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## The effect of fasting and refeeding on temperature preference, activity and growth of roach, *Rutilus rutilus*

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**Abstract** Most fish species are regularly subjected to periods of starvation during which a reduction of energy turnover might be favourable for the animal. This reduction of energy flux may be achieved by changes in thermal behaviour and/or swimming activity. We investigated such behavioural changes during starvation and subsequent refeeding in roach, *Rutilus rutilus*, with respect to energetic benefits and growth maximisation. Roach, acclimated to a wide range of temperatures (4, 12, 20, 24, 27 and 30 °C), were fed to excess, subjected to 3 weeks of starvation and subsequently refed in order to determine the temperature dependence of feeding rates, growth rates and conversion efficiency ( $K_1$ ) under control conditions and during compensatory growth. When exposed to a thermal gradient, control animals preferentially selected a temperature of  $26.8 \pm 0.9$  °C, which is in the range of the optimal temperatures for feeding, growth and conversion efficiency. Starving fish showed a distinct circadian pattern of the mean selected temperature (MST). They migrated to cooler water in the dark ( $MST_{\text{dark}} = 22.8 \pm 1.1$  °C) but returned to warmer water during daytime. This behaviour may be regarded as a trade-off between the potentially higher food density in warmer water areas and the energetic benefit of selecting cooler water patches. The circadian pattern of MST was gradually abandoned upon refeeding and control values were reached again after 3 weeks. Energetically more effective than behavioural hypothermia was the reduction of swimming activity. During starvation, activity peaks were slightly lower than under control conditions and mean daily activity decreased by about 50%. Swimming velocity, however, was not affected by feeding regime. After a period of starvation fish showed compensatory growth at all temperatures, even below 12 °C, where these animals normally do not grow. This suggests that

after a period of starvation the critical temperature for growth shifts to lower values.

**Keywords** Behavioural thermoregulation · Compensatory growth · Conversion efficiency · Fish · Starvation

### Introduction

Due to seasonal variations of food supply in the aquatic environment, many fish species are regularly subjected to periods of starvation during which they have to rely on body reserves. In order to survive extended bouts of starvation the organism has to spare body resources by reducing total energy turnover (Wieser et al. 1992; Yang and Somero 1993). The reduction of total energy flux leads to a redistribution of the available energy between energy-consuming processes. The energy is mainly channelled into maintenance functions while other processes (such as growth) are down-regulated or even arrested.

Behavioural changes may also contribute to the reduction of the overall energy requirement. For example, some fish reduce swimming activity during starvation (Beamish 1964). A general reduction of all energy-consuming processes can be achieved by a decrease of body temperature (behavioural hypothermia). In an ectothermic organism, body temperature is generally very close to that of the ambient medium. Fish can detect and respond to temperature differences as small as 0.03 °C (Murray 1971). When exposed to thermal gradients they are able to regulate body temperature by seeking warmer or cooler water areas (behavioural thermoregulation). The maximum power principle suggests that in a natural aquatic system fish should select thermal habitats where “surplus power” is maximised, i.e. maximum energy is available for growth processes (Crowder and Magnuson 1983; Bryan et al. 1990). The optimum temperature for growth ( $T_{\text{opt}}$ ) of fish is greatly dependent on food availability. If food is limited,  $T_{\text{opt}}$  decreases, because low temperatures are correlated with low metabolic rates and,

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therefore, less energy is expended on maintenance processes (Jobling 1994). In consequence, a greater percentage of the assimilated energy is available for growth processes. If the fish tries to optimise the net energy gain (=“surplus power”), it seems logical that the preferred temperature ( $T_{\text{pref}}$ ) of a given species decreases at a lower ration level. However, the results given in the literature are not consistent. Most studies revealed the expected decrease, but some examples can be found where  $T_{\text{pref}}$  increases during starvation (Javaid and Anderson 1967; Boltz et al. 1987; Morgan and Metcalf 2001). This indicates that processes other than energetic optimisation may play a role in determining  $T_{\text{pref}}$ .

When refed after a long period of starvation many species show increased growth rates when compared to control fish (compensatory growth, Wieser et al. 1992). However, it is not known whether behavioural changes exhibited during starvation in order to reduce energy consumption (behavioural hypothermia and hypoactivity) are sustained during the period of compensatory growth.

In this study we investigated whether behavioural changes play a role in the optimisation of energy utilisation during energetic stress in roach. To this end, we determined temperature preference and swimming activity of roach under feeding, starvation and refeeding conditions. In a second set of experiments we determined the effects of temperature on growth and feeding rates in control and refed fish.

## Materials and methods

### Thermal gradient

Juvenile roach were collected during summer from Lake Mueggelsee, Germany. Fish were acclimated to 28 °C for several weeks prior to the experiment. Previous measurements had shown that the  $T_{\text{pref}}$  of juvenile roach lies around 28 °C (Staaks 1996). The photoperiod was kept constant 12 h L:12 h D throughout the acclimation period and the experiments.

For determination of the thermal preference, 10 fish [mean body mass (bm)=8.6±1.0 g] were placed in a 600 l aquarium with a horizontal thermal gradient from 21 °C to 33 °C in steps of 3 °C as described by Staaks (1996). In brief, the aquarium was partially divided into five interconnected compartments (dimensions: 50×50×50 cm) by plastic panels. Fish were allowed to distribute freely between compartments through gaps in these walls. Each compartment was thermostatted by a cooling system and electric heaters regulated by PT100 thermometers. The movements of the fish were recorded by a vertical array of eight infrared transmitters in each compartment.

