

ENERGETIC SIGNIFICANCE OF CHANGES IN SWIMMING MODES DURING GROWTH OF LARVAL ANCHOVY, *ENGRAULIS MORDAX*

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ABSTRACT

The swimming behavior of larval northern anchovy, *Engraulis mordax*, in the first few days after hatching is different from the intermittent beat-and-glide mode used by older larvae and later stage fish. It is shown mathematically that the bursts of continuous swimming typical of these yolk-sac larvae is the more efficient form of locomotion at this stage, because of their small size. This advantage changes as the larva grows out of the size range in which water viscosity is the dominant factor (small Reynolds number). When the larva reaches a length of 5 mm, typical Reynolds numbers are such that intermittent swimming gradually becomes the more economical mode, and this mode is dominant when the larvae reach 15 mm. These analytical results compare well with observed behavioral changes.

Swimming behavior of the northern anchovy, *Engraulis mordax*, changes dramatically during growth in the larval stage (Hunter 1972). At hatching, the motion of yolk-sac larvae consists of bouts of continuous, very energetic swimming. This behavior persists for the first 3-4 days of growth, changing to beat-and-glide swimming at the close of the yolk-sac period. The beat-and-glide mode is then retained during the rest of the fish's life.

Intermittent swimming, or beat and glide, is an efficient mode of locomotion for adult fish, enabling increases by a factor of two or more in the range achieved for a given energy expenditure (Weihs 1974). The problem addressed in the present paper is whether the changes in swimming behavior mentioned above also have an energy-saving function. The energetic advantage of intermittent swimming may not exist during the early life stages of fishes because of the importance of viscous effects on small organisms. This study includes setting up a theoretical framework for the analysis of energetics of swimming during the various stages of the fish's life history. The forces and energy required for swimming in the continuous and intermittent modes are then calculated and compared at different stages of larval development. These stages are hydrodynamically distinguished by the nondimensional Reynolds number, Re , which is a function of both length and

speed. The value of the Re defines the relative importance of viscous and inertial effects on the hydrodynamic resistance to motion.

THEORETICAL MODEL

Consider a fish swimming in a straight line at constant depth. We shall assume the fish to be neutrally buoyant so that the only forces acting are in the horizontal plane. Fish of negative buoyancy can be included in the following analysis by equating the excess weight of the fish in water (which is usually not more than 6% of its weight in air) and lift forces produced on the body and fins. However, this is not directly relevant to the present discussion as these forces are perpendicular to the plane of motion, and shall therefore be left out for simplicity.

Returning to the horizontal plane, the forces acting are the thrust applied by the fish, T , and the drag on the fish, D , acting in the opposite direction. The drag is a combination of viscous drag due to friction and form drag, which also is an indirect result of the friction caused by areas over which the flow is separated from the fish body. The drag force can be written (Hoerner 1965) as

$$D = \frac{1}{2} \rho A C_D u^2 \quad (1)$$

where ρ is the water density; A the frontal area (seen in frontal projection); C_D a nondimensional drag coefficient dependent on shape, roughness, and other factors to be discussed below; and u the relative velocity between the fish and the water

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some distance away, which is not disturbed by the fish's passage.

The drag coefficient C_D has been found experimentally to be a similar function of Re for various shapes. Thus, for all shapes tested (Hoerner 1965, chapter 3), the coefficient C_D is a decreasing function up to Re 200-300, being a constant for larger Re up to the turbulent regime which starts at about $Re = 500,000$, where a new, lower, constant value is obtained. Thus when $Re > 200$, hydrodynamic drag becomes proportional to the velocity squared, as the other factors in Equation (1) do not change for a fixed body.

The $Re > 200$ regime was examined by the author (Weihs 1974) previously and will therefore be mentioned here for comparisons only. When $Re < 200$, two main regimes are observed, that of $Re < 10$ and $10 < Re < 200$. The low Re range, in which velocity plays a much more important role than the inertial (acceleration) force effects, has $C_D \propto Re^{-1}$. Strictly speaking, this regime ends when $Re = 1$, but experiments have shown that this relationship can be applied up to $Re = 10$ with good accuracy. Vlymen (1974) actually used this relationship at $Re = 30$, where C_D , estimated by the low Re formula, still is within 10% of the exact value, for his analysis of larval anchovy swimming. The remaining range is a transition regime where C_D gradually changes from the low Re form to the high Re ($C_D \propto Re^0$) form.

