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The effect of the length of repeated feed deprivation between single meals on compensatory growth of pikeperch *Sander lucioperca*

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ABSTRACT

Juvenile pikeperch (Sander lucioperca) were reared for 58 days according to one of the following feeding regimes: control (fed once every day); 1+1 (fed every other day); 1+3 (one-day feeding followed by a three-day feed deprivation); and 1+6 (fed once a week). Control fish had significantly higher growth rate than the 1 + 3 and 1 + 6 fish, and consequently the final weight of the controls $(125.2 \pm \text{SD } 30.0 \text{ g}, n = 4)$ was higher than that of the 1 + 3 (84.0 \pm 17.9 g) and 1 + 6 fish (64.7 \pm 7.2 g). Fish in the treatment groups were capable to compensate for the reduced number of feedings by increasing intake relative to the controls when feed was available. This hyperphagic response induced enlargement of the stomach but no difference in feed conversion ratio between any groups. Compensatory ability improved during the course of the experiment and it was almost identical in 1+3 and 1+6 groups. However, it appeared that only at the lowest feeding frequency the compensatory response as weight gain occurred slower than compensation of feed intake. Final visceral fat (%), total body fat (%) and energy content of the 1 + 3 and 1 + 6 fish were significantly lower and water content (%) higher than in the controls and 1 + 1 fish, but protein content was unaffected by the treatments. In conclusion, this experiment indicated that feeding pikeperch every other day (1+1) did not significantly affect any other measured or calculated parameter than relative feed intake when compared to the controls which indicated full compensation. At lower feeding frequencies (1+3 and 1+6) pikeperch was capable to compensate only partially for the decreased number of feedings.

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1. Introduction

Pikeperch *Sander lucioperca* is a highly valued predatory fish in northern Eurasia and research to develop aquaculture practices for its cultivation has increased during the last few years (Nyina-wamwiza et al., 2005; Schulz et al., 2006, 2008; Luchiari et al., 2006, 2009; Zakęś et al., 2006; Bódis et al., 2007; Szkudlarek and Zakęś, 2007). As a predatory fish pikeperch may naturally experience large variations in food availability which can be supposed to affect its tactics in surviving and allocating energy for growth and sexual maturation. One possible option for coping with infrequent availability of food is through morphological adjustments of stomach size.

Compensatory growth is a commonly observed phenomenon amongst fish and most compensation related research has concentrated on the effects of feed cycling. During compensation previously growth restricted (e.g. through feed restriction) animals show faster growth during refeeding than those fed continuously. In most growth compensation experiments associated with feed restriction, the length of the refeeding period has been similar to (Quinton and Blake, 1990; Jobling et al., 1993) or longer (Bilton and Robins, 1973; Hayward et al., 1997; Xie et al., 2001; Wu et al., 2002; Nikki et al., 2004) than the length of feed deprivation. The current study was designed to evaluate the capacity of pikeperch for growth compensation when the fish were given only a single satiation meal after a designated period of feed deprivation. It was hypothesised that as a predatory fish naturally experiencing large variability in food availability, pikeperch is able for morphological adjustments to increase food intake in the cases when food is available only temporarily.

2. Materials and methods

2.1. Fish and experimental conditions

The experiment was carried out in the wet laboratory of the Department of Biological and Environmental Science, University of Jyväskylä, between 26 November 2007 and 24 January 2008, in a total of 58 days. Ninety-six one-year old second generation hatchery raised (but originally hatched and started in a natural pond, and transferred indoors and weaned to dry feed at the age of 1 month) pikeperch (mean initial weight \pm SD 42.8 \pm 8.9 g) from the lake Vanajavesi stock were acclimated for four weeks in 16 15 L flow-through aquaria. Well



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water was heated to 22 °C and aerated. Water flow was set to 0.6– 0.7 L min⁻¹ tank⁻¹, and each tank was also aerated with an aquarium air pump, and tank oxygen concentration was always above 6 mg L⁻¹ (measured by YSI model 55 Oxygen meter, YSI Inc., Yellow Springs, Ohio, USA) and NH₃ varied between 0.004 and 0.006 mg L⁻¹ about 2 h after feeding. Water pH was about 7.8 and conductivity around 196 μ S cm⁻¹. Tanks were lighted continuously by fluorescent tubes and the light intensity was set to 50 lx at the surface. Sunset red gelatine filters (Lee Filters, New Hampshire, England) were taped underneath the lights, as red colour was earlier observed to be the most advantageous for rearing pikeperch (Luchiari et al., 2009).

During the acclimation in the aquaria the fish refused to eat pelleted fish dry feed which they had previously eaten. Therefore the feed was changed to skinless rainbow trout fillet pieces (c. 5×5 mm; proximate composition: energy 7.7 kJ g^{-1} , fat 8.6%, protein 19.2%, and water 70.9%). The fish immediately accepted fillet pieces and therefore the fish were fed with rainbow trout meat for three weeks before the start of the experiment. During acclimation there were some extra fish in the tanks but the number was decreased to six fish at the start of the experiment. The fish which had deformities or had not eaten (based on their body shape) were taken out of the tanks. At the start of the experiment still about 10% of the fish had different kinds of eye deformations which however did not affect their feeding or growth in any noticeable manner. Many of the fish had also different types of abrasions in their tail fin, which did not appear to affect their feeding. Fish with deformed eyes or abraded fins were equally assigned to each test group.

