

A mechanism for the juvenile-to-adult transition in fishes¹

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The mechanisms used by physiologists and fishery biologists to explain why fish become mature are shown to be wanting. The hypothesis is presented that diminishing oxygen supply per unit weight serves in growing fish as the master factor in inducing the transition from juvenile to adult.

Introduction

The conventional view (Hoar, 1970; Liley, 1970; Harvey and Hoar, 1979) of the sequence of events which, in fish, leads to first gonadal maturation and subsequent spawning, starts with "environmental stimuli" which the brain and pineal gland process and pass on to the hypothalamus, which passes its information to the pituitary; gonadotropic hormones are then synthesized and released which leads to the maturation and release of gametes, given suitable environmental conditions (including a mate). Other more elaborate schemes allow for feedback loops (Kuo and Nash, 1975), but share with the linear sequence outlined above the feature that they invariably *start* with "environmental" or "external" stimuli.

The conventional view of the link between growth and reproduction in fish is that of a "reproductive drain", i.e., the notion that fish, once they have reached sexual maturity, have a slower growth because the "energy" previously available for growth is, in mature fish, redirected toward the production of gonadal material (Jones, 1976; Lagler *et al.*, 1977). It is argued here that these conventional views can be replaced by a single hypothesis with the help of which a number of otherwise irreconcilable observations on the growth and reproduction of fish can be explained.

Definitions of concepts

Conceptually, three time scales can be defined for spawning and related processes:

- a) a short time scale (seconds to days) for those processes that occur just before shedding and fertilization of ova (e.g., courtship, final maturation, etc.);

- b) a medium time scale (weeks to months) during which gonadal maturation takes place, as triggered by environmental stimuli; and
- c) a long time scale, in which the age and the size at which a fish becomes sexually mature for the first time are determined.

It is only time scale (c) which concerns us here, and to which the hypothesis below applies. The elements in (a) and (b) are appropriately covered by conventional explanations and they are part of the sequence of events which occurs during the spawning season (in which (a), however, succeeds (b)).

The length and weight at which juvenile fish become sexually mature adults for the first time are coded L_m and W_m , respectively.

The maximum length and weight reached, on the average, by the fish of a given population are L_u (ultimate), and W_u , respectively.

Relative oxygen consumption (Q) is defined as the rate of oxygen consumption of a fish per unit weight, or

$$Q = \frac{p_1 L^a}{q L^b} \quad (1)$$

while similarly (G), the relative gill surface area, is defined by

$$G = \frac{p_2 L^a}{q L^b} \quad (2)$$

with both equations having the same exponent (a) for the oxygen consumption/length and gill surface area/length relationships because oxygen consumption is, other factors being equal, a function of gill surface area (Pauly, 1981).

The length/weight relationship of fish, finally, is expressed by

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$$W = q \times L^b \quad (3)$$

where the exponent (b) generally has a value of, or close to 3 (Carlander, 1969).

Equations (1), (2), and (3) imply that absolute gill size and O_2 consumption grow, in fish, in proportion to a power ($d = a/b$) of less than unity which generally ranges between 0.6 and 0.9 (Pauly, 1981).

Problem definition

Numerous studies indicate that the ratio L_m/L_u is relatively constant within most families of fish, with, for example, values of 0.6 to 0.7 in Clupeidae, and about 0.4 to 0.5 in tunas (Beverton and Holt, 1959; Beverton, 1963; Mitani, 1970).

Although this phenomenon is well known among fishery biologists, and has been used to estimate L_m from L_u or vice versa, it has rarely been investigated specifically. The reason for this is possibly that the "reproductive drain" concept offers such a handy explanation for it.

However, in a large number of fishes, the females grow not only larger but also faster than the males (see e.g. data in Beverton and Holt, 1959) while producing the larger amount of gonadal material (Lagler *et al.*, 1977). Clearly, their growth does not suffer from a reproductive drain.

