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Longer wavelengths of light improve the growth, intake and feed efficiency of individually reared juvenile pikeperch *Sander lucioperca* (L.)

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Abstract

We tested the effects of monochromatic light on the specific growth rate (SGR), feed intake and feed efficiency (FE) of juvenile pikeperch, *Sander lucioperca* (L.). Pikeperch were reared individually for 42 days in aquaria covered with blue, green, yellow or red gelatin filters or white paper (control; $n = 5$). Linear regression analysis indicated a significant positive effect of longer wavelengths of light on the condition factor (CF), FE and SGR. The final weight, SGR and CF were significantly higher in fish reared under red than under white light, and FE was better under green, yellow and red light than under white light (Dunnett's *post hoc* test, $P < 0.05$) while blue was comparable to white light in terms of the measured parameters. After the growth trial, the spectral sensitivity of photoreceptor cells in the retina was tested using microspectrophotometry, which revealed the presence of rods with λ_{max} at ca. 530 nm and two cone classes, absorbing maximally at ca. 535 and 603 nm, all containing a porphyropsin-based pigment. These results suggest that the presence of mid and long wavelength-sensitive cones enhances visual sensitivity under mid-wavelength and long-wavelength environments, and thus supports the finding that longer wavelengths of incoming light can improve FE and SGR of the cultivated pikeperch.

Keywords: light colour, cortisol, food intake, specific growth rate, percids

Introduction

Pikeperch, *Sander lucioperca* (L.), is a predatory fish in temperate waters of Eurasia (Rennert, Wirth, Günther & Schulz 2004). As a new potential candidate for intensive aquaculture in Europe (Hilge & Steffens 1996), the interest to develop methods for commercial pikeperch culture has increased during the last decade (Kestemont & Melard 2000; Barry & Malison 2004). In order to make the culture of this non-domesticated species economically profitable, new know-how must be obtained about optimal rearing conditions and practices especially regarding the effects of environmental parameters on food intake and growth. Food intake and growth can be regarded as valuable parameters for estimating performance because environmental factors that cause the animal to experience distress leads to decreased intake and growth, among other physiological responses (Moberg & Mench 2000). Thus, under conditions that improve fitness, the animal may spend more energy on growth than under unsuitable conditions.

Light is one of the environmental factors that profoundly affects the life of fish. From the fish's point of view, light can have several characteristics: quality, quantity and periodicity, and, of these light characteristics, light quality is the least studied (Boeuf & Le Bail 1999). Controlled experiments regarding light colour have shown significant differences in the behavioural and physiological responses of different fish (e.g. Volpato, Duarte & Luchiari 2004; Luchiari, Duarte, Freire & Nissinen 2007). These differences can be explained by the fact that the aquatic environment includes many colours, from ultraviolet to infrared (Levine & MacNichol Jr 1982), and different types of visual systems have evolved in fish depending on the environment they live in (Brown 1957; Wheeler 1982), and the spectral sensitivity of the photoreceptor pigments may be correlated with the predominant colour available in that ambient (Munz 1958).

Pikeperch is a crepuscular predator inhabiting turbid waters (Ali, Ryder & Anctil 1977) and it displays some retinal adaptations such as tapetum lucidum (Wunder 1930) and macroreceptors (Braekevelt, McIntyre & Ward 1989), improving vision under low ambient light. Ali *et al.* (1977) have also shown the presence of green and red cones in the retina of other percid species (from genera *Sander* and *Perca*) but no blue-absorbing cones have been found in percids.

Colours can be expected to influence fish that have a physiological substrate to colour vision (Brown 1957; Wheeler 1982; Pitcher 1993). For instance, haddock larvae, *Melanogrammus aeglefinus* (L.), show high survival in blue and green light (Downing 2002), silver carp, *Hypophthalmichthys molitrix* (Valenciennes), and common carp, *Cyprinus carpio* L., show the best growth under green light (Radenko & Alimov 1991; Ruchin, Vechkanov & Kuznetsov 2002) and Atlantic salmon, *Salmo salar* L., smolts have decreased gill Na^+, K^+-ATPase activity under yellow light (Gaignon, Quemener & Roux 1993). On the other hand, Stefansson and Hansen (1989) found no differences in growth or smolting characteristics in Atlantic salmon when they were reared for 7 months under artificial lights of colour temperatures ranging between 2.500 and 6.500 K. As it seems that the effects of light colours are not similar for all species, it is possible that the colour that improves growth and well-being in certain species may be related to the species-specific colour preference (Luchiari & Pirhonen 2008).

