Reproduction of pike (*Esox lucius*) in reed belt shores of the SW coast of Finland, Baltic Sea: a new survey approach

Antti Lappalainen[1]*, Meri Härmä[1,2], Sanna Kuningas[2] and Lauri Urho[1]

[1] *Finnish Game and Fisheries Research Institute, P.O. Box 2, FI-00791 Helsinki, Finland (*corresponding author's e-mail: antti.lappalainen@rktl.fi)*

[2] *Department of Biological and Environmental Sciences, Faculty of Biosciences, P.O. Box 56, FI-00014 University of Helsinki, Finland*

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The coastal reproduction areas of pike in the western Gulf of Finland were surveyed during spring 2004 and 2005 using a new approach. The locations of reed belts, the most important spawning substratum, were first identified using aerial photos, and 36 sites in three archipelago zones were selected for field sampling. The occurrence of pike larvae at each 100 m long site was observed with the aid of a white plate and a scoop. The majority of pike larvae were found in a habitat formed by the previous season's flattened reeds at a water depth of 20–80 cm. The comparison between archipelago zones revealed that reed belt shores in the innermost archipelago and bay area, substantially influenced by freshwater inputs in the spring, are the key reproduction areas of pike. Pike larvae were abundant in these areas, in contrast to the intermediate and outer archipelago, where pike larvae were found only sporadically. It is likely that productive habitats in the inner archipelago serve as a source and the outer archipelago as a sink, the latter maintaining pike population with the aid of juvenile immigrants from the main reproduction areas. The results also indicate that pike can not take full advantage of the slowly increasing spatial coverage of reed belts in the intermediate and outer archipelago of the western Gulf of Finland.

Introduction

Pike (*Esox lucius*) is a freshwater fish species with a distribution area covering almost the entire northern hemisphere (Raat 1988, Crossman 1996), including 45% of the total freshwater area of North America (Carlander *et al*. 1978). In the Baltic Sea, pike is also common in shallow coastal and archipelago areas up to a salinity of 10‰ (Raat 1988, Karås and Lehtonen 1993). Here it is also a target species for the coastal fishery, especially the recreational fishery, with annual catches of around 1400 tonnes at the Finnish coast (Anon. 2004). Locally, decreasing trends in pike catches have been reported in the Baltic Sea (Anttila 1973, Lehtonen 1986, Nilsson *et al*. 2007). Some of these observations have been linked to eutrophication (Anttila 1973). In the early 1990s, fishermen along the Swedish coast of the Baltic Proper reported decreasing catches of pike, and further studies revealed a widespread recruitment failure. Virtually no young-of-the-year pike were found in large coastal areas, but no unambiguous explanation was confirmed (Nilsson *et al*. 2004). Decreased catches have also been reported by

Lehtonen (1986) in the outer archipelago of the western Gulf of Finland.

In fresh waters, the overall reproductive biology and spawning habitat requirements of pike have been fairly well studied (e.g. Casselman and Lewis 1996, Bry 1996, Farrell and Werner 1996). In the northern areas, pike spawn in shallow water over vegetation shortly after ice-break in the spring, when these shallow waters have warmed to 8–12 °C (Casselman and Lewis 1996). Grasses and sedges are preferred, but other vegetation may be used. The shelter provided by vegetation is essential for the larvae and also the young pike. The larvae are 8–9 mm long after hatching and remain attached to vegetation during the first 4–6 days (Franklin and Smith 1963, Kennedy 1969). Thereafter, the larvae are 11–12 mm long, almost all of the yolk sac has been used, and they start to seek food (Franklin and Smith 1963). The larvae remain close to the spawning site for several weeks and gradually disperse to adjacent areas in the same habitat after they have reached a length of 20 mm (Raat 1988, Urho 1999).

