

Effects of ambient colour on colour preference and growth of juvenile rainbow trout *Oncorhynchus mykiss* (Walbaum)

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Colour preference of individual juvenile rainbow trout *Oncorhynchus mykiss* was tested at 1 and 12° C, and also at 12° C after a 42 day growth experiment under white, blue, green, yellow or red ambient colour. All experiments were carried out under controlled laboratory conditions and the preference was assessed by the location of the fish in a preference tank with four chambers. Rainbow trout showed a preference for blue and green at 1° C and for green at 12° C. After the growth experiment the fish reared in blue tanks preferred blue and green but green was the most preferred colour for the fish reared in green, yellow and red tanks. Yellow and especially red chambers were avoided, irrespective of the ambient colour during the growth trial. The final mass of fish reared in the red aquaria was significantly smaller than that of the fish in green tanks. In addition, when the data of the preference tests were correlated with the data of the growth experiment using mean values of the four tested colours, a very good linear relationship was observed between the preference (*i.e.* visit frequency in coloured compartments) and growth rate as well as food intake. When considering the results both from the preference and growth trials it is suggested that green is the best environmental colour for rearing juvenile rainbow trout while rearing in a red environment cannot be recommended.

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INTRODUCTION

Colour vision is an important feature for fishes inhabiting bright environments, where they are able to discriminate details in the ambient surroundings that bring advantages on feeding, defence, migration or mating (Levine, 1980; Wheeler, 1982). The ambient light and the visual tasks that fishes experience

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during their life are selective forces modulating visual systems (McFarland & Munz, 1975) and in some species, spectral sensitivity changes according to ontogenetic development (Douglas, 1989; Alexander *et al.*, 1994) and the season of the year (Whitmore & Bowmaker, 1989). These changes in colour sensitivity arise from the switch of different opsins, density of different cone types in the retina or shifts in the chromophore source (Cheng & Flamarique, 2004; White *et al.*, 2004).

It has been shown that temperature affects the composition of visual pigments in the retina of salmonids (Tsin & Beatty, 1977). This change enables the fishes to see at night during the winter and shifts vision towards the blue end of the spectrum during the summer (Tsin & Beatty, 1977). There is also evidence that environmental colour can affect growth and even survival of fishes (Radenko & Alimov, 1991; Downing, 2002; Ruchin *et al.*, 2002). The colours that improve growth and survival in populations of certain species may be related to the ambient colour in which the populations have evolved, because the spectral sensitivity of visual pigments is correlated with the predominant light colour available in the environment (Munz, 1958).

Under fish farm conditions different environmental colours may affect the vision of fishes, influencing for example food intake, signals for hierarchical status and reproduction. As the environmental colour can also affect stress or stress responses of fishes (Gilham & Baker, 1985; Papoutsoglou *et al.*, 2000) the optimal species-specific light or tank colour may improve growth and productivity of intensively cultivated species. Food intake and growth can be regarded as valuable variables for estimating general performance and well-being of fishes under culture conditions, but these variables are also the most important ones for economical profitability of an aquaculture operation. Thus, under colour conditions that improve fitness, the fishes may spend more energy on growth than under unsuitable conditions. Despite the possible positive effects of certain ambient wavelengths on feed intake and growth, this area has received surprisingly little attention among fish researchers.

The aim of this study was, firstly, to test the light colour preference by observing the location of a rainbow trout *Oncorhynchus mykiss* (Walbaum) in a four-chamber test tank and, secondly, to test the effects of the same colours on growth and food intake of rainbow trout. The four colours used in the experiments were chosen from the two ends of the visible spectrum of light (blue and red) and green and yellow were chosen to represent mid-wavelengths of the visible spectrum. It was hypothesized that (1) water temperature and (2) prior residence in a certain colour environment would affect the colour preference and also that (3) preference or avoidance of certain ambient colours would influence feed intake and growth when used for rearing.

