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Effects of turbidity and zooplankton availability on the condition and prey selection of pike larvae

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Along with increasing eutrophication the pike (*Esox lucius*) has decreased in numbers in some parts of the Baltic Sea. We undertook a field study to identify the environmental factors affecting condition of pike larvae around the southwestern coast of Finland. We also sampled the natural zooplankton community to reveal food preferences of pike larvae. Our mixed model showed that larval condition decreased with increasing turbidity, whereas temperature, salinity and stomach content were non-significant factors. One third of the variation in larval condition was explained by sampling site, indicating that site characteristics influenced the condition index significantly. The prey selection index showed that pike larvae preferred adult copepods and cladocerans, whereas they ignored rotifers and seemingly copepod nauplii as well. Together, our data show that food availability and several environmental factors are crucial for the condition of pike larvae, and probably also survival and recruitment.

Introduction

Several environmental factors affect larval fish growth, survival and recruitment to the adult population (Craig 2008). Food quantity and food quality are — in addition to temperature, salinity, oxygen, nutrients and light — often considered the most important factors affecting the growth rate of fish (Brown 1957, Moyle and Cech 1996, Brett and Müller-Navarra 1997). Temperature is crucial and may account for more than half of the variability in average growth, survival and energy use in fish larvae (Houde 1989). A good reproduction area offers both food and shelter for fish larvae, because the primary sources of mortality for young stages are predation and starvation (Hutchings 1997).

During recent decades due to human activities, many lakes and coastal sea areas have become eutrophicated, as evidenced by drifting algal mats, deep-water hypoxia, cyanobacterial blooms and turbidity (Sandén and Håkansson 1996, Bonsdorff *et al*. 1997, Valiela *et al*. 1997). An increase in phytoplankton abundance may lead to an increase in zooplankton production. Turbidity and changes in food quantity may alter the success of growth, survival and recruitment of fish larvae (Utne-Palm 2002, Sandström 2004). In the Baltic Sea, eutrophication is a serious problem that also affects shallow and shel-

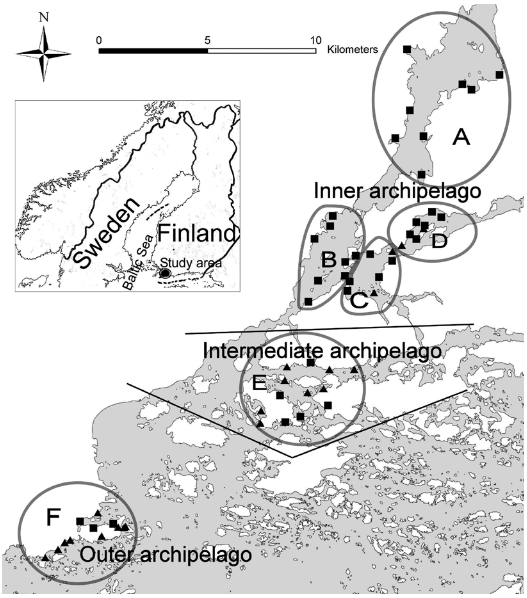

Fig. 1. Map of the study zones [I = inner zone (Pojo Bay), M = intermediate zone (Danskogen), O = outer zone (Tvärminne)], including different areas (circles A–F) with sampling sites, where pike larvae were either present (squares) or absent (triangles). Tvärminne Zoological Station (59°50´N, 23°15´E) is located in the rightmost triangle in the outer area.

tered areas (Bonsdorff *et al*. 1997), which are important nursery areas for many fish.

