



## Does the zooplankton prey availability limit the larval habitats of pike in the Baltic Sea?

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### ABSTRACT

The objectives of this study were to (1) investigate whether the availability of suitable zooplankton prey limits the distribution of the coastal larval areas of pike (*Esox lucius*) in two archipelago areas of the northern Baltic Sea and (2) compare the availability of zooplankton prey in spring between different types of coastal littoral habitat. According to the results, reed belt habitats formed by *Phragmites australis* constitute hot spots for zooplankton prey in the coastal ecosystem. During the spring, reed-covered shores of the inner archipelago maintained more than 10 times higher densities of copepods and cladocerans, the preferred prey for larval pike, compared to the other studied shores. Temperature conditions were also most favourable in the reed belt habitat. Thus, the reed belts of the inner and middle archipelago were shown to form the best habitat for larval pike in the coastal area of the northern Baltic Sea, and this was also the only habitat where pike larvae were found. Our results suggest that the poor survival and recruitment of pike in the outer archipelago, however, cannot exclusively be explained by sub-optimal feeding conditions of the larvae. There are also other important factors, presumably connected to the exposure to the open sea, that affect the distribution of the pike larvae. Our results, however, highlight the importance of sheltered coastal reed belt shores as reproduction habitat for spring-spawning fish in the northern Baltic Sea. Further, this study disproves the assumption that the seaweed bladder wrack (*Fucus vesiculosus*) forms a reproduction habitat for pike in the coastal area.

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### 1. Introduction

The year-class strength of a fish population is determined during the larval stage (Cushing, 1990), and the quality and quantity of spawning and larval habitats thus establish the basis for fish production (Urho, 1996). A larval habitat has to maintain appropriate environmental conditions, such as an optimal temperature, as well as contain suitable prey organisms and a sufficiently low density of predators and competitors for the eggs to hatch and the larvae to survive and successfully recruit to juvenile and adult populations (Leggett and Deblois, 1994; Urho, 1996). Food limitation during the larval stage is suggested to be an especially important regulator of recruitment. According to Hjort's 'critical period' hypothesis (Hjort, 1914, 1928) it is already shown that larval survival is strongly linked to food abundance during the transition of larvae from endogenous, i.e. yolk sac, to exogenous feeding. Cushing (1972) proposed the match-mismatch hypothesis, according to which food adequacy is crucial

during the entire larval period. Further, he demonstrated the importance of abiotic factors in regulating the timing and intensity of plankton production, and hence the abundance of food for larval fish (Cushing, 1972).

The pike (*Esox lucius*) is a freshwater fish species appearing in inland waters of the entire northern hemisphere (Raat, 1988; Crossman, 1996). Pike also spawn in the brackish coastal archipelago areas of the northern Baltic Sea and occur up to a salinity of 10 (Raat, 1988). Pike can spawn over beds comprised of a range of macrophyte species. The newly hatched larvae remain close to these shallow, vegetated, littoral spawning areas (Casselman and Lewis, 1996) and spend most of their first summer within the same vegetated habitat (Raat, 1988). After hatching, larval pike are sustained for a few days by an internal store of energy consisting of the yolk sac. However, for the larvae to survive, exogenous feeding on zooplankton has to take place before full yolk resorption (Billard, 1996). At a few weeks of age, the diet of larval pike is formed of zooplankton, mainly of copepodites and adult copepods, especially cyclopoid copepods, but also to a smaller extent of cladocerans (Desvillettes et al., 1994; Lehtiniemi et al., 2007; Salonen et al., 2009). These two zooplankton taxa usually dominate the prey communities of the coastal waters of the Baltic Sea (Hansson et al., 1990; Heerkloss and Schnese, 1999). Larval pike feed

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selectively and prefer larger sized prey, since large prey items offer a better energy source for the growing larvae (Lehtiniemi et al., 2007). At a size of 20–40 mm, depending on the environmental conditions and prey availability, larval pike begin to prey more on insect and fish larvae, and from then on their growth rate consequently increases (Raatt, 1988; Urho et al., 1989 and references therein).

It has earlier been argued that the seaweed bladder wrack (*Fucus vesiculosus*) may serve as a spawning and larval habitat for pike in the outer archipelago of the northern Baltic Sea (Lehtonen, 1986), but this has never been subsequently documented. Instead, coastal reed belt shores, formed by *Phragmites australis*, have been shown to serve as a major coastal spawning and larval area for pike (Lappalainen et al., 2008). In spring, during the spawning season of pike, the previous year's cut and flattened reeds in the outer parts of the belt form a sheltered habitat for pike larvae. The abundance and range of reed belts have increased and nowadays they are a dominant feature of sheltered shores along the entire coastal zone of the northern Baltic Sea (Roosaluste, 2007).

However, larval pike have not been found equally on all coastal reed-covered shores. According to Lappalainen et al. (2008), the reed belt shores in the inner archipelago area form particularly important reproduction habitats for coastal pike. For some still unknown reason, larval pike were only found to be abundant in these inner archipelago areas, while along similar reed belt shores in the intermediate or outer archipelago they occurred more sporadically. Abiotic environmental variables such as turbidity and salinity during the spawning season have been shown to explain the coastal distribution of the larval areas of pike, but not comprehensively, since these factors have an indirect effect on the occurrence of larvae (Sundblad et al., 2009). It is likely that the distribution of the coastal larval areas of pike strongly depends on biotic interactions, and sub-optimal feeding conditions have been offered as a possible explanation for the poor survival and recruitment of pike larvae in the reed belt shores of the outer parts of the archipelago zone (Lappalainen et al., 2008; Sundblad et al., 2009). Sub-optimal feeding conditions are also a possible reason for the widespread recruitment failure of pike observed on the Swedish coast of the northern Baltic Sea (Nilsson et al., 2004a). It has recently been suggested that the recruitment failure is connected to high water exchange between