MATERIALS AND METHODS

Juvenile rainbow trout originated from the Hanka Taimen Ltd fish farm (62°37' N; 26°49' E) where they were raised in green tanks. After transportation to the laboratory of the Department of Biological and Environmental Science, University of Jyväskylä, Finland, the fish were held in a stainless steel stock tank (water volume 550 l) supplied with filtered well water (12° C), exposed to continuous light (c. 100 lx at water

surface; all light-intensity measurements taken with a HD9221 lux metre; Delta OHM, Padua, Italy) and fed by commercial trout dry food (size 2.5 mm; proximate composition according to manufacturer: protein 46%, fat 26% and energy 23.8 MJ kg⁻¹; Rehuraisio Ltd, Raisio, Finland). The experiments were done with the permissions (46/29.8.2005 and 17/27.3.2006) of the experimental animal committee of the University of Jyväskylä.

COLOUR PREFERENCE TRIAL

For the colour preference tests, three 1 m² (1000 × 1000 mm) light yellow plastic tanks were divided into four lateral compartments of similar size (500 × 500 mm) with a 150 mm hole in the central region to allow the fish to move between compartments. Water depth was 200 mm and one air stone supplied oxygen in the middle of each tank. The laboratory was illuminated by fluorescent tubes (DURA lamp, F36W840, 3350 lumen) for 24 h. Different environmental light colours [blue (λ_{\max} 435 nm), green (λ_{\max} 534 nm), yellow (λ_{\max} 546 nm) and red (λ_{\max} 610 nm); wavelengths measured with a USB-2000 spectrometer (Ocean Optics Inc., Dunedin, FL, U.S.A.)] were randomly chosen for each compartment, by covering the chosen compartment with a gelatin filter (LeeFilters, Hampshire, England). Light intensity was set *c.* 60 lx for each compartment by adding layers of the same gelatin filter; adding the layers had no effect on wavelengths mentioned above.

Colour preference of individuals (one fish per tank) was observed for a period of 5 days. Each fish was placed in the experimental tank 1 day before observations started. During the first and fifth day of each 5 day period, the compartments were not covered and light intensity was *c.* 300 lx. During these days, fish visit frequency in each compartment was observed to check possible preference between non-coloured compartments. On the second, third and fourth days the observations were made with compartments set with different colours. Visiting frequency was directly observed throughout 5 days by checking the compartment location of fish at 2 min intervals for 20 min periods at 0800, 1100, 1400 and 1700 hours, making a total of 40 observations per day. Food was not offered during the experimental days in order to prevent any stimulus that could propel the fish to choose one specific compartment due to any other driving force than light colour. As it is well documented that juvenile *Oncorhynchus* species are able to withstand prolonged periods of starvations (Bilton & Robins, 1973; Simpkins *et al.*, 2003; Montserrat *et al.*, 2007) it is likely that the 5 day starvation during the preference test has not affected well-being of the tested individuals in any significant manner.

To test the effects of different water temperatures on colour preference, two experiments were done: one testing colour preference at 1° C (3 October to 21 November 2005), a typical winter temperature at fish farms in Finland, and the other at 12° C (20 August to 13 September 2005). At 1° C, nine rainbow trout (mean \pm s.d. 133 \pm 12 mm total length, L_T ; 48.6 \pm 12.3 g wet mass, M) and at 12° C, eight rainbow trout (113 \pm 11 mm; 24.5 \pm 6.8 g) were tested. The fish were acclimated in the experimental temperature for a minimum of 14 days before starting the measurements. In both experiments, the same procedure was carried out, changing only water temperature. Each individual fish was tested only once.

To test the effects of prior residence in a certain environmental colour on colour preference, groups of 10 rainbow trout were reared in coloured tanks (blue, green, yellow, red or white). After the growth trial (*i.e.* after 2 to 3 months under monochromatic light), five randomly chosen rainbow trout (101 \pm 10 mm; 13.1 \pm 3.7 g) from each colour condition were tested individually for colour preference (19 June to 3 August 2006). In this experiment, the first control day (without colours on the compartments) was skipped to avoid possible influence of the prior residence on the preference; thus only one control day at the end of the test was carried out. All the observation procedures were the same as stated above, and these preference tests were also done at 12° C.

The 120 observations of every individual were used to calculate the mean preference for each 3 day measuring period and 40 observations for the control days. For statistical analyses, the non-parametric procedure of Friedman ANOVA was used for multiple group analyses of visit frequency. A Friedman test was used because fish preference for one compartment instead of the others provides dependent data. In cases where the Friedman test was significant ($P < 0.05$), the non-parametric Dunn's *post hoc* test was used to determine significant differences among compartments.

