Hydrobiologia (2006) 553:161–169
DOI 10.1007/s10750-005-1949-8
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Predation of northern pike (*Esox lucius* L.) eggs: a possible cause of regionally poor recruitment in the Baltic Sea

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Received 7 January 2003; in revised form 23 May 2005; accepted 23 May 2005

Key words: egg loss, *Gasterosteus aculeatus*, numerical response, predator–prey interactions, spawning

Abstract

Northern pike (*Esox lucius*) spawning habitat and egg mortality were studied in three spawning areas in 2001 along the Swedish coast of the Baltic proper: the Blekinge Archipelago, Kalmar Sound and coastal freshwater streams. Spawning peaked during the last week of April in streams, at temperatures ranging from 7.7 to 8.9 °C and during the first week of May in brackish waters, at temperatures ranging from 8.9 to 13.8 °C. Spawning occurred in shallow waters, at depths between 0.2–1.5 m, but generally most of the spawn was found in the shallowest areas. In streams, eggs were mainly attached to emersed vegetation, while in brackish sites pike eggs were well scattered among flooded emersed plants, submersed plants and filamentous algae. Mean egg density varied between 469–1829 m^{-2} with the lowest density observed in Kalmar Sound. The calculated egg loss occurring from approximately one day after spawning to one day before hatching ranged from $41 \pm 7\%$ in coastal streams to $67 \pm 6\%$ in the Blekinge Archipelago and 100% in Kalmar Sound. The significant removal of eggs from spawning sites in Kalmar Sound and Blekinge was most likely due to predation from several fish species. In situ observations and stomach analyses suggested that many pike eggs in Kalmar Sound were lost to the three-spined stickleback (*Gasterosteus aculeatus*), a species that presently dominate the littoral small fish community. This study therefore suggests that egg predation by sticklebacks and other fishes may be a possible cause of the reported poor recruitment of coastal pike populations in the Kalmar Sound region.

Introduction

The recruitment of new individuals to a fish population is determined both by physical mechanisms like water currents and temperature (Sissenwine, 1984) and by biological mechanisms such as starvation (Cushing, 1990) and predation (Leggett & Deblois, 1994). Predation is increasingly viewed as an important ecological process regulating the survival of fish eggs and larvae, which could have great significance in the dynamics of fish populations in marine and freshwater ecosystems (e.g. Bailey & Houde, 1989; Swain & Sinclair, 2000).

Fish display many different reproductive strategies, each of which has evolved to be successful in a specific reproduction area (Wootton, 1998). Populations of northern pike (*Esox lucius* L.) in the Baltic Sea spawn either in shallow brackish waters or in coastal freshwater streams (Müller, 1986; Westin & Limburg, 2002). The eggs are scattered in small clutches among vegetation, to which they immediately adhere due to their sticky outer layer. Over a period of approximately 2–5 days, a single female may lay 8000–100 000 eggs, depending on her size and health. The eggs are left unattended and hatch in approximately 120 degree days. The deposited eggs are extremely vulnerable during this period. Factors, such as oxygen concentration, salinity, siltation and temperature, have been shown to affect embryo survival (Raat, 1988). The eggs are relatively large, 2.5 mm in diameter, non-toxic and palatable, allowing predators to feed on them during all developmental stages. A number of studies have examined pike egg survival in freshwater spawning grounds (e.g. Svärdson, 1947; Franklin & Smith, 1963; Bryan, 1967; Gillet & Dubois, 1995), but only a few consider predation (e.g. Monten, 1948; Forney, 1968; Wright & Shoesmith, 1988). Monten (1948) reported egg loss of over 96% and Forney (1968) of about 82% in single natural spawning grounds. Wright & Shoesmith (1988) reported a daily egg loss of 9–10%, which gives a 30% survival over an incubation period of 11–12 days.

Although pike is a well-studied fish in many respects, there is a lack of knowledge pertaining to the survival of their eggs on natural spawning grounds in the Baltic. The Baltic environment is changing rapidly due to eutrophication, pollution and other processes, particularly in coastal areas (Jansson & Dahlberg, 1999). In North America, such disturbances resulted in the loss or alteration of pike spawning habitats, which negatively affected pike production (Casselman & Lewis, 1996). The decline of pike stocks in some Baltic areas has been explained by similar environmental changes, such as a decline in suitable spawning vegetation (Lehtonen, 1986; Sapota & Skora, 1996).

