

RESPIRATION AND DEPTH CONTROL AS POSSIBLE REASONS FOR SWIMMING OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, YOLK-SAC LARVAE

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ABSTRACT

Larval northern anchovy in the yolk-sac (nonfeeding) stage exhibit regular bursts of continuous swimming during the first 3 days after hatching. It has been suggested that this behavior may have a respiratory function. A different possibility is depth control, countering the tendency of the larvae to sink when motionless. This paper includes a theoretical and experimental investigation of the possible functions of these swimming bouts.

The theoretical approach was to define a model and calculate the oxygen available to the larva when resting and while moving, and experiments were performed as a check of the theoretical results. The experiments were conducted on yolk-sac larvae in sealed tanks with varying dissolved oxygen concentrations to determine the effects of reducing the available oxygen on the frequency and duration of the swimming bursts. Results of the experiments confirmed the theoretical model. They indicate that the swimming bouts both help the larva stay at a constant depth and have a respiratory function when the oxygen concentration in seawater is less than 60% of saturation.

Newly hatched northern anchovy, *Engraulis mordax*, larvae exhibit a pattern of regular short bouts of continuous swimming interspersed with periods of resting. These larvae are still in the yolk-sac stage and are not feeding so that the locomotory behavior must have some other purpose, as these motions are energy consuming and also endanger the animal by attracting predators (Lillelund and Lasker 1971). Hunter (1972) suggested that these swimming bouts might have a respiratory function. Respiration has to be by cutaneous diffusion through the 2-3 μm thick skin (Lillelund and Lasker 1971) of the larvae as the gills develop only at a later stage. The purpose of this paper is to test this hypothesis and another possibility, depth control, to counter sinking due to the negative buoyancy, using theoretical and experimental methods.

First, I develop a theoretical model for oxygen transport to motionless and swimming yolk-sac larvae and estimate the possible oxygen uptake. Next, I describe the experiments to test the prediction of the theory for both proposed mechanisms and compare their results.

METHODS

Analytical Model

A mathematical model is now introduced to consider the possible respiratory function of the bouts of continuous swimming of yolk-sac anchovy larvae. First, we calculate the oxygen transport to a motionless larva. This transport is then compared with the metabolic requirements. If the metabolic requirements are not met, larval motion (and the resulting convective diffusion) is required.

The size of yolk-sac larvae (2.7-4.0 mm total length) and their swimming speeds (Hunter 1972) lead to typical Reynolds numbers, based on larval length (Weihs 1980) of <20 . (The Reynolds number is a nondimensional factor indicating the relative importance of pressure and viscous effects on a body moving in a fluid under given circumstances—the higher the Reynolds number, the smaller the influence of the viscosity.) The larvae, as a direct result of their small size, are in a highly viscous laminar flow situation in which turbulent effects can be neglected. Thus, the larvae and their immediately surrounding water would be transported together in oceanic turbulent eddies, which are of the order of tens of centimeters in diameter. As a result, a nonswimming larva would stay for a relatively long period in the same mass

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of water, even though that mass is convected on a much larger scale.

The motionless larva and its surrounding water mass may therefore be analyzed separately, as a distinct system in the thermodynamic sense. Within this system, oxygen transport to the larva is controlled by molecular diffusion because the gill system is not developed at this stage. This process is time dependent, beginning when the larva arrives in a certain location (by swimming) and rests, ending when swimming begins again. Initially the oxygen concentration in the water mass surrounding the larva is uniform, but the larva now starts acting as an oxygen sink, gradually depleting the oxygen content of the water surrounding it. This concept of the larva as an oxygen sink simplifies the calculations, as knowledge of the exact distribution of oxygen diffusivity on the animal's surface is not required. The sink model also is useful here as it averages out the direction of local transport and the body of the larva into which the oxygen diffuses can be taken as an equivalent sphere of equal surface area (Figure 1).

Diffusion into a sphere is most conveniently analyzed in the spherical coordinate system. The governing conservation of mass equation can be written (Crank 1975) as

$$\frac{\partial c}{\partial t} = D \left(\frac{\partial^2 c}{\partial r^2} + \frac{2}{r} \frac{\partial c}{\partial r} \right) \quad (1)$$

where c is the mass fraction of oxygen (a function of the distance and time); r is the radial distance, measured for the center of the equivalent spherical body (the sink); t is the time; and D is the diffusion coefficient of oxygen in seawater.

