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Effects of temperature and hypoxia on the metabolic performance of juvenile striped bass (*Morone saxatilis*)

Katie V. Anweiler (contact author)[1]
Karl Brenkert[1]
Tanya L. Darden[1]
Eric J. McElroy[2]
Michael R. Denson[1]

Email address for contact author: anweilerk@dnr.sc.gov

[1] Marine Resources Research Institute
South Carolina Department of Natural Resources
P.O. Box 12559
Charleston, South Carolina 29422

[2] Department of Biology
College of Charleston
66 George Street
Charleston, South Carolina 29424

Abstract—Striped bass (*Morone saxatilis*) found in estuaries and rivers of North America face many environmental challenges. These challenges may have led to local extirpations of striped bass, as has been observed in the Ashley River in South Carolina. The link between environmental challenges and extirpation may be physiological capacities, such as standard metabolic rate (SMR), maximum metabolic rate (MMR), and aerobic metabolic scope (AMS). The objective of this study was to determine the effect of temperature and oxygen availability on the metabolic capacities of striped bass, thereby assessing the physiological capability for survival under varying environmental conditions. After being acclimated to water temperatures of 20°C, 25°C, and 32°C, striped bass swam at their acclimation temperature while being acutely exposed to dissolved oxygen (DO) levels of 2.5, 3.0, and 4.0 mg/L. The highest values of SMR, MMR, and AMS were observed at 32°C, a temperature approaching the upper lethal limit. The MMR, AMS, and exhaustion time were significantly reduced at DO concentrations below 4.0 mg/L. These results indicate that juvenile striped bass are metabolically limited as DO concentrations fall below 4.0 mg/L. However, juvenile striped bass in the Ashley River may be minimally affected by this potential challenge because these conditions are rarely observed.

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The striped bass (*Morone saxatilis*) is an ecologically and economically important finfish species along the Atlantic coast of North America. Its native range extends from the St. Lawrence River in Canada to the Gulf of Mexico (Setzler et al., 1980). Striped bass have also been introduced into rivers and reservoirs throughout the United States and are a valuable recreational fishery in many areas. North of Cape Hatteras, in North Carolina, up through New England, adults leave their native estuaries and migrate along the coast, ascending into rivers to spawn (ASMFC[1]; Coutant, 1985). South of Cape Hatteras, striped bass rarely undertake coastal migrations and remain associated with rivers and estuaries (Coutant, 1985).

Across the range of this species, dissolved oxygen (DO) concentration and temperature are important water-quality parameters that affect the survival and reproductive success of striped bass (Coutant, 1985; Coutant and Benson, 1990). Both field observations and experimental results from inland impoundments, rivers, and estuaries indicate that striped bass become physiologically stressed by hypoxic conditions of DO levels of approximately 3 mg/L and that they cannot inhabit areas with DO concentrations less than approximately 2 mg/L (Coutant, 1985). Although resource managers and fisheries biologists commonly measure oxygen preferences and limits and develop habitat suitability index models in terms of DO concentration (e.g., ASMFC[1]; Coutant, 1985; Greene et al.[2]; Ruane et al., 2013), it should be noted

[1] ASMFC (Atlantic States Marine Fisheries Commission). 1981. Interstate fisheries management plan for the striped bass of the Atlantic coast from Maine to North Carolina. Atl. States Mar. Fish. Comm., Fish. Manage. Rep. 1, 329 p. [Available from website.]

[2] Greene, K. E., J. L. Zimmerman, R. W. Laney, and J. C. Thomas-Blate. 2009. Atlantic coast diadromous fish habitat: a review of utilization, threats, recommendations for conservation, and research needs. Atl. States Mar. Fish. Comm., Habitat Manage. Ser. 9, 463 p. [Available from website.]

that the gradient in partial pressure of oxygen (PO_2), rather than in DO concentration, drives the rate of oxygen diffusion and, therefore, oxygen uptake for an organism (Farrell and Richards, 2009). The ability of water to hold oxygen decreases with increasing temperature, but the PO_2 at any given oxygen concentration increases with temperature.

Thermal tolerance of striped bass varies by several degrees depending on experimental methodology, differences among fish stocks, geographic location, age of fish, and the ranges of water temperature and oxygen concentration available to the fish (Crance[3]). Merriman (1941) reported a maximum thermal tolerance of 25–27°C on the basis of field distribution records in New England. However, Tagatz[4] found that adult striped bass sampled in North Carolina tolerated temperatures of 0–30°C in the laboratory. Gift (1970) observed a median lethal temperature of 31.5°C for adult striped bass sampled in New Jersey, acclimating them to 20°C and raising the temperature to the lethal level over a period of approximately 24 h. The same experimental procedure showed a higher temperature tolerance for juvenile striped bass, with a median lethal temperature of 37°C. Likewise, Coutant et al. (1984) reported the optimum temperatures for juvenile striped bass (80–300 mm in total length [TL]) as 24–27°C, and Coutant and Carrol (1980) reported an optimal temperature range of 20–24°C for larger juvenile striped bass (430–680 mm TL). These findings agree with the premise that juvenile striped bass are more tolerant of high temperatures than adults.

Nearly all observations of physiological limits of striped bass have been on migratory northern populations (i.e., those above Cape Hatteras), which likely have different physiological tolerances than southern populations (i.e., those below Cape Hatteras) because of their different life history. Southern populations of striped bass are essentially non-migratory (Greene et al.[2]). In South Carolina, populations of striped bass are small, reproductively isolated, and exist either in inland impoundments or in coastal rivers (Bulak et al., 2004; Sessions et al.[5]). The results of field studies exploring habitat preferences in inland impoundments indicate that striped bass choose habitats with temperatures of 20–24°C during the summer and occupy habitats with temperatures up to 26°C when a cooler habitat is unavailable (Schaffler et al., 2002; Young and Isely, 2002). However, the coastal rivers and estuaries that some southern populations inhabit do not have the degree of thermal refuge of inland impoundments. In a coastal river of South Carolina, Bjorgo et al. (2000) observed that striped bass chose habitats with temperatures of 25–27°C during periods when downstream habitats were as much as 5°C higher.

