

Effects of macroalgal exudates and oxygen deficiency on survival and behaviour of fish larvae

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Abstract

Filamentous algae may create anoxic, i.e. oxygen free, conditions during night and fish larvae that commonly spend their first months in the littoral may therefore be subject to anoxia. We conducted two different experiments; firstly, we measured behaviour of pike larvae (*Esox lucius* L.), such as frequency of prey attacks and time in vegetation, in the presence of a chemical predator cue and oxygen deficiency. In the second experimental set-up, pike larval survival was monitored in water with added macro-algal exudates (excreted from *Pilayella littoralis*) and a low oxygen level (3 mg l⁻¹). Our results showed that oxygen concentration and the chemical predator signal, caused by three-spined sticklebacks, had strong significant effects on the larval prey attacks. The prey attacks were strongly reduced at 3 mg oxygen l⁻¹. However, survival of the larvae was not affected by low oxygen and macro-algal exudates. Pike larvae are very tolerant to hypoxia and exudates excreted by the littoral vegetation, whereas prey attacks are strongly decreased in hypoxia when a predator is around. This may have negative consequences for pike larval growth and recruitment in eutrophicated environments.

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1. Introduction

The eutrophication of coastal sea areas is today a widespread phenomenon, and this process may have far-reaching consequences to the biota in areas, such as the Baltic Sea where it has continued for several decades. The eutrophication of the aquatic environment depends to a large extent on increasing influx of nitrogen and phosphorus (Perttilä et al., 1995). Drifting algal mats, deep-water hypoxia, turbidity and cyanobacterial blooms

are typical symptoms of high production (Bonsdorff et al., 1997).

The occurrence of “macroalgal blooms” or “green tides”, consisting of e.g. fast-growing filamentous algae or seaweeds, has increased greatly in many parts of the world (Hodgkin and Birch, 1986; Pihl et al., 1995; Fletcher, 1996, Lehto and Bäck, 2001). Apart from community composition changes, such as replacements of marine perennials (Kautsky et al., 1986; Middelboe and Sand-Jensen, 2000), these macroalgae, e.g. *Ulva* sp., *Ulvaria* sp., *Pilayella* sp. and *Enteromorpha* sp. may also produce potentially harmful exudates (Aneer, 1987; Larson, 1997; Nelson et al., 2003; Råberg et al., 2005) and form nocturnal hypoxia when respiration

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exceeds photosynthesis (Johnson and Welsh, 1985). Algal exudates and hypoxia have severe consequences for littoral animals, such as various invertebrates and fish larvae (Nelson et al., 2003; McNatt and Rice, 2004), e.g. by interfering with larval development and lowering egg and larval survival probability. Even though not lethal, oxygen concentrations in the range of 1–4 mg l⁻¹ are physiologically stressful (Rombough, 1988) and impact on behaviour, growth and survival of many fish species (Kramer, 1987; Pihl, 1994; Weltzien et al., 1999). Hypoxia affects a wide range of other factors too, such as vertical movement and trophic interactions (Breitburg, 1994; Breitburg et al., 1997). Breitburg (1994) showed that fish larvae strongly avoided oxygen-depleted sub-pycnocline water. Low oxygen may also affect the predation mortality of fish larvae because of its effect on the vertical distribution of larvae and their predators (Breitburg et al., 1999). Hypoxia may further affect prey capture rates by decreasing the feeding activities of predators (Breitburg et al., 1994), and by changing prey behaviour and thereby influencing their susceptibility to predation (Breitburg et al., 1997).

The pike (*Esox lucius*) is an important piscivore, controlling other fish species, in the boreal northern hemisphere (Craig, 1996), and it is also important catch for fishermen in the Baltic Sea (Lappalainen, 2002). The pike is considered a highly adaptive species due to its wide distribution (Casselman, 1996), but despite its flexibility, populations have collapsed during the last decades in areas where environmental change has been considerable (reviewed by Casselman and Lewis, 1996; Nilsson et al., 2004). Previous studies have shown that young-of-the-year pike showed increased mortality due to oxygen depression caused by prolonged respiration of dense vegetation (Casselman, 1978). However, newly hatched pike larvae prefer the dense filamentous alga *Cladophora glomerata* to the brown alga *Fucus vesiculosus*, which has a more open architecture (Engström-Öst et al., submitted for publication). There may be trade-offs associated with this habitat choice, because anoxia can form in dense filamentous algae at night when metabolic demands for oxygen exceed production (Johnson and Welsh, 1985; Norkko et al., 2000; Isaksson, unpublished data).