Along the Baltic Sea coast, river mouths such as those in the Gulf of Bothnia are known to be important spawning and nursery areas for pike (Lehtonen and Hudd 1990, Urho *et al*. 1990). It has earlier been argued that a marine alga, the bladder wrack (*Fucus vesiculosus*), can serve as a spawning and nursery habitat for pike in the outer archipelago of the northern Baltic Sea, but this has never been documented. Pike can spawn over a range of macrophyte species. However, reed belts formed by *Phragmites australis* are a dominant feature in sheltered shores, bays and estuaries in wide regions of the northern Baltic Sea coast, and this common habitat serves as a major spawning and larval area for pike (Lehtonen 1986, Urho *et al*. 1990). The abundance and range of the reed belts increased along the southwestern coast of Finland from the beginning of the 1960s to the mid-1990s due to land uplift, decreased grazing of cattle, and especially in the outer areas due to general eutrophication of the Baltic Sea (Suominen 1998). These reed belts extend from supra-littoral zone to a depth of usually 1–1.5 m. The parts of the reeds above the substratum have an annual growth pattern. Winter ice and waves typically cut down and flatten the reeds in the outer parts of the belt into a horizontal position, after which they are piled up by waves closer to the shore. This shallow part of the reed belt forms a habitat where pike often spawn (Urho *et al*. 1990), mostly during May when the water temperature reaches 10 °C. However, the occupation of reed belts by pike larvae, such as in various archipelago zones, has never been systematically surveyed.

One reason for the scarcity of studies is that there have been no widely used field sampling methods for young pike in brackish waters. Electro-fishing with portable apparatus has been successfully used in fresh waters (e.g. Sutela *et al*. 2004) to catch one-summer-old pike in the late summer, but this method does not work effectively in brackish waters due to high water conductivity. One-summer-old pike have also been captured with small underwater detonations (Sandström and Karås 2002, Sandström *et al*. 2005), which are not effective for fish less than 2 cm long, and with a beach seine, which cannot be used efficiently among dense vegetation.

In this study we therefore developed a new and cost-effective approach to survey pike reproduction areas in the coastal environment. As a first step, the locations of coastal reed belts were mapped using aerial photography. Selected shores with reed belts were then sampled using a white plate and scoop to locate pike larvae that were a few weeks old. Our main hypotheses was that some shores with reed belts are more valuable habitats and spawning areas for pike than others, and that the suitability of a reed belt shore for pike reproduction can be predicted from variables such as the width of the reed belt and the calculated wave exposure index that can be derived from aerial photos or nautical maps without actually visiting the sites. Finally, we aimed to investigate the effects of environmental factors on pike reproduction in the northern Baltic Sea.
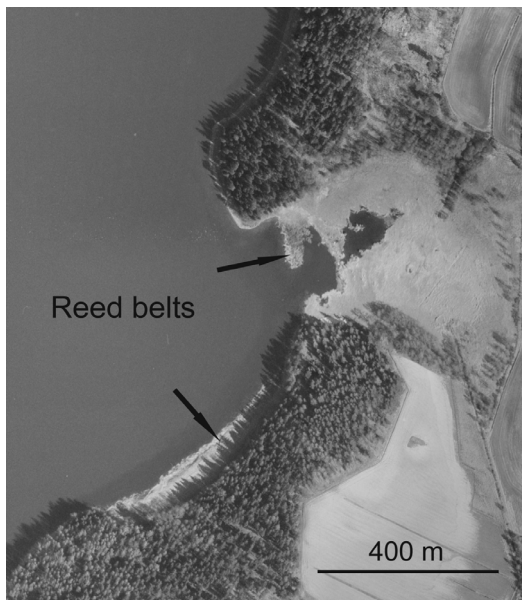
Materials and methods

Study area

The study area was located in the Tammisaari region in the northwestern part of the Gulf of Finland (Fig. 1). The shoreline of the northern
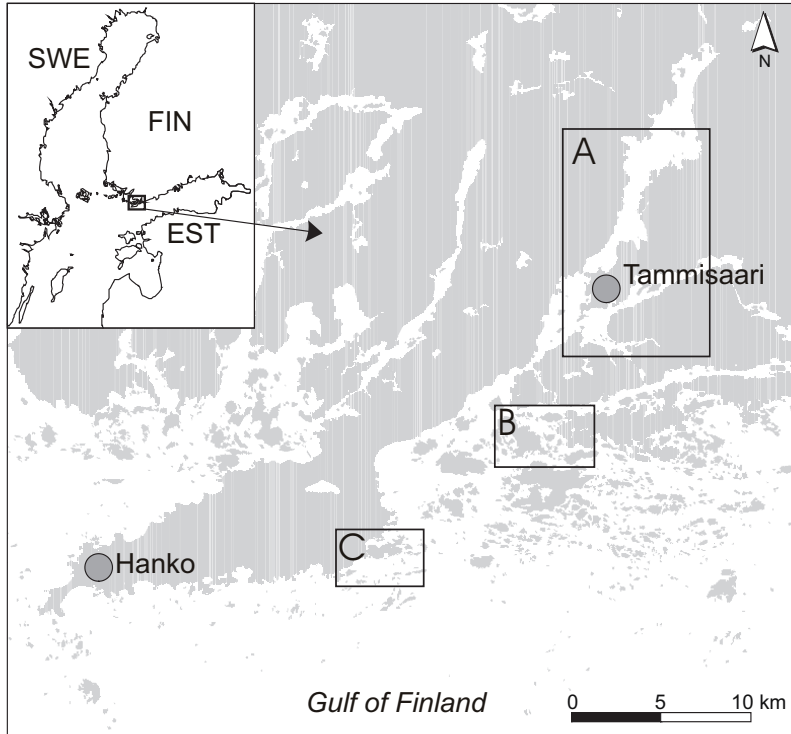
**Fig. 1**. Location of the study area, and the three sub-areas (A–C).