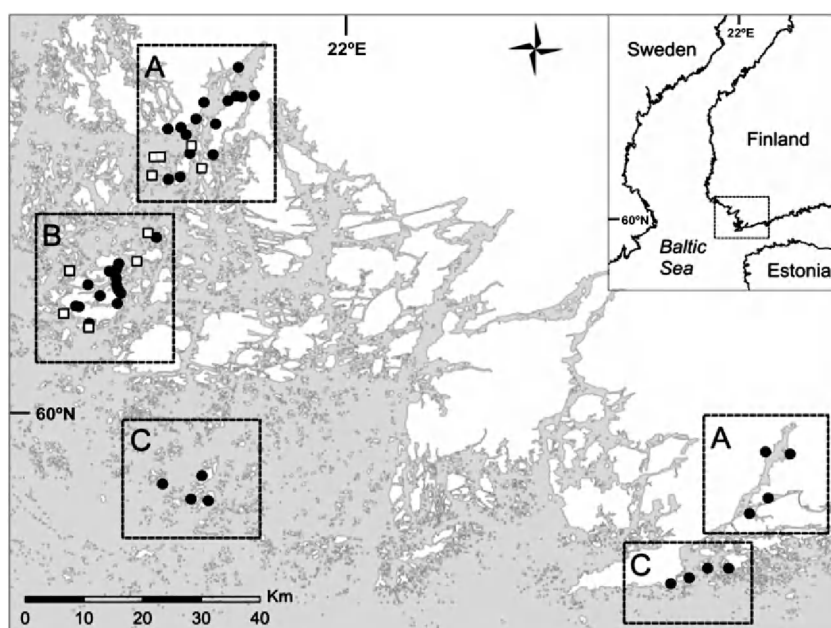
the coastal area and the open sea, and that the main reason for the recruitment failure could be the changes in the zooplankton community of the open Baltic proper, i.e. a reduced total biomass and, notably, a lower proportion of copepods reported by Möllmann et al. (2000) and Alheit et al. (2005).

The aims of this study were to (1) evaluate whether the availability of suitable zooplankton prey limits the distribution of the coastal larval areas of pike in the northern Baltic Sea, especially in the archipelago areas exposed to the open sea, and in addition to this, (2) compare the availability of zooplankton prey between different types of coastal littoral habitat. Our main hypotheses were that pike prefer reed belt shores as larval habitats and that some reed belt shores contain more suitable zooplankton prey for the larval pike to prey on, therefore forming more valuable larval habitats. In addition to the abundance of suitable prey organisms, abiotic environmental variables were also used as indicators of the suitability of areas as larval pike habitats. Simultaneous larval, zooplankton and environmental data were gathered at the same critical time and place where a few weeks old pike larvae were found at two separate archipelago areas in the northern Baltic Sea.

## 2. Methods

### 2.1. Study area and selection of study sites

The study area consisted of two coastal brackish water areas, the Archipelago Sea (60N, 21E) and the Ekenäs (Tammisaari in Finnish) archipelago (60N, 23 E), both located on the south-western coast of Finland in the northern Baltic Sea (Fig. 1). The archipelago zone in this area is very complex and extensive with several islands and long shoreline, and defined by strong environmental gradients in, e.g. salinity and turbidity. No tides exist, only air pressure driven water level variation. Both freshwater plants, such as reed, and marine algae, such as bladder wrack, occur next to each other in this area. However, shores covered with reed belts constitute a considerable part of the shoreline in the study area, especially in the shallow near-shore waters of the inner archipelago. In the Ekenäs archipelago the reed belt coverage of the shoreline was 9%



**Fig. 1.** Location of the study areas (Archipelago Sea A–C on the left and Ekenäs archipelago A, C on the right side) and the study sites. The boxes indicate the inner archipelago area (A), intermediate archipelago area (B) and outer archipelago area (C). The reed-covered sampling sites are marked with solid circles and other sites with open squares.

in the outer archipelago and increased to 58% in the innermost archipelago area (Härmä et al., 2008).

Altogether, 51 littoral sampling sites, each consisting of a 100-m-long stretch of shoreline, were selected. Of these, 43 sites were located in the Archipelago Sea (Fig. 1). Here, the selection of the study sites was conducted by stratified random sampling within three archipelago zones (inner, middle, outer) and two habitat types (reeds, no reeds). The locations of shores with reed belts were determined from GIS maps produced from Landsat TM/ETM+ satellite images by computer-based interpretation (Pitkänen et al., 2007). The shores without reeds were furthermore divided into bladder wrack-covered shores, i.e. rocky shores where bladder wrack was attached to stones or other hard substrates, and shores without vegetation. In the Archipelago Sea, the simultaneous larval pike and zooplankton sampling and environmental data collection were carried out between 25 May and 21 June 2006. In addition to these, 8 sampling sites were located in the Ekenäs archipelago (Fig. 1). Here, the selection of study sites was conducted by stratified random sampling within two archipelago zones (inner, outer) and all sites were located on reed belt shores. In the Ekenäs archipelago, simultaneous larval pike, zooplankton and environmental background data samplings were carried out between 21 May and 21 June 2007.

## 2.2. Environmental data

Abiotic conditions (surface water temperature, salinity, Secchi depth, wave exposure) were recorded at each sampling site at each visit. Temperature and salinity (Practical Salinity Scale) were measured with a portable temperature and conductivity meter (Thermo Fisher Scientific Inc., Waltham, MA) close to shoreline, whereas the Secchi depth was measured with a white plate ( $\emptyset$  25 cm) at the closest possible depth, usually outside vegetation. The exposure of a site to wave action was estimated using an effective wave exposure (fetch) index (see *Isæus, 2004*) with a 25-m resolution. The abiotic conditions were recorded as average values and ranges, since the number of measurements and timing varied between sites. Additionally, water temperature loggers were placed in some of the study sites to monitor the surface water temperature: two loggers in the Archipelago Sea (one in inner, one in middle archipelago) from 18 May to 22 June 2006 and eight loggers in the Ekenäs archipelago from 18 May to 22 June 2007 (four in inner, four in outer archipelago).

