

Coastal reed belts as fish reproduction habitats

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Received 2 Dec. 2009, accepted 9 May 2010 (Editor in charge of this article: Johanna Mattila)

Kallasvuo, M., Lappalainen, A. & Urho, L. 2011: Coastal reed belts as fish reproduction habitats. *Boreal Env. Res.* 16: 1–14.

In this study, we investigated the temporal and spatial occurrence of early life stages of fish within shores covered by reeds (*Phragmites australis*) in two coastal areas of the northern Baltic Sea in spring and summer. Fish larvae of ten species were found, with cyprinids being the most common family comprising five species. The first occurring early life stages of fish in early May were the larvae of burbot (*Lota lota*) and pike (*Esox lucius*), which mainly utilized the previous year's old and flattened reeds, whereas larvae hatching later in June, such as some cyprinids, utilized the new reed growth. The reed belts in the inner bay areas with a low salinity, high water temperature and dense vegetation were especially productive fish reproduction habitats, since 74% of all captured larvae were found there. Therefore, according to the results of this study, reed belts particularly in the inner bay areas can be described as regionally significant key fish reproduction habitats in the northern Baltic Sea.

Introduction

The majority of the fish species occurring in the northern Baltic Sea spawn in spring or early summer and use shallow archipelago areas for reproduction. In these large archipelago areas, reed belts formed by *Phragmites australis* are a dominant feature on littoral shores (Pitkänen *et al.* 2007). Spring-spawning fish species usually begin spawning in late April or early May after ice breakup. During this time, sheltered, soft-bottomed littoral shores covered by the previous year's reeds essentially form the only available vegetated littoral habitat, since the breaking ice removes other perennial littoral vegetation and the growing season of annual plants and algae has not yet begun. The perennial reeds extend from the littoral zone to a depth of usually 1.5 m, and new growth arises annually (Roosaluste

2007). The reed belt zone can be divided into two sub-habitats: (1) the previous year's reeds in the shallow part of the belt, which have often been cut down and flattened by winter ice and waves, and (2) the new emergent reed growth, which begins to appear in May, encompasses the old flattened reeds and expands the reed belt horizontally to deeper littoral areas as spring advances.

Reproduction is critical for fish production (Cushing 1990), and the quality of reproduction habitats is therefore essential. A good reproduction habitat maintains appropriate environmental conditions and also contains suitable prey organisms and a sufficiently low density of competitors and predators for the eggs and larvae to survive and successfully recruit to juvenile and adult populations (Leggett and DeBlois 1994, Urho 1996). Certain reproduction habitats can

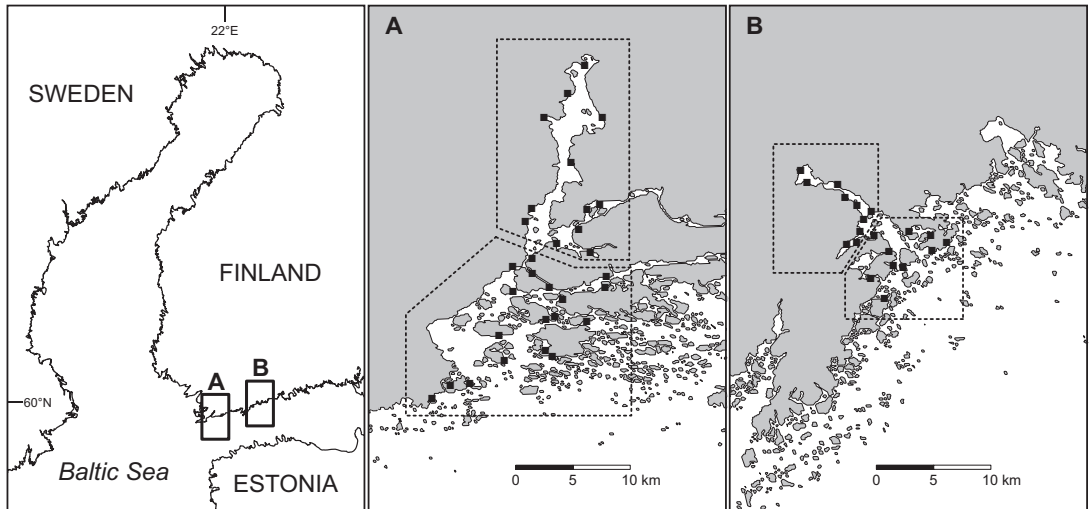


Fig. 1. Location of the study areas (A) Pohja Bay and (B) Espoo Bay, and the sampling sites. The dashed boxes in A and B indicate the inner bay areas (top) and the outer archipelago areas (bottom).

offer suitable conditions for several fish species, which may lead to partitioning of the available resources (Schoener 1974). Inter-specific resource partitioning can be temporal (Floyd *et al.* 1984, Lawler and Morin 1993, Alanärä *et al.* 2001) or spatial (Ross 1986). It often also leads to food resource partitioning (Olson *et al.* 1988), and it is usually greatest among the earlier life stages of fish (Ross 1986 and references therein).

It has been suggested that coastal reed belts could form reproduction habitats for several freshwater fish species in the northern Baltic Sea (Kallasvuo *et al.* 2009). Species such as pike (*Esox lucius*), roach (*Rutilus rutilus*) and burbot (*Lota lota*) have been shown to use reed belts as spawning or larval habitats (Hudd *et al.* 1983, Härmä *et al.* 2008, Lappalainen *et al.* 2008). In the coastal areas of the northern Baltic Sea, several other common fish species, such as perch (*Perca fluviatilis*), bream (*Abramis brama*), white bream (*Abramis bjoerkna*), rudd (*Scardinius erythrophthalmus*), bleak (*Alburnus alburnus*) and sticklebacks (*Gasterosteus aculeatus*, *Pungitius pungitius*), which are known to reproduce along vegetated littorals also occur (Lemetyinen and Mankki 1975, Urho *et al.* 1990, Mann 1996, Snickars *et al.* 2010). However, the dynamics of reed belts as fish reproduction habitats have so far not been studied, even though they form the prevailing vegetated habitat type

in spring along large coastal areas of the northern Baltic Sea.

