

Effect of Temperature and Salinity on Growth Performance in Anadromous (Chesapeake Bay) and Nonanadromous (Santee-Cooper) Strains of Striped Bass *Morone saxatilis*

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During the first year of life of Striped Bass *Morone saxatilis*, the effect of estuarine habitat use on growth rate is poorly understood. In a split-plot experiment, growth and feeding rates were compared between anadromous (Chesapeake Bay) and non-anadromous (Santee-Cooper) broods of juvenile striped bass (45–90 days posthatch) exposed to a range of salinity levels (0.5, 7, and 15 ppt) and temperatures (20, 24, and 28 C). At 28 C, which best simulated the summertime conditions of young juveniles, Chesapeake Bay fish showed highest growth performance. For this temperature and strain, growth was approximately 40% higher at 7 ppt than at 0.5 or 15 ppt. Santee-Cooper juveniles showed no response to salinity. Over combined temperature and salinity levels, Chesapeake Bay juveniles experienced 22% higher growth rates than did Santee-Cooper juveniles, supporting a proposal that early growth rates are inversely related to latitude. Because salinity had a strong effect on Chesapeake Bay striped bass growth rate, we also conclude that variation in distribution patterns within and among estuaries can substantially modify the expected latitudinal gradient in growth rate.

THE Chesapeake Bay comprises the largest number and volume of nurseries for Striped Bass (*Morone saxatilis*). A portion of Chesapeake Bay striped bass is anadromous (Kohlenstein, 1981); following springtime migrations from coastal regions, adults spawn in freshwater. Eggs are spawned just upriver to the salt front (Secor and Houde, 1995). With increasing size, larvae and young-of-the-year (YOY) juveniles gradually move into higher salinity waters (Dovel, 1992; Secor and Houde, 1995; Robichaud-LeBlank et al., 1998). Down-estuary dispersal by YOY may be related to increased prey abundance in brackish waters (Rathjen and Miller, 1957; Markle and Grant, 1970; Wainwright et al., 1996). Alternatively, this dispersal may be directional, related to improved overwintering refuge habitats expected to occur in lower estuaries (Dovel, 1992).

Habitat use by YOY striped bass during the first summer and fall of life may be related to metabolic responses to both temperature and salinity as has been shown for Juvenile Weakfish (*Cynoscion regalis*) in the Delaware Bay (Lankford and Targett, 1994). Temperature control of growth rates is well studied for juvenile striped bass (Otwell and Merriner, 1975; Cox and Coutant, 1981; Hartmann and Brandt, 1993). Salinity effects on juvenile growth and metabolic rates are commonly reported for estuarine and coastal fishes (Perez-Pinzon and Lutz, 1991; Lankford and Targett, 1994; Heyward et al., 1995). For striped bass YOY, however, few stud-

ies have directly addressed the effect of salinity. Otwell and Merriner (1975) reported “relative” growth rates (percent deviation from reference growth rates) for Chesapeake Bay juvenile striped bass (43–69 days old) across a range of temperatures and salinities. Results from that study (their table 6) indicated maximal relative growth rate at 12 ppt and 24 C.

The initial growth season experienced by YOY (summer and fall) varies in duration across the broad range of latitudes where striped bass occur. Conover (1990) hypothesized and later observed (Conover et al., 1997) that YOY growth rate was inversely related to the latitude of a given population’s nursery. Winter mortality at higher latitudes is size dependent which led to the proposal that natural selection favored higher growth rates in northern populations (Hurst and Conover, 1998). Tests for latitudinal clines in larval and YOY striped bass growth rates (Conover et al., 1997; Brown et al., 1998) have emphasized temperature and ration level as principal factors controlling growth rate. These studies were conducted at a common salinity level (5 ppt) and did not consider how variability in habitat use within estuaries (i.e., salinity levels) might affect growth responses. Additionally, striped bass populations vary in their dependence upon estuarine and coastal habitats. Striped bass populations in Florida, Georgia, and South Carolina exhibit semianadromous or potamodromous lifecycles (Raney and Wolcott, 1955; Dudley et al., 1977; Bulak et al., 1997).

