

# Growth: Environmental Effects

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## Glossary

**Abiotic** The chemical and physical (nonbiological, physical) variables of the environment (e.g., temperature).

**Ad libitum** Amount of food consumed when food is always present for individual fish.

**Anabolism** Synthesis of materials via metabolic processes; a series of chemical reactions that builds larger molecules from smaller components, usually requiring energy in the process.

**Biotic** Environmental factors related to living organisms. The biological variables of the environment, e.g., predation and competition.

**Catabolism** Metabolic processes that result in the release of energy from organic molecules.

**Conspecifics** Other individuals of the same species.

**Dominance** Behavioral ability of an individual to sequester resources in the presence of other individuals.

**Ectothermic** An organism whose body temperature is largely determined by heat exchange with its

surroundings. It does not produce and retain enough metabolic heat to elevate its body temperature above ambient temperature, but may use behavioral mechanisms to regulate body temperature.

**Heterospecifics** Individuals from different species.

**Ontogeny** Changes in the phenotype of an individual during its life span. Ontogeny is the outcome of a developmental program, encoded in an organism's genes, as well as interactions between the genotype of the individual and the environments it encounters, together with any maternal effects mediated through the egg itself.

**Photoperiod** Durations of day and night during the 24-h diel cycle.

**Ram ventilation** A passive method of driving oxygen-containing water over the gills. The fish swims with its mouth open, so water flows in through the mouth and out past the gills.

**Thermocline** Zone of high rate of temperature change that separates a shallow, less-dense, warm water layer (epilimnion) from a deeper, more-dense colder-water layer (hypolimnion) in lakes, seas, and estuaries.

## Introduction

Growth is central to the ecology of fishes because many factors relevant to fitness are size dependent, including prey size, risk of predation, survival during harsh conditions, and fecundity of females. In terms of the energy content of fish, growth is the difference between energy obtained in the food and the outputs of energy in the form of fecal and excretory losses and the heat generated by metabolic processes (see also **Energy Utilization in Growth: Energetics of Growth**).

The growth that an individual fish achieves depends on three constraints. The first is the genetic constitution of the individual. Growth responds to artificial selection indicating that there is underlying heritable, genetic variation for growth in fish populations. Second, the abiotic environment experienced by the fish will set constraints on growth. Third, the biotic environment will determine the extent of the growth potential that the fish can achieve as defined by its genotype and the abiotic environment experienced.

This article focuses on the effects of abiotic and biotic factors on growth. In analyzing the effect of abiotic and biotic factors on growth, a further factor has to be included. If the quality and quantity of food available does not change significantly, the growth rate, expressed as specific growth rate,  $g$ , decreases as the size of the fish increases. Specific growth rate is a measure of the size-specific growth rate. In mathematical terms, it is  $g = dW/W dt$ , where  $W$  is size (mass, length, or total energy content).

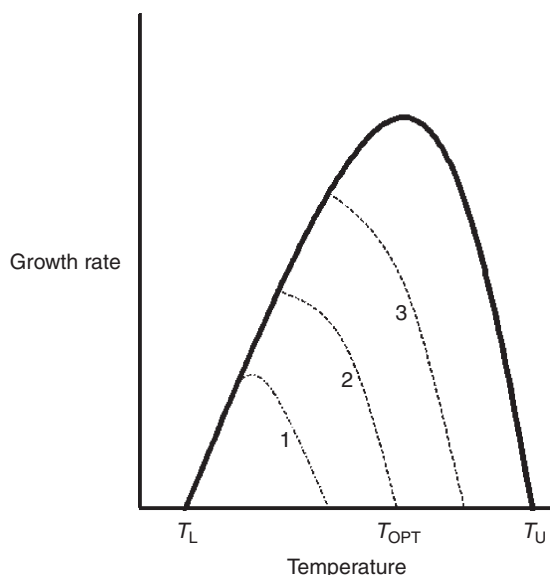
## Abiotic Factors

### Temperature

Metabolism, both anabolic and catabolic, is a set of chemical reactions catalyzed by enzymes; consequently, all physiological rates depend on temperature (see also **Swimming and Other Activities: Cellular Energy Utilization: Environmental Influences on Metabolism**). Temperature controls the maximum rate at which growth can occur