Striped bass will select habitats with water that is warmer than their preferred range when DO concentration is low in cooler water (Farquhar and Gutreuter, 1989). During summer, when temperatures are highest and DO levels are lowest, striped bass select the coolest habitat available with DO concentrations over 2.0–2.5 mg/L (Zale et al., 1990). Water temperatures in summer (June–August) at our study site, the Ashley River in South Carolina, have been 19–33°C (M. Denson, unpubl. data; Fig. 1), with temperatures of 24–31°C being the most frequent (80% of observations). Concentrations of DO typically range from 3.5 to 5.5 mg/L during the summer, with levels ≤4.0 mg/L for 28% of observations and levels ≤3.0 mg/L for 1% of observations. Tolerance of both high temperatures and low DO concentrations is likely important to survival of striped bass in the coastal rivers and estuaries of the southeastern United States.

Temperature is the principal controlling factor of metabolic demand; within an ectotherm's temperature range, metabolism is expected to increase 2–3 fold for every 10°C increase in temperature (Hochachka and Somero, 2002). Aerobic metabolic scope (AMS) is defined as the mathematical difference between the maximum metabolic rate (MMR) and the standard metabolic rate (SMR) (Fry, 1947, 1971). Aerobic metabolic scope represents the metabolic confines within which all aerobic energetic processes (e.g., somatic and gonadal growth, digestion, and activity) must be performed (Fry, 1947, 1971; Neill and Bryan, 1991; Lapointe et al., 2014). Although SMR increases with temperature (Fry and Hart, 1948), MMR levels off, or even decreases, when temperatures become too high (Fry and Hart, 1948; Pörtner and Knust, 2007). Therefore, at high temperatures, AMS is expected to decrease because of tissue oxygen demand outpacing oxygen supply from the environment (Pörtner, 2001, 2002). Many studies have quantified AMS as a proxy for biological performance in a given environment (e.g., Pörtner and Knust, 2007; Farrell et al., 2008; Clark et al., 2011; Lapointe et al., 2014) and have found that the time it takes for a swimming fish to exhaust (i.e., *exhaustion time*) is positively correlated with AMS (Reidy et al., 2000; Metcalfe et al., 2016).

This study is the first to examine the interactive effects of temperature and low DO concentration on aerobic metabolism and swimming performance in southern stocks of striped bass. The objective of this study was to compare changes in AMS during acute exposure to hypoxic treatments (DO levels of 2.5, 3.0, and 4.0 mg/L) in striped bass that were acclimated and exercised at 3 temperatures (20°C, 25°C, and 32°C). These temperatures span the range of the summer thermal regime in the Ashley River, and the DO levels mimic the lower end of DO concentrations observed in this river (Fig. 1). Although environmental PO_2 has a more direct effect on fish oxygen uptake than environmental oxygen concentration, specific oxygen concentrations were chosen on

[3] Crance, J. H. 1984. Habitat suitability index models and instream flow suitability curves: inland stocks of striped bass. U.S. Fish Wildl. Serv., Div. Biol. Serv. Res. Dev. FWS/OBS-82/10.85, 63 p. [Available from website.]

[4] Tagatz, M. E. 1961. Tolerance of striped bass and American shad to changes of temperature and salinity. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 388, 8 p. [Available from website.]

[5] Sessions, F., S. Lamprecht, J. Bettinger, J. Bulak, and M. Scott. 2015. Striped bass. *In* South Carolina's state wildlife action plan (SWAP) 2015. Suppl. vol.: species of conservation concern. South Carolina Dep. Nat. Resour., Columbia, SC. [Available from website.]