As a result of a poor recruitment the abundance of pike in the coastal waters of Kalmar Sound along the Swedish coast of the Baltic proper decreased substantially during the 1990s (Andersson et al., 2000). Spawning pike were observed annually, but virtually no young-of-the-year were captured in surveys at the end of the first growth season. Thus, the impact likely affected life stages during the first summer. At reference sites south of Kalmar Sound, in Blekinge Archipelago, and north of Kalmar Sound, in Kvädöfjärden, there was no indication of a similar recruitment problem. Consequently, the poor recruitment in Kalmar Sound appeared to be connected to a rapid change in regional environmental conditions as Y–O–Y abundance was considered to be normal in 1989–1990 (Nilsson et al., 2004). The structure of the littoral small fish community in Kalmar Sound has changed remarkable. Perch (*Perca fluviatilis* L.), sticklebacks (*Gasterosteus aculeatus* L. and *Pungitius pungitus* L.) and roach (*Rutilus rutilus* L.) dominated in 1989 and 1990, whereas sticklebacks, mainly the three-spined stickleback, dominated from 1997 and onwards (Nilsson et al., 2004).

During the pike and stickleback spawning periods, filamentous brown algae usually cover large parts of the bottom of the brackish water spawning and nursery grounds. These nuisance algae have increased in many littoral areas around the Baltic Sea over the past few decades (Kangas et al., 1982; Plinski & Florczyk, 1984; Vogt & Schramm, 1991). Furthermore, during recent years a dominance of three-spined sticklebacks has been reported in some of these shallow areas (e.g. Sundell, 1994; Sapota & Skora, 1996; Ziliukas et al., 1998). The great abundances of sticklebacks in the shallow vegetated habitats in Kalmar Sound may be a consequence of this altered littoral vegetation structure, as it provides ideal shelter against predators and is at the same time a suitable nest-building environment (Wheeler, 1980). A changed vegetation structure in combination with a concurrent decline in perch and pike stocks could be another possible explanation for the dominance of sticklebacks in Kalmar Sound (Andersson et al., 2000; Nilsson et al., 2004). In coastal areas with low pike stocks, such as Kalmar Sound, egg consumption by sticklebacks or other predators may suppress recruitment. Observations of transplanted pike eggs on spawning sites in Kalmar Sound showed that sticklebacks ate all eggs shortly after deposition (Andersson et al., 2000).

The aims of the current study were: (1) to give a description of the pike's spawning habitat and (2) to estimate the survival of pike eggs in natural spawning sites in coastal freshwater streams and in brackish waters along the Baltic Sea coast.

Materials and methods

Pike spawning habitat and egg survival were surveyed from April to May, 2001. Spawning sites, at depths of 0.2–1.5 m, were visited in three areas along the Swedish coast of the Baltic proper: the Blekinge Archipelago ('Blekinge'), northern and central Kalmar Sound ('KS'), and small coastal freshwater streams ('streams') discharging into the Kalmar Sound area (Fig. 1). A qualitative survey of dominant spawning substrates was conducted by snorkelling in the pike-spawning grounds. All twelve spawning sites, four in each area, were surveyed within 24 h of sighting spawning pike. Data on deposited egg densities were collected by visual estimates by scuba divers of the number of eggs within 0.01 m^2 quadrates. Thirty quadrates per spawning site were sampled. Each quadrate was a square constructed of steel with sides measuring 10 cm. To ensure that only freshly deposited eggs were counted, two quadrates from each spawning site were gently emptied and the vegetation and eggs placed in net bags. The samples were immediately preserved in a 4% formalin/seawater solution buffered with borax. Spawning dates were later determined from the observed developmental stage of the preserved eggs (Lindroth, 1946). Water temperature and salinity were recorded with a conductivity meter (WTW LF 191) during the first visit. To quantify egg loss sampling was repeated after the remaining eggs had further incubated approximately 90 degree days, (i.e. after 7–10 days). A second spawning event took place at two of the Blekinge sites; therefore before calculating the mean egg loss for these two sites, the proportion of the second spawn was subtracted from the first.

In the brackish water spawning grounds, three-spined sticklebacks were visually censused while snorkelling along 25 m long and 0.5 m wide transects (12.5 m^2). Five transects were made within each site, covering a total area of 62.5 m^2. In addition to the original four spawning sites surveyed, an additional four sites in Blekinge and Kalmar Sound were censused. A visual census for sticklebacks could not be performed in the freshwater streams because of poor water visibility. During the first trip three-spined sticklebacks were caught for stomach analysis using one gill net, 10 m long and with 10 mm mesh size, and five minnow traps, 0.4 m long with 5 mm mesh size, at each site. The fish were immediately killed and preserved in a 4% formalin/seawater solution buffered with borax. In the laboratory their stomach contents were classified according to taxonomic group. The contribution of different prey taxa to the diet was

