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## ORIGINAL ARTICLE



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# Spatial differences in estuarine utilization by seasonally resident species in Mid-Atlantic Bight, USA

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**Abstract**

Climate-driven distributional shifts have been well-documented for fisheries resources along the East Coast of the United States, yet little attention has been given to adjacent estuarine systems. The Chesapeake Bay is the largest estuary in the continental United States and serves as important habitat for a diversity of fishes and invertebrates, many of which are seasonal residents. Survey data indicate that relative abundance of finfish in Chesapeake Bay has diminished substantially, while coastwide stock status has remained unchanged. In response to warming, seasonal estuarine residents may remain in coastal waters or inhabit a northerly estuary, but the extent to which changing environmental conditions may drive exchange between the coastal ocean and estuarine systems remains unresolved. This study analyzed data collected from 2008 to 2019 by three fisheries-independent trawl surveys to explore temporal patterns and associated environmental drivers of the estuarine-coastal ocean exchange in the Mid-Atlantic for eight economically and ecologically important species. Relative habitat utilization of Chesapeake Bay declined for most species, while utilization patterns for Delaware Bay were largely constant or increasing over time. Broad-scale, multispecies analyses of relative habitat utilization time series revealed that the North Atlantic Oscillation (NAO) was an important driver of Chesapeake Bay exchange, but that average Apr/May coastal ocean bottom temperature was significant for Delaware Bay. Collectively, the results demonstrate that several Mid-Atlantic species have altered their estuarine habitat use over time, climate drivers associated with estuarine-coastal ocean exchange operate on different time scales, and that the impacts of warming within the Mid-Atlantic vary spatially.

**KEYWORDS**

Chesapeake Bay, climate change, dynamic factor analysis, ecosystem exchange, quantitative fisheries ecology

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## 1 | INTRODUCTION

Ocean basins serve as the predominant sink of the energy accumulated in response to anthropogenic greenhouse gas emissions, which has led to global increases in sea surface temperature (IPCC, 2015; Levitus et al., 2000). The Atlantic Ocean has been disproportionately impacted by warming (Cheng et al., 2020; Levitus et al., 2005), with temperatures increasing on the northwestern Atlantic shelf at rates nearly three times the global average (Saba et al., 2016). Adjacent estuaries along the East Coast of the United States also have been impacted by climate change, with systemic warming documented in Narragansett Bay (Collie et al., 2008; Langan et al., 2021; Oviatt, 2004), Long Island Sound (Howell & Auster, 2012), and Chesapeake Bay (Ding & Elmore, 2015; Hinson et al., 2021; Tian et al., 2021).

The Chesapeake Bay is the largest estuary in the continental United States and serves as an important habitat for an array of fish and invertebrate species that represent a variety of life history modes and occupy unique ecological niches. Several of these species support economically valuable recreational and commercial fisheries, as well as a host of non-market ecosystem services (Kirkley et al., 2005; Lellis-Dibble et al., 2008; NMFS, 2018). Although several species are resident to this estuary, the bay is also utilized seasonally by a diverse assemblage of boreal, temperate, and subtropical species as a foraging, spawning, nursery, and refuge habitat (Murdy et al., 1997).

Most of the seasonally resident species in Chesapeake Bay immigrate into the estuary during spring (March to May) and emigrate to the coastal ocean in the fall (September to November). The effects of climate change on this ecosystem have not only led to increased water temperatures year round but have also impacted the seasonal temperature cycles that are associated with the timing of migratory patterns. Specifically, the rate of warming in the spring has increased (Friedland & Hare, 2007), and the earlier physical onset of spring, defined by the thermal environment, is leading to altered timing of associated spring phenological events for many marine species (Burrows et al., 2011; Parmesan & Yohe, 2003; Thackeray et al., 2010; Thomas et al., 2017). These changes likely will affect residence times of migratory species, as has been documented in Narragansett Bay (Langan et al., 2021), and may ultimately lead to modifications of their seasonal usage of the Chesapeake Bay.

Numerous studies conducted along the northwestern Atlantic shelf have documented significant shifts in distribution of individual marine species and assemblages poleward or to deeper waters in response to warming temperatures (e.g., Bell et al., 2015; Kleisner et al., 2016; Lucey & Nye, 2010; Nye et al., 2009; Pinsky & Fogarty, 2012). For seasonal estuarine residents, the combination of distributional shifts, faster spring warming, and earlier spring onset may result in seasonal migrations that bypass Chesapeake Bay in favor of a more northern estuary. Furthermore, the lowered solubility of dissolved oxygen in warmer water temperatures is expected to cause an increase in the frequency, volume, and onset of hypoxia in this estuary (Irby et al., 2018; Najjar et al., 2010; Tian et al., 2021).

This phenomenon has been suggested as a critical factor driving distributional shifts in other ecosystems (Deutsch et al., 2015; Pörtner & Knust, 2007), and fish hypoxia avoidance behaviors have been documented within Chesapeake Bay (Buchheister et al., 2013) and elsewhere (Eby & Crowder, 2002).

The Chesapeake Bay is considered a nursery habitat for many species due to the provisions afforded in support of increased density, growth, and survival for juveniles (Beck et al., 2001; Nagelkerken et al., 2015; Schloesser & Fabrizio, 2019). However, continued use of this estuary in light of the emerging suboptimal environmental conditions resulting from climate change could create negative impacts on vulnerable life stages that may cascade to population-level effects. The availability of more suitable nursery habitats is considered a key factor in driving the distributional shifts of demersal fishes in other coastal systems (Rijnsdorp et al., 2009). As there are several estuaries north of the Chesapeake Bay, estuarine-dependent Mid-Atlantic fishes may modify their seasonal migrations to inhabit a more amenable environment. Alternatively, some adult fishes less reliant on an estuarine system may forgo seasonal residency and instead remain in the coastal ocean.

For some fish species, declines in catch-per-unit-effort (CPUE) of up to 90% have been documented in Chesapeake Bay (Buchheister et al., 2013). However, these same precipitous drops in relative abundance are not apparent in coastwide stock assessments, which often indicate that populations are not overfished and overfishing is not occurring. The mismatch in realized relative abundance trends between localized and regional scales indicates that there may be ecological factors driving an exchange of these populations between the Chesapeake Bay and adjacent ecosystems, which have yet to be quantified. The term “exchange” is used throughout this manuscript to refer to within-stock habitat partitioning that occurs when a proportion of the population of a given marine species enters an estuary after overwintering in the ocean.

To gain insights into the interannual patterns of relative habitat usage and the potential drivers of exchange between the coastal ocean and Chesapeake Bay, this study paired catch data on several species collected from fisheries-independent surveys that were complementary in both space and time: a spring (April/May) survey conducted in nearshore coastal waters coupled with a Chesapeake Bay summer (May to September) survey provided measures of relative abundance for the same populations lagged in time. To explore spatial differences along the coast, analogous methods were applied to summer (June to September) survey data collected within Delaware Bay, a more northern estuary, and the same spring coastal survey. Overall, there were two objectives in this investigation: (1) to create time series of relative habitat usage representing estuarine-coastal ocean exchange for a suite of sampled species and (2) to characterize the common trends shared among these time series with the goal of identifying the broad-scale factors associated with these trends. Results from this study can be used to better understand the nuances of distributional shifts of ecologically and economically important seasonal estuarine residents within the Mid-Atlantic.

