



# Hypoxia influences the extent and dynamics of suitable fish habitat in Chesapeake Bay, USA

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**ABSTRACT:** Intra-annual patterns of hypoxia in Chesapeake Bay have been recorded since the mid-1900s, but anthropogenic inputs and climate change have exacerbated the volume and extent of hypoxic waters, which mobile marine fishes avoid. This estuary provides important habitat for many seasonally resident species but declines in relative abundance and relative habitat usage have been documented. An understanding of the relationship between environmental conditions and habitat suitability could assist in evaluating the stock status of these species. To characterize baseline habitat associations for *Micropogonias undulatus*, *Leiostomus xanthurus*, *Paralichthys dentatus*, and *Cynoscion regalis*, ecological niche models were developed relating catch-per-unit-effort data from a fisheries-independent trawl survey conducted within Chesapeake Bay to environmental covariates. Model output indicated that impacts of climate change on the environmental conditions, including continued increases in temperature and decreases in dissolved oxygen (DO) concentration, will likely further the decline in estuarine utilization of these species. The niche envelopes were then paired with hindcasts from an estuarine-carbon-biogeochemical regional model to derive estimates of spatiotemporal habitat suitability. The patterns in habitat suitability do not match those of declining abundance, indicating that dynamics outside of Chesapeake Bay are likely driving the shift. An auxiliary model was used to replace hypoxic DO concentrations with normoxic concentrations to evaluate the influence of hypoxia on habitat suitability. Both hypoxic severity and extent displayed significant associations with the quantity of suitable habitat available to each species in the bay. Results characterize the complexity of the dynamics underpinning observed trends in habitat utilization.

**KEY WORDS:** Climate change · Ecological niche · Habitat suitability · Estuarine usage · Mid-Atlantic fishes

## 1. INTRODUCTION

In recent decades, anthropogenic nutrient inputs and climate change have amplified the extent of aquatic hypoxic zones, defined as areas with low dissolved oxygen (DO) concentrations (Diaz & Rosenberg 2008, Rabalais et al. 2014, Altieri & Diaz 2019). Hypoxia can manifest seasonally (typically during warmer

months), periodically (days to weeks), or episodically (infrequent, <1 event per year; Diaz & Rosenberg 2008). Seasonal oxygen depletion can cause mortality of sessile benthic organisms (Sagasti et al. 2001) and it influences the physiological processes of more mobile fishes, as evidenced by decreases in growth rates (Eby et al. 2005), reproduction (Wu et al. 2003), antipredator behaviors (Domenici et al. 2007, Chapman & McKenzie

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2009), and swimming speeds (Craig et al. 2023). Thus, persistent hypoxia has the potential to impact the population dynamics of species and ecosystem functioning more broadly.

Hypoxia is known to occur in waters worldwide, with the physical properties of the water body itself and the local anthropogenic impacts contributing to the severity and extent of hypoxia (Breitburg et al. 2018). The physical attributes of the Chesapeake Bay, the largest estuary in the continental USA, provide benefits in the form of supporting a nursery habitat (Schloesser & Fabrizio 2019), while also contributing to the persistent hypoxia experienced by the system (Breitburg et al. 2018). The bay is characterized by a deep channel (20–30 m) that is surrounded by shallow (primarily <10 m) water environments (Boicourt et al. 1999, Kemp et al. 2005). The bay is partially-mixed through estuarine circulation that is primarily driven by freshwater inputs (Pritchard 1956, Kemp et al. 2005). A strong salinity gradient (oligohaline to polyhaline) and riverine flow lead to stratification of the water column, particularly in summer months (Boicourt 1992, Hagy 2002, Kemp et al. 2005). The Chesapeake Bay also displays large seasonal fluctuations in temperature, allowing it to serve as critical habitat seasonally, from the spring (Mar–May) through fall (Sep–Nov), for a diversity of post-juvenile (age > 1) marine fishes (Murphy et al. 1997). Specifically, these taxa, several of which support highly valuable recreational and commercial fisheries (Kirkley et al. 2005, Lellis-Dibble et al. 2008, Able & Fahay 2010, NMFS 2022), utilize the bay as refuge, foraging, and spawning habitat (Murphy et al. 1997, Able & Fahay 2010).

Water temperatures in Chesapeake Bay have been increasing as a result of climate change (Ding & Elmore 2015, Hinson et al. 2022, Tian et al. 2022), consistent with documented changes occurring in other estuaries on the US East Coast, including Long Island Sound (Howell & Auster 2012) and Narragansett Bay (Oviatt 2004, Collie et al. 2008, Langan et al. 2021), as well as throughout the global ocean basins (Levitus et al. 2000, IPCC 2014). The cumulative impacts of climate change are expected to be greatest in coastal and estuarine systems (Najjar et al. 2010, Wetz & Yoskowitz 2013), and include additional effects on the physical environment such as decreasing DO, increasing frequency and intensity of precipitation, and changes to salinity and the seawater chemistry (e.g. Karl & Trenberth 2003, Najjar et al. 2010, Muhling et al. 2018, Hinson et al. 2023).

There has been a significant increase in hypoxic volume in the Chesapeake Bay since the 1950s (Hagy

et al. 2004, Murphy et al. 2011), which is expected to continue in response to the decreased solubility of DO in warmer waters (Irby et al. 2018, Tian et al. 2022). Fish avoidance of hypoxic zones, in the form of spatial displacement, has been documented within the bay (Buchheister et al. 2013) and in other systems (e.g. Eby & Crowder 2002, 2004, Craig et al. 2023). Further, temperature-related reductions in DO have been suggested as a main driver of distributional shifts of mobile marine species throughout the Atlantic Ocean (Pörtner & Knust 2007, Deutsch et al. 2015). Similarly, to maintain their optimal thermal range, fish are expected to shift poleward or to deeper water in response to warming (Murawski 1993, Walther et al. 2002, Parmesan & Yohe 2003, Perry et al. 2005). This behavior has been extensively documented in coastal waters adjacent to Chesapeake Bay (e.g. Nye et al. 2009, Lucey & Nye 2010, Pinsky & Fogarty 2012, Bell et al. 2015, Kleisner et al. 2016).

The relative abundance of several fish species in Chesapeake Bay has decreased substantially, with declines in survey catch rates of up to 90% from 2002–2011 for some taxa (Buchheister et al. 2013). Many of these species inhabit the bay only seasonally (spring–fall), and over approximately the same time period, the seasonal usage of this estuary relative to the coastal ocean has also declined for several species (Schonfeld et al. 2022). As fishery managers seek to improve the status of living marine resources in Chesapeake Bay, it is important to understand the relationship between environmental factors, habitat suitability, and relative abundances of those species. Ecological niche models (ENMs) and species distribution models (SDMs) are 2 tools commonly employed to achieve such a goal (Peterson et al. 2015, Melo-Merino et al. 2020). While these approaches are similar, the aim of each is distinct (Peterson & Soberón 2012). ENMs explicitly model a subset of the ecological elements experienced by a species to allow for inference regarding the processes driving the distribution and potential habitat, while SDMs model the realized occupied space (Peterson & Soberón 2012, Melo-Merino et al. 2020). This investigation seeks to (1) develop ENMs for 4 seasonally resident fish species inhabiting Chesapeake Bay: Atlantic croaker *Micropogonias undulatus*, spot *Leiostomus xanthurus*, summer flounder *Paralichthys dentatus*, and weakfish *Cynoscion regalis*; (2) pair these niche envelopes with an estuarine-carbon-biogeochemical regional ocean model to evaluate changes in suitable habitat in Chesapeake Bay over time (2002–2020); and (3) quantify the influence of hypoxia on spatiotemporal patterns of habitat suitability.

## 2. MATERIALS AND METHODS

### 2.1. Data sources

The 4 finfish species common to the Chesapeake Bay included in this study, Atlantic croaker, spot, summer flounder, and weakfish, were selected due to their status as key recreational and commercial species in the Mid-Atlantic (NMFS 2022), as well as their ecological importance. The analyses were supported by 16 yr (2003–2018) of data collected by the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP), a fisheries-independent trawl survey conducted within the mainstem of the bay. ChesMMAP cruises occur bimonthly from early spring to fall, the extent of seasonal estuarine residency in Chesapeake Bay, sampling approximately 80 sites according to a stratified random design based on latitude and depth (3.0–9.1 m, 9.1–15.2 m, and >15.2 m; Fig. 1). To gain insight into the relationship between habitat suitability and hypoxia, and how it has changed over time, data from ChesMMAP cruises conducted during May (pre-hypoxic peak), July (during hypoxic peak), and September (post-hypoxic peak; Smith et al. 1992, Kemp et al. 2005, Murphy et al. 2011), were included. Data collected during 2007, 2009, and 2010 were excluded due to incomplete cruises during the months of interest.

Environmental conditions, including bottom water temperature, bottom DO concentration, bottom salinity, and depth, are measured at each ChesMMAP sampling site. A 4-seam bottom trawl (13.7 m head-rope length with 7.6 cm codend mesh) is towed for 20 min in the direction of the current. Specimens are then sorted by species and enumerated (Latour et al. 2003, 2023). For each species, only regions in which the fish are expected to be present based on life history were included in the analysis to reduce the number of uninformative zeros in the data (Latour et al. 2017). Specifically, regions were excluded if <5% of tows captured the species of interest and catch in the region represented <5% of the overall catch throughout the time series.