Iles (1974) presented data in support of the view that fishes do not suffer from reproductive drain and made an attempt to explain the relative constancy of the ratio L_m/L_u in fish. He suggested that it was a sort of pre-recorded growth "programme" which is run in the ontogeny of a given fish, and determined when fish spawn, spawning being thus an "event" of the growth programme.

Both the "reproductive drain" concept and Iles's "programmed" growth, however, fail to link up the relative constancy of the ratio L_m/L_u in fish with the sequence of physiological events leading to spawning.

Moreover, the sequence of physiological events mentioned above implies that fish exposed to "environmental stimuli" do perceive these stimuli. Juvenile fish, if their youth lasts for several years, (as for example in cod, halibut, sea perches, and other fishes capable of reaching high ages) go, however, through several sequences of those environmental events which their elders perceive as "spawning season" – yet they do not spawn.

Clearly, the right "environmental stimuli" during a "spawning season" are *not sufficient* for fish to mature and spawn; they must also have reached a certain critical size (near L_m) from which on they perceive the environmental stimuli that trigger gonadal maturation.

Development of the new hypothesis

Fish need – in order to grow and to elaborate gametes – both food and oxygen. While food is generally available in relatively large chunks (as compared with the O_2 needed to metabolize that food), and can be stored, in one form or the other, for considerable periods of time, O_2 must be extracted, most often at great energetic expense from a dense medium which is relatively poor in oxygen, and cannot be stored for later use in more than small quantities.

I have shown elsewhere (Pauly, 1981) that the growth of fish is generally oxygen limited, as evidenced by the relationship of fish growth to ambient oxygen concentration and to habitat temperature, as well as by the inverse relationship between food conversion efficiency and body weight. The major cause for this oxygen lim-

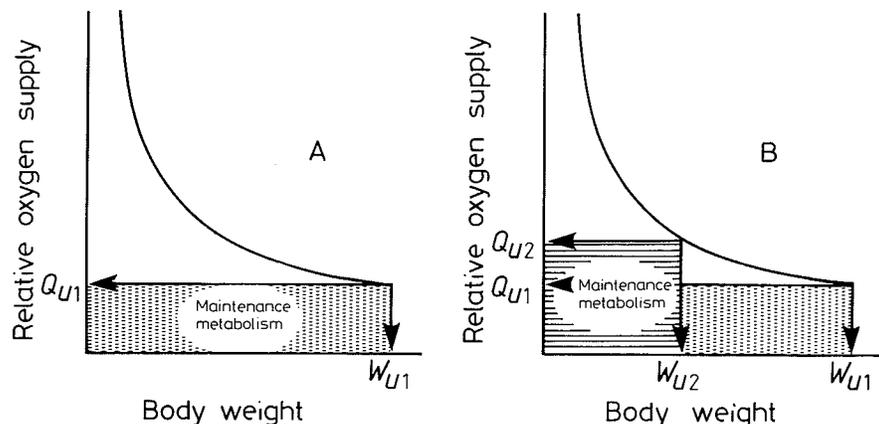


Figure 1. Relationship between gill surface area per unit weight (or oxygen supply per unit weight) and weight in growing fish. Note (in A) that growth must cease when O_2 supply is equal to maintenance requirements. Note further (in B) that anything that increases maintenance metabolism (e.g., elevated temperature, reduced food density, etc.) will also tend to raise the level at which O_2 supply becomes limiting to further growth (see text).