Light and/or tank colour are relatively easy methods to apply to optimize productivity and they can be varied according to species-specific requirements to improve feeding, growth or reproduction. Thus, the aim of this study was to test the effects of different light colours on feed intake (FI) and growth. In addition, the spectral sensitivities of the photoreceptor cells were analysed and it was hypothesized that growth and FI could be explained by the morphological features of the pikeperch eye.

Materials and methods

One-year-old (1+) pikeperch used in these experiments came from the stocks of a private fish farm (Hankataimen, Hankasalmi, Finland). Fish were transported to the laboratory of the University of Jyväskylä 4 months before the experiments. Until the start of the experiments, the fish were held in a partially covered flow-through stainless-steel stock tank (water volume 500 L) supplied with fresh, heated (22 °C) and aerated well water and exposed to continuous light (to mimic the summertime photoperiod at northern latitudes) provided by fluorescent tubes (ca. 100 lx at water surface). Fish were fed a commercial dry diet (proximate composition according to Raisio Feed, Raisio, Finland: protein 460 g kg^{-1}, fat 260 g kg^{-1}, energy 23.8 MJ kg^{-1}) in excess by belt feeders for 15 min every 3 h.

Growth trial

Twenty-five flow-through aquaria (40 × 20 × 25 cm; water volume 15 L, temperature 22 °C, flow rate 0.8 L min^{-1}) were covered from the sides with blue, red, yellow, green or white canson paper ($n = 5$ for each colour, one fish in each aquarium) and the top was covered with blue (λ_{max} 435 nm), green (534 nm), yellow (546 nm) or red (610 nm) gelatin filter (Lee Filters, Hampshire, UK; manufacturer codes for the filters were lagoon blue-172, jade-323, yellow-101 and sunset red-025) or white paper, setting the illuminance at ca. 50 lx by adding layers of filters, continuously illuminated with white fluorescent tubes (Duralamp, Florence, Italy; model F36W840, 3350 lumen).

Pikeperch were reared individually in the aquaria and acclimated in them for 15 days before the start of the experiment. The experiment lasted for 42 days, during which food intake and growth were measured. When transferred to the aquaria, the fish refused to eat dry pellets. Therefore, the diet was switched to rainbow trout (*Oncorhynchus mykiss*) meat containing 74.4% water, 18.9% crude protein (analysed as Kjeldahl-N × 6.25) and 5.2% crude lipid (Soxhlet method); the energy content was 6.4 kJ g^{-1} (adiabatic bomb calorimetry). During the experiment, the fish were fed twice a day in excess and uneaten food was removed 2 h after feeding. Uneaten food was weighed, freeze dried and reweighed for calculation of relative FI as food wet and dry weight (g kg^{-1} day^{-1}) but also as energy content (kJ kg^{-1} day^{-1}). Fish length (to 0.1 cm) and weight (to 0.1 g) were measured under anaesthesia (with a clove oil: ethanol mixture, 1:9, using clove oil concentration 40 mg L^{-1}) at the beginning of the experiment and then every 14 days.

At the termination of the experiment, the fish were netted from the aquaria and killed with a sharp blow on the head. Blood was withdrawn from caudal vessels using heparinized syringes, and plasma was separated and frozen (− 20 °C) for later analysis of cortisol. Haematocrit was measured after centrifuging micro haematocrit tubes (Brand GmBh+Co KG, Wertheim, Germany) for 5 min at 10300 g. Cortisol was analysed (Spectria Cortisol RIA 06119-kit; Orion diagnostica, Turku, Finland) from 20 μL samples in triplicate for each fish using the Beckman (Fullerton, CA, USA) LS-6500 multipurpose scintillation counter. As a new assay for pikeperch, we also verified the parallelism of the standard and an unknown sample.

