RESEARCH ARTICLE

The indirect effects of eutrophication on habitat choice and survival of fish larvae in the Baltic Sea

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Abstract The structure of the habitat is usually crucial for growth and survival of young life stages. Presently, some nursery areas of fish larvae are changing due to eutrophication, e.g. due to enhanced growth of ephemeral filamentous algae at the expense of perennial species. We studied the influence of two habitats, one with filamentous algae (*Cladophora glomerata*) and the other with bladder wrack (*Fucus vesiculosus*), on habitat choice of pike larvae (*Esox lucius*) in the absence/presence of a predator or a competitor. We further tested whether the habitat choice is adaptive in increasing survival under predation threat. In contrast to expectations, pike larvae preferred the habitat with ephemeral filamentous algae to the bladder wrack, thriving in clean waters, independent of the presence/absence of both predator/competitor. In addition, the survival of the larvae was higher in the filamentous algae in the presence of predators, which suggested that the habitat preference of the larvae was adaptive. The structure of the bladderwrack habitat was probably too open for newly hatched larvae, which implies that *F. vesiculosus* and other large brown algae are not as important refuges for young larvae as previously thought.

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Introduction

When choosing a habitat, an individual has to balance between the costs and benefits of occupying a particular patch, such as between predation risk and foraging. The structure of a habitat can have profound effects on these costs and benefits, by influencing factors like susceptibility to predators, competitive interactions, foraging rate and the quality of food (Werner et al. 1983). In general terms, as the physical habitat structure increases, the diversity of different organisms also increases (Kohn and Leviten 1976; Downes et al. 1998). This might be due to a higher amount of structure providing more surfaces, and therefore more resources, such as food, mates and living space (reviewed by Connor and McCoy 1979). However, refuge use could also limit foraging (Sih 1997), which could retard growth (reviewed by Persson and Crowder 1997) and extend the stage of increased predation susceptibility (Milinski 1986; Pedersen 1997).

Deterioration of habitats has been considered a primary cause for the decline of many animals worldwide, such as waders (Koivula and Rönkä 1998), butterflies (Pöyry et al. 2005), elephants (Armbruster and Lande 1993), and fish (Amaral and Jablonski 2005). Changes in habitat structure and visual conditions in aquatic systems, due to man-made processes, such as eutrophication, are considered to be serious threats to fish larval

nursery areas worldwide due to a decline in food resources (Diehl 1988 and references therein). Habitat decline and changes in structure are therefore important factors to take into account when studying fish larval behaviour and predation risk. One typical example of a nursery area change is the enhanced growth of annual, rapidly growing filamentous algae (Wennhage and Pihl 1994; Isaksson et al. 1994), which are increasing at the expense of slow-growing perennial key species (Wallentinus 1984).

The pike (*Esox lucius*) is an important solitary piscivore, controlling populations of smaller fish species (Craig 1996). Further, it is an important catch for professional as well as for recreational fishermen in the Baltic Sea (Lappalainen 2002). The pike is a widely distributed species and considered highly adaptive to different environmental conditions (Casselman 1996). Despite this high flexibility, populations in environments characterized by human-induced changes have collapsed during the last decades (reviewed by Casselman and Lewis 1996; Nilsson et al. 2004). In addition, pike is considered sensitive to turbid water (Vøllestad et al. 1986; Craig and Babaluk 1989). Studies have shown that juvenile pike prefer structured habitats (Skov et al. 2002), and that survival is slightly higher in these habitats (Skov et al. 2003).

The aim of the present study was to experimentally study the habitat choice of pike larvae when confronted with two environments, one of which is increasing due to eutrophication, and to further determine if the choice depends on the presence of a predator and/or a competitor. Habitat choice could be influenced by predation risk and competitive interactions if these factors determine the pay-off of staying in each habitat. We therefore investigated whether the presence of predators and competitors influenced time spent in the two habitats, and swimming activity and foraging rate. To determine if the habitat preference is adaptive in relation to survival, we monitored survival of pike larvae in the two habitats in a predation experiment. Since it has been suggested that pike juveniles do not thrive in dense vegetation mats (reviewed by Casselman and Lewis 1996), we hypothesised that also pike larvae would reject dense ephemeral algae in favour of habitats with bladder wrack with a more open structure.

