10. Some Aspects of Thermal Stress on Freshwater Teleosts

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Abstract. Thermal stress is defined as any temperature change that produces a significant disturbance in the normal functions of a freshwater teleost and thus decreases the probability of survival. As stress responses at the population and community level are very complex and poorly understood, thermal stress is considered only at the level of the individual fish and emphasis is placed on ecological, rather than physiological, effects.

The thermal limits, optimum temperature range and preferred temperatures of freshwater teleosts are reviewed, and information on 27 European species is summarized. The concepts of tolerance and resistance to thermal stress are discussed and illustrated by original work on brown trout, *Salmo trutta*. Some comparisons are made between fish species with examples of cold-water stenotherms, mesotherms, and warm-water eurytherms. The temperature limits for spawning and egg development are shown to be much narrower than the normal thermal limits for older fish. Some factors that may affect thermal tolerance are briefly discussed.

The subtle effects of thermal stress within the normal tolerance range are discussed and illustrated by work on brown trout. Within the lethal limits, temperature can act as a loading stress by affecting functions such as growth and metabolism, especially when food intake is reduced. Temperature can also act as an inhibiting stress by affecting functions such as feeding and spawning.

Changes in body temperature and thermoregulation are briefly discussed. As well as combating thermal stress by tolerance, resistance and metabolic adjustments, fish may be able to change their body temperature by physiological regulation in a few species and by behavioural regulation in many species. The latter response is one of the chief factors responsible for fish movements.

I   INTRODUCTION

There is little uniformity in the use of the term "thermal stress" (see also Pickering, 1981, this volume). In the present contribution, thermal stress

will be used to refer to any temperature change that produces a significant disturbance in the normal functions of a freshwater teleost and thus decreases the probability of survival. This definition is similar to that proposed by Brett (1958) and assumes that the response is a stochastic variable that can be measured quantitatively. It also assumes that thermal stress is harmful. Although this is a reasonable assumption for the individual fish it is not always true for the population or community. For example, increased mortality in a crowded population may be beneficial to the fish population as a whole if space and/or food resources are limited. An extreme example is the death of the entire population through the severe stress of a thermal discharge, but even this may be beneficial to other members of the community.

It has been traditionally assumed in ecology that increasing complexity or diversity in a community produces increasing stability (e.g. Elton, 1958), but a more recent proposition is that complexity begets instability not stability, and that ecological communities persist despite, not because of, their complexity (e.g. May, 1973, 1976; Pimm and Lawton, 1980). It is, therefore, not surprising that stress responses at the population and community level are very complex and that little is known about the response of a freshwater ecosystem (for general reviews of stress and ecosystems see Odum, 1967, 1974; Slobodkin and Sanders, 1969; Gibbons, 1976; Lugo, 1978; Leffler, 1978). Therefore the present paper considers thermal stress only at the level of the individual fish.

The responses of a fish to stress can be broadly classed as either primary or secondary. Primary responses include neuro-endocrine and endocrine reactions which are reviewed in detail elsewhere in this volume (see contributions by Donaldson, 1981; Mazeaud and Mazeaud, 1981). Examples of primary responses to thermal stress include work on juvenile coho salmon, *Oncorhynchus kisutch* (Wedemeyer, 1973), goldfish, *Carassius auratus* (Fryer, 1975), juvenile sockeye salmon, *Oncorhynchus nerka* (Mazeaud *et al.*, 1977), and juvenile cutthroat trout, *Salmo clarki* (Strange *et al.*, 1977). As the fish were subjected to rapid increases of 10–15°C in these experiments, it is not surprising that the primary responses were so large. Such temperature increases rarely occur naturally in fresh water, and it would be of more ecological value to know the primary responses to smaller temperature changes at different acclimation temperatures and the level of temperature change at which there is no significant primary response.

There are numerous secondary responses to thermal stress and these include disturbances in osmotic and ionic regulation, metabolic processes, growth, reproduction and behaviour. The ultimate response is death. Metabolic and osmoregulatory disturbances during stress are effected by neuro-humoral changes (see reviews by Love, 1970; Maetz, 1974; Fontaine,

1975; Mazeaud et al., 1977; Eddy, 1981, this volume; Mazeaud and Mazeaud, 1981, this volume). The marked effects of thermal stress on the cardiovascular and respiratory system of freshwater fish have been described in detail by several workers (e.g. Hughes, 1964; Hughes and Shelton, 1962; Hughes and Roberts, 1970; Shelton, 1970; Heath and Hughes, 1973; Randall and Cameron, 1973; Burton, 1979), and the large amount of information on the relationship between temperature and metabolic rates of whole fish or their organs and tissues is summarized in several reviews (e.g. Brett, 1956, 1970; Fry, 1957, 1967, 1971; Fry and Hochachka, 1970; Hochachka and Somero, 1971). There is therefore an enormous literature on the physiological responses of freshwater fish to thermal stress, and there is a similar amount of information on thermal discharges and their effects on fish (see recent reviews by Esch and McFarlane, 1976, Coutant and Talmage, 1975, 1976, 1977; Talmage and Coutant, 1978, 1979; Alabaster and Lloyd, 1980).

The present paper cannot deal with all these effects and emphasizes those aspects of thermal stress that directly affect the ecology of freshwater teleosts. These are: thermal limits and the optimum temperature range, thermal tolerance and resistance, subtle effects of thermal stress within the normal tolerance range, body temperature changes and thermoregulation. Extensive use has been made of the excellent work of F. E. J. Fry and J. R. Brett. Although their approach to the problem has usually been through the laboratory experiment, they have always asked questions that are relevant to the ecology of the fish. Their influence on my own thinking is therefore considerable and evident in this contribution.

II THERMAL LIMITS, OPTIMUM TEMPERATURE RANGE AND PREFERRED TEMPERATURES

Fish are obligate poikilotherms (ectotherms) some of which can perceive temperature changes of less than $0.5°C$ (Murray, 1971). Their gills are an effective heat exchanger, but most heat transfer is by conduction directly through the body wall and heat transfer at the gills accounts for only 10–30% of the total heat exchange between the fish and the surrounding water (Stevens and Sutterlin, 1976; Beitinger et al., 1977; Erskine and Spotila, 1977; Kubb et al., 1980). Although there is some thermoregulation by local conservation of muscular heat in at least two groups, the tunas and the lamnid sharks (Fry and Hochachka, 1970; Stevens and Neill, 1978), most fish lack a mechanism to maintain an independent body temperature and are therefore essentially thermal conformers. When the water temperature changes, the rate of thermal equilibration is usually rapid. The

thermoregulatory mechanism in the central nervous system is similar to that of other vertebrates but the interrelationship between thermal acclimation and the thermoregulatory centres is somewhat ambiguous (see review by Crawshaw, 1977).

Although fish occur in habitats with temperatures from −2·5°C to 44°C, no species can survive over this entire range and each species has a characteristic range with upper and lower lethal limits. At one extreme are the polar species that live under ice and in ice tunnels, and have a narrow thermal range with limits of −2·5°C and 6°C (Sholander *et al.*, 1957; Somero and de Vries, 1967; Crawshaw and Hammel, 1971). The North American desert pupfish (*Cyprinodon* spp.) are at the other extreme and are the most eurythermal of fish with limits of about 2°C and 44°C (Lowe and Heath, 1969; Brown and Feldmuth, 1971; Otto and Gerking, 1973). Although different species may live within different thermal ranges, their metabolic rates may be similar. For example, the respiration rates of tissues from polar species (*Trematomus* spp.) are as high at 0–5°C as the rates of comparable tissues from goldfish at 20–25°C (Somero and de Vries, 1967). Freshwater teleosts in temperate regions usually live within the range 0–30°C. Minimum temperatures may reach 0°C in upland streams in winter, and maximum values may exceed 30°C in shallow ponds in summer or in waters that receive a thermal discharge. Brown trout, *Salmo trutta*, and carp, *Cyprinus carpio*, are good examples of temperate stenotherms and eurytherms respectively, and the marked contrast in their thermal requirements is illustrated in Fig. 1. Thermal stress, or even death, in each species occurs at temperatures that are optimal for feeding in the other species, but both species have a relatively narrow range for egg development.