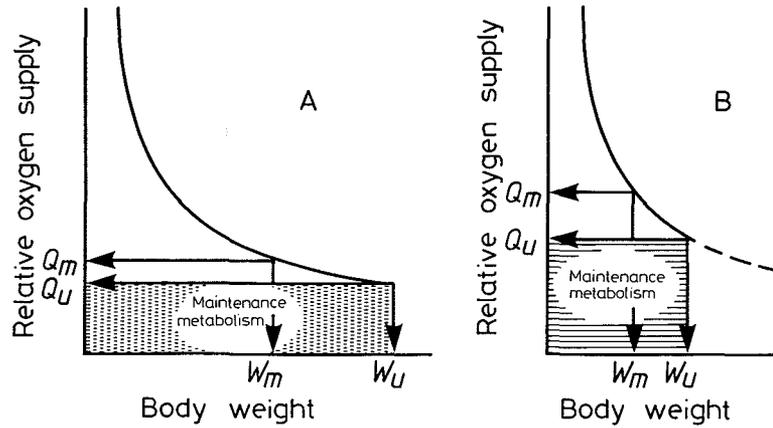


Figure 2. Interrelationships between oxygen supply at maintenance level (Q_u), oxygen supply near first maturity (Q_m), and the weight of fish. Note that the Q_m/Q_u ratio is constant for two different habitats, one of which (A) is linked with large ultimate size and a large size at first maturity, the other (B) being associated with a small ultimate size and a small size at first maturity. Note also that the constancy of Q_m/Q_u can only be imperfectly mirrored in the ratio L_u/L_m (which can be derived from W_u and W_m).

itation is that fish gills cannot grow as fast as the body they have to supply with oxygen because a surface, even when growing with a strong positive allometry cannot keep up with a growing volume (i.e., $a < b$ in Equations 1, 2, and 3). An immediate result of this is that, as fish grow larger, their relative O_2 supply diminishes down to a point (at W_u) where growth ceases because O_2 supply (Q_u) is just sufficient for maintenance metabolism (Fig. 1 A). Thus, anything (e.g., elevated temperature or osmotic stress) which in a given population causes an elevated maintenance metabolism will result in a reduced ultimate size (Fig. 1 B). Such reduction of ultimate sizes in conjunction, e.g., with elevated temperatures, osmotic stress, crowding, or other factors are well documented in the literature (Taylor, 1958; Liu and Walford, 1966; Iles, 1973).

Fish obviously will be able to invest energy into gonad production and spawning only if W_m is less than W_u , and consequently if G_m is greater than G_u and Q_m is greater than Q_u . Thus, the relative constancy of the ratio L_m/L_u in fish may be viewed in fact as an imperfect expression of the underlying constancy of the ratio Q_m/Q_u (Fig. 2) which, when reached by growing juveniles effectively turns these juveniles into potential adults, capable of registering appropriate environmental stimuli.

The relation between the ratios Q_m/Q_u and L_m/L_u can be obtained, based on Equations (1), (2), and (3) by defining

