In situ estimation of gastric evacuation and consumption rates of burbot (*Lota lota*) in a summer-warm lowland river

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Summary

The burbot (*Lota lota*) is the only cold-stenothermal gadoid inhabiting freshwaters with high temperature amplitudes. Summer temperatures up to 25°C have been reported as being far above the thermal preferendum of this species. Thus this study aimed to determine gastric evacuation, daily food consumption and energy uptake of burbot at high temperatures under *in situ* conditions. These data are prerequisites for bioenergetics modelling of the adaptive physiological behaviour of burbot in summer-warm freshwaters. The study was conducted in the lower Oder River, Germany between May and October 2003 covering a temperature range between 4.6 and 23.4°C. A total of 1683 burbot was caught in five successive 24-h fisheries. The mean index of stomach fullness showed a significant decrease with rising temperature. Highest stomach fullness values were reached at 4.6°C in October. A negative correlation was observed between gastric evacuation and temperature. In contrast to the data reported in the literature gastric evacuation was found to be high at 4.6°C, which may indicate an ongoing compensatory adaptation to the long period of high temperatures in July and August, when a significant reduction of the mean daily ration was observed. Balancing the energy flux probably resulted in a decrease in the hepatosomatic index at high temperatures and an increase during the cool period, when the liver energy was restored. The endogenous energy pool of the liver may determine the survival of burbot during summer months. The ability of burbot to actively forage during winter and to rapidly digest high amounts of food at cold temperatures was considered an adaptation to increase survival chances in an environment with high environmental, especially thermal, heterogeneity as is typical for a summer-warm lowland river. Limitations of the energy budget have to be expected with extended periods of high temperatures.

Introduction

The burbot (*Lota lota*) is the only member of the cold-stenothermal family Gadidae that has invaded freshwater habitats and is widely distributed throughout the Holarctic region. Spawning occurs during winter at low temperatures (1–4°C) over coarse substrata; eggs optimally develop between 4°C and 7°C and larvae hatch after 30 (at 6°C)–41 (2°C) days. After an initial pelagic stage, juveniles shelter in weed beds and under rocks in the littoral. Adults typically inhabit deep lakes and cool rivers, where it is suggested they avoid temperatures above 13°C (temperature requirements reviewed by McPhail and Paragamian, 2000). Temperatures above 20°C have been considered stressfully high as indicated by reduced oxygen consumption and feeding (Shodjai, 1980; Pääkkönen and Marjomäki, 1997). Accordingly, feeding was modelled to cease at 23°C (Rudstam et al., 1995). In contrast, Pääkkönen and Marjomäki (2000) observed feeding at 23.4°C in an experimental setup. Thermal limits for burbot survival have been determined in several ways: In an experimental tank, 89% of 0 + fish died within 9 weeks at 28°C (Shodjai, 1980). During growth experiments mortality began at 23°C when the first burbot died after 6 days, increased successively with increasing water temperature, and reached 60% at the highest temperature 25.5°C (Hofmann and Fischer, 2003). Pääkkönen et al. (2003) experimentally determined lethal levels for burbot acclimated from 2 to 20°C. The lethal temperature (27°C) was the lethal rate for burbot acclimated to 12°C. Critical thermal maxima, i.e. temperatures tolerated no longer than 10 min, have been experimentally determined using burbot acclimated to 5.2–5.9°C and 19.6°C with 27.1–26.8°C and 31.5–31.7°C, respectively (Hofmann and Fischer, 2002). Nevertheless, stressfully high temperatures were found to be maintained by burbot in a state of metabolic depression, with down regulated enzyme expression, low food intake and low energy expenditure (Hardewig et al., 2004).