## 2.3. Larval pike sampling

Larval pike that were a few weeks old were sampled by wading in shallow water and searching for them using a white plate and a white scoop (for more details see *Lappalainen et al., 2008*). The white plate and scoop method has been developed to sample unevenly distributed larvae in dense vegetation and shallow water. It is a rapid and cost-effective method and can be used to determine the presence or absence of larval pike at the study sites. In both years (2006 and 2007), sampling was started earlier in the inner areas because of the earlier increase in water temperature and consequently earlier onset of spawning, and the sampling was continued until the entire spawning season was over, i.e. no spawning fish had not been observed at the previous visit. The inner archipelago sampling sites were therefore visited three times at 12–18 days intervals, whereas the middle and outer archipelago sites were each visited only two times at 12–26 days intervals. At each site and visit, 100 m of shoreline was checked by criss-cross searching, with a sampling duration of half an hour per study site using two samplers. Only larval pike that had already absorbed their yolk sac and started exogenous feeding on zooplankton were recorded in this study. The total number of pike larvae found at each sampling

site per visit was counted and total length of the larvae measured. The number of larvae observed is here treated as a semi-quantitative variable and in the statistical analysis only the binary variable 'larvae presence/absence' was used. Positive observation of pike larvae at least at one of the visits per site was enough to treat that particular site as present observation.

## 2.4. Zooplankton sampling

Zooplankton sampling consisted of two parts. First, each of the 51 sampling sites was sampled once to quantitatively determine the zooplankton density and species composition. The zooplankton samples were gathered at the same time and from the same habitat as zooplankton-feeding larval pike. At sites where no pike larvae were observed, zooplankton samples were collected at the same time and from similar conditions to the nearby sites where pike larvae were found. In addition to this, four reed-covered sampling sites, two sites in the inner archipelago and two in the middle archipelago in the Archipelago Sea, were selected to examine the changes in zooplankton density and species composition over time. These four sites were sampled five times at one-week intervals between 25 May and 21 June 2006. At each visit at the four sites, also the occurrence of pike larvae was examined and zooplankton-feeding larval pike were detected during the first three weeks of sampling.

From one sampling site and on each visit, a total of three parallel zooplankton samples were gathered at the ends and in the middle of the 100-m stretch of shoreline to gain a representative view of the zooplankton population. One sample, totalling 15 l of water, was gathered with a 2-l scoop from a littoral area of about 3 m<sup>2</sup>. Using the scoop as a sampling instrument enabled the water sample to be collected from exactly the same habitat where pike larvae were detected, this usually being in shallow water (<1 m depth). Larval pike occasionally caught in the water sample were immediately removed. The water sample was passed through a 50  $\mu$ m sieve and the sample retained on the sieve was then transferred to a 200 ml glass bottle. Lugol's solution was added to the samples in the field and sample bottles were stored in the dark and chilled for later analysis.

Species determination and counting took place later in the laboratory. There, the zooplankton samples were filtered through a 90  $\mu$ m mesh to remove detritus. The samples were divided by eye and, in total, 1/10 or 1/4 of each 200 ml sample was counted, depending on the overall density of the sample. The zooplankton community was counted in a cuvette using 6 $\times$  objectives with a Wild M40 microscope (Wild Heerbrugg, Gais, Switzerland) and identified to species. The three parallel samples per study site and visit were combined as one pooled sample, and the zooplankton densities were counted and recorded as individuals per litre (ind l<sup>-1</sup>) per species per site and visit.

## 2.5. Data analysis

Since sampling began earlier at the inner archipelago sites, it was not possible to compare the abiotic conditions between sites within one sampling round. Therefore, with the dataset for the Archipelago Sea, the difference in the surface water temperature and Secchi depth between reed-covered sites and "other sites" (pooled bladder wrack or non-vegetated sites) was tested with paired *t*-tests to exclude the effect of sampling time on the results. A reed-covered counterpart site was selected for each "other shore" site ( $n = 16$ ) based on geographical closeness, and only environmental variables measured during the same day at both of the paired sites were used in the analysis.

Zooplankton species were combined to form five larger prey taxa to enable comparisons between sites in the statistical analysis. First three taxa represented prey items preferred by larval pike (according to Desvillettes et al., 1994; Lehtiniemi et al., 2007; Salonen et al., 2009): (1) Cladocera, (2) copepodites and adult Cyclopoida copepods and (3) copepodites and adult Calanoida copepods. The next 2 taxa represented prey items not preferred by pike larvae: (4) Copepoda nauplii and (5) Rotifera. The zooplankton data were log-transformed to produce normal distributions for the comparison of averages and further analysis. The following tests and analysis were carried out. (1) The difference in zooplankton density between habitat types was tested using parametric one-way ANOVA and Tukey's multiple comparisons. Only the Archipelago Sea dataset ( $n = 39$ ) was used and the sites in the inner and middle archipelago were pooled in this test. (2) The difference in zooplankton density between archipelago zones was tested using parametric one-way ANOVA and Tukey's multiple comparisons. Only reed-covered study sites were included in the analysis and the Archipelago Sea ( $n = 33$ ) and Ekenäs archipelago ( $n = 8$ ) datasets were tested separately. (3) A principal component analysis (PCA) was employed to identify the basic structure of the zooplankton community from the Archipelago Sea dataset ( $n = 43$ ). The densities of the five zooplankton taxa were reduced to two non-correlated principal components, using the criterion of eigenvalues greater than one. This approach accounted for 68% of the variation in the variables. The principal component scores were further used to examine the differences among the various groups of sampling sites. (4) Logistic regression models were fitted to the data from the Archipelago Sea ( $n = 43$ ) in order to examine the effects of environmental factors (Secchi depth, salinity, wave exposure) and zooplankton prey density (sum of Copepoda and Cladocera ind  $l^{-1}$ ) on the occurrence of pike larvae. Models with various combinations of explanatory variables and interactions were constructed, but the final models only included statistically significant ( $P < 0.05$ ) explanatory variables. The goodness of fit of the models was evaluated by comparing Akaike's Information Criterion (AIC) values and classification power by comparing the observed and predicted responses (occurrence of pike larvae) and the sensitivity and specificity of the models. Here, a jack-knife approach was used to reduce the bias of classifying the same data from which the classification criterion was derived. (5) The correlations between the environmental variables and zooplankton densities were tested using non-parametric Spearman's Correlation Analysis. Only reed-covered study sites were included in the analysis. The Archipelago Sea ( $n = 43$ ) and Ekenäs archipelago ( $n = 8$ ) datasets were tested separately. (6) Temporal variation in the density of the preferred zooplankton prey groups was examined and presented graphically. All analyses were carried out using the SAS 9.1 software package (SAS Institute Inc., Cary, USA).

