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An Eulerian perspective on habitat models of striped bass occurrence in an offshore wind development area

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Abstract

Offshore wind energy development, including along the US Atlantic coast, frequently occurs within important multispecies migration corridors; however, assessing the regional factors influencing the local Eulerian occurrence of these species poses a significant challenge. We used generalized models incorporating lagged variables and hierarchical formulations to account for temporal dependencies and hierarchical structure that occur outside the narrower frame of a sampled project area. Acoustically tagged striped bass, the most frequently detected species regionally, were sampled using a gridded acoustic telemetry array in the Maryland Wind Energy Area of the US Mid-Atlantic Bight. The daily occurrence of striped bass was better explained by broad-scale sea surface temperature warming patterns than by local concurrent environmental conditions, demonstrating the importance of drivers that occur across the wider spatial scales of migration. Weekly residency patterns were similar between tagging origin groups, suggesting that Chesapeake Bay, Hudson River, Delaware Bay, and other Northwest Atlantic populations migrate synchronously through the Southern Mid-Atlantic Bight and are similarly influenced by sea surface temperature. Our study demonstrates that adapting an Eulerian approach to include lagged variables can improve regional assessments of fish on the move until richer Lagrangian insights become possible through future coordination of telemetry arrays throughout the Mid-Atlantic flyway.

Introduction

Globally, offshore wind energy development is increasing in both scale and pace. In particular, vast regions of the US Atlantic shelf slated for offshore wind farms (OWFs) overlap broadly with known migration corridors of fishes, marine mammals, and birds (Gulka and Jenkins 2020). As of December 2020, 16 sites amounting to 7051 km² along the US Mid-Atlantic Bight (MAB) have been leased for future construction (Fig. 1; Bureau of Ocean Energy Management, 2022). Although OWF development is already prompting an increase in focused offshore monitoring efforts, few design approaches have been developed or applied to test how changes in the coastal environment will influence migrating animals. Previous marine fauna impact studies have typically focused on explanatory factors occurring only within focal study regions, overlooking the importance broader-scale habitat, or population dynamics may hold for mobile species. One potential approach to address this gap is through sampling and modeling frameworks that consider the influence of environmental gradients and demographic structure on migration behaviors (Bailey et al. 2014). In this study, we analyze the influence of both local and broad-scale factors on the occurrence of Atlantic striped bass *Morone saxatilis* using an Eulerian approach that may help improve future studies

of migratory fishes in coastal movement corridors (Fig. 1a). Striped bass was chosen as a model migratory species because it is the most frequently detected acoustically-tagged species within the large MAB region of study (Secor et al. 2020a).

To improve the accuracy of models predicting migratory species incidence, it is crucial to measure flyways (also known as multispecies migration corridors; Rothermel et al. 2020) at the same temporal and spatial scales experienced by moving fish, taking into account past environmental cues (Kavanaugh et al. 2016, Scales et al. 2017, Schneider 2018). Due to the transience of migrating species in specific habitats, it is often necessary to continuously track individual animals over time to gather data at a sufficiently fine level of detail to support reliable distribution models (Royer et al. 2005, Maxwell et al. 2011, Hazen et al. 2017). These methods can be considered as a Lagrangian approach to monitoring, in which environmental variables, and the animal's selection of these variables, are known for each location and time step (Fig. 1b). However, when there are specific areas of concern, as is the case with OWFs, we believe targeted monitoring of discrete project areas will likely be prioritized initially over larger regional assessments of individual movements due to resource constraints.
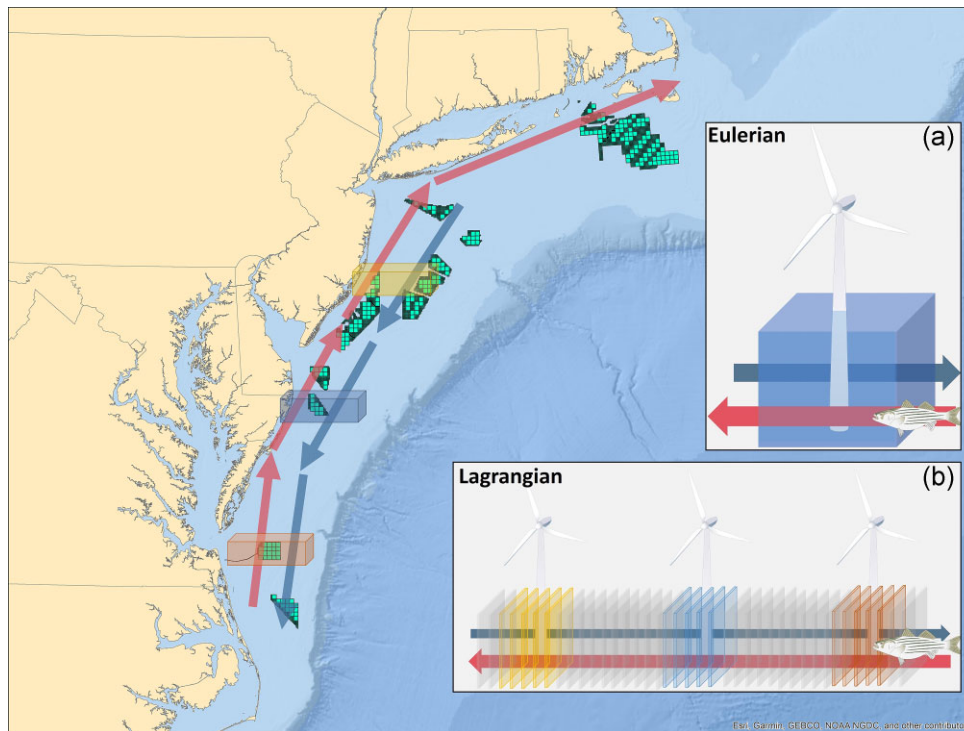
Figure 1 Conceptual overview of habitat modeling through OWFs (main figure) along the MAB migration corridor of striped bass. Locations of proposed OWFs (turquoise-colored grid fields; left, map) overlap with known migration routes of striped bass north in the Spring/Summer (red arrows) and south in the Autumn/Winter (blue arrows). An Eulerian modeling approach (a) is based on a fixed sampling window (transparent boxes; left, map) but can incorporate habitat variables both within and outside the impact region to account for broader drivers of animal movement. Under Lagrangian approaches (b), continuous tracking of individual animals allows for direct correlation between fish behavior and measured environmental variables; however, in a stationary telemetry array, this method would entail multiple discrete snapshots of data taken along a migration pathway such that the sampling frame instantaneously resets over time.

Although acoustic telemetry methods now support both remote (i.e. >20 km offshore) and long-term (> 1y) deployments, stationary receiver arrays are typically small and discrete compared to the coast-wide scale of marine fish migration pathways. Within this framework, habitat or species occurrence models that assume stationary (resident behaviors) might falsely ascribe coincident habitat variables as driving incidence (Haulsee et al. 2020). Alternatively, migration could be modeled throughout an entire flyway, but this remains impractical for most species due to limited telemetry assets and the dynamic, wide-ranging nature of coastal migrations. Instead, when monitoring is constrained to a given project area, as will likely occur on an individual OWF basis (Fig. 1a), analysis should include adjustments for species on the move. Multivariate and generalized modeling approaches support tests of lagged variables and can include unique hierarchical formulations that account for habitat and demographic information gathered from outside the window of an individual detection event.

