



## THE INFLUENCE OF ENVIRONMENTAL TEMPERATURE ON GROWTH AND CONVERSION EFFICIENCY IN FISH

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Temperature is the most all-pervasive environmental factor that influences aquatic organisms. Nearly all fish species are, for practical purposes, thermal conformers, i.e. they are not able to maintain body temperature by physiological means, and their body temperatures fluctuate in close accord with the temperature of the surrounding water. Intimate contact between body fluids and water at the gills, and the high specific heat of water, assure this near-identity of internal and external temperatures (Brill *et al.*, 1994). Consequently, fish species are largely dependent on behavioural control of their body temperatures (Beitinger & Fitzpatrick, 1979; Coutant, 1987). Behavioural thermoregulation is widespread among fish species, and in laboratory studies it has often been found that there is good agreement between preferred temperatures and temperatures at which the fish can grow well and perform efficiently (Brett, 1971; Beitinger & Fitzpatrick, 1979; Jobling, 1981; Kellogg & Gift, 1983).

Natural water bodies will seldom, if ever, provide the fish with conditions under which maximum rates of growth can be achieved. Such water bodies will, however, present varied thermal environments offering a wide range of feeding opportunities. It is within such habitats that the ability to thermoregulate by behavioural means may be particularly beneficial to the fish, enabling it to reduce the potentially harmful effects of unfavourable thermal regimes on physiological performance.

The main focus of this overview is the examination of the effects of temperature upon fish growth under various feeding conditions. The interactions between feeding and growth are discussed in relation to behavioural thermoregulation, temperature selection in the natural environment and temperature compensatory mechanisms.

## Thermal sensitivity of physiological processes

A graph showing the relationship between the rate of a physiological process and temperature is known as a rate-temperature curve. Increases in temperature usually result in increases in the rates of physiological processes, but there is an upper limit above which the effects of temperature become debilitating. Thus, a rate-temperature curve typically consists of an ascending limb within the lower temperature range, and a descending limb at higher temperatures, when increased temperatures result in decreases in physiological rates. The temperature at which the rate is greatest is known as the optimum temperature.

The ascending limb of the rate-temperature curve encompasses temperatures usually considered to be within the 'normal range' of the species under consideration. Thus, within the normal range of temperatures an increased temperature results in increased rate, whilst above the normal range an increased temperature results in a decreased rate. There have been numerous attempts to provide quantitative descriptions of the effects of temperature upon a range of processes (e.g. developmental rates, metabolic rates, growth rates), and several empirical equations have been fitted to rate-temperature data (for discussion see Cossins & Bowler, 1987; Kamler, 1992).

At one time it was thought that the time taken for a biological process to occur (e.g.  $D$  in days) multiplied by temperature ( $T$  in  $^{\circ}\text{C}$ ) was constant, i.e.  $T \times D = \text{constant}$ . This expression of thermal summation has, for example, become established as the 'degree-day' concept that is widely used by fish hatchery managers for the prediction of developmental times of eggs and larvae. Since many biological processes are completely inhibited at temperatures several degrees above zero it has been suggested that it might be more appropriate to consider temperatures reckoned from the 'biological zero' than from  $0^{\circ}\text{C}$  (Cossins & Bowler, 1987; Blaxter, 1992; Kamler, 1992). The biological zero ( $T_0$ ) is the temperature at which infinite time would be required for the given process to reach completion. This form of correction gives  $(T - T_0)D = \text{constant}$ . The plotting of the times required for the biological process to reach completion against temperature yields a curvilinear relationship in the form of a rectangular hyperbola.

The rate of a process ( $V$ ) may be calculated as the reciprocal of the time taken ( $V = 1/D$ ). Consequently, the principle of thermal summation can be expressed as  $V = a(T - T_0)$ , where  $a$  is a constant. This type of expression usually provides a good fit to the observations over only part of the temperature range, with rates at low temperatures being greater than, and rates at high temperature being less than, those predicted by this type of rate-temperature curve.

These problems can usually be partially overcome by fitting an exponential equation ( $V = ab^T$ , where  $a$  and  $b$  are constants) to the observations. The logarithmic form of the exponential equation is:  $\log V = \log a + T \log b$ , and plotting  $\log V$  against  $T$  gives a straight line with slope  $\log b$  and

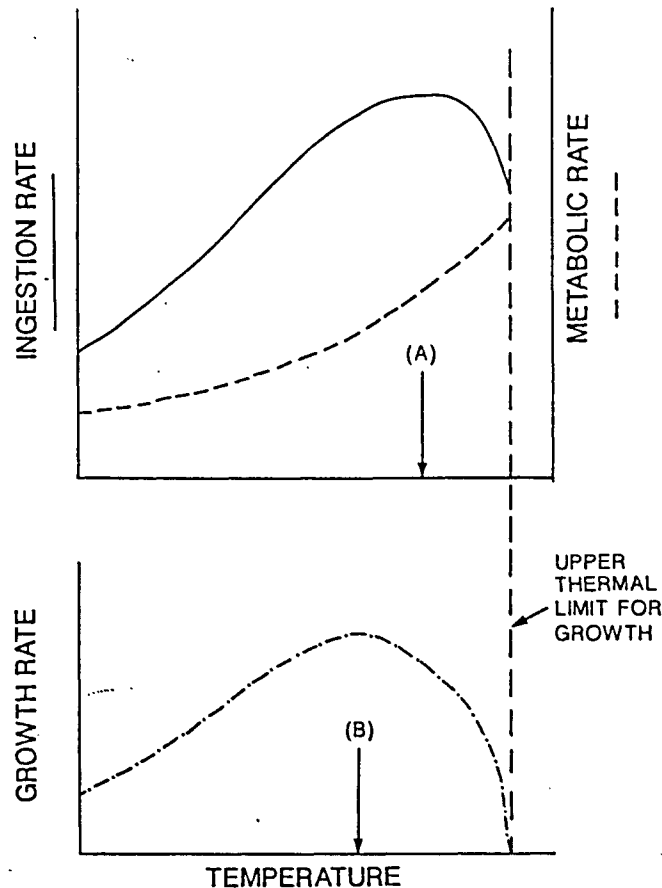
intercept  $\log a$ . In the exponential expression the ratio of rates over a given temperature interval is constant. This forms the basis of the  $Q_{10}$  relationship ( $Q_{10} = V_{T+10}/V_T$ , where  $V_{T+10}$  and  $V_T$  are the rates at temperatures  $T + 10$  and  $T$ , respectively). Accordingly, the  $Q_{10}$  and the constant  $b$  in the exponential equation are related as  $\log Q_{10} = 10b$ .