The pike (*Esox lucius*) is a central species in many northern lakes and brackish waters (Casselman 1996), and is an important catch in recreational fishing (Finnish Game and Fisheries Research Institute 2007). Pike populations have diminished in some coastal areas of the Baltic Sea since the 1970s. Due to its wide distribution, the pike is considered to be an adaptive species (Casselman 1996), but despite its high flexibility, catches have collapsed in areas where environmental changes have been considerable (Lehtonen 1986, Nilsson *et al*. 2004, Nilsson 2006). The decrease in pike numbers appears to be spatial, and the species has mainly diminished in places that are influenced by harsh pelagic circumstances (Lappalainen *et al*. 2008). Pike catches have decreased, but the average weight of (caught) fish has simultaneously increased in the outer archipelago (Lehtonen 1986). Recruitment failure was suggested to be the main reason for this phenomenon (Lehtonen 1986, Nilsson *et al*. 2004), but more information is needed to clarify this issue. Winkler (2002) stated that pike catches have decreased because of diminishing macrophytes and eutrophication.

The aim of the present study was to identify the environmental factors affecting condition of pike larvae in a coastal area of the Baltic Sea. We measured environmental background variables and sampled the zooplankton communities to reveal prey selection of pike larvae. The field study was performed in late spring and early summer 2005 around the southwest coast of Finland. We hypothesized that abiotic factors and food availability are highly important for pike larval condition and prey selection. The abiotic factors shifted from a more freshwater environment to a more harsh sea environment at our study sites, resulting in changes in the zooplankton community and thus prey preferences and condition.

Material and methods

Pike larval samples were collected in May and June 2005 from the south-western coast of Finland, northern Baltic Sea (Fig. 1). Potential pike reproduction areas were randomly chosen from the reed belt zone traced from aerial photos. In all, 56 sites were chosen for this study. Due to the subsequent warming, fish were caught later from the outer parts of the study area. The timing of environmental sampling and larval pike capture in different study areas was chosen according to egg hatching. The study area was monitored before collecting the data to ensure the correct timing for the fieldwork. The sites were visited several times to ensure that all the possible larval sites were found and that enough data would be available for the analysis.

We divided the study area into three zones: the inner (I), intermediate (M) and outer (O) archipelago, which were further divided into six areas: A, B, C and D in the inner archipelago, E in the intermediate archipelago and F in the outer archipelago. Within each area, pike were caught at several sites (Fig. 1). The inner archipelago is sheltered and influenced by freshwater from the river running down to the northernmost part of the study area. The intermediate archipelago has many outer archipelago characteristics, but is rather sheltered. The outer archipelago is fairly exposed and open.

We located pike larvae using a white plate and caught them rapidly with a scoop. Further details about the larval fish capture method used can be found in Lappalainen *et al*. (2008). The larvae were taken from 32 sites and preserved in denatured ethanol (75%).

We collected water samples and measured some environmental data from all the sites. Only the sites with pike larvae were included in our data. Sampling was performed once before capturing the larvae to avoid stirring of the water and mixing of the bottom substrate with water. Water temperature, dissolved oxygen concentration (YSI model 95; YSI Inc., Yellow Springs, OH, USA) and conductivity (Hanna Instruments 9835; Hanna Instruments, Woonsocket, RI, USA) were measured in the field. Turbidity was measured in the laboratory (Hach 2100P; Hach Co., Loveland, CO, USA) from a water sample. Salinity was calculated accordingly:

$$\text{Salinity } (‰) = 0.6701(\text{conductivity (mS)} - 0.3723) \quad \text{(Eq. 1)}.$$

Water for the zooplankton-composition analyses was taken with a Limnos sampler (Limnos Oy, Turku, Finland) from a depth of approximately 60 cm. In some shallow areas, this depth was found at the edge of the reed-belt zone. Three Limnos samples were taken from each location and thoroughly mixed in a container. A 100-ml sample was preserved with acid Lugol's solution. The abiotic data (salinity, temperature and turbidity) for areas A, B, E, F (Fig. 1) were similar to the data of Lappalainen *et al*. (2008). The present study includes data only from sites where pike were found (excluding sites with no pike).