The aim of the study was to measure pike larval behaviour, such as prey attacks and time in vegetation in hypoxic water, in the presence of a chemical predator signal. We further monitored the combined effect of hypoxia and macro-algal exudates on pike larval survival. Our main questions were: 1) how is larval behaviour affected by hypoxic water when a predator is nearby and 2) are pike larvae sensitive to macro-algal exudates in hypoxic water? We hypothesised that oxygen deficiency

may include additional stress for newly hatched pike larvae in the presence of a chemical predator signal, or algal exudates derived from a common coastal macro-alga *Pilayella littoralis* (L.) Kjellman.

2. Material and methods

We studied the effects of macro algal exudates (*P. littoralis*) and oxygen conditions on survival and behaviour of newly hatched pike larvae, *E. lucius*. Two experiments were performed at Tvärminne Zoological Station in SW Finland (59°50' N, 23°15' E) in May and June 2005: 1) the effect of oxygen and predator signal on behaviour, and 2) the effect of algal exudates and oxygen concentration on survival.

2.1. Pike larvae

Pike (*E. lucius*) yolk sac larvae, 4-days post-hatch, were obtained from Trollböle fish hatchery in SW Finland. The larvae originated from five females and five males, all of which were caught in the wild and are of freshwater origin. The eggs were fertilised and hatched in river water in the hatchery and thereafter the larvae were transported to Tvärminne Zoological Station. The larvae were acclimatised to the temperature and salinity for ca. 2 h and then let into a 628 l tank with aeration and seawater flow-through (9.0±0.3 °C, unfiltered) at a concentration of approximately 5 larvae l⁻¹. The larvae were fed with a dense brackish-water zooplankton community (16±3 prey ml⁻¹) three times a day. The main prey species were rotifers *Synchaeta* sp. and adult copepods *Eurytemora affinis* (Poppe). Since the fish tanks were outdoors, the light regime was natural, varying between c. 17L:7D to 19L:5D. Salinity in culture water and in all experiments was 5.4 psu.

2.2. Zooplankton

The zooplankton used as food for pike larvae were sampled with a 100 µm net from 23 m depth to the surface. Sampling was performed every second day in an open pelagic area (Storfjärden) at the SW coast of Finland, Baltic Sea. Upon arrival to the laboratory, the zooplankton container was aerated in a climate chamber (11–17 °C, 16L:8D).

2.3. Algae

For the behaviour experiment we collected *P. littoralis* from c. 1 m depth. The algae were not detached from the substrate (stones) and stored in an aerated tank

under constant light in the same climate chamber as mentioned above until they were used in an experiment the following day. After the experiment, *P. littoralis* was carefully detached from the stones with a scalpel and dried on aluminium foil at 60 °C until dry, and then weighed (Mettler AE100). For the survival experiment fresh *P. littoralis* was removed from the stones in the field. The algae were placed in a 45 l container with 36 l seawater to a concentration of 9.3 g dry weight algae l⁻¹ water (measured after the experiment). The container was placed under weak light (0.19±0.05 μE m⁻² s⁻¹) and lightly aerated for two days to let the algae decay before the experiment was initiated. Decaying algae are known to produce more exudates than fresh ones (Råberg et al., 2005). The experiment was thereafter conducted during three days and each day approximately 1/3 of the water was removed to use in the experiment, and 1/3 of the algae were removed to keep the initial concentration even. The algal exudate water was filtered through a 200 μm mesh prior to addition to the experimental containers. After finishing the experiment, the algae were dried in 60 °C until dry and finally weighed. In order to control algal decay, samples were taken from the algal exudate water in the containers, and analysed for total nitrogen and total phosphorus concentrations, according to Koroleff and Grasshoff (1976).

2.4. Predators

The predator-conditioned water, used in the behaviour experiment, originated from pike larvae-fed three-spined sticklebacks (*Gasterosteus aculeatus* L., L_T : 5.7±0.1 cm). The fish were caught from the littoral zone with a beach seine close to the field station. Prior to the experiments the sticklebacks were fed daily with mysid shrimps *Neomysis integer* Kåre, whereas on the days of the experiment, sticklebacks were fed with pike larvae. The mysid shrimps were caught in the littoral zone with a beach seine. Both sticklebacks and mysid shrimps were kept in 30 l containers with aeration.

2.5. Behaviour experiment: the effect of oxygen and predator signal

An experiment was conducted to assess the effect of oxygen and predator signal on pike larval behaviour. Pike larvae (13.9±0.2 mm, 20–22 days old) were subjected to four treatment combinations: 1) high oxygen level (normoxic, cf. below) with or 2) without a chemical predator signal, 3) low oxygen level (moderately hypoxic, cf. below) with or 4) without a chemical predator signal. The oxygen concentrations tested were

normoxic (>6.0 mg O₂ l⁻¹) and moderately hypoxic (3.0 mg O₂ l⁻¹). Twelve replicates were performed during three days (31 May–2 June). To assure that zooplankton used as prey survived the low oxygen treatment, zooplankton were visually inspected prior to and after the experiment. Zooplankton activity was compared and no visual difference could be revealed between the samples.