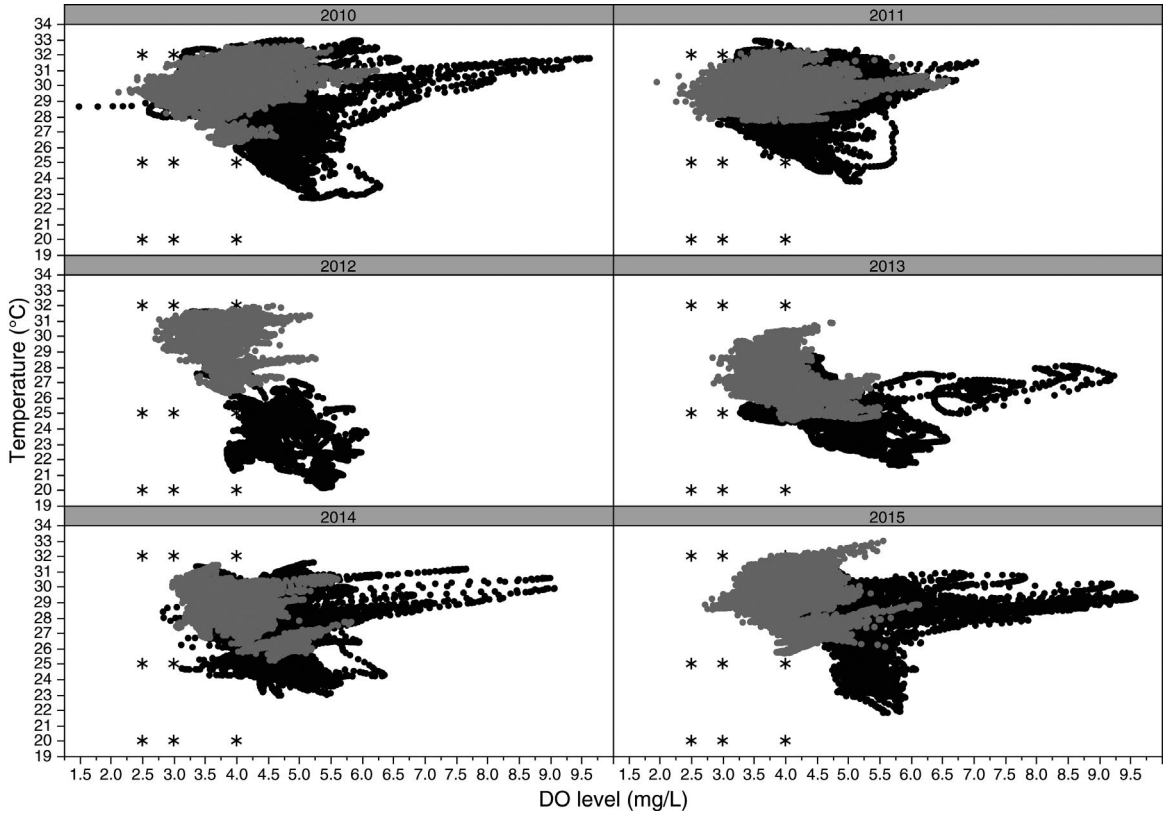

Figure 1

Relationships of temperatures to dissolved oxygen (DO) levels recorded at 2 sites in the Ashley River in South Carolina during the summers (June–August) of 2010–2015. Observations were recorded in 15-min intervals by using 2 YSI 6600EDS V2-2 multiparameter water-quality monitoring devices (or sondes; YSI Inc., Yellow Springs, OH). Sondes were deployed in the Ashley River at river kilometer (rkm) 21 and rkm 39, measured from the river's confluence with Charleston Harbor. Gray dots indicate values recorded at the site at rkm 21, a location that represents a marsh-dominated estuarine habitat. Black dots indicate values recorded at the site at rkm 39, which is a transition zone between estuarine emergent wetland and palustrine forested wetlands. For comparison, asterisks indicate temperatures and DO concentrations used in treatments in this study.

the basis of how natural resource managers monitor systems and estimate fish survival in systems.

Changes in AMS of juveniles due to temperature and DO level were measured to understand how these conditions might affect the survival of stocked fish during their first summer in the Ashley River. Because AMS, when expressed as a function of temperature, typically takes the approximate form of a bell-shaped curve that aligns with organismal performance (Neill and Bryan, 1991; Pörtner and Farrell, 2008; Pörtner, 2010), we predicted that 1) SMR would increase with increasing temperature; 2) MMR, AMS, and exhaustion time would be greatest at 25°C and would be lower at 20°C and 32°C, consistent with the recorded temperature preference for juveniles (Coutant and Carrol, 1980; Coutant et al., 1984); and 3) MMR, AMS, and exhaustion time would decrease with decreasing DO concentration. Hypotheses 2 and 3 are consistent with observations that striped bass avoid DO levels less than 3.0 mg/L and prefer temperatures less than 30°C (Zale et al., 1990; Bjorgo et al., 2000; Schaffler et al., 2002).

Materials and methods

Experimental animals and acclimation conditions

Experiments were conducted at the Marine Resources Research Institute (MRRI), South Carolina Department of Natural Resources (SCDNR), in Charleston, South Carolina. Striped bass larvae (2013 year class) were produced from wild-caught adults from the Santee Cooper reservoirs. Larvae were grown to small juveniles in fertilized, brackish ponds (salinity: ~7) at the SCDNR Waddell Mariculture Center and transported to the MRRI, located in Charleston Harbor. Fish were initially held indoors in circular 1600-L fiberglass tanks in order to acclimate them to feeding routines until they were 1 year old.

Table 1

Results from trials with different treatment combinations conducted on striped bass (*Morone saxatilis*) at the Marine Resources Research Institute, South Carolina Department of Natural Resources, during June–December 2014. Partial pressure of oxygen in water (PO_2), fish wet weight, fish total length (TL), fish relative condition factor (*Kn*), standard metabolic rate (SMR), maximum metabolic rate (MMR), aerobic metabolic scope (AMS), exhaustion time, and fish sample size (*n*) were measured for each combination of temperature and dissolved oxygen (DO) concentration. Lettered subscripts indicate significant differences between temperature treatments, and numbered subscripts indicate significant differences between DO-level treatments. Standard deviations of means are given in parentheses.

Temp. (°C)	DO level (mg/L)	PO_2 (kPa)	Wet weight (g)	TL (mm)	*Kn*	SMR ($mg \cdot kg^{-1} \cdot h^{-1}$)	MMR ($mg \cdot kg^{-1} \cdot h^{-1}$)	AMS ($mg \cdot kg^{-1} \cdot h^{-1}$)	Exhaustion time (s)	*n*
20	2.5	5.74_{a} (0.01)	404_{b} (67)	340_{b} (17)	1.00_{a} (0.04)	79_{ab} (15)	$274_{a,1}$ (60)	$194_{a,1}$ (47)	8499_{1} (957)	5
20	3.0	6.89_{b} (0.04)	447_{b} (37)	348_{b} (13)	1.04_{a} (0.04)	73_{ab} (21)	$294_{a,2}$ (36)	$221_{a,2}$ (27)	8994_{1} (1118)	5
20	4.0	9.14_{c} (0.02)	386_{b} (53)	337_{b} (13)	0.99_{a} (0.03)	64_{ab} (13)	$398_{a,3}$ (42)	$334_{a,3}$ (43)	$10{,}954_{2}$ (923)	5
25	2.5	6.27_{d} (0.01)	504_{a} (67)	364_{a} (17)	1.03_{ab} (0.07)	75_{b} (15)	$279_{ab,1}$ (29)	$203_{ab,1}$ (21)	9932_{1} (1497)	7
25	3.0	7.55_{e} (0.01)	512_{a} (43)	366_{a} (14)	1.03_{ab} (0.04)	83_{b} (25)	$311_{ab,2}$ (34)	$227_{ab,2}$ (31)	$10{,}135_{1}$ (1460)	7
25	4.0	10.04_{f} (0.03)	504_{a} (65)	364_{a} (18)	1.03_{ab} (0.08)	66_{b} (9)	$429_{ab,3}$ (80)	$363_{ab,3}$ (77)	$12{,}016_{2}$ (2148)	7
32	2.5	6.83_{b} (0.02)	410_{b} (62)	349_{b} (11)	0.95_{b} (0.09)	106_{a} (34)	$334_{b,1}$ (28)	$227_{b,1}$ (46)	8727_{1} (1147)	5
32	3.0	8.16_{g} (0.01)	436_{b} (19)	353_{b} (10)	0.98_{b} (0.05)	101_{a} (21)	$376_{b,2}$ (28)	$275_{b,2}$ (33)	8710_{1} (1054)	5
32	4.0	10.91_{h} (0.04)	426_{b} (58)	354_{b} (12)	0.95_{b} (0.06)	93_{a} (8)	$530_{b,3}$ (37)	$436_{b,3}$ (35)	$10{,}440_{2}$ (610)	5

Fish were moved to an outside 12,000-L brackish-water flow-through system (salinity: ~5) on 9 April 2014 and held until they were brought indoors for acclimation. While held outside, they experienced natural lighting and temperature conditions similar to those of the Ashley River during spring and summer (ratio of hours of daylight to hours of night: ~12 h:12 h in spring and ~14 h:10 h in summer; temperature range: 20–30°C).