Information on the thermal limits of common European species that also occur in Britain is summarized in Tables I and III. These tabulated values are my own interpretation of the data, and the number of references is a rough index of the amount of information on each species. Although the methods and objectives of studies on the same species often vary considerably, there is usually a remarkable similarity in the estimates of thermal limits. Other useful compilations have been made by Coutant (1977) who summarizes information on the "preferred" temperatures and upper and lower "avoidance" temperatures for 110 species from North America, and Alabaster and Lloyd (1980) who list the upper lethal and "disturbing" temperatures for 23 species, using data chiefly from Eastern Europe.

The "optimum temperature range" in Table I is the range over which feeding occurs and there are no external signs of abnormal behaviour, i.e. thermal stress is not obvious. This range is similar to the "normal physiological range" of some workers and is usually slightly wider than the range for growth and maturation. The optimum temperature range usually meets
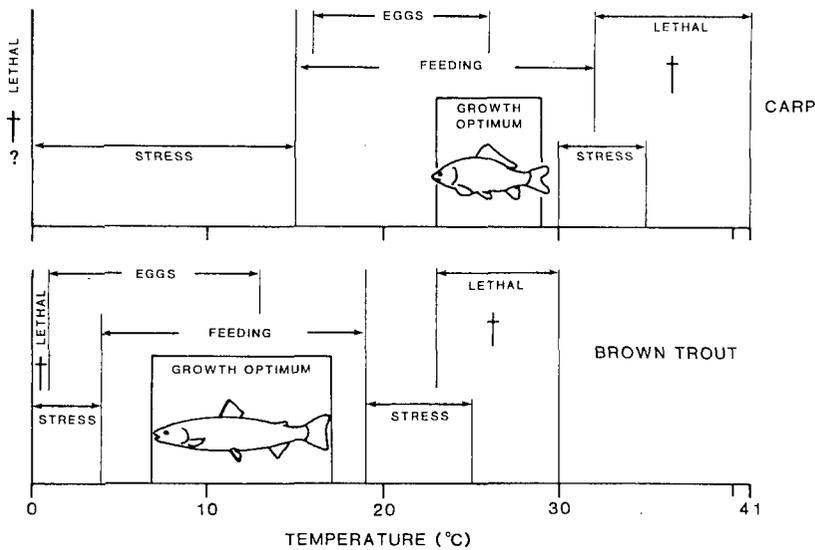
Fig. 1 Comparison of the thermal requirements of carp, *Cyprinus carpio*, and brown trout, *Salmo trutta*.

or overlaps the upper and lower critical temperature ranges (defined in Section III(a)) in Table I, but this does not occur for a few species because of a lack of reliable information.

Many workers have also used the concept of a "selected" or "preferred" temperature (see review of Richards *et al.*, 1977). The preferred temperature is often defined as the temperature at which fish are most frequently found when they are allowed to move freely in a temperature gradient. Usually the value is the modal, median or mean selected temperature and the fish generally occur over a temperature range rather than at one specific temperature. This preferred range is usually similar to, or lies within, the optimum temperature range. A second definition of preferred temperature is the value at which acclimation and preference temperatures are equal. The two definitions have led to different experimental designs. Methods for determining the final preferendum include temperature-gradient tanks, electronic shuttleboxes, body-core-temperature telemetry and calorimetry (McCauley, 1977).

As there are two definitions, several methods and additional variability due to differences in acclimation temperature, age, size and physiological conditions of the fish, it is not surprising that estimates of a single preferred temperature often vary considerably for the same species. For example, values in different studies ranged from about 21°C to 29°C for carp (Fry and Hochachka, 1970) and from 11·6°C to 19°C for rainbow trout (Spigarelli

TABLE I   Summary of Optimum Temperature Range, Upper and Lower Critical Ranges for Different Freshwater Species (All Values to Nearest °C).

Species	Common name	Optimum range (°C)	Lower critical range (°C)	Upper critical range (°C)	No.	Reference
Coregonus lavaretus	whitefish	8–15		20–25	2	
Thymallus thymallus	grayling	4–18		18–24	2+	Hellawell (1969, 1971)
Salmo salar	Atlantic salmon	6–20		20–34	6+	Jones (1959), Bishai (1960), Spaas (1960), Garside (1973)
Salmo trutta	brown trout	4–19	0–4	19–30	8+	Spaas (1960), Frost and Brown (1967), Elliott (Tables II, IV)
Salmo gairdneri	rainbow trout	10–22	0–9	19–30	10+	Bidgood and Berst (1969), McCauley and Huggins (1976), Kaya (1978)
Salvelinus alpinus	charr	5–16	c.0	c.22–27	0+	McCauley (1958), Swift (1964), Johnson (1980)
Salvelinus fontinalis	American brook trout (speckled trout)	8–20	0–7	20–29	14+	Fry *et al.* (1946), McCormick *et al.* (1972), Hokanson *et al.* (1973)

Species	Common name				References
Esox lucius	pike	9–25		30–34	5
Cyprinus carpio	carp	15–32	.0–15	30–41	7 + Aston and Brown (1978)
Carassius carassius	crucian carp	c.27		35–38	2
Carassius auratus	goldfish	16–30	0–17	27–42	6 + Fry et al. (1942)
Gobio gobio	gudgeon			27–37	3
Tinca tinca	tench	20–26		26–39	3 + Weatherley (1959)
Abramis brama	bream	8–28		28–36	3
Alburnus alburnus	bleak	?–20		20–38	2
Phoxinus phoxinus	minnow	13–25	c.0	23–31	1 + Frost (1943), Barrington and Matty (1954), Fortune (1955)
Scardinius erythrophthalmus	rudd	14–28		29–38	3
Rutilus rutilus	roach	8–25	0–12	25–38	2
Leuciscus cephalus	chub	8–25		27–39	1
Anguilla anguilla	eel	8–29	0–8	30–39	3 + Aston and Brown (1978), Sadler (1979)
Gasterosteus aculeatus	3-spine stickleback	4–20		22–37	0 + Baggerman (1957), de Sylva (1969), Jordan and Garside (1972), Wootton (1976)
Perca fluviatilis	perch	8–27		23–36	3 + Hokanson (1977)
Stizostedion lucioperca	zander	12–30		32–37	3 + Hokanson (1977)
Cottus gobio	bullhead	c.10–15			0 + Mann (1971)
Ctenopharyngodon idella	grass carp	20–30	0–2	34–39	1 + Stott (1977), Timmermans (1978)

The number of references is given for each species, and references are given if they are not in Reichenbach-Klinke (1976), Coutant (1977) or Alabaster and Lloyd (1980).

and Thommes, 1979). Therefore the concept of a single preferred tempera-
ture is difficult to apply to most species, and the preferred temperature
range, which is usually similar to the optimum temperature range, is
probably a more realistic concept in studies on thermal stress. The role of
temperature preference in relation to thermoregulation is discussed in the
second part of Section V.

III TOLERANCE AND RESISTANCE TO THERMAL STRESS

(a) Upper and Lower Critical Ranges

The "critical temperature ranges" in Table I are the ranges over which a
significant disturbance in the normal behaviour of a fish may occur, i.e. there
may be obvious signs of thermal stress. As most work on thermal stress has
been to predict the effects of thermal discharges on fish, information on the
upper critical range is more numerous than on the lower critical range. The
lowest value in the upper critical range is close to the "avoidance", "rest-
lessness" or "disturbing" temperature of other workers (see references in
Coutant, 1977; Alabaster and Lloyd, 1980), whilst the highest value is the
maximum temperature ("critical thermal maximum" of some workers) at
which fish can survive for brief periods.

As temperature increases within the upper critical range, the stress
response of the fish can be divided into three progressive phases. The first
external indications of abnormal behaviour are a reluctance to feed, sudden
bursts of activity with frequent collisions with the side of a tank in the
laboratory, rolling and pitching, defaecation and rapid ventilatory move-
ments. In the second phase, the fish becomes quiescent with short bursts of
weak swimming, often floats on its side or back, may rapidly change colour
and increases its ventilatory movements. Movements are restricted in the
third phase to the opercula, pectoral fins and eyes, and cease with the death
of the fish. I have observed all three phases in brown trout and have found
that when fish are transferred to cooler well-oxygenated water, they usually
recover from the first and second phases, but never from phase three.
Cocking (1959) has made similar observations on roach, *Rutilus rutilus*,
subjected to thermal stress.

