FIELD AND LABORATORY OBSERVATIONS ON DIURNAL SWIM BLADDER INFLATION-DEFLATION IN LARVAE OF GULF MENHADEN, *BREVOORTIA PATRONUS*

D. E. HOSS[1] AND G. PHONLOR[2]

ABSTRACT

Diurnal swim bladder inflation-deflation in gulf menhaden larvae was studied at sea and in the laboratory. At sea, the larvae filled their swim bladders at night and deflated them during the day. Laboratory experiments in which the larvae were either prevented or allowed to reach the air-water interface demonstrated that the larvae fill their swim bladder each night by swallowing air. These results agree with the findings of other investigators and suggest that diurnal swim bladder inflation may be a common characteristic in the late stage larvae of clupeoid species.

The swim bladder in fishes has been assigned various functions, the most widespread being the regulation of buoyancy. Recent work on clupeoid species, however, has shown that the function of the swim bladder changes with ontogeny. In adults of at least two clupeoids—Atlantic herring, *Clupea harengus*, and Atlantic menhaden, *Brevoortia tyrannus*—the swim bladder is thought to serve as a reserve of gas for the adjustment of hydrostatic pressure in the gas-filled bulla, allowing the bulla membrane to maintain acoustic sensitivity independently of depth. The swim bladder's role as a buoyancy regulating organ is secondary (Blaxter and Hunter 1982). During the late larval stages of some clupeoids, however, buoyancy provided by an inflated swim bladder may have an important function. Hunter and Sanchez (1976), working with the pelagic larvae of the northern anchovy, *Engraulis mordax*, proposed that an observed diurnal inflation and deflation of the swim bladder by larvae is an energy-sparing mechanism. In this case, one function of the inflated swim bladder is to provide buoyancy that allows the larvae to "rest" during the night when they are unable to see to feed. This diurnal inflation and deflation of the swim bladder has also been reported for other larval clupeoids by Uotani (1973).

The objective of this study was to determine if a diurnal swim bladder inflation-deflation rhythm exists in larval gulf menhaden, *Brevoortia patronus*, under natural conditions and, if so, to evaluate the mechanism of inflation in the laboratory.

The swim bladder in gulf menhaden is similar to that described for Atlantic menhaden by Hoss and Blaxter (1981). In the Atlantic species the anlage of the swim bladder is present at 10 mm standard length (SL), and the pro-otic bullae first appear at 12.5 mm and may contain gas soon after. The swim bladder first contains bubbles of gas in 13 mm SL larvae, and the lateral line first appears in larvae of about 17 mm. In the fully developed system, narrow ducts connect the swim bladder to the gas-filled bullae which are close to the labyrinth of the inner ear. The bullae-swim bladder system is in turn connected to the extensive lateral line on the head of adult fish through a membrane in the skull. As in other clupeoid species (Blaxter and Hunter 1982), menhaden apparently swallow air to initially fill both the bullae and the swim bladder. As there is no evidence for gas secretion in menhaden, it is also assumed that they replace lost gas by regularly swallowing air into the alimentary canal and then by transferring it to the swim bladder through the pneumatic duct. The swim bladder is deflated by diffusion and by reversing gas movement in the above pathway. Unlike some clupeoids, menhaden have no direct connection between the swim bladder and the anal opening (Tracy 1920).

METHODS

At Sea

Gulf menhaden larvae were obtained in the northern Gulf of Mexico off Southwest Pass, La.,

[1]Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516-9722.
[2]Fundacao Universidade do Rio Grande, 96.200 Rio Grande, RS, Brazil.

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at the mouth of the Mississippi River in December 1981 (RV *Oregon II* cruise 123) and December 1982 (RV *Oregon II* cruise 131). On cruise 123, larvae were collected by oblique or surface tows of either a multiple-opening closing net and environmental sensing system (MOCNESS) (Wiebe et al. 1976), a neuston net, or an opening-closing paired BFN-1 net[3]. The sampling scheme was modified on cruise 131 in that only the MOCNESS system was used and duplicate samples were taken at fixed depths (1, 8, and 20 m) during a 24-h period of time. On board the ship, menhaden larvae were removed from the samples, measured to the nearest 0.1 mm SL, and examined for the presence of gas in the swim bladder. Gas in the swim bladder was easily observed before pigmentation of larvae (Fig. 1). In inflated bladders, a light-refractive bubble is obvious while a deflated bladder appears under the microscope as a flattened sac (Doroshev et al. 1981). Maximum width and length of the swim bladder (with or without gas) was measured to the nearest 0.02 mm, and volume was calculated by the equation for a prolate spheroid, $V = 4/3\ \pi ab^2$, where a is half the maximum bladder length and b is half the maximum bladder width (Hunter and Sanchez 1976). Approximate changes in volume of the swim bladder due to increased pressure at increased depth of capture were calculated from Boyle's law $\frac{P_1}{P_2} = \frac{V_2}{V_1}$ where P is pressure and V is volume, and temperature is assumed to be constant. After being measured, larvae were preserved in 5% Formalin[4].