Interestingly, in temperate, large lowland rivers of Central and Eastern Europe, burbot was one of the most abundant fish species prior to excessive damming. In the free-flowing lower Oder River (Germany) this species still constitutes about 20% of the littoral fish assemblage (Wolter and Freyhof, 2004). In their lower stretches, these rivers typically reach temperatures above 20°C for months and maximum temperatures of up to 25–26°C in summer. Burbot not only survive these stressfully high temperatures, but also grow rapidly in summer (Hölker et al., 2004). A potentially insufficient energy uptake was suggested to be compensated by the metabolism of energy-rich liver tissue to provide energy for growth (Hölker et al., 2004) and the down regulated basal metabolism (Hardewig et al., 2004). Replenishment of the liver energy store was suggested to occur at lower temperatures, when increased feeding provides surplus energy. Hofmann and Fischer (2003) calculated the maximum daily food consumption at 17.9°C and the maximum daily growth at 16°C; Shodjai (1980) found this to be 12–20°C and 16°C, respectively. For adult burbot Pääkkönen and Marjomäki (2000) determined 13.6°C as an optimum temperature for mean daily food intake, and Hofmann and Fischer (2002) calculated a final temperature preferendum of 14.2°C. Corresponding to the optimum temperature for growth determined by Shodjai (1980), Hölker et al. (2004) assumed that gastric evacuation reached its maximum at 15–16°C.

In contrast to initial expectations, Lake Constance burbot have been observed to migrate into cooler profundal waters despite optimum temperatures for feeding and growth in the littoral, questioning the role of temperature as proximate factor for habitat shifts (Hofmann and Fischer, 2003). However, when temperature refuges are lacking, which will be the case in most lowland rivers, burbot maintain growth at the expense of liver energy (Hölker et al., 2004) probably in a state of metabolic stress (Hardewig et al., 2004).

The study aimed to determine gastric evacuation and daily food consumption of burbot at high temperatures under *in situ* conditions, where burbot were not fed *ad libitum* in contrast to the experimental setups (Shodjai, 1980; Pääkkönen and Marjomäki, 2000; Hofmann and Fischer, 2002, 2003). These data are prerequisites for bioenergetics modelling of the adaptive physiological behaviour of burbot in summer-warm freshwaters.

Materials and methods

Field sampling

The study was performed in the lower River Oder, within the National Park 'Lower Oder Valley', Germany. In the study area, the Oder River is a 200–250 m wide and 4–5 m deep lowland floodplain river with a medium discharge of $522 \text{ m}^3 \text{ s}^{-1}$ and a mean flow velocity of 1 m s^{-1}. Further site details are given in Wolter and Freyhof (2004).

The Water and Navigation Authority in Eberswalde, Germany, provided daily means of water temperature, which were recorded continuously at the automatic water level gauge 'Schwedt Oderbrücke', situated at the upstream end of the sampling site. Water temperatures typically exceed 20°C for at least 1 month during the summer, while winter temperatures drop to −0.2°C, with an absolute range between <0°C and 28.8°C.

Five successive 24 h fisheries were carried out between May and October 2003. At each sampling date, every 2 h 30 burbot were caught using a generator-powered DC electrofishing gear, in total 12 samples and 360 specimens each.

All burbot were anaesthetized immediately after capture using Tricaine Methane Sulfonate (MS-222), measured (total length to the nearest mm below), weighed (nearest g), and their stomach content collected before the next sampling. At each sampling, 10 specimens were dissected to weigh stomach content, the empty body the and liver. All other specimens were rereleased into the River Oder after recovering from anaesthesia. The proportion of liver to the whole body mass was calculated as hepatosomatic index (HSI): HSI (%) = liver weight / mass of carcass*100. As there was a significant increase of HSI with carcass mass in May and a significant decrease in August (P < 0.05) HSI was standardised to a 100 g fish based on the HSI-carcass mass relationship in May and August, respectively.

Stomach contents of all other specimen were flushed out using a water pump sprayer. This non-destructive technique (reviewed in detail by Hyslop, 1980) was evaluated as most effective method of recovering stomach items from a variety of fishes (Kamler and Pope, 2001; Schulze et al., 2006). In a pretest, 25 flushed out burbot stomachs were found to be empty when thereafter dissected. All stomach contents were preserved in 4% formaldehyde.