The occurrence of thermal stress in the critical ranges is affected by several
variables, the most important being the period of exposure to the critical
temperature and the acclimation temperature, i.e. the temperature at which
the fish are kept prior to the change in temperature. The different experi-
mental methods of investigating the upper limits of thermal tolerance can be
divided into two broad categories. In the first group are the methods used to

determine the "critical thermal maximum" by raising the temperature from ambient acclimation level at a constant rate so that there is no significant time lag between the water temperature and the internal temperature of the fish. The critical thermal maximum is usually defined as the temperature at which the fish loses its ability to escape from lethal conditions, and is quickly followed by the lethal maximum when temperature continues to rise. In the second group of methods, the fish are kept at an acclimation temperature and then abruptly transferred to a higher constant temperature. This method is frequently used to determine the "incipient lethal temperature" which is the temperature beyond which the fish cannot live for an indefinite period. Some workers also determine the temperatures at which the fish can live for shorter periods of time, often 100 and 1000 min. Both groups of methods have their supporters and critics (see Fry, 1947, 1967, 1971; Hutchison, 1976; Becker and Genoway, 1979). Acclimation temperature is a common variable to both groups, but the important effects of the exposure period to the critical temperature are not included in the first group whilst the effects of rate of change in temperature are not included in the second group. In general, methods in the second group provide more information on the overall thermal tolerance and resistance of a fish, but have the added disadvantage that the final stress response may be due not only to thermal stress but also to handling stress when the fish are transferred from the acclimation temperature to the new temperature.

The complexity of thermal stress within the critical ranges can be illustrated by original work on brown trout. These experiments were performed to provide background data for a detailed study on feeding, growth and energetics (Elliott, 1972, 1975a, b, c, d, 1976a, b, c). The trout were in three distinct size groups with mean lengths (to nearest cm) and live weights (range to nearest g) of 10 cm and 10–12 g, 15 cm and 37–40 g, 25 cm and 175–185 g. The experimental tanks are described in detail by Swift (1961). Each tank contained about 100 litres of water that was stirred and aerated by compressed air (oxygen concentration >85% saturation) and maintained within ±0·1–0·2°C of a constant temperature. The tanks were covered with transparent polyethylene so that there was natural illumination with a light intensity at the water surface of c. 100 lux during the day.

Trout of similar size were acclimated to the same constant temperature (either 5, 10, 15, 20 or 22°C) for two weeks with one fish in each tank. Water temperature was then raised at a rate of about $1°C\ h^{-1}$ so that the final mean temperature in each tank was either 18, 20, 22, 24, 26 or 28°C. For acclimation temperatures of 20 and 22°C, there was an additional final temperature of 30°C but no final temperatures of 18–20°C and 18–22°C respectively. The rate of temperature increase was chosen because it is similar to mean rates of change in upland trout streams in summer, but rates

as high as $2 \cdot 2 - 2 \cdot 5°C\,h^{-1}$ occasionally occur (Macan, 1958; Crisp and Le Cren, 1970; J. M. Elliott, unpublished). Two fish were kept at the acclimation temperature throughout the experiment and served as controls. Freshly killed *Gammarus pulex* were fed to the fish at satiation levels which had been determined from other experiments (Elliott, 1975a). Therefore the trout were not subjected to the additional stresses of handling and food deprivation. These stresses are ignored in most studies of thermal stress but are clearly important. When trout were handled during early experiments on feeding and growth, they refused to feed for periods between 1–6 days after handling, even when the fish were simply transferred between tanks with the same water temperature.

The survival and feeding rate (see Elliott, 1975b for experimental details) of the trout were recorded every 10 min for the first 100 min, every 100 min for the period 100–1000 min, and every 1000 min for the period 1000–10 080 min (= 7 days). These observations were used to record the highest temperature for normal feeding and survival over 10 min, 100 min, 1000 min and 7 days. The normal rate of feeding was determined in a separate series of experiments (Elliott, 1975b), and there was usually no problem in detecting a marked decrease in this rate because feeding became spasmodic or ceased. The experiment was repeated five times with different fish to give five estimates for each size group of fish at each acclimation temperature. As there were no significant differences ($p > 0 \cdot 05$) between the values for the three size groups at the same acclimation temperature, the samples were combined to give 15 values which were used to calculate arithmetic means and standard errors (Table II).

Several fish that survived for 7 days were kept at the same temperature for up to a month and it was therefore assumed that values for 7 days survival are the "incipient lethal levels", i.e. the temperatures that define a "tolerance zone" within which the fish can live for a considerable time (all definitions follow the terminology of Fry, 1947, 1971). The upper, incipient lethal temperature increased linearly with increasing acclimation temperature until the latter was just above 15°C. Above this level, there was no increase with increasing acclimation temperature and an ultimate upper incipient lethal temperature of $24 \cdot 7 \pm 0 \cdot 25°C$ was reached (Table II). Values for survival at 10 min, 100 min and 1000 min followed a similar pattern at slightly higher temperatures and were within the "zone of thermal resistance" outside the tolerance zone and between the incipient lethal temperature and ultimate lethal temperature. The latter temperature was estimated by the temperature for survival over 10 min. There was an exponential relationship between the "resistance time" (or "effective time" of some workers) to death and the lethal temperature (Fig. 2). Trout acclimated at 15, 20 or 22°C were able to survive at temperatures close to

TABLE II *Salmo trutta*: Highest and Lowest Temperatures (°C) for Survival over 10 min, 100 min, 1000 min and 7 days or Longer, and for Normal Feeding; all Values are Arithmetic Means ±SE ($n = 15$).

| | Acclimation temperature | | | | |
	5°C	10°C	15°C	20°C	22°C
Highest temp. for:					
Survival over 10 min	25·6±0·21	27·3±0·25	—	29·9±0·13	29·7±0·18
100 min	24·3±0·18	25·9±0·31	27·7±0·18	27·9±0·13	27·7±0·18
1000 min	22·7±0·37	24·4±0·21	25·6±0·35	26·5±0·31	26·7±0·25
7 days+	21·5±0·36	22·9±0·38	24·4±0·45	24·7±0·25	24·7±0·25
Normal feeding	18·7±0·25	19·5±0·41	19·1±0·27	None	None
A and D, survival 100 min	23·9 (6°C)	—	27·4	28·2	—
1000 min	23·2 (6°C)	—	26·0	26·4	—
B, survival 1000 min	24·3 (6°C)	—	25·9	26·7	—
7 days	22	23	—	23	—
F and B, survival 7 days	22·5	24·2	24·5	24·8	25·3 (23°C)
Lowest temp. for:					
Survival over 100 min	0	0	0	0	0
1000 min	0	0	0	0	0·3±0·18
7 days+	0	0	0	0·7±0·25	1·3±0·25
Normal feeding	0·4±0·21	2·9±0·27	3·6±0·29	4·3±0·18	None

Values of other workers are included for comparison: A and D = Alabaster and Downing (1966), B = Bishai (1960), F and B = Frost and Brown (1967) who reproduced data from the Ph.D. thesis of E. S. Gibson (1951, University of Toronto).
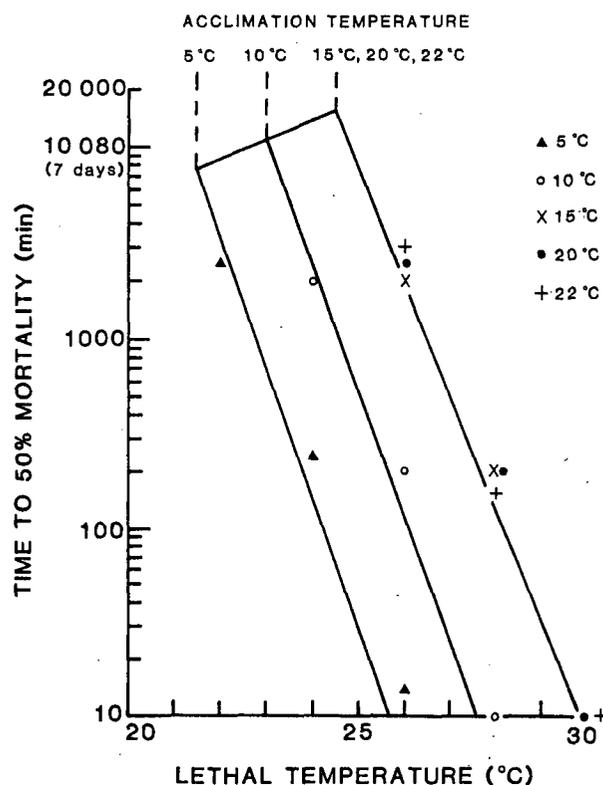
Fig. 2   Relationship between the time (min) for 50% mortality of brown trout, *Salmo trutta*, and the lethal temperature (°C) at different acclimation temperatures.