In this study, we investigated the coastal reed belts and aimed at obtaining an overview of their importance as habitats for early life stages of fish during spring and summer. We examined both the temporal and spatial occurrence of early life stages of fish and the environmental conditions within reed belt shores in two separate coastal areas of the northern Baltic Sea. Two spatial scales were used when investigating the occurrence of early life stages: (1) between reed belts located in inner bays and those in outer archipelago areas and (2) within reed belts. The results of this study could be used to provide recommendations for monitoring fish reproduction within coastal reed belt shores.

Material and methods

Study area and selection of sampling sites

The study area consisted of two coastal bays, Pohja Bay (59.9°N, 23.4°E) and Espoo Bay (60.1°N, 24.7°E), both located on the southern coast of Finland in the northern Baltic Sea, and the outer archipelago areas facing them (Fig. 1). The archipelago zone in the study area is very

complex and extensive, and the large inner bays are sheltered by several small islands. No tides exist in the area. 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 Pohja Bay area, for example, the reed belt coverage of the shoreline was 9% in the outermost archipelago and increased to 58% in the inner bay area (Härmä *et al.* 2008).

Altogether, 50 littoral sampling sites, each consisting of a 100-m-long stretch of a shoreline, were selected. Of these, 30 sites were located in the Pohja Bay area and 20 sites in the Espoo Bay area, with the sites being distributed between inner bay and outer archipelago areas (Fig. 1). The sampling sites were selected randomly within the reed-covered shores in the two bay areas by using “Select random points” function in ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, California, USA) with minimum distance of 1.0 km between the sites. 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). In the Pohja Bay area, fish sampling and environmental data collection were carried out five times at two-week intervals between 7 May and 5 July 2007 and in the Espoo Bay area four times at two-week intervals between 15 May and 1 July 2008.

Collection of environmental data

Abiotic conditions (surface water temperature, salinity, turbidity, Secchi depth) were recorded at each sampling site during each visit. Temperature, salinity and turbidity were measured with portable temperature, conductivity and turbidity meters (Thermo Fisher Scientific Inc., Waltham, MA) within the reed belt from shallow water close to the shoreline, whereas the Secchi depth was measured with a white plate (\varnothing 25 cm) at the closest possible location, usually outside vegetation. A variety of reed-belt characteristics were measured at each site and during each visit: the total width of the reed belt and its width in water, the width of the flattened reed area in water and the width and height of the new reed

growth outside the flattened reed zone. The total percentage cover of the reed belt and of the flattened reeds in water were also measured, as well as the coverage of moss (*Fontinalis* sp.) and loose-lying bladder wrack (*Fucus vesiculosus*) that waves had brought into the reed belts.

Sampling of early life stages of fish

Fish eggs and larvae 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 fish eggs and 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 early life stages of fish at the sampling sites. Furthermore, with a fixed sampling effort and time, it is possible to compare the total number of visually-observed larvae per species at each sampling site per visit, but since these numbers are estimates, they should be treated as relative abundances. The early life stages of fish were sampled exclusively during daytime. Previous studies in shallow freshwater lakes have shown that fish larvae or juveniles may migrate horizontally between sheltered and open water zones during diel cycles. Our own systematic sampling with ichthyoplankton nets in the bays during both day and night revealed, however, that only perch and gobiid larvae occurred in open water areas outside the reed belts. Therefore, we believe that the daytime sampling was appropriate to catch the majority of fish larvae.

At each site and visit, 100 m of shoreline was checked with a sampling duration of half an hour per sampling site using two samplers. The larvae were searched for horizontally along the entire 100 m of the reed belt, starting from the shoreline at one end of the site and proceeding through the cut-down and flattened previous year's reeds in the inner shallow part of the reed belt until 100 m of shoreline had been checked and the other end of the site was reached. The search then continued back again, slowly proceeding through the newly-grown reeds in deeper water, and this pattern was continued until the outer

edge of the belt at a water depth of approximately 1.2 m was reached. The width of the surveyed area varied between approximately 10 m and 50 m. When eggs or larvae were found, they were counted on the white plate and the depth, surrounding vegetation and distance to the outer edge of the flattened reeds were recorded. The minimum, maximum and average water temperature and salinity were determined for each species at sites where they were found from the combined *in-situ* observations from Pohja and Espoo Bay areas. A few individuals were also always collected with a scoop in order to identify the species later in the laboratory. The fish eggs were incubated in the laboratory and identified to species after hatching. Three-spined and nine-spined sticklebacks were combined as “sticklebacks” and sand and common gobies (*Pomatoschistus minutus*, *P. microps*) as “gobies”.

Data analysis

The difference in the sum abundance of larvae per species per site between the inner bay areas and the outer archipelago was tested with the non-parametric Mann-Whitney *U*-test performed on pooled data from Pohja and Espoo Bays ($n = 50$). Since in the field surveys pike eggs and yolk-sac larvae often seemed to be found among moss that grew within the reed belts, we wanted to test this relationship statistically. Therefore, the connection between the occurrence of moss and loose unattached bladder wrack and the occurrence of pike early life stages (eggs, larvae) was tested with Fisher's exact tests ($n = 50$) performed on pooled data from Pohja and Espoo Bays ($n = 50$).