Striped bass exhibit regular seasonal migrations in shelf regions where OWFs will operate (Secor et al. 2020b, 2020c) and are the focal species of our study. They have received >1000 acoustic tags within the region (Rothermel et al. 2020) and are the most-detected species within our study array. The range and seasonality of their migrations are similar to other MAB migratory species (Secor et al. 2020a). Coastal striped bass in the MAB mostly originate from either the Hudson River, Delaware Bay, or Chesapeake Bay estuaries (Wirgin et al. 1997, Kneebone et al. 2014, ASMFC,

2016). Within these populations, larger individuals (>80 cm total length) undertake shelf migrations; smaller individuals are more resident to natal estuaries (Secor et al. 2020b). Though individual striped bass may vary in their propensity to migrate, many undergo predictable oceanic movements in which they mix with members of multiple populations during northward migrations in the spring and southward migrations in the autumn and winter (Wirgin et al. 2020). Still, little is known regarding habitat selection while on the move. Additionally, shelf migration pathways could vary by population or demographic attributes, as found for salmon (Crossin et al. 2007, Hanson et al. 2008, Rogers and Schindler 2008).

As striped bass and other migratory fish transit OWFs, they will encounter fields of turbine subfoundations, transmission grids, and substations, and regions of increased vessel traffic. The addition of structure to the water column by wind turbines in particular is predicted to alter food webs (Degraer et al. 2020, Hutchison et al. 2020, Perry and Heyman 2020) in regions currently dominated by unstructured sand and sediment (Rothermel et al. 2020). Such changes in habitat or prey availability could elicit novel migration and movement behaviors by striped bass. Species across the MAB are also likely to experience continued fishing pressure and changing environmental conditions that could further alter migratory patterns. Detecting the response of migratory fauna will thus depend on a baseline understanding of broader regional cues that likely vary seasonally, and influence striped bass occurrence in any given OWF.
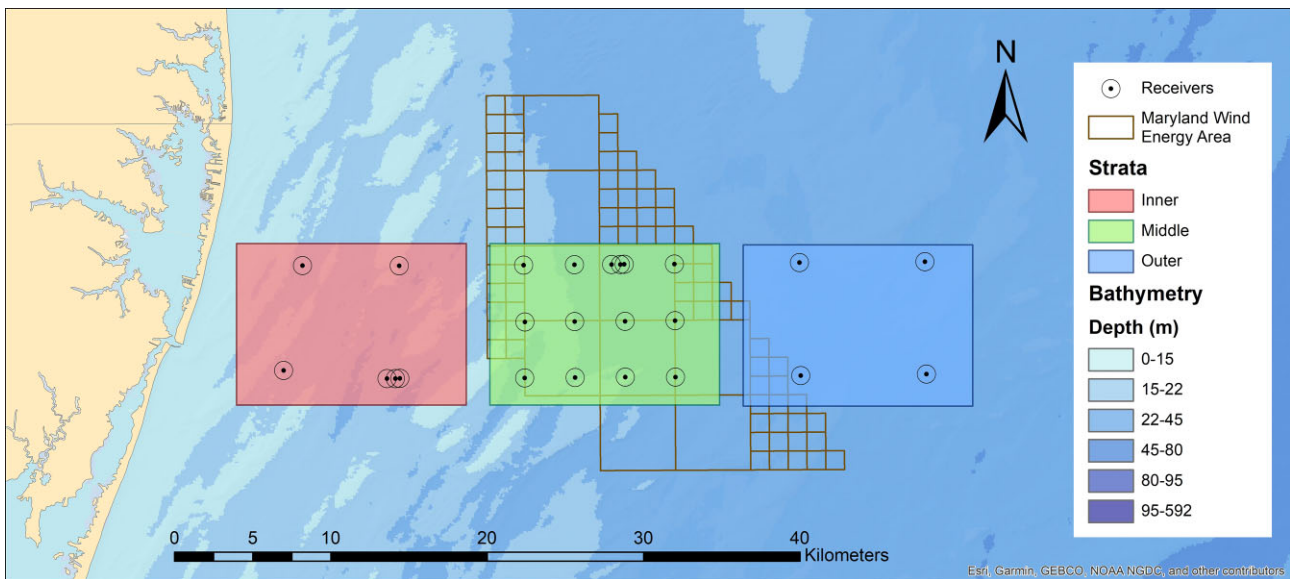
Figure 2 Map of the study region off the coast of Maryland (Fig. 1; blue box on the map, left), including acoustic receiver array design, the gridded MD WEA, and bathymetry features. Circles surrounding receivers represent the maximum expected 1000 m detection radius and range test sites are shown within the Inner and Middle Strata as overlapping circles of presumed mean detection range.

The goal of this study was to present a modeling framework for assessing the drivers of occurrence for species migrating through discrete acoustic telemetry monitoring areas. Here, striped bass was used as a test species to examine the importance of variables occurring both within and outside a section of their migration corridor slated for OWF development. This study utilizes baseline data that were collected and initially analyzed empirically by Rothermel et al. (2020) for a 2-year biotelemetry study within the Maryland Wind Energy Area (MD WEA), located 16–46 km offshore of Ocean City, MD, USA (Fig. 2). Past habitat-selection modeling in the Mid-Atlantic indicated that temperature, depth, and satellite-derived measures of productivity should influence marine fish distributions (Manderson 2016, Breece et al. 2018, Haulsee et al. 2018). We also anticipated that occurrence within these transit habitats is influenced by environmental conditions occurring elsewhere across the broader MAB. Additionally, migration timing could differ by population (Hudson, Delaware, or Chesapeake), for which tagging location can be used to inform likely population sources. Thus, for a single region along the MAB flyway slated for OWF development, we tested the influence of both coincident and lagged variables and included hierarchical formulations of population structure to account for complex drivers of occurrences during seasonal migrations. The presented modeling framework and the results are used to discuss applications for future assessments of occurrence and migration behaviors of striped bass or other species with similar demographic complexities that undertake coastal migrations through OWF regions.

Materials and methods

The study site is an OWF area planned for c. 2 GW capacity and >100 monopile turbines, which is leased to US Wind Inc. in the southern MAB (ESS Group 2022) and termed here as the MD WEA (Maryland Wind Energy Area). The shelf habitat off Maryland is biologically productive, in part due to land-based inputs from the Delaware Bay, with phytoplankton biomass fluctuating according to seasonal cycles of strat-

ification (O'Reilly and Busch 1984, Townsend et al. 2006). While a strong thermocline exists for most of the year (Spring–early Fall), this "cold-pool," in which warmer surface waters overlay cooler residual winter bottom water, is disrupted with the onset of storms in late fall that de-stratify the water column and replenish shelf nutrients, leading to phytoplankton blooms (Houghton et al. 1982, Xu et al. 2013). Our study area was 10–50 km offshore with depths of 10–45 m depth (Fig. 2).