### 3. Results

#### 3.1. Environmental conditions

Strong increasing gradients in salinity and Secchi depth were detected from the inner to the outer archipelago, both in the Archipelago Sea and in the Ekenäs archipelago (Table 1). However, the range of salinity and Secchi depth values varied between the two study areas (Table 1). The Secchi depth range was wider in the Archipelago Sea (70–740 cm) compared to the Ekenäs archipelago (90–460 cm). According to the logger data, variation in the surface water temperature between the inner and the outer archipelago was more prominent in the Ekenäs archipelago, where inner areas were in average 3.3 °C warmer than outer areas, than in the Archipelago Sea, where inner areas were in average only 0.3 °C warmer than middle areas. The minimum temperatures of the surface water were 8–9 °C in the Archipelago Sea and 9–10 °C in the Ekenäs archipelago. In the inner Ekenäs archipelago, temperatures remained higher throughout the study period. However, during the sampling period, reed belt sites were found to be warmer and more turbid, the surface water temperature being on average 2.8 °C higher and the Secchi depth 1.5 m lower compared to other nearby shores, i.e. bladder wrack or non-vegetated sites (paired *T*-test,  $n = 16$ ,  $P < 0.001$ ). Wave exposure (fetch) was also on average 60% higher on the other shores than on the reed-covered shores (Table 1).

#### 3.2. Pike larvae

Larval pike were only observed on reed-covered shores, being found at 85% of the reed-covered sampling sites in the Archipelago Sea. Comparing the three archipelago zones, pike larvae were found at 100% of the reed-covered sites in the inner archipelago, 86% in the middle archipelago and 0% in the outer archipelago. No pike larvae were detected on bladder wrack shores or shores without vegetation. In the Ekenäs archipelago, where all sites were reed-covered, pike larvae were found at all of the four inner archipelago sites but only at one of the four outer archipelago sites. On average, pike larvae were more abundant in the inner Ekenäs archipelago (29 larvae per site) compared to inner Archipelago Sea (8 larvae per site), but sampling was conducted in consecutive years. The length distribution of larvae caught ( $n = 292$ ) was 11–28 mm. In the Archipelago Sea, zooplankton-feeding larval pike were found from 17 May to 12 June in 2006, and in the Ekenäs archipelago from 21 May to 6 June in 2007.

#### 3.3. Zooplankton prey

The zooplankton community ( $>90 \mu\text{m}$ ) at the study sites consisted of cladocerans, different stages of copepods (nauplii,

**Table 1**

Archipelago Sea	Reed belt shores			Other shores	
	Inner ( $n = 15$ ) Mean (min-max)	Middle ( $n = 14$ ) Mean (min-max)	Outer ( $n = 4$ ) Mean (min-max)	Inner ( $n = 5$ ) Mean (min-max)	Middle ( $n = 5$ ) Mean (min-max)
Salinity	5.1 (4.0-5.8)	6.1 (5.9-6.2)	6.1 (6.0-6.3)	5.8 (5.7-5.9)	6.0 (5.9-6.1)
Secchi depth (cm)	140.3 (70.0-245.0)	287.1 (120.0-710.0)	715.0 (650.0-740.0)	248.0 (160.0-450.0)	478.0 (380.0-670.0)
Fetch ( $\text{m}^2 \text{s}^{-1}$ )	6031.8 (1455.1-11739.0)	3410.3 (1414.0-7361.0)	4232.8 (2215.0-8792.0)	11564.0 (4775.5-17518.1)	11471.0 (5987.0-20589.0)
Ekenäs archipelago	Reed belt shores				
	Inner ( $n = 4$ ) Mean (min-max)		Outer ( $n = 4$ ) Mean (min-max)		
Salinity	2.3 (1.8-3.1)		5.9 (5.8-6.0)		
Secchi depth (cm)	130.0 (90.0-150.0)		340.0 (200.0-460.0)		
Fetch ( $\text{m}^2 \text{s}^{-1}$ )	4261.0 (3651.0-4578.0)		3544.5 (1756.0-5688.8)		

Table 2

	Archipelago Sea		Ekenäs archipelago
	Reed belt shores Mean (min-max)	Other shores Mean (min-max)	Reed belt shores Mean (min-max)
Cladocera	11.4 (0.9–56.0)	1.8 (0–4.7)	458.4 (0–2601.3)
Copepoda	58.5 (3.0–272.0)	7.6 (1.1–21.6)	258.1 (5.7–994.0)
Cyclopoida	54.3 (1.3–264.0)	2.7 (0.2–11.3)	254.6 (5.7–994.0)
Calanoida	3.0 (0–20.0)	3.3 (0.4–14.4)	3.1 (0–12.0)
Copepoda nauplii	68.9 (1.3–358.2)	31.7 (6.6–104.0)	135.5 (13.7–434.0)
Rotifera	211.9 (20.4–1274.7)	91.5 (20.7–226.4)	181.8 (21.7–780.0)
Total	350.6 (34.0–1761.8)	132.6 (37.8–354.7)	1033.6 (50.3–3225.3)

copepodites and adults) and rotifers (Table 2). Differences in the average densities of copepodites and adult cyclopoid copepods as well as cladocerans, the prey items preferred by pike, were significant among the three habitats studied (ANOVA,  $n = 39$ ,  $P < 0.001$ ), the averages being significantly higher on reed belt shores compared to bladder wrack shores or shores without vegetation (Tukey's,  $n = 39$ ,  $P < 0.001$ ) (Fig. 2). The proportion of calanoid copepods was higher on the bladder wrack (5 ind  $l^{-1}$ , 42% of copepods) and non-vegetated shores (2 ind  $l^{-1}$ , 57% of copepods) compared to the reed-covered shores (3 ind  $l^{-1}$ , 5% of copepods).