Water temperatures, number of burbot caught, length and body mass ranges on the five sampling dates are presented in Table 1. Stomach fullness was expressed as fullness index (FI): FI (%) = total stomach content mass / total fish mass*100.

FI-values were calculated using stomach content wet mass determined to the nearest 0.01 g. Changes of the stomach content relative to fish mass have been frequently used to assess diel feeding rhythms (Hölker and Temming, 1996). To exclude allometric size dependent influences on FI, the size adjusted FI_{adj} of a 100 g standard fish was calculated based on the FI-total mass relationships of all investigated burbot.

Gastric evacuation

Determining gastric evacuation in the field is hampered by the individual variability of the specimen in fasting, sporadic food uptake and meal size, the latter inversely correlated to evacuation constant (Pääkkönen et al., 1999). In contrast to experiments, in the natural environment there was neither a defined extended period in which the entire population was fasting, nor a defined amount of food provided. However, nearly all fish species show clear diurnal behavioural patterns (Helfman, 1993), including burbot (Wolter and Freyhof, 2004). Accordingly, the average FI_{adj} of the subsamples (30 burbot) varied during the 24 h surveys. The steepest decline of average FI_{adj} observed among a minimum of four consecutive subsamples was used to estimate the evacuation constant for each sampling date separately.

Estimates of the evacuation constant were based on analysis of percentiles (medians and upper quartiles) according to Temming et al. (2002), which has proven to be an appropriate method to avoid bias arising from inclusion of empty stomachs in the means in combination with uncontrolled variation in the initial meal sizes. According to Pääkkönen and Marjomäki (1997), an exponential model provides the best description of the relationship between stomach content and time and therefore was used to calculate gastric evacuation constant between sub-samples:

$$FI_{adj\,t} = FI_{adj\,0} \, e^{-Rt},$$

where $FI_{adj\,t}$ is the stomach content at time t (h), $FI_{adj\,0}$ is the initial stomach content and R is the gastric evacuation constant (1 h^{-1}). Only if the relationship between FI_{adj} and time during the period of steepest decline was significant (P < 0.05), the resulting R was used for further analysis.

Estimation of daily ration

Daily food consumption rate (C) was calculated according to Eggers (1977) as

$$C\,(\%) = 24\,R\,FI24_{adj},$$

with $FI24_{adj}$ = adjusted median stomach content over the 24 h period of all specimens caught in one sampling campaign, and R = instantaneous gastric evacuation constant.

Diurnal feeding intensities at day and night have been compared using the simplified Eggers (1977) model,

$$C_h\,(\%\,h^{-1}) = R\,FIh_{adj},$$

to calculate the relative consumption rate per hour.

Statistical analysis

Median values have been first calculated at the level of sub-samples, for example to estimate the average variations of FI_{adj} during 24 h. Each sampling date formed a group of nested sub-samples. These groups were analysed for seasonal

Table 1
Food consumption of burbot. Sampling dates, temperatures, number of specimens (n = 1683), ranges of length and biomass, indices of fullness and daily rations

Date	20/21 May 2003	25/26 June 2003	16/17 July 2003	20/21 August 2003	28/29 October 2003
T (°C)	17.2	18.7	23.4	21.4	4.6
Number (n) of burbot	248	360	360	355	360
n with empty stomachs	22	49	161	159	1
TL (cm)	11–32	14–32	16–37	13–32	11–31
M (g)	18–277	26–258	34–373	21–188	12–194
FI24 (%)	0.68^a (0.26–1.22)	0.81^b (0.23–1.64)	0.13^c (0–0.28)	0.02^c (0–0.21)	4.0^d (2.53–5.35)
FI24$_{adj}$ (%)	0.58^a (0.23–0.99)	0.78^a (0.21–1.44)	0.01^b (0–0.27)	0.01^b (0–0.14)	1.8^c (1.14–2.59)
C (%)	0.52^a (0.21–0.89)	2.07^b (0.56–3.81)	0.01^c (0–0.23)	0.01^c (0–0.12)	5.13^d (3.22–7.33)

