THE INFLUENCE OF HYPOXIA ON THE PREFERRED TEMPERATURE OF RAINBOW TROUT *ONCORHYNCHUS MYKISS*

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Summary

The behavioural thermoregulation of rainbow trout *Oncorhynchus mykiss* was investigated in a shuttlebox at normoxia and at three levels of hypoxia: 13.3, 9.3 and 5.3 kPa. The final preferred temperatures at normoxia, and at 13.3, 9.3 and 5.3 kPa, were 16.1, 14.9, 15.0 and 12.7°C, respectively. A decreased rate of metabolism and an increased blood oxygen-affinity are among the physiological advantages of selecting a lower temperature during hypoxia. It is suggested that catecholamines may play a part in controlling temperature selection during hypoxia. In natural environments, this behaviour may result in habitat shifts of fish living in heterothermal environments with changing oxygen tensions.

Introduction

Fish placed in a temperature gradient will initially select temperatures that depend on the acclimation temperature. The selected temperature during the first 2 h in the gradient is termed the acute preferred temperature. If left in the gradient for a longer period, usually 24 h (Reynolds and Casterlin, 1980), the fish will select a species-specific preferred temperature. This temperature is termed the final preferendum and is defined by Fry (1947) as 'the temperature at which the individuals will ultimately congregate regardless of their thermal experience before being placed in the gradient, and at which acclimation temperature and acute preferred temperatures are equal'. Usually the selected temperature consists of a range of temperatures bounded by an upper and lower avoidance temperature, so the final preferendum is actually a statistical measure of central tendency in the temperature distribution (Reynolds and Casterlin, 1979).

Recently, the acute preferred temperature for fish (Bryan *et al.* 1984) has been shown to decrease as a result of exposure to hypoxia. Similar results were obtained in reptiles (Hicks and Wood, 1985), salamanders and crayfish (Dupré and Wood,

1988). These animals were tested for 8–24 h in hypoxia, but the authors did not discuss whether these results represent acute or final preferred temperatures. In the terrestrial environment the oxygen pressure (P_{O_2}) is rather stable, whereas it may be labile in aquatic environments. Thus, especially for aquatic ectotherms, this behaviour could be important.

Bryan *et al.* (1984) concluded that the acute preferred temperature for the plains minnow *Hybognathus placitus* decreased when the water oxygen content was lower than $5 \, \text{mg} \, \text{l}^{-1}$. To show this, they placed the fish in a tube, in which a horizontal temperature gradient ranging from 13 to 36°C, as well as the pre-set water oxygen content, was established within 45 min. The acute preferred temperature was determined during the following 30 min. During experiments with dissolved oxygen concentrations below $6 \, \text{mg} \, \text{l}^{-1}$, the oxygen content was the same throughout the gradient. Owing to the temperature-dependent solubility of gases in water, there must have been a gradual increase in oxygen tension from the cold to the warm end of the gradient of approximately 50 %. Since the driving force in the exchange of respiratory gases is the difference in their partial pressures, the question may be raised as to whether the selected temperature was influenced by the oxygen tension gradient. Furthermore, the fish were not acclimated to experimental hypoxia, which raises another question as to whether hypoxia-acclimated fish would respond in the same way. If they do, not only the acute preferred temperature but also the final preferendum may depend on the water oxygen tension (P_{O_2}). This could be of biological significance for fish inhabiting water with changing P_{O_2} and temperature.

The aim of the present study was to investigate whether the final preferendum as well as the upper and lower avoidance temperatures are influenced by the oxygen tension of the water.