when food availability or other factors are not restricting growth rate. As the majority of fish are ectothermic (for exceptions, see also **Pelagic Fishes: Endothermy in Tunas, Billfishes, and Sharks**), their body temperature will essentially follow the temperature of the surrounding water. Experimental studies on the effect of temperature on growth rate show that three temperatures can be defined. There is a minimum ( $T_L$ ) and a maximum temperature ( $T_U$ ) at which the growth rate is zero. Between the minimum and maximum temperatures for growth, there is a temperature at which growth rate is maximized, identified as the optimum temperature for growth ( $T_{OPT}$ ). This means that the relationship between growth rate and temperature is an asymmetric bell shape (Figure 1). This pattern largely reflects the relationship between *ad libitum* food consumption and temperature. For fish supplied with maximum rations,  $T_L$ ,  $T_{OPT}$ , and  $T_U$  for growth in the European trout, *Salmo trutta*, a cold-water species, are approximately 5, 14, and 23°C, respectively. Experimentally determined values will also depend on the population from which the experimental fish are taken and the details of the experimental protocols. If the ration size is restricted, the optimum temperature for growth decreases (Figure 1), reflecting the lower metabolic costs at low temperatures (see also **Swimming and Other Activities: Cellular Energy Utilization: Environmental Influences on Metabolism**).

Most laboratory studies of the relationship between growth and temperature use constant temperatures. However, fish in natural populations may experience



**Figure 1** Schematic diagram of the relationship between growth rate and temperature, identifying the minimum,  $T_L$ ; optimum,  $T_{OPT}$ ; and maximum,  $T_U$ , temperatures for growth. Unbroken line shows relationship when fish fed *ad libitum*, broken lines show the relationship at restricted rations levels with level 1 < level 2 < level 3.

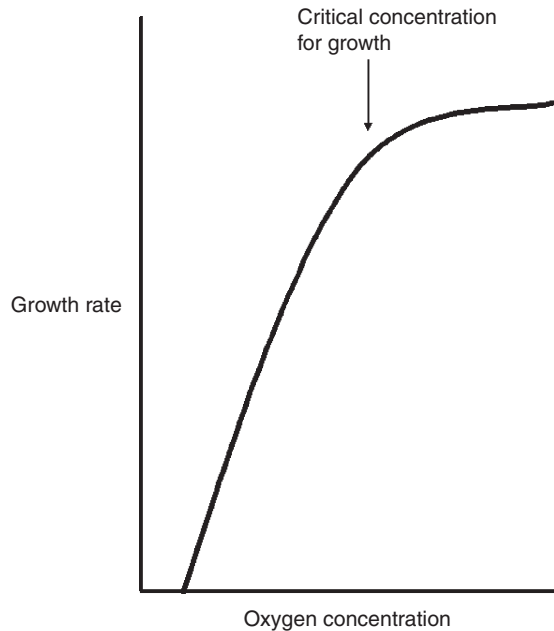
cyclical changes in temperature, either because of day–night cycles in temperature or because voluntary movements of the fish take them into different thermal regimes. Experimental studies on the effect of cyclical temperature regimes on growth have not provided consistent results, probably because of differences in the experimental designs. The vertical migrations of juvenile sockeye salmon, *Oncorhynchus nerka*, through the thermocline, in some lakes in summer, may reflect the advantage of feeding in the warm surface waters, but metabolizing the results of feeding in the cooler, deeper waters.

The relationship between temperature and growth rate for a given species of fish may vary with latitude. Experimental studies on the Atlantic silverside, *Menidia menidia*, which is found along the Atlantic seaboard of North America, demonstrated a pattern of counter-gradient selection. At a given temperature and with abundant food, silversides from northern populations grew faster than fish from southern populations. This was true even at high temperatures, even though the temperatures in which the northern population naturally live are lower throughout the year. This counter-gradient variation means that although silversides in the northern populations have a shorter growing season than that in the south, the higher growth potential of the northern fish means they can reach a size similar to that of the southern fish by the end of the growing season.

