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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.

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 (Desvilettes 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 (Raat, 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%

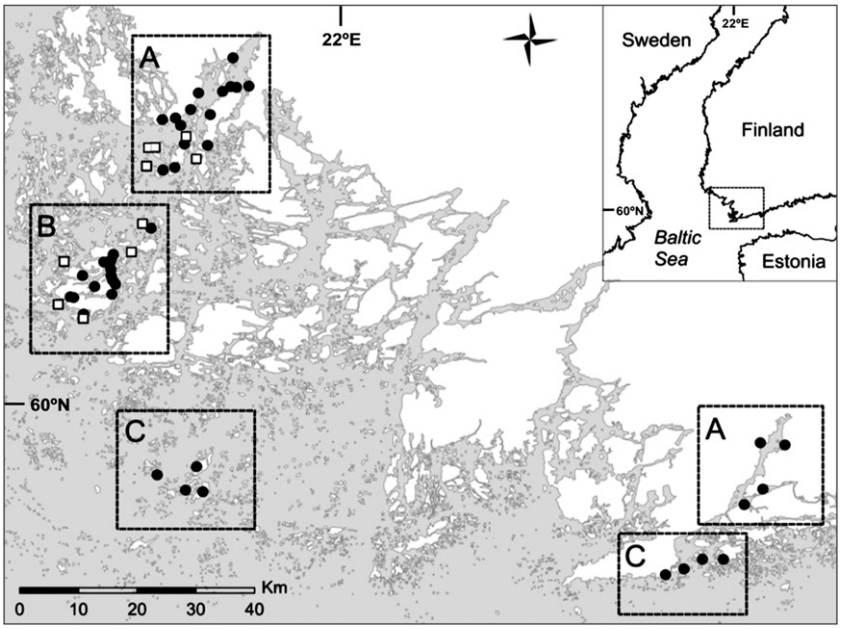

Fig. 1. Location of the study areas (Archipelago Sea A–C on the left and Ekenäs archipelago A, C on the right side) and the study sites. The boxes indicate the inner archipelago area (A), intermediate archipelago area (B) and outer archipelago area (C). The reed-covered sampling sites are marked with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