Logarithmic equations ( $V = aT^b$ , where  $a$  and  $b$  are constants) have also been proposed as being appropriate descriptors of rate-temperature relationships. The logarithmic transformation of the equation ( $\log V = \log a + b \log T$ ) shows that  $\log V$  is a linear function of  $\log T$ , so that plotting a graph of  $\log V$  against  $\log T$  results in a straight line with a slope  $b$  and an intercept  $\log a$ . In some cases the fit of empirical data to logarithmic equations can be improved if corrections are made to relate the rates to biological zero. The corrected equation becomes  $V = a(T - T_0)^b$ , where  $T_0$  is the biological zero. The constant  $b$  is a temperature coefficient, and if this constant is unity the logarithmic equation becomes identical to the expression of rate-temperature relationships in terms of thermal summation.

Various other expressions, including logistic, catenary, a range of polynomials, and the Hoerls function ( $V = aT^b e^{cT}$ ) have also been used to describe rate-temperature curves (see Cossins & Bowler, 1987; Kamler, 1992 for discussion of applications). It is, however, logarithmic and exponential expressions, particularly the exponential and  $Q_{10}$ , that have been the most frequently employed. The popularity of the  $Q_{10}$  relates to its simplicity, in that it gives an easily understood expression of the effect of temperature on rates, but  $Q_{10}$  varies with temperature and this tends to limit its usefulness. As a result, comparisons of  $Q_{10}$ s recorded for different species should only be made when studies have been carried out over the same temperature intervals. Such comparisons may, however, still be suspect because a given temperature interval may fall within different portions of the rate-temperature curves for the species being compared, i.e. a temperature range of 20-25°C may incorporate temperatures that are close to the upper thermal tolerance of stenothermal, coldwater species, but the same range may be below the optimum temperature for warmwater species. It should also be obvious that any attempt at comparison will be invalidated if the 'thermal history' of the animals under test has not been considered. For example, when physiological rates are recorded at the temperature of acclimation (test temperature = acclimation temperature) the slope of the rate-temperature curve (and hence  $Q_{10}$ ) will tend to differ from the slope obtained when measurements are carried out under conditions of 'acute' temperature change (for discussion see Jobling, 1994). In addition, it must be realised that the relationship between temperature and physiological rates can be influenced by a range of other environmental parameters, such as photoperiod and salinity, which may, or may not, be adequately controlled in experimental studies of rate-temperature effects (Roberts, 1964; Evans, 1984; Woilode & Adelman, 1991, 1992). Failure to account for any of these factors will reduce the precision with which rate-temperature relationships are described by the various mathematical formulations, and can invalidate the use of such formulations for comparative purposes.

## Temperature and growth - Maximum feeding

The simplest view of energy partitioning and growth is based upon the concept that 'any change in body weight results from the difference between what enters the body and what leaves it' (Jobling, 1994). This can be represented algebraically as  $\delta W/\delta t = pR - M$ , where  $\delta W/\delta t$  is the change in weight per unit time (somatic and reproductive growth),  $R$  is the amount of food consumed (ration),  $p$  is a coefficient indicating the availability of nutrients or food energy, and  $M$  represents catabolic losses (metabolism). Both  $R$  and  $M$  are expressed in terms of units per unit time, and therefore represent feeding (or ingestion) and metabolic rates, respectively. The metabolic rate term  $M$  incorporates fasting metabolism, activity metabolism, and feeding metabolism, the latter being defined as the metabolism linked to the processing of nutrients and the elaboration of tissues. The coefficient  $p$  can be considered to account for faecal and excretory losses.



**Figure 1.** Rate-temperature curves illustrating the effects of temperature on rates of ingestion, metabolism and growth. Note that the temperature at which ingestion rate reaches its maximum (A) is a few degrees higher than the optimum temperature for growth (B).

Numerous workers have investigated the effects of temperature upon the metabolic rate of fishes. Within the range of temperatures under which growth is possible the metabolic rate is almost invariably found to increase with increasing temperature (Figure 1), and the data are usually found to give a good fit to an exponential equation (Jobling, 1994).

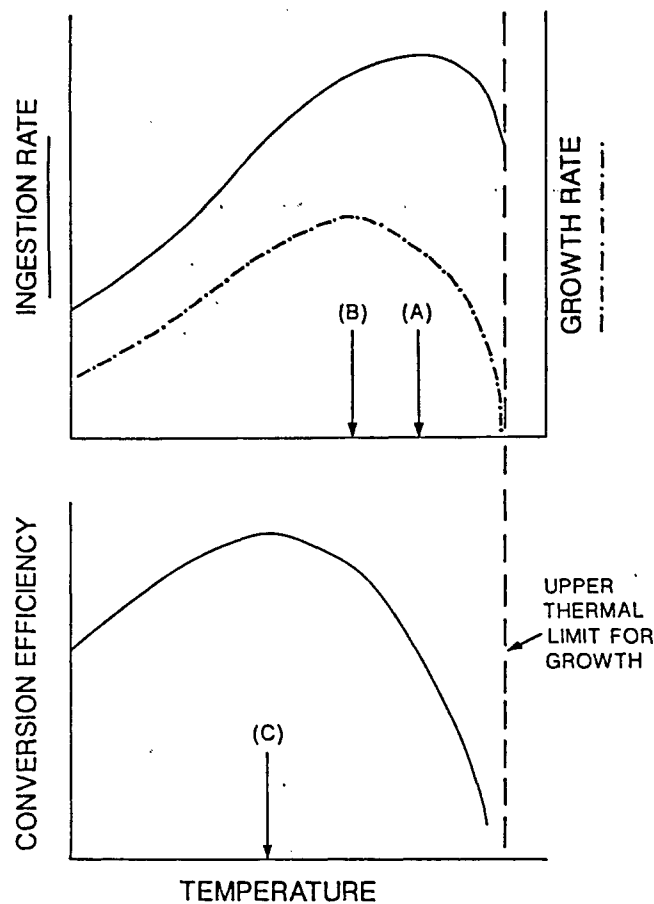
There are fewer studies of the effects of temperature on food consumption, and the fitting of ingestion rate data to mathematical functions is problematic (Elliott, 1982, 1994; Hogendoorn *et al.*, 1983; Binkowski & Rudstam, 1994). Most workers have not attempted to describe the effects of temperature on ingestion rates in mathematical terms, a few have fitted the data to polynomials and others have fitted logarithmic equations to the ascending limb of the rate-temperature curve (Cox & Coutant, 1981; Elliott, 1982, 1994; Wurtsbaugh & Cech, 1983; Woiwode & Adelman, 1991). Occasionally, more complex functions have been fitted to the data using non-linear regression procedures (Binkowski & Rudstam, 1994).