First, we sought to construct a model of relative occurrence to predict the spatial density of striped bass at a daily resolution, for combined detection data, not including potential population as a factor. To better understand drivers of transient occurrence, this model included regional sea surface temperature (SST) change over the recent past (e.g. Reyier et al. 2014). Second, we evaluated the time that individuals spent in the region depending on environmental conditions and tagging region of origin (index of potential population source or behavioral group), which owing to data limitations, analysis was conducted at a weekly resolution for the entire array. Sampling assumptions differed between these objectives and associated scales of response, so three unique modeling approaches were employed for daily, weekly, and population-based research objectives (Table 1). Through random effects and hierarchical fixed effect structures within a generalized additive mixed model (GAMM) framework, we adjusted for biases associated with central spatiotemporal autocorrelation and group-based heterogeneity (Bolker et al. 2009). The analysis was weighted by the detection efficiency of acoustic telemetry receivers, which varied with stratification and ambient noise (principally surface winds), both seasonally and subregionally within the study array. Detection efficiency for each receiver was incorporated based on tests and an analysis within the same array (O'Brien and Secor 2021).

Acoustic telemetry array and transmitters

The occurrence of striped bass was monitored in the Maryland shelf region using an acoustic telemetry array spanning from the coast to 10–50 km offshore (Fig. 2). Approximately

Table 1. Summary of intended purpose and modeling approach for each research question. See "Methods" section for additional explanation. GAMM = generalized additive mixed model; HGAM = hierarchical generalized additive mixed model.

Category	Objective	Modeling approach	Response variable	Level of organization	Autocorrelation compensation	Random effects
Relative daily occurrence	Predict fine-scale relative occurrence of test species	GAMM	Number of individuals per receiver	Temporal: daily spatial: receiver-based	Distributed temperature lag, Range test offset	Receiver site and year of study
Individual weekly residence	Determine predictors of individual residence	GAMM	Number of days per week	Temporal: weekly spatial: array-wide	Lagged residency response	Individual ID
	Evaluate residence response by population (tagging origin)	HGAM submodel	Number of days per week	Temporal: weekly spatial: array-wide	Lagged residency response	Tagging origin

500 acoustically tagged striped bass, of which 315 were detected within the project array (Rothermel et al. 2020, Secor et al. 2020b), were at large during the course of this study. The array of 20 acoustic-release receivers (VR2AR, 69 kHz; VEMCO-INNOVASEA, Bedford, Nova Scotia, Canada) was deployed November 2016–December 2018 to detect the presence of acoustically-tagged striped bass both inshore (inner stratum: 10–20 km from shore) and offshore (outer stratum: 40–50 km offshore). The design allowed sampling of depth (10–45 m; Fig. 2) and temperature gradients. The middle MD WEA stratum contained 12 receivers spaced at 3.2 km (E-W) or 3.6 km (N-S) intervals. The other strata each consisted of four receivers with 8 km spacing. Additional sets of two receivers each were deployed in the inner and middle strata as part of a concurrent range test study (see the section "Detection efficiency adjustments"). Each bottom-moored receiver recorded bottom temperature (°C) and noncalibrated, relative ambient noise at 69 kHz (mV) at hourly intervals. Detections of unique transmitter codes were logged on a continuous basis. Data were downloaded during tri-annual maintenance cruises. Detected codes were matched to species and tagging information provided by data-sharing agreements and the regional Atlantic Cooperative Telemetry (ACT) Network (Bangley et al. 2020). Detections were filtered to include only those codes heard more than once to correct for false detection and code collision (Pincock 2012).

Detection efficiency adjustments

To reduce temporal autocorrelation caused by underlying fluctuations in acoustic transmitter detectability, site- and day-specific adjustments were incorporated into the relative occurrence model. Seasonal and environmental effects on VR2AR detection range were quantified and modeled in a 1-year field test concurrent to the array deployment (O'Brien and Secor 2021), and directly incorporated into the model formulations of the present study. Testing took place at both a shallow Inner stratum site and a relatively deeper Middle stratum site (Fig. 2). The distance at the 50th percentile detection efficacy (D50) was estimated for each day using a GAMM model. Predicted D50 ranged from ~10 to 1100 m, and was added as an offset to the GAMM habitat models. The predicted range represented an index of sampling effort and was used to adjust each day's sum of detections such that occurrence recorded on days with lower D50 values were up-weighted and in-

cidence recorded on days with larger detection ranges were down-weighted. Additional details of range test modeling procedures can be found in O'Brien and Secor (2021).

Environmental and demographic data

Environmental and oceanographic variables were obtained *in situ* from deployed receivers and remotely through satellite-derived values accessed via Environmental Research Division's Data Access Program (ERDDAP) servers (Simons 2017, Table 2). Most variables were available on a daily basis at the scale of the telemetry array with the exception of chlorophyll-a concentration (CHL-A; http://oceancolor.gsfc.nasa.gov/), wherein cloud cover prevented matches for nearly 80% of the daily detection events. CHL-A values were averaged over 8 days, which allowed retention of 90% of the dataset, and log-transformed prior to modeling to reduce the influence of skewed outlier values. Temperature variables included an index of water column temperature stratification (ΔT), where higher absolute values of ΔT represent increased stratification strength.

Species demographic data were included in hierarchical formulations of individual weekly residency GAMMs to allow different responses according to population (Table 1). Though we did not have information on genetic origin, tagging region was known for all telemetered individuals (Table 2). The tagging location was often informative of the population of origin as, aside from those tagged in mixing areas in offshore Massachusetts (Kneebone et al. 2014), much of the tagging occurred on spawning runs. Despite the lack of true population data (e.g. populations defined through lineage), location of tagging was retained as a variable of interest related to past group migration behaviors that could have implications for management. Here, we anticipated that fish tagged with transmitters during their likely spawning runs in the Kennebec River, ME; Hudson River, NY; Potomac River, MD; and Delaware River, DE might exhibit migratory behavioral patterns unique to their population of origin, whereas mixed stocks of fish tagged off the coast of Massachusetts on summer feeding grounds might represent a mix of behavioral tendencies across tagging groups.

Daily relative occurrence model

The daily relative occurrence of striped bass within the array (incidence) was modeled using a GAMM with a distributed

Table 2. Metadata of variables to be used in range test, relative occurrence, and individual weekly residence models. Units, spatiotemporal resolution, and general description are provided.

| Variable | Units | Resolution | | Description |
		Time	Space	
Bottom temperature	Degrees C	Hourly	Receiver	Average water temperature recorded by receivers
Absolute noise	Millivolts	Hourly	Receiver	Average noise level at 69 kHzrecorded by receivers
SST	Degrees C	Daily	Array	Multi-scale Ultra-high Resolution SST satellite derived; JPL MUR MEaSUREs Project 2015
ΔT (stratification)	Degrees C	Daily	Array	SST- Bottom temperature
Bathymetry	Meters	N/A	3 arc-seconds (90 meters, Receiver)	NCEI's Southeast Atlantic Coastal Relief Model; National Geophysical Data Center 1999
Log-transformed chlorophyll-a concentration (CHL-A)	$\log(\text{mg m}^{-3})$	Weekly	Array	MODIS-Aqua; NASA Goddard Space Flight Center 2018
Location of tagging	Categorical	N/A	MAB	Region where fish were tagged by researchers with data-sharing agreements in place

lag non-linear modification (Gasparrini et al. 2017). Individual incidence was calculated by tallying the total number of unique tag codes detected at each receiver each day. The resulting skewed and over-dispersed data were modeled using a zero-inflated Poisson distribution. To account for differences in behavior between northern and southern migration phases (Kneebone et al. 2014, Secor et al. 2020b, 2020c), relative occurrence was modeled separately for Autumn/Winter (Sep–Feb) and Spring/Summer (Mar–Oct) seasons, respectively. Receiver site and study year were added as random intercepts to limit spatial autocorrelation and to account for inter-annual differences in the number of fish detected. All modeling was conducted in R statistical software (R Core Team 2020) using the mgcv package (Wood and Wood 2019).

