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

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1 Abstract

2   Large-scale shifts in marine species biogeography have been a notable impact of

3   climate change. An effective explanation of what drives these species shifts, as well as

4   accurate predictions of where they might move, is crucial to effectively managing these

5   natural resources and conserving biodiversity. While temperature has been implicated

6   as a major driver of these shifts, physiological processes suggest that oxygen, prey, and

7   other factors should also play important roles. We expanded upon previous temperature-

8   based distribution models by testing whether oxygen, food web productivity, salinity, and

9   scope for metabolic activity (the Metabolic Index) better explained the changing

10   biogeography of Black Sea Bass (*Centropristis striata*) in the Northeast US. This species

11   has been expanding further north over the past 15 years. We found that oxygen

12   improved model performance beyond a simple consideration of temperature (ΔAIC =

13   799, ΔTSS = 0.015), with additional contributions from prey and salinity. However, the

14   Metabolic Index did not substantially increase model performance relative to

15   temperature and oxygen (ΔAIC = 0.63, ΔTSS = 0.0002). Marine species are sensitive to

16   oxygen, and we encourage researchers to use ocean biogeochemical hindcast and

17   forecast products to better understand marine biogeographic changes.

18
19   **Keywords**: marine biogeography, species distribution modeling, fisheries, species shifts,

20   physiology, temperature, oxygen, metabolic index

21
22

23 # Introduction

24

25 Ongoing global climate change has had substantial impacts on species biogeography

26 (Sunday et al., 2012). This is especially visible in the ocean, where there are many

27 examples of species and communities shifting to new locations as environmental

28 conditions change (Lenoir et al., 2020). These shifts impact ecological communities,

29 ecosystems, and coastal economies (Allison et al., 2009; Brander, 2010; Kleisner et al.,

30 2016). For scientists and resource managers, understanding historical distribution shifts

31 is an important step towards understanding the mechanisms most relevant to making

32 future projections and developing effective management plans.

33

34 Approaches to modeling marine species distribution under climate change have often

35 focused on responses to temperature change (Kleisner et al., 2017; Nye et al., 2009).

36 Temperature is widely measured and has clear impacts on species physiology and

37 demography, including metabolism, growth, and reproduction (Angilletta Jr., 2009; Free

38 et al., 2019). However, effectively explaining past shifts in distribution and accurately

39 projecting future shifts will require a more complete understanding of the factors

40 determining species habitat. Previous research has found that models using only

41 temperature can result in less accurate and overly optimistic projections (McHenry et al.,

42 2019).

43

44 For marine species, physiological experiments and ecological theory suggest that key

45 factors are likely to include dissolved oxygen, prey availability (Morgan, 1972; Velasco et

46 al., 2019). In particular, metabolic processes suggest that temperature and dissolved

47   oxygen interact to determine marine species habitat suitability (Portner & Knust, 2007).

48   This physiological interaction has been explained through the mechanism of temperature

49   induced hypoxia, which can be measured with the Metabolic Index (ϕ). The Metabolic

50   Index measures the metabolic capacity of an individual organism relative to the

51   environmental supply of oxygen at a certain temperature (Deutsch et al., 2015). For a

52   marine habitat to be metabolically viable for a species, the dissolved oxygen supply rate

53   must exceed the basal metabolic demand of the individual (Seibel & Deutsch, 2020).

54   The Metabolic Index has been used to explain the boundaries of extant species

55   distributions (Deutsch et al., 2020; Howard et al., 2020) as well as species extinction

56   events over geological time (Penn et al., 2018), and is therefore expected to be useful

57   for explaining contemporary changes in species distributions. However, it remains

58   unclear how the Metabolic Index performs relative to and in combination with other

59   environmental factors likely to influence species distributions and their changes through

60   time (Essington et al., 2022). In particular, oxygen and the Metabolic Index have proven

61   useful for explaining static biogeography (Essington et al., 2022; Howard et al., 2020)

62   and changes in abundance (Howard et al., 2020), but it remains unclear whether these

63   factors are more important for explaining changes in biogeography over decadal

64   timescales than other factors like temperature. In addition, the use of the Metabolic

65   Index requires species-specific physiological measurements, which impedes widespread

66   application. A more widely applicable alternative may be to estimate the interaction of

67   temperature and oxygen from historical records of species occurrence.

68

69   Food or prey availability is also an important determinant of species niche and habitat.

70   The availability of prey is a first-order constraint on predator presence and abundance

71   (Mammides et al., 2009; Morgan, 1972; Trainor et al., 2014). Despite the clear

72   importance of prey availability, using such information to understand marine species

73   spatial distributions is difficult in part because many marine predators are generalists, or

74   their prey remain unknown. One solution may be to consider aggregate measures of

75   lower food web productivity. For example, fisheries productivity has been related to the

76   overall productivity of planktonic food chains (Stock et al., 2017).