The mean selected temperature (MST) was calculated as:

$$\text{MST} = \left( \left( \sum_{i1}^{i2} D_1 \times T_1 \right) + \left( \sum_{i1}^{i2} D_2 \times T_2 \right) \dots + \left( \sum_{i1}^{i2} D_5 \times T_5 \right) \right) / \sum D_{\text{total}} \quad (1)$$

where  $D_1$  is the duration of all infrared impulses in compartment 1 and  $T_1$  is temperature in compartment 1. All sums were calculated over periods of 1 h.

Activity (arbitrary units) was calculated as:  $\sum_{i1}^{i2}$  impulses in all compartments.

Swimming velocity was estimated according to the formula:

$$\text{Velocity [arbitrary units]} = \frac{\sum_{i1}^{i2} \text{impulses in all compartments}}{\sum_{i1}^{i2} \text{duration of all impulses [s]}} \quad (2)$$

For these estimations, no distinction was made between active swimming and passive drift. If we assume fish are passing the transmitters horizontally and vertical movements can be neglected, the duration of one impulse equals the time a fish takes to swim one body length (BL). So these measurements can be considered as an approximation of swimming velocity in BLs<sup>-1</sup>.

Photoperiod was kept constant at 12 h light from 0900–2100 hours. Fish were fed at 1000 hours each day with living chironomid larvae (20% bm) from day 1 to 26, then starved for 3 weeks from day 27 to day 47 before the feeding regime was resumed for additional 5 weeks (days 48–85).

### Growth experiments

Fish (mean body mass=7.2±3.0 g) were kept in thermostatted 200 l aquaria at 4, 12, 20, 24, 27, 30 and 33 °C. Each aquarium was subdivided into four compartments by gauze walls, each compartment containing two fish. Feeding rates were determined for each pair of fish, while growth rates were determined for each fish individually. Animals were acclimated to final temperatures and the experimental set up for at least 6 weeks prior to experimentation.

Fish were fed to excess with preweighed living chironomid larvae each morning. Excess of food was removed and weighed the following day. After a 2-week period of feeding, fish were starved for 3 weeks and refed to excess for an additional 3 weeks. During the experiment fish were weighed once a week. Specific growth rates (SGR) were calculated as:

$$\text{SGR [\% bm day}^{-1}] = 100 * \frac{\ln m_{t1} - \ln m_{t0}}{t1 - t0} \quad (3)$$

where  $m_{tx}$  is the fish mass at time  $x$ . Growth rates of fish during the first week of refeeding were corrected for the weight of gut contents, since animals had empty guts at  $t_0$  but full guts at  $t_1$ . Fish were killed at the end of the experiments and gut content was determined to be 1.18, 1.39, 0.79, 0.60, 0.57 and 0.52% bm in ad libitum fed fish at 4, 12, 20, 24, 27 and 30 °C, respectively.

Conversion efficiency  $K_1$  was calculated according to the formula:

$$K_1 [\%] = \frac{\text{specific growth rate}}{\text{specific feeding rate}} * 100 \quad (4)$$

### Statistics

Statistical significance was tested at the  $P \leq 0.05$  level using analysis of variance (one factor ANOVA, temperature=factor) and Tukey's post hoc test. All data are given as means±SD.