The experiments were carried out in constant air temperature (15 °C). The water temperature of the experimental units was 15.5±0.2 °C. The aquaria were illuminated by overhead fluorescent tubes, and the light intensity was 17.99±0.33 μE m⁻² s⁻¹ (Li1000 Data Logger LiCor). The experiments were performed in 5 l rectangular aquaria (width 28×depth 9×height 20 cm) filled with 2 l of seawater. All walls of the aquaria, except the front, were covered by black plastic to avoid disturbance from the surrounding environment. The bottom of each aquarium was covered by 500 ml sand. Vegetation was planted in one half of each aquarium while the other half was kept without vegetation. The vegetation was first rinsed under running seawater and shaken vigorously, subjected to visual inspection and all visible fauna were manually removed.

The small stones that *P. littoralis* was growing on, were buried in the sand. The vegetation extended up to ca. 6 cm in the water column.

Each pike larva was acclimatised to the experimental oxygen concentration and temperature. Fish larvae subjected to the low oxygen treatments were first introduced to containers with 5.2 mg oxygen l⁻¹ for 15 min., and thereafter moved to a container with 3.1 mg oxygen l⁻¹ for 15 min. The fish larvae subjected to the high oxygen treatments were handled similarly, although they were put into containers with high oxygen concentration. The reduction of the oxygen level was conducted, before fish were added, by bubbling nitrogen directly into the acclimatisation containers and experimental aquaria, respectively.

The chemical predator signal was obtained by adding 200 ml of normoxic water from the stickleback container to the experimental aquaria. Time spent in the vegetation was recognised when the fish larva was in the vegetation half of the aquarium.

After the acclimatisation, the fish larvae were gently introduced individually to each experimental aquarium. The fish larvae were acclimatised for another 5 min. to its new environment, and then 100 ml of well-mixed dense zooplankton community and 200 ml of either seawater or chemical predator signal were carefully and uniformly added to each aquarium. The aquaria were not covered by plastic film, due to the short experiment. During the experiment we counted the number of

feeding attacks on prey and measured time spent in vegetation during 15 min. When the larva formed an s and rushed forward to catch a prey, we considered it as a feeding attack. Special care was taken not to disturb the fish larvae.

2.6. Survival experiment: the effect of algal exudates and oxygen concentration

Effects of algal exudates and oxygen concentration on survival of newly hatched pike larvae (13.4±0.1 mm, 15–17 days old) were investigated in an experiment with two treatments with two levels each: oxygen concentration (high/low; Table 1) and exudates (present/absent). Nine replicates were made over three days time. The experimental unit was a 5 l container (diameter=21 cm), filled with 4 l water (2 l algal exudate water+2 l seawater, i.e. 50% exudate water concentration). The containers were randomly placed in groups of four, with all treatments represented in each group. The light intensity was 0.171±0.03 μE m⁻² s⁻¹ (Li1000 Data Logger, LiCor). The water temperature of the experimental units was 11.5±0.1 °C.

Experiments were conducted from c. 1 p.m. to 11 a.m. the following day. The containers were aerated for two hours before the experiment was initiated. At t_0 ten fish larvae were gently introduced to each container. The fish were fed with natural zooplankton (16±3 prey ml⁻¹). During the first six hours the oxygen concentration was kept high (10.3 mg l⁻¹) in all containers. At t_6 , after six hours with normoxia, the oxygen concentration was reduced in the containers with low oxygen treatment. The reduction in oxygen concentration was conducted in two steps to simulate naturally occurring diurnal fluctuations of oxygen levels in the field within areas of filamentous algae. Nitrogen was bubbled directly into the containers to reach an oxygen concen-

tration of 5.5 mg l⁻¹. All containers were thereafter covered by plastic film and left for 6 h. At t_{12} , the second reduction in oxygen concentration was performed by exchanging 2.5 l of water in each container with water of low oxygen level (1.2 mg l⁻¹) to obtain an oxygen concentration of ca 3 mg l⁻¹. This procedure was performed to better allow us to control the oxygen concentration. The oxygen concentration of the added water had been reduced in advance by bubbling nitrogen to the bottom of water tube. The high oxygen treatments were connected to air instead of nitrogen in the first step, and water was exchanged to water with a high oxygen concentration in the second step. After this water exchange the exudate water concentration was 33%. Containers were covered by plastic film and left for 6 h, after which the experiment was terminated at t_{18} . We measured oxygen concentration and temperature every 2–3 h (YSI 95 Oxygen Microelectrode Array). The oxygen measurements were calibrated with Winkler titration at t_{12} (Anonymous, 1990). During these occasions survival of fish larvae was also monitored. At termination of the experiment, we checked survival of fish larvae in each container. Length measurements were conducted on a random sample of live fish after both the behaviour and the survival experiment.

