

RESEARCH ARTICLE

The importance of oxygen for explaining rapid shifts in a marine fish

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Abstract

Large-scale shifts in marine species biogeography have been a notable impact of climate change. An effective explanation of what drives these species shifts, as well as accurate predictions of where they might move, is crucial to effectively managing these natural resources and conserving biodiversity. While temperature has been implicated as a major driver of these shifts, physiological processes suggest that oxygen, prey, and other factors should also play important roles. We expanded upon previous temperature-based distribution models by testing whether oxygen, food web productivity, salinity, and scope for metabolic activity (the Metabolic Index) better explained the changing biogeography of Black Sea Bass (*Centropristis striata*) in the Northeast US. This species has been expanding further north over the past 15 years. We found that oxygen improved model performance beyond a simple consideration of temperature ($\Delta AIC = 799$, $\Delta TSS = 0.015$), with additional contributions from prey and salinity. However, the Metabolic Index did not substantially increase model performance relative to temperature and oxygen ($\Delta AIC = 0.63$, $\Delta TSS = 0.0002$). Marine species are sensitive to oxygen, and we encourage researchers to use ocean biogeochemical hindcast and forecast products to better understand marine biogeographic changes.

KEYWORDS

fisheries, marine biogeography, Metabolic Index, oxygen, physiology, species distribution modeling, species shifts, temperature

1 | INTRODUCTION

Ongoing global climate change has had substantial impacts on species biogeography (Sunday et al., 2012). This is especially visible in the ocean, where there are many examples of species and communities shifting to new locations as environmental conditions change (Lenoir et al., 2020). These shifts impact ecological communities, ecosystems, and coastal economies (Allison et al., 2009; Brander, 2010;

Kleisner et al., 2016). For scientists and resource managers, understanding historical distribution shifts is an important step toward understanding the mechanisms most relevant to making future projections and developing effective management plans.

Approaches to modeling marine species distribution under climate change have often focused on responses to temperature change (Kleisner et al., 2017; Nye et al., 2009). Temperature is widely measured and has clear impacts on species physiology and demography,

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including metabolism, growth, and reproduction (Angilletta Jr., 2009; Free et al., 2019). However, effectively explaining past shifts in distribution and accurately projecting future shifts will require a more complete understanding of the factors determining species habitat. Previous research has found that models using only temperature can result in less accurate and overly optimistic projections (McHenry et al., 2019).

For marine species, physiological experiments and ecological theory suggest that key factors are likely to include dissolved oxygen and prey availability (Morgan, 1972; Velasco et al., 2019). In particular, metabolic processes suggest that temperature and dissolved oxygen interact to determine marine species habitat suitability (Portner & Knust, 2007). This physiological interaction has been explained through the mechanism of temperature-induced hypoxia, which can be measured with the Metabolic Index (ϕ). The Metabolic Index measures the metabolic capacity of an individual organism relative to the environmental supply of oxygen at a certain temperature (Deutsch et al., 2015). For a marine habitat to be metabolically viable for a species, the dissolved oxygen supply rate must exceed the basal metabolic demand of the individual (Seibel & Deutsch, 2020). The Metabolic Index has been used to explain the boundaries of extant species distributions (Deutsch et al., 2020; Howard et al., 2020) as well as species extinction events over geological time (Penn et al., 2018) and is therefore expected to be useful for explaining contemporary changes in species distributions. However, it remains unclear how the Metabolic Index performs relative to and in combination with other environmental factors likely to influence species distributions and their changes through time (Essington et al., 2022). In particular, oxygen and the Metabolic Index have proven useful for explaining static biogeography (Essington et al., 2022; Howard et al., 2020) and changes in abundance (Howard et al., 2020), but it remains unclear whether these factors are more important for explaining changes in biogeography over decadal timescales than other factors like temperature. In addition, the use of the Metabolic Index requires species-specific physiological measurements, which impedes widespread application. A more widely applicable alternative may be to estimate the interaction of temperature and oxygen from historical records of species occurrence.

Food or prey availability is also an important determinant of species niche and habitat. The availability of prey is a first-order constraint on predator presence and abundance (Mammides et al., 2009; Morgan, 1972; Trainor et al., 2014). Despite the clear importance of prey availability, using such information to understand marine species spatial distributions is difficult in part because many marine predators are generalists, or their prey remain unknown. One solution may be to consider aggregate measures of lower food web productivity. For example, fisheries productivity has been related to the overall productivity of planktonic food chains (Stock et al., 2017).

Beyond prey, salinity is an important habitat determinant of marine species, especially in coastal and lagoon environments with variable freshwater outflow and dry conditions (Barletta et al., 2005). Because many marine species spend at least a part of their life cycle nearshore, salinity can impact the overall distribution of a species (Pauly & Yáñez-Arancibia, 1994). Salinity has been used in previous efforts to predict marine species habitat (Miller et al., 2016).

While oxygen, prey availability, and salinity are likely to be important for defining marine fish biogeography, the absence of long-term, spatially resolved datasets for oxygen and prey has made testing these hypotheses difficult. The development of coupled physical-biogeochemical oceanographic model hindcasts that resolve historical planktonic food web dynamics may help to fill in these details (Doney, 1999; Quere et al., 2005).