T, water temperature, measured at the day of sampling; TL, total length; M, mass; FI24, median index of fullness (% of body mass); FI24$_{adj}$, adjusted median index of fullness (% of body mass); C, median relative daily ration (% of body mass); lower/upper quartiles in parentheses, proc multtest feature by SAS to perform multiple comparisons of nonparametric data, letters mark significant differences.

variations in FI$_{adj}$, R and C as well as for the effects of temperature. Median FI24$_{adj}$ and C were compared using the proc multtest approach of the SAS software package (Release 8.2, SAS Institute Inc.) to perform multiple comparisons of nonparametric data. FI$_{adj}$-percentiles of all specimens caught during 24 h were used to analyse the impact of temperature on FI$_{adj}$ and C using regression analysis. Medians of HSI related to temperature and season were compared by Kruskal–Wallis one-way analysis of variance with multiple comparisons of all groups. Diurnal variations of feeding rations were compared using the Mann–Whitney U-test. If not otherwise indicated, all tests were performed at the 0.05 level of significance using SPSS for Windows (SPSS Inc. 2005, release 14.0.1).

Results

Gastric evacuation and temperature

Gastric evacuation constants correlated slightly with temperature T (Fig. 1, $R = -0.0042\ T + 0.142$, $r^2 = 0.48$, P < 0.05). Decreasing R-values with increasing temperature were observed between October and August, with the lowest R-value registered at the maximum temperatures >20°C in July and August (Fig. 1).

Stomach fullness

The median index of fullness FI24$_{adj}$ increased from May to June, and declined significantly in July and August (SAS, proc

multtest, P < 0.001) when it approached zero (Fig. 2a). In October the stomach fullness significantly increased, indicating an inverse correlation between water temperature and FI24$_{adj}$ (SAS, proc multtest, $r^2 = 0.94$, P < 0.01, Fig. 2b). Reduced feeding intensity at high water temperatures was further indicated by an increasing proportion of fish with empty stomachs (Table 1). The proportion of burbot with empty stomachs was low in May and June, increased in July and August, while in October at low temperatures only a single specimen was found with an empty stomach.
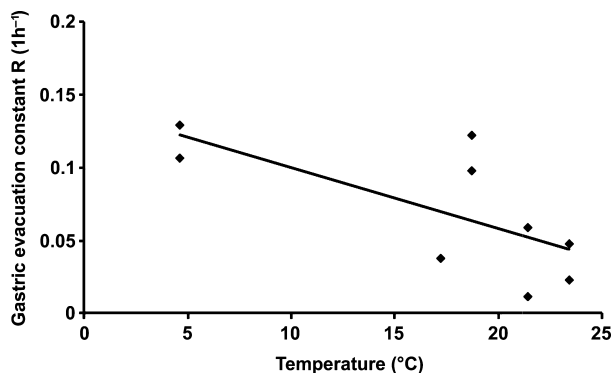