When only the reed-covered study sites were taken under examination, the differences in the average densities of copepodites and adult cyclopoid copepods were significant among the three archipelago zones in the Archipelago Sea (ANOVA,  $n = 33$ ,  $P < 0.01$ ), the averages being significantly higher in the inner archipelago reed belts compared to reed belts in the outer parts of the archipelago (Tukey's,  $n = 33$ ,  $P < 0.01$ ) (Fig. 3). Also in the Ekenäs archipelago, differences in the average densities of copepodites and adult cyclopoid copepods were significant between the inner and outer archipelago (ANOVA,  $n = 8$ ,  $P < 0.001$ ) (Fig. 3). Cyclopoids were the most abundant copepod taxa within the reed belts, and their densities were considerably higher both in the inner Archipelago Sea (75 ind  $l^{-1}$ , 94% of copepods) and the inner Ekenäs archipelago (492 ind  $l^{-1}$ , 99% of copepods) compared to the reed belts in the outer Archipelago Sea (11 ind  $l^{-1}$ , 65% of copepods) or in the outer Ekenäs archipelago (18 ind  $l^{-1}$ , 93% of copepods). In the Ekenäs archipelago, the differences in the average cladoceran densities were also significant between the two archipelago zones (ANOVA,  $n = 8$ ,  $P < 0.001$ ), being significantly higher in the inner archipelago reed belts compared to the reed belts of the outer archipelago (Fig. 3). Here, the cladoceran species *Chydorus* sp. dominated the cladoceran community and its average density was higher in the inner reed belts (910 ind  $l^{-1}$ , 99% of cladocerans) compared to the outer reed belts (<2 ind  $l^{-1}$ , 99% of cladocerans). *Chydorus* sp. was

also the most abundant cladoceran species in the Archipelago Sea reed belts (8 ind  $l^{-1}$ , 80% of cladocerans). Overall, cyclopoid density was 7 times higher and cladoceran density almost 100 times higher in the inner parts of the Ekenäs archipelago compared to densities of the same taxa in the inner parts of the Archipelago Sea in the previous year (Fig. 3).

#### 3.4. Interactions between zooplankton, environmental conditions and occurrence of pike larvae

The first principal component given by the PCA had high positive loadings for the abundance of copepod nauplii, cyclopoid copepods and cladocerans (Table 3), the latter two being important food items for larval pike (e.g. Salonen et al., 2009). Loadings were also positive for the abundance of rotifers and calanoid copepods. Therefore, the first principal component appeared to indicate the general abundance of zooplankton. The second principal component had negative loadings for the abundance of cyclopoid copepods and cladocerans, both taxa being typical for sheltered bay areas on the south-western coast of Finland (Koski et al., 1999), but a high positive loading for the abundance of calanoid copepods, which is a taxa common in exposed archipelago areas and in the open sea (Koski et al., 1999). Therefore, higher loadings on the second principal component were positively connected to exposed conditions. A co-ordinate figure based on these two principal components revealed that the littoral shores without reed were fairly well separated from the reed-covered shores, the former showing on average lower scores on the first principal component and higher scores on the second principal component, as compared to the reed belt shores (Fig. 4). Most of the reed-covered sites without pike larvae were located in the co-ordinate close to the sites without reed belt, except for one observation (Fig. 4). Respectively, the combined densities of cyclopoid copepods and cladocerans were low both at the reed-covered sites without pike larvae (median 8.7 ind  $l^{-1}$ , range 3.0–40.0 ind  $l^{-1}$ ) and at the sites without reed nor larvae (median 4.3 ind  $l^{-1}$ , range 0.7–11.3 ind  $l^{-1}$ ) compared to reed-covered sites where pike larvae were found (median 62.4 ind  $l^{-1}$ , range 6.2–2980.0 ind  $l^{-1}$ ). The Secchi depth, indicating exposition to the pelagic environment, was also usually higher at reed belt sites without pike larvae compared to reed belt sites where pike larvae were found (Fig. 5).

In the logistic regression models, the only site-specific variables significantly ( $P < 0.05$ ) explaining the occurrence of pike larvae were the density of suitable zooplankton prey (copepods and cladocerans combined) and Secchi depth. When the zooplankton prey density was the only explaining variable, the formula of logistic regression model was:

