DIEL CHANGES IN SWIM BLADDER INFLATION OF THE LARVAE OF THE NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

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ABSTRACT

Laboratory and field studies demonstrated that larval anchovy 10 mm standard length and larger inflate their swim bladders each night and deflate them in the day. Maximum night levels of inflation were attained 2 h after the onset of dark and typical day levels occurred about 2 h after the onset of light. Laboratory experiments indicated that larvae fill their bladders at night by swallowing air at the water surface and the vertical distribution of sea-caught larvae suggested that they migrate to the surface each night to fill their swim bladders. Gas is released by passing bubbles through the pneumatic duct into the alimentary canal. The diel rhythm of inflation was viewed as an energy sparing mechanism. Measurements of sinking speed of larvae with and without inflated bladders suggested that the energy saved at night by inflation of the swim bladder would exceed the cost of vertical migration to the surface and that the migratory range over which energy savings are possible would be greater as larvae increased in length.

Northern anchovy, *Engraulis mordax* Girard, are more vulnerable to starvation in the larval stage than at any other time of life, consequently, energy sparing mechanisms may be critical to their survival. In a recent paper Uotani (1973) showed that the larvae of several clupeoid fishes, *Engraulis japonicus* (Houttuyn), *Sardinops melanosticta* (Temminck and Schlegel), and *Etrumeus teres* (DeKay) have expanded swim bladders when captured at night in the sea and deflated ones when captured during the day. Energy conservation is certainly one of the possible adaptive advantages of such behavior, but the energy saved must be evaluated in terms of the energy cost of daily filling the bladder. This requires that the mechanism of filling be known. The object of the present study was to determine if the larvae of the northern anchovy display a similar rhythm and to evaluate this behavior as a possible energy sparing mechanism.

The swim bladder in adult northern anchovy is a tubular vesicle that extends the length of the body cavity. It is connected to the alimentary canal by a pneumatic duct which originates from the dorsal wall of the cardiac stomach; no anal duct exists as it does in some clupeoids (O'Connell 1955). Two tubules on each side of the body extend from the anterior end of the bladder into the cranium where they expand into two pairs of capsules, termed prootic and pterotic bullae (O'Connell 1955). The swim bladder of the larva is basically similar to that of the adult. At the time of initial filling of the swim bladder, the pneumatic duct is functional and the bullae become filled with gas. No histological evidence exists for gas secretion in adult *E. mordax* nor for the larvae (O'Connell 1955, and pers. commun.).

The swim bladder is deflated by passing gas bubbles through the pneumatic duct into the alimentary canal and out the anus. On a number of occasions we have observed this process while examining a live anchovy larva under a dissection microscope. We have also captured larvae with deflated swim bladders that had gas bubbles in the alimentary canal.

METHODS

Fertilized anchovy eggs were obtained from a captive population of adults maintained in spawning condition in the laboratory (Leong 1971) and the larvae were reared using the techniques, foods, and tanks described by Hunter (1976). The larvae were reared at temperatures of 16.5° ± 0.2°C and 16.9° ± 0.9°C. A 12-h photoperiod was used without a dawn or dusk transition in light intensity. Incident light at the surface was about 2,000 lx in the day and at night no light was provided in the closed room which contained the rearing tanks.

Larvae reared in the laboratory were sampled at

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various times of day commencing at age 1 day to determine if a daily rhythm of inflation existed and to determine the larval length at which the swim bladder was inflated. Samples of preserved specimens from California Cooperative Oceanic Fisheries Investigations (CalCOFI) ichthyoplankton collections were also examined to determine if differences existed in swim bladder inflation in sea-caught specimens.

The standard length was measured to the nearest 0.1 mm and the maximum width and length of the swim bladder to the nearest 0.02 mm. The volume of the swim bladder was calculated by using 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 width. For larvae 16 mm and larger, the calculated swim bladder volume may be converted to actual gas volume by multiplying it by the coefficient 0.82 (Figure 1). This conversion is based on data obtained while measuring the composition of swim bladder gas. The larvae used in that experiment were larger (mean length 15.6 to 29.6 mm) than most of the larvae in the rest of the experiments. For this reason we have used the calculated swim bladder volume in all computations.