Hogendoorn *et al.* (1983) suggested that a useful empirical approach was to use Hoerls function to describe the effects of temperature on both feeding and metabolic rates. Nevertheless, irrespective of the approach adopted, it is almost invariably found that increases in temperature initially lead to increased rates of ingestion, feeding rates peak at some intermediate temperature and then decline precipitously as the temperature continues to rise (Figure 1). Thus, ingestion rate will have an optimum at an intermediate temperature, whereas metabolic rate will tend to show an exponential increase with temperature within the range at which growth is possible.

The difference between the rate-temperature curves for ingestion rate and metabolic rate indicates the resources available for growth under different temperature conditions. The plotting of growth rate-temperature relationships indicates that growth rate reaches a peak at an intermediate temperature (Figure 1). The optimum temperature for growth is, however, slightly lower than that at which ingestion rate reaches its maximum.

When both ingestion rates and growth rates are known it is possible to examine the influence of temperature upon the efficiency with which the ingested food is used for growth. The temperature at which conversion efficiency is maximized is slightly lower than the optimum temperature for growth (Figure 2).

The generality of these relationships is demonstrated by the results obtained in a number of growth studies conducted on fish species (e.g. Brett, 1971; Cox & Coutant, 1981; Elliott, 1982; Wurtsbaugh & Cech, 1983; Keast, 1985; Xiao-Jun & Ruyung, 1992). For example, Woiwode and Adelman (1991) reported that the food consumption of hybrid bass (female *Morone saxatilis* x male *Morone chrysops*) increased with temperature to 29.2°C, whereas the optimum temperature for growth was 26.8°C, and conversion efficiency peaked at 21.2°C.



**Figure 2.** Rate-temperature curves illustrating the effects of temperature on rates of ingestion and growth, and the influence of temperature upon conversion efficiency. Conversion is defined as growth per unit food ingested. Note that most efficient conversion (C) is achieved at a lower temperature than those at which ingestion (A) and growth (B) rates are at their respective maxima.

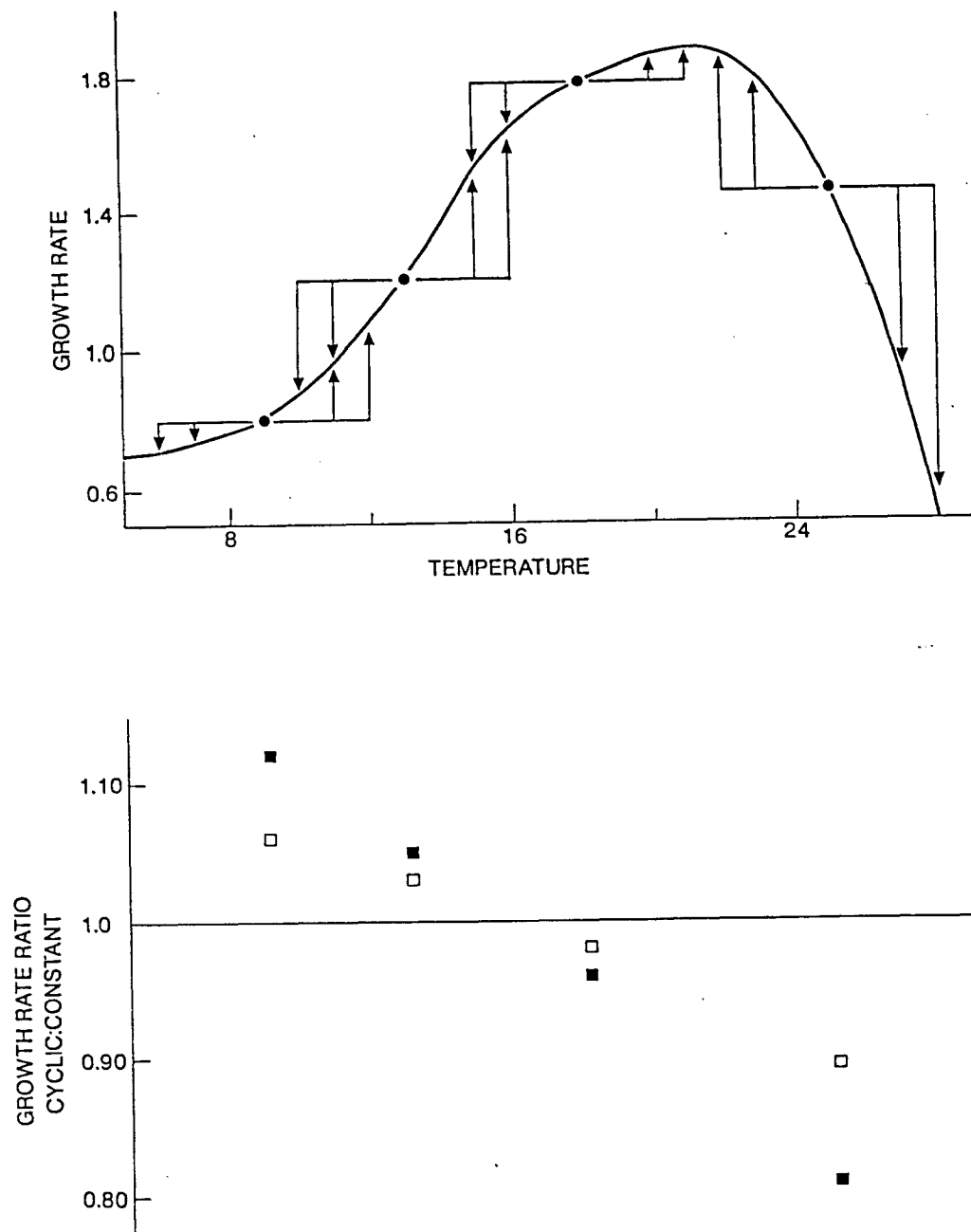
Examination of the results of behavioural thermoregulation studies points to there being general agreement between preferred temperatures and those that permit good growth. Optimum temperatures for growth often coincide with the final preferendum zone for temperature (Jobling, 1981; Kellogg & Gift, 1983). Thus, the impression is gained that there is a closer correspondence between thermal preferenda and optimum temperatures for growth, than between preferred temperatures and the temperatures at which either food consumption or conversion would be maximized.

