

**OSMOREGULATORY RESPONSES IN STRIPED BASS *MORONE*
SAXATILIS LARVAE: SURVIVAL, GROWTH, YOLK ABSORPTION,
AND DEVELOPMENT OF CHLORIDE CELLS IN BODY SKIN**

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Summary

Survival, growth, and number of chloride cells were measured during and after exposure to a range of osmotic conditions in anadromous Striped bass *Morone saxatilis* larvae (ages: 9-41 days post hatch). Larvae were held at 0.7ppt prior to salinity challenge tests at 0, 0.1, 0.7, 5, 11, and 33ppt. Higher survival rates were recorded at 11 and 5ppt, while unexpectedly low survival was observed at 0.7ppt. Late yolk-sac larvae showed particularly low survival at 0.7ppt. During this stage, few chloride cells were observed on the integument; these chloride cells increased gradually as larvae developed. Higher yolk absorption rates and lower growth in postflexion larvae occurred at 0.7ppt than at 5 or 11ppt. These results suggest that 5-11ppt result in minimal osmoregulatory expenditures. However, wild larvae mainly distribute in estuarine tidal freshwater habitats (<2ppt) above the salt front. The salt front and associated maximum turbidity zone concentrate the zooplankton prey of larval striped bass. Therefore, we examined salinity tolerance in both starved and fed larvae. At 0.7ppt fed larvae exhibited higher survival than the starved larvae. No significant differences occurred between fed and starved larvae at higher salinities. We speculate that increased energetic costs due to osmoregulation in freshwater may be offset by higher zooplankton prey availability in these habitats.

Introduction

Striped bass *Morone saxatilis* is an anadromous teleost occurring on the eastern coast of North America, which spawns in tidal freshwater habitats in spring and invades salt water during the early juvenile stage. During juvenile

and adult periods, striped bass occur across the broad range of freshwater, estuarine, and marine salinity (Setzler-Hamilton et al. 1981). The early development of eury-haline osmoregulation is poorly known for striped bass, but salinity is known to influence larval and young-of-the year survival and growth rate (Lal et al. 1977; Otwell and Merriner 1977; Secor et al. 2000). Further the ontogeny of osmo-regulation may provide insight to the evolution of this taxa. Waldman (1986) has proposed that anadromy in Moronidae which may be derived from an ancestral marine form despite the general proposal by Gross (1987) that anadromy is derived exclusively from freshwater ancestors.

During larval period, striped bass in the Chesapeake Bay distributes in 0-2ppt, which is the area of salt front between FW and brackish water overlapping broadly with the maximum turbidity zone (Secor and Houde 1995; Secor et al. 1995), but in rearing experiments, 3-12ppt is believed to be optimal for their survival and growth (Lal et al. 1977). In teleosts occurring in freshwater, branchial chloride cells play a chief role in ion uptake (Flik et al. 1996). Because larvae have undifferentiated gills, chloride cells in body skin are believed to be important in ionoregulation (Hiroi et al. 1998). This study examines the osmotic response of fed and starved striped bass larvae to a range of estuarine salinity (0.7-11ppt), by observing differences in survival, growth, yolk absorption, and number of chloride cells.

Materials and Methods

Striped bass larvae (9 days post hatch) originating from Patuxent River broodstock (Chesapeake Bay, Maryland) were obtained from a Maryland Department of Natural Resources hatchery on April 26th, 1999. Larvae were transported to Chesapeake Biological Laboratory (CBL) at 19 °C and 0.7ppt salinity, and were subsequently held under these same conditions in 100-liter tanks. Water temperature in the stock tanks increased gradually to simulate natural conditions in the Patuxent River so that at experiments' end (41 days post hatch), temperature reached to 25 °C. Twenty percent of the water in stock tanks was changed daily. Finfold larvae (9-19 days post hatch) were fed *Artemia* spp. nauplii cultured at 5ppt and enriched by DHA (Docosahexaenoic acid). From 20 days post hatch, larvae were fed artificial diet (0.4mm Kyowa ©). Subsamples of 30 larvae were drawn from the stock tank on the first day of salinity challenge trials. They were fixed by 4% normal formalin in phosphate buffer (pH 7.1) or Bouin solution for 24 hours and preserved in 70% ethanol at 4 °C for later immunocytochemical analysis.