We also sampled larvae reared in the laboratory to determine the effect of swim bladder development and swim bladder inflation on sinking rate. The method of Blaxter and Ehrlich (1974) was used to measure sinking rates of larvae. Larvae anesthetized in MS 222[2] were measured and added to a 1-liter graduated cylinder without contact with the air. The larvae were allowed to sink a few centimeters, then the rate of descent was timed with a stopwatch for a distance of 7 to 35 cm. Only one measurement was made per larva and larvae were reexamined after the test to determine if they were still alive (dead larvae sank faster than live ones) and if any gas had been lost from their bladders. Fresh seawater was used in the graduated cylinder for each day's run and the specific gravity and temperature of the seawater were measured before each larva was tested. The specific gravity averaged 1.0262 and ranged from 1.0259 to 1.0266. The graduated cylinder was immersed in a temperature-controlled water bath which was maintained within 1°C of the rearing temperature. One rearing group was tested at 15.9° ± 0.2°C and another at 18.0° ± 0.1°C. In the Results section we have combined the data from these two rearing groups because covariance analysis indicated that the differences in sinking speed when adjusted for swim bladder volume and larval length were not significant.

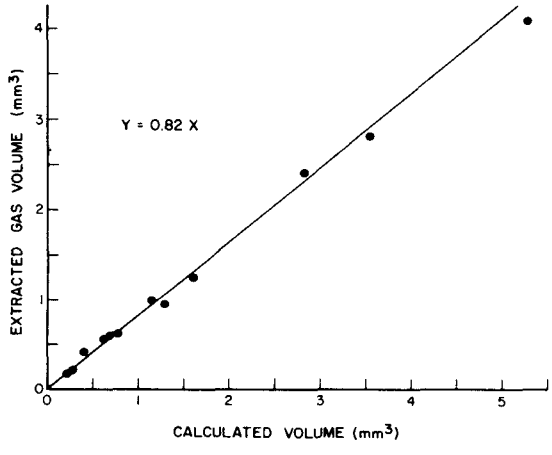

FIGURE 1.—Relation between the volume of the swim bladder calculated from the equation $V = 4/3\,\pi\,ab^2$ and the actual volume of gas extracted from the swim bladder for northern anchovy larvae of mean length 15.6 to 29.6 mm. Each point is the mean volume of the swim bladder calculated for a sample of two to eight larvae taken at night and the average volume of gas extracted from that sample. Sample means were weighted by their variances to calculate the regression line; intercept for line did not differ from 0; and the standard error of line was 0.0428.

To determine if anchovy larvae filled the swim bladder by gulping air at the water surface, the following experiment was performed. Commencing 4 h after the onset of dark, larvae in a 400-liter rearing tank were sampled and the lengths and dimensions of the swim bladder of each larva in the sample measured. Just before the onset of dark on the following day, the surface of the tank was sealed with a 0.5-cm layer of mineral oil. A second sample was taken commencing at 2400 h, 4 h after the onset of dark and ending just before the beginning of light at 0800. A third sampling was taken of larvae in the sealed tank during the day beginning at 1000 h, 2 h after the onset of light, and ending at 1400.

The gas content of the swim bladders of laboratory-reared larvae captured in the dark was analyzed using the micro gasometric method and apparatus described by Scholander et al. (1955). Swim bladders were dissected from the larvae in acid citrate solution, removed with a Pasteur pipette, and injected into an acid citrate filled capillary tube sealed at one end. After two to eight

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

swim bladders had been collected, they were macerated in the tube and the gas withdrawn with a Pasteur pipette and inserted into the syringe gas analyzer (Scholander et al. 1955). In the analyzer, the carbon dioxide was absorbed with alkaline citrate, oxygen by pyrogallol, and the volume of gas determined before and after each treatment. The remaining gas was considered to be nitrogen. The volume of gas was read under a dissecting microscope using an optical micrometer. Reading error was about ± 0.09 μl or from 1 to 2% depending on the volume of the sample.

RESULTS

Diel Rhythm in Swim Bladder Inflation

The volume of the swim bladder of larvae captured at night in the sea was greater than that of larvae collected in the day (Table 1). Similarly, the volume of the swim bladder of larvae reared in the laboratory was greater at night than in the day. To illustrate these daily changes for laboratory-reared larvae, the mean volume of the swim bladder for 2-h intervals was calculated for each of three length classes (10.0 to 11.9 mm, N = 121; 12.0 to 13.9 mm, N = 202; 14.0 to 15.9 mm, N = 129). No evidence existed for anticipation of the onset of dark at 2200 h nor for the onset of light at 1000 h (Figure 2). In all three length classes the mean volume did not return to the daytime level until about 2 h after the onset of light nor did they reach the maximum at night until about 2 h after the onset of dark.

The swim bladder of larvae at night was frequently so inflated that it constricted the gut (see fig. 8 in Uotani 1973). Larvae in the dark with filled swim bladders were motionless or slowly sinking. The body was oriented head down at an oblique angle to the water surface. After sinking a short distance, the larvae swam back to the water surface, a behavior closely resembling that of yolk-sac larvae (Hunter 1972).

TABLE 1.—Swim bladder volume (mm³) of preserved northern anchovy larvae from standard CalCOFI oblique plankton tows taken at night and in the day in southern California inshore waters.