Black Sea Bass (*Centropristis striata*) is an important fishery species that has expanded its range 80km/decade north over the past five decades (McMahan, 2017; Morley et al., 2018). Because of this notable range expansion and the extensive distribution data available from scientific trawl surveys of the continental shelf, Black Sea Bass is a useful species against which to test hypotheses for the factors driving range shifts. Fishermen have reported a higher number of sightings of Black Sea Bass in the southern Gulf of Maine since an ocean heatwave in 2012 (McMahan, 2017). Subsequent investigations determined that Black Sea Bass have been slowly expanding into the Gulf of Maine over 15 years and have spawned there at least once (McBride et al., 2018). This represents a range expansion of nearly 1° north from the previous range limit for the Mid-Atlantic stock (McBride et al., 2018; McMahan, 2017). More broadly, Black Sea Bass are distributed across the northwest Atlantic Ocean and, historically, the species has been recorded from Texas in the Gulf of Mexico up to Cape Cod, Massachusetts (Drohan et al., 2007; McCartney et al., 2013; Roy et al., 2012). Black Sea Bass supports both commercial and recreational fisheries throughout their range and has been managed as three separate stocks: Mid-Atlantic, South Atlantic, and Gulf of Mexico (Mercer, 1978). Black Sea Bass has been identified as a warm water species, and it undertakes southward migrations triggered by low ocean temperatures each fall. In the face of ocean warming caused by climate change, it has been categorized as a “winning” species in the northeast United States because of its expanding range and increased productivity (Free et al., 2019; Hare et al., 2016). Black Sea Bass has been the focus of previous modeling studies (Miller et al., 2016; Morley et al., 2018) in which temperature and shelf water volume (as a proxy for productivity) were important determinants of seasonal habitats in fall and spring.

In this study, we tested several environmental variables and one physiological variable for their utility to explain Black Sea Bass habitat and changes in spatial distribution through time in the Northwest Atlantic. The major questions that we address in this study are (1) whether dissolved oxygen, prey availability, and salinity more effectively explain Black Sea Bass biogeography and changes through time than does ocean temperature alone; and (2) whether the Metabolic Index outperforms other environmental factors for explaining shifting marine species distributions. There are broad concerns over how shifts of important marine species under climate change may impact local economies and our work addresses this by defining a metabolic habitat for Black Sea Bass.

2 | MATERIALS AND METHODS

Our approach was to test alternative hypotheses expressed as statistical species distribution models. Our baseline model used sea

bottom temperature, ocean floor rugosity, and sediment type (grain size) as explanatory variables, which have been useful for previous Black Sea Bass distribution models (Morley et al., 2018). We then tested whether adding salinity, zooplankton density (as a proxy for prey availability), dissolved oxygen, and Metabolic Index improved the ability to explain changes in distribution. In situ observations of oxygen and prey were too sparse for this purpose, so we used oceanographic hindcasts for these environmental conditions and for salinity. Models were assessed on their ability to predict out-of-sample presence-absence and biomass.

2.1 | Species data

We used species occurrence and biomass data from scientific bottom trawl hauls conducted in four regions of the Atlantic North American continental shelf. Surveys were conducted primarily by NOAA Fisheries (USA) and by DFO (Canada) and were compiled by Morley et al. (2018; Figure S1, Table S1). The dataset included corrections for method changes in the northeast United States following Miller et al. (2010). The original dataset spanned nearly 50 years from 1963 to 2010, but we trimmed it to 1982–2010 to match the environmental data and oceanographic hindcasts. This trimming left 2802 Black Sea Bass presences and 40,542 absences (Figure S2). A majority of Black Sea Bass presences were in the Mid-Atlantic (2125), and the rest were in the South Atlantic.

2.2 | Environmental data

Oxygen concentration, zooplankton density, and salinity values were obtained from a biogeochemical oceanographic hindcast model for the period 1982–2010 (Kang & Curchitser, 2013; Zhang et al., 2019). This ROMS-COBALT (Regional Oceanic Modeling System-Carbon, Ocean, Biogeochemistry and Lower Trophics) model covers most of the northwest Atlantic and has a grid configuration of 7 km × 7 km and 40 vertical layers from the sea surface to the sea bottom. The accuracy of this model has been verified by comparing it against historical data for sea surface temperature, sea surface chlorophyll, and nitrate concentrations (Kang & Curchitser, 2013; Zhang et al., 2018). We used zooplankton density as a proxy for prey availability. While Black Sea Bass are generalist predators that do not directly feed on zooplankton (Drohan et al., 2007), zooplankton productivity supports the food web that feeds Black Sea Bass.

At the location of each haul in our species dataset, we extracted the seasonal averages of dissolved oxygen, zooplankton, and salinity by calculating the average value over 3 months (the month the haul took place and the preceding and following months). Dissolved oxygen concentration (mol/kg of seawater) and salinity (ppm) were taken from the bottom-most vertical layer of the ROMS dataset. Zooplankton densities (zooplankton body nitrogen mol/kg of seawater) were defined separately for three size classes in the ROMS-COBALT model. Small zooplankton were less than 200 μm equivalent

spherical diameter (ESD), medium zooplankton were small to medium copepods between 200 and 2000 μm ESD, and large zooplankton were large copepods and euphausiids between 2 and 2 mm ESD (Stock et al., 2014). We calculated the total zooplankton density as the sum of the three size classes across the 40 vertical layers.

In addition, we used sea bottom temperature, seafloor rugosity, and seafloor sediment grain sizes as compiled by Morley et al. (2018). To summarize their methods, temperature data were originally from the Simple Ocean Data Assimilation (SODA) v3.3.1 (Carton et al., 2018). While Morley et al. used several temperature variables, including sea surface temperature and annual maximums and minimums, we only used seasonal bottom temperature because of the high correlation between the various temperature measurements (Figure S3). The temperature metrics were positively correlated to a large degree ($r > .5$), while dissolved oxygen was negatively correlated with the various temperature metrics ($r < -.5$). Rugosity and grain size were potentially useful because Black Sea Bass are known to be associated with rocky bottom structures (Able, 1995; Drohan et al., 2007; Steimle, 1996). Rugosity was calculated from the General Bathymetric Chart of the Oceans (GEBCO) gridded bathymetry dataset at a 1 km resolution (Becker et al., 2009). While coarse, this scale has proven useful for explaining the distribution of marine fishes (Hare et al., 2012; Morley et al., 2018, 2020). Rugosity of a cell was calculated as the absolute difference between its depth and the depth of the surrounding eight cells. Sediment grain size was interpolated from several sources (see Morley et al., 2018) and was measured on the Phi Wentworth scale in which a higher value indicates a finer sediment and a lower value indicates a coarser sediment. The distribution of these variables for both Black Sea Bass presences and absences is shown in Figure S4 (presences) and Figure S5 (absences).