77

78   Beyond prey, salinity is an important habitat determinant of marine species, especially in

79   coastal and lagoon environments with variable freshwater outflow and dry conditions

80   (Barletta et al., 2005). Because many marine species spend at least a part of their life

81   cycle near-shore, salinity can impact the overall distribution of a species (Pauly & Yáñez-

82   Arancibia, 1994). Salinity has been used in previous efforts to predict marine species

83   habitat (A. S. Miller et al., 2016).

84

85   While oxygen, prey availability, and salinity are likely to be important for defining marine

86   fish biogeography, the absence of long term, spatially resolved datasets for oxygen and

87   prey has made testing these hypotheses difficult. The development of coupled physical-

88   biogeochemical oceanographic model hindcasts that resolve historical planktonic food

89   web dynamics may help to fill in these details (Doney, 1999; Quere et al., 2005).

90

91   Black Sea Bass (*Centropristis striata*) is an important fishery species that has expanded

92   its range 80 km/decade north over the past five decades (McMahan, 2017; Morley et al.,

93   2018). Because of this notable range expansion and the extensive distribution data

94   available from scientific trawl surveys of the continental shelf, Black Sea Bass is a useful

95   species against which to test hypotheses for the factors driving range shifts. Fishermen

96   have reported a higher number of sightings of Black Sea Bass in the southern Gulf of

97   Maine since an ocean heatwave in 2012 (McMahan, 2017). Subsequent investigations

98   determined that Black Sea Bass have been slowly expanding into the Gulf of Maine over

99   15 years and have spawned there at least once (McBride et al., 2018). This represents a

100   range expansion of nearly 1° north from the previous range limit for the Mid-Atlantic

101   stock (McBride et al., 2018; McMahan, 2017). More broadly, Black Sea Bass are

102   distributed across the northwest Atlantic Ocean and, historically, the species has been

103   recorded from Texas in the Gulf of Mexico up to Cape Cod, Massachusetts (Brodziak,

104   2007; McCartney et al., 2013; Roy et al., 2012). Black Sea Bass supports both

105   commercial and recreational fisheries throughout their range and has been managed as

106   three separate stocks: Mid-Atlantic, South Atlantic, and Gulf of Mexico (Mercer, 1978).

107   Black Sea Bass has been identified as a warm water species, and it undertakes

108   southward migrations triggered by low ocean temperatures each fall. In the face of

109   ocean warming caused by climate change, it has been categorized as a "winning"

110   species in the northeast U.S. because of its expanding range and increased productivity

111   (Free et al., 2019; Hare et al., 2016). Black Sea Bass has been the focus of previous

112   modeling studies (A. S. Miller et al., 2016; Morley et al., 2018) in which temperature and

113   shelf water volume (as a proxy for productivity) were important determinants of seasonal

114   habitats in fall and spring.

115

116   In this study, we tested several environmental variables and one physiological variable

117   for their utility to explain Black Sea Bass habitat and changes in spatial distribution

118   through time in the Northwest Atlantic. The major questions that we address in this study

119   are 1) whether dissolved oxygen, prey availability, and salinity more effectively explain

120   Black Sea Bass biogeography and changes through time than does ocean temperature

121   alone; and 2) whether the Metabolic Index outperforms other environmental factors for

122   explaining shifting marine species distributions. There are broad concerns over how

123   shifts of important marine species under climate change may impact local economies

124   and our work addresses this by defining a metabolic habitat for black sea bass.

125

126

Materials and Methods

127

128 Our approach was to test alternative hypotheses expressed as statistical species

129 distribution models. Our baseline model used sea bottom temperature, ocean floor

130 rugosity, and sediment type (grain size) as explanatory variables, which have been

131 useful for previous Black Sea Bass distribution models (Morley et al., 2018). We then

132 tested whether adding salinity, zooplankton density (as a proxy for prey availability),

133 dissolved oxygen, and Metabolic Index improved the ability to explain changes in

134 distribution. *In situ* observations of oxygen and prey were too sparse for this purpose, so

135 we used oceanographic hindcasts for these environmental conditions and for salinity.

136 Models were assessed on their ability to predict out-of-sample presence-absence and

137 biomass.

Species data

138

139 We used species occurrence and biomass data from scientific bottom trawl hauls

140 conducted in four regions of the Atlantic North American continental shelf. Surveys were

141 conducted primarily by NOAA Fisheries (USA) and by DFO (Canada) and were compiled

142 by Morley et al. (2018) (Fig. S1 and Table S1). The dataset included corrections for

143 method changes in the Northeast U.S. following Miller et al. (2010). The original dataset

144 spanned nearly 50 years from 1963 to 2010, but we trimmed it to 1982-2010 to match

145 the environmental data and oceanographic hindcasts. This trimming left 2802 Black Sea

146 Bass presences and 40,542 absences (Fig. S2). A majority of Black Sea Bass

147 presences were in the Mid-Atlantic (2125) and the rest were in the South Atlantic.