GROWTH TRIAL

Twenty-five aquaria (400 × 200 × 250 mm; water volume 15 l) were covered from the sides with blue, red, yellow, green or white canson paper and the top was covered with blue, green, yellow or red gelatin filter or white paper, respectively, setting illumination at c. 60 lx (five aquaria of each colour) with white fluorescent tubes (type: see above) using a photoperiod of 24 L:0 D.

The tanks were supplied with filtered and aerated 17° C well water (pH 7.6, conductivity 31 mS m⁻¹, total hardness 0.8 mmol l⁻¹, Mn 10 µg l⁻¹, Fe 80 µg l⁻¹) at c. 0.4 l min⁻¹ (equal to a minimum of 5 l kg⁻¹ min⁻¹ at the end of the experiment). The temperature was set at 17° C in order to obtain maximum growth rates during the experiment (Wedemeyer, 1996). Air was provided in each aquarium through air stones connected to aquarium air pumps. Oxygen concentration was measured by a YSI oxygen metre (YSI 550 DO; YSI Inc., Yellow Springs, OH, U.S.A.) three times per week between feedings and was always >7.5 mg l⁻¹, which is c. 1.5 mg l⁻¹ above the estimated safe oxygen concentration for salmonid culture (Wedemeyer, 1996).

Groups of 10 rainbow trout, with five replicates of each colour, were reared in the aquaria for 42 days (3 April to 15 May 2006) after acclimation of 14 days to the treatment colours. For the first 28 days, the fish were fed by hand twice per day (at c. 0800 and 1600 hours) with commercial dry food (Skretting Nutra 1.0 mm; protein 53%, fat 19% and energy 20 MJ kg⁻¹, according to manufacturer) until apparent satiation, and the amount of food offered was weighed. All pellets were delivered at once by slightly moving the cover glass. During the first month the fish could not eat pellets larger than 1 mm, and because of the small size of the pellets the amount of uneaten food could not be measured. The appetite in each aquarium, however, was visually estimated by feeding the fish to apparent satiation (*i.e.* some more food was added until a few pellets remained uneaten on the tank bottom), avoiding overfeeding. During the last 14 days, fish received 1.5 mm pellets, twice per day, and remaining food was siphoned out and counted 30 min after delivery. As the mass of one pellet was calculated from 10 samples of 50 pellets, it was possible to estimate the amount of food eaten in each aquarium by subtracting the number of uneaten pellets from the fed amount. The M (to 0.1 g) of every individual was measured at the beginning of the experiment and then every 14 days. Before measurements the fish were anaesthetized with clove oil:ethanol mixture (1:9), using a clove oil concentration of 40 mg l⁻¹. The L_T was measured only at the end of the experiment (to 1 mm). After the experiments the fish were held in coloured tanks until the preference had been tested and then returned to a stock tank.

The condition factor (K) was calculated from: $K = 10^5 M L_T^{-3}$ (M in g and L_T in mm), specific growth rate (G) from: $G = 100 (\ln M_2 - \ln M_1) t^{-1}$, where M_1 and M_2 = masses in g at the start and end of the measuring period and t = period in days) and intake and feed efficiency (E_F) from: $E_F = (M_2 - M_1) I^{-1}$, where I = food intake. One-way ANOVA was used (after testing for the homogeneity of variances) to compare the means of measured and calculated parameters of the five different colour regimes, and the tank mean was used as an observational unit for each variable, *i.e.* $n = 5$; however, differences in mass were tested using RM ANOVA. *Post hoc* comparisons between sample means were tested by Student–Newman–Keuls and $P = 0.05$ was taken as the level of significance.

RESULTS

COLOUR PREFERENCE TRIALS

During the first observation day of the experiment at 1° C (compartments without colours) rainbow trout showed equal distribution among the compartments (Friedman ANOVA, d.f. = 8, $P > 0.05$). When the coloured gelatine filters were placed over the compartments (days 2, 3 and 4) the average visit frequency in blue and green compartments was significantly higher than in yellow and red compartments [d.f. = 8, $P < 0.01$; Fig. 1(a)]. On the fifth day (coloured gelatine filters were removed the previous evening), the fish showed again no preference for any of the compartments ($P > 0.05$).