2.7. Statistical analyses

All data were tested for normality and homogeneity of variances. The data were analysed with a factorial ANOVA and Tukey post hoc tests. The statistical power was also calculated for all tests and the result was good. Number of prey attacks and time [seconds] spent in the vegetation were log-transformed (log $x+1$) to improve the normal distributions. All data in the paper are given as means±S.E. and all tests are two-tailed.

3. Results

3.1. Behaviour experiment: the effect of oxygen concentration and predator signal

Generally, pike larval behaviour was strongly affected by the presence of a chemical predator signal (Factorial ANOVA, multivariate results, $F_{2,47}=5.0$, $p<0.05$) and oxygen concentration ($F_{2,47}=20.0$, $p<0.001$). There was not an interactive effect of chemical predator signal and oxygen concentration on larval behaviour ($F_{2,47}=0.5$, $p>0.05$). In more detail, prey attacks towards zooplankton prey by pike larvae were decreasing significantly in the presence of the chemical predator signal (Factorial ANOVA, univariate results, $F_{1,44}=10.3$, $p<0.01$). Further,

Table 1

Mean pike larval survival after 18 h exposure to high or low oxygen concentrations in the presence or absence of filamentous algal exudates (*Pilayella littoralis*)

| | High O ₂ | High O ₂ +ex | Low O ₂ | Low O ₂ +ex |
|--------------------------------------|------------------------|----------------------------|-----------------------|---------------------------|
| Survival (%) | 100 | 99.17 | 100 | 100 |
| O ₂ (mg l ⁻¹) | 10.0±0.4 | 9.7±0.2 | 3.1±0.2 | 2.8±0.2 |
| Total N (μg l ⁻¹) | 273 | 412 | 293 | 374 |
| Total P (μg l ⁻¹) | 14 | 39 | 18 | 41 |

Replicate number=9 (10 fish replicate⁻¹). Oxygen concentrations, total nitrogen (N) and phosphorus (P) concentrations measured from the experimental units are presented. ex=macro-algal exudates. See Materials and methods section for more details.

the number of prey attacks decreased significantly in a low oxygen concentration ($F_{1,44}=38.7$, $p<0.001$). The interactive effect of chemical predator signal and oxygen concentration was not significant in the behaviour experiment (exp. 1) ($F_{1,44}=0.9$, $p>0.05$) (Fig. 1a). Pairwise comparisons showed that prey attacks in low oxygen water with a chemical predator cue was significantly lower than in the other treatments, i.e. high oxygen with or without a chemical predator cue (Tukey HSD, $p<0.001$; $p<0.001$, respectively), or in low oxygen without a predator cue (Tukey HSD, $p<0.05$). Further, the number of prey attacks was also significantly different between the treatments with low and high level oxygen, both lacking the predator signal (Tukey HSD, $p<0.01$). On the other hand, vegetation use did not seem dependent on any of the factors mentioned above; the chemical predator signal did not increase vegetation use (Factorial ANOVA, univariate results, $F_{1,44}=1.6$, $p>0.05$), and neither did the oxygen concentration ($F_{1,44}=1.2$, $p>0.05$) (Fig. 1b). The

interactive effect of the two factors was neither significant ($F_{1,44}=0.5$, $p>0.05$).

3.2. Survival experiment: the effect of algal exudates and oxygen concentration

Total nitrogen (TotN) and phosphorus (TotP) concentrations showed that algal decay had initiated at the time of the experiment (Table 1). No mortality of pike larvae occurred in our 18-h trials, where we exposed the larvae to high or low oxygen concentrations in combination with (or without) exudates obtained from the filamentous alga *P. littoralis*, except for one larva that died in the high oxygen treatment with exudates (Table 1).

4. Discussion

In the present study, we demonstrated that oxygen concentration in combination with a predator chemical cue significantly affected pike larval foraging. Habitat use, on the other hand, was not affected by predator cue or oxygen level. In another experimental set-up, pike larvae did not show a decrease in survival in hypoxic water containing algal exudates. The results are discussed in more detail below.