Length class (mm)	Night samples		Day samples	
	N	Swim bladder vol (mean ± 2 SE)	N	Swim bladder vol (mean ± 2 SE)
11.0-11.9	23	0.044 ± 0.007	28	0.018 ± 0.008
12.0-12.9	20	0.073 ± 0.015	30	0.015 ± 0.004
13.0-13.9	24	0.124 ± 0.011	17	0.030 ± 0.016
14.0-14.9	14	0.128 ± 0.011	6	0.029 ± 0.003

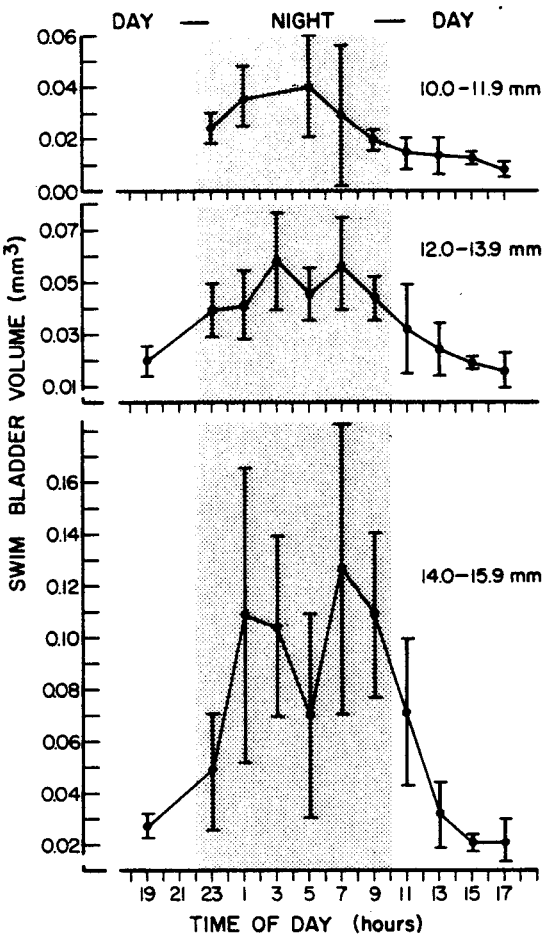

FIGURE 2.—Mean swim bladder volume ± 2 SE of mean for 2-h class intervals plotted at midpoint of each 2-h class. Data shown for three length classes of laboratory-reared northern anchovy larvae; the onset of dark was at 2200 h and onset of light at 1000 h. No transitional level of illumination existed between night and day.

Specimens with obviously inflated swim bladders occurred occasionally in day samples from the sea and laboratory but these were only a few percent of the larvae examined if the first 2 h after the onset of light are excluded. On the other hand, the occurrence of larvae with deflated bladders at night was more common. About 10% of the wild larvae and 20% of the laboratory-reared (12.0 to 12.9 mm) larvae had swim bladder volumes at night comparable to those in the day (Figure 3). The proportion of larvae with deflated bladders at night decreased with larval length.

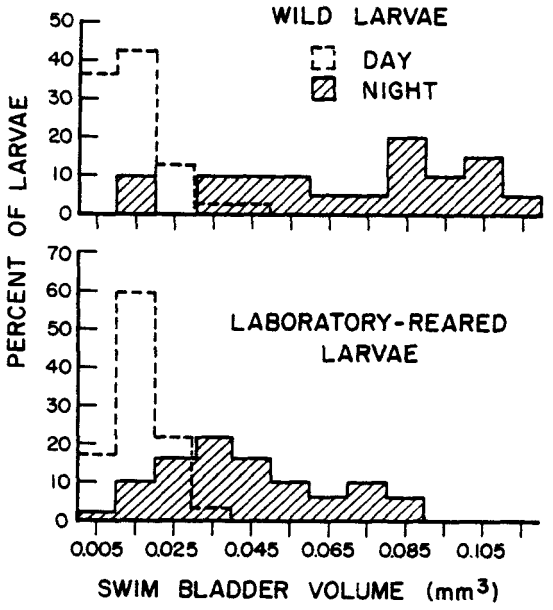

FIGURE 3.—Percent of northern anchovy larvae, 11.9 to 12.0 mm, at night (solid bars) and in day (dashed bars) having swim bladder volumes in various 0.01-mm^3 classes; numbers on abscissa are midpoints of swim bladder volume classes. Upper panel, larvae from CalCOFI ichthyoplankton collections (preserved specimen length), $N = 20$ for night, and $N = 30$ for day. Lower panel, larvae reared in laboratory (live specimen length), $N = 49$ for night, and $N = 29$ for day. Data from 2-h after onset of dark and 2-h after onset of light were excluded in laboratory-reared larvae.