2.3 | Metabolic Index

The Metabolic Index is defined as the ratio of the rate of oxygen supply to an individual relative to the oxygen demand necessary for sustaining basic life functions at a certain temperature. Experiments have confirmed that the Metabolic Index is a useful indicator of temperature-dependent hypoxia in Black Sea Bass (Slesinger et al., 2018). The Metabolic Index is calculated as

$$\varphi = \frac{A_o B^n P_{O_2}}{\exp(-E_o/k_B T)}$$

where A_o is the species-specific ratio of rate coefficients for O_2 supply and metabolic demand, B^n is the per-mass rate of gas transfer between water and the animal and its scaling with body mass for the species of interest (measured in kPa^{-1}), P_{O_2} is the partial pressure of dissolved oxygen measured in kPa, E_o is the temperature dependence of metabolic activity measured in eV, k_B is Boltzmann's constant measured in eV/K, and T is temperature measured in K. We used Black Sea Bass-specific values of $A_o = 0.00040728$, $B^n = 10^{-2}$, and $E_o = 0.27$ measured in physiological experiments (Seibel & Deutsch, 2020; Slesinger et al., 2018).

We used seasonal bottom temperature (referred to as temperature from now on) from SODA in K for temperature. Dissolved oxygen from the ROMS-COBALT model in mol/kg of seawater units was converted to kPa using the “Respirometry” package in R (Birk, 2020). For the unit conversion, ROMS-COBALT seasonal salinity values (in ppm) and temperature (in K) were also used.

2.4 | Species distribution modeling

We expressed alternative hypotheses for the factors driving Black Sea Bass distribution as a set of statistical models. We used a two-stage modeling approach, also called a hurdle model, that included a presence/absence model and a biomass conditional on presence model to account for the large number of zeros in the data (Barry & Welsh, 2002; Cragg, 1971; Morley et al., 2018). To model presence-absence, we utilized a generalized additive model (GAM) with binomial errors fit with the *mgcv* package in R (Wood, 2017). For biomass models, we then added a second-stage GAM that modeled the log-transformed biomass with a normal error distribution. The GAM for presence-absence included all hauls in order to include observed absences, while the log-biomass GAM was fit for all hauls with nonzero biomass. Because the biomass model was only fit to nonzero biomass observations and in order to model biomass across the full range of environmental conditions and surveys, we followed

the methods of Morley et al. (2018) and added a small set of artificial near-zero biomass values (10^{-10}) to a fraction of hauls in regions where the species was never encountered (10% of the hauls in a region or 10% of total observations, whichever was the smaller value).

We then designed sets of explanatory variables to compare against each other as our alternative hypotheses. These included models with only a single oceanographic variable as well as multi-variable models. All models (whether single or multivariable) included the ocean floor variables (rugosity and sediment grain size) and a categorical variable for the bottom trawl survey (to account for differences in vessels and sampling methods; Table S1). To reduce overfitting, we used the recommendation to set a gamma value for each GAM as the log of the number of samples included in the model divided by two (Wood, 2017). We investigated higher gamma values (up to gamma=50) for greater smoothing but doing so degraded out-of-sample predictive skill and we did not pursue this further (Wood, 2017).

The null model contained only the ocean floor and survey variables. Single-variable models also included temperature, Metabolic Index, dissolved oxygen, salinity, or zooplankton. Multivariable models included different combinations of the abovementioned variables in order to test the explanatory value of Metabolic Index and other variables relative to temperature (Table 1). We examined models in several classes, including traditional temperature-based models (T models), Metabolic Index-based models (MI models),

| Model class | Model name | Abbreviation |
|---------------|--|--------------|
| - | Ocean floor only (Null model) | - |
| T models | Temperature + Dissolved Oxygen | T+O |
| | Temperature + Salinity | T+S |
| | Temperature + Zooplankton | T+Z |
| | Temperature + Metabolic Index | T+MI |
| | Temperature + Dissolved Oxygen + Zooplankton | T+O+Z |
| | Temperature + Dissolved Oxygen + Salinity | T+O+S |
| | Temperature + Dissolved Oxygen + Salinity + Zooplankton | T+O+S+Z |
| Hybrid models | Temperature + Dissolved Oxygen + Temperature-Oxygen interaction | T+O+T:O |
| | Temperature + Dissolved Oxygen + Metabolic Index | T+O+MI |
| | Temperature + Dissolved Oxygen + Salinity + Zooplankton + Metabolic Index | T+O+S+Z+MI |
| | Temperature + Dissolved Oxygen + Salinity + Zooplankton + Temperature-Oxygen interaction | T+O+S+Z+T:O |
| MI models | Metabolic Index + Salinity | MI+S |
| | Metabolic Index + Zooplankton | MI+Z |
| | Metabolic Index + Salinity + Zooplankton | MI+S+Z |
| T:O models | Temperature-Oxygen interaction + Salinity | T:O+S |
| | Temperature-Oxygen interaction + Zooplankton | T:O+Z |
| | Temperature-Oxygen interaction + Salinity + Zooplankton | T:O+S+Z |

TABLE 1 List of models used to explain Black Sea Bass habitat.

temperature–oxygen interaction models (T:O models), and hybrid models (those that contained a combination of temperature, Metabolic Index, and/or temperature–oxygen interaction). The T:O models examined whether the interaction between temperature and oxygen could be estimated statistically and the relative performance of this estimation against the physiologically calibrated MI values.

