging) from transit movements, we examined how environmental factors influence movement, and how forage fish species distributions and surface aggregations influence habitat use by gannets and loons that have greater dietary reliance. Our results suggest that chlorophyll *a* concentration significantly affected movement behavior across species, highlighting the importance of higher-productivity areas around estuaries during colder months when regional productivity is low. Though variable across species and seasons, spatial cross-correlation analysis revealed that herring species (Family Clupeidae), including Atlantic menhaden *Brevoortia tyrannus*, may be important resources; it also showed positive spatial correlations with forage fish aggregations. This suggests that prey patch dynamics and factors driving aggregation formation may be as important as species composition. However, spatial patterns were generally low (<0.3), suggesting a mismatch in spatiotemporal resolution, exemplifying the challenges in quantifying trophic relationships in marine systems. Disentangling predator–prey relationships is critical to understanding the mechanisms driving marine bird behavior in rapidly changing marine systems.

KEY WORDS: Predator–prey dynamics · Marine birds · Forage fish · Movement · Behavior · Trophic links · Hidden Markov model · HMM

1. INTRODUCTION

Multiple factors, including abiotic and biotic constraints (e.g. habitat quality, species interactions, behavioral characteristics), influence species distributions, with food availability as a critical driver (Soberón 2007, Pettex et al. 2010, Boulangeat et al. 2012). Food resources drive habitat use in marine ecosystems, where predators contend with dynamic ocean systems to track and access patchily distributed and often unpredictably located prey (Fauchald et al. 2005, Weimerskirch et al. 2005, Sims et al. 2006). Thus, mar-

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ine predators may rely on environmental cues to locate prey patches and utilize habitats where spatiotemporal predictability of resources is higher (Cox et al. 2018). Understanding the links and mechanisms driving predator–prey dynamics, and the potential effects of anthropogenic activities on these patterns, is imperative to implement effective ecosystem-based management and conservation (Chimienti et al. 2020).

Marine birds are wide-ranging upper trophic level predators often touted as indicators of marine ecosystem health (Cairns 1987, Piatt et al. 2007). Many marine birds rely heavily on forage fishes as a primary resource, which in turn represent a key link in the energy transfer web between these predators and lower trophic levels (i.e. phyto- and zooplankton; Pikitch et al. 2012). Other marine bird species may utilize lower trophic level prey directly. To realize the potential for marine birds to act as ecosystem indicators, it is helpful to first have a more comprehensive understanding of connections among trophic levels within marine food webs, particularly the strength of species interactions and the environmental factors driving these relationships. Most research on marine bird resource use focuses on foraging behavior during the breeding season and has linked foraging behavior to shelf and frontal features that operate at variable spatiotemporal scales, such as sea surface temperature (SST), chlorophyll *a* (chl *a*), and wind patterns, among other factors (e.g. Louzao et al. 2009, Scales et al. 2016, Poli et al. 2017, Frankish et al. 2020, Jakubas et al. 2020). These abiotic conditions likely relate to the abundance and accessibility of prey resources, which form a hierarchical patch system (Fauchald 1999). While these processes may contribute to predictability of resources at large scales (10s to 1000s of km), with marine species associating with persistent features, these patterns can become unpredictable at smaller spatial scales (<10 km), depending on the processes driving their formation (Weimerskirch et al. 2005, Mannocci et al. 2017). While abiotic conditions contribute to spatiotemporal patterns of prey, including ephemeral patch-level (10s of m) aggregation patterns, direct information on prey availability is often lacking. In addition, there is less research on trophic relationships during the non-breeding period, even though this represents the largest portion of the annual cycle for many marine birds. Indeed, the non-breeding period may be when birds face the greatest environmental and physiological pressures and presents the potential for carry-over effects influencing survival and breeding success (Daunt et al. 2006, Deakin et al. 2019, Schaefer et al. 2020). Prey availability is likely to influence non-breeding distributions and behaviors, but constraints differ from the breeding season with a shift from central-place foraging to self-centered foraging, and predator–prey interactions can be difficult to quantify during this period.

In this study, we used satellite telemetry data from northern gannets *Morus bassanus* (hereafter 'gannets'), red-throated loons *Gavia stellata* (hereafter 'loons'), and long-tailed ducks *Clangula hyemalis* (hereafter 'ducks') that utilize marine habitats off the US Atlantic coast during the non-breeding period. These species have different life histories and foraging strategies with varying levels of reliance on forage fishes, allowing for examination of inter-specific variation in relationships with environmental variables and direct measures of forage fish availability. Gannets are plunge-divers (mean dive depth 20 m; Brierley & Fernandes 2001), that, during the breeding season, primarily exploit pelagic shoaling fishes, such as mackerel *Scomber scombrus*, capelin *Mallotus villosus*, and Atlantic herring *Clupea harengus* (Kirkham et al. 1985, Garthe et al. 2007, Montevecchi 2007), and will scavenge on fisheries discards when available (Cleasby et al. 2015). Information on non-breeding season diet is lacking. Loons are opportunistic pursuit-divers (mean dive depth 5 m; Duckworth et al. 2021) that locate prey visually from the surface or by hunting underwater, and in other marine regions have been found to forage both benthically and pelagically (Duckworth et al. 2021). Little is known about their winter diet off the US Atlantic coast, though winter diet in Labrador and Europe is composed primarily of forage fishes, including capelin, Atlantic herring, and sand lance *Ammodytes* spp. (Guse et al. 2009, Rizzolo et al. 2020). Long-tailed ducks are diving ducks (mean dive depth 20–25 m; Žydelis & Richman 2015) that feed primarily benthically but also pelagically on a generalist diet including epibenthic crustaceans, bivalves, gastropods, and fishes, during the non-breeding period (Jamieson et al. 2001, Perry et al. 2007, White et al. 2009, Robertson & Savard 2020). Ducks were included in this study mainly for contrast with the other 2 species that focus on pelagic fishes.

Biologging technology, including satellite telemetry, has improved the tracking of marine bird movement patterns throughout the annual cycle. A key research gap is the paucity of data linking these movement patterns to pelagic prey distributions at relevant spatiotemporal scales (Fauchald 1999, Scales et al. 2014a). Consequently, studies often use oceanographic variables, such as chl *a* and SST, as proxies for prey. In fact, the movement behavior of gannets in relation to environmental factors has been well-studied during the breeding season (Stauss et al. 2012, Scales et al. 2014a, Cox et al. 2016, Bennison et al. 2018, Grecian et al. 2018, Deakin et al. 2019). However, the relationship between marine birds and such environmental proxies for prey can be highly variable (Kane et al. 2020), with process and measurement uncertainty contributing to poor inference. As such, validation of these associations through incorporation of prey data reduces the likelihood of spurious and inaccurate associations and also improves understanding of how best to manage marine systems for desired outcomes. Forage fishes are often monitored using trawl surveys (Suca et al. 2021) or other fisheries monitoring techniques (Sydeman et al. 2017), as well as hydroacoustic surveys (Zamon 2001, Couto et al. 2022). While these data are valuable, fisheries monitoring techniques are often best suited for large-scale species distribution modeling (Friedland et al. 2020a) rather than quantifying distribution patterns at higher spatiotemporal resolutions. In contrast, while hydroacoustic surveys can provide high-resolution information about forage fish distributions and biomass, they are typically limited in time and space and lack species-level information. Recently, digital aerial surveys have collected high-quality observations of surface-schooling (<10 m depth) forage fish aggregations over large areas of the US Atlantic (Williams et al. 2015, Robinson Willmott et al. 2021). This new source of fine-scale prey availability data (i.e. number and size of surface-level aggregations) can improve our understanding of the factors influencing prey aggregations and their relationship to predator distributions and foraging behaviors, particularly for marine predators that detect prey visually from the air or water surface, such as gannets and loons.

The aims of this study were to (1) examine how environmental factors influence the movement behaviors of 3 marine bird species during the non-breeding period and (2) explore the degree to which incorporating direct measures of prey can improve understanding of these relationships, with a focus on gannets and loons, which have greater dietary reliance on forage fishes. Foraging theory regarding hierarchical patch structure predicts that detections of prey should correspond with changes in predator movement behavior (e.g. area-restricted movement; Fauchald 1999). Thus, using discrete-time hidden Markov models (HMMs), we classified movement behavior into generalized states (e.g. transit vs. area-restricted) based on step length and turning rate derived from the tracking data (Faaborg et al. 2010). We then examined (1) how environmental proxies for resources and other environmental conditions influence movement behavior (e.g. transitions between movement states) across marine bird species; and (2) the relationship between density of area-restricted behavior for gannets and loons and forage fish occupancy and aggregation distributions, using spatial cross-correlation analysis.

2. MATERIALS AND METHODS

2.1. Satellite tag deployment

Adult gannets (n = 75) were captured via dipnet and spotlight at night at sea during the non-breeding period in the US Mid-Atlantic region, as well as at breeding colonies in Newfoundland, Canada, via noose pole or dip-net during daylight hours (Table 1, Fig. 1). Loons (n = 86) in the mid-Atlantic were also captured via dipnet and spotlight at night at sea during the non-breeding period (Stenhouse et al. 2020). Long-tailed ducks in the Great Lakes and northeastern USA were captured using a variety of techniques, including dipnet and spotlight, lift nets, and mist nets (n = 188; Lamb et al. 2019). At capture, individuals were banded with a standard US Geological Survey or Canadian Wildlife Service metal band. A 0.5–4.0 ml blood sample was taken from the metatarsal or brachial vein from gannets for molecular sexing (methods described in Spiegel et al. 2017). Loons and ducks were sexed based on plumage characteristics and cloacal examination, respectively; loons and gannets were aged based on plumage, and ducks were aged based on bursal depth and plumage (Sea Duck Joint Venture 2015). Age and sex information was explored for inclusion in movement modeling (described in Section 2.3), as some species exhibit intraspecific differences in foraging strategies.