4.1. The effect of oxygen deficiency and predator signal on behaviour

Fishes are considered more sensitive to reduced oxygen concentrations than crustaceans, annelids, bivalves (Rosenberg et al., 1991; Nilsson and Rosenberg, 1994), and gelatinous species (Decker et al., 2004). Generally speaking, all early life stages of fishes seem to be more susceptible to low oxygen than adult stages (Werner, 2002). But on the whole, there is little information available concerning larval survival in low oxygen levels, compared with the papers on adult and immature fish (Shoji et al., 2005a). Our results showed that larval pike performed significantly fewer prey attacks in low oxygen water compared to normoxic water; even the difference between prey attacks in hypoxic water with or without predator cue were significant, whereas pike larval habitat use, measured as time spent in or above vegetation, did not differ significantly between treatments in the present study. The results by Sandberg et al. (1996) support our study; predation rates of *Crangon crangon* upon *Bathyporeia pilosa* were decreasing with declining oxygen concentration. Breitburg et al. (1994, 1997) showed similar results with fish. Our results suggest that low oxygen levels, even though not lethal, add stress to newly hatched larvae when a predator is around. If feeding is

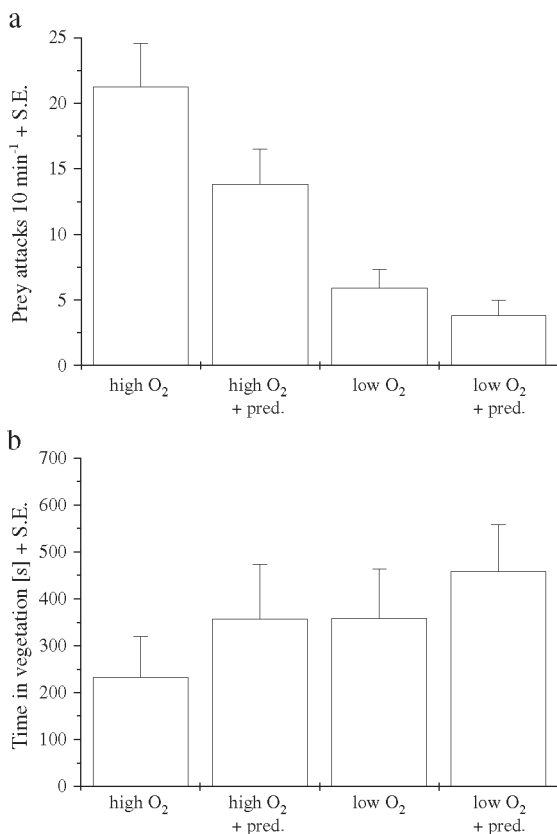


Fig. 1. (a) Number of attacks towards zooplankton prey and (b) time spent in or above vegetation by pike larvae exposed to four environments: high (c. 9 mg l⁻¹) or low oxygen (c. 3 mg l⁻¹) in the presence or absence of water conditioned with predator signals from the three-spined stickleback (*Gasterosteus aculeatus*). Replicate number=12.

reduced for a longer period of time, growth and survival may also decrease (McNatt and Rice, 2004). This is shown in a study by Shoji et al. (2005b) where fish larvae were more heavily preyed upon by *Aurelia aurita* in hypoxic waters, due to decreased activity level of fish larvae. Further, the presence of vegetation in the experimental units may have reduced the frequency of prey attacks made by pike larvae, as shown by Manatunge et al. (2000). Despite the short experiment, we consider the oxygen concentration in the experimental units relatively stable, because Häder et al. (1997) reported negative oxygen production of *Cladophora* spp., when the algae were exposed to light close to the surface (similarly as in our experimental set-up).

In the field oxygen concentrations were above 5 mg l⁻¹ in summer 2005 in typical pike larval habitats on the SW coast of Finland, Baltic Sea (Salonen et al. unpubl. data). On the other hand, Casselman (1996) report that YOY mortality may result from oxygen depression due to prolonged respiration by dense vegetation. Feeding by pike larvae seems to respond easily to changes in oxygen, which also could affect the behaviour and survival of pike larvae in the field. In case of local hypoxia combined with predator presence, pike larval feeding may decrease considerably. This change in behaviour further has implications on the survival and recruitment, because larvae may become easy prey for predators. One has to remember though, that common pike larval predators, such as perch are less active during night, when the probability of hypoxia increases. Another factor that affects the situation for fish larvae in the field is whether the population is locally adapted to hypoxia (Decker et al., 2003). The larvae used in the current study were hatched in river water in the hatchery and have not experienced hypoxia previously, which makes them respond more sensitively to changes in oxygen level.