Output from an implementation of the Regional Ocean Modeling System (ROMS; Shchepetkin & McWilliams 2005) coupled with an Estuarine-Carbon-Biogeochemistry (ECB) module configured specifically for the Chesapeake Bay (ROMS-ECB; St-Laurent et al. 2020, Frankel et al. 2022, St-Laurent & Friedrichs 2024) was used to provide daily values of the environmental parameters of interest (i.e. water temperature, DO concentration, and salinity) at 600 m horizontal resolution from 2002–2020. This time series includes

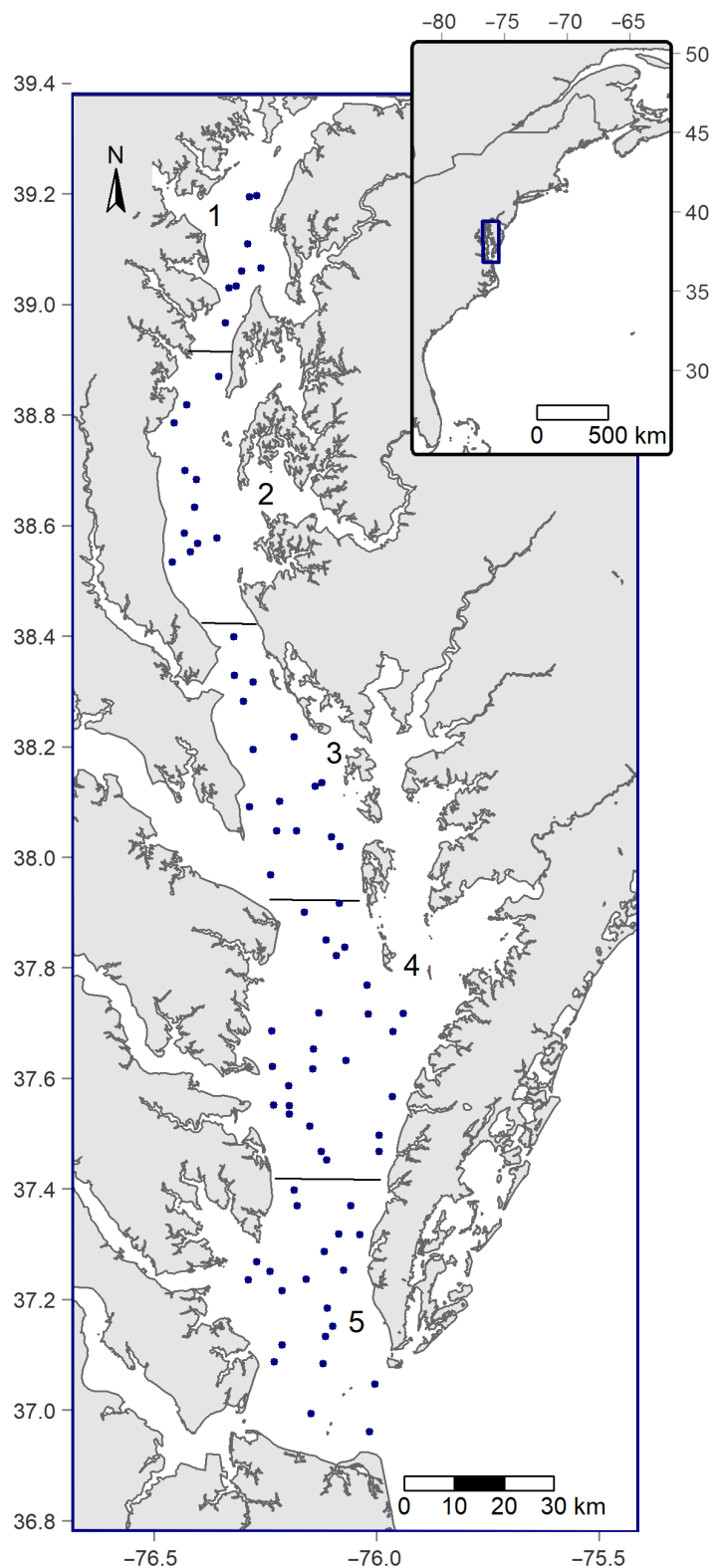


Fig. 1. Sampling sites for a representative cruise (July 2013) conducted by the Chesapeake Bay Multispecies Monitoring and Assessment Program. Circles: tow locations; horizontal lines: stratification scheme (i.e. sampling regions, 1–5)

years outside of the ChesMMA data analyzed, as the ENM formulation is not constrained temporally. ROMS-ECB output for all months within the range of the ChesMMA cruises was used (May–Sep), while the spatial grid of this model was trimmed to include only cells within the sampling frame of the ChesMMA cruises used for each species. Although ROMS-ECB is a 3-dimensional model with 20 vertical levels, only the bottom level was used in this analysis as the species included in this study are demersal and specimens were collected using a bottom trawl.

## 2.2. Ecological niche models

The habitat associations for the suite of species were characterized through the development of ENMs (Peterson & Soberón 2012), whereby catch-per-unit-effort, quantified as count per tow, was related to the 4 environmental parameters measured synoptically at each site: bottom water temperature (°C), bottom DO concentration ( $\text{mg O}_2 \text{ l}^{-1}$ ), bottom salinity, and depth (m). Collinearity was assessed through calculation of the variance inflation factor of all model terms in a fully saturated (i.e. included all parameters) linear model before proceeding with model selection. The generalized additive modelling (GAM) framework was used to develop the ENMs, as these models can include both parametric (i.e. linear) and non-parametric (i.e. non-linear) components (Zuur et al. 2009). The count data were assumed to follow a negative binomial distribution and the natural logarithm of the area swept by the survey trawl, the measure of effort, was included as an offset variable. Significant correlations between latitude and salinity ( $r < -0.7$ ;  $p < 0.001$ ) and between day-of-year (DoY) and temperature ( $r > 0.7$ ;  $p < 0.001$ ) precluded the possibility of including either latitude or DoY in the model. Akaike's information criterion (Akaike 1973, Burnham & Anderson 2002), the Bayesian information criterion (Burnham & Anderson 2004), and diagnostic plots (QQ plots, analysis of residuals) were used in model selection. For continuous covariates, the number of knots included in the smoothing function was adjusted based on information criteria to avoid extraneous smoothing without losing important information on the relationships. Concurvity of the selected model was evaluated to confirm that there were no problematic relationships among the smoothed covariates, and Kolmogorov-Smirnov, dispersion, and outlier tests were applied to simulated model residuals to verify distributional assumptions. Marginal means (Searle et al. 1980) were then used to estimate

the relationship between predicted abundance across the domain of each covariate of the selected models. All analyses were conducted using the software program R (v4.2.0; R Core Team 2022). The package 'mgcv' (Wood 2017) was accessed to fit the ENMs, and the package 'DHARMA' (Hartig 2022) was used to evaluate residuals and model assumptions.

## 2.3. Habitat suitability and hypoxia

ROMS-ECB provided simulated environmental conditions for each individual cell (area  $0.36 \text{ km}^2$ ) in the sampling grid every day for 5 mo (May–Sep) over 19 yr (2002–2020). These water quality outputs were then coupled with the selected ENM for each species and used to predict the expected count based on those environmental conditions in each grid cell (Fig. 2a). These predicted counts were used as a proxy for suitable habitat, where a larger predicted count represented greater habitat suitability. After predicting this value in each grid cell daily, the estimates for each cell were averaged within each month and year (Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m748p117\\_supp.pdf](http://www.int-res.com/articles/suppl/m748p117_supp.pdf)). That is, a single value was calculated to represent the habitat suitability of each cell for a given month and year. Then, the overall annual habitat suitability index (HSI) for each species in Chesapeake Bay was calculated by summing the averaged values in the sampling frame across the 5 months. Annual HSI values were then scaled by dividing by the mean of all annual HSI estimates (Fig. 2a). Trends in the HSI time series were analyzed using Theil-Sen regressions (Sen 1968, Theil 1992), a non-parametric approach (R package 'RobustLinearReg'; Hurtado 2020).

Spatial patterns of habitat suitability within Chesapeake Bay were also evaluated by calculating the average HSI value per cell on an annual scale (i.e. averaged across all months, May–Sep, within a given year), to allow for visualization of the suitability throughout the full sampling frame at an annual scale (Fig. S1). For each species, quantiles were calculated from the estimates of all 19 years of estimated values and mapped. To derive a measurement of stability in the annual averages, the SE of the predictions within a single cell across all months in a year was used to calculate 95% confidence intervals (CIs) surrounding the mean. Dividing the range of the CI by the annual average value in the corresponding cell provided a value akin to a coefficient of variation, which hereafter is referred to as the instability or variability of the suitability of the cell.