28°C for 100 min and 30°C for 10 min. Therefore, trout can survive for short periods at temperatures that would be eventually lethal. This resistance to the lethal effects of thermal stress enables the fish to survive in waters where daily maximum values exceed the incipient lethal temperature.

The highest temperatures for survival were very similar to those obtained in three other studies on brown trout (cf. values in Table II), in spite of the different experimental methods and fish sizes. Methods and sizes are not given for the data quoted by Frost and Brown (1967), but in both the other studies the fish were transferred abruptly from the acclimation temperature to the higher temperature, and the trout were newly-hatched alevins (Bishai, 1960) and either 7·4 cm or 10·1 cm long (Alabaster and Downing, 1966). These comparisons show that sudden or slower (1°C h^{-1}) changes in temperature, some handling and size differences within the length range c.

2–25 cm had no obvious effects on the temperatures for survival over different periods.

The trout did not feed at acclimation temperatures of 20°C and 22°C, and the normal rate of feeding decreased markedly at temperatures above c. 19°C in the other experiments (Table II). As a marked decrease or a cessation of feeding will obviously have an important effect on the growth and ultimately the survival of the fish, it must be considered a stress response within the tolerance zone. Therefore, thermal stress can occur at temperatures that are below the incipient lethal level.

Detailed information on the lower critical range is scarce, but there are several records of "cold shock" during sudden decreases in temperature (see references in Brett, 1956; Ash et al., 1974; Block, 1974). As the freezing point of the body fluids of freshwater fish is close to -0.5°C, there is little danger of death through freezing. In lakes that freeze to the bottom, some species such as the Arctic black fish, *Dallia pectoralis*, and the crucian carp, *Carassius carassius*, avoid freezing by burrowing into the warmer mud at the bottom (de Vries, 1971). Thermal stress within the lower critical range usually produces a cessation of feeding and sudden bursts of activity followed by a state of coma in which there is failure of the respiratory centre and the ion-osmoregulatory mechanism (see references in Fry, 1971; see also Eddy, 1981, this volume). It is often difficult to determine when death occurs in comatose fish and death in the following experiments was assessed by the ability of the trout to recover when transferred to warmer water. It is worth noting that the gradual cooling of fish to less than 4°C (depending on the species and its thermal history) is one of the oldest methods of anaesthetizing fish (Randall and Hoar, 1971).

The experimental procedure used to determine lower temperature limits for brown trout was very similar to that used to determine upper limits. The same acclimation temperatures were used but the water temperature was then lowered at about 1°C h^{-1} to final mean temperatures of 0, 2, 4, 6°C (not 6°C for acclimation temperature of 5°C). This rate was close to the maximum rate of decrease in upland trout streams (Crisp and Le Cren, 1970; J. M. Elliott, unpublished). It was difficult to control the temperature at 2°C or less and iced water had to be added to maintain a temperature near 0°C. Records were made of the lowest temperatures for normal feeding and survival over 100 min, 1000 min and 7 days. Once again, there were no significant differences ($p > 0.05$) between the values for the three size groups of fish at each acclimation temperature and therefore the data were combined for the final estimates of means and standard errors.

Most fish survived for at least 7 days at temperatures close to 0°C, but some fish died at 0°C after acclimation at 20°C and 22°C, and the lowest temperatures for survival were therefore just above 0°C (Table II). The

ultimate lower incipient lethal temperature could not be determined because it was obviously below the freezing point of freshwater. The lowest temperature at which normal feeding occurred increased with increasing acclimation temperature. Trout did not feed at acclimation temperatures of 20°C and 22°C, but those at 20°C started to feed at 4°C and 6°C. To check if trout could survive sudden decreases in temperature, fish kept at about 10°C in the laboratory were transferred abruptly in winter to outdoor tanks containing water to which snow was frequently added. The trout survived for 7 days, but refused to feed, at temperatures in the range 0·5–2°C, and were then returned to the laboratory where they soon returned to their normal feeding behaviour.

(b) Tolerance of Different Freshwater Species

The results presented in the last section were used to construct a thermal tolerance diagram for brown trout (Fig. 3). Thermal stress is lethal outside the tolerance zone enclosed by the incipient lethal level and death is a function of the exposure time to the thermal stress. The incipient lethal level
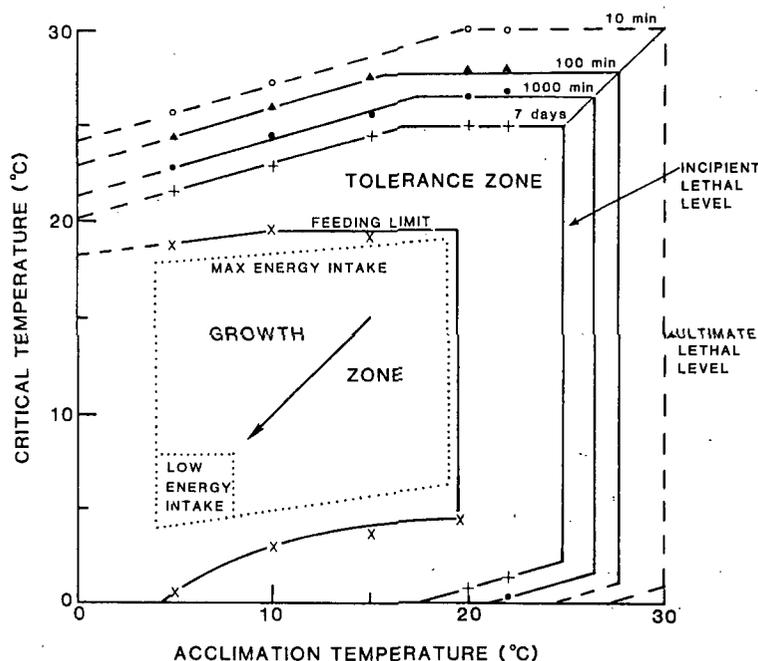
Fig. 3 Thermal tolerance diagram for brown trout, *Salmo trutta*, showing the tolerance zone, feeding zone and growth zone which decreases with decreasing energy intake.

is therefore the boundary between tolerance and resistance. Within the tolerance zone, temperature acts as a "loading" and "inhibiting" stress by limiting functions such as feeding, spawning, growth and metabolism (see Section IV).