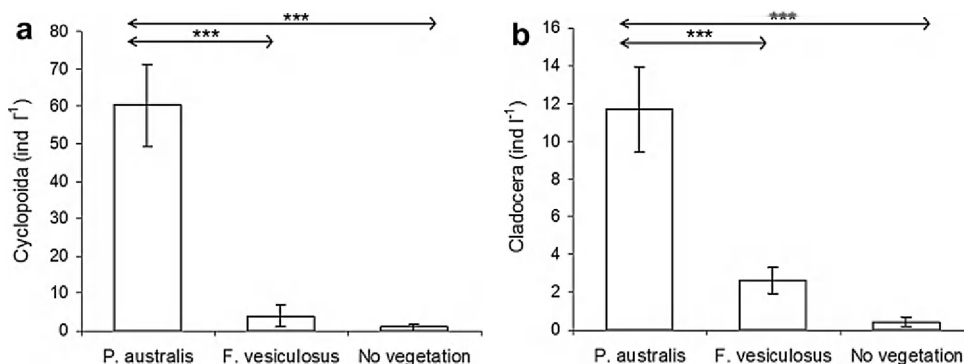
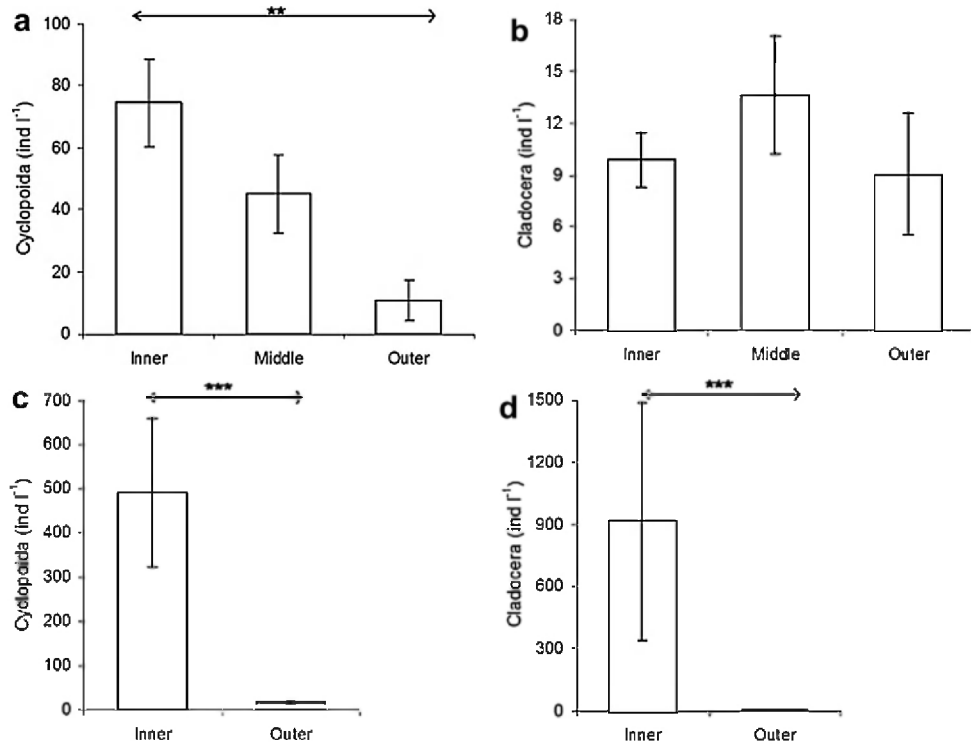


Fig. 2. Average ( $\pm$ S.E.) prey density for (a) cyclopoid copepods (Cyclopoida) and (b) cladocerans (Cladocera) in reed (*Phragmites australis*), bladder wrack (*Fucus vesiculosus*) and non-vegetated habitats. Significant differences are indicated by asterisks (\*\*\*)  $P < 0.001$ . Note the different scales on the y-axis.



**Fig. 3.** Average ( $\pm$ S.E.) zooplankton density for (a) cyclopoid copepods (Cyclopoida) and (b) cladocerans (Cladocera) in reed belts of the inner, middle and outer archipelago in the Archipelago Sea, and for (c) cyclopoid copepods (Cyclopoida) and (d) cladocerans (Cladocera) in the inner and outer archipelago in the Ekenäs area. Significant differences are indicated by asterisks (\*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ). Note the different scales on the y-axis.

$$\pi(x) = 1 / (1 + e^{-(\alpha + \beta x)})$$

where  $\pi(x)$  is the probability of occurrence of pike larvae at a certain value of the explanatory variable ( $x$ ), and  $\alpha$  and  $\beta$  are estimated model parameters. The estimated model parameters ( $\pm$ SE) were  $\alpha = -5.80 \pm 1.85$  and  $\beta = 2.04 \pm 0.61$  and the model predicted correctly 79.1% of the observations ( $n = 43$ , AIC = 34.2, sensitivity 81.5%, specificity 75.0%), and higher abundance of zooplankton prey meant higher probability for the occurrence of the pike larvae. Similarly, the model based on Secchi depth ( $\alpha = 3.89 \pm 1.10$ ,  $\beta = -0.01 \pm 0.004$ ) predicted 81.4% of the observations correctly ( $n = 43$ , AIC = 37.7, sensitivity 88.9%, specificity 68.8%), here high Secchi depth indicating low probability for the occurrence of pike larvae. The combined model with both of the variables as explanatory variables was:

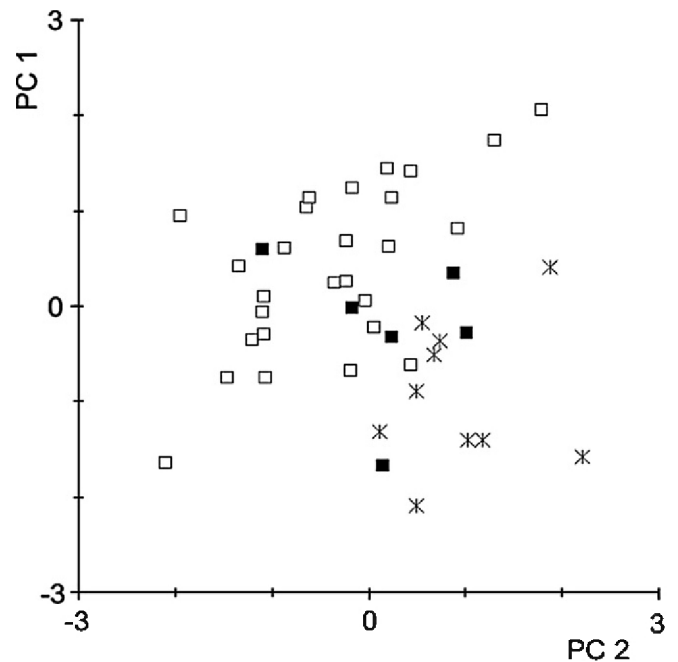
$$\pi(x_{1,2}) = 1 / (1 + e^{-(\alpha + \beta x_1 + \gamma x_2)})$$

where, the model parameters ( $\pm$ SE) were  $\alpha = -3.48 \pm 2.72$ ,  $\beta = -0.01 \pm 0.01$ ,  $\gamma = 2.49 \pm 1.11$ , with  $x_1$  and  $x_2$  being zooplankton prey density and Secchi depth, respectively. The combined model predicted 86.0% of the observations ( $n = 43$ ) correctly (sensitivity 88.9%, specificity 81.3%). The goodness of fit of the combined model