In the experiment at 12° C, rainbow trout showed equal distribution among the compartments on the first test day (Friedman ANOVA, d.f. = 7, $P > 0.05$). During the days 2, 3 and 4 with coloured filters the visit frequency in green compartment was significantly higher than in the other compartments [d.f. = 7, $P < 0.05$; Fig. 1(b)]. On the last experimental day, again without colours, the fish showed no preference for any specific compartment ($P > 0.05$).

When fish were tested in different colours after the growth experiment, the results were similar for the fish that had been reared in green, yellow and red tanks. In those cases green was the preferred environmental colour while visit

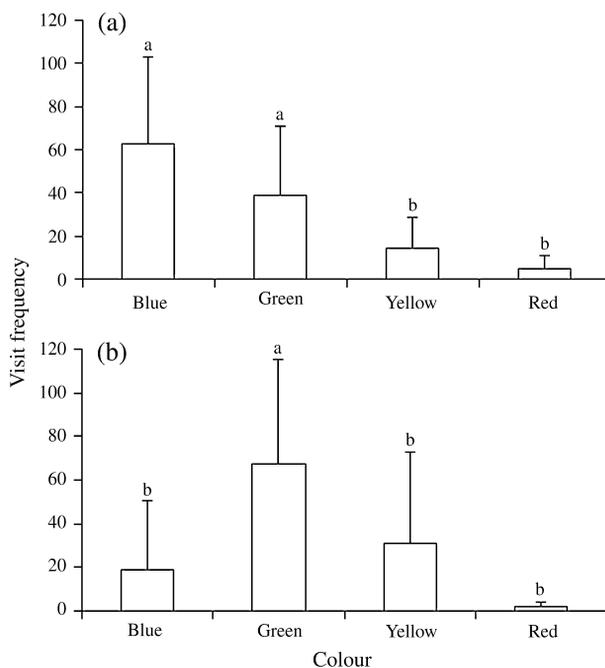


FIG. 1. Preference of juvenile rainbow trout for blue, green, yellow and red ambient at (a) 1° C and (b) 12° C. Bars represent the mean + s.d. visit frequency of 20 min observation periods at 0800, 1100, 1400 and 1700 hours over the 3 day period (in total 120 observations per individual). Statistical difference of fish visit frequency in each compartment is indicated by different lower case letters (Friedman ANOVA, d.f. 1° C = 8, d.f. 12° C = 7, $P < 0.05$).

frequency in blue, red and yellow compartments was lower, and usually significantly so [Fig. 2(b), (c), (d)]. Rainbow trout from the blue aquaria had significantly higher visit frequency in blue and green compartments than in yellow and red compartments [d.f. = 4, $P < 0.05$; Fig. 2(a)]. On the control day, no differences in visit frequency were observed in any occasion (d.f. = 4, $P > 0.05$)

GROWTH TRIAL

Fish mass increased from a mean \pm s.d. of 1.33 ± 0.3 g to 7.96 ± 0.69 g during the 42 day experiment. At the end of the experiment there were significant differences between treatments both in M (ANOVA, d.f. = 4, $P < 0.05$) and L_T (ANOVA, d.f. = 4, $P < 0.001$), *post hoc* comparisons indicating that the fish reared in the green environment were significantly larger than the fish in blue, white and red tanks, but not different from fish reared in the yellow environment (Table I). The value of K was not significantly different between colours (d.f. = 4, $P > 0.05$) (Table I). The value of G was significantly higher in fish reared in the green ambient than in the red (d.f. = 4, $P < 0.05$) (Table I). The mean I per day for the last 14 days was around 4.2% of body mass, however I was significantly higher in the green than in the blue tanks (d.f. = 4, $P < 0.05$). Feed efficiency, E_F , during the last 14 days was lower in green, yellow and red than in blue tanks (d.f. = 4, $P < 0.05$), white tanks not differing from any other colour (Table I). Mortality was observed on some occasions right after weighing and the total number of dead fish varied between three to six per treatment over the whole experiment.