Thermal tolerance diagrams provide a useful method for comparisons between species, but the detailed information required to construct such a diagram is lacking for most species. Notable exceptions (based on the work of Fry et al., 1942, 1946; Cocking, 1959) are compared in Fig. 4. The
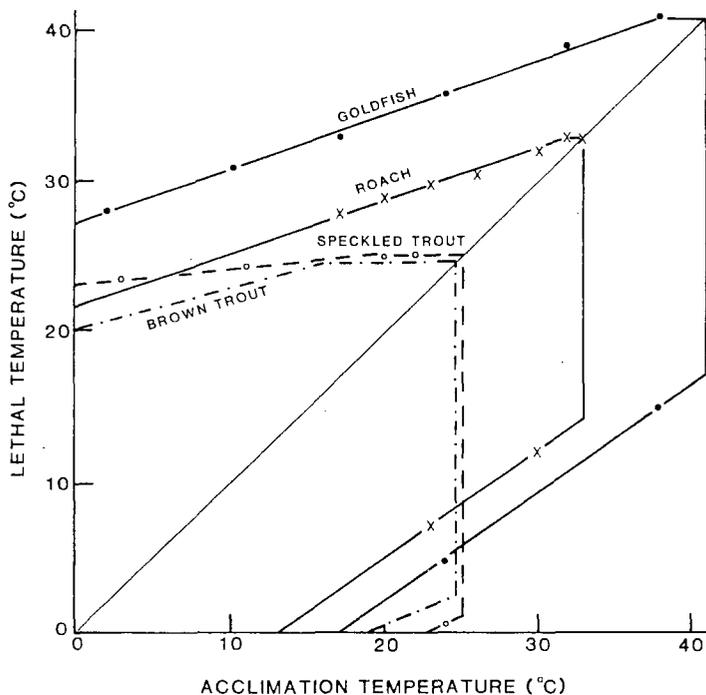
Fig. 4   Thermal tolerance diagrams for four species: brown trout, speckled trout or American brook trout (Fry et al., 1946), roach (Cocking, 1959), and goldfish (Fry et al., 1942).

thermal tolerance of brown trout and American brook trout, *Salvelinus fontinalis*, is very similar and both species are typically cold-water steno-therms. Roach have a much higher tolerance and the extremely high tolerance of goldfish shows why they can survive in habitats varying from a small lake to a jam-jar or polyethylene bag full of water! A 1°C increase in the upper incipient lethal temperature below the ultimate lethal level requires an increase in acclimation temperature of about 7°C for American

brook trout, about 5°C for brown trout and about 3°C for roach and goldfish. The area of the tolerance zone is a useful index of thermal tolerance and is usually expressed as °C squared. The value of $583°C^2$ for brown trout is slightly lower than that of $625°C^2$ for American brook trout, but much lower than $770°C^2$ and $1220°C^2$ for roach and goldfish respectively. Brett (1956) gives values for 23 species from North America, and these decrease from goldfish to five *Oncorhynchus* spp. with extremely low values between 450 and $529°C^2$. There is a lack of detailed information on the temperature tolerance of most species in Table I, but a simple comparison between families (Fig. 5) shows the marked contrast between the cold-water steno-therms (Coregonidae, Thymallidae, Salmonidae), mesotherms (Esocidae, most Cyprinidae, Gasterosteidae, Percidae, Anguillidae), and the warm-water eurytherms (Cyprinidae: carp, goldfish, grass-carp).
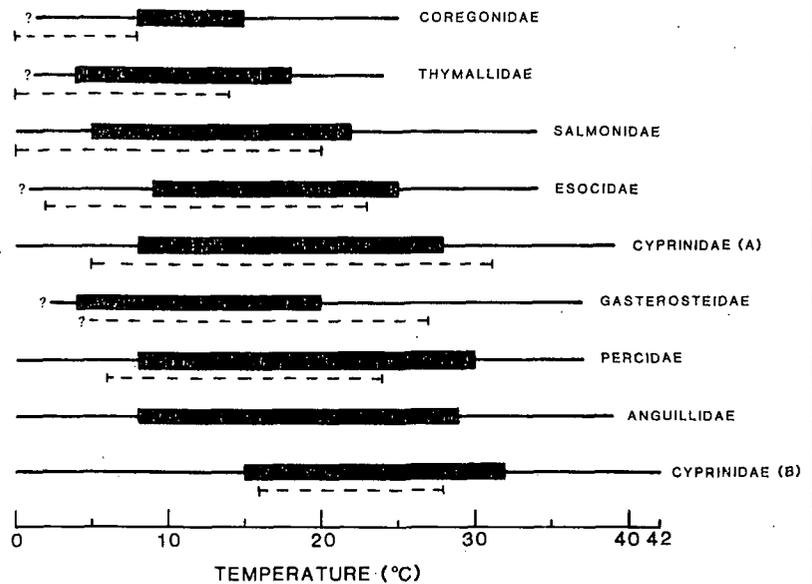
Fig. 5   Thermal tolerance of different families, using data for different species in Tables I and III: single line indicates upper and lower critical limits, solid bar indicates the optimum range, and broken line indicates the limits for development of the eggs (carp, goldfish and grass-carp constitute Cyprinidae B, all others in Cyprinidae A).

There is usually an inverse relationship between tolerance and resistance to thermal stress. Cold-water stenotherms have fairly low tolerance but high resistance (e.g. brown trout in Figs. 2, 3), whilst warm-water eurytherms usually have high tolerance but low resistance, i.e. the resistance time to temperatures outside the tolerance zone is very short (e.g. goldfish).

(c) Temperature Limits for Spawning and Egg Development

Information on the temperature range for spawning and the limits for egg development is summarized in Table III, and the tolerance ranges for the eggs of different families are compared in Fig. 5. It is obvious that the critical limits for successful spawning and egg development are narrower than those for older fish (see also Fig. 1). An extreme example is the desert pupfish with critical thermal limits of 2–44°C but a reproductive tolerance range of only 24–30°C (Shrode and Gerking, 1977; Gerking et al., 1979). Therefore, for most species, the eggs are more stenothermal than the juvenile or older fish and are the most vulnerable stage in the life cycle to the effects of thermal stress. These effects will influence not only the survival of the individual fish but also the ultimate survival of the population.

(d) Other Factors that may Affect Thermal Tolerance

Most workers agree that acclimation temperature and the period of exposure to temperatures outside the tolerance zone are the two most important factors that affect thermal tolerance and ultimately the lethal temperature for fish. There is less agreement over other factors, some of which are now considered. A full review is impossible because of lack of space and therefore only a selection of relevant examples can be given.

It is generally agreed that the egg is the critical stage for thermal stress (see previous section) but there is less agreement over a relationship between thermal tolerance and the age or size of the fish. Lack of any influence of size has been reported in the majority of studies, especially on upper temperature tolerance (see references in Brett, 1970). Smaller juvenile Pacific salmon (Oncorhynchus spp.) were more susceptible than larger juvenile fish to extremes of low temperature but not to high temperature (Brett, 1952). It has already been shown that values for brown trout in the size range c. 2–25 cm were not significantly different, but Spaas (1960) did find that as age and size increased, there was a corresponding increase in the upper lethal temperatures for brown trout and salmon, Salmo salar, with respective values close to 25°C and 28°C for alevins, 26°C and 29°C for yearlings and 29°C and 30°C for parr. These differences may be partially due to differences in experimental technique.

There may be seasonal variations in thermal tolerance and these variations are often related to changing photoperiod. Fish maintained on a long-day photoperiod may be more resistant to higher temperatures than those on a short-day photoperiod, e.g. goldfish (Hoar, 1956, 1965), carp (Roberts, 1961). Increased heat resistance under a long photoperiod and increased cold resistance under a short photoperiod may be of adaptive

TABLE III Summary of Usual Temperatures and Months for Spawning and Lethal Temperatures for Eggs of each Species (all Values to Nearest °C).

