

Jari-Pekka Pääkkönen

Feeding Biology of Burbot, *Lota lota* (L.):  
Adaptation to Profundal Lifestyle?



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## ABSTRACT

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Diss.

The aims of this thesis are to determine the role of burbot in the freshwater ecosystem and clarify how the feeding biology and behaviour have been affected by the profundal life style of burbot.

The gastric evacuation rates of burbot fed single fish meals were measured under various experimental conditions. The gastric evacuation rates of the burbot were affected by water temperature and meal size in the temperature range of 1.3-12.6°C, as has earlier been observed about several fish species. However, the stomach emptying rates were low compared to other freshwater fish species. As stomach emptying is prolonged, the stomach can act as a reserve of food during the periods of low prey availability.

In the experimental conditions, the estimated optimum temperature for food intake ( $\text{g g}^{-1}$ ) was 13.6°C. Food consumption estimates suggest that burbot are potential competitors for food with other piscivorous fish. Seasonal changes in burbot's diet may, however, decrease their impact on prey fish species.

Indeed, the profundal life style provides the adaptation to nearly zero illumination and low temperatures. Ambush feeding behaviour with low metabolic rates are characteristic of the burbot, a major predator in various freshwaters. The burbot has adapted to use dark periods of the day for activity during most of the year. Food composition and stomach fullness data suggest that burbot are periodic and opportunistic feeders, that have adapted to prey under unpredictable food conditions.

Key words: Activity; burbot; feeding; gastric evacuation; metabolic rate; oxygen consumption; temperature.

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## List of original publications

This thesis is based on five original articles, which will be referred to by their Roman numerals (I-V). Some additional data are also presented.

I. Pääkkönen, J.-P. J. & Marjomäki, T. J. 1997: Gastric evacuation rate of burbot fed single-fish meals at different temperatures. - *Journal of Fish Biology* 50: 555-563.

II. Pääkkönen, J.-P. J., Myyrä, R. & Marjomäki, T. J. 1999: The effect of meal size on the rate of gastric evacuation of burbot, *Lota lota* (L.). - *Ecology of Freshwater Fish* 8: 49-54.

III. Pääkkönen, J.-P. J. & Marjomäki, T. J. 2000: Feeding of burbot, *Lota lota*, at different temperatures. - *Environmental Biology of Fishes* 58: 109-112.

IV. Pääkkönen, J.-P. J. & Lyytikäinen, T. 2000: Oxygen consumption of Burbot (*Lota lota*) fed different rations of vendace (*Coregonus albula*). - *Journal of Applied Ichthyology* (in press)

V. Pääkkönen, J.-P. J., Laitinen, M. & Marjomäki, T. J. 2000: Total activity of burbot *Lota lota* (L.) measured with bioelectronic monitoring system: seasonal differences in activity length. In: V. L. Paragamian and D. W. Willis (eds), *Burbot: biology, ecology, and management*. American Fisheries Society, Fisheries Management Section, Publication Number 1, Bethesda. (in press)

# 1 INTRODUCTION

The burbot (*Lota lota* L.) is the only true freshwater gadoid species (Scott & Crossman 1973). Along with the pike (*Esox lucius*), the burbot has the widest longitudinal distribution of all freshwater fish ranging from the British Isles across Europe and Asia to the Bering Strait and from Alaska across the North American continent to the Atlantic coast (McPhail 1997).

The burbot is an opportunistic feeder, preying on zooplankton, invertebrates and fish in varying proportions during its lifetime (Daan et al. 1990, Guthruf et al. 1990, Ghan & Sprules 1993, Fratt et al. 1997, Wang & Appenzeller 1998). Juveniles live in shallow water near shores. At their third or fourth year, they become mature and move to deeper water areas. The depth distribution of the adult burbot has been observed to reflect the preference for cooler water (Bernard et al. 1993). In dimictic lakes with cool epilimnia (<12°C), adult burbot are distributed across all depths and are seldom observed at temperatures higher than 12°C (Bernard et al. 1993, Carl 1995).

As the burbot grows, the proportion of fish in its diet becomes larger and in many lakes, the burbot is one of the most abundant predatory fish species. Burbot population size may be up to 600 ind. ha<sup>-1</sup> and it varies, of course, between lakes and years. In small and moderate sized Alaskan lakes the population density estimates were 0.4 to 15 burbot ha<sup>-1</sup> (Bernard et al. 1993). In Julian's Reef, Lake Michigan, the burbot population density ranged from 0 to 571 burbot ha<sup>-1</sup>, the average being 139 burbot ha<sup>-1</sup> (Edsall et al. 1993). Since its diet overlaps with other piscivorous species, a question has been raised whether the burbot is able to compete for food with more valuable fish species (e.g. salmonids) or even with fisheries (Carl 1992, Edsall et al. 1993, Carl 1995, Rudstam et al. 1995, Fratt et al. 1997; Tolonen et al. 1999). However, due to the lack of knowledge of burbot feeding processes and the effect of temperature on the physiology of burbot these suggestions have been based on the physiological parameters of other gadoids.

The food consumption rates of fishes is commonly estimated with two methods: fish bioenergetics or gastric evacuation models. In this paper, the gastric evacuation approach has been chosen for two reasons: firstly, there is no bioenergetics model for burbot, and secondly, the gastric evacuation models have been suggested to predict well the food consumption of predatory fish. Gastric evacuation approach assumes that the amount of food evacuated in a time unit mirrors the amount of food eaten (Bromley 1994). Stomach emptying has been studied for various fish species in order to find out the gastric evacuation rates on artificial and natural diets and the factors affecting the evacuation rates (e.g. Persson 1981, Grove et al. 1985, dos Santos & Jobling 1991, Elliott 1991, dos Santos & Jobling 1992, Singh-Renton & Bromley 1996, Ruohonen et al. 1997, Hop & Tonn 1998, Andersen 1999). Food consumption models have been derived from the gastric evacuation rates (Elliott & Persson 1978, Eggers 1979, Bromley 1991, dos Santos & Jobling 1995).

The adaptation of organisms is commonly divided into two components: genetic and non-genetic adaptation (Cossins & Bowler 1987). Genetic adaptation is the fundamental element of evolution. Genetically determined characters that enhance individuals' survival and reproduction in their environment will gradually be fixed over time. Non-genetic adaptations or acclimatisation involve changes in individuals' performance over life-time. Thus, acclimatisation causes changes in the phenotype within the limits of the genotype. Variation in the environmental cues, e.g. temperature, light regime and salinity induces the acclimatisation processes of the individual in nature.

