Reference: *Biol. Bull.*, **141**: 176–188. (August, 1971)

# SWIMBLADDER DEVELOPMENT AND FUNCTION IN THE HADDOCK, *MELANOGRAMMUS AEGLEFINUS* L.[1]

ABBY SCHWARZ

*Department of Zoology, University of California, Berkeley, California 94720*

Some of the earlier embryological studies on the teleostean swimbladder attempted to elucidate its evolutionary relationship to the lungs (*e.g.*, Spengel, 1904; Moser; 1904; Makuschok, 1913; Ballantyne, 1927), while others were done in recognition of its uniquely piscine nature (*e.g.*, Vogt, 1842; Ryder, 1884; Tracy, 1911; Maier and Scheuring, 1923). More recent investigations of swimbladder development have included studies of its initial inflation (*e.g.*, von Ledebur, 1928; von Ledebur and Wunder, 1937; Powers, 1932; Jacobs, 1938; McEwen, 1940; Wickler, 1959). However, these studies concentrated on morphological changes and concurrent larval behavior rather than on larval gas gland function.

The functioning of the swimbladder in adult fish presents some unique physiological aspects (Copeland, 1952; Fänge, 1953; Scholander, van Dam and Enns, 1956; Scholander, 1954; Copeland, 1969; Deck, 1970), which have not been extrapolated backward to early stages of development. Therefore, physiological observations are included where appropriate in this paper. Haddock was the species of choice since it has been thoroughly investigated as an important food fish. Much is known about its life cycle, vertical distribution of eggs and larvae, and rearing of larvae in the laboratory.

The swimbladder may originate in one of three ways. Most commonly it develops as a dorsal or lateral diverticulum of the gut, as in *Lepomis macrochirus macrochirus* (Duwe, 1952), but in *Coregonus palaea* (Vogt, 1842) it originates from the esophagus as a solid cell mass in which a cavity later appears. This cavity then grows down towards and establishes communication with the esophagus. Finally, it may originate as a solid cell mass, later to be invaded by an evagination of the gut, as in *Salmo salar* (Hoar, 1937). Sinnce Meek (1924) found the swimbladder of *Gadus morhua* (=*callarias*) to originate as a diverticulum of the gut, a major objective of this study was to determine its mode of origin and course of development in another member of the Gadidae, the haddock.

At least two methods exist by which the swimbladder may be first inflated. Many larval physoclists swim to the surface and gulp air at or shortly after hatching, while they are still morphologically physostomous. This air may somehow stimulate production of gas by the gas gland (Jacobs, 1938), which in some species is already present in connection with the rete mirabile. On the other hand, the duct may degenerate prior to hatching or, if present, its lumen may be closed. Fishes in this category would not swallow surface air, and some internal mechanism would have to stimulate gas production. Thus an attempt was made to determine the method of swimbladder inflation in the haddock.

Swimbladder gas gland cells in the adults of a number of species store glycogen when not secreting and metabolize it during periods of activity (Copeland, 1952;

[1] This work forms part of a dissertation submitted in partial fulfillment of the requirements for the Ph.D. degree at Boston University, Boston, Massachusetts 02215.

Fänge, 1953). No work of this kind has been done on larval fishes. I thought it possible that, prior to initial inflation, the gas gland might concentrate glycogen which could be used as the energy source for the process. A third objective therefore was to test for the presence of glycogen in gas glands of larval haddock.

Adult and juvenile haddock live near the ocean floor. The eggs are spawned at the bottom between February and May but develop in the upper layers of the ocean. The larvae remain pelagic until August or September, when they return to the bottom (Miller, Colton and Marak, 1963). An attempt was made to determine what role, if any, the swimbladder plays in the vertical distribution of the larvae during their pelagic phase.

## Methods and Materials

About 250 fertilized haddock eggs were incubated at 5.5° C in quart jars three-fourths filled with seawater, 50–75 eggs to a jar. Aeration was facilitated by twice-daily stirring. Temperatures were checked daily.

Every morning, from the time of blastopore closure (day 7) on, 10–15 eggs were fixed for 24 hours at 27° C in 10% Lillie's neutral buffered formalin. After removal of the vitelline membranes, specimens were dehydrated and cleared in graded alcohols, toluene, and cedarwood oil, and bathed and embedded in Paraplast. Transverse serial sections at 4 $\mu$ were stained routinely with Harris' hematoxylin and eosin.

The behavior of the larvae upon hatching was observed and recorded. A five-gallon polyethylene tank was filled with two gallons of seawater, and the whole cooled by circulating tap water. The temperature stabilized at 10° C and the larvae underwent a 1.3° C per day rise in temperature until 10° C was reached on the fourth day of larval life, when they were introduced into the tank. The culture temperatures gradually rose from the initial 10° to 13° C because of seasonal warming of the tap water.

From the day after hatching on, the larvae were given one teaspoon daily of *Artemia salina* nauplii. Due to the large surface area of the tank, twice-daily stirring provided the only further aeration.