This study compares growth performance between Chesapeake Bay and Santee-Cooper broods of striped bass exposed to a range of temperature and salinity levels. The Santee-Cooper population (South Carolina) inhabits a large system of freshwater rivers and reservoirs, and the juvenile nursery is entirely freshwater (Bulak et al., 1997). The purpose of this study was to quantify the interactive effects of salinity and temperature on growth and feeding rates and gross growth conversion efficiency. We expected that Santee-Cooper and Chesapeake Bay broods would show improved growth performance in freshwater habitats and oligohaline habitats (< 15 ppt), respectively.

MATERIALS AND METHODS

The experiment used YOY striped bass provided by hatcheries in Maryland (Chesapeake Bay) and South Carolina (Santee-Cooper). Broodstock were collected from either the Choptank River (Maryland strain) or the Santee River (South Carolina strain). For each strain, three separate broods were used. Each brood comprised the progeny of one female and several males (> 3). Half-sib broods were maintained during larval and early juvenile stages under identical conditions (20 C and 0.5 ppt) and combined in equal proportion just prior to the experiment. No effort was made to track brood performance during the experiment. Larvae were initially fed live *Artemia* and then weaned onto a pelleted diet (Biokyowa®) which was used during the experiment.

Three salinity levels (0.5, 7, and 15 ppt), three temperature levels (20, 24, and 28 C), and two strain levels were investigated. Wet weights at the start of each run were 0.65 ± 0.28 and 5.06 ± 1.56 g, respectively, for juveniles aged 45 and 75 days posthatch. Prior to each experimental run, juveniles were transferred from holding tanks to 40-liter aquaria. The temperature and salinity were raised two degrees and two ppt per day until the appropriate experimental conditions were achieved. The fish were then allowed to acclimate for 10 days, during which they were fed ad libitum. Near the end of the acclimation period, fish were individually marked by injection with acrylic dye. The two strains were then combined in equal numbers for each experimental unit (total 6–8 fish per tank). Experimental duration was 15 days. On the first day of the experiment, the fish were weighed in water to determine the initial weight. During the experiment, preweighed artificial pellet food was provided three times daily—0900, 1300, and 1700. Fifteen minutes after

feeding, remaining pellets were siphoned out of the tank and counted. The weight of food consumed was determined by multiplying the number of pellets remaining by the average pellet weight ($1.058 \text{ mg} \pm 0.283$; $n = 200$) and subtracting this from the weight of offered pellets. One 50% water change was performed each day. On the last day of the experiment, the fish were reweighed, sacrificed, then placed in a 60 C drying oven for 48 h. A regression based upon samples collected at the end of experimental runs was used to convert the initial wet weights into dry weight [dry weight (g) = $-0.122 + 0.3038 \cdot \text{wet weight}$; $r^2 = 0.97$].

Temperature was controlled within 0.4 C, and salinity was maintained within 0.3 ppt during the acclimation and experimental period. There were 14 deaths during the experimental runs; nine of these were from the 0.5 ppt treatment level. The number of deaths was more evenly distributed among temperature levels (six deaths at 28 C, six deaths at 24 C, two deaths at 20 C), strains (seven deaths for each strain), and tanks (two deaths in three tanks, all others no more than one death per tank).

Instantaneous daily growth rate (G), feeding rate (FR), and gross growth efficiency (K_1) were calculated as,

$$G = (\ln W_t - \ln W_0)15^{-1}$$

$$FR = \left(\sum_{t=0}^{t=15} C_t W_t \right) 15^{-1}$$

$$K_1 = AI^{-1} \cdot 100$$

where W_0 = initial body weight; W_t = body weight on day t , (for FR expression, $W_t = W_0 e^{Gt}$); C_t = weight of food consumed on day t ; $A = W_t - W_0$; and I = total amount of consumed feed. Growth and feeding rates were calculated based upon the 15-day experimental duration.