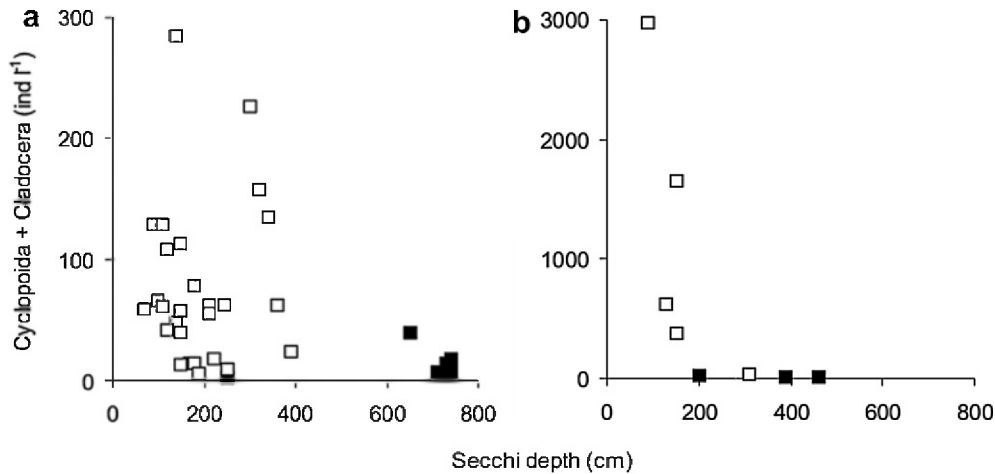
**Table 3**  
Loadings of the principal components given by the PCA.

	PC 1	PC 2
Cladocera	0.6919	-0.4669
Cyclopoida	0.8055	-0.3678
Calanoida	0.3286	0.7519
Copepoda nauplii	0.8471	0.1695
Rotifera	0.5865	0.3910

was best (AIC = 23.8) of the three models, even though combining the two explanatory variables into the same model improved the classificatory power of the model only moderately, possibly due to the moderate correlation between these two variables in the



**Fig. 4.** Comparison of the sampling sites based on the principal component analysis. The mean scores of principal components are shown for reed belt sites with pike larvae (open squares), reed belt sites without larvae (solid squares) and other shores without larvae (asterisks).

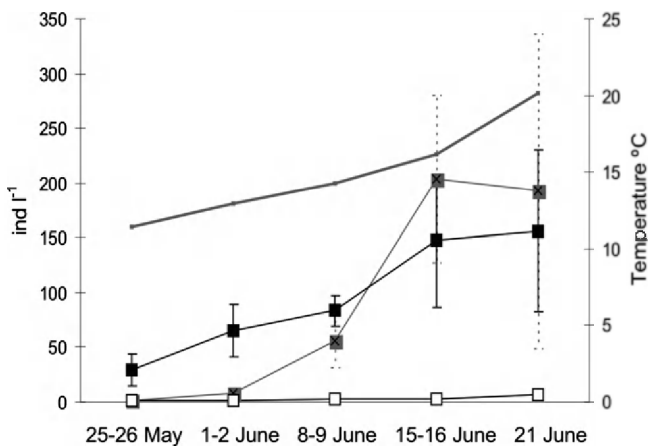


**Fig. 5.** The combined density of copepod (Copepoda) and cladoceran (Cladocera) prey plotted against Secchi depth at reed-covered study sites in (a) the Archipelago Sea (open squares, larval pike present; solid squares, larvae absent) and (b) the Ekenäs archipelago (open squares, larval pike present; solid squares, larvae absent). Note the different scales on the y-axis.

dataset from the Archipelago Sea ( $r = -0.51$ ,  $P = 0.001$ ,  $n = 43$ ). There, the prey density was low at sites where the Secchi depth was high, but at sites with a low Secchi depth, prey density showed large variation (Fig. 5). However, in the data from Ekenäs the correlation between prey density and Secchi depth was higher ( $r = -0.93$ ,  $P < 0.001$ ,  $n = 8$ ).

### 3.5. Temporal variation in the zooplankton community

Cyclopoid copepods were generally the only substantially abundant prey taxa present during the time when zooplankton-feeding larval pike were found in the Archipelago Sea reed belts, although cladocerans increased in abundance during the last few days that pike larvae were detected (Fig. 6). The relative proportion of cyclopoid copepods in the total zooplankton community of reed belt shores varied from 15 to 30%. Calanoid copepods accounted for less than 2% of zooplankton during the entire study period. Cladocerans increased in abundance later in the summer (Fig. 6), their proportion of the total zooplankton community ( $>90 \mu\text{m}$ ) increasing from less than 1% in May to 22% in June.



**Fig. 6.** Average ( $\pm$ S.E.) cyclopoid copepod (Cyclopoida, solid line and squares), calanoid copepod (Calanoida, solid line and open squares) and cladoceran (Cladocera, grey line and squares) density during the 5-week sampling period between 25 May and 21 June 2006 in the Archipelago Sea. Temperature development is marked with a grey line. Zooplankton-feeding larval pike were present from 17 May to 12 June.

## 4. Discussion

According to the results, reed belt habitats form hot spots for zooplankton during spring in the coastal area of the northern Baltic Sea. This suggests that they are important habitats for larval fish, as they are also the prevailing habitat type in several coastal areas. Surface water temperatures were higher and both cyclopoid copepods and cladocerans, known to be the most important prey for larval pike (Desvillettes et al., 1994; Lehtiniemi et al., 2007; Salonen et al., 2009), were almost 10 times more abundant in reed belts than in other nearby littoral habitats during the time when zooplankton-feeding pike larvae were detected. Earlier field observations (Jeppesen et al., 1994) and experimental studies (Schriver et al., 1995) have also demonstrated that submerged macrophytes enhance zooplankton density, and cladocerans and cyclopoid copepods in particular have been shown to be more abundant in the vegetated littoral zone than in the open sea (Jeppesen et al., 1998; Geraldes and Boavida, 2004; Telesh, 2004). In this study, the average meso-zooplankton density in the inner archipelago reed belts was even 20–280 times higher than the density of 5–20  $\text{ind l}^{-1}$  reported from the pelagic waters of the northern Baltic Sea (Viitasalo, 1992).