In the laboratory, we weighed the larvae to the nearest 0.0001 g (Mettler Toledo AX205; Mettler-Toledo International Inc., Greifensee, Switzerland) and measured their total length (LT) to the nearest 0.5 mm under a binocular microscope (Leica; Microsystems, Wetzlar, Germany). The stomachs were carefully emptied and the contents analysed under a microscope (Wild M40; Wild Heerbrugg, Gais, Switzerland). We counted the prey individuals from the stomach content and identified the individuals as accurately as possible. Forty-nine pike stomachs of the total 201 were empty. The zooplankton samples were filtered through a 43-μm mesh to remove detritus, microzooplankton and preservative. The zooplankton samples were identified to species and counted in a chamber under a microscope (Wild M40) with a 10× objective.

Larval pike condition was estimated from residuals of log-transformed weights and lengths (Ormerod and Tyler 1990). We estimated the larval condition from the residuals of each data point on the logarithmic regression line; the more positive the residual the better the larval condition was and vice versa.

We conducted a general linear mixed model (GLMM) analysis using restricted maximum likelihood (REML) estimation to explain pike larval condition in relation to environmental factors. This analysis technique accounts for the lack of independence of observations due to the grouping variables (areas and sites). Prior to fitting our general mixed model on the fixed effects of interest, we compared all combinations of grouping variables, including nesting, to determine the random effect structure that best fit our data. Based on Akaike's information criterion (AIC) (Burnham and Anderson 2002), the random effect of site (cf. Fig. 1) best explained our data. Only variables with no missing data were included in our analysis, and thus we included stomach content, turbidity, salinity, temperature and exposure gradient ranked on an ordinal scale from 1 to 7 as fixed effects. Oxygen was not included in the model, due to missing data, and so were sites with no larvae (Fig. 1). Some multicollinearity occurred between some of the environmental variables, but if slight, it was considered of little consequence (Zar 1999).

We also calculated a selectivity index for comparing zooplankton in the stomach with the zooplankton community in the surrounding environment (Pearre 1982). The index was analysed with Fisher's exact test. Pearre's (1982) selectivity index is a χ^2-based index:

$$C = \frac{a_d b_e - a_e b_d}{\sqrt{abde}} \quad \text{(Eq. 2)}$$

(for explanation *see* Table 1). The index values range from 1 (always consumed) to –1 (always ignored), values close to zero indicate no selection.

Results

Environmental data and condition of pike larvae

The environmental parameters varied spatially and temporally (Table 2). Salinity increased and temperature decreased towards the outer archipelago areas. The oxygen concentration varied throughout the study area between 5.3 and 11.7 mg l^{-1}. Highest turbidities were measured in the inner archipelago and the lowest in the middle archipelago (Table 2). In total, 201 pike larvae were caught at 32 sites (Fig. 2); 88% of the fish were 10.0–17.0 mm long, at which size they mainly use zooplankton as prey. There were more sites with no pike or few pike larvae in the outer archipelago zone (Table 2). The average condition index of pike larvae was highest in the intermediate archipelago and lowest in the outer archipelago (Fig. 3).

The condition of pike larvae significantly decreased with increasing water turbidity (GLMM: $F_{1,165} = 5.94$, $p = 0.0159$) (Fig. 4). The lack of larvae in good condition in the most turbid areas mainly seems to determine the trend. Neither salinity, temperature, stomach content nor the site exposure gradient were significant predictors of larval condition (GLMMs, all $p > 0.5$). However, the random effect of sampling site explained 35.6% of the total variation in condition.

Table 1. Explanation of terms used to calculate Pearre's (1982) selectivity index (Eq. 2). Relative abundance (percentage) of each zooplankton prey item ingested in relation to the total prey standing stock, where *a* and *b* represent the relative abundance of a particular species (A) and all others, respectively, and subscripts d and e indicate the diet and the environment.