As continuous swimming in anchovy larvae is observed mainly in the yolk-sac stage (2.8-5 mm long), the low Re regime is relevant. Thus, $Re = 8$ corresponds to a 3 mm long larva moving at 3 mm/s, and a 5 mm long larva, moving at 5 mm/s, experiences a $Re < 30$.

Applying the relationship for low Re ($C_D \propto Re^{-1}$), Equation (1) can be written

$$D = \frac{1}{2} \rho ACu \quad (2)$$

where C is a numerical constant depending on the shape.

When a fish is actively swimming by means of body and fin oscillations, the drag force is affected, both through the increase in frontal area A , and through the change in the numerical coefficient C . Thus, for example, $C = 20.37$ for a disc moving in a direction normal to its plane, and is equal to 13.6 when moving parallel to its plane. Experimental data collected by Webb (1975) show that the drag coefficient for fish swimming at high Re can be up to four times that of a rigidly gliding fish. For the

low Re regime considered here, the increase in drag coefficient caused by swimming motions does not exceed a factor of 2, for a long slender body (Wu et al. 1975). This increase is written as

$$D_s = \frac{1}{2} \rho AC\alpha u \equiv \alpha Ku \quad (3)$$

where α is the ratio of swimming to gliding drag and the subscript s stands for active swimming. The equation of motion for fish, while actively producing a thrust T is

$$T = m \frac{du}{dt} + \alpha Ku \quad (4)$$

where m is the fish mass (slightly augmented by the added mass at higher Re), and K is defined in Equation (3).

The energy (E) required to traverse a distance L within time τ is

$$E = \int_0^\tau T u dt \quad (5)$$

There is no available information on the dependence of propulsive efficiency on swimming speed for larval anchovy, so that we have to perform the calculations on the energy required, and not the energy actually expended by the fish. However, for comparison of different swimming modes, these are equally applicable.

The purpose of the present study is to compare the effectiveness of continuous and intermittent swimming of larval fish so that we start by finding the energy, E_c , required for swimming at constant speed U_c over the same distance L . From Equation (5),

$$E_c = T_c U_c \tau = T_c L \quad (6)$$

where the subscript c stands for continuous swimming. Defining the energy expenditure per unit distance as $\bar{E} = E/L$ we obtain, by applying also Equation (4),

$$\bar{E}_c = T_c = \alpha K U_c \quad (7)$$

Intermittent swimming, on the other hand, requires energy only during the beating part of the cycle so that the total energy for one beat-and-glide cycle is described by

$$E_v = \int_0^{t_1} T u dt = \int_0^{t_1} \left(m u \frac{du}{dt} + \alpha K u^2 \right) dt \quad (8)$$

where t_1 is the time spent in active swimming during the cycle. In order to integrate Equation (8) we have to obtain the functional dependence of u on the time t . This is done with the aid of Equation (4). Taking the thrust applied to be constant (T_0), Equation (4) can be solved in closed and general form. It was previously shown (Weihs 1974) that constant thrust production is the most efficient procedure so that we can use this assumption here, recognizing that any other behavior will probably be more wasteful in terms of energy. After some rearrangement, Equation (4) is

$$\frac{du}{dt} + \frac{\alpha K}{m} u - \frac{T_0}{m} = 0 \quad (9)$$

with boundary condition

$$u = U_i \text{ at } t = 0 \quad (10)$$

where U_i is the initial velocity at the beginning of the beat phase, which is equal to the speed at the end of the gliding phase. The solution is

$$u = (U_i - U_0) \exp\left(-\frac{\alpha K}{m} t\right) + U_0 \quad (11)$$

where $U_0 = T_0/K$ is the final velocity which the larva would attain if the beating phase were sustained for a long enough period. U_0 is higher than the final speed actually obtained during the beat phase U_f . Substituting Equation (11) into Equation (8) and integrating, recalling that the speed at t_1 is U_f , we have

$$E_v = mU_0(U_0 - U_f) + \alpha KU_0^2 t_1. \quad (12)$$

To find t_1 , we substitute U_f in Equation (11) with $t = t_1$ and obtain, after algebraic reduction

$$t_1 = \frac{m}{\alpha K} \ln \frac{U_0 - U_i}{U_0 - U_f} \quad (13)$$

so that the energy required during one beat-and-glide cycle is

$$E_v = mU_0^2 \left[\left(1 - \frac{U_f}{U_0}\right) + \ln \frac{1 - \frac{U_i}{U_0}}{1 - \frac{U_f}{U_0}} \right]. \quad (14)$$