Satellite tags were deployed primarily via surgical implantation of intra-abdominal platform transmitter terminal (PTT) tags with an external antenna. At capture, birds were administered a mild sedative and transported to an onshore veterinarian, who performed the surgical implantation using standard techniques (Korschgen et al. 1996, Mulcahy & Esler 1999). After the procedure, birds were released on the water near the capture area during daylight. The surgical implantation method is detailed in Spiegel et al. (2017). Tail-mounted tags on gannets were attached to the underside of tail feathers using self-amalgamating tape (Tesa tape™) and cable ties (Montevecchi et al. 2012). We used 5 types of ARGOS PTT transmitters

Table 1. Sample sizes (n) of northern gannets *Morus bassanus*, red-throated loons *Gavia stellata*, and long-tailed ducks *Clangula hyemalis* tracked using satellite telemetry in the northwest Atlantic between 2008 and 2016 that were included in spatial analysis by deployment location (see Section S1, Tables S1–S3 in the Supplement, www.int-res.com/articles/suppl/m711p077_supp.pdf for full details). Years indicate years tags were deployed; attachment methods include tail-mounted tags or surgical implantation

Species	Location	Years	Tag[a]	Attachment method	n
Northern gannet	Cape St Mary's Reserve	2008–2012[b]	Sirtrack KiwiSat202; Telonics TAV-2630	Tail	17
	Chesapeake Bay	2012–2015	Telonics TAV-2630; Telonics IMPTAV-2640	Tail, Implant	2, 36
	Delaware Bay	2012–2014	Telonics IMPTAV-2640	Implant	6
	Pamlico Sound	2013–2014	Telonics IMPTAV-2640	Implant	9
Red-throated loon	Chesapeake Bay	2012–2013, 2015	Telonics IMPTAV-2640	Implant	12
	Delaware Bay	2012–2014	Telonics IMPTAV-2640	Implant	13
	Pamlico Sound	2012–2015	Telonics IMPTAV-2640	Implant	26
Long-tailed duck	Chesapeake Bay	2012	Microwave PTT100-26g; Telonics IMPTAV-2630	Implant	5
	Lake Ontario	2012	Telonics IMPTAV-2630	Implant	1
	Long Island Sound	2016	Telonics IMPTAV-2630	Implant	1
	Nantucket Sound	2008–2010, 2015–2016	Microwave PTT100-26g	Implant	50

[a]Mass of tags: Telonics TAV-2630 ~29 g; Telonics IMTAV-2640 ~49 g; Sirtrack KiwiSat202 32–39 g; Microwave PTT100 26 g
[b]All northern gannets captured between 2008 and 2010 were juveniles; all others were adults

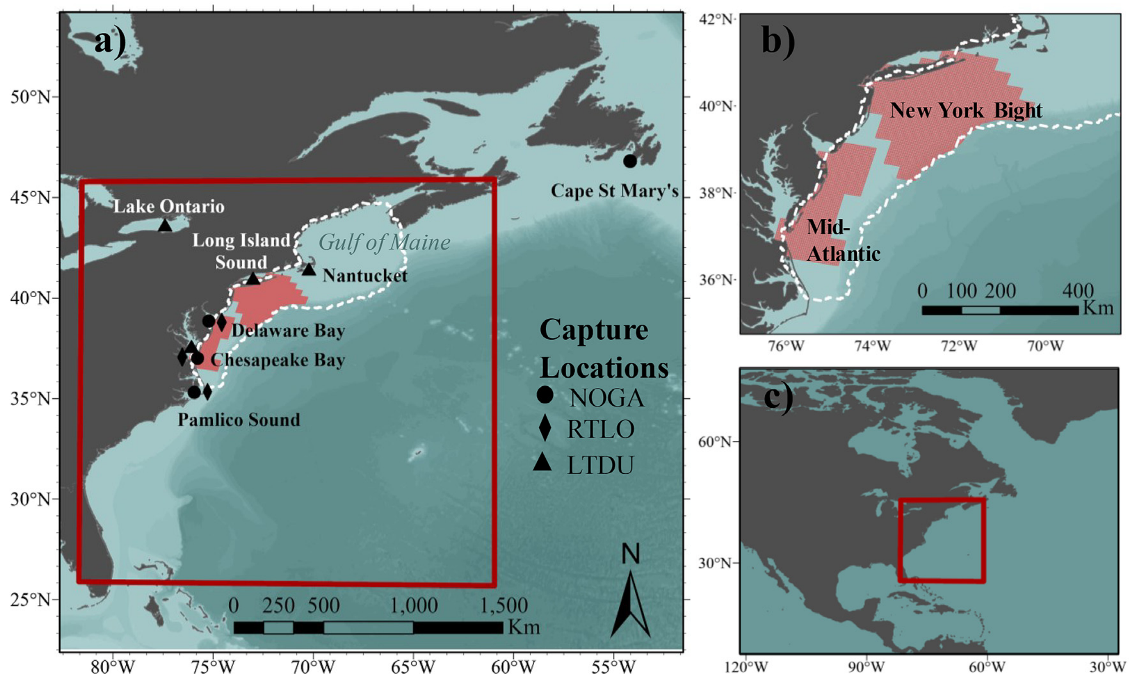

Fig. 1. Study area for marine bird movement analysis in relation to environmental variables and forage fish distributions. (a) Capture locations of satellite-tagged northern gannets *Morus bassanus* (NOGA), red-throated loons *Gavia stellata* (RTLO), and long-tailed ducks *Clangula hyemalis* (LTDU) in the eastern USA and Canada from 2008 to 2017. The red box indicates the US Atlantic coast (the spatial extent of marine bird movement models), the white dashed area represents the Northeast Continental Shelf (the spatial extent of the forage fish occupancy models). (b) Red-filled areas indicate forage fish aggregation prediction areas in the Mid-Atlantic and New York Bight. (c) Location of study area in North America

(www.argos-system.org/; Table 1). Tag mass was <5% of overall body mass for all deployments (Phillips et al. 2003). Transmitters had varying duty cycles during the non-breeding season, with 4–5 h 'on' periods followed by 13–72 h 'off' periods. For detailed information on transmitter deployments, tag types, and duty cycles, see Section S1 in the Supplement (www.int-res.com/articles/suppl/m711p077_supp.pdf).

Tracking data were assessed using a data filter (Douglas Argos Filter) to remove redundant locations and flag errant points. A hybrid filter was applied that used both the distance, angle, and rate and minimum redundant distance filters to remove outliers, which was developed to handle avian tracking data characterized by periods of sedentary behavior (e.g. breeding) interspersed with rapid directional movement (e.g. migration; Douglas et al. 2012). In addition, given the marine distribution of these species during the non-breeding period, we removed points that were located on land due to errors in location estimates.

2.2. Data management

All data management and analysis were conducted using statistical software (R v.4.1.0, R Core Team 2023; and ArcMap v.10.8.1, Esri). Individual movement data were excluded from modeling if there were <30 d of data from an individual due to tag failure or loss, or if there was a suspected mortality within 60 d of deployment based on inactivity and/or internal temperature loggers (see Spiegel et al. 2017 for more details). Individuals that did not utilize the study area (US Atlantic coast; Fig. 1) during any period were excluded; this included subsets of gannets captured in Newfoundland, and ducks tagged on Lake Ontario. Our final dataset included 75 gannets (32 with data from 2 non-breeding seasons), 51 loons (39 with data from 2 non-breeding seasons), and 57 ducks (12 with data from 2 non-breeding periods; Table 1).

Telemetry data were truncated to focus on movements during the non-breeding period, which we defined spatiotemporally based on species-specific phenological cutoffs (gannets: 1 October to 20 May; loons: 1 November to 31 May; ducks: 1 November to 30 April; Powers & Cherry 1983, Veit & Petersen 1993, Mowbray 2020, Robertson & Savard 2020), distance threshold from a breeding colony (gannets), and movement outside of the study area (loons and ducks). The distance thresholds were used to account for individual variation in breeding ground arrival and departure for colonial breeding gannets. As gannets of all ages migrate southward from breeding colonies in Canada starting in the fall, we created colony distance buffers (432 km based on maximum breeding foraging ranges from published studies; Garthe et al. 2007, Pettex et al. 2010, Scales et al. 2014a, D'Entremont et al. 2022). As loons and ducks are non-colonial nesting species with breeding ranges exclusively north of the study area, we truncated movement data to locations within the study area.

2.2.1. Environmental covariates

Initial environmental covariates for potential inclusion in models were chosen based on *a priori* knowledge on drivers of marine bird habitat use (Warden 2010, Scales et al. 2014a, Cox et al. 2016, Grecian et al. 2018, Lamb et al. 2020) and additional variables that may influence the abundance and distribution of prey resources and foraging tactics (Table 2). Choice of covariates focused primarily on those related to resource use. These included static habitat (e.g. bathymetric features), dynamic habitat (e.g. SST), and resource aggregating features (e.g. fronts and eddies). We also considered covariates related to foraging tactics, including factors that might influence behavior, such as wind and fishing vessels (Table 2). Environmental data were obtained from publicly accessible data sources at the finest available spatial resolution.