Salinity challenge trials were initiated 13, 18, 23, 30, 37 days post hatch. Six salinity levels (0, 0.1, 0.7, 5, 11, and 33ppt), each replicated thrice were established using 1-liter beakers. Thirty larvae were transferred from the stock tank (0.7ppt) to each beaker, and they were observed at 0, 1, 3, 6, 12, 24, 48, and 72 hours after transfer. Dead larvae were removed by pipette. After the test, surviving larvae were fixed and preserved as described above. Larvae were not fed in this set of salinity challenge trials.

The effect of feeding on osmotic responses was examined for the second series of trials. Larvae (18, 23, 30, 37 days post hatch) were introduced to 3 salinity levels (0.7, 5, 11ppt) and two feeding levels (unfed and fed *Artemia* spp. nauplii with 500 individuals l^{-1}), each replicated thrice in 1-l beakers. Larvae in fed treatments were fed at 1 and 24 hours after transfer. Temperatures were maintained between 18-22 C and did not differ among treatment levels. Dead larvae were recorded during the trials and all larvae at trials end were fixed and preserved as described above.

A third set of short-term 4-days growth trials were conducted for post-flexion larvae (30 days post hatch) supplied with artificial diet and reared at 0.7, 5, 11ppt in 30 liter tanks. Each of three replicates was supplied with 300 larvae and samples (n=30) were fixed in formalin 0, 2 and 4 days. Temperature ranged 20-22 C and larvae were fed artificial diet (600mg day^{-1}) in each treatment.

From preserved material in the first set of trials (0.7, 5, and 11ppt), yolk absorption during the period of 13 days post hatch was estimated by measuring the largest lateral areas of yolk. The yolk areas were traced on paper using a light microscope with a camera lucida. Images were digitized with a flat bed scanner (Canon, Japan) and were measured using public domain U.S. National Institute of Health image analysis software. A mean diameter was calculated for yolk areas. Yolk was assumed to be spherical ($4/3\pi r^3$), and its volume was calculated by the mean diameter.

To detect chloride cells in the yolk-sac membrane and body skin, antiserum specific for Na^+ , K^+ -ATPase α -subunit was used as a specific probe (Ura et al. 1996). Chloride cells were stained by whole mount immunocytochemistry based on the avidin-biotin-peroxidase complex (ABC) method (Hsu et al. 1981) using commercial reagents (DAKO sABC kit, Glostrup, Denmark). The method of staining followed the method of Hiroi et al. (1998). For the quantitative analysis, three sites each 1 mm^2 were selected randomly in the larva's body, and densities and sectional areas of chloride cells were

estimated. These measurements were performed by the same method described above for estimation of yolk volume.

All data are expressed by means and standard errors. For the comparison of salinity tolerance between experimental salinity, survival rates of unfed larvae at 72 hours were analyzed in each phase. Also, comparison of salinity tolerance between fed and unfed fish was analyzed with the survival at 48 hours. Significant differences in all data were conducted by Turkey-Kraimer test for multiple comparison after one way analysis of variance.

Results

Striped bass larvae under unfed condition showed highest survival at 5 or 11ppt throughout the early ontogeny, despite acclimation to 0.7ppt in the stock tank (Table 1). Late yolk-sac larvae exhibited particularly low survival at 0.7ppt compared to other stages. In addition, the density of chloride cells in body skin was lower during this stage. Although the sectional area of chloride cells did not change through development (Figure 1), the density of chloride cells tended to increase throughout the ontogeny.

