

Zeynep Pekcan-Hekim · Jyrki Lappalainen

Effects of clay turbidity and density of pikeperch (*Sander lucioperca*) larvae on predation by perch (*Perca fluviatilis*)

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Abstract Increased turbidity reduces visibility in the water column, which can negatively affect vision-oriented fish and their ability to detect prey. Young fish could consequently benefit from high turbidity levels that can provide a protective cover, reducing predation pressure. Perch (*Perca fluviatilis*) are commonly found in littoral zones of temperate lakes and coastal areas of the Baltic Sea. Pikeperch (*Sander lucioperca*) spawn in these areas, so perch is a potential predator for pikeperch larvae. We conducted laboratory experiments to test the predation of perch on pikeperch larvae at different turbidity levels (5–85 nephelometric turbidity units), densities of pikeperch larvae (2–21 individuals l^{-1}) and volumes of water (10–45 l). The logistic regression showed that the probability of larvae eaten depended significantly on turbidity and volume of water in the bags, while density of larvae was not significant. However, because container size is known to affect predation, the data was divided into two groups based on water volume (10–20 and 25–45 l) to reduce the effects of container size. In either group, probability of predation did not significantly depend on volume, whereas turbidity was significant in both groups, while density was significant in larger water volumes. Thus, high turbidity impaired perch predation and protected pikeperch larvae from perch predation. Because density of larvae was also a significant factor affecting predation of perch, the dispersal of pikeperch larvae from spawning areas should also increase the survival of larvae.

Introduction

Water turbidity can have both negative and positive impacts on visually feeding fish in aquatic systems (Utne-

Palm 2002). Clay turbidity caused by suspended particles in the water column results in scattering of light and, therefore, interferes with vision of fish (Bruton 1985). The negative effects of turbidity on predation have been experimentally shown in several studies (e.g. Vinyard and O'Brien 1976; Gregory and Northcote 1993; Utne-Palm 1999). However, a certain degree of turbidity can even increase the contrast between the prey and its background, enabling the predator to detect its prey (Horppila et al. 2004). Increased turbidity can also lead to higher feeding motivation of the fish caused by lowered predation risk (Gregory and Northcote 1993).

Several fish species appear to prefer turbid waters during their early life stages (Cyrus and Blaber 1987). High turbidity can reduce predation pressure on larval and juvenile stages of fish, providing a protective cover enabling them to avoid detection or capture by predators (Gregory 1993). Besides high turbidity, decreased density of prey increases the time spent searching for the prey by the predator (Walton 1980).

Pikeperch (*Sander lucioperca*) spawn in shallow and turbid areas of lakes and also in the coastal areas of the Baltic Sea in late spring (Lappalainen et al. 2003). During this period, turbidity is usually the highest in several bays in the Baltic Sea (Lappalainen and Lehtonen 1995). High turbidity can protect pikeperch larvae from predators during the critical first 3–4 days after hatching (Svärdson and Molin (1973) and references therein). Hatched pikeperch larvae show alternate phases of upward swimming and passive falling that can be connected to avoidance of less oxygenated bottom layers or to dispersal from spawning areas (Schlumberger and Proteau 1996).

Pikeperch is a potential prey species for several littoral predators such as perch (*Perca fluviatilis*) (Dörner et al. 1999). Kjellman et al. (2003) found that the relative year-class strength of pikeperch was established approximately 1 to 2 months after the supposed hatching and suggested that the mortality during the larval and early juvenile stages determines the year-class strength of pikeperch in the coastal areas of the Baltic. The positive effects of temperature on the year-class strength of pikeperch are evident

Z. Pekcan-Hekim (✉) · J. Lappalainen
Department of Biological and Environmental Sciences/
Aquatic Sciences, University of Helsinki,
P.O. Box 65, FI-00014 University of Helsinki, Finland
e-mail: zeynep.pekcan@helsinki.fi
Tel.: +358-9-19158993
Fax: +358-9-19158257

(Lappalainen and Lehtonen 1995; Kjellman et al. 2003), but the effect of predation remains unknown.

Perch are primarily adapted to daylight feeding (Bergman 1988) and low light can significantly reduce their feeding efficiency (Diehl 1988). Sandström (2004) showed that increased turbidity (from 3 to 35 nephelometric turbidity units (NTU)) and reduced density of prey (*Bosmina longirostris*) decreased the feeding success of perch. However, Granqvist and Mattila (2004) did not find any clear effect of turbidity on the feeding of juvenile perch on mysids at turbidity levels ranging from 1 to 30 (NTU). Radke and Gaupish (2005) found that phytoplankton-induced turbidity had more pronounced effect on perch feeding than bentonite-induced turbidity; however, the turbidity levels used by Radke and Gaupish (2005) were only up to 8 NTU. In Finnish lakes and in the coastal areas of the Baltic Sea, clay turbidity can reach up to 90–100 NTU caused by sediment resuspension and inflowing rivers.