Before each set of experiments was conducted, a subset of striped bass (~50 fish for each temperature treatment) were moved into a circular 1600-L recirculating tank housed in an environmental chamber. Fish were held in lighting conditions with a ratio of 13 h of light to 11 h of dark and were acclimated to the desired salinity (1) and test temperature (20°C, 25°C, or 32°C) before testing. Dechlorinated tap water and Instant Ocean[6] sea salt (Instant Ocean, Blacksburg, VA) were used to make water with a salinity of 1. Fish in the group held in 20°C water were acclimated for a mean of 64 d (standard deviation [SD] 7) and range of 51–75 d, fish in the group held in 25°C water were acclimated for a mean of 26 d (SD 11) and a range of 9–47 d, and fish in the group held in 32°C water were acclimated for a mean of 46 d (SD 15) and a range of 26–70 d. Therefore, acclimation times ranged from 9 d to several weeks. Although 9 d is a relatively short thermal acclimation period, it was considered adequate because the temperature of the outside tank from which fish were collected before each experiment was similar to the temperatures of the experimental tanks (i.e., fish were moved to the 20°C tank in the spring and to the 25°C and 32°C tanks in the summer).

[6] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

To account for any effect of acclimation time on metabolic rates or swimming performance, we included acclimation time as a covariate in the statistical models. During the acclimation period, fish were fed to satiation once daily with a commercially pelleted diet (5.0-mm, slow-sinking Finfish Silver, Zeigler Bros. Inc., Gardners, PA).

Seven days prior to use in a trial, individual fish were transferred from the holding tank into a 70-L rectangular aquarium equipped with an air-driven Hydro-Sponge 1 filter (Aquarium Technology Inc., Decatur, GA) and an air stone to promote water mixing and oxygenation; all fish were held at air saturation >90% and at their test temperature. Water was changed in aquaria daily to prevent buildup of nitrogenous waste. Food was withheld during this 7-d period, which is an adequate amount of time to ensure that digestion and specific dynamic action do not influence oxygen consumption rates (Clark et al., 2013). Five fish held in 20°C water and 5 fish held in 32°C water were tested at each DO level; 7 fish held in 25°C water were tested at each DO level (Table 1).

Oxygen consumption measurements

Standard metabolic rate, MMR, and AMS were determined by using intermittent-flow respirometry at temperatures of 20°C, 25°C, and 32°C and DO concentrations of 4.0, 3.0, and 2.5 mg/L in a full factorial design. The PO_2 of each treatment combination is reported in Table 1. Trials on temperature-acclimated fish were conducted during 19 June–19 December 2014. The day prior to a trial, a single fish was anesthetized directly in its aquarium with Finquel tricaine methanesulfonate (Argent Chemical Laboratories Inc., Redmond, WA) at a concentration of 0.1 g/L. Fish were removed from the aquarium with a dip net and then measured and weighed (Table 1)

before transfer to a 90-L swim tunnel respirometer (Loligo Systems, Tjele, Denmark) containing water at a salinity of 1 and the treatment temperature. Blinders were placed over the front, working portion of the inner chamber to create a darkened environment for the fish and prevent accidental startling from personnel monitoring the swim chamber. Approximately 30 min was allowed for recovery from the effects of anesthesia, and recovery was defined as the return of fish to resting on the bottom of the respirometer in a normal posture and with normal patterns of resting gill ventilation.

After recovery, flow in the tunnel was set to 10 cm/s, and fish were left overnight (~1600–0900). The overnight period allowed fish to recover from any stress due to handling or effects of anesthesia because the results of preliminary overnight trials indicate that oxygen consumption returned to baseline approximately 5 h after transfer. The overnight period also allowed a fish time to orient itself in the swim tunnel against a low-velocity flow. The darkened front portion of the chamber aided fish in using the working portion of the chamber instead of resting against the back grid. During the overnight recovery period, the swim tunnel respirometer was continually flushed with water from the outer bath. An air stone was placed in the outer bath to achieve a constant ambient DO level of over 90%.

On the morning of each trial, a DO galvanic probe (MINI-DO, Loligo Systems; with accuracy of ±1% air saturation) was calibrated with a 2-point calibration method and secured in the inner chamber of the flume through a port. A bright light was placed over the back portion of the swim chamber to further encourage fish to use the darkened portion of the swim chamber. Water in the outer bath was deoxygenated by bubbling nitrogen gas through a high-pressure air stone. A solenoid valve, linked to the DO galvanic probe, controlled the flow of nitrogen gas in the outer chamber. The oxygen saturation in the inner chamber was lowered from the ambient level by continuously flushing in deoxygenated water from the outer bath. The treatment DO level was typically reached within 1 h. Once the treatment DO concentration was reached, fish were held at this concentration for 30 min to allow for acclimation.

After acclimation, flow in the chamber was increased and intermittent respirometry was used to repeatedly measure oxygen consumption. Oxygen consumption measurements were recorded in milligrams per kilogram per hour in 7-min intervals that consisted of a 2-min flush, followed by a 1-min equilibration period then a 4-min measurement period in which oxygen saturation was recorded once every second. The flush cycle served, among other things, to restore oxygen that had been depleted during each equilibration and measurement period. The speed of water flow in the chamber was increased by 15 cm/s every 42–56 min, resulting in 6–8 oxygen consumption measurements at each speed. At least 3 of those measurements were more than 20 min after the speed change; these measurements were required for SMR calculations (see the next section).