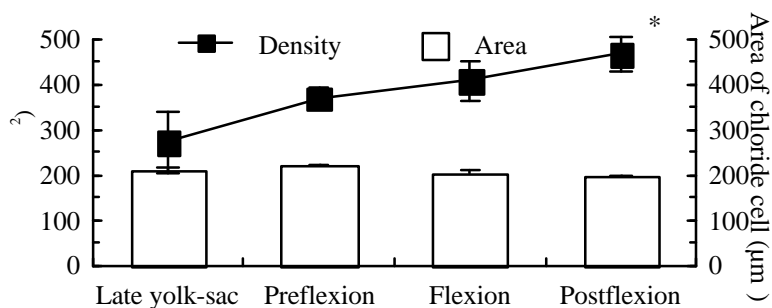


Figure 1. Development of skin chloride cells in density and sectional areas. Data are means±S.E.M. An asterisk in density indicates significant differences ($p>0.05$).

No larvae survived at both 0ppt and 33ppt, and survival was very low at 0.1ppt. A significant ontogenetic effect on salinity tolerance occurred for 0.7ppt: survival at this level was higher for post-flexion larvae and juveniles than for early stage larvae. Further in development, juveniles exhibited some tolerance to 33ppt level (11% survival) but not at 0ppt (Table 1).

Table 1. Survival rate of striped bass at 72 hours exposed to test salinities during early life history. Data are means±S.E.Ms based on three replicates. Within a column, means with the same letter are not significant differences ($P>0.05$).

Salinity	Late Yolk-sac	Prelexion	Flexion	Postflexion	Juvenile
0ppt	0.0±0.0 a	0.0±0.0 a	0.0±0.0 a	0.0±0.0 a	0.0±0.0 a
0.1ppt	0.0±0.0 a	1.6±1.6 a	2.0±2.0 a	5.5±4.0 a	14.5±12.8ab
0.7ppt	3.2±3.2 a	29.9±29.9ab	6.7±18.9ab	35.7±15.6ab	50.0±14.7b
5ppt	67.9±7.7 b	46.4±11.6ab	82.1±7.8 b	59.2±10.4 b	55.5±8.5 b
11ppt	80.3±10.7 b	77.5±5.5 b	67.2±17.7b	41.4±11.5ab	56.8±13.0 b
33ppt	0.0±0.0 a	0.0±0.0 a	.0±0.0 a	0.0±0.0 a	11.0±6.6 a

Estimated yolk volumes of late yolk-sac larva (13 days post hatch) in 0.7ppt was significantly smaller after 72 hours transfer than those of larvae in 5 or 11ppt, indicating a higher yolk utilization rate (Figure 2). Growth increments of post-flexion larvae indicated significant differences at 4 days after transfer; growth increments were highest, intermediate, and lowest at 11ppt, 5ppt, and 0.7ppt, respectively (ANOVA: $p<0.05$) (Figure 3).

At 0.7ppt salinity level, fed larvae at pre-flexion and flexion phases showed substantially higher survival (92%, 94%, respectively) than unfed larvae (30%, 37%, respectively). During these phases, in contrast to unfed larvae that showed lower survival at 0.7ppt than at higher salinities, fed larvae showed no significant differences in survival among salinities. Regardless of feeding level, post-flexion larvae and juveniles did not exhibit similar survival responses across salinity levels (Table 1, Table 2).

