The effect of ocean warming on black sea bass (*Centropristis striata*) aerobic scope and hypoxia tolerance

Ocean warming and *C. striata* physiology

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Key Words

Black sea bass, *Centropristis striata*, climate change, metabolic index, aerobic scope

Summary Statement

Laboratory-based physiological studies focused on aerobic scope and hypoxia tolerance of black sea bass presented here support the recently observed poleward shift of their range on the U.S. Northeast Shelf.

Abstract

Over the last decade, ocean temperature in the U.S. Northeast Continental Shelf (U.S. NES) has warmed faster than the global average and is associated with observed distribution changes of the northern stock of black sea bass (*Centropristis striata*). Mechanistic models based on physiological responses to environmental conditions can improve future habitat suitability projections. We measured maximum (MMR), resting metabolic rate (RMR), and hypoxia tolerance (S_{crit}) of the northern adult black sea bass stock to assess performance across the known temperature range of the species. A subset of individuals was held at 30˚C for one month ($30_{chronic}$°C) prior to experiments to test acclimation potential. MMR and absolute aerobic scope (AAS = MMR-RMR) reached a maximum at 24.4°C (AS: 367.21 mgO_2 kg^{-1} hr^{-1}) while S_{crit} continued to increase in proportion to RMR up to 30°C. The $30_{chronic}$°C group had a significant decrease in MMR and AAS but RMR or S_{crit} were not affected. This suggests a decline in performance of oxygen demand processes (e.g. muscle contraction) beyond 24°C despite maintenance of oxygen supply. The Metabolic Index, calculated from S_{crit} as an estimate of potential aerobic scope, closely matched the measured factorial aerobic scope (FAS = MMR/RMR) and declined with increasing temperature to a minimum below 3. This may represent a critical value for the species. Temperature in the U.S. NES is projected to increase above 24°C in the southern portion of the northern stock's range. Therefore, these black sea bass will likely continue to shift north as the ocean continues to warm.

Introduction

Marine environments are progressively warming as a consequence of climate change (Belkin, 2009). Along the U.S. Northeast Shelf (U.S. NES), ocean temperature is rising faster than the global average (Pershing *et al.*, 2015; Caesar *et al.*, 2018) resulting in a significant temperature increase (Friedland and Hare, 2007; Kavanaugh *et al.*, 2017). Sea surface and bottom temperatures in the U.S. NES are projected to rise an additional 4.1°C and 5.0°C,

77 respectively, along the U.S. NES (Saba *et al.*, 2016; Kleisner *et al.*, 2017). Contemporary ocean
78 warming in the U.S. NES has been associated with distribution shifts of many economically and
79 ecologically important fish species both in latitude and/or depth (Nye *et al.*, 2009; Bell *et al.*,
80 2015; Kleisner *et al.*, 2016, 2017; Morley *et al.*, 2018), associated with tracking local climate
81 velocities (Pinsky *et al.,* 2013). Understanding and projecting shifts in fish distribution will be
82 important for characterizing potential ecological and economic impacts and anticipating and
83 resolving fishery management conflicts (Pinsky *et al.*, 2018).
84 Temperature directly affects metabolic rates of marine ectotherms (Clarke and Johnston,
85 1999; Verberk *et al.*, 2016) and is believed to set the boundaries of species ranges (Pörtner and
86 Farrell, 2008; Deutsch *et al.*, 2015). One explanation for the effects of temperature on
87 ectothermic species, oxygen and capacity-limited thermal tolerance (OCLTT; Pörtner, 2010),
88 postulates that thermal limitation occurs due to a mismatch in oxygen demand and supply at sub-
89 optimal temperatures, which ultimately determines suitable thermal habitat (Pörtner and Knust,
90 2007). In this framework, the thermal optimum occurs where absolute aerobic scope (AAS), the
91 difference between maximum (MMR) and resting metabolic rate (RMR) (Schulte, 2015), is
92 highest. RMR is the cost of maintenance for an organism and increases with temperature (Clarke
93 and Johnston, 1999). MMR may be constrained differently across a temperature range by oxygen
94 uptake, transport or utilization. The drop in AAS beyond the thermal optimum is associated with
95 the failure of MMR to increase relative to the continuing rate of increase in RMR (Farrell, 2016).
96 Absolute AAS is thought to represent the capacity for oxygen uptake, beyond that supporting
97 maintenance metabolism, that can be utilized for activities that promote individual fitness (e.g.
98 growth, reproduction, predator avoidance; Pörtner & Peck 2010). Hence, the adaptive benefit of
99 living at suitable temperatures to maintain metabolic scope may provide a mechanistic
100 explanation for where fish may be distributed in their environment.
101 While the general distribution of fishes is broadly confined by thermal preferences,
102 oxygen availability can further constrain suitable habitat. The hypoxia tolerance of a fish can be
103 estimated as the critical oxygen saturation level (S_{crit}), the $\%O_2$ below which oxygen supply
104 cannot match the demands of maintenance metabolism. Further reductions in $\%O_2$ cause a
105 proportional decrease in RMR (Schurmann and Steffensen, 1997). Below the S_{crit}, a fish has
106 time-limited survival as ATP production progressively relies on unsustainable anaerobic
107 pathways and metabolic suppression (Nilsson and Renshaw, 2004; Seibel, 2011). Generally, a

108 fish with a low S_{crit} is tolerant of lower sustained oxygen levels (Claireaux and Chabot, 2016). As
109 ocean temperature increases, oxygen demand concomitantly increases (Del Toro-Silva *et al.*,
110 2008; Capossela *et al.*, 2012), potentially reducing hypoxia tolerance (Collins *et al.*, 2013;
111 McDonnell and Chapman, 2015). The S_{crit} further provides a means of calibrating the Metabolic
112 Index, which is a ratio of oxygen supply to demand that provides an estimate of sustained
113 factorial aerobic scope and metabolically suitable habitat (Deutsch et al., 2015). At S_{crit}, by
114 definition, supply exactly matches demand allowing statistical estimation of the equations'
115 physiological parameters.
116 The northern stock of black sea bass (*Centropristis striata*) on the U.S. NES extends from
117 Cape Hatteras to the Gulf of Maine and is centered in the Mid-Atlantic Bight (MAB; Roy *et al.*,
118 2012). These fish seasonally migrate from the continental shelf edge in cooler months to inshore
119 depths (5-50m) in warmer months (Musick and Mercer, 1977; Moser and Shepherd, 2008).
120 Seasonally migrating black sea bass thus experience a wide range of temperatures throughout the
121 year, ranging from 6°C during winter and up to 27°C during summer/early fall months (Steimle
122 *et al.*, 1999). Off the coast of New Jersey, periodic hypoxic events can occur during the summer
123 as a result of high biological activity (Schofield *et al.*, 2012) fueled by upwelling of nutrient rich
124 waters (Glenn *et al.*, 2004). Therefore, during the warm summer months, black sea bass are
125 potentially subject to hypoxia in this region, contributing to the oxygen limitation that contains
126 suitable habitat.
127 The northern stock of black sea bass may already be exhibiting poleward shifts, likely
128 due to ocean warming (Hare *et al.*, 2016; Kleisner *et al.*, 2017). Evidence for current black sea
129 bass distribution shifts comes primarily from bottom trawl survey data (Kleisner *et al.*, 2017),
130 and is supported anecdotally through fishermen. Laboratory-based process studies focused on the
131 physiology of an organism provide detailed mechanistic relationships between the environment
132 and the animal (Wikelski and Cooke, 2006). The objectives of this study were to determine the
133 AAS and S_{crit} for the northern stock of adult black sea bass. We measured AAS and S_{crit} at a
134 range of temperatures similar to those experienced by black sea bass during their summer inshore
135 residency to compare thermal optima, if present, and metabolic index against the known
136 temperature range of the species. Results from these physiological studies may be useful for
137 modeling suitable habitat based on environmental parameters (Lefevre *et al.*, 2017) and model