## Results

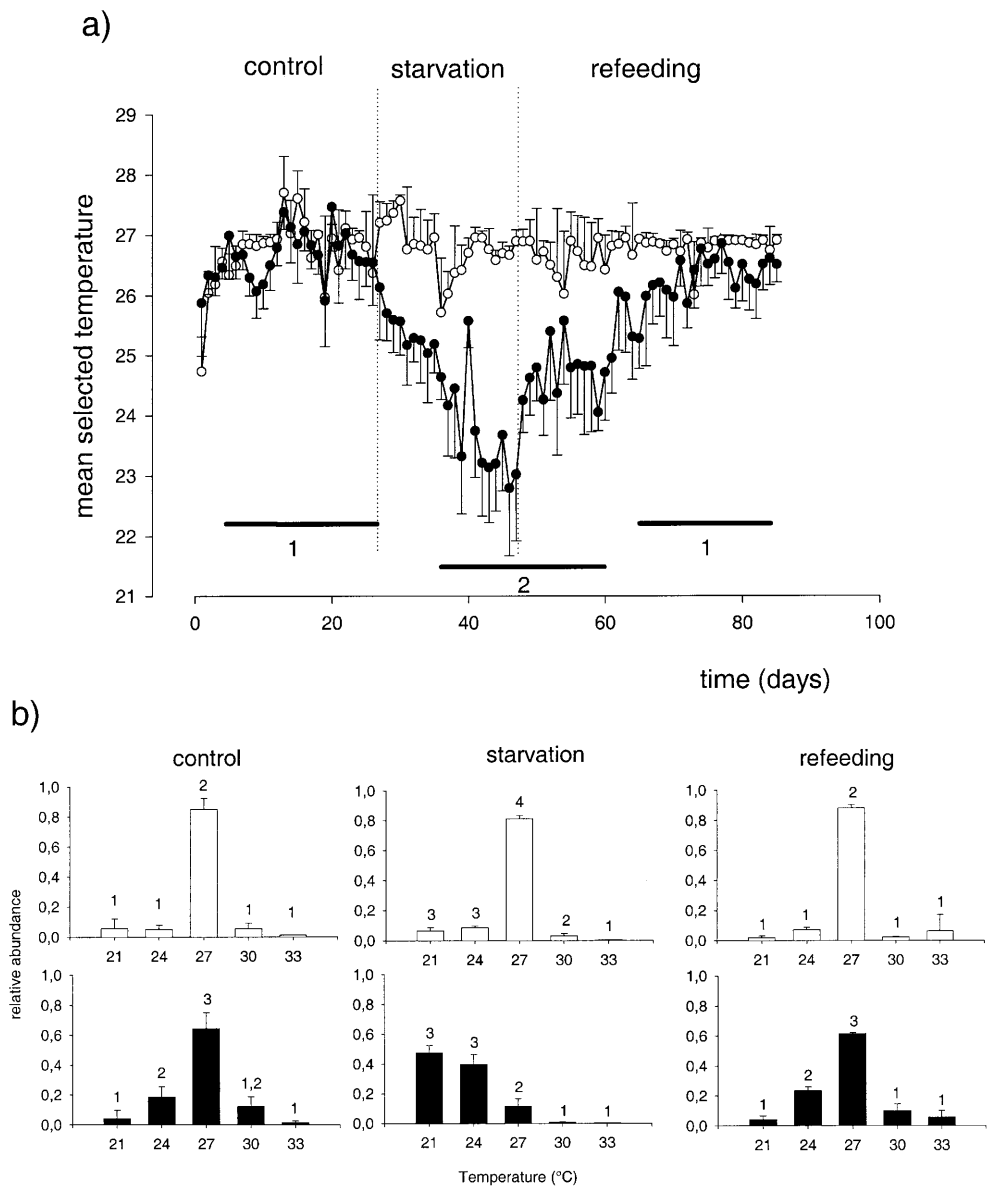
### Mortality

There was no mortality in any experimental group except at 33 °C, at which temperature all fish died during the acclimation period or the early phase of the experiment.

### Behavioural changes during starvation and refeeding

Roach preferentially selected water with a temperature of 27 °C (MST=26.8±0.94) under control conditions

**Fig. 1** **a** Mean selected temperature of 10 roach, *Rutilus rutilus*, during light (*open symbols*) and dark periods (*filled symbols*). Values are given as mean $\pm$ SD of twelve 1-h intervals. **b** Relative abundance of roach in each compartment of the thermal gradient during 6 representative days of the control, starvation and refeeding periods (days 17–22, days 41–46 and days 81–86, respectively). *Open bars* light period, *black bars* dark period. Numbers denote significantly different groups