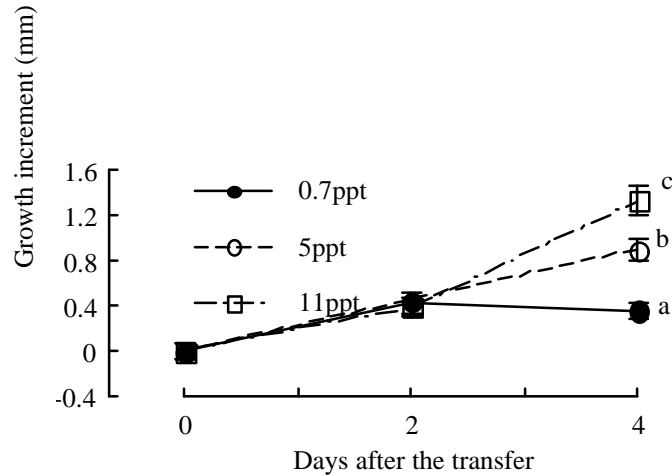


Figure 3. Growth increments to salinity in larval striped bass (30 days posthatch; post-flexion period). Growth increments are calculated as follow: Growth increment (mm) = SL (mm) at each days - Mean SL (mm) at Day 0. The letters on right shoulder of mean at Day 4 indicate significant differences ($p>0.05$).

Table 2. Comparison with survival at 48 hours after exposure between fed and unfed larvae. All data are means and standard error based on three replicates. The same letter below means is not significant differences ($p>0.05$).

Salinity	Feeding	Preflexion	Flexion	Postflexion	Juvenile
0.7ppt	Unfed	29.9±29.9 a	36.7±18.9 a	35.7±15.6 a	50.0±14.7 a
	Fed	91.7±3.4 ab	94.0±0.5 b	64.3±8.9 a	69.9±18.3 a
5ppt	Unfed	46.4±11.6ab	79.2±4.5 ab	59.2±10.4 a	55.5±8.5 a
	Fed	97.0±1.8 b	93.8±3.8 b	78.6±5.4 a	53.6±16.1 a
11ppt	Unfed	77.5±5.5 ab	67.2±17.7 ab	41.4±11.5 a	56.8±8.5 a

Fed	98.5±0.8 b	96.1±2.4 b	78.4±5.5 a	100.0±0.0 a
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Discussion

Survival rate of larvae transferred to 0.7ppt increased in later stages of development, but no larvae could survive at 0ppt and 33ppt until transformation to juvenile. On the other hand, in young juveniles, moderate survival was observed even exposed to SW (33ppt) (Table 1.), suggesting the lack of full-euryhalinity prior to the completion of larva to juvenile transformation. Although the larvae used for experiments were reared at 0.7ppt, higher survival was recorded at 5 and 11ppt than those at 0.7ppt. Similar to our results, Lal et al. (1977) reported 3-12ppt as the optimal salinity for larval survival of striped bass. Morgan II et al. (1981) found that salinity tolerance of newly hatched larvae varied with temperature, and that the highest survival at optimal temperature conditions (ca. 18 C) was obtained at 10ppt. Other studies also provide evidence that the optimal salinity of striped bass larvae is in the range of 5-11ppt as observed in this study (Minton and Harrell 1990; Winger and Lasier 1994). Body fluid of teleosts is osmotically equivalent to one third SW (11ppt) (Evans, 1984), therefore the fish reared at 11ppt is expected to consume minimal energy for osmoregulation. Maybe this is the most probable explanation for higher survival rate found at 5 or 11ppt.

Density of chloride cells in body skin in striped bass larvae at 0.7ppt increased gradually as development proceeded (Figure 1), in parallel to the increase of survival rate at 0.7ppt. Although not statistically significant ($p=0.1326$), late yolk-sac larvae (13 d post hatch) had less chloride cells than pre-flexion larvae and flexion larvae. Chloride cells in body skin is suggested to serve a role for SW adaptation during larval stages of teleosts (Shiraishi et al.1997; Hiroi et al.1998; Katoh et al. 2000). Moreover, yolk-sac larvae reared in FW also have chloride cells on their yolk-sac membrane, with size changing in response to environmental salinity (Kaneko et al. 1995;

Shiraishi et al. 1997). Taken together with our result, chloride cells in larval striped bass possibly support hyperosmoregulation in low salinity areas of nursery habitats. Distribution of branchial chloride cells in chum salmon fry in FW (Uchida et al. 1996) and FW acclimated Japanese sea bass (Hirai et al. 1999), are different from those of SW adapted fish. Chloride cells of FW fish also increase their density when transferred to soft water or experimentally prepared low calcium water (Perry and Wood 1985, McCormick et al. 1992, Greco et al. 1996), suggesting a role of gill chloride cells play a role to ion uptake in freshwater. Therefore, it is expected that chloride cells in body skin of striped bass larvae is similarly involved in ion uptake in hypo-osmotic environments.