Materials and methods

Rainbow trout, *Oncorhynchus mykiss* (Walbaum), of body mass 100–220 g and acclimated to 18°C and a 12 h:12 h light/dark cycle, were allowed to thermoregulate in an electronic shuttlebox (Fig. 1), a modification of the system described by Neill *et al.* (1972). It consists of two chambers, each $50 \, \text{cm} \times 50 \, \text{cm}$, connected by a 40 cm long tube with a diameter of 10 cm. The water depth in the chambers was approximately 20 cm. The temperature difference between the chambers was always kept at 2°C, and a smooth temperature gradient existed in the connecting tube. When a fish was in the 'warm' section, both sections were continuously heated. Likewise, when the fish swam to the 'cold' section, both sections were cooled. Each passage was registered by two photocells, which initiated either cooling or heating, depending on the sequence of triggering. By shuttling between the chambers the fish could regulate the ambient temperature and, thereby, its own temperature.

The temperature in the chamber that the fish left, as well as the time, was recorded by a computer. Furthermore, the temperatures of the two chambers, a
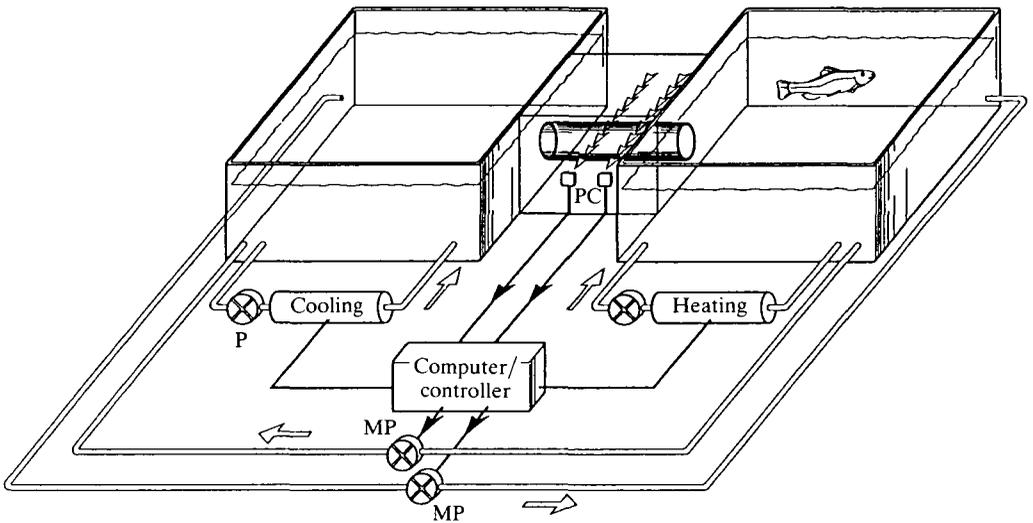
Fig. 1. The shuttlebox in which the fish could regulate ambient and, thereby, its own temperature. The two chambers were connected by a tube. The water was recirculated in both chambers by the pumps (P). Cooling took place in a heat exchanger by pumping fluid at −15°C countercurrent to the recirculating water from the 'cold' section. Heating was accomplished by leading the recirculating water from the 'warm' section through a heated water bath; it was turned off by shunting it through a bypass. The mixing pumps (MP), controlled by the computer, maintained a constant temperature difference of 2°C between the two chambers. Passage in the tube was registered by two photocells (PC). If the fish swam from the warm to the cold section, the heating was turned off and the cooling on, and *vice versa*.

calculated fish temperature (see below) and the oxygen tension of the water were recorded by the computer every minute.

Experimental procedure

The fish was introduced into the shuttlebox containing air-saturated water at 18°C. The light/dark cycle was the same as in the holding tank. The fish was allowed a 1-day period of acclimation to the shuttlebox. After the acclimation period, the fish was allowed to thermoregulate for 1 day at each of the following oxygen tensions: normoxic (P_{O_2}>20 kPa), 13.3, 9.3 and 5.3 kPa. The shift in oxygen tension was made 1 h before the light was switched off, and the new P_{O_2} was established in approximately 45 min. Four out of 15 fish did not 'learn' to thermoregulate and were thus omitted.