Fig. 1. Effect of water temperature on gastric evacuation of burbot. Data points = evacuation constants based on median and upper quartile percentiles of stomach fullness values (sampled at five temperatures, n = 248–360 each). All values standardised for a 100 g fish. Fitted linear model ($R = -0.0042\ T + 0.142$, $r^2 = 0.48$, P < 0.05) covers temperature range 4.6–23.4°C
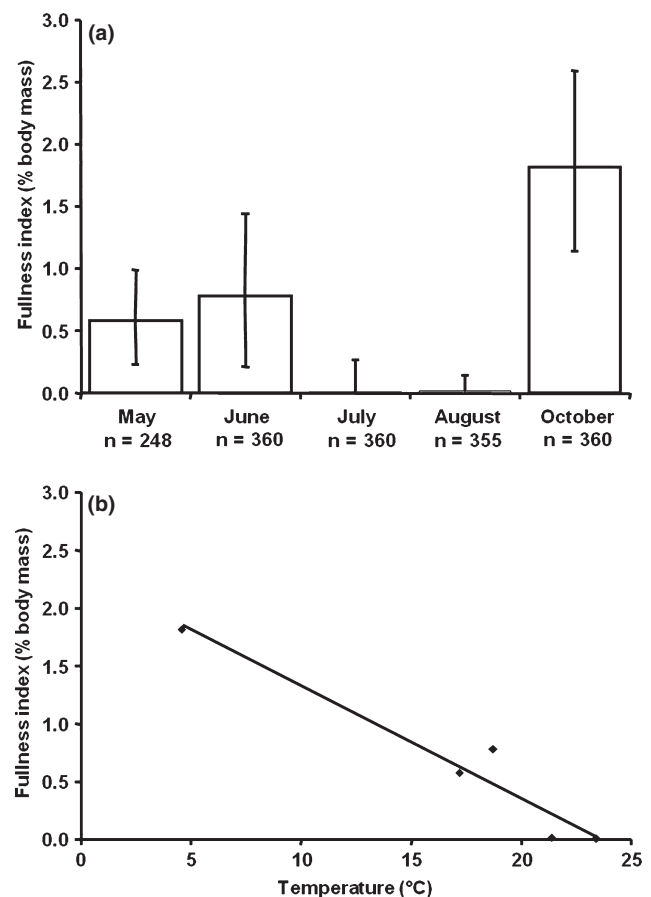
Fig. 2. Seasonal stomach fullness (FI$_{adj}$, % body mass) of 1683 burbot in relation to a) months (medians with upper and lower quartiles) and b) water temperature. Single black dots = median FI$_{adj}$ at each temp. Fitted model (FI$_{adj} = -0.0973x + 2.3006$, $r^2 = 0.94$, P < 0.01) covers temperature range 4.6–23.4°C. All values standardised for a 100 g fish

Daily ration

Mean daily rations of burbot varied seasonally between 0.01 and 5.13% of body mass (Table 1). Daily rations significantly rose until June (SAS, proc multtest, $P < 0.01$), and significantly decreased in July and August (SAS, proc multtest, $P < 0.01$) when temperatures increased above 20°C (Fig. 3). The minimum of daily rations was observed in August at 21.4°C. In October at lower temperatures a substantial increase of daily rations was observed (SAS, proc multtest, $P < 0.001$, Fig. 3).

The consumption rate per hour indicates the nocturnal behaviour of burbot. However, in October there was only a slight trend and in July the feeding intensity did not differ significantly between day and night (Mann–Whitney U-test, $P > 0.05$, Fig. 4).
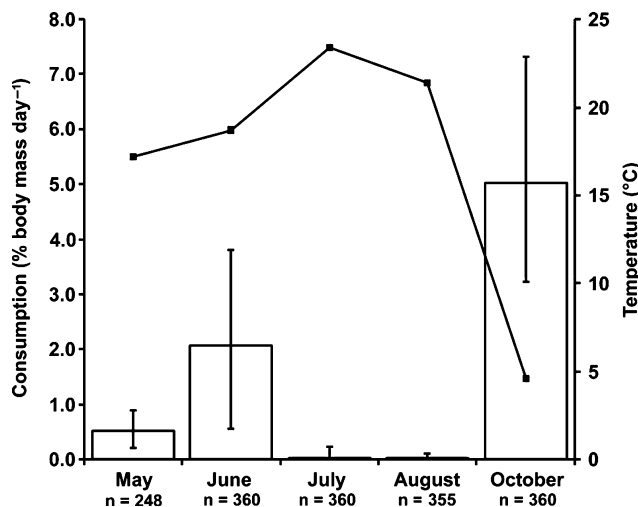