Optimal habitat selection theory predicts that an animal should select the habitat which produces the highest fitness (Godin 1997). Fitness is constructed of various components and it is not usually possible to maximise all of them at the same time, and trade-offs occur. For example, fish can select between predation risk, prey capturing and energetic costs. The prediction of the habitat selection requires information on all major effects of the habitat on the fitness of the fish. Usually, complex life-history or bioenergetics models are required to determine the fitness function and spatial distribution of fish (Godin 1997). As a cold water fish, the burbot spends most of its adult life in profundal habitats at low temperatures. This profundal life provides physiological and behavioural adaptations which have been studied in this thesis.

## 2 OBJECTIVES

The aims of this thesis are to determine the role of burbot in the freshwater ecosystem and clarify how the feeding biology and behaviour have been affected by the profundal life style of burbot.

A series of experiments has been carried out in order to:

- 1) measure the gastric evacuation rate of burbot fed fish meals under various experimental conditions
- 2) evaluate the validity of the gastric evacuation model
- 3) estimate how much food a burbot population can consume during a year
- 4) and finally, find out whether food composition, growth, gastric evacuation, and both seasonal and daily activity indicate adaptation to living in profundal environment at low temperatures.

### 3 MATERIAL AND METHODS

The burbot used in the experiments were caught with trapnets and stake nets from Lake Päijänne (central Finland) during the spawning season in January–March. The burbot were transferred to the Tammen Mylly Laboratory of the University of Jyväskylä, Leivonmäki, Finland (Rutajoki 62°N, 26°E) and held under laboratory conditions in a 2 m<sup>3</sup> tank (2 x 2 x 0.5 m) prior to the experiment. The burbot were fed a variety of food organisms [chironomids, smelt *Osmerus eperlanus* (L.), perch *Perca fluviatilis* (L.) and vendace *Coregonus albula* (L.)] before the experiments. A natural photoperiod was used before and during the experiments. The inlet water was extracted from the River Rutajoki. All the feeding of the burbot was voluntary. The burbot were offered meals by hand and if a burbot did not eat, the meal was offered to another fish.

#### 3.1 Food composition and growth of burbot

Stomach samples were collected from a total of 190 burbot from 1993 to 1999. The samples were from February to November. The winter time samples (February–April) were pooled. The burbot were caught by fishing overnight with gillnets from the profundal (>10 m) of six lakes located in central Finland (Table 1). The total length was measured to the nearest millimetre (mm) and the burbot were weighed to the nearest gram (g). The age was determined from the otoliths. The stomach contents was weighed (0.01g accuracy) and related to the corrected burbot mass (= burbot mass - stomach content mass). The stomach contents were frozen (-18°C) for further analysis. In the laboratory, prey items were divided into fish and invertebrate classes. Occurrence was defined as the percentage of all the burbot stomachs which contained at least one of the prey taxon under consideration.

TABLE 1 The number of burbot caught (n) for stomach content and growth analysis.

	Latitude	Longitude	n
Lake Puulavesi	61°40' N	26°30' E	63
Lake Päijänne	61°54' N	25°35' E	48
Lake Leppävesi	62°18' N	26°00' E	35
Lake Konnevesi	62°20' N	26°30' E	28
Lake Kynsivesi	62°05' N	26°15' E	11
Lake Suontee	61°40' N	26°05' E	5

### 3.2 Gastric evacuation rates at different temperatures (I)

The temperature effect on the gastric evacuation rate (GER) of the burbot fed a single meals (4 or 8 grams) of vendace was studied at five different temperatures. Stomach samples were collected at varying intervals after feeding, and observations were terminated when first empty stomachs were observed. Three different models (linear, square root and exponential) were fitted to the dry-weight based data. Any temperature effect on the gastric evacuation rate was estimated by fitting an exponential equation into instantaneous gastric evacuation estimates. The adjusted non-linear coefficient of determination (adj.  $r^2$ ) provided a measure of the goodness of the model.

$Q_{10}$  values were used to examine more closely the effect of temperature on the stomach evacuation of burbot.  $Q_{10}$  values were calculated from the equation:

$$\text{Log}_{10}Q_{10} = \frac{10(\log_{10}R_2 - \log_{10}R_1)}{T_2 - T_1}$$

where  $R_1$  and  $R_2$  were instantaneous gastric evacuation rates and  $T_1$  and  $T_2$  were water temperatures.

### 3.3 The effect of meal size on the GER (II)

The meal size effect on the gastric evacuation rate of the burbot was studied at the constant temperature of 1.5°C. The burbot were fed single meals of whole vendace at the beginning of the experiment. The wet weight of a vendace meal ranged from 2.0 to 16.8 g (1.0-12.6 % of burbot weight). The burbot were randomly selected to be fed different meals. At fixed intervals from 6 to 24 h, the burbot were killed and stomach samples were collected. The stomach

samples were dried at 60°C and the data was divided into six meal size categories.

An exponential model was fitted in each size category and the relationship between the instantaneous gastric evacuation rate ( $R_e$ ) and the mean relative meal size ( $W_v/W_b$ ) was examined by fitting a power function in the data. Modified versions of exponential and power exponential models were fitted in the pooled data to estimate the best model to describe the meal size effect on the gastric evacuation rate of the burbot. Power exponential model was used to estimate daily gastric evacuation rates of a standard-sized burbot.

Goodness of fit values was justified on the basis of an adjusted  $r^2$ -value. The coefficient of determination was considered to be valid if the residuals did not correlate with dependent factors, were normally distributed and if the parameter estimates were statistically significant.

### **3.4 The effect of meal composition on the GER (I, II)**

The effect of different food species on the gastric evacuation rate (I) was studied using perch, smelt and vendace as meal objects at 2.6°C. The mean energy content of each prey species was measured using the bomb calorimetric method. The differences in the instantaneous gastric evacuation rates of the different food species were tested with ANOVA, and the mean energy content of the different food species was tested with Bonferroni-test.

In the experiment determining the effect of the number of prey items in the meal on the GER in the burbot (II), the fish were fed meals consisting of one vendace or three smaller vendace of an equal total weight of 3 grams at 1.5°C. The data were pooled and a dummy parameter (D) was introduced in the power exponential model to find possible differences in stomach emptying between various meal compositions.