	Zooplankton species		
	A	Others	Total
Diet	a_d	b_d	$a_d + b_d = d$
Environment	a_e	b_e	$a_e + b_e = e$
Total	$a_d + a_e = a$	$b_d + b_e = b$	$a_d + a_e + b_d + b_e = n$

Zooplankton communities and prey selection index

The total amount of zooplankton (Table 2) as well as the number of most preferred prey (cladocerans and cyclopoids) diminished towards the outer archipelago. In the outer archipelago, the zooplankton community consisted of three groups, whereas in the inner archipelago zone, 12 groups were represented. In the inner zone, rotifers, cyclopoid copepods and cladocerans predominated, while rotifers and calanoid copepods dominated the zooplankton community in the outer zone (Figs. 5 and 6). Most of the species found among zooplankton were free-swimming, but a few live on the surfaces of vegetation or on the bottom (e.g., harpacticoids, *Alona* sp.). The differences in abundance between the sampling zones varied between 570 and 9160 ind. l^{-1} (Table 2).

Table 2. Environmental data for the study area (Fig. 1). The data were collected between 17 May and 6 June 2005 and are presented as means ± SE and ranges (in parentheses). NFU = nephelometric units, ZPL = zooplankton. The study zones are: I = inner area (Pojo Bay), M = intermediate area (Danskogen), O = outer area (Tvärminne).

Zone	Pike (ind.)	Temperature* (°C)	O_2 (mg l^{-1})	Salinity* (‰)	Turbidity* (NFU)	ZPL density (ind. l^{-1})
I	184	16.9 ± 0.2	9.0 ± 0.1	1.3 ± 0.02	3.8 ± 0.2	3779.9 ± 194
		(10.8–20.6)	(5.3–11.7)	(0.9–2.5)	(1.6–14.6)	(570–9160)
M	10	15.1 ± 0.9	8.7 ± 0.2	3.5 ± 0.3	1.6 ± 0.2	1437.5 ± 114
		(9.9–16.8)	(8.5–10.3)	(2.9–5.2)	(1.3–2.7)	(1310–2330)
O	7	11.4 ± 0	9.8 ± 0	5.0 ± 0	3.16 ± 0	1790 ± 0

* Abiotic data are published in Lappalainen *et al.* (2008).

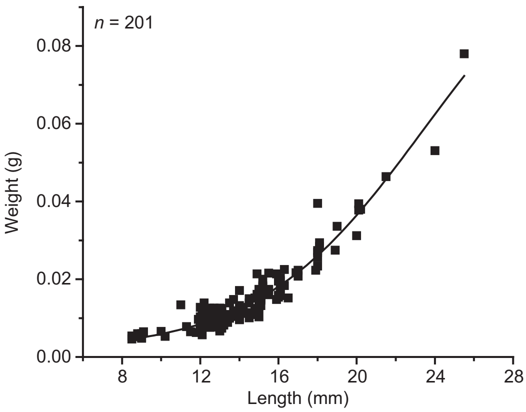

Fig. 2. Relationship between larval weight and length ($R^2 = 0.754$, df = 200, $p < 0.001$).

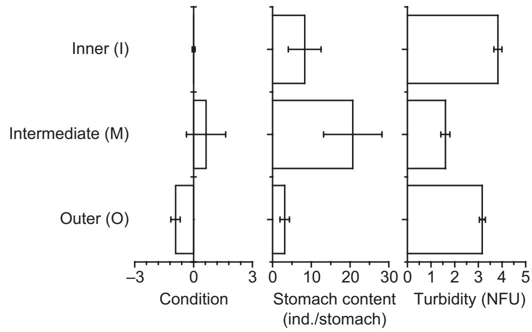

Fig. 3. Pike larval condition index, stomach content (number of food particles in stomachs) and turbidity (mean ± S.E.) in different zones. NFU = nephelometric units.