Materials and methods

Study organisms

We picked up pike larvae (*Esox lucius*) with yolk sac, 4-days post-hatch, from a fish hatchery in SW Finland (Trollböle fish hatchery). The larvae originated from

five females and five males, which all were wild and of freshwater origin. Pike is a common species along the coastline of the brackish Baltic Sea (Ojaveer et al. 1981). Large amounts of pike larvae of freshwater origin are annually introduced to the brackish Baltic Sea (Selén 1999). Pike uses pre-dominantly habitats with *Phragmites australis* or *Fucus vesiculosus* in the Baltic Sea (Lehtonen 1986). The larvae were divided into two 628 l tanks with seawater flow-through (6.6 ± 0.07 psu, 10°C, unfiltered) at a concentration of approximately 2,000 larvae tank^{-1}. We added macroalgae and stones to both containers. The larvae were fed with a thoroughly mixed, dense brackish-water zooplankton community (25 ± 3 prey ml^{-1}) twice a day. Since the fish tanks were outdoors, the light regime followed was natural, varying between 17L:7D and 19L:5D. The fish were kept in the tanks until the experiment (exp. 1 = 18 days, exp. 2 = 40 days).

The zooplankton used as food for pike larvae in the holding tanks and the experiments were collected with a 100 μm net from 20 m depth to the surface from an open pelagic area (Storfjärden) at the SW coast of Finland, Baltic Sea. The zooplankton container was kept aerated in the climate chamber (14–15°C, 16L:8D). The main zooplankton species were *Synchaeta* sp. and *Acartia* sp. nauplii and adults. The zooplankton community did not change much under the course of the experiment.

We used perch as a predator in experiment 1 and sticklebacks in experiment 2, due to logistic reasons. The perch (Eurasian perch, *Perca fluviatilis*, L_T: 18–20 cm) were caught by a fish trap, from a shallow bay close to the Tvärminne Zoological Station (depth: 1–2 m). The perch were kept in an outdoor 628 l tank with seawater flow-through (similar as above). The perch were fed ad lib once daily with mysid shrimps. Perch is a common predator on pike larvae in the Baltic Sea area (Selén 1999 and references therein).

The three-spined sticklebacks (*Gasterosteus aculeatus*, L_T: 6.0 ± 0.04 cm) were caught from the littoral zone with a beach seine close to the Tvärminne Zoological Station. The sticklebacks were kept in an outdoor 628 l tank with brackish-water flow-through (similar as above). They were fed daily with mysid shrimps or daphnids. The stickleback feeds on fish larvae in the Baltic Sea (Lemmetyinen and Mankki 1975), and it is hypothesised that the stickleback may be a significant factor affecting the pike recruitment negatively due to egg and larval predation (Nilsson et al. 2004).

Mysid shrimps (*Neomysis integer*, L_T: 1.74 ± 0.16 cm, Lindén et al. 2003) were caught from the littoral zone with a beach seine as above. The mysids were kept in a 30 l container with aeration in the climate-chamber and

fed daily with zooplankton. The temperature and light conditions in the climate chamber were the same as mentioned above. *N. integer* is highly omnivorous and feeds especially on rotifers *Synchaeta* sp. (Koho 2005), which are also readily fed upon by newly-hatched pike larvae (unpublished data; the current study). The two species also partially share the same habitat (Lehtonen 1986; Rudstam et al. 1986).

Bladder wrack (*F. vesiculosus*) was collected close to the shoreline at the Tvärminne Zoological Station from 1 m depth (salinity: 6) and detached from the stones by a rake. Filamentous green algae *Cladophora glomerata* were collected from 1 m depth (salinity: 6) by hand and were not detached from the stones. The algae were stored in an aerated tank in the same climate chamber as mentioned above until the experiment. After the experiment, *C. glomerata* were carefully removed from the stones with a blade and all algae were dried on aluminium foil at 60°C for 24 h and then weighed.