### **3.5 Feeding of burbot at different temperatures (III)**

The feeding of burbot was studied at four temperatures. The burbot were offered vendace meals once a day consisting of ten vendace resulting a mean total weight of 30.2 g (+1.1). The burbot were allowed to feed 10 minutes and the uneaten vendace were removed and the amount of the food eaten was calculated.

Mean daily food intake (MDI) and relative food intake (RDI) values were calculated for each fish. The effect of the temperature on the daily food

intake was tested with general ANOVA analysis with burbot weight as a covariate. The maximum food intake values and temperatures were calculated from MDI and RDI values after fitting a quadratic model.

Annual food consumption estimates were calculated from the RDI values for different burbot densities.

### 3.6 The amount of previous meals remaining in the stomach at the moment of feeding on the next meal

A modified version of the exponential model that included the effect of the meal weight in relation to the burbot weight and the effect of temperature on gastric evacuation (I) was applied to each set of data obtained from the burbot feeding experiment (III). This allowed the estimation of the mean amount of food remaining in the burbot stomach at the moment of feeding the next meal at different temperatures (2.4, 5.1, 10.8 and 23.4°C). Each item of food consumed was expected to be evacuated separately, and the quantity of the meal remaining in the stomach at the moment feeding on the next meal ( $t$ ) was therefore calculated as:

$$W_t = W_0 e^{(-0.068e^{0.023T} + 0.087(W_w / W_b)^{0.110})t},$$

where  $W_t$  is the dry weight of the food remaining in the stomach,  $W_0$  is the dry weight of the meal and  $W_w$  and  $W_b$  are the wet weight of the meal at the moment moment of feeding and the weight of the burbot, respectively, and  $t$  is the time period between meals (h).

The cumulative amount of previous meals remaining in the stomach (g dry weight) at the moment of feeding ( $t$ ) on the next meal ( $W_f$ ) was

$$W_f = \sum_{m=1}^n W_{t_m},$$

where  $m$  is the number of separate meals eaten before the next meal. Values were then transformed into wet weights

$$W_w = (W_f + 0.013) / 0.206$$

and related to the burbot weight.

An analysis of variance (ANOVA) with Tukey Honest *post hoc*-test was used to determine the differences in the meal weight at the moment of the next meal at different temperatures.



### 3.7 Estimation of the daily amount of food evacuated from the stomach

The daily amount of food evacuated from the stomach was estimated from an exponential model of the daily food intake values at temperatures 2.4, 5.1, 10.8 and 23.4°C (III). The evacuation of each meal was treated separately and was estimated as:

$$W_{t+24} = W_t e^{(-0.068e^{0.023 \cdot T} + 0.087(W_w / W_b)^{0.110})24}$$

where  $W_{t+24}$  is the weight of the meal remaining in the stomach of fish 24 h after the moment of feeding.

The amount of each food item ( $DE_m$ ) evacuated from the stomach within 24 h was calculated as

$$DE_m = W_t - W_{t+24}$$

The daily amount of food evacuated from the stomach ( $g\ d^{-1}$ ;  $DE_{tot}$ ) was calculated as

$$DE_{tot} = \sum_{m=1}^n DE_m$$

where  $m$  is the number of meals in the stomach.

$DE_{tot}$  values were transformed into wet weight (MDE;  $g\ d^{-1}$ ) and related to the burbot weight (RDE;  $g\ g^{-1}\ d^{-1}$ ). Mean values were calculated and compared to the observed food intake values (MDI and RDI) obtained from III.

### 3.8 Oxygen consumption measurements (IV)

The oxygen consumption of 19 burbot was measured at 2.1°C prior to and after feeding of a vendace meal. Meals consisted of one or several vendace and the total weight of meals varied from 2.6 to 17.8 g (1.1-8.5 % of the burbot weight). Oxygen consumption ( $mg\ kg^{-1}\ h^{-1}$ ) was measured once a day for 13 to 15 days after feeding.

The fasting metabolic rate was estimated as a mean oxygen consumption rate of four day pre-feeding. The effect of the meal size on the oxygen consumption of the burbot ( $M_{75}$ ) was estimated with an exponential gastric evacuation model for the time period required to digest 75% of a meal ( $t_{75}$ ). Linear regression was used to estimate the dependence of  $M_{75}$  on the meal

ratio and the fasting metabolic rate. Apparent heat increment was estimated as the difference between the mean metabolic rate for  $t_{75}$  and the fasting rate of each fish.

The proportion of the energy of an ingested meal used in the apparent heat increment ( $AHI_{PROP}$ ; %) was estimated from the difference between the mean fasting metabolic rate and the mean metabolic rate of each fish during  $t_{75}$ . The difference was converted to energy with an oxyenergetic equivalent (13.59  $\text{kJ g}^{-1}$  oxygen consumed) and related to the energy concentration of the vendace meal that an individual had consumed.

The peak value of the apparent heat increment ( $AHI_{PEAK}$ ) was estimated as the highest oxygen consumption value within the period  $t_{75}$ . The correlation between the meal ratio and  $AHI_{PEAK}/MO_{2FAST}$  was estimated with a non-parametric Spearman-test.

### 3.9 Total activity of burbot (V)

Nine measurements of activity were made with the bioelectronic monitoring system [BEM, (Microvolt Oy, Helsinki)] in March 1997 - February 1998. The first experiment was started after the spawning in March 1997. The burbot were placed individually in a 53 l monitoring aquarium (174 l aquaria were used in the experiment no. 6, V) and allowed to acclimate for 3 d after the transfer. The burbot were then monitored for 7 - 22 d.

Diurnal activity was studied by comparing the mean activity rates of each burbot for day and night on each valid 24h period starting from midnight. The distributions of day and night observations were tested by  $\chi^2$ -test. The length of the activity period of the burbot was studied by correlating the observed length of the activity period of the burbot with the day length (h) and the mean water temperature during the experimental period. Spectral analysis (single series Fourier analysis) was used to reveal a possible cyclical patterns in the activity of the burbot in different experiments. Spectral analysis periods greater than 48 h were excluded from the results.

## 4 RESULTS AND DISCUSSION

### 4.1 Food composition and growth of burbot

Adult burbot (total length 159-710 mm, n=192) had seasonal variation in their food composition (Table 2). Fish was common during winter and early summer (February-June). In July-August, invertebrates became common, and their occurrence decreased towards the winter.