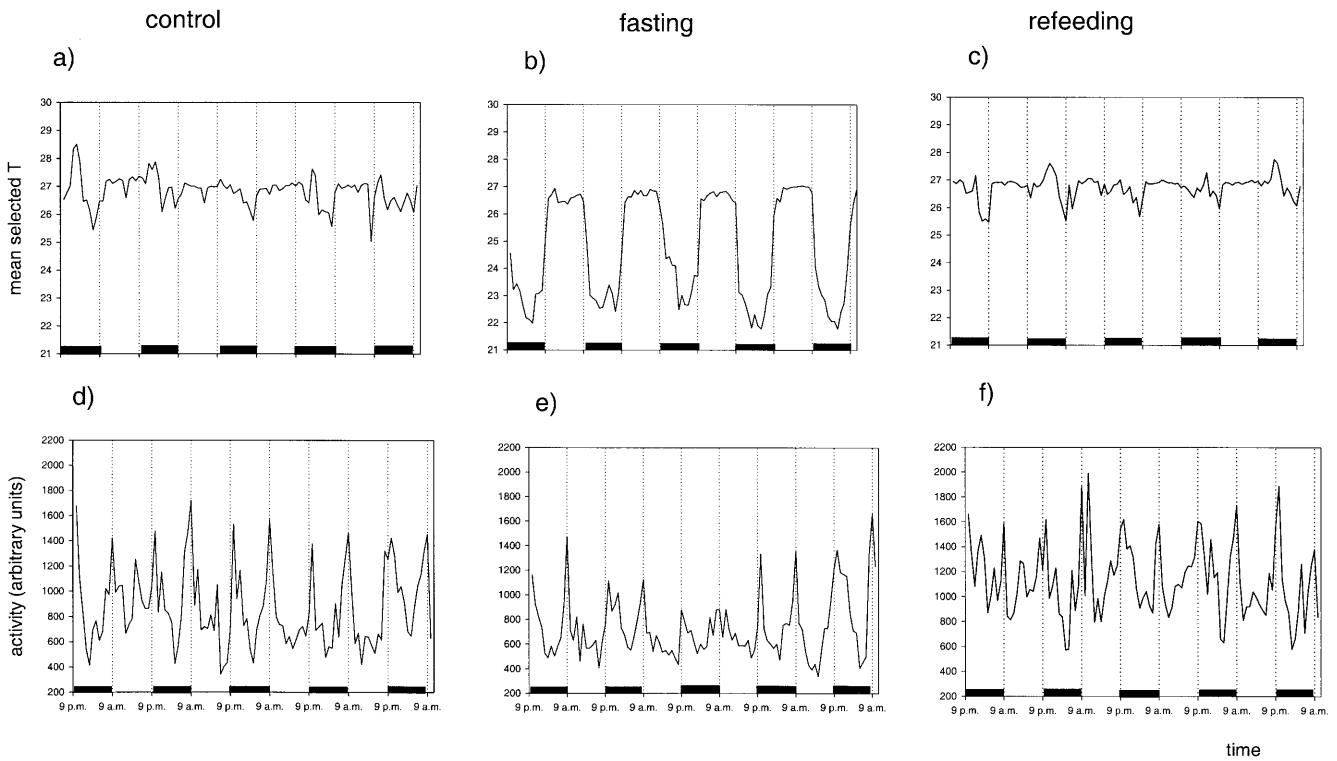


(Fig. 1a). The preference for 27 °C was very distinct since the relative abundance at that temperature was as high as  $85\pm 7\%$  under control conditions. Only at night did fish make occasional excursions into water of 24 °C and 30 °C (Fig. 1b). There was no clear diurnal pattern of the mean selected temperature and MST varied maximally about 3 °C within 24 h (Fig. 2a).

As soon as feeding was stopped, the animals started to select cooler water areas during the dark period.  $MST_{\text{dark}}$  gradually declined until it reached a value of  $22.8\pm 1.1$  °C after 3 weeks of fasting (Fig. 1a, b). After refeeding,  $MST_{\text{dark}}$  displayed a mirror image of that during fasting, reaching control values after 3 weeks.  $MST_{\text{light}}$  did not change significantly during the whole experiment. Due to the decrease of  $MST_{\text{dark}}$  fish showed a very distinct circadian pattern of MST during the fasting period (Fig. 2b). As soon as the light was turned off the animals selected cooler water and within a few hours

MST dropped by 5 °C. After a recovery period of 3 weeks this pattern had disappeared again and MST showed only a small circadian variation (Fig. 2c).

Swimming activity of the fish showed no clear circadian rhythm (Fig. 2d–f). Activity peaked when light was switched on and off. These peaks were slightly lower during starvation (Fig. 2b) and mean daily activity decreased (Fig. 3). Refeeding resulted in an immediate increase of the mean activity by a factor of 2 (Fig. 3). Swimming velocity was similar during day and night and was not affected by feeding regime (Fig. 4a). Fish showed lowest swimming speeds at their  $T_{\text{pref}}$  (27 °C under control conditions and refeeding, 21–27 °C during dark period in fasting fish). Swimming speed increased with increasing deviation of the ambient temperature from  $T_{\text{pref}}$ , and was highest at 33 °C (Fig. 4b).



**Fig. 2** Circadian patterns of mean selected temperature (a–c) and swimming activity (d–f) of 10 roach during control conditions, starvation and refeeding

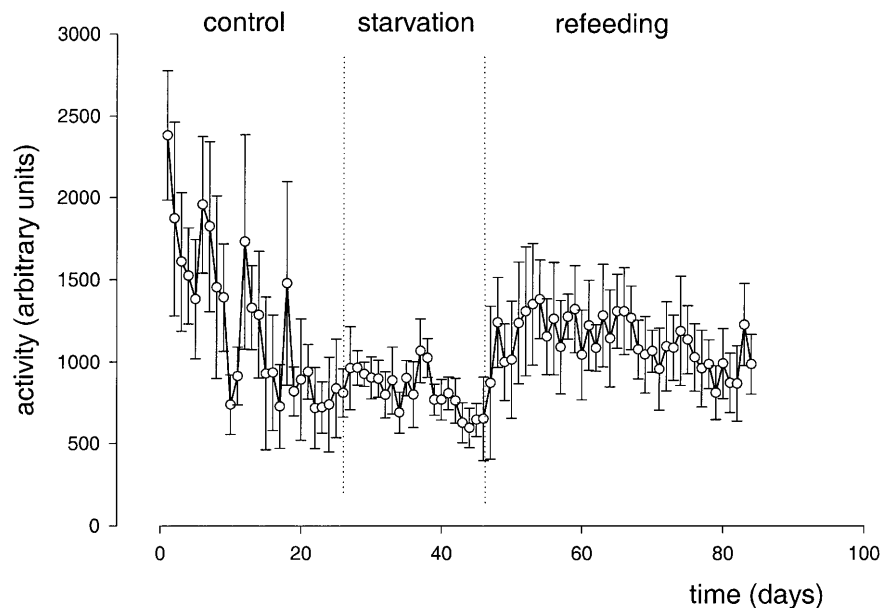
#### Temperature effects on feeding and growth rates

Feeding rates of control animals increased with ambient temperature and reached a maximum value of  $29.0 \pm 7.4\%$  bm at  $20^\circ\text{C}$ . At higher temperatures feeding rates dropped and levelled off at about 17% (Fig. 5). Although feeding at low rates, fish did not grow at temper-