Experiment 1: Habitat choice

Pike larvae were allowed to choose between two common habitats in the presence and absence of competitors and predators. One pike larva was placed in a 5 l aquarium ($20 \times 28 \times 9$ cm^3) that had been divided into two habitats by putting filamentous algae, *C. glomerata* and bladder wrack, *F. vesiculosus* at opposite ends of the aquarium. The pike larva was subjected to one of the following treatments: (1) five competitors present (mysid shrimps *N. integer*), (2) visual contact with a predator (Eurasian perch *Perca fluviatilis*) and (3) five competitors present + visual contact with a predator and (4) control (no competitor or predator present). Each pike larva was used only once. The pike larvae were 20–24-days post-hatch (mean L_T: 13.8 ± 0.1 mm, mean W: 0.01 ± 0.0003 g). To create the two habitats, *F. vesiculosus* was attached with strings to a plastic net, which was covered by washed commercial fine sand. *C. glomerata* was growing on small stones, which were also covered by sand. Each of the algae took up approximately 25% of the volume of the aquarium both vertically and horizontally, whereas the rest of the area consisted of open water.
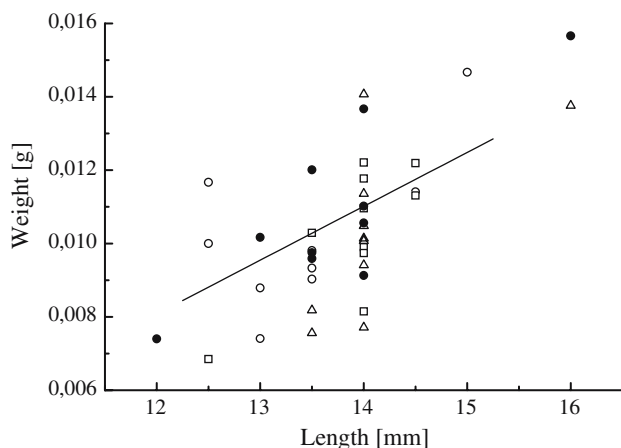
The average biomass (dry weight) of *F. vesiculosus* was 2.01 ± 0.15 g and that of *C. glomerata* was 0.14 ± 0.04 g per unit area in the test tank. The biomass difference was due to the marked morphological differences between the two species: *F. vesiculosus* is a thick, robust brown alga with an open and highly curved structure, whereas *C. glomerata* consists of long, thin and simple filaments. *F. vesiculosus* is usually considered the more structurally complex alga (Borg et al.

1997). The aquarium was filled with filtered seawater (10 μm filtered, salinity 6, 16.3 ± 0.1°C).

Pike larvae and mysid shrimps were starved for 70 ± 2 min prior to the experiment and they were acclimatised to the environment for 10 min. The acclimatisation took place in the middle of the experimental aquarium in a plastic bottle, which was open in one end and with a hole on the side covered with a net, to allow water exchange. The mysid shrimps were acclimatised simultaneously with the pike larva in the same tube, and they were free ranging in the experiment to reveal the natural interaction between the two species. After the acclimatisation, the bottle was carefully emptied over the open water area in the middle of the aquarium. After pike release, 100 ml of dense well-mixed natural zooplankton community (25 ± 3 prey ml^{-1}) was added uniformly. For the predator treatment, we used two Eurasian perch (*Perca fluviatilis*). One of the perches was placed in a separate 19 l aquarium ($25 \times 30 \times 25$ cm^3) next to the long side of the rectangular experimental aquarium. Pike larvae always had visual contact to the predator aquarium (with or without predator, depending on the treatment).

During the experiment, the fish were filmed for 10 min from the rectangular side of the aquarium. The video sessions were recorded in 36.5–58.9 μE m^{-2} s^{-1} light. The replicate number was 10 for each of the 4 treatments, indicating 40 video recordings in total. All experimental runs were conducted in random order. Use of the two predators was also random. Further, before every experimental run, we alternated which of the two habitats in the experimental aquarium was closer to the wall, in case of differences in light. During analysis of the video sessions, we measured total swimming time of the pike larvae, time spent in each vegetation, and open water, and number of attacks towards zooplankton prey. The total number of prey attacks may sometimes be a slight underestimation, if the fish was behind the vegetation and could not be seen on the videotape. The pike larvae did not change habitat often after the choice had been made (Times visited: *F. vesiculosus*: 1 ± 0.2; *C. glomerata*: 2.4 ± 0.5).