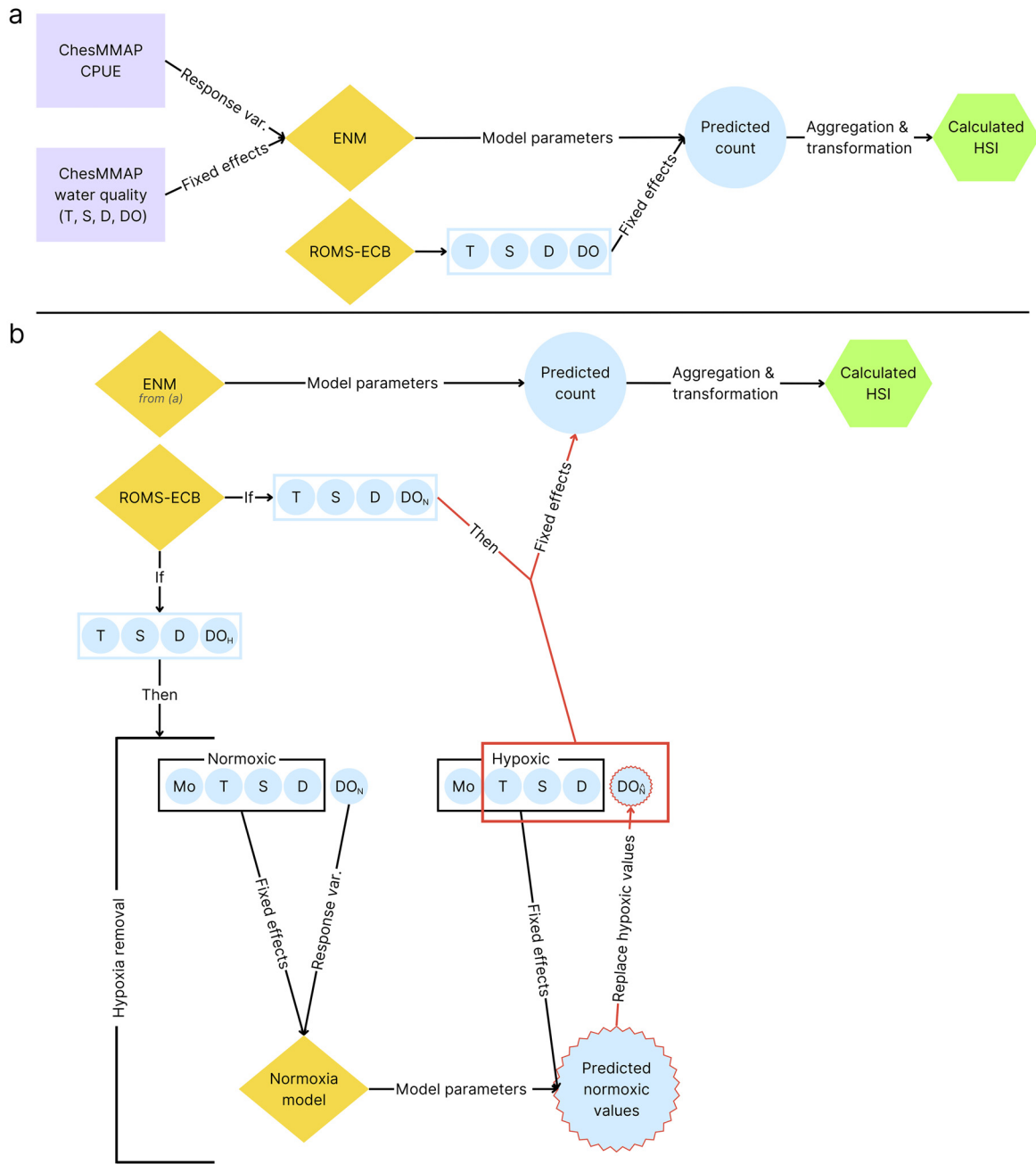


Fig. 2. Flow of model development and predictions to generate habitat suitability indices (HSI). Purple boxes: observational data from the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAAP); yellow diamonds: models; blue bubbles: predictions; green hexagons: final calculated values of interest. (a) Observational catch-per-unit-effort (CPUE) and water quality measurements (T: temperature; S: salinity; D: depth; DO: dissolved oxygen) were used to build the ecological niche model (ENM) for the selected species. ROMS-ECB (Regional Ocean Modeling System – Estuarine Carbon Biogeochemical; St-Laurent & Friedrichs 2024) output was then used in the ENM to predict the count of a given species per cell, which was used to calculate the HSI. (b) Hypoxia ‘removed’ calculations. Specifically, the ROMS-ECB output (T, S, D, DO) was separated into normoxic ( $>2.5 \text{ mg O}_2 \text{ l}^{-1}$ ;  $\text{DO}_N$ ) cells and hypoxic ( $\leq 2.5 \text{ mg O}_2 \text{ l}^{-1}$ ;  $\text{DO}_H$ ) cells. If the cells were hypoxic, then the hypoxia removal process was implemented. A normoxia model was developed by relating the ROMS-ECB normoxic DO values ( $\text{DO}_N$ ) to the other associated parameters (month [Mo], T, S, D). Then, the ROMS-ECB Mo, T, S, and D associated with hypoxic cells were used in the normoxia model to predict replacement normoxic DO values ( $\text{DO}_N$ ). Temperature, salinity, and depth in the hypoxic cells were not affected by the DO modification. Finally, the ROMS-ECB output associated with normoxic cells (T, S, D,  $\text{DO}_N$ ) and the hypoxia ‘removed’ output (T, S, D,  $\text{DO}_N$ ) were used in the same way as in (a) to generate theoretical estimated species counts per cell and calculate HSIs. Red outlines and arrows in (b) aid in the visualization of the flow following the predicted normoxic DO values ( $\text{DO}_N$ )



To evaluate the impacts of hypoxia on available habitat for each species, all ROMS-ECB DO concentrations that were hypoxic were replaced with a normoxic value. While  $2.0 \text{ mg O}_2 \text{ l}^{-1}$  is often used to categorize waters as hypoxic, the DO concentration that induces behavioral and physiological responses is more ecologically relevant. Species-specific thresholds of hypoxia tolerance vary, and species included in this study have been shown to avoid areas with DO concentrations of  $2.3 \text{ mg O}_2 \text{ l}^{-1}$  and lower (Eby & Crowder 2002). Thus, a threshold value of  $2.5 \text{ mg O}_2 \text{ l}^{-1}$  was used to better encapsulate the habitat association of each species in this analysis. The replacement of hypoxic values with normoxic values was accomplished by filtering the ROMS-ECB output to only include normoxic cells (i.e.  $>2.5 \text{ mg O}_2 \text{ l}^{-1}$ ) and subsequently fitting a GAM to this dataset, where DO ( $DO$ ) concentration at space  $s$  and time  $t$  was the response variable, assumed to follow a gamma distribution:

$$DO_{s,t} = b + f_1(T_{s,t}) + f_2(Sa_{s,t}) + f_3(D_{s,t}) + \alpha_t(\text{Mo}_t) \quad (1)$$

and where  $b$  is the intercept,  $f_1$ ,  $f_2$ , and  $f_3$  are the smoothing functions for the other simulated environmental conditions: water temperature ( $T$ ), salinity ( $Sa$ ), and depth ( $D$ ). Additionally,  $\alpha_t$  is the estimated mean effects for each month ( $\text{Mo}$ ). The R package 'gamlss' (Rigby & Stasinopoulos 2005) was utilized to develop this model.

This model was then coupled with the ROMS-ECB output containing hypoxic values to provide estimated normoxic DO concentrations ( $\hat{DO}_{s,t}$ ) at times and cells that were hypoxic based on the outputs of the other variables. All other environmental conditions from the ROMS-ECB simulation (i.e. water temperature, salinity, and depth) were unchanged. This method provides a quantitative alternative to replacing hypoxic values with a single constant normoxic value (e.g.  $2.5 \text{ mg O}_2 \text{ l}^{-1}$ ). The estimated concentrations are more likely to reflect true normoxic values encountered, given the other environmental conditions and time of year. These outputs with hypoxia 'removed' were then paired with the selected ENM and the same methods as above were used to calculate the hypoxia 'removed' annual HSI (Fig. 2b). For comparison, the hypoxia 'removed' annual HSI was also scaled by dividing by the mean of the 'true' annual HSI estimates (i.e. calculated from the outputs that included hypoxia).

The approximate area gained each month by removing hypoxia was calculated through the comparison of the average monthly predicted value in each cell in the sampling frame. Each estimate, for both

'true' outputs and hypoxia 'removed' outputs, was divided by the mean 'true' value within a month across years (e.g. mean cell estimate in May 2002–2020). Any values that were greater than or equal to the mean were considered to be good habitat. If a cell was below average in the 'true' output calculations, but became suitable once hypoxia was removed, the cell was classified as area gained. The number of cells that changed from below average to equal or greater than average was summed in the month and multiplied by  $0.36 \text{ km}^2$  (the area of a ROMS-ECB cell) to generate the total area gained in that month. The total area gained was also divided by the total area in the sampling frame for a given species (no. of cells  $\times 0.36 \text{ km}^2$ ) to calculate the proportional increase in suitable habitat area.

To further evaluate the influence of hypoxia on habitat suitability, ENM predictions for July were analyzed, since this month most often corresponds to the peak of hypoxia in Chesapeake Bay. Daily abundances were predicted in each cell in a given July, then averaged to generate a spatial field of cell-specific July averages (Fig. S1). The same calculations were applied to the ROMS-ECB output with hypoxia 'removed,' and at each cell, the average value from the 'true' outputs was subtracted from the average hypoxia 'removed' value, which populated the full sampling frame with the difference in suitability with no hypoxia. The quantiles were calculated from these differences and mapped. Additionally, the averaged values from the 'true' ROMS-ECB outputs were summed to get a single HSI value for the entire Chesapeake Bay sampling frame in July for each year. This calculation was repeated for the hypoxia 'removed' ROMS-ECB outputs and the proportional increase in July HSI was calculated by subtracting the 'true' July HSI from the hypoxia 'removed' July HSI, then dividing by the 'true' July HSI.