A few larvae died each day. This plus periodic sampling depleted their numbers so that fixations were not done beyond larval day 12. Visual observations were continued on the remaining larvae until day 19.

The 10 larvae in each sample were fixed, dehydrated, cleared, bathed and embedded using the same procedure as for the eggs. Four larvae per sample were sectioned transversely at 4 $\mu$ and stained with Harris' hematoxylin and eosin. The other six were sectioned transversely at 5 $\mu$ and treated using the PAS technique with a hematoxylin counterstain; three of these six were incubated with malt diastase prior to staining. The diastase treatment (and subsequent PAS on diastase-treated slides) was performed by Histology Service Inc., Philadelphia, Pennsylvania.

Out of 60 plankton sampling attempts I made while on board the R/V Albatross IV (cruise 68–8), five haddock larvae were obtained. These were examined for swimbladder glycogen using the method described above.

A number of other larvae, collected during surveys made on the R/V Albatross IV in 1967 and 1968, were obtained as preserved material from the Bureau of Commercial Fisheries, Woods Hole, Massachusetts.

## Results

Embryogenesis took 17 days at 5.5° C. Four of the 250 eggs died during this period. Larval mortality rose sharply after yolk sac absorption, although the larvae were feeding on *Artemia* nauplii. The last larva died 19 days after hatching. (Previous attempts to rear haddock larvae in the laboratory had been unsuccessful in that the larvae did not survive beyond 21 days; David Miller, Bureau of Commercial Fisheries, Woods Hole, Massachusetts, personal communication).

### *Morphology of laboratory-reared eggs*

*Day 11.* The swimbladder anlage appeared on day 11, when embryogenesis was two-thirds completed. It showed as a shallow evagination of the dorsal gut wall at the level of the pectoral fins. A narrow lumen opened into the gut opposite and just posterior to the connection of the gut with the liver.

The gut wall in this area was composed of stratified columnar cells surrounded by one to two layers of mesenchyme. These were enclosed in turn by a thin layer of fibroblasts. The bladder anlage was constructed similarly, but there was only one layer of columnar epithelium lining its lumen. There was little indication of blood vessels serving the swimbladder region.

*Day 12.* The anlage had become a narrow inverted U with a distinct lumen patent throughout its length. No distinction could be made between pneumatic duct and swimbladder proper. The inner lining of the anlage consisted of a single layer of tall columnar cells; near its origin from the gut, however, another columnar layer appeared, reflecting the stratification of the cells of the gut lining. The cytoplasm of the columnar cells was intensely basophilic, a characteristic which persisted throughout embryogenesis and during early larval life.

Around the columnar lining there was a pronounced agglomeration of irregularly-layered, undifferentiated mesenchymal cells. Venous sinusoids and capillaries were occasionally observed in the mesenchymal mass.

*Day 13.* The inverted U of the swimbladder had elongated somewhat more. The mesenchymal cells had proliferated in an antero-posterior direction, although they were still evenly distributed up and down the outgrowth. The layers of fibroblasts and fibers surrounding the swimbladder had increased in number and in thickness. Venous sinusoids and capillaries appeared with increasing frequency, especially in the outer layers of the swimbladder and at its base on the side nearest the liver.

*Day 14.* A distinction was apparent between pneumatic duct and swimbladder proper, due in part to the lumen's enlargement at its distal end. Also contributing was a new concentration of mesenchyme around the distal end of the outgrowth, forming a ball surrounded by several layers of fibroblasts and collagenous fibers and enclosed by the layer of pigmented peritoneum characteristic of the adult condition.

The swimbladder had become more dorsal in position. The mesenchyme had increased in bulk antero-posteriorly and had begun organizing into layers.

*Day 15.* In contrast to the duct lumen, the swimbladder cavity had continued to expand. The concentration of fibroblasts and fibers had increased over the anterior and posterior ends of the bladder. Within the mass of mesenchyme, more capillaries and one venule were present, situated as before on the side of the swimbladder near the liver.

*Day 16.* The swimbladder cavity had undergone pronounced expansion in a dorso-ventral direction. The pneumatic duct was now seen to emerge from the right side of the bladder. Its lumen was patent throughout and its walls were intact.

A well-developed basement membrane appeared beneath the epithelial cells lining the cavities of swimbladder and pneumatic duct. Several venules were present in the mesentery between swimbladder and liver.

*Day 17.* The swimbladder had lengthened antero-posteriorly, so that the pneumatic duct entered it approximately midway along its length.

The structure of the duct had not altered significantly since its first appearance. A single row of cuboidal cells bordered on the patent lumen. These were enclosed by a layer of small cuboidal mesenchymal cells which were continuous around the swimbladder. The mesenchyme was surrounded by one or two layers of loose fibrous connective tissue and a layer of pigmented peritoneum.

*Morphology of laboratory-reared larvae*

*Day 1* (average total length = 3.5 mm). By the time of hatching, the swimbladder had grown more anteriorly. The pneumatic duct thus appeared far posterior in position.

