Foraging, growth and habitat choice in turbid water: an experimental study with fish larvae in the Baltic Sea

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ABSTRACT: Eutrophication is a large problem in many marine and brackish-water areas. One of the consequences is algae-induced turbidity affecting visually feeding organisms, and behavioural changes of fish and other animals are common in turbid water. The aim of this study was to compare the performance of larval pike *Esox lucius* in turbid and clear water. We experimentally studied habitat choice, prey attacks and swimming activity of newly hatched larvae in the presence of a predator and competitors in relation to algae-induced turbidity. Our results demonstrated that the larvae spent less time in vegetation, performed more prey attacks and spent less time swimming in turbid water than in clear conditions. The presence of competitors increased the number of prey attacks, while the presence of a visual predator decreased the number of attacks. We also showed that pike larval weight was lower in high turbidity than in low turbidity. Our results show that algae-induced water turbidity affects both direct (i.e. feeding and habitat choice) and indirect qualities (i.e. weight) of pike larvae and may therefore affect larval survival and potentially even recruitment into the population.

KEY WORDS: Turbidity · Pike larvae · Habitat choice · Prey attacks · Growth · Shelter · Perception of threat

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INTRODUCTION

Algae-induced turbidity has greatly increased in coastal areas worldwide due to nutrient runoffs into rivers, lakes and seas. The increasing amount of nutrients leads to algal blooms and higher turbidity (Utne-Palm 2002). With elevated turbidity, light attenuation increases, limiting visibility (Eiane et al. 1999). However, some species benefit from elevated turbidity levels, because their visual acuity is enhanced due to increased scattering of light increasing the contrasts in the water. Algae-induced turbidity within certain levels is desirable, since algae add oxygen and remove nutrients from the water (Boyd 1982). The phenomenon may have both positive and negative effects on the behaviour of visually feeding fish. For a large piscivore that detects its prey from a long distance, increasing turbidity will be more disruptive than for a small planktivore

that detects its prey at a shorter distance (Chesney 1989). Negative effects caused by turbidity include decreased reactive distance to prey, changes in the amount or type of prey, lower opportunity for sexual selection in fish with visual mate choice, and decreased growth due to reduced capture success (Järvenpää & Lindström 2004, Stuart-Smith et al. 2004, Ljunggren & Sandström 2007). In contrast, positive effects include increased feeding rate due to a lower risk of predation (Gregory & Northcote 1993). Turbidity may also induce other activities, such as migration, reduced use of shelter and increased use of open water (reviewed by Utne-Palm 2002). Finally, turbidity, as such, may also provide shelter against predators (Maes et al. 1998, Snickars et al. 2004, Engström-Öst et al. 2006).

The pike *Esox lucius* is an important piscivore in many northern areas and is also an important catch for fishermen in the northern Baltic Sea (Lappalainen

2002). The pike is considered to be a very adaptive species due to its wide distribution (Casselman & Lewis 1996), but despite high flexibility, populations have collapsed during the last few years in areas where environmental changes have been considerable (reviewed by Casselman & Lewis 1996, Nilsson et al. 2004). The Baltic Sea, where our study was performed, has become increasingly turbid during the last few decades (Sandén & Håkansson 1996).

The aim of this study was to study pike larval behaviour, including habitat choice, foraging and swimming in the presence of a competitor species and a visual predator in an environment with algal turbidity. We also analysed stomach contents and measured larval condition. Finally, weight of pike larvae in high and low turbidity was monitored. We hypothesised that the behaviour of pike larvae, such as habitat choice, is less pronounced in turbid water, because predators are more difficult to detect, and the larvae thus perceive less threat. Further, we expected that open turbid water would be used more frequently than open clear water due to increased protection from visual predators. Pike are usually considered to be sensitive to turbid water (Vøllestad et al. 1986, Craig & Babaluk 1989, Lehtiniemi et al. 2005), but few studies have investigated the behaviour of larval stages as a consequence of this environmental change. Freshwater, brackishwater and marine species inhabit the Baltic Sea, where this study was conducted. Therefore, all organisms used in the current study (pike larvae, mysid shrimps, copepods) are common species in the Baltic Sea and co-occur within the habitats (Lehtonen 1986, Engström-Öst 2002, Kotta et al. 2004).