Trials ended when the fish was exhausted, which was defined as failure to swim against the current and use of the tail to maintain position against the back screen for at least 15 s. A recent review of methods for eliciting MMR found that the swim-tunnel method is acceptable for species, such as the striped bass, that are active swimmers (Norin and Clark, 2016). The timing of exhaustion was calculated by subtracting the time that we increased speed for the first speed increment of the trial from the time at which the fish became exhausted. After exhaustion, flow in the chamber was decreased to 10 cm/s, water was brought to a DO level of 100%, and fish were left to rest for 15 min before being transferred to the recovery tank. After the fish was removed, the chamber was closed again and 3 measurements of background oxygen consumption were recorded by using the previously described 7-min cycle.

Metabolic calculations

Mean background bacterial oxygen consumption was appreciable at each temperature (20°C: 12.1 mg/h [SD 2.8]; 25°C: 28.9 mg/h [SD 8.9]; and 32°C: 32.6 mg/h [SD 12.3]). Note that these levels represent a substantial portion of the measured oxygen consumption values (39% [SD 12] when measuring SMR and 13% [SD 6] when measuring MMR, averaged across all temperature and DO-level treatments). Although these values are relatively high, they likely occurred because 1) fish were acclimated in the respirometry system for ~12–16 h prior to measurements being recorded and 2) the dechlorinated tap water used to fill the flume was held in 200-L bins for 2–3 d prior to testing to allow it to reach the testing temperature (also see Svendsen et al., 2016). Therefore, the average background bacterial oxygen consumption (computed from the 3 measurements made for that trial) was subtracted from the total recorded oxygen consumption to calculate the oxygen consumption of the fish (Svendsen et al., 2016).

The SMR for each individual was calculated by fitting a linear function to the log of oxygen consumption on swimming speed (Fig. 2) and then by using this function to extrapolate the SMR at a speed of zero (Brett, 1964; Fry, 1971). Only oxygen consumption values measured 20 min after each speed change were used in the calculations for SMR. The MMR was the single maximum oxygen consumption rate achieved by the fish during the entire trial. This reading occurred approximately 50% of the time at the maximum speed step and the other 50% of the time at the speed step just before the maximum. The AMS for each fish was calculated as follows:

$$AMS = MMR - SMR, \quad (1)$$

where AMS = aerobic metabolic scope ($mg \cdot kg^{-1} \cdot h^{-1}$);
MMR = maximum metabolic rate ($mg \cdot kg^{-1} \cdot h^{-1}$); and
SMR = standard metabolic rate ($mg \cdot kg^{-1} \cdot h^{-1}$).

Statistical analysis

All analyses were completed in JMP 13 (SAS Institute Inc., Cary, NC). Differences in weight and relative condition factor (Kn; Le Cren, 1951) between treatments were analyzed

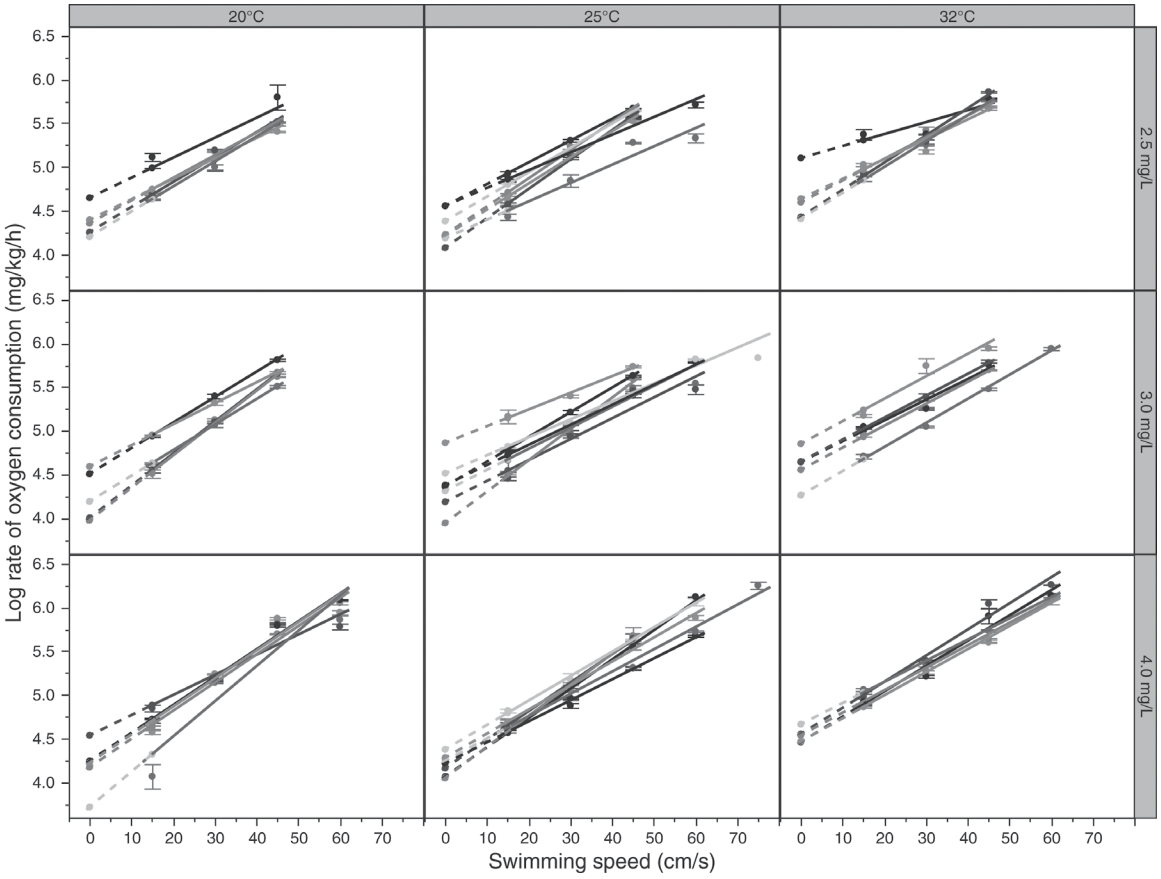

Figure 2

Mean log rate of oxygen consumption by striped bass (*Morone saxatilis*) as a function of swimming speed for each treatment combination of temperature and dissolved oxygen (DO) level. Individual replicates are differentiated by differently shaded lines within each panel. The dashed lines on the left side of each panel show the extrapolation of log standard metabolic rate to a speed of zero. Error bars indicate the standard error of mean oxygen consumption at each speed for each individual. Trials were conducted in aquarium tanks at the Marine Resources Research Institute, South Carolina Department of Natural Resources, from June through December 2014.

by using analysis of variance with the Tukey's honestly significant difference (HSD) test (Table 1). The Kn was calculated with the following equation:

$$Kn = \left(\frac{W}{\hat{W}}\right), \quad (2)$$

where W = weight (in grams) and

$\hat{W}$ = the fish weight (in grams) predicted from the least squares regression of log W on the log of the fish TL.