The temporal boundary condition is the initial, uniform state

$$c(r, 0) = c_0 \quad (2)$$

while the spatial conditions are

$$c(\infty, t) = c_0 \quad (3)$$

which states that far from the animal the oxygen concentration stays unchanged at all times. Strictly, the condition should be defined at some finite distance but as that distance is much larger than the animal equivalent radius, it can be ap-

proximated by ∞ . Next, the oxygen concentration boundary condition at the surface of the equivalent sphere $r = a$ is obtained. Muscles and vascularized tissues have much higher oxygen transport rates than seawater, due to internal uptake augmented by active transport. Thus, oxygen will be absorbed at the surface of the larva as fast as it arrives by diffusion from the surrounding water. The oxygen concentration c at the larva's surface ($r = a$) is thus constant, and very low, i.e.,

$$c(a, t) = c_1 \quad (4)$$

where $c_1 \rightarrow 0$ and $t > 0$.

Equations (2)-(4) enable solving equation (1) analytically, by classical methods. The solution can be written in nondimensional form for the concentration as

$$\frac{c - c_0}{c_1 - c_0} = \frac{a}{r} \operatorname{erfc} \frac{r - a}{2\sqrt{Dt}} \quad (5)$$

where the complementary error function, erfc , is defined as

$$\operatorname{erfc}(z) = \frac{2}{\sqrt{\pi}} \int_z^{\infty} e^{-z^2} dz \quad (6)$$

Numerical values of the complementary error function are found in most mathematical tables (e.g., Abramowitz and Stegun 1965).

The rate of mass transfer (flux) J to the animal is now obtained from

$$J = -\rho D \int_A \frac{\partial c}{\partial r} dA \quad (\text{surface } A) \quad (7)$$

where ρ is the density and A the surface area of the body. For the equivalent sphere of radius a , $A = 4\pi a^2$. $\partial c / \partial r$ is assumed spherically symmetric so that

$$J = -\rho DA \left. \frac{\partial c}{\partial r} \right|_{r=a} \quad (8)$$

where the concentration derivative is obtained from Equation (5). Substituting this, and the value for the surface area, and setting $c_1 = 0$ as in Equation (4), the total mass flux per unit time J_d is