Oxygen tension

The oxygen tension was measured with a Radiometer PHM 72 acid–base analyzer and a Radiometer oxygen electrode (E-5046). Since the electrode is temperature sensitive, the measurements of oxygen tension could not be made

directly in the chambers, where the temperature fluctuated. Instead, it was thermostatted in a cuvette at 25°C, and a constant flow of water was maintained past the electrode by a roller pump. The measured oxygen tension was corrected by the computer to the actual water oxygen tension. The computer used the corrected value to regulate oxygen tension by triggering the addition of pure N_2 or air into the recirculating water.

The oxygen tension was measured in the warm section of the shuttlebox. Control measurements of the oxygen tension in the cold section showed that the actual oxygen tensions in the two sections never differed by more than 0.4 kPa.

Fish temperature

With a few exceptions, fish have a body temperature that deviates little from the ambient temperature if the latter is stable (Stevens and Fry, 1970, 1974; Stevens and Sutterlin, 1976). The core temperature of a fish in a heterothermal environment is dependent on the thermal history of the fish. Reynolds et al. (1976) concluded that the core temperature of a fish in a shuttlebox does not differ significantly from the mean water temperature. A better estimate of the temperature of the fish may be obtained by using Newton's law of cooling. This states that the instantaneous rate of temperature change is proportional to the difference between ambient and body temperature:

$$T_b = T_a + (T_i - T_a)e^{-kt},$$

where T_b is body temperature, T_a is ambient temperature, T_i is initial body temperature, t is time (min) and k is the rate of temperature change (degrees min^{-1}). Values of $k = 3.32W^{-0.536}$, where W is body mass in grams, given by Stevens and Sutterlin (1976), for cooling rates of the sea raven Hemitripterus americanus, were used.

Data sampling

The fish were usually most active during the light period, and the fluctuations in fish temperature were smallest during this period (Fig. 2). Hence, the data are collected from 2 h after the light was turned on until 2 h before it was switched off. After a change in oxygen tension, the fish were thus allowed 15 h of acclimation before data collection started.

Data handling

If the preferred temperature is given as a single value, the central tendency described as mode, mean or median selected temperature is usually used. It can be argued that the mode temperature fits the definition of final preferendum (Fry, 1947) best, as it is the temperature most frequently occupied by the fish. Fig. 3 shows that the mode temperature is not always distinct. If the temperature distribution shows a broad plateau, the mode may be altered by changing the class intervals of the distribution. The mean preferred temperature is affected by
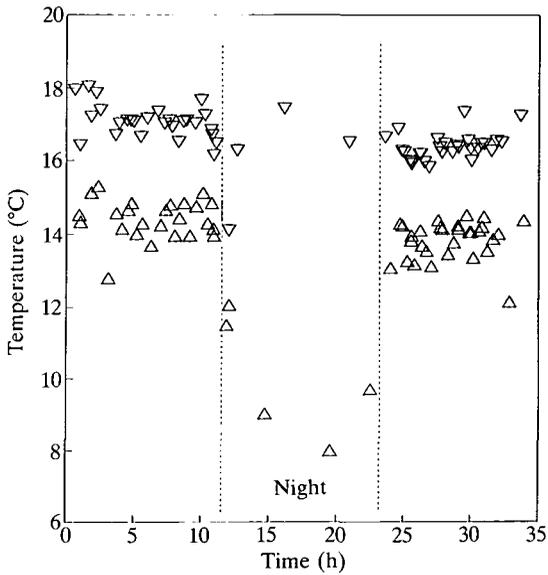
Fig. 2. An example of diurnal rhythm in thermoregulatory behaviour. The figure shows the ambient water temperature when the fish left the warm (∇) and the cold ($\triangle$) sections of the shuttlebox. The fish thermoregulated most actively during the day.
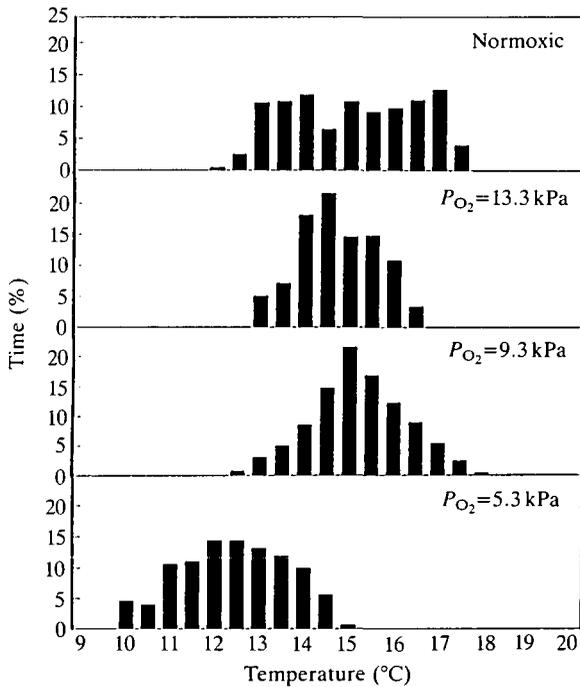