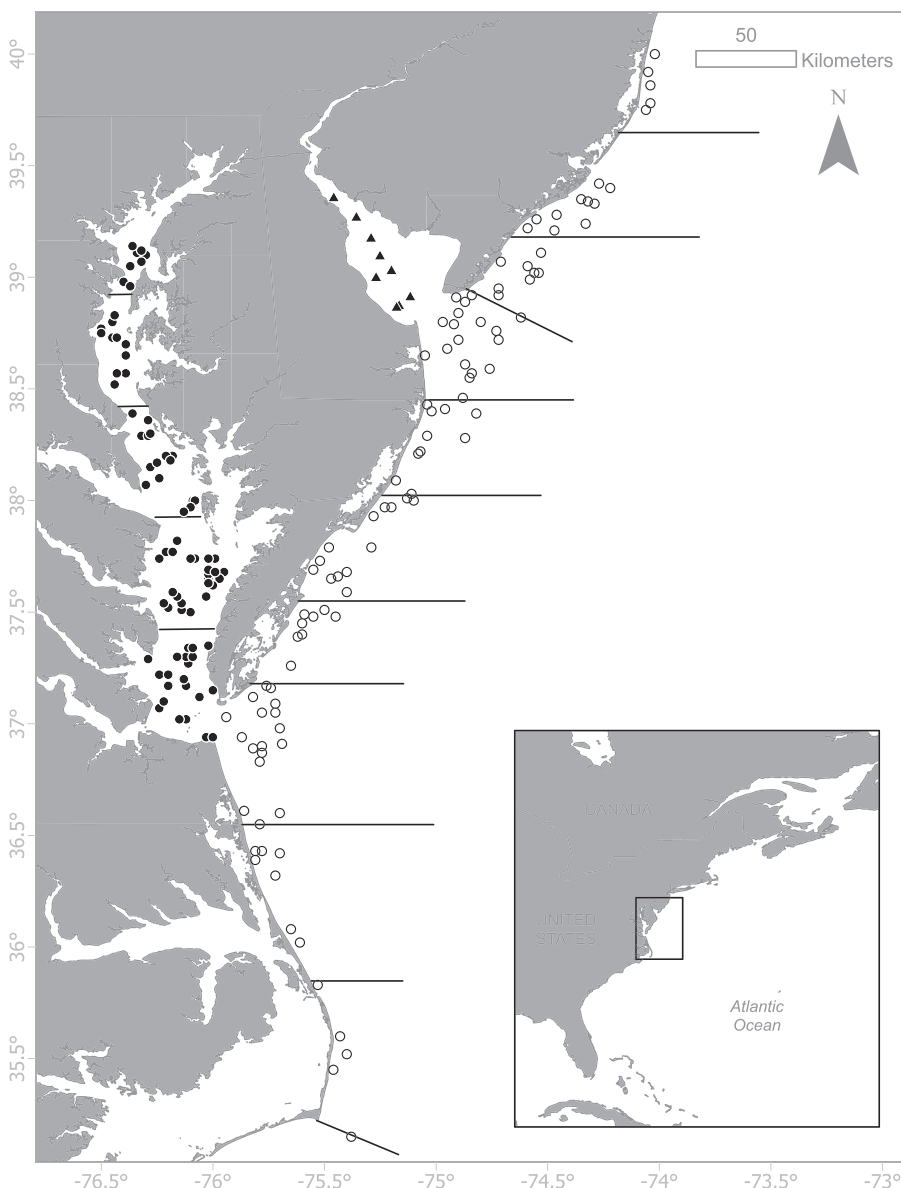
## 2 | METHODS

### 2.1 | Field sampling

Data for this study span 2008–2019 and were collected by the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP, May to September, 2008–2018), the Northeast Area Monitoring and Assessment Program (NEAMAP, April/May, 2008–2016, 2018–2019), and the Delaware Bay Adult Trawl Survey (DBATS, June to September, 2008–2019). All three programs are fisheries-independent bottom trawl surveys; NEAMAP and ChesMMAP are conducted by the Virginia Institute of Marine Science, while DBATS is administered by the Delaware Division of Fish & Wildlife. ChesMMAP data are restricted to 2018 due to a gear and vessel change in following years, while NEAMAP data exclude 2017 because of incomplete sampling during that year.

ChesMMAP samples at approximately 80 sites throughout the main stem of Chesapeake Bay bimonthly from March to November each year. Sites are selected using a stratified random design based on depth (3.0–9.1 m, 9.1–15.2 m, and >15.2 m) and latitude (Figure 1). A four-seam bottom trawl (13.7 m headrope length with 7.6 cm codend mesh) is deployed for 20 min in the direction of the current at each site (Latour et al., 2003). NEAMAP samples the near-shore continental shelf waters from Cape Hatteras, North Carolina, to Martha's Vineyard, Massachusetts. Two cruises are conducted annually, during spring (April/May) and fall (September/October), with 150 sites sampled each cruise. Sites are selected using a stratified random design, with stratification based on latitudinal/longitudinal regions and depth (6.1–12.2 m and 12.2–18.3 m south of Montauk, New York; 18.3–27.4 m and 27.4–26.6 m in Block Island Sound and Rhode Island Sound; Figure 1). At each site, a 400 × 12 cm (fishing circle circumference), three-bridle, four-seam bottom trawl with a

**FIGURE 1** Sampling sites for the fisheries independent trawl surveys. The filled circles are the sampling locations from a representative Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP) cruise (July 2018). The open circles are trawl sites from a representative Northeast Area Monitoring and Assessment Program (NEAMAP) cruise (Spring 2018). The triangles are the nine fixed stations sampled by the Delaware Bay Adult Trawl Survey (DBATS). Horizontal lines delineate the sampling regions of ChesMMAP (lines within Chesapeake Bay) and NEAMAP (along US coastal waters).



2.54 cm lined codend is towed for 20 min (Bonzek et al., 2017). DBATS conducts monthly cruises nearly year-round (March to December) where nine fixed stations are sampled throughout Delaware Bay (Figure 1). This survey utilizes a 9.3 m (headrope length) trawl with 5.1 cm codend mesh, and tow duration is 20 min (Greco, 2017).

Each survey records site variables and hydrographic measurements (e.g., bottom temperature) at every sampling location. Catches are sorted by species, with ChesMMAP and NEAMAP separating size-classes within species, if distinct. Specimens are enumerated, and individual length measurements are recorded. ChesMMAP subsamples five individuals of each species and size-class for age determination (Latour et al., 2003, 2017), while NEAMAP subsampling of species and size-classes for aging is restricted to those species with a Fisheries Management Plan (FMP; Bonzek et al., 2017).