The data sets from the two study bays were gathered in separate years and, therefore, they were not pooled for the multivariate analyses and only the Pohja Bay data set ($n = 30$) gathered in 2007 was used, since the number of observations ($n = 20$) in the Espoo Bay data set was considered to be too low. Principal component analysis (PCA) was employed to identify the basic vegetation structure of the reed-covered sampling sites. Six variables describing the reed belt characteristics (total width, width of reed belt in water, width of flattened reeds in water,

width of new reeds) and other vegetation (coverage of loose unattached bladder wrack and of moss) used in the analysis were log-transformed average values from all visits to the sites. These six variables were reduced to two non-correlated principal components using the criterion of eigenvalues greater than one. This approach accounted for 80% of the variation in the variables. The principal component scores were further used to examine the differences among the various groups of sampling sites. In order to find general structures in the occurrence of fish larvae of various species at the sampling sites in the Pohja Bay area, a nonmetric multidimensional scaling (NMS) was employed. Two variables containing a high number of zero observations (occasionally occurring gobiid and perch larvae) were excluded from the analysis and bream and white-bream larvae were combined into “breams”, the final number of variables being thus seven. All larvae per species found at each sampling site during the five visits were summed, bringing the total number of observations to 30. The distances used in the NMS were based on Bray-Curtis dissimilarity matrix (see McCune and Grace 2002). The final stress value in the NMS was 3.9, which is considered excellent according to Clarke's rule (McCune and Grace 2002). To test whether the groups of sites indicated in NMS differed significantly ($p < 0.05$) with respect to their vegetation structure, the difference in the average scores of both principal components given by the PCA between the fish-defined groups was tested using a one-way ANOVA and Tukey's multiple comparisons ($n = 30$). Analyses were conducted using the SAS 9.1 software package (SAS Institute Inc., Cary, USA) and PC-ORD 5.0 (MjM Software Design, Oregon, USA).

Results

Environmental conditions in the study areas

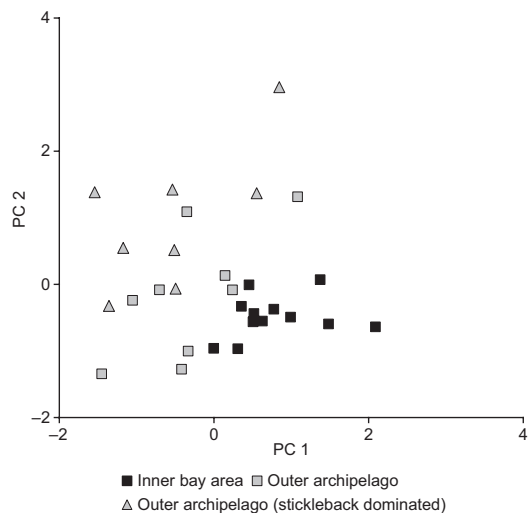
Within the reed belts in the inner bay areas the salinity was on average 2.0 ppm lower and turbidity 2.5 NTU higher as compared with those in the reed belts in the outer parts of the archipela-

Table 1. Average (\pm SE) environmental conditions measured *in situ* in the study areas.

	Pohja Bay		Espoo Bay	
	Inner bay (n = 11)	Outer parts (n = 19)	Inner bay (n = 10)	Outer parts (n = 10)
Temperature ($^{\circ}$ C)	17.1 (\pm 1.2)	16.2 (\pm 1.1)	15.7 (\pm 1.0)	15.3 (\pm 0.9)
Salinity (ppm)	2.2 (\pm 0.2)	5.0 (\pm 0.2)	3.8 (\pm 0.2)	4.7 (\pm 0.1)
Secchi depth (m)	1.6 (\pm 0.2)	2.3 (\pm 0.2)	1.1 (\pm 0.1)	2.0 (\pm 0.3)
Turbidity (NTU)	3.5 (\pm 0.5)	2.7 (\pm 0.3)	8.9 (\pm 1.3)	4.8 (\pm 0.9)
Total width of reed belt (m)	83.7 (\pm 15.2)	40.5 (\pm 6.1)	185.9 (\pm 32.5)	121.0 (\pm 28.3)
Width of reed belt in water (m)	41.3 (\pm 8.2)	21.3 (\pm 3.5)	53.5 (\pm 12.0)	42.1 (\pm 13.2)
Width of flattened reeds in water (m)	12.3 (\pm 2.9)	7.5 (\pm 2.1)	6.5 (\pm 3.0)	4.1 (\pm 1.5)
Width of new reeds outside flattened zone (m)	24.2 (\pm 7.3)	12.1 (\pm 2.8)	29.2 (\pm 10.7)	24.8 (\pm 9.6)
Flattened reed coverage in water (%)	75.7 (\pm 7.2)	60.0 (\pm 8.3)	66.5 (\pm 11.7)	55.1 (\pm 11.4)
Total reed belt coverage (%)	64.1 (\pm 10.1)	52.1 (\pm 7.7)	64.3 (\pm 7.2)	54.0 (\pm 6.0)
Bladder wrack coverage (%)	0	4.8 (\pm 1.7)	3.3 (\pm 5.6)	7.3 (\pm 3.5)
Moss coverage (%)	15.0 (\pm 5.0)	7.5 (\pm 2.4)	24.5 (\pm 5.8)	13.9 (\pm 3.7)

gos (Table 1). The average differences in surface water temperatures in shallow water within the reed belts were more moderate: the reed belts in Pohja Bay were on average only 0.9 $^{\circ}$ C and in Espoo Bay 0.4 $^{\circ}$ C warmer than the respective reed belts in the outer archipelago areas (Table 1).

In the inner bay areas, the average reed belt width in water was 47 m, of which flattened reeds covered 9 m, and the average total reed coverage was 64%. These inner reed belts were in general wider and denser, since the reed belt width in water was 15 m and the total reed coverage 11% higher than at the outer reed belt sites (Table 1). Moreover, moss coverage was on average 9% higher and the average bladder wrack coverage 4% lower at the inner archipelago sites as compared with those at the sites in outer parts of the archipelago. This was also shown by the PCA, where the first principal component had high positive loadings for the reed belt width variables and for moss coverage and low loadings for bladder wrack coverage (Table 2). Therefore, the first principal component appeared to indicate the level of shelter and the gentleness of the slope in the shore profile at the sampling sites. The second principal component had negative loadings for the reed belt width, but a high positive loading for bladder wrack coverage, indicating a positive association with exposed marine conditions. A PCA plot (Fig. 2) revealed that the wider, moss-rich reed-covered shores in the inner bay area were

**Fig. 2.** Comparison of the basic vegetation structure of the reed-covered sampling sites in the Pohja bay area in 2007 based on principal component analysis.**Table 2.** Loadings of the principal components in the Pohja Bay study area (n = 30) given by PCA.