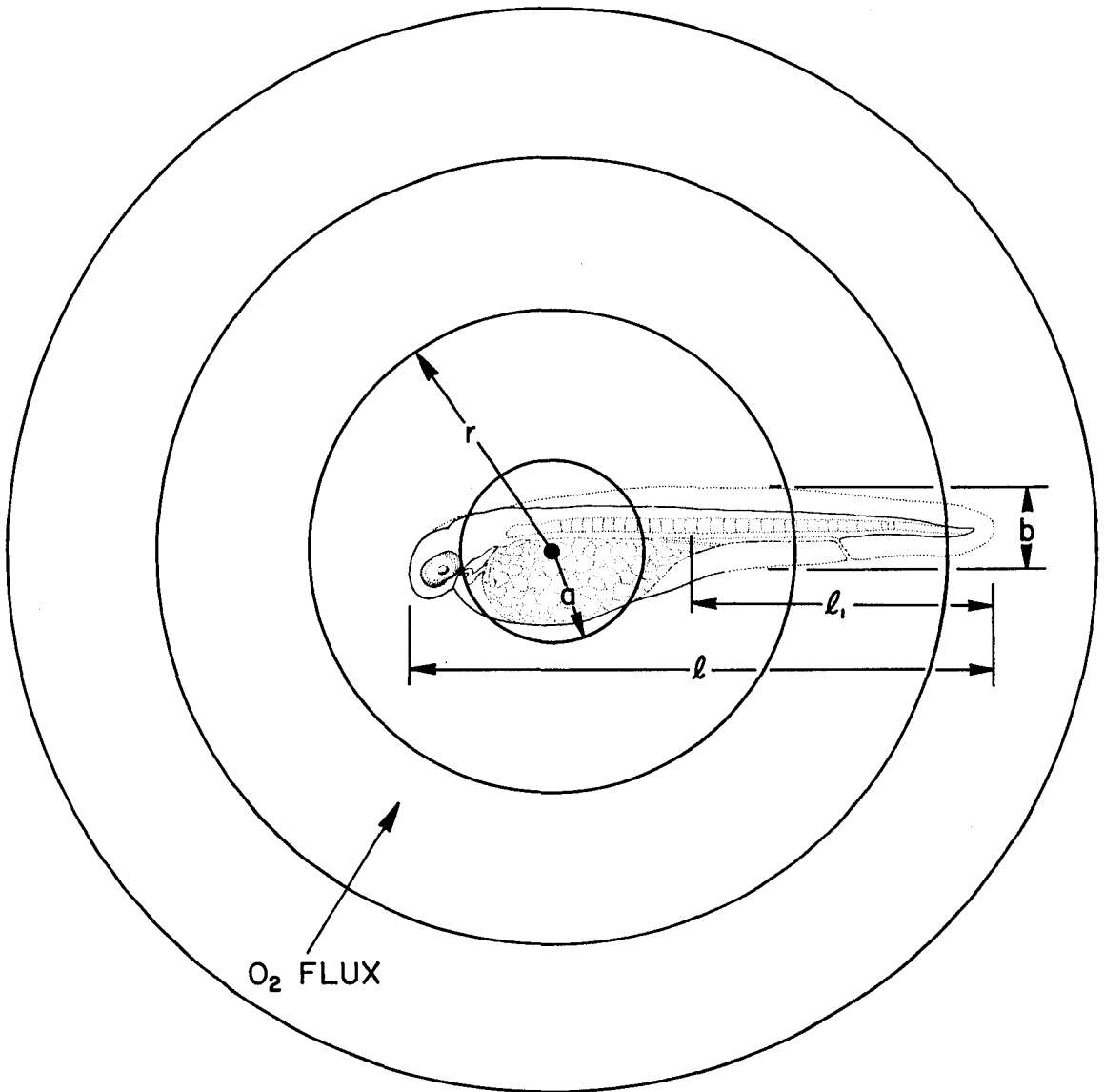


FIGURE 1.—Schematic description of model and spherical coordinate system centered on the center of mass of a northern anchovy larva: a is the radius of an equivalent sphere of equal surface area (not to scale), l is the larval length, and b and l_1 are the average tail strip depth and length.

$$J_d = -\rho D c_0 \cdot 4\pi r^2 \frac{a}{r} \operatorname{erfc} \left(\frac{r-a}{2\sqrt{Dt}} \right) \cdot \left(\frac{1}{2\sqrt{Dt}} + \frac{1}{r} \right) \quad (9)$$

and when $r = a$, this simplifies to

$$J_d = 4\pi\rho D c_0 a^2 \left(\frac{1}{a} + \frac{1}{2\sqrt{Dt}} \right). \quad (10)$$

Equation (10) consists of two terms in the brackets, multiplied by a constant factor. The first term in the brackets is the constant, time-independent contribution while the second describes the initial

transient. The latter drops rapidly, proportionally to the square root of time elapsed since arrival of the larva. Substituting numerical values into Equation (10), the oxygen flux can be compared with oxygen requirements of larval anchovy to see if the swimming motions are required for respiration.

The equivalent radius, a , of the larval anchovy is found by equating the surface area of the larva and the equivalent sphere. The larva, at this yolk-sac stage, is described for diffusion purposes as a sphere of radius q (the yolk sac) attached to an almost flat ribbon of length l_1 and average breadth b . The combined surface area of the sphere and ribbon is then taken to be equal to the area of the equivalent sphere appearing in Equation (10). Thus

$$4\pi a^2 = 2l_1 b + 4\pi q^2. \quad (11)$$

Using typical values for these parameters for newly hatched larvae we obtain $l_1 = 1.4$ mm, $b = 0.3$ mm, and $q = 0.3$ mm (from drawings by E. H. Ahlstrom, Senior Scientist, Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038), i.e., $a = 0.0395$ cm. The mass content of oxygen in seawater at 20° C is $c_0 = 7.8 \times 10^{-6}$ g/cm³ (Prosser 1973), and the mass fraction is obtained by dividing by the density of seawater, which then cancels out in Equation (10). Finally, the diffusion coefficient of oxygen is approximately equal for freshwater and seawater (Riley and Skirrow 1965) so that a reasonable value for 20° C is 1.8×10^{-5} cm²/s (O'Brien et al. 1978), or $D = 1.08 \times 10^{-3}$ cm²/min. Substituting all these values into Equation (10) we obtain