Species	Spawning range (°C)	Spawning months	Lethal for eggs Lower (°C)	Lethal for eggs Upper (°C)	No.	References
Coregonus lavaretus	0–4	October–January	c. 0	>8	3+	Bagenal (1970)
Thymallus thymallus	6–10	March–May	c. 0	>14	4+	Kokurewicz et al. (1980)
Salmo salar	0–8	October–January	c. 0	>16	3+	Peterson et al. (1977)
Salmo trutta	1–10	September–January	c. 0	>13	4	
Salmo gairdneri	4–19	October–March (May)	c. 0	>20	4+	Kwain (1975), Kaya (1977)
Salvelinus alpinus	3–15	September–April	c. 0	>8	0+	Frost (1965), Swift (1965a)
Salvelinus fontinalis	2–16	October–March	c. 0	>12	1+	Embody (1934), Needham (1961), Webster (1962), Hokanson et al. (1973)
Esox lucius	4–17	February–May	<2	>23	12+	Swift (1965b), Lillelund (1966)
Cyprinus carpio	12–30	May–July	<16	>26	6+	Sigler (1958), Swee and McCrimmon (1966)
Carassius carassius	16–18+	May–June			2	
Carassius auratus	17–24	May–July		>28	2+	Yamazaki (1965)

Species					
Barbus barbus	14–20	May–July	<14?	>20	3 + Hancock (1975)
Gobio gobio	c.12	May–June			1
Tinca tinca	18–27	May–July	<14	>31	6
Abramis brama	8–24	May–July	<8	>28	11
Alburnus alburnus	14–28	April–June	<14	>31	4
Phoxinus phoxinus	c.17–20	April–August			0 + Papadopol and Weinberger (1975)
Scardinius erythrophthalmus	14–28	April–June	<14	>31	7
Rutilus rutilus	5–22	April–June	<5	>27	14
Leuciscus cephalus	c.18	April–June	<16	>30	1
Leuciscus leuciscus	5–10+	March–May			3 + Kennedy (1969)
Gasterosteus aculeatus	12–18	April–June		>27	0 + Craig–Bennett (1931), Baggerman (1957), de Sylva (1969)
Perca fluviatilis	5–19	February–August	<6	>16	9 + Swift (1965b), Guma'a (1978), Hokanson (1977)
Stizostedion lucioperca	4–26	February–July	<9	>24	9 + Hokanson (1977)
Cottus gobio	7–14	February–June			0 + Fox (1978)
Ctenopharyngodon idella	c.20–30	May?–July	<20	>28	0 + Stott (1977), Timmermans (1978)

The number of references is given for each species, and references are given if they are not in Reichenbach-Klinke (1976) or Alabaster and Lloyd (1980).

value in temperate and polar regions (Hoar and Robinson, 1959; Tyler, 1966), but there are no really detailed studies on the seasonal effect or the extent to which changes in photoperiod can modify the lethal temperature. A clear demonstration of endocrine involvement is that the pituitary must be intact for a goldfish to acclimate to a higher temperature (Johansen, 1967). There may be also diel changes in thermal tolerance, similar to those shown by reptiles and amphibians (Hutchison, 1976), but there is no comparable evidence for fish, except that they may show diel changes in the "preferred" temperature (see Section V).

Thermal tolerance may be affected by diet and nutritional status, and varies in relation to levels of fats, cholesterol and phospholipids in the diet of goldfish (Hoar and Dorchester, 1949; Hoar and Cottle, 1952; Irvine et al., 1958). There is considerable evidence that thermal tolerance to high temperature is related to the reduction of free, body water (Fry, 1958). A high fat content and a low water content is usually indicative of fish in good condition. The "condition" of a fish (ratio of body mass to length^3) will therefore affect its thermal tolerance because fish in poor condition exchange heat more rapidly than those in good condition (Kubb et al., 1980).

Although two different rates of change in temperature (abrupt transfer and a slow change of $1°C\,h^{-1}$) had no obvious effects on the thermal tolerance of brown trout (cf. values in Table II), an increase from $1°C\,h^{-1}$ to $60°C\,h^{-1}$ increased the upper lethal temperature by about 4°C for juvenile coho salmon and young pumpkinseed fish, Lepomis gibbosus (Becker and Genoway, 1979), and an increase of $6°C\,h^{-1}$ to $60°C\,h^{-1}$ elevated the critical thermal maximum of bluegill, Lepomis macrochirus, by about 3°C (Cox, 1974). Most workers use constant acclimation temperatures in experimental studies, but there is some evidence that thermal tolerance and resistance increase if slightly fluctuating acclimation temperatures are used or there is a brief exposure to sublethal high temperatures (see references in Heath, 1963; Hutchison, 1976).

There may be geographical or genetic differences in thermal tolerance between populations of the same species, i.e. there may be physiological races (see references in Hart, 1952; McCauley, 1958). An example of the perils of assuming genetic differences is a study of a geothermal river where both brown and rainbow trout were apparently unaffected by daily maximum values of 28·8°C in summer (Kaya, 1977). The trout were therefore found at temperatures which are normally regarded as lethal (Table II), and it would have been easy to conclude that these populations were genetically different from other populations. However, it was later shown experimentally that the rainbow trout had not developed a greater resistance to high temperatures when they were compared with trout from two hatcheries (Kaya, 1978). Some of the apparent geographical variation in the thermal

tolerance of the same or closely related species, may be due to differences in experimental technique and acclimation temperatures (Brett, 1956). There may be also different interpretations of the same data. For example, Hall *et al.* (1978) concluded that the preference temperatures of three populations of white perch, *Morone americana*, were significantly different and thus provided an example of geographical variation in temperature response, but Mathur and Silver (1980) later showed that these apparent differences were not significant when the correct number of degrees of freedom was used in the analysis.

IV THERMAL STRESS WITHIN THE TOLERANCE ZONE

To obtain a complete picture of the possible effects of thermal stress, it is important to know how temperature affects the various functions of a fish. The most complete information is for sockeye salmon and Brett (1971) has collated information on 25 responses to temperature. A similar summary is now possible for 19 responses of brown trout (Nos 1–19 in Table IV). Tolerance and preference (Nos 1, 2, 3) were discussed in Sections II and III, but it is worth noting that the upper lethal temperature is the only response with an increase to an upper plateau. If the rather short response of lower lethal temperature is excluded, there are four responses with a continuous increase to a maximum, namely rate of gastric evacuation (No. 7), energy losses of fish deprived of food (No. 15), standard metabolic rate (No. 9) and maintenance energy intake (No. 13). The two latter aspects also determine the lower limits of the "scope for activity" and "scope for growth" respectively (Fig. 6c, d).

All the remaining responses show an increase with increasing temperature to maximum values at optimum temperatures, and then a decrease as temperature continues to increase. Feeding rate (No. 6) has the widest optimum range of 7–19°C, whilst both appetite, as measured by voluntary food intake, and satiation time (Nos 4, 5) have narrower ranges of 13–18°C (Figs 6a, b). The active metabolic rate, maximum energy intake and scopes for activity and growth (Nos 10, 11, 12, 16) all have maximum values at about 18°C (Figs 6c, d), but there is a lower optimum of about 15°C for the optimum energy intake (No. 14), i.e. the value that produces the greatest growth for the least energy intake at each temperature. Although the scope for growth is greatest at *c.* 18°C, the energy losses in the faeces and excretory products increase markedly with temperature and therefore the energy available for growth is greatest in the narrow range 13–14°C. This is the optimum temperature for growth of all sizes and ages of trout on maximum rations (No. 17), but the growth rates at all temperatures decrease with

TABLE IV Responses of Brown Trout to Temperature Increases (Information is from Table II for Aspects 1 and 2, from Coutant (1977), Reynolds and Casterlin (1979) for Aspect 3, and from Elliott (1972, 1975a, b, c, d, 1976a, b, c, 1979) for Other Aspects).

