

## Troubled by the humics — effects of water colour and interspecific competition on the feeding efficiency of planktivorous perch

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In humic lakes in addition to various density-dependent interactions, dark water may be partly causing a bottleneck in perch (*Perca fluviatilis*) growth. This study focuses on clarifying the role of water colour and increasing fish density on the plankton feeding efficiency of perch. Both aquarium experiments and field data were used in this study. In the experiments, perch fed clearly less in highly humic water than in clear water, but the presence of roach had no significant effect on the feeding efficiency of perch. According to the field data, water colour had a significant effect on the length at which perch shifted from feeding primary on plankton to other food sources.

### Introduction

Fish can respond to environmental demands in several ways, one of which is niche shift in search of suitable prey (Eklöv and Persson 1995). Species that change habitat or prey target during ontogeny are often subject to selection pressure and competition at different life stages (Werner 1988). Morphology of the common Eurasian perch (*Perca fluviatilis*) is claimed to be a trade-off between specialized ontogenic niches since perch show morphological preadaptation to two major niche shifts during its life history, starting from planktivory, switching to macroinvertebrates, and ending up as a piscivorous predator (Persson 1988, Eklöv and Persson 1995,

Hjelm *et al.* 2000). Coexisting perch and roach (*Rutilus rutilus*) are claimed to compete for food, especially during the small planktivorous stage (Persson 1990, Persson *et al.* 1999). Roach has been suggested to force young perch to switch to benthic food at a relatively early age, resulting in an earlier niche shift from planktivory to benthivory (Persson and Greenberg 1990). This early niche shift results in reduced growth rate of perch due to increased intraspecific competition and delayed shift to piscivory, or prohibits the shift to piscivory, causing a growth bottleneck (Persson and Greenberg 1990).

Earlier studies have shown that decreased visibility, turbidity caused by e.g. inorganic or dissolve organic matter in water, severely

disturbs prey detection by fish (Vinyard and O'Brien 1976, Horppila *et al.* 2004, Nurminen and Horppila 2006, Estlander *et al.* 2010). Perch is a vision-oriented selective particulate feeder and predator (Helfman 1979), whereas roach is known for its capability of efficient zooplanktivory by filter-feeding in simple-structured turbid waters and at low light intensities (Bohl 1980, Nurminen *et al.* 2010a). Therefore, predation efficiency and prey detection of perch is more dependable on vision and light (Helfman 1979, Nurminen and Horppila 2006).

High concentrations of humic substances in water causes light attenuation (Kirk 1994). During the last decades, lakes in northern and central Europe and North America had become darker due to the increase in dissolved organic carbon (DOC) concentrations (Vuorenmaa *et al.* 2006, Monteith *et al.* 2007). This fundamental change in light conditions underwater must have an effect on prey detection by vision-oriented fish, such as perch. In food selection and diet-analysis studies based on field data collected from humic lakes in southern Finland, Estlander *et al.* (2010) found that water colour caused by humic substances affected prey selection and diet of perch more than prey selection and diet of roach. The effect on perch was pronounced in the most vision-oriented concomitant planktivorous stage. According to Heibo *et al.* (2005), occurrence of the niche shifts in perch is determined by prevailing environmental conditions and various density-dependent interactions. Rask and Raitaniemi (1988) demonstrated a high 2nd-year growing capacity of perch at the planktivorous stage which was strongly related to prevailing environmental variables.

In this study, we focus on clarifying the effect of water colour and density-dependent interactions between perch and roach, on plankton feeding of perch. We conducted aquarium experiments with trials including perch shoals and mixed shoals of perch and roach at different densities feeding in clear- and highly-humic water on planktonic phantom midge (*Chaoborus flavicans*) which is a typical prey organism for perch in humic lakes (Estlander *et al.* 2010). To support experimental studies, field data from Estlander *et al.* (2010) were reanalyzed using a logistic regression to reveal a probability of

perch diet-shift occurring at a given size, in lakes with varying water colour. We also added to the analysis new data from a clear-water lake. We hypothesized that (1) dark water has pronounced effects on plankton feeding of perch, (2) presence of roach should reduce feeding efficiency of perch through interspecific competition, and (3) in addition to competitive density-dependent causes, in humic lakes also water colour may partly affect the diet-shift size of perch at the vision-dependent planktivorous stage.