$$J = (4.18 + 2.51 t^{-1/2}) 10^{-9} \text{ g/min} \quad (12)$$

when the water is 100% saturated. Reducing the oxygen content of the water causes the value of the oxygen flux, J , to go down proportionally, i.e., by multiplying J from Equation (12) by the fraction of saturation. Some typical values of J appear in Figure 2 with the percent of saturation as the parameter.

When the larva starts swimming, two changes in the oxygen supply occur. First, the animal's motion produces a convective local flow relative to the body, thus bringing new, oxygen-rich water closer and removing the respiratory waste products. Secondly, the absolute motion will bring the larva to an area where the oxygen concentration is

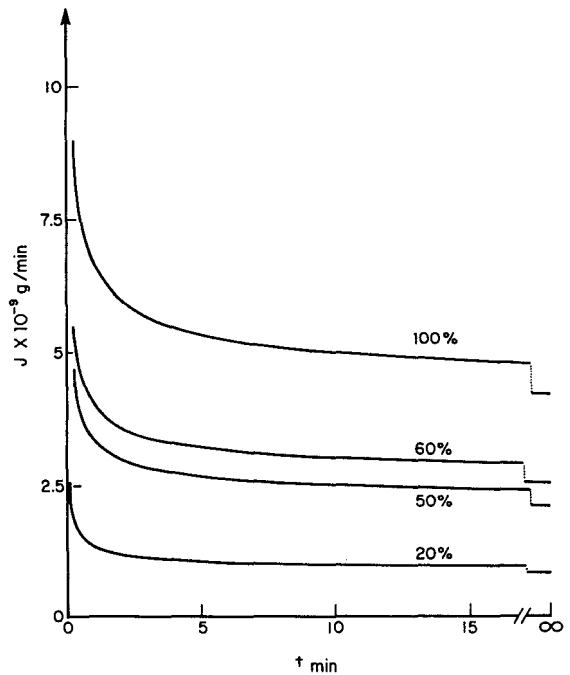


FIGURE 2.—Rate of oxygen transport (J) to motionless northern anchovy larva by diffusion versus time (t). Broken part of curve shows asymptotic value, after the initial transient has disappeared. Parameter is oxygen concentration in percentage of saturation.

still at the initial ambient value, starting the process described by Equations (1)-(4) again.

Following this reasoning, even relatively slight motions causing just a local flow around the animal's body would suffice for respiratory functions. Thus, actual swimming would not be required. However, the yolk-sac larvae are increasingly negatively buoyant with age (Hunter and Sanchez 1976), which causes them to sink. Therefore, active absolute motion is necessary for the larva to stay at a given depth for feeding and future schooling.

When the larva is swimming, the process of transport of oxygen changes to convective diffusion, and as such is described by a different model (Daykin 1965). Daykin's work dealt with stationary eggs in a moving river environment, but for mass transfer purposes this is equivalent to a larva (or egg) moving at constant speed relative to the water. In the convective diffusion process (Levich 1962; Daykin 1965), the mass transfer to the larva can be roughly described by

$$J_{con} = 4\pi a^2 (c_0 - c_1) k \quad (13)$$

where k is a diffusion coefficient obtained from experimental correlations of the diffusional flux with the Reynolds (Re) and Schmidt numbers (Sc). (The Schmidt number is the ratio of the kinematic viscosity to the diffusivity and nondimensionally indicates the relative importance of these two effects in a given flow situation.) For the present circumstances

$$k = \frac{D}{2a} (2 + 0.6 \text{Re}^{1/2} \text{Sc}^{1/3}) \quad (14)$$

for average swimming speeds of approximately 5 cm/s (Hunter 1972) and a Schmidt number of 600 we have