We derived slope, surface wind velocity magnitude, surface current velocity magnitude, SST fronts, and chl *a* fronts. Slope was derived from bathymetric depth (using the 'Slope' tool in ArcMap). Surface wind and current velocity magnitude were calculated from the eastward and northward (u and v) wind component vector data. Fronts were detected from daily SST and chl *a* raster data, using the Cayula-Cornillon single image edge detection algorithm (Cayula & Cornillon 1992; using the Marine Geospatial Ecology toolbox version 0.8175 in ArcMap; Roberts et al. 2010). Algorithm parameters for SST fronts included a 32 × 32 pixel window, a 3 × 3 kernel, and a 0.4°C temperature threshold. Parameters for chl *a* fronts included a 16 × 16 pixel window, 5 × 5 kernel, and a 0.5 mg m^{-3} threshold (Roa-Pascuali et al. 2015, Swetha et al. 2017). Frontal gradients were calculated (in the 'grec' R package; Lau-Medrano 2020) using the gradient algorithm of Belkin & O'Reilly (2009). Composite frontal maps (7 d and 30 d rolling windows; Scales et al. 2014a) were used to calculate

Table 2. Covariates considered for movement modeling analysis of marine birds. 'Model' indicates if the covariate was included in the northern gannet *Morus bassanus* model (NOGA), red-throated loon *Gavia stellata* model (RTLO), long-tailed duck C*langula hyemalis* model (LTDU), all 3, or none due to high correlation with other covariates. Additional information includes temporal resolution (Temp.) of data, spatial resolution of raw data, and predicted relationship with marine bird area-restricted movement, indicated as a positive (+) or negative (–) association. SST: sea surface temperature

Covariate	Model	Temp.	Spatial	Predicted relationship	Data source
Bathymetric depth (m)	All	Static	1 km	(–) Accessibility and coastal prey distribution	General Bathymetric Chart of the Oceans (GEBCO Compilation Group 2020)
Slope	All	Static	1 km	(+/–) Mixing, convergence, prey distributions	Derived from depth
Rugosity	None	Static	0.5 km	(+) Bottom complexity relating to resource availability	Derived measure of ratio of the real to the geometric surface area (Friedland et al. 2020a)
Sediment grain size (mm)	LTDU	Static	0.5 km	(–) Influence on benthic species composition, diversity, and abundance	Northwest Atlantic Marine Ecoregional Assessment (NAMERA; The Nature Conservancy 2016)
SST	All	Daily	1 km	(+/–) Thermal conditions linked to prey occurrence and activity levels	A Group for High Resolution Sea Surface Temperature (GHRSST) Version 4 Multiscale Ultrahigh Resolution (MUR) l4 interpolated (JPL MUR MEaSUREs Project 2015)
SST front strength (*Fmean*)	All	30 d	1 km	(+) Frontal conditions aggregate resources	Fronts derived from daily SST using the Cayula-Cornillon algorithm (Cayula & Cornillon 1992); combined with gradient information into composites of mean front strength
Chlorophyll *a*	All	Daily	4 km	(+) Lower trophic level productivity linked to forage fish abundance	Copernicus Marine Environment Monitoring Service interpolated GlobColour (Bertrand et al. 2019)
Chlorophyll *a* front strength (*Fmean*)	All	30 d	4 km	(+) Frontal conditions aggregate resources	Fronts derived from daily chl *a* using the Cayula-Cornillon algorithm; combined into composites representing probability of observing a front over a sequence
Salinity	None	Daily	8 km	(–) Areas of freshwater influence, tidal mixing fronts that aggregate resources	Sea surface salinity from the Global Ocean Physics Reanalysis (GLORYS 12V1) global ocean eddy-resolving model, https://doi.org/10.48670/moi-00021
Mixed layer depth	None	Daily	8 km	(–) Indication of stratification, aggregates prey in water column	GLORYS12V1 global ocean eddy-resolving model
Sea surface height anomaly (m)	RTLO LTDU	Daily	0.25°	(–) Physical forcing stimulates primary productivity, aggregates prey; indication of eddies	Copernicus Marine Environment Monitoring Service (CMEMS) Sea Level Anomaly, https://doi.org/10.48670/moi-00021; computed with respect to a 20 yr mean (1993–2012)
Surface wind velocity magnitude	All	Daily	0.25°	(–) Influences water mixing, aerial maneuverability, and cost of flight	Derived from surface wind velocity *u* and *v* direction from National Center for Atmospheric Research Cross-Calibrated Multi-platform Wind Vector Analysis (Wentz et al. 2015)
Surface current velocity magnitude	NOGALTDU	Daily	0.08°	(+) Relates to visibility, upwelling, and resource aggregation	Derived from current velocity *u* and *v* direction from GLORYS12V1 global ocean eddy-resolving model
Fishing vessel density	NOGA	Static	4 km	(+/–) Species level attraction or avoidance	Derived using point location Automatic Identification System (AIS) data collected by the US Coast Guard from Marine Cadastre from 2009–2016, https://marinecadastre.gov/ais/

2 frontal metrics (in R): *Fprob,* representing front persistence, and *Fmean*, representing front strength (Miller 2009). *Fprob* is the probability of a front being detected over the temporal window, while *Fmean* is the average of the gradient of values within identified fronts over the temporal window (Miller 2009,

Suberg et al. 2019). These frontal metrics were chosen due to ease of interpretation and high correlations between these and other commonly used metrics (Suberg et al. 2019).

In addition to the environmental covariates described above, fishing vessel density was calculated given its potential importance in foraging tactics (i.e. attraction), particularly for gannets (Bodey et al. 2014). Fishing vessel density was derived from vessel traffic data (i.e. Automatic Identification System; AIS) collected by the US Coast Guard through onboard navigation devices (2009–2016), which is required by all vessels over 65 feet (19.8 m) in length. AIS data were filtered to include only fishing vessels within the study area. Vessel tracks were interpolated to a 1 min time step, assuming that points from the same vessel with a gap of >1 d were separate trips ('adehabitatLT' package, v.0.3.25; Calenge 2006). We created monthly density rasters from the interpolated vessel tracks, using non-parametric fixed kernel density analysis ('adehabitatHR' package, v.0.4.19; Calenge 2006). To account for interannual differences in vessel reporting rates and lack of data for 2007–2008, we averaged monthly rasters into a static density raster.

Environmental covariate data were projected to a North American Albers Equal Area Projection, resampled to a common 4 km resolution using bilinear interpolation, scaled, and zero-centered. Log transformations were applied to variables with high levels of skew. Pairwise correlations between variables informed the final covariate suite, with a representative covariate chosen when Pearson's correlation coefficient was >0.4. Exploratory analysis of *Fmean* and *Fprob* 7 d and 30 d scales revealed that 30 d *Fmean* had the most explanatory power (based on Akaike's information criterion, AIC) for both SST and chl *a* fronts; therefore, these were the only front metrics considered in our final models. In instances where bird locations did not correspond to a covariate value (e.g. coastal grid cells), the nearest cell with a covariate value was used (0.09–0.16% of locations). Maps of multiyear (2008–2017) average covariate values for candidate environmental covariates can be found in Section S2.

2.2.2. Forage fish data

To compare marine predator habitat use with existing forage fish species-level information, we used annual seasonal (fall, spring) occupancy (e.g. probability of occurrence) models from Friedland et al. (2020a). This study used fisheries-independent bottom trawl data collected by the NOAA Northeast Fisheries Science Center to model occupancy of 48 finfish and macroinvertebrate species for the Northeast Continental Shelf (white dashed line Fig. 1) at a 0.1° resolution. We selected 11 forage fish species from these models based on diet information of our study species: Atlantic herring *Clupea harengus*, northern sand lance *Ammodytes dubius*, American butterfish *Peprilus triacanthus*, Atlantic silverside *Menidia menidia*, striped anchovy *Anchoa hepsetus*, bay anchovy *A. mitchilli*, Atlantic menhaden *Brevoortia tyrannus*, Atlantic mackerel *Scomber scombrus*, blueback herring *Alosa aestivalis*, alewife *Alosa pseudoharengus*, and round herring *Etrumeus acuminatus*. Forage fish occupancy estimates, developed using remotely sensed marine environmental covariates, were averaged within season across years (with selected years defined based on marine bird movement date range by species) to create a single occupancy estimate per forage fish species per season. As the temporal span of marine bird data varied by species, averaged forage fish occupancy was calculated separately for gannets and loons for the time periods of interest. In addition, occupancy of all 11 species was summed by season to create an estimate of cumulative forage fish occupancy. To examine forage fish aggregations (e.g. surface availability), we used data on the size and location of surface shoals of forage fish identified in seasonal digital aerial surveys in the Mid-Atlantic (2012–2014; Williams et al. 2015) and New York Bight (2016–2017; Robinson Wilmott et al. 2021). These surveys represent a novel method for surveying forage fish aggregations and may provide important information about accessibility of forage fish to visual aerial predators that is not available using more traditional survey methods. Aggregation size was measured based on the visible areal extent of the shoal at the ocean surface (<10 m depth) using a custom measurement tool, and aggregation location was defined as the centroid of each shoal (Robinson Willmott et al. 2021). We used seasonal (fall, winter, spring) predictions from a concurrent study (Goetsch et al. preprint doi:10.22541/au.167163077.72855489/v1) using this dataset and a suite of environmental covariates to model the availability of forage fish aggregations (number and size) in a hierarchical Bayesian framework. Prediction rasters of aggregation number, size, and number × size were calculated using the seasonal averages of the included covariates across the spatiotemporal extent of the study (2008–2016).

2.3. Data analysis

2.3.1. Movement models

Hidden Markov models provide a powerful tool to examine underlying behavior states based on movement trajectories. These models are made up of an observation time series, in this case step length and turning angle, and an underlying non-observable (hidden) state sequence (Patterson et al. 2008, Langrock et al. 2012, McClintock & Michelot 2018). To meet the assumption of equal time steps between sequential locations in discrete-time HMMs, the data were interpolated using a continuous-time correlated random walk (CTCRW) model (using the 'crawl' R package version 2.2.3; Johnson et al. 2008). The CTCRW model was fit using the Kalman filter on a state–space version of the continuous-time stochastic movement process and included an observation model accounting for ARGOS error based on location class. Position uncertainty was modeled by including a prior distribution for each error class, represented as a normal distribution of the log(estimated error) for each location class based on ARGOS estimates (Collecte Localisation Satellites 2011, Douglas et al. 2012). Locations were predicted by individual at a 17 h time step for gannets and loons, and a 48 h time step for ducks to align with the duty cycle of most tags for each species. Given the primarily marine distribution of study species and the extent of the covariates, we used a function ('fix_path' in 'crawl') to avoid predicted locations on land. This function simulates multiple paths using the fitted CTCRW model and associated location uncertainty and adjusts predicted paths that cross a user-defined land raster onto the nearest valid path (if available; Johnson et al. 2008).