## Oxygen

Oxygen is required for the aerobic metabolic processes that make energy available to do useful work (see also **Energetics: General Energy Metabolism**). However, oxygen has a low solubility in water, and this solubility decreases as water temperature increases. The oxygen content of water can be expressed either as the absolute concentration in  $\text{mg L}^{-1}$  or as a percent of saturation. Due to the effect of temperature on the solubility of oxygen, 100% saturation at a high temperature represents a relatively low absolute concentration (see also **Transport and Exchange of Respiratory Gases in the Blood:  $\text{O}_2$  Uptake and Transport: The Optimal  $P_{50}$** ). Thus, at 10°C and 100% air saturation (at sea level), dissolved oxygen is at a concentration of 11.3  $\text{mg L}^{-1}$ , but at 25°C, the oxygen concentration at 100% air saturation is at 8.2  $\text{mg L}^{-1}$ . A further complication is that the oxygen concentration also decreases with an increase in water salinity.

There is the possibility that the rate of oxygen uptake by the fish is too low to support the rate of growth that would be permitted by the prevailing temperature. Thus, in some circumstances, oxygen can act as a limiting factor on growth and observed growth is lower than that predicted for the given temperature and available food (Figure 2). The



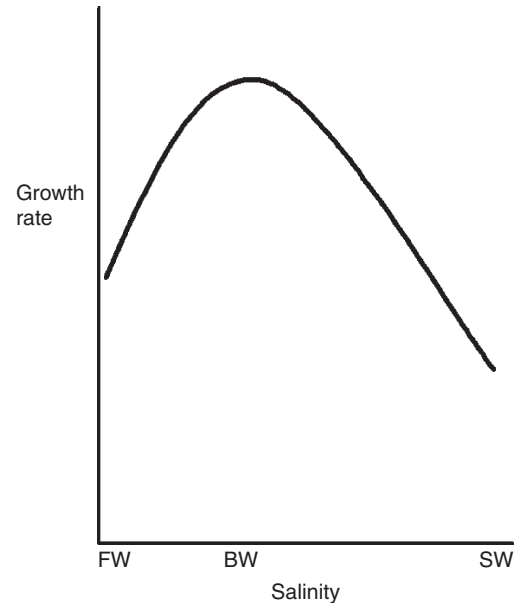
**Figure 2** Schematic diagram of the relationship between growth rate and oxygen concentration, showing a representative critical oxygen concentration for growth.

environmental conditions in which oxygen may act as a limiting factor on growth are unusually high water temperatures, water in which there is a high demand for dissolved oxygen by decaying organic matter (biological oxygen demand, BOD), high densities of fish in a limited volume of water, and low rates of oxygen diffusion from air to water because of a barrier formed by ice or snow or stratification.

Experimental studies suggest that across a range of species, the critical threshold level of air saturation at which growth starts to be inhibited by hypoxia (i.e., low oxygen) is 50–70%. In the freshwater tropical species *Poecilia reticulata*, the critical concentration was about  $3.0 \text{ mg L}^{-1}$  and at  $30^\circ\text{C}$ , 100% saturation would be about  $7.6 \text{ mg L}^{-1}$ . Most laboratory studies of the relationship between growth and oxygen level use a constant oxygen concentration. In natural environments, fish may experience regular or stochastic changes in oxygen concentrations such as those associated with day–night cycles in oxygen generated photosynthetically, or through water mixing induced by winds and storms.

### Salinity

Fish have to do metabolic work to maintain a homeostasis of ionic concentrations in their body fluids. For those species that live the whole of their lives either in the sea water or in freshwater, this metabolic work will be consistent. However, some fish species move between waters of different salinities. Many salmonid species, for



**Figure 3** Schematic diagram of the relationship between growth rate and salinity for a euryhaline species. FW, freshwater; BW, brackish water; SW, seawater.