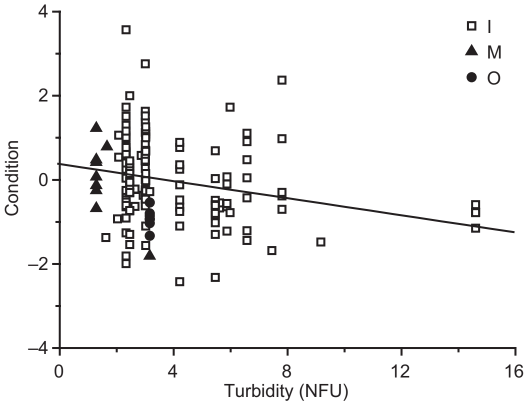

Fig. 4. Relationship between the condition index of pike larvae and turbidity. Formal analysis in the text. I = inner zone (Pojo Bay), M = intermediate zone (Danskogen), O = outer zone (Tvärminne).

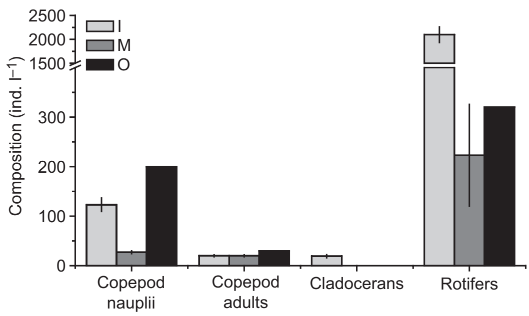

Fig. 5. Zooplankton community composition (ind. l^{-1}) (mean ± S.E.) in inner zone (I), intermediate zone (M), and outer zone (O).

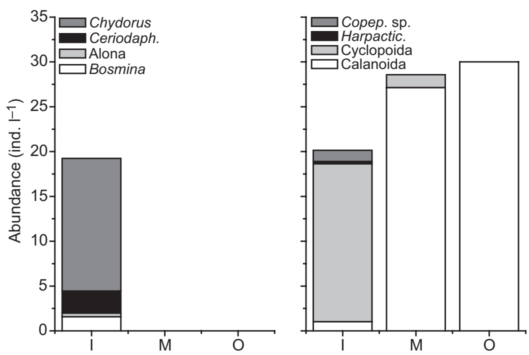

Fig. 6. Cladoceran and copepod abundances (ind. l^{-1}) in inner zone (I), intermediate zone (M), and outer zone (O).

The main prey of pike larvae were different copepods (calanoids, cyclopoids) and cladocerans, of which *Chydorus* sp. was the main taxa. The selectivity for different prey species was more or less similar throughout the study area (Fig. 7). Rotifers were strongly ignored by pike larvae in all areas (Fig. 7). Copepod nauplii were not selected by pike larvae in any area, as indicated by the selection index, which was often close to zero (Fig. 7). No nauplii were found in the stomachs of pike larvae, even when they were abundant or nearly the only available prey at some sites. Adult calanoid copepods (mainly *Eurytemora affinis*), different cyclopoid copepods and many cladoceran species (*Bosmina* sp., *Ceriodaphnia* sp., *Chydorus* sp., *Daphnia* sp.) were readily selected by pike larvae (Fig. 7).

Discussion

In the present study, we showed that the condition of pike larvae was related to turbidity and the archipelago zone. The variation of larval condition could also be explained by site specifi-