Fig. 3. An example of the temperature distributions for a fish thermoregulating at normoxia ($P_{O_2} > 20$ kPa) and oxygen tensions of 13.3, 9.3 and 5.3 kPa (fish 8).

Table 1. *Mean of median upper (UAT) and lower (LAT) avoidance temperatures, the final preferendum (temppref), given as mean of median preferred temperatures, and the occupied temperature range, at normoxia (P_{O_2}>20 kPa) and oxygen tensions of 13.3, 9.3 and 5.3 kPa*

| P_{O_2} (kPa) | N | Mean of median temperature (°C) | | | Temperature range (°C) | |
		LAT	UAT	Temppref	Maximum	Minimum
20.0	11	15.6±1.1	16.3±1.1	16.1±1.1	13.3±1.1	18.9±1.3
13.3	9	14.1±2.3	15.1±2.2	14.9±1.9	12.1±2.7	18.6±1.8
9.3	10	14.1±2.6	15.6±2.2	15.0±1.9	11.6±2.9	18.1±2.2
5.3	7	11.8±2.7	12.6±3.2	12.7±2.8	10.3±2.4	15.6±2.9

Standard errors (S.E.) are given for each value.

extreme or unusual values and might distort the picture if the distribution is skewed.

Since the distribution of selected temperatures in the present study was sometimes skewed, sometimes normally distributed and sometimes showed a broad plateau, the median selected temperature was chosen as a measure of the final preferendum of the fish (Table 1).

The upper and lower avoidance temperatures are described by the medians of the upper and lower turnaround temperatures (Neill and Magnuson, 1974). Furthermore, the temperature range is given to complete the picture (Table 1).

Statistics

The medians of the selected temperatures and the medians of the upper and lower avoidance temperatures for different P_{O_2} values are compared in a Wilcoxon–Mann–Whitney test (Siegel and Castellan, 1988).

Results

The results of experiments with 11 fish are shown in Table 1. In general, the experimental procedure described above was followed. Some data at lower P_{O_2} values are missing, however, as a result of inactivity or the inability of the fish to thermoregulate. During this period of inactivity the fish usually stayed in the cold chamber. The possibility exists that these fish selected the lowest possible temperature, but a more likely explanation is that the stressing effect of hypoxia caused the inactivity. For technical reasons, fish 7 and 9 were not tested at 13.3 kPa.