example, are anadromous, moving from freshwater, where they spend an early juvenile phase, into the seawater, where they undergo growth to sexual maturity. As a consequence, energy that could have appeared as growth (see also **Energy Utilization in Growth: Energetics of Growth**) is expended on ionic homeostasis (**Figure 3**). Salinity acts as a masking factor for growth. The costs of ionic homeostasis will change as the fish move between salinities. The juveniles of some species that spawn in the sea, such as the European sea bass, *Dicentrarchus labrax*, move into estuaries, perhaps because of the growth advantage accrued by living at a reduced salinity. For a range of euryhaline species ( $N=23$ ), the best growth was achieved at salinities ranging from 0 to 35 ppt, but with a median value of 15 ppt. A study of growth in the early juvenile, glass-eel stage of the American eel, *Anguilla rostrata*, found that they grew faster in brackish water than freshwater, but that growth rates differed depending on the sites in eastern Canada from which the eels had been collected. This may be an example of an interaction between an abiotic factor and the genetic capacity for growth in eel populations.

### Current Speed

The speed of water flow potentially has opposing effects on growth. First, the energy the fish spends in swimming against a current will not be available to invest in growth. Second, the current flow may allow the fish to use, at least partly, ram ventilation for respiration, rather than the energetically more costly method of pumping the dense

and viscous water over the gills. In some salmonids, including European trout and Arctic charr, *Salvelinus alpinus*, fish grew faster when forced to swim at speeds of about 1.5 body lengths  $s^{-1}$ . This is a relatively slow speed for salmonids. However, some species of fish showed no effect or even reduced growth if subjected to exercise, including the goldfish (*Carassius auratus*). A preliminary study detected no effect of speed of swimming over the range 0–1.0 body lengths  $s^{-1}$  in juvenile cod, *Gadus morhua*, a marine species.

### Photoperiod

The effect of the diel cycle of light and dark on the growth of fish has, potentially, two components. For species that depend primarily on vision to detect their food, a longer period of light during the cycle will provide more time in which to feed. Other things being equal, this should result in faster growth. A second effect may be mediated through the control systems of the fish, due to the effect of photoperiod on the neuroendocrine system – as a consequence of light reception at the retina of the eye, the pineal gland, or perhaps other extra-retinal light receptors. In many species, these effects of photoperiod on the neuroendocrine system control important processes in the life cycle, most notably sexual maturation. In salmonids, photoperiod is important in the control of smoltification, the physiological processes that prepare the juvenile salmonid for life in the sea. Experimental studies and studies using aquaculture systems demonstrate an increase in growth rates in some species, including Atlantic salmon, *S. salar*, subjected to long day lengths or even continuous light. Three possible mechanisms may lead to higher growth: the increased time for feeding; neuroendocrine changes that stimulate feeding; and neuroendocrine changes that direct resources into growth rather than other activities. Most of the research on the effect of photoperiodic regime on growth has focused on the light regimes that increase growth rates under aquaculture conditions and less has been directed at teasing apart the mechanisms by which higher growth rates are achieved.

### Other Abiotic Factors

Although temperature, oxygen, salinity, and photoperiod are likely to be the most important factors influencing growth rates, in some contexts, other abiotic factors may become important. At high fish densities and low water-filtration/replacement rates, the ammonia/ammonium excreted by the fish can reach levels, in the water, that inhibit growth. Growth can also be inhibited at low pH levels or high  $[CO_2]$  such as those observed in areas affected by acid rain or decomposition of organic molecules.

### Interactions of Abiotic Factors

Although experimental studies on the effects of abiotic factors on fish growth tend to study only one or two factors, under natural conditions, fish experience many factors simultaneously, with some of those factors showing short- and long-term variations. The factors also interact (e.g., the effects of temperature and salinity on oxygen concentration), while some are confounded (e.g., day length and temperature in temperate and boreal areas). Thus, while experimental studies are essential for an understanding of the effects of abiotic factors on growth, care needs to be taken in extrapolating experimental results to natural populations.