4.2. The effect of algal exudates and oxygen level on survival

Previous studies show that exudates of *Ulva* species had negative effects on oyster larval development (Nelson et al., 2003), and crab larval survival (Johnson and Welsh, 1985). Other studies suggest that the initial attachment of brown algae were reduced by *P. littoralis* exudates (Råberg et al., 2005). In the present study, no effect by *P. littoralis* exudates, or the combination of exudates and low oxygen was detected on pike larval survival. Even though algae were in a decaying stage as shown by the nutrient concentrations (Table 1), and therefore, the concentration of exudates presumably high (Råberg et al., 2005), larval

mortality was low. Recently, several studies show negative effects on fish, crustaceans and algae by macro-algal exudates. However, we believe that our experiments were long enough (18 h) to show a potential effect by exudates on survival, if the exudate concentration was not low. Incubation lengths in similar studies have been similar or slightly longer than our experiment, varying between 6 and 96 h (Johnson and Welsh, 1985; Aneer, 1987; Larson, 1997; Nelson et al., 2003; Råberg et al., 2005). The concentration of algal exudate water (50%) in our experiment was also within the ranges (0.1–100%) used in the studies mentioned above. The most probable explanation to high survival in hypoxic water containing exudates is that pike larvae are extremely tolerant and adaptive to fluctuating abiotic environmental factors. It has been shown that pike larvae are generally rather tolerant to low oxygen; Siefert et al. (1973) found that embryos and larvae survived low oxygen levels well, because mortality did not start to increase until after 12 days at 12.5% oxygen saturation. Further, pike larvae often hatch in dense vegetation, such as reed (Kuningas, 2005), where oxygen concentrations may fluctuate due to plant decay.

Concerning algal exudates, pike larvae were highly tolerant to exudates in the present study. To our knowledge, no previous studies have monitored survival of pike larvae in the presence of macroalgal exudates. Other fish, such as the three-spined stickleback show low mortality in the presence of *Myriophyllum spicatum* exudates. Swimming and foraging are, however, reduced and stickleback larvae also show avoidance behaviour towards *M. spicatum* (Lindén and Lehtiniemi, 2005). Aneer (1987) found that *P. littoralis* exudates have negative effects on fish egg survival and plaice larvae showed reduced survival and possibly reduced growth due to combined effects by hypoxia and *Enteromorpha* sp. exudates (Larson, 1997). In addition, anti-herbivorous substances, e.g. dimethyl sulfide and acrylic acid, are formed by macro-algae (*Enteromorpha*, *Ulva*), but these are usually produced only within the consumed plant tissue (Alstynne van, 2001). We do not know with certainty which exudates and which concentrations are likely to be present in the field, because few data exist. Besides nutrients, such as nitrate, phosphate and ammonium that are released when algae decay (Vahteri et al., 2000, Table 1), *Pilayella* sp. may also excrete chemicals or secondary metabolites that can be harmful or have toxic properties (McInnes et al., 1984; Aneer, 1987; Råberg et al., 2005). Johnson and Welsh (1985) collected water from macroalgal beds in the field and found similar mortality of littoral animals as in experimental conditions, which suggests that exudate concentrations in the field may be considerable.

To conclude, in the present study we showed that prey attacks of pike larvae were heavily reduced in hypoxic water in the presence of a chemical predator cue. This fact may have serious consequences on the anti-predator behaviour of larval stages, but also on pike larval growth and survival on a long-term perspective. Due to the eutrophication of coastal areas, filamentous algae, which may form nocturnal hypoxia, have increased, and therefore various larval stages may suffer more than adults due to their restricted mobility. Although, fish larvae are known to move away from local hypoxia (Breitburg, 1994), and because common fish larval predators (such as perch and stickleback) are less active at night (Koli, 1998), the predation impact on larval stages may, however, not be so large as previously thought. Future studies should focus on the potential changes in predator–prey interactions due to local hypoxia in the field.

