

EFFECTS OF LAKE AND POND AERATION ON FISH GROWTH AND RELATED PROCESSES²⁰

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ABSTRACT

The basic principles of the growth of fish (and aquatic invertebrates) are recalled, with emphasis on the fact that oxygen, while continuously required for maintenance, cannot be stored for later use. Hence the rate at which oxygen is extracted via the gills and transported into the body of fish limits, at any time, their scope for activity, growth and food conversion efficiency. This is shown to be consistent with the increased growth and food conversion efficiency observed by aquaculturists who aerate their ponds. Some implications for aeration of larger water bodies, such as lakes and reservoirs, are presented.

INTRODUCTION

The following is a brief presentation of a theory, elaborated in more detail in Pauly (1979, 1981, 1984, 1986, 1998) and in Longhurst and Pauly (1987) of how fish grow. Emphasis is given to the fact that it explains some of the observed direct and indirect effects of pond aeration on fish growth and related processes (Loyacana, 1974; Hollerman and Boyd, 1980), and that it can be used to predict some of the effects of aerating larger water bodies such as lakes and reservoirs.

This theory applies to any submerged animal breathing through gill; the example presented below refers to fish in the narrow sense (i.e., to teleosts), although the principles it illustrates also apply to other fishes and aquatic invertebrates (see Pauly, 1998). We shall assume for simplicity's sake that fish consist of, and feed, only on proteins. The theory presented below can accommodate more realistic body composition and diets (van Dam and Pauly, 1995), but dealing with this does not change its main points.

THEORY OF FISH GROWTH

Fish are aerobic heterotrophs – with some exceptions, such as common carp (*Cyprinus carpio*), which may operate anaerobically at very low temperatures, a feature which is not a concern here.

As fish feed, their food is assimilated i.e., broken down into amino acids; part of the amino acid pool is oxidized, and the energy thus bound used to form ATP, used for activity (i.e., muscle contraction), and, along with building blocks drawn from the amino acid pool, used for synthesis of native protein.

This synthesis is required for net growth, but also, even more importantly, for replacing proteins that have spontaneously denatured (i.e., lost their quaternary and tertiary structures). Such spontaneous denaturation – a mildly exergonic reaction requiring neither O₂ nor ATP – is a characteristic of live proteins. Indeed, it expresses a basic feature of life itself: that living organisms will spontaneously decay, i.e., fail to maintain their structure integrity unless entropy is 'pumped out' (Schrödinger, 1944).

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Important here are:

- That the rate of spontaneous denaturation of proteins can be assumed proportional to protein mass (i.e., roughly proportional to body weight); and
- That this rate of spontaneous denaturation, being due to thermally-induced vibrations of protein molecules, increases with temperature, with a Q_{10} usually ranging from 2 to 4 (Winberg, 1971; Regier *et al.*, 1990).
- That the relation between the metabolic rate of fish and water temperature is reasonably well described by Krogh's 'normal curve' (Table 1).

Protein synthesis as mentioned above requires O_2 to be where needed (in cells' mitochondria); for this to be the case O_2 must have been brought in via the circulatory system, through the gills from the water surrounding a fish. Transfer of O_2 through the gills of fish follows Fick's Law:

$$Q = dP \cdot G \cdot U / WBD \quad \dots 1)$$

where Q is the O_2 uptake (e.g., ml·hour⁻¹), dP is the O_2 pressure difference on either side of the gill membrane (in atm), G is the respiratory area of the gills (total area of respiratory lamellae), U is Krogh's diffusion constant, i.e., the quantity of O_2 (in ml) which diffuses through an area of 1 mm² in one minute for a given type of tissue when the pressure gradient is one atm O_2 μ^{-1} , and WBD is the water-blood distance, i.e., the thickness of the membrane separating water and blood, in μ (Hughes and Morgan, 1973; Hughes, 1984).

Of the four parameters which influence Q , only G varies with body weight (W), i.e.,

$$G = a \cdot W^d \quad \dots 2)$$

where 'a' is a multiplicative factor used here as 'gill area index', and 'd' is an exponent ranging in fish between 0.50 (in cyprinodonts, Winberg, 1961) and 0.95 (in tuna, Muir and Hughes, 1969), but never reaching unity, at least not in well-studied cases covering a wide range of body weight.

Thus, gill surface area can be expected to be a key variable when attempts are made to explain the wide difference of growth performance occurring among species of fishes.