TABLE 2 Seasonal variation in the food composition of burbot. Occurrence (%) is defined as the number of burbot in which prey taxon (fish or invertebrate) occurs as a percentage of the number of predators with prey.

	Burbot length range (mm)	Fish %	Invertebrate %	Empty stomachs n	Total n
Feb-Apr	310-495	100	8.3	2	14
May	200-710	92.3	30.8	5	31
Jun	159-419	81.3	62.5	1	17
Jul	228-362	35.3	88.2	3	20
Aug	220-412	47.1	100	1	18
Sep	194-385	60.0	90.0	5	15
Oct	162-523	47.7	81.8	7	51
Nov	200-535	54.5	72.7	4	26

In July, the dominant invertebrate species was *Mysis relicta* and in August *Pallasea quadrispinosa*. The lowest stomach contents (g) were observed during July-September (Table 3). The occurrence of invertebrate species (chironomids, *Mysis relicta* and *Pallasea quadrispinosa*) was larger during the summer months, and therefore, the proportion of fish in the diet declined. In summer,

the high occurrence for invertebrates might have been caused by the changes in prey fish swimming speeds compared to burbot swimming speeds due to the higher water temperature. During the warmer water period, prey fish are suspected to be capable of escaping the ambush predator more efficiently. Also, the habitat shift of prey fish from profundal wintering areas to pelagic areas

TABLE 3 The observed and relative weights of burbot stomach contents.

	Mean stomach content g (s.d.)	min-max g	Relative mean stomach content % burbot weight ( $\pm$ s.d)	min-max % burbot weight	n
Feb-Apr	16.7 ( $\pm$ 16.12)	0-42.3	4.2 ( $\pm$ 5.46)	0-20.4	14
May	18.2 ( $\pm$ 29.11)	0-119.3	3.4 ( $\pm$ 4.07)	0-12.8	31
Jun	17.5 ( $\pm$ 49.85)	0-209.2	4.8 ( $\pm$ 8.17)	0-34.3	17
Jul	2.7 ( $\pm$ 5.20)	0-18.9	1.5 ( $\pm$ 3.06)	0-10.7	20
Aug	5.7 ( $\pm$ 8.00)	0-23.8	2.6 ( $\pm$ 3.09)	0-8.9	18
Sep	2.8 ( $\pm$ 5.29)	0-16.8	1.1 ( $\pm$ 1.77)	0-5.2	15
Oct	15.8 ( $\pm$ 43.41)	0-275.5	3.6 ( $\pm$ 7.16)	0-36.6	51
Nov	22.3 ( $\pm$ 40.43)	0-162.4	4.0 ( $\pm$ 4.91)	0-18.7	26

may reduce encounter probabilities. The results are in agreement with previous studies on burbot diet in different lakes, although the number of the fish examined in our study were low in February-April (Bailey 1972, Sandlund et al. 1985, Guthruf et al. 1990). Burbot can eat large amounts of food in their stomachs (Table 3). Higher maximum stomach contents were observed in months when fish were predominant prey species. The highest observed stomach content was observed in October, and was almost 40% of the burbot's own weight (Table 3). Empty stomachs were observed in all months.

The growth of burbot seems to be lower than the growth of other large pelagic predators (pike, pike-perch, *Stizostedion lucioperca*) and brown trout, *Salmo trutta*). Especially after the age of 3 to 4 years, the growth of the burbot decreased (Fig. 1). The decline in growth occurs at the same time as the burbot matures and moves from the littoral to profundal life style.

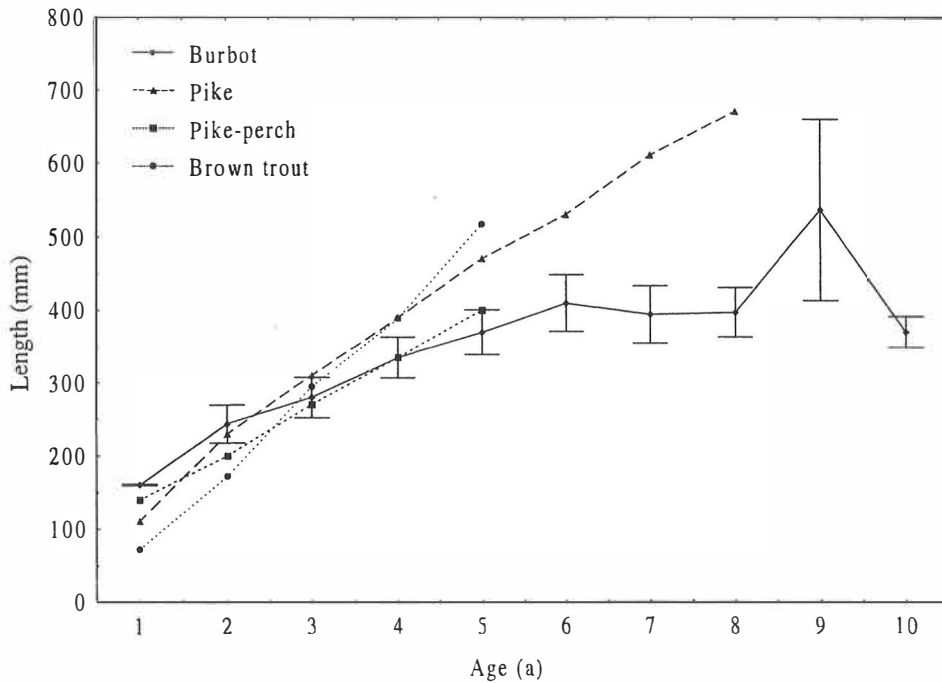


FIGURE 1 Length per age of burbot and some pelagic predators (from Lake Saimaa, Viljanen et al. 1982).

## 4.2 Gastric evacuation rates at different temperatures (I)

An exponential model fitted best in the gastric evacuation pattern of the burbot (Table 2 in I). The gastric evacuation rates of the burbot were affected by changes in the temperature. The GER of the burbot increased with temperature but was lower than that observed in other freshwater species (Fig. 2).

The effect of the temperature on the GER was low suggesting that the benefit of temperature change is low for burbot. Similar low gastric evacuation results have been obtained from polar cod (*Boreogadus saida*) which constantly lives in near-zero temperatures (Hop & Tonn 1998. Sæther et al. 1999).