Function	No.	Fig.	Aspect	(a) Continuous increase to maximum (range in °C)	(b) Increase to optimum, then decrease (optimum in °C)	(c) Increase to upper plateau (Plateau range in °C)
Tolerance	1	3	Upper lethal temp.			25–30
	2	3	Lower lethal temp.	0–c.2		
Preference	3	—	Selected temp.		10–14	
Appetite + feeding	4	6a	Voluntary food intake		13–18	
	5	6b	Satiation time		13–18	
	6	—	Feeding rate		7–19	
Digestion	7	—	Gastric evacuation rate	4–19		?
Metabolism + growth	8	—	% energy intake		$14 \to 4$	
Metabolism	9	6c	Standard metabolic rate	4–20		
	10	6c	Active metabolic rate		c. 18	
	11	6c	Scope for activity		c. 18	
Energetics + growth	12	6d	Maximum energy intake		c. 18	
	13	6d	Maintenance energy intake	4–20		
	14	6d	Optimum energy intake		c. 15	
	15	—	Energy losses (starvation)	4–20		?
	16	6d	Scope for growth		c. 18	
	17	6e	Growth rate (max. rations)		13–14	
	18	6e	Growth rate (reduced rations)		$14 \to 4$	
	19	6f	Gross efficiency (all rations)		8–11	
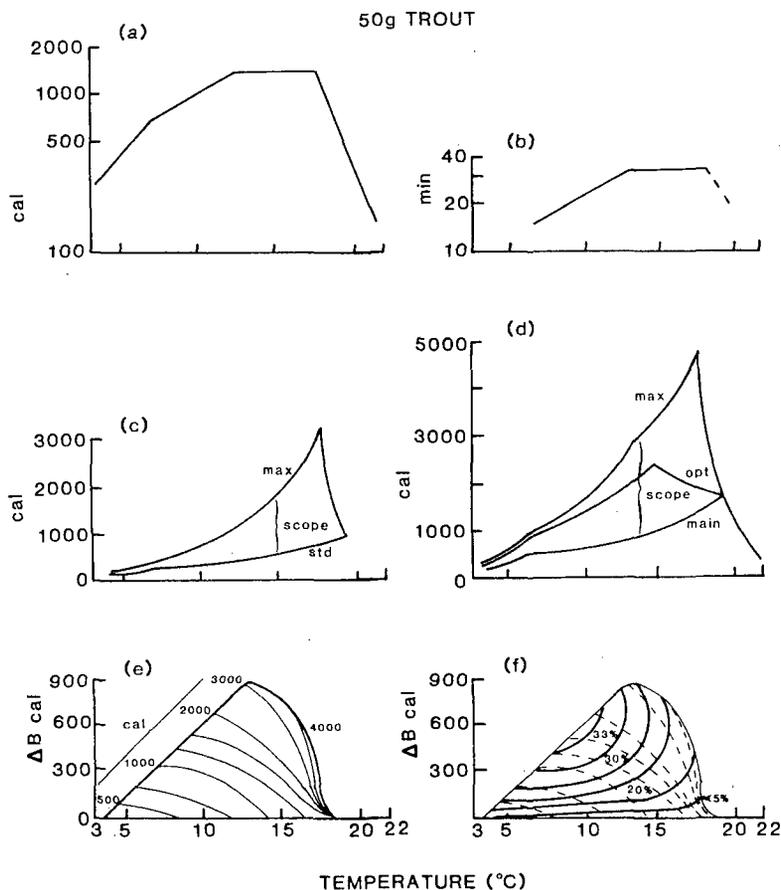
Fig. 6   Examples of some of the responses of brown trout (live weight 50 g) to temperature: (a) appetite (energy intake per meal); (b) satiation time (min); (c) daily energy requirements for standard (std) and active (max) metabolic rates with scope for activity; (d) maintenance (main), optimum (opt) and maximum (max) energy intake with scope for growth; (e) energy available for growth (ΔB) for different levels of energy intake (C cal day^{-1}); (f) gross efficiency isopleths (%).

increasing size and age (Elliott, 1979). When the energy intake (ration level) is reduced progressively, there is a corresponding reduction in the optimum temperature for the maximum growth rate (No. 18) and for the proportion of the energy intake available for growth and metabolism (No. 8). There is also a reduction in the upper temperature at which growth occurs, e.g. range for growth in 50 g trout is about 4–19°C on maximum rations but only about 4–8°C at a ration of 500 cal day^{-1} (Fig. 6e). The lowest optimum temperature range is for gross efficiency (energy for growth as a percentage of energy

intake) at all ration levels (No. 19). For 50 g trout, gross efficiency exceeded 33% in the range 8–11°C and then decreased with both increasing and decreasing values for temperature, energy intake and energy available for growth (Fig. 6f).

Although this brief summary of temperature effects on brown trout is no substitute for the detailed descriptions in the original publications, it does show that the form of the response to temperature and the optimum temperatures are not always the same for different functions, and that the optimum temperature for the response may change if there is a change in another factor such as energy intake. Some of these responses can be used to illustrate the subtle effects of stress within the tolerance zone, but some further concepts of stress must first be defined.

Fry (1947, 1971) classified environmental effects into five groups of factors: lethal, controlling, limiting, masking and directive. This approach was followed by Brett (1958) who divided stresses on fish into four categories: lethal (self-explanatory), limiting (restriction in the supply of essential metabolites or interference with the chain of energy release), inhibiting (reduction in the ability of the fish to carry out its normal functions, and hence a reduction in its probability of survival), and loading (an undue burden on the fish with a rapid or steady release of energy). Limiting, inhibiting and loading stresses may also be lethal when they continue over a long period.

The effects of temperature as a lethal stress outside the tolerance zone have been discussed in detail in Section III. An example of temperature as an inhibiting stress is cessation of feeding and this has also been discussed in Section III. Temperature limits for feeding at the normal rate were used to construct a feeding zone within the tolerance zone (Fig. 3). The range between the feeding limit and the incipient lethal level is the "zone of resistance to starvation", using a concept similar to that for the zone of thermal resistance, and the resistance time to death within this starvation zone is also a function of temperature (see No. 15 in Table IV), and the size and body composition of the fish (Elliott, 1975d, 1976a, b). Another example of temperature as an inhibiting stress is the limited range for spawning (Table III). Outside this range, temperature may be acting as an inhibiting stress by affecting the normal endocrine balance necessary for spawning (Brett, 1958).

The best example of temperature as a loading stress is the limit for growth and activity. In brown trout on maximum rations, growth occurs between 4°C and 19°C, and the lack of energy for growth outside this range is due to a combination of reduced energy intake, high energy losses in waste products, high metabolic demands above 19°C and perhaps the inhibition of metabolism below 4°C. These limits were used to construct a growth zone within the

feeding zone (Fig. 3). Thermal stress can continue even within this growth zone when there are also limiting stresses, e.g. reductions in oxygen concentration, enzyme substrates, nutrients and essential ions (see review of Fry, 1971). It has already been shown that when the food supply is reduced, both the optimum temperature and temperature range for growth are reduced (Fig. 6e). These changes are due to the combined effects of two stresses: the limiting stress of reduced energy intake and the loading stress of temperature. As the energy intake is reduced, there is a marked decrease in the upper limits of the growth zone (Fig. 3).

These examples have shown that thermal stress is not only lethal outside the tolerance zone, but can also act subtly within the tolerance zone as an inhibiting stress, a loading stress, or a loading stress in conjunction with other limiting stresses. All these effects are within the definition of thermal stress in the introduction and show that thermal stress can affect most functions of a fish.

V BODY TEMPERATURE AND THERMOREGULATION

Body temperature is usually less than $0.6°C$ above water temperature but the excess body temperature usually increases slightly as a function of fish size and weight (Stevens and Fry, 1970, 1974; Spigarelli et al., 1974). For example, body temperatures of brown trout were measured with a thermistor (precision at least $0.05°C$, see Mortimer and Moore, 1970) inserted 1–2 cm inside the anal aperture. The measurements were made within 30 s of the removal of the fish from the water. Mean values ($\pm$SE) for samples of 10 trout kept at $15°C$ or $6°C$ were $15.07 \pm 0.02°C$ and $6.07 \pm 0.02°C$ for trout with a mean length of 10 cm (live weight 10–12 g), $15.12 \pm 0.02°C$ and $6.13 \pm 0.02°C$ for 15 cm trout (37–40 g), $15.28 \pm 0.03°C$ and $6.25 \pm 0.03°C$ for 25 cm trout (175–185 g). Other workers have measured body temperatures by implanting thermistors or using miniature transmitters that are small enough to be swallowed (see review by McCauley, 1977).

Rates of thermal equilibration in body temperature following a change in water temperature are affected by many factors, including rates of gill ventilation and blood flow, circulatory anatomy, water movement and the shape, size and activity of the fish (see references in Crawshaw, 1977; Kubb et al., 1980). Between 70 and 90% of the heat transfer occurs through the body wall, rather than the gills, and body diameter, insulation thickness and tissue thermal conductivity are the chief factors affecting heat transfer. It is therefore not surprising that rates of heat exchange are generally related to body size and weight.