$$Q_m = \frac{p_1}{q} \times \frac{L_m^a}{L_m^b}$$

$$Q_u = \frac{p_1}{q} \times \frac{L_u^a}{L_u^b}$$

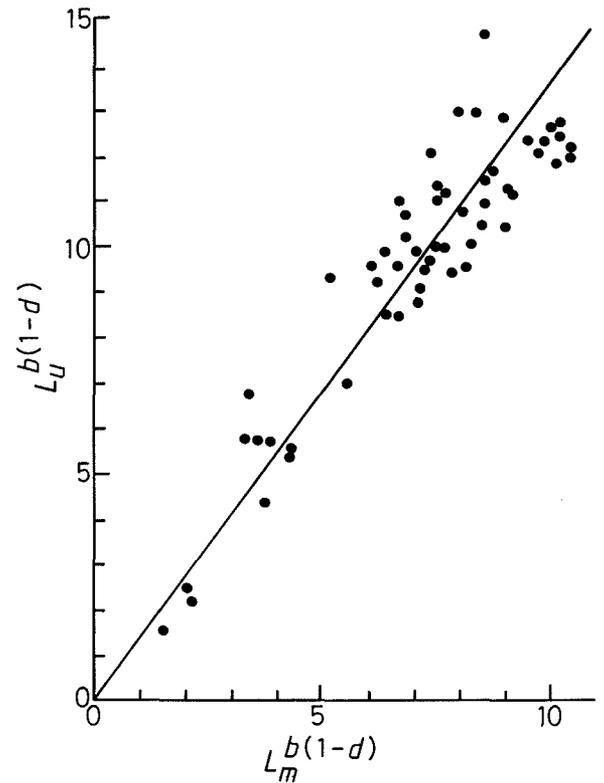


Figure 3. Plot of ultimate length (L_u), raised to the power $3(1-d)$, on length at first maturity (L_m) raised to the power $3(1-d)$; for each pair of L_m/L_u values, the same value of d was used, as estimated from an empirical relationship established earlier linking W_u and d (Pauly, 1981). The conversion from L_u to W_u was done using the best available length/weight relationship; the L_m/L_u data pairs were obtained from Beverton and Holt (1959), Beverton (1963), and Mitani (1970) and cover a wide variety of fishes, ranging in size from guppies to tuna ($n = 56$). The data provide an estimate of $Q_m/Q_u = 1.36$.

from which

$$Q_u/Q_m = \frac{L_u^a}{L_u^b} \times \frac{L_m^b}{L_m^a}$$

which after some re-arranging leads to

$$Q_u/Q_m = \left(\frac{L_m}{L_u} \right)^{b(1-d)} \quad (4)$$

where $d = a/b$ and where the exponent $b(1-d)$ is equal to the parameter "D" in Pauly (1981), when $b = 3$.

I have shown elsewhere (Pauly, 1981) that fish which stay small (e.g., guppies) tend to have low values of d (as defined above) while fish that can reach large sizes as adults (e.g., tuna) have high values of d .

The quantitative relationship linking d and maximal body weight in Pauly (1981) was used, in conjunction with L_u and L_m values taken from the literature to obtain the plot of $L_m^{b(1-d)}$ on $L_u^{b(1-d)}$ shown in Figure 3. This plot suggests a mean value of about 1.4 as a mean Q_m/Q_u in fishes.

Discussion

The scenario resulting from these considerations is as follows: the fish of a given stock grow rapidly until $Q_m/Q_u = 1.4$ is approached, at which point increasing amounts of a substance (or substances) are produced which enable the brain to respond to environmental stimuli for reproduction. At first, the level of the substance(s) will be low, and/or environmental stimuli will begin to be perceived (too) late in the spawning season. The fish will then either be irresponsive or undergo a "trial-run" or "abortive" maturation (Hickling, 1930; Iles, 1974), followed at the end of the spawning season by a resorption of whatever material was elaborated. Then, as a result of subsequent growth, $Q_m/Q_u = 1.4$ is reached, and environmental stimuli are responded to from the onset of the next spawning season.

Having lost gonadal material – up to 20 % of their body weight (Lagler *et al.*, 1977) – spent fish have a value of Q greater than Q_m . Thus much of their oxygen can go back into growth (rather than maintenance) which brings them back to $Q_m/Q_u \approx 1.4$ such that at the onset of the next spawning season, maturation may be quickly re-initiated.

Higher environmental temperatures, low food densities (which increase foraging time), or low O_2 availability, crowding, and other growth-reducing factors act on fish by increasing Q_u . With a constant Q_m/Q_u as a regulator, fish, however, "know" that they will stop growing at smaller sizes, and can adapt to this by spawning at an even smaller size – a major problem of aquaculturists working, for example, with tilapias (Iles, 1973).

It will be noted that the hypothesis proposed here of a constant Q_m/Q_u in fishes eliminates the need to postulate a "biological clock" to explain the relative constancy of the ages at first maturity occurring within a given population. "Precocious" spawning (Iles, 1973) is explained as well.

The major corollary of the hypothesis presented here is that a substance (or several of them) is (are) produced by fish experiencing a steady decrease in the availability of O_2 per unit weight and which activates those parts of the brain that are capable of responding to stimuli for reproduction.

Substances produced by animals exposed to permanent stress – which is what reduced oxygen supply may amount to – are well documented in the physiological literature and any of these is a potential candidate for the link between metabolic stress and the brain.

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