After the experiments, all pike larvae and mysid shrimps were killed according to Engström-Öst et al. (2005). The fishes were preserved 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). To ensure that all experimental fishes were in equally good condition we performed a linear regression between larval weight and length ($R^2 = 0.45$, $F_{1,39} = 30.6$, $P < 0.001$) (Fig. 1), and then tested the residuals with each other (Ormerod and Tyler 1990). No differences were found between the four

Fig. 1 *Esox lucius*. The relationship between larval length (mm) and weight (g) given as a linear regression. *Open circle* control, *open square* mysid shrimps present, *open triangle* predator (visual contact), *filled circle* mysid shrimps present + predator (visual contact)

treatment groups (One-way ANOVA: $F_{3,39} = 1.5$, $P = 0.22$). Finally, stomach analysis was done in order to reveal whether prey switching occurs in the presence of competitors.

Experiment 2: Habitat dependent survival

A predation experiment was done with pike larvae as prey (39–42 days post-hatch, 15 mm) and adult three-spined sticklebacks (*Gasterosteus aculeatus*) as predators. The sticklebacks were starved overnight before the experiment. The experiment was performed in two plastic 30 l containers with washed commercial fine sand on the bottom. The containers were kept on two separate tables in a climate chamber (14°C) and treatments were alternated between the two tables during every new experimental session, because light conditions varied slightly (0.0433 and 0.0453 µE m^{-2} s^{-1}, respectively). One replicate of each treatment (*F. vesiculosus* or *C. glomerata*) was conducted simultaneously with one container on each table. The algae were evenly distributed in one patch and covered 40% of the bottoms of respective container. *F. vesiculosus* was attached by strings to a plastic net, which was covered by sand, and *C. glomerata* was growing on stones, which were also covered by sand. The water was changed and thoroughly oxygenised between every experimental run. The water temperature was 11.5 ± 0.1°C in the experiment.

The fish larvae were acclimatised to the environment for 10 min. before the start of the experiment. Acclimatisation took place by adding 20 pike larvae to a plexi glass tube in the container, and three three-spined sticklebacks to the same container outside the tube allowing

visual contact between the prey and predator during acclimatisation. We decided to add three sticklebacks because the species forms schools in nature (Wootton 1984). The experiment was started after the acclimatisation by slowly removing the plexi glass tube and setting the larvae free. We finished the experiment after 60 min. by removing the sticklebacks. Finally, the survived pike larvae were counted. We did not make observations during the experiment, in order not to disturb the fish. The number of replicates in the experiment was 15. *F. vesiculosus* mean biomass (dry weight) was 6 g in the experimental unit, and that of *C. glomerata* 0.68 g.

Statistical analyses

All data were tested for normality and homogeneity of variances, using Wilk–Shapiro and Bartlett's test for equal variances, respectively. If assumptions were not met, non-parametric tests were employed. Pooling of data was performed in order to reveal one important factor: the potential preference for filamentous algae by pike larvae. The pooled samples (4 × 10 samples) have equal sample size, are fully independent, are sampled with the same method, and collected within a 5-day period of time. Therefore, the potential bias caused by pooling of data is likely to be negligible (cf. Leger and Didrichsons 1994). Pooling of data should not be done without statistical justification, that is, prior to confirming that no significant difference between the data sets to be pooled exists (cf. Results). To determine whether habitat choice (experiment 1) depended on treatment, the habitat choice data were given as percentages of time in *C. glomerata* to total time in both algae in the two-way ANOVA analysis. The habitat choice data were not arcsine-transformed because it did not improve the normality of the data to any significant extent (Sokal and Rohlf 1995). The non-parametric Scheirer-Ray-Hare 2-way ANOVA was used when normality could not be achieved (Sokal and Rohlf 1995). The habitat dependent survival data (experiment 2) were log-transformed (log $x + 1$). All data in the paper are given as mean ± SE and all tests are two-tailed. 95% confidence intervals are provided in Figs. 3 and 4.

