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DEVELOPMENTAL ANATOMY AND INFLATION OF THE GAS BLADDER IN STRIPED BASS, *MORONE SAXATILIS*

In 1974, a percentage of striped bass, *Morone saxatilis*, fingerlings reared at the Cooperative Fishery Research Laboratory, Southern Illinois University, lacked an inflated gas bladder. The purpose of this study was to describe the de-

velopmental anatomy of the gas bladder and its associated structures in striped bass so that a better understanding of the inflation mechanism could be obtained.

With regard to gas bladder morphology, bony fishes are classified as physostomes or physoclists. Generally, the more ancient, soft-rayed fishes (Malacopterygii) are physostomous, while the more modern, spiny-rayed fishes (Acanthopterygii) are physoclastic (Lagler et al. 1962). A physotome possesses a hollow connection, the pneumatic duct, between the gut and the gas bladder throughout its entire life. Some physotomes gulp surface air through the pneumatic duct to initiate inflation of the gas bladder (Tait 1960). Fish that are physoclastic do not possess this open connection as adults. Some physoclists, however, do possess a pneumatic duct as larvae, but the duct atrophies prior to adulthood. Günther's (1880) examinations have shown that adult striped bass are physoclastic. Doroshev and Cornacchia (1979) give a partial description of the development of the gas bladder in striped bass.

Several theories have been advanced to explain how the gas bladder is initially inflated in fishes that do not gulp surface air or are physoclastic prior to initial inflation. Some of these theories include: gases produced by the disintegration of organic materials (Powers 1932); production of gasses as a result of digestion (Johnston 1953); vacuolation of the gas bladder epithelia (McEwen 1940); and functioning of a rete mirabile, or gas gland (Schwarz 1971).

Methods

Histomorphological Studies

Striped bass larvae were obtained from the Hudson River, N. Y., and Lake Charles, La. Upon arrival, the 1- to 4-day-old larvae were transferred into 200 l aquaria and maintained at 16°-18° C. Brine shrimp, *Artemia salina*, were fed regularly to the larvae. Eighty-three striped bass larvae 4.3-24 days old (from the time of hatching) were removed from the aquaria and prepared for histological study. The larvae were fixed in either 10% Formalin¹ or Bouin's fluid, dehydrated in a series of graded alcohols, cleared in benzene, and embedded in Carbowax. From a representative

¹Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

series of 34 larvae, we prepared transverse and longitudinal series sections 7 and 10 μm thick (Table 1). The mounted specimens were stained with either Harris's hematoxylin and eosin or a modification of Mallory's connective tissue stain (Martan²).

TABLE 1.—Number of striped bass larvae sectioned to determine the internal anatomy of the gas bladder and its associated structures.

Age (days)	With inflated gas bladder	Without inflated gas bladder
4.3	1	2
4.8	2	3
5.5	2	2
6.0	5	1
7.0	2	0
8.0	2	2
14.0	0	3
21.0	0	1
24.0	4	2

Results

During laboratory aquaria experiments, striped bass larvae were observed with inflated gas bladders as early as day 4. A peak period of inflation occurred during day 5, closely corresponding with the absorption of the yolk sac. Doroshev and Cornacchia (1979) found that striped bass inflated their gas bladder from the 5th to the 7th day.

Striped bass larvae with inflated gas bladders were easily distinguished from larvae with uninflated gas bladders. Morphologically, the newly inflated gas bladder has the general appearance of a small air bubble, located dorsal to the gut. Behaviorally, larvae that had inflated gas bladders oriented horizontally within the water column and maintained their position without continual swimming motion. Larvae without inflated gas bladders assumed a vertical swimming position, sinking when swimming movements ceased. This characteristic swimming behavior of larvae with noninflated gas bladders was defined as "swim-up" behavior.

In 4.8-day-old striped bass larvae, the noninflated gas bladder primordium was dorsal and slightly posterior to the junction of the esophagus and the stomach. The stomach was at the right of the dorsomedial gas bladder primordium. The walls of the noninflated gas bladder primordium were much thicker ventrally than either dorsally

or laterally. Columnar epithelium comprised the ventral mass of the gas bladder primordium. The noninflated gas bladder possessed a slight, dorsally located lumen. An open pneumatic duct connected the foregut with the right side of the posterior wall of the gas bladder primordium. The duct was composed of a single layer of cuboidal epithelium, surrounded by a layer of connective tissue.