	PC 1	PC 2
Total width of reed belt	0.911	-0.046
Width of reed belt in water	0.948	-0.131
Width of flattened reeds in water	0.766	0.369
Width of new reeds outside flattened reed zone	0.789	-0.376
Moss coverage	0.796	0.441
Bladder wrack coverage	-0.021	0.825

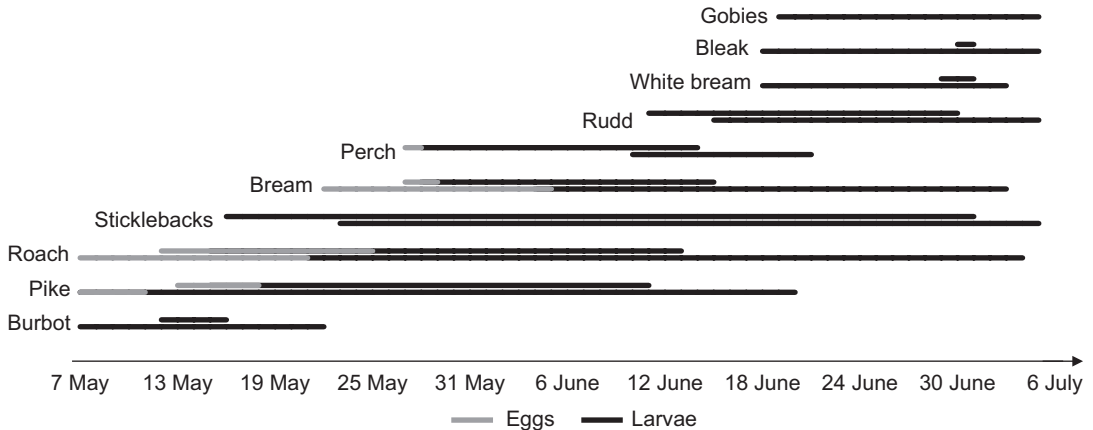


Fig. 3. Timing of the occurrence of eggs and larvae in the Pohja Bay in 2007 (lower lines), and in the Espoo Bay in 2008 (upper lines). Gobies were only found in 2007.

fairly well separated from the narrow, bladder-wrack-containing reed-covered shores located in the archipelago outside the bay areas, the former showing on average higher scores on the first principal component as compared with the reed belt shores in the outer archipelago.

The average total reed belt width of the studied sites was 96 m, of which the majority grew on land and only 38% of its average width was in water. However, the reed belt width and coverage changed considerably over time during the study period. In early May, the previous year's reeds formed almost the only cover, and the average reed belt width in water was only 10 m, of which cut down and flattened reeds covered 9 m. As spring advanced, the reed belt width in water increased on average by 10 m and the total reed coverage by 13% every two weeks as a consequence of new reed growth, which began in May. The height of the new reed growth also increased by an average of 44 cm every two weeks, and during the study period the average height of the new reed growth increased from 2 cm to 180 cm above the water surface.

Species composition and temporal occurrence of the early life stages of fish

Altogether, 56 739 fish larvae representing ten species (burbot, pike, roach, sticklebacks, bream, perch, rudd, white-bream, bleak and gobies) were recorded within the reed belts during this

study. Cyprinids were the most common family, with five species, and roach larvae formed the largest proportion (65%) of the total catch. Both yolk-sac larvae and larger larvae were found for most species and the ranges of larval sizes were as follows: burbot 4–10 mm, pike 8–40 mm, roach 5–27 mm, sticklebacks 5–19 mm, bream 5–21 mm, perch 6–11 mm, rudd 4–16 mm, white-bream 7–20 mm, bleak 5–13 mm and gobies 4–12 mm. Eggs of pike (455 eggs), roach (428), bream (57) and perch (3 egg strands) were also found along the reed-belt shores during this study.

Even though the species composition varied, larval fish communities along the reed belt shores occurred over several months from May to July and over a wide range of temperatures. Since water temperatures increased earlier in the inner bay areas, spawning and the appearance of fish larvae were detected a few days earlier there than in the outer reed belts. In general, the larvae appeared in the same species order in both study areas, but with a considerable temporal overlap of larvae of different species. With some exceptions, the overall order of appearance of the larvae was as follows: the first larvae observed in early May were burbot and pike (Fig. 3), and the minimum water temperature when these species were first found was 9 °C. In mid-May, roach (10 °C) and stickleback larvae (11.5 °C) and at the end of May bream (14 °C) and perch larvae (16 °C) began to appear. The larval species recorded in mid-June were rudd

(15.5 °C), white bream (17 °C) and bleak (16 °C) and finally, during the end of June, gobiid larvae (16 °C) were observed in the reed belt shores. The average minimum temperatures were similar in both Pohja and Espoo Bay areas in consecutive years, and the minimum temperatures for the occurrence of fish eggs were also similar to the minimum temperatures of the first larval occurrence. However, the larvae of individual species occurred over variable time periods. Stickleback larvae were recorded during the longest period: 6–7 weeks out of the 9-week study period in 2007 and the 7-week period in 2008 (Fig. 3). Larvae of both pike and roach were found during 4–6 weeks and larvae of the other cyprinids, perch and gobies only for shorter periods. Burbot larvae were present for the shortest time (1–2 weeks).