Fig. 3. Water temperature (solid line) and daily ration (% body mass h^{-1}, median, upper and lower quartiles) calculated from *in situ* determined burbot food consumption, lower Oder River, 2003. Temperature measured at day of sampling. All values standardised for a 100 g fish
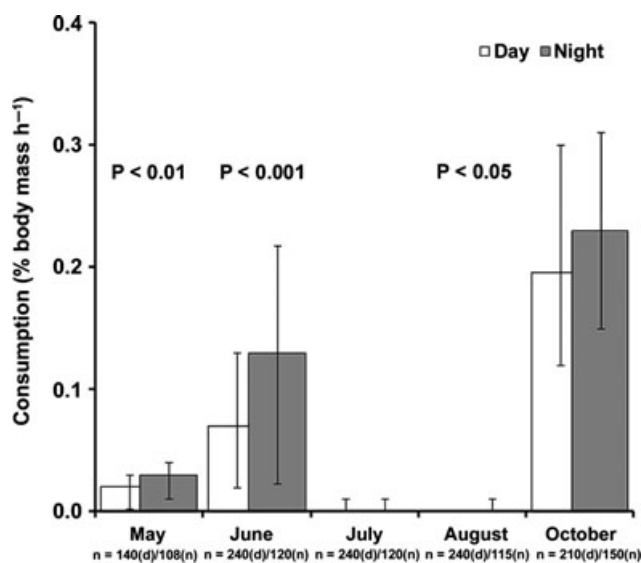

Fig. 4. Diurnal variations in burbot consumption rate (% body mass h^{-1}, median with upper and lower quartiles). Significant differences are indicated by P values (Mann–Whitney U-test, $P < 0.05$). All values standardised for a 100 g fish
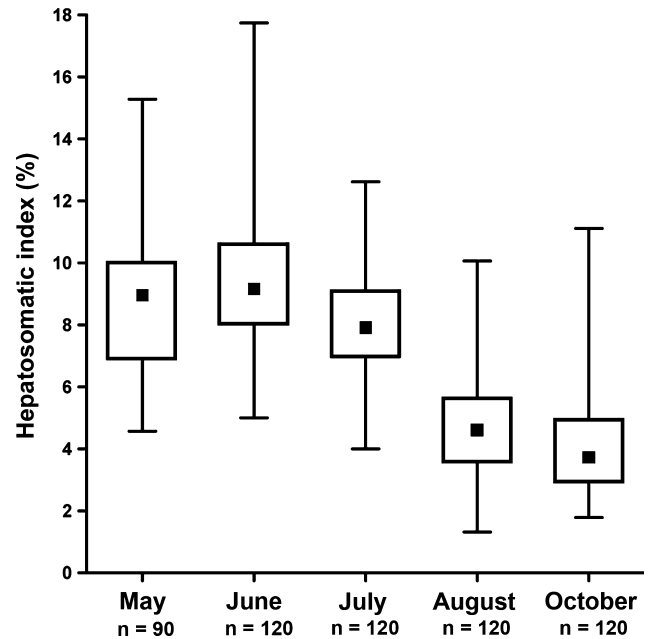

Fig. 5. Seasonal changes of burbot HSI (%), lower Oder River, 2003. Boxes indicate 50% of observations, whiskers 90% and black squares the medians. All values standardised for a 100 g fish

Hepatosomatic index

Medians of HSI slightly increased from May (8.96) to June (9.17) and significantly decreased from June to October (3.7; Kruskal–Wallis test, $P < 0.001$, Fig. 5).