The aim was to study the effects of clay turbidity, density of pikeperch larvae and volume of water on feeding of perch in laboratory experiments. We hypothesised that the feeding success of perch on pikeperch larvae will reduce towards higher turbidity levels and lower prey densities. Turbidity levels analysed in the present study were higher (up to 85 NTU) than that used previously by Radke and Gaupish (2005) and by Granqvist and Mattila (2004).

Materials and methods

The perch (6.3–10.6 cm total length) used in experiments were acclimatised for 2–3 weeks at 16°C in 450-l aquaria before the tests. Fluorescent lights were fixed above the aquaria and a daily light regime of 8-h dark and 16-h light was used. Perch were fed daily on a diet of invertebrates such as chironomid's, krill and white and black mosquito larvae. Pikeperch larvae (4.4–6.5 mm total length) were obtained from pikeperch cultures. All experiments were done in transparent plastic bags, which were placed in aquaria filled with water at 16°C. The aquariums were covered with black plastic to prevent disturbance from

outside. Fluorescent lights were fixed above the aquariums and the light intensity above the bags was kept constant for each experiment. On the day before each experiment, three perch were moved to each bag. The turbidity levels used in the experiments ranged from 5–85 NTU and water volumes in bags were 10, 15, 20, 25, 35 and 45 l. The dimensions of the empty bags were 30×70 cm. Turbidity levels were created with clayish bottom sediment and slight air bubbling was used to prevent sedimentation of the suspended material during the experiments. The experiments started at 12:00 when pikeperch larvae (100 or 200) were added to bags and ended at 14:00. After each experiment, perch were taken out and water temperature, pH, turbidity and concentration of dissolved oxygen were measured with a YSI-6600 sonde. The water temperature (16°C), pH (7.4–7.9) and dissolved oxygen (80–100%) were similar in each experiment. The light intensity (400–700 nm) was measured with a LI-1400 datalogger equipped with quantum sensors at the surface, at the middle and at the bottom of every bag. The density of larvae in bags was calculated as the number of larvae divided by the volume of water in the bag. Perch were measured by total length to nearest millimeter and weighed and their stomach contents were analysed after each experiment for pikeperch larvae eaten.

The effect of turbidity, density of prey and volume of water on feeding of perch was analysed using stepwise logistic regression (SAS, proc LOGISTIC). The dependent variable was the number of perch feeding divided by the number of perch in the bag. Thus, the dependent variable had four different levels (0/3=none of the perch feeding, 1/3=one perch feeding, 2/3=two perch feeding and 3/3=all perch feeding in a bag). As earlier experimental studies have shown that container size influences predation rates in predator–prey systems (de Lafontaine and Leggett 1987), we divided the data into two groups based on water volume (10–20 and 25–45 l) to reduce the possible effects of container size on predation. Logistic regression was also used to analyse if feeding was size-dependent using either length or weight of perch. Besides these, logistic regression was also used to analyse the possible effects of light levels on feeding of perch.

Table 1 Effects of turbidity, density of larvae and volume of water on predation of perch based on stepwise logistic regression

Model	Volumes (l)	<i>n</i>	Parameter	Estimate	Chi-square	<i>P</i>
1	10–45	54	Intercept	1.167	3.1	ns
			Turbidity	–0.039	9.6	0.002
			Density of larvae ^a	–	–	ns
			Volume of water	–0.055	9.2	0.002
2	10–20	17	Intercept	0.7	0.9	ns
			Turbidity	–0.052	5.8	0.016
			Density of larvae ^a	–	–	ns
			Volume of water ^a	–	–	ns
3	25–45	37	Intercept	–3.615	11.1	0.001
			Turbidity	–0.033	5.2	0.023
			Density of larvae	0.491	8.0	0.005
			Volume of water ^a	–	–	ns

First, all data were analysed (model 1) and then divided into two groups based on volume (models 2 and 3)
n Number of experiments,
 ns *P*>0.05

^aNot significant and dropped during stepwise selection

Results

The logistic regression showed that the probability of larvae eaten depended significantly on turbidity and volume of water in the bags, while density of larvae was not significant (Table 1). However, when the data was divided into two groups based on water volume (10–20 and 25–45 l), turbidity had significant effect on the probability of pikeperch larvae eaten in both groups, while density had significant effect only in larger volumes (Table 1; Fig. 1).