This can be shown by using the parameters W_∞ and K of the von Bertalanffy growth function (VBGF), whose simplest version has, for weight, the form

$$W_t = W_\infty (1 - e^{-K(t-t_0)})^3 \quad \dots 3)$$

where W_t is the weight at age t , W_∞ is the mean weight the fish would reach if they were to live indefinitely, K expresses the rate at which W_∞ is approached, and t_0 is the theoretical 'age' the fish would have at $W = 0$.

From W_∞ and K , a growth performance index Φ can be derived, i.e.,

$$\Phi = \log_{10}(K) + 2/3 \log_{10}(W_\infty) \quad \dots 4)$$

which takes similar values among different populations of the same species, and hence can be used to compare the growth performance of different fishes (Pauly, 1979; 1994).

Figure 1 shows that the gill area index of 37 species of teleosts, ranging from guppies to tunas, i.e., selected to cover a wide range of asymptotic sizes and ecologies, significantly and positively correlates with their

Table 1 Values of the temperature (t) correction factor (q) for converting respiratory rates to 20°C, according to the 'normal curve' of Krogh (1914) (from Winberg, 1971).

t	q	t	q	t	q	t	q
5	5.19	12	2.16	19	1.09	26	0.609
6	4.55	13	1.94	20	1.00	27	0.563
7	3.98	14	1.74	21	0.920	28	0.520
8	3.48	15	1.57	22	0.847	29	0.481
9	3.05	16	1.43	23	0.779	30	0.444
10	2.67	17	1.31	24	0.717	-	-
11	2.40	18	1.20	25	0.659	-	-

growth performance index. It might be argued at this point that if gill size is limiting, then fish should, over evolutionary time, have developed larger gills. The answer to this is that they have: their gills are suitable for rapid growth up to the size at (first) reproduction, i.e., to the size which is crucial to their evolutionary fitness. It is only from that size that the limiting effect of low relative gill area manifests itself (Pauly, 1984; 1994). Moreover, a growth limitation would occur at some stages: whatever the initial endowment, gill area, being a *surface* cannot, for geometrical reasons, keep up with the growing *volume* it is supposed to supply with oxygen.

Given (2), we also have:

$$Q = a' \cdot W^d \quad \dots 5)$$

in which Q is defined as in (1), W and d as in (2), and a' is a proportionality constant. Equation (5) implies that relative gill area, and hence the O₂ available for growth and routine metabolism in fish, decline as size increases. This decline occurs in proportion to a power of weight equal to 1-d, down to a level where Q is, at W_∞, just enough for maintenance, i.e., that level of activity and of protein synthesis that is sufficient to compensate for spontaneous protein denaturation (Figure 2A). Thus the level of metabolism corresponding to W_∞ is, by definition, an estimate of maintenance metabolism, and any factor that increases maintenance metabolism (e.g., elevated temperature, or reduced food density, by increasing the level of activity required to secure the required food) will have the effect of reducing W_∞ (Figure 2B). This explains why, e.g., the fish of North American freshwaters tend to reach larger maximum sizes at their cold northern end than at the warm, southern ends of their range (see data in Carlander, 1969; 1977), or why Australian fishes have asymptotic sizes that are higher in the (cold) south than in the north of that country (Andersen and Pauly, 2006, this volume).

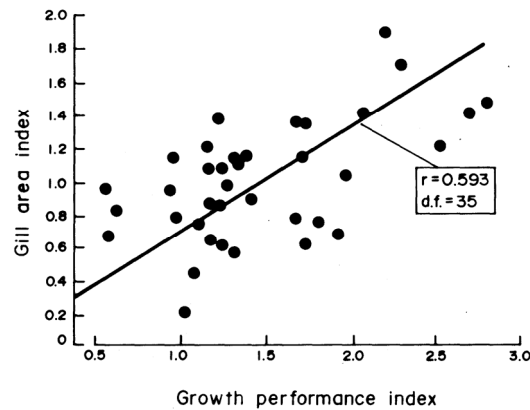


Figure 1 Relationships between an index of the gill area (a' in Equation 2) and the growth performance of 35 species of teleosts and two sharks as expressed by their value of Φ (see Equation 4; adapted from data in Pauly 1979).