MATERIALS AND METHODS

Study organisms. Larval pike *Esox lucius* with yolk sacs at 4 d post hatch (dph) were obtained from a fish hatchery in SW Finland (Trollböle). The larvae originated from 5 females and 5 males, caught from the natural environment. The eggs were fertilised and hatched in river water according to the normal procedures at the hatchery. The larvae were transported in a plastic bag containing oxygen-enriched river water to the Tvärminne Zoological Station. The larvae were acclimated for 2 h to the ambient temperature and then divided into two 628 l tanks with brackish-water flowthrough (salinity 6.6 ± 0.07, 10°C, unfiltered). Macroalgae and stones were added to both containers. The larvae were fed with a dense zooplankton community twice a day (32 ± 6 prey ml^{-1}). The main species were rotifers *Synchaeta* sp. and *Acartia bifilosa* copepod adults and nauplii. Since the fish tanks were outdoors, the light regime was natural, varying between ca.

17:7 h and 19:5 h light:dark during the study period. The fish were not removed from the tanks until the experiment. Pike are common along the coastline of the brackish Baltic Sea and are well adapted to brackish water (Engström-Öst et al. 2005). Large numbers of stocked pike larvae of freshwater origin are annually released to the brackish Baltic Sea (Selén 1999). Pike usually use habitats with *Phragmites australis* or *Fucus vesiculosus* in the Baltic Sea (Lehtonen 1986).

The zooplankton (*Synchaeta* sp., *Acartia bifilosa*) that were used as food for the pike larvae were collected with ca. 8 hauls with a 100 µm net from 0 to 25 m depth. Collection was performed daily in an open pelagic area (Storfjärden). Upon arrival in the laboratory, the zooplankton container was transferred to a climate chamber (14 to 15°C, 16:8 h light:dark) and aerated.

The predators (Eurasian perch *Perca fluviatilis*, total length [L_T] 18 to 19 cm) were caught from a shallow bay (depth 1 to 2 m) with fish traps. The traps were checked twice a day. The perch were kept in an outdoor 628 l tank on a brackish-water flow-through system (similar as above). The perch were fed ad libitum with mysid shrimps once a day. Perch are common predators of pike larvae in the Baltic Sea area (Selén 1999 and references therein).

The competitors (mysid shrimps *Neomysis integer*) were caught from the littoral zone with a beach seine. The mysids were kept in an aerated 30 l container in the climate chamber and fed once daily ad libitum with natural zooplankton. The temperature and light conditions in the climate chamber were the same as mentioned above. *N. integer* is the most common and widespread mysid shrimp in the Baltic Sea, occupying mainly shallow coastal areas (Kotta et al. 2004).

Turbidity was created using the green flagellate *Brachiomonas submarina*, diameter 7.5 µm. We obtained *B. submarina* from the culture collection at Tvärminne Zoological Station, University of Helsinki, where it was cultured in TV2 medium (Hällfors & Hällfors 1992). The algal culture density was quantified by particle counting (ELZONE particle counter, Particle Data).

Bladder wrack *Fucus vesiculosus* was collected close to the shoreline from ca. 1 m depth and detached from the stones with a rake. The filamentous green alga *Cladophora glomerata* was collected manually from ca. 1 m depth and was not detached from the stones. The algae were stored under light in the same climate chamber as mentioned above and aerated. After the experiment, *C. glomerata* was removed from the stones with a blade. All algae were dried on aluminium foil at 60°C for 24 h or until dry and then weighed.