SST, lagged SST, bathymetry, and CHL-A were considered as environmental covariates. The dlnm package (Gasparrini 2011) was used to define an exposure history to SST in the form of lagged values of SST: the difference between SST on each of the 30 days prior to the sampled incidence and the SST on the day of sampled incidence. The resulting temperature-difference-by-lag-number interaction was used as an index representing the effect of SST in unsampled regions that could drive migration through, and occurrence in, the sampled region. Although a coarse assumption, lagged values should represent those values occurring at lower and higher latitudes during migration seasons, owing to strong latitudinal gradients in SST (Richaud et al. 2016). The effects of concurrent and lagged SST and the other environmental covariates were evaluated for each migration season.

The exposure-lag-response associations between relative abundance and SST were implemented in the standard mgcv R package framework using a bi-dimensional cross-basis spline. To account for seasonality in the data, day-of-year (DOY) was included as a cyclic spline predictor variable. All other variables were modeled using thin plate regression splines. Knots were constrained to avoid overfitting based on our *a priori* expectations on the scale at which each parameter would be relevant (Wood 2003); results from Rothermel et al. 2020 regarding temperature and depth selection, daily residency, and transit rate were used to infer general assumptions of striped bass sensitivity to environmental variables. The maximum-allowable number of knots was set to 11 for lagged SST, which

assumes that there is limited sensitivity of the fish to temperature changes <2°C, and to 16 for days of lag, which assumes limited sensitivity to changes that occur on a scale <2 days (Table 3). Additional knot constraints included 15 for depth (assumed limited sensitivity to changes of depth <2 m), 11 for day-of SST (changes less than 2°C), 10 for CHL-A (changes <0.5 log mg m^{-3}), and 14 for DOY (changes less than biweekly). Interactions between depth, day-of SST, CHL-A, and DOY were included using a tensor product smooth term to account for differing units among interaction variables (Wood et al. 2013). Only one of these interactions was allowed per modeling iteration to limit complexity.

All possible model combinations were tested and ranked according to the AIC score. Final model residuals were visually checked for temporal and spatial correlation using autocorrelation function (ACF), partial autocorrelation function (PACF), and semivariogram plots. Overall model performance was evaluated with k-fold cross validation in which the data were randomly split into training (75%) and testing (25%) sets over each of 5-folds. The root mean square error (RMSE) and average error between observed abundance in testing data and training model-predicted abundance were then calculated and used to assess model predictive error (Potts and Elith 2006).

Weekly residence model

For weekly residency models, the total number of days with confirmed detections within each week (0–7) were regressed against environmental variables using a quasibinomial GAMM approach (Table 1) to account for underdispersion produced by frequent zero-detection weeks. A zero-inflated binomial approach was also considered, but not used, due to similar results and a much longer model runtime (Rothermel 2019). Transmitter code was included as a random intercept to account for correlation from repeated measures of the same individual. "Population"-level differences in individual response were tested by considering tagging region as a fixed effect in the model. Differences between tagging regions were evaluated using the *post-hoc* multiple comparison Wald test in the *itsadug* R Package (Van Rij et al. 2015).

Table 3. Summary of configuration details and assumptions for each modeling approach. GAMM = generalized additive mixed model; HGAM = hierarchical generalized additive mixed model.

Modeling approach	Candidate smooths	Spline	Knots	Limit of effect on response
GAMM	SST	Thin plate	11	2°C
	Depth	Thin plate	15	2 m
	CHL-A	Thin plate	10	0.5 log mg m^{-3}
	DOY	Cyclic Cubic	14	14 days
	SST lagged exposure	Distributed non-linear		
	Lagged SST		11	2°C
	Days of Lag		16	2 days
GAMM	SST	Thin plate	11	2°C
	Depth	Thin plate	15	2 m
HGAM	CHL-A	Thin plate	6	0.5 log mg m^{-3}
submodel	Week	Cyclic Cubic	27	2 weeks

Week-of-year, CHL-A, and SST were examined for their effect on weekly residency. Lagged SST was not considered for the weekly residency model as it was not possible to define an exposure history within the necessary random and fixed effects framework and because the analysis was focused on potential population-level differences in response to environmental variables occurring within the WEA. Each covariate was specified using thin plate splines with the exception of week-of-year, which was modeled with a cyclic spline. Based on *a priori* expectations for the scale at which biological responses might occur as outlined in section "Daily relative occurrence model", knots were limited to 11 for SST (changes <2°C), 6 for CHL-A (changes <0.5 log mg m^{-3}), and 27 for week-of-year (changes less than bi-weekly). Although models likely suffered from concurvity, thus increasing the potential for biased estimates or Type I error, SST and week-of-year were both retained so that the influence of each term could be evaluated while accounting for individual-level variability.

Preliminary analysis showed that inclusion of individual random intercepts did not resolve all residual temporal autocorrelation and, in contrast to the daily-resolution incidence modeling (see previous section), the use of a D50 offset did not effectively diminish correlation at the weekly timescale. A state-dependence approach, in which past states are allowed to influence the current state of a variable, was used to model and reduce remaining serial autocorrelation in weekly residence probability. The state-dependence model for lagged residency was created using a first-order smoothed autocorrelation term that corresponded to the number of days an individual fish was detected in the previous week. Residual autocorrelation was checked using ACF and PACF plots. Residual spatial correlation was not a concern in this analysis, as residency was modeled over the entire array.

Population-level differences in residency response

When significant differences in weekly residency were identified between tagging regions (populations) in GAMM *posthoc* tests, hierarchical generalized additive models (HGAMS) were used to further evaluate the group-level differences in response to environmental and temporal covariates (Table 1). HGAMs allow for varying degrees of nonlinear response over different grouping levels (Pedersen et al. 2018). Significant predictors of residency were each tested individually; the smoothed functional response in each model was allowed to vary by group (tagging region), but group-level functions

were pooled in a common response. The hierarchical relationship between predictor variables and tagging-region groupings was specified using different variable and factor relationships. First, the global response of all groups to the variable of interest (either week-of-year, SST, or CHL-A) was specified using a thin plate regression spline for SST and CHL-A or a cyclic spline for week-of-year with the same knot specifications that were allowed in the base weekly residence models (see section "Weekly residence model"). Next, the predictor was modeled according to each tagging group factor using the factor-by-smooth model specification to allow additive responses to differ. A random intercept for tagging group was included to properly scale the response as by-factor smooths are centered due to identifiability constraints (Pedersen et al. 2018). Collinearity between the global response and group-level responses was deliberately penalized and reduced, thereby increasing certainty around the global smoothed predictor (Wieling et al. 2016, Baayen et al. 2018). Model diagnostics and performance were not assessed for HGAMs since they were intended to visualize the group-level differences in response to individual environmental covariates and not to predict residency.