## Material and methods

### Experimental study

Experimental study was conducted at the Evo Fisheries Research Station in May 2010. The licence for animal experiments was granted by the Finnish Animal Experiment Board (licence number ESAVI-2010-04859/Ym-23). The fish were captured with wire traps (perch) and a pound net (roach) from Majajärvi, a highly humic lake. After capture, the fish were acclimatized to laboratory conditions for one week at 15 °C in a 3500-l pool. The mean ( $\pm$  95%CI) total length of the perch was 10.0  $\pm$  0.20 cm, weight 9.9  $\pm$  0.7 g, and age 2–3 years. The mean ( $\pm$  95%CI) total length of the roach was 11.1  $\pm$  0.13 cm, and weight 11.2  $\pm$  0.6 g. The experiments were conducted in plastic tanks (100  $\times$  100  $\times$  100 cm) filled with 15 °C water. The water was filtered to the tanks through a 50  $\mu$ m net to remove any food items from the water. The light levels above the water surface were adjusted to represent twilight conditions (0.1  $\mu$ mol m<sup>-2</sup> l<sup>-1</sup>, measured with quantum sensors). Light attenuation (cm<sup>-1</sup>) (LI-1400 data logger equipped with a LI-192SA quantum sensor) in the clear-water and highly humic experiments was calculated from light intensity measurements at the surface (1 cm below the water surface) and at 90-cm depth (Nurminen and Horppila 2006).

The fourth instar larvae (body length ca. 10 mm) of *C. flavicans* used in the experiments as prey were collected with net hauls from Majajärvi. The prey density (1 indiv. l<sup>-1</sup>) was adjusted to represent the typical density of *C. flavicans* in Majajärvi (Estlander *et al.* 2009,

Valonen 2009). Chaoborids are a popular planktonic food item for fish and compose a high percentage in the diet of perch in Majajärvi and other humic lakes in the area (Estlander *et al.* 2010). The experiments were conducted both in highly-humic water (Majajärvi: 340 mg Pt l<sup>-1</sup>) and clear water (Syrjälanun: < 10 mg Pt l<sup>-1</sup>) with different fish assemblages (pure perch shoals and mixed shoals) and densities. In the trials, the basic fish assemblage was 3 perch to which we added 3, 6, or 9 perch or roach (three replicates each, total number of experiments 42), total experiment densities thus being 3, 6, 9 and 12 fish (Table 1). After starvation for 2 days, fish were moved to the experimental tanks and were left to acclimatize for six hours before the trials. At the beginning of each trial, 1000 individuals of *C. flavicans* were released into the tanks. The short duration time of the trials (20 min) was set according to preliminary experiments to ensure that the prey density would be sufficient for all used fish densities (3, 6, 9 and 12), thereby all prey individuals would not be consumed during the trials at any fish density. After each experiment, fish were captured with a small net and immediately killed by cutting the neck and weighed to the nearest mg, measured to the nearest mm ( $L_T$ ), after which the digestive tracts were removed. The ingested prey items from the mouth, pharynges and the stomach content of perch and the gut content of roach, were counted under a microscope by counting the number of *C. flavicans* head capsules.

## Field study

### Study lakes

The five study lakes are situated in the Evo district (61°13'N, 25°12'E) in southern Finland, and are small and humic brown-water lakes typical for the temperate regions of northern Europe. The surface area of the lakes varies between 2.1 and 13.8 ha, mean depth between 2.2 and 6.1 m, total P concentration between 8 and 22 µg l<sup>-1</sup>, total N concentration between 440 and 700 µg l<sup>-1</sup>, and water colour between 50 and 340 mg Pt l<sup>-1</sup> (Table 2). The crustacean zooplankton biomass varied between 6 and 21 µg C l<sup>-1</sup> (Table 2). The biomass of cladoceran zooplankton varied

between 2 and 12 µg C l<sup>-1</sup>, and biomass and average size of cladocerans in the study lakes decreased with the Secchi depth (Table 2). The density of chaoborids varied among the study lakes independently of water colour (222–1198 indiv. m<sup>-2</sup>) (Table 2). The benthic invertebrate densities varied among the lakes between 327 and 958 indiv. m<sup>-2</sup> with no dependence on water colour; however, its is worth pointing out that the oxygenated littoral area in darker lakes was remarkably reduced as compared with that in the clearer lakes (7.07–0.54 ha) (Table 2). More detailed description of zooplankton and zoobenthos assemblages and fish diet in the study lakes is given in Estlander *et al.* (2010). Roach and perch comprised 96%–100% of the total gillnet catch and were clearly the most important fish species in the studied lakes (Table 2); detailed methodology and lake characteristics are available from Estlander *et al.* (2010), Horppila *et al.* (2010) and Olin *et al.* (2010).