138 black sea bass distributions (e.g., Manderson *et al.*, 2011; Deutsch *et al.*, 2015), and projecting
139 future distribution shifts in black sea bass with continued ocean warming.
140
141 **Methods**
142 *Fish Collection and Husbandry*
143 Adult black sea bass (*Centropristis striata*) from the northern stock (length = 221-
144 398mm; weight = 193.7-700.4g) were collected off the coast of New Jersey, USA at depths of
145 15-20m in early June from Sea Girt and Manasquan Reefs by fish traps (2016), and from local
146 reefs off Sandy Hook by hook-and-line (2017). Fish were housed in the NOAA James J. Howard
147 Marine Laboratory, held at ambient temperature (22 ± 1°C) and salinity (26ppt), maintained at a
148 natural photoperiod for New Jersey summer, and fed daily to satiation on a diet of sand lance and
149 silversides. Water temperature and salinity was monitored daily using a YSI (Pro-30; Yellow
150 Springs, Ohio, USA), and water chemistry remained at suitable levels (< 20 uM nitrate,
151 undetectable nitrite, < 0.05 uM ammonia, pH range of 7.98-8.04). Fish were acclimated to
152 captive conditions two weeks prior to the trials, after which all experimental fish ate regularly
153 and were in good condition. Any fish exhibiting apparent health issues (i.e. lack of appetite,
154 difficulties with buoyancy or orientation) were not used in experiments. After acclimation, fish
155 were measured for length (TL mm), weight (g), and tagged with individually numbered T-bar
156 Floy tags inserted underneath the dorsal rays. For each temperature treatment, fish were
157 acclimated at a rate of 2°C day^{-1} to reach experimental temperature, then held at the target
158 treatment temperature for at least 48hr prior to the start of experiments. Fish were starved 48hr
159 prior to the start of each experiment to eliminate effects of specific dynamic action (Chabot *et*
160 *al.*, 2016a). At the end of each experiment, fish were euthanized with an overdose of MS-222
161 (250 mgL^{-1}). Fish were collected under New Jersey permits #1610 & #1717. Treatment of all
162 animals was held in accordance with Rutgers IACUC protocol 15-054.
163
164 *Experimental Set-Up*
165 Experimental tanks (1,200L) were filled with treated seawater from Sandy Hook Bay that
166 continuously circulated through a closed system. Circulating seawater was treated using filters
167 (sand and biological) and UV-light, and salinity was adjusted to mimic average summertime
168 inshore NJ bottom water (32±1). Experimental temperatures were achieved using in-line chillers

169 (Aqua Logic Delta Star; San Diego, California, USA) and/or titanium exchanger heaters
170 (Innovative Heat Concepts, Homestead, Florida, USA), and maintained at ±1°C from target
171 temperature.
172 Metabolic rates were measured using intermittent respirometry under the protocols
173 outlined in Clark *et al.*, (2013) and Svendsen *et al.*, (2016a). Flow-through respirometers (13.5
174 liter volume; 23[H]x26[W]x37[L] cm plexiglass) were placed into the two experimental tanks
175 (two respirometers per tank; four respirometers per trial). Flush pumps (Eheim Universal 600
176 l//h; Deizisau, Germany) connected to the respirometer were used to pull water from the
177 surrounding temperature bath to replenish dissolved oxygen and eliminate metabolic waste
178 buildup within the respirometer. The duration and timing of flushes set the intermittent cycles,
179 which were controlled through a pre-determined time sequence using a DAQ-M instrument
180 (Loligo Systems; Viborg, Denmark), and were set based on the trial temperature so that oxygen
181 saturation was never below 75% (Svendsen *et al.*, 2016b). For each closed measure period
182 (when flush pumps were off), the rate of decline in dissolved oxygen concentration within the
183 sealed chamber was used to calculate a mass specific rate of oxygen consumption, or metabolic
184 rate (MO_2: $mgO_2\ kg^{-1}\ hr^{-1}$). A closed recirculation loop connected with a smaller pump (Eheim
185 Universal 300 l/h; Deizisau, Germany) was also utilized to uniformly disperse dissolved oxygen
186 within the chamber and provide waterflow across the oxygen dipping probe optical mini sensor
187 (PreSens Pst3; Regensburg, Germany). Oxygen probes were calibrated in accordance with the
188 supplier's manual (Oxygen dipping probe PSt3, PreSens GmbH, Regensburg, Germany) and
189 checked with a YSI (ProSolo ODO; Yellow Springs, Ohio, USA) that was calibrated in 100%
190 and 0% oxygen saturation sample waters. Autoresp computer software (Loligo Systems; Viborg,
191 Denmark) and a Witrox-4 instrument (Loligo Systems; Viborg, Denmark) were used to
192 continuously monitor dissolved oxygen and temperature within the chamber over the course of
193 the experiment.
194 For hypoxia experiments, intermittent respirometry was also used to avoid a CO_2 and
195 metabolite build up (Rodgers et al. 2016). Each respirometer flush pump was connected to an
196 external water bath that was filled with the same system water. Within the external water bath, a
197 pump (Eheim Universal 1200 l/h; Deizisau, Germany) connected to a piece of Tygon tubing held
198 an oxygen optode to monitor source O_2 and served as a mixing device. Also within the external
199 water bath, four small microdiffusers were connected to a N_2 gas canister (Schurmann and

200 Steffensen, 1997) to allow for diffusion of nitrogen gas into the external bath and subsequent
201 displacement of O_2 within the external water bath and control of environmental $\%O_2$ within the
202 chambers over the course of the hypoxia experiment.
203 Background respiration was measured by taking background MO_2 (MO_{2br}) pre- and post-
204 trial in empty chambers for ~1.5hr. A linear regression between pre- and post-MO_{2br} was used to
205 apply a correction factor to each MO_2 value recorded throughout an experiment.
206 Experiments were conducted at a range of temperatures (12, 17, 22, 24, 27 and 30°C). An
207 additional subset of black sea bass were held at 30°C for one month to test acclimation potential
208 (Table 1). We used two different methods in an attempt to elicit maximum metabolic rate
209 (MMR): exhaustive-chase and swim-flume. For the chase method, individual black sea bass
210 (Table 1) were placed in a 4ft-diameter chase tank filled with water from the experimental tanks.
211 Fish were chased via tactile stimulation on the caudal tail and were determined exhausted when
212 unresponsive to further tactile stimulation and air exposure. Fish were then immediately
213 transferred to individual respirometers that were sealed within ~1 min from the end of the chase
214 and remained in the metabolic chambers for ~23hr allowing for resting metabolic rate (RMR)
215 measurement (Chabot *et al.*, 2016b). Once the experiment was finished, fish were either
216 exercised in a swim-flume (Loligo Systems 90L; Viborg, Denmark) after a 24hr rest period or
217 remained in the chamber for the hypoxia experiments. For the swim-flume, fish were tested
218 using a sprint protocol. Swimming speed was increased over a 5min period up to 0.95 BL s^{-1} with
219 a flush pump on as the fish adjusted to the flume. After an adjustment time (~10 minutes), the
220 speed was increased over a period of 5 minutes until the fish was sprinting (designated as >10
221 tail bursts during 30s intervals and an inability to maintain position in the working section
222 without burst swimming). Once a fish was sprinting, the flush pump was turned off and the
223 flume was sealed. Fish were held at their sprint speed for at least 10 minutes or until failure,
224 determined when the fish rested at the backgrate for >10s. Aerobic scope was calculated in
225 absolute (AAS = MMR-RMR) and factorial terms (FAS = MMR/RMR). An additional subset of
226 black sea bass was held at 30°C for one month to test acclimation potential. In 2016, fish were
227 only tested at 24, 27, and 30°C due to restrictions in maintaining temperatures. See Table 1 for
228 sample size at each temperature.
229
230 *Critical $\%O_2$ determinations*