Discussion

Gastric evacuation and temperature

Temperature is probably the most widely studied variable influencing digestion and gastric evacuation and most studies have found an exponential relationship between temperature and gastric evacuation (Bromley, 1994). However, Tyler (1970) and Temming (1995) proposed a domed temperature relationship for cod, with peak evacuation occurring at around 15°C. According to a temperature preferendum determined for burbot at a similar temperature range (e.g. Shodjai, 1980; Pääkkönen and Marjomäki, 2000; Hofmann and Fischer, 2002) and an exponential relationship between R and T for burbot at experimental temperatures between 1.3°C and 12.6°C (Pääkkönen and Marjomäki, 2000), a dome shaped function was expected to describe the gastric evacuation of burbot where the evacuation constant reached its maximum at 15–16°C (Hölker et al., 2004). In contrast, in the present study a linear model fitted best to the data. The complete data set (n = 1683) revealed a continuous decrease of mean gastric evacuation with rising temperatures, while a domed temperature relationship for burbot was not supported, possibly because of the limited number of data points in the intermediate temperature range between 5°C and 18°C. However, our data appeared adequate, since the data points are within the domed temperature relationship for burbot (Hölker et al., 2004) and a similar relationship for cod (Tyler, 1970; Temming, 1995; Fig. 6).

At low temperatures (5°C) the R values of 0.12 estimated from field samples were approximately eight times higher compared to the results of Pääkkönen and Marjomäki (1997), who reported extremely low gastric evacuation constants
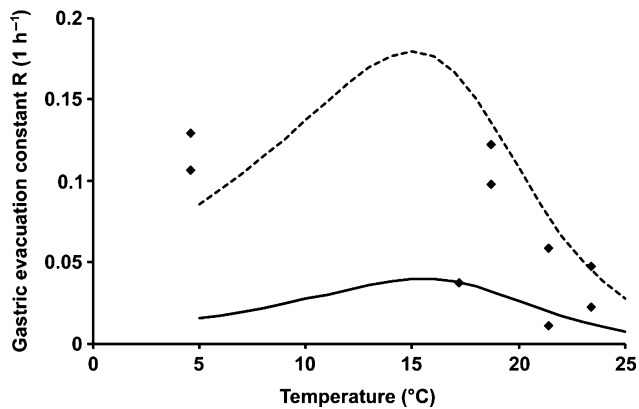
Fig. 6. Gastric evacuation constant (♦) of burbot vs water temperature (°C). All values standardised for a 100 g fish. Dashed curve = adapted results of Tyler (1970) to a temperature optimum model for gastric evacuation developed by Temming (1995) for cod. Solid line = temperature optimum model for gastric evacuation of burbot by Hölker et al. (2004) using the gastric evacuation constants determined by Pääkkönen and Marjomäki (1997)

Table 2
Comparison of gastric evacuation constants (R). Burbot data from this study as well as burbot and cod values from the literature

Author	Species	T (°C)	R (h^{-1})
This study	*Lota lota*	4.6	0.118
		17.2	0.037
		18.7	0.110
		21.4	0.035
		23.4	0.035
Pääkkönen and Marjomäki (1997)	*L. lota*	1.3	0.009
		2.6	0.012
		4.8	0.016
		9.4	0.023
		12.6	0.034
Durbin et al. (1983)	*Gadus morhua*	5.8	0.077
		9.3	0.114
Jones (1974)	*G. morhua*	6.0	0.35
		12.0	0.57
Tyler (1970)	*G. morhua*	2.0	0.051
		5.0	0.063
		10.0	0.143
		15.0	0.184
		19.0	0.139