Following temporal smoothing, HMMs were implemented using statistical software (the 'momentuHMM' R package version 1.5.4; McClintock & Michelot 2018). In the context of animal movement, hidden states in HMMs can be interpreted as proxies for behavior states. Based on *a priori* understanding of behavior (Grecian et al. 2018), 2 movement states were chosen with the expectation that they represent: (1) transit behavior state, represented by strong directionality (i.e. high angle concentration) and larger step lengths; and (2) area-restricted behavior state, represented by greater turning angles (i.e. low angle concentration) and shorter step lengths. While 2-state models were implemented for gannets and loons, exploratory analysis of duck data revealed that the model was unable to distinguish multiple states; thus, a single-state model was used in this case. This inability to distinguish multiple states for ducks may relate to the coarser temporal resolution of this dataset or to specifics of the species' foraging ecology.

Turning angle was assumed to have a wrapped Cauchy distribution and step length a gamma distribution (Fisher 1993, Michelot et al. 2016). To incorporate the uncertainty associated with ARGOS position error, we fitted each model with 50 simulations of tracks and reported the pooled parameter estimates, standard deviations, and confidence intervals, using multiple imputation (McClintock & Michelot 2018). Step length mean and standard deviation along with angle mean and concentration were estimated for each state. We verified that the models identified global likelihood maxima (an issue for some HMMs) by refitting the null model with randomized initial parameter values (n = 1000) and used parameter starting values for the best fit iteration (based on AIC) for subsequent models, as well as implemented n = 15 randomizations of initial parameters for all models. For 2-state models, we constrained natural scale parameters for step length such that area-restricted state < transit state to prevent label switching among model simulations.

2.3.2. Environmental modeling

Following initial model exploration (described above), we examined how environmental covariates influenced the movement states of marine birds, by running a single model for each of our study species, including all potential environmental covariates with <0.4 Pearson correlation with other covariates to avoid model multicollinearity (Table 2). For all 3 species, salinity was negatively correlated to chl *a*, as was mixed layer depth with depth. Thus, we chose the latter as the representative covariate in both cases. To account for multiple non-breeding periods for individuals that were tracked for multiple years, as well as differences in tracking duration due to tag attachment type (gannets only, as implanted tags lasted much longer than taped tags), a categorical fixed effect 'type' was included in all models. For gannets, this fixed effect had 3 categories: tail-mounted tags, implanted tags non-breeding period 1, and implanted tags non-breeding period 2. For loons and ducks, only the latter 2 categories were included. We also explored the inclusion of sex and age as fixed effects in addition to type (and all combinations of these fixed effects) in the models to examine potential influence on transition probabilities, using AIC and model convergence to determine final fixed effects based on model fit for each species. For gannets and loons, type only resulted in the best fit, while for ducks, the inclusion of sex as well as type resulted in the best fit. Thus, these fixed effects were included in the environmental covariate models for each species. For the 2-state models (gannets, loons), environmental covariates were allowed to influence transition probabilities between states, while for the 1-state models (ducks), environmental covariates were allowed to influence step length directly. This difference leads to models that address the effects of environmental covariates on 2 aspects of movement (e.g. transitions between movement modes and step length). As we were focused on understanding the factors influencing resource use, and therefore why birds might slow down or spend more time in a particular area, these patterns are similarly represented by a transition to area-restricted movement or shorter step lengths. To examine the importance of each covariate for these movement patterns, we assessed parameter estimates and associated 95 % confidence intervals from environmental models for each species. Parameters were considered statistically significant if 95 % confidence intervals did not overlap with zero. Pseudo-residuals and decoded state sequences were calculated and examined as model diagnostics. All models converged in <12 min (per simulation), and there was no indication of numerical issues during model fitting. As the large number of candidate covariates would have required high computational costs in a model selection framework, we explored a subset of 16 candidate models per species to help ensure models were not overfit by comparing AIC and parameter estimates across models. As we did not find large differences in parameter estimates across models, we present the results of the model with all candidate covariates. Additional details and model comparisons can be found in Section S3.

The Viterbi algorithm was used to compute the most likely sequence of states, assigning a state to each location in the time series using the environmental models (McClintock & Michelot 2018). To compare space use across species, we calculated non-parametric fixed kernel densities by movement state and season: fall (September–November), winter (December–February), and spring (March–May), using predicted point locations assigned to each state for gannets and loons (e.g. transit, area-restricted), and all predicted locations combined by season for ducks. Smoothing factors were chosen based on reference bandwidth calculation. Core (50 %) and overall (95 %) volume contours were calculated for each species–season–state combination to examine utilization distributions.

2.4. Forage fish comparison

To compare spatial patterns between forage fish and gannets and loons, we used the seasonal kernel density estimates of area-restricted states clipped to match the extent of forage fish information (occupancy: Northeast Continental Shelf; aggregations: Mid-Atlantic and New York Bight; Fig. 1). We made pairwise comparisons between seasonal marine bird densities and forage fish species occupancy, cumulative forage fish occupancy, and surface aggregations (number, size, and number × size) by calculating an overall Pearson correlation coefficient and conducting a spatial cross-correlation analysis ('spatialEco' package, version 1.3-7; Evans 2021). Cross-correlation analysis calculates (1) the local spatial cross-correlation index (SCI), the gridwise cross-correlation between 2 variables based on spatial distance, indicating where there are strong positive or negative spatial correlations; (2) the global SCI, the summation of gridwise cross-correlation; (3) local indicators of spatial association (LISA) clusters, categorical indicators of spatial clustering of similar (high–high or low–low) or dissimilar (high–low) grid cells; and (4) spatial goodness of fit (R^2), which represents the proportion of spatial change of marine bird density explained by forage fish predictions. The product of local SCI and LISA clusters (−1 = negative local SCI correlation, 1 = positive local SCI correlation) was used for visualizing spatial patterns. Forage fish occupancy models were only available for fall and spring, while forage fish aggregation models were available for all 3 seasons we assessed (fall, winter, spring), and spatial cross-correlation analysis was conducted for each species–season combination available. In instances where forage fish data were highly non-Gaussian in form, transformations were performed prior to spatial cross-correlation analysis. Given our interest in examining similarity between marine birds and forage fish, results focus on positive SCI patterns as an indication of potential trophic links as opposed to negative patterns, which would indicate absence of both marine birds and forage fish.

3. RESULTS

3.1. State distributions

The HMMs revealed 2 distinct movement states for gannets and loons that matched the hypothesized transit and area-restricted states (Fig. 2). For gannets (17 h predicted time step), the transit state had a

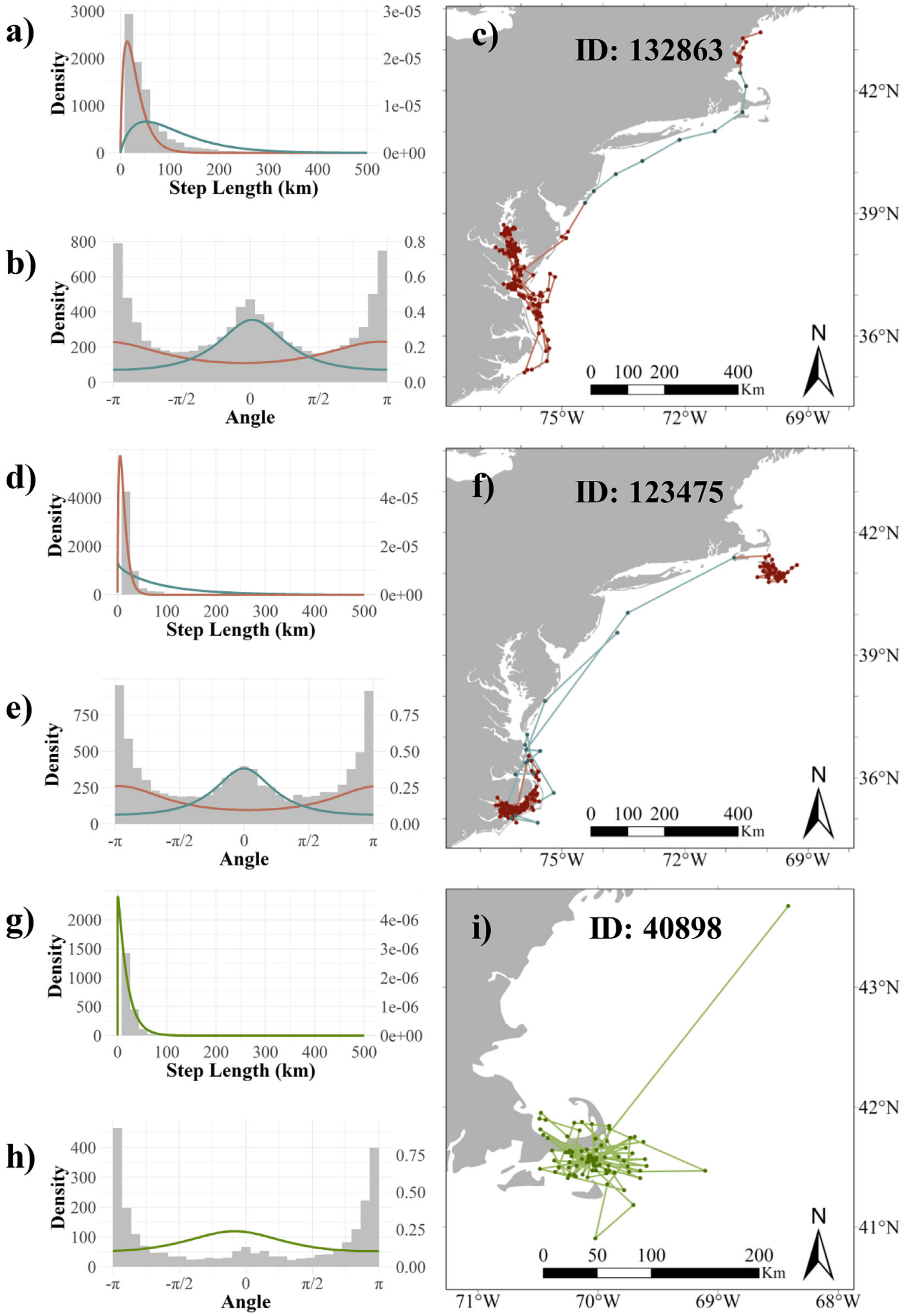

Fig. 2. State distributions and assignments from the hidden Markov models for non-breeding (a–c) northern gannet *Morus bassanus*, (d–f) red-throated loon *Gavia stellata*, and (g–i) long-tailed duck C*langula hyemalis* satellite telemetry data off the US Atlantic coast. Step length and turning angle distributions for the movement states, including transit (blue), area-restricted (red) for gannets (a,b) and loons (d,e), and all movement (green) for ducks (g,h). Sample tracks of individuals classified into discrete behavioral states based on step length and turning angle distributions using the Viterbi algorithm for gannets (c), loons (f), and ducks (i)