231 Hypoxia (S_{crit}) experiments were conducted on the last 4 fish of each temperature
232 treatment trial. This allowed us to reliably use fish that were already acclimated to the
233 respirometers and had reached RMR overnight. Starting with 100% dissolved oxygen (DO)
234 saturation within the chambers, environmental $\%O_2$ was incrementally decreased by 10%. Three
235 intermittent (flush, wait, measure) cycles were measured per DO level until S_{crit} was determined
236 to have been reached, indicated by a substantial decline in fish metabolic rate or loss of
237 equilibrium, and the experiment ended.
238
239 *Data Analysis*
240 Fish MO_2 was calculated via the AutoResp program from the slope of oxygen saturation
241 decline during each closed measurement period. Validation of each MO_2 value was conducted
242 using R_2 values from each measure period. MO_2 measurements with R_2 values < 0.9 were not
243 used.
244 We report our baseline metabolic rate as resting (RMR) instead of standard (SMR)
245 metabolic rate because the amount of time in the chamber was ~23 hours, which does not allow
246 for determination of full diel cycles (Chabot *et al.*, 2016b). RMR was calculated from a
247 truncated dataset without the first two hours of elevated MO_2 values following exercise and by
248 using the 20th quantile of the RMR data in the *calcSMR* package in R (Chabot *et al.*, 2016b).
249 Briefly, a frequency distribution of MO_2 values from the truncated data set was created and the
250 values at the 20th quantile were taken to calculate RMR. MMR in the chase protocol was defined
251 as the highest MO_2 value recorded during the trial and MMR was calculated for the duration of
252 the sprint interval in the swim-flume. AAS was taken as the difference between MMR and RMR.
253 There was a significant effect of mass on MO_2 ($F_{1,117} = 4.651$; $P < 0.05$; Fig. 1). Therefore, the
254 effect of temperature on MO_2 was analyzed using a one-way ANCOVA with weight as a
255 covariate. A Tukey's HSD *post hoc* was used to determine significant pair-wise comparisons
256 between temperatures. MO_2 was adjusted for weight using the estimated marginal means from
257 the ANCOVA centered around a fish mean weight of 346.9g. Because the average weight of fish
258 in the 24°C treatment (253.9g) was lower than the mean weight of all other experimental fish, the
259 adjusted MO_2 for 24°C was slightly overestimated and had larger standard error for AAS and
260 MMR. Curves for aerobic scope were modeled using a 3rd degree polynomial fit and were used

261 to estimate a thermal optimum (temperature at the highest AS). All graphs and results report the
262 adjusted MO_2 (MO_{2adj}).
263 Q_{10} values were calculated for the adjusted MO_2 between temperature increments, and
264 between the range of temperatures using the formula:

265 $$Q_{10} = \frac{R_2}{R_1}^{10/(T_2 - T_1)}$$

266 where Q_{10} is the temperature coefficient for MO_2, R_1 is the MO_2 at T_1 and R_2 is the MO_2 at T_2.
267 S_{crit} was determined by fitting two regression lines through the data: one through the region
268 where RMR was independent of $\%O_2$ and one through the portion where MO_2 decreased linearly
269 with a decrease in $\%O_2$. The intersection of the two regression lines is the critical point used for
270 S_{crit} (Yeager and Ultsch, 1989). This was analyzed using R code in the *calcO2crit* package from
271 Claireaux and Chabot (2016). Because we had a sample size of 4 fish per temperature trial, a
272 power analysis was run to determine the statistical power of this small sample size and four fish
273 provided enough statistical power (*Power* = 1, $n = 4$, $f = 1.71$, *sig. level* = 0.05). A one-way
274 ANOVA was used to assess the effect of temperature on S_{crit} and a Tukey's HSD *post hoc* test
275 was used to determine significant pair-wise comparisons between temperatures.
276 All statistical analyses were performed in R (Version 3.4.1). Data were checked for
277 assumptions of normality by the visual Q-Q norm plot and statistically with the Shapiro-Wilk
278 test where $P > 0.05$ indicate normally distributed data. Assumptions of homogeneity were
279 assessed using the Levene's test where a $P > 0.05$ indicates homogeneity. Data that did not fit
280 assumptions of normality were log-transformed prior to further statistical analysis. Data are
281 presented as mean ± SE and results from statistical analyses are defined as significant at $P <$
282 0.05.
283
284 **Results**
285 *Metabolic rates and aerobic scope*
286 RMR increased significantly with temperature (Figs 2a and 2b) and there was a
287 significant effect of weight and temperature*weight interaction on RMR ($P < 0.05$; Table 2).
288 While the results for the two MMR methods differed considerably, temperature, weight and
289 temperature*weight interaction all had a significant effect on MMR using either method ($P <$
290 0.05; Table 2). The chase MMR increased continuously with temperature, while flume MMR

291 increased with temperature until ~22°C (Fig 2a & 2b). The MMR values from the flume were
292 consistently higher across the temperature range than from the chase method, indicating that the
293 metabolic rate reached during the chase likely was not the maximum possible for this species.
294 While the chase method did not achieve MMR, it still provided an estimate of
295 submaximal exercise performance across a temperature range. The MMR using the chase
296 method increased continuously with temperature and reached a maximum adjusted value of
297 396.65±11.48 mg O_2 kg^{-1} hr^{-1}at 30.0°C (the highest temperature measured; Table 3; Fig 1a).
298 The MMR measured using the flume reached a maximum of 497.96±21.92 mgO_2 kg^{-1} hr^{-1} at
299 27°C (Table 3; Fig 1b). The absolute aerobic scope using the flume method reached a
300 maximum, typically referred to as "T_{opt}" at ~24.4°C (Fig. 2B). There was a significant effect of
301 temperature, weight, and the temperature*weight interaction on AAS ($P < 0.05$) using both
302 MMR methods (Table 2). Using different MMR methods resulted in differences in the shape of
303 the AAS curve and the estimated thermal optimum with consequences for its interpretation. All
304 RMR, MMR and AAS values are reported in Table 3 and Q_{10} values are reported in Table 4.
305
306 *Critical %O_2*
307 The critical %O_2 (S_{crit}) increased significantly with increasing temperature (Fig 4a; $F_{5,18}$ =
308 14.023, $P < 0.05$), directly correlated with RMR (Fig 4b). There was no significant difference
309 between 12˚C (19.65 ± 1.72 %O_2), 17˚C (21.325 ± 1.75 %O_2) and 22˚C (21.80 ± 1.21 %O_2), but
310 S_{crit} increased significantly at 27˚C (31.60 ± 1.67 %O_2) and further at 30˚C (37.875 ± 3.39 %O_2).
311 However, non-significance between 12, 17 and 22°C could be due to low sample size.
312
313 *Chronic high temperature exposure*
314 The $30_{chronic}$°C group AAS using both MMR methods significantly decreased when
315 compared to the 30°C treatment where fish were only held at this temperature for a week. Based
316 on Tukey *post hoc* differences, RMR did not change significantly between the $30_{chronic}$°C and
317 30°C treatments but there was a significant decrease in MMR between the 30°C and $30_{chronic}$°C
318 treatments. There was no significant difference in S_{crit} between 30°C and $30_{chronic}$°C treatments.
319
320 **Discussion**

321 The primary objective of this study was to assess the use of physiological measurements
322 to determine habitat suitability for the northern stock of black sea bass at current and future
323 temperatures. We measured the oxygen consumption rate during two different exercise
324 protocols. The flume yielded much higher metabolic rates, indicating that the chase method did
325 not elicit MMR. Using the flume MMR, we found that AAS peaked at 24.4°C. S_{crit} increased
326 with increasing temperatures as is typical of most (but not all, Wishner et al., 2018) animals,
327 including fishes (Rogers et al. 2016). Chronic exposure to 30°C resulted in a significant drop in
328 AAS with no change in RMR or S_{crit}. That S_{crit} increased with temperature in proportion to RMR,
329 while MMR in the flume did not, suggests that chronic exposure to high temperature did not alter
330 the capacity for oxygen uptake and transport, but that the capacity to generate ATP was reduced,
331 perhaps due to a decrement in muscle function. The capacity for submaximal exercise (oxygen
332 consumption following a chase to exhaustion) also increased across the entire temperature range
333 further suggesting that the failure was not in the capacity for oxygen supply. Chronic exposure
334 to 30°C led to further reductions in MMR using both methods, but no loss of oxygen supply
335 capacity as estimated from S_{crit}, suggesting continued deterioration in muscle function with
336 longer exposure to warm temperatures.
337 Absolute AS typically increases with temperature up to a point, often termed "optimal",
338 and then declines at higher temperatures resulting in a roughly bell-shaped curve as has been
339 identified in fishes that include, but is not limited to, juvenile European sea bass *Dicentrarchus*
340 *labrax* (Claireaux *et al.*, 2006), turbot *Scophthalmus maximus* (Mallekh and Lagardere, 2002),
341 coho salmon *Oncorhynchus kisutch* (Raby *et al.*, 2016), and sockeye salmon *Oncorhynchus*
342 *nerka* (Farrell *et al.*, 2008). However, some studies have found left- or right-skewed curves (e.g.
343 Healy and Schulte 2012) while others find that AAS continues to increase up to the critical
344 temperature for the species (i.e. no temperature optimum for AAS is identifiable; e.g. Norin *et al.*
345 2014). In our study, the black sea bass AAS curve was more bell-shaped with an estimated
346 optimal temperature of 24.4°C. Bottom temperature in the southern portion of the black sea bass
347 range typically hovers around 24-26°C during the summer (Houghton *et al.* 1982; Castelao *et al.*
348 2008; from U.S. East Coast Regional ESPreSSO model, Wilkin and Hunter 2013), which would
349 suggest this area to be thermally optimal. However, if the loss in AAS at higher temperatures is
350 due to a failure in muscular performance rather than potential oxygen supply, then 24°C may
351 represent a maximum tolerable temperature rather than a temperature that allows optimal