A network of arterioles and venules, a rudimentary rete mirabile, ran parallel and ventral to the noninflated gas bladder primordium. At the posterior end of the gas bladder, the rete arterioles and venules turned dorsoanteriorly and entered a layer of loose connective tissue adjacent to the ventral columnar epithelium of the gas bladder. Within this connective tissue, a network of capillaries connected the arterioles and venules. Since the rete mirabile proceeded directly to the secretory epithelium of the gas bladder, the whole structure may properly be called a gas gland (Steen 1970). A gas gland is formed in striped bass before the initial inflation of the gas bladder.

In older (8 days) striped bass larvae that still had a noninflated gas bladder, the capillary network was more developed and pushed closer to the ventral columnar epithelium of the gas bladder. This gave the epithelium a festooned appearance.

In striped bass larvae that were in the process of inflating their gas bladders, the initial inflation occurred at the anterior end of the gas bladder. The columnar epithelium, which previously had dominated the ventral wall of the gas bladder, became confined to the posterior portion of the gas bladder as inflation progressed. At no time were distinct vacuoles visible within the ventral, columnar epithelium.

In 5.5-day-old striped bass larvae that possessed an inflated gas bladder, the ventral epithelium was reduced to cuboidal epithelium and was restricted to the posteriorventrad portion of the gas bladder where it was in close association with the gas gland. The remaining walls of the inflated gas bladder were composed of stretched epithelium. The rete mirabile still ran parallel and ventral to the newly inflated gas bladder. Capillaries of the rete mirabile made contact with secretory epithelium towards the posterior of the gas bladder.

In all striped bass larvae which were 4.3-5.5 days old and possessed an inflated gas bladder, a

²Martan, J. 1968. Laboratory instructions: Histological techniques in zoology. South. Ill. Univ., Carbondale, 98 p.

pneumatic duct with a well-defined lumen still appeared to form a connection between the gut and the gas bladder. However, in the older larvae of this group, the lumen of the pneumatic duct was smaller. In some sections, the openings between the pneumatic duct and the gut and the pneumatic duct and the gas bladder were not plainly visible, indicating that the pneumatic duct was beginning to atrophy.

We examined 14- and 21-day-old striped bass larvae without inflated gas bladders, and 24-day-old larvae with and without inflated gas bladders. In 14-, 21-, and 24-day-old larvae that had noninflated gas bladders, a well-developed rete mirabile still ran ventral and parallel to the gas bladder, turning dorsally to make a medial connection. The retail capillary network was developed, distending the overlaying connective tissue into a villuslike structure which was bordered by the ventral, columnar (secretory) epithelium of the gas bladder. The villuslike projections occupied most of the internal volume of the gas bladder. The pneumatic duct was well defined and continued to connect the gut with the gas bladder.

In 24-day-old striped bass larvae that had inflated gas bladders the pneumatic duct was absent. Unfortunately, we did not collect any striped bass larvae with inflated gas bladders between day 8 and day 24. We were thus unable to accurately describe the atrophication of the pneumatic duct, which seemingly occurs after inflation of the gas bladder. The rete mirabile was connected to a narrow band of cuboidal epithelium at the ventromedial wall of the gas bladder.

Discussion

Striped bass larvae possess an open pneumatic duct. An experiment designed to determine if striped bass have to gulp surface air to initiate gas bladder inflation was inconclusive, as was a similar experiment conducted by Doroshev and Cornacchia (1979). However, allowing striped bass larvae unobstructed access to the surface did not guarantee inflation in either study.

In our study, the pneumatic duct had atrophied in 24-day-old larvae which had inflated their gas bladders, but an open pneumatic duct was still present in 24-day-old larvae which had not inflated their gas bladders. This suggests that inflation of the gas bladder stimulates the at-

rophication of the pneumatic tube in striped bass. Johnston (1953) observed a similar phenomenon in the largemouth bass, *Micropterus salmoides*.

The rete mirabile, or gas gland, is developed before initial inflation of the gas bladder in larval striped bass. Since the gas gland concentrates gases within the gas bladders of many adult fishes, it is reasonable to assume that the gas gland plays a role in achieving initial inflation of the gas bladder in larval striped bass. The continued presence of a gas gland, and the prolonged retention of an open pneumatic duct in striped bass larvae that had not achieved initial inflation of the gas bladder within 24 days suggests that initial inflation may occur over an extended period of time.