Results

Experiment 1: Habitat choice

Pike larvae varied the time they spent in different habitats (Kruskal–Wallis 1-way ANOVA, $H_{2,117} = 11.4$, $P = 0.003$). Larvae spent more time in the filamentous algae *C. glomerata* habitat than in the bladder wrack

F. vesiculosus habitat (Tukey HSD, *P* < 0.01) (Fig. 2), whereas no differences were found when compared to the open water habitat (Tukey HSD, *P* > 0.05). The preference for the *C. glomerata* habitat did not differ regardless of the presence of a predator (Scheirer–Ray–Hare 2-way ANOVA: $H_{1,36} = 0.68$, $P = 0.41$), or competitors ($H_{1,36} = 0.09$, $P = 0.77$), or an interaction between the two ($H_{1,36} = 0.11$, $P = 0.74$) (Fig. 3a).

The rate of prey attacks by pike larvae decreased significantly in the presence of a predator (2-way ANOVA: $H_{1,36} = 10.3$, $P = 0.003$), and increased in the presence of competitors ($H_{1,36} = 4.3$, $P = 0.048$). No interaction between predator and competitors on attack rate was found ($H_{1,36} = 0.4$, $P = 0.553$) (Fig. 3b).
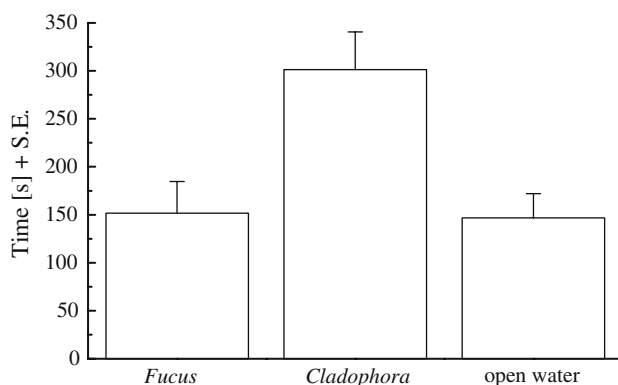
Swimming activity of pike larvae was not significantly affected by the presence of a predator (Scheirer–Ray–Hare 2-way ANOVA: $H_{1,36} = 0.01$, $P = 0.90$) or competitors ($H_{1,36} = 0.4$, $P = 0.52$) or an interaction between the two of them ($H_{1,36} = 0.80$, $P = 0.37$) (Fig. 3c).
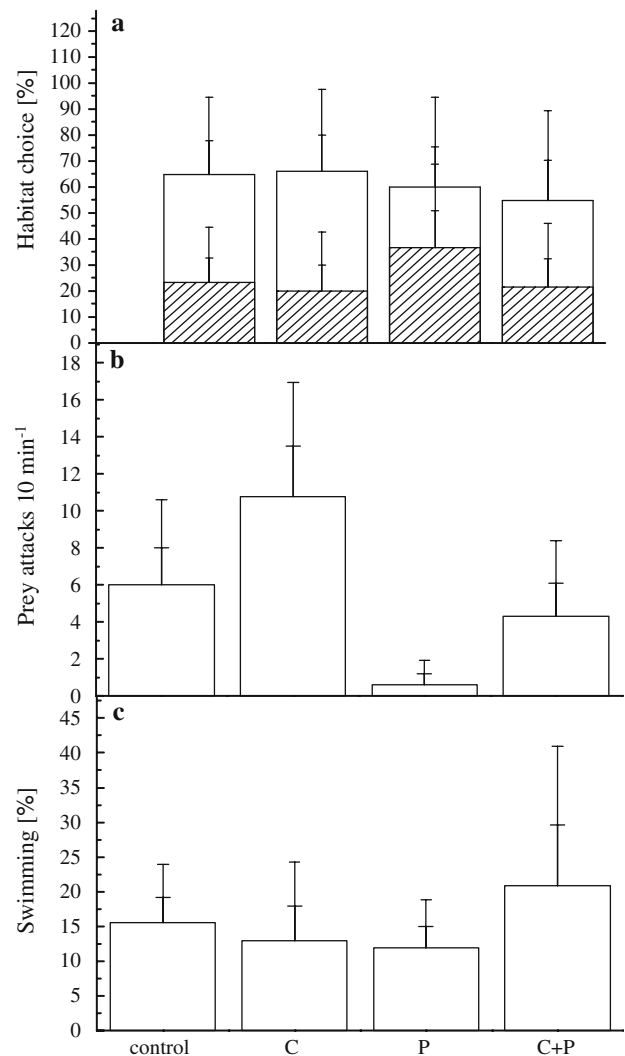
Stomach analysis