352 performance. In support of this interpretation, the Metabolic Index (which closely matches the
353 factorial aerobic scope) declines with increasing temperature toward levels (~3 at 27°C in black
354 sea bass) known to limit the geographic range of some species (Deutsch et al., 2015). While the
355 average bottom temperature in the southern portion of the northern stock of black sea bass is near
356 24°C during the summer months, there has still been a consistent expansion of their range
357 northward into lower temperatures (NEFSC 2017) further suggesting that the temperature
358 eliciting maximum AAS is not, in fact, optimal. It is important to note that AAS is only a
359 measured capacity to supply oxygen under maximum sustained exercise (Farrell, 2016). The
360 required scope for other metabolic expenses (i.e. feeding, digestion; Holt and Jørgensen, 2015)
361 change with temperature in unknown ways and metabolic needs can change seasonally and with
362 ontogeny (Clark *et al.*, 2013). Thus, AAS may in this case be an inappropriate predictor of
363 fitness.

364 Black sea bass in the $30_{chronic}$°C treatment did not acclimate, indicated by no change in
365 RMR or S_{crit} and a significant decrease in their MMR and AS. Norin et al. (2014) similarly found
366 that MMR and AAS in juvenile barramundi decreased significantly following 5 weeks at the
367 highest study temperature (38°C). However, unlike black sea bass in our study, the juvenile
368 barramundi RMR also decreased after the 5-week exposure. This same response has also been
369 found for short-horn sculpin (*Myoxocephalus scorpius*) whose RMR was restored after being
370 held at 16°C for 8 weeks to RMR values that were measured at 10°C (Sandblom *et al.*, 2014).
371 The decrease in RMR can be an acclimation response to lower their energetic costs at high
372 temperatures, but comes with its own caveats as this sometimes can reduce MMR. Importantly,
373 black sea bass in the $30_{chronic}$°C treatment may have suffered stress from long-term captivity,
374 which could also reduce AAS and time did not permit for a control chronic trial at a cooler
375 temperature (although all fish were held for at least 5 days). Understanding the acclimation
376 potential of black sea bass would benefit from future studies focusing on effects of a chronic
377 treatment at each temperature tested.

378 S_{crit} decreased as temperature increased, most likely caused by rising RMR with higher
379 temperatures, which has been shown in a majority of fish hypoxia studies (e.g. Schurmann and
380 Steffensen, 1997; although see Wishner et al., 2018). The $30_{chronic}$˚C group did not have a
381 significant decrease in hypoxia tolerance compared to the 30˚C group, which agrees with no
382 change in RMR between the two 30˚C treatments. This suggests that the reduced MMR in

383 $30_{chronic}$°C animals resulted from reduced capacity to generate ATP, rather than to supply
384 oxygen. Black sea bass had lower S_{crit} than striped bass *Morone saxatilis* (Lapointe *et al.*, 2014)
385 and summer flounder *Paralichthys dentatus* (Capossela *et al.*, 2012), two important species
386 found throughout the MAB that periodically experience hypoxic water during the summer
387 months. However, when compared with fish that frequently experience hypoxia, such as
388 largemouth bass and crucian carp (Yamanaka *et al.*, 2007) and juvenile barramundi (Collins *et*
389 *al.*, 2013), black sea bass were less hypoxia tolerant, especially in warmer water. Deutsch et al.
390 (2015) proposed a metabolic index (MI), as the ratio of oxygen supply to demand, which is
391 effectively an estimate of a species' time-averaged aerobic scope. By definition, the MI is equal
392 to 1 at the S_{crit}. A minimum MI of 2-5, indicating the capacity to supply oxygen at 2-5x the rate
393 required at rest, is supportive of a population and delineates the equatorward distribution limit in
394 the few species studied to date. Black sea bass factorial AS and MI both decreased with
395 increasing temperature (Fig. 6). During the summer months when bottom water temperature is
396 warmest along the coastal MAB, periodic hypoxic events occur after large phytoplankton blooms
397 in the surface waters. In the past, these hypoxic events decreased bottom water PO_2 below
398 ~5.5kPa (26% saturation; 2.2 mg L^{-1} at 14°C Schofield et al. 2012), providing a metabolic index
399 of ~1.3 at those temperatures for black sea bass. Such environments can be tolerated for short
400 periods but are not likely supportive of a thriving population. At 30°C, even air-saturated water
401 provides a MI of only 2.6 which is near the physiological limits of many species (Deutsch *et al.*,
402 2015). Therefore, when determining the suitable habitat, both temperature and oxygen must be
403 taken into consideration as the interacting effects of these variables will effectively decrease
404 optimal thermal habitat.
405 The chase method did not elicit MMR in black sea bass since MMR from the flume
406 method was consistently higher. Which method, chase or flume, provides a more reliable
407 measure of MMR and AAS is actively debated (Norin and Clark, 2016; Killen *et al.*, 2017).
408 Whether a maximum rate of oxygen uptake is achieved by either method could depend on the
409 type of swimming the study fish species naturally exhibits in the wild. Norin et al (2014)
410 purposefully used a chase method for juvenile barramundi (*Lates calcarifer*), an ambush
411 predator, that typically swims in quick bursts. In other cases, a fish will exhibit marked post-
412 exercise oxygen consumption (EPOC; Plambech *et al.*, 2013), sometimes eliciting MMR minutes
413 to hours after the cessation of exercise (Reidy *et al.*, 1995). The swim flume method may be

414 more appropriate for endurance swimming exhibited by pelagic fish such as tunas (Killen *et al.*,
415 2017). Different MMR methods may promote a certain type of swimming which could exhaust a
416 fish before reaching MMR by depleting anaerobic stores, a noteworthy contributor to AAS
417 (Ejbye-Ernst *et al.*, 2016). For this study, we employed a sprint protocol for the swim-flume,
418 which prompted similar burst swimming as in the chase method. However, during the chase
419 protocol, black sea bass switched almost immediately to burst swimming accompanied with
420 quick turning/flipping movements, compared to a slower transition and continuously straight
421 burst swimming in the swim flume. The differences in MMR between the two methods could
422 have been related to different swimming types, durations and/or speeds which could recruit more
423 anaerobic resources (Svendsen *et al.*, 2010) in the chase method, leading to exhaustion before
424 reaching MMR.
425 In summary, the results from this study indicate that the northern stock of black sea bass
426 reach a peak in AAS at ~24°C, which is warmer than in the northern portion of their range in the
427 U.S. NES. The MI of 3.8 in air-saturated water, calculated from S_{crit} at 24°C, suggests relatively
428 limited scope for sustained activity at that temperature (Deutsch *et al.*, 2015). We suggest that,
429 rather than an optimal temperature, the peak in MMR and AAS indicates the maximum tolerable
430 temperature, beyond which black sea bass experience a failure in some subcellular or organ
431 systems that contribute to muscle performance. Our study only used individuals from the
432 northern stock that were collected during the summer off of the New Jersey coastline. Metabolic
433 research on the southern stock (south of Cape Hatteras, NC) and/or individuals from the northern
434 stock in waters outside of New Jersey could reveal variation in some of these physiological
435 metrics. However, the distribution of the northern stock of black sea bass has shifted northward
436 (Kleisner *et al.*, 2017) and this newly expanded habitat is almost 10°C colder than their apparent
437 thermal optimum for AAS. We believe the preference for cooler waters reflects physiological
438 limitation at higher temperatures, including possible limitation of oxygen supply relative to
439 demand for growth and reproduction (reduced Metabolic Index) despite maintenance of oxygen
440 supply capacity. However, many other factors, including food availability, additional energetic
441 costs (e.g., evading predators, mating), or lower optimal temperatures for other critical processes
442 may be important. This suggests AAS may not be the most appropriate predictor for habitat
443 suitability in this species. Additionally, the northern stock of black sea bass population size has
444 been increasing in the last decade (NEFSC 2017), and this increase in biomass could be pushing

part of the population northward. Regardless, the chronic exposure experiments presented here suggest little capacity for physiological adjustment to future temperatures. Black sea bass thermal habitat may shrink considerably in the southern region of the MAB as bottom water temperatures reach >27°C and continue to expand into the northern region of the MAB as ocean waters continue to warm, significantly impacting fisheries in these two regions.