The mean swim bladder volume at night was greater for wild than for laboratory-reared larvae of the same length. The effect of preservation on larval length for larvae of this size is not known but a shrinkage of about 10% in length in the Formalin-preserved ichthyoplankton specimens would account for this difference. The effect of preservation on swim bladder volume is also unknown. In some of the preserved specimens, we noticed the bladder was filled with fluid but we did not routinely make an examination of the bladder contents.

Swim Bladder Inflation and Larval Length

The swim bladder was fully formed when larvae reached 8 to 9 mm but it usually was not inflated. To determine the larval size at which nightly inflation commenced, night and day samples from the laboratory were grouped into 1-mm length classes (9.0 to 9.9 mm, 10.0 to 10.9 mm, etc.), and the mean volume for day and night samples for each class calculated, and compared using the t test. The first 2 h after the onset of dark and the onset of light were excluded from the classes.

Some of the 9.0 to 9.9 mm larvae appeared to have inflated swim bladders at night but the night-day difference in swim bladder volume was not significant ($0.2 > P > 0.1$). Mean volumes for day and night samples were different in larvae 10.0 to 10.9 mm as were those for larvae in all succeeding length classes ($P < 0.001$). Thus, the threshold larval length for nightly inflation of the swim bladder occurred at about 10 mm, the point at which the means for day and night volumes diverge (Figure 4).[3] From this point, mean volume of night samples increased exponentially with length whereas that for day samples increased linearly.

Relation Between Sinking Speed, Swim Bladder Volume, and Larval Length

We observed that larvae with inflated bladders sank more slowly than those with uninflated

[3]Swim bladder inflation is reported to occur at 7 mm in *E. japonicus* (Uotani 1973). Comparison of his illustrations to those of Uchida et al. (1958) suggests Uotani's reported lengths are in error and that *E. japonicus* also inflates the bladder at about 10 mm.

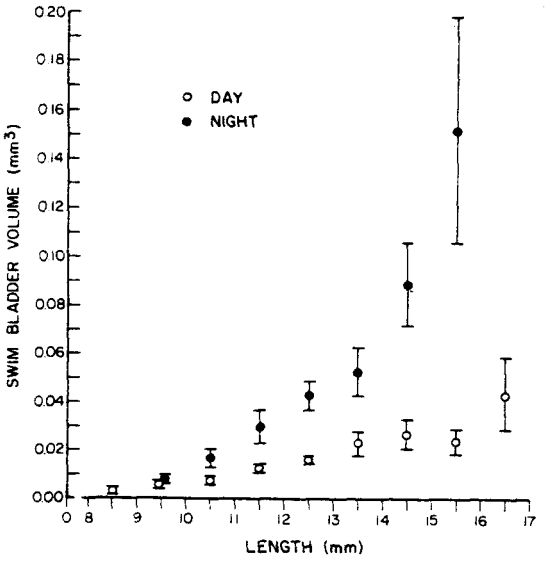

FIGURE 4.—Mean swim bladder volume ± 2 SE for laboratory-reared northern anchovy larvae for 1-mm classes of length plotted at the midpoint of each class. Solid circles are night (first 2-h after onset of dark omitted) and open circl day (first 2-h after onset of light omitted).

bladders. At night, larvae were occasionally neutrally buoyant but most were slightly negatively buoyant.

To develop an equation for expressing sinking speed in terms of larval length and swim bladder volume, the data on sinking speeds were grouped into four classes of larval length: 10.0 to 11.9 mm, $N = 30$; 12.0 to 13.9 mm, $N = 41$; 14.0 to 15.9 mm, $N = 54$; and 16.0 to 17.9 mm, $N = 14$. A regression of sinking speed on swim bladder volume for each length class yielded the following slopes and standard errors for the regression lines: -3.040, SE = 2.339; -4.001, SE = 1.297; -4.8796, SE = 0.616; and -5.070, SE = 1.680, respectively. Covariance analysis of these data indicated that the slopes were not different whereas the intercepts for the regression lines were statistically different ($P = 0.01$). Since no difference existed in the slopes among the four groups, the common slope from the covariance analysis, -4.769, SE = 0.487, was used to express the relation between sinking rate and swim bladder volume for each length class (Figure 5, lower panel). When adjusted for the common slope, the sinking rate intercepts of the four regression lines showed a precise linear relationship when plotted against the midpoints of their respective length classes (Figure 5, upper panel). The equation for the intercept-length relationship was $y = 0.18L - 1.51$ where L is larval length (the midpoints of the larval length classes) and y is the intercept for the regression of sinking rate on swim bladder volume (the sinking rate at $V = 0$ in Figure 5). This equation was combined with the common slope to provide the equation given below:

$$S = 0.18L - 1.51 - 4.77V$$

where S = sinking speed in centimeters per second
L = larval length in millimeters
V = swim bladder volume (outside dimensions) in cubic millimeters.