2.5 | Model assessment

In order to understand model skill, we assessed both in-sample model fit and out-of-sample forecasting skill. Each model was fit to a training dataset of all hauls before the year 2000 and two metrics were calculated. Akaike Information Criterion (AIC) is a measure of model performance that is proportional to the model complexity minus the log likelihood. With certain assumptions, the model with the lowest AIC score is expected to have the best performance (Burnham & Anderson, 2004). We calculated Δ AIC as the difference between the AIC of each model and of the lowest scoring model. As a simple guideline, Δ AIC values <2 indicate models that do not have substantially different performance, and Δ AIC values >10 indicate very little support (Burnham & Anderson, 2004). In addition, the models were evaluated against all the hauls, including and after the year 2000 with the True Skill Statistic (TSS) as a true out-of-sample test. TSS compares the number of correct forecasts, minus the ones attributed to random guessing, to that of a hypothetical set of perfect forecasts (Allouche et al., 2006). A TSS value of 1 suggests perfect prediction capability, and values at 0 or below indicate no better than random capability.

The code for accessing the ROMS-COBALT hindcast data and calculating seasonal averages for dissolved oxygen, salinity, and zooplankton was written in Python programming language version 2.7 (Perez & Granger, 2007; van Rossum & Drake, 2002). The code for all remaining analyses was written in R version 4.0 (R Core Team, 2021). The code can be accessed on GitHub at <https://github.com/wajra/bsb-shift-drivers>.

3 | RESULTS

Black Sea Bass distribution shifted northward from 1980 to 2010 (Figure 1a,b), and by the 2000s, they were highly prevalent off the coast of New Jersey and into southern New England. This is apparent by prevalence anomalies (2000s–1980s; Figure S6a). As one measure of spatial distribution, their centroid shifted north from 37.15°N latitude in the 1980s to 38.79°N latitude in the 2000s (Figure 1a,b). Over the same period of time, the environment had also changed considerably, with the most noticeable changes in temperature and dissolved oxygen (Figure 2). The bottom waters in the Gulf of Maine warmed by around 1°C over these two decades. This region also showed some deoxygenation (loss of 1 mg/dL over a 20-year period). However, zooplankton density and salinity remained constant through the 1980s to the 2000s.

While we fitted presence–absence and biomass models using single or multiple oceanographic variables, we focus our presentation of results here on the presence–absence model. The best-performing single-variable model for presence–absence used the Metabolic Index, as determined from out-of-sample TSS and AIC

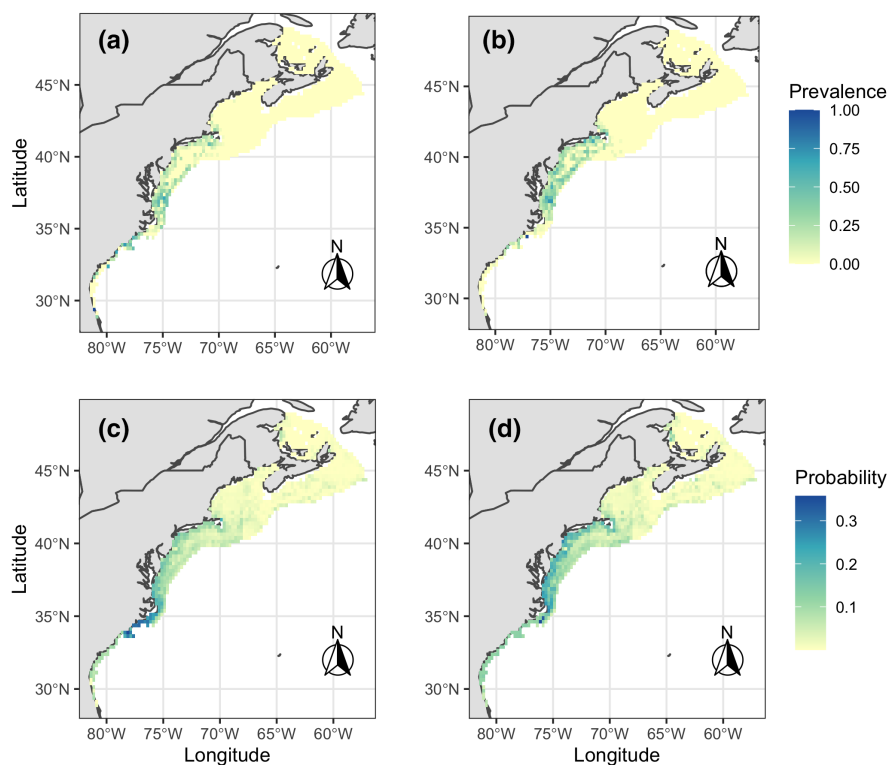


FIGURE 1 Distribution of Black Sea Bass across time. (a) and (b) show Black Sea Bass prevalence (proportion of hauls with Black Sea Bass) in bottom trawl surveys. Subfigures (c) and (d) show hindcast probability of presence from the preferred model (Temperature + Dissolved Oxygen + Salinity + Zooplankton model; T+O+S+Z). Maps are for 1980–1990 (a, c) and for 2000–2010 (b, d). Both prevalence and probability have been averaged into $\frac{1}{4}^\circ$ latitude \times longitude grid cells.