The experiment represented a balanced split plot design with one replicate (i.e., two experimental runs). Temperature and salinity levels were applied to whole experimental units (tanks), and strain was applied to split units (tagged fish within tanks). Experimental run was considered a random effect. Analysis of variance on instantaneous growth rates was performed using mixed model analysis with initial dry weight as a covariate; temperature, salinity, and strain as fixed effects; and experimental run as a random effect (Littel et al., 1996). Growth rates, adjusted for initial size, met assumptions of normality and homogeneity. Least-square means for growth rates were contrasted for fixed effects using a priori t -tests. Feeding rate and conversion efficiency were computed

TABLE 1. ANALYSIS OF VARIANCE FOR SPLIT PLOT DESIGN OF SALINITY, TEMPERATURE, AND STRAIN EFFECTS ON JUVENILE STRIPED BASS GROWTH RATE (g d^{-1}).

		df	F	Type II error (<i>P</i>)
Main effects	temperature	2	25.73	0.003
	salinity	2	0.02	0.98
	strain	1	4.36	0.04
Interactions	temperature \times salinity	4	1.68	0.25
	temperature \times strain	2	13.49	<0.001
	salinity \times strain	2	2.56	0.08
	temperature \times salinity \times strain	4	4.70	0.001
Residual		187		

for combined fish within tanks, rather than by strain (split unit). Therefore, strain effects could not be determined for these responses. Mixed model analysis of variance (SAS PROC MIXED) was used rather than a general linear variance model because the former provides correct and conservative standard error estimates for main and crossed effects (R. C. Littell, G. A. Millikin, W. W. Stroup, and R. D. Wolfinger, SAS System for Mixed Models, Cary, NC, 1996, unpubl.).

RESULTS

Instantaneous growth rate was significantly affected by temperature, strain, and temperature-strain and temperature-salinity-strain crossed effects (Table 1). Growth rate increased 70% between 20 C (0.057 d^{-1}) and 28 C (0.097 d^{-1}). Growth at 28 C was significantly higher than at 24 C ($P = 0.005$) and 20 C ($P = 0.001$). Growth rates did not differ between 20 and 24 C ($P = 0.20$). Overall, Maryland juveniles showed 22% higher growth rates than did South Carolina juveniles (Table 2). At 28 C, Maryland juveniles exhibited significantly higher growth rates ($P = 0.005$) than did South Carolina juveniles (Fig. 1). No strain effect was detected at 20 C ($P = 0.75$) or 24 C ($P = 0.15$). Contrasts for juveniles reared at 28 C (Fig. 1) showed that Maryland

strain juveniles grew faster than did South Carolina strain fish at 7 ppt ($P < 0.0001$). Within Maryland strain fish, growth rate at 7 ppt was approximately 40% higher than at 15 ppt ($P = 0.01$) and 0.5 ppt ($P = 0.07$).

Temperature had a strong positive effect on *FR* ($P = 0.002$) (Table 3). Feeding rate was 54% higher at 28 C ($12.3\% \text{ d}^{-1}$) than at 20 C ($8.0\% \text{ d}^{-1}$). Salinity and its interaction with temperature showed no detectable effect on *FR* ($P > 0.1$). Temperature, salinity, and their crossed effects showed no significant influence on K_1 ($P > 0.1$). Across temperature and salinity levels, K_1 -values ranged from 27.2–30.7% (Table 3).

DISCUSSION

Maryland strain fish showed higher growth performance under conditions that they would likely encounter in nature during their first summer of life: > 25 C temperatures and oligohaline salinities (Ritchie and Koo, 1968; Dorazio et al., 1991). South Carolina strain juveniles did not show higher performance at 28 C and freshwater conditions (0.5 ppt) that simulated their nursery habitat. Alternatively, because Maryland YOY showed reduced growth at 0.5 ppt and SC fish did not, one could infer "higher-than-expected" growth occurred for South Carolina juveniles in freshwater conditions.