Survey data on eight species (five demersal species, one pelagic, one elasmobranch, and one arthropod; Table 1) were included in this study, due to the ecological and economic importance of these taxa in the Mid-Atlantic Bight: Atlantic croaker (*Micropogonias undulatus*), scup (*Stenotomus chrysops*), spot (*Leiostomus xanthurus*), summer flounder (*Paralichthys dentatus*), windowpane flounder (*Scophthalmus aquosus*), weakfish (*Cynoscion regalis*), clearnose skate (*Raja eglanteria*), and horseshoe crab (*Limulus polyphemus*).

## 2.2 | Data filtering

NEAMAP and the estuarine surveys (i.e., ChesMMAP or DBATS) provide measures of the same populations lagged in time. The NEAMAP data were spatially restricted to include only sites sampled between central New Jersey and Cape Hatteras, North Carolina, given that these boundaries encompass a biotic ecotone (Stratton, 2017). The species-specific datasets from each survey were filtered to remove catch data on young-of-year (YOY) animals, as only individuals actively undergoing migration (Murdy et al., 1997; Swan, 2005) were of interest. Age data are not routinely collected by DBATS, so ChesMMAP data were used to create an age-length key based on 5 mm length bins for each species, and these were applied to the DBATS length-frequency data to remove YOY specimens from survey collections. No survey captured horseshoe crab less than 20 mm prosoma width, which is the maximum size for YOY animals (Sekiguchi et al., 1988). While DBATS does not measure clearnose skate, the lengths observed in ChesMMAP and NEAMAP far exceeded the threshold of 33 cm total length to be considered age one (Packer et al., 2003).

The survey datasets for each species were also filtered to include only the key habitat regions, and thereby the most informative data, by removing locations where the species of interest was not expected to occur based on known life history characteristics and general

**TABLE 1** Characterizations of species evaluated in this investigation

Species	Family	Description	Spawning location (Able & Fahay, 2010)	Timing of spawning (Able & Fahay, 2010)	Focal stock range	Stock status
Atlantic croaker	Sciaenidae	Demersal finfish	Ocean	Summer to Fall	ME to FL	Of concern (ASMFC, 2019a)
Scup	Sparidae	Demersal finfish	Estuaries	Spring to Summer	MA to NC	Not overfished/overfishing not occurring (Terceiro, 2021a)
Spot	Sciaenidae	Demersal finfish	Ocean	Fall to Winter	ME to FL	Of concern (ASMFC, 2021b)
Summer flounder	Paralichthyidae	Demersal finfish	Ocean	Fall	ME to NC	Not overfished/overfishing not occurring (Terceiro, 2021b)
Windowpane flounder	Scophthalmidae	Demersal finfish	Estuaries and ocean	Spring and Fall	MA to NC	Not overfished/overfishing not occurring (NEFSC, 2020)
Weakfish	Sciaenidae	Pelagic finfish	Estuaries and ocean	Spring to Summer	NY to NC	Depleted (ASMFC, 2019b)
Clearnose skate	Rajidae	Elasmobranch	Unknown	Egg deposition in spring (Packer et al., 2003)	MA to NC	Not overfished/overfishing not occurring (Sosebee, 2020)
Horseshoe crab	Limulidae	Marine arthropod	Estuaries (ASMFC, 2019a)	Spring to Summer (ASMFC, 2019a)	ME to FL	Not overfished/overfishing not occurring (ASMFC, 2019a)

*Note:* Information on timing of spawning reflects the season(s) during which active spawning occurs within the Mid-Atlantic region. Each species included in this investigation is managed as one or more unit stocks, and focal stock range provides the geographic bounds of the unit stock evaluated in this study. Stock status provides the most recent classification given of the stock as determined by the governing management body.

absence in survey samples (Latour et al., 2017). Due to differences in sampling designs and the magnitude of catch rates, the definition of uninformative samples varied by survey. For ChesMMA, these were defined as latitudinal regions in which less than approximately 5% of tows encountered the species of interest and contributed less than 5% of the total catch of the target species. For NEAMAP, the restriction was based on the joint region and depth strata, and the threshold for designation as uninformative was less than 2% for both frequency of encounter and overall catch. Due to the lower number of seasonal DBATS samples, sampling locations were excluded if they contributed less than 2% of the total catch or less than 5% and had a low number of positive occurrences. This filtering approach resulted in datasets that varied in size by species and survey.

### 2.3 | Relative habitat usage

Species-specific catch data from spring NEAMAP and each estuarine survey's summer cruises were randomly paired within year, such that the maximum number of pairs per year was equal to the minimum number of tows in either survey during that year. Data on relative habitat usage ( $H_{s,i,y}$ ) were generated as the ratio of catches from each paired tow:

$$H_{s,i,y} = \frac{E_{s,i,y}}{E_{s,i,y} + N_{s,i,y}} \quad (1)$$

where  $E_{s,i,y}$  represents the number of species  $s$  captured in the  $i$ th estuarine tow in year  $y$  and  $N_{s,i,y}$  is the number in the complementary NEAMAP tow. Although there are differences in capture efficiency between NEAMAP and the estuarine surveys, the sampling gears and vessels have not changed during the time periods included in this investigation and thus support the assumption of constant gear efficiency within each survey. While the absolute value of the ratio is not meaningful, the trend of the ratio over time is indicative of changes in estuarine utilization as compared to the coastal ocean.

Generalized linear models (GLMs, McCullagh & Nelder, 1989) that included a fixed categorical year covariate were applied to estimate a time series of annual relative habitat usage

$$g(H_{s,i,y}) = a + \alpha_{s,y} + \epsilon_{s,i,y} \quad (2)$$

where  $g$  is the link function,  $a$  is the intercept representing year 2008,  $\alpha_{s,y}$  is the estimated mean effect level  $y$  of the year covariate for species  $s$ , and  $\epsilon_{s,i,y}$  is the error vector. Additionally, in the Delaware Bay models, the station sampled by DBATS was included as a random effect to account for the fixed station sampling design.

The response data were assumed to follow a beta (BE) binomial (BI) distribution (Miller, 2013), which is a joint distribution in which the species-specific probability from the binomial distribution,  $\pi_s$ , follows a beta distribution. That is,  $H_s \sim BI(n_s, \pi_s)$ , where  $n_s$  is the known number of observations of species  $s$  and  $\pi_s \sim BE(\alpha_s, \beta_s)$ , such that  $\alpha_s = \frac{\mu_s}{\sigma_s}$ ,  $\beta_s = \frac{1-\mu_s}{\sigma_s}$ ,  $0 < \mu_s < 1$ , and  $\sigma_s > 0$  (Rigby et al., 2019).

The process of random-stratified pairing of an estuarine dataset with the NEAMAP dataset and subsequent model fitting was repeated 1000 times. The final time series of annual indices of relative habitat usage for each species was calculated as the yearly means over the full set of model estimates. Subsequently, beta regression analyses (Ferrari & Cribari-Neto, 2004) were applied to each of these 16 final time series (i.e., eight species and two estuaries) to identify significant trends in the relative habitat usage.