Results

Drivers of daily relative occurrence

Twenty-five daily occurrence models were considered for each season and SST formulation (day-of vs lagged SST), resulting in 100 total models. The top-ranked lagged SST models performed better than equivalent day-of SST models for both migration seasons (Autumn/Winter and Spring/Summer; Table 4). For the Autumn/Winter migration season, the two best models both contained lagged SST and an interaction between depth and DOY (Table 4), with the top-ranked model also including CHL-A concentration as a predictor of occurrence. During the Spring/Summer season, the top-ranked model contained an interaction between Depth and CHL-A along with terms for lagged SST and DOY.

The top-ranked model for Autumn/Winter showed that large decreases (>5°C) in SST over the previous 5–10 days increased the likelihood of striped bass presence in the MD WEA. However, smaller increases (0°C–5°C) in SST over the previous 15–20 days led to the highest predicted striped bass incidence (Fig. 3). A similar pattern was observed during Spring/Summer, with slightly larger increases (3°C–10°C) in SST over still longer time scales (>20 days) leading to the

Table 4. Summary of GAMM models of daily relative occurrence including equation terms, degrees of freedom (df), Akaike information criterion (AIC), and % deviance explained for the top five predictive habitat models for each season and SST formulation, ordered by AIC score. Considered predictors are chlorophyll-a concentration (CHL-A), magnitude of SST change (SST Δ1–13), DOY, and depth. Model term "s" represents singular smooth terms (single factors) and "t2" represents tensor-product smooth interactions (interaction between factors with different scales). Selected models are at the top of the table for each season and SST formulation.

Model terms	df	AIC	Deviance explained
Autumn/Winter, lagged SST			
∗s(SST lag) + s(CHL-A) + t2(DOY, Depth)	113.83 097	5378.974	68.5%
s(SST lag) + t2(DOY, Depth)	105.93 167	5429.422	67.7%
s(SST lag) + t2(DOY, CHL-A)	101.78 233	5621.409	63%
s(SST lag) + s(Depth) + t2(DOY, CHL-A)	101.61 817	5621.946	62.9%
s(CHL-A) + t2(DOY, Depth)	49.59 834	5780.423	58.9%
Autumn/Winter, day-of SST			
s(CHL-A) + s(SST) + t2(DOY, Depth)	58.89 882	5635.680	61.8%
s(DOY) + s(CHL-A) + t2(Depth, SST)	61.32 394	5650.450	61%
s(SST) + t2(DOY, Depth)	54.33 912	5667.180	61.4%
s(DOY) + t2(Depth, SST)	54.95 134	5711.257	59.8%
s(CHL-A) + t2(DOY, Depth)	53.34 980	5741.745	55.4%
Spring/Summer, lagged SST			
∗s(SST lag) + s(DOY) + t2(Depth, CHL-A)	78.20 265	1552.545	84.8%
s(SST lag) + s(CHL-A) + t2(DOY, Depth)	93.23 887	1561.920	85.7%
s(SST lag) + t2(DOY, Depth)	75.23 726	1572.276	83.9%
s(SST lag) + +s(Depth)+ t2(DOY, CHL-A)	84.76 680	1574.357	84.2%
s(SST lag) + s(CHL-A) + s(DOY) + s(Depth)	83.25 533	1577.961	84%
Spring/Summer, day-of SST			
s(SST) + t2(DOY, Depth)	40.97 988	1606.529	79.9%
s(Depth) + s(CHL-A) + t2(DOY, SST)	40.01 305	1608.050	79.2%
s(DOY) + s(CHL-A) + t2(Depth, SST)	43.20 768	1611.401	79.5%
S(CHL-A) + s(SST) + t2(DOY, Depth)	56.99 946	1615.082	81.2%
S(DOY) + s(SST) + t2(Depth, CHL-A)	42.57 925	1616.297	79.7%
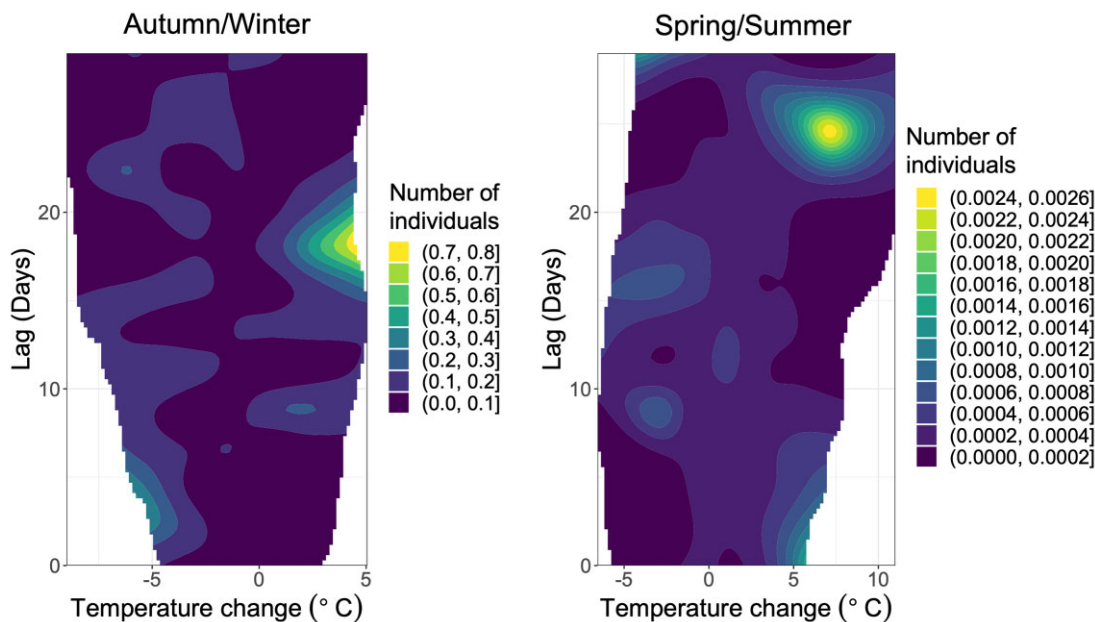
Figure 3 GAMM response function for the relative occurrence of striped bass in Autumn/Winter (left) and Spring/Summer (right) specific to SST change over the previous 30 days, estimated using a distributed lag GAMM. Negative values of temperature change represent cooling conditions and positive values represent warming conditions. Visualizations are on the response scale and warmer colors indicate a higher predicted number of individuals.

greatest likelihood of striped bass occurrence. These dominant patterns suggest that during both seasons, warming conditions are largely prompting the migratory movements of striped bass. However, cooling temperatures appear to influence movement behaviors to some extent during the Autumn/Winter season, though the effect is less.