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References

- Alstynne van, K.L., 2001. Are bloom-forming green algae chemically defended? *J. Phycol.* 37, 50.
- Aneer, G., 1987. High natural mortality of Baltic herring (*Clupea harengus*) eggs caused by algal exudates? *Mar. Biol.* 94, 163–169.
- Anonymous, 1990. O₂-titraus. Finnish Standards Association SFS 3040, pp. 1–10 [in Finnish].
- Bonsdorff, E., Blomqvist, E.M., Mattila, J., Norkko, A., 1997. Coastal eutrophication: causes, consequences and perspectives in the archipelago areas of the northern Baltic Sea. *Estuar. Coast. Shelf Sci.* 44 (Suppl. A), 63–72.
- Breitburg, D.L., 1994. Behavioral response of fish larvae to low dissolved oxygen concentrations in a stratified water column. *Mar. Biol.* 120, 615–625.
- Breitburg, D.L., Steinberg, N., DuBeau, S., Cooksey, C., Houde, E.D., 1994. Effects of low dissolved oxygen on predation on estuarine fish larvae. *Mar. Ecol. Prog. Ser.* 104, 235–246.
- Breitburg, D.L., Loher, T., Pacey, C.A., Gerstein, A., 1997. Varying effects of low dissolved oxygen on trophic interactions in an estuarine food web. *Ecol. Monogr.* 67, 489–507.
- Breitburg, D.L., Rose, K.A., Cowan Jr., J.H., 1999. Linking water quality to larval survival: predation mortality of fish larvae in an oxygen-stratified water column. *Mar. Ecol. Prog. Ser.* 178, 39–54.
- Casselman, J.M., 1978. Effects of environmental factors on growth, survival, activity and exploitation of northern pike. *Am. Fish. Soc. Spec. Publ.* 11, 114–128.
- Casselman, J.M., 1996. Age, growth and environmental requirements of pike. In: Craig, J.F. (Ed.), *Pike: Biology and Exploitation*. Chapman and Hall, London, pp. 70–101.
- Casselman, J.M., Lewis, C.A., 1996. Habitat requirements of northern pike (*Esox lucius*). *Can. J. Fish. Aquat. Sci.* 53 (Suppl. 1), 161–174.
- Craig, J.F., 1996. *Pike — Biology and Exploitation*, 1st ed. Chapman and Hall, London.
- Decker, M.B., Breitburg, D.L., Marcus, N.H., 2003. Geographical differences in behavioral responses to hypoxia: local adaptation to an anthropogenic stressor? *Ecol. Appl.* 13, 1104–1109.
- Decker, M.B., Breitburg, D.L., Purcell, J.E., 2004. Effects of low dissolved oxygen on zooplankton predation by the ctenophore *Mnemiopsis leidyi*. *Mar. Ecol. Prog. Ser.* 280, 163–172.
- Engström-Öst, J., Immonen, E., Candolin, U., Mattila, J., The indirect effects of eutrophication on habitat choice and survival of fish larvae in the Baltic Sea. (submitted MS).
- Fletcher, R.L., 1996. The occurrence of “green tides”—a review. In: Schramm, W., Nienhuis, P.H. (Eds.), *Marine Benthic Vegetation — Recent Changes and the Effects of Eutrophication*. Springer Verlag, Heidelberg, pp. 7–43.
- Häder, D.-P., Herrman, H., Schäfer, J., Santas, R., 1997. Photosynthetic fluorescence and oxygen production in two Mediterranean *Cladophora* species measured on site. *Aquat. Bot.* 56, 253–264.
- Hodgkin, E.P., Birch, P.B., 1986. No simple solution: proposing radical management options for a eutrophic estuary. *Mar. Pollut. Bull.* 17, 399–404.
- Johnson, D.A., Welsh, B.L., 1985. Detrimental effects of *Ulva lactuca* (L.) exudates and low oxygen on estuarine crab larvae. *J. Exp. Mar. Biol. Ecol.* 86, 73–83.
- Kautsky, N., Kautsky, H., Kautsky, U., Waern, M., 1986. Decreased depth penetration of *Fucus vesiculosus* (L.) since the 1940s indicates eutrophication of the Baltic Sea. *Mar. Ecol. Prog. Ser.* 28, 1–8.
- Koli, L., 1998. Suomen kalat. Wemer Söderström Oy, Porvoo. 357 pp. (in Finnish).
- Koroleff, F., Grasshoff, K., 1976. Determination of nutrients. In: Grasshoff, K. (Ed.), *Methods of Seawater Analysis*. Verlag Chemie, Weinheim, pp. 117–181.
- Kramer, D.L., 1987. Dissolved oxygen and fish behaviour. *Environ. Biol. Fishes* 18, 81–92.
- Kuningas, S., 2005. Hauen lisääntymisalueet ja kartoitusmenetelmät Pohjanpitäjänlahden ja Tvärminnen rannikkoalueella vuonna 2004. M.Sc. Thesis, Univ. Helsinki. 47 pp. (in Finnish).
- Lappalainen, A., 2002. The effects of recent eutrophication on freshwater fish communities and fishery on the northern coast of the Gulf of Finland, Baltic Sea. Ph.D. Thesis, Univ. Helsinki. 24 pp.
- Larson, F., 1997. Survival and growth of plaice (*Pleuronectes platessa*) larvae and juveniles in mats of *Enteromorpha* sp. M. Sc. thesis, Göteborg University. 12 pp.