### Fish data

The perch used for stomach analyses (Iso Valkjärvi  $n = 202$ , Hokajärvi  $n = 191$ , Haarakjärvi  $n = 142$ , Haukijärvi  $n = 162$ , Majajärvi  $n = 167$ ; total  $n = 864$ ) were sampled from 18 July to 16 August 2006 (in total, six times from each lake) with Nordic multimesh gillnets (Estlander *et al.* 2010, Olin *et al.* 2010). The lakes were divided into 2–3 depth zones from which the net sites were chosen randomly. The stomachs were analysed for fullness (12 level scale) and volume proportions of different food items (Windell 1971). For between-lake comparisons, different food items were pooled into two groups: zoo-

**Table 1.** The summary of experimental design. P = perch, R = roach.

	Clear water		Dark water	
	Pure shoals	Mixed shoals	Pure shoals	Mixed shoals
3 ×	3 P		3 P	
3 ×	6 P	3 P + 3 R	6 P	3 P + 3 R
3 ×	9 P	3 P + 6 R	9 P	3 P + 6 R
3 ×	12 P	3 P + 9 R	12 P	3 P + 9 R

plankton and other (benthic macroinvertebrates and fish). The proportions of both groups of food items were calculated for every 1-cm-length class of perch (5–21 cm). The perch ages were determined from opercula bones, and the aging was verified from otoliths (Horppila *et al.* 2000).

## Statistical analyses

In the aquarium experiments, the effects of water colour, fish species and density of fish on perch and roach predation rates were tested with ANCOVA using fish density as a covariate; although this study focused on perch, roach was also considered a treatment. A logistic regression model was used to analyze the proportion of perch utilizing zooplankton as a function of perch length ( $L$ ) following Tolonen *et al.* (1999):

$$y = \exp(\alpha + \beta L + \gamma C + \delta LC) \times [1 + \exp(\alpha + \beta L + \gamma C + \delta LC)]^{-1},$$

where  $y$  is the occurrence of a food category or item in a single fish assuming values between 0 (does not occur) and 1 (does occur),  $L$  is the perch length,  $C$  is the water colour; and  $\alpha$ ,  $\beta$ ,  $\gamma$  and  $\delta$  are parameters. This model was used to test if utilization of zooplankton was dependent on perch length, and if there was an interaction with perch length and water colour. Fish with empty stomachs (9% from Iso Valkjärvi and Haarakjärvi, 10% from Hokajärvi and Majajärvi,

and 3% from Haukijärvi), were not used in the analysis. The fit of logistic regression model was estimated with a likelihood-ratio test. The between-lake differences in length of 2–3-year-old perch were tested with ANOVA. The statistical analyses were performed using SYSTAT ver. 15.0 (SPSS Inc.).