Fig. 4 shows the mean final preferendum, the mean upper and lower avoidance temperatures, and the mean temperature range at normoxia and at oxygen tensions of 13.3, 9.3 and 5.3 kPa. The mean normoxic final preferendum is 16.1°C, which is in accordance with values given by other investigators for rainbow trout
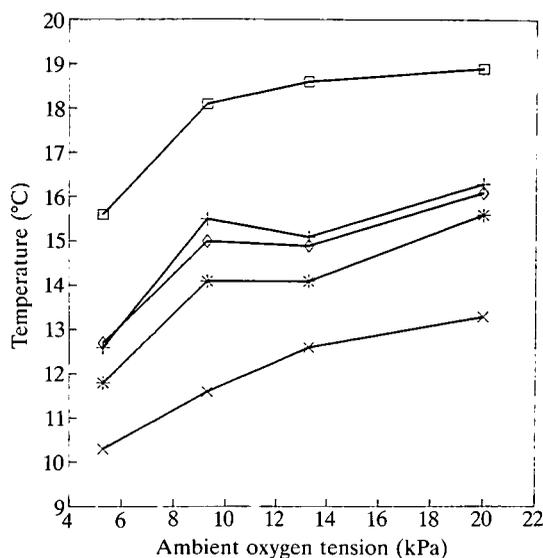
Fig. 4. The temperature range (□×), upper (+) and lower (*) avoidance tempera-tures and the final preferendum (◇) at normoxia (P_{O_2}>20 kPa, N=11) and at oxygen tensions of 13.3 (N=9), 9.3 (N=10) and 5.3 (N=7) kPa. The graph shows the mean of absolute maximum and minimum temperatures, the mean of median upper and lower avoidance temperatures, and the mean median temperatures.

(Garside and Tait, 1958; Javaid and Anderson, 1967; McCauley and Pond, 1971; Cherry *et al.* 1975; McCauley *et al.* 1977; Spigarelli and Thommes, 1979).

The final preferenda for 13.3, 9.3 and 5.3 kPa are 14.9, 15.0 and 12.7°C, respectively. The final preferendum at 5.3 kPa was significanly lower than those at normoxia, 13.3 kPa and 9.3 kPa (P<0.001, P<0.025 and P<0.025, respectively). There was no significant difference between the final preferenda at normoxia, 13.3 and 9.3 kPa.

The mean median upper avoidance temperatures for normoxia, 13.3, 9.3 and 5.3 kPa were 16.3, 15.1, 15.6 and 12.6°C, respectively. The upper avoidance temperature for 5.3 kPa was significantly lower than those for normoxia, 13.3 and 9.3 kPa (P<0.001, P<0.025 and P<0.01, respectively).

The mean median lower avoidance temperatures for normoxia, 13.3, 9.3 and 5.3 kPa were 15.6, 14.1, 14.1 and 11.8°C, respectively. The lower avoidance temperature at 5.3 kPa was significantly lower than those at normoxia, 13.3 and 9.3 kPa (P<0.001, P<0.025, and P<0.05, respectively). For the upper as well as the lower avoidance temperatures there were no significant differences between normoxia, 13.3 and 9.3 kPa.

Two different control experiments were performed. (1) In two experiments, normoxia was re-established after exposure to hypoxia. In one of these, the experimental and post-experimental normoxic selected temperatures were the same. In the other, the post-experimental normoxic selected temperature was
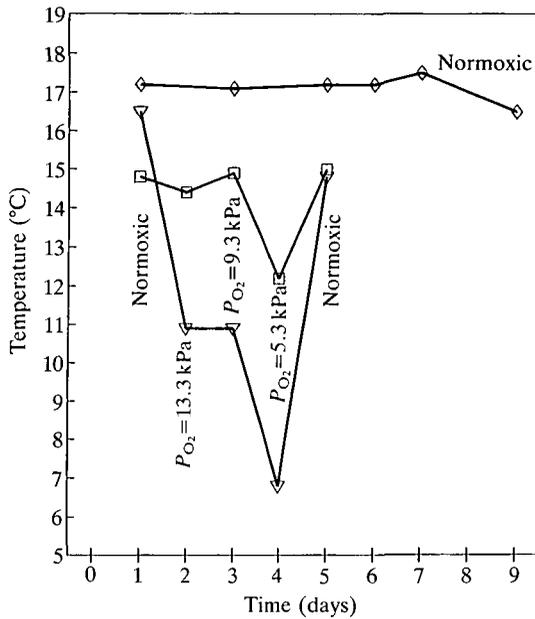
Fig. 5. The uppermost curve (◇) shows the median temperatures for a fish thermoregulating for 9 days at normoxia without being fed. There was no significant change in selected temperature during the 9 days of starvation. The other two curves are for fish 8 (□) and 10 (▽) and show the median temperatures at normoxia (day 1), 13.3 kPa (day 2), 9.3 kPa (day 3), 5.3 kPa (day 4) and normoxia (day 5).