### 2.4 | Drivers of ecosystem exchange

Dynamic factor analysis (DFA) was used to estimate the underlying shared patterns among the time series of relative habitat usage. DFA is a multivariate analysis technique in which the common trends in temporal variation of  $n$  time series are quantified through linear combinations of  $m$  hidden random walks, where  $1 \leq m < n$ . The general form of a DFA is as follows (Holmes et al., 2012; Zuur, Fryer, et al., 2003):

$$\mathbf{y}_t = \Gamma \boldsymbol{\alpha}_t + \mathbf{D} \mathbf{x}_t + \boldsymbol{\epsilon}_t \text{ where } \boldsymbol{\epsilon}_t \sim MVN(\mathbf{0}, \mathbf{R}) \quad (3)$$

$$\boldsymbol{\alpha}_t = \boldsymbol{\alpha}_{t-1} + \boldsymbol{\eta}_t \text{ where } \boldsymbol{\eta}_t \sim MVN(\mathbf{0}, \mathbf{Q})$$

where  $\mathbf{y}_t$  is the z-scored (i.e., standardized to a mean of zero and variance of one) vector ( $n \times 1$ ) of time series of estimated relative habitat usage for  $n$  species in year  $t$ ,  $\boldsymbol{\alpha}_t$  is the vector ( $m \times 1$ ) of  $m$  common trends,  $\Gamma$  is the matrix ( $n \times m$ ) of species-specific factor loadings on the common trends,  $\mathbf{x}_t$  is the vector ( $q \times 1$ ) of  $q$  covariates,  $\mathbf{D}$  is the matrix ( $n \times q$ ) of covariate effects, and  $\mathbf{R}$  and  $\mathbf{Q}$  are the variance-covariance matrices associated with the observation error vector  $\boldsymbol{\epsilon}_t$  ( $n \times 1$ ) and process error vector  $\boldsymbol{\eta}_t$  ( $m \times 1$ ), respectively.

While  $\mathbf{Q}$  is constrained to the identity matrix to ensure the model is identifiable,  $\mathbf{R}$  may take several forms and is used to define the noise component of the model (Zuur, Fryer, et al., 2003). The three forms of the variance-covariance matrix explored were diagonal with equal variance and zero covariance, diagonal with unequal variance and zero covariance, and nondiagonal with equal variance and equal covariance.

Twelve annualized covariates were considered as explanatory variables in the DFA model fitting, 10 of which were classified as climate variables, one as a biological covariate, and one as a metric of exploitation. Four of the climate variables considered reflect processes of broad spatial scales: the Atlantic Multidecadal Oscillation index (AMO; <https://psl.noaa.gov/data/correlation/amon.us.data>), the Gulf Stream Index (GSI; Bastille et al., 2021), the winter North Atlantic Oscillation index, defined as the average value from Dec-Mar (NAO; <https://psl.noaa.gov/data/correlation/nao.data>), and winter NAO lagged by 1 year. The remaining six climate variables reflect localized conditions: the sea surface temperature anomaly of the Mid-Atlantic Bight (Bastille et al., 2021), average bottom temperature and bottom salinity from the NEAMAP spring cruise (April/May) in the restricted geographical range, average winter-spring (January to May)



precipitation and cooling degree days of the season, defined as the summation of the difference between average daily temperature and 18.3°C from six NOAA stations (the Naval Air Station Oceana in Virginia Beach, VA, USA; the Norfolk International Airport, VA, USA; the Baltimore Washington International Airport, MD, USA; the Ocean City Municipal Airport, MD, USA; the Wilmington-New Castle Airport, DE, USA; and the Atlantic City International Airport, NJ, USA; <https://www.ncdc.noaa.gov/cdo-web/>), and the year-day of spring onset defined as the first day in a sequence of 8 days that the sea surface temperature within the geographic range of the coastal waters considered exceeded a threshold temperature of 8°C (Thomas et al., 2017; <https://www.ncei.noaa.gov/access>). The biological metric was the small-large copepod abundance anomaly in the Mid-Atlantic Bight (Bastille et al., 2021), and exploitation was represented as the sum of recreational and commercial species-specific landings (lbs) coastwide for all species except windowpane flounder, which is managed as two stocks and thus New England landings were excluded (<https://www.fisheries.noaa.gov/foss>).

DFA model selection was based on Akaike's information criterion (AIC; Akaike, 1973; Burnham & Anderson, 2002) corrected for small sample sizes (AICc) and species-specific fit ratios, defined as  $\sum \hat{\epsilon}_t^2 / \sum \hat{Y}_t^2$ , where smaller values indicate better model fit (Zuur, Tuck, & Bailey, 2003). Models were first fitted with 1, 2, or 3 common trends for each of the variance-covariance error structures and no covariates. Model parameterizations where the mean of fit ratios was  $\geq 0.6$  or  $\Delta AICc$  (i.e., AICc minus minimum AICc) was greater than 10 were eliminated from consideration. The remaining parameterizations were then fitted with a single covariate or two covariates from different variable classifications. Final model selection was based on a combination of  $\Delta AICc$  and mean fit ratio. All statistical analyses were performed using the R software program (v4.0.3, R Core Team, 2020). Packages “gamlss” (Rigby & Stasinopoulos, 2005), “betareg” (Cribari-Neto & Zeileis, 2010), and “MARSS” (Holmes et al., 2012) were

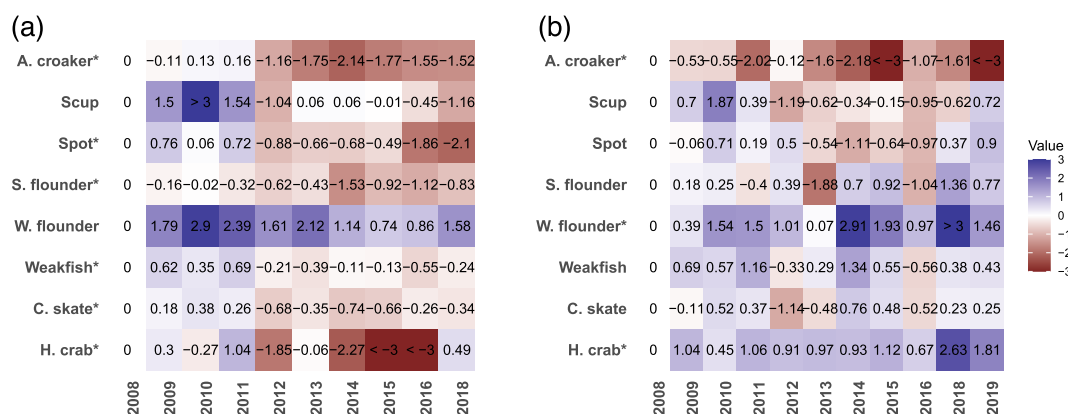
accessed to fit the beta-binomial time series models, the beta regressions, and DFAs, respectively.