between 1.3°C (R = 0.009) and 12.6°C (R = 0.034, Fig. 6). This difference may result partly from the different prey items found (at least 90% invertebrates in all sub-samples of stomach content, data not shown) compared to lean fish prey used by Pääkkönen and Marjomäki (1997) in their experiments. However, changes in prey composition alone may not explain gastric evacuation constants that were eight times higher. The burbot used by Pääkkönen and Marjomäki (1997) originated from a Finnish lake, where at least the benthic adult burbot are exposed to a homogeneous water body with low temperatures most of the year. Thus, the differences compared to the burbot population of a summer-warm lowland river may indicate an evolutionary adaptation to very low temperatures and an environment favouring low metabolic rates and low food intake resulting in low growth rates of the Finnish population (Pääkkönen and Marjomäki, 1997). Svärdson (1979) hypothesized that being small-sized might be an adaptation for living in cold environments at reduced food densities (see also Ohlberger et al., 2008). In contrast, the strategy of burbot living in a summer-warm lowland river is to go into energetic debt during summer and boosting it during winter, which requires certain physiological adaptations to maintain a high level of metabolic activity at low water temperatures in winter (Hölker et al., 2004; Binner et al., 2008). The gastric evacuation constant of burbot at 5°C was similar to the R-value of another gadoid species, the cod (Tyler, 1970; Fig. 6). An overview of gastric evacuation constants of burbot and cod is given in Table 2. Other cold adapted fish species showed intermediate values at 5°C. The piscivorous brown trout *Salmo trutta* (L.) had a gastric evacuation constant of 0.064 (Elliott, 1972, 1991) and arctic charr *Salvelinus alpinus* (L.) of 0.062 (Amundsen and Klemetsen, 1988).

In conclusion, the ability of burbot to actively forage during winter and to rapidly digest food at low temperatures provides a mechanism broadening the capacity to survive and successfully colonise environments with high thermal heterogeneity.

Daily ration

The *in situ* determination of temperature effects on daily ration and gastric evacuation was carried out for burbot in a summer-warm lowland river. The increasing daily rations observed at rising temperatures from May to June corresponded well with previous investigations of cod and burbot, indicating an optimum temperature for food consumption (Shodjai, 1980; Rudstam et al., 1995; Temming, 1995; Pääkkönen and Marjomäki, 1997; Hölker et al., 2004). Pääkkönen and Marjomäki (2000) described a polynomial function for the relationship between temperature and consumption and estimated a maximum food intake of 2.62% d^{-1} at 13.6°C, which is close to the ration determined in the lower Oder in June (2.07% d^{-1} at 18.7°C). In contrast, this study revealed the highest value in October at 4.6°C. However it cannot be excluded that the maximum in daily ration will be reached at a temperature between 4.6 and 17.2°C, because this range was not covered by field samplings.

The quantification of the day/night ration (h^{-1}) reflected a nocturnal behaviour of burbot. Therefore, the duration of the night strongly influenced the absolute amount of food consumed. Although nocturnal behaviour was classified as stenotypical for burbot with little modulation by external stimuli (Fischer, 2004), this study revealed very little difference in the feeding activity between day and night in July and August, in particular at the highest temperature in July.

Burbot strongly reduce feeding activity during summer months (Pulliainen and Korhonen, 1990; Pääkkönen and Marjomäki, 1997). Given the length increment of juvenile burbot observed in the lower Oder River in summer (Hölker et al., 2004), an endogenous source was considered to supply the energy required. Within the fish family Gadidae, in general the liver provides an important energy reservoir and a main storage for fat and glycogen (Love, 1980). Balancing the energy flux probably resulted in the decrease of the hepatosomatic index at high temperatures (see also Fig. 5) and its increase during the cool period, when the liver energy was restored. In contrast to most freshwater fish, which reduce growth during the winter months, the evolutionary burden of being cold-adapted inherited from its marine ancestors enables *L. lota* to maintain somatic growth throughout the year (Hölker et al., 2004).

The present study fills gaps in the estimation of *in situ* gastric evacuation rates and food consumption at high

temperatures to enhance bioenergetics modelling approaches for burbot. The reduced food consumption as well as the low gastric evacuation constants at high temperatures confirmed the hypothesis that the liver has to serve as an essential endogenous energy pool to provide energy for maintenance and growth during the summer months (cf. Hölker et al., 2004).

The predicted global change will potentially affect this adaptive strategy of burbot if periods of stressfully high temperatures become substantially longer. An elongated period of higher energy requirements, less food consumption and lower gastric evacuation may not be compensated by energy-rich liver tissue or may exhaust the energy storage of the liver to a degree that it cannot be restored during the shorter periods of preferred temperatures.

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