*Day 3* (average total length = 3.8 mm). Swimbladder growth in an anterior direction had continued, and the tissue layers showed signs of increasing organization. At least two layers of columnar cells now lined the cavity, and the mesenchyme was now compacted into distinct layers that closely surrounded the epithelial lining.

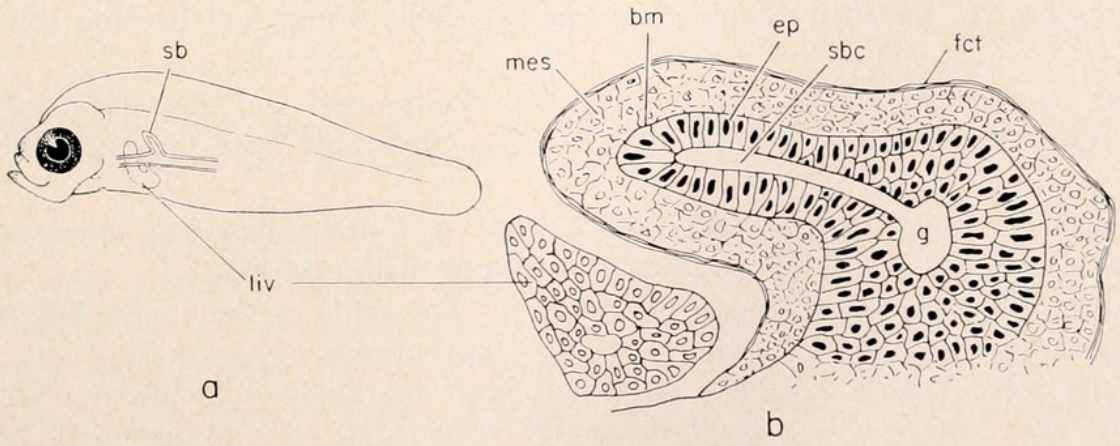


FIGURE 1. (a) Diagram of swimbladder position, newly hatched *Melanogrammus aeglefinus*. Dorsal is at top in all figures. (b) Cross-section through swimbladder region of a day 12 embryo. Abbreviations are: sb = swimbladder, liv = liver, mes = mesenchyme, bm = basement membrane, ep = epithelium, sbc = swimbladder cavity, fct = fibrous connective tissue, g = gut lumen; × 156.

The rounded bladder tapered caudally to meet the pneumatic duct. The duct appeared short, thick, and fairly straight, passing through the fibrous coats before turning to enter the posterior end of the swimbladder cavity on the right side. The duct lument was patent throughout and showed no sign of narrowing. However, the layer of mesenchymal cells distal to the cuboidal epithelium lining the duct appeared somewhat disorganized, and this proved to be the first sign of duct degeneration.

The cytoplasm of the epithelium and mesenchyme was now much more acidophilic; this increased in later stages.

*Day 6* (average total length = 4.3 mm). The yolk sac had been absorbed by now and feeding had begun. The swimbladder had assumed a shape generally similar to that observed after inflation.

The cavity itself varied in shape among specimens examined, but no changes in size were evident. It was lined by stratified cuboidal epithelium, distal to which were polygonally-shaped mesenchymal cells and some blood vessels.

The epithelial cells bordering the duct lumen appeared flatter, and the structure of the mesenchymal layer more chaotic, although the lumen still exhibited a uniform diameter. No structure resembling a sphincter was evident in the duct region. Although the duct was located at the anteriormost end of the midgut, the common bile duct had appeared to enter the midgut anteriorly to it. This was now seen to have been caused by a craniad expansion of the midgut at this point.

This day marked the appearance of the rete mirabile, which resembled a collar almost completely surrounding the bladder and set on a diagonal to it. Posteriorly, the rete extended past the entrance point of the pneumatic duct to cover the bladder's posterior wall. Erythrocytes were present within its vessels, which at this stage were mainly venules and capillaries. The rete extended poorly-defined, branching projections into the main bladder mass. This arrangement suggested that seen in older larvae and adults, where the rete resembles a tree whose vascular branches are traced by singly-layered cuboidal glandular cells and whose trunk is composed of thick bundles of parallel blood vessels. The rete was surrounded by a layer of fibrous tissue which was continuous around the bladder.

*Day 10* (average total length = 4.8 mm). A single layer of columnar cells now appeared to line the swimbladder cavity. This lining had become somewhat folded.

The mesenchyme distal to the lining had proliferated and now enclosed many blood vessels containing erythrocytes. More erythrocytes were present within the rete.

The cells lining the pneumatic duct were still more flattened and appeared to form a syncytium. The basement membrane had disappeared.

*Day 12* (average total length = 4.8 mm). The folds of the cavity lining were more pronounced, suggesting the convoluted appearance of the mature gas gland. The cells were larger and less stratified, with markedly acidophilic cytoplasm. In some areas there was a proliferation of very small cells immediately beneath the prominent basement membrane. The rete was packed with erythrocytes.