$$J_{\text{con}} = 1.27 \times 10^{-7} \text{ g/min.} \quad (15)$$

Hence, oxygen transport due to convective diffusion is over 20 times higher than for the motionless larva (Equation (12)). The calculation leading to Equation (15) is approximate, as the larva's shape will influence the coefficient 0.6 in k (Equation (14)) and also change the form of Equation (13). It is, however, accurate to at least an order of magnitude (Levich 1962). Thus, once the larva starts swimming, the mass transfer of oxygen to its surface increases by at least an order of magnitude. Recently, an additional mechanism for oxygen transport to stationary eggs was identified by O'Brien et al. (1978) who showed that under certain riverbed conditions natural convection, due to the oxygen and metabolite gradients, may contribute to the oxygen transfer. This effect may play a supplementary role in the present (pelagic) case as the natural convection effects are much smaller than the forced convection.

Tests with Larvae

Egg batches were obtained once a week from groups of adult northern anchovy maintained in the laboratory and induced to spawn. Measurements were made each week during a 6-wk period to minimize bias due to a single cohort group. Water temperature ranged from 19° to 21° C, and overhead fluorescent lighting was used. The 50% hatching point was determined and defined as "day 0" for each batch. Experiments were carried out on age day 0 larvae every week (six times).

A set of five 2,000 ml graduated cylinders filled with filtered seawater was used for the environmental tests. Oxygen concentrations of 100, 80,

60, 40, and 20% of saturation at the measured temperature were produced by bubbling nitrogen through each of the cylinders. After the larvae were added (about 25 individuals/cylinder), the cylinders were sealed off with rubber stoppers. Oxygen concentrations were measured periodically during the experiments with a Beckman Instrument Model 160 Physiological Gas Analyzer² to check on initial values and possible drift.

Individual fish were monitored for a 5-min period, and duration and number of swimming bursts were recorded on a Esterline-Angus Operation Recorder Model AW. Records were also made of approximate swimming direction (measured from horizontal) as well as the change in orientation of motionless larvae while they were sinking during the resting periods. Five active larvae were monitored in each container every week, for both day 0 and day 1 tests.

After the day 0 experiments were finished each week, the equipment was reset and the day 1 tests conducted 24 h later with additional larvae from the same batch. The latter larvae were kept in oxygen-saturated water from hatching to minimize stress due to oxygen starvation.

RESULTS

No appreciable change in the proportion of time spent in burst swimming was observed when the measurement at 100% of saturation concentration of oxygen (which is the oxygen level in the natural state in the sea because of turbulent interchange with the atmosphere) was compared with the time spent in motion at the 80 and 60% oxygen levels (Figure 3).

When oxygen levels were <60% of saturation, large increases in the time spent swimming were observed. The rate of increase of swimming time in both ages (day 0 and day 1) were similar. Various attempts at describing all five data points for each age-group by means of a single empirical exponential function were not successful (low coefficients of determination). Thus, it seems that a different behavioral mechanism is triggered when oxygen levels fall below 60% of saturation at the given temperatures, i.e., much lower than expected oxygen concentrations in the upper layers of the sea, where the anchovy larvae are usually found.

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

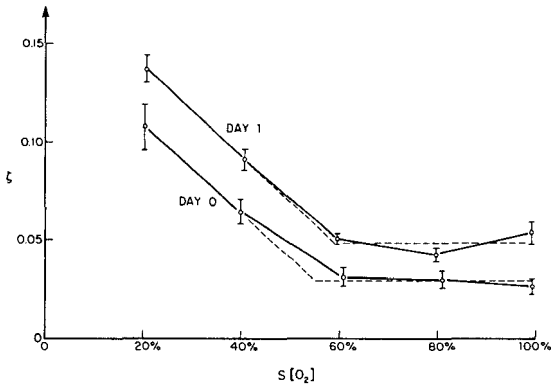


FIGURE 3.—Fraction of time spent actively swimming, ζ , versus oxygen concentration in percentage of saturation, $S[O_2]$, for newly hatched (day 0) and 24-h-old (day 1) northern anchovy larvae. Each point on the full curves is an average of between 20 and 25 individual 5-min observations. Bounds are standard errors. Dashed lines indicate idealized model of constant fraction, ζ , at high $S[O_2]$ and linearly increasing ζ at low $S[O_2]$.