Spatial occurrence of the early life stages of fish

The spatial occurrence of the larvae of different species varied considerably, even though the early life stages of fish were found from all sampled reed-belt sites (Fig. 4). However, 74% of all the larvae caught were recorded from the sheltered reed belts in the inner bay area and only 26% from the reed belts in the archipelago area outside the bays (Fig. 5). In particular, cyprinid larvae of roach ($U = 4.65$, $p < 0.001$), bream ($U = 3.90$, $p < 0.001$), white bream ($U = 1.97$, $p < 0.05$) and rudd ($U = 2.14$, $p < 0.05$), as well as burbot ($U = 3.28$, $p < 0.001$) and pike larvae ($U = 2.18$, $p < 0.05$) were significantly more abundant in the inner bay areas as compared with the outer sampling sites (Mann-Whitney U -test, Fig. 6). Eggs and newly-hatched larvae of roach, bream and white bream were only found at sites with salinities < 4.1 ppm, even though some larger roach larvae were found in salinities between 4.0 ppm and 4.7 ppm (Fig. 6). No significant differences ($p > 0.05$) were observed in the abundance of bleak larvae and they were almost as abundant at the sites outside the bay areas as at those inside the bays, although only very few bleak larvae were detected at the outermost sampling sites. Only larvae of sticklebacks ($U = -3.04$, $p < 0.01$) and gobies ($U = -1.80$,

$p < 0.05$) were significantly more abundant in the outermost archipelago. White bream and perch larvae ($p > 0.05$) were found in low numbers and at few sites. Altogether, 80% (32/40) of the reed-covered sites where early life stages of pike were found also contained moss, and only 20% (2/10) of the sites were without moss (Table 3). This positive relationship between the availability of moss and the occurrence of pike larvae and eggs was significant (Fisher's exact test: $p < 0.001$). However, no significant relationships were found between the occurrence of the early life stages of pike and the availability of loose bladder wrack within the reed belts (Fisher's exact test: $p > 0.05$, Table 3).

According to the results of the NMS, the eight outermost sampling sites in the Pohja Bay area formed a distinct group separate from the other sampling sites (Fig. 7). At these eight sites, the larvae of sticklebacks were abundant (50–1800 ind./site) in contrast to all other sites, where they were absent or few in numbers (max. 1–6 ind./site). At these eight sites, in addition to the stickleback larvae, only few bleak larvae were found at five sites and pike larvae at two sites. These eight stickleback-dominated sites did not considerably differ from other outer archipelago sites in terms of basic vegetation structure (Fig. 2). There were no significant differences in the average PCA scores for the first principal component between the two outer archipelago groups, but instead the average scores for the second principal component were significantly higher (one-way ANOVA: $F_{2,27} = 8.78$, $p = 0.001$, Tukey's for PC2: $p < 0.05$) for the stickleback-dominated sites as compared with the other outer archipelago sites. The stickleback-dominated outer archipelago sites were also of high salinity (> 5.6 ppm) and low turbidity (< 2.4 NTU).

In the early spring, the first hatching or arriving larvae were usually found close to the previous year's old and flattened reeds. As spring advanced and the width of the reed belts increased, more horizontal habitat became available for the later hatching or arriving larvae, which were usually found among the newly-grown reeds. Thus, the first hatching pike larvae were found closest to the shoreline, and 83% of the newly-hatched pike larvae were caught within the flattened reeds (Fig. 8). Almost all

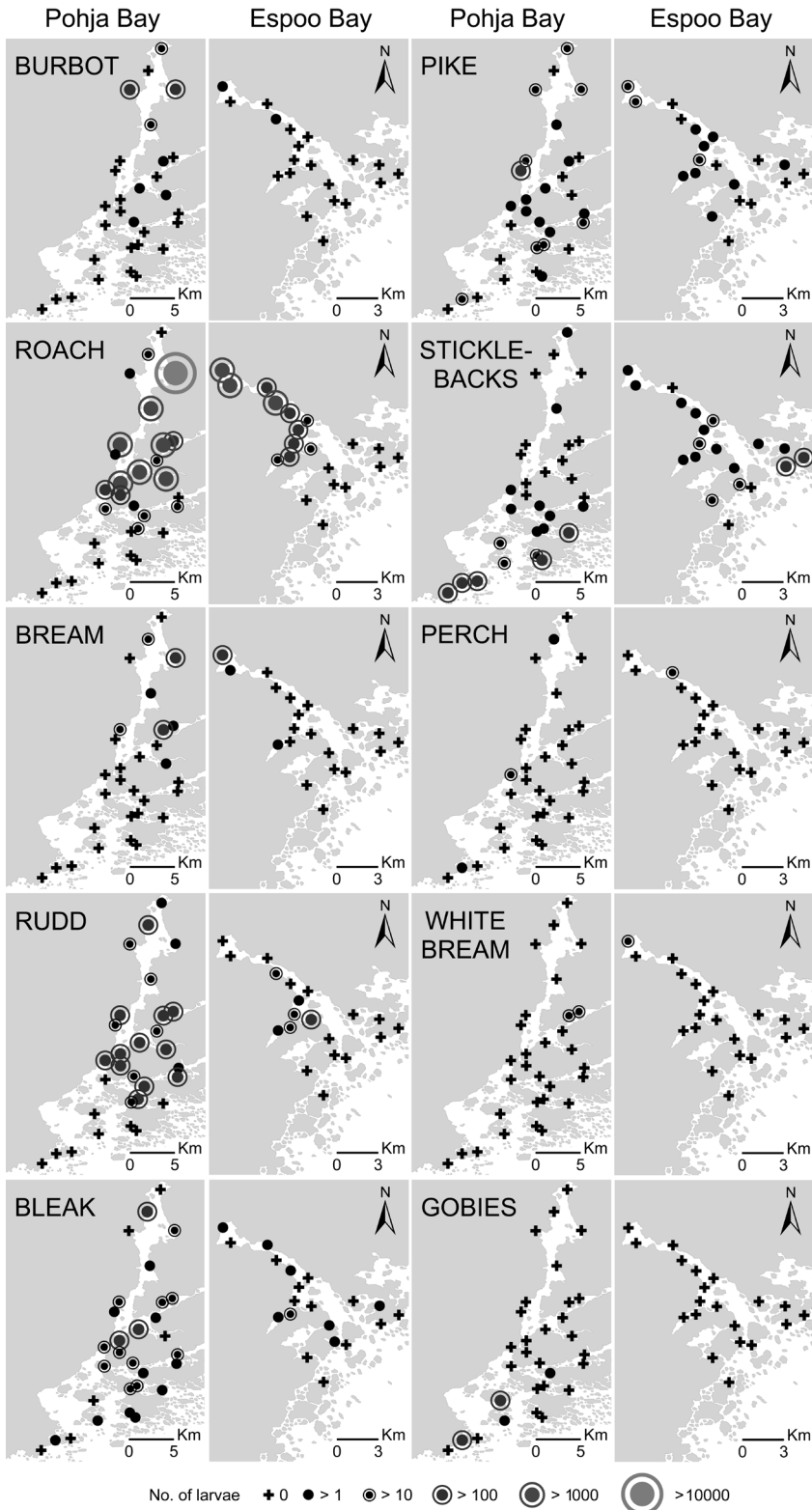


Fig. 4. Larval occurrence of fish species in the Pohja Bay area in 2007, and in Espoo Bay area in 2008.