The lumen of the pneumatic duct had altered in diameter. Although unchanged at the swimbladder end, it was extremely narrow where it opened into the gut. In six specimens it appeared open and in two others it appeared closed.

The mesenchymal cells had disappeared from the duct wall, leaving only a chaotic syncytial epithelium.

*Morphology of collected specimens*

Collected larvae were obtained from the Bureau of Commercial Fisheries and from seining by the author. Larvae in the first category measured 4–17.5 mm while in the second group four averaged 6.3 mm and one measured 8.0 mm in total length.

Major features of swimbladder development in these specimens were cavity expansion, increasing antero-ventral localization of most of the cuboidal (?glandular) epithelium, rete development, and the appearance of accessory tissue layers. Swimbladder development was arbitrarily divided into three stages on the basis of larval size; *viz.* 4–5 mm, 5–10 mm, and 10–17.5 mm.

In laboratory-reared larvae of 4–5 mm the cavity was small and the lining deeply folded. In collected specimens of similar length the cavity was noticeably larger and the folds not as deep. Cuboidal epithelium surrounded the cavity, as did rete vessels, except most postero-dorsally where a small area was lined by thin squamous epithelium. Occasionally vacuoles were evident within the cuboidal cells.

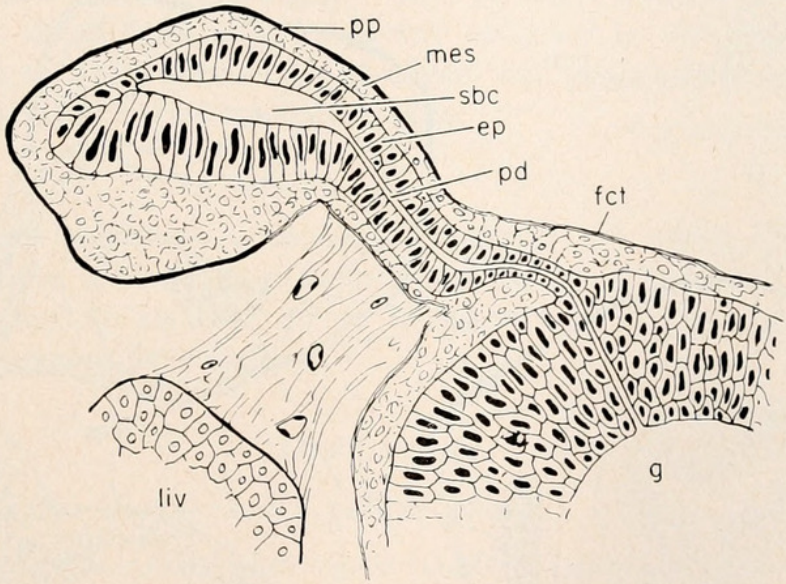


FIGURE 2. Cross-section through swimbladder region of a day 16–17 embryo. Abbreviations are: pd = pneumatic duct, pp = pigmented peritoneum; × 156.

In 5–10-mm collected larvae the cavity was still further expanded. The swimbladder appeared teardrop-shaped in lateral view, tapering posteriorly. The trunk of the rete ran along the outside of the ventral swimbladder wall and divided in two before entering the cavity anteriorly. Its vessels were most abundant here, but it also sent branches caudally along the lateral walls of the bladder. This organization apparently determined the localization of the cuboidal epithelium, which had proliferated over the anterior and antero-ventral walls of the bladder and in some specimens covered a small portion of the antero-dorsal wall as well. In these areas it was complexly folded around elements of the rete. From here

it extended as two tongue-shaped masses running posteriorly along the lateral walls almost to the end of the cavity. In these places the epithelium was unfolded and each cell appeared to be in contact with a rete vessel. Intra- and intercellular vacuoles were present. Caudally there was a slight decrease in the size of the cuboidal cells. The tongue-shaped masses tapered slightly at their caudal ends. The dorsal wall was almost uniformly thin, exhibiting only one layer of squamous cells, but the ventral wall anteriorly sometimes showed a few layers of squamous epithelium underlying the cuboidal tissue. Further posteriorly, its lining cells were transitional between cuboidal and squamous, and its caudal end was covered by a very thin sheet of squamous epithelium.

The cavity in third-stage swimbladders was very large, accounting in part at least for the size reduction and sharp tapering of the lateral masses mentioned earlier. Third-stage bladders also exhibited two to four layers of circular smooth muscle ventrally. These seemed to diminish dorsally, and in fact the dorsal wall was uniformly thin and histologically almost featureless.

In the third stage, as in the second, the anterior concentration of cuboidal epithelium was at least partly divided into two masses, following the division of the rete where it entered the bladder.