Expt 1: habitat choice in turbid water. Pike larvae were exposed to turbid and clear water and allowed to choose between 2 different habitats in the presence of competitors and/or a predator. The control data (i.e. clear

water treatment; see Fig. 1) were obtained from Engström-Öst et al. (2007). One pike larva was placed in a 5 l aquarium (20 × 28 × 9 cm, height × width × depth) that had been divided into 3 habitats by putting filamentous algae *Cladophora glomerata* and bladder wrack *Fucus vesiculosus* at opposite ends of the rectangular aquarium. The third habitat, an open brackish-water area, separated the 2 vegetation patches. The length of each vegetation habitat was ca. 8 cm, and the distance between the 2 habitats was ca. 12 cm. The pike larva was subjected to 1 of the following treatments: (1) 5 competitors present (*Neomysis integer*), (2) visual contact with a predator (*Perca fluviatilis*), (3) 5 competitors present + visual contact with a predator or (4) the control (no competitors or predator present). Each pike larva was used only once in 1 video session. The pike larvae were 26 to 31 dph (L_T: 14.0 ± 0.1 mm, weight [W]: 0.013 ± 0.0003 g) during the experimental period. The 2 vegetated habitats were created by attaching *F. vesiculosus* by strings to a plastic net, which was covered by washed commercial fine sand, and by embedding small stones with attached *C. glomerata* in sand, respectively. Each of the algae took up ca. $\frac{1}{5}$ of the volume of the aquarium. The average biomass (dry weight) of *F. vesiculosus* was 2.01 ± 0.15 g and that of *C. glomerata* was 0.14 ± 0.04 g. The biomass difference depended on the marked morphological differences of the 2 species: *F. vesiculosus* is thick, robust and has an open and highly curved structure, whereas *C. glomerata* consists of long, thin and simple filaments. The aquarium was filled with filtered brackish water (10 μm filtered, ca. 6 psu).

The pike larvae and mysid shrimps were starved for 74 ± 4 min prior to the experiment and were acclimatised to the environment for 10 min. Prior to the acclimatisation, the plankton algae were added to the aquarium to make the water turbid. Chlorophyll (chl) *a* concentration was 42.7 ± 3.0 μg l^{-1} in the experimental units, which corresponded to 30 ± 2.3 NTU (i.e. very turbid conditions). Turbidity in the Baltic Sea may vary between 0.5 and 45 NTU (Granqvist & Mattila 2004). The acclimatisation of experimental organisms was performed in a plastic bottle, which was placed in the middle of the aquarium. The bottle had net-covered holes at 1 end and on 1 side to allow water exchange. The mysid shrimps were acclimatised simultaneously with the pike larva in the same bottle. After the acclimatisation, the bottle was carefully emptied in the middle of the aquarium, and 100 ml of dense natural zooplankton community was poured uniformly into the water (32 ± 6 prey ml^{-1}). We used 2 Eurasian perch as predators. One of the perch was placed in a separate 19 l aquarium (25 × 30 × 25 cm) next to the long side of the rectangular fish larval aquarium so that the pike larva only had visual contact with it. The water temperature in the predator aquaria was 16.7 ± 0.3°C.

During the experiment, the pike larvae were filmed for 10 min. The video sessions were recorded at room temperature in 36.5 to 58.9 μE m^{-2} s^{-1} light. The water temperature in the fish larval aquaria was 15.3 ± 0.2°C. We used 1 video camera (JVC) to record a total number of 40 video sessions. The sample size was 10 per treatment (4 treatments). Individual fish were used for independent observations. All experimental trials were conducted in random order. Use of the 2 predators was also random. Further, before every experimental run, we alternated which of the 2 habitats in the fish larval aquarium was closer to the wall to avoid any systematic differences due to position of the aquarium. During the analysis of the video sessions, we measured time spent in each vegetation type (*Fucus vesiculosus* versus *Cladophora glomerata*), number of attacks on zooplankton prey, and total swimming time of the pike larvae. Preliminary observations suggested that the mysid shrimps did not show any distinct distribution pattern during the experiments (authors' unpubl. data).

After the experiment, all pike larvae and mysid shrimps were killed according to Engström-Öst et al. (2005). The fishes were conserved in unbuffered formalin (37%). Weight of preserved specimens was measured on a scale (Mettler AE 101-S) and length measured under a binocular microscope (Leica). We calculated a condition index for all fish to ensure their well-being and suitability for the experiments (Ormerod & Tyler 1990). The length and weight data of the larvae were log-transformed, analysed with linear regression, and residuals used as an index for condition. Negative values denote low condition and positive values denote good condition. Stomach analysis was performed under a binocular microscope. The stomach was removed and carefully opened with 2 sharp forceps in a petri dish. The content was spread out in a small amount of water; thereafter, the zooplankton were identified to species and the numbers counted.