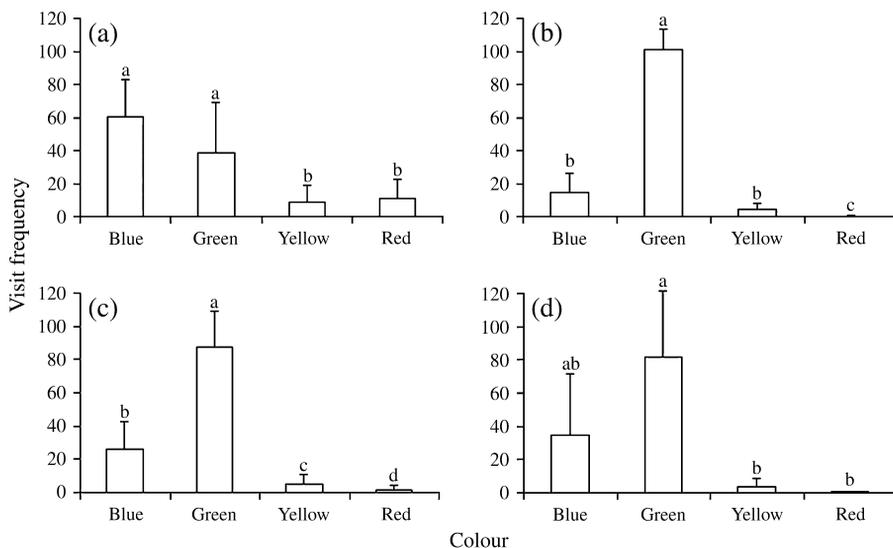


FIG. 2. Preference of juvenile rainbow trout for blue, yellow, green and red ambient after rearing for 2–3 months under (a) blue, (b) green, (c) yellow and (d) red environment. Bars represent the mean \pm s.d. visit frequency of 20 min observation periods at 0800, 1100, 1400 and 1700 hours over the 3 day period (in total 120 observations per individual). Statistical difference of fish visit frequency in each compartment is indicated by different lower case letters (Friedman ANOVA, d.f. = 4, $P < 0.05$).

TABLE I. Mean \pm S.D. ($n = 5$) initial (M_1) and final (M_2) masses, final total length (L_{T_2}), condition factor (K), specific growth rate (G), feed intake (I , last 14 days) and feed efficiency (E_F , last 14 days) of rainbow trout reared in groups of 10 individuals under different colours for 42 days at 17° C

	Ambient colour				
	White	Blue (435 nm)	Green (534 nm)	Yellow (546 nm)	Red (610 nm)
M_1 (g)	1.30 \pm 0.14	1.33 \pm 0.08	1.32 \pm 0.14	1.37 \pm 0.16	1.36 \pm 0.07
M_2 (g)	7.77 \pm 0.24 ^a	7.64 \pm 0.65 ^a	8.65 \pm 0.34 ^b	8.32 \pm 0.72 ^{ab}	7.40 \pm 0.66 ^a
L_{T_2} (mm)	87.5 \pm 0.8 ^{ab}	86.6 \pm 1.5 ^a	91.4 \pm 1.0 ^c	89.4 \pm 2.3 ^{bc}	87.2 \pm 1.7 ^{ab}
K	1.16 \pm 0.03	1.18 \pm 0.06	1.13 \pm 0.02	1.16 \pm 0.03	1.11 \pm 0.05
G (% day ⁻¹)	4.28 \pm 0.24 ^{ab}	4.16 \pm 0.26 ^{ab}	4.49 \pm 0.19 ^b	4.30 \pm 0.28 ^{ab}	4.03 \pm 0.12 ^a
I (g)	23.1 \pm 1.3 ^{ab}	22.0 \pm 3.2 ^a	25.4 \pm 1.3 ^b	23.2 \pm 2.6 ^{ab}	21.3 \pm 1.1 ^{ab}
E_F	1.53 \pm 0.09 ^{ab}	1.64 \pm 0.16 ^a	1.35 \pm 0.19 ^b	1.44 \pm 0.09 ^b	1.42 \pm 0.13 ^b

Values denoted by different lower case superscripts indicate statistical differences between colours ($P < 0.05$, RM ANOVA for final mass, one-way ANOVA for other variables).