We examined the changes in sinking speed of larvae from the time of hatching through the development of the swim bladder. These changes are of interest because they illustrate the timing of swim bladder development, its effect on buoyancy, and the advantage of a nightly inflation cycle. Data for sinking rates for larvae 4.0 to 9.9 mm were grouped into 1-mm classes and the means plotted at the midpoints of the class intervals except for the yolk-sac larvae (3.7 mm) which were all about the same length. For larvae 10.0 mm or larger, we calculated sinking speeds from the mean swim bladder volume given in Figure 4 using the equation given in the preceding paragraph.

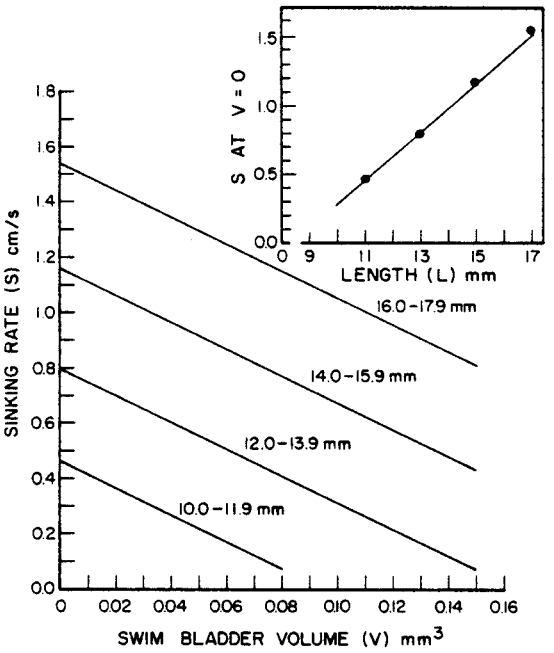

FIGURE 5.—The relation in larval northern anchovy between sinking speed (S), swim bladder volume (V), and larval length (L). Lower panel, regression lines show relation between sinking speed and swim bladder volume for the four classes of larval length indicated in the figure, when a common slope of -4.769 is used (see text). Upper panel, the regression of the y intercepts (S at $V = 0$) of the four regression lines on larval length (midpoints of the four length classes); equation for intercept line was $y = 0.18L - 1.51$. Final equation is $S = 0.18L - 1.51 - 4.77V$.

Sinking speed increased exponentially with length, when larvae sampled at night are excluded (Figure 6). The increase is roughly proportional to the cube of the length (curved line in Figure 6). This might be expected since sinking speed is dependent upon buoyancy which varies with the volume (L^3) and the difference in specific gravity between the fish and its medium. For estimating mean sinking speed for larvae with swim bladders in the day, or for those without swim bladders the equation $S = 0.094 + 0.000264L^3$ where L is length in millimeters and S is sinking speed in centimeters per second, gives a good fit to the data.

The length threshold for filling the swim bladder (about 10 mm) coincides with a rapid acceleration

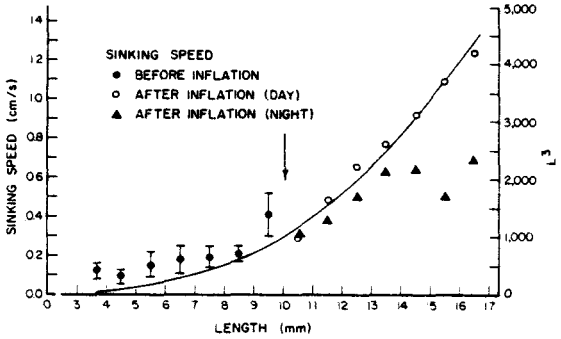

FIGURE 6.–Change in sinking speed from hatching through threshold of the initial inflation of swim bladder (arrow) of northern anchovy larvae. For larvae <10 mm, mean sinking speed ± 2 SE were plotted against the midpoint of 1-mm length classes, except for the first point which was for yolk-sac larvae and is plotted at average length for the class. For larvae >10 mm, sinking rates are estimated from the mean swim bladder volume given in Figure 3 using the general equation for sinking speed given in Figure 5. Open circles are estimates for the day and solid triangles for the night. Line is the cube of the length (L^3) plotted against length.

in the volume of the larva and its sinking speed. Thus, the timing of the swim bladder inflation may be related to these events.

The effect of night inflation of the swim bladder is also illustrated in Figure 6. For larvae 12 mm and larger, the average sinking speed at night appears to be relatively constant at about 0.6 ± 0.1 cm/s (22 m/h) while the sinking speed in the day increased exponentially with length. A larva 16.5 mm long had a sinking speed at night nearly half that of the day. Swimming speeds of larval anchovy while searching for food in the day, range from about 0.6 to 1.0 body length/s (Hunter in press). If a larva did not inflate the swim bladder at night, the swimming required just to maintain a position in the water would be equivalent to that used in the search for food in the day. Since larvae do not feed at night, filling the swim bladder would clearly be advantageous as an energy conserving mechanism.