In the Laboratory

Experiments to determine if larvae filled the swim bladder by gulping in air at the water surface utilized larvae hatched from eggs in the laboratory (Hettler 1983). Larvae were reared on the rotifer *Brachionus plicatilis*, also cultured in the laboratory. As larvae grew older, their diet was supplemented with newly hatched *Artemia* nauplii. Before being used, larvae were held in 80 l tanks at a water temperature of 20°C, salinity of ca. 25‰, and a 12 h light-12 h dark photoperiod without a dawn or dusk transition.

Three hours before the start of the experiment, 15-20 larvae were transferred from the rearing tanks to each of eight 10 l tanks, and 10 larvae were measured and observed for the presence of gas in the swim bladder. A 500 μm screen was then placed below the water surface (Fig. 2) in four of the experimental tanks to prevent access of the larvae to the air-water interface. In the other four tanks, larvae had access to the air-water interface. During the experiment, the 12-h-light photoperiod was continued. Larvae sampled at ca. 1800, 2100, 0630, 0900, and 1230 h were measured and observed for gas in the swim bladder.

[3]Tarez and Co., 8460 S.W. Street, Miami, FL 33143.

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

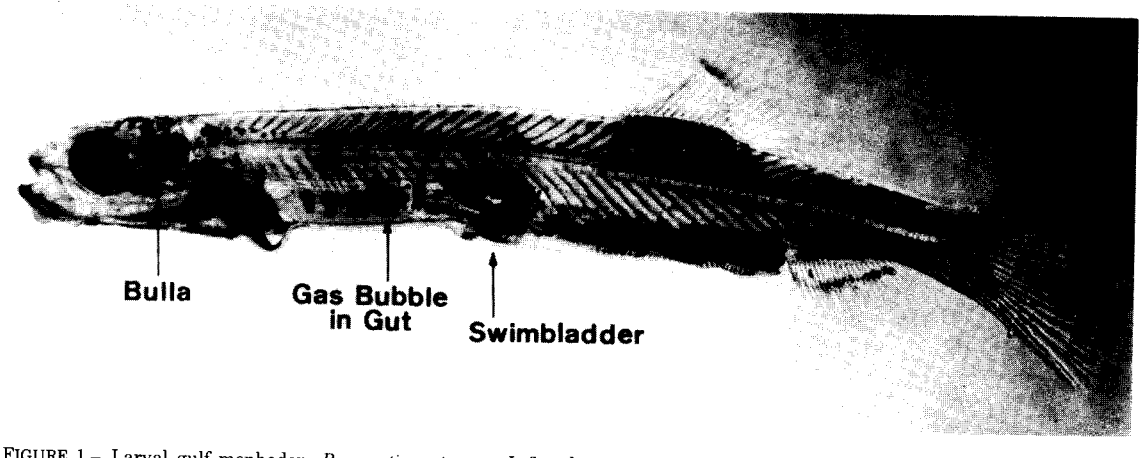

FIGURE 1.—Larval gulf menhaden, *Brevoortia patronus*. Inflated swim bladder, gas-filled bullae, and gas bubble in foregut are indicated by arrows.

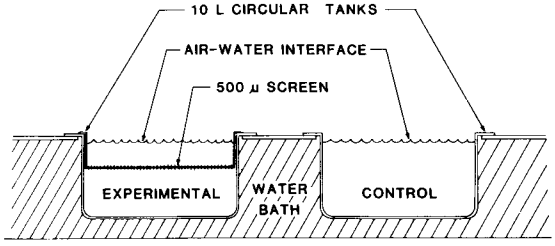

FIGURE 2.—Cross section view of tanks used in laboratory experiments to determine if larvae of gulf menhaden, *Brevoortia patronus*, fill the swim bladder at the water surface.

RESULTS

At Sea

The percentage of larvae having gas in the swim bladder was much greater at night than during the day (Fig. 3). The number of larvae with gas increased within an hour of sunset and decreased within an hour of sunrise (i.e., within the twilight periods). Although sample size was sometimes small (8-10 fish), the combined data for the two cruises were consistent.