### 3 | RESULTS

#### 3.1 | Time series of relative habitat usage

When comparing Chesapeake Bay and the coastal ocean, the beta regressions fit to the mean ratios of relative habitat usage (Figure S1) indicated a significant trend in relative habitat usage over time for six of the eight species: Atlantic croaker ( $p < 0.001$ ), spot ( $p < 0.001$ ), summer flounder ( $p < 0.001$ ), weakfish ( $p = 0.01$ ), clearnose skate ( $p = 0.01$ ), and horseshoe crab ( $p = 0.003$ ). The relationship was negative for each of these species, indicating a multispecies decrease in the usage of Chesapeake Bay relative to the coastal ocean over time. Compared to the baseline relative habitat usage value for Chesapeake Bay in 2008, seven species displayed largely negative changes, particularly since 2012 (Figure 2a). Although windowpane flounder exhibited an increase in relative usage of Chesapeake Bay for each year compared to 2008, peak estuarine usage occurred in 2010 followed by a notable decrease thereafter.

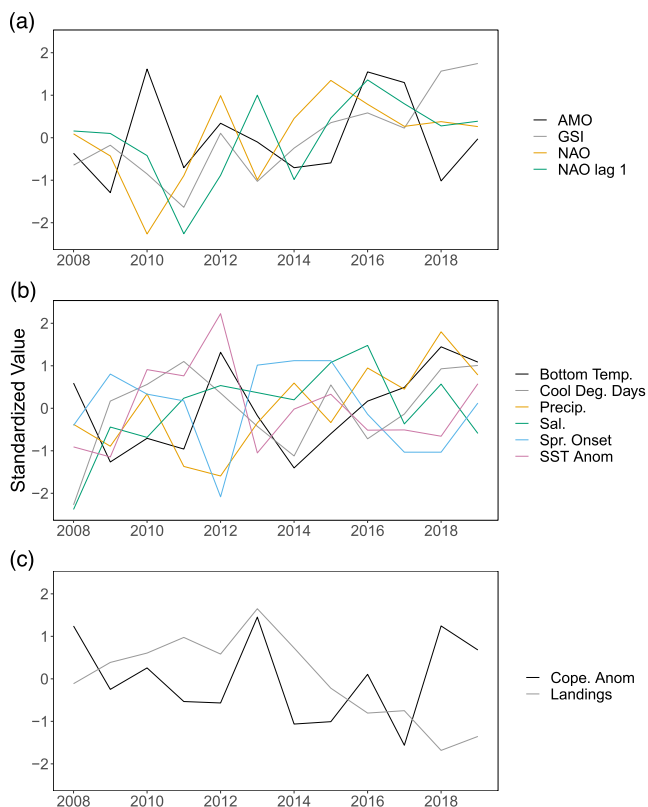
Only three species exhibited significant changes in relative habitat usage when comparing Delaware Bay to the coastal ocean over time: Atlantic croaker ( $p = 0.002$ ), windowpane flounder ( $p = 0.027$ ), and horseshoe crab ( $p < 0.001$ ). Of these significant relationships, the trends for horseshoe crab and windowpane flounder were positive, and the trend for Atlantic croaker was negative. Five of the species displayed an increase in relative usage of Delaware Bay compared to the 2008 baseline for the majority of years (Figure 2b). Collectively, the general lack of significant relationships across species suggests fewer changes in the relative habitat usage of Delaware Bay when compared to Chesapeake Bay.



**FIGURE 2** Mean estimated coefficients associated with levels of the year covariate for the eight species derived from 1000 beta-binomial model fits for (a) Chesapeake Bay-coastal ocean comparison and (b) Delaware Bay-coastal ocean comparison. Positive values (purple tones) represent an increase compared to the 2008 baseline, while negative values (red tones) signify a decrease. Species names followed by an asterisk indicate a significant trend in relative habitat usage over time based on beta regressions. A. croaker: Atlantic croaker; S. flounder: summer flounder; W. flounder: windowpane flounder; C. skate: clearnose skate; H. crab: horseshoe crab

### 3.2 | Time series of annualized covariates

For the broad scale climate variables considered, NAO, NAO-lag-1, and GSI generally increased over time, whereas AMO displayed



**FIGURE 3** Time series of (a) broad-scale climate variables (Atlantic Multidecadal Oscillation [AMO]; Gulf Stream Index [GSI]; North Atlantic Oscillation [NAO]; North Atlantic Oscillation lagged by one [NAO lag 1]), (b) localized environmental variables (average spring bottom temperature from NEAMAP trawls [Bottom Temp.]; cooling degree days [Cool Deg. Days]; precipitation [Precip.]; average spring bottom salinity from NEAMAP trawls [Sal.]; spring onset [Spr. Onset]; sea surface temperature anomaly [SST Anom]), and (c) biological and exploitation covariates (copepod abundance anomaly [Cope. Anom]; landings of focal species [Landings]) considered in dynamic factor analysis (DFA). See Section 2 for descriptions and data sources.

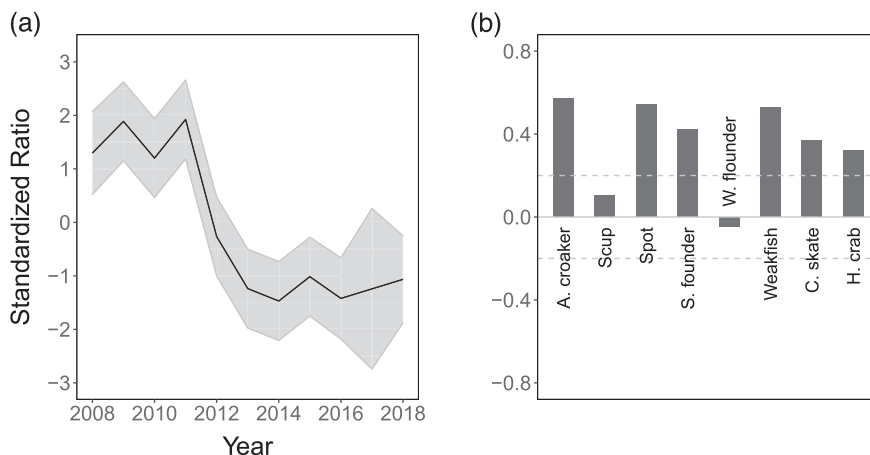
relatively large fluctuations but remained stable (Figure 3a). The localized climate covariates were generally more variable than the broad scale metrics (Figure 3b). Average springtime bottom temperature from NEAMAP cruises, sea surface temperature anomaly in the Mid-Atlantic Bight, and average winter–spring precipitation have all steadily increased since 2014, 2013, and 2012, respectively. In contrast, average springtime bottom salinity from NEAMAP cruises increased from 2008 to 2016, then decreased in the most recent years. Cooling degree days increased rapidly between 2008 and 2011 and has fluctuated at these higher levels since. Spring onset has varied over time without a clear trend. The copepod abundance anomaly had a negative trend through 2017, but increased in recent years, while combined recreational and commercial landings of the species included in this investigation increased to a peak in 2013 and steadily declined after (Figure 3c).