148

149 Environmental data

150 Oxygen concentration, zooplankton density, and salinity values were obtained from a

151 biogeochemical oceanographic hindcast model for the period 1982 to 2010 (Kang &

152 Curchitser, 2013; Zhang et al., 2019). This ROMS-COBALT (Regional Oceanic Modeling

153 System-Carbon, Ocean, Biogeochemistry and Lower Trophics) model covers most of the

154 northwest Atlantic and has a grid configuration of 7 km x 7 km and 40 vertical layers

155 from the sea surface to the sea bottom. The accuracy of this model has been verified by

156 comparing it against historical data for sea surface temperature, sea surface chlorophyll

157 and nitrate concentrations (Kang & Curchitser., 2013; Zhang et al., 2018). We used

158 zooplankton density as a proxy for prey availability. While Black Sea Bass are generalist

159 predators that do not directly feed on zooplankton (Brodziak, 2007), zooplankton

160 productivity supports the food web that feeds Black Sea Bass.

161

162 At the location of each haul in our species dataset, we extracted the seasonal averages

163 of dissolved oxygen, zooplankton, and salinity by calculating the average value over

164 three months (the month the haul took place and the preceding and following months).

165 Dissolved oxygen concentration (mol/kg of seawater) and salinity (ppm) were taken from

166 the bottom-most vertical layer of the ROMS dataset. Zooplankton densities (zooplankton

167 body nitrogen mol/kg of seawater) were defined separately for three size classes in the

168 ROMS-COBALT model. Small zooplankton were less than 200 μm equivalent spherical

169 diameter (ESD), medium zooplankton were small to medium copepods between 200 and

170 2000 μm ESD, and large zooplankton were large copepods and euphausiids between 2

171 and 2 mm ESD (Stock et al., 2014). We calculated the total zooplankton density as the

172 sum of the three size classes across the 40 vertical layers.

173

174

175   In addition, we used sea bottom temperature, seafloor rugosity, and seafloor sediment

176   grain sizes as compiled by Morley et al. (2018). To summarize their methods,

177   temperature data were originally from the Simple Ocean Data Assimilation (SODA)

178   v3.3.1 (Carton et al., 2018). While Morley et al. used several temperature variables,

179   including sea surface temperature and annual maximums and minimums, we only used

180   seasonal bottom temperature because of the high correlation between the various

181   temperature measurements (Fig. S3). The temperature metrics were positively

182   correlated to a large degree ($r > 0.5$), while dissolved oxygen was negatively correlated

183   with the various temperature metrics ($r < -0.5$). Rugosity and grain size were potentially

184   useful because Black Sea Bass are known to be associated with rocky bottom structures

185   (Able, 1995; Brodziak, 2007; Steimle, 1996). Rugosity was calculated from the General

186   Bathymetric Chart of the Oceans (GEBCO) gridded bathymetry dataset at a 1 km

187   resolution (Becker et al., 2009). While coarse, this scale has proven useful for explaining

188   the distribution of marine fishes (Hare et al. 2012; Morley et al., 2018, Morley et al.,

189   2020). Rugosity of a cell was calculated as the absolute difference between its depth

190   and the depth of the surrounding eight cells. Sediment grain size was interpolated from

191   several sources (see Morley et al. 2018) and was measured on the Phi Wentworth scale

192   in which a higher value indicates a finer sediment, and a lower value indicates a coarser

193   sediment. The distribution of these variables for both Black Sea Bass presences and

194   absences are shown in Fig. S4 (presences) and Fig. S5 (absences).

195
196

197 ## Metabolic Index

198 The Metabolic Index is defined as the ratio of the rate of oxygen supply to an individual

199 relative to the oxygen demand necessary for sustaining basic life functions at a certain

200 temperature. Experiments have confirmed that the Metabolic Index is a useful indicator

201 of temperature-dependent hypoxia in Black Sea Bass (Slesinger et al., 2018). The

202 Metabolic Index is calculated as

203
$$\varphi = \frac{A_o B^n P_{O_2}}{exp(-E_o/k_B T)}$$

204 where A_o is the species-specific ratio of rate coefficients for O_2 supply and metabolic

205 demand, B^n is the per-mass rate of gas transfer between water and the animal and its

206 scaling with body mass for the species of interest (measured in kPa^{-1}), P_{O2} is the partial

207 pressure of dissolved oxygen measured in kPa, E_o is the temperature dependence of