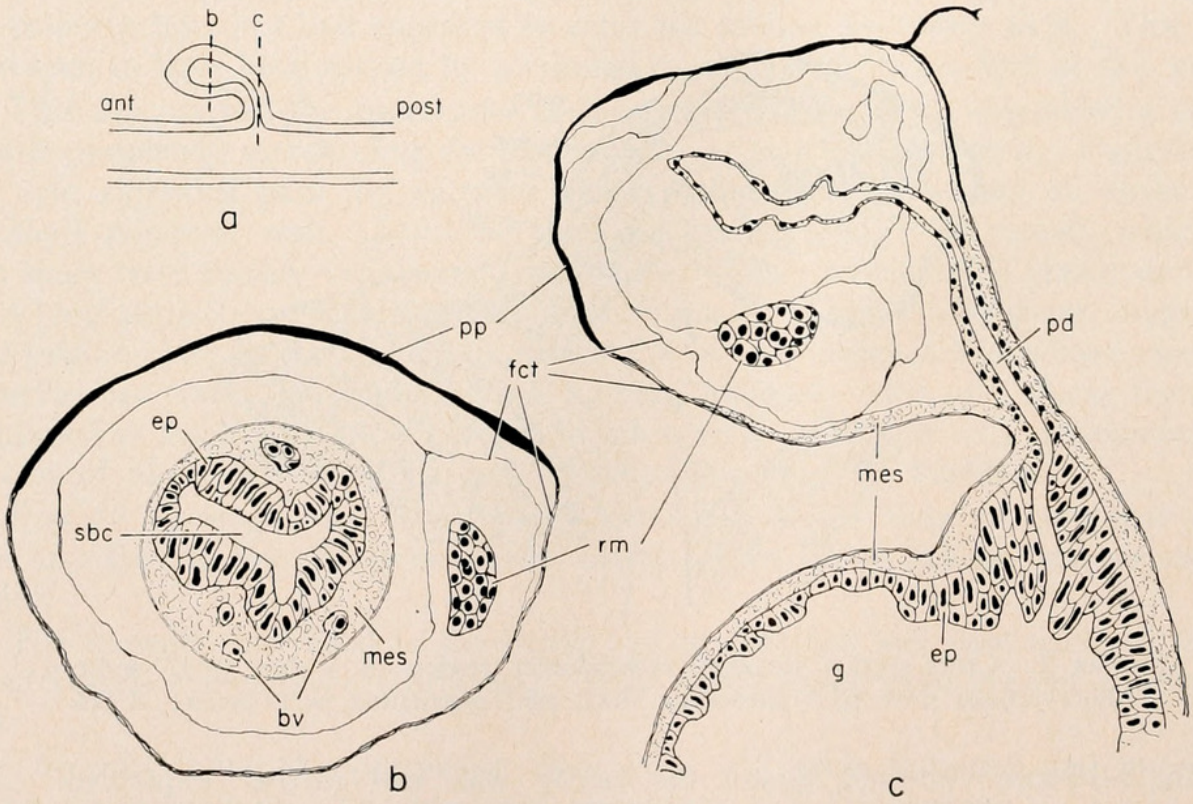


FIGURE 3. (a) Diagram showing area of sections (b) and (c). (b) cross-section through swimbladder cavity of a day 10 larva. Abbreviations are: bv = blood vessel, rm = rete mirabile. × 156. c, cross-section through region of pneumatic duct, day 10 larva; × 156.

The state of the pneumatic duct in laboratory-reared larvae averaging 4.8 mm has been described. In collected specimens, the duct was closed at the opening into the gut in three 4.5-mm individuals, and had become composed largely of connective tissue fibers. A small depression where the duct opened into the

swimbladder was apparent in specimens up to about 7.0 mm in length, and was always to be found on the lower right bladder wall. In larger specimens only a few connective tissue strands were left to represent the duct. The lumen first closed at the opening into the gut, but a small thickening of the outer gut wall marked its former position even in a 17.5-mm specimen.

*Glycogen in laboratory-reared larvae*

All these animals had uninflated swimbladders. The concentration of glycogen in swimbladder epithelium increased from the time of hatching on, reaching a maximum on day 10. The mesenchymal cells did not exhibit glycogen until after yolk sac absorption was completed, after which they showed an increasing glycogen concentration. Other PAS-positive material was absent from the mesenchyme at hatching, most evident on day 6, and then declined.

All PAS-positive material in both epithelium and mesenchyme remained evenly distributed in the cytoplasm throughout the course of observed development.

*Glycogen in collected larvae*

These larvae had inflated swimbladders. Specimens obtained from the Bureau of Commercial Fisheries had been kept in formalin for long periods of time and so could not be examined for glycogen. The glycogen content in inflated swimbladders was thus determined only for larvae collected by the author. In swimbladder epithelium of these specimens, glycogen was absent from the paravascular areas but was abundant elsewhere in the cells.

*Behavior*

Hatching in the laboratory occurred throughout the water column, not just at the surface. None of the larvae swam towards the surface at this time. The animals were not seen to swallow air or to attempt to do so at any time in the course of their subsequent development.