Fig. 2. A sample aerial photograph showing reed belts. ©National Land Survey of Finland 238/MYY/07.

coast of the gulf, as well as the Archipelago Sea west of the Gulf of Finland, is very irregular, having numerous deeply-extended bay areas and a unique archipelago zone off the shoreline. Abiotic conditions vary considerably in the gradient between the innermost bay areas and the open sea, with salinity in the latter being around 5‰–7‰. In the outer archipelago the period of winter ice cover usually begins in January and the ice breaks up in April. In the innermost areas, salinities are much lower and spring water temperatures are higher than in the open sea. The Mustionjoki, with a mean runoff of 19 m^3 s^{-1}, is the only larger river in the study area, running into the northern end of the innermost bay area.

The study area was further divided into three sub-areas representing the three archipelago zones: (A) the innermost bay area, (B) the intermediate archipelago and (C) the outer archipelago (Fig. 1). The total length of the shoreline was 58.8 km in the largest sub-area A, 55.8 km in sub-area B and 30.0 km in sub-area C. The location of shores with reed belts in the study area was visually determined using black and white aerial orthophotographs in digital format, provided by the National Land Survey of Finland (Fig. 2). These photographs were taken during spring 1997 and 2000 from a height of
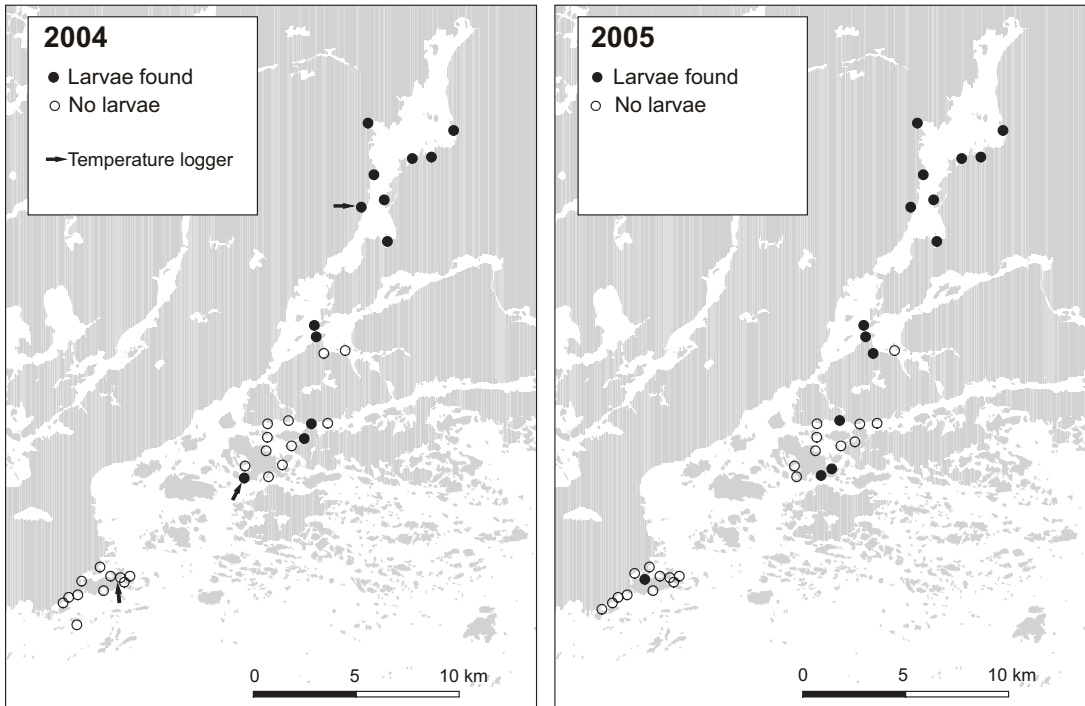
Fig. 3. The occurrence of pike larvae at the study sites in spring 2004 and 2005. The location of temperature loggers in 2004 are indicated in the left map.