Measures of SMR, MMR, AMS, and exhaustion time were log transformed to meet assumptions of normality of residuals and homogeneity of variance, which were verified by using Shapiro-Wilk and Levene tests, respectively. Separate linear models that use standard least squares were used to test the effects of treatment temperature, DO concentration, weight, Kn, and acclimation time of fish on SMR, MMR, AMS, and exhaustion time. A similar set of linear models were also generated with the PO_2 in place of DO concentration; this second set of models was used to examine the effect of uneven PO_2 across combinations of temperature and dissolved oxygen on the metabolism and exhaustion time. This entire analysis was repeated except the SMR, MMR, and AMS values were not adjusted for weight (i.e., values were not divided by fish weight; therefore, they were absolute, or raw, metabolic rates in milligrams per hour). This second round of analysis with unadjusted values was done to understand differences in the effects of temperature or DO concentration due to estimating SMR, MMR, and AMS as ratios (with weight in the denominator) rather than using raw metabolic rates. For all analyses, Tukey's HSD tests were used where appropriate to assess differences among treatments. For all statistical tests, the significance level or alpha level was set at 0.05.

Ethical approval

All applicable international, national, and institutional guidelines for the care and use of animals were followed. All procedures in this study involving animals were performed in accordance with the ethical standards of the institution or practice at which the procedures were conducted. Procedures used in this research were covered under College of Charleston Institutional Animal Care and Use Committee protocol 2016-01-29-081028.

Results

During all trials, the decrease in oxygen saturation in the chamber during the measurement period was linear (mean coefficient of determination [r^2]: 0.99 [SD 0.01]), indicating that the chamber had no leakage (Svendsen et al., 2016). The decrease in oxygen saturation observed while measuring background oxygen consumption was also linear (mean r^2: 0.92 [SD 0.13]). Groups of fish used to compare among treatment temperatures had significantly different wet weights ($F_{2,46}$=16.76, P<0.01), TL ($F_{2,46}$=12.60, P<0.01), and *Kn* ($F_{2,46}$=6.31, P<0.01) (Table 1), although these same factors were similar across all DO-concentration treatments (weight: $F_{2,46}$=0.50, P=0.61; TL: $F_{2,46}$=1.12, P=0.34; *Kn*: $F_{2,46}$=1.05, P=0.36; Table 1).

Strong linear relationships of the log of oxygen consumption on swimming speed allowed for calculation of SMR by extrapolation to zero for each individual (mean r^2: 0.95 [SD 0.07]). The SMRs of striped bass were significantly different across temperatures, with the SMR at 25°C being significantly lower than the SMR at 32°C and with the SMR at 20°C being intermediate and not significantly different from the SMRs at the other temperatures (Tables 1 and 2, Fig. 3A). Standard metabolic rate was not significantly affected by treatment DO concentration, the interaction of temperature and DO level, weight, or *Kn* (Table 2). The results were slightly different when DO concentration was replaced with PO_2 in the linear models: PO_2 was marginally negatively related to SMR (Table 2), and the SMR was higher for the 32°C treatment than for the 20°C and 25°C treatments. The models that used raw SMR were qualitatively similar (Table 2), with the exception that fish wet weight was positively related to SMR as would be expected.

The MMRs were significantly different across temperature and DO-level treatments, although the interaction of these 2 factors was not significant (Table 2). The MMR at 20°C was significantly lower than the MMR at 32°C, and the MMR at 25°C was intermediate and not significantly different from the MMRs at other temperatures (Table 1, Fig. 3). The MMRs increased significantly with increasing DO concentration (Table 1, Fig. 3). Maximum metabolic rate was negatively related to *Kn* but not to weight (Table 2). When DO level was replaced with PO_2 in the linear models, PO_2 was positively related and *Kn* was still negatively related to MMR. However, treatment

Table 2

Results from linear models used to test the effects of treatment temperature, dissolved oxygen (DO) concentration, partial pressure of oxygen (PO_2), fish wet weight, fish relative condition factor (*Kn*), and acclimation time of striped bass (*Morone saxatilis*) on standard metabolic rate (SMR), maximum metabolic rate (MMR), aerobic metabolic scope (AMS), and exhaustion time. The top half of the table shows results for models with DO concentration at fixed-level treatments (2.5, 3.0, and 4.0 mg/L). The bottom half shows actual PO_2 in each treatment (a continuous variable). Values for SMR, MMR, and AMS were calculated by dividing oxygen consumption per hour by fish wet weight. Absolute or raw SMR, MMR, and AMS were calculated as metabolic rates not divided by fish wet weight. The degrees of freedom (df) numerator and denominator used to test each parameter in each model are separated by a comma. An alpha level of 0.05 was used to establish significance. Data used in models came from trials conducted at the Marine Resources Research Institute, South Carolina Department of Natural Resources, from June through December 2014.