## Discussion

I. *Role of swimbladder during larval pelagic phase*

Colton (1965) demonstrated that while haddock eggs were present throughout the water column, they were most abundant at the surface, decreasing linearly with depth. Miller *et al.* (1963) showed that this was not the case with the larvae, although since spawning occurred earlier than usual in that year, only 5–10% of the total catch consisted of newly-hatched animals. The water column was sampled to 75 meters, but over 80% of the larvae from almost 4.0 mm to 21 mm in total length were found between 10 and 40 meters. They constituted two groups, the first containing larvae of 8.0 mm and less, and the second including those over 9.0 mm. Larvae in the first group were dispersed over a greater depth range than those in the second, exihibiting a random distribution with no region of maximum density. However, over 80% of the larger larvae were concentrated within the thermocline. No vertical migration was observed for any of the animals, although further studies were deemed necessary.

It is possible that the swimbladder becomes functional when the larvae reach about 9.0 mm, with the result that they may better adjust their density and thus stratify out at some preferred level, in this case the thermocline. I examined 40 collected larvae measuring 4–17.5 mm, half of which were 4–9 mm. In all specimens the swimbladder was at least partly inflated, and in larvae of 5.0 mm and over it occupied the same percentage of the body area in cross-section as it did in the adult. Therefore the swimbladder was probably functional in larvae less than 9.0 mm in length. A possible role for it is discussed below.

The thermocline in the area studied by Miller *et al.* (1963) generally does not form until April or May, and before this time most of the larvae average less than 9.0 mm in length (Robert Marak, Bureau of Commercial Fisheries, Woods Hole, Massachusetts, personal communication). Although admittedly little is known of the ability of the small larvae to cross barriers posed by temperature gradients and current velocities, their swimming ability is probably relatively undeveloped. Their random vertical distribution might thus indicate a passive dispersal caused by hydrographic factors that thoroughly mix the water column. However, the inflated swimbladder decreases the density of the fish, so that as the winter mixing decreases, the smaller larvae might be carried up into a range able to be affected by the forming thermocline. By the time of its formation, the larvae would be larger and of greater swimming ability, and would be able to maintain themselves among food concentrations such as exist within it.

II. *Time of swimbladder inflation*

The pelagic phase of the haddock includes animals from 3.5 mm (hatching size, Bigelow and Schroeder, 1953) to about 100 mm (Miller *et al.*, 1963). It is within the pelagic period that the swimbladder begins functioning as a hydrostatic organ.

Examination of the liver and gut, as well as body length measurements, revealed a disparity in development between laboratory-reared and collected larvae in favor of the latter. This may have been due to a lack of optimum food and temperature conditions in the laboratory. Laboratory animals were reared at temperatures averaging up to five degrees higher than those to which larvae less than 8.0 mm would naturally be exposed. Furthermore, most collected specimens had ingested several planktonic forms whereas laboratory-reared larvae were given only *Artemia* nauplii.

Swimbladder inflation commonly occurs either upon hatching as in *Hippocampus* (Jacobs, 1938) or just after yolk sac absorption as in some salmonoids (Tait, 1960). Yolk sac absorption was finished and swimbladder inflation completed or nearly so in all collected larvae. Although laboratory-reared specimens of equal size (4–4.5 mm) had completed yolk sac absorption, they never showed inflated swimbladders. Thus this study did not furnish a definite time for initial inflation, but such evidence as is available (hatching occurs throughout the water column, not just at the surface; laboratory-reared larvae do not swallow air upon hatching; the rete does not appear until after yolk sac absorption) indicates that it occurs soon after yolk sac absorption rather than upon hatching.

III. *Mechanism of swimbladder inflation*

If swimbladder inflation resulted from swallowing surface air, larvae less than 4.5 mm might be most abundant at the surface. However, Miller *et al.* (1963) found small larvae to be concentrated well below the surface. Although in that study the larvae were not observed at the time of hatching, hatching may occur anywhere in the upper 20 meters (Colton, 1965) and did not always occur at the surface in the laboratory. Laboratory-reared larvae were not observed to gulp air upon hatching or at any time thereafter. However, the natural behavior of the larvae upon hatching can still only be conjectured. Moreover, since collected larvae 4–4.5 mm all had closed pneumatic ducts, while in laboratory animals of equal size the duct remained open, the state of the duct gave no clue as to method of inflation. Nevertheless, use of a mechanism other than swallowing air is suggested.

An interesting alternative was suggested by Powers (1932) who stated that initial inflation should normally occur before gas gland function ensued. Although not certain how this would come about, he postulated the disintegration of certain organic materials within the bladder epithelium, producing carbon dioxide within its lumen. Some support for this was given by McEwen (1940) and Johnston (1953).

McEwen found that the swimbladder lining in *Hemichromis bimaculatus* was at first composed of cells resembling those lining the gut, but within 24 hours they became greatly vacuolated and expanded to fill the bladder lumen. Two to nine hours later the cells had transformed into a flat epithelium, leaving a gas-filled bladder lumen. McEwen thought that this gas came from the vacuoles, but as the bladder's cross-sectional area was not as great after lumen obliteration as after cellular flattening, he suggested that additional disintegration of cellular material was going on continuously during this time.