The influence of 'removing' hypoxia on habitat suitability was evaluated by relating the proportion change in available habitat in July to 2 measures of environmental quality from the ROMS-ECB outputs: extent and severity of hypoxia. Hypoxic extent was represented as the proportion of hypoxic area in July, which was calculated by determining the total number of hypoxic cells in the bottom-most layer of ROMS-ECB in July of that year divided by the total number of cells in the spatial field and days in the month. Hypoxic severity was quantified as the average bottom DO concentration in July from the ROMS-ECB outputs. The trends in the relationships between the proportion change in available habitat to the extent and severity of hypoxia were analyzed through Theil-Sen regressions (Sen 1968, Theil 1992).

### 3. RESULTS

#### 3.1. Ecological niche models

The selected ENM for each species included all 4 covariates and all displayed nonlinearity in the relationships between survey count and the predictor variables (exception: the depth covariate was linear for the summer flounder ENM; Table S1). The marginal mean predicted catches for 3 of the 4 species (Atlantic croaker, spot, and summer flounder) displayed a bimodal relationship with temperature, with the second peak larger than the first (Fig. 3a). For spot and summer flounder, this second peak occurred at approximately 25°C, while for Atlantic croaker, the second maximum occurred at approximately 22.5°C. Although the relationship between the weakfish marginal mean prediction and temperature was not bimodal, this species also displayed a maximum predicted relative abun-

dance at approximately 25°C (Fig. 3a). Marginal mean predictions for all 4 species were very low under hypoxic (<2.5 mg O<sub>2</sub> l<sup>-1</sup>) conditions (Fig. 3b). Peak marginal mean predictions for Atlantic croaker, summer flounder, and weakfish in relation to salinity occurred at approximately 20–30 (Fig. 3c). For spot, the marginal mean prediction for salinity showed the highest association with areas <10 and a secondary peak in the 20–30 range, as noted for the other species (Fig. 3c). The relationship between the marginal mean predictions and depth for all 4 species was highest at the lower to middle depth ranges sampled (Fig. 3d).

#### 3.2. Habitat suitability and hypoxia

For the 4 focal species, annual estimates of bottom habitat suitability generally fluctuated without a clear trend from 2002–2014, but showed a declining pattern

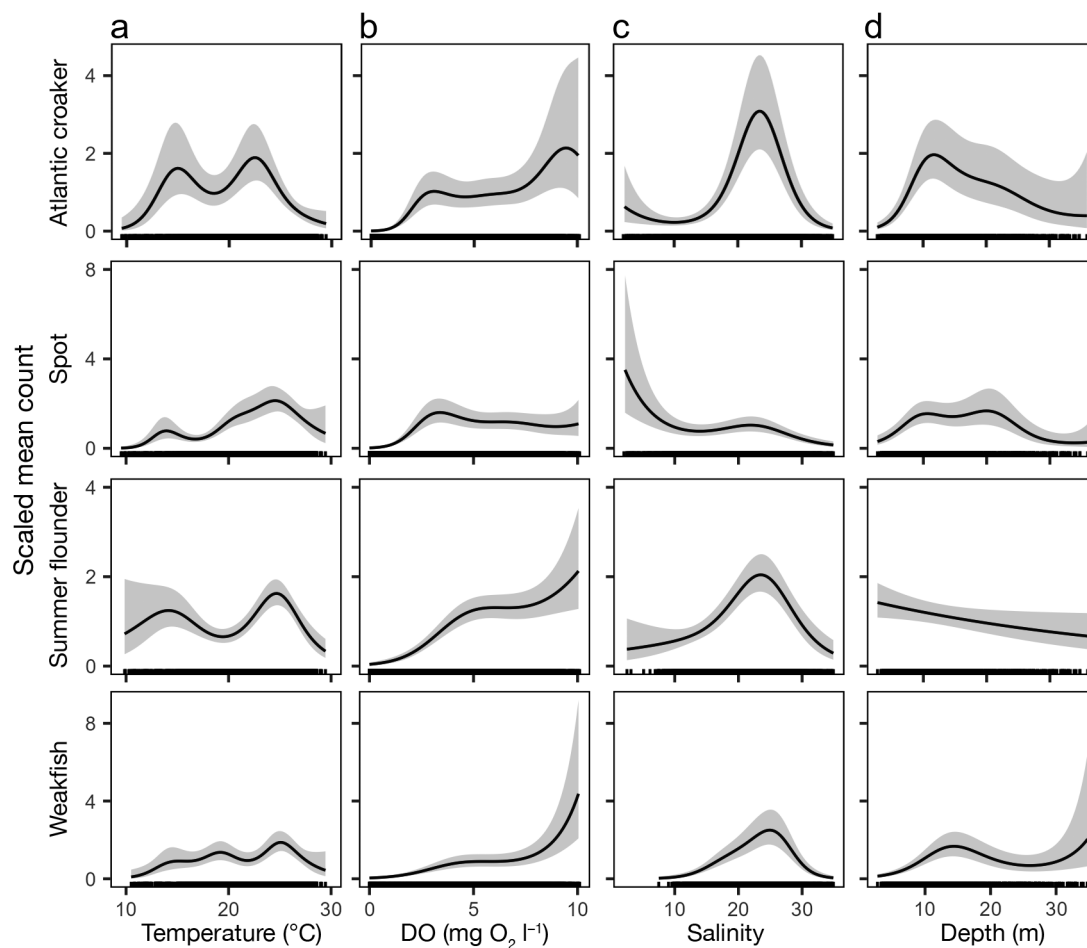


Fig. 3. Ecological niche model (ENM) output of the relationship between mean relative abundance and (a) temperature, (b) dissolved oxygen (DO), (c) salinity, and (d) depth for each species developed using survey data collected by ChesMMAAP. Measurements of environmental covariates in sparsely recorded ranges (i.e. on the upper and/or lower bounds of the observed;  $\leq 0.5\%$  of values) were omitted for visualization purposes. Gray bands: 95% CIs; rug plot: individual observations at each value of the covariate

thereafter (Fig. 4). Theil-Sen regressions indicated that these fishes did not have a significant temporal trend in annual HSI ( $p > 0.05$ ). For spot and weakfish, the minimum annual HSI occurred in 2003 (Fig. 4b,d), while the minima for Atlantic croaker and summer flounder were in 2018 (Fig. 4a,c). During both of those years, the Chesapeake Bay experienced high spring and summer freshwater inputs, as evidenced by having the 2 lowest average bottom salinities (17.9 and 16.9, respectively; Fig. S2a) from ROMS-ECB output within

the sampling frame and during the time span of this study (i.e. May–Sep 2002–2020), and thus were classified as wet years. For spot, summer flounder, and weakfish, the maximum estimated annual HSI occurred in 2002 (Fig. 4b–d), while for Atlantic croaker the maximum was in 2009 (Fig. 4a). In terms of freshwater inputs to the bay, 2002 was a dry year (i.e. one of the highest average bottom salinities, 20.7, from the ROMS-ECB output) and 2009 (salinity 20.2) was drier than average (salinity 19.3), but more typical.