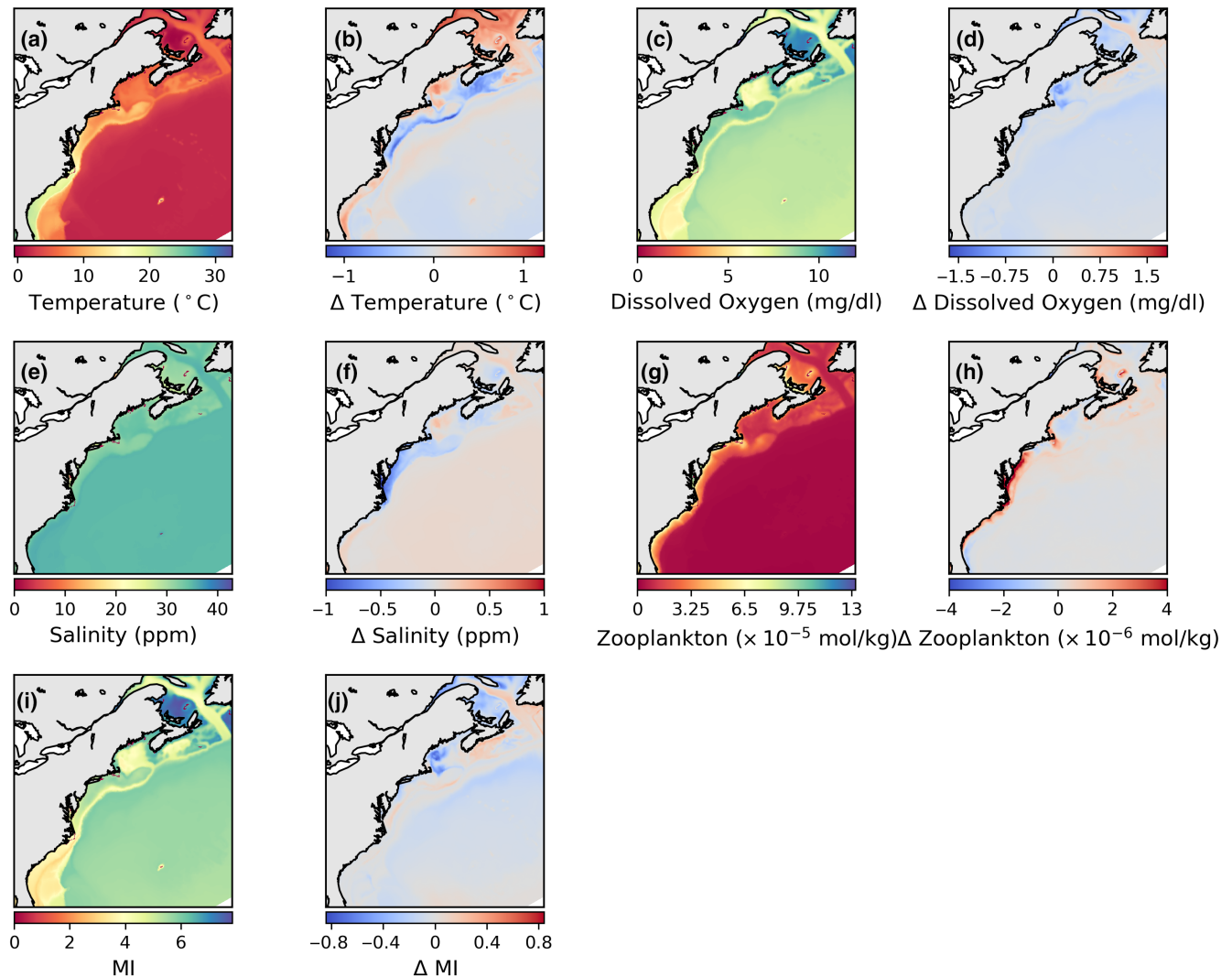


FIGURE 2 Decadal averages for the 1980s and decadal change in mean values between the 1980s and 2000s for bottom temperature (a, b), bottom dissolved oxygen (c, d), bottom salinity (e, f), vertically integrated zooplankton density (g, h), and bottom Metabolic Index (i, j). Note that the change in zooplankton scale is an order of magnitude smaller than the mean zooplankton scale. The 1% most extreme values for change in salinity, zooplankton, and dissolved oxygen have been removed to improve legibility of the map.

TABLE 2 Performance metrics for presence–absence models with single oceanographic variables measured as Δ AIC and as out-of-sample TSS. The best-performing model (MI) is highlighted in bold.

| Model name | TSS | AIC | Δ AIC |
|------------|--------------|-------------|--------------|
| Null | 0.113 | 10,613 | 993 |
| S | 0.117 | 10,325 | 706 |
| SBT | 0.129 | 9860 | 240 |
| O | 0.131 | 9643 | 24 |
| Z | 0.109 | 10,449 | 830 |
| MI | 0.132 | 9619 | 0 |

(Table 2). Models had similar but relatively low out-of-sample TSS at the scale of the individual bottom trawl haul, while AIC differences among the models were large (>20). The next-best model

was oxygen, which had a Δ AIC of 24. The null model performed poorly on all metrics. The low skill of the models could be partially attributed to testing against individual hauls rather than testing over a larger averaged area (e.g., a $\frac{1}{4}$ degree grid square as shown in Figure 1).

In presence–absence models combining multiple oceanographic factors, there were three equivalently well-performing models according to both out-of-sample TSS and Δ AIC (Table 3). In order of increasing complexity, these were T+O+S+Z (Δ AIC=0.625), T+O+MI+S+Z (Δ AIC=0), and T+O+T:O+S+Z (Δ AIC=0.698). The addition of an extra explanatory variable to the T+O+S+Z model, in the form of either a temperature–oxygen interaction (T:O) or the Metabolic Index (MI), produced only a very minor increase in model performance. Therefore, we selected T+O+S+Z as the preferred model for plotting in Figure 1. In terms of model classes, the MI

TABLE 3 Performance metrics for presence/absence models with multiple explanatory variables. The three best-performing models are highlighted in bold.