Johnston (1953) found similar vacuolated cells temporarily comprising the ventral swimbladder epithelium in *Micropterus.* Although *Micropterus* did not swallow air to fill its bladder, the organ increased in size and in gas volume, and the pneumatic duct remained open during inflation. Johnston thought it possible that some of the initial gas resulted from digestion.

How the presence of gas released from vacuoles eventually stimulates gas gland activity is unknown. The problem is further complicated in *Hemichromis* and *Micropterus,* neither of which possesses a rete at the time of initial inflation. Further studies in this area would be desirable.

Swimbladder inflation in the haddock was not observed to occur in this manner. Vacuoles in swimbladder epithelium only appeared after inflation. Moreover, no cellular expansion was seen.

It is possible that glycogenolysis is the major energy source for production of swimbladder gas in the haddock. Support for this statement derives from studies showing that much of the gas in the swimbladder of *Gadus morhua,* another gadid, could be derived from glycogenolysis (Fänge, 1953). Moreover, in some other genera (*Perca,* Fänge, 1953; *Fundulus,* Copeland, 1952), glycogen disappeared from gas gland cells during inflation and reappeared during gas resorp-

tion. Histochemical studies on these fishes revealed a distribution of glycogen in the gas gland similar to that observed here in the inflated haddock swimbladder.

As epithelial cells in the uninflated haddock swimbladder were found to concentrate glycogen, it is proposed that the initial gas supply is derived from glycogenolysis. The intra- and intercellular vacuoles observed in the inflated bladder's epithelium may have been associated with glandular function rather than with intracellular disintegration of organic materials as postulated for other species by Powers (1932). The rete was developed well before inflation, and made apparent contact with each epithelial cell examined. Additional data necessary to support this proposed mechanism could most profitably accrue from studies of gas gland ultrastructure.

While glandular function may provide the initial gas, how the gas gland cells are first stimulated to function remains unanswered. It is possible that secretion begins when the concentration of specific metabolites in the blood passing through the rete reaches a certain level, the buildup perhaps resulting from the onset of feeding.

It is of interest that mesenchymal cells just distal to the swimbladder lining concentrated glycogen. These cells differentiated into blood vessels of the rete. Glycogen may have been an energy source for cellular differentiation (Donald Patt, Department of Biology, Boston University, Boston, Massachusetts, personal communication), further illustrating the need for ultrastructural studies of differentiating tissue.

Oval development was not studied, but it is doubtful that the oval in the haddock develops from the degenerating pneumatic duct as in *Opsanus* (Tracy, 1911). Inflation resulted in a uniformly thin-walled roof even in 5.0-mm larvae, and an oval was not seen in any specimen. Furthermore, the opening of the duct into the bladder was always found on the lower right swimbladder wall. It seems unlikely that the entire swimbladder would shift position by ninety degrees in order that this opening be located dorsally. Some support for this view is given by Srivastava (1957), who found the duct coexisting with the oval in several species of Mugilidae.

I gratefully acknowledge the support and encouragement of Drs. W. R. Courtenay, Jr., D. I. Patt, R. D. Estes, A. L. Kelly and D. Shepro, and of Mr. Robert Marak and Mr. David Miller. This study was supported in part by grants-in-aid from the National Science Foundation (GB-3866 and GB-6522, Dr. W. R. Courtenay, Jr., Principal Investigator), and by an NSF Summer Predoctoral Traineeship.

## Summary

The swimbladder in the haddock appears on the 11th day of embryogenesis as a dorsal outgrowth of the gut just posterior to the liver diverticulum. In later stages its true position just anterior to the liver becomes visible.

Swimbladder inflation occurs very soon after yolk sac absorption. At this time the larvae measure 4–4.5 mm and have begun feeding.

Haddock larvae probably do not swallow air to fill their swimbladders. The initial gas volume may be derived from glycogenolysis, as glycogen is present in substantial amounts in uninflated swimbladder epithelium. Glycogen is absent from the paravascular portions of the epithelium in inflated swimbladders but is well-represented elsewhere in the cells.

It is proposed that the inflated swimbladder in larvae less than 8.0 mm serves to decrease their density and thereby carry them up towards the level of the forming thermocline. By the time the thermocline is well-established, the larvae are larger and of greater swimming ability, and with the aid of a functioning swimbladder should be able to maintain themselves within it.

## LITERATURE CITED


BALLANTYNE, M., 1927. Air-bladder and lungs: a contribution to the morphology of the air-bladder of fish. *Trans. Roy. Soc. Edinburgh,* **55**: 371–394.

BIGELOW, H. B., AND W. C. SCHROEDER, 1953. Fishes of the Gulf of Maine. *Fish. Bull. Fish Wildlife Serv. U. S.,* **74**: 199–213.

COLTON, J. B., JR., 1965. The distribution and behavior of pelagic and early demersal stages of haddock in relation to sampling techniques. *Int. Comm. Northwest Atlan. Fish. Spec. Publ.,* **6**: 317–335.