Expt 2: effects of turbidity on growth. In the growth experiment, the pike larvae were exposed to (1) high (34.9 ± 1.6 NTU) and (2) low turbidity (5.3 ± 1.3 NTU). Turbidity was measured with a nephelometer (Hach 2100P Portable Turbidimeter). The high turbidity treatment corresponded to 59.3 ± 3.7 μg chl *a* l^{-1}. Chl *a* analysis was done according to Engström-Öst (2002). The aim of the experiment was to identify whether high turbidity constrains growth of pike larvae. Turbidity was induced by adding a suspension of the alga *Brachiomonas submarina* to the experimental water. No algae were added to the low turbidity treatment. Single fish larvae were put into individual 1 l white plastic containers. There was no significant difference between the starting weights of larvae put into high and low turbidity water (two sample *t*-test, $t_{14} = 1.3$, p = 0.22). The containers did not contain stones or plants in order to make the growth environ-

ments as similar as possible among replicates. The water in each container was changed daily without disturbing the larva, and oxygen saturation was monitored (high turbidity: $128.6 \pm 0.8\%$, low turbidity: $106.3 \pm 0.4\%$) in the early morning in all experimental units. The light was not switched off during the night, due to the light environment larvae experience in nature. The water temperature was $14.6 \pm 0.03°C$ in the high turbidity units and $14.7 \pm 0.03°C$ in the low turbidity units. The experiment lasted 15 d, and fish larval wet weight (0.0001 g) was determined with a scale (Mettler AE100) every second day. At the start of the experiment (Day 0), all experimental fish were weighed. For weight measurements, the fish larva was caught in a small plankton net spoon. The spoon was dried and the fish was transferred to a small cup of water of known weight. The water in each weighing originated from the respective experimental unit. The experimental units were cleaned daily by changing the water to pre-aerated, 10 µm filtered water of high or low turbidity and larvae were fed by adding 100 ml of dense zooplankton community (32 ± 6 prey ml^{-1}; *Synchaeta* sp., *Acartia bifilosa*). The sample size was 8. None of the fish died during the experimental period. The fish were released to a vegetated shoreline after the experiment.

Light intensity was 5.933 µE m^{-2} s^{-1} during the experiment and was monitored once above the experimental units at the end of the experiment (Li1000 Data Logger LiCor). Water conductivity (µS cm^{-1}) was measured once during the experimental period (CDM83 Conductivity Meter, Radiometer Copenhagen). Salinity was 6.67 and was calculated as follows: (Conductivity −60.9)/163. Fish larval pellet production was measured once a week. Pellets were collected with a glass Pasteur pipette before the daily cleaning of the aquarium and carefully transferred to plastic petri dishes and counted immediately under a microscope.

All data were tested for normality (Wilk-Shapiro) and homogeneity of variances (Bartlett's test for equal variances). If assumptions were not met, non-parametric tests were employed. All tests were 2-tailed (MANOVA, 2-sample *t*-test), and all data are given as mean ± SE. For the analyses concerning Expt 1, we used data from the 40 video sessions conducted in turbid water (present study) and 40 sessions from clear water (data obtained from Engström-Öst et al. 2007).

RESULTS

Expt 1: behaviour in turbid water

Differences in the behaviour of pike larvae in general, including habitat choice, prey attacks and swimming activity, were highly significant between the treatments (i.e. control, competitor, predator, competitor + predator) and between clear and turbid water (treatment: MANOVA, Pillai's trace = 0.24, $F_{9,216} = 2.1$, p = 0.03; water clarity: Pillai's trace = 0.31, $F_{3,70} = 10.3$, p < 0.001, Fig. 1). The interaction term (Treatment × Water Clarity) was not significant (Pillai's trace = 0.115, $F_{9,216} = 0.96$, p > 0.05).