### 3.3 | Dynamic factor analysis: Drivers of ecosystem exchange

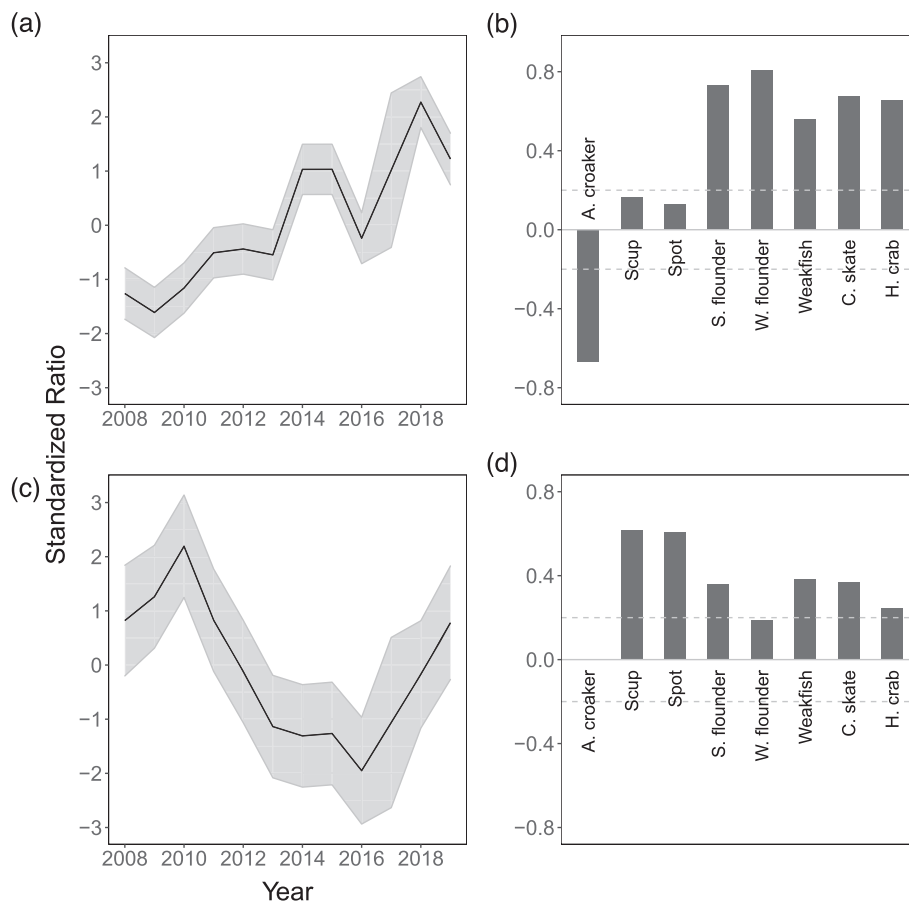
The final DFA model chosen for the Chesapeake Bay–coastal ocean exchange included one common trend, a diagonal and equal variance–covariance structure, and winter NAO as a covariate. The common trend peaked to its highest values during the first few years of the time series, before steadily declining from 2011 to 2014 and remaining low since 2014 (Figure 4a). Six of the species exceed the factor loading threshold of 0.2, and thus loaded strongly and positively on the common trend (Figure 4b). The usage of Chesapeake Bay by scup, windowpane flounder, and clearnose skate was significantly and negatively associated with NAO (Table S1).

For the Delaware Bay–coastal ocean comparison, the most empirically supported DFA model had two common trends, a diagonal and equal variance–covariance structure, and the average springtime coastal bottom temperature from NEAMAP cruises as a covariate. The first common trend showed an increase throughout the span of the time series (Figure 5a). Five species loaded strongly and positively and one strongly and negatively on the first common trend (Figure 5b). The second common trend increased over the first 2 years of the time series, then followed a parabolic shape, decreasing until

**FIGURE 4** The (a) common trend from the Chesapeake Bay–coastal ocean dynamic factor analysis (DFA) with the confidence interval represented by the gray ribbon and (b) factor loadings, where the threshold ( $\pm 0.2$ ) indicating strong loading on the common trend is represented by the dashed lines. A. croaker: Atlantic croaker; S. flounder: summer flounder; W. flounder: windowpane flounder; C. skate: clearnose skate; H. crab: horseshoe crab







**FIGURE 5** The (a) first common trend and (b) factor loadings on common trend one, and (c) the second common trend and (d) resultant factor loadings on common trend two from the Delaware Bay-coastal ocean dynamic factor analysis (DFA). The confidence intervals are represented by the gray ribbon in (a) and (b), and the threshold ( $\pm 0.2$ ) indicating strong factor loading on the common trend is represented by the dashed lines in (c) and (d). A. croaker: Atlantic croaker; S. flounder: summer flounder; W. flounder: windowpane flounder; C. skate: clearnose skate; H. crab: horseshoe crab

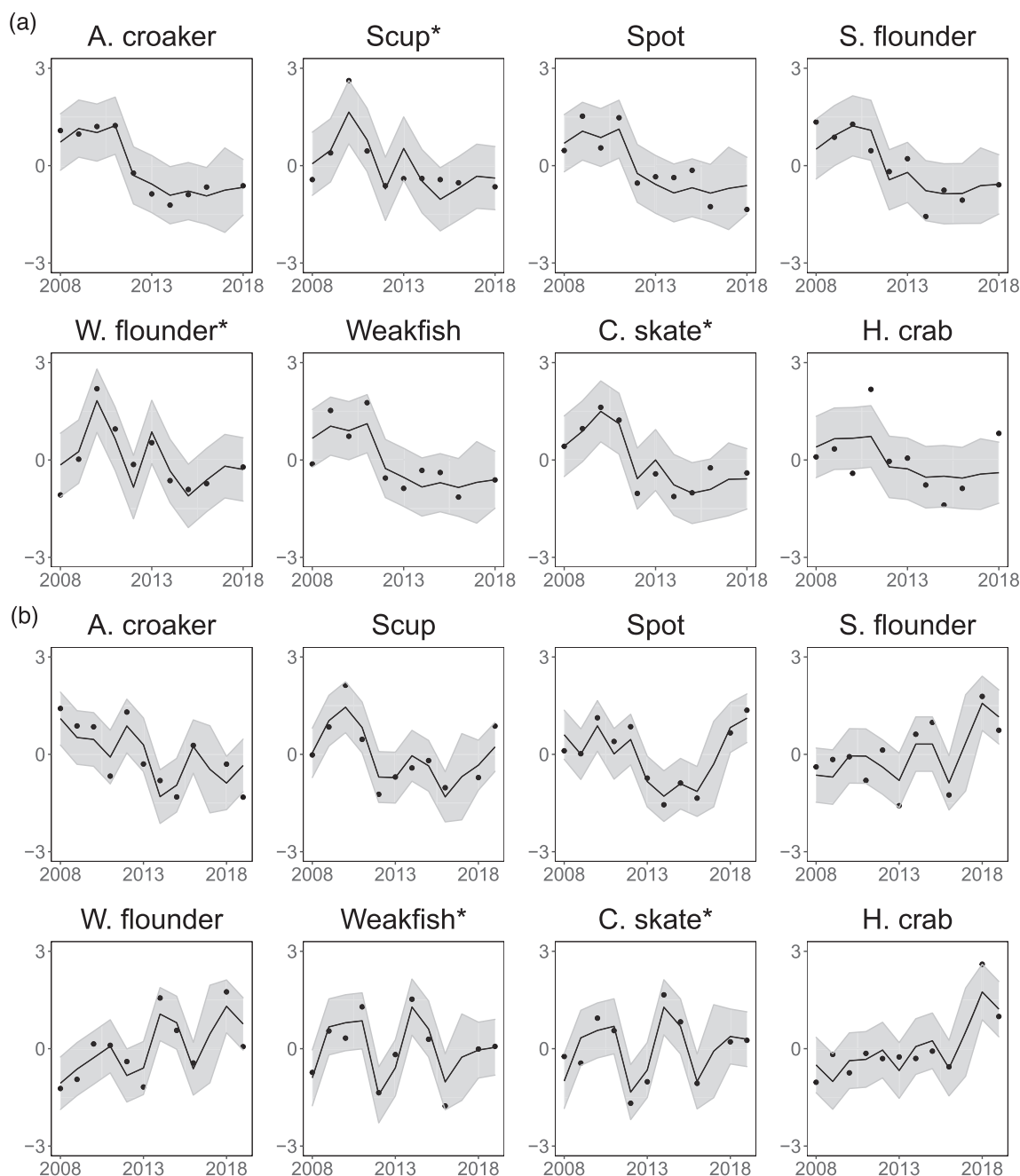
2016, after which it increased (Figure 5c). Six species loaded strongly and positively on the second common trend (Figure 5d). Summer flounder, weakfish, clearnose skate, and horseshoe crab loaded strongly on both common trends while the remaining four species loaded strongly on one common trend. Average bottom temperature from the NEAMAP spring cruises had a significant and negative impact on the usage of Delaware Bay by weakfish and clearnose skate (Table S2). The model fits for both the Chesapeake Bay-coastal ocean and Delaware Bay-coastal ocean comparisons were generally good (Figure 6a,b). For the Chesapeake Bay DFA, only the time series of horseshoe crab relative habitat usage was considered to have a poor fit, with a fit ratio of 0.67. The remaining time series had fit ratios ranging from 0.05 (Atlantic croaker) to 0.3 (scup). The Delaware Bay DFA fit ratios were from 0.08 (spot) to 0.29 (Atlantic croaker).