6000 m and have a resolution of approximately 0.5 m. The identification of reed belts from aerial photos was easy in the inner archipelago (sub-areas A and B) where the reed belts were broad and approximately 90% of the reed belts were correctly identified. In the outer archipelago, a small proportion of the reed belts were narrow and thus difficult to identify, and there some field verification was carried out. Reed belts extended along 68% of the shoreline in sub-area A, 39% in sub-area B and 21% in sub-area C.

Sampling of pike larvae

The study sites, comprising 100 m long stretches of reed belt shores, were randomly selected from each sub-area. Altogether, 12 sites were selected in sub-areas A and B for sampling in two con-secutive years, 2004 and 2005. In sub-area C, 11 sites were sampled in 2004 and 12 in 2005 (Fig. 3). Moreover, one site in sub-area C was moved by approximately 400 m in 2005 due to dredging at the original site, and another site was moved

by approximately 2 km because the reed belt at the original site was too sparse.

In May, the reed belts are comprised of reeds from the previous year, which at the outer edge are usually partly twisted and flattened in the water. Pike larvae were sampled by wading in the reed belt and seeking them using a white plate and a white scoop (Fig. 4). The zone sampled typically covered the outer parts of the reed belt reaching from water depth of 5–10 cm to the outermost flattened reeds, and the width of this zone was usually a few metres. The white plate is an approximately 20 × 30 cm white plastic plate fixed to an approximately one metre long arm at 100°–120° angle. The plate is slowly moved between a depth of 10–40 cm below the surface, enabling the typically 13–25-mm-long larvae to be easily observed against the white background. An ordinary 2–3 litre white water scoop was used with a swift movement to sample water from the suitable habitat, and larvae could be observed against the bottom of the scoop. The observers had the white plate in one hand and the scoop in the other, and the latter was mostly used

Fig 4. Sampling of pike larvae in a potential habitat using a white plate and a scoop.

in spots, where the layer of flattened and buoyant reed was dense. Generally, both sampling equipments were equally effective to reveal pike larvae, but the scoop was needed when larvae were collected for laboratory examination. The white-plate method was developed at the end of the 1980s (L. Urho unpubl. data). The scoop had been used earlier to search for burbot (*Lota lota*) larvae along shores (Hudd *et al*. 1983).

Our aim was not to estimate larval abundance but to determine the presence/absence of pike larvae at the sites. Each site was visited at least three times, 8–10 days between visits, or until the first pike larvae were detected. The visits were carried out during the day between 09:00 and 17:00, and during occasional heavy rains searching was postponed. The rate at which water temperature increases in May is highest in the inner sub-area A and lowest in the outermost sub-area C. Thus, the first visits to sub-area A were carried out during the first two weeks in May, and the last visits at the beginning of June. Correspondingly, the first visits to sub-area C were carried out in the latter half of May and the last visits in the middle of June. In spring 2005, the first pike larvae were recorded on 17 May in sub-area A, 19 May in sub-area B, and as late as 6 June at the only site in sub-area C. The maximum searching time for two observers at one site and during one visit, if larvae were not found,

was half an hour. In cases where larvae were found, the number of observed larvae was typically from 1 to 20–30.

Background information and data analysis

The surface-water temperature and salinity were measured at each site and visit using a Hanna Instruments Microprocessor conductivity/TDS meter. In 2004, the spring and summer water temperature at 1-m depth was measured and registered by automatic temperature loggers at one site in each sub-area (*see* Fig. 3). The mean width (from land to sea) of the reed belt in each site was estimated from aerial photographs or measured in the field, both methods yielding similar results. In 2005, the water depth at the outer edge of the flattened reeds was measured. The data from water depth measurements were adjusted according to the prevailing sea water level. The exposure of a site to waves was estimated using the effective fetch index (*see* Isaeus 2004) with a 10-m resolution.