The volume of gas in the swim bladder of larvae captured at night was greater than the volume of gas in larvae captured during the day (Table 1). There was a significant difference between the day and night volumes, where sample size was sufficient to allow testing. Sunrise and sunset samples were not significantly different (t-test, $P > 0.05$) from daylight samples.

Gulf menhaden larvae showed a diurnal pattern of depth distribution that seemed to contrast the pattern of swim bladder inflation (Table 2). Night sampling (1700-0600) indicated that larvae were present from the surface down to at least 20 m, the deepest samples taken. Maximum water depth at

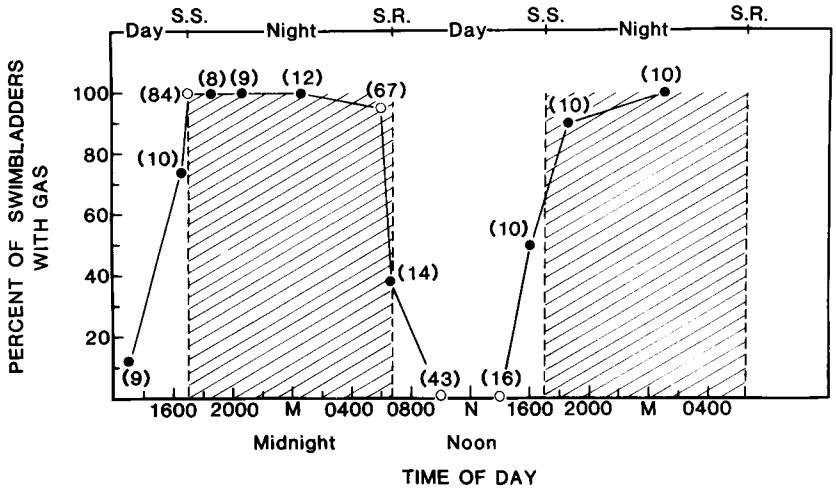

FIGURE 3.—Diurnal change in percent of gulf menhaden, *Brevoortia patronus*, larvae with gas in their swim bladders (S.S. = sunset, S.R. = sunrise). Numbers of fish examined are in parentheses. Data from two cruises (Dec. 1981, open circles; Dec. 1982, closed circles) are combined and presented in chronological order.

TABLE 1.—Swim bladder volume of gulf menhaden, *Brevoortia patronus*, larvae measured immediately after capture. Samples are from oblique and surface net tows.

Length class (mm)	Night samples N	Night samples: Swim bladder vol. (mm^3) (mean ± 2 SE)[1]	Day samples N	Day samples: Swim bladder vol. (mean ± 2 SE)[1]	t	df	P
<14.9	7	0.44 ± 0.19	1	0.03	—	—	—
15-16.9	13	0.89 ± 0.21	9	0.05 ± 0.02	7.97	20	<0.001
17-18.9	18	1.71 ± 0.52	12	0.17 ± 0.10	5.81	28	<0.001
>19.0	11	1.78 ± 0.75	8	0.32 ± 0.19	3.77	17	<0.01

[1]SE = standard error of the mean.

TABLE 2.—Swim bladder volume of gulf menhaden, *Brevoortia patronus*, larvae captured in MOCNESS tows and measured immediately after capture. Volumes were corrected for expansion of the swim bladder due to the change in pressure (0.1 atm/m of water).

Water depth (m)	Night samples N	Night samples Swim bladder vol. (mm^3) (mean ± 2 SE)[1] At surface	Night samples Corrected for pressure change	Night samples % with gas	Day samples N	Day samples Swim bladder vol. (mean ± 2 SE)[1] At surface	Day samples Corrected for pressure change	Day samples % gas
1	55	0.422 ± 0.148	NA	97	54	0.033 ± 0.013	NA	0
8	75	0.593 ± 0.136	0.329 ± 0.075	99	3	([2]) —	—	0
20	21	0.336 ± 0.123	0.126 ± 0.044	97	0	— —	—	—

[1]SE = standard error of the mean.
[2]Swimbladder volume of the three fish captured was not measured.

this station varied between 23 and 27 m. During the day nearly all the larvae were taken at the surface and only three larvae were captured as deep as 8 m. Without exception, fish examined from daylight samples did not have gas in the swim bladder, while almost all of the fish from the night samples contained some gas. In some cases, the volume of the swim bladder was such that it constricted the gut (Hunter and Sanchez 1976) or burst through the body wall.