mean step length of 110.1 ± 80.3 km (±SD) and angle mean of 0.04 and concentration of 0.38, while the area-restricted state had a mean of 30.7 ± 23.0 km and an angle mean of 2.98 and concentration of 0.18. For loons (17 h predicted time step), the transit state had a mean step length of 87.8 ± 90.0 km and an angle mean of 0.00 and concentration of 0.41, while the area-restricted state had a mean step length of 12.6 ± 9.6 km and angle mean of −3.04 and concentration of 0.24. The single movement state for ducks (48 h time step) had a mean step length of 18.6 ± 18.2 km and an angle mean of −0.27 and concentration 0.20. The proportion of time spent in the area-restricted state was much higher than transit for gannets (74–78% across simulations) and loons (85–88% across simulations).

Kernel density estimates (KDEs) by movement state showed spatial variation across species and seasons (Fig. 3). Gannets exhibited a broad distribution along the US Atlantic coast, although core (50%

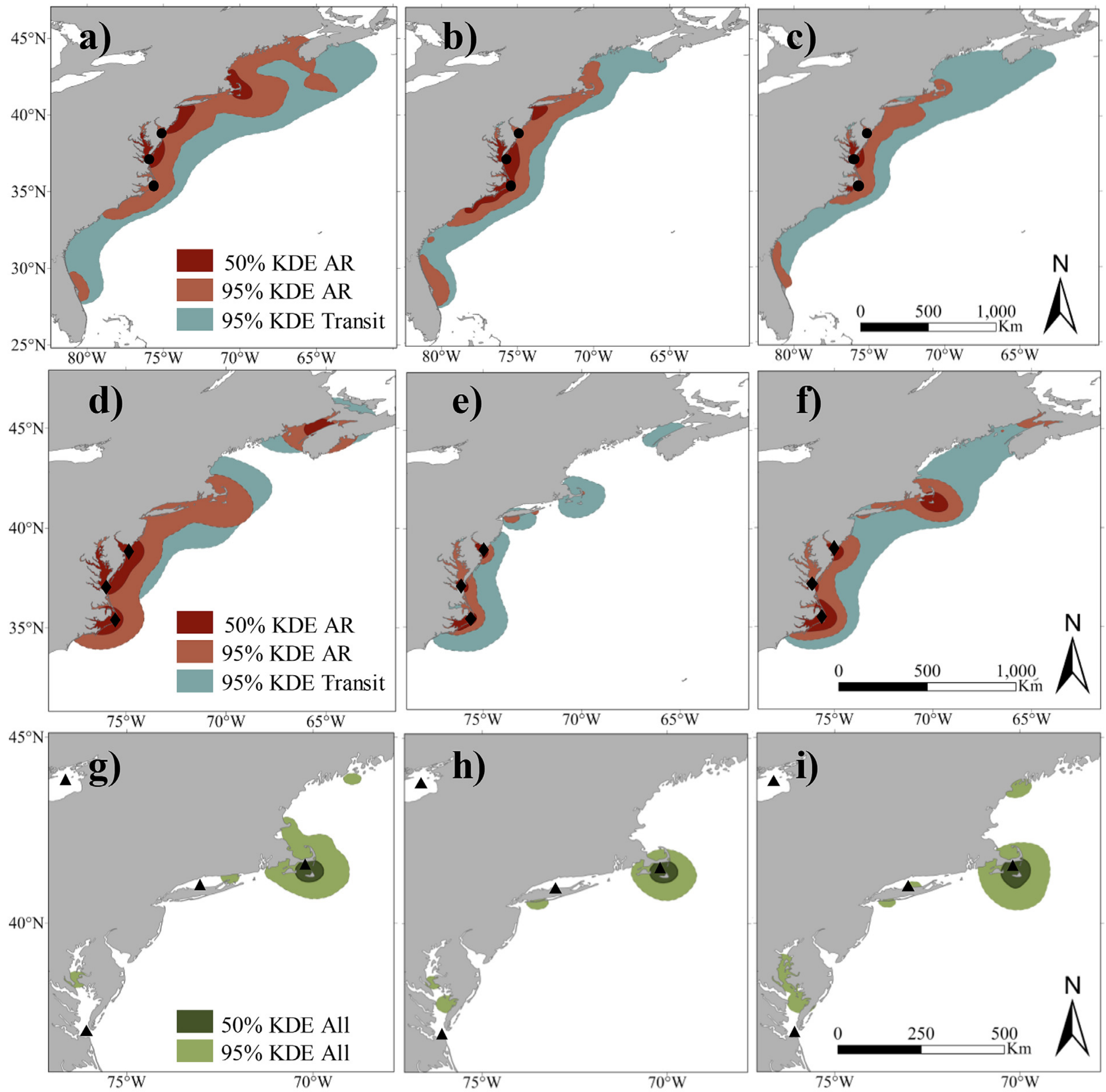

Fig. 3. Core (50%) and overall (95%) utilization distributions of non-breeding northern gannets *Morus bassanus* for (a) fall, (b) winter, and (c) spring, red-throated loons *Gavia stellata* for (d) fall, (e) winter, and (f) spring, and long-tailed ducks *Clangula hyemalis* for (g) fall, (h) winter, and (i) spring off the US Atlantic coast by movement state (transit: blue, area-restricted [AR]: red, overall: green). Capture locations indicated by black symbols for gannets (circles; except Cape St Mary's; see Fig. 1), loons (diamonds), and ducks (triangles)

KDE) area-restricted movement was most concentrated in the spring around the Mid-Atlantic, while the fall and winter core habitat spanned areas of the New York Bight and the Gulf of Maine. Loon seasonal distributions exhibited less use of the south Atlantic, with core area-restricted use in the Mid-Atlantic across seasons and additional use of the Gulf of Maine and areas near Nantucket in the fall and spring, respectively. Finally, ducks exhibited a more constrained and consistent spatial distribution, with core movement concentrated near Nantucket across seasons with little activity in Chesapeake Bay and the Gulf of Maine.

3.2. Influence of environmental covariates

Parameter estimates from environmental models were examined to determine the importance and directionality of individual variables (Fig. 4). This assessment revealed that for gannets, only chl *a* was significant (β = –0.43, CI = –0.75, –0.12). As chl *a* increased, gannets were significantly less likely to switch to the transit state. Though non-significant, gannets exhibited a trend with depth, with birds more likely to remain in a transit state as water depth increased (β = –0.25, CI = –0.57, 0.06) as well as with wind, where gannets were less likely to switch from transit to an area-restricted state as wind speed increased (β = –0.20, CI = –0.42, 0.02). Similar to gannets, loon movement was also influenced by chl *a*, with birds significantly less likely to switch to a transit state (β = –0.29, CI = –0.49, –0.08), and significantly more likely to switch to the area-restricted state (β = 0.49, CI = 0.23, 0.76) as chl *a* increased. Loons also exhibited a similar relationship with chl *a* fronts (transit → area-restricted: β = 0.45, CI = 0.12, 0.78; area-restricted → transit: β = –0.24, CI = –0.45, –0.03), and sea surface height anomaly (SSHA; transit → area-restricted: β = 0.23, CI = 0.02, 0.44), where increasing covariate values were related to higher probability of area-restricted movement and lower likelihood of switching to transit movement. Loons also exhibited a significant relationship with depth, where decreasing depth (e.g. shallower water) was related to higher probability of area-restricted movement (transit → area-restricted: β = –0.34, CI = –0.61, –0.05; area-restricted → transit: β = 0.37, CI = 0.05, 0.68). Finally, loons exhibited a significant relationship with wind, whereby birds were less likely to switch to area-restricted (e.g. remain transiting) as wind speed increased (β = –0.22, CI = –0.45, 0.00). Showing similar directional patterns with the other 2 species, step length for ducks significantly decreased as chl *a* (β = –0.05, CI = –0.08, –0.02) and SSHA (β = –0.03, CI = –0.06, –0.00) increased. Ducks also exhibited an affinity towards shallow, flat, sandy areas, with step length increasing with increased depth (β = 0.05, CI = 0.00, 0.09), slope (β = 0.04, CI = 0.01, 0.07), and sediment size (β = 0.04, CI = 0.00, 0.07). Overall, the only shared relationships among all 3 marine bird species were the relationships with chl *a* (significant for all species) and depth (non-significant for gannets).