In studies of behavioural thermoregulation it has often been assumed that the final preferendum is a species-specific characteristic, and warmwater, coolwater and coldwater species have been distinguished on the basis of temperature selection and growth performance criteria (Magnuson *et al.*, 1979; Jobling, 1981; Coutant, 1987). Some modification of the definition of the final preferendum may, however, be required because there is convincing evidence that there are ontogenetic changes in the thermal preferenda of some species of fish. Thus, there may be differences in selected temperatures at different stages of the life history, with the juveniles of several temperate zone freshwater species tending to select higher temperatures than do adults (McCauley & Huggins, 1979; Coutant, 1987; Jobling, 1994). If it is taken as axiomatic that there is a close correspondence between preferred temperatures and optimum temperatures for growth, then effects of temperature on growth performance will also be expected to differ among the different ontogenetic stages within any given species. Only a few studies have been conducted in which the influence of fish size or age on the optimum temperature for growth has been examined, but there is evidence that the thermal optimum tends to decline with increasing age and size of the fish (Coutant & Cox, 1976; Hogendoorn *et al.*, 1983; Keast, 1985).

#### Constant versus fluctuating temperatures

There are several reports that growth rates may be increased by exposure of fish, and other aquatic organisms, to fluctuating temperature regimes (Biette & Geen, 1980; Spigarelli *et al.*, 1982; Diana, 1984; Konstantinov & Zdanovich, 1986; Vondracek *et al.*, 1988; Berg *et al.*, 1990; Miao, 1992), the 'acceleration effect' of fluctuating temperatures being known as the *Kaufmann effect* (Cossins & Bowler, 1987). The growth acceleration resulting from exposure of fish to fluctuating temperatures is usually assessed by comparing the rate of growth observed under conditions that cycle regularly between two temperatures with that obtained at the 'mean' temperature. This method of calculation creates problems for the interpretation of experimental results because it assumes that there is a linear relationship between growth rate and temperature, something which is usually not the case. For example, if growth rates increased exponentially with temperature and the fish simply proportioned growth according to this relationship they should grow faster in fluctuating regimes than at a constant temperature equal to the 'mean' of the thermocycle.

The apparent growth-promoting effect of thermocycling is not universal, and there are also reports that growth rate is either depressed or unaffected by fluctuating temperature regimes (Hokanson *et al.*, 1977; Cox & Coutant, 1981; Vondracek *et al.*, 1989; Woiwode & Adelman, 1991). The extent to which growth rate will be either depressed or accelerated, or be unaffected by a fluctuating temperature regime will depend both upon the amplitude of the thermocycle and the 'mean' temperature about which the temperature fluctuates (for discussion see Cossins & Bowler, 1987).



**Figure 3.** Rate-temperature curve illustrating growth rates at different constant temperatures (●) and the possible influences of thermocycling upon rates of growth ( $\uparrow \downarrow$ ). The growth rate ratio refers to the rate of growth observed under thermocycling conditions relative to that attained under constant temperature at the cycle 'mean'. Comparisons were made using growth rate data for different constant temperatures and thermocycles of 'mean'  $\pm 2^\circ\text{C}$  (□) and 'mean'  $\pm 3^\circ\text{C}$  (■).



The nature of rate-temperature curves leads to the expectation that growth promotion will be greatest when cycles fluctuate around a low 'mean' temperature, thermocycling will have less effect on growth when the 'mean' is close to the optimum temperature, and growth will be markedly depressed when temperatures fluctuate around temperatures above the optimum (Figure 3; Table 1).

**Table 1.** Influence of thermocycling upon the growth of various fish species. The growth ratio refers to the rate of growth observed under thermocycling conditions relative to that attained under constant temperature at the cycle 'mean'. Data are from the following sources: Berg *et al.* (1990), Cox & Coutant (1981), Hokanson *et al.* (1977), Spigarelli *et al.* (1982), Vondracek *et al.* (1988), Woiwode & Adelman (1991).

Species	Temperature (°C)		Growth Ratio Cyclic : Constant
	Constant	Cyclic	
Atlantic salmon <i>Salmo salar</i>	13	10 $\rightleftharpoons$ 16	1.06
Mosquitofish <i>Gambusia affinis</i>	25	20 $\rightleftharpoons$ 30	1.07
Brown trout <i>Salmo trutta</i>	13	8 $\rightleftharpoons$ 18	1.39
Striped bass <i>Morone saxatilis</i>	18	14 $\rightleftharpoons$ 22	1.26
	24	20 $\rightleftharpoons$ 28	0.83
	30	26 $\rightleftharpoons$ 34	0.84
Rainbow trout <i>Oncorhynchus mykiss</i>	12	8 $\rightleftharpoons$ 16	1.16
	17	13 $\rightleftharpoons$ 21	0.95
	19	15 $\rightleftharpoons$ 23	0.99
	22	18 $\rightleftharpoons$ 26	Cyclic groups lost weight
Hybrid bass <i>Morone saxatilis</i> x <i>M. chrysops</i>	20	16 $\rightleftharpoons$ 24	1.07
	24	20 $\rightleftharpoons$ 28	0.99
	28	24 $\rightleftharpoons$ 32	0.87

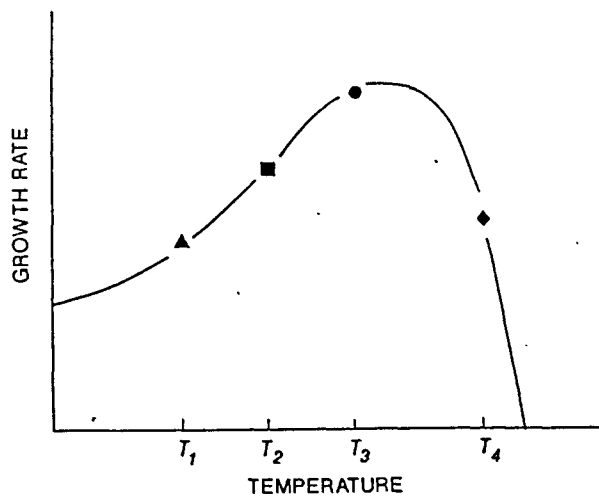
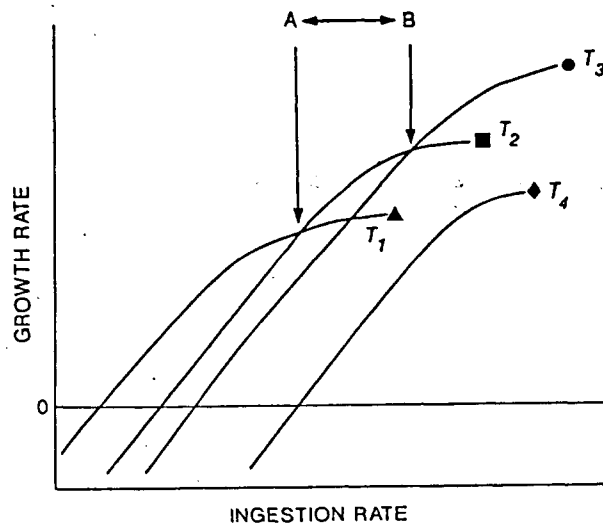
## Temperature and growth - Restricted feeding