To visualize the distribution of pike reproduction areas on a map, the entire study area, reaching from the inner archipelago to the open sea, was covered by a grid of 2 km × 2 km squares, using ArcGIS (ArcMap 9.1) software package. The length of reed belt shoreline, based on the aerial photos, was measured for each square. The occurrence (present/absent) of pike larvae in the 100-metres-long study sites of the three sub-areas (data from years 2004 and 2005 combined) were used to estimate rough probabilities for pike larvae to be found in a given 100-metres-long stretch of a reed belt shore in inner, intermediate and outer archipelago. Finally, these rough probabilities for the three archipelago zones were combined into the data on length of reed belt shore in each square, yielding grid-specific estimates for the length of reed belt shores occupied by pike larvae.

The occurrence (presence/absence) of pike larvae at the study sites is a binary response variable and the site-specific potential explanatory variables (salinity, wave exposure index, width of the reed belt, water depth at the outer flattened reed belt) are continuous variables. Linear

logistic regression models were separately fitted to the data for 2004 and 2005. 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 classificatory power of the final models was evaluated by comparing the observed and predicted responses (occurrence of pike larvae). Here, a jack-knife approach was used to reduce the bias of classifying the same data from which the classification criterion is derived. The analyses were performed using the LOGISTIC procedure of the SAS 8.2 software package.

Results

Main abiotic characteristics of sub-areas A, B and C

The surface water salinity in May was generally lowest in the innermost sub-area A and increased towards the outer sub-areas B and C (Table 1). A temporal increase in salinity during May–June was also recorded, especially in sub-area A, where the effects of spring fresh water runoff diminish during late spring and early summer, and a rise in sea water level pushes cold saline water into the area. In the spring of 2004 for instance, the mean salinity in sub-area A increased from 1.3‰ in early May to 3.3‰ in mid-June. Spring water temperatures were generally higher in sub-area A than in sub-areas B and C (Table 1 and Fig. 5), except during a period in mid May when cold saline water entranced into the inner areas, too. The wave exposure index
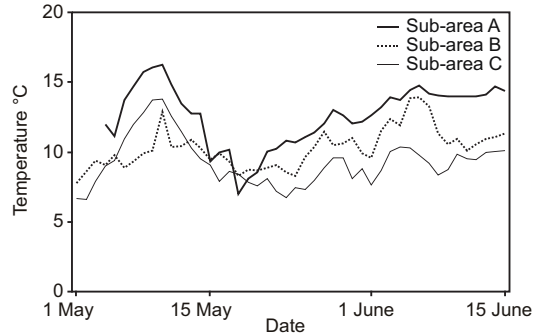

Fig. 5. Spring temperatures in 2004 in three sub-areas of the Tammisaari archipelago.

(fetch), as well as the mean width of the reed belt and the mean depth at the outer edge of the flattened reed zone was highest in the innermost sub-area A (Table 1).

Occurrence of pike larvae in various archipelago zones

Pike larvae were most frequently recorded in sub-area A, where they were found at 10 out of 12 sites in 2004 and 11 of 12 sites in 2005 (Fig. 3). In sub-area B, pike larvae were found at three of 12 sites both in 2004 and 2005. In the sub-area C, no larvae were observed in 2004, but pike eggs had earlier been found with the scoop at two sites. In 2005, larvae were found at one out of 12 sites in sub-area C. Within individual sites, pike larvae were most often detected in a habitat formed by flattened reeds from the previous season at a water depth of 20–80 cm.

Out of each 10 km of shoreline, 6.8 km was covered by reed belts in the innermost sub-area A, 3.9 km in sub-area B and 2.1 km in sub-area

Table 1. Mean (± SE) abiotic characteristics of the sites in sub-areas A, B and C. Surface water salinity, temperature and turbidity were measured in mid-May. Figures are averages of 12 measurements (one per site) in each sub-area, except in 2004, when the number of sites in sub-area C was 11.