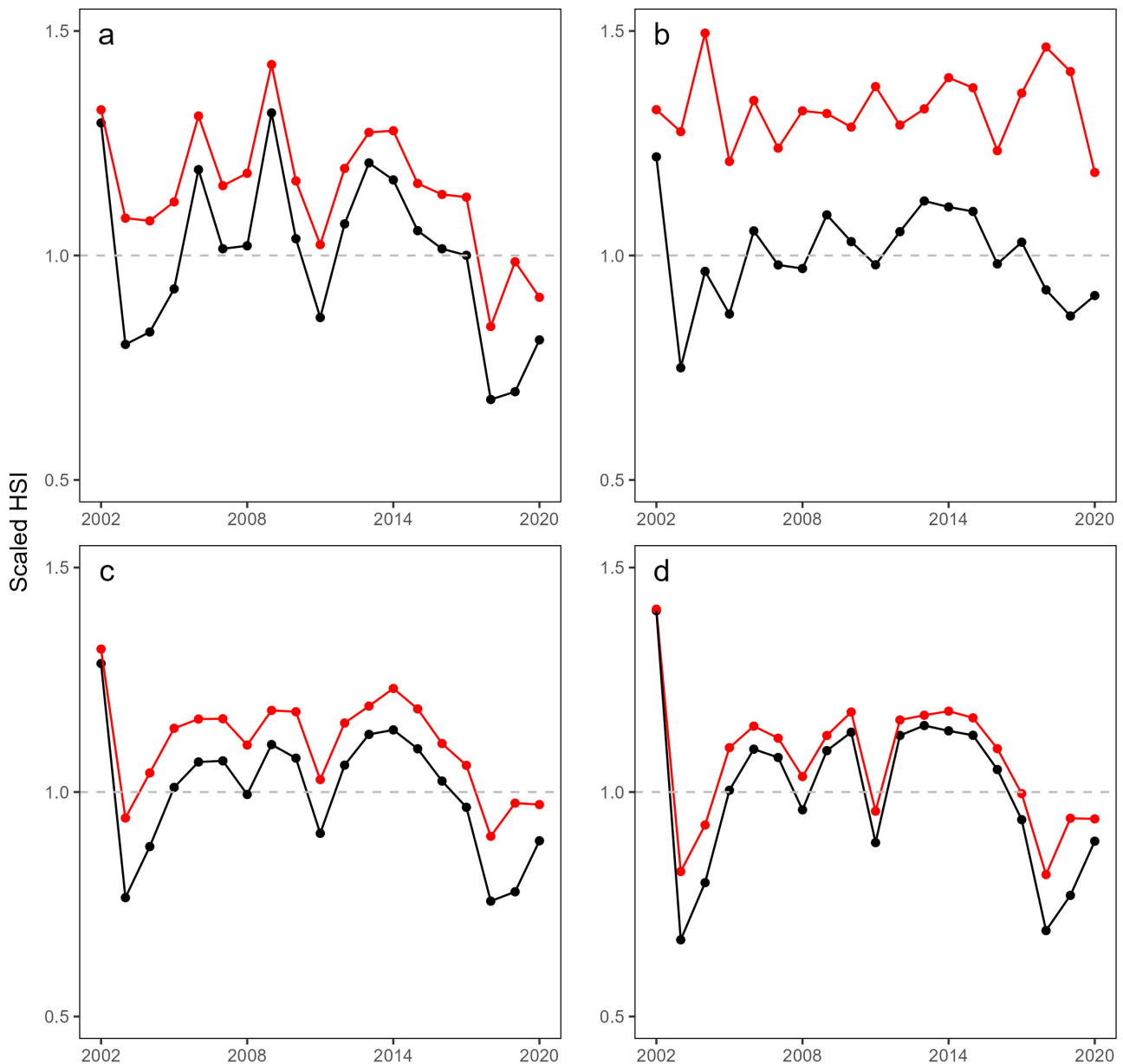


Fig. 4. Time series of habitat suitability indices (HSI) derived from the pairing of the ecological niche models (ENMs) and the simulated environmental conditions from the estuarine-carbon-biogeochemical Regional Ocean Modeling System for (a) Atlantic croaker, (b) spot, (c) summer flounder, and (d) weakfish. Black lines: HSI based on 'true' ROMS-ECB values; red lines: HSI based on data with hypoxia 'removed'; gray dashed line at scaled HSI of 1: average annual 'true' HSI across the time series



The most obvious difference in the spatial distribution of suitable habitats during years with high and low HSI for the 4 species was the increase in extent of high-quality habitat towards the head of Chesapeake Bay (Fig. 5). There were some areas that remained low quality for a species regardless of whether the year was estimated as having a maximum or minimum annual HSI. For example, the waters in the northernmost region of Chesapeake Bay were consistently low-quality habitat for summer flounder (Fig. 5c). The lower bay was relatively stable for all species during high and low years of estimated HSI, but there was markedly more instability in the mainstem during the years with the estimated minimum HSI compared to years of estimated maximum HSI (Fig. S3).

The time series of proportional increase in suitable habitat when hypoxia was 'removed' were highly similar among the 4 species, with the primary difference being the scale of the proportional increase (Fig. 6). Spot showed the largest increases in habitat with approximately a 70% increase in some years (Fig. 6b). Removing hypoxia appeared to have the smallest impact on the quantity of suitable habitat for weakfish, with less than a 25% increase over the years of this study (Fig. 6d). For both spot and weakfish, the maximum proportion increase occurred coincident with the minimum HSI (2003; Fig. 6b,d). Atlantic croaker and summer flounder exhibited a maximum proportion increase in suitable habitat in 2019 (Fig. 6a,c), which was not the same year associated with their respective minimum HSIs.

There was a clear seasonality in the potential increase in suitable bottom habitat without hypoxia for all 4 species, with the highest increase occurring primarily in July, and in June for some years (Fig. 7). Spot exhibited the highest potential gains in suitable habitat under the hypoxia 'removed' scenario, reaching approximately 2250 km<sup>2</sup> in June 2019, which is over 40% of the sampling frame (Fig. 7b). That increase was nearly 3 times the amount of area gained by summer flounder, which had the second highest increase of approximately 700 km<sup>2</sup> in July 2019 (Fig. 7c). While weakfish displayed the least amount of above-average habitat quality area to be potentially gained with hypoxia 'removed', namely a maximum of about 465 km<sup>2</sup> (June 2019), weakfish also had the smallest sampling frame included in the analyses (and therefore used to predict suitable habitat) due to the removal of the 2 northernmost regions in which they are not commonly found. Therefore, the largest increase in area for weakfish was about 12% of the Chesapeake Bay mainstem analyzed (Fig. 7d). Although Atlantic croaker displayed a larger potential

increase in suitable habitat, nearly 540 km<sup>2</sup> in July 2003, that area comprised only about 10% of the area of the mainstem, the least of all 4 species (Fig. 7a).

The peak in hypoxic extent and severity in Chesapeake Bay primarily occurred in July. According to the ROMS-ECB outputs within the ChesMMAP sampling frame, over 40% of the cells were hypoxic at some point throughout the month of July. Habitat gains from 'removing' hypoxia for Atlantic croaker and spot were higher than those for summer flounder in the more northern regions of the bay (Fig. 8a–c, respectively). Removal of the small hypoxic areas off several main tributaries in the southern portion of the bay resulted in larger effects on the habitat suitability for Atlantic croaker and weakfish (Fig. 8a,d) when compared to spot and summer flounder (Fig. 8b,c).

The relationship between the proportional increase in habitat suitability in July and both the severity and extent of hypoxia was significant for all species ( $p < 0.001$ ), as showcased by the fitted Theil-Sen regressions (Fig. 9). There was a significant positive trend in the proportional increase in suitable habitat when hypoxia was 'removed' in years with increasing hypoxic extent (i.e. proportion of hypoxic cells; Fig. 9a) and a significant decline with decreasing hypoxic severity (i.e. an increase in average DO concentrations; Fig. 9b).

#### 4. DISCUSSION

The Chesapeake Bay is undergoing alterations in its physical environment in response to climate change (Hinson et al. 2023), which will affect whether the environmental conditions remain within the optimal ranges of the seasonally migrant species that inhabit the bay. This estuary has warmed significantly in recent years (Ding & Elmore 2015, Hinson et al. 2022), and despite the ENMs of all 4 species displaying the largest peak in the relationship between mean relative abundance and temperature at fairly high values (22.5–25°C), continued warming will likely result in temperatures that will surpass those upper values. Of the 19 yr of ROMS-ECB bottom outputs used in this study, the 3 years with the highest number of cells reaching temperatures above 25°C all occurred within the last 5 yr. Accordingly, and based on the ENMs developed, continued increases in temperature will likely correspond to lower relative abundance of all 4 species, as temperatures in a portion of Chesapeake Bay are expected to exceed their optimal ranges. However, lab experiments have found significant increases in the critical thermal maximum when

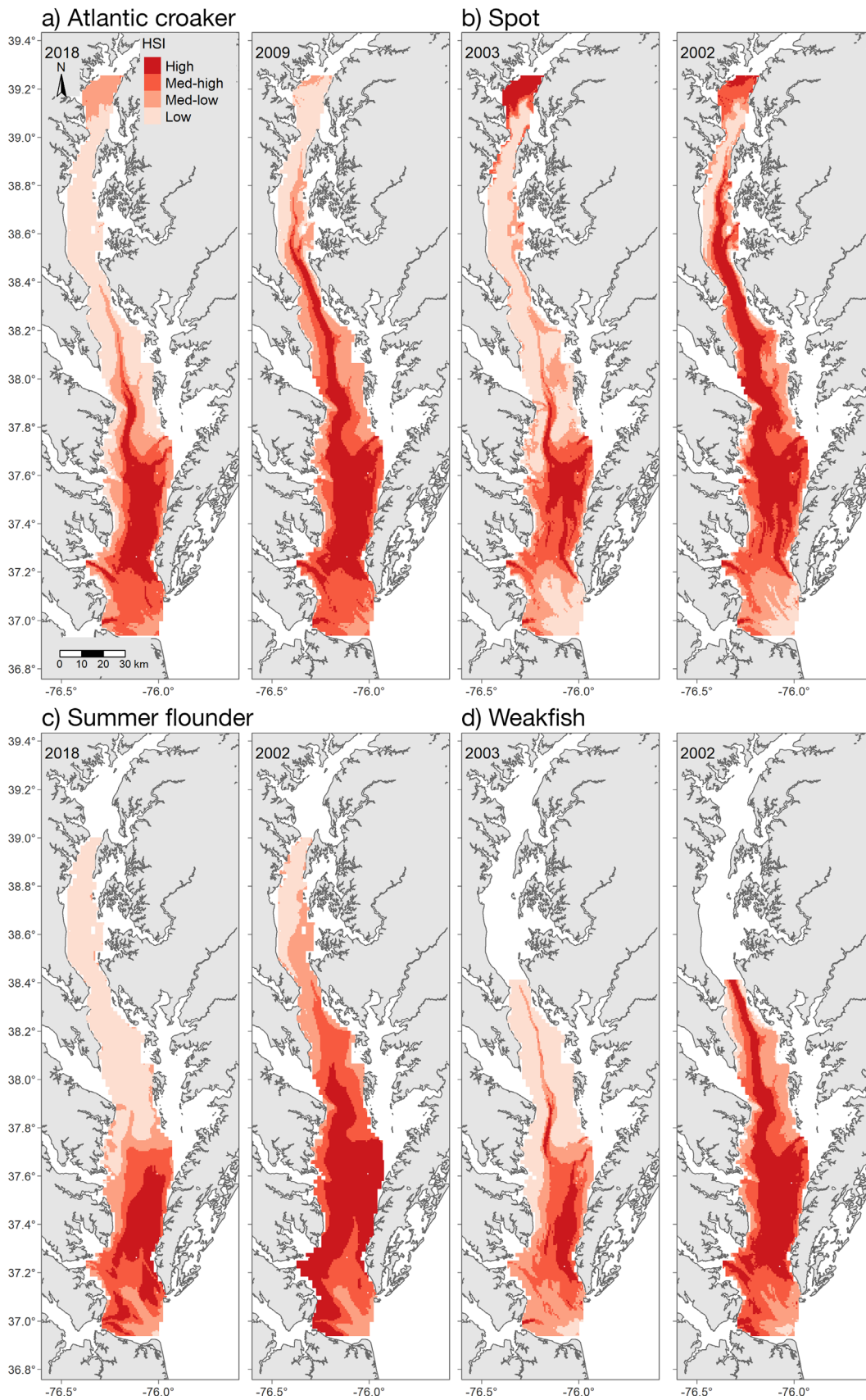


Fig. 5. Spatial distribution of suitable habitat during years with minimum and maximum annual habitat suitability indices (HSI) for (a) Atlantic croaker (min. 2018, max. 2009), (b) spot (min. 2003, max. 2002), (c) summer flounder (min. 2018, max. 2002), and (d) weakfish (min. 2003, max. 2002), generated by pairing the ecological niche model (ENM) with daily output from an estuarine-carbon-biogeochemical Regional Ocean Modeling Systems (ROMS-ECB). Mapped values represent averaged estimated suitability per cell from May–Sep. Quantiles were calculated using all years of habitat suitability, with the top 25% in the darkest red and the lowest quantile in the lightest