208 metabolic activity measured in eV, k_B is Boltzmann's constant measured in eV K^{-1}, and T

209 is temperature measured in K. We used Black Sea Bass-specific values of

210 $A_o=0.00040728$, $B^n=10^{-2}$, and $E_o=0.27$ measured in physiological experiments (Seibel &

211 Deutsch, 2020; Slesinger et al., 2018). We used seasonal bottom temperature (referred

212 to as temperature from now on) from SODA in K for temperature. Dissolved oxygen from

213 the ROMS-COBALT model in mol/kg of seawater units was converted to kPa using the

214 'Respirometry' package in R (Birk, 2020). For the unit conversion, ROMS-COBALT

215 seasonal salinity values (in ppm) and temperature (in K) were also used.

216 ## Species distribution modeling

217 We expressed alternative hypotheses for the factors driving Black Sea Bass distribution

218 as a set of statistical models. We used a two-stage modeling approach, also called a

219   hurdle model, that included a presence/absence model and a biomass conditional on

220   presence model to account for the large number of zeros in the data (Barry & Welsh,

221   2002; Cragg, 1971; Morley et al., 2018). To model presence-absence, we utilized a

222   generalized additive model (GAM) with binomial errors fit with the mgcv package in R

223   (Wood, 2017). For biomass models, we then added a second-stage GAM that modeled

224   the log-transformed biomass with a normal error distribution. The GAM for presence-

225   absence included all hauls in order to include observed absences, while the log-biomass

226   GAM was fit for all hauls with non-zero biomass. Because the biomass model was only

227   fit to non-zero biomass observations and in order to model biomass across the full range

228   of environmental conditions and surveys, we followed the methods of Morley et al.

229   (2018) and added a small set of artificial near-zero biomass values (10^{-10}) to a fraction of

230   hauls in regions where the species was never encountered (10% of the hauls in a region

231   or 10% of total observations, whichever was the smaller value).

232

233   We then designed sets of explanatory variables to compare against each other as our

234   alternative hypotheses. These included models with only a single oceanographic

235   variable as well as multivariable models. All models (whether single or multivariable)

236   included the ocean floor variables (rugosity and sediment grain size) and a categorical

237   variable for the bottom trawl survey (to account for differences in vessels and sampling

238   methods) (Table S1). To reduce overfitting, we used the recommendation to set a

239   gamma value for each GAM as the log of the number of samples included in the model

240   divided by two (Wood, 2017). We investigated higher gamma values (up to gamma = 50)

241   for greater smoothing but doing so degraded out-of-sample predictive skill and we did

242   not pursue this further (Wood, 2017).

243

244   The null model contained only the ocean floor and survey variables. Single variable

245   models also included temperature, Metabolic Index, dissolved oxygen, salinity, or

246   zooplankton. Multivariable models included different combinations of the above-

247   mentioned variables in order to test the explanatory value of Metabolic Index and other

248   variables relative to temperature (Table 1). We examined models in several classes,

249   including traditional temperature-based models (T models), Metabolic Index-based

250   models (MI models), temperature-oxygen interaction models (T:O models), and hybrid

251   models (those that contained a combination of temperature, Metabolic Index, and/or

252   temperature-oxygen interaction). The T:O models examined whether the interaction

253   between temperature and oxygen could be estimated statistically and the relative

254   performance of this estimation against the physiologically calibrated MI values.

255

256   Model assessment

257   In order to understand model skill, we assessed both in-sample model fit and out-of-

258   sample forecasting skill. Each model was fit to a training dataset of all hauls before the

259   year 2000 and two metrics were calculated. Akaike Information Criterion (AIC) is a

260   measure of model performance that is proportional to the model complexity minus the

261   log likelihood. With certain assumptions, the model with the lowest AIC score is

262   expected to have the best performance (Burnham & Anderson, 2004). We calculated

263   ΔAIC as the difference between the AIC of each model and of the lowest scoring model.

264   As a simple guideline, ΔAIC values <2 indicate models that do not have substantially

265   different performance, and ΔAIC values >10 indicate very little support (Burnham &

266   Anderson, 2004). In addition, the models were evaluated against all the hauls including

267   and after the year 2000 with the True Skill Statistic (TSS) as a true out-of-sample test.

268   TSS compares the number of correct forecasts, minus the ones attributed to random

269   guessing, to that of a hypothetical set of perfect forecasts (Allouche et al., 2006). A TSS

270   value of 1 suggests perfect prediction capability, and values at 0 or below indicate no

271   better than random capability.