An important variable for managers of aquaculture ponds is food conversion ratio (FCR), defined as the amount of food required to produce a given amount of fish flesh. This is related to a concept commonly used in fisheries science, the food conversion efficiency (K_1) of Ivlev (1966) through $1/\text{FCR} = K_1$, the latter being defined, for any time interval by:

$$K_1 = \text{growth increment}/\text{food consumption} \quad \dots 6)$$

Various approaches exist to relate K_1 and growth (e.g., Paloheimo and Dickie, 1966), or more precisely equation (6), with the VBGF as represented in equation (3). One of these was presented by Temming (1994a), i.e.,

$$K_1 = A \cdot (1 - W/W_\infty)^{1-d} \quad \dots 7)$$

where K_1 is the food conversion efficiency at weight W, W_∞ is as defined in equation (3), d is set at 2/3, as implied in the version of the VBGF presented here [there are other version of the VBGF, incorporating other, more realistic values of d, see Pauly, 1981; Temming, 1994b; and Essington *et al.*, 2001], and A is a factor constrained between zero and one, and expressing the fraction of the ingested food that is available for protein synthesis. It can be expected that A will be related to the nitrogen content of the food (Pandian and Marian, 1985).

APPLICATION OF THE THEORY TO AQUACULTURE POND AERATION

There is an extensive literature on pond aeration, which tends to emphasize its technological aspects (see e.g., Boyd *et al.*, 1988), and only one of its numerous biological effects: the reduction of mortality due to (early-morning) oxygen deficiency. However, aeration has numerous other biological effects, notably, beneficial effects on food conversion and growth (see Table 2). Strangely enough, these effects of aeration appear to date not to have been related to any theory of growth.

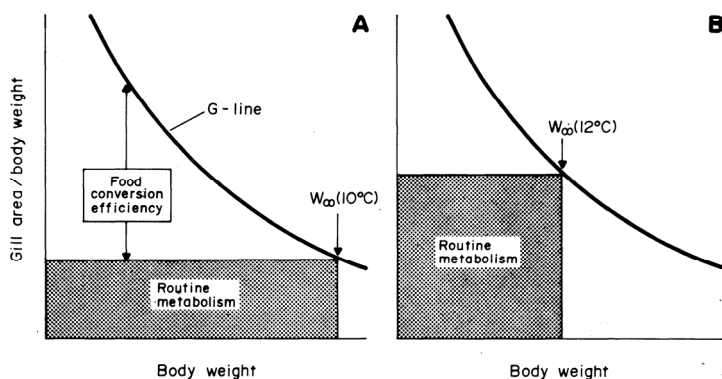


Figure 2 Illustrating how, given a certain G-line (determined by 'a' and 'd' in Equation 5), maintenance metabolism determines asymptotic weight (W_{∞}), because relative gill area (and hence oxygen supply) *must* decline with body weight. **A.** Fish exposed to a low level of stress (e.g., environmental temperature, abundant food). **B.** Fish exposed to a higher level of stress (high temperature, causing rapid denaturation of body protein, and/or low food density, requiring O_2 to be diverted to foraging, rather than protein synthesis). Note that 'scope for growth' and food conversion efficiency can both be directly related to the difference, in these graphs, between the G-line and the level of routine metabolism.

increased (Fast and Hulquist, 1989) should result, other things being equal, in improved growth of the fish therein, both by directly facilitating respiration, and by increasing the size of those water layers that have both suitable temperature and food.

The point here is that the observations in Table 2 are fully consistent with the theory presented above stating that fish growth is generally oxygen-limited. On the other hand, they flatly contradict conventional theories of fish growth, which tend to concentrate exclusively on *ad hoc* postulates of local food scarcity (see, e.g., Weatherley and Gill, 1987).

This suggests that quantitative predictions (i.e., hypotheses) concerning the response of fish to pond aeration made on the basis of that theory, represent 'strong inferences' *sensu* Platt (1964), the testing of which is likely to advance a field still dominated by empirical approaches.

APPLICATION OF THE THEORY TO LAKE AND RESERVOIR AERATION

One of the corollaries of the above theory is that destratifying a lake such that its overall oxygen content is

Table 2 Response to aeration of some cultivated fish species (√: increase explicitly noted; -: item not mentioned).