Between treatments, significant differences were found for the number of prey attacks (MANOVA between subjects, $F_{3,79} = 5.3$, p = 0.002; Fig. 1B), whereas habitat choice (Fig. 1A) and swimming activity (Fig. 1C) showed no significant differences ($F_{3,79} = 0.7$, p > 0.05 and $F_{3,79} = 1.3$, p > 0.05, respectively). In contrast, water turbidity affected all fish behaviours (Fig. 1). The number of prey attacks was significantly higher in turbid water than in the control (clear water; $F_{1,79} = 22.1$, p < 0.001), whereas swimming activity was significantly lower and *Cladophora glomerata* habitat less preferred in turbid water than in clear water conditions ($F_{1,79} = 8.8$, p = 0.004, $F_{1,79} = 6.0$, p = 0.017, respectively). The interaction terms (Treatment × Water Clarity) were not significant (prey attacks: $F_{3,79} = 1.5$, p > 0.05, swimming: $F_{3,79} = 0.6$, p > 0.05, habitat choice: $F_{3,79} = 0.4$, p > 0.05).

The multiple comparisons showed that prey attacks differed significantly between the control and the visual predator (European perch) treatment (Tamhane's T2, p = 0.012), as well as between the competitor treatment (5 *Neomysis integer* present) and the predator treatment (p = 0.037). Swimming activity and habitat choice did not differ between the treatments (p > 0.05).

There was a significant trend for higher use of open water by pike larvae in turbid conditions, compared to clear water (2-sample *t*-test, $t_{40} = -1.81$, p = 0.07).

The main prey in pike larval stomachs were copepodite stages and adults of the calanoid copepods *Acartia bifilosa* and *Eurytemora affinis*, as well as rotifers *Synchaeta* sp. Stomach analyses of pike larvae showed no differences between the number of copepods (repeated-measures ANOVA, $F_{3,36} = 0.5$, p > 0.05), or rotifers ($F_{3,36} = 0.3$, p = 0.05) between the treatments, i.e. with and without a predator respective competitors.

Expt 2: effect of turbidity on weight and growth

Pike larval weight was significantly lower in high turbidity than in low turbidity (2-sample *t*-test, $t_{63} = 4.92$, p < 0.001, Fig. 2), whereas weight-specific growth rates did not differ between treatments (low turbidity: $6.50 \pm 0.70\%$ weight d^{-1}, high turbidity: $6.53 \pm 0.65\%$ weight d^{-1}; 2-sample *t*-test, $t_{14} = -0.03$, p > 0.05). Oxygen saturation levels were high in the high turbidity units due to the photosynthesising algae, but levels were also high in the low turbidity

units throughout the experiment. The weight differences were not reflected in the faecal pellet production of pike larvae, because pellet numbers (low turbidity: 8.2±0.5; high turbidity: 8.6±0.5 pellets d^{-1}, respectively), were not different between the high turbidity treatment and the low turbidity control (2-sample t-test, $t_{15} = -0.51$, p > 0.05).
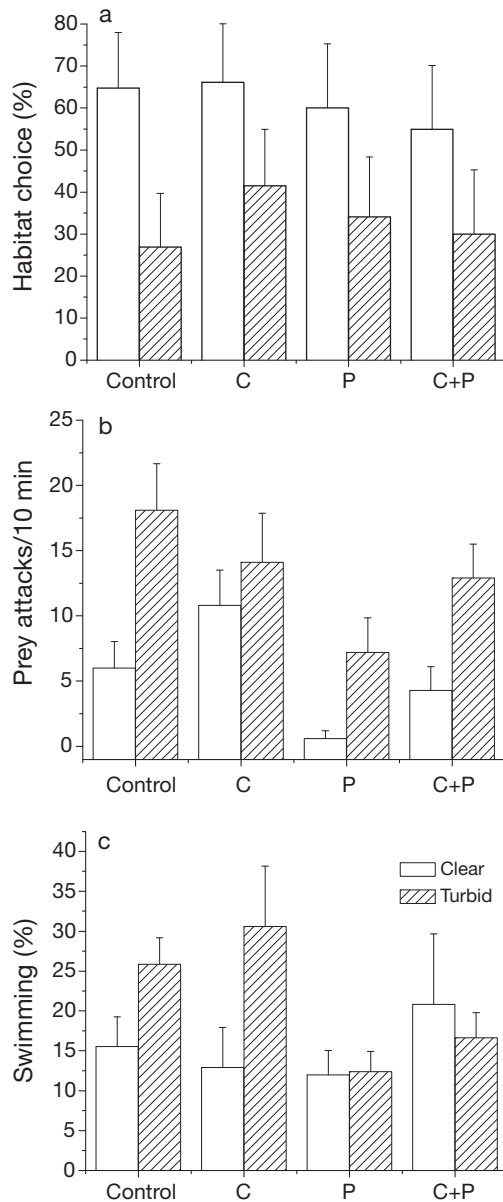