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Competing Interests

The authors declare no competing interests.

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List of Abbreviations

AAS	Absolute aerobic scope
FAS	Factorial aerobic scope
MO_2	Oxygen consumption rate
MO_{2adj}	Adjusted oxygen consumption rate
MO_{2br}	Background oxygen consumption rate
MMR	Maximum metabolic rate
RMR	Resting metabolic rate
S_{crit}	Critical oxygen saturation
SMR	Standard metabolic rate
$\%O_2$	Oxygen saturation

Tables

Table 1. Number of black sea bass used in both the chase and flume MMR trials at each temperature.

Temperature (°C)	**Sample Sizes**	
	Chase MMR	*Flume MMR*
12	16	10
17	16	12
22	16	12
24	17	0
27	30	12
30	17	10
$30_{chronic}$	9	4

482 Table 2. ANCOVA results for AS, MMR (both methods) and RMR. Bolded *P*-values are
483 significant.
484

Variable	**Effect**	**DF**	***F*-value**	***P*-value**
AAS (chase)	Temperature Weight Temperature*weight	6, 105 1, 105 6, 105	13.877 2.082 2.106	**< 0.001** > 0.05 0.0586
AAS(flume)	Temperature Weight Temperature*weight	5, 48 1, 48 5, 48	6.185 6.599 4.033	**< 0.001** **< 0.05** **< 0.01**
MMR (chase)	Temperature Weight Temperature*weight	6, 105 1, 105 6, 105	50.327 9.267 2.281	**< 0.001** **< 0.01** **< 0.05**
MMR (flume)	Temperature Weight Temperature*weight	5, 48 1, 48 5, 48	16.244 8.927 3.147	**< 0.001** **< 0.01** **< 0.05**
RMR	Temperature Weight Temperature*weight	6, 105 1, 105 6, 105	136.613 12.282 2.489	**< 0.001** **< 0.001** **< 0.05**

485

Table 3. The MO_{2adj} mean ± S.E. values for RMR, MMR (both methods), AS (both methods) and S_{crit} for each temperature treatment. * = the adjusted MO_2 values for MMR and AAS at 24°C are overestimated due to the average weight of fish in the 24°C group to be smaller than the average weight for all study fish combined.

Temperature (°C)	RMR	Chase MMR	Flume MMR	Chase AS	Flume AS	S_{crit} (% O_2 saturation)
12	46.44±1.94	169.12±11.78	286.57±24.02	117.67±7.55	242.67±24.24	19.65
17	65.27±3.27	215.05±14.15	369.27±24.47	143.63±11.07	303.55±24.70	21.33
22	95.69±4.51	266.03±13.32	462.30±22.01	167.18±12.13	363.73±22.21	21.80
24	106.61±11.03	342.06±29.20*	NA	230.39±36.65*	NA	NA
27	140.55±4.48	357.44±8.99	497.96±21.92	208.96±10.24	351.65±22.12	31.60
30	173.36±7.05	396.65±11.48	479.88±25.29	213.20±13.33	310.20±25.52	37.88
$30_{chronic}$	163.14±9.28	306.62±16.06	356.82±53.05	136.03±11.90	198.33±53.54	38.63

Table 4. Q_{10} values for AS, MMR (both methods) and RMR separated between each temperature increment. * = the slightly overestimated adjusted MO_2 for the 24°C fish is reflected in calculated Q_{10} values.

	12-17°C	17-22°C	22-24°C	22-27°C	24-27°C	27-30°C	27-30$_C$°C
AS_{chase}	1.49	1.35	4.97*	1.56	0.72*	1.07	0.24
AS_{flume}	1.56	1.44	NA	0.93	NA	0.66	0.15
MMR_{chase}	1.62	1.53	3.51*	1.81	1.16*	1.41	0.60
MMR_{flume}	1.66	1.58	NA	1.16	NA	0.88	0.33
RMR	1.96	2.15	1.72	2.16	2.51	2.01	1.64

Figures

Figure Captions

Figure 1. Temperature and body weight both affect resting metabolic rate in black sea bass. RMR (n=121) for each temperature treatment is plotted against body weight (g). A fitted regression line demonstrates that in addition to the effect of temperature on RMR, body weight also has an effect ($P<0.05$). 30c = $30_{chronic}$°C treatment.

Figure 2A and 2B. Effect of temperature on resting metabolic rate and maximum metabolic rate measured with a chase and a flume method. MMR (solid circles) and RMR (open circles) presented as mean ± s.e. normalized to a mean weight of 350g for each temperature treatment for chase method MMR (A) and flume method MMR (B). RMR is slightly different between (A) and (B) based on which fish were used for the respective MMR method. The $30_{chronic}$°C group is denoted by triangles. Tukey *post hoc* significance between treatments is shown by letters where data points with different letters indicate a significant difference ($P<0.05$). **2A**: n=9 for $30_{chronic}$°C ; n=16 for 12, 17, and 22°C; n=17 for 24 and 30°C; n=30 for 27°C. **2B**: n=4 for $30_{chronic}$°C; n=10 for 12 and 30°C; n=12 for 17, 22, and 27°C.

Figure 3a and 3b. Effect of temperature on black sea bass aerobic scope. Aerobic scope (mean ± s.e.) of black sea bass normalized around a mean weight of 350g at each temperature treatment with the 30°C chronic group denoted by the black triangle. Letters indicate Tukey *post hoc* significance between groups where data points sharing a letter are not significantly different ($P<0.05$). Aerobic scope curves were generated from a) the chase MMR treatment ($y = 180.17 + 89.15x - 15.40x^2 - 21.55x^3$; $R^2 = 0.878$) and b) flume MMR treatment ($y = 314.36 + 63.29x - 68.26x^2 - 19.65x^3$; $R^2 = 0.994$). **3A**: n=9 for $30_{chronic}$°C ; n=16 for 12, 17, and 22°C; n=17 for 24 and 30°C; n=30 for 27°C. **3B**: n=4 for $30_{chronic}$°C; n=10 for 12 and 30°C; n=12 for 17, 22, and 27°C.

Figure 4. S_{crit} increases with increasing temperature. S_{crit} presented as $\%O_2$ air saturation for each temperature treatment. $30_{chronic}$°C treatment is denoted by a triangle and there is no significant difference between the $30_{chronic}$°C and acute 30°C treatments. A linear-regression was fitted for these data points ($R_2 = 0.793$, $P<0.001$) showing an increase in S_{crit} (e.g. a decrease in hypoxia tolerance) with increasing temperature.

Figure 5. S_{crit} dependence on resting metabolic rate. S_{crit} is plotted against resting metabolic rate measured during the hypoxia experiment. A linear-regression was fitted for these data points ($R_2 = 0.823$, $P<0.001$) and shows an increase in S_{crit} as metabolic rates also rise.

Figure 6. Factorial aerobic scope and metabolic index response to temperature. Factorial aerobic scope (FAS) and metabolic index (MI) plotted against temperature. Trends illustrate a decreasing trend in both measures as temperature increases. Both FAS and MI are unitless measures, but both measures scale similarly.

Figures

Figure 1.

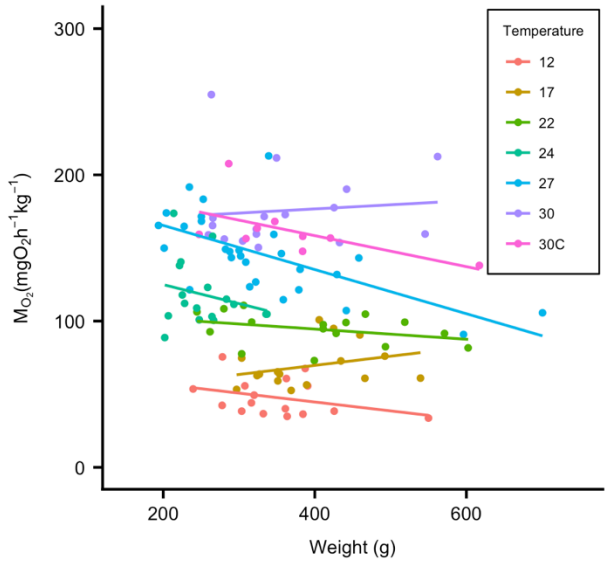


Figure 2.