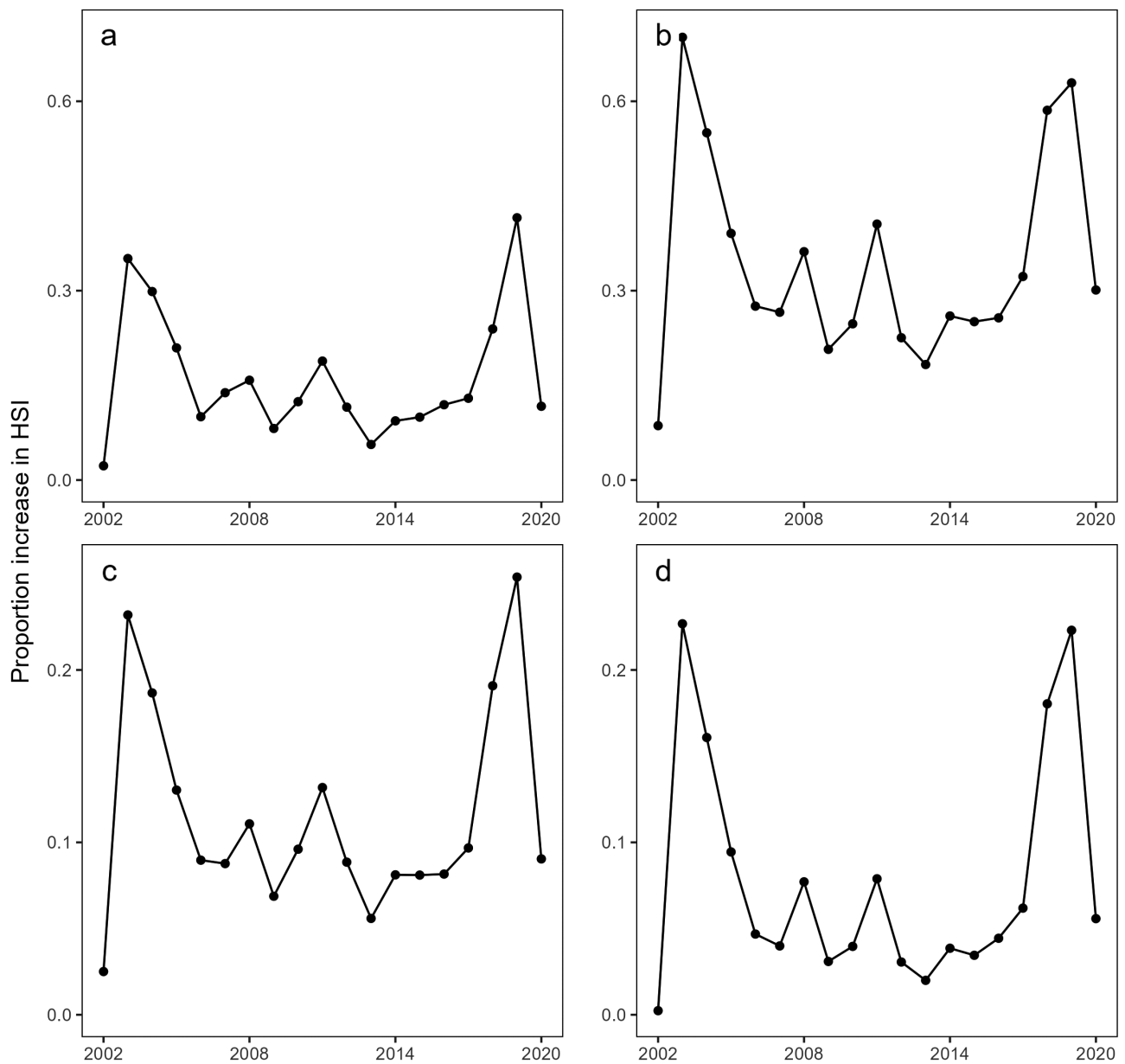


Fig. 6. Proportion increase in habitat suitability each year when hypoxia was 'removed' for (a) Atlantic croaker, (b) spot, (c) summer flounder, and (d) weakfish

juvenile spot were acclimated at higher temperatures (Hodson et al. 1981), indicating the potential for these fishes to adapt to a warming environment.

The ENMs for all species indicated low relative abundance or absence at the lowest DO concentrations (e.g. hypoxic waters,  $\leq 2.5 \text{ mg O}_2 \text{ l}^{-1}$ ). Similarly, studies conducted individually on each of these species have documented hypoxia avoidance behaviors (e.g. Tyler 2004, Craig & Crowder 2005, Sackett et al. 2008, Brady & Targett 2013, Craig et al. 2023). Since the 1950s, DO concentrations in Chesapeake Bay have declined appreciably and hypoxic volume has

increased (Hagy et al. 2004, Murphy et al. 2011). This trend is likely to continue, due to continued atmospheric warming and the lowered solubility of DO in warmer waters (Najjar et al. 2010, Irby et al. 2018, Tian et al. 2022, Hinson et al. 2023), thus potentially leading to further declines in the relative abundance of these 4 species in this estuary.

The possible impacts of climate change on the salinity in Chesapeake Bay are highly variable and largely unpredictable. Climate change is expected to lead to increases in precipitation frequency and intensity, extreme climatic events, and sea level rise

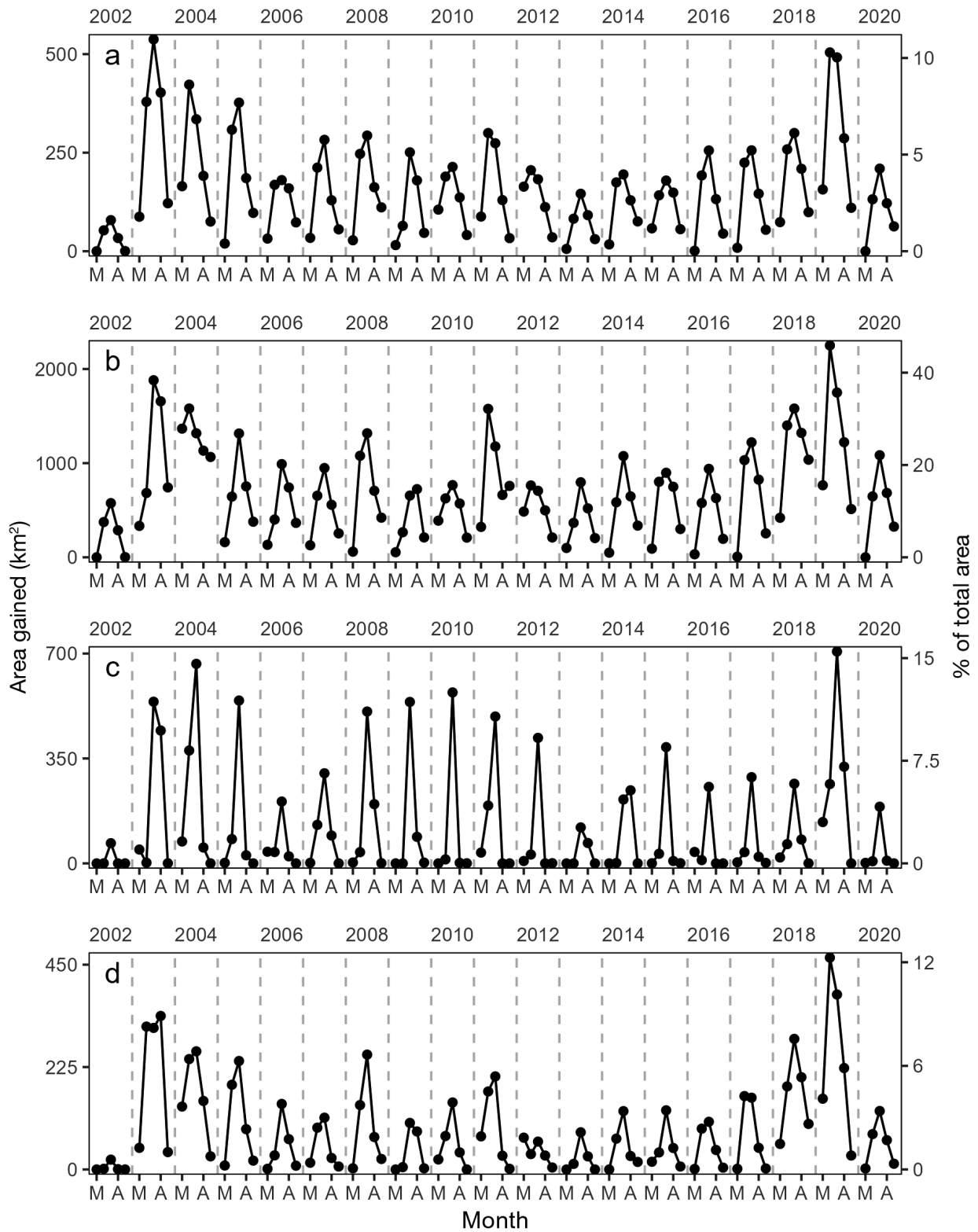


Fig. 7. Quantity of area gained each month (May–Sep; x-axis labels show May [M] and August [A]) when hypoxia was 'removed' for (a) Atlantic croaker, (b) spot, (c) summer flounder, and (d) weakfish. Right-hand y-axis is the corresponding percentage of the total area of the sampling frame that was gained. Any cells that changed from below-average to average or above-average once hypoxia was 'removed' were classified as area gained; see Section 2.3 for calculation details