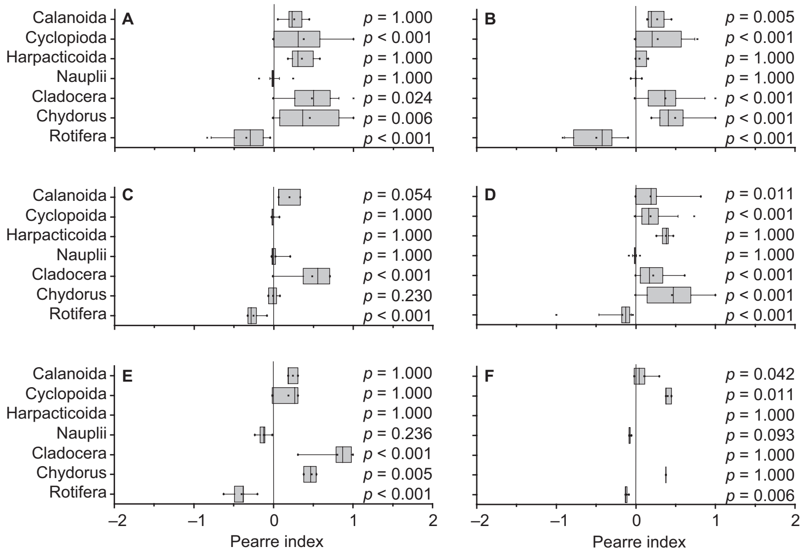

Fig. 7. Food selection indices of pike larvae (Pearre 1982) for different groups of prey in the monitored zones. The zones are divided into sampling areas. The inner zone consists of areas A–D, the intermediate zone E and the outer zone F. More details in Fig. 1.

city. Temperature, salinity and stomach content were less important factors. We calculated the prey selection index to reveal diet preferences of pike larvae. The larvae selected copepods and cladocerans and ignored rotifers. They did not select copepod nauplii. In support, Samardina (1957) does not list rotifers or copepod nauplii in the diet of pike larvae. Preferred prey, cladocerans, did not occur commonly in the outer archipelago, which possibly contributing to the low number of larvae in that zone.

Condition of pike larvae in relation to environmental factors

In the present study, condition of pike larvae was significantly dependent on one main environmental factor: water turbidity. The relationship between condition and turbidity was negative, which is supported by Craig and Babaluk (1989), who showed that 21% of the variance in adult pike weight was explained by Secchi depth, pike weight decreasing with a decrease in Secchi depth. The variance within the data in the present study (Fig. 4) was quite large and some of the noise in the condition–turbidity relation could have been better explained by using a more biologically meaningful measurement, such as Secchi depth. Vøllestad *et al*. (1986) reported that adult pike showed slower growth in the turbid Halden River system in comparison to Lake Tyrifjorden, even though prey densities were high.

The Baltic Sea has become increasingly turbid during recent decades (Sandén and Håkansson 1996). Turbidity is a phenomenon that affects species and life stages differently, but can be problematic for fish that use visual cues for capturing prey (reviewed by Utne-Palm 2002). This effect may appear as a decrease in reaction distance to the prey (Barret *et al*. 1992, Sweka and Hartman 2001), as a change in the type of prey selected or captured (Rowe *et al*. 2003) or as a change in the amount or ratio of prey consumed (Sweka and Hartman 2001, Engström-Öst *et al*. 2006, Engström-Öst and Mattila 2008). In brown trout (*Salmo trutta*), turbidity altered the isopod-dominated diet in clear water to a diet dominated by cladocerans under turbid conditions. Simultaneously, stomach fullness decreased progressively (Stuart-Smith *et al*. 2004). In our data, no correlation between turbidity and stomach content was detected. Turbidity may also lead to differing behaviour of the prey species (Abrahams and Kattenfeld 1997). The relationship between foraging success and turbidity may not always be straightforward; enhanced contrast at intermediate turbidity can also increase the foraging success of larval fish (Utne 1997).

The relationship between salinity and larval condition was non-significant. Pike are genuine freshwater fish (Crossmann 1996), and growth is expected to decrease with increasing salinity (Craig 1996, Engström-Öst *et al*. 2005), due to the higher energy costs of osmotic and ionic regulation (Wootton 1990). Lappalainen *et al*. (2008) found that pike occurrence and spring salinity were negatively related. In the inner archipelago zone, the water is nearly fresh (0.9‰), indicating that pike larvae live in habitats with salinities close to that of their original habitat, while salinity in the outer parts of the study area is higher (Table 2).