During the Autumn/Winter migration season, the partial effect of CHL-A was a small peak of increased likelihood of occurrence at ∼0.5 log mg m^{-3} concentration, with an analogous decrease in likelihood of occurrence at 1 log mg m^{-3} (Supplemental Fig. S1). Concentrations above 2.5 log mg m^{-3} also led to higher predicted incidence. Striped bass occurrence
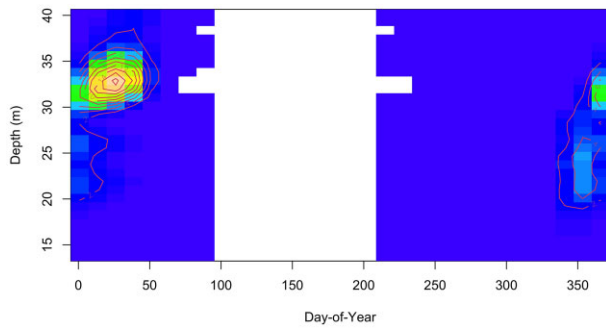
Figure 4 GAMM response function for the interaction between DOY and Depth for the best Autumn/Winter model of striped bass occurrence. Visualizations are on the response scale and warmer colors indicate a higher predicted number of individuals. Predicted number of individuals are shown on contour bands of colors.

varied in depth, reflecting the inshore-offshore gradient: during early winter, relative abundance was highest at mid-range depths (20–30 m) but shifted toward greater depths (>30 m) during later winter months (Fig. 4). Although the top model in Spring/Summer contained terms for DOY and an interaction between Depth and CHL-A, these terms were not significant predictors of occurrence in the model output (thus, figures are not shown). The effect of lagged SST was the only significant predictor in the top-ranked model for striped bass occurrence in Spring/Summer.

The 5-fold cross-validation RMSE of the best-performing Autumn/Winter model was 0.93 ± 0.03, meaning that the model-predicted abundance was 0.05 of the maximum number of striped bass per receiver deployed (maximum = 19). Meanwhile, the optimal model for the Spring/Summer migration season had a 0.03 error rate compared to the maximum (maximum = 19; RMSE 0.64 ± 0.13). Overall, model predictions were off by <1 individual for both migration seasons (RMSE calculations are on the same scale as the response variable: the number of individuals detected), though the Spring/Summer model had slightly less error. Model diagnostics did not show spatial or temporal autocorrelation in residuals.

Weekly residence model

The weekly residency models for striped bass showed that SST, week-of-year, and CHL-A were significant predictors of the number of days individuals were present in the array (Table 5). However, the random effect of the transmitter was not significant. Pairwise comparison between tagging regions revealed differences in response between the Delaware River vs. Coastal Massachusetts and Delaware River vs. Hudson River origins (Table 4: Wald test, $P < 0.05$).

Partial effects of environmental and temporal variables in species residency GAMMs were largely consistent with the responses observed in daily relative abundance models, but revealed variation in how these factors affected the amount of time individuals spent in the area. Partial effects showed that temperatures <15°C were associated with higher residency while temperatures higher than this threshold negatively affected residency duration (Supplemental Fig. S2). Similar to the GAMM occurrence model, striped bass were likely to occur for more days per week during winter and spring months and were unlikely to reside in the area during summer. Striped

Table 5. Parameter and pairwise factor comparison significance for weekly species residency GAMMs. Significance of model parameters and pairwise tagging region factors (Origin) are indicated by asterisks (<0.001= ***; 0.001–0.009 =**; 0.01–0.009=*; 0.05–0.1 = .). Striped bass tagging regions are: Hudson = Hudson River, New York; Potomac = Potomac River, Maryland; MA = Coastal Massachusetts; Kennebec = Kennebec River, Maine.

Term	P-value	df	AIC	Deviance explained
s(SST)	<0.001 ***	46.12	9350.70	64.5%
s(Week)	<0.001***			
s(CHL-A)	<0.001***			
s(Lag 1 Residency)	<0.001***			
s(Transmitter)	0.409			
Origin				
Hudson with Potomac	0.159			
Hudson with Kennebec	0.351			
MA with Potomac	0.236			
Hudson with MA	0.548			
Kennebec with Potomac	0.796			
DE River with Potomac	0.963			
DE River with Kennebec	0.780			
Kennebec with MA	0.476			
DE River with MA	0.020 *			
DE River with Hudson	0.014*			

bass occupancy had an inverse relationship with CHL-A in which occupancy was predicted to be higher at low values of CHL-A concentrations and decreased as concentrations increased (Supplemental Fig. S2).

### Population-level differences in residency response

Group-level differences occurred in how striped bass responded to SST and week-of-year (Figs. 5, 6), but variation in response to CHL-A concentration was less apparent (Supplemental Fig. S3). Residency predictions were highest when SST was <15°C, with striped bass tagged in the Delaware and Potomac Rivers showing peaks in the number of days detected just above 10°C. Individuals tagged in coastal Massachusetts and the Kennebec River had a slightly flatter response to SST and were predicted to reside for less time over a broader range of temperatures (∼5°C–12°C) compared to the other groups. Striped bass tagged in the Hudson River appeared to have a bimodal response to temperature in which residency was highest at 10°C but also peaked near 5°C. All tagging regions showed a similar pattern of lower residency in the spring (weeks 10–22) and slightly higher and more protracted residency in the winter (from week 48 to week 9 the following year), but individuals tagged in the Hudson River were predicted to occupy the region for the greatest amount of time in the spring (Fig. 6). The Hudson fish were also the only group that did not have a second, smaller peak in residency following the initial spring peak. Group-level heterogeneity was not obvious in the response of striped bass to CHL-A concentration (Supplemental Fig. S3).

Discussion

Is the Eulerian perspective sufficient?

Here we used modeling approaches that were dynamic in allowing the incorporation of time-varying and hierarchical variables to understand the local occurrence of a highly mobile, migratory species within the context of a standard teleme-
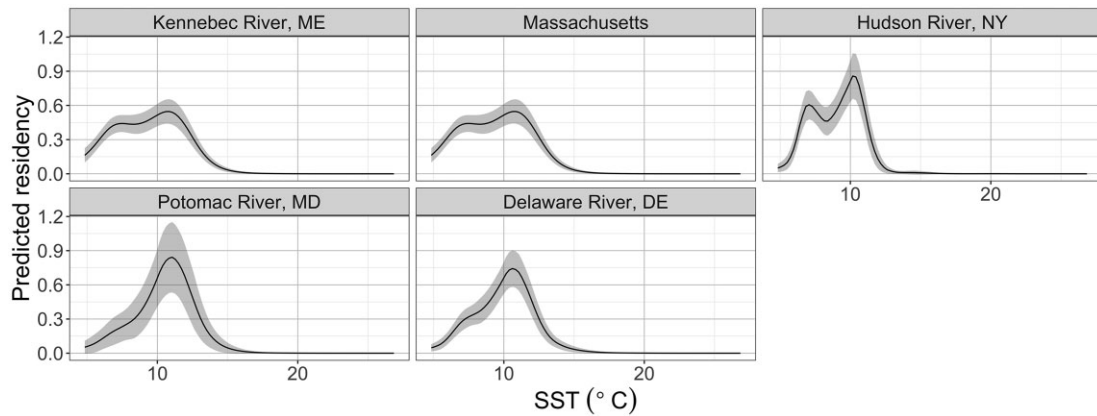
Figure 5 Predicted residency function (days per week ± 2 SE) of striped bass for each tagging region based on the SST across the MD WEA.
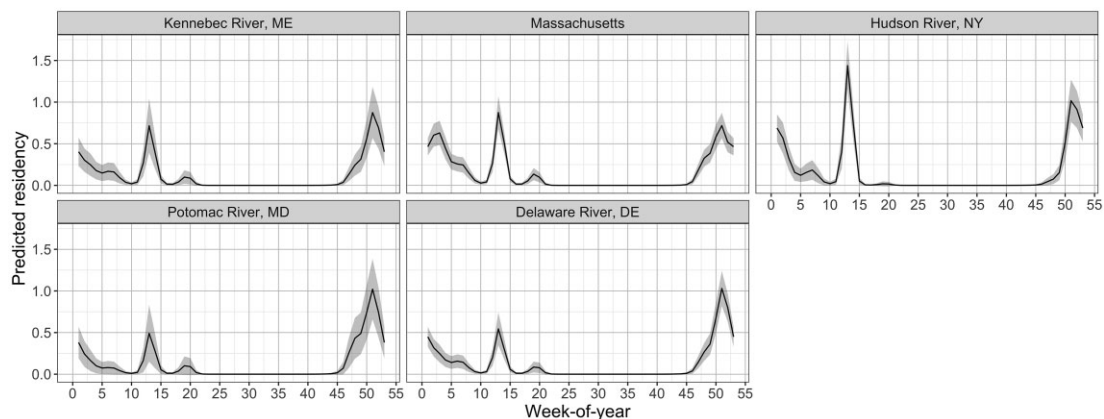
Figure 6 Predicted residency function (days per week ± 2 SE) of striped bass in the MD WEA array for each tagging region based on week-of-year.