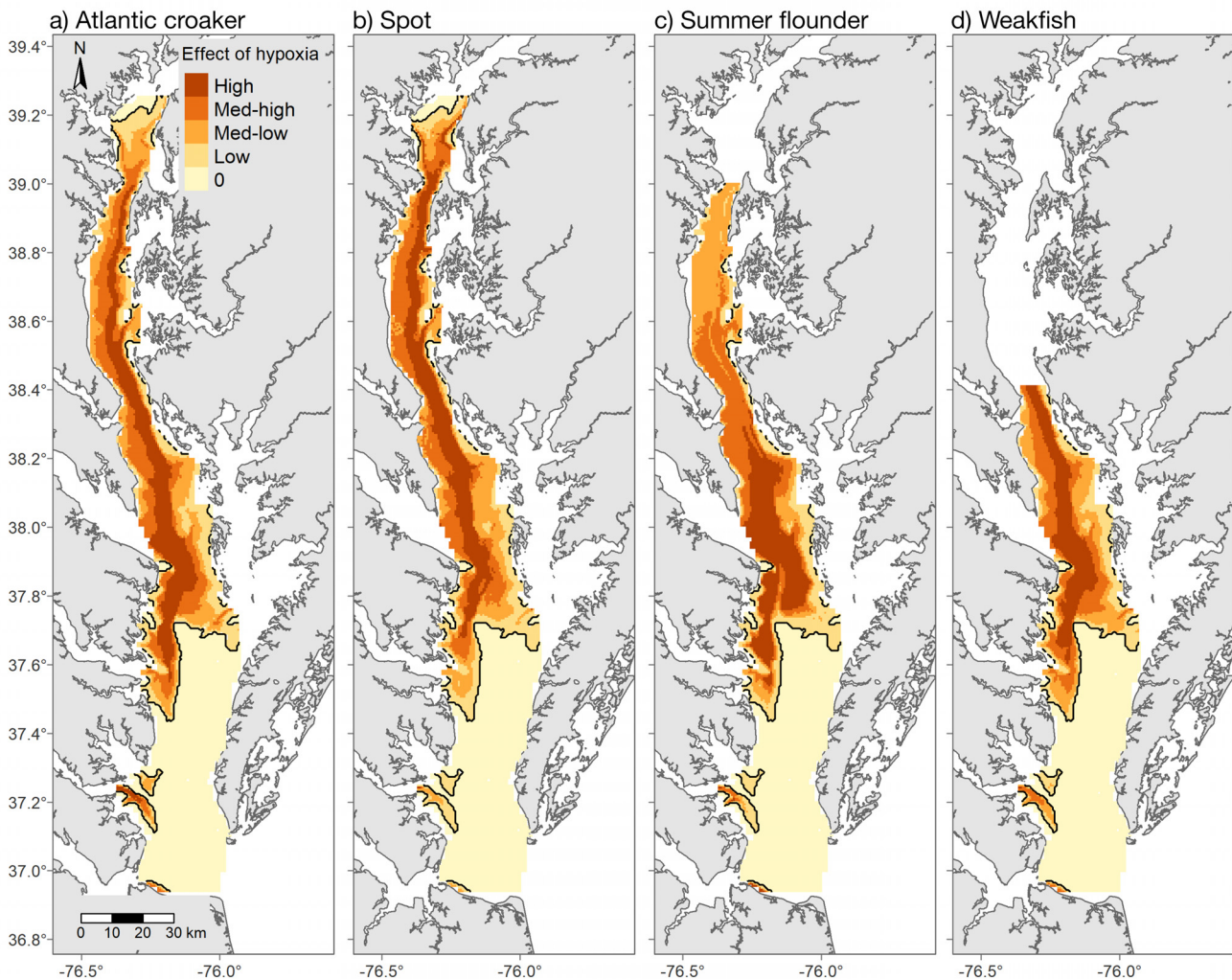


Fig. 8. Effects of 'removing' hypoxia in July 2019, the year with the largest change on habitat suitability, for (a) Atlantic croaker, (b) spot, (c) summer flounder, and (d) weakfish. Quantiles were calculated based on all nonzero values (i.e. only cells where hypoxia occurred) and mapped. Yellow cells were normoxic throughout July (i.e. no alterations in habitat suitability); black outline surrounds the areas where hypoxia occurred. See Section 2.3 for calculation details

(Karl & Trenberth 2003, Trenberth 2005, 2007, Sun et al. 2007). Sea level rise is expected to increase salinity in Chesapeake Bay (Hilton et al. 2008, Hong & Shen 2012). However, the influence on salinity caused by the weather-based changes is dependent upon seasonality and the specifics of the events. For example, increased precipitation will increase stream flow and lead to a decrease in salinity. However, if heavy precipitation events are interspersed with periods of drought, salinity will increase during the drought periods. Current models predicting stream flow vary widely (Najjar et al. 2010, Hinson et al. 2023), so concrete conclusions cannot be drawn about expected salinity trends in Chesapeake Bay relative to climate change, but it is likely that variability in salinity would increase. The ENMs for both summer flounder

and weakfish display clear, discrete ranges of salinity associated with highest predicted relative abundances. Thus, any changes in salinity that extend beyond the bounds of these ranges would likely lead to a decrease in relative abundance of these species.

Overall, based on the ENMs, the expected changes to the physical environment of the Chesapeake Bay due to climate change will likely result in decreases of relative abundance of all 4 species, continuing trends of many species previously recorded (Buchheister et al. 2013). However, none of the effects of climate change are occurring individually. The occurrence of multiple stressors acting simultaneously can result in different physiological responses to the same stimuli. The presence of 2 stressors could dampen the individual effects (i.e. an antagonistic interaction), or it could



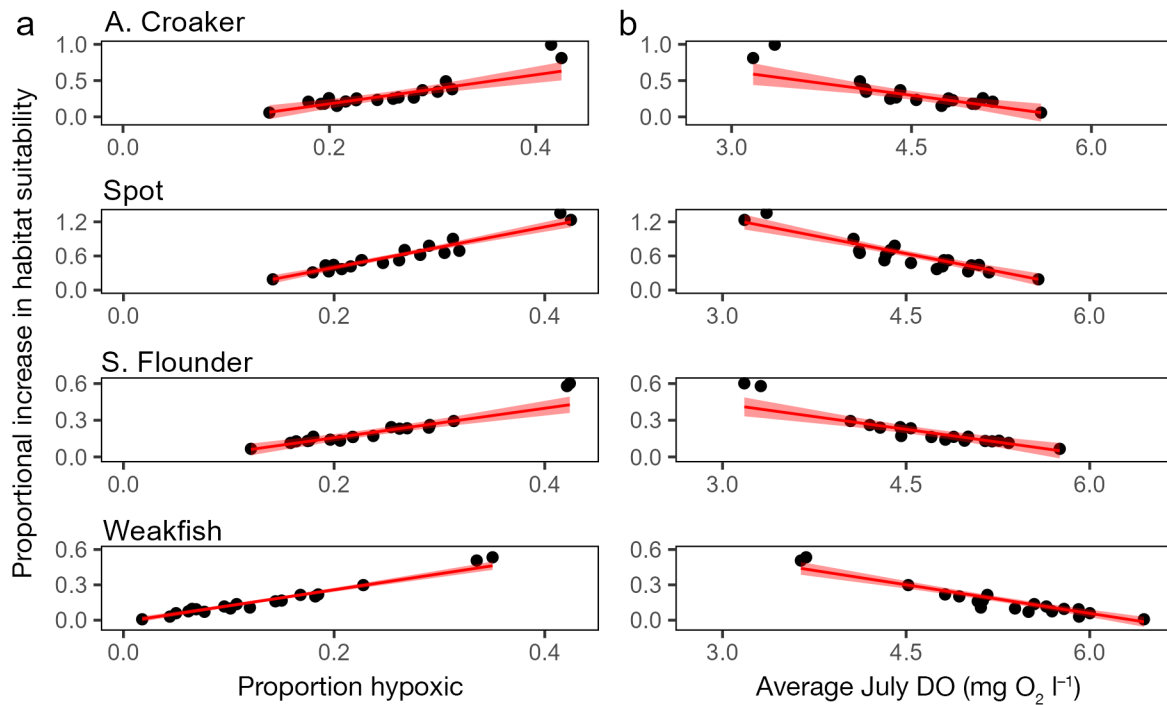


Fig. 9. Relationship between the proportional increase in habitat suitability in July with (a) hypoxic extent and (b) hypoxic severity for each species included in the analysis. Hypoxic extent was calculated as the proportion of the estuarine-carbon-bio-geochemical Regional Ocean Modeling System (ROMS-ECB) cells that had simulated dissolved oxygen (DO) concentrations  $<2.5 \text{ mg O}_2 \text{ l}^{-1}$ . Hypoxic severity was calculated as the average bottom DO in July. See Section 2.3 for details on the proportional increase in habitat suitability calculations. The black dots are the calculated values, the red lines are the fitted Theil-Sen regressions, and the red ribbons are the 95% confidence intervals. A. Croaker: Atlantic croaker; S. Flounder: summer flounder