COPELAND, D. E., 1952. The histophysiology of the teleostean physoclistous swimbladder. *J. Cell. Comp. Physiol.,* **40**: 317–334.

COPELAND, D. E., 1969. Fine structural study of gas secretion in the physoclistous swim bladder of *Fundulus heteroclitus* and *Gadus callarias* and in the euphysoclistous swim bladder of *Opsanus tau. Z. Zellforsch.,* **93**: 305–331.

DECK, J. E., 1970. Lactic acid production by the swim bladder gas gland *in vitro* as influenced by glucagon and epinephrine. *Comp. Biochem. Physiol.,* **34**: 317–324.

DUWE, A. E., 1952. The embryonic origin of the gas bladder in the centrarchid fish, *Lepomis macrochirus macrochirus. Copeia,* **1952**(2): 92.

FÄNGE, R., 1953. The mechanisms of gas transport in the euphysoclist swimbladder. *Acta Physiol. Scand.,* **30**(*Suppl.* 10): 1–133.

HOAR, W. S., 1937. The development of the swim bladder of the Atlantic salmon. *J. Morphol.,* **61**: 309–320.

JACOBS, W., 1938. Untersuchungen zur Physiologie der Schwimmblase der Fische. IV. Die erste Gasfüllung der Schwimmblase bei jungen Seepferdchen. *Z. Vergl. Physiol.,* **25**: 379–388.

JOHNSTON, P. M., 1953. The embryonic development of the swim bladder of the largemouth black bass *Micropterus salmoides salmoides* (Lac.). *J. Morphol.,* **93**: 45–67.

LEDEBUR, J. VON, 1928. Beiträge zur Physiologie der Schwimmblase der Fische. *Z. Vergl. Physiol.,* **8**:445–460.

LEDEBUR, J. VON, AND W. WUNDER, 1937. Beiträge zur Physiologie der Schwimmblase. IV. Beobachtungen an Stichlingen, die ihre Schwimmblase nicht mit gas Füllen könnten. *Z. Vergl. Physiol.,* **25**: 149–155.

MCEWEN, R.S., 1940. The early development of the swimbladder and certain adjacent parts in *Hemichromis bimaculatus. J. Morphol.,* **67**(1): 1–59.

MAIER, H. N., AND L. SCHEURING, 1923. Entwicklung der Schwimmblase und ihre Beziehungen zum statischen Organ und der Kloake bei Clupeiden. *Wiss. Meeresunters. (Abt. Helgoland),* **15**(6): 1–22.

MAKUSCHOK, M., 1913. Über genetische Beziehung zwischen Schwimmblase und Lungen. *Anat. Anz.,* **44**: 33–55.

MEEK, A., 1924. The development of the cod (*Gadus callarias* L.). *Fish. Invest. Min. Agr. Fish. Food (Gt. Brit.), Series II,* **7**(1): 1–26.

MILLER, D., J. B. COLTON AND R. R. MARAK, 1963. A study of the vertical distribution of larval haddock. *J. Cons. Int. Explor. Mer,* **28**: 37–49.

MOSER, F., 1904. Beiträge zur vergleichenden Entwickslungsgeschichte der Schwimmblase. *Arch. Mikrosk. Anat.,* **63**: 532–574.

Powers, E. V., 1932. The relation of respiration of fishes to environment. *Ecol. Monogr.*, **2**: 385–473.

Ryder, J. A., 1884. A contribution to the embryology of osseous fishes, with special reference to the development of the cod, *Gadus morhua*. *U. S. Comm. Fish. Rept.*, **1882**: 455–605.

Scholander, P. F., 1954. Secretion of gases against high pressures in the swimbladder of deep-sea fishes. II. The rete mirabile. *Biol. Bull.*, **107**: 260–277.

Scholander, P. F., L. van Dam and T. Enns, 1956. The source of oxygen secreted into the swimbladder of the cod. *J. Cell. Comp. Physiol.*, **48**: 517–522.

Spengel, J. W., 1904. Ueber schwimmblasen, lungen und kiementaschen der wirbelthiere. *Zool. Jahrb., Suppl.*, **7**: 727–749.

Srivastava, P. N., 1957. The air bladder of Mugilidae and the relationship of the oval and pneumatic duct. *Trans. Amer. Microscop. Soc.*, **76**: 346–352.

Tait, J. S., 1960. The first filling of the swimbladder in salmonoids. *Can. J. Zool.*, **38**: 179–187.

Tracy, H. C., 1911. The morphology of the swimbladder in teleosts. *Anat. Anz.*, **38**: 600–606.

Tracy, H. C. 1911. The morphology of the swimbladder in teleosts. *Anat. Anz.* **38**: 638–649.

Vogt, C., 1842. Embryologie des Salmones. Page 177 in L. Agassiz, *Histoire Naturelle des Poissons d'Eaus Douce de l'Europe Centrale. Neuchâtel.*

Wickler, W., 1959. Über die erste Schwimmblasenfüllung bei Cichliden (Pisces Acanthopterygii). *Naturwiss.*, **46**: 94.