| Model class | Model name | TSS | AIC | Δ AIC |
|---------------|--------------------|---------------|---------------|--------------|
| Null | Null | 0.1132 | 10612.7 | 1551.92 |
| T models | T+O | 0.1361 | 9481.9 | 421.17 |
| | T+MI | 0.1342 | 9540.4 | 479.62 |
| | T+S | 0.1305 | 9732.6 | 671.82 |
| | T+Z | 0.1296 | 9590.1 | 529.30 |
| | T+O+Z | 0.1386 | 9119.1 | 58.37 |
| | T+O+S | 0.1380 | 9368.0 | 307.24 |
| | T+O+S+Z | 0.1438 | 9061.4 | 0.63 |
| Hybrid models | T+O+T:O | 0.1361 | 9481.9 | 421.17 |
| | T+O+MI | 0.1363 | 9458.4 | 397.61 |
| | T+O+MI+S+Z | 0.1440 | 9060.8 | 0.00 |
| | T+O+T:O+S+Z | 0.1438 | 9061.5 | 0.70 |
| MI models | MI+S | 0.1334 | 9517.9 | 457.14 |
| | MI+Z | 0.1374 | 9236.6 | 175.87 |
| | MI+S+Z | 0.1429 | 9186.1 | 125.37 |
| T:O models | T:O+S | 0.1353 | 9643.7 | 582.97 |
| | T:O+Z | 0.1368 | 9368.9 | 308.12 |
| | T:O+S+Z | 0.1374 | 9368.2 | 307.46 |

TABLE 4 Fit statistics for the best-performing presence/absence model (T+O+S+Z). Table shows the empirical degrees of freedom (EDF) and the approximate chi-squared and *p*-values for each term. The *p*-values were below machine tolerance values.

| Variable | EDF | Chi-squared value | <i>p</i> -value |
|------------------|-------|-------------------|----------------------|
| Temperature | 5.253 | 240.54 | $<1 \times 10^{-11}$ |
| Dissolved oxygen | 6.682 | 467.83 | $<1 \times 10^{-11}$ |
| Zooplankton | 4.730 | 457.484 | $<1 \times 10^{-11}$ |
| Salinity | 5.908 | 98.016 | $<1 \times 10^{-11}$ |
| Rugosity | 3.536 | 46.63 | $<1 \times 10^{-11}$ |
| Grain size | 7.840 | 301.28 | $<1 \times 10^{-11}$ |

and T:O models generally did not perform well, illustrating the importance of including a temperature factor. In the T class of models with only one additional factor, adding dissolved oxygen resulted in the greatest improvement in model skill and was substantially better than adding MI. Comparing models with T+O, the addition of S, Z, or S+Z (from T+O to T+O+Z, T+O+S, or T+O+S+Z) yielded better model performance compared with hybrid models.

In the T+O+S+Z model, all explanatory variables were statistically significant ($p < 1 \times 10^{-11}$; Table 4). The probability of presence generally increased with rising temperature up to at least 10°C (Figure 3). The probability of presence decreased substantially at dissolved oxygen levels higher than 2.5×10^{-4} mol/kg. The probability of presence increased with zooplankton density up to 8×10^{-5} zooplankton body nitrogen mol/kg of seawater. Probability of presence also increased in general with salinity and rugosity. Grain size

was the only parameter to which probability of presence did not show a clear directional response (Figure 3).

Species biomass (Table S2) also showed a positive relationship with temperature, peaking at 10°C and then slowly declining at higher temperatures (Figure S7). Species biomass showed a similar positive relationship with dissolved oxygen and peaked at 2.5×10^{-4} mol/kg and declined after. Biomass also showed a positive nonlinear relationship with zooplankton density (Figure S7).

Both the statistically estimated temperature–oxygen interaction and the Metabolic Index represent similar concepts, with the latter more tightly constrained by physiological theory. We, therefore, compared the two effects (Figure 4). The temperature–oxygen interaction suggested that probabilities of presence were highest at dissolved oxygen levels from 0 to 9 mg/L) and from 5 to 30°C, which did not align with MI isoclines. In particular, the statistical interaction did not suggest a higher minimum tolerable oxygen concentration at higher temperatures, as suggested by MI. Nearly all hauls considered for the study (99%) were above a MI of 2. Black Sea Bass were encountered in 6% of these hauls. Black Sea Bass were also encountered in 14% of the hauls below an MI of 2. Black Sea Bass were notably absent from hauls below 3°C or above 10 mg/L O₂ (i.e., at particularly high MI values).

Hindcasting the T+O+S+Z model revealed that the model successfully predicted the northward expansion of Black Sea Bass through time (Figure 1c,d). In particular, the model predicted a northward shift of the centroid from 35.23°N to 35.80°N, similar to but not as large as the observed shift (37.15–38.79°N). The suitable habitat was concentrated around North Carolina in the 1980s and shifted northward to New York and offshore to Georges Bank by the 2000s.

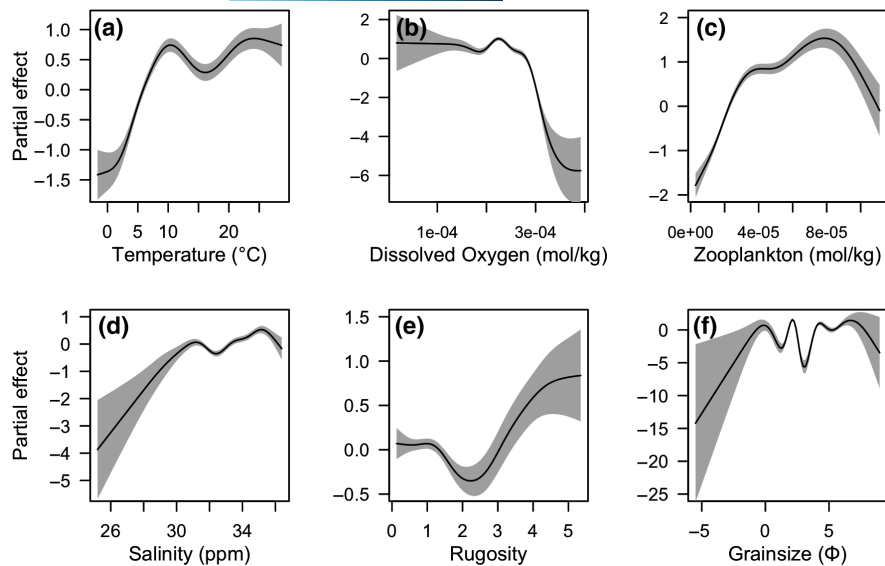


FIGURE 3 Response curves for predictors in the T+O+S+Z presence-absence model. The predictors include bottom temperature (a), bottom dissolved oxygen (b), vertically integrated zooplankton density (c), bottom salinity (d), seafloor rugosity (e), and seafloor sediment grain size (f). The shaded areas show the 95% confidence interval. This figure and [Figure S7](#) show the partial or additive effect that each covariate in the model has on the predicted variable.