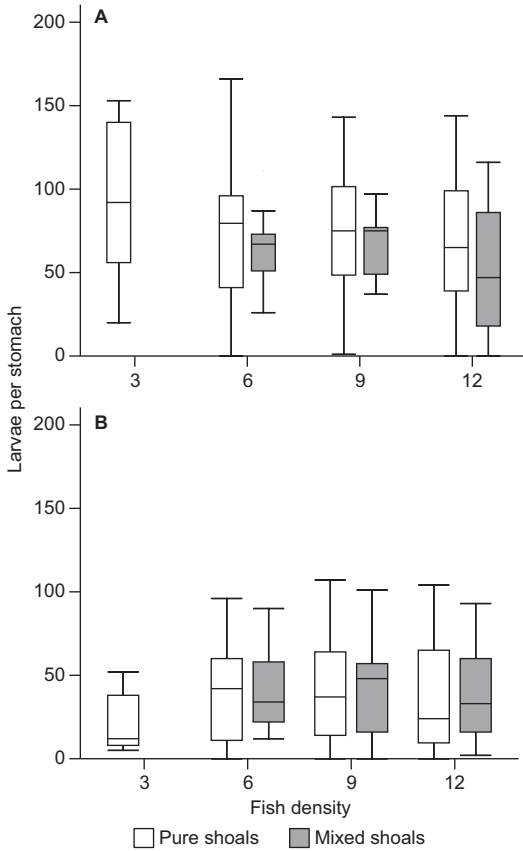
## Results

The mean ( $\pm$  95%CI) values of light attenuation in the highly-humic-water experiments were  $0.027 \pm 0.005 \text{ cm}^{-1}$  and in clear-water experiments  $0.0069 \pm 0.002 \text{ cm}^{-1}$ . Dark water significantly decreased the feeding efficiency of perch ( $p < 0.0001$ ) (Table 3). Fish species had no significant effect on the feeding rate of perch ( $p = 0.372$ ). There was no significant change in the feeding efficiency of perch when perch or roach density was increased (Fig. 1). The average feeding efficiency of roach was overall lower and did not significantly ( $p > 0.05$ ) differ between clear-water and highly-humic water trials (clear-water 29 and highly-humic water 31 larvae fish<sup>-1</sup> on average) or among different fish densities (average 32 larvae fish<sup>-1</sup>) ( $p > 0.05$ ).

The logistic regression analysis showed that in the study lakes, the probability of perch to shift from feeding primary on plankton to other food resources was dependent on perch length and water colour (Fig. 2): i.e., the higher the water-colour value, the greater the probability of

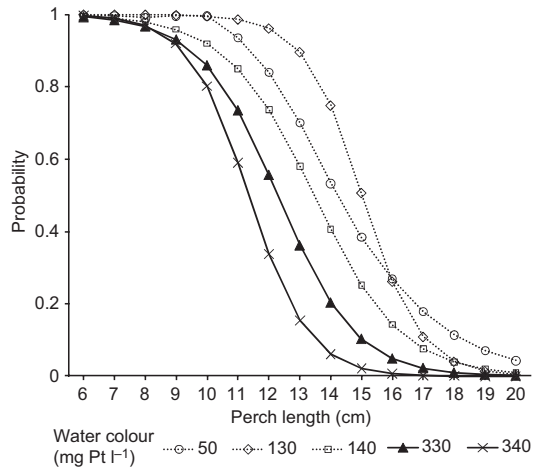
**Table 2.** The abiotic and biotic variables in the study lakes. Iso Valkjärvi data from: <sup>a</sup>own measurements 2007, <sup>b</sup>Grönroos 2009, <sup>c</sup>Olin *et al.* 2010. DO = dissolved oxygen.

	Iso Valkjärvi	Hokajärvi	Haarakjärvi	Haukijärvi	Majajärvi	Reference
Surface area (ha)	2.1	8.4	13.8	2.1	3.4	Horppila <i>et al.</i> 2010
Mean depth (m)	3.8	2.2	6.1	3.8	4.6	Horppila <i>et al.</i> 2010
Max depth (m)	8	6	12	8	12	Horppila <i>et al.</i> 2010
Water colour (mg Pt l <sup>-1</sup> )	50	130	150	330	340	Horppila <i>et al.</i> 2010
Secchi depth (cm)	260	170	150	110	90	Horppila <i>et al.</i> 2010
Crustacean biomass ( $\mu\text{g C l}^{-1}$ )	13 <sup>a</sup>	15	6	12	21	Estlander <i>et al.</i> 2010
Cladoceran biomass ( $\mu\text{g C l}^{-1}$ )	9 <sup>a</sup>	7	2	6	12	Estlander <i>et al.</i> 2010
Cladocera mean length ( $\mu\text{m}$ )	444 <sup>a</sup>	422	478	552	594	Estlander <i>et al.</i> 2010
<i>Chaoborus flavicans</i> (indiv. m <sup>-2</sup> )	1198 <sup>a</sup>	518	600	222	1044	Immonen 2008
Benthic macroinv. (indiv. m <sup>-2</sup> )	958 <sup>b</sup>	327	791	388	856	Immonen 2008
DO $\geq$ 2 mg l <sup>-1</sup> littoral area (ha)	2.19	7.07	6.88	0.54	0.78	own measurements 2010
Roach (CPUE indiv. per net)	0.2	20	43	28	12	Horppila <i>et al.</i> 2010
Perch (CPUE indiv. per net)	18 <sup>c</sup>	10	16	38	15	Estlander <i>et al.</i> 2010