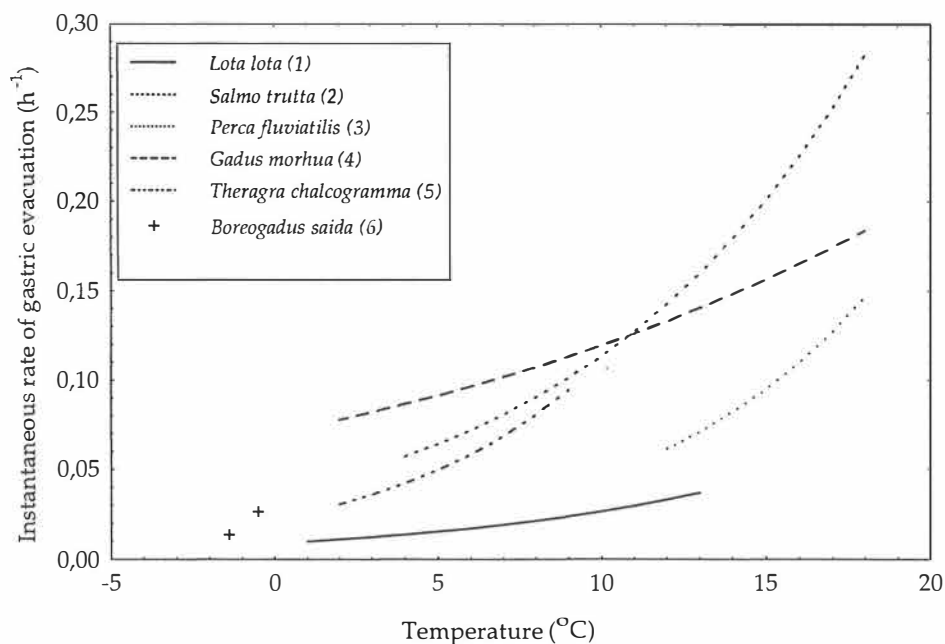


FIGURE 2 Instantaneous gastric evacuation rates of (1) burbot (I), (2) brown trout (*Salmo trutta*) (Elliott 1991), (3) perch (*Perca fluviatilis*) (Persson 1981), (4) Atlantic cod (*Gadus morhua*) (Tyler 1970), (5) walleye pollock (*Theragra chalcogramma*) (Smith et al. 1989) and (6) Arctic cod (*Boreogadus saida*) (Hop & Tonn 1998) at different temperatures estimated from temperature dependence functions (except for observed rates for Arctic cod (6)).

TABLE 4  $Q_{10}$  values (between temperatures) calculated from the observed instantaneous gastric evacuation rates ( $R_e$ ) for burbot at different temperatures

Temperature (°C)	$R_e$ ( $h^{-1}$ )	$Q_{10}$
1.3	0.009	9.14
2.6	0.012	3.70
4.8	0.016	2.20
9.4	0.023	3.39
12.6	0.034	

$Q_{10}$  value for temperature range calculated from the function between the temperature and gastric evacuation rate was 2.97 (p. 559 in I). However,  $Q_{10}$

values were much higher in lower temperatures if calculated from the actual instantaneous gastric evacuation values, suggesting that metabolic rates are strongly affected in low temperatures (Table 4). Generally,  $Q_{10}$  values do not remain constant over an entire temperature range, and are often found to be high at low temperatures (Jobling 1994). Hop & Graham (1995) observed values of 6.7 to 7.1 for juvenile arctic cod when the temperature increased by 2.3°C (temperature range -0.5 to 2.7°C). In burbot,  $Q_{10}$  value for a temperature increase of 1.3°C was 9.14.

### **4.3 The effect of the meal size on the GER (II)**

Meal size affected the gastric evacuation rate of the burbot as observed in other gadoids (Table 1 in II, Jones 1974, dos Santos & Jobling 1991, Andersen 1999). The instantaneous rate of evacuation ( $h^{-1}$ ) decreased but the absolute rate ( $g d^{-1}$ ) increased with increase in meal size. The meal size factor ( $b=0.744$ ) was observed to be between surface-area ( $b=0.66$ ) and volume-dependent ( $b=1$ ) gastric evacuation models (Table 2 in II). Due to the decreased instantaneous gastric evacuation rates, the stomach emptying times were prolonged when the burbot fed large meals. The food in the burbot stomach, however, was observed to form a single bolus, which may suggest that the surface-area of the total bolus is more important for the regulation of the evacuation process than the total volume of the bolus.

### **4.4 The effect of meal composition on the GER (I, II)**

Energy concentration of fish meal or meal composition had no effect on the gastric evacuation rate of the burbot (Table 4 in I, Table 4 in II). Generally, diets with a high energy content are evacuated from the stomach more slowly than low energy diets (Grove et al. 1978, Flowerdew & Grove 1978, dos Santos & Jobling 1988). The number of eaten prey items did not affect the instantaneous gastric evacuation rate in the burbot. Thus, the total surface area of bolus is a more important factor on the gastric evacuation rate than the total surface-area of the individual prey items. This is in agreement with the result obtained for cod (dos Santos & Jobling 1991). The same instantaneous gastric evacuation rate can be used for the examined prey fish species (vendace, smelt and perch) in gastric evacuation models for burbot. Also, the total number of single items eaten is negligible for the gastric evacuation estimation on burbot, but the original mass of the whole bolus must be known.

#### 4.5 Feeding of burbot at different temperatures (III)

The daily food intake of the burbot ranged from 2.3 to 4.8 g d<sup>-1</sup>, the estimated maximum food intake value was 5.4 g d<sup>-1</sup> at 13.6°C, and the maximum relative food intake was 0.029 g g<sup>-1</sup>d<sup>-1</sup> at 14.4°C (Table 1 in III). Food consumption estimates of burbot with different biomass estimates (Table 3 in III) suggest that burbot are potential competitors for food with other piscivorous fish. Burbot have, however, seasonal changes in their diet and consume more invertebrate food items during the warm water period (Guthruf et al. 1990), which decreases burbot impact on the prey fish species. Also, the body shape of the burbot indicates adaptation to sedentary life compared to most predatory fish common in northern freshwaters.