lower than the experimental normoxic selected temperature, but substantially higher than the selected temperature at 5.3 kPa (Fig. 5). (2) One fish was allowed to thermoregulate for 9 days at normoxia to determine the effect of starvation. During this period the median selected temperature did not change (Fig. 5).

Discussion

Bryan *et al.* (1984) found that the acute selected temperature for plains minnows decreased from 30°C at normoxia to 17°C at a water oxygen content of $2 \, mg \, l^{-1}$, which corresponds to an oxygen tension of 4.3 kPa. The decrease in selected temperature in hypoxia in the present study is smaller. Although it is not the same species, we conclude that hypoxia exerts a stronger influence on the acute preferred temperature than on the final preferendum. This might be explained by the difference in hypoxia acclimation status of the fish in the two experiments. Bryan *et al.* (1984) exposed their fish to the final level of hypoxia within 45 min and measured the temperature response immediately afterwards. In the present experiment, the fish were also exposed to hypoxia over a period of 45 min, but they were allowed 15 h of acclimation before data sampling started. Furthermore, the deepest hypoxia in this experiment was reached over 4 days, compared to a change

from normoxia to hypoxia within 45 min in all the experiments of Bryan *et al.* (1984), regardless of the degree of hypoxia.

In general, the final preferendum, at least in a normoxic environment, corresponds to the optimum temperature for several physiological functions. The consequences of selecting a lower temperature include decreases in maximum swimming speed, growth rate, food intake and digestion rate (Brett, 1971) as well as changes in enzyme and structural protein composition, membrane structure, acid–base regulation and osmotic balance (Reynolds and Casterlin, 1980).

There are at least three reasons why it is of physiological advantage to select a lower temperature in a hypoxic environment: (1) metabolic rate decreases because biochemical reactions are slower at lower temperatures. If Q_{10} is 2.5, decreases in temperature of 2 and 4 °C will cause decreases in oxygen consumption of 17 and 31 %, respectively (Fig. 6). (2) Consequently, assuming that oxygen extraction from the water *via* the gills is unchanged, the ventilation volume would decrease by 17 and 31 %, respectively, when the temperature was decreased by 2 and 4 °C (Q_{10}=2.5) (Fig. 6). However, the solubility of oxygen in water increases by about 2.1 % degree^{-1} as temperature decreases. Thus, as the inspired oxygen tension is constant and, assuming a constant decline in oxygen tension from inspired to expired water, the oxygen extraction *via* the gills increases as temperature decreases. This will further reduce the ventilatory requirement. As ventilation volume increases during hypoxia (Randall, 1982) and as the branchial pump has a maximal capacity (Farrell and Steffensen, 1987), this might enhance survival for a fish in a hypoxic environment. (3) The blood oxygen-affinity is higher, for at least three reasons. First, as a direct effect, a decrease in temperature will increase the blood oxygen-affinity (Riggs, 1970). Second, the blood pH, and thereby oxygen-
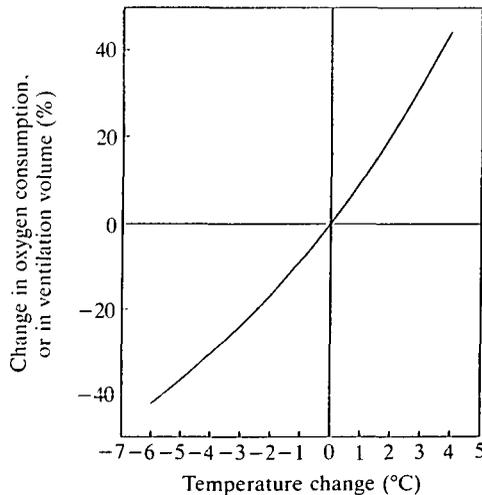