The most abundant species in the environment as well as in the stomach contents of pike larvae was *Synchaeta* sp. (5.0 ± 1.3 individuals; all treatments pooled). Few *Acartia bifilosa* and *Eurytemora affinis* were found (1.1 ± 0.3 and 0.3 ± 0.2 individuals, respectively; all treatments pooled). The total number of prey items in the stomachs of pike larvae was not significantly affected by the presence of a predator (2-way ANOVA: $F_{1,36} = 2.8$, $P = 0.1$) or competitors ($F_{1,36} = 0.7$, $P = 0.4$).

Experiment 2: Habitat dependent survival

The number of surviving pike larvae in the predation experiment with adult three-spined sticklebacks was

Fig. 2 *Esox lucius*. Total time (s) spent in each habitat (*Fucus*, *Cladophora*, open water) by larvae in the habitat choice experiment. Data of all treatments (4) were pooled. *N* = 40. *Error bars* denote SE
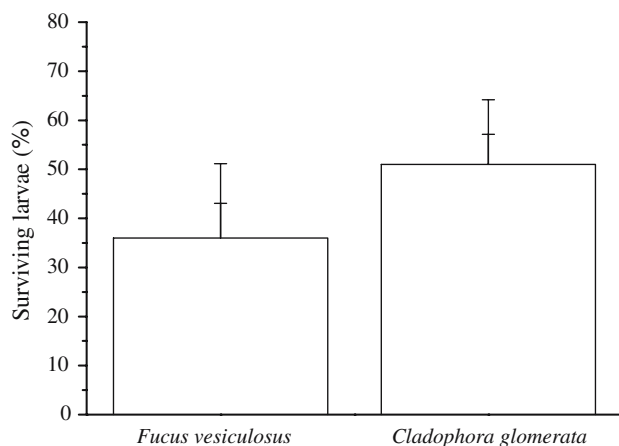

Fig. 3 *Esox lucius*. Habitat choice (%) where white bars denote time in *Cladophora glomerata* to the total time in both algae, and striped bars denote total time (%) spent in *Fucus vesiculosus* (**a**), total number of prey attacks (**b**), and swimming activity (% of total time) (**c**), by larvae in the habitat choice experiment. Open water time omitted from **a**. *C* Mysid shrimps present, *P* predator (visual contact), *C* + *P* mysid shrimps present + predator (visual contact). The *lower error bars* denote SE and the *upper bars* 95% confidence intervals

significantly higher in the habitat treatment with filamentous algae than in the *F. vesiculosus* habitat (Two sample *t*-test: $t_{14} = -2.09$, $P = 0.0485$) (Fig. 4).

Discussion

In the present study, we demonstrated that newly hatched pike larvae preferred ephemeral filamentous algae, induced by eutrophication, to a structurally more robust macroalga, bladderwrack, that thrives in clean waters. Further, the survival of the pike larvae

Fig. 4 *Esox lucius*. Number of surviving larvae in two different habitats, *Cladophora glomerata* and *Fucus vesiculosus*, in the predation experiment with three-spined stickleback. The *lower error bars* denote SE and the *upper bars* 95% confidence intervals

was higher in the filamentous algal habitat during predation threat by three-spined sticklebacks, 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. Commonly, *F. vesiculosus* is considered more complex than *C. glomerata* when considering habitats for juveniles and larger fish (Borg et al. 1997), whereas it seems that *C. glomerata* may have a preferable complex structure to small fish larvae, because they have no problem entering the filamentous algal mats (Borg et al. 1997, the present study).