	SMR		MMR		AMS		Raw SMR		Raw MMR		Raw AMS		Exhaustion time		
Model	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	df
Temperature	8.55	<0.01	8.42	<0.01	4.02	0.03	9.18	<0.01	9.16	<0.01	4.21	0.02	3.13	0.05	2,39
DO (mg/L)	2.22	0.12	54.0	<0.01	72.4	<0.01	2.23	0.12	52.6	<0.01	71.8	<0.01	15.2	<0.01	2,39
Temp*DO	0.24	0.91	0.29	0.88	0.68	0.61	0.22	0.92	0.33	0.86	0.73	0.58	0.23	0.92	4,39
Acclimation	2.24	0.14	0.70	0.41	0.13	0.72	2.56	0.12	1.08	0.31	0.04	0.85	1.70	0.20	1,39
Kn	0.21	0.65	4.89	0.03	3.81	0.06	0.09	0.76	3.63	0.06	2.95	0.09	3.66	0.06	1,39
Wet weight	0.41	0.53	1.87	0.18	4.03	0.05	16.6	<0.01	26.1	<0.01	11.0	<0.01	5.70	0.02	1,39
Temperature	10.4	<0.01	0.85	0.44	0.69	0.51	11.2	<0.01	1.31	0.28	0.37	0.69	6.87	<0.01	2,42
PO_2 (kPa)	4.49	0.04	116	<0.01	150	<0.01	4.45	0.04	113	<0.01	148	<0.01	30.9	<0.01	1,42
Temp*PO_2	0.21	0.77	0.03	0.97	0.11	0.90	0.22	0.81	0.04	0.96	0.10	0.91	0.75	0.48	2,42
Acclimation	2.88	0.10	0.60	0.44	0.31	0.58	3.26	0.08	0.97	0.33	0.14	0.71	2.02	0.16	1,42
Kn	0.31	0.58	5.26	0.03	3.55	0.07	0.14	0.71	3.73	0.06	2.58	0.12	4.76	0.03	1,42
Wet weight	0.44	0.51	1.96	0.17	3.92	0.05	18.4	<0.01	30.9	<0.01	13.2	<0.01	5.44	0.02	1,42

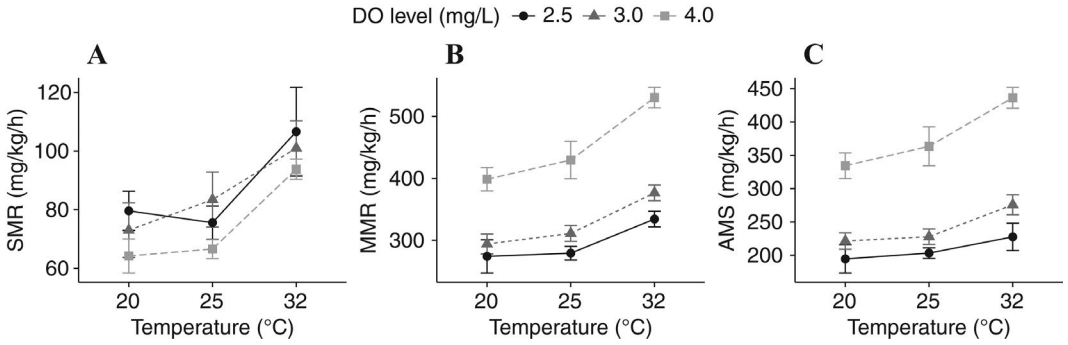

Figure 3

Effects of temperature and dissolved oxygen (DO) level on (**A**) standard metabolic rate (SMR), (**B**) maximum metabolic rate (MMR), and (**C**) aerobic metabolic scope (AMS) of juvenile striped bass (*Morone saxatilis*) during trials conducted in aquarium tanks at the Marine Resources Research Institute, South Carolina Department of Natural Resources, from June through December 2014. Error bars indicate standard errors of the mean.

temperature was no longer related to MMR (Table 2). The results were similar when these analyses were run with raw MMR as the response, except that the MMR at 32°C was significantly greater than the MMRs at both 20°C and 25°C, *Kn* was not related to raw MMR, and weight was positively related to raw MMR (Table 2).

The values of AMS were significantly different across temperatures and DO levels, although the interaction between treatments was not significant (Table 2). The AMS at 20°C was significantly lower than the AMS at 32°C, and the AMS at 25°C was intermediate and not significantly different from the AMS values at other temperatures (Table 1, Fig. 3). The AMS values increased with increasing DO concentration (Table 1, Fig. 3). Aerobic metabolic rate was negatively related to weight but was not related to *Kn* (Table 2). The results were similar when DO level was replaced with PO_2 in the linear model, except that treatment temperature was no longer related to AMS and PO_2 was positively related to AMS (Table 2). The results were similar when raw AMS was used as the response, except that fish wet weight was positively related to AMS (Table 2).

Exhaustion time was significantly different across DO levels (Table 2). Fish in the 4.0-mg/L treatment had significantly longer exhaustion times compared with fish in the 3.0-mg/L and 2.5-mg/L treatments (Table 1). Neither temperature nor the interaction between treatments were significant terms in the model (Table 2). Exhaustion time was positively related to fish wet weight (Table 2). When DO concentration was replaced with PO_2 in the linear model, PO_2 and fish wet weight were both positively related to exhaustion time and *Kn* was negatively related to exhaustion time. Treatment temperature was a significant predictor of exhaustion time when PO_2 was used (Table 2), with exhaustion times significantly longer at 25°C than at 32°C and with exhaustion time at 20°C being intermediate and not significantly different from the exhaustion times at 25°C or 32°C.

Discussion

This study is the first to investigate the effects of temperature and DO concentration on the metabolism of striped bass in coastal waters of the southeastern United States. Within the range tested, SMR was greatest at 32°C. The SMRs increased with increasing temperature at DO levels of 3.0 and 4.0 mg/L (Fig. 2), supporting our first prediction. Notably, at a DO concentration of 2.5 mg/L, SMR was lowest at 25°C, a result that may have been influenced by high variability and small sample size. The MMRs increased with increasing temperature at all DO levels. Contrary to our second prediction, MMR was highest at 32°C at every DO level. The increase in both SMR and AMS with temperature caused a net increase in AMS across temperature. Again, contrary to predictions, AMS was highest at 32°C. Although increases in SMR and MMR are predicted within a normal temperature range, the magnitude of these changes was lower than expected. The Q_{10} temperature coefficient is a measure of the rate of change of a process as a consequence of increasing the temperature by 10°C. In a normal temperature range, Q_{10} values of 2–3 are expected, but in this study a Q_{10} value of approximately 1.3 was observed for SMR and MMR. The relatively parallel changes in SMR and MMR led to a Q_{10} value of 1.2 for AMS, indicating wide thermal breadth for striped bass in the study area. This result may indicate that southern stocks of striped bass are well equipped to cope with temperature fluctuations, which are common in their estuarine habitat.