The energy per unit distance crossed during one cycle in intermittent swimming is

$$\bar{E}_v = \frac{E_v}{l_1 + l_2} = \frac{E_v}{U_i \tau} = \frac{E_v}{U_i(t_1 + t_2)} \quad (15)$$

where l_1 , and l_2 are the distances crossed during beating and gliding phases, respectively. The sum of l_1 and l_2 is taken to be equal to the continuous swimming speed U_c multiplied by the total cycle time, as we compare energy required for crossing the same distance $l_1 + l_2$. Thus, U_c is also the average velocity during the whole intermittent swimming cycle

$$U_c = \frac{l_1 + l_2}{t_1 + t_2} \quad (16)$$

To compare energy expenditure in intermittent and continuous swimming, we define a ratio S

$$S = \frac{\bar{E}_v}{E_c} = \frac{E_v}{\alpha KU_c^2(t_1 + t_2)} = \frac{E_v(t_1 + t_2)}{\alpha K(l_1 + l_2)^2} \quad (17)$$

Intermittent swimming is more efficient only when the numerical value of S is less than unity. To calculate values of S we need explicit expressions for l_1 , l_2 , t_1 , and t_2 . The beat phase velocity has already been found, Equation (11), so that l_1 is easily obtained by integration, using t_1 , Equation (13), as the upper bound

$$l_1 = \frac{m}{\alpha K} \left[U_0 \ln \frac{U_0 - U_i}{U_0 - U_f} - (U_f - U_i) \right]. \quad (18)$$

The gliding phase of intermittent swimming is described by

$$m \frac{du}{dt} + Ku = 0 \quad (19)$$

which is obtained from Equation (4) when no thrust is applied, and gliding drag is experienced by the fish. The relevant initial condition is

$$u = U_f \text{ when } t = 0 \quad (20)$$

and the speed is

$$U = U_f \exp\left(-\frac{K}{m} t\right) \quad (21)$$

with the time spent gliding t_2 obtained from the fact that at t_2 the speed is back to U_i . After some reshuffling

$$t_2 = \frac{m}{K} \ln \frac{U_f}{U_i} \tag{22}$$

Integrating Equation 20 gives l_2

$$l_2 = \int_0^{t_2} U_f \exp\left(-\frac{K}{m}t\right) dt = \frac{m}{K}(U_f - U_i) \tag{23}$$

To nondimensionalize, we now divide all velocities by U_0 . Substituting Equations (13), (14), (18), (22), and (23) into S (Equation (17)) and simplifying results in

$S =$

$$\frac{\left[(1 - \bar{U}_f) + \ln \frac{1 - \bar{U}_i}{1 - \bar{U}_f} \right] \left[\ln \frac{1 - \bar{U}_i}{1 - \bar{U}_f} + \alpha \ln \frac{\bar{U}_f}{\bar{U}_i} \right]}{\left[(\alpha - 1) (\bar{U}_f - \bar{U}_i) + \ln \frac{1 - \bar{U}_i}{1 - \bar{U}_f} \right]^2} \tag{24}$$

where the line over the speeds signifies values divided by U_0 . The ratio S serves now as a quantitative criterion, showing which mode of swimming is more efficient. The advantages of the comparison approach are now clear, as the only parameter specific to the fish is α which, as mentioned before, can vary between 1 and 2 only. All other factors, such as fish mass, frontal area, and the numerical coefficient of drag, have cancelled out, dropping many of the uncertainties of such calculations.