Biomass or density of burbot are difficult to be estimate. It is problematic to count fish that are mostly sessile and stay in deep lightless water bodies. Submersible vessels have been successfully used in order to make estimates of burbot densities in Great Lakes (Edsall et al. 1993), but more studies are needed to be able to estimate accurate burbot biomasses.

#### 4.6 The amount of previous meals remaining in the stomach at the moment of feeding on the next meal

The stomach fullness at the moment of feeding the next meal was estimated with the modified exponential gastric evacuation model, and it varied between different temperatures ( $F_{3,53}=6.75$ ;  $p<0.001$ ). However, only at 23.4°C did stomach fullness differ statistically significantly from other experimental temperatures (Fig. 3). At temperatures below 11°C, the return of appetite in the burbot was observed when about 3 % of the total wet weight of the previous meals relative to the burbot weight remained in the stomach. At 23.4°C this percentage was 0.5%. These stomach fullness observations are in agreement with previous studies that most fish will take food before their stomachs are fully emptied (Bromley 1994). For burbot, however, this period between feedings is long.



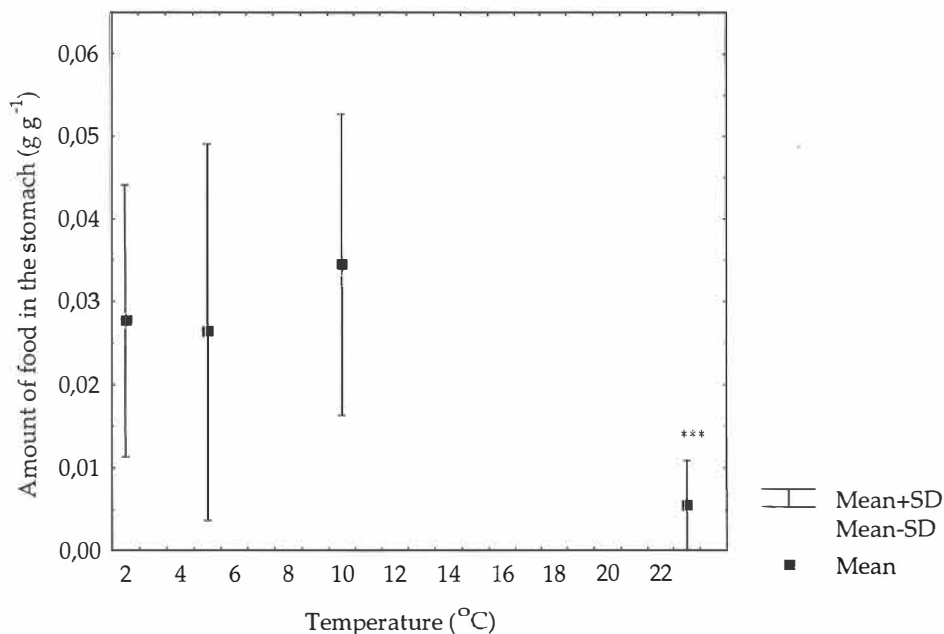


FIGURE 3 Estimated amount of food left ( $\text{g g}^{-1}$ ) in the stomach of the burbot at the moment of feeding the next meal at different temperatures. (symbol \*\*\* indicates significant difference between groups (Tukey Honest test,  $p < 0.05$ ).

#### 4.7 Estimation of the daily amount of food evacuated from the stomach

Temperature has a significant effect on the daily amount of food evacuated from the stomach ( $\text{Kruskal-Wallis } H(3, N=814) = 108.438; p < 0.001$ ; Table 5). The predicted mean daily evacuated (MDE,  $\text{g d}^{-1}$ ) and the relative amount of food evacuated (RDE,  $\text{g g}^{-1} \text{d}^{-1}$ ) estimates were close to the observed mean daily (MDI) and relative food intake (RDI) values and the difference was not statistically significant (Wilcoxon matched pairs test,  $p > 0.05$ ; Table 5).

Thus, in the experimental conditions the amount of food evacuated from the stomach of the burbot equals the average food intake rate in the same time unit. Similar results have been obtained for other gadoids. Observed and estimated daily consumption values ( $\text{g d}^{-1}$ ) of Atlantic cod were similar for the different food species (dos Santos & Jobling 1995). Our exponential gastric evacuation model predicts well the gastric evacuation process in burbot. With the data of temperature and the amount of food eaten it is possible to predict daily ration estimates for burbot within the temperature range of 1.3- 12.4°C.

TABLE 5 The predicted mean daily evacuated (MDE,  $\text{g d}^{-1}$ ) and the relative amount of food (RDE,  $\text{g g}^{-1}\text{d}^{-1}$ ) from the stomach of burbot (*Lota lota* (L.)) at different temperatures fed vendace (*Coregonus albula* (L.)). MDI and RDI values are from III.

Temperature °C	MDE $\text{g d}^{-1}$ (s.e.)	MDI $\text{g d}^{-1}$ (s.e.)	RDE $\text{g g}^{-1}\text{d}^{-1}$ (s.e.)	RDI $\text{g g}^{-1}\text{d}^{-1}$ (s.e.)	n
2.4	2.12 (0.298)	2.31 (0.31)	0.010 (0.001)	0.011 (0.001)	18
5.1	3.01 (0.555)	3.42 (0.74)	0.012 (0.002)	0.014 (0.002)	15
10.8	5.07 (0.719)	4.83 (0.76)	0.025 (0.003)	0.024 (0.004)	16
23.4	2.75 (0.558)	2.58 (0.53)	0.017 (0.004)	0.016 (0.003)	12

#### 4.8 Oxygen consumption measurements (IV)

The fasting oxygen consumption values for the burbot were lower than those observed for another gadoid fish, *Gadus morhua* (Lydon et al. 1992; Blaikie and Kerr 1996). The increase in the oxygen consumption of the burbot was observed for several days after feeding and the apparent heat increment (AHI) correlated positively with the meal ration (Fig. 2 in IV). Also, the observed AHI peak values correlated significantly with the meal ration. The meal ration had no effect on the proportion of the ingested energy used in the apparent heat increment. The metabolic rates of the burbot were close to the rates of Arctic and sedentary temperate fish that have adapted to live in constant low temperatures (Holeton 1974, Johnston et al. 1991, Hop & Graham 1995). The observed low oxygen consumption rates indicate that the metabolic processes of burbot are reduced during day time at low temperatures. These low oxygen consumption rates are in contrast to the hypothesis that fish adapted to cold should have considerably elevated resting or standard metabolic rates compared to fish adapted to live in warmer waters (Krogh 1914). The benefits of high resting or standard metabolism have been questioned because they tend to imply high energy costs (Holeton 1974). In fact, for burbot, it is probably beneficial to have low metabolic rates with periodic feeding because more energy is then left for the growth.