### Biotic Factors

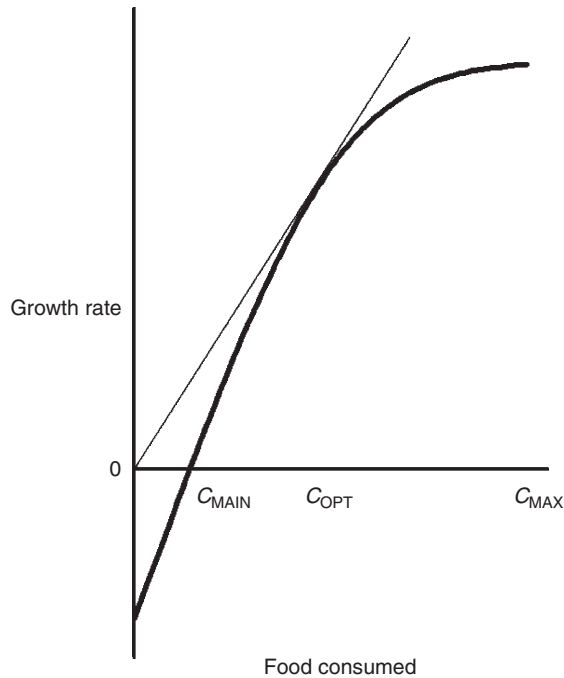
The abiotic factors provide the framework, which defines the maximum rate at which an individual fish can grow. Biotic factors determine what proportion of that maximum can be realized.

### Food

Food is the biotic factor that controls the rate of growth (see also **Energy Utilization in Growth: Energetics of Growth**). If a fish cannot obtain food, it will lose mass and eventually starve, although fish can often survive long periods without food. Both the quantity and the quality of food available control the growth rate.

### Food Quantity

Experimental studies show that the relationship between the growth rate and the quantity of food consumed is an asymptotic, curvilinear relationship (**Figure 4**). This relationship is defined by four levels of consumption. The growth rate of starved fish, that is, the rate at which the fish is losing mass, is defined by the value at which the curve intercepts the  $y$ -axis. The maintenance ration,  $C_{MAIN}$ , is defined by where the curve intercepts the  $x$ -axis. At this ration, there is no growth; the fish maintains a constant size. The optimum ration,  $C_{OPT}$ , is the ration at which the conversion of food into fish flesh is most efficient. Finally,  $C_{MAX}$  is the maximum ration the fish will consume under the prevailing abiotic conditions. With an increase in temperature, the loss of mass with starvation and  $C_{MAIN}$  increase, reflecting the effect of temperature on the rate of metabolism. Initially,  $C_{OPT}$  and  $C_{MAX}$  also increase, but at higher temperatures, beyond the optimum temperature for growth, they decline. The relationship also shows that a fish cannot maximize its growth rate and its growth efficiency simultaneously. Detailed, quantitative descriptions of



**Figure 4** Schematic diagram of the relationship between growth rate and food consumption, identifying the maintenance ration, at which growth is zero,  $C_{\text{MAIN}}$ ; ration at which growth efficiency is maximized,  $C_{\text{OPT}}$ ; and growth rate with *ad libitum* food consumption,  $C_{\text{MAX}}$ .

the relationship between growth, rate of food consumption, and temperature have been determined for the European trout. A feature of these results was that the temperature and ration size at which growth efficiency was maximized were both lower than the temperature at which the growth rate was maximized. However, there are still relatively few studies on other fishes that define the relationships in detail as is available for the European trout.

### Food Quality

Food quality in relation to fish growth has two aspects. The first is the nutritional quality of the food. Fish tend to have high requirements for protein and lipid in their diets. This is particularly true of carnivorous fish, such as the salmonids and gadoids. A consequence of this is that in the aquaculture of such species, to obtain good growth, the food provided contains good-quality protein, usually in the form of fish meal (see also **Energetic Models: Bioenergetics in Aquaculture Settings**). Omnivorous species such as the roach, *Rutilus rutilus*, one of the most common freshwater fishes of Western Europe, consume both plant and animal material. Roach fed on mealworms grew far faster than roach fed on grass, though the rates of consumption in both diets were close to the maximum. The growth

efficiency for the roach fed on grass was 9%, whereas for those fed on mealworms it was 46%. These differences reflect the higher quality of animal foods.