**Fig. 1.** The effect of increasing fish densities on perch feeding on *C. flavicans* (larvae eaten fish<sup>-1</sup>) in perch shoals and in mixed shoals with roach in (A) clear-water and (B) highly humic water experiments. The bottom and top of the boxes are the lower and upper quartiles, and the bars inside the boxes are the median values. The ends of the whiskers represent the minimum and maximum values of the whole data.

perch to shift from feeding primary on plankton at a smaller size. The length and length–water colour interaction estimates in the model were significant ( $p < 0.0001$ ) (Table 4). The age range



**Fig. 2.** Probability of ingestion of zooplankton against perch length estimated with logistic regressions for different water colours.

of planktivorous perch was 2–3 years, but their size varied significantly ( $F_{4,13} = 25.578, p < 0.0001$ ), see also Horppila *et al.* (2011). The average length of 2-year-old perch was 96, 87, 78, 74 and 75 mm in Iso Valkjärvi, Hokajärvi, Haarajärvi, Haukijärvi and Majajärvi, respectively.

## Discussion

Corroborating the hypothesis, in the experiments, feeding efficiency of perch on chaoborids was severely disturbed in dark water most likely because plankton feeding is dependent on good light conditions (e.g. Helfman 1979, Nurminen and Horppila 2006, Nurminen *et al.* 2010b). Expectedly, the foraging technique of roach was not similarly affected by dark water or lack of light (Bohl 1980, Diehl 1988, Nurminen *et*

**Table 3.** Results from ANCOVA using the fish density as a covariate for effects of water colour, fish species and density of fish on perch predation rate.

	df	Mean square	F	p
Density	1	1919.962	1.551	0.214
Colour	1	32062.881	25.895	< 0.0001
Fish species	1	991.167	0.800	0.372
Colour × Fish species	1	3322.293	2.683	0.103

*al.* 2010a). Contrary to our hypothesis, in the experiments, the presence of roach had no significant effect on perch feeding. Persson (1987) suggested the competitive interaction of the species to be asymmetric and in favour of roach. Interestingly, in our clear-water trials, the perch feeding efficiency was slightly lower in the presence of roach but the effect was not statistically significant. This may have resulted from perch limiting its movements in the presence of roach (S. Estlander pers. obs.). However, Persson and Greenberg (1990) showed a clear negative effect of roach on perch growth and diet already at lower fish densities (115–156 fish/1640 m<sup>3</sup>) and much longer duration of experiments (three months). In darker water, movement, success of hunting activity and prey search by perch is fundamentally more limited.

Supporting the experimental results on the hampering effect of water colour on the feeding efficiency of perch, the field data indicated that water colour had a significant effect on the length at which perch shifted from a primarily plankton diet to other food resources. The darker the water in the lake, the smaller the size at which perch shifted from feeding on plankton to feeding on benthic organisms. According to Persson and Greenberg (1990), juvenile perch shift earlier and at a smaller size to feeding on macroinvertebrates, if zooplankton resources were severely limited by e.g. density-dependent interactions such as competition. In our study lakes, high competition for zooplankton resources was unlikely the ultimate reason for the earlier shift by perch from planktivory, because the crustacean zooplankton resources were most plentiful in the most dark-watered Majajärvi where perch shifted to benthivory at the smallest size. According to Estlander *et al.* (2009, 2010) in the study lakes there was a significant positive relation between cladoceran

mean size and water colour as cladocerans are overall larger in more humic lakes, indicating refuge provided by dark water against vision-oriented fish predators. Additionally, there was no clear relation between water colour and chaoborid density among the study lakes, highest densities occurring in the clearest and darkest lakes, as the density is also dependent on the occurrence of anoxic refuge rather than on visibility alone (Liljendahl-Nurminen *et al.* 2008). Therefore, it is conceivable that dark water hampered the vision of planktivorous perch by reducing detection of zooplanktonic prey, and forced perch to concentrate on macroinvertebrate prey as benthic feeding is less vision-oriented (Crowl 1989, Horppila *et al.* 2010).