Other workers have indicated that failure to initiate inflation of the gas bladder may lead to slower growth rates (Tait 1960), a higher percentage of morphological abnormalities (Baker³), and an increased susceptibility to stress (Lewis et al.⁴). Studies designed to define the stimuli responsible for the initiation of gas bladder inflation in striped bass, an important sport fish species that is often cultured, would be beneficial.

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³Baker, J. F. 1975. The rearing of Hudson River striped bass at the Edenton National Fish Report prepared for Consolidated Edison Company of New York, Inc., 30 p.

⁴Lewis, W. M., R. C. Heidinger, and B. L. Tetzlaff. 1977. Striped bass rearing experiments 1976. Report prepared for Consolidated Edison Company of New York, Inc., 197 p.

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FOOD OF AGE 1 AND 2 ATLANTIC TOMCOD, *MICROGADUS TOMCOD*, FROM HAVERSTRAW BAY, HUDSON RIVER, NEW YORK

Atlantic tomcod, *Microgadus tomcod* (Walbaum), are opportunistic feeders (Howe 1971; Grabe 1978) with amphipods *Gammarus* spp. and the decapod *Crangon septemspinosa* identified as primary prey (Howe 1971; Alexander 1971; Scott and Crossman 1973; Grabe 1978; Nittel¹). Limited data are available on the biology of yearling and older Hudson River tomcod due to their low overall abundance and because they are most abundant during winter when ice cover restricts sampling. This note summarizes feeding data of 339 tomcod, ages 1 and 2, from the Haverstraw Bay area of the Hudson River (37.5-41.5 mi north of the Battery, New York City) on 19 dates, January 1973-June 1976, and supplements food preference data on juveniles (Grabe 1978). All fish were collected as part of an ecological monitoring program conducted by Lawler, Matusky & Skelly Engineers for Orange and Rockland Utilities, Inc.

Methods

Collections (Table 1) were made with a 9.1 m

¹Nittel, M. 1976. Food habits of Atlantic tomcod (*Microgadus tomcod*) in the Hudson River. In Hudson River Ecology. Fourth Symposium on Hudson River Ecology. Bear Mountain, N.Y., March 28-30 1976. Hudson River Environmental Society, Inc.

TABLE 1.—Collections of age 1 and 2 Atlantic tomcod from Haverstraw Bay, Hudson River, 1973-76.

Season	Sample size	Total length (mm)	
		Mean	95% confidence limits
Winter (Jan.-Feb.)	72	130.5	126.2-134.7
Spring (Apr.-June)	166	158.7	155.8-161.6
Summer (July-Aug.)	10	156.3	142.2-170.3
Fall (Oct.-Dec.)	91	182.6	178.3-186.8

otter trawl (64 mm mesh cod end liner) towed against the tide at 1.5-2.0 m/s during both day and night. The data are likely to be biased towards daytime feeding preferences since almost twice as many tows were taken during daytime as at night. Diel differences in feeding could not be evaluated because day and night collections were often combined for other analyses. Fish were preserved in 10% buffered Formalin.² In the laboratory they were measured (± 1 mm total length, TL) and weighed (± 0.1 g), and the stomachs were removed and preserved in 70% ethanol. Prey were identified and counted, and the contents of 195 stomachs were dried at 103° C. The number of fish per sampling period whose stomach contents were analyzed were limited by contract and were randomly selected from the total catch. Whenever possible, I analyzed additional fish to increase both sample size and temporal coverage. Yearling and older tomcod collected during fall 1973 were separated from young-of-the-year by examination of length-frequency histograms drawn from larger samples (Lawler, Matusky & Skelly Engineers³); by this method age 1 and 2 fish were those ≥ 160 mm TL. On other sampling dates young-of-the-year were present only as larvae or as juveniles < 110 mm TL.

Food preference data were classified seasonally and examined as percentage occurrence (number of fish in which prey item "a" occurred/total number of fish), percentage composition (number of prey item "a"/total number of prey), and as importance, I, the geometric mean of these two measurements (Windell 1971). This approach, however, may overestimate the utilization of smaller prey (e.g., copepods) but should provide a better indication of feeding preference than either percent occurrence or percent composition taken singly. An index of fullness (Windell 1971), I_f , was calculated to evaluate feeding intensity (dry

²Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

³Lawler, Matusky & Skelly Engineers. 1976. Environmental impact assessment—water quality analysis: Hudson River. Natl. Comm. on Water Quality. NTIS PB-251099.