In the discussion of the effects of temperature upon growth presented hitherto it has been assumed that the fish have had unlimited access to food. In other words, the fish have been able to consume the maximum rations that could be achieved under the given temperature conditions. It should, however, be obvious that growth rates will be influenced by food supply. Thus, there is a close relationship between ingestion rates and growth rates (the *growth-rations* curve) at sub-maximal rates of feeding. The relationship between growth rate and ingestion rate is often reported not to be a simple linear one (Elliott, 1982, 1994; Jobling, 1994).

At zero ingestion the fish starve and lose weight. As the rate of ingestion increases above zero, the curve rises steeply to reach the point at which the fish are ingesting food at the maintenance rate. The maintenance rate of ingestion is defined as the rate at which food must be ingested by the fish in order to maintain bodily functions without either loss or gain in weight. In other words, at maintenance ingestion rate the rate of growth is zero. With steadily increasing rates of ingestion the curve begins to flex, and it finally plateaus at the point of maximum ingestion rate and maximum growth rate.

Some variations in the form of the growth-rations relationship have been reported, but in many studies a curvilinear relationship is indicated (Elliott, 1982, 1994; Hogendoorn *et al.*, 1983; Wurtsbaugh & Cech, 1983; Vondracek *et al.*, 1989; Xiao-Jun & Ruyung, 1992; Jobling, 1994). There have been some attempts to find suitable mathematical expressions for the description of growth-rations relationships, but in many cases investigators have resorted to the fitting of smooth curves 'by eye'. A straight line has sometimes been used to depict the growth-rations relationship, especially when data points have shown considerable scatter and the point of maximum growth rate and maximum ingestion rate has not been well defined. Mathematical expressions that have been used to describe the relationship between ingestion rate and growth rate include exponential and quadratic equations, and hyperbolic functions (Wurtsbaugh & Cech, 1983; Woiwode & Adelman, 1991; Xiao-Jun & Ruyung, 1992; Jobling, 1994).

Since temperature influences metabolic rate, and governs the processes involved in ingestion and growth, the growth-rations relationship responds in a manner dependent upon the temperature-induced changes in the different physiological rate processes. At a comparatively low temperature (curve denoted by  $T_1$  in Figure 4) the growth-rations curve is far to the left by virtue of the fish having a low metabolic rate, and hence a low maintenance requirement. The curve rises to a low plateau in keeping with the low maximum rate of ingestion and generally depressed growth rate at low temperatures (Figure 4).



**Figure 4.** Curves illustrating the relationships between growth rate and ingestion rate (growth-rations curves) at increasing temperatures ( $T_1 \rightarrow T_4$ ). The symbols indicate the points of maximum ingestion and maximum growth at each of the four temperatures. The rate-temperature curve is also shown to illustrate the growth rates attained when ingestion rates are at their respective maxima for each of the four temperatures.

As temperature increases ( $T_1 \rightarrow T_2 \rightarrow T_3$  in Figure 4) the growth-rations curves are moved to the right as increasing temperature leads to metabolic rates, and hence maintenance requirements, being increased. The growth-rations curves also become elevated as temperatures approach the optimum and growth rate peaks (Figure 4).

Higher temperatures ( $T_4$  in Figure 4), above the optimum, lead to the growth-rations curve being shifted further to the right as maintenance requirements continue to increase. Thus, at temperatures slightly above the optimum there is a decrease in maximum growth rate despite high rates of ingestion.

Examination of the series of growth-rations curves reveals certain key features relating to the influences of temperature upon growth and conversion under different feeding conditions. Firstly, at high temperatures (e.g.  $T_4$  in Figure 4), when the rates of ingestion required to meet the costs of maintenance are high, growth rates and conversion efficiencies will be poorer than those at somewhat lower temperatures (e.g.  $T_2$  and  $T_3$  in Figure 4) irrespective of the rate of ingestion.

At temperatures below the optimum for growth (e.g.  $T_1$ ,  $T_2$  and  $T_3$  in Figure 4) the temperature at which the best growth and most efficient conversion is observed will be dependent upon ingestion rate. For example, when food is ingested at a low rate the best growth and most efficient conversion of food will occur at low temperature. In other words, the temperature at which best growth is achieved under any given conditions of restricted fixed rations reflects the partitioning of the resources available from the ingested food. At low temperature less of the ingested energy will be required for maintenance than at high temperatures. Hence, under conditions of low rates of ingestion more of the food energy is available for growth at the lower temperature.

As food supply increases, permitting increases in rates of ingestion, best growth and conversion are achieved at progressively higher temperatures. Thus, in the example shown in Figure 4, conditions that restrict ingestion to low rates result in the best growth and conversion being shown by fish held at  $T_1$ . At intermediate rates of ingestion (denoted by  $A \leftrightarrow B$ ) fish held at  $T_2$  would grow most rapidly, but if food supplies permitted ingestion rates to be high the most rapid growth and most efficient food conversion would be observed in fish held at  $T_3$ .