Results and Discussion

Equation (24) is now studied for various values of the parameters involved. As mentioned before, the numerical value of S indicates the relative efficiency of intermittent and steady swimming. When $S > 1$ beat-and-glide swimming is more costly. The three variables appearing in S are bounded by well-defined limits, which makes the parametric study of Equation (24) easier. The nondimensional "final" velocity, at the end of the beat phase, is limited by $0 < \bar{U}_f < 1$ as U_0 is the highest velocity obtainable by the animal (see Equation (11)) under present conditions. By definition, $0 < \bar{U}_i < \bar{U}_f$. The yolk-sac larvae and later stage larvae are combinations of elongated

and round shapes so that the limits of α are $1 \leq \alpha \leq 2$. The range of values of α is obtained from the fact that for elongated (fish) bodies, the ratio of drag in normal motion to resistance to tangential relative motion does not exceed 2 in the viscous domain. Only some sections of the fish bodies are in pure normal motion (perpendicular to the local flow direction), consequently the average ratio is always < 2 .

It is also clear that the larger the numerical value of α , the larger the possible gains by means of intermittent swimming, because the drag when actively swimming is proportionally greater than while gliding so that breaks in the swimming phase will be more advantageous. Therefore, we first take $\alpha = 2$ as a reasonable upper limit. Figure 1 shows the results of such calculations. The coordinates are the energy ratio S versus the normalized average velocity U_c . The calculations were performed for different values of the final

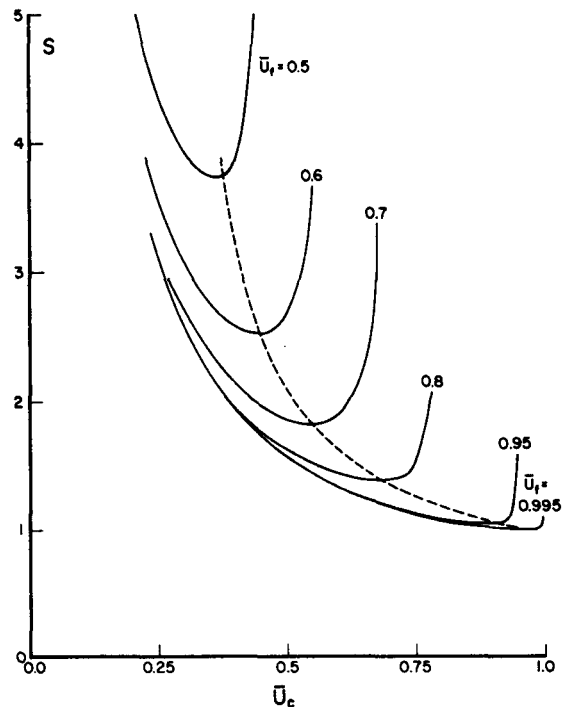


FIGURE 1.—The ratio of energy required per unit distance S for intermittent swimming and continuous swimming respectively, versus the nondimensional average speed \bar{U}_c , for various values of speed at the end of the beating phase, \bar{U}_f . All speeds are normalized by the speed U_0 attained at maximum sustained thrust T after a long time. Dashed line shows locus of minimal energy ratio at different \bar{U}_f . Ratio of swimming to gliding drag $\alpha = 2$.

velocity U_f , varying the initial velocity U_i to obtain different average speeds.

The main result of this Figure is that S is always >1 , i.e., for the speeds and sizes at which viscous effects dominate continuous swimming is always more efficient. This calculation is based on the relation $C_D \propto Re^{-1}$ and is therefore valid for Re up to 10. Larval anchovy tend to swim at speeds of about 0.8 body length/s (Hunter 1972) when swimming intermittently. Thus the Re typical of 3-day-old larvae whose length (Zweifel and Hunter²) is about 4 mm at 18°C is also about 10. At age 3 days, larvae spent $<20\%$ of the time swimming intermittently, but 2 days later (Hunter 1972, fig. 1) about 90% of the time is spent in beat-and-glide motion. This level of intermittent swimming is retained thereafter. This sharp change coincides with the time the animal "grows out" of the viscous regime (the Re is essentially proportional to fish length squared), e.g., when the larvae is 5 mm long, the Re is 20.

Recalling that at high Re , beat-and-glide swimming is the more efficient motion (Weihs 1974), the energy saving obtained is probably one of the reasons for the observed change in swimming behavior.