TABLE 2. MEAN GROWTH RATE OF JUVENILE STRIPED BASS (\pm SE) BY STRAIN FOR TEMPERATURE AND SALINITY LEVELS. Sample sizes for each level ranged 35–39 observations.

Effect	Level	South Carolina	Maryland
Temperature	20 C	0.054 ± 0.005	0.057 ± 0.007
	24 C	0.080 ± 0.005	0.063 ± 0.007
	28 C	0.085 ± 0.005	0.109 ± 0.007
Salinity	0.5 ppt	0.074 ± 0.005	0.072 ± 0.007
	7 ppt	0.072 ± 0.005	0.086 ± 0.007
	15 ppt	0.073 ± 0.005	0.072 ± 0.007
Grand mean		0.067 ± 0.004	0.082 ± 0.004

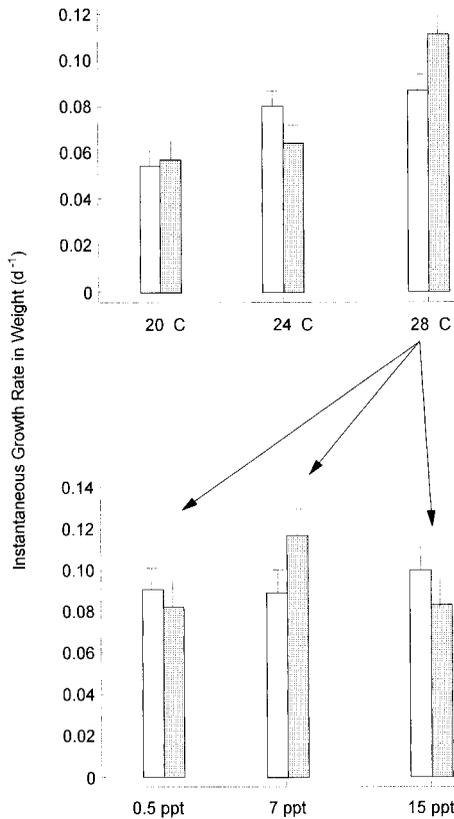


Fig. 1. Growth rate responses of Chesapeake Bay (shaded bars) and Santee-Cooper strain (open bars) young-of-the-year striped bass to temperature (upper panel) and salinity (lower panel). Salinity responses are shown for 28 C only. Standard error bars are shown.

Across temperature levels, similar magnitudes of change in growth rate (70%) and feeding rate (54%), and lack of change in conversion efficiency, indicated that higher growth rates were due to higher consumption rather than by increased assimilation efficiency. In research on Santee-Cooper YOY striped bass (1–3 g), Klyash-

torin and Yarzhombek (1975) reported that routine metabolism increased 73% from 20 C to 28 C, a similar change to that observed for growth rate in our study. Elevated temperatures may cause similar rates of change in routine metabolism, consumption, and growth rates. By similar reasoning, we might expect that higher growth at 28 C by Maryland juveniles was due to rates of consumption that exceeded those of South Carolina juveniles. Unfortunately, the experimental design did not permit a direct evaluation of feeding rates and conversion efficiencies between strains.

Based upon the range of rearing conditions tested, Maryland striped bass reared at 28 C and 7 ppt would be expected to yield highest yield per cost in commercial aquaculture ventures. Because there is no difference in growth conversion efficiency among temperatures, decreased cost would arise through shorter rearing times. Growth probably declines rapidly at temperatures greater than 30 C when temperature becomes sublethal in its effect on metabolism. Cox and Coutant (1981) observed that growth in yearling striped bass (40–300 g wet weight) was maximal at 26 C and became negative at > 30 C.