A second aspect of food quality is the size of the prey eaten (see also **Food Acquisition and Digestion: Energetics of Prey Capture: From Foraging Theory to Functional Morphology; Energetics of Foraging Decisions and Prey Handling**). As fish grow, the size of the mouth (gape size) increases, which allows the fish to take larger prey, with the result that each prey taken provides more energy. However, the time taken to handle an individual prey tends to increase with prey size. Consequently, for a fish of a given size, there is a prey size that maximizes the rate of return per unit time. This is the optimum prey size. In species such as the European perch, *Perca fluviatilis*, or the European trout, if an individual can reach a size that allows it to switch from feeding exclusively on invertebrate prey to feeding on fish, the individual often shows an increase in growth rate after this switch. This is a reflection of the increased profitability of the prey. In aquaculture, the size of the food pellets fed to the fish reflects the changing size of the gape of the fish as they grow.

### Social Interactions

The social environment of the individual fish can affect growth through several mechanisms, which influence the rate of feeding. The amount of food available can be affected by the presence of other animals. The propensity to feed may be affected by the presence of other, more dominant fish, even when food is available. Interactions with other animals can affect the time that can be spent on feeding or the energy expended on interactions. Social dominance is an excellent example of a social interaction (see also **Social and Reproductive Behaviors: Dominance Behaviors**) that results in differential growth.

### Presence of conspecifics

The effect of conspecifics on feeding and hence growth depends on the nature of the behavioral interactions. One possibility is that there is competition by exploitation for food. This occurs simply because items of food consumed by one individual are then not available for being eaten by another individual. When food availability is limiting, individual fish have essentially the same chance of obtaining food. Differences in food consumption and, therefore, differences in growth are largely determined by the chance of encountering suitable food items.

However, if the behavioral interactions include dominance relationships, the dominant fish can sequester food at the expense of the subordinate fish. This leads to compensatory growth. The dominant fish grows at a faster rate than the subordinate fish and so the variance



of fish size increases over time. Since dominance in fish is often related to fish size, as the dominant fish grow faster, their size advantage over the subordinate fish increases, which reinforces the ability of the dominants to sequester food. Observations on stream populations of salmonid fishes suggest that dominant fish can acquire the better localities for feeding. In the aquaculture of salmonids, fish are size-graded at regular intervals to reduce the differences in size among fish kept in a single tank, in an attempt to reduce the depensatory growth.

Even when food is readily available, the presence of dominant fish may inhibit the food intake of subordinate fish. The presence of the dominant fish stresses the subordinates and this leads to a loss of appetite in the subordinates. The importance of such a behavioral inhibition of feeding and hence growth in natural populations is uncertain (see also **Social and Reproductive Behaviors: Dominance Behaviors**).

In contrast, in fish species that typically live in shoals, the presence of conspecifics may stimulate feeding. This is because for such fish, isolation is a stressful condition, again leading to a suppression of appetite.

### **Presence of heterospecifics**

If species that coexist in the same habitat have similar diets, there may be interspecific competition for food, with adverse consequences on the growth of individuals. In some North American lakes, juveniles of bluegill (*Lepomis macrochirus*) and pumpkinseed sunfish (*L. gibbosus*) both occur in the littoral zones and have similar diets and act as interspecific competitors. As they increase in size, the diets of the two species diverge such that interspecific competition relaxes.

The presence of predators can also affect growth rates because the predators may restrict their prey to habitats that are less favorable for feeding. Largemouth bass, *Micropterus salmoides*, feed on juvenile bluegill sunfish. In the presence of the largemouth bass, the bluegill juveniles tend to be restricted to the vegetated littoral and are not able to move in to more open water, where zooplankton is an abundant source of food, but the risk of predation by largemouth bass is much higher. The presence of a predator may also inhibit a fish from foraging for food.

Such interspecific interactions and their effect on fish growth can be complex. An example can be found among European perch and roach in lakes in northern Europe. In the early life-history stages, the two species can be interspecific competitors for zooplankton, with roach tending to be the superior competitor. Later in ontogeny, the perch may become predators of roach. The presence of roach may both inhibit and stimulate the growth of perch,

depending on the ontogenetic stages of the individuals that are interacting.