272

273   The code for accessing the ROMS-COBALT hindcast data and calculating seasonal

274   averages for dissolved oxygen, salinity, and zooplankton was written in Python

275   programming language version 2.7 (Perez & Granger, 2007; van Rossum & Drake,

276   2002). The code for all remaining analyses was written in R version 4.0 (R Core Team,

277   2021). The code can be accessed on GitHub at https://github.com/wajra/bsb-shift-

278   drivers.

279

280   Results

281   Black sea bass distribution shifted northwards from 1980 to 2010 (Fig. 1a,b) and by the

282   2000s, they were highly prevalent off the coast of New Jersey and into southern New

283   England. This is apparent by prevalence anomalies (2000s – 1980s; Fig. S6 (a)). As one

284   measure of spatial distribution, their centroid shifted north from 37.15 °N latitude in the

285   1980s to 38.79 °N latitude in the 2000s (Fig. 1a,b). Over the same period of time, the

286   environment had also changed considerably, with the most noticeable changes in

287   temperature and dissolved oxygen (Fig. 2). The bottom waters in the Gulf of Maine

288   warmed by around 1 °C over these two decades. This region also showed some

289   deoxygenation (loss of 1 mg/dl over a 20 year period). However, zooplankton density

290   and salinity remained constant through the 1980s to the 2000s.

291

292   While we fitted presence-absence and biomass models using single or multiple

293   oceanographic variables, we focus our presentation of results here on the presence-

294   absence model. The best performing single-variable model for presence-absence used

295   the Metabolic Index, as determined from out-of-sample TSS and AIC (Table 2). Models

296   had similar but relatively low out-of-sample TSS at the scale of the individual bottom

297   trawl haul, while AIC differences among the models were large (>20). The next-best

298   model was oxygen, which had a ΔAIC of 24. The null model performed poorly on all

299   metrics. The low skill of the models could be partially attributed to testing against

300   individual hauls rather than testing over a larger averaged area (for example, a ¼ degree

301   grid square as shown in Fig. 1)

302

303

304   In presence-absence models combining multiple oceanographic factors, there were

305   three equivalently well-performing models according to both out-of-sample TSS and

306   ΔAIC (Table 3). In order of increasing complexity, these were T+O+S+Z (ΔAIC=0.625),

307   T+O+MI+S+Z (ΔAIC=0), and T+O+T:O+S+Z (ΔAIC=0.698). The addition of an extra

308   explanatory variable to the T+O+S+Z model, in the form of either a temperature-oxygen

309   interaction (T:O) or the Metabolic Index (MI), produced only a very minor increase in

310   model performance. Therefore, we selected T+O+S+Z as the preferred model for

311   plotting in Fig. 1. In terms of model classes, the MI and T:O models generally did not

312   perform well, illustrating the importance of including a temperature factor. In the T class

313   of models with only one additional factor, adding dissolved oxygen resulted in the

314   greatest improvement in model skill and was substantially better than adding MI.

315   Comparing models with T+O, the addition of S, Z, or S+Z (from T+O to T+O+Z, T+O+S,

316   or T+O+S+Z) yielded better model performance compared to hybrid models.

317

318

319   In the T+O+S+Z model, all explanatory variables were statistically significant ($p<1 \times 10^{-11}$)

320   (Table 4). The probability of presence generally increased with rising temperature up to

321   at least 10 °C (Fig. 3). The probability of presence decreased substantially at dissolved

322   oxygen levels higher than 2.5×10^{-4} mol/kg. The probability of presence increased with

323   zooplankton density up to 8×10^{-5} zooplankton body nitrogen mol/kg of seawater.

324   Probability of presence also increased in general with salinity and rugosity. Grain size

325   was the only parameter to which probability of presence did not show a clear directional

326   response (Fig. 3).

327

328   Species biomass (Table S2) also showed a positive relationship with temperature,

329   peaking at 10 °C and then slowly declining at higher temperatures (Fig. S7). Species

330   biomass showed a similar positive relationship with dissolved oxygen and peaked at 2.5

331    $\times 10^{-4}$ mol/kg and declined after. Biomass also showed a positive nonlinear relationship

332   with zooplankton density (Fig. S7).

333

334

335   Both the statistically estimated temperature-oxygen interaction and the Metabolic Index

336   represent similar concepts, with the latter more tightly constrained by physiological

337   theory. We, therefore, compared the two effects (Fig. 4). The temperature-oxygen

338   interaction suggested that probabilities of presence were highest at dissolved oxygen

339   levels from 0 to 9 mg/L) and from 5 to 30 °C, which did not align with MI isoclines. In

340   particular, the statistical interaction did not suggest a higher minimum tolerable oxygen

341   concentration at higher temperatures, as suggested by MI. Nearly all hauls considered

342   for the study (99%) were above a MI of 2. Black Sea Bass were encountered in 6% of

343   these hauls. Black Sea Bass were also encountered in 14% of the hauls below an MI of

344   2. Black Sea Bass were notably absent from hauls below 3 °C or above 10 mg/L O_2 (i.e.,

345   at particularly high MI values).