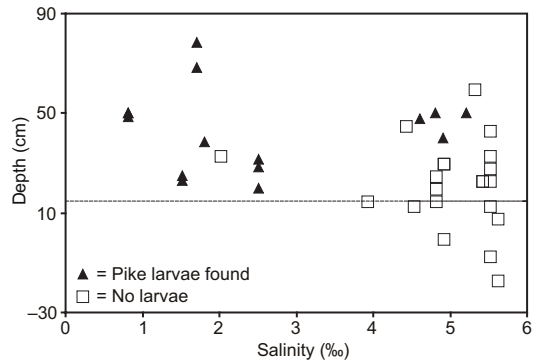| Variable	Sub-area A	Sub-area B	Sub-area C
Salinity 2004 (‰)	1.7 (± 0.2)	5.6 (± 0.1)	6.2 (± 0.1)
Salinity 2005 (‰)	1.7 (± 0.2)	4.8 (± 0.1)	5.3 (± 0.1)
Temperature 2004 (°C)	13.3 (± 0.2)	11.0 (± 0.6)	9.8 (± 0.4)
Temperature 2005 (°C)	11.7 (± 0.3)	10.5 (± 0.4)	10.8 (± 0.5)
Turbidity 2004 (NTU)	4.6 (± 0.3)	2.6 (± 0.4)	2.9 (± 0.8)
Fetch (m² s⁻¹)	3417 (± 263)	1504 (± 263)	1644 (± 222)
Reed belt width (m)	23.3 (± 4.5)	20.0 (± 4.1)	13.4 (± 2.3)
Depth (m) at outer edge of the reed belt in 2005	0.41 (± 0.05)	0.32 (± 0.05)	0.19 (± 0.05)
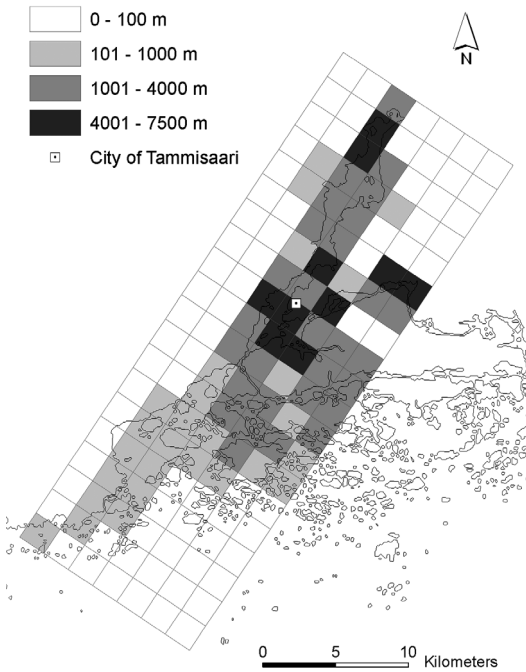
Fig. 6. Estimated length of shoreline used for reproduction of pike in 2 km × 2 km squares in the Tammisaari archipelago.

Fig. 7. The occurrence of pike larvae at the study sites in 2005. The salinity in the spring is presented on the *x*-axis and the water depth at the outer edge of flattened reeds, corrected to the normal water level, on the *y*-axis. The fallen reeds were probably dry at sites below the dotted line in late May 2005, when the sea water level decreased to 15 cm below the mean sea level.

C. In 2004, for instance, 10/12 (83%) of the shores with reed belts in the innermost sub-area were sites of pike reproduction, while the respective proportions for sub-areas B and C were 3/12 (25%) and 0/11 (0%). Thus, combining these two elements, it can be roughly estimated that in the innermost sub-area A, a total of 5.6 km of each 10 km of shoreline was used for pike reproduction. The respective figures for sub-areas B and C, 1.0 km and 0 km, were much lower. This same result is illustrated in Fig. 6, which combines the presence/absence data of pike larvae in the three archipelago zones to the grid-specific data on distribution of reed belt shores.

In the logistic regression models for both 2004 and 2005, the only variable significantly ($p < 0.05$) explaining the occurrence of pike larvae was the salinity in the spring. No other site-specific variables, including the wave exposure index, width of the reed belt and water depth at the outer edge of the fallen reeds, had a significant explanatory effect. The final logistic regression model with one explanatory factor was:

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

where $\pi(x)$ is the probability of occurrence of pike larvae at a certain salinity x, and α and β are estimated model parameters. The final models for 2004 data ($\alpha = 3.57$ and $\beta = -0.896$) and 2005 data ($\alpha = 4.68$ and $\beta = -1.257$) respectively predicted 82% and 86% of the observations correctly.

In May 2005, the minimum daily mean sea water level was –15 cm at the monitoring station in Hanko, 20 km west of sub-area C. This level was reached on both 21 and 23 May. Thus, the zone of flattened reeds was at least temporarily dry (above the water level) at some sites in sub-areas B and C (Fig. 7) during or soon after the spawning period of pike. The logistic regressions for 2005 data were run excluding the seven sites where the water depth at the edge of flattened reeds was 15 cm or less. However, this had little effect on the final model and the salinity in spring remained the only significant ($p < 0.05$) explanatory variable.