Common name	Scientific name	Location	Increase of:					Source
			Con ^a	Growth	Survival	Harvest	Profits	
Common carp	<i>Cyprinus carpio</i>	Szarvas, Hungary	-	-	-	√	√	Abdul Amir (1988)
Silver carp	<i>Artisticthys nobilis</i>	Szarvas, Hungary	-	-	-	-	√	Abdul Amir (1988)
Bighead carp	<i>Hypophthalmichthys molitrix</i>	Szarvas, Hungary	-	-	-	-	√	Abdul Amir (1988)
Japanese eel	<i>Anguilla japonica</i>	Lukang, Taiwan	√	√	-	-	√	Anon. (1988a)
Tilapia	<i>Cichlidae</i>	Singapore	-	√	√	-	√	Anon. (1988b)
Channel catfish	<i>Ictalurus punctatus</i>	Alabama, USA	√	√	√	√	√	Hollerman and Boyd (1980)
Hybrid carp	<i>Ctenopharyngodon idella</i> X <i>Aristichthys nobilis</i>	Florida, USA	-	√	√	-	-	Shireman <i>et al.</i> (1983)

a) food consumption and/or conversion

This is illustrated here by a scheme in which stratification reduces the habitat of a fish population. Let us assume a lake with a warm epilimnion, a cool (10°), well-oxygenated mesolimnion and a small, oxygen-free hypolimnion (Figure 3). Let us further assume a population of cold-water fish, limited to the mesolimnion, feeding at 10°C, and having, for a value of $d = 0.8$, the VBGF parameters $W_{\infty(10^{\circ}\text{C})} = 1,000\text{g}$ (Figure 3), and $K_{(10^{\circ}\text{C})} = 0.5 \text{ year}^{-1}$.

Let us now imagine a change in the lake's stratification such that the O₂-free hypolimnion moves up, reducing the amount of benthos accessible in 10°C water. In such a case, the fish will have to undertake feeding forays into the warm epilimnion, and thus expose themselves to higher temperatures. Let us further assume that integrating time/temperature profiles of these forays suggests the fish to live, on the average, in a temperature of 12°C.

Other things being equal, and given Krogh's normal curve (Table 1), this will raise O₂ consumption by about 25%. Thus we have:

$$1.25 = (W_{\infty(10^{\circ}\text{C})}/W_{\infty(12^{\circ}\text{C})})^{1-d} \quad \dots 6)$$

from which $W_{\infty(12^{\circ}\text{C})} = 328\text{g}$.

Given equation (4) and the initial value of $K_{(10^{\circ}\text{C})} = 0.5 \text{ year}^{-1}$, one can also estimate the value of K corresponding to $W_{\infty(12^{\circ}\text{C})}$, i.e., $K_{(12^{\circ}\text{C})} = 1.05 \text{ year}^{-1}$.

Thus, given the above theory and ancillary field information, we can predict qualitatively and quantitatively how food conversion efficiency and growth (and hence also natural mortality, see Pauly 1980) will change, given changes in the thermal stratification of a lake (Figure 3).

Similar procedures can be applied to assess the impact of the distribution of O₂, and thus to reexamine as an example, the work of Coutant (1985, 1987, 1990), which documents a habitat – Chesapeake Bay – then in need of destratification, i.e., where striped bass – especially the large ones, for which oxygen supply was a problem – had become unable to grow and feed in certain areas of their original habitat.

CONCLUSION

The theory presented above, based on first principles and easily verifiable assumptions, can be easily developed to provide a comprehensive framework both for interpreting aeration experiments and for predicting potential effects of aeration in various water bodies.

Without such development of the above theory, or of a modification thereof, the observed impacts of aeration on ponds and lakes will continue to be perceived as isolated facts, and not as elements of a well-articulated system of principles allowing strong inferences and rapid advances.

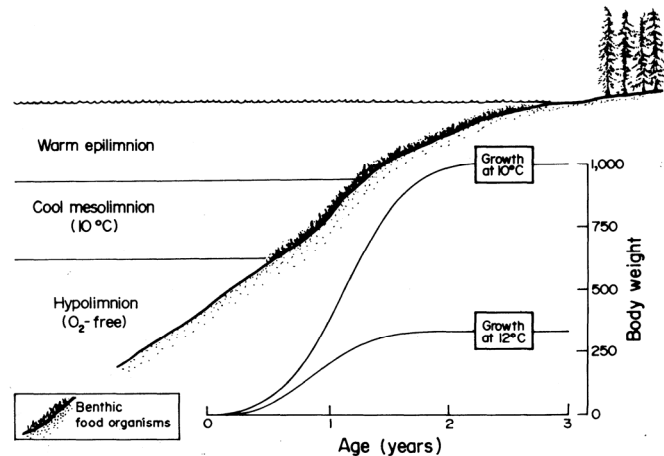


Figure 3 Schematic representation of a stratified lake, with each layer offering a different O₂/temperature combination to resident fishes. The insert in the lower right corner shows the growth curves resulting from the two scenarios in the text.

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