try framework. Our results present methods that can be used by other researchers and managers to better understand the drivers of migratory species occurrence in regions where they are relatively transient. Although a singular, static acoustic receiver array can never fully capture the range of environmental factors influencing a species like striped bass during long-range migrations, the model formulations presented herein provide options for approximating conditions and variables that exist outside the window of observation. Dynamic modeling of telemetry detections in our study demonstrated that striped bass occurrence was influenced by conditions occurring both within and outside the MD WEA. A separate telemetry study by Ingram et al. 2019 showed that the presence of Atlantic sturgeon in the NY WEA was similarly driven by long-term environmental cues, including photoperiod and temperature, occurring outside the window of detection. Despite the fact that we could not account for all potential environmental or population factors that shape striped bass migration and occurrence patterns, evidence suggests that future telemetry studies on the migration behavior of species transiting through coastal OWF regions will be improved by the inclusion of broad-scale variables in addition to variables occurring at the local scale of OWF monitoring arrays.

We found that lagged SSTs, acting as proxies for warming or cooling patterns across the broader region, were better predictors of daily incidence than surface temperatures experienced by striped bass within the study region. Dur-

ing both migration seasons, daily striped bass occurrence was largely driven by warming regional SSTs, with some evidence of cooling temperatures driving incidence in the Autumn/Winter. Within the MD WEA, warming temperatures during spring likely emulate warmer conditions to the South, thus aligning with striped bass migrations northward toward cooler temperatures. Meanwhile, warming temperatures during the autumn or winter seasons correspond with cooler temperatures to the north, which aligns with the movement of striped bass southward toward warmer waters. Although shelf SST patterns may influence the speed of oceanic migrations by striped bass (Rothermel et al. 2020), their timing is likely dependent on temperature and other variables occurring within areas of extended residency, such as estuaries or summer feeding grounds. Similar to other anadromous species, temperature changes are widely considered the primary cue for striped bass to initiate migrations and spawning behavior (Crozier and Hutchings 2014, Peer and Miller 2014, Lombardo et al. 2020). These environmental responses allow migratory species to depart an area before it becomes unfavorable (Dingle and Drake 2007). While SST may modify prey availability or metabolic demands during shelf transit once migrations begin, the importance of lagged temperature in our study supports emerging evidence that the oceanic movements of striped bass are generally rapid (Secor et al. 2020b); like spawning behaviors, regional temperature cues likely prompt individuals to move toward more-favorable feeding grounds

to the North in Massachusetts or to warmer overwintering waters in the South. Other regional migratory species, such as Atlantic sturgeon, likely exhibit similar regional temperature cues (Rothermel et al. 2020).

Although environmental variables recorded within the array were retained in daily incidence models, the influence of these factors was not consistent among seasons. For instance, the best model for relative occurrence during the spring migration season contained terms for DOY and an interaction between Depth and CHL-A, but these terms were not significant. In contrast, the model for Autumn/Winter showed that striped bass incidence was associated with certain CHL-A concentrations and that depth selection depended on DOY; striped bass were more likely to occur in deeper shelf waters as the winter season progressed. Relative occurrence models therefore support previously observed seasonal differences in oceanic striped bass behavior in which spring migrations are more-rapid and Autumn/Winter migrations are protracted or develop into an extended offshore residency during winter months (Kneebone et al. 2014, Rothermel et al. 2020).

Temperature changes over the broader region, represented by lagged variables, likely present over-arching cues for striped bass to migrate, with *in-situ* factors seasonally varying in their importance. Depth and productivity variables may be less influential during the spring because striped bass are rapidly departing southern spawning locations in favor of cooler northern summer feeding grounds. In comparison, migrations to the South, initiated by cooling temperatures, may be altered by local environmental conditions in the Southern MAB. For instance, during winter, individuals may shift toward greater depths as the season progresses in order to take advantage of waters that are relatively warm compared to shallow, near-shelf regions (Rothermel et al. 2020).

Multistock flyways

The Eulerian flyway approach allowed comparison between striped bass stocks in their migration timing under the assumption that stocks were represented by tagging region. Across single-origin and mixed-stock tagging groups, individuals were more likely to be detected for multiple days during winter months compared to spring, when transit rates were more rapid across groups. This finding was consistent with previous results showing faster migrations for striped bass during spring with increased likelihood of residency during winter (Kneebone et al. 2014, Callihan et al. 2015). However, weekly residency for individuals tagged in Chesapeake and Delaware estuaries peaked just above 10°C temperatures, while fish tagged in regions north of Delaware were likely to reside for a longer period when SSTs were between 0°C–10°C. Broader- and lower-temperature preferences for fish tagged in Maine may reflect their northern origin, and acclimatization and/or genetic selection to colder temperatures. Similar patterns of temperature response observed in the Massachusetts-tagged fish may suggest that these mixed stocks contained a higher proportion of individuals with northern natal origin. The bimodal pattern in weekly residence response to temperature of Hudson River fish reflected their two pulsed migrations, which were more protracted than other groups, where selection for lower temperatures occur during spring than during late Autumn/Winter (Rothermel et al. 2020).

Because tagging region cannot be definitively related to genetic origin (source population), group-level findings should

thus be considered preliminary and warranting further investigation with regard to genetic assignments to populations of origin. Many striped bass were tagged in known spawning regions that may correspond with genetic origin, but fish tagged in Massachusetts are likely comprised of multiple spawning stocks (Kneebone et al. 2014) and a small degree of straying (<5%) has been observed for Hudson and Chesapeake Bay striped bass (Gahagan et al. 2015, Secor et al. 2020b, 2020c). Still, these analyses offer a potential means of comparing migration behaviors between groups of striped bass or indeed between other marine fish species that transit the Mid-Atlantic flyway (Rothermel et al. 2020, Lowerre-Barbieri et al. 2021).