Maryland juveniles showed a trend of highest growth at oligohaline salinities (7 ppt) over freshwater and mesohaline salinities (Fig. 1), which suggests that physico-chemical preferences correspond with habitat use observed in the field (Ritchie and Koo, 1968; Markle and Grant, 1970). In contrast, growth rates for Santee-Cooper juveniles were relatively invariant across salinity levels at 28 C. In their study on salinity-acclimatized South Carolina juveniles, Klyash-torin and Yarzhombek (1975) observed no significant differences in routine metabolism among salinity levels 0, 7, and 14 ppt. Increased assimilation efficiencies at near iso-osmotic conditions might explain why South Carolina juveniles did as well at 7 and 15 ppt than at the natural salinity level (approximately 0.5 ppt),

TABLE 3. MEAN DAILY FEEDING RATE (g g^{-1} FISH WT) AND CONVERSION EFFICIENCY FOR JUVENILE STRIPED BASS (\pm SE) FOR TEMPERATURE, SALINITY, AND STRAIN LEVELS.

Effect	n	Level	Feeding rate	Conversion efficiency
Temperature	18	20 C	0.080 ± 0.005	0.27 ± 0.02
		24 C	0.092 ± 0.005	0.30 ± 0.02
		28 C	0.122 ± 0.005	0.29 ± 0.02
Salinity	18	0.5 ppt	0.098 ± 0.003	0.27 ± 0.02
		7 ppt	0.099 ± 0.003	0.31 ± 0.02
		15 ppt	0.097 ± 0.003	0.28 ± 0.02
Grand mean	36		0.098 ± 0.001	0.29 ± 0.01

which we assumed would yield an optimum growth rate.

With the exception of the 0.5 ppt, all experimental levels yielded higher growth rates in Maryland than in South Carolina striped bass. Increased growth performance by Chesapeake Bay over South Carolina juvenile striped bass supported Conover's proposal for growth rate variation among latitudes (Conover, 1990; Conover et al., 1997; Brown et al., 1998). In experiments on larvae (8–28 day posthatch) and post-metamorphic juveniles (30–50 days posthatch), Brown et al. (1998) and Conover et al. (1997) observed higher growth rates of Chesapeake Bay, Hudson River, and Nova Scotia strains in comparison to North Carolina, South Carolina, and Florida strains. Temperature levels for their YOY experiments (17 C, 21 C, and 28 C) were similar in range to those chosen in our study, but salinity was held constant at 5 ppt. At 28 C, we observed a similar difference in growth rate between South Carolina and Maryland strains (approximately 20%) to that reported by Conover et al. (1997). In contrast to their study, we observed no strain effect at 24 C, whereas Conover et al. (1997) reported consistent differences in growth rates across all tested temperatures. Differences between the design of the two studies include age (size) of YOY and consideration of salinity effects. Utilization of a larger size range in this study (0.3–11 g wet weight) allowed inferences to be applied to a substantial period of the first growth season of striped bass, but statistical compensation for this large range in sizes (using initial weight as a covariate) probably reduced sensitivity in statistical contrasts among temperature and salinity levels. Statistical inferences on strain effects for our study were mostly limited to salinity level 7 ppt and were similar to Conover et al.'s (1997) results at their nominal 5 ppt level. However, our results did suggest that strains respond differently to salinity. The oligohaline salinity level (7 ppt) resulted in substantially higher growth (40%) than lower or higher salinities in Maryland juveniles only.

Within estuaries and across systems, dispersive behaviors of YOY striped bass are variable (Dorazio et al., 1991; Dovel, 1992; Robichaud-LeBlank et al., 1998). Although we investigated a limited number of broods from only two strains, our results suggest that realized growth rates for a population depend upon distribution patterns and strain-specific responses to hydrographic conditions. In particular, annual variations in distribution within estuaries, thought to be largely determined by year-class strength (Able and Fahay, 1998), could substantially

modify the ecological consequences of a latitudinal cline of YOY growth rates.

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