346

347

348   Hindcasting the T+O+S+Z model revealed that the model successfully predicted the

349   northward expansion of Black Sea Bass through time (Fig. 1c, d). In particular, the

350   model predicted a northward shift of the centroid from 35.23 °N to 35.80 °N, similar to

351   but not as large as the observed shift (37.15 to 38.79 °N). The suitable habitat was

352   concentrated around North Carolina in the 1980s and shifted northwards to New York

353   and offshore to Georges Bank by the 2000s.

354   # Discussion

355   Species range shifts have both ecological and economic impacts. In order to best

356   understand how to mitigate and prepare for these shifts, it is important to understand

357   their major drivers. In this study, we examined whether oxygen, temperature-dependent

358   hypoxia, food availability, and salinity from oceanographic hindcasts were useful for

359   explaining historical shifts in Black Sea Bass distributions in the northwest Atlantic. We

360   found that a multi-variate model including temperature and dissolved oxygen in particular

361   described the Black Sea Bass habitat in the Northwest Atlantic and changes through

362   time. While fish physiology suggests an interaction between temperature and oxygen is

363   important for metabolic considerations, considering this mechanism did not appreciably

364   improve explanatory or forecast skill for species distributions.

365

366   The Metabolic Index has been shown in experimental studies (Seibel & Deutsch, 2020;

367   Slesinger et al., 2018) to accurately reflect the factorial aerobic scope (measured as

368   maximum/standard metabolic rate) of a species. As fish were exposed to higher

369   temperatures and lower Metabolic Indices, Black Sea Bass exhibited less ability to

370   increase their metabolic activity above their resting rate (Slesinger et al., 2018). A

371   Metabolic Index of 3 has been suggested as a lower limit for population persistence

372   (Seibel & Deutsch, 2020). Using Metabolic Index to explain species distributions could

373   therefore provide a physiological and mechanistic link between the environment and

374   species biogeography. Previous work has suggested that the Metabolic Index more

375   accurately describes species boundaries experiencing higher temperatures and lower

376   oxygen concentrations than does temperature or oxygen alone (Deutsch et al., 2015,

377   2020). While we found some evidence that Metabolic Index could explain historical Black

378   Sea Bass distributions, we also found that including temperature and oxygen separately

379   produced models that were effectively as skillful and parsimonious. Considering

380   Metabolic Index in addition to temperature and oxygen was not as useful as considering

381   salinity and proxies for prey.

382

383   One potential explanation for this result is that Metabolic Index is a better predictor of the

384   warm edge (retracting range) of a species than of the cold edge (expanding range), and

385   our data were focused on the cold range edge of Black Sea Bass. An organism's ability

386   to supply oxygen to its organs may decline at cold temperatures more than does

387   metabolic demand, creating temperature-dependent hypoxia at the cold range edge

388   (Pörtner et al., 2017). If this process is important at cold range edges, the MI would need

389   to be reformulated to include this process. However, the concept of oxygen- and

390   capacity-limited thermal tolerance itself also remains controversial, including at cold

391   range edges (Jutfelt et al., 2018). Alternatively, temperature alone (without an oxygen

392   interaction) may limit the cold range edge because of difficulty acquiring food or avoiding

393   predators when metabolic, movement and growth rates are slow, or because of limits on

394   reproduction or other processes (Dahlke et al., 2020; Slesinger et al., 2018). Lower

395   zooplankton concentrations in the Gulf of Maine (Fig. 2g) may also play a role and

396   interact with cold temperatures to help limit the Black Sea Bass distribution, perhaps by

397   further reducing the ability to find food. Better understanding of the ecological limits at

398   cold temperatures will be helpful for understanding cold range edge dynamics.

399

400   Our findings contribute to other research finding limited utility of the Metabolic Index for

401   explaining species distributions beyond the utility of oxygen and temperature. Recent

402   research on sablefish (*Anoplopoma fimbria*) on the west coast of the US has highlighted

403   that static species distributions may be more closely related to oxygen than to Metabolic

404   Index, though, in contrast to Black Sea Bass, temperature was not a particularly useful

405   explanatory factor for sablefish beyond oxygen (Essington et al., 2022). Some of the

406   differences between these two species may be explained by their depth distributions.

407   Sablefish inhabit deeper depths where low oxygen provides a strong constraint on

408   occupancy, whereas Black Sea Bass occupy shelf habitats with less oxygen limitation.

409   The sablefish paper did not directly examine changes through time, and our Black Sea

410   Bass results show additionally that changes in temperature and oxygen can skillfully

411   predict changes in species distribution through time.