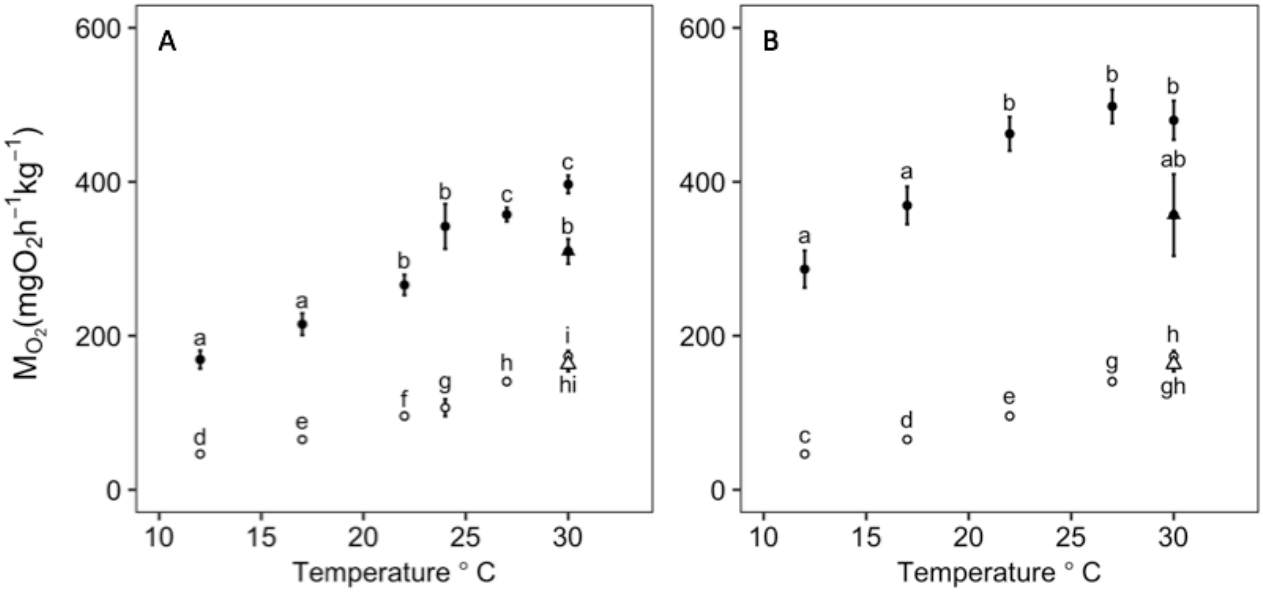
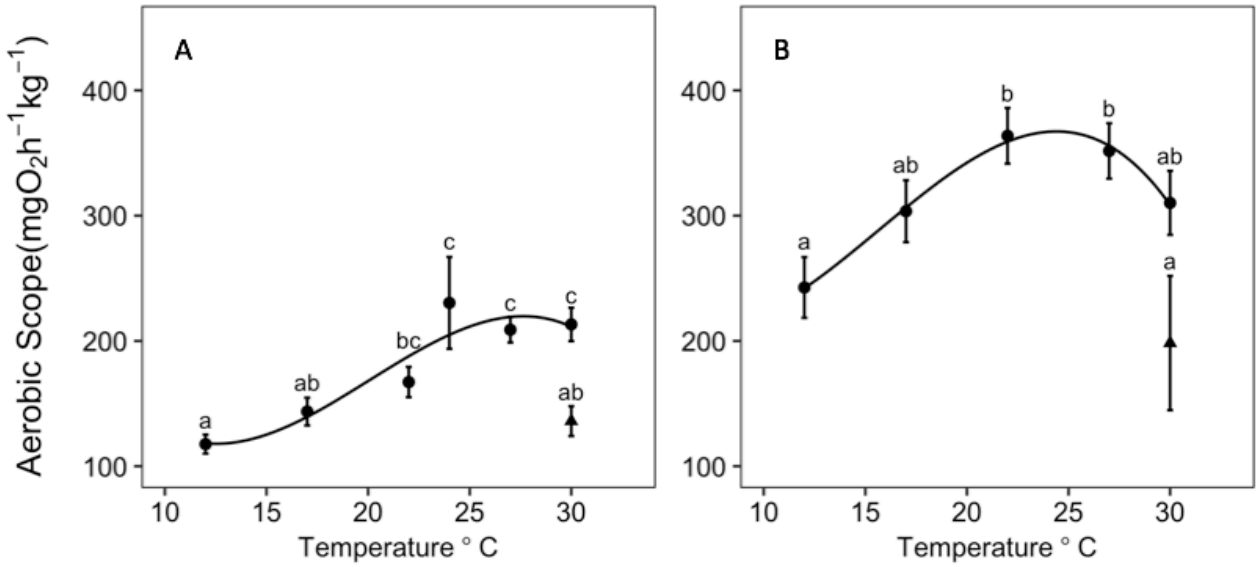


Figure 3



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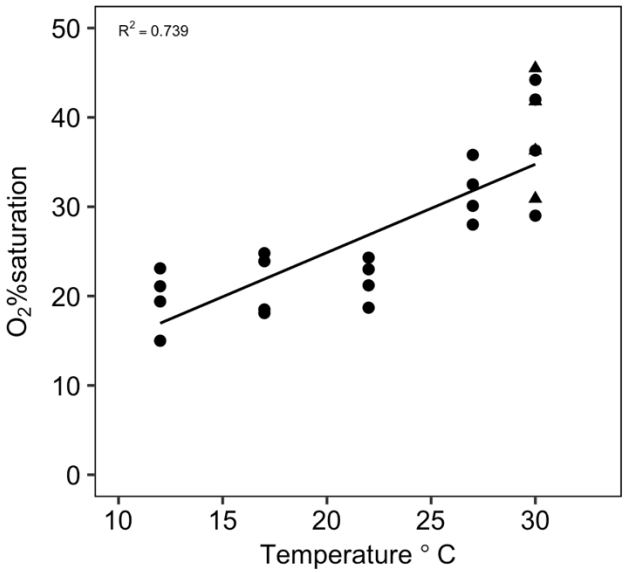


Figure 5

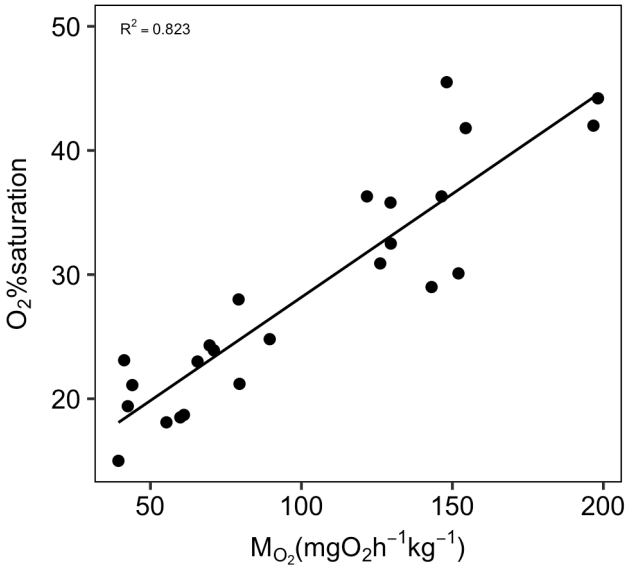
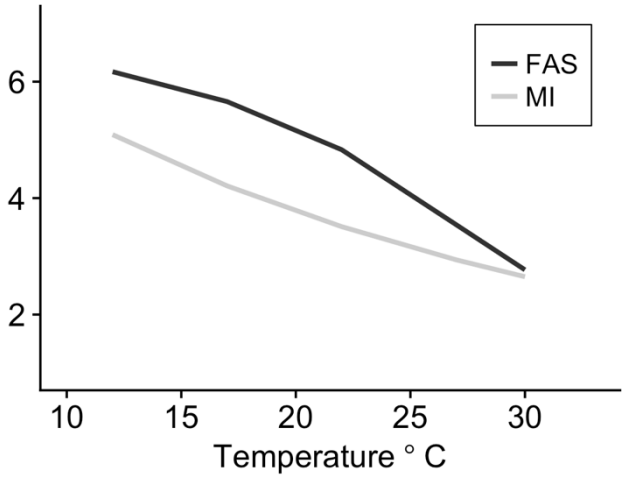


Figure 6



References

Belkin, I. M. 2009. Rapid warming of Large Marine Ecosystems. Progress in Oceanography, 81: 207–213.