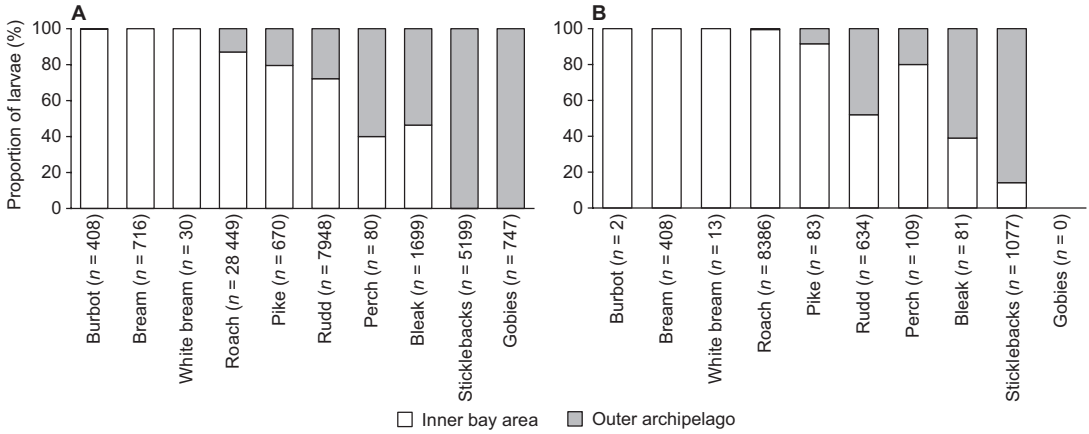


Fig. 5. Proportion of larvae found at sampling sites in the inner bay area and at the archipelago sites outside the bays in (A) the Pohja Bay area in 2007, and (B) the Espoo Bay area in 2008.

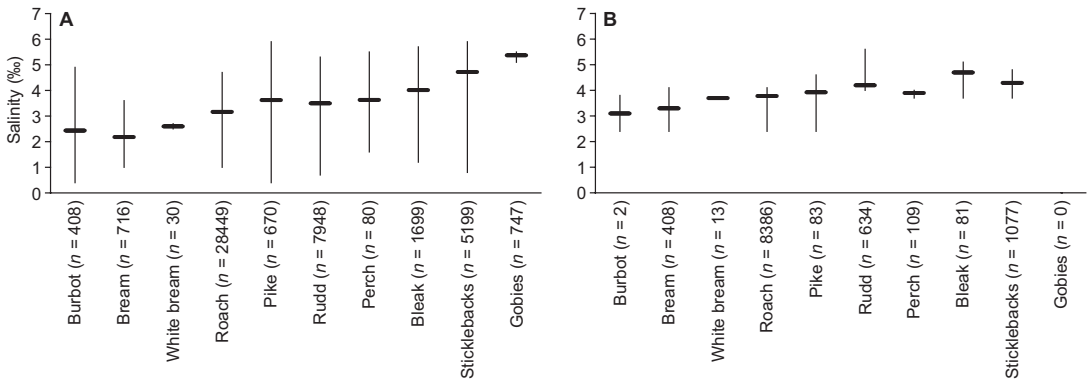


Fig. 6. Average and range (error bars) of salinity values measured *in situ* at sites occupied by fish larvae in (A) the Pohja Bay area in 2007, and (B) the Espoo Bay area in 2008.

burbot larvae were found at the outer edge of the flattened reeds and cyprinid larvae were found at the outer edge of the flattened reeds as well as in greater numbers among the newly-grown reeds outside flattened reed areas. The horizontal order from the shoreline to the open water for the newly-hatched cyprinids was roach (average

minimum distance to the edge of the flattened reeds 2 m), bream (4 m), white bream (5 m), rudd (6 m), and bleak (12 m). These larval distributions for the cyprinids were most distinct during the spawning period and the first two weeks after hatching, and as the larvae grew in size their distributions became wider and overlapped with

Table 3. Number and proportions of reed-covered sampling sites (n = 50) where moss or bladder wrack were present/absent and their division into sites where early life stages of pike were present/absent.

		Moss		Bladder wrack	
		Pres.	Abs.	Pres.	Abs.
Pike eggs and larvae	Pres.	32 (80%)	2 (20%)	19 (61%)	15 (79%)
	Abs.	8 (20%)	8 (80%)	12 (39%)	4 (21%)
	Tot.	40 (100%)	10 (100%)	31 (100%)	19 (100%)

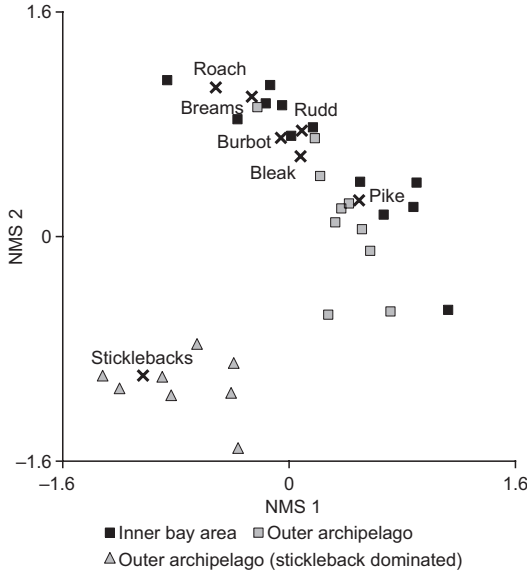


Fig. 7. A nonmetric multidimensional scaling ordination of the sampling sites in the Pohja Bay in 2007 based on cumulative abundances of the fish larvae. Crosses represent the location of the species in the two-dimensional space.

the distributions of other species. Sticklebacks had the widest distribution within the reed belts, since their average minimum distance from flattened reeds was low (3 m) and some larvae at some sites were found within the flattened reeds, but most of the larvae were found throughout the newly-grown reed zone. All perch and goby larvae were found in the outer parts of the newly-grown reed belt (11–14 m). Moreover, the average water depth where the larvae were found

varied between species and correlated weakly with the horizontal distance from the shoreline: pike, burbot and sticklebacks were on average found at a water depth of 30 cm, roach and bream at 45 cm, rudd and perch at 55 cm, and white bream, bleak and gobids at 65 cm.