Condition factor [$K = 100 \times$ weight (g)/length $(\mathrm{cm})^3$], FI, specific growth rate [SGR = (ln final weight − ln initial weight) × 100/time in days; Jobling 1994] and feed efficiency (FE = gain/FI; separately for wet and dry food) were calculated. Wavelength was regarded as a continuous variable, and therefore linear regression analysis was used for estimating the effects of wavelength on the measured and calculated parameters. Data of fish reared under white light (control) were not included in the regression analyses but the average values of fish reared under blue, green, yellow and red light were compared with those of the controls using ANOVA and the two-sided Dunnett's *post hoc* test. $P < 0.05$ was considered to indicate as a level of significance. Statistical tests were performed using SPSS 14.0 software package.

Retinal preparation and MSP measurements

Retinal preparation was performed as described in Carleton, Parry, Bowmaker, Hunt and Seehausen (2005). Twenty pikeperch were dark adapted for 24 h to avoid stimulation of visual pigments. Under dim red illumination, fish were anaesthetized with a clove oil:ethanol mixture, killed by a blow on the head and the eyes were removed, wrapped in tin foil and kept on ice until analyses. The eyes were dissected under dim red light, and small sections of the retina were removed to a coverslip with a small drop of saline and dextran, covered with a second coverslip and sealed with wax. Dim red light was used because it minimally reaches the visual pigments and allows the cells to keep the pigments intact.

Microspectrophotometric analyses were performed of three eyes of randomly chosen individuals according to Bowmaker, Astell, Hunt and Mollon (1991). Spectra were recorded from 400 to 750 nm at a 2-nm interval. In total, 10 double cones, eight single cones and four rods were chosen for the measurements by their appearance and integrity. After measuring the baseline absorbance spectrum of a chosen cone or rod cell, it was scanned again after full bleaching with white light. the λ_{max} of the two absorbance spectra were subtracted to obtain the absorbance difference. In all cells, the spectrum fitted well to the vitamin A2 (porphyropsin) template.

Results

Growth trial

The colour of the ambient light had no significant effect on FI of pikeperch; however, the final weight, SGR and final CF of the fish reared in red ambient were significantly higher than those of the control fish reared under white light (Dunnett's test, $P < 0.05$; Table 1). In addition, the final CF and SGR were positively correlated with wavelength.

The feed efficiency of the fish reared in green, yellow and red ambient was significantly higher and the energy intake per gain was significantly lower than those of the control fish while these efficiency values were not different between the fish reared under blue or white light (Table 1). Feed efficiency values were also linearly correlated with the used wavelength ($P = 0.002$; Table 1).

Haematocrit was similar in all tested colours, averaging 27.6 ± 6.65 (Table 1). Cortisol levels showed a wide variation between individuals, from 5.9 to 635 ng mL^{-1}, and no significant correlation between cortisol concentration and wavelength was observed (Table 1). There was no mortality during the experiment.

MSP measurements

The retina of pikeperch had two types of cones: identical double cones containing a long-wavelength pigment with λ_{max} at 603 ± 3 nm ($n = 10$), and a single cone with medium wavelength pigments with λ_{max} at 535 ± 3 nm ($n = 8$). Rods were also found, presenting λ_{max} at 531 ± 3 nm ($n = 4$; Fig. 1). Although all pigments fitted a porphyropsin (vitamin A2) template, it does not exclude the possibility of a small percentage of rhodopsin (vitamin A1) being used for pigment formation.

Table 1 Measured and calculated parameters of individually reared pikeperch under different colours for 42 days