When mean G and I values of the growth trial (Table I) were correlated with the mean visit frequencies in respective colours of the preference test at 12° C [Fig. 1(b)] there were significant positive correlations with these variables (Fig. 3) and 97 and 99% of the variation in G and I , respectively, was explained with linear regression.

DISCUSSION

In this study rainbow trout showed a difference in light colour preference when tested at 1 and 12° C. Fish preferred blue and green environments when tested at 1° C but at 12° C green was the most preferred colour (Fig. 1). The

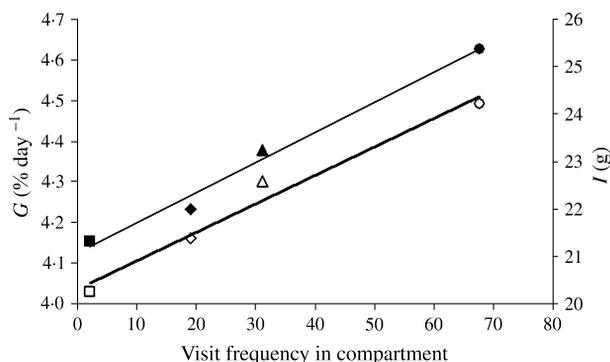


FIG. 3. Relationship between preference for different colours, indicated by visit frequency in blue (◆, ◇), green (●, ○), yellow (▲, △) and red (■, □) compartments at 12° C, and specific growth rate [G , ◇, ○, △, □, —; $y = 0.007x + 4.035$ ($r^2 = 0.97$, $P < 0.05$)] or food intake [I , ◆, ●, ▲, ■, —; $y = 0.19x + 21.07$ ($r^2 = 0.99$, $P < 0.01$)] during the growth experiment in juvenile rainbow trout.

change in the preference can be explained by an earlier observation of the temperature-dependent change in the proportion of visual pigments, namely rhodopsin and porphyropsin, in the retina of rainbow trout reared at 6 and 16° C (Tsin & Beatty, 1977), even though the direct proof of this switch between the two pigment types of the present fish is lacking. Such a change in the proportion of these two pigments may permit the fish to alter the spectral sensitivity of the visual system to match the prevailing light environment (Bowmaker, 1990). Allen *et al.* (1973) could, however, not explain the functional significance of seasonal changes in the visual pigments but they showed that different trout species have clear differences in the rhodopsin:porphyropsin balance, possibly indicating that underlying mechanisms controlling that balance is species specific.

Rainbow trout is a temperate-zone fish experiencing very different light conditions during a cold dark winter and a warm bright summer. Thus, it can be expected that the change in the spectral sensitivity is advantageous for rainbow trout, and that change was observed as a change in the preferred light colour between the two temperatures of the present experiment. The change in colour preference is also in agreement with the idea that as the vision sensitivity is adjusted to the spectral quality of the ambient light, this change enables the fish to catch the greatest number of photons available and enhance visual activity to improve the detection of predators or prey all year around (Munz, 1958; Loew & Lythgoe, 1978).

In this experiment the fish were held under constant light, which is an unnatural photoperiod for rainbow trout when temperature is low (*i.e.* during winter) but on the other hand it is a natural photoperiod during summer at the northern latitudes. In recent experiments with rainbow trout continuous light or constant long days have been shown to have some influence on the immune system (Leonardi & Klempau, 2003), plasma IGF-I levels (Taylor *et al.*, 2005) and haematological variables (Valenzuela *et al.*, 2007) but growth rates have been unaffected (Leonardi & Klempau, 2003) or increased (Taylor *et al.*, 2005) when compared to fish held under natural photoperiod or constant short days. As the use of continuous light in the present experiment probably did not decrease the growth of rainbow trout it permitted 'sieving out' the possible seasonal change in visual pigments and allowed concentrating on the effects of temperature. Even though the season (and consequently photoperiod) can have an effect on the proportions of rhodopsin and porphyropsin (Allen *et al.*, 1973) through modulation of neuroendocrine factors (Flamarique, 2005), Tsin & Beatty (1977) demonstrated that low water temperature favours higher proportion of porphyropsin both at constant darkness and at a 12L:12D light cycle.