That a decrease in food supply leads to a decrease in the temperature at which growth is best has been observed in studies carried out on a range of fish species (Brett, 1971; Elliott, 1982; Woilwode & Adelman, 1991; Jobling, 1994). If fish tend to select temperatures at which their growth rates are highest (Jobling, 1981; Kellogg & Gift, 1983), it would be predicted that lower temperatures would be selected under conditions of severe food-limitation than under those that permitted ingestion rates to be high. This prediction is supported by the findings of a number of studies into behavioural thermoregulation, links between selected temperatures and the 'nutritional status' of the

fish having been found (Javaid & Anderson, 1967; Stuntz & Magnuson, 1976; Mac, 1985). In other words, well-fed fish select higher temperatures than do those that are severely food-restricted. Selection of higher temperatures by well-fed fish would lead to the promotion of rapid digestion and food processing, thereby permitting high rates of ingestion and growth to be maintained (Neverman & Wurtsbaugh, 1994). On the other hand, the selection of lower temperatures under conditions of severe food restriction would lead to energy conservation via reductions in maintenance requirements. In some cases, however, the magnitude of the reduction in preferred temperature in response to food limitation appears to be less than would be required for the fish to achieve the highest possible growth under the given food-restriction (Mac, 1985).

### Feeding, growth and behavioural thermoregulation in nature

A number of workers have discussed the possible energetic advantages of behavioural thermoregulation in water bodies with discontinuous thermal environments and localised food supplies, but there have been few experimental tests of the ideas (Brett, 1971; Biette & Geen, 1980; Diana, 1984; Clark & Levy, 1988; Wurtsbaugh & Neverman, 1988; Bevelhimer & Adams, 1993; Neverman & Wurtsbaugh, 1994). For example, Brett (1971) provided a review of the influences of temperature on feeding, metabolism and growth of juvenile sockeye salmon, *Oncorhynchus nerka*, and discussed the findings in relation to vertical migration patterns of the fish in thermally stratified lakes. He hypothesized that energetic advantages might accrue if fish migrated between the warm epilimnion, where they fed on zooplankton, and the cooler waters of the hypolimnion where metabolic costs would be reduced. The energetic advantages of making vertical migrations between warm and cool waters were expected to be greatest under conditions of limited food supply (Brett, 1971).

Biette & Geen (1980) attempted to test these ideas by conducting experiments under conditions that simulated those found in thermally stratified lakes. They were able to demonstrate that juvenile sockeye salmon usually grew more rapidly under conditions of thermal cycling than when they were held in either warm or cool water throughout the experiment. There were, however, two exceptions to the general trend of better growth under thermal cycling: severe food restriction resulted in growth being best under constant low temperature conditions, and when food supply permitted high ingestion rates the greatest rates of growth were observed under constant warm water conditions. Thus, it was concluded that under feeding conditions prevailing in thermally stratified lakes there would be a growth advantage to be gained by making vertical migrations between the warm waters of the epilimnion and the cooler hypolimnetic waters (Biette & Geen, 1980).

In the discussion given above it is assumed that the growth advantage that accrues from migrating between waters of different temperature relates to the fact that metabolic rates will be low in cool

waters, thereby leading to 'energy conservation' and improved growth. More recently, Wurtsbaugh & Neverman (1988) proposed an alternative viewpoint: it may be advantageous for fish to move into warmer waters after feeding if this stimulates digestion and thereby promotes increased rates of ingestion during subsequent feeding periods. Their hypothesis arose following observations that juvenile sculpin, *Cottus extensus*, fed on benthic organisms during the day and then migrated vertically, to spend the night in water that was 10°C warmer than that occurring close to the lake bottom. The results of laboratory experiments provided evidence that there could be a substantial feeding and growth advantage to be gained by feeding in cool waters and then moving into warmer waters, rather than residing permanently in water at low temperature (Wurtsbaugh & Neverman, 1988; Neverman & Wurtsbaugh, 1994). These conclusions were drawn on the basis of laboratory experiments in which the fish were permitted to feed at, or close to, maximum rates.

The two views of the mechanisms underlying the growth advantages to be gained by fish that display behavioural thermoregulation - 'minimization of metabolic costs' and 'maximization of feeding' - are not in conflict because both are essentially part of an hypothesis based upon 'growth maximization'. This can be illustrated by reference to the growth-rations relationships shown in Figure 4. If food resources were localised in areas of high temperature and fish remained in such areas, they would display a growth response denoted by a point on curve  $T_4$  in Figure 4. Fish feeding in areas of high water temperatures could, however, gain a growth advantage if they moved into areas of lower temperature following the completion of a feeding bout. That is, on moving to cooler water the growth performance of the fish would correspond to the appropriate points on curves  $T_1$ ,  $T_2$  or  $T_3$  for the given ingestion rate. The improved growth at the lower temperatures would arise because the fish would incur very high metabolic costs if they stayed permanently in areas with high water temperatures.

In cases where food supplies occur in waters of intermediate temperature (e.g.  $T_3$  in Figure 4) the fish should reside permanently in the area in which they feed provided that the amounts of food available enable high rates of ingestion to be maintained. On the other hand, should food supplies be limited, thereby reducing ingestion rates, the fish will achieve the best growth by moving to waters of lower temperature following feeding. For example, if food availability results in an ingestion rate lower than that indicated by point B in Figure 4 the fish would gain a growth advantage by moving from waters at  $T_3$  to those at  $T_2$  following completion of a feeding bout.

In cases where food is localised within areas of low water temperature, the fish should both feed and reside within such areas when conditions are such that food availability imposes a restriction on rates of ingestion (i.e. at ingestion rates below those indicated by point A in Figure 4 a fish would grow most rapidly if it remained in cool water at a temperature of  $T_1$ ). Under feeding conditions that permitted higher rates of ingestion the fish would gain a growth advantage by feeding at low temperature and then moving into warmer water to digest its food during intermeal

intervals (i.e. when food supply enables ingestion rates to exceed that indicated by A, the fish would increase its growth rate by migrating from water at  $T_1$  to water at a temperature of  $T_2$  during non-feeding periods).

Thus, the general rules for behavioural thermoregulation, as determined from considerations of growth maximization, are as follows:

- 1) When food supply is limited, fish should feed in areas where ingestion rates are maximized and then move, when not feeding, to areas where energetic costs are reduced.
- 2) Movement into cooler water following the completion of a feeding bout should only occur provided that the digestion and processing of food continues sufficiently rapidly to ensure that consumption during the next feeding period is not limited by the amount of undigested food remaining in the stomach.
- 3) When rates of ingestion are limited by low temperature *per se*, rather than food availability, the fish should migrate into warmer waters during non-feeding periods, thereby ensuring increased rates of food processing and improved growth.