Improving Eulerian models

Dynamic habitat models for marine fishes, turtles, birds, and mammals have shown that mesoscale oceanographic features such as eddies, thermal fronts, upwelling zones, and wind-driven mixing play key roles in structuring species distribution in pelagic habitats (Bigelow et al. 1999, Nel et al. 2001, Kai and Marsac 2010, Benson et al. 2011, Hobday and Hartog 2014, Hazen et al. 2017), features that could not be represented in the current analysis owing to limitations in the temporal resolution of environmental data. Although variables such as CHL-A or DOY could act as proxies for other key variables such as ocean currents or prey availability, additional analysis would be needed to verify these connections. To better understand the biological drivers of striped bass behavior along their migration route, future studies could incorporate modeled oceanographic dynamics from products like the Finite-Volume Community Ocean Model (FVCOM: Chen et al. 2003) or the Regional Ocean Modeling System (ROMS; www.myroms.org), which may enable more-robust inferences surrounding species behavior and movement decisions (Zemeckis et al. 2017, Breece et al. 2018, Secor et al. 2018).

Biological inferences surrounding striped bass migration behavior could be further improved through the addition of Lagrangian methods to the current fixed framework. State-space modeling and particle tracking are two key approaches that have been applied in modeling how individuals interact with their environment (Royer et al. 2005, Phillips et al. 2018). Dynamic habitat modeling, or dynamic ocean management, links animal tracks to satellite oceanographic products and is a particularly promising framework in this area (Žydelis et al. 2011, Vandeperre et al. 2016, Hazen et al. 2017). These models often rely on satellite telemetry and have been biased toward larger marine fauna (Block et al. 2011). Increased acoustic receiver coverage of ocean environments has recently allowed individuals to be tracked across broader regions. Modeling movement behaviors between arrays can allow for quasi-Lagrangian migration inputs in the development of dynamic habitat models (Breece et al. 2018, Lowerre-Barbieri et al., 2021). Acoustic telemetry technologies such as depth-transponding tags, accelerometers, or condition-sensing transponders may further help elucidate potential biological or physiological drivers of shelf habitat selection at the individual level. Advances in autonomous underwater vehicle (AUV) technology (Skomal et al. 2015, Dodson et al. 2018) also allow direct tracking of individuals or groups through time, environments, and space. An additional promising direction for future research lies in fish-deployed mobile telemetry receivers, which allow investigators to take a Lagrangian approach to group sociality, which could help researchers bet-

ter understand the interactions driving movement patterns of striped bass and other migratory species along the shelf (Barkley et al. 2020, Roose et al. 2022).

Implications for understanding the cumulative impacts of OWFs on megafauna

The modeling framework presented herein can be used to improve regional assessments of migratory species behaviors through project-scale sampling efforts. Previously, applications of dynamic ocean management have focused on evaluating the imposition of local impacts such as ship strikes, fishery bycatch, and marine protected areas as marginal impacts on habitat and species risk (Maxwell et al. 2011, Hazen et al., 2018); Abrahms et al. 2019). A key challenge is in understanding the influence of many distributed OWFs on changing and curtailing fish habitats and distributions (Gill et al. 2020). Owing to staggered developments and data sharing constraints, past and ongoing monitoring efforts have been focused on single OWFs. This piecemeal monitoring may initially necessitate an Eulerian perspective to develop a broader understanding of possible regional-scale impacts. Designs that incorporate lagged variables can further add to the power of cumulative impact inferences, as these will allow for consideration of dynamics occurring at times and places outside the immediate footprint of the OWF project area, where monitoring is most likely to occur.

Moving forward, OWF developers could choose to monitor SST changes or use past seasonal trends to predict when species interactions may be most likely to occur. For instance, it may be advisable to avoid construction disturbances during early spring months when strong regional (MAB) warming is most likely to occur if limited interaction with striped bass is desired. Modeled incidence also confirmed that summer months will provide the most favorable window for wind turbine installation since striped bass were consistently absent during these time frames in our study. Results suggest that behavioral differences between tagging groups are limited and that coastal stocks of striped bass can be treated similarly at the level of concern to wind energy developers. Here, interactions with all tagging origin groups examined could be broadly avoided in the MD WEA by limiting construction activities between November and May. Though our results provide an explanation of drivers of striped bass incidence off the coast of Maryland, previous studies suggest that habitat models developed in one coastal shelf region do not always apply to another (Haulsee et al. 2020). Thus, similar studies will need to be applied across the MAB to fully understand the appropriate timing of activities at other OWF locations; gradients, lagged variables, and hierarchal formulations could also be applied to monitoring frameworks to establish better understanding of the factors driving incidence for any species of concern.

As wind energy development progresses along the MAB and elsewhere, dynamic modeling techniques could provide crucial information on changes in species behavior in response to wind turbine construction and maintenance. Such techniques will also be crucial in determining changes to coastal migrations caused by climate change and other anthropogenic pressures; already marine fish distributions are being impacted by shifting temperatures (Nye et al. 2009, Pinsky et al. 2013). Seasonal temperature changes, especially within estuaries, may differentially alter spawning phenol-

ogy and migration timing among population contingents of striped bass and other anadromous fish (Pan et al. 2023). For instance, striped bass have been documented to shift their arrival on Chesapeake Bay spawning grounds by ~ 3 days earlier for every $1°C$ increase in spring water temperature (Peer and Miller 2014), a shift which is likely to vary by population and natal spawning location. A comprehensive and coordinated monitoring approach, using appropriate modeling techniques, will therefore be needed to understand the confounding effects of development and climate change on the timing or speed of anadromous species migrations. Ideally, networks of receiver arrays, strategically located in OWFs, could be used to inform a shelf-wide Eulerian-Lagrangian perspective on migratory species in a cumulative impact framework. Corresponding models developed within this study align with impact study frameworks such as Before-After-Control-Impact and Before-After-Gradient designs, which include year or phase of development as factors to efficiently test for significant changes in species response according to the impact of interest. Within such a framework, past (lagged) and current environmental variables, as well as population factors, would be used to evaluate the incidence along the entire migratory route of any telemetered species of concern, providing managers and developers with a more comprehensive view of the dynamics that drive movement behavior.

Supplementary data

Supplementary material is available at the *ICES Journal of Marine Science online*.

Conflict of interest: None declared.

Author contributions

E. Rothermel provided Data curation, Formal analysis, Investigation, Methodology, Resources, Software, Visualization, and Writing—original draft. D. Secor provided Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Validation, Visualization, and Writing—original draft. M. O'Brien provided Conceptualization, Data curation, Investigation, Methodology, Resources, Software, Supervision, Visualization, and Writing—review & editing. J. Best, F. Fox, B. Gahagan, A. Higgs, I. Park, and G.

Wippelhauser contributed Resources and Writing—review & editing.

Data availability

All the telemetry detection data underlying this analysis are available in .csv files on Dryad (https://doi.org/10.5061/drya d.6hdr7sqx3) and R code for modeling described below will be shared on reasonable request to the corresponding author.

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