Discussion

According to the results of this study, reed belt shores form important reproduction habitats for several fish species on the southern coast of Finland in the Baltic Sea. The early life stages of different fish species occurred at least partially asynchronously in the reed belts, and this yielded some benefits. Firstly, it reduced the risk of inter-specific competition and led to temporal resource partitioning (e.g. Floyd *et al.* 1984, Lawler and Morin 1993) within the reed belts. Secondly, it enabled the earlier-hatching predatory fish larvae to reach a larger size and prey upon the later-hatching larvae of other species, as has been shown in Scandinavian inland waters (Berg *et al.* 1997). The first larval species, burbot and pike, were already observed along the reed belt shores in early May, and they utilized the previous year’s cut-down and flattened reeds, which formed the only available vegetated and sheltered habitat at that time. It has earlier been shown that pike reproduce within coastal reed belts (Lappalainen *et al.* 2008) and not in surrounding shore habitat types (Kallasvuo *et al.* 2009, Sundblad *et al.* 2009). In this study, we

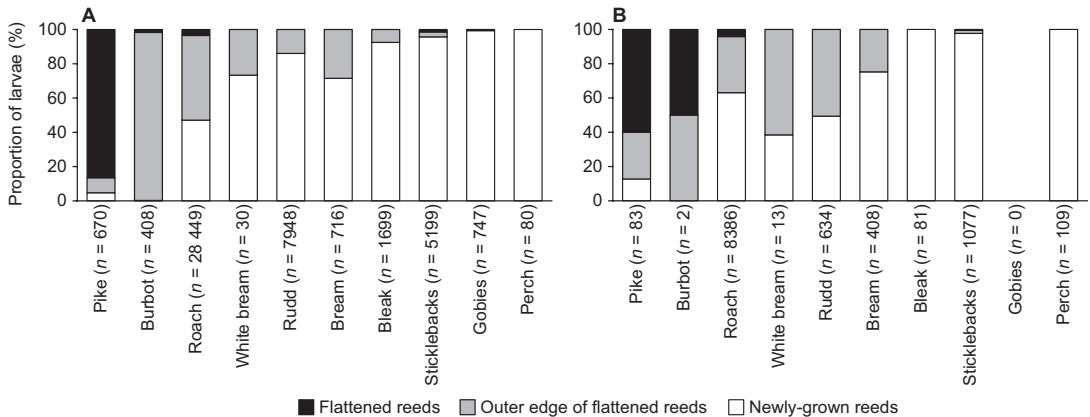


Fig. 8. Proportion of larvae found among flattened reeds, on the outer edge of the flattened reeds and among newly-grown reeds (A) in the Pohja Bay area 2007, and (B) in the Espoo Bay area in 2008.

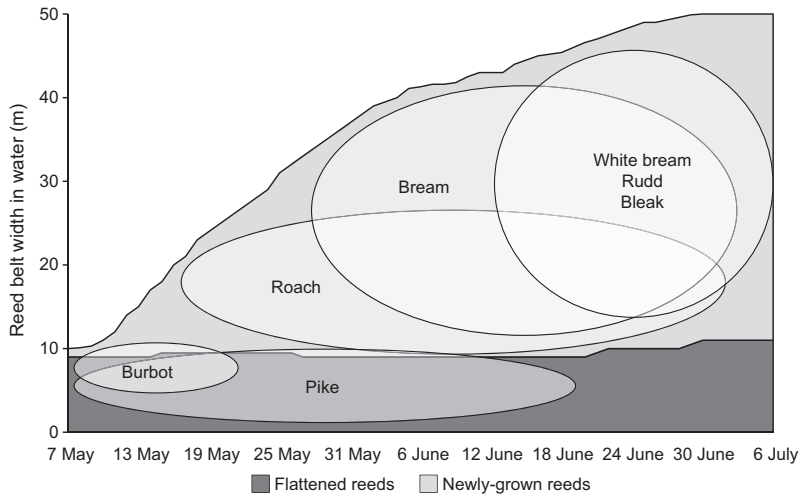


Fig. 9. The typical spatial and temporal distributions of burbot, pike and cyprinid larvae during the study period from 7 May to 5 July. Average increase in the horizontal reed belt width in water on the y-axis.

further showed that pike eggs and larvae were significantly more abundant within reed belt shores where moss was also found. Thus, moss could be used as an indicator when surveying suitable reed-covered spawning habitats for pike. Burbot spawn on non-vegetated bottoms where water currents are present (Sorokin 1971), but the results of this study support the finding of Hudd *et al.* (1983) that burbot larvae arrive at reed-covered shores very early in spring.

The new reed growth began to appear in mid-May at the latest, and during this time roach and stickleback larvae hatched and began to appear in the reed belts, where their larvae utilized both the flattened old reeds and the new reed growth. The occurrence of roach larvae was mainly limited to the inner bay areas, as earlier reported by Härmä *et al.* (2008). Previous experimental studies (Jäger *et al.* 1981, Klinkhardt and Winkler 1989) and field surveys (Härmä *et al.* 2008) have demonstrated that roach reproduction is strongly limited by salinity (< 4 ppm), and the results of this study support this finding. On the other hand, the larvae of sticklebacks, which are known to spawn on a variety of coastal shores (Lemmetynen and Mankki 1975), were dominating in the exposed reed belts in the outermost archipelago, where environmental conditions were marine and harsh and larvae of competing species were almost absent. The high water turbidity in the inner archipelago reed belts may also affect the visually based mating system of the sticklebacks (Engström-Öst and Candolin 2006).