	Ambient colour (λ_{max}, nm)					Linear regression	
	White	Blue (435)	Green (534)	Yellow (564)	Red (610)	R^2	*P*-value
Initial weight (g)	37.06 ± 8.54	46.23 ± 13.78	38.54 ± 6.96	36.13 ± 7.23	39.82 ± 11.51	0.086	NS
Final weight (g)	72.06 ± 14.91	87.02 ± 14.32	95.93 ± 23.49	88.19 ± 18.49	106.05 ± 24.77*	0.078	NS
Final length (cm)	19.52 ± 1.47	20.96 ± 1.37	21.18 ± 1.42	20.32 ± 1.46	20.84 ± 1.61	0.006	NS
Condition factor	0.96 ± 0.06	0.93 ± 0.35	1.07 ± 0.16	1.04 ± 0.03	1.16 ± 0.04*	0.516	0.000
SGR (% day^{-1})	1.59 ± 0.34	1.56 ± 0.35	2.15 ± 0.51	2.12 ± 0.39	2.37 ± 0.64*	0.308	0.011
Wet feed intake (g kg^{-1} day^{-1})	46.9 ± 5.2	41.8 ± 3.9	46.4 ± 9.3	46.1 ± 6.3	48.1 ± 9.5	0.107	NS
Dry feed intake (g kg^{-1} day^{-1})	12.0 ± 1.3	10.7 ± 1.0	11.9 ± 2.1	11.8 ± 1.6	12.3 ± 2.4	0.107	NS
Energy intake (kJ kg^{-1} day^{-1})	301 ± 33	268 ± 25	298 ± 53	296 ± 40	309 ± 61	0.107	NS
Wet feed efficiency	0.33 ± 0.05	0.36 ± 0.06	0.43 ± 0.03*	0.43 ± 0.04*	0.45 ± 0.04*	0.433	0.002
Dry feed efficiency	1.27 ± 0.20	1.39 ± 0.23	1.67 ± 0.1*	1.68 ± 0.1*	1.75 ± 0.15*	0.433	0.002
Energy intake/gain (MJ kg^{-1})	20.1 ± 3.4	18.4 ± 3.3	15.0 ± 0.8*	15.0 ± 1.4*	14.4 ± 1.3*	0.408	0.002
Haematocrit	28.75 ± 6.02	27.40 ± 5.94	28.80 ± 10.23	28.60 ± 6.11	24.80 ± 7.66	0.008	NS
Cortisol (ng mL^{-1})	280.54 ± 299.9	135.99 ± 195.2	76.53 ± 116.5	45.97 ± 33.5	80.67 ± 114.8	0.050	NS

Data are presented as means of five aquaria ± SD. Effect of wavelength on each parameter was tested with linear regression; coefficient of determination (R^2) and significance of the slope are presented, NS indicates a non-significant slope ($P>0.05$), $n=20$. Fish held under white light (control) were not included in the regression analysis but the possible difference of the colour treatments from the controls is indicated by an asterisk ($P<0.05$) within each parameter (tested by ANOVA and Dunnett's *post hoc* test).
SGR, specific growth rate.

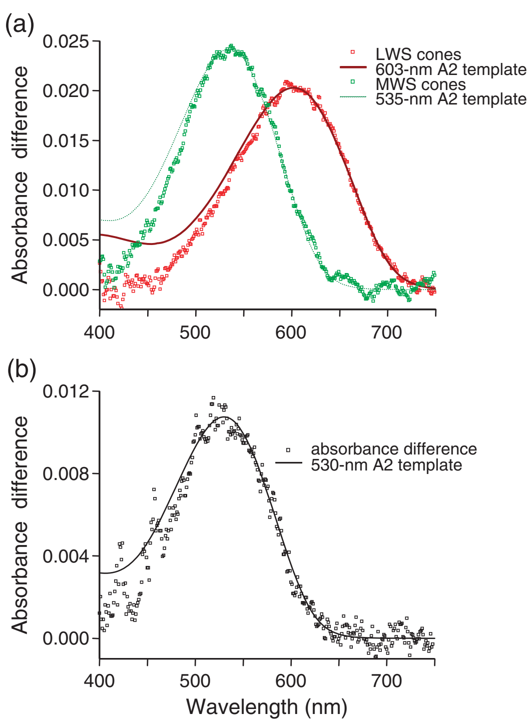

Figure 1 Absorbance difference curves of MSP measurements using the retina of juvenile pikeperch: (a) medium (MWS)- and long-wavelength (LWS) cones and (b) rods. All scans were best fitted by the porphyropsin (A2) visual pigment template.

Discussion

Based on the present results, the increase in the light wavelength within the visible spectrum improves the growth rate, CF and FE of pikeperch. This result suggests that light colour should be taken into account when developing an economically sound culture for pikeperch. Other studies that have studied the effects of light colours on fish suggest positive effects of green light on the growth of silver carp, common carp and rainbow trout (Radenko & Alimov 1991; Ruchin *et al.* 2002; Luchiari & Pirhonen 2008) while guppy, *Poecilia reticulata* Peters, and whitefish, *Coregonus peled* (Gmelin), appear to show increased growth rates under blue light (Ruchin 2004). Ruchin (2004) found a negative effect of red light on the growth rate of three different fish species, and Luchiari and Pirhonen (2008) recorded a lower growth rate of rainbow trout in red than in green ambient. Thus, the present findings of the advantageous effects of long-wavelength light, especially red light, with pikeperch differ from earlier findings with other fish species and highlight the need for testing light colour when new species are introduced for aquaculture. It must be noted that the fish were reared individually and the result would not necessarily be identical if the fish had been reared in groups (Luchiari & Freire 2008). However, as there is no information on the optimal rearing density for juvenile pikeperch, the possible negative impacts of social hierarchies were ruled out by individual rearing.