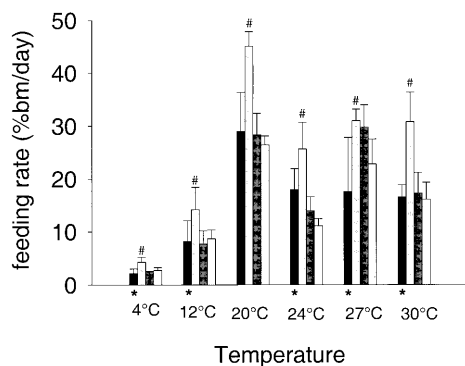
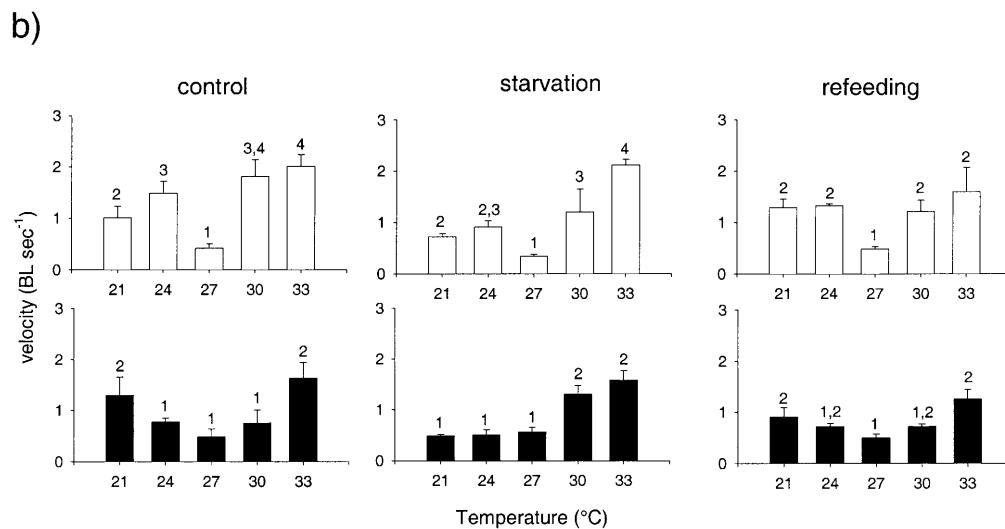
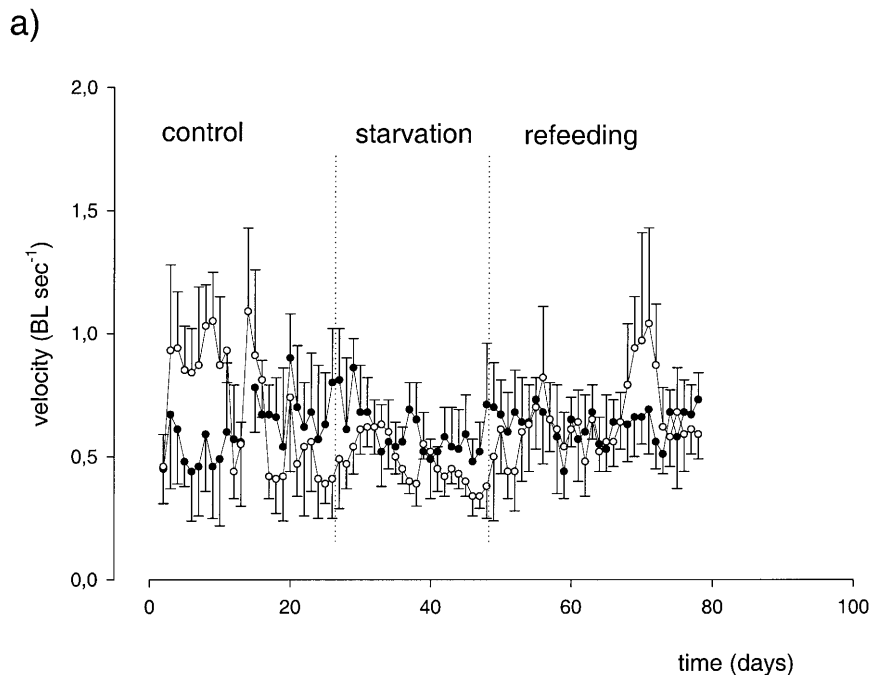
atures of  $12^\circ\text{C}$  and lower. Growth rates showed a broad maximum between  $20^\circ\text{C}$  and  $27^\circ\text{C}$ , thus  $T_{\text{opt}}$  for growth may be slightly higher than  $T_{\text{opt}}$  for feeding (Fig. 6a).  $K_1$  values of control fish showed a similar temperature dependence as growth rates (Fig. 8).

When provided with excess food after a 3-week period of starvation all fish fed about twice as much as control fish, but after 1–2 weeks feeding rates returned to control levels (Fig. 5). Interestingly, fish showed compensatory growth during the first week of refeeding at all temperatures, even below  $12^\circ\text{C}$ , where they did not

**Fig. 3** Mean daily activity of 10 roach in a thermal gradient during control conditions, starvation and refeeding



**Fig. 4 a** Mean velocity of 10 roach during light (*open symbols*) and dark periods (*filled symbols*). Values are given as mean $\pm$ SD of twelve 1-h intervals. **b** Swimming velocity of roach in each compartment of the thermal gradient during 6 representative days of the control, starvation and refeeding periods (days 17–22, days 41–46 and days 81–86, respectively). *Open bars* Light period, *black bars* dark period. Numbers denote significantly different groups



**Fig. 5** Feeding rates of roach under control conditions (*black bar*) and during the 1st, 2nd and 3rd week of refeeding after a 3-week period of starvation (*shaded bars*) at different temperatures. Values are given as mean $\pm$ SD,  $n=4$ . \* denotes a significant difference with the group at 20 °C; # denotes a significant difference with the control group at the same temperature