Interestingly, the presence of a predator and competitors had no significant effects on the habitat preference, despite the fact that both factors influenced prey attack rate; visual predation risk reduced attack rate whereas the presence of competitors increased attack rate. *Neomysis integer* is an active swimmer and performs bioturbation (Roast et al. 2004), and seems to have facilitated prey availability for the pike larva. *N. integer* used predominantly the open water area in the present study, and this has been shown also by Lindén et al. (2003). Recently, Lehtiniemi (2005) has shown that pike larvae increase their use of refuge in the presence of both visual and chemical predator signals. However, refuge use, prey attack rate and swimming in the present study did not differ markedly to Lehtiniemi's results obtained in the presence of both visual and chemical predator signals. Thus, in the present study pike larvae appeared to inherently prefer filamentous algae to bladderwrack, independent of perceived predation risk or the level of competition. Pike larvae swim only 15–20% of their time (Engström-Öst

and Lehtiniemi 2004), and after detecting the predator they often freeze, even in open water, instead of swimming to a shelter, which may have affected the choice of habitat in the predator treatment. Stomach analysis did not either reveal changes in behaviour, such as prey switching. The preference for filamentous algae in the absence of predators and competitors may be due to factors other than predation risk or competition that induced a preference for filamentous algal habitats, for example differences among habitats in food availability. *Cladophora glomerata* has more substrate for prey items due to its high area/volume relationship than *F. vesiculosus* (Salovius-Laurén 2004, and references therein).

The preference for filamentous algae and the favourable consequence of this for survival were contrary to our hypothesis. Large brown macroalgae, such as *F. vesiculosus*, have traditionally been considered to provide better refuges for juvenile/small-sized fish than dense mats consisting of ephemeral filamentous algae (Borg et al. 1997; reviewed by Salovius-Laurén 2004). Predators that actively chase prey, such as the three-spined stickleback, are therefore supposed to be more efficient foragers in less structured environments (Eklöv and Diehl 1994; Flynn and Ritz 1999). In support of this, Isaksson and Pihl (1992) showed that the field abundance of three-spined sticklebacks correlated positively with filamentous algae, common in eutrophicated environments. The stickleback also builds its nest out of filamentous algae, so they are familiar with this environment that also is an important refuge against their own predators (Candolin and Voigt 1998). Despite these facts, the prey capture rate of sticklebacks seem to be more efficient in macro-algae in our study, since pike larvae showed higher survival in *F. vesiculosus* than in filamentous algae.

Studies supporting our results exist in the literature; Isaksson et al. (1994) showed that the survival of young cod was enhanced by the addition of filamentous algae to a sandy substrate. Moksnes et al. (1998) found that filamentous algae constitute an important refuge for crab juveniles and that the increased distribution of these algae may have a positive effect on the recruitment of juveniles. Thus, contrary to the general expectation, filamentous algae might be a preferred habitat among larval stages that are more susceptible to predation than adults (Werner 2002), if dense filamentous algae offer more effective shelter than large macroalgae with a more open structure.

However, it has been shown that slightly older pike, juveniles, avoid dense macrophyte beds, which may be due to low oxygen levels within the macrophytes during night (reviewed by Casselman and Lewis 1996) or

to that larger fish have difficulties in entering the plants (Borg et al. 1997). Filamentous algal mats, e.g. *C. glomerata*, can turn anoxic during nights (Norkko et al. 2000), and hypoxia may therefore have modified the results in the present study. Several studies report toxic algal exudates from macroalgae (Johnson and Welsh 1985; Aneer 1987). It has been shown that filamentous algal exudates neither affect the survival of pike larvae, nor the hatching success of pike eggs (Nilsson et al. 2004; Engström-Öst and Isaksson 2006), whereas the potential effects on larval habitat choice are not known.

To conclude, the results show that pike larvae prefer to stay in filamentous green algae that are increasing in the nursery areas of the pike in eutrophic waters, to the morphologically more robust bladder wrack, which thrives in clean water. This behaviour is adaptive in increasing survival under predation threat. Local hypoxia may, however, occur in filamentous algal mats and therefore change the results presented here slightly, because pike larvae most likely have to balance between different costs and benefits, such as predation risk, foraging rate and hypoxia, when choosing between different habitats. Future studies should attempt to estimate these costs and benefits to determine the further consequences that the increased growth of filamentous algae may have for pike populations in eutrophicated environments.

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