#### 4.9 Total activity of burbot (V)

The burbot had clear seasonal variation in activity patterns (Table 2 in V). The fish were nocturnally active during July-February and the mean length of the activity period was longer during winter than summer (Fig. 8 in V). In mid winter (February), activity started immediately after sunset and continued until sunrise. The highest activities were observed a few hours before sunrise or after sunset. In summer (July), activity peaks were observed randomly and the

duration of activity was only few hours at a time. Spectral analysis distinguished clear rhythms in the activity. Activity periods were shorter in the summer experiments and the cycles became longer towards the winter (Table 6).

Fish may avoid contact with predatory fish by selecting an opposite activity rhythm and take advantage of light conditions unfavourable for visual predators (Greenwood & Metcalfe 1998). Adult burbot, however, have only few predators and activity changes are probably not due to predation but more likely due to the change in light conditions and temperature.

TABLE 6 Three longest observed and predicted periods (h) of spectral analysis (single Fourier analysis) for burbot in different activity experiments. Frequency is the number of cycles per hour. Cosine and sine coefficients and periodogram values are also given. Spectral analysis periods greater than 48h were excluded from the results.

Experiment date	Observed period (h)	Spectral analysis periods (h)	Frequency	Cosine coefficient	Sine coefficient	Periodogram value
Jan 1-9, 1998	21.79	12.00	0.0833	-314.38	81.83	107638532
		25.50	0.0392	-14.82	-219.21	4923889
		7.55	0.1324	18.18	182.93	3446893
Jan 30-Feb 6, 1998	19.38	25.43	0.0393	-16.89	-619.68	34201884
		22.25	0.0449	-284.15	521.61	31395830
		11.87	0.0843	-389.43	-203.66	17188976
Mar 20-31, 1997	7.19	9.67	0.1034	-175.69	5.411	4479719
		36.25	0.0276	-118.73	-13.25	2069484
		9.36	0.1069	89.20	79.13	2061605
Apr 3-17, 1997	6.12	12.00	0.0833	-15.34	-129.91	2874972
		6.22	0.1607	-97.94	29.04	1756220
		24.00	0.0417	25.26	73.56	1016218
Jul 2-9, 1997	5.08	42.00	0.0238	37.39	204.63	3634672
		28.00	0.0357	28.96	124.68	1376227
		4.00	0.250	80.28	81.27	1096109
Jul 11-18, 1997	5.58	5.68	0.1761	22.39	162.94	2606315
		5.87	0.1704	107.44	72.89	1483299
		11.00	0.091	-2.39	124.41	1362585
Sep 1-7, 1997	4.00	4.06	0.2466	188.68	31.89	2673001
		6.08	0.1644	86.80	128.00	1745988
		4.42	0.2260	-118.12	-72.39	1401148
Sep 10-22, 1997	12.95	23.23	0.0430	-72.52	273.97	12128521
		15.10	0.0662	203.94	-68.82	6995445
		25.17	0.0397	76.28	-195.62	6666967
Nov 19-28, 1997	15.46	23.00	0.0435	495.76	664.817	79092144
		28.75	0.0348	-529.54	-202.13	36946138
		25.56	0.0391	-233.69	-255.68	13797947

## 5 CONCLUSIONS

The burbot has adapted to use dark periods of day for activity during most of the year. Food composition and stomach fullness data suggest that burbot are periodic and opportunistic feeders, that have adapted their feeding behaviour to irregular feeding conditions. When the chance for feeding comes burbot are capable of catching and eating large quantities of prey at low temperatures due to their very elastic stomachs. As an ambush predator, the burbot benefits from the ability to feed large meals. Also the low food processing rates may be a sign of adaptation to irregular feeding of the burbot at low temperatures. When stomach emptying is prolonged, the stomach can act as a reserve of food during the seasons of poor capture success. During abundant food supply (summer), however, low food processing rates would result in reduced growth rates (Hop & Tonn 1998). Indeed, in adult burbot, the reduced growth is likely to be caused by the preference for invertebrate food species during July-September and by the lower food intake ( $\text{g d}^{-1}$ ). Thus, in the experimental conditions, food consumption increased with the temperature suggesting that burbot are able to consume larger amounts of food during summer if they are able to catch enough prey.

As a poor swimmer (Jones 1974) and ambush predator, the burbot may take advantage of the low water temperature and poor light conditions in prey catching. Cold temperatures reduce swimming speeds of fish, and fish reach fatigue at lower swimming speeds due to the greater demand for red muscle activity compared to higher temperatures (Randall & Brauner 1991). As the swimming speed of prey fishes decreases with low temperature, burbot are able to catch prey efficiently. During warmer water seasons the burbot switches its food on invertebrates which are numerous and easier to catch. At low water temperatures the burbot can maintain its metabolism for several weeks without feeding due to the low stomach emptying rates. With the help of low food processing rate during the daytime combined with low activity (low metabolic costs), the burbot is able to use a large proportion of the energy of food into

somatic growth. In spite of that, the growth of a mature burbot remains low due to the profundal environmental conditions .

The temperature affects the feed intake and food processing rate of the burbot. As the temperature increases, energy demands increase. Total activity pattern changes and burbot are active for short periods at a time. The food evacuation rate, however, does not increase as much as supposed when compared to other fish species. This may be a sign of adaptation to live in cool water. The metabolic rate, which is relatively insensitive to temperature, will have ecological advantages for the species because it will minimise the loss of energy reserves during the periods of limited food supply (Davenport 1992).

An adult burbot has adapted to benthic life style in profundal areas, resulting trade-offs in growth, prey capturing and energetic cost. Benefits to burbot, however, are that the predation pressure by day active pelagic predators (pike, pike-perch , brown trout) and the competition of feeding habitat use with other predators are reduced. This habitat use combined with enormous fecundity may explain the wide Holarctic distribution of the burbot, the only true freshwater gadoid.