The fact that the average continuous speeds are much higher also results in savings of energy. For a 3-4 mm long larva, swimming at over 1 cm/s brings it again to Re of over 20, so that the drag coefficient is smaller, and some coasting at the end of the bout of continuous swimming is possible. At lower Re , in the purely viscous regime, no coasting is possible as the inertial effects are negligible and motion ceases immediately when oscillations stop. It is therefore advantageous for the fish, for hydrodynamic reasons, to swim continuously during the first few days of the larval phase, changing to beat-and-glide swimming later on. It should be noted here that the present calculations and data are for a water temperature of 17°-18° C. Both viscosity of water and the growth rate of larvae (see footnote 2) depend on the temperature, so that data collected under different ambient conditions might lead to a later (or earlier, if the temperature is higher) change of swimming mode.

Further examination of Figure 1 shows that for each terminal velocity in the beating stage there is

²Zweifel, 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., 13 p. Southwest Fisheries Center, NMFS, NOAA, P.O. Box 271, La Jolla, CA 92038.

a value of \bar{U}_c for which the ratio S attains a minimum (marked by the dashed line). The value of this minimum approaches unity and the curves become more shallow as \bar{U}_f increases. Thus, if an anchovy larva swims intermittently at low Re , it should do so at high average speeds, so that the energy penalties incurred due to swimming in the beat-and-glide mode are minimal.

Figure 1 also shows that the lowest penalties for using intermittent swimming are obtained when \bar{U}_f approaches unity, for the whole range of average speeds. Therefore, the value $\bar{U}_f = 0.995$ was chosen for calculations of the effect of varying α (the ratio of swimming to coasting drag). These appear in Figure 2, where the dependence of S on \bar{U}_c is shown. The range of values of α to be expected in nature is described by the shaded area, showing as expected that the smaller the α the more advantageous is continuous swimming. When $\alpha > 2$, which can only happen at higher Re , a range of values of \bar{U}_c and \bar{U}_f exists where S is smaller than unity, i.e., intermittent swimming is more efficient. This is shown by the dashed curve on Figure 2 where for $\bar{U}_f = 0.995$ and $0.79 < \bar{U}_c < 1$, $S < 1$. This curve will be discussed later, in reference to the transition region between the low and high Re domains.

The results discussed above all dealt with the low Re range. For comparison, we now show the equivalent energy ratio for high Re , i.e., the domain relevant to larger larvae as well as adult anchovy (>15 mm long). The results presented

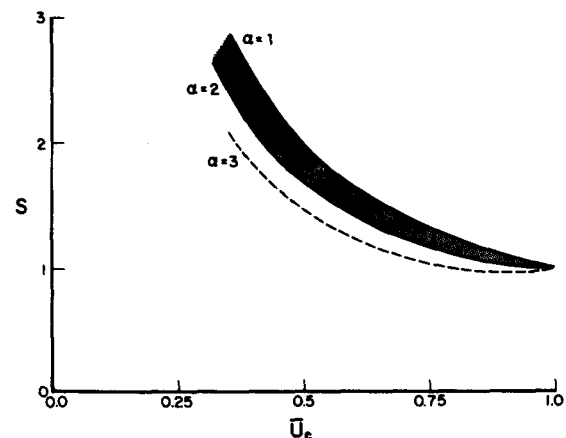


FIGURE 2.—Influence of changes in ratio of swimming drag to gliding drag α on the energy ratio S , versus nondimensional average speed \bar{U}_c . Shaded area is the range of possible α at low Reynolds numbers. $\bar{U}_f = 0.995$ (See Figure 1 for definitions).

stem from calculations based on the analysis in Weihs (1974). The ratio of energy per unit distance traversed in intermittent swimming to that of continuous swimming at the same average speed R , can be shown to be, in present notation,

$$R = \frac{\tanh^{-1}\left(\frac{\bar{U}_f - \bar{U}_i}{1 - \bar{U}_i \bar{U}_f}\right) \left[\tanh^{-1}\left(\frac{\bar{U}_f - \bar{U}_i}{1 - \bar{U}_i \bar{U}_f}\right) + \alpha \left(\frac{1}{\bar{U}_i} - \frac{1}{\bar{U}_f}\right) \right]}{\left[\ln \left\{ \cosh \left[\tanh^{-1}\left(\frac{\bar{U}_f - \bar{U}_i}{1 - \bar{U}_i \bar{U}_f}\right) \right] + \bar{U}_i \sinh \tanh^{-1}\left(\frac{\bar{U}_f - \bar{U}_i}{1 - \bar{U}_i \bar{U}_f}\right) \right\} + \alpha \ln \frac{\bar{U}_f}{\bar{U}_i} \right]^2} \quad (25)$$