## 4 | DISCUSSION

This investigation provides a quantitative evaluation of the patterns of estuarine utilization and ecosystem exchange for a suite of key fisheries resources in the southern Mid-Atlantic Bight. Gaining insight into the relative habitat usage of estuarine and coastal environments for these species contributes to the understanding of both their population dynamics and possible responses to climate change. Together, commercial landings of these species generate more than \$20 million

in revenue annually, and five of these species are among the most targeted by recreational fishers in the Mid-Atlantic (NMFS, 2018); thus, an improved understanding is critical for the continued delivery of these desirable ecosystem services. Further, the information generated from this study can serve as a valuable baseline when evaluating the overall changes in the use of these three ecosystems over time, and may prove useful when considering benefits derived from these habitats, as these trends in relative usage identify systems that are seemingly becoming more (when positive) and less (when negative) favorable to these taxa.

A decrease (increase) in relative habitat usage of a given estuary can be attributed to one of four possible scenarios: (1) a decrease (increase) in estuarine relative abundance while coastal relative abundance is constant, (2) coastal relative abundance decreases (increases) at a slower rate than estuarine relative abundance, (3) an increase (decrease) in relative abundance in the coastal ocean while estuarine relative abundance remains constant, or (4) a relative abundance increase (decrease) in the estuary that is outpaced by an increase (decrease) in relative abundance in the coastal ocean. Given that the same NEAMAP datasets were used to evaluate exchange for both Chesapeake Bay and Delaware Bay, any changes in coastal abundance, including potential phenological shifts of earlier estuarine entrance affecting the availability to the NEAMAP spring survey, were captured in both ratios. If changes in relative habitat usage were being driven purely by a signal in coastal relative abundance, then the time



**FIGURE 6** Model fits from the dynamic factor analysis (DFA) for (a) Chesapeake Bay–coastal ocean comparison and (b) Delaware Bay–coastal ocean comparison. The gray ribbons represent the confidence intervals and the points are the estimates from the beta-binomial time series models. Species names followed by an asterisk indicate a significant relationship between the time series of relative habitat usage and the covariate included in the selected DFA. A. croaker: Atlantic croaker; S. flounder: summer flounder; W. flounder: windowpane flounder; C. skate: clearnose skate; H. crab: horseshoe crab

series of relative habitat usage in the two estuaries would have been similar, which was not found, except for Atlantic croaker. Thus, it can be concluded that the observed trends in relative habitat usage were being driven by changes in proportional relative abundance within the estuaries. Overall, for the species analyzed, relative habitat usage of Chesapeake Bay compared to the coastal ocean has decreased since 2008, while relative usage of Delaware Bay by those taxa has either increased or remained constant.

Of the eight species included in this investigation, the stock status of five species (scup, summer flounder, windowpane flounder, clearnose skate, and horseshoe crab) was recently assessed as healthy at the regional scale (ASMFC, 2019a; NEFSC (Northeast Fisheries Science Center), 2020; Sosebee, 2020; Terceiro, 2021a, 2021b) and the remaining three (Atlantic croaker, spot, and weakfish) displayed population characteristics that caused management concern (ASMFC, 2019b, 2021a, 2021b). This provides important context for

the trends in relative habitat usage and further supports the conclusion that the trends are not driven by coastal abundance. Of the five species with healthy coastwide stock status, three species (summer flounder, clearnose skate, and horseshoe crab) displayed a significant decline in relative habitat usage in Chesapeake Bay, while the same declining relationship was not found in Delaware Bay relative habitat usage. Atlantic croaker was the only species that had a significant trend in the same direction (declining) in relative habitat usage in both estuaries. As abundance levels are of concern for Atlantic croaker, and associated management efforts have been implemented (ASMFC, 2021a), it is possible that the trends in relative habitat usage of this species is being driven by the dynamics of the coastwide stock.

Previous studies have documented significant northward shifts in the distributions of many species in the Mid-Atlantic Bight, including several evaluated in this study (e.g., Bell et al., 2015; Lucey & Nye, 2010; Nye et al., 2009). Additionally, seven of the eight species evaluated were considered to have a high potential to exhibit distributional shifts in response to climate change; only horseshoe crab was deemed to have low potential (Hare et al., 2016). These distributional changes likely would cause a decline in the localized abundance of these species in the vicinity of the mouth of Chesapeake Bay. As such, these shifts may have driven the trends of decreasing relative usage of Chesapeake Bay, as overwintering individuals would likely have to migrate well past this estuary to encounter amenable conditions for the summer season.