According to Estlander *et al.* (2010), in the study lakes the interspecific diet overlaps between perch and roach were highest at the concomitant planktivorous stage, but were nevertheless insignificant. In addition to interspecific interactions, Svanbäck *et al.* (2008) suggested that intraspecific competition within perch populations may also be important in habitat distribution and resource partitioning. Corroborating the results of Persson and Greenberg (1990), after the plankton-feeding phase the availability of benthic macroinvertebrates restricted the growth rate of perch in the study lakes (Horppila *et al.* 2010). Benthic-macroinvertebrate densities per square meter varied among the lakes regardless of water colour, but when taking into account the areas with dissolved-oxygen concentrations below 2 mg l<sup>-1</sup>, total benthic macroinvertebrate densities were lower in the highly humic lakes due to smaller oxygenated areas (Estlander *et al.* 2010). The thickness of the oxygenated water layer may, therefore, be an important factor limiting the foraging possibilities of fish in strongly-stratified humic lakes (Rask *et al.* 1999). In darker lakes, the coverage of the oxygenated littoral area was particularly small, which most likely limits the availability of benthic macroinvertebrates and confines perch benthivory to a smaller area, and increases intraspecific competition for benthic food (Estlander *et al.* 2010, Horppila *et al.* 2010).

Size and growth are interrelated, and in the study lakes perch growth was overall quite slow indicating restricted resources typical for humic lakes (Estlander *et al.* 2010, Horppila *et al.* 2010,

**Table 4.** Results of the logistic regression analysis.

Parameter	Estimate	SE	Wald $\chi^2$	<i>p</i>
$\alpha$	14.207	1.886	56.738	< 0.0001
$\beta$ (length)	-0.976	0.146	44.836	< 0.0001
$\gamma$ (colour)	-0.038	0.007	30.003	< 0.0001
$\delta$ (length $\times$ colour)	0.002	0.001	17.519	0.001

Olin *et al.* 2010). In the study lakes, the diet shift from plankton to benthos occurred on average at the age of 2–3 years, and at a variable size, indicating heterogeneity in growth. Fast growth by efficient plankton feeding is important for perch survival and early maturation (Heibo *et al.* 2005). Slow growth during the plankton-feeding phase may lead to delay and inhibition of the second niche shift from benthivory to piscivory and, according to Heibo *et al.* (2005), the second-year growth seems to determine the likelihood of the shift to piscivory. Corroborating our results, Horppila *et al.* (2010, 2011) reported that in the study lakes the growth rate of perch during the second year of life was significantly dependent on water transparency.

Factors affecting habitat distribution, resource partitioning, diet selection and also the timing of ontogenic niche shifts may be numerous. The study lakes vary in morphometry, productivity, availability of resources, biomass of planktivores and piscivores and littoral habitats (e.g. Estlander *et al.* 2010, Horppila *et al.* 2010). However, humic lakes are relatively stable ecosystems (Wetzel 2001), and in our study lakes, the year-to-year timing of diet shifts of perch is quite consistent. Olin *et al.* (2010) studied the effects of several abiotic and biotic factors on various population parameters of perch in humic lakes, including our study lakes, and suggested that perch populations are affected by biotic factors such as interspecific competition by roach and predation by pike, but the intensity of the interactions is regulated by abiotic factors, such as lake size and general productivity, with water colour as the most important single factor.

Water colour clearly had a negative effect on perch feeding, but did not affect roach. Dark water could thus favour roach over perch in humic lakes in competition for the same food resources. According to Persson and Greenberg (1990), a dense roach population may create a bottleneck in perch growth in the macroinvertebrate feeding phase by forcing young planktivorous perch to switch to benthic food resources at a smaller size. Estlander *et al.* (2010) predicted a possible bottleneck in perch growth in highly humic lakes. Here, we confirmed this prediction in both experimental and field studies. We conclude that in humic waters, in addition to the

density-dependent interactions (e.g. fish density and competition), occurrence of a benthic bottleneck in perch growth is dependent on prevailing environmental factors such as water colour.

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