The duration of bursts increased monotonically as the oxygen levels decreased, while the number of bursts dropped significantly to a minimum of 1/min at 60-80%, increasing sharply after that (Figure 4). No satisfactory explanation has been found for the drop in the number of bursts at 80% of saturation. The main result illustrated by Figure 4 is that both the frequency and duration of bursts increase markedly at low oxygen concentrations, both contributing to the increase in time spent swimming.

The center of gravity of anchovy larvae is in the vicinity of the head and therefore they tend to be oriented in an oblique head-down configuration after swimming ceases. More mature larvae, which have converted significant amounts of yolk into denser tissue are negatively buoyant (Hunter and Sanchez 1976) and tend to sink head downward at rates of approximately 1-2 mm/s. To check the vertical station-keeping hypothesis, the direction of swimming was recorded, as well as the body

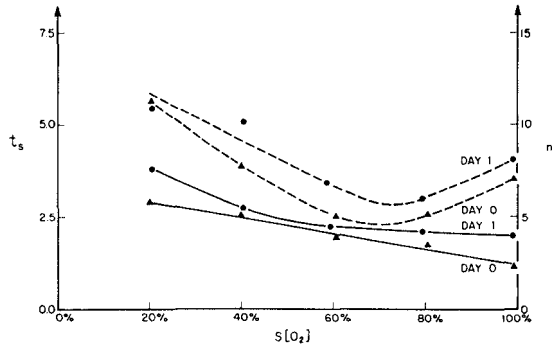


FIGURE 4.—Average duration (t_s) of swimming bouts (full lines) and number of bouts (n) in 5 min (dashed lines) for day 0 (solid triangles) and day 1 (solid circles) larvae, versus oxygen in percentage of saturation concentration ($S[O_2]$).

orientation, when swimming started. The results of over 1,400 recorded swimming periods appear in Table 1, which lists average values of the body angle at the onset of swimming and the direction of swimming.

No significant variation in swimming direction with oxygen concentration was found for either day 0 or day 1 larvae (Table 1). The spread in results was large, as is noticeable from the standard errors. The total possible spread of data is $\pm 90^\circ$, which suggests that swimming direction is actually a random phenomenon for day 0 larvae. At age 1 day, a positive bias was observed in the swimming direction, still with large variation. The body inclination at the beginning of the swimming periods was consistent, at around -65° with the exception of the day 0, 20% oxygen data, which is influenced by additional factors, discussed below.

DISCUSSION

The analytical model predicted that a motionless larva would be able to pick up oxygen at a decreasing rate at any given spot (Equation 12).

TABLE 1.—Initial orientation of the body and duration of swimming during bouts of continuous swimming by newly hatched and 1-d-old northern anchovy larvae. Error bounds are standard error. Angles are measured from the horizontal. Positive values indicate upward motion. Averages of day 0 do not include 20% O_2 values as these (indicated by question marks) include different phenomena.

Oxygen concentration (% of saturation)	N, number of observed events		Orientation of body at start of swimming period (degrees)		Direction of swimming relative to horizontal (degrees)	
	Day 0 larvae	Day 1 larvae	Day 0 larvae	Day 1 larvae	Day 0 larvae	Day 1 larvae
100	106	157	-68.9 ± 23.7	-74.6 ± 11.8	-4.7 ± 56.1	44.7 ± 45.8
80	103	113	-66.3 ± 29.4	-80.0 ± 9.2	-15.0 ± 59.0	28.2 ± 58.1
60	109	112	-72.1 ± 15.6	-66.7 ± 17.6	-3.9 ± 73.6	51.9 ± 31.9
40	161	140	-61.0 ± 30.3	-69.2 ± 22.0	12.3 ± 54.0	33.2 ± 45.9
20	210	204	$-45.6 \pm 36.7(?)$	-63.8 ± 27.8	$38.7 \pm 43.3(?)$	37.4 ± 52.3
Weighted average			-66.4 ± 25.2	-70.2 ± 16.9	-2.8 ± 58.3	39.0 ± 48.1