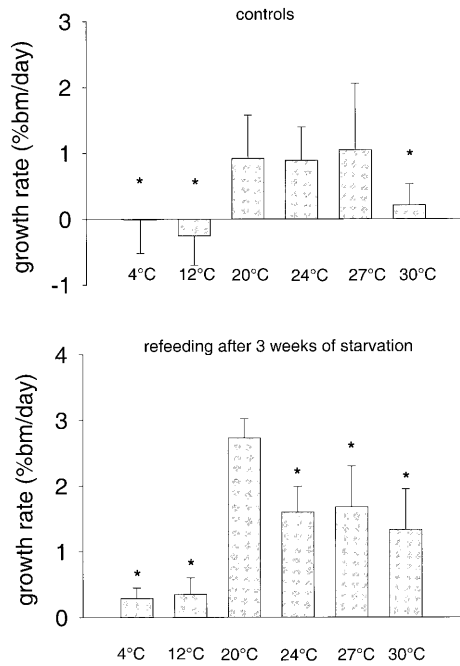
grow under control conditions (Fig. 6). Compensatory growth was highest at 20 °C. This may indicate that normal growth processes and compensatory growth may have slightly different temperature optima. Growth rates returned to control levels after 1–2 weeks (Fig. 7).  $K_1$  values were increased during compensatory growth at all temperatures except 27 °C (Fig. 8).

## Discussion

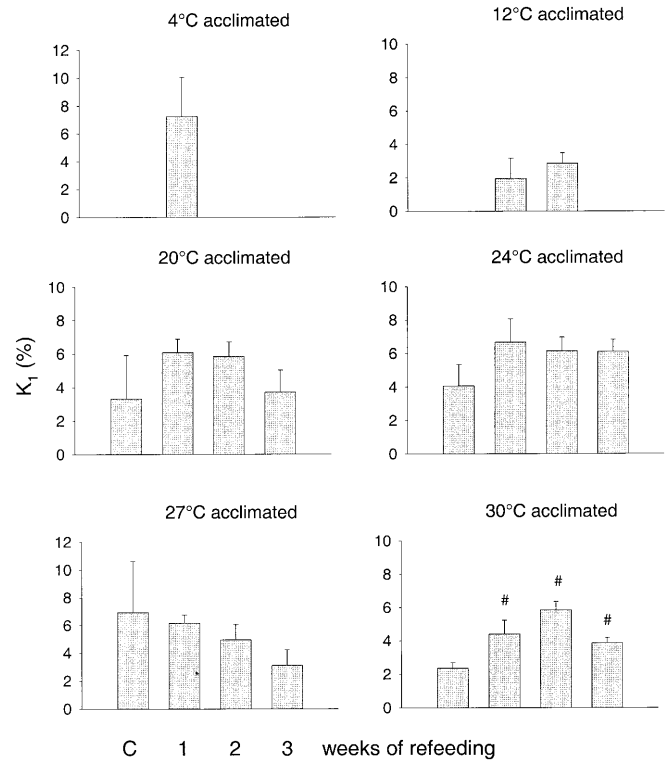
### Temperature preference

When fed ad libitum, roach preferentially selected a temperature of  $26.8\pm 0.9$  °C. This temperature can be considered the final temperature preference of roach since fish were kept under control conditions for 26 days until

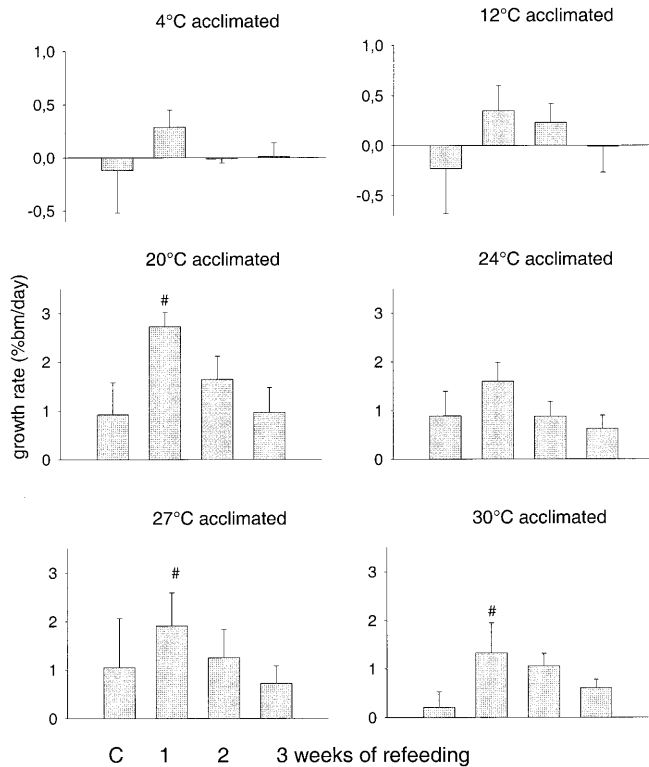




**Fig. 6** Temperature dependence of growth rates **a** under control conditions and **b** during compensatory growth. Values are given as mean $\pm$ SD,  $n=8$ . \* denotes a significant difference with the group at 20 °C



**Fig. 8** Growth efficiency ( $K_1$ ) under control conditions and during the 1st, 2nd and 3rd week of refeeding after a 3-week period of starvation at different temperatures. Values are given as mean $\pm$ SD,  $n=4$ . # denotes a significant difference with the control group at the same temperature



**Fig. 7** Growth rates under control conditions and during the 1st, 2nd and 3rd week of refeeding after a 3-week period of starvation at different temperatures. Values are given as mean $\pm$ SD,  $n=8$ . # denotes a significant difference with the control group at the same temperature

treatment started. The preferred temperature of roach lies at the high end of the optimal temperature range for growth (20–27 °C). This complies with the maximum power principle, which predicts that fish select thermal habitats where maximum energy is available for growth processes (Bryan et al. (1990). Jobling (1981) found a close correlation between MST and  $T_{opt}$  for growth when comparing these parameters in 19 different fish species, supporting the view that MST is mainly determined by the optimisation of growth processes. It is surprising, however, that the preference of 27 °C is very distinct (85% relative abundance at that temperature) while the  $T_{opt}$  for growth covers a broad range between 20 °C and 27 °C. This indicated that processes other than growth maximisation contribute to the determination of  $T_{pref}$  (see below).