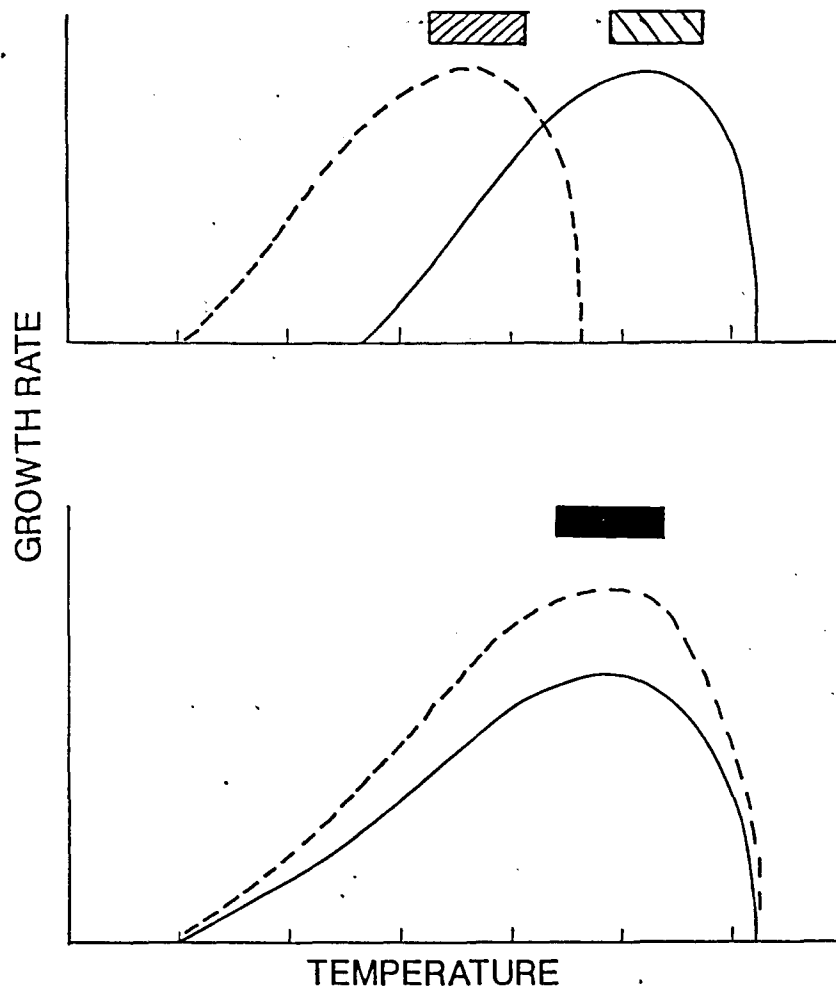
#### **Growth at different latitudes: Thermal compensation of growth?**

A number of fish species are distributed over a wide range of latitudes, and different populations inhabit environments that differ in both mean annual temperature and length of the growing season. In several of these species, fish in low-latitude environments grow faster than do high-latitude fish. There are, for example, numerous examples of northern hemisphere, temperate zone freshwater fish species in which the annual growth increment is lower for fish from northern populations than for those living further to the south. The conventional wisdom appears to be that high latitude populations tend to grow more slowly than those at lower latitudes as a result of the low temperature conditions experienced at high latitudes.

However, when reared at the same temperature, fish from high-latitude environments may grow faster than do low-latitude conspecifics (Isely *et al.*, 1987; Conover & Present, 1990; Williamson & Carmichael 1990; Philipp & Whitt, 1991; Nicieza *et al.*, 1994a, b) suggesting that there is some form of growth rate compensation in individuals from high-latitude populations. This compensation of growth rate with respect to latitude could represent a form of adaptation to the thermal regime most frequently encountered in high- and low-latitude environments, respectively.

Growth rate compensation could be expressed via the rate-temperature curves for growth being shifted to a lower range of temperatures in fish from high-latitude environments (Figure 5). This means that the optimum temperature for growth would be lower in fish from high-latitude populations, but the maximum growth rate need not differ among fish from high- and low-latitude

populations. The capacity to grow rapidly at low temperatures is envisaged to impose physiological constraints that preclude rapid growth at high temperatures such that individuals from high-latitude populations grow faster than those from low latitudes at low temperatures but the reverse is the case at high temperatures (Figure 5).



**Figure 5.** Rate-temperature curves illustrating two ways in which compensatory adjustments could be made in order to counteract the effects of latitudinal differences in temperature upon growth. In the upper figure the rate-temperature curve of the high-latitude population is shifted to the left; fish in the high-latitude population will, therefore, have a lower optimum temperature for growth, and grow faster at low temperatures, than do fish from low-latitude populations. In the lower figure, compensation is envisaged to occur by means of an elevation of the rate-temperature curve of the high-latitude population with respect to that of the low-latitude population. Bars indicate the zones of thermal preferenda predicted for fish of high- and low-latitude populations.



Based upon the premise that there is a close link between thermal preferenda and optimum growth temperatures (Jobling, 1981; Kellogg & Gift, 1983), a shift in the growth rate-temperature curve towards lower temperatures in fish from high latitudes would be predicted to be accompanied by a corresponding change in preferred temperatures (Figure 5). When temperature preferences and tolerances have been examined for fish populations inhabiting different thermal environments locally adaptive differences in thermal tolerance have been found in some species, but the thermal characteristics of other species appear to be invariant across numerous populations (McCauley, 1958; Kaya, 1978; Winkler, 1979; Hirshfield *et al.*, 1980; McCormick & Wegner, 1981; Matthews, 1986; Fields *et al.*, 1987; Koppelman *et al.*, 1988; McGeer *et al.*, 1991; Kaya *et al.*, 1992). Intraspecific differences in temperature tolerances are usually found to be small among populations from different thermal environments, and temperature preferenda may not differ significantly among high- and low-latitude fish populations. Koppelman *et al.* (1988) cautioned, however, that the failure to find significant differences among populations in thermal preferenda might be related to the combined effects of the general insensitivity of behavioural thermoregulation tests and a failure to adequately control for the various biotic and abiotic factors that are known to influence the temperatures selected by fish. Nevertheless, the impression is gained that there may be only small intraspecific differences in temperature tolerances and preferenda among fish populations, and this would, in turn, tend to call into question the idea that there is a marked downward shift in the optimum temperature for growth in high-latitude populations (Figure 5).

When growth rates of fish from high- and low-latitude populations have been examined at various temperatures, and rate-temperature curves plotted, optimum temperatures for growth for the different populations have been found to be very similar (McCormick & Wegner, 1981; Conover & Present, 1990). These observations led Conover (1990, 1992) to conclude that individuals of a given species grow at essentially the same temperatures independent of latitude, and that the reduced growth recorded for fish in high-latitude populations was a result of the decline in the length of the growing season with increasing latitude.