412

413   The Metabolic Index represents an interaction between temperature and oxygen, but the

414   use of the Metabolic Index requires physiological experiments to derive species-specific

415   values that are available to date for only a few dozen species (Deutsch et al., 2020). In

416   theory, this interaction could be estimated statistically for a wider range of species from

417   spatial observations of occupancy or biomass. In support of this idea, our model that

418   estimated the temperature-oxygen interaction statistically (the T:O model) performed

419   equivalently well as the MI model. However, statistical estimation of the temperature-

420   oxygen interaction in Black Sea Bass produced a response surface that did not align

421   with Metabolic Index predictions. This statistical approach may allow insights from

422   physiology (such as the temperature-oxygen interaction) to be applied more widely

423   across species in the absence of the extensive lab work required to estimate the MI

424   directly. There has been a push in the literature to incorporate more mechanistic

425   approaches into species distribution modeling where the species habitat is explained by

426   variables with measurable impact on physiological function (Buckley et al., 2011), such

427   as the Metabolic Index. In advance of extensive physiological experiments, it may be

428   productive to infer metabolic traits from more widely measured species characteristics

429   and from phylogenetic history, as is now possible (Schrodt et al., 2015; Thorson et al.,

430   2017). Alternatively, statistical estimation of the temperature-oxygen interaction may be

431   suitable in many cases for species with sufficient occurrence data.

432

433   The use of hindcast zooplankton density to explain Black Sea Bass distributions proved

434   to be effective, and the most skillful models included zooplankton. In many ways, this

435   was a surprising finding. Our zooplankton data were not observations, but instead

436   hindcast quantities reconstructed by a biogeochemical oceanographic model. Despite

437   the potential biases and errors in such hindcasts, the zooplankton fields were skillful for

438   explaining Black Sea Bass observations. However, using zooplankton as a proxy for

439   prey availability might be dependent on the species in question, and other metrics of

440   prey availability would be worth exploring. The inclusion of biotic interactions in the form

441   of density or coverage of other species has shown to improve certain species distribution

442   models (Mod et al., 2015). Therefore, it might be valuable to consider prey species that

443   interact with Black Sea Bass. However, single prey species are less likely to be useful

444   for a generalist predator like Black Sea Bass. Joint species distribution modeling in

445   which associated species covary with environment variables may be useful in this

446   context if the prey species have also been sampled (Tikhonov et al., 2017). Other

447   studies have suggested that shelf water volume as a proxy for cross-shelf migration

448   distance may be useful in explaining Black Sea Bass habitat at a regional scale (A. S.

449   Miller et al., 2016).

450

451   Going forward, the rapid redistribution of many marine species in recent decades,

452   including Black Sea Bass, provide an ideal opportunity to test hypotheses about the

453   factors constraining and changing species spatial distributions. Many continental shelf

454   ecosystems are well-observed and have been for decades (Maureaud et al., 2021),

455   setting the stage for further research. For Black Sea Bass, future directions could include

456   a consideration of both minimum and maximum annual temperatures, new data sources

457   to better survey rocky habitats, and separately investigating juvenile and adult

458   distributions. Seasonal temperature changes (that may be captured by seasonal

459   minimums and maximums) are known to trigger Black Sea Bass migratory movements

460   in fall and spring (Able, 1995), and temperature extremes have been suggested to be

461   important determinants of species ranges edges (Hutchins, 1947). In the face of climate

462   change and phenomena such as the increased frequency of heatwaves (Oliver et al.,

463   2018; Stillman, 2019), it has become even more important to investigate how these

464   temperature extremes may drive redistribution of species. In addition, Black Sea Bass

465   are known to associate with complex bottom structures (such as reefs) and with coarse

466   sediment (Fabrizio et al., 2013; Schweitzer & Stevens, 2019). However, bottom trawl

467   surveys are typically conducted over muddy and sandy substrate and do not sample

468   rocky habitats well (Azarovitz, 1981). Therefore, more focused sampling of Black Sea

469   Bass over their preferred habitats, such as with traps or rod-and-reel (Provost et al.,

470   2017), will be helpful to fully observe their association with complex bottom structures.

471   Finally, separate models for juveniles and adults may be useful because juveniles are

472   more often found in shallow water bodies and adults alternate between deeper and

473   shallow waters. Previous work conducted to determine the wintering habitat preferences

474   of adult and juvenile Black Sea Bass in the mid-Atlantic Bight found that the wintering

475   period was important for explaining recruitment to the adult population (A. S. Miller et al.,

476   2016). The extensive history and spatial extent of data available for Black Sea Bass and

477   other species provides an important resource for testing these and related hypotheses.