Mechanism of Swim Bladder Inflation

It was not possible to determine if larvae in the tank sealed with mineral oil swam just below the layer of oil or into it because our view was from above rather than from the side. However, the mean swim bladder volume for larvae sampled at night in the sealed tank was less than that for larvae sampled on the previous night when the tank was not sealed (t test, $P = 0.001$, Table 2). The mean volumes of the swim bladders for larvae in the day and at night in the sealed tank were not different. This experiment suggests that anchovy larvae in the laboratory fill their swim bladders by swallowing air at the surface.

TABLE 2.–Mean swim bladder volume and mean length of northern anchovy larvae in sealed and unsealed containers.

Treatment	N	Mean length of larvae (mm ± 2 SE)	Mean swim bladder vol (mm^3 ± 2 SE)
Unsealed tank:			
Night	12	13.9 ± 0.37	0.094 ± 0.037
Sealed tank:			
Night	18	14.1 ± 0.41	0.035 ± 0.008
Day	17	13.8 ± 0.86	0.026 ± 0.019

An analysis of the oxygen content of the swim bladder could suggest whether or not the gas in the swim bladder was secreted or taken from the air. Newly secreted gas would be expected to be oxygen (Wittenberg 1958), but if larvae were swallowing air the concentration should be about 21% oxygen. Our analysis did not agree with either pattern even though some measurements were made 30 min after the onset of dark. Samples averaged about 11% oxygen, consistently less than the atmospheric concentration (Table 3). Carbon dioxide levels (0.9 to 2.2%) were higher than atmospheric levels but little can be concluded because our experimental reading error was 1 to 2% owing to the small volumes used. It is probable that oxygen was lower than atmospheric concentration because it was absorbed from the bladder by the larva. Except for the first two observations in Table 3, oxygen concentration tended to decrease with time from the onset of dark. It should be noted that preferential removal of oxygen from swim bladder gases is not unique to anchovy larvae but is found in most fishes which have been studied (Wittenberg 1958).

The rate at which the swim bladder was filled also suggests that the filling is accomplished by gulping air. Larvae with filled swim bladders were captured 20 to 30 min after the onset of dark and the means were at a maximum by 2 h after dark. Uotani (1973) reported for *E. japonicus* that filling was completed by 1 h in the sea. Fishes that fill the swim bladder by secretion require much more time to fill the bladder, for example, *Stenotomus versicolor* (Mitchill) requires 10 to 12 h; *Anguilla rostrata* (LeSueur), 12 to 24 h; *Opsanus tau* (Linnaeus), *Prionotus carolinus* (Linnaeus), and *P. evolans* (Linnaeus), 24 h; and *Tautoga onitis*

TABLE 3.–Percent composition of swim bladder gas of laboratory-reared northern anchovy larvae sampled at night, listed in order of time of sampling.

Elapsed time after onset of darkness (h)	(min)	Number of larvae	Mean larval length (mm)	Composition of swim bladder gas (%) CO_2	O_2	N_2	Sample volume (μl)	Oxygen in tank (ml/liter)
0	30	2	27.1	1.2	9.6	89.2	5.54	5.4
0	30	2	29.6	1.6	8.2	90.2	8.12	—
0	50	4	22.1	1.3	14.2	84.5	4.99	5.7
3	15	5	21.0	1.8	13.1	85.0	6.08	5.0
4	20	3	25.3	2.2	11.1	86.7	7.18	5.1
6	25	8	19.3	0.9	12.7	86.4	4.85	4.6
6	25	7	18.9	0.6	12.6	86.9	4.05	5.0
7	35	6	22.1	1.4	9.1	89.5	6.06	4.9
8	10	6	20.1	0.6	9.5	89.9	3.70	4.8

Linnaeus, about 24 h (Wittenberg 1958). Considering the evidence presented here, and the apparent lack of gas secretion in clupeoid fishes in general (Brawn 1962), the most tenable hypothesis is that swim bladder inflation is accomplished in larval anchovy by taking in air at the water surface.

Vertical Migration

If anchovy larvae fill their swim bladders each night by swallowing air, they must either remain near the surface throughout the day and night or migrate to the surface at dusk.