Discussion

Survey methods

The reasonable ground resolution and the wide geographical coverage of already-existing high-altitude black and white aerial photographs make them a useful tool to identify various coastal

habitats such as sandy beaches, lagoons and submerged sandbanks (Ekebom and Erkkilä 2003). The high-altitude photographs used here were taken in the spring, when reed belts were pale brown and easily distinguishable in black and white photos from the surrounding habitats. After mapping of reed belts, various sampling techniques can be used in the selection of study sites. Stratified random sampling is one technique to improve efficiency and reduce the variance of estimates, but it requires advance knowledge of valid background variables in order to form strata. As this was the first attempt to carry out larger-scale mapping of the reproduction areas of pike along the northern Baltic coast, no such variables were available. Nevertheless, we assumed that there are differences in the occurrence of pike larvae between the inner, intermediate and outer archipelago zones and thus selected study sites in all three different zones.

The white plate and scoop proved suitable tools for detecting pike larvae. It usually takes some hours or up to a day to learn how to observe larvae among the reeds using the white plate or the scoop, but thereafter the method becomes routine. One advantage of this inexpensive sampling method is that the larvae can be released if no detailed measurements in laboratory are needed. The larvae found using this method were typically 13–26 mm long, but some individuals still attached to vegetation were also caught with the scoop. Thus, most the larvae found in this study had survived two critical stages in their life, as mortality is generally very high during both the embryonic period and the stage of first feeding. A white scoop has earlier been used to observe burbot larvae in an archipelago area outside a river mouth in the Gulf of Bothnia, northern Baltic Sea (Hudd *et al*. 1983, Urho *et al*. 1990).

The length of the sample sites (100 m) appeared appropriate to reveal the distribution of pike larvae in the study area and adequate to detect larvae at almost all sites in sub-area A, where they were most abundant. In most cases, where larvae were detected, the first individuals were found rather easily and soon. Thus, based on a subjective experience, the half an hour maximum searching time for two observers at one site and during one visit was long enough.

Considering that each site was visited three times or until the first larvae were found, the risk for false negative observation, i.e. pike larvae were present but not observed, is relatively low. Binary presence/absence data of this kind can also be used in various multivariate analyses. In the dense vegetation, collection of quantitative data on larval abundance would be difficult and laborious. The surface area of potentially suitable patches for larvae sometimes varies considerably between the 100-metre-long sites, and that larvae are not evenly distributed even in patches with flattened reeds. Intensive sampling of one site would take excessively long time, and a quantitative estimation of larval numbers would require several consecutive visits to each site after the first larvae in an area have been detected in order to catch the peak of larval abundance and to observe separate cohorts.

The two variables that can be derived by remote sensing and using existing data, namely the width of the reed belt and wave exposure index (fetch), were expected to be useful variables when modeling the probability of pike larval occurrence at a certain site. However, this hypothesis was rejected. These variables were unconnected with the pike reproduction in our models, or the connections were overwhelmed by the superior explanatory variable, salinity. There are also various ways to calculate the wave exposure index, and it is possible that an index based on another calculation could have worked better.

Pike reproduction in various archipelago zones

The survey results from two successive years, 2004 and 2005, revealed that the innermost archipelago and the bay area are the most important reproduction areas for pike in the northwestern Gulf of Finland. Earlier results of Lehtonen and Hudd (1990) and Urho *et al*. (1990) from the Gulf of Bothnia, in an area several hundred kilometres northwest of the Gulf of Finland, support our finding, as they reported that there river mouths are locally important reproduction areas for pike.

Pike reproduction was more sporadic along the reed belt shores in the intermediate and

outer archipelago. A partial reason for this was revealed in the spring of 2005 when, due to the low water level, it was noted that at some sites in these outer areas the potential habitats for pike larvae, flattened reeds, had been on dry land during or just after the spawning period in late May, or in extreme cases throughout May and during the first half of June. The reed belts were generally narrower in the outer areas than in the inner archipelago and bay area, which may increase the risk of flattened reeds being washed up too high up on the shore.