This prediction has now to be compared with the requirements of the organisms to determine if additional oxygen is needed. Data for oxygen consumption at 17° C of late-stage anchovy eggs and larvae of differing ages as a function of time since spawning has been obtained by Theilacker,³ by measurement in a respirometer. These data were adjusted to 20° C, the temperature at which most of my experiments were conducted (Figure 5), by means of a temperature-growth correlation for larval northern anchovy (Zweifel and Hunter⁴). This adjustment was made by calculating the size of the larvae at 17° C at the ages recorded by Theilacker, then translating these into age for the same size at the new temperature, which gave a smaller size because growth rates increase with temperature. Thus, an estimate for the oxygen requirements at 20° C of size-defined larvae was obtained as a function of their age (the 20° C line in Figure 5).

The value of the ratio of oxygen consumption 1 d after hatching to that at hatching was about 1.6 (Figure 5). Returning now to Figure 3 we see that the ratio for the average percent of time spent swimming of the two age-groups is approximately 1.66. I conclude, therefore, that the distance between the day 0 and day 1 curves in Figure 3 is an indication of the increased general activity of the larvae as they grow. This correlation indicated in Figures 3 and 5 serves as an additional verification of both Theilacker's respirometer data and the present swimming data.

To compare experimental values of oxygen consumption to the prediction of the model we plot the data as Figure 6, where the horizontal lines show the range of oxygen requirements (from Theilacker's data) at hatching and 24 h later. The steady-state oxygen available by steady-state diffusion only (after the initial transient) obtained from the time-dependent first term in Equation (12) is now superimposed. Figure 6 indicates that pure diffusion supplies all the oxygen required for the day 0 larvae only when $<42 \pm 4\%$ of the O_2 saturation concentration is available. This changes to $63 \pm 4\%$ of saturation for the day 1 larvae. The sharp discontinuity in the swimming data, occurring be-

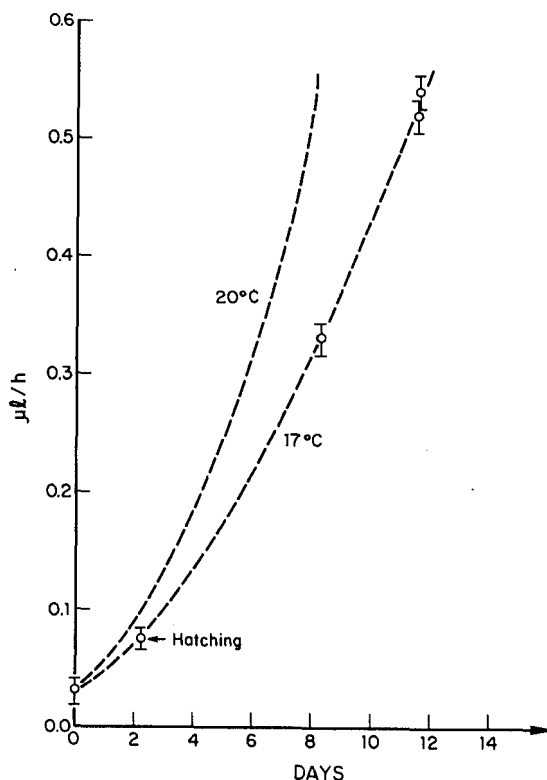


FIGURE 5.—Oxygen consumption by northern anchovy eggs and larvae versus time elapsed since spawning. Open circles indicate experimental data for 17° C. The line for 20° C is extrapolated from the 17° C data with the aid of the Zweifel and Hunter model (see text).

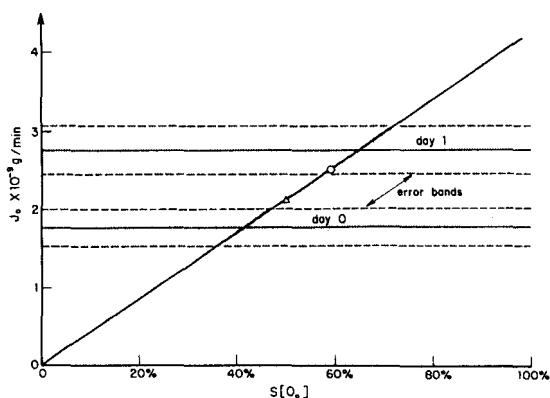


FIGURE 6.—Estimated oxygen requirements (J_o) of northern anchovy larvae at day 0 (hatching) and day 1, and steady-state oxygen supply by diffusion versus oxygen in percentage of saturation concentration ($S[O_2]$). The triangle and circle denote concentrations at which observed swimming behavior changes at day 0 and day 1, respectively (see Figure 3).