By early June, the newly-grown part of the reed belt had on average increased to cover an area almost three times as wide as the flattened reed zone (Fig. 9), and during this time the overall abundance of larvae also peaked. Pike, stickleback and especially roach larvae were abundant and larvae of bream and perch also occurred within the reed belts. By the end of June, cyprinid species dominated the larval fish communities, since rudd, white bream and bleak larvae, which are known to prefer higher water temperatures (Mills 1991), appeared in the reed belts. At this stage, the larval community mainly exploited the newly-grown reeds, and the larvae were therefore found further from the edge of the flattened reeds as compared with the species occurring in the reed belts in May. Eggs and larvae of bream and white bream were only found in low salinities (bream < 4.1 ppm, white bream < 3.7 ppm), similarly to roach, but the spawning and larval areas of bream and white bream were more spatially limited and scattered around the inner bay areas than those of roach, which may be due to their preference for higher water temperatures (Shikhshabekov 1969). Larvae of rudd and bleak, on the other hand, were also found to occur on reed belt shores outside the inner bay areas, which indicates less limited reproductive requirements compared to other cyprinids, and they can certainly tolerate higher salinities than roach (rudd at least 5.6 ppm, bleak at least 5.7 ppm). Gobies do not spawn on vegetated shores (Nellbring 1993), but both gobies and

perch have pelagic larvae (Nellbring 1993, Urho 1996), which according to our results could also be found in rather low numbers in the outer parts of the newly-grown reed belt in June. In the Åland archipelago, Snickars *et al.* (2010) found several perch egg strands spawned on reeds. With the methods used here, however, surprisingly few egg strands were found, considering the high abundance of the species in coastal waters.

Only 30% of all captured larvae were found from the flattened reeds or the edge of this area in May, and larval abundance peaked in the newly-grown reed zone in June. However, the fish species found in this study occurred in a particular temporal order, which reflected interspecific differences in their breeding phenology. The larvae hatched or arrived in reed belts when water temperatures reached their reported species-specific physiological minima for successful embryological and larval development, e.g. 4 °C for burbot (Sorokin 1971), 9 °C for pike (Hassler 1982), 10 °C for roach and 14 °C for bream (Shikhshabekov 1969), and for this reason the newly-hatched roach and especially bream, rudd and white bream larvae appeared considerably later than burbot and pike in the studied habitats.

Burbot, pike and roach are widely distributed throughout northern Eurasia, but the northern distribution limit of roach is confined to 68°N and it is absent from northern Scandinavia (Wheeler 1978, Ojaveer *et al.* 2003). The northernmost distributions of bream (67°N), rudd (63°N) and white bream (66°N) are even more limited compared to roach (Wheeler 1978, Ojaveer *et al.* 2003). These cyprinid species require considerably higher temperatures during the first summer (Černý 1975, Gulidov and Popova 1979, Mills 1991) in order for the juveniles to reach a sufficient size and avoid over-winter mortality (Kirjasniemi and Valtonen 1997). Global climate change is expected to cause extensive changes in aquatic ecosystems (e.g. Kennedy 1990, Reist *et al.* 2006, The BACC Author Team 2008). If global climate warming causes earlier increases in spring temperatures and extends the autumn growing season, these late-spawning cyprinid species could potentially benefit considerably from the global climate change. Some signs of climate warming have already been reported

from the northern Baltic Sea region, including a shorter duration of the sea ice period and a trend towards earlier ice breakup (Jevrejeva *et al.* 2004, Seinä *et al.* 1996, 2001). Roach, bream and white bream stocks have also been reported to have considerably increased in the coastal areas of the northern Baltic Sea (Lappalainen *et al.* 2001, Ådjers *et al.* 2006), although eutrophication has been suggested as the main cause for this (Lappalainen *et al.* 2001).

The early life stages of ten fish species were recorded from littoral reed habitats in this study, and these comprised more than 30% of the fish species with spring or summer larval stages occurring in the studied coastal areas. In particular, freshwater fish species, which have a known preference for vegetated littoral areas during their early life stages (Mann 1996, Weaver *et al.* 1997), were shown to extensively exploit the reed habitats as spawning and larval areas. Migratory fish species and species with pelagic or non-phytophilous larval stages were almost completely lacking from the reed belts. Reed-covered shores have also been shown to maintain higher temperatures and prey densities than other surrounding littoral shore habitats in the coastal area of the northern Baltic Sea (Kallasvuo *et al.* 2009). However, strong spatial differences in environmental conditions and vegetation cover were detected between the inner and outer reed belt shores in our study area. Respectively, this had an influence on the occurrence of fish larvae, since some species had more limited environmental requirements than others. Thus, the reed belt shores in the inner bay areas with a low salinity, high water temperature and dense vegetation were emphasized as especially productive fish reproduction areas in this study. Previous studies conducted in the northern Baltic Sea (Lehtonen and Hudd 1990, Urho *et al.* 1990, Karås and Hudd 1993) and globally in other estuarine and coastal marine systems (Beck *et al.* 2001) also support this finding by emphasizing the importance of coastal bays and lagoons. The regional importance of the reed belt shores as fish reproduction habitats in the northern Baltic Sea arises from the scarcity of other suitable vegetated habitats, especially in early spring. According to studies conducted in inland waters, also some other shallow littoral habitats with

complex submerged vegetation form important habitats for juvenile fish as e.g. Kafemann *et al.* (1998) have shown. However, these alternative habitats are rare in the northern Baltic Sea. Therefore, temperate reed habitats, especially in inner bays areas, can be considered as regionally significant productive systems, comparable even to marshlands or mangrove swamps that have been recognized as key fish reproduction habitats in the subtropical and tropical latitudes (Weinstein 1979, Boesch and Turner 1984, Manson *et al.* 2005).

Acknowledgements: We thank V. Vuorenperä and J. Salmi for assistance in the field. Tvärminne Zoological Station provided us with accommodation and working facilities during part of the field studies. Dr. Z. Pekcan-Hekim provided valuable comments that substantially improved this paper.

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