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## YHTEENVETO

### Mateen, *Lota lota* (L.), ravinnonkäytön erityispiirteet: sopeumia pohjaelämään?

Väitöskirjatyössäni olen tutkinut elinympäristön valinnan vaikutuksia kalan fysiologiaan. Tutkimus kuuluu kalabiologian tieteenalaan. Optimi habitaatinvalinta teorian mukaan eläin valitsee elinympäristön, joka tuottaa suurimman elinkyvyn. Elinkyky koostuu useista eri tekijöistä, joiden yhdenaikainen maksimointi ei ole yleensä mahdollista. Tämä johtaa allokaatiokustannuksiin (trade-off), kuten valintaan ravinnon saannin ja saaliiksi joutumisen välillä. Tutkimuksessani kohteena on made (*Lota lota*), joka viettää suurimman osan aikuisvaiheestaan järvien syvänteissä viileässä vedessä. Työn tavoitteena on tutkia, miten elinympäristön valinta on vaikuttanut mateen käyttäytymiseen ja fysiologiaan.

Aikuisen mateen ravinnonkäyttöä ja kasvua luonnossa tutkittiin pyytämällä näytteitä kuudesta Keski-Suomessa sijaitsevasta järvestä. Kalaravinto muodosti suurimman osan ravinnosta talvella ja keväällä, mutta syksyllä ja loppuvuodesta selkärangattomat muodostivat suuren osan mateen ravinnosta. Selkärangan ravinto koostui pääosin jäännöshalkoisjalkaäyriäisistä (*Mysis relicta*) ja okakatkasta (*Pallasea quadrispinosa*). Suurimmat mahan täyteisyydet (lähes 40% mateen massasta) havaittiin, kun ravinto koostui kalaravinnosta. Mateen kasvu luonnossa oli hitaampaa kuin muiden suurten pelagiaalin petokalojen [hauki (*Esox lucius*), kuha (*Stizostedion lucioperca*) ja taimen (*Salmo trutta*)].

Mateen syömän ravinnon sulamisnopeus eri lämpötiloissa on alhainen verrattaessa muihin kaloihin, vaikka  $Q_{10}$ -arvo mateelle onkin 2.97 (elintoimintojen nopeus liki kominkertaistuu lämpötilan noustessa 10°C). Made kykenee syömään kerralla suuria annoksia, jolloin ravinnonsulamisnopeus edelleen hidastuu. Eri ravintokohteiden välillä [ahven (*Perca fluviatilis*), kuore (*Osmerus eperlanus*), muikku (*Coregonus albula*)] ei havaittu eroja sulamisnopeudessa, vaikka ravintokohteiden energiapitoisuus vaihteli merkittävästi. Myöskään syötyjen ravintokohteiden lukumäärä ei vaikuttanut ravinnon sulamisnopeuteen, kun syödyn annoksen kokonaisuudessa pysyi samana.

Koeolosuhteissa mateen ravinnonkulutus vaihteli eri lämpötiloissa. Aineiston avulla arvioitu mateen maksimiravinnonkulutus oli 5.4 g d<sup>-1</sup> kun lämpötila on 13.6°C. Ravinnonkulutusarvoja käytettiin arvioitaessa eri madepopulatioiden vuotuista ravinnonkulutusta. Made kykenee kilpailemaan kalaravinnosta muiden petokalojen kanssa, mutta ravinnon koostumuksen vuodenaikaisvaihtelu vähentää tätä kilpailua.

Ravinnonotto vaikutti mateen hapenkulutukseen. Hapenkulutuksen kasvu havaittiin useiden päivien ajan ravinnonoton jälkeen. Ravinnonoton aiheuttama hapenkulutuksen kasvu korreloi positiivisesti annoksen koon kanssa. Annoksen koolla ei kuitenkaan ollut vaikutusta siihen, kuinka paljon ravinnon sisältämästä energiasta kului kohonneeseen aineenvaihduntaan.



Mateen vuodenaikais- ja vuorokausiaktiivisuutta mitattiin bioelektro-nisella monitorointilaitteistolla. Talvella (tammikuu) mateet olivat aktiivisia koko auringonnousun ja -laskun välisen ajan. Kesällä (heinäkuu) mateet olivat aktiivisia vuorokauden ympäri ja aktiivisuusjakso kesti muutamia tunteja kerrallaan. Mateet olivat yöaktiivisia heinäkuusta helmikuuhun. Selkeä aktiivisuuden vuorokausirytmikka oli havaittavissa syyskuusta helmikuuhun.

Mateet ovat opportunistisia ravinnonottajia, jotka ovat sopeutuneet satunnaiseen ravinnonsaantiin. Tilaisuuden tullen ne kykenevät syömään kerralla suuria määriä ravintoa ja elämään sen turvin pitkiä aikoja alhaisissa lämpötiloissa. Mateet ovat sopeutuneet elämään syvänteiden pohjilla, mikä näkyy hidastuneena kasvuna ja aineenvaihduntana. Hyötynä mateelle on ollut saaliiksi joutumisriskin pieneneminen ja ravintohabitaateista kilpailun väheneminen muiden petokalojen kanssa. Elinympäristön valinta ja suuri hedelmällisyys on mahdollistanut mateen, makean veden ainoan turskakalan, laajan holarktisen levinneisyyden.

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**ORIGINAL PAPERS**

**I**

**Gastric evacuation rate of burbot fed single-fish meals  
at different temperatures**

By

Jari-Pekka Pääkkönen and Timo Marjomäki

Journal of Fish Biology 50: 555-563, 1997

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II

**The effect of meal size on the rate of gastric evacuation of burbot, *Lota lota* (L.)**

By

Jari-Pekka Pääkkönen, Riitta Myyrä and Timo Marjomäki

Ecology of Freshwater Fish 8: 49-54, 1999

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III

**Feeding of burbot, *Lota lota*, at different temperatures**

By

Jari-Pekka Pääkkönen and Timo Marjomäki

Environmental Biology of Fishes 58: 109-112, 2000

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**IV**

**Oxygen consumption of Burbot (*Lota lota*) fed different rations of vendace (*Coregonus albula*)**

By

Jari-Pekka Pääkkönen and Tapani Lyttikäinen

Journal of Applied Ichthyology (In press), 2000

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<https://doi.org/10.1046/j.1439-0426.2000.00251.x>



V

**Total activity of burbot *Lota lota* (L.) measured with bioelectronic monitoring system: seasonal differences in activity length**

By

Jari-Pekka Pääkkönen, Markku Laitinen and Timo Marjomäki

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