The feeding of perch on pikeperch larvae was not size-dependent (10–45 l), because neither length ($\chi^2=2.1$, $P=0.15$) nor weight ($\chi^2=1.17$, $P=0.3$) was significant among the analysed size range (6.3–10.6 cm total length, 3.0–6.7 g) of perch. The same was observed also in two different groups of volumes (10–20 l: $\chi^2=3.4$, $P=0.06$; 25–45 l: $\chi^2=0.6$, $P=0.4$). Light levels ranging from 0.6 to 4.2 $\mu\text{E m}^{-2} \text{s}^{-1}$ similarly had no effect on predation by perch on pikeperch larvae in any of the analysis (10–45 l: $\chi^2=2.75$, $P=0.1$; 10–20 l: $\chi^2=1.9$, $P=0.16$; 25–45 l: $\chi^2=0.6$, $P=0.5$).

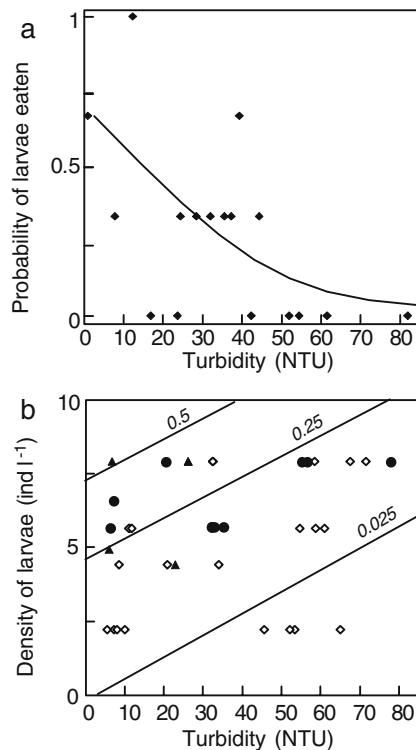


Fig. 1 Probability of pikeperch larvae eaten by perch: **a** different turbidity levels in smaller water volumes (10–20 l) (probability marked with line); **b** different densities of larvae and turbidity levels in larger water volumes (25–45 l) (probability marked with isopleths), each marker represents the number of perch feeding in each bag with different turbidity and density. *Open square* is for 0 perch feeding, *solid dot* is for 1 perch feeding and *solid triangle* is for two perch feeding

Discussion

The success of perch feeding on pikeperch larvae decreased with increasing clay turbidity despite water volume in the bags. Pikeperch larvae should be safer in highly turbid waters due to decreased reaction distance of the predator. Reaction distance is the maximum distance at which the predator detects and attacks its prey (Vinyard and O'Brien 1976). With increasing turbidity, the reaction distance of the predator will shorten, increasing the probability of detection of the predator by its prey (Abrahams and Kattenfeld 1997). Pike (*Esox lucius*) larvae showed decreased anti-predator behaviour in the presence of perch in more turbid waters (Lehtiniemi et al. 2005). Reduced anti-predator behaviour of larvae could lead to increased feeding efficiency of larvae (Boehlert and Morgan 1985).

Container size has been found to influence predation in experimental studies (de Lafontaine and Leggett 1987). This was also the case in our experiments. To reduce the effects of volume, we divided our data in two groups based on the volumes of water in the bags and found that turbidity was a significant factor affecting perch predation in both groups, whereas density of larvae was significant only in larger volumes. The latter result coincides with the experiments conducted by Utne (1997) and Sandström (2004), who showed that the reaction distance declined faster with increasing turbidity in low than in high prey densities. Thus, our results suggest that turbidity is an important environmental factor that has negative effects on predation of perch, while comparisons of predation over a large range of container sizes could be problematic.

The size of predator had no effect on the probability of larvae eaten within the studied size range. This is in line with Richmond et al. (2004) who found that total length of yellow perch (*Perca flavescens*) (3.1–8.8 cm total length) did not significantly influence the reaction distance. Light scattering increases linearly with higher turbidity and impairs the feeding success of visually hunting fish (Kirk 1981). Experimental studies with piscivorous and planktivorous predators have shown that the reaction distance between predator and prey increased rapidly with increasing light intensity and reached a constant level at the threshold light level (Vinyard and O'Brien 1976; Utne 1997; Mazur and Beauchamp 2003; Horppila et al. 2004). Because the light levels used in our experiments were above the suggested threshold level, no effects of light on the predation rate of perch on pikeperch larvae were found.

We can conclude that high turbidity levels impair perch predation and protect the pikeperch larvae from perch. Because density was also a significant factor, especially in larger water volumes, the dispersal of pikeperch larvae from spawning areas could also be seen as a factor increasing the survival probabilities of larvae.

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