The volume of gas in the larval swim bladder would, of course, be reduced due to increased pressure as the larvae moved deeper in the water. As the volume of the swim bladder decreased, its capacity as a buoyancy organ would decrease, causing the larvae to expend more energy in swimming or to sink more rapidly. Since our measurements were all made at the surface, we corrected the volumes of the swim bladders in larvae collected at 8 and 20 m to reflect the increased pressure at these depths (Table 2). Since swim bladder volume is related to size of the fish, a t-test was used to compare the mean standard length of the larvae from each depth. This test showed no significant difference in lengths of fish captured at the three depths (t-test, $P > 0.05$).

In the Laboratory

Swim bladder volume was much greater in tanks where the larvae had direct access to air (Fig. 4). Swim bladder volume of the larvae without access to air remained essentially the same throughout the experiment. It appears from this experiment that gulf menhaden larvae, like a number of other clupeoid species, fill their swim bladders by swallowing air at the surface.

DISCUSSION

Our findings for swim bladder inflation in larval gulf menhaden generally agree with the findings of Hunter and Sanchez (1976) and Uotani (1973) for other clupeoid species. Our field studies showed conclusively that gulf menhaden inflate their swim bladders at night and deflate them during the day. Hunter and Sanchez (1976) suggested that nighttime swim bladder inflation in larvae of the northern anchovy is an energy-sparing mechanism that allows larvae to reduce swimming activity during nonfeeding periods while maintaining their depth in the water column. These authors further suggest that a reduction in swimming activity may reduce predation, since some predators of larval fish (e.g., chaetognaths) use the water movement caused by swimming activity to detect their prey.

In the laboratory we found that larvae were unable to fill their swim bladders when they were prevented from reaching the air-water interface. This too agrees with the previous hypothesis on

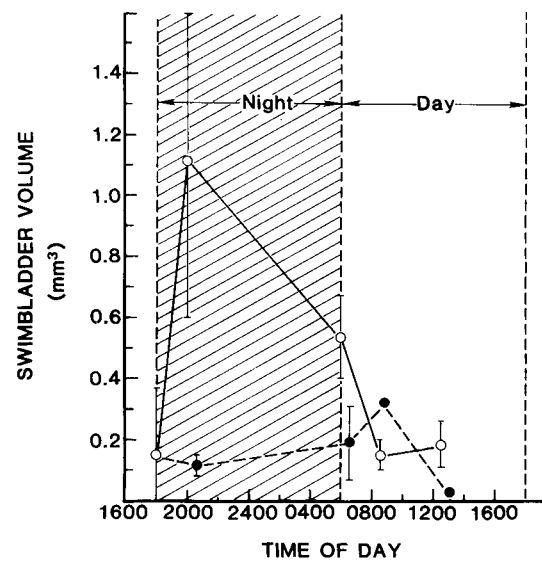

FIGURE 4.—Swim bladder volume ($X \pm 2$ SE) of gulf menhaden, *Brevoortia patronus*, held in the laboratory with access (solid line) and without access (dashed line) to the air-water interface.

how larvae of physostomatous clupeoid fishes initially inflate the swim bladder (Blaxter and Denton 1976).

Under field conditions, gulf menhaden larvae began to fill and empty their swim bladders during the approximately 45 min of twilight preceding sunset and sunrise. The numbers of fish with gas in their bladders increased and decreased gradually (i.e., it is not an all or none phenomenon) prior to darkness (or daylight). This observation suggests to us that larvae are responding as individuals to gradually changing light levels. This response is probably better developed in larger larvae.

The relation of diurnal vertical migration to swim bladder inflation that we found is different from the generally accepted position that larvae are near the sea surface with well-inflated swim bladders at night and are deeper in the water with deflated swim bladders during the day. We captured menhaden larvae at three discrete depths at night (down to 20 m) and over 95% of the larvae captured at 8 and 20 m had gas in their swim bladders. On four previous cruises, collections in the same location also showed that menhaden larvae were distributed throughout the water column at night but concentrated at the surface during the day (unpubl. data[5]).

In conclusion, the swim bladder of the larval stages of gulf menhaden acts as a buoyancy regulator that allows the fish to maintain a position in the water column at night without movement. By day the swim bladder is deflated, and the larvae must actively swim to maintain their position near the water surface. At some point during development, the swim bladder's primary function switches to that of a pressure-adjusting mechanism for the otic bullae.

[5]Sogard, Susan M., Donald E. Hoss, and John J. Govoni. In prep. Density and depth distribution of larval fishes at selected sites in the northern Gulf of Mexico. Southeast Fish. Cent. Beaufort Lab., Natl. Mar. Fish. Serv., NOAA, Beaufort, NC 28516-9722.

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