The effects of light colours on growth have been tested on several fish species, and there appear to be interspecific differences in this respect, possibly linked to the environment typically inhabited by the given species. For example, it has been shown that the colour red has negative effects on performance and behaviour of several fish species (Ruchin *et al.*, 2002; Ruchin, 2004; Luchiari *et al.*, 2006), which also concurs with the present results with rainbow trout. The low mass gain observed in red and blue environments suggests that these colours affects negatively on growth of juvenile rainbow trout at summer temperatures. Ruchin (2004) suggested that the negative effect of red light on growth rate was induced through changes in energy metabolism, endocrinology

or physiology. On the other hand, red light is probably the most favoured for rearing pikeperch, *Sander lucioperca* (L.), a crepuscular predator inhabiting turbid waters (A. C. Luchiari, F. A. Morais Freire, J. Koskela & J. Pirhonen, unpubl. data). Mid-wavelength colours (green and yellow) provided the most favourable conditions for growth of rainbow trout in the present experiment, and green light has also been shown to promote growth of cyprinids (Radenko & Alimov, 1991; Ruchin *et al.*, 2002). In contrast, guppy *Poecilia reticulata* Peters and whitefish *Coregonus peled* (Gmelin) appear to show increased growth rates in a blue light (Ruchin, 2004).

Karakatsouli *et al.* (2007) found no significant difference in growth rates of gilthead seabream *Sparus aurata* L. (at 20.7° C) or rainbow trout (16.6° C) reared for 11 weeks either in blue, red or white light conditions. Blue light, however, appeared to impose negative effects on growth of rainbow trout after 8 weeks when compared to red and white light. The levels of brain neurotransmitters were also different in fish reared under blue light than in white or red light. Thus, the results of the present experiment seem to contrast the results of Karakatsouli *et al.* (2007) to some extent possibly because of the differences in the length of the rearing period or fish size which in turn may indicate ontogenetic changes in visual and neurohormonal systems in juvenile rainbow trout. This suggestion is supported by the findings of Hawryshyn *et al.* (1989), Beaudet *et al.* (1993) and Allison *et al.* (2003) of the size-related change of visual system in juvenile rainbow trout, especially regarding the loss of ultraviolet wavelength-sensitive cones.

Even though mid-wavelength colours appear to promote growth when compared to the colours at either end of the visible spectrum these results suggest that feed efficiency is not necessarily improved when using mid-wavelength lights. This result is difficult to explain and it must be considered cautiously. Especially, it must be remembered that the feed efficiency result based only on the last 14 day measurement period, so more data would be needed to confirm this result. Also the mechanisms underlying the differences in intake and consequent growth between different colours remain unclear. The differences may have partly been associated with the increased stress under unsuitable colour (Papoutsoglou *et al.*, 2000) or perception of food under different colours.

In this study it was also observed that earlier residence in tested colours (at 17° C) had some influence on the colour preference (tested at 12° C); the fish reared in blue tanks preferred blue compartments while in other cases green was clearly the preferred colour (Fig. 2). Kröger *et al.* (1999) reported that rearing under monochromatic light (blue, green and red) did not change absorbance spectra of the cones in the fish eye which is in contrast to the present finding of the preference for blue when the fish were reared in a blue environment. It has also been reported that the adaptation to a new environmental colour takes around 14 days for Nile tilapia *Oreochromis niloticus* (L.) (Volpato & Barreto, 2001) and this adaptation is possibly linked to the proportions of vitamins A1 and A2 in the retinal pigment epithelium. Therefore, the fact that exposure to different colours varied from 2 to 3 months before the preference test has probably not influenced the results.

In conclusion, these experiments suggest that preference tests can be used as an indicator of an optimal rearing environment. When the results of the

preference test and growth trial were combined (Fig. 3) a very good correlation was observed with the preference and growth and food intake under the tested colours. Consequently, the results support the original research hypothesis (3). The hypothesis (2) of the effects of prior residence in a certain colour environment on subsequent colour preference was supported only partly. The results also support the hypothesis (1) that water temperature influences colour preference. Based on these observations made under laboratory conditions it is suggested that the mid-wavelength light colour environment is the most favourable for rearing rainbow trout <10 g.

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