The computed values of R , for $\alpha = 2$, appear in Figure 3. Each full line describes the values of R for a given \bar{U}_f as a function of the average velocity U_c . Each of these curves ends at $\bar{U}_c = \bar{U}_f$ and, in a similar manner to Figure 1, has a minimum for a lower value of U_c . Here, however, all curves have a large section in the range $R < 1$, i.e., intermittent swimming is more efficient. In fact, the slower the average velocity, the higher the possible gains, as shown by the dashed line which is the locus of lowest values of R as a function of \bar{U}_c . As already mentioned in Weihs (1974), this curve goes monotonously from unity at $\bar{U}_c = 1$ (continuous swimming by definition) to $1/\alpha$ at $U_c \rightarrow 0$. One can therefore predict that fish species using the anguilliform swimming mode (Breder 1926) will find

intermittent swimming relatively more efficient than carangiform swimmers as α is greater for anguilliform swimming in which most of the body is oscillated. Another result is that for greatest gains, the average speed during the whole beat-

and-glide should be as low as possible, with small differences between \bar{U}_i and \bar{U}_f .

Anchovy, which swim in the anguilliform mode, fulfill both these predictions as adults and more mature larvae usually swim by means of a single beat followed by a long glide, so that 1) \bar{U}_i and \bar{U}_f are not too different and 2) \bar{U}_c is rather low.

Having examined the low and high Re domains, where the drag coefficient is proportional to the reciprocal of Re, and constant, respectively, we now look at the transition regime between them. Based on average swimming speeds of 0.8 body length/s, larvae will be in this regime when they are from 5 to 15 mm in length. Analysis of the forces and energy is much more complicated here because the hydrodynamic drag is

$$C_D \propto Re^{-\beta} \quad (26)$$

where β is not constant, but itself is a function of both Re and body shape. This results in Equation (4) taking the form

$$T = m \frac{du}{dt} + \alpha K u^{2-\beta} \quad (27)$$

a differential equation that has to be solved numerically when β is not zero or one (the two cases discussed previously). While this in itself is a relatively straightforward task, the generality and accuracy of the previous solutions is immediately lost as numerical values for the mass and K have to be included. K especially is known very inaccurately as it includes the numerical drag coefficient and the frontal area (which varies at different speeds and times). The setting of β is even more problematical as it depends on the instantaneous swimming speed in an empirical manner (which

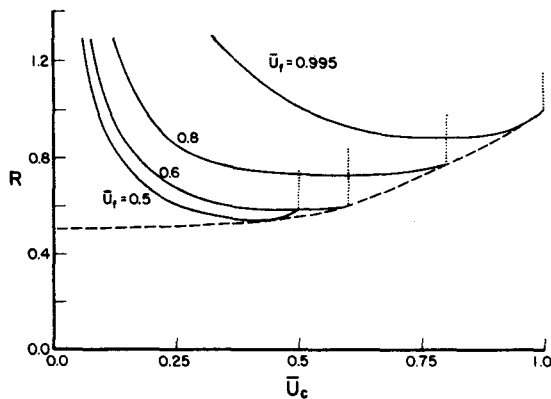


FIGURE 3.—The ratio of energy required per unit distance R , for intermittent and continuous swimming at high Reynolds numbers, respectively, versus nondimensional average speed U_c . Dashed lines shows locus of minimum values of R attainable as a function of U_c . See Figure 1 for definitions.

is, however, not known at the present time), thus changing during the beat-and-glide cycle. No single value may therefore be taken to describe a given beat-and-glide behavior and an average value has to be used. This adds greatly to the inaccuracy as β is an exponent. Bearing especially the latter factor in mind, no smooth curves of the type appearing in Figures 1-3 can be expected.