Bell, R. J., Richardson, D. E., Hare, J. A., Lynch, P. D., and Fratantoni, P. S. 2015. Disentangling the effects of climate, abundance, and size on the distriubtion of marine fish: an example based on four stocks from the Northeast US shelf. ICES Journal of Marine Science, 72: 1311–1322.

Caesar, L., Rahmstorf, S., Robinson, A., Feulner, G., and Saba, V. 2018. Observed fingerprint of a weakening Atlantic Ocean overturning circulation. Nature, 556: 191–196.

Capossela, K. M., Brill, R. W., Fabrizio, M. C., and Bushnell, P. G. 2012. Metabolic and cardiorespiratory responses of summer flounder *Paralichthys dentatus* to hypoxia at two temperatures. Journal of Fish Biology, 81: 1043–1058.

Castelao, R., Glenn, S., Schofield, O., Chant, R., Wilkin, J., and Kohut, J. 2008. Seasonal evolution of hydrographic fields in the central Middle Atlantic Bight from glider observations. Geophysical Research Letters, 35: 6–11.

Chabot, D., McKenzie, D. J., and Craig, J. F. 2016a. Metabolic rate in fishes: definitions, methods and significance for conservation physiology. Journal of Fish Biology, 88: 1–9.

Chabot, D., Steffensen, J. F., and Farrell, A. P. 2016b. The determination of standard metabolic rate in fishes. Journal of Fish Biology, 88: 81–121.

Claireaux, G., Couturier, C., and Groison, A. 2006. Effect of temperature on maximum swimming speed and cost of transport in juvenile European sea bass (*Dicentrarchus labrax*). Journal of Experimental Biology, 209: 3420–3428.

Claireaux, G., and Chabot, D. 2016. Responses by fishes to environmental hypoxia: integration through Fry's concept of aerobic metabolic scope. Journal of Fish Biology, 88: 232–251.

Clark, T. D., Sandblom, E., and Jutfelt, F. 2013. Aerobic scope measurements of fishes in an era of climate change: respirometry, relevance and recommendations. Journal of Experimental Biology, 216: 2771–2782.

Clarke, A., and Johnston, N. 1999. Scaling of metabolic rate with body mass and temperature in teleost fish. Journal of Animal Ecology, 68: 893–905.

Collins, G. M., Clark, T. D., Rummer, J. L., and Carton, A. G. 2013. Hypoxia tolerance is conserved across genetically distinct sub-populations of an iconic, tropical Australian teleost (*Lates calcarifer*). Conservation Physiology, 1: doi:10.1093/conphys/cot29.

Del Toro-Silva, F. M., Miller, J. M., Taylor, J. C., and Ellis, T. A. 2008. Influence of oxygen and temperature on growth and metabolic performance of *Paralichthys lethostigma* (Pleuronectiformes: Paralichthyidae). Journal of Experimental Marine Biology and Ecology, 358: 113–123.

Deutsch, C., Ferrel, A., Seibel, B., Pörtner, H. O., and Huey, R. B. 2015. Climate change tightens a metabolic constraint on marine habitats. Science, 348: 1132–1136.

Ejbye-Ernst, R., Michaelsen, T. Y., Tirsgaard, B., Wilson, J. M., Jensen, L. F., Steffensen, J. F., Pertoldi, C., *et al.* 2016. Partitioning the metabolic scope: The importance of anaerobic metabolism and implications for the oxygen- and capacity-limited thermal tolerance (OCLTT) hypothesis. Conservation Physiology, 4: 1–13.

Fabrizio, M. C., Manderson, J. P., and Pessutti, J. P. 2013. Habitat associations and dispersal of black sea bass from a mid-Atlantic Bight reef. Marine Ecology Progress Series, 482: 241–253.

Farrell, A. P., Hinch, S. G., Cooke, S. J., Patterson, D. A., Crossin, G. T., Lapointe, M., and

Mathes, M. T. 2008. Pacific salmon in hot water: applying aerobic scope models and biotelemetry to predict the success of spawning migrations. Physiological and Biochemical Zoology, 81: 697–709.

Farrell, A. P. 2016. Pragmatic perspective on aerobic scope: peaking, plummeting, pejus and apportioning. Journal of Fish Biology, 88: 322–343.

Friedland, K. D., and Hare, J. A. 2007. Long-term trends and regime shifts in sea surface temperature on the continental shelf of the northeast United States. Continental Shelf Research, 27: 2313–2328.

Glenn, S., Arnone, R., Bergmann, T., Bissett, W. P., Crowley, M., Cullen, J., Gryzmski, J., *et al.* 2004. Biogeochemical impact of summertime coastal upwelling on the New Jersey Shelf. Journal of Geophysical Research C: Oceans, 109: 1–15.

Hare, J. A., Morrison, W. E., Nelson, M. W., Stachura, M. M., Teeters, E. J., Griffis, R. B., Alexander, M. A., *et al.* 2016. A vulnerability assessment of fish and invertebrates to climate change on the northeast u.s. continental shelf. PLoS ONE, 11: e0146756.

Healy, T. M., and Schulte, P. M. 2012. Thermal acclimation is not necessary to maintain a wide thermal breadth of aerobic scope in the common killifish (*Fundulus heteroclitus*). Physiological and Biochemical Zoology, 85: 107–119.

Holt, R. E., and Jørgensen, C. 2015. Climate change in fish: effects of respiratory constraints on optimal life history and behaviour. Biology Letters, 11: 20141032.

Houghton, R. W., Schlitz, R., Beardsley, R. C., Butman, B., and Chamberlin, J. L. 1982. The Middle Atlantic Bight Cold Pool: Evolution of the Temperature Structure During Summer 1979. Journal of Physical Oceanography, 12: 1019–1029.

Kavanaugh, M. T., Rheuban, J. E., Luis, K. M. A., and Doney, S. C. 2017. Thirty-three years of ocean benthic warming along the U.S. Northeast Continental shelf and slope: patterns, drivers, and ecological consequences. Journal of Geophysical Research: Oceans: 1–16.

Killen, S. S., Norin, T., and Halsey, L. G. 2017. Do method and species lifestyle affect measures of maximum metabolic rate in fishes? Journal of Fish Biology, 90: 1037–1046.

Kleisner, K. M., Fogarty, M. J., McGee, S., Barnett, A., Fratantoni, P., Greene, J., Hare, J. A., *et al.* 2016. The effects of sub-regional climate velocity on the distribution and spatial extent of marine species assemblages. PLoS ONE, 11: 1–21.

Kleisner, K. M., Fogarty, M. J., McGee, S., Hare, J. A., Moret, S., Perretti, C. T., and Saba, V. S. 2017. Marine species distribution shifts on the U.S. Northeast Continental Shelf under continued ocean warming. Progress in Oceanography, 153: 24–36.

Lapointe, D., Vogelbein, W. K., Fabrizio, M. C., Gauthier, D. T., and Brill, R. W. 2014. Temperature, hypoxia, and mycobacteriosis: effects on adult striped bass *Morone saxatilis* metabolic performance. Diseases of Aquatic Organisms, 108: 113–127.

Lefevre, S., McKenzie, D. J., and Nilsson, G. E. 2017. Models projecting the fate of fish populations under climate change need to be based on valid physiological mechanisms. Global Change Biology, 23: 3449–3459.

Mallekh, R., and Lagardère, J. P. 2002. Effect of temperature and dissolved oxygen concentration on the metabolic rate of the turbot and the relationship between metabolic scope and feeding demand. Journal of Fish Biology, 60: 1105–1115.

Manderson, J., Palamara, L., Kohut, J., and Oliver, M. J. 2011. Ocean observatory data is useful for regional habitat modeling of species with different vertical habitat preferences. Marine Ecology Progress Series, 438: 1–17.