However, zooplankton prey availability varied between reed belt shores in various archipelago zones. The results of this study demonstrate that prey density was highest in the inner archipelago reed belts. Earlier studies from the northern Baltic Sea pelagial have also shown cyclopoids and cladocerans to be generally more abundant in the less marine inner bay area than in the open sea (Vuorinen et al., 1998; Koski et al., 1999; Telesh, 2004). In the outermost archipelago reed belts, on the other hand, the zooplankton density was generally low and the zooplankton community resembled the communities of non-vegetated shores and bladder wrack shores in the inner and middle archipelago. The zooplankton communities in the outer archipelago reed belts were also more similar to that of pelagic waters, which according to Viitasalo et al. (1995) lack freshwater zooplankton, such as some of the larger copepod species and most of the cladocerans.

The zooplankton prey community within reed belt shores also changed over time. In general, the cyclopoid copepods were the most abundant prey taxa present in reed belts during the few weeks when zooplankton-feeding larval pike were observed. Cladocerans were also abundant, especially in the inner Ekenäs archipelago and later in the season in the Archipelago Sea. However, in the Archipelago Sea, during the critical time for larval pike, they were fewer in number

and absent from the outer archipelago, which matches their known low tolerance of salinity (Jeppesen et al., 1994; Vuorinen et al., 1998; Koski et al., 1999). Cladocerans benefit from the effects of warm and eutrophicated waters (Heerkloss and Schnese, 1999), which are typical later in the summer in the coastal area. Therefore, cladocerans increased in abundance after the zooplankton-feeding stage and probably did not considerably contribute to the diet of larval pike, at least in the Archipelago Sea.

Pike larvae were only found in the reed belt habitats in the inner and middle archipelago in this study. In addition to the higher prey availability, environmental conditions for pike larvae were generally also more favourable on reed belt shores, since the average temperature was higher compared to the other studied habitats. Both Secchi depth and the density of suitable zooplankton prey explained rather well the distribution of pike larvae. The zooplankton density was low in all reed-covered shores in the outer archipelago lacking pike larvae, but at similar low zooplankton densities larvae were still found in the inner and middle archipelago, indicating that the low prey abundance was not the only factor limiting the distribution of pike larvae. Thus, our results did not give any new support to the hypothesis that the lack of zooplankton prey would be the exclusionary reason for the widespread pike recruitment failure in the Swedish coast of the Baltic proper (Nilsson et al., 2004a). In our study area, the outer archipelago reed belts were also more vulnerable to the harsh influence of the pelagic zone and less vulnerable to the turbid runoff waters from land, compared to the sheltered inner archipelago reed belts. As an indication of this, a high Secchi depth was shown to increase the probability of a reed belt habitat lacking pike larvae. Even so water turbidity has only indirect effects on the occurrence of pike larvae. However, in the outer archipelago reed belts, also other factors such as a low number of spawning fish or water level fluctuations during the spawning season, causing temporary drying out of suitable spawning and larval habitats in these usually narrow reed belts, could also contribute to the poor recruitment of pike. Temperature or salinity turned out not to be the limiting factors in the outer reed belts, since both remained within the optimal range, temperature between 9 and 15 °C (Hassler, 1982) and salinity <7 (Lindroth, 1946; Westin and Limburg, 2002), during the embryological stage in the entire study area.

Bladder wrack and non-vegetated shores were rather similar in having low prey densities and very different from the inner archipelago reed-covered shores. At these sites the proportion of cyclopoid copepods was lower and the proportion of calanoid copepods, which are fast-swimmers and more difficult for newly hatched pike larvae to catch (Hwang and Turner, 1995; Nassal et al., 1998), was higher. Even though the presented data from the bladder wrack shores was rather scarce, the results of this study nevertheless quite explicitly disprove the persistent assumption of bladder wrack forming a reproduction habitat for pike in the coastal area of the northern Baltic Sea (e.g. Lehtonen, 1986). In experimental studies, larval pike have also been shown not to prefer a bladder wrack habitat (Engström-Öst et al., 2007). Littoral areas covered by dense growths of bladder wrack are mostly found on exposed rocky shores (Ruuskanen, 2000; Nilsson et al., 2004b). This habitat type is perhaps even more exposed to waves and the effects of the open sea than the outer archipelago reed belts and cannot therefore maintain optimal feeding and environmental conditions for zooplankton prey or, further, for larval pike survival.

Both copepods and cladocerans reached 10–100 times higher densities in the inner Ekenäs archipelago compared to similar inner archipelago reed belts in the Archipelago Sea. Respectively, larval pike were abundant at the sampling sites in the inner Ekenäs archipelago, and water temperature was also comparatively high there. This suggests that the inner parts of the Ekenäs archipelago formed, at least in 2007, highly productive key reproduction areas

for pike and perhaps for many other spring-spawning fish species on the south-western coast of Finland. The results by Härmä et al. (2008) support this statement, since they have shown the reed-covered shores in this area to form regionally important reproduction area for roach (*Rutilus rutilus*).

As MacKenzie et al. (1994) have stated, the dynamics of feeding and survival of larval fish can, however, be complex and quite independent of simple measures such as food abundance and distribution. Overall, it has not unequivocally been demonstrated that the availability of food when larval fish begin to feed solely contributes to their survival and recruitment. Whilst this certainly plays an important role, other factors such as environmental conditions, predation and competition may interact and dominate the dynamics of larval survival and recruitment (Leggett and DeBlois, 1994). This could also be seen in the present study; the overall distribution of the coastal larval areas of pike could not be explained by a single factor. Sub-optimal feeding conditions certainly contribute to the poor survival and recruitment of larval pike in the outer parts of the archipelago area, but other factors associated with a high Secchi depth also appeared to influence the occurrence of larval pike. Abiotic non-direct predictors, such as Secchi depth and salinity, together with reed belt data have been used in modelling the distribution of coastal larval areas of pike (Lappalainen et al., 2008; Sundblad et al., 2009). According to our results, Secchi depth could be a useful abiotic predictor in this type of modelling as it (1) correlates with cyclopoid density in reed belts and (2) indicates the influence of the open sea and, furthermore, is rather easy and cost-effective to collect by remote sensing methods.

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