In order to try and make clear how the transition regime influences the energetics of swimming, in spite of the difficulties mentioned, curves such as those from Figures 1 and 3 are reproduced in Figure 4. The purpose of this Figure is to show that by using the correct nondimensional description, curves for the viscous and nonviscous regimes can be compared. Both the dashed and full curves have similar shape, going to infinity for $\bar{U}_c \rightarrow 0$ and having a minimum at the higher values of \bar{U}_c , the values increasing again for $\bar{U}_c \rightarrow \bar{U}_f$. One must recall that the absolute speeds and sizes are very much different for the two cases, this resulting from the difference in U_0 , the maximum sustained speed. U_0 is much larger for the full curves. The dashed curves have $\beta = 1$ while the full lines are for $\beta = 0$. Therefore, calculations at any intermediate values of β are expected to fall between them.

Some calculated values appear in Figure 4, for two values of average β . While they show the expected behavior, their actual values are, as men-

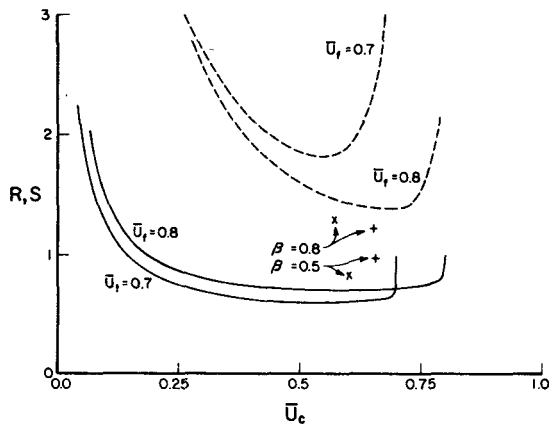


FIGURE 4.—Energy ratio versus nondimensional speed at various Reynolds numbers. Dashed lines show the low Reynolds number (viscous) regime, full lines are for high Reynolds numbers (boundary layers) and, \times , $+$ are at intermediate Reynolds numbers, for $\bar{U}_f = 0.7$ and $\bar{U}_f = 0.8$, respectively. See Figures 1 and 3 for other definitions.

tioned before, unreliable, because they are based on rough estimates of various coefficients which do not have to be made when $\beta = 0$ or 1. These computations are to be taken only as an indication that the expected gradual transition actually occurs and are not to be used for actual calculations.

Keeping these limitations in mind, one can tentatively come to the conclusion that the intermediate Re regime is one of gradual transition. The advantage of beat-and-glide intermittent swimming becomes more and more significant as the larva grows, after the 4th day after hatching.

This conclusion can be strengthened, in a roundabout manner, by a different approach. The ratio of swimming to gliding drag for a given animal is 2 in the low Re regime, and up to 4 for high Re. Therefore taking a higher value of α for the viscous domain calculations can indicate, in a different manner, the trend of results when increasing Re. This appears in Figure 2, where the dashed line stands for $\alpha = 3$. It can be seen that this curve is intermediate between typical curves for the viscous (Figure 1) and inertial regimes (Figure 3).

CONCLUDING REMARKS

It was demonstrated in the previous section that the change in swimming style observed when anchovy larvae reach the age of 4-5 days is correlated with the passage of the animal from the highly viscous regime to the boundary layer regime. My calculations show that this behavioral change is an adaptive energy sparing mechanism. When the larva is <5 mm long, it can only progress by actively swimming as the enhanced effect of viscosity will bring it to a rapid halt when coasting. The yolk-sac, which still exists as a spherical protrusion, increases the drag even further at this stage. The drag coefficient here is inversely proportional to the velocity so that any low-speed motion is very costly in terms of energy. As a result, interspersing coasting and accelerating is not an efficient way of progressing. When the larva is larger (>5 mm) and moving faster, viscous effects are concentrated in a thin layer surrounding the fish and the influence of speed and shape on drag changes. At this stage, it is shown that intermittent motion is the more efficient for fish species such as anchovy which swim in the anguilliform mode. Intermittent motion is much less efficient for carangiform swimmers at all sizes (Weihs 1974) which may explain why species such as mackerel swim continuously at all phases of life.

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