2.2. Experimental procedures and measurements

The 16 tanks were divided into four treatments: control (fed every day); 1 + 1 (fed one day followed by one day of feed deprivation); 1 + 3 (fed one day followed by three days of feed deprivation); and 1 + 6 (fed one day followed by six days of feed deprivation). During the feeding days the fish were fed in excess a weighed amount of rainbow trout meat by hand, and uneaten pieces were siphoned out from the tanks 30-90 min after feeding. For the calculation of food intake in each tank during each feeding the uneaten food was blotted dry, weighed and multiplied by 1.076 to correct for the change in food weight before and after feeding.

Fish weight (to 0.1 g) and standard length (to 1 mm) were measured 26 Nov. 2007 (start date) and 25 Dec. 2007 under anaesthesia using clove oil:ethanol mixture (1:10, clove oil concentration 40 mg L^{-1}). At the termination of the experiment (24 Jan. 2008) the anaesthetic was added directly into the aquaria and after sedation the fish were netted out and killed with a sharp blow on the head. This procedure was carried out because we attempted to get unstressed measurement of plasma cortisol. However, cortisol values (6–700 ng mL⁻¹) varied unexplainably and as widely as in an earlier experiment with pikeperch without sedation (Luchiari et al., 2009) and are therefore not reported here. The fish were fasted for one day before each measurement. The fish were individually marked with a Panjet needleless injector using Alcian blue dye at the beginning and remarked during the second measurement because the marks tended to fade in most individuals.

After the final measurement of weight and length the body cavity was opened, viscera removed and the carcass was reweighed. Visceral fat was separated by fingers and weighed (to 0.01 g). Gastrointestinal tract of each fish was frozen (-20 °C) for later measurement of stomach volume: a string was tied around the pyloric sphincter and oesophagus was tied to a burette. Stomach volume (to 0.1 mL) was estimated as the volume of water required to dilate the stomach with a pressure head of 50 cm water (Jobling et al., 1977). After the volume measurement the stomach was weighed (to 0.01 g).

Body and feed composition was measured after freeze drying and homogenization of the samples. Total lipids were analysed using Soxhlet method, proteins as Kjeldahl-N×6.25 and energy $(kJ g^{-1})$ using adiabatic bomb calorimetry. The initial values were analysed from a pooled sample of 10 fish and final values from tank wise samples in which all individuals of each tank were pooled.

Two individuals died during the experiment for unknown reasons (one in 1 + 1 and one in 1 + 6 group) and four fish (three control fish and one from 1 + 3 group) died because of a technical failure in the cold water pumping system (day 40) and as a consequence water temperature rose momentarily to about 30 °C. Those individuals which died were excluded from all calculations.

2.3. Calculations and statistical analyses

Specific growth rate was calculated as $SGR = 100(\ln W_2 - \ln W_2)$ W_1) * t^{-1} , where W_1 and W_2 were weights in g at the start and end of the measuring period and *t* was that period in days. Condition factor was calculated as $CF = 100W^*L^{-3}$, where *L* was the standard length in cm. Coefficient of variation was calculated for each tank as $CV = 100SD^*mean^{-1}$. Relative feed intake feeding⁻¹ was calculated as $I_{\rm R} = (\text{total intake } (g)^* \text{number of feedings}^{-1})^* W^{-1}$, where W was the average weight of the fish. Feed conversion ratio was calculated as FCR = intake $(g)^*$ gain $(g)^{-1}$. Possible compensation (in terms of weight and feed intake) in the treatment groups during both four-week periods was estimated by a compensation coefficient which was calculated as $CC = \Delta T^* \Delta C^{-1}$, where ΔT was the average weight gain or intake (g) in the treatment group tanks divided by the number of feeding days and ΔC was the average weight gain or intake (g) in the control group tanks divided by the number of feeding days; thus, CC>1.0 would indicate compensation. Relative stomach volume was calculated by dividing the absolute value by fish weight and multiplying by 100. Apparent nutrient (protein and fat) and energy retention was calculated as $NR = (N_2$ $(-N_1)^* N_{\text{intake}}^{-1}$, where N_1 and N_2 were nutrient (g) or energy (kJ/g) contents at the start and end of the experiment and N_{intake} was the amount of nutrient or energy eaten during the experiment. Protein efficiency ratio was calculated as $PER = gain (g)^* protein fed (g; dry$ weight basis).

Statistical analyses were performed using SPSS 14.0 for Windows. Possible differences in weight, length and CF were tested using Repeated Measures ANOVA and other parameters (intake, SGR, FCR, CV, composition, NR, PER, stomach weight and volume) were tested using one-way ANOVA and the tank average value as observational unit, i.e. n = 4. One-sample *t*-test was used to test the possible difference of the average (mean of the two measuring periods) CC of the treatment groups from 1 (expected value when no compensation). Post-hoc comparisons between sample means were tested by Tukey's test and P = 0.05 was taken as the level of significance. Equality of variances was tested with Levene's test and normality with Shapiro-Wilk's test. Linear and non-linear regression analyses were used to test possible relationship between stomach volume, visceral fat weight or condition factor with other measured variables of individual fish (individuals from different tanks from each treatment were combined for analyses).

3. Results

3.1. Intake, growth and condition factor

Numbers of feeding days were 55, 28, 15 and 9 in the control, 1 + 1, 1+3 and 1+6 groups, respectively. Total absolute feed intake was significantly affected by the treatment. Control fish ate significantly more than the fish in the 1+3 and 1+6 treatments and also the 1+1 group fish ate more than the 1+6 group fish (Table 1). The average (\pm SD) absolute intake per feeding was significantly less in the controls (2.94 ± 0.92 g) than in the treatment groups (4.59 ± 1.1 g, 5.09 ± 0.94 g and 5.04 ± 0.99 g in 1+1, 1+3 and 1+6 groups,

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