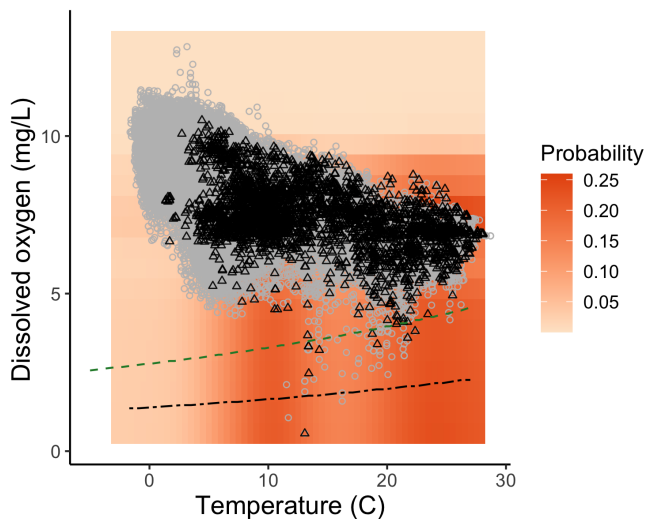


FIGURE 4 Effect of the interaction between seasonal bottom temperature and dissolved oxygen on the probability of presence (from the T+O+T:O+S+Z model). Black Sea Bass presences (black triangles), absences (gray circles), and Metabolic Index (ϕ , lines) are plotted against seasonal temperature and dissolved oxygen. Lines indicate a ϕ of 1 (dashed black) and 2 (dashed green).

4 | DISCUSSION

Species range shifts have both ecological and economic impacts. In order to best understand how to mitigate and prepare for these shifts, it is important to understand their major drivers. In this study, we examined whether oxygen, temperature-dependent hypoxia, food availability, and salinity from oceanographic hindcasts were useful for explaining historical shifts in Black Sea Bass distributions in the northwest Atlantic. We found that a multivariate model including temperature and dissolved oxygen in particular described the Black Sea Bass habitat in the Northwest Atlantic and changes through time. While fish physiology suggests an interaction between

temperature and oxygen is important for metabolic considerations, considering this mechanism did not appreciably improve explanatory or forecast skill for species distributions.

The Metabolic Index has been shown in experimental studies (Seibel & Deutsch, 2020; Slesinger et al., 2018) to accurately reflect the factorial aerobic scope (measured as maximum/standard metabolic rate) of a species. As fish were exposed to higher temperatures and lower Metabolic Indices, Black Sea Bass exhibited less ability to increase their metabolic activity above their resting rate (Slesinger et al., 2018). A Metabolic Index of 3 has been suggested as a lower limit for population persistence (Seibel & Deutsch, 2020). Using Metabolic Index to explain species distributions could therefore provide a physiological and mechanistic link between the environment and species biogeography. Previous work has suggested that the Metabolic Index more accurately describes species boundaries experiencing higher temperatures and lower oxygen concentrations than does temperature or oxygen alone (Deutsch et al., 2015, 2020). While we found some evidence that Metabolic Index could explain historical Black Sea Bass distributions, we also found that including temperature and oxygen separately produced models that were effective as skillful and parsimonious. Considering Metabolic Index in addition to temperature and oxygen was not as useful as considering salinity and proxies for prey.

One potential explanation for this result is that Metabolic Index is a better predictor of the warm edge (retracting range) of a species than of the cold edge (expanding range), and our data were focused on the cold range edge of Black Sea Bass. An organism's ability to supply oxygen to its organs may decline at cold temperatures more than does metabolic demand, creating temperature-dependent hypoxia at the cold range edge (Pörtner et al., 2017). If this process is important at cold range edges, the MI would need to be reformulated to include this process. However, the concept of oxygen- and capacity-limited thermal tolerance itself also remains controversial, including at cold range edges (Jutfelt

et al., 2018). Alternatively, temperature alone (without an oxygen interaction) may limit the cold range edge because of difficulty acquiring food or avoiding predators when metabolic, movement and growth rates are slow, or because of limits on reproduction or other processes (Dahlke et al., 2020; Slesinger et al., 2018). Lower zooplankton concentrations in the Gulf of Maine (Figure 2g) may also play a role and interact with cold temperatures to help limit the Black Sea Bass distribution, perhaps by further reducing the ability to find food. Better understanding of the ecological limits at cold temperatures will be helpful for understanding cold range edge dynamics.

Our findings contribute to other research finding limited utility of the Metabolic Index for explaining species distributions beyond the utility of oxygen and temperature. Recent research on sablefish (*Anoplopoma fimbria*) on the west coast of the US has highlighted that static species distributions may be more closely related to oxygen than to Metabolic Index, though, in contrast to Black Sea Bass, temperature was not a particularly useful explanatory factor for sablefish beyond oxygen (Essington et al., 2022). Some of the differences between these two species may be explained by their depth distributions. Sablefish inhabit deeper depths where low oxygen provides a strong constraint on occupancy, whereas Black Sea Bass occupy shelf habitats with less oxygen limitation. The sablefish paper did not directly examine changes through time, and our Black Sea Bass results show additionally that changes in temperature and oxygen can skillfully predict changes in species distribution through time.