With respect to FI, the daily ration size of predatory percids during the growing season is about 3–7% of body weight (Popova & Sytina 1977; Swenson 1977). In the present study, pikeperch ate ca. 4–5% of body weight and intake was unaffected by light colour. However, there was a significant positive correlation in FE with wavelength. Feed efficiency values (range on a dry matter basis 1.27–1.75) in the present experiment were much higher than those reported for 5–20 g pikeperch fed a commercial dry diet (FE = ca. 0.8; Zakęś, Kowalska, Czerniak & Demska-Zakęś 2006); however, the growth rate in that study (ca. 2.45% day^{-1}) was comparable to our pikeperch reared in the red ambient (2.37% day^{-1}). Because the increase in fish size is accompanied by a decline in the growth rate (Jobling 1994), it seems that the fish in our experiment grew well, and keeping them under isolation apparently did not decrease the growth rates.

The increase in growth performance in the long-wavelength environment may be related to the enhancement of visual sensitivity in the ambient where the visual pigments are able to maximize photon capture (Cohen & Forward Jr 2002), in the case of pikeperch, the red environment. Pikeperch lakes are typically eutrophic with low visibility (Nagięć 1977), and in that type of lakes with high amounts of organic matter no light of wavelengths below 600 nm penetrates below 1 m (Wetzel 1983). Hence, visual pigments of pikeperch appear to match better the light wavelength present in the long-wavelength environment, thus improving the growth rate and FE under such an ambient. In the white environment, where all visible wavelengths are combined, FE and growth rate were comparable to the blue environment. It must be noted here that the growth rate in green and yellow ambient was not significantly different from the control fish in the white ambient although the growth rate increased significantly in a linear manner along with an increase in wavelength. These observations suggest that the shorter wavelengths of the spectrum in white light may partly inhibit the growth and FE, and the advantage of having longer wavelengths mixed within the white light is lost.

The retina of the pikeperch was composed of single mid-wavelength cones and double long-wavelength cones, absorbing maximally at 535 and 603 nm respectively. Our results are in agreement with the findings of Ali *et al.* (1977), who reported the presence of double red and single green cones and the absence of blue cones in other percids from the genera *Sander* and *Perca*. Also, the photoreceptors' absorbance shown in this study is very similar to those found by Loew and Lythgoe (1978) for *Perca fluviatilis*. These authors found single cones absorbing maximally at 535 nm and both cones of the double cones absorbing maximally at 615 nm.

Loew and Lythgoe (1978) reported that double cones almost always contain pigments well matched to the ambient light in which the fish is found, and the additional single cones contain pigments that are offset to shorter wavelengths from the maximum water transmission. Moreover, McFarland and Munz (1975), after studying different fish species, concluded that the most versatile eye would have one visual pigment that matches the background light and one that has shorter wavelengths, because visual sensitivity is enhanced in environments where the visual pigments are able to maximize photon capture (Cohen & Forward Jr 2002). Thus, the presence of single green and double red cones in pikeperch suggests that their natural environment mainly comprises long-wavelength light.

To our knowledge, this is the first time that plasma cortisol values have been reported on pikeperch. Cortisol concentrations showed an unusually wide variation and the highest values were also unexpectedly high for seemingly unstressed fish (cf. Barton & Zitzow 1995). No statistically significant trend in cortisol with the increase in wavelength was observed, but interestingly, the average cortisol concentrations of fish reared in white and blue tanks (280 and 136 ng mL^{-1} respectively) were higher (although not statistically significantly) than in green, red and yellow tanks (46–81 ng mL^{-1}), which concurs with the differences in FE and growth rate in those treatments.

In conclusion, our results suggest that pikeperch should be reared under red environmental colour and under dim light conditions (Luchiari, Freire, Koskela & Pirhonen 2006). The original hypothesis was supported as spectral sensitivity of the pikeperch eye matched the results of the improved growth along with the increase in the light wavelength.

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