³G. Theilacker, Fishery Biologist, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92030, pers. commun. November 1978.

⁴Zweifel, J. R., and J. R. Hunter. 1978. Temperature specific equations for growth and development of anchovy (*Engraulis mordax*) during embryonic and larval stages. Unpubl. manusc., 37 p. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

tween 60 and 40% oxygen concentration (Figure 3) can now be understood in terms of the theoretical results above. When the oxygen concentration in this water is 60% or higher, diffusion alone can satisfy the respiratory requirements of both day 0 and day 1 motionless larvae. Thus, the swimming activity at the higher concentrations is due to other factors, such as depth control. The measured activity level (Figure 3) does not change between 60 and 100% oxygen concentration, as expected from the theoretical model's predictions.

The increased swimming activity observed when the concentration drops below the 40-60% level must therefore be a respiratory reaction. Active swimming causes convective diffusion (which, as shown in the Analytical Model section, leads to much higher oxygen transport rates) and moves the larva to a new, nondepleted position. As expected from this mechanism, activity increases with decreasing ambient oxygen concentration, as oxygen transport rates drop below the required level faster at low ambient concentration, initiating motion more often. The dashed lines in Figure 3 verify this theoretical reasoning and the obtained values of 59% concentration (day 1) and 55% concentration (day 0) for the beginning of respiration-driven swimming are in very good agreement with Figure 6, especially considering the experimental errors involved in the various data sources.

Next, I consider the significance of swimming activity at higher oxygen concentration. The most plausible reason for the swimming behavior is to keep the larvae, which are negatively buoyant, from sinking out of the preferred depth zone in the sea. Day 1 larvae swim at an average angle of 39° upwards from the horizontal with no significant variation with oxygen concentration (Table 1). The large standard error is an indication of the wide spread of observed directions. The average swimming speed at this stage is 5.2 ± 4.1 cm/s (Hunter 1972) and the average duration of a swimming bout (at oxygen concentration of 60-100%) is about 2.1 s (Figure 4). The average vertical component of the distance moved during a single bout is therefore

$$h_{\text{up}} = Vt \sin \alpha = 5.2 \cdot 2.1 \sin 39^\circ = 6.9 \text{ cm.} \quad (16)$$

The uncertainty in this value is large due to the standard errors in both the swimming angle and

the average swimming speed, but it is probably accurate at least to an order of magnitude. Between swimming periods, the larvae sink at a speed of 0.12 ± 0.03 cm/s (Hunter and Sanchez 1976). The average number of swimming bouts per 5-min period was found to be about 7 (Figure 4), i.e., giving an average sinking time of 43 s. This leads to a vertical distance of 5.2 cm, which is close enough to the value of 6.9 cm of Equation (16) to show that the swimming of day 1 larvae at high oxygen levels most probably is a depth-control mechanism.

The newly hatched (day 0) larvae present a different situation. Pelagic eggs are slightly positively buoyant (Blaxter 1969) while the chorion, which is shed during hatching, is somewhat negatively buoyant. Thus, while no measurements independent of the present ones exist, it is reasonable to assume that these newly hatched larva are approximately neutrally buoyant due to their large yolk sac. As the yolk is consumed, the specific gravity increases and the sinking rates for day 1 are obtained. The larvae are approximately neutrally buoyant during the first hours after hatching so that no net sinking or upward swimming is expected. Table 1 shows that this is actually the case at day 0, where the average direction is very close to horizontal and the large error indicates almost random swimming direction. Some upward swimming may be discerned at the very low O_2 concentration experiments (20% O_2). This may be a result of an inadvertent oxygen gradient in the tank or a phototactic response induced by the low oxygen concentration. Phototaxis is probably the means by which the older larvae choose swimming direction, and is directed upwards as light in the present experiments comes from the surface.

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