The Metabolic Index represents an interaction between temperature and oxygen, but the use of the Metabolic Index requires physiological experiments to derive species-specific values that are available to date for only a few dozen species (Deutsch et al., 2020). In theory, this interaction could be estimated statistically for a wider range of species from spatial observations of occupancy or biomass. In support of this idea, our model that estimated the temperature–oxygen interaction statistically (the T:O model) performed equivalently well as the MI model. However, statistical estimation of the temperature–oxygen interaction in Black Sea Bass produced a response surface that did not align with Metabolic Index predictions. This statistical approach may allow insights from physiology (such as the temperature–oxygen interaction) to be applied more widely across species in the absence of the extensive lab work required to estimate the MI directly. There has been a push in the literature to incorporate more mechanistic approaches into species distribution modeling where the species habitat is explained by variables with measurable impact on physiological function (Buckley et al., 2011), such as the Metabolic Index. In advance of extensive physiological experiments, it may be productive to infer metabolic traits from more widely measured species characteristics and from phylogenetic history, as is now possible (Schrodt et al., 2015; Thorson et al., 2017). Alternatively, statistical estimation of the temperature–oxygen interaction may be suitable in many cases for species with sufficient occurrence data.

The use of hindcast zooplankton density to explain Black Sea Bass distributions proved to be effective, and the most skillful models included zooplankton. In many ways, this was a surprising finding. Our zooplankton data were not observations, but instead hindcast quantities reconstructed by a biogeochemical oceanographic model. Despite the potential biases and errors in such hindcasts, the zooplankton fields were skillful for explaining Black Sea Bass observations. However, using zooplankton as a proxy for prey availability might be dependent on the species in question, and other metrics of prey availability would be worth exploring. The inclusion of biotic interactions in the form of density or coverage of other species has shown to improve certain species distribution models (Mod et al., 2015). Therefore, it might be valuable to consider prey species that interact with Black Sea Bass. However, single-prey species are less likely to be useful for a generalist predator like Black Sea Bass. Joint species distribution modeling in which associated species covary with environment variables may be useful in this context if the prey species have also been sampled (Tikhonov et al., 2017). Other studies have suggested that shelf water volume as a proxy for cross-shelf migration distance may be useful in explaining Black Sea Bass habitat at a regional scale (Miller et al., 2016).

Going forward, the rapid redistribution of many marine species in recent decades, including Black Sea Bass, provides an ideal opportunity to test hypotheses about the factors constraining and changing species spatial distributions. Many continental shelf ecosystems are well observed and have been for decades (Maureaud et al., 2021), setting the stage for further research. For Black Sea Bass, future directions could include a consideration of both minimum and maximum annual temperatures, new data sources to better survey rocky habitats, and separately investigating juvenile and adult distributions. Seasonal temperature changes (that may be captured by seasonal minimums and maximums) are known to trigger Black Sea Bass migratory movements in fall and spring (Able, 1995), and temperature extremes have been suggested to be important determinants of species range edges (Hutchins, 1947). In the face of climate change and phenomena such as the increased frequency of heatwaves (Oliver et al., 2018; Stillman, 2019), it has become even more important to investigate how these temperature extremes may drive redistribution of species. In addition, Black Sea Bass are known to associate with complex bottom structures (such as reefs) and with coarse sediment (Fabrizio et al., 2013; Schweitzer & Stevens, 2019). However, bottom trawl surveys are typically conducted over muddy and sandy substrates and do not sample rocky habitats well (Azarovitz, 1981). Therefore, more focused sampling of Black Sea Bass over their preferred habitats, such as with traps or rod-and-reel (Provost et al., 2017), will be helpful to fully observe their association with complex bottom structures. Finally, separate models for juveniles and adults may be useful because juveniles are more often found in shallow water bodies and adults alternate between deeper and shallow waters. Previous work conducted to determine the wintering habitat preferences of adult and juvenile Black Sea Bass in the

mid-Atlantic Bight found that the wintering period was important for explaining recruitment to the adult population (Miller et al., 2016). The extensive history and spatial extent of data available for Black Sea Bass and other species provides an important resource for testing these and related hypotheses.

Black Sea Bass is expanding into the Gulf of Maine and has been widely noted as an example of redistributing marine species (McBride et al., 2018). However, it is one of many species in the northwestern Atlantic that is expanding into this region (Hare et al., 2016; Nye et al., 2009). In the Gulf of Maine, several species have been projected to gain suitable thermal habitat in the next 60–80 years (Kleisner et al., 2017). The introduction of novel species into the Gulf of Maine may produce novel species interactions that have substantial impact on the ecology as well as economic activities. An example would be the impact that Black Sea Bass may have on the American lobster populations in the Gulf of Maine as a novel predator (McMahan & Grabowski, 2019).

Our results suggest that integrating temperature plus oxygen into a wide range of marine species distribution models will be productive for allowing a better understanding of species distributions and their changes through time. Continuing to link physiological processes to biogeographic patterns has strong promise for improving our understanding of the impacts of global climate change on species biogeography.

AUTHOR CONTRIBUTIONS

Rathnayaka Mudiyansele Wajra Jeewantha Bandara: Data curation; formal analysis; funding acquisition; investigation; methodology; software; visualization; writing – original draft; writing – review and editing. **Enrique N. Curchitser:** Data curation; project administration; resources; validation; writing – review and editing. **Malin L. Pinsky:** Conceptualization; funding acquisition; investigation; methodology; project administration; resources; supervision; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

All authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The code and data used for this study are available in a public GitHub repository (<https://github.com/wajra/bsb-shift-drivers>). These data and code are also archived in a Zenodo repository (<https://doi.org/10.5281/zenodo.10023533>).

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SUPPORTING INFORMATION

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