Fig. 2. *Esox lucius.* Cumulative growth (mg) of pike larvae during 2 wk in low and high turbidity conditions

DISCUSSION

We demonstrated that pike larvae showed less habitat choice and performed more prey attacks in turbid water than in clear water. In clear water, pike larvae generally show distinctive habitat choice and active feeding (Engström-Öst et al. 2007). In the current study, we also showed that pike larvae gained significantly less weight in high turbidity than in low turbidity. The benefits and disadvantages of the 2 habitats used, i.e. *Cladophora glomerata* and *Fucus vesiculosus*, for pike larvae were discussed by Engström-Öst et al. (2007), and will only be described in short here. Newly hatched pike larvae preferred ephemeral filamentous algae (*C. glomerata*), common in eutrophic waters, to a structurally more robust macroalga, bladderwrack *F. vesiculosus*, which thrives in clean waters. Pike larval survival was also higher in the filamentous algal habitat during predation threat by three-spined stickleback *Gasterosteus aculeatus* (Engström-Öst et al. 2007), which suggests that the habitat preference of the pike larvae is adaptive when it comes to avoiding predation. Filamentous algae seemingly provide good protection against predation despite their simple morphology.

Behaviour of pike larvae in turbid water

In the present study, we showed that choice *Cladophora glomerata* habitat decreased considerably in turbid water compared to experiments conducted in clear water (cf. Snickars et al. 2004, Engström-Öst et al. 2007). Results from previous studies support our

Fig. 1. *Esox lucius.* (a) Habitat choice as time spent in *Cladophora glomerata* to total time spent in both habitats (%), (b) number of prey attacks, and (c) total swimming time (%), by pike larvae in the different experimental treatments in clear and turbid water. C: mysid shrimps present, P: predator (visual contact), C+P: mysid shrimps present + predator (visual contact). Error bars denote SE. Data for the control experiment from Engström-Öst et al. (2007). In general, turbidity had a significant effect on pike larval behaviour
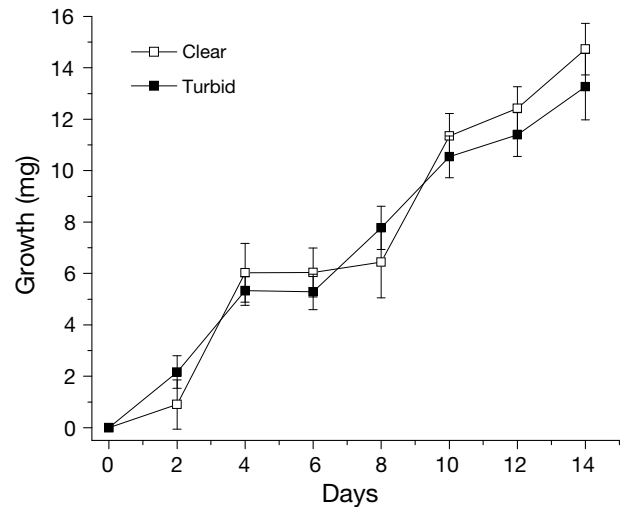
findings. Reduced water transparency provides shelter against predators (Gregory 1993, Gregory & Northcote 1993, Maes et al. 1998), and hence the prey is able to redistribute more evenly between habitats (Skov & Koed 2004). This may include a more active use of open water areas and a reduced use of vegetative shelter (Utne-Palm 2002 and references therein, Snickars et al. 2004). When the larvae perceive less threat, they can engage in activities that would be more risky in clear water, such as diverting effort from seeking shelter (Gregory 1993, De Robertis et al. 2003) to increased foraging (Gregory & Northcote 1993). Our results support these 2 assumptions, because feeding activity was considerably greater and use of sheltering habitat much lower in turbid conditions than in clear water conditions. Pike larvae also showed less activity in terms of swimming in turbid water, which has also been reported by Sirois & Dodson (2000). Reduced activity in turbid water may partly be a consequence of larvae perceiving less threat (Abrahams & Kattenfeld 1997) and partly a reduced need to seek shelter (Vøllestad et al. 1986, Gregory 1993). Pike larvae and other fish decrease their anti-predator behaviour in turbid water (Abrahams & Kattenfeld 1997, Lehtiniemi et al. 2005). This phenomenon is supported further by our data, because feeding activity decreased significantly in the presence of a visible predator (*Perca fluviatilis*) compared to the control. In addition, the presence of a competitor (*Neomysis integer*) clearly increased the foraging activity of pike larvae. We do not know why increased feeding occurs in the presence of mysid shrimps, because growth in pike larvae is inversely related to density of other pike larvae (Grimm & Klinge 1996).