The results of previous studies of northern populations of striped bass indicate an optimum temperature in the mid-20s (degrees Celsius) (Coutant and Carrol, 1980; Coutant et al., 1984) and a lethal temperature in the lower 30s (degrees Celsius), depending on life stage (Tagatz[4]; Gift, 1970). These findings indicate that our highest treatment temperature (32°C) may be approaching the lethal

limit. In this study, MMR increased with temperature all the way up to 32°C (Table 1, Fig. 3). The rise in MMR, in concurrence with the smaller increase in SMR, resulted in a steady rise in AMS across all temperatures. In effect, the decrease in MMR and, therefore, in AMS at high temperatures that should signal the onset of thermal intolerance (Pörtner, 2001, 2002) was absent in our sample of juvenile striped bass.

Although high temperature did not decrease the AMS available for striped bass, low DO levels did decrease it, with both MMR and AMS declining at the lower DO levels tested. These results support our third prediction. In fact, DO concentration clearly played an important role in limiting MMR and AMS. Most notably, the sharp differences between the values of AMS at the DO level of 4.0 mg/L and the values of AMS at DO levels of 2.5 or 3.0 mg/L (Fig. 3, B–D) indicate that DO level has a greater influence on AMS than the range of water temperatures used in our study. Even when DO concentration remained above a level that would directly cause fish mortality (e.g., 2 mg/L), the reduction in AMS that was observed in this study with low environmental DO concentration could limit the capacity of striped bass for locomotion, foraging, growth, or reproduction (Coutant, 1990; Neill and Bryan, 1991). These conclusions are further supported by the results of our analyses based on PO_2 because, in models that used it, PO_2 was significantly positively related to AMS and MMR but temperature was not (Table 2).

Fish that were exercised at lower DO levels had shorter exhaustion times, further supporting the findings that low DO concentration plays a larger role in limiting metabolic capacities than temperature. At every temperature tested, fish exercised at a DO level of 4.0 mg/L had significantly longer exhaustion times (Table 1). Although there was no statistically significant effect of temperature on exhaustion time, fish that were acclimated and exercised at 25°C had slightly longer exhaustion times on average, and swam to greater speeds, than their counterparts at other temperatures (Table 1, Fig. 2). This trend is more pronounced when PO_2 is substituted in the model, with exhaustion time being significantly longer at 25°C (Table 2). This result indicates that, although AMS may not be optimal at 25°C, swimming performance may be higher at this intermediate temperature.

The overall effects of high temperature on survival of southern populations of striped bass remain unknown; however, the striped bass used in this study were not likely to have been metabolically limited in the Ashley River. Temperatures above 32°C are rare and brief in this river. Although DO levels between 3.0 and 4.0 mg/L are common, DO concentrations below 3.0 mg/L account for only 1% of all values recorded at water-quality stations during June–August (M. Denson, unpubl. data). Several caveats, however, should be noted.

First, because of the decline in AMS with decreasing DO concentration, occupancy of hypoxic habitats (DO levels <3 mg/L) may have long-term metabolic costs, which could eventually affect growth and reproduction depending on the amount of time spent under such conditions. Second, temperatures in the southeastern United States are projected to increase by 2.2–4.4°C by the end of this century, with an additional 10–40 d over 35°C per year in South Carolina (Carter et al., 2014). The maximum temperature that fish will be exposed to and the amount of time spent at high temperatures will increase. If 32°C is near the optimum for AMS, an increase in temperature by a few degrees could drastically decrease AMS, limiting available summer habitat for wild striped bass in rivers of the southeastern United States. Lastly, metabolic tolerances in relation to temperature and DO concentration may change as fish grow and age. In northern populations, adult striped bass have a lower temperature tolerance than juveniles. Additionally, Johnson (2015) found that age-0 striped bass in the Ashley River have positive growth rate potential over a wider range of temperatures than older fish. It is reasonable to conclude that in southern populations, AMS of adult striped bass will decrease at a lower temperature than it would for juveniles. Lower AMS at high temperatures will likely increase mortality and reduce the reproductive potential of a population.

Larger fish had greater raw MMR and AMS and longer exhaustion times, a finding similar to those of several previous studies (Clarke and Johnston, 1999; Killen et al., 2006; Norin and Malte, 2011). This observation reflects the greater abilities of larger individuals. Although raw AMS is greater in larger fish, larger fish will also face absolutely greater metabolic demands from the physiological systems that support swimming. Therefore, the larger AMS of larger fish may not convey a greater ability to deal with variable environmental conditions. Conversely, heavier fish had lower relative AMS and MMR (i.e., size-adjusted metabolic rates). The negative relationship between weight and size-adjusted active metabolism can be explained by the supposition that heavier fish contain more stored reserves that are not involved in active metabolism (Brett, 1964). Lapointe et al. (2014) measured the AMS of larger Chesapeake Bay striped bass (mean weight: 1300g) under hypoxic conditions with a DO level of 3 mg/L. At 20°C, the striped bass used in our study had 80% greater AMS than the larger striped bass used by Lapointe et al. (2014), although a portion of this difference could be due to differences between northern and southern populations. We note that the aim of our study was to determine the AMS of striped bass that were most comparable to large age-1 or small age-2 wild fish during the summer in South Carolina. Therefore, a relatively small range of weights and *Kn* were intentionally used in this study. The consequence of this narrow size range is that the significant relationship between weight and AMS may not hold for striped bass of other sizes in South Carolina.

Given trends in the recapture of striped bass by the SCDNR in the Ashley River and knowledge of the physical conditions within this river, juvenile striped bass are occupying habitats that, during the warmest days of summer, are near the edge of their thermal tolerance. We predict

that these same habitats will become less tolerable as fish age. Additionally, they will likely become less habitable, even for juveniles, as the warm periods of summer increase in duration and in maximum temperature as a result of climate change.

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