During 3 weeks of starvation MST decreased gradually down to  $22.8\pm 1.8$  °C during dark periods, while it remained at high values during daytime. A decrease in body temperature is correlated with a decrease in metabolic rate and, therefore, a reduction of energy expenditure. In acclimated fish the rate of weight loss was  $0.54\pm 0.09\%$   $\text{bm day}^{-1}$  at 27 °C compared to  $0.47\pm 0.07\%$   $\text{bm day}^{-1}$  at 24 °C (data not shown). This corresponds to a  $Q_{10}$  value of 1.58, which is in agreement with the  $Q_{10}$  for routine metabolic rate of roach in this temperature range (Koch et al. 1992). Based on a  $Q_{10}$  of 1.58 a drop

of MST from 26.8 °C to 22.8 °C would induce a reduction of weight loss by 17%. Taking into account that the MST is reduced only during the dark period, the mean reduction of weight loss can be estimated to 8.5%. Thus, behavioural hypothermia creates energetic advantages. However, the selection of cooler water may also have detrimental effects for the animal, which may explain why behavioural hypothermia is restricted to the dark period in roach (see below).

Literature data on the effect of starvation on temperature preference are not consistent, but the majority of studies showed at least a minor decrease of MST during starvation or low ration feeding. However, in most studies published so far, fish were not kept in a thermal gradient and observed continuously over the whole experimental period. Rather, fish were placed in the gradient for 2–3 days and the selected temperature was determined by visual observation only during daytime. With such an experimental design gradual shifts or circadian fluctuations of MST cannot be detected. Morgan (1993) kept American plaice (*Hippoglossoides platessoides*) on low rations for 10 weeks followed by 4 weeks of starvation. At the end of the treatment, fish were placed in a thermal gradient for 48–96 h and the positions of the fish were recorded once in 24 h. The author determined a drop of MST by 0.8 °C. Visual observations of walleye pollock (*Theragra chalcogramma*) revealed a decrease of MST by 3–4 °C after 30–54 days of starvation (Sogard and Olla 1996). Lake charr (*Salvelinus namaycush*) fed on low rations for 2 weeks shifted their MST by 3.4 °C (Mac 1985, determined in a shuttle box system). A comparative study on different salmonids showed a decrease of MST about 2–4 °C in fasted brook and rainbow trout (Javaid and Anderson 1967). In contrast, Atlantic salmon (*Salmo salar*) showed a significant increase of MST during 3 weeks of starvation (Javaid and Anderson 1967). This surprising result was verified in a recent study by Morgan and Metcalfe (2001). The authors speculate that Atlantic salmon increases MST during starvation in order to optimise foraging behaviour since this species shows much better swimming abilities, e.g. position holding ability and acceleration during burst swimming, at higher temperatures. This may be one of the reasons why roach maintain a high MST during daytime, when these fish normally feed. Unfortunately there are no literature data available on the  $T_{opt}$  for swimming abilities in roach. Another explanation for the high MST maintained during daytime in starving roach may arise from the behavioural energetics hypothesis. According to Crowder and Magnuson (1983) fish choose the habitat that provides optimal bioenergetic benefits (i.e. maximum surplus power), based on integration of food and temperature distributions. This means that the optimal habitat is determined by the integration of the  $T_{opt}$  of growth processes and the availability of food. However, several studies suggest that some fish are not able to integrate temperature and food availability during their decision-making in habitat choice, but “automatically” correlate high temperature with high food availability

(Wildhaber and Crowder 1990; Krause et al. 1998). This behaviour may have evolved since in freshwater lakes patches with higher temperatures (e.g. the littoral zone and surface water) are often correlated with higher plankton densities (Wildhaber and Crowder 1990). Therefore, planktivorous fish, like roach, may have shifted their MST to higher values in order to optimise feeding success.

Thus, roach may follow different strategies during light and dark periods. During light, the fish optimises feeding success by selecting higher temperatures where expected food abundance is high and swimming abilities are maximised. At night, however, energetic parameters dominate temperature selection behaviour, the fish choosing cooler water, where energy expenditure is reduced.

In our experiments, fish decreased their swimming speed once they reached their  $T_{pref}$ , which is a further contribution to energy conservation (Fig. 4b). Bryan et al. (1990) proposed that “fish swim through a thermal gradient at velocities proportional to the derivative of metabolic scope with respect to temperature ( $dPm/dT$ )”. According to this hypothesis swimming speed is zero at the temperature where metabolic scope is maximal and increases with a progressing decrease of metabolic scope. We indeed found in our experiments that swimming speed was lowest at  $T_{pref}$  and increases with increasing deviation of the ambient temperature from  $T_{pref}$ .