Although optimum temperatures for growth may be similar among fish in different populations, the growth rate-temperature curves of high-latitude fish may be elevated in comparison with those of the fish from low-latitude populations (Figure 5)(Conover & Present, 1990). This elevation of the growth rate-temperature curve of high-latitude, relative to that of low-latitude, populations is viewed as being a compensation that counteracts the decrease in the length of the growing season at higher latitudes (Conover, 1990, 1992; Conover & Present, 1990; Present & Conover, 1992). In other words, fish from high-latitude populations are thought to have a greater capacity for growth than those from lower latitudes across the full range of temperatures that permit growth, i.e. there is 'latitudinal compensation' for growth (Figure 5).

Similarly, latitudinal compensations in metabolic rate have been observed in many species, i.e. when

compared at the same temperature, individuals from high-latitude populations usually have higher metabolic rates than do conspecifics from low latitudes (Cossins & Bowler, 1987). Whilst this metabolic compensation has often been interpreted as being a response to temperature *per se*, the basis of the compensatory response remains a matter of debate (Cossins & Bowler, 1987; Hochachka, 1988; Clarke, 1991, 1993).

The links between metabolic rates, feeding and growth have been pointed out by several workers (for discussion see Clarke 1991, 1993; Jobling, 1994) and the increase in growth capacity of high-latitude fish may be accompanied by increased rates of ingestion (Present & Conover, 1992). It has also been reported that the digestive performance of Atlantic salmon, *Salmo salar*, from a northern population is potentially greater than that of salmon from a low-latitude population (Nicieza *et al.*, 1994a). Feed digestibility increased with increasing temperature, but fish from both populations were equally efficient at digesting and absorbing nutrients at the three temperatures tested (5, 12 and 20°C). By contrast, the times taken for food to be passed through the gut were longer for the salmon from the southern population. When digestibilities and passage rates were integrated and expressed as digestion rates (food digested and absorbed per unit time) it was found that the salmon from the high-latitude population had digestion rates that were potentially as much as 1.6 times greater than those of the low-latitude fish (Nicieza *et al.*, 1994a). Thus, it is possible that the high rates of ingestion, food processing and growth in high-latitude populations may be coupled to high metabolic rates. The maintenance of high metabolic rates may be a prerequisite if the fish are to exploit the available food resources over the course of a short growth season.

A latitudinal compensation of growth, resulting from an elevation of rate-temperature curves in fish from high-latitude populations, has only been demonstrated for a single species of fish - the Atlantic silverside, *Menidia menidia*. There is, however, some evidence that this type of growth rate compensation may also be present in other fish species (Conover, 1990, 1992; Nicieza *et al.*, 1994a, b). Clearly, further research is required in order to fully elucidate the mechanisms of latitudinal compensations in fish species. Laboratory studies of growth rate-temperature curves, coupled to the study of temperature preference, of fish populations from different latitudes may prove to be a fruitful approach for the examination of compensatory mechanisms at the whole-animal level.

### **Thermal limits for somatic and reproductive growth**

Temperature influences growth processes in a number of ways, but one consistent feature that emerges is that somatic and reproductive growth are only possible within relatively narrow temperature ranges. The range of temperatures within which growth is possible is usually much narrower than that which permits short-term survival. Furthermore, somatic growth is usually possible over a wider temperature range than that under which reproduction can be successfully

completed (Cossins & Bowler, 1987; Blaxter, 1992; Kamler, 1992; Elliott, 1994; Jobling, 1994).

This illustrates one of the problems in defining the thermal requirements of a species. It would be meaningless to define the thermal requirements of a species simply in terms of the critical limits for short-term survival of adults. There are narrower limits for feeding, even narrower limits for growth, and there are usually found to be very narrow thermal requirements for the completion of the reproductive cycle. Further, the thermal requirements for gametogenesis and spawning may differ from those for successful egg and larval development.

Temperature may have a profound influence upon various aspects of reproduction, from the hormonal regulation of gonadal growth, to the timing of spawning, and the relative timing of organogenesis in developing embryos. Unfavourable temperatures experienced by the adult fish may lead to disorders in gonad development, oocyte atresia and degeneration, inhibition of ovulation or a delay in the timing of spawning (Hokanson *et al.*, 1973; Gerking, 1979; Gerking & Lee, 1983; Gillet, 1991; Gillet & Breton, 1992; Luksiene & Sandström, 1994; Jobling *et al.*, 1995). On the other hand, incubation temperatures experienced by developing eggs and embryos may have profound effects upon the differentiation of different organ systems and the timing of organogenesis (Johnston, 1993; Brooks & Johnston, 1994). Any negative influences of unfavourable temperatures upon reproductive and developmental events would be expected to lead to reduced reproductive success, and in extreme cases could lead to recruitment failure.

Thus, reproductive performance - oogenesis, ovulation, egg and embryonic development - is much more sensitive to temperature than is somatic growth. Both reproductive and somatic growth have thermal limits that are considerably narrower than the temperature tolerance range, and successful reproduction might be expected over only about 10-20% of the range of temperatures tolerated by the adult fish (Gerking, 1979).

### Concluding comments

Temperature has a profound influence upon growth, and since growth is an important parameter with obvious implications at the population level it is often considered to be a useful indicator in the study of the effects of thermal stress on fish and other aquatic organisms. The value of using growth as an indicator in studies of thermal stress is that the temperature range over which growth is possible is much narrower than that permitting short-term survival. Nevertheless, the thermal limits for somatic growth are often broader than those for reproductive growth and development. Consequently, examination of reproductive success will generally provide a more sensitive indication of thermal stress in fish than will the study of somatic growth.

Temperature effects upon growth should never be viewed in isolation, and any discussion of the influences of temperature on growth should also include considerations of food availability. In other words, attention must be directed towards considerations of whether or not rates of ingestion are being constrained by limited supplies of food. This is important because feeding conditions will obviously have profound influences upon growth, the best growth being observed at low temperatures under conditions of restricted food supply and at higher temperatures when supplies of food are in excess of those capable of being ingested by the fish.

When food is limited fish appear to select cool water in order to reduce their metabolic costs and thereby increase the proportion of ingested nutrients available for growth. On the other hand, under conditions of unlimited food availability fish tend to prefer to remain within waters at temperatures that are close to the thermal optimum for growth. Thus, behavioural thermoregulation appears to provide a means by which the fish can counteract the suppressive effects of high or low temperatures on growth performance under different conditions of food availability.

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