We reexamined the original data collected by Ahlstrom (1959) to determine if any evidence existed for vertical movements in northern anchovy larvae. Ahlstrom (1959) made extensive horizontal tows for fish larvae with opening and closing nets and presented the average number of larvae of all lengths at various depths. We separated his original length data into two length classes: larvae <11.75 mm (preserved standard length) and larvae ≥11.75 mm for night and day collections; we omitted those collections occurring near dawn and dusk. Unfortunately, only 14 larvae ≥11.75 mm were taken in the day while 279 were taken at night but the depth pattern in the day collections was relatively consistent. Larvae <11.75 mm were more abundant: N = 6,456, night; and N = 331, day.

At night, over 50% of the larvae ≥11.75 mm were taken in the upper 10 m whereas in the day the upper 10 m contained less than 10% of the larger larvae (Figure 7). About 50% of the larvae <11.75 mm occurred in the upper 10 m, but no obvious difference between day and night samples existed. These results are in general agreement with those of Ida (1972) who studied the vertical distribution of the Japanese anchovy, *E. japonicus*, a closely related species that also has a diel rhythm in swim bladder inflation (Uotani 1973). Ida (1972) found a striking diel change in the vertical distribution of *E. japonicus* with the maximum numbers occurring at the surface at night and at 20 to 30 m during the day with the movement to the surface occurring at twilight. Examination of the size frequency histograms from some of the collections

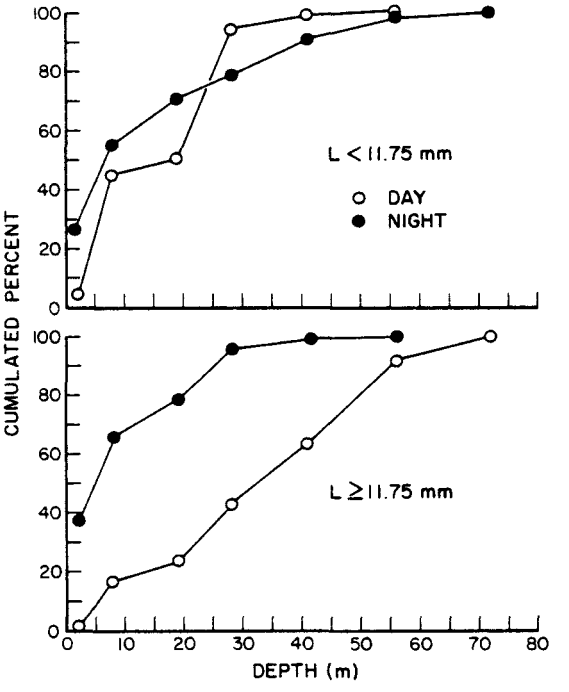

FIGURE 7.–The vertical distribution in the sea of northern larvae at night and in the day for two length classes; length <11.5 mm, upper panel, and length ≥11.5 mm, lower panel (lengths for preserved specimens). Numbers of larvae taken at each depth were cumulated starting at the shallowest tow (5 m) and expressed as the cumulated percent of the total larvae taken. Data are from Ahlstrom (1959).

led Ida to conclude that the diurnal change was caused by the vertical migration of the larger larvae (10 to 15 mm).

The diel vertical movements that appear in larval anchovy at the time of swim bladder inflation probably persist into adult life. The adults, however, are quite variable in their behavior which changes with size of school and season (Mais 1974). Vertical migration is most noticeable in large schools which are deep during the day (119 to 220 m) and rise to the surface and disappear as sonar targets at dusk. These schools reform and descend at first light in the morning (Mais 1974).

Possible Adaptive Advantages

Inflation of the swim bladder reduces the energy required for maintaining a position in the water column. This reduction in sinking speed could represent an important energy savings for larval anchovy because they do not feed at night and swimming can not be used in the search for food. The major energy cost of a diel rhythm of swim bladder inflation is the required vertical migration to the surface. Laboratory work suggests that anchovy larvae, by modification of swimming speed and direction of turning, are able to find and remain in area of high food density (Hunter and Thomas 1974). Thus, it is possible that a larva could follow an upward and downward movement of food at dusk and dawn. In this case the added cost for vertical movements would be slight since the energy spent in swimming could be used in searching for food. It is unlikely, however, that this condition could always be met. Thus, the energy saved at night by inflation of the swim bladder should exceed that used in vertical migration. Assuming the energy used per centimeter swum is the same for vertical migration as for maintaining a position in the water at night, the energy used in a round trip vertical migration of 100 m would be equivalent to that used to maintain a position for 10 h at night when the sinking speed was 0.28 cm/s. Thus, the difference between day and night sinking speeds would have to exceed 0.28 cm/s before a 100-m round trip could be considered an energy sparing mechanism. The difference in sinking rates exceeds 0.28 cm/s for larvae 13.5 mm and larger (Figure 6). This difference increases with larval length suggesting that the vertical range of migration over which energy savings are possible increases with length. In addition, the difference between day and night sinking speeds may be underestimated because sinking speeds were measured at the surface. If larvae descend during the day the gases in the swim bladder would be compressed, increasing body density and thereby increasing the sinking speed for larvae in the day.