Experimental results indicate that larvae encountering hypo-osmotic conditions might expend greater amounts of energy on basal metabolism. Yolk absorption of the late yolk-sac larvae at 0.7ppt was significantly higher than at 5 or 11ppt and growth at post-flexion larvae at 0.7ppt was significantly slower than at 5 or 11ppt. Finally, for low salinity treatment survival was substantially enhanced by feeding larvae (Table 2). Eggs and larvae of teleosts generally regulate their internal osmolarity at a level near those of the body fluids of adults (Alderdice, 1988). To maintain this level, Na^+ , K^+ -ATPase within chloride cells is well known to regulate ionic balance (Kamerky et al. 1976). Low osmotic stress and rate of yolk utilization was reported for catadromous *Chanos chanos* larvae at 15ppt, perhaps due to iso-osmotic conditions (Swanson, 1996). Under osmotic stress, larvae may consume their yolk to produce this enzyme and ATP, and the consumption might make higher mortality of unfed striped bass larvae at 0.7ppt. However, for a Canadian population of striped bass, Peterson et al. (1996) observed yolk utilization in larvae originating from a Canadian population, and found higher yolk utilization in larvae at 10ppt than those at 1 or 5ppt. Although the difference between fish in our study and Canadian population might be caused by populational differences, our study suggests that iso-osmotic condition (11ppt) is an optimal salinity of survival and growth of striped bass larvae in Chesapeake Bay.

In the field, striped bass eggs and larvae distribute in 0-2ppt (Setzler-Hamilton et al. 1981, Uphoff 1989, Secor et al. 1995, Robichaud-LeBlanc et al. 1996, Rutherford et al. 1997), which is a substantially lower salinity than the optimum indicated by our laboratory experiments. Our feeding experiment, however, demonstrated that survival of fed larvae in expected natural nursery conditions (0.7 ppt) was nearly two-fold higher than survival of unfed larvae (Table 2). We believe that food provided an important subsidy of internal stores of energy and ions and needed to maintain osmolarity at iso-osmotic salinity. To determine specifically the role of diet on osmore-gulation will require more detailed.

Our result suggests that increased osmotic costs associated with hypo-osmotic nursery conditions could be offset by increased foraging opportunities in these environments. Indeed, tidal salt front regions (0-2ppt) are also often characterized by local peaks in zooplankton is commonly observed (Beaven and Mihursky 1980, Setzler-Hamilton et al. 1981, Tsai et al. 1991, Secor et al. 1995, McGovern et al. 1996). Also, the ichthyoplankton surveys in the upper Chesapeake Bay indicate that the salt front and associated maximum turbidity zone contain high abundance of both striped bass and white perch *Morone americana* larvae distribute in that zone (North and Houde, Chesapeake Biological Laboratory, personal communication,) and in the Patuxent and Potomac sub-estuaries, peak density of Moronidae larvae occur where conductivity is $< 800 \mu\text{mhos}/\text{cm}^2$, near or upriver from the maximum turbidity zone (Secor and Houde 1995, Rutherford et al. 1997). In a larval tagging study by fluorescent marker, Secor et al. (1995) released striped bass larvae above and below the salt front and observed complete mortality of those released below the salt front. They suggested that the salt front is an important retention feature curtailing downstream dispersal by early stage larvae. Dovel (1981) in his critical zone hypothesis proposed that benefits attributed to this oligohaline nursery zone included both increased prey availability due to a hydraulic retention front, and lower predation due to high turbidity (Dovel 1981, Secor et al. 1998).

Thus, although oligohaline nurseries may impose energetic costs due to osmoregulation, these costs may be offset by ecological attributes of the nursery zone.

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