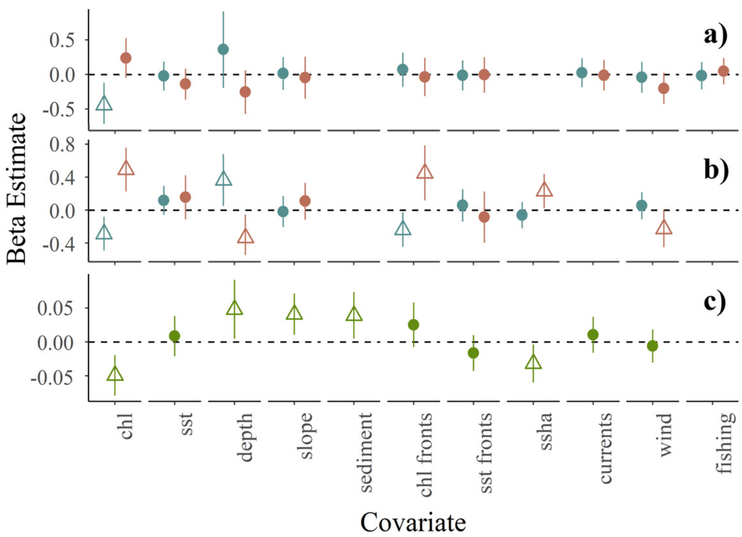

Fig. 4. Relationship between environmental covariates and movement patterns of non-breeding (a) northern gannets *Morus bassanus*, (b) red-throated loons *Gavia stellata*, and (c) long-tailed ducks *Clangula hyemalis* off the US Atlantic coast from hidden Markov models. For gannets and loons, positive beta parameters represent a positive relationship with transition probabilities for transit → area-restricted (red), and area-restricted → transit (blue). For ducks, positive beta parameters represent a positive relationship with step length (green). Covariates include chlorophyll *a* (chl *a*), sea surface temperature (SST), depth, slope, sediment size, chl *a* fronts (chl fronts), SST fronts, sea surface height anomaly (SSHA), current velocity (current), wind speed (wind), and fishing vessel density (fishing). Shape represents parameter significance (triangles) or non-significance (circles). Not all covariates are included in each model

3.3. Spatial patterns with forage fish occupancy

Correlations between seasonal marine bird densities and forage fish species occupancy ranged from –0.55 to 0.67 for fall and –0.32 to 0.42 for spring (Section S4), and SCI values ranged from −0.28 to 0.27 for fall and −0.12 to 0.16 for spring (Fig. 5). Spatial cross-correlation analysis revealed similar magnitudes of spatial patterns between gannets and loons, with positive SCI values for both species in the fall and spring for menhaden, bay anchovy, striped anchovy, and round herring. Butterfish in fall, and silverside and blueback herring in spring, were also positively correlated with both bird species, and mackerel in spring were positively correlated with gannets (Fig. 5). Spatial goodness-of-fit varied across species and season (gannets in fall 0.00–0.35, spring 0.00–0.41; loons in fall 0.02–0.59, spring 0.00–0.08). For gannets, round herring explained the most spatial variance in fall ($R^2 = 0.32$), while Atlantic menhaden explained the most in spring ($R^2 = 0.41$). Similarly, for loons, round herring explained the most spatial variance in the fall ($R^2 = 0.55$), while menhaden had the highest goodness of fit in spring though it explained little variation ($R^2 = 0.08$). For gannets and loons, the LISA analysis of the forage fishes with the highest SCI values showed consistent positive spatial associations (i.e. regions of high seabird density and forage fish occupancy) along the Mid-Atlantic coast across seasons (Fig. 6). Conversely, positive spatial associations in the New York Bight and Nantucket for these birds were limited to specific forage fish species (Fig. 6).

3.4. Spatial patterns with forage fish aggregations

Correlations between seasonal gannet and loon densities and forage fish aggregation number, size, and number × size (hereafter 'surface availability') ranged from 0.31 to 0.74 for fall, 0.00 to 0.62 for winter, and 0.28 to 0.56 for spring (Table 3). For gannets and loons in all seasons, the aggregation surface availability metric had the highest spatial cross-correlation with marine bird distributions. Spatial goodness of fit was highest in fall for gannets ($R^2 = 0.43$) and loons ($R^2 = 0.39$). For gannets, positive spatial associations with forage fish aggregations were concentrated in the southern portion of the Mid-Atlantic (near Chesapeake Bay) across seasons, contrasting with loons, which had positive spatial associations primarily in the northern region of the Mid-Atlantic closer to Delaware Bay (Fig. 7).

4. DISCUSSION

Large-scale movement patterns of gannets, loons, and ducks were best explained by dynamic and static environmental gradients. Chl *a* was significant for all 3 species, suggesting a link between seabird movement and lower trophic level productivity that is also strongly associated with lower-saline estuaries. In contrast, the importance of resource-aggregating covariates (i.e. sea surface fronts and eddies) varied by species and were not as important for gannets. Correlations with forage fish occupancy varied by species combination and season, exemplifying the potential dynamism of these trophic relationships. Atlantic menhaden exhibited the most consistently high positive spatial associations across species and seasons, suggesting that menhaden is a key prey resource in this region during the non-breeding period. Forage fish aggregations exhibited slightly stronger or similar spatial associations with marine birds than did species occupancy, suggesting that prey patch distribution and factors driving the formation of surface-level aggregations

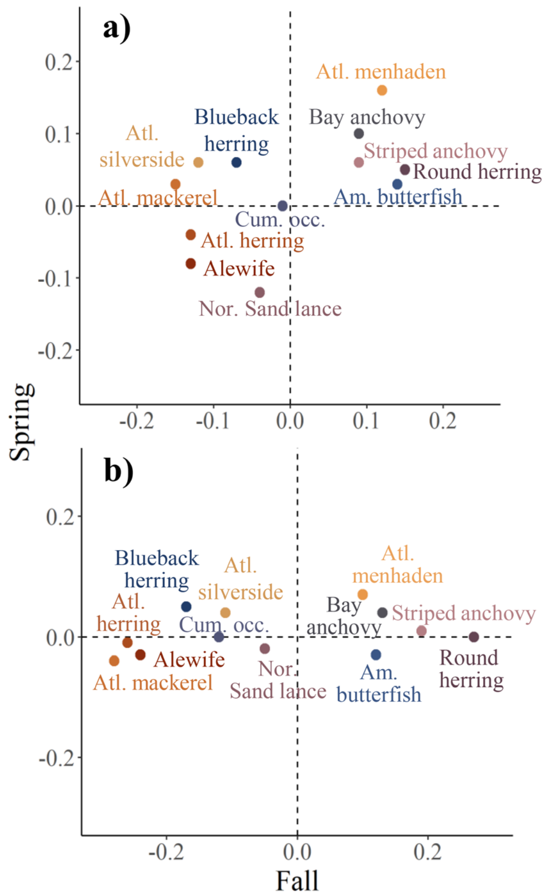

Fig. 5. Fall and spring spatial cross-correlation index (SCI) values of pairwise comparisons of 11 forage fish species and cumulative occupancy (Cum. Occ.) with area-restricted locations of non-breeding (a) northern gannets *Morus bassanus* and (b) red-throated loons *Gavia stellata* off the US Atlantic coast. Quadrants represent positive and negative SCI by season, with positive values representing spatial associations (high–high or low–low) while negative values represent spatial mismatch (high–low) between marine birds and forage fish species occupancy

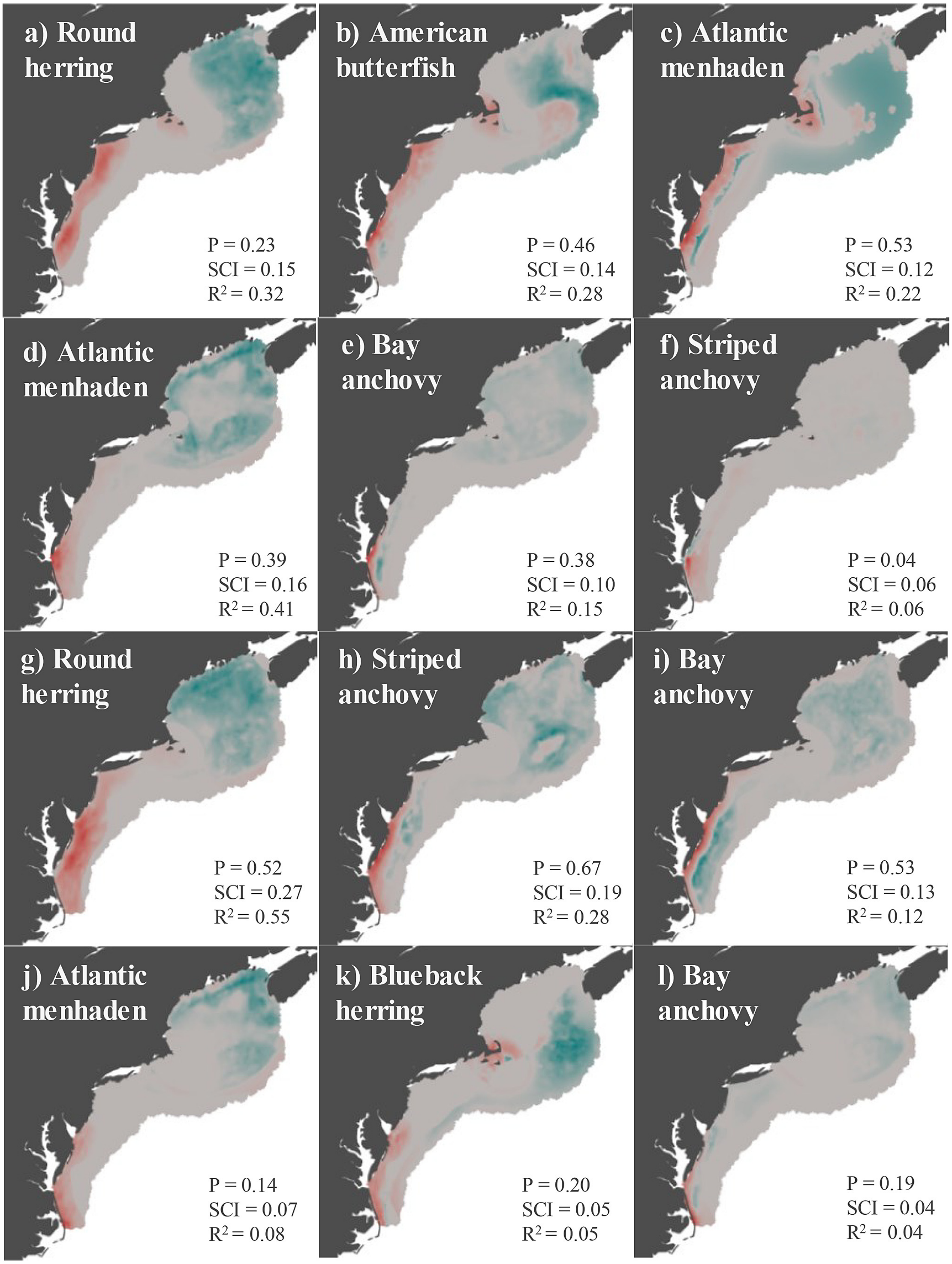

Fig. 6. Spatial association patterns for seasonal forage fish occupancy and marine bird density for the 3 forage fish species with the highest spatial variance (R^2) explaining seabird activity for northern gannets *Morus bassanus* in (a–c) fall and (d–f) spring and red-throated loons *Gavia stellata* in (g–i) fall and (j–l) spring. Colors indicate areas of positive (red), negative (blue), and zero (grey) spatial associations (product of local indicators of spatial association and local spatial cross-correlation analyses). Colors are scaled independently for each panel based on minimum and maximum values. Values indicate overall Pearson correlation (r), spatial cross-correlation index (SCI), and spatial goodness of fit (R^2). Correlation values and spatial associations for all forage fish species by seabird species and season can be found in Section S4 in the Supplement, www.int-res.com/articles/suppl/m711p077_supp.pdf