McDonnell, L. H., and Chapman, L. J. 2015. At the edge of the thermal window: effects of

elevated temperature on the resting metabolism, hypoxia tolerance and upper critical thermal limit of a widespread African cichlid. Conservation Physiology, 3: 1–13.

Morley, J. W., Selden, R. L., Latour, R. J., Frölicher, T. L., Seagraves, R. J., and Pinsky, M. L. 2018. Projecting shifts in thermal habitat for 686 species on the North American continental shelf. PLoS ONE, 13: 1–28.

Moser, J., and Shepherd, G. R. 2008. Seasonal distribution and movement of black sea bass (*Centropristis striata*) in the Northwest Atlantic as determined from a mark-recapture experiment. Journal of Northwest Atlantic Fishery Science, 40: 17–28.

Musick, J. A., and Mercer, L. P. 1977. Seasonal distribution of Black Sea Bass, *Centropristis striata*, in the Mid-Atlantic Bight with comments on ecology and fisheries of the species. Trans. Amer. Fish. Soc., 106: 12–25.

NEFSC. 2017. The 62nd northeast regional stock assessment workshop (62nd SAW). Ref. Doc. 17-03, NEFSC, Woods Hole, MA.

Nilsson, G. E., and Renshaw, G. M. C. 2004. Hypoxic survival strategies in two fishes: extreme anoxia tolerance in the North European crucian carp and natural hypoxic preconditioning in a coral-reef shark. The Journal of Experimental Biology, 207: 3131–3139.

Norin, T., Malte, H., and Clark, T. D. 2014. Aerobic scope does not predict the performance of a tropical eurythermal fish at elevated temperatures. The Journal of Experimental Biology, 217: 244–251.

Norin, T., and Clark, T. D. 2016. Measurement and relevance of maximum metabolic rate in fishes. Journal of Fish Biology, 88: 122–151.

Nye, J. A., Link, J. S., Hare, J. A., and Overholtz, W. J. 2009. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. Marine Ecology Progress Series, 393: 111–129.

Pershing, A. J., Alexander, M. A., Hernandez, C. M., Kerr, L. A., Le Bris, A., Mills, K. E., Nye, J. A., *et al.* 2015. Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. Science, 350: 809–812.

Pinsky, M. L., Worm, B., Fogarty, M. J., Sarmiento, J. L., and Levin, S. A. 2013. Marine taxa track local climate velocities. Science, 341: 1239–1242.

Pinsky, M. L., Reygondeau, G., Caddell, R., Palacios-Abrantes, J., Spijkers, J., and Cheung, W. W. L. 2018. Preparing ocean governance for species on the move. Science, 360: 1189–1192.

Plambech, M., Van Deurs, M., Steffensen, J. F., Tirsgaard, B., and Behrens, J. W. 2013. Excess post-hypoxic oxygen consumption in Atlantic cod *Gadus morhua*. Journal of Fish Biology, 83: 396–403.

Pörtner, H. O., and Knust, R. 2007. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. Science, 315: 95–97.

Pörtner, H. O., and Farrell, A. P. 2008. Physiology and climate change. Science, 322: 690–692.

Pörtner, H. O. 2010. Oxygen- and capacity-limitation of thermal tolerance: a matrix for integrating climate-related stressor effects in marine ecosystems. Journal of Experimental Biology, 213: 881–893.

Pörtner, H. O., and Peck, M. A. 2010. Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. Journal of Fish Biology, 77: 1745–1779.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Raby, G. D., Casselman, M. T., Cooke, S. J., Hinch, S. G., Farrell, A. P., and Clark, T. D. 2016.

Aerobic scope increases throughout an ecologically relevant temperature range in coho salmon. The Journal of Experimental Biology, 219: 1922–1931.

Reidy, S. P., Nelson, J. A., Tang, Y., and Kerr, S. R. 1995. Post-exercise metabolic rate in Atlantic cod and its dependence upon the methos of exhaustion. Journal of Fish Biology, 47: 377–386.

Rodgers, G. G., Tenzing, P., and Clark, T. D. 2016. Experimental methods in aquatic respirometry: the importance of mixing devices and accounting for background respiration. Journal of Fish Biology, 88: 65–80.

Rogers, N. J., Urbina, M. A., Reardon, E. E., Mckenzie, D. J., and Wilson, R. W. 2016. A new analysis of hypoxia tolerance in fishes using a database of critical oxygen level (P_{crit}). Conservation Physiology, 4: cow012.

Roy, E. M., Quattro, J. M., and Greig, T. W. 2012. Genetic management of black sea bass: influence of biogeographic barriers on population structure. Marine and Coastal Fisheries, 4: 391–402.

Saba, V. S., Griffies, S. M., Anderson, W. G., Winton, M., Alexander, M. A., Delworth, T. L., Hare, J. A., *et al.* 2016. Enhanced warming of the Northwest Atlantic Ocean under climate change. Journal of Geophysical Research: Oceans, 120: 1–15.

Sandblom, E., Gräns, A., Axelsson, M., and Seth, H. 2014. Temperature acclimation rate of aerobic scope and feeding metabolism in fishes: implications in a thermally extreme future. Proceedings of Royal Society of Biology, 281: 20141490.

Schofield, O., Roarty, H., Saba, G. K., Xu, Y., Kohut, J., Glenn, S., Manderson, J., *et al.* 2012. Phytoplankton dynamics and bottom water oxygen during a large bloom in the summer of 2011. Oceans, 2012, IEEE: 1–6.

Schulte, P. M. 2015. The effects of temperature on aerobic metabolism: towards a mechanistic understanding of the responses of ectotherms to a changing environment. The Journal of Experimental Biology, 218: 1856–1866.

Schurmann, H., and Steffensen, J. F. 1997. Effects of temperature, hypoxia and activity on the metabolism of juvenile Atlantic cod. Journal of Fish Biology, 50: 1166–1180.

Seibel, B. 2011. Critical oxygen levels and metabolic supression in oceanic oxygen minimum zones. The Journal of Experimental Biology, 214: 326-336.

Steimle, F., Zetlin, C., Berrien, P., and Chang, S. 1999. Essential fish habitat source document: Black sea bass, *Centropristis striata*, life history and habitat characteristics. NOAA Tech Memo NMFS NE 143: 42.

Svendsen, J. C., Tudorache, C., Jordan, A. D., Steffensen, J. F., Aarestrup, K., and Domenici, P. 2010. Partition of aerobic and anaerobic swimming costs related to gait transitions in a labriform swimmer. Journal of Experimental Biology, 213: 2177–2183.

Svendsen, M. B. S., Bushnell, P. G., and Steffensen, J. F. 2016a. Design and setup of intermittent-flow respirometry system for aquatic organisms. Journal of Fish Biology, 88: 26–50.

Svendsen, M. B. S., Bushnell, P. G., Christensen, E. A. F., and Steffensen, J. F. 2016b. Sources of variation in oxygen consumption of aquatic animals demonstrated by simulated constant oxygen consumption and respirometers of different sizes. Journal of Fish Biology, 88: 51–64.

Verberk, W. C. E. P., Bartolini, F., Marshall, D. J., Pörtner, H. O., Terblanche, J. S., White, C. R., and Giomi, F. 2016. Can respiratory physiology predict thermal niches? Annals of the New York Academy of Sciences, 1365: 73–88.

Wikelski, M., and Cooke, S. J. 2006. Conservation physiology. Trends in Ecology and Evolution, 21: 38–46.

Wilkin, J. L., and Hunter, E. J. 2013. An assessment of the skill of real-time models of Mid-Atlantic Bight continental shelf circulation. Journal of Geophysical Research: Oceans, 118: 2919–2933.

Wishner, K. F., Seibel, B. A., Roman, C., Deutsch, C., Outram, D., Shaw, C. T., Birk, M. A., *et al.* 2018. Ocean deoxygenation and zooplankton: very small oxygen differences matter. Science Advances, 4: eaau5180.

Yamanaka, H., Kohmatsu, Y., and Yuma, M. 2007. Difference in the hypoxia tolerance of the round crucian carp and largemouth bass: Implications for physiological refugia in the macrophyte zone. Ichthyological Research, 54: 308–312.

Yeager, G. R., and Ultsch, D. P. 1989. Physiological regulation and conformation : A BASIC program for the determination of critical points. Physiological Zoology, 62: 888–907.