- Lehvo, A.-M., Bäck, S., 2001. Survey of macroalgal mats in the Gulf of Finland, Baltic Sea. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 11, 11–18.
- Lindén, E., Lehtiniemi, M., 2005. The lethal and sublethal effects of the aquatic macrophyte *Myriophyllum spicatum* on Baltic littoral planktivores. *Limnol. Oceanogr.* 50, 405–411.
- Manatunge, J., Asaeda, T., Priyadarshana, T., 2000. The influence of structural complexity on fish–zooplankton interactions: a study using artificial submerged macrophytes. *Environ. Biol. Fishes* 58, 425–438.
- McInnes, A.G., Ragan, M.A., Smith, D.G., Water, J.A., 1984. High-molecular-weight phloroglucinol-based tannins from brown algae: structural variants. *Hydrobiologia* 116/117, 597–602.
- McNatt, R.A., Rice, J.A., 2004. Hypoxia-induced growth rate reduction in two juvenile estuary-dependent fishes. *J. Exp. Mar. Biol. Ecol.* 311, 147–156.
- Middelboe, A.L., Sand-Jensen, K., 2000. Long-term changes in macroalgal communities in a Danish estuary. *Phycologia* 39, 245–257.
- Nelson, T.A., Lee, D.J., Smith, B.C., 2003. Are “green tides” harmful algal blooms? Toxic properties of water-soluble extracts from two bloom-forming macroalgae, *Ulva fenestrata* and *Ulvaria obscura* (Ulvophyceae). *J. Phycol.* 39, 874–879.
- Nilsson, H.C., Rosenberg, R., 1994. Hypoxic responses of two marine benthic communities. *Mar. Ecol. Prog. Ser.* 115, 209–217.
- Nilsson, J., Andersson, J., Karås, P., Sandström, O., 2004. Recruitment failure and decreasing catches of perch (*Perca fluviatilis* L.) and pike (*Esox lucius* L.) in the coastal waters of southeast Sweden. *Boreal Environ. Res.* 9, 295–306.
- Norkko, J., Bonsdorff, E., Norkko, A., 2000. Drifting algal mats as an alternative habitat for benthic invertebrates: species-specific responses to a transient resource. *J. Exp. Mar. Biol. Ecol.* 248, 79–104.
- Perttilä, M., Niemistö, L., Mäkelä, K., 1995. Distribution, development and total amounts of nutrients in the Gulf of Finland. *Estuar. Coast. Shelf Sci.* 41, 345–360.
- Pihl, L., 1994. Changes in the diet of demersal fish due to eutrophication-induced hypoxia in the Kattegat, Sweden. *Can. J. Fish. Aquat. Sci.* 51, 321–336.
- Pihl, L., Isaksson, I., Wennhage, H., Moksnes, P.-O., 1995. Recent increase of filamentous algae in shallow Swedish bays: effects on the community structure of epibenthic fauna and fish. *Neth. J. Aquat. Ecol.* 29, 349–358.
- Råberg, S., Berger-Jönsson, R., Björn, A., Granéli, E., Kautsky, L., 2005. Effects of *Pilayella littoralis* on *Fucus vesiculosus* recruitment: implications for community composition. *Mar. Ecol. Prog. Ser.* 289, 131–139.
- Rombough, P.J., 1988. Respiratory gas exchange, aerobic metabolism, and effects of hypoxia during early life. In: Hoar, W.S., Randall, D.J. (Eds.), *Fish Physiology XI. The Physiology of Developing Fish. A. Eggs and Larvae*. Academic Press, San Diego, pp. 59–161.
- Rosenberg, R., Hellman, B., Johansson, B., 1991. Hypoxic tolerance of marine benthic fauna. *Mar. Ecol. Prog. Ser.* 79, 127–131.
- Sandberg, E., Tallqvist, M., Bonsdorff, E., 1996. The effects of reduced oxygen content on predation and siphon cropping by the brown shrimp, *Crangon crangon*. *P. S. Z. N. I. Mar. Ecol.* 17, 411–423.
- Shoji, J., Masuda, R., Yamashita, Y., Tanaka, M., 2005a. Effect of low dissolved oxygen concentrations on behavior and predation rates on sea bream *Pagrus major* larvae by the jellyfish *Aurelia aurita* and by juvenile Spanish mackerel *Scomberomorus niphonius*. *Mar. Biol.* 147, 863–868.
- Shoji, J., Masuda, R., Yamashita, Y., Tanaka, M., 2005b. Predation on fish larvae by moon jellyfish *Aurelia aurita* under low dissolved oxygen concentrations. *Fish. Sci.* 71, 748–753.
- Siefert, R.E., Spoor, W.A., Syrett, R.F., 1973. Effects of reduced oxygen concentrations on northern pike (*Esox lucius*) embryos and larvae. *J. Fish. Res. Board Can.* 30, 849–852.
- Vahteri, P., Mäkinen, A., Salovius, S., Vuorinen, I., 2000. Are drifting algal mats conquering the bottom of the Archipelago Sea, SW Finland? *Ambio* 29, 338–343.
- Weltzien, F.-A., Døving, K.B., Carr, W.E.S., 1999. Avoidance reaction of yolk-sac larvae of the inland silverside *Menidia beryllina* (Atherinidae) to hypoxia. *J. Exp. Biol.* 202, 2869–2876.
- Werner, R.G., 2002. Habitat requirements. In: Fuiman, L.A., Werner, R.G. (Eds.), *Fishery Science — the Unique Contributions of Early Life Stages*. Blackwell, Oxford, pp. 161–182.