Table 3. Spatial correlation patterns comparing northern gannet *Morus bassinus* and red-throated loon *Gavia stellata* with seasonal forage fish aggregation predictions in the New York Bight and Mid-Atlantic. Forage fish aggregations (metrics) include predicted number, size, and surface availability (number multiplied by size). Patterns examined include Pearson's correlation (r), spatial cross-correlation (SCI), and corresponding goodness of fit (R^2)

Species	Metric	Fall			Winter			Spring		
		r	SCI	R^2	r	SCI	R^2	r	SCI	R^2
Northern gannet	Number	0.64	0.23	0.40	0.45	0.19	0.18	0.28	0.13	0.14
	Size	0.31	0.09	0.05	0.00	–0.05	0.01	0.30	0.09	0.06
	Surface availability	0.66	0.24	0.43	0.62	0.28	0.38	0.36	0.16	0.20
Red-throated loon	Number	0.72	0.30	0.36	0.46	0.12	0.24	0.53	0.20	0.26
	Size	0.34	0.11	0.05	0.00	–0.02	0.00	0.30	0.10	0.06
	Surface availability	0.74	0.31	0.39	0.45	0.15	0.39	0.56	0.22	0.32

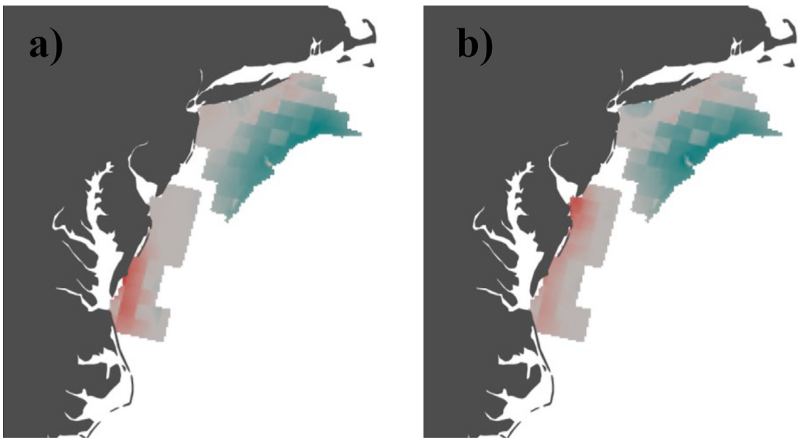

Fig. 7. Spatial association patterns for forage fish surface availability and marine bird density averaged across seasons (fall, winter, spring) for the New York Bight and Mid-Atlantic regions for (a) northern gannets *Morus bassanus* and (b) red-throated loons *Gavia stellata*. Colors indicate areas of positive (red), negative (blue), and zero (grey) spatial associations (product of local indicators of spatial association and local spatial cross-correlation analyses) between marine birds and forage fish aggregations. Colors are scaled independently for each panel based on minimum and maximum values

are as influential as individual or cumulative forage fish species distributions. While forage fish occupancy and aggregations only explain some of the variation in marine bird movements, these analyses represent a key first step in understanding food web dynamics of marine predators and forage fish off the US Atlantic coast during the seabird non-breeding period.

4.1. Influence of environmental covariates

4.1.1. Key patterns across species

Chl *a* was the most important dynamic covariate, with individuals of all 3 species exhibiting an affinity towards foraging in areas of higher chl *a*, which is thought to be underpinned mechanistically via enhanced primary productivity supporting high biomass of forage fish (Winiarski et al. 2013). This relationship is seen broadly across marine taxa and regions, including breeding northern gannets (Grecian et al. 2018), manx shearwaters *Puffinus puffinus* (Kane et al. 2020), Cape gannets *Morus capensis* (Grémillet et al. 2008), non-breeding red-throated loons (Skov & Prins 2001), and leatherback sea turtles *Dermochelys coriacea* (Dodge et al. 2014). In recent years, the US Northeast Continental Shelf ecosystem has undergone climate-induced declines in chl *a* concentration, representing a fundamental change in lower trophic levels supporting the food web, with a corresponding decrease in pelagic fishes and macroinvertebrates (Friedland et al. 2020b). While predicting future trends is difficult, these ecosystem-level changes could strongly affect non-breeding marine birds, given the strength of the relationship between movement patterns and chl *a*. Given the high correlation between chl *a* and salinity in our dataset, these patterns may relate to areas of freshwater and estuarine influence at tidal river and bay inlets, where the combination of shallow depth, SST, and chl *a* enhance foraging conditions (Skov & Prins 2001). In addition, both loons and gannets exhibited similar relationships with depth, with birds more likely to switch to transit behavior as depth increased. The high correlation between depth and mixed layer depth in our dataset point to the use of areas with a limited water column that may reflect the coastal distribution of some forage fish species (Maravelias 1999, Friedland et al. 2020a). For example, Atlantic menhaden use estuaries, such as the Chesapeake Bay, and coastal habitats as foraging areas (Friedland et al. 2011). It also could indicate associations with coastal stratified waters, similar to the findings of Wakefield et al. (2015). The relationship between seabird movement and these covariates may also relate to accessibility and predictability of prey, as shallow coastal habitats could more consistently constrain the vertical distribution of forage fish, resulting in more stable and predictable distribution patterns (Holland et al. 2021). From late fall through early spring, areas of freshwater influence (e.g. estuaries, coastal regions) may represent enhanced and predictable foraging opportunities when region-wide productivity is reduced (Benjamins et al. 2015).

Duck movement, in contrast, was influenced by multiple static covariates, with localized movement in shallower, flatter, sandy-bottomed regions (i.e. low slope with small sediment grain size). The greater importance of static, bathymetric habitat is consistent with their non-breeding season diet of lower trophic level and benthic resources including clams, mussels, and gammarid amphipods (Perry et al. 2017, White & Veit 2020). Bathymetric habitat characteristics may play a key role in aggregating non-sessile benthic prey, such as amphipods. In fact, Theroux & Wigley (1998) found the highest densities of amphipods in sandy-bottom areas off the northeastern US Atlantic coast. Thus, knowledge of species-specific differences in diet composition, foraging strategies, and energy requirements is necessary for understanding the relationships between habitat features, prey availability, and animal movement (Cox et al. 2018).

Finally, gannet and loon movements were affected by wind velocity, with birds more likely to remain in a transit state as wind velocity increased. This relationship is likely due to movement constraints rather than prey distribution, particularly the energetic costs of flight (Amélineau et al. 2014). Indeed, flap-gliding species like gannets are able to glide more often in higher winds to reduce energy expenditure (Birt-Friesen et al. 1989, Furness & Bryant 1996), while pure flappers like loons must instead utilize tailwinds during high wind conditions to reduce their energy costs (Elliott et al. 2014). During the non-breeding period, when not constrained as central-place foragers, gannets and loons may select and exploit high wind speeds to more efficiently move between prey patches, reducing energy costs.

4.1.2. Role of surface frontal features

Heterogeneity of oceanographic processes, such as frontal features and eddies, play a key role in structuring marine food webs and influencing marine predator–prey interactions. Mechanistically, fronts and eddies enhance primary productivity and contribute to plankton transport via convergence processes, aggregating prey and attracting predators (Bost et al. 2009). Increased marine predator and fish biomass and higher biodiversity has been associated with proximity to frontal features, emphasizing their role in aggregating resources (reviewed by Belkin 2021). Loons were more likely to switch to an area-restricted state with stronger chl *a* fronts and increasing SSHA. This is consistent with previous studies of marine predators, including seabirds, marine mammals, and fishes, in relation to various types of fronts (reviewed by Scales et al. 2014b). The influence of chl *a* fronts on loon movement was weaker than that of chl *a* concentration, possibly indicating interplay between high concentrations and front strength, particularly in estuarine waters, where multiple factors, including freshwater influence, temperature, salinity, and depth characteristics, likely interact in frontal formation (Scales et al. 2014b). Ducks exhibited a similar relationship, with higher SSHA relating to localized movement. Eddies (indicated by higher SSHA) may provide enhanced foraging opportunities. In particular, the Nantucket Shoals, where ducks were concentrated, are characterized by shallow banks with a sandy bottom and anticyclonic currents (e.g. eddies) which act to aggregate phyto- and zooplankton, with *Gammarid* amphipods as an important prey item (White & Veit 2020).