478

479   Black Sea Bass is expanding into the Gulf of Maine and has been widely noted as an

480   example of redistributing marine species (McBride et al., 2018). However, it is one of

481   many species in the northwestern Atlantic that is expanding into this region (Hare et al.,

482   2016; Nye et al., 2009). In the Gulf of Maine, several species have been projected to

483   gain suitable thermal habitat in the next 60 to 80 years (Kleisner et al., 2017). The

484   introduction of novel species into the Gulf of Maine may produce novel species

485   interactions that have substantial impact on the ecology as well as economic activities.

486   An example would be the impact that Black Sea Bass may have on the American lobster

487   populations in the Gulf of Maine as a novel predator (McMahan & Grabowski, 2019).

488

489   Our results suggest that integrating temperature plus oxygen into a wide range of marine

490   species distribution models will be productive for allowing a better understanding of

491   species distributions and their changes through time. Continuing to link physiological

492   processes to biogeographic patterns has strong promise for improving our

493   understanding of the impacts of global climate change on species biogeography.

494
495

496   Acknowledgments

505   Data availability

506

507   The code and data used for this study are available in a public GitHub repository

508   (https://github.com/wajra/bsb-shift-drivers). This data and code are also archived in a

509   Zenodo repository (https://doi.org/10.5281/zenodo.10023533).

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780 # Tables

781

782 **Table 1**: List of models used to explain Black Sea Bass habitat.

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 +	T:O+S

	Salinity	
	Temperature-Oxygen interaction + Zooplankton	T:O+Z
	Temperature-Oxygen interaction + Salinity + Zooplankton	T:O+S+Z

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784   **Table 2.** Performance metrics for presence-absence models with single oceanographic

785   variables measured as ΔAIC and as out-of-sample TSS. The best performing model (MI)

786   is highlighted in bold.

Model name	TSS	AIC	ΔAIC
Null	0.113	10613	993
S	0.117	10325	706
SBT	0.129	9860	240
O	0.131	9643	24
Z	0.109	10449	830
MI	**0.132**	**9619**	**0**

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789   **Table 3.** Performance metrics for presence/absence models with multiple explanatory

790   variables. The three best-performing models are highlighted in bold.

Model class	Model name	TSS	AIC	ΔAIC
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**
	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**
Hybrid models	**T+O+T:O+S+Z**	**0.1438**	**9061.5**	**0.70**
	MI+S	0.1334	9517.9	457.14
	MI+Z	0.1374	9236.6	175.87
MI models	MI+S+Z	0.1429	9186.1	125.37
	T:O+S	0.1353	9643.7	582.97
	T:O+Z	0.1368	9368.9	308.12
T:O models	T:O+S+Z	0.1374	9368.2	307.46

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792

793   **Table 4**: Fit statistics for the best-performing presence/absence model (T+O+S+Z).

794   Table shows the empirical degrees of freedom (EDF) and the approximate chi-squared

795   and p-values for each term. The p-values were below machine tolerance values.

Variable	EDF	Chi-Squared value	p-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	$<1 \times 10^{-11}$

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Figure legends

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817   **Figure 1:** Distribution of Black Sea Bass across time. (a) and (b) show Black Sea Bass

818   prevalence (proportion of hauls with Black Sea Bass) in bottom trawl surveys.

819   Subfigures (c) and (d) show hindcast probability of presence from the preferred model

820   (Temperature + Dissolved Oxygen + Salinity + Zooplankton model; T+O+S+Z). Maps

821   are for 1980 to 1990 (a, c) and for 2000 to 2010 (b, d). Both prevalence and probability

822   have been averaged into ¼ ° latitude x longitude grid cells.

823

824   **Figure 2.** Decadal averages for the 1980s and decadal change in mean values between

825   the 1980s and 2000s for bottom temperature (a,b), bottom dissolved oxygen (c,d),

826   bottom salinity (e,f), vertically integrated zooplankton density (g,h), and bottom Metabolic

827   Index (i,j). Note that the change in zooplankton scale is an order of magnitude smaller

828   than the mean zooplankton scale. The 1% most extreme values for change in salinity,

829   zooplankton, and dissolved oxygen have been removed to improve legibility of the map.

830

831   **Figure 3.** Response curves for predictors in the T+O+S+Z presence-absence model.

832   The shaded areas show the 95% confidence interval. This figure and Fig. S7 show the

833   partial or additive effect that each covariate in the model has on the predicted variable.

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835   **Figure 4**: The effect of the interaction between seasonal bottom temperature and

836   dissolved oxygen on the probability of presence (from the T+O+T:O+S+Z model). Black

837   Sea Bass presences (black triangles), absences (gray circles), and Metabolic Index (ϕ,

838   lines) are plotted against seasonal temperature and dissolved oxygen. Lines indicate a ϕ

839   of 1 (dashed black) and 2 (dashed green).

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