Temporary drying out of suitable habitats was a potential reason for the lack of pike larvae at some sites, but does not completely explain the sparse occurrence of pike larvae in the intermediate and outer archipelago. There were still several apparently suitable sites where the depth below the important habitat was adequate during the reproduction season but no larvae were recorded. Adult pike were commonly seen in shallow waters at sites in the outer archipelago in May, and the finding of pike eggs at some sites where larvae were not subsequently detected proves that pike do spawn there. Logistic regression models identified the water salinity in spring as the best explanatory variable among the set of variables tested. A directly harmful effect of salinity on pike eggs or larvae is, however, unlikely. According to Lindroth (1946), a salinity of over 7‰ might be harmful to the development of pike eggs, but the salinity in the outer parts of our study area (5‰–6‰) was lower than this. Westin and Limburg (2002) reported that pike is capable of reproducing at salinities of up to 6‰–7‰ at the Swedish coast of the Baltic Proper. Furthermore, we noted successful reproduction at some sites even in the outer archipelago areas.

Environmental conditions are harsher in the outer archipelago that in the inner areas, as the outer areas are more vulnerable to effects of upwelling and currents from the open sea. However, water temperature measurements in spring 2004 revealed strong fluctuation, not only in the outer and intermediate archipelago but also in the innermost bay area around mid May. Nevertheless, pike larvae were abundant in the inner archipelago and the bay area. The temperature levels were yet a little lower in the outer areas,

which might be harmful for the early life stages of pike. Pike larvae feed on zooplankton and also the feeding condition for pike larvae may be worse in the outer area. Upwelling and fluctuating sea water level can bring colder and more saline water especially to the outer archipelago, which may inhibit zooplankton development and cause a fatal decrease in food availability for pike larvae. In the inner archipelago the water salinity remained relatively low during the spring, indicating far lesser effects of sea water. However, the mechanisms should be further studied and verified by comprehensive zooplankton surveys.

Reproduction failures of pike and perch have recently been reported in some areas along the Swedish coast of the Baltic Proper (Nilsson *et al.* 2004), which is closely connected to the open sea. The total abundance of zooplankton as well as the abundance of rotifers and nauplii in the spring were clearly lower in the affected area that in non-affected areas, and sub-optimal feeding conditions were suggested as a possible explanation for the poor recruitment. Lehtonen (1986) reported a long term decline in pike catches and a simultaneous increase in the mean size of pike captured around a group of small islands in the outer archipelago of the western Gulf of Finland, approximately 20 km east of our outermost subarea. Lehtonen (1986) suggested that the reason for this decline was a local recruitment failure, probably due to the decline in occurrence of the bladder wrack. This is a typical algal species on shallow (1–5 m) hard bottoms in the Gulf of Finland and needs at least 4‰ salinity to thrive in the long term (Luther 1981). The bladder wrack has been assumed to serve as a spawning and nursery habitat for pike in the outer archipelago, although this has never been well documented. The poor reproduction success of pike in the outer areas of our study, however, question the successful reproduction of pike among bladder wrack in the Gulf of Finland, as littoral areas covered by dense growths of this alga are found only in the outer archipelago zone and there in shores that are much more exposed to waves and to the effects of the open sea than shores with reed belts. It is possible that the conception of pike reproduction in the bladder wrack in the outer archipelago has been wrongly based on observations of juveline pike feeding among

bladder wrack. There is, nevertheless, another possibility that in the earlier decades, conditions such as the availability of suitable zooplankton have been more favourable in the outer archipelago for the early life stages of pike, and that recent changes such as the general eutrophication of the Baltic Sea (e.g. Cederwall and Elmgren 1990, Bonsdorff *et al*. 1997) or decreasing salinity (e.g. Hänninen *et al*. 2000) have caused dramatic deterioration in the conditions.

The observations of the spatial distribution of pike reproduction in the study area fit well to the idea of source-sink dynamics (e.g. Pulliam 1988, Howe *et al*. 1991, Kristan 2003), which suggest that populations can persist indefinitely in poor habitat when they receive immigrants from productive habitat (source), and the poor habitats (sinks) can also stabilize source population size fluctuations (Howe *et al*. 1991). The source-sink models also predict that the changes in population density are first detected at the sink. According to this, a possible decrease in pike densities in the inner archipelago could be a potential explanation for the assumed decline in pike population in the outer archipelago of the western Gulf of Finland, reported by Lehtonen (1986). Furthermore, reed belts have become increasingly abundant in outer archipelago areas around northern Baltic Sea during the last few decades (Suominen 1998), partially due to large-scale eutrophication, but our results suggest that coastal pike has not yet been able to take full advantage of this phenomenon.

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