Additionally, long-term warming, rather than annual temperature fluctuations, has been found to drive the northward distributional shift of marine taxa in the northwest Atlantic Ocean (Nye et al., 2009). While NAO has not yet been implicated as the primary driver responsible for these shifts in the near coastal waters of the Mid-Atlantic region, NAO was found to be positively associated with the overall trend shared among several broad-scale climatic indices, which was significantly correlated with shifts in species assemblages (Lucey & Nye, 2010). Further, NAO was significantly correlated with a shift in an estuarine community in New England from primarily demersal to dominated by pelagic species (Collie et al., 2008), and was significantly related to the community composition and seasonal usage of estuarine environments by juvenile fishes elsewhere (Attrill & Power, 2002). NAO has also been shown to impact the population dynamics of several marine species by shaping recruitment, abundance, and predatory interactions (Drinkwater et al., 2003; Ottersen et al., 2001, 2010).

In recent decades, the NAO index has been primarily in a positive phase, which is associated with warmer conditions in the Mid-Atlantic (Hurrell, 1995; Hurrell et al., 2003; Visbeck et al., 2001). This investigation found that NAO was associated with exchange between the Chesapeake Bay and coastal ocean, while average spring bottom temperature from NEAMAP cruises was related to the Delaware Bay-coastal ocean exchange. Thus, the climatic variables related to relative habitat usage in the two estuaries are operating on different temporal scales: NAO is a signal of longer-term warming, while average spring bottom temperature from NEAMAP cruises represent annual fluctuations. For individuals in the vicinity of Delaware Bay, spring

temperature may serve as a signal to begin estuarine migration, or to remain in coastal waters if temperatures are higher than preferred. The significant relationship between spring bottom temperatures measured during NEAMAP cruises and the Delaware Bay-coastal ocean exchange underscores the importance of local-scale processes driving relative habitat usage of this estuary.

NAO is a mesoscale climate pattern impacting multiple environmental factors, including wind speed and direction, precipitation, storm intensity, circulation patterns, and heat transport in the ocean (Hurrell, 1995; Hurrell et al., 2003). Thus, despite the difference in temporal scales, the significant covariates in each model were measures of water temperature, albeit indirectly for NAO. Overall, the results of this investigation contribute to the growing body of information on the influences of climate on marine taxa in the Mid-Atlantic by finding that NAO likely is an important driver of estuarine utilization at the boundaries of a species' range (i.e., edge-effects), while local-scale drivers influence relative estuarine usage within its range.

The varying degrees of site fidelity or natal homing exhibited by the species included in this investigation introduces added complexity when attempting to evaluate the impact of changes in relative habitat usage on overall population dynamics. Four of the species in this investigation (scup, windowpane flounder, weakfish, and horseshoe crabs) spawn within estuaries (Able & Fahay, 2010; ASMFC, 2019a). The reliance upon an estuarine environment to complete their reproductive cycle denotes some degree of estuarine dependency (Able, 2005; Whitfield, 2020). However, evidence suggests that scup spawn only in estuaries north of this study region (Able & Fahay, 2010; Eklund & Targett, 1990; NEFSC, 1999) and both windowpane flounder and weakfish can also spawn in ocean waters (Able & Fahay, 2010). The degree to which weakfish exhibit site fidelity is still not fully resolved, as some studies have found high levels of spawning site fidelity (e.g., Thorrold et al., 2001), while others have found low levels or evidence of a single panmictic population (Graves et al., 1992; Krause et al., 2020). Similarly, the level of site fidelity exhibited by horseshoe crabs is still unclear, as there is evidence that populations within estuaries are genetically distinct, indicating high rates of natal homing (Pierce et al., 2000). However, multiple long-term tagging studies have found that while horseshoe crabs remain close to their tagging sites for several days, the fraction recovered at the same spawning site the subsequent year diminished greatly, demonstrating a lack of site fidelity across years (McGowan, 2018; Swan, 2005).

In general, if strong site fidelity is a life history characteristic of a species, then the changes in estuarine relative habitat usage would likely be reflected in the future abundance of the overall coastwide population. That is, declines in relative usage of Chesapeake Bay would likely indicate a future decline in the localized coastal population of that species. However, changing environmental conditions could lead to improved survival and recruitment in the local population of a more northern estuary. In Delaware Bay, for example, this study has found that the relative habitat usage of horseshoe crabs has increased significantly over the time series. Thus, if horseshoe crabs do display strong natal homing, then the increase could result in the

horseshoe crab population increasing overall. For windowpane flounder, studies have not yet been conducted on the site fidelity of the Mid-Atlantic or New England stocks, and so it is unclear if changes in relative habitat usage can be interpreted as influencing trends in the overall population.

Future work on estuarine fidelity of these non-obligate estuarine users (i.e., those that are not fully dependent upon estuaries; Able, 2005; Whitfield, 2020) would help contextualize the results of this study and the implications for the coastwide populations. An additional area of focus for future work is on the spawning location of coastal shelf spawners, as juvenile abundances of summer flounder and spot, two of three coastal shelf spawners included in this study, have declined in recent years (Tuckey & Fabrizio, 2021), while coastwide assessments have not found similar declines in adult biomass (Able et al., 2017; ASMFC, 2021b; NEFSC, 2019), although spot harvest levels have recently triggered management actions. Finally, while this investigation quantified ratios of relative habitat usage by pairing a spring coastal and summer estuarine survey, evaluating the within-season egress of migrant species back into coastal waters and the role of bay-specific covariates, such as measures of habitat quality (e.g., temperature or hypoxic volume) or fishing pressure, in driving that migration represent a valuable area of future research.

While this study cannot support explicit inference on abundance trends for the eight species included in an absolute sense, this work provides valuable information on relative habitat utilization and ecosystem exchange in the southern Mid-Atlantic Bight. For example, the relative usage of Delaware Bay by horseshoe crabs has increased significantly, while declining significantly within Chesapeake Bay. The trends can be used to provide a “ranking” of the relative usage of each ecosystem, with Delaware Bay usage the strongest, followed by the coastal ocean, and finally Chesapeake Bay.

Water temperatures are expected to continue to rise, and thus these general trends in relative habitat usage likely will continue. It is expected that Chesapeake Bay will be utilized less frequently, as important fisheries resources will instead inhabit coastal waters or more northerly estuaries. Shifting distributions of living marine resources have already caused management conflicts (Dubik et al., 2019), and the impacts of range changes on estuarine utilization will only further the discourse. This study contributes to the growing body of information focused on characterizing the dynamics in the Northwest Atlantic Ocean along the US continental shelf by resolving trends in relative habitat utilization and ecosystem exchange for two major estuaries in the southern Mid-Atlantic Bight.

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## CONFLICTS OF INTEREST

The authors have no conflicts of interest.

## AUTHOR CONTRIBUTIONS

AJS, JG, and RJL contributed to the study design. Statistical analyses were conducted by AJS with input from JG and RJL. The first draft of the manuscript was written by AJS and subsequently revised based on comments provided by JG and RJL. All authors approved the final manuscript.

## DATA AVAILABILITY STATEMENT

All data used to generate the annualized covariates are publicly accessible online with access information provided in the main text. Catch data from ChesMMAP and NEAMAP are available from the authors upon reasonable request, and data from DBATS were provided to the authors by Delaware Division of Fish & Wildlife following a written request.

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## SUPPORTING INFORMATION

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