In contrast, we found no relationship between gannet movements and resource-aggregating features, although gannets have exhibited associations with fronts in other regions during the breeding season (Skov et al. 2008, Votier et al. 2011, Scales et al. 2014a). While we found evidence that loons use estuarine fronts, these are often characterized by high turbidity (Belkin et al. 2009), which may not prove fruitful for plunge-diving gannets that rely more heavily on detecting prey from the air. Thus, gannets may utilize resource-aggregating features as cues for area-restricted behavior that we may not have adequately captured due to front-detection methods or the suite of environmental covariates and frontal metrics considered. Alternatively, gannets may not be reliant on frontal features during the non-breeding period. The absence of a discernible influence may relate to regional or seasonal dynamics given that the strength of physical and biological forcing can vary widely across ecosystems and time (Dodge et al. 2014, Byrne et al. 2019). For example, Byrne et al. (2019) found relationships between mako sharks

Isurus oxyrinchus and frontal zones in the Gulf of Mexico, but not in the temperate waters off the US Atlantic coast. Thus, differences in gannet response to fronts throughout their range and across seasons may be due to regional and seasonal changes in frontal formation driven by upper ocean mixing and stratification (Olsen 2002). The northeast US Shelf ecosystem is characterized by thermal destratification during the winter and spring, though vertical salinity gradients persist to influence stratification (Li et al. 2015). Indeed, sub-surface level variables, including mixed layer depth and bottom temperature, were important variables in the forage fish distribution and aggregation models included in this study (Friedland et al. 2020a, Goetsch et al. preprint doi:10.22541/au.167163077.72855489/v1), and are key to structuring the occurrence and biomass of prey (Evans et al. 2021). Mixed layer depth was a candidate variable in our models but was excluded due to high correlation with bathymetric depth, again exemplifying interplay across variables contributing to the aggregation of resources. Thus, it is possible that stratification plays a key role in area-restricted behavior for gannets, as has been found in previous studies (Wakefield et al. 2015).

4.2. Spatial patterns with forage fish

We found relatively consistent spatial patterns between gannet and loon movements and forage fish species distributions and aggregations, with variation in the strength and location of these patterns across seasons. Round herring (fall) and Atlantic menhaden (spring) exhibited the highest spatial cross-correlation with both gannets and loons, in addition to bay and striped anchovies and butterfish, suggesting that these could be important prey resources during the non-breeding season. While much less is known about most of these forage fish species, Atlantic menhaden represents an important prey species for many marine predators, including piscivorous fish, seabirds, and marine mammals (Fifield et al. 2014, Anstead et al. 2021), and has been subject to the largest commercial fishery by volume on the Atlantic coast for the last century (Anstead et al. 2021). Moreover, menhaden undergo an extensive seasonal migration which corresponds to the spatial associations we observed, with menhaden migrating southward offshore in the fall, and northward, near-shore in the spring, with multiple age classes seasonally inhabiting estuarine and coastal habitats (Bowen & Avise 1990, Anstead et al. 2021). While little is known about the diet composition of gannets and loons in the non-breeding period in the region, evidence from gannets in the breeding season in Atlantic Canada suggests that diet includes menhaden (Mowbray 2020), in addition to Atlantic mackerel, capelin, various herring species, and squid (Montevecchi 2007, Garthe et al. 2011, Davoren 2013). Anecdotal observations of menhaden in gannet regurgitate during the at-sea captures for this study corroborate our findings. Thus, clupeids, including menhaden, may represent a key trophic link for seabirds during the non-breeding season, as well as during the breeding season.

Spatial associations with other forage fish species varied in strength across marine bird species, season, and location. Overall, seasonal species distributions of forage fishes explained relatively little spatial variation in marine bird movement patterns (<10%). This suggests that these trophic links are complex and variable, with other factors, such as community-level and prey-patch dynamics, likely influencing these patterns at multiple spatial and temporal scales. Spatial linkages between marine predators and forage fish could be weakening over time with the rapid nature of climate change (Hollowed et al. 2012), or there may be other unexamined factors that cause tradeoffs in marine bird behavior in the non-breeding period and result in weaker spatial connectivity with prey than predicted.

Further investigation of non-breeding period diet for gannets and loons would help to clarify these potential linkages. Given that these forage fishes are also experiencing multiple pressures due to climate change (Friedland et al. 2019, 2021), in addition to fishing pressure, careful management of these species could help to ensure future population viability to support both fisheries and marine predators (Cury et al. 2011).

Forage fish aggregations were more spatially correlated with gannet and loon movements than were distributions of forage fish species as measured via bottom trawl surveys. Aggregation number and surface availability (a combination of number and size) showed the highest spatial associations. Particularly for visual predators, the number of aggregations likely increases detectability of prey patches. A study of black-legged kittiwakes, thick-billed murres *Uria lomvia*, and northern fur seals *Callorhinus ursinus* found similar patterns, in which marine predator species had stronger spatial links to patchiness of prey than to distribution of biomass (Benoit-Bird et al. 2013). This suggests that the number of aggregations making up prey patches may be key to explaining marine predator use of those patches. Spatial associations where surface-level forage fish aggregations and marine bird densities were both high primarily occurred in coastal areas near Chesapeake Bay, Delaware Bay, and the New York Bight. Thus, resource availability as measured by surface aggregations may be a stronger predictor of bird movements given higher predictability in transition zones that are highly influenced by estuarine waters with freshwater influence (Woodland et al. 2021) than in more stable waters farther offshore during periods of thermal destratification (Li et al. 2015).

4.3. Limitations and sources of uncertainty

4.3.1. Mismatch in spatiotemporal scales

While these patterns provide insight into trophic links, spatial correlation patterns between marine birds and forage fish were generally low (<0.3), and relationships with resource-aggregating features (e.g. fronts) were weak. Mismatch in temporal and spatial resolution of predator and prey data and resource proxies (Grémillet et al. 2008, Campbell et al. 2019) can lead to weak or ephemeral spatial associations (Benoit-Bird et al. 2013). Given the coarse resolution of satellite telemetry data in this study, the area-restricted states identified represent large-scale movement patterns, and therefore may not capture finer-scale behaviors used for locating prey. Similarly, the forage fish data used in this study have a seasonal temporal resolution, and the spatial extents of forage fish occupancy and aggregation models differed; while large-scale prey distribution patterns may broadly shape foraging ranges, finer patch-scale dynamics, such as daily activity patterns, distance between prey patches, and patch characteristics, may influence predator–prey interactions (Carroll et al. 2017, Suraci et al. 2022). Prey patch-level analysis may provide stronger coherence between predators and their prey than a larger arbitrarily defined grid (Benoit-Bird et al. 2013). In particular, prey patch persistence is important to marine predators (Clapham et al. 1993, Hedd et al. 2012, Davoren 2013) as they need to reliably locate resources while minimizing energy expenditure in order to survive; however, aggregation persistence was not included in this study.

4.3.2. Data collection biases

While individual tracking is a powerful tool to understand the movement and behavior of marine species, this sampling methodology can introduce biases such as population sampling bias (Soanes et al. 2013), and capture location and tag failure/loss biases (Hays et al. 2020). This study included a large number of tagged individuals, but capture locations were concentrated in a few coastal areas (e.g. Chesapeake Bay, Nantucket) where we in turn found high use. As such, we recognize that these spatial patterns may not be fully representative of the non-breeding distributions of these species.

Biases may also be introduced in the forage fish species occupancy estimates used in this study, which are based on bottom-trawl data that are influenced by methodology (e.g. net type, mesh size, towing speed), as well as biological factors (e.g. avoidance behavior, patchiness of distribution, benthic–pelagic habitat preference; Stoeckle et al. 2021). In addition, these models lack coastal distribution information, particularly in bays and estuarine habitats such as the Chesapeake Bay, which represent high-use areas by our study species during the non-breeding season, and serve as crucial nursery areas and foraging grounds for many fish populations (Wood & Austin 2009). Integrating coastal trawl data with the bottom trawl data used in this study could improve our understanding of trophic links in key areas for marine birds.

Digital aerial surveys represent a novel method for surveying forage fish aggregations, but the depth at which forage fish aggregations are detectable in aerial imagery, and the oceanographic conditions that affect this detectability, are not well understood (Buckland et al. 2012) and warrant further investigation. In particular, oceanographic conditions likely influence the level of survey effort in a vertical plane (e.g. depth of aggregation detection; Colefax et al. 2018) that is not accounted for in the forage fish modeling. These same conditions may also affect detectability of forage fish by marine birds, which likely varies by foraging strategy, as the eyes of pursuit- and plunge-divers have different adaptations for underwater versus aerial vision (Machovsky-Capuska et al. 2012), but it is unknown the degree to which detectability by digital aerial surveys and marine predators correspond and how other visual cues (e.g. movement) beyond visibility affect prey detection by marine predators. This survey method also lacks information on the species composition, 3-dimensional volume, and within-aggregation density of detected aggregations. In particular, the relationship between horizontal and vertical dimensions of fish aggregations is highly variable, unstable, and dependent on various characteristics, including species, age class, behavior, and environmental conditions (Pavlov & Kasumyan 2000, Gerlotto & Paramo 2003). These biases likely limit our ability to link patterns of marine birds and forage fish, and integration among multiple methods may help to address these issues.

4.4. Conclusions

This study provides insight into the environmental factors influencing marine bird movement behavior, highlighting the importance of productivity and freshwater influences in aggregation and predictability of resources. Water depth also drove movement behaviors in these species, perhaps through further connection with water column stratification. In exploring seasonal patterns of spatial overlap between marine birds and forage fish species distributions and surface aggregations, we found evidence of the importance of round herring, Atlantic menhaden, and surface aggregations of forage fish to foraging distributions of gannets and loons.

This study represents a first step in understanding trophic relationships between non-breeding marine birds and forage fish in the US Atlantic. Understanding the nature of scale-dependent predator–prey dynamics can help provide the knowledge needed to effectively implement conservation management strategies (Allen & Singh 2016, Cox et al. 2018). In particular, anthropogenic activities and climate change are driving alterations in the distributions and behavior of marine species, which can have consequences for energy flow, population dynamics, and ecosystem structure (Grémillet et al. 2008). With continued technological and analytical advancements, direct incorporation of lower trophic level information into our understanding of marine predator behavior could help us to better understand the drivers of movements and foraging activities, as well as to identify the important prey populations and habitats, such as estuaries, upon which upper trophic level predators rely. Such information could help to effectively balance human use of the oceans with the conservation of marine predators.

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