Effect of turbidity on weight and growth rates

In the present study, weight gain of larval pike was significantly lower in high turbidity than in low turbidity, whereas weight-specific growth rates showed no differences between the 2 treatments. Evidence from the literature regarding the effect of turbidity on larval growth is inconclusive. Many studies have shown that turbidity reduces growth (Vøllestad et al. 1986, Sweka & Hartman 2001, Sandström 2004), whereas others found no effect of turbidity on growth (e.g. Van de Meutter et al. 2005), and some reported positive effects (e.g. Sirois & Dodson 2000). In an experimental study by Lehtiniemi et al. (2005), pike larvae were observed to be stressed in turbid water, since the time until the first prey attack was considerably longer in turbid conditions than in clear water, due to longer acclimation times. We suggest that pike larvae are not able to compensate for lost feeding opportunities, because weight decreased in our study.

We believe that the most likely cause of decreased weight was that pike larvae were not able to capture as much food as in low turbidity, or as a result of increased energy expenditure when searching for food in turbid conditions. On the other hand, the visual contrast between the environment and the prey should increase in turbid water (Utne-Palm 2002), and make it easier for larvae to detect and catch prey, if prey densities are high enough. Larval fish may be less affected by turbidity than adult fish. We have previously shown that pike larvae feed less in turbid water caused by a filamentous non-toxic cyanobacterium (Engström-Öst et al. 2006). In the present study, where high turbidity was caused by the harmless green flagellate *Brachiomonas submarina* that has been widely used in Baltic studies (e.g. Engström-Öst 2002), pike larvae had a higher attack rate than in clear water but nevertheless gained weight at a slower rate. This indicates that the success of the prey attacks must have been low in high turbidity.

To conclude, water turbidity caused by elevated phytoplankton concentrations showed multiple effects on pike larval weight and behaviour. In turbid water, the larvae performed more prey attacks, and appeared to perceive less threat, since they did not use the vegetation as shelter as much as in clear water. Even though the number of prey attacks was higher in turbid water, the larvae were probably not able to catch as many prey as in clear water, or their energy expenditure was higher, because their weight decreased. On the other hand, even though larval growth would remain at a lower rate than in clear water, pike larvae may benefit from turbid environments, if the predation pressure decreases due to low visibility. Our results show that algae-induced water turbidity affects behavioural aspects of fish larvae both directly and indirectly, and may therefore affect larval survival and potentially the recruitment into the population. Turbidity is a common problem in eutrophicated coastal areas and may have more far-reaching effects on the organisms than previously thought. However, turbidity effects differ widely depending on species, size and distribution, and environmental condition is just one stress factor among many others in eutrophicated systems.

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