These changes are illustrated by original data for brown trout in three size groups with mean lengths of 10 cm, 15 cm, 25 cm (see above for weight ranges). Ten fish in each size group were transferred abruptly from 15°C to 6°C or the reverse, and one fish was then removed every minute after the transfer so that ten measurements of anal temperature were made with a thermistor. The temperature difference (ΔT°C) between body temperature and water temperature decreased exponentially with time for both cooling (15 to 6°C) and warming (6 to 15°C), but the exponential rate was not the same for the two processes nor for the different size groups (Fig. 7a, b). The exponential relationship follows Newton's law of cooling and has been used by other workers (e.g. Stevens and Fry, 1970, 1974).

As the mean temperatures of the trout in each size group were already known for water temperatures of 15°C and 6°C (see above), exponential rates of change in body temperature were estimated for each fish (R°C per min per ΔT°C, where $R = (\log_e \Delta T_t - \log_e \Delta T_0)/t$ and ΔT_0 and ΔT_t were the temperature differences at the beginning and end of a period of t min). When the values of R for the three size groups and a small number of trout of intermediate weights were plotted against the live weight (W g) of the fish (Fig. 7c), the relationship between the two variables followed a power law with a negative exponent ($R = aW^{-b}$ where a and b are constants). The rate of cooling was clearly lower than the rate of warming for trout of similar weight, and both rates decreased as the weight of the trout increased (for cooling: $a = 1 \cdot 862$, $b \pm 95\% CL = 0 \cdot 390 \pm 0 \cdot 033$, $r^2 = 0 \cdot 95$, $n = 32$; for warming: $a = 2 \cdot 290$, $b \pm 95\% CL = 0 \cdot 375 \pm 0 \cdot 025$, $r^2 = 0 \cdot 97$, $n = 30$). These relationships can be used to estimate the time taken to reach thermal equilibrium for trout of different weights exposed to different changes in temperature. Sudden changes in water temperature rarely exceed 2°C but may be as high as 5–7°C when a thermal discharge enters a river, or as high as 10°C when a fish crosses the thermocline in a stratified lake. If trout are exposed to these changes within the extremes of 2°C to 10°C, the time taken to attain thermal equilibrium is only 3–6 min for 10 g trout, but about 7–15 min for 100 g trout, and about 23–35 min for cooling and 18–27 min for warming in 1000 g trout. Other workers have also found that the internal temperature of smaller fish (<100 g) changes rapidly, usually in less than 10 min, to the ambient temperature whereas larger fish may require over an hour (Spigarelli et al., 1974; Kubb et al., 1980). Several studies have also shown that rates of heat exchange are usually higher for warming than for cooling, at least in larger fish (McCauley and Huggins, 1976; Reynolds, 1977; Beitinger et al., 1977). Some physiological changes may be responsible for this difference, e.g. circulatory rates may decrease with cooling and thereby reduce the rate of heat exchange across the gills.
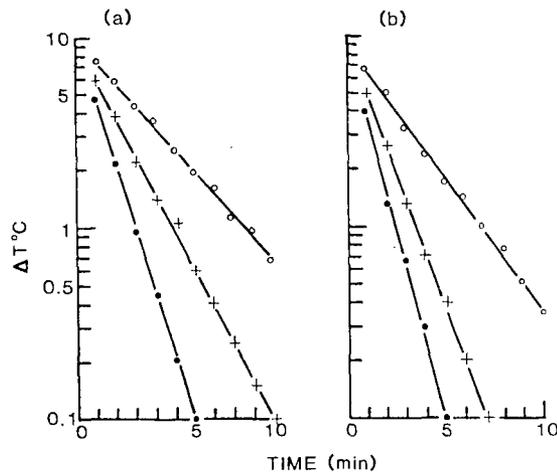
Fig. 7a, b Relationship between the temperature difference ($\Delta T°C$ = difference between body and water temperatures) and time (min) for brown trout subjected to (a) cooling (15 to 6°C) and (b) warming (6 to 15°C); mean lengths of trout were 10 cm (●), 15 cm (+) and 25 cm (O).
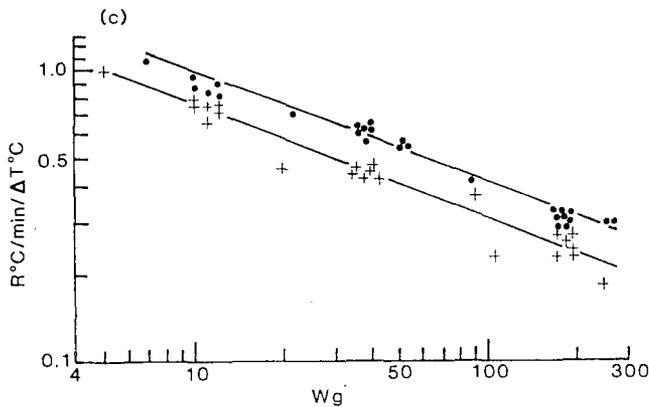
Fig. 7c Relationship between the exponential rate of change in body temperature ($R°C$ per min per $\Delta T°C$) and the live weight of brown trout (Wg) subjected to warming (●) and cooling (+).

Rates of change in body temperature are important because they determine the time lag in thermal equilibration. This time lag increases as fish weight increases and therefore the short-term fluctuations in the body temperature of larger fish are less than temperature fluctuations in the surrounding water. For example, gut temperatures of 200 g rainbow trout

remained within $16 \pm 0.5°C$ whilst water temperatures varied continuously within about 13·5–18·5°C (McCauley and Huggins, 1976). Thus, the body temperatures of larger fish are independent of small and rapid fluctuations in water temperature. Freshwater teleosts do not show any physiological thermoregulation by local conservation of muscular heat as seen in tunas and lamnid sharks (Fry and Hochachka, 1970; Stevens and Neill, 1978), but there may be a limited control of heat exchange by a restriction of blood circulation through the gills (Fry and Hochachka, 1970).

The only other mechanism available to a freshwater fish is behavioural thermoregulation. Fish can detect temperature changes of less than 0·5°C (Murray, 1971) and are able to select a particular temperature or range of temperatures. The concept of "selected" or "preferred" temperatures has already been discussed in Section II. A spectacular demonstration of temperature preference is the work of Rozin and Mayer (1961) who trained goldfish to press a lever and cause a fall in water temperature when it was too warm. Thus, the goldfish maintained their environmental temperature at about 34°C and their precision was similar to that achieved by a rat in a similar experiment. Thermoregulatory behaviour has not been adequately studied in many species and is not well understood (see reviews of Fry and Hochachka, 1970; Richards et al., 1977). It is remarkable that several species show diel rhythms of preferred temperature, e.g. goldfish (Reynolds, 1977; Reynolds et al., 1978), brown trout (Reynolds and Casterlin, 1979), but other species do not, e.g. striped bass, Morone saxatilis (Coutant and Carroll, 1980). These rhythms may be related to varying temperature optima for different physiological functions (see Section IV). The diel migration of sockeye salmon smolts into deep, cold water may be due to a lower ration level and hence a lower optimum temperature for growth (Brett, 1971). Brown trout of 50 g live weight will not grow on a daily energy intake of about 1000 cal at 14·5°C, but growth will be about 350 cal day^{-1} for the same energy intake at 8°C (Fig. 6e). Therefore trout may also move into colder water, especially in lakes, when the food supply is reduced (Elliott, 1979). Both these examples show that thermoregulatory behaviour is one of the chief factors responsible for fish movements, but a discussion of fish movements in relation to temperature is beyond the scope of this contribution.

VI   GENERAL CONCLUSIONS

This account has shown that a fish is subjected to a hierarchy of thermal stresses, ranging from lethal effects outside the tolerance zone to inhibiting and loading effects within the tolerance zone. The fish can counteract these

effects by resistance, acclimation with metabolic adjustment, and thermo-regulation chiefly by behaviour. There is clearly a need for more complete studies on the effects of temperature on various functions connected with feeding, metabolism and growth. It is also important to know more about the thermal requirements of different species in the field and the critical limits for all forms of thermal stress. Although they have not been discussed in the present contribution, fish movements and the synergistic effects of temperature in conjunction with other stresses are clearly important aspects of thermal stress. Effects at the population and community levels are probably the least understood aspects of thermal stress and are probably the most important in relation to the impact of man's activities on the freshwater ecosystem.

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