Fig. 6. The relationship between a change in temperature and the concurrent change in oxygen consumption, or ventilation volume, assuming constant oxygen extraction and that Q_{10} is 2.5.

affinity, increases when the temperature decreases (Albers, 1970). Third, as a response to hypoxia, the concentrations of GTP and ATP in the red blood cells decrease, causing an increase in oxygen-affinity (Weber *et al.* 1976; Boutilier *et al.* 1988). All these factors contribute to an increase in oxygen affinity.

Possible mechanisms involved

Wollmuth *et al.* (1987, 1988) showed that injections of noradrenaline into the forebrain of goldfish *Carassius auratus* led to a consistent dose-dependent decrease in selected temperature. Boutilier *et al.* (1988) measured the concentrations of adrenaline and noradrenaline in arterial plasma of rainbow trout acclimated to various oxygen tensions. The concentrations of these catecholamines increased as oxygen tension decreased. The observations of these authors suggest that catecholamines may be involved in regulating the influence of hypoxia on thermal preference.

Ecological implications

Fish raised under hypoxic conditions have reduced growth rates (Brett and Blackburn, 1981). Thus, in an ecological sense, oxygen fits the definition of a resource as 'any substance or factor which can lead to increased growth rates as its availability in the environment is increased, and which is consumed by an organism' (Tilman, 1982). In behavioural ecology, optimality theory assumes that an organism will maximize the net rate of resource uptake or minimize the cost of obtaining a required amount of that resource (Kramer, 1987). As already discussed, fish can do this by selecting colder water when the environment becomes hypoxic.

In an aquatic environment fluctuations in oxygen tension occur frequently. Factors such as photosynthesis, respiration, temperature fluctuations, stagnation of the water body, ice cover and eutrophication contribute to this. Kramer (1987) describes four principal categories of behavioural responses to reduced ambient oxygen availability: (1) a change in activity, (2) an increased use of air-breathing, which is only possible for some species, (3) an increased use of aquatic surface-breathing and (4) vertical and horizontal habitat changes. The present investigation concerns the fourth category, and provides further information on this. Kramer (1987) does not discuss the possible advantage of movement to habitats with colder water.

The distribution of temperatures in an aquatic environment (the thermal structure) provides habitats that are important to fish distribution (Coutant, 1987). The results of this investigation show that hypoxia alters the thermal behaviour of the fish and that warmer areas of the water body would be avoided as a result of hypoxia. If hypoxia were persistent, as a result of eutrophication, this effect could be pronounced. The consequences of a habitat shift could, for example, be depletion of food resources and/or disturbance of the ecological equilibrium, such as predator–prey interactions (Coutant, 1987; Kramer, 1987). This experimental situation is, of course, not to be compared with a natural situation, and the

question of whether fishes in natural environments behave as predicted by this investigation remains unanswered.

It is difficult to quantify the energetic benefit of selecting a lower temperature when exposed to hypoxia. Measurements of the activity level at different oxygen tensions of a thermoregulating fish would provide more information concerning the daily energy budget of the fish. As the spontaneous swimming activity is reduced during hypoxia (Metcalfe and Butler, 1984), the fish save more energy than can be predicted from the simple Q_{10} calculations used above.

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