More than 35% of the variance in larval condition was explained by site, indicating that condition was strongly dependent on the site at which the larvae were captured. Most of pike larvae were found in the inner archipelago zone, which poses the question of whether survival of larvae is low in the outer zone. Lappalainen *et al*. (2008) suggested that the outer and inner archipelago act as sink and source, respectively, for pike. Due to eutrophication, reed belts that are suitable habitats for pike larvae are covering increasingly larger areas in the outer archipelago. But some environmental conditions probably decrease the survival of pike larvae in the outer archipelago.

In the outer archipelago, prey species diversity was lower than in the inner archipelago. Moreover, zooplankton in the outer archipelago consisted of prey that was either not preferred by pike larvae or simply unavailable to them which may partly explain why there were only few larvae in the outer archipelago. In the outer areas, colder and less nutrient rich waters are more extreme both for pike larvae and their prey. In this area, as well as in the recruitment failure area in the Kalmar Sound (Nilsson *et al*. 2004), the probability for cold water upwelling is also higher (Myrberg and Andrejev 2003). Favourable condition index values in the intermediate area (Fig. 3) can be explained by a combination of preferred zooplankton species and low turbidity.

Roach (*Rutilus rutilus*) have increased in the Baltic Sea since the 1970s (Lappalainen *et al*. 2001). Roach larvae eat cladocerans (Lange 1960, Grigorash *et al*. 1972) and may compete with pike larvae, if occurring in high abundances. Roach reproduces in areas with low salinities (Härmä *et al*. 2008), and the larvae are, therefore, present almost only in the inner archipelago zones. The three-spined stickleback (*Gasterosteus aculeatus*) has increased in some areas of the Baltic Sea (Nilsson *et al*. 2004), and use partly the same prey as pike larvae (Peltonen *et al*. 2004). In present study, larvae of these fish species were mainly found in the outer archipelago areas.

Prey selection

Little is known about the prey preferences of fish larvae, especially in brackish water. Pike are generalists that feed on a variety of prey in a proper size range (Mamcarz *et al*. 1998). During the first few weeks of their life, pike feed mainly on zooplankton. We found a few fish in the stomachs analysed, indicating that pike may change to a piscivorous diet very early in life (Urho *et al*. 1989). In the present study, we examined the stomach contents and compared them with the natural zooplankton community composition. Pike larvae selected adult copepods and cladocerans as food, but they ignored rotifers, even though they were of appropriate size. Only moving prey releases the hunting reaction of pike larvae (Braum 1964), and evenly moving rotators, even as big as *Asplanchna* species, seem not to attract the attention of pike larvae (visual observation by L. Urho).

Our results are, in general, supported by the size-selection hypothesis (Brooks and Dodson 1965), stating that planktivores should select the largest prey items, because it is energetically the best choice. Lehtiniemi *et al*. (2007) showed that pike larvae prefer large prey. On the other hand, our study also showed that the small round cladocerans of the genus *Chydorus* sp. were also frequent prey for pike larvae (Bry 1996), at sites where they were not found in the water samples. These *Chydorus* species may be attractive prey especially for newly hatched larvae, due to their slow swimming motion and dark coloration.

To conclude, we showed that the condition of pike larvae was related to turbidity and that the variation in condition was explained by site differences. In general, larval condition was higher in less turbid and slightly more saline waters.

Few larvae (3.4%) were found in the outer zone, which suggests that reproduction and perhaps survival is lower there. Temperature, salinity and stomach content were not important factors explaining condition in the present study. Pike larvae generally preferred large prey, such as adult copepods and cladocerans, but ignored small prey, e.g., rotifers, whereas copepod nauplii were not selected. We also showed that there was less suitable prey for pike larvae in the more hazard outer archipelago, which may also have affected larval condition and survival. Future studies should focus on the spatial and temporal differences in food quality of prey items for pike larvae, as well as on the effect of turbidity on prey capture of larvae. In addition, the abundance of competitors, such as roach, has increased tremendously in the area (Lappalainen *et al*. 2001), and may also affect the success of pike via larval competition for prey and habitats.

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