### **Compensatory Growth**

Compensatory growth is a phenomenon which has been demonstrated in the laboratory, but whose importance in natural populations is still uncertain. It occurs when fish, which have experienced a period of unusually slow growth (e.g., due to low rations or high levels of swimming activity), are returned to favorable conditions (e.g., in which food is unlimited and/or activity is low). Such fish then grow at an unusually high rate and may catch up in size with individuals that have never suffered the growth depression. It is of interest because it suggests that, even in good conditions, fish tend to grow at a rate slower than their maximum physiological capacity. This suggests, also, that there are costs, in terms of fitness, of high growth rates. Notably, some studies have described an inverse relationship between growth rate and swimming performance. Growth rates may be regulated by neuroendocrine and endocrine mechanisms to reduce these costs.

### **Conclusion**

Growth patterns are adaptive responses to the environmental conditions. The growth potential of an individual is defined by its genotype. However, the extent to which that potential can be realized will depend on the abiotic conditions experienced during the ontogeny of the individual, further modified by biotic factors, particularly the availability of food.

See also: **Energetics: General Energy Metabolism.**

**Energy Utilization in Growth: Energetics of Growth.**

**Food Acquisition and Digestion: Energetics of Foraging Decisions and Prey Handling; Energetics of Prey Capture: From Foraging Theory to Functional Morphology. Pelagic Fishes: Endothermy in Tunas, Billfishes, and Sharks.**

**Social and Reproductive Behaviors: Dominance Behaviors. Swimming and Other Activities: Cellular Energy Utilization: Environmental Influences on Metabolism.**

**Transport and Exchange of Respiratory Gases in the Blood: O<sub>2</sub> Uptake and Transport: The Optimal P<sub>50</sub>.**

### **Further Reading**

Ali M, Nicieza A, and Wootton RJ (2003) Compensatory growth in fishes: A response to growth depression. *Fish and Fisheries* 4: 147–190.  
Boeuf G and Le Bail P-Y (1999) Does light have an influence of fish growth? *Aquaculture* 177: 129–152.

- Boeuf G and Payan P (2001) How should salinity influence fish growth? *Comparative Biochemistry and Physiology Part C* 130: 411–423.
- Brett JR and Groves TD (1979) Environmental factors and growth. In: Hoar WS, Randall DJ, and Brett JR (eds.) *Fish Physiology*, vol. 8, pp. 599–675. London: Academic Press.
- Conover DO, Clarke LM, Munch SB, and Wagner GN (2006) Spatial and temporal scales of adaptive variation in marine fishes and their implications for conservation. *Journal of Fish Biology* 69 (supplement C): 21–47.
- Davison W (1997) The effects of exercise on teleost fish, a review of recent literature. *Comparative Biochemistry and Physiology* 117A: 67–75.
- Elliott JM (1994) *Quantitative Ecology and the Brown Trout*. Oxford: Oxford University Press.
- Fry FEJ (1971) The effect of environmental factors on the physiology of fish. In: Hoar WS and Randall DJ (eds.) *Fish Physiology*, vol. 6, pp. 1–98. London: Academic Press.
- Halver JE and Hardy RW (2002) *Fish Nutrition*, 3rd edn. London: Academic Press.
- Jobling M (1994) *Fish Bioenergetics*. London: Chapman and Hall.
- McCullough DA, Barthololow JM, Jager HI, et al. (2009) Research in thermal biology: Burning questions for coldwater stream fishes. *Reviews in Fisheries Sciences* 17: 1–26.
- Persson L and de Roos AM (2006) Food-dependent individual growth and population dynamics in fishes. *Journal of Fish Biology* 69 (supplement C): 1–20.
- Ricker WE (1979) Growth rates and models. In: Hoar WS, Randall DJ, and Brett JR (eds.) *Fish Physiology*, vol. 8, pp. 677–743. London: Academic Press.
- Volkoff H, Canosa LF, Unniappan S, et al. (2005) Neuropeptides and the control of food intake in fish. *General and Comparative Endocrinology* 142: 3–19.
- Wootton RJ (1998) *Ecology of Teleost Fishes*, 2nd edn. London: Chapman and Hall.