diminish the individual's ability to respond to the stressors such that the negative consequences would be greater than the sum of the individual effects (i.e. a synergistic interaction; Folt et al. 1999, Côté et al. 2016). A plethora of studies have been dedicated to determining the influence of multiple stressors on the physiological response of an animal, including many on the 4 species included in this analysis. Such investigations have documented the influence of salinity on temperature tolerance of spot (Hodson et al. 1981), the interaction of temperature and salinity on feeding and growth rates of juvenile weakfish (Lankford & Targett 1994), and the interaction of temperature and  $\text{pCO}_2$  on hypoxia tolerance of summer flounder (Schwieterman et al. 2019). The concurrence of multiple stressors in Chesapeake Bay due to climate change could cause the expected declines in relative abundance to occur more rapidly than the ENMs would suggest.

One of the more interesting, and somewhat unexpected, relationships produced by the ENMs was the multimodal distribution of mean relative abundance as a function of temperature for all 4 species. The differences in the temperatures corresponding to the local maxima for each species indicates that this mul-

timodal relationship is not solely due to the seasonality of the ChesMMAAP sampling design. While the ranges of temperatures encountered vary based on cruise month, peaks in abundance of the species occurring at different temperatures indicates a reflection of species-specific temperature associations, rather than representing a mean or mode associated with a cruise month.

For summer flounder, the predicted maximum mean relative abundance occurred at approximately  $25^\circ\text{C}$ , which is beyond the temperature ( $20^\circ\text{C}$ ) of waters they were most commonly distributed within, and is near the maximum temperatures in which these fish were found during a tagging study conducted in Delaware Bay, a neighboring northern estuary (Sackett et al. 2008). Further, the movement rates of summer flounder peak at  $24^\circ\text{C}$  and decrease at higher temperatures (Henderson et al. 2014). Atlantic croaker exhibited a second peak in mean relative abundance at approximately  $22.5^\circ\text{C}$ , which is in contrast to 2 other studies conducted in estuarine environments of South Carolina and the Gulf of Mexico that found this species to be most abundant at temperatures above  $24^\circ\text{C}$  (Miglares et al. 1982, Craig & Crowder 2005). Previously re-

ported optimal temperature ranges for spot and weakfish are more similar to the temperature associated with the maximum predicted relative abundance in this study. Ideal temperatures for juvenile weakfish range from 27–29°C (Lankford & Targett 1994), and spot have been found in a wide range of temperatures, regularly exceeding 30°C (Parker 1971), with lab experiments showing the upper incipient lethal temperature for juvenile spot to be about 35°C (Hodson et al. 1981).

The Chesapeake Bay, as an estuarine system, experiences the influence and input of both saline ocean water and freshwater from its tributaries. The salinity difference between these 2 water sources is one of the major drivers of water column stratification, which prevents DO from mixing to the bottom and thereby contributing to hypoxia at depth (Boicourt 1992, Murphy et al. 2011, Scully 2013). As displayed by the ENMs developed in this study, as well as described in numerous other investigations, including those specific to the 4 focal species of this analysis and the Chesapeake Bay overall (Tyler 2004, Craig & Crowder 2005, Sackett et al. 2008, Buchheister et al. 2013, Brady & Targett 2013), fish avoid hypoxic areas. Given that hypoxia occurs in cooler, deeper waters of the bay, fish likely relocate to the periphery of these hypoxic areas, which are shallower and warmer. Such displacements may explain the peak in predicted relative abundance associated with higher temperatures exhibited in the ENMs, and may act as a hyperstabilizing phenomenon. That is, survey catch remains stable due to aggregation behaviors of the fish, thus presenting the illusion of a robust population, but the high and stable catches are not reflective of the true trends in abundance (Hilborn & Walters 1992). Displacement due to hypoxia and aggregation along the hypoxic edge have been associated with changes in the mean temperature occupied by several species, including Atlantic croaker in the Gulf of Mexico (Craig & Crowder 2005).

Anthropogenic nutrient runoff is correlated with hypoxia in Chesapeake Bay (Officer et al. 1984, Hagy et al. 2004, Murphy et al. 2011), as large nutrient inputs fuel phytoplankton blooms, and subsequent high benthic respiration rates at depth deplete oxygen as bacteria remineralize this organic matter (Kemp & Boynton 1992, Diaz & Rosenberg 1995, Rabalais et al. 2010). As such, historic total maximum daily load (TMDL) reductions of nutrients have had large impacts in reducing hypoxic volume in Chesapeake Bay (Frankel et al. 2022). Therefore, the maps displaying the largest increases in HSI when hypoxia was 'removed' (Fig. 8), could be utilized by managers

to guide policies related to the TMDL. For example, the hypoxic zones at the mouths of several main tributaries in the southern portion of Chesapeake Bay, namely the James River, the York River, Mobjack Bay, and the Rappahannock River, represent areas where TMDL restrictions might be most beneficial. Adjusting TMDLs in these areas could result in an increase in suitable habitat if the measures were able to reduce summertime hypoxia, especially for Atlantic croaker and weakfish, since these species displayed the largest increases in habitat suitability by the mouths of these tributaries. Further, the clear seasonality in the theoretical increase in area of suitable habitat with the potential elimination of hypoxia (Fig. 7) supports temporally dynamic TMDL policies, indicating that the limitation of nutrient inputs in the months preceding the highest habitat losses due to hypoxia could be advantageous.

This study has shown that hypoxia plays a large role in determining the quantity of suitable bottom habitat for 4 ecologically and economically important species in Chesapeake Bay. The time series of HSIs developed in this analysis do not display a notable trend, but instead, results showed large annual fluctuations in the quantity of suitable habitat, similar to results found for juvenile spot and other species in the bay (Fabrizio et al. 2021). Concurrently, however, trends in relative abundance of important species have declined in Chesapeake Bay (Buchheister et al. 2013, Bonzek et al. 2022) and the usage of this estuary relative to the coastal ocean has also decreased (Schonfeld et al. 2022). Therefore, the environmental conditions of the Chesapeake Bay itself are likely not the only factor contributing to the documented declines in relative abundance and seasonal estuarine utilization patterns. As described, these species inhabit the Chesapeake Bay only seasonally, spending the remainder of the year in the coastal ocean. The Atlantic Ocean is also affected by climate change, and the rate of warming of the northwestern Atlantic shelf is nearly 3 times the global average (Saba et al. 2016). Many studies conducted using data from these coastal waters have documented significant shifts in distribution of fishes poleward or to deeper habitats in response to warming, several of which include the 4 species in this investigation (e.g. Bell et al. 2015, Kleisner et al. 2016, Lucey & Nye 2010, Nye et al. 2009, Pinsky & Fogarty 2012). Consequently, the dynamics of climate change and processes in the coastal ocean may contribute to the recent decrease in relative abundance and estuarine utilization of many fishes in Chesapeake Bay, in addition to the physical environment of the bay itself.

A valuable area of future research involves the pairing of the ENMs developed in this analysis with projections of future conditions within Chesapeake Bay (Hinson et al. 2023), as this study only utilized hindcasts from ROMS-ECB. While this analysis did not find notable trends in the time series of HSI, future environmental conditions under various climate change scenarios may result in forecasted values of the environmental covariates that are outside the optimal ranges estimated by the ENMs, and subsequent annual HSI estimates may begin to exhibit directionality. Further, including potential TMDL policy adjustments with the climate change scenarios could quantify the value of specific management actions aimed at increasing suitable habitat. Additionally, the hypothesis that the hypoxic waters at depth are leading to aggregation at the periphery (i.e. hyperstabilization or edge effects) could be evaluated through more directed fieldwork. Finally, this analysis included only bottom waters, as observational data were gathered through a bottom trawl; collections throughout the water column could improve understanding of the vertical dynamics of habitat suitability.

This study has provided valuable information on the relationship between the physical environment of Chesapeake Bay and abiotic habitat of 4 key seasonally resident species that had previously not been quantified for their adult life stage. Insight into these relationships allows for increased understanding of species-specific habitat utilization and the potential impacts of climate change. Additionally, this investigation analyzed the role of hypoxia as it relates to habitat suitability, and the resultant spatial HSI maps provide awareness of relative habitat quality within the bay mainstem that can aid directed management efforts. Although hypoxia in Chesapeake Bay remains problematic, this study did not find clear declining patterns in abiotic habitat quality, which raises important questions regarding impacts of larger scale, coastal ocean processes on the distribution and ecology of fishes commonly found in estuaries within the mid-Atlantic.

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