#### Effects of starvation on swimming activity

Besides behavioural hypothermia the reduction of swimming activity is a potential strategy to reduce energy expenditure during starvation. Mendez and Wieser (1993) proposed three phases in the sequence of behavioural responses to starvation, namely stress, transition, and adaptation. During the initial stress phase, fish may react to food deprivation by hyperactivity, reflecting increased food searching behaviour. This phase is only short (about 24 h) and is followed by the subsequent transition phase where the fish gradually reduce swimming activity and, therefore, routine oxygen consumption. Activity and metabolism is maintained at the low level during the adaptation phase until fish are refed. In our experiments the overall swimming activity of roach did not show a clear response to food deprivation. An initial increase of activity did not occur. According to Mendez and Wieser (1993), this behaviour is more pronounced in young fish. During the whole period of starvation, the activity level of roach was slightly decreased (Fig. 3), due to a reduction of peak activity at dawn and dusk (Fig. 2, and shown by the reduction of error bars of activity levels during the starvation period in Fig. 3). Swimming activity increased about 2-fold immediately upon refeeding, showing a similar circadian pattern as under control conditions. Overall, a reduction of swimming activity apparently contributes to the reduction of energy expenditure in starving roach. The energetic costs of routine swim-

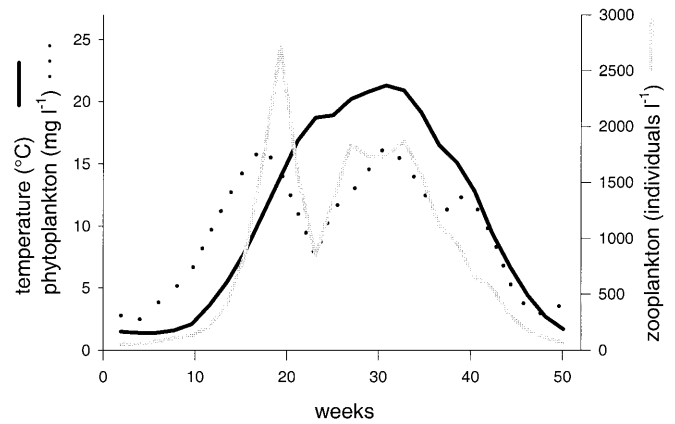
ming have been estimated to be 1–2 times the standard metabolism (Ware 1975). Based on this assumption, a reduction of swimming activity by 50% would correspond to a reduction of the overall energy expenditure of 25–33%. Therefore, in our experiment, the energetic benefit of reduced swimming activity is much more pronounced than that of behavioural hypothermia. However, not all species use the strategy of activity reduction during starvation: Atlantic cod show the same level of swimming activity under ad libitum feeding and starvation (Björnson 1993). Similarly, the burbot, *Lota lota*, maintains high activity levels even during prolonged starvation (P.L.M. van Dijk, G. Staaks, I. Hardewig, unpublished results).

Our results suggest that roach, when subjected to starvation, remain in their normal microhabitat during daytime but migrate to cooler water areas at night. This strategy may be regarded as a trade-off between the potentially higher food density in warmer water areas and the energetic benefit of selecting cooler water patches. More important than behavioural hypothermia is the energetic benefit of reduced swimming activity observed in this species.

### Compensatory growth

After 3 weeks of starvation fish showed increased growth rates for 1–2 weeks. This compensatory growth is partly fuelled by increased food uptake (Fig. 5). However, the high values of  $K_1$  during the first week of re-feeding indicate that food energy is more efficiently used for growth under these conditions. Apparently, other energy-consuming processes remain depressed during this phase in order to maximise growth rates. Our data show that swimming activity goes back to control levels as soon as food becomes available. Behavioural hypothermia, however, is maintained and only gradually returns to control levels within 3 weeks of refeeding. This may be a mechanism to save metabolic energy, which is then channelled into growth.

Roach showed compensatory growth at all investigated temperatures, even below 12 °C, where control animals did not grow. This indicates that the critical temperature for growth is lower in previously starved than in control fish. Apparently, the growth curve is shifted to lower temperatures during compensatory growth. Accordingly,  $T_{opt}$  for compensatory growth is slightly lower than  $T_{opt}$  for normal growth (Fig. 6). To our knowledge, this is the first study investigating the effects of temperature on compensatory growth. The ecological relevance of this shift is quite clear. During early winter when water temperatures drop below 12 °C, plankton densities decline and food becomes scarce (Fig. 9). Under these conditions, the animals rapidly enter a state of non-growth and winter rest. In spring, however, both phyto- and zooplankton starts to increase before water temperature reaches 12 °C. Thus, plankton densities are generally higher during spring than at a comparable tem-



**Fig. 9** Mean water temperatures and plankton densities from Lake Müggelsee, Germany, averaged from 1978 to 1998. Data source: Gerten and Adrian (2001) and D. Gerten and R. Adrian, personal communication

perature during autumn and winter. After the winter fast, when body reserves are depleted, it is crucial for the fish to be able to feed and grow as soon as food becomes available even at low water temperatures. The physiological mechanisms underlying this shift in growth curve are as yet unknown, but will be the subject of our future investigations. To this end, we will have to determine what is limiting growth below 12 °C in control animals. Possible factors may be energy limitation due to reduced food uptake, or adverse thermodynamic effects of low temperature on biochemical reactions involved in growth processes.

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