These calculations are, of course, a great oversimplification, but they do illustrate that the energy saved by inflation of the swim bladder at night could exceed the cost of a vertical migration and that the possible range of migration could be greater for larger larvae.

The energy costs of maintaining a position in the water column for fish with and without swim bladders have been calculated by Alexander (1972). His calculations are not appropriate for anchovy larvae at night because he considered fish without a bladder to be continuously swimming and gaining lift from the pectoral fins. The behavior of an anchovy at night that failed to inflate the swim bladder would probably resemble one with an inflated bladder. It would sink motionless at an oblique angle to the water surface and interrupt sinking by bursts of near vertical swimming. To maintain a position, these bursts of swimming would have to be of longer duration or of greater frequency than if the swim bladder were filled.

In addition to an energy sparing mechanism, a nightly pattern of swim bladder inflation could possibly reduce predation. Some predators of larval fishes, for example chaetognaths and medusae, use the movement or turbulence produced by prey for detection and attack (Horridge 1966; Newbury 1972). Thus, the reduction of activity produced by slower sinking speeds could reduce predation. The vertical migration of the larvae could also result in exposure to different and possibly less hazardous predators at night. It would also serve to aggregate larvae, thus facilitating social contacts necessary for the development of schooling which begins at about 15 mm.

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LITERATURE CITED

AHLSTROM, E. H.
1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish Wildl. Serv., Fish. Bull. 60:107-146.

ALEXANDER, R. McN.
1972. The energetics of vertical migration by fishes. Symp. Soc. Exp. Biol. 26:273-294.

BLAXTER, J. H. S., AND K. F. EHRLICH.
1974. Changes in behaviour during starvation of herring and plaice larvae. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 575-588. Springer-Verlag, Berl.

BRAWN, V. M.
1962. Physical properties and hydrostatic function of the swim-bladder of herring (*Clupea harengus* L.) J. Fish. Res. Board Can. 19:635-656.

HORRIDGE, G. A.
1966. Some recently discovered underwater vibration receptors in invertebrates. *In* H. Barnes (editor), Some contemporary studies in marine science, p. 345-405. George Allen & Unwin Ltd., Lond.

HUNTER, J. R.
1972. Swimming and feeding behavior of larval anchovy, *Engraulis mordax*. Fish. Bull., U.S. 70:821-838.
1976. Culture and growth of northern anchovy, *Engraulis mordax*, larvae. Fish. Bull., U.S. 74:81-88.
In press. Behavior and survival of northern anchovy *Engraulis mordax* larvae. Symposium on Fishery Science Cienca Marinas, Spec. Suppl.

HUNTER, J. R., AND G. L. THOMAS.
1974. Effect of prey distribution and density on the searching and feeding behaviour of larval anchovy *Engraulis mordax* Girard. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 559-574. Springer-Verlag, N.Y.

IDA, H.
1972. Some ecological aspects of larval fishes in waters off central Japan. Bull. Jap. Soc. Sci. Fish. 38:981-994.

LEONG, R.
1971. Induced spawning of the northern anchovy, *Engraulis mordax* Girard. Fish. Bull., U.S. 69:357-360.

MAIS, K. F.
1974. Pelagic fish surveys in the California Current. Calif. Dep. Fish Game, Fish Bull. 162, 79 p.

NEWBURY, T. K.
1972. Vibration perception by chaetognaths. Nature (Lond.) 236:459-460.

O'CONNELL, C. P.
1955. The gas bladder and its relation to the inner ear in *Sardinops caerulea* and *Engraulis mordax*. U.S. Fish Wildl. Serv., Fish. Bull. 56:505-533.

SCHOLANDER, P. F., L. VAN DAM, C. L. CLAFF, AND J. W. KANWISHER.
1955. Micro gasometric determination of dissolved oxygen and nitrogen. Biol. Bull. (Woods Hole) 109:328-334.

UCHIDA, K., S. IMAI, S. MITO, S. FUJITA, M. UENO, Y. SHŌJIMA, T. SENTA, M. TAHUKU, AND Y. DÔTU.
1958. Studies on the eggs, larvae and juveniles of Japanese fishes. [In Jap.] Kyushu Univ., Fac. Agric., Fish. Dep., 2d Lab. Fish. Biol., Ser. 1, 89 p.

UOTANI, I.
1973. Diurnal changes of gas bladder and behavior of postlarval anchovy and other related species. [In Jap., Engl. abstr.] Bull. Jap. Soc. Sci. Fish. 39:867-876.

WITTENBERG, J. B.
1958. The secretion of inert gas into the swim-bladder of fish. J. Gen. Physiol. 41:783-804.