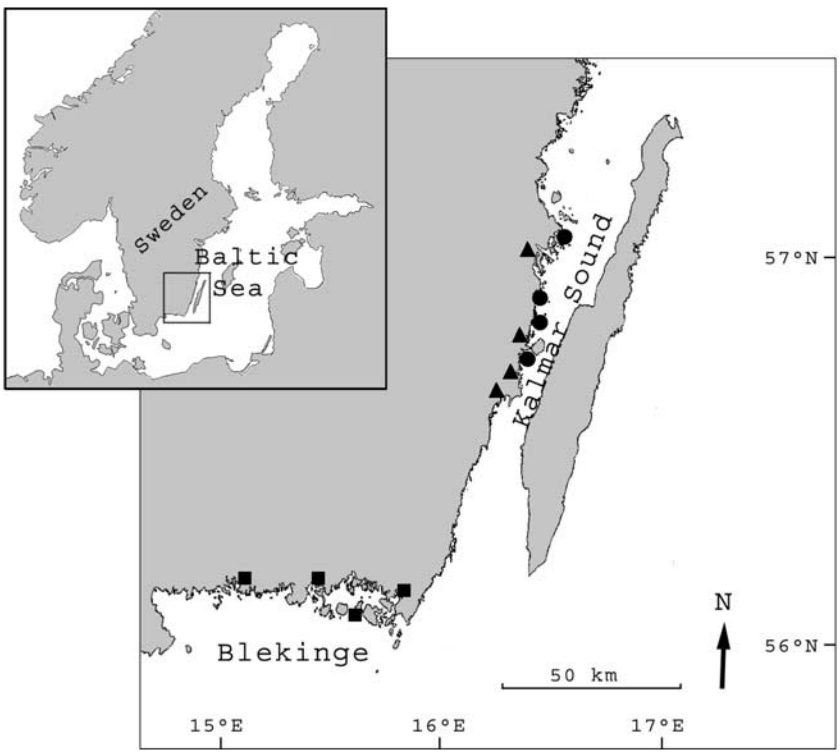

Figure 1. Location of pike spawning sites in Blekinge Archipelago (■), Kalmar Sound (●) and coastal freshwater streams (▲). Streams are from north to south; Kronobäcken, Ryssbyån, Stävlö and Törnebybäcken.

determined in two ways: (1) the proportion of each prey to the total volume of stomach content and (2) the percentage frequency of occurrence of the number of stomachs in which a prey item occurred to the total number of stomachs.

At each of the four spawning sites in Kalmar Sound and at three out of four sites in Blekinge, about 10 000 unfertilized pike eggs, obtained by stripping a female and estimating volumetrically, were dispersed by hand on a nylon net (0.5 m^2). Due to a shortage of eggs only three sites in Blekinge were possible to study. The eggs were observed underwater by a snorkeller for one hour, or until all eggs were consumed, and the foraging species were determined.

Daily consumption of pike eggs per square metre by sticklebacks (C) at Kalmar Sound spawning sites was estimated using the following equation: $C = A_s \times F_s \times (W_s \times C_s \ / \ W_{pe})$. A_s denoted the abundance of sticklebacks; F_s denoted the frequency of egg-consuming sticklebacks; W_s denoted the mean body weight of sticklebacks; W_{pe} denoted the mean weight of a pike egg, and C_s denoted the daily food consumption of stickleback body weight.

Results will be provided that measure mean abundance of young-of-the-year pike and sticklebacks (Nilsson et al., 2004). Small explosive charges were detonated underwater at approximately half the water depth in shallow (1–3 m) and sheltered areas potentially suitable as nurseries for the targeted fish. Detonations stunned or killed fish within an area of about 50 m^2. All fish floating to the surface were collected and counted. The aim was to collect fish from fifteen stations at each site.

Statistica TM 99 (Statsoft Inc.) was used for data analyses. Where ANOVA was used, the homogeneity of variances was tested using Cochran's test and differences between sites were tested with a post hoc test according to Tukey. All measurements are given as means ± standard error (SE).

Results

The first sightings of spawning pike were on April 12th in one of the freshwater streams, Stävlö, at a temperature of 5.4 °C. The main spawning peaked, however, during the last week of April in streams, at temperatures ranging from 7.7 to 8.9 °C and during the first week of May in the brackish waters, at temperatures ranging from 8.9 to 13.8 °C (Fig. 2). Spawning temperatures were significantly lower in streams (ANOVA $F_{2,9} = 9.82$, $p = 0.005$). Salinity reached a maximum of 6.8‰ in the brackish areas (Fig. 2). Spawning depth varied between 0.2–1.5 m, but generally most of the spawn was found in the shallowest areas. In brackish water spawning sites pike eggs were well scattered among different kinds of vegetation, on flooded emersed plants such as *Carex* spp., *Phragmites* sp. and other Gramineae, on submersed plants such as *Myriophyllum spicatum*, *Potamogeton* spp., *Ruppia* spp. and *Chara* spp., and on filamentous algae. Neither density nor type of vegetation seemed to correlate closely with egg deposition; however, eggs were only occasionally found on loose-lying *Fucus vesiculosus*. In the streams, the eggs were mainly attached to emersed vegetation chiefly composed of different grasses.

Egg densities on spawning vegetation ranged from 469 ± 210 eggs m^{-2} in Kalmar Sound, to 1129 ± 206 eggs m^{-2} in Blekinge and 1829 ± 453 eggs m^{-2} in streams. The density in Kalmar Sound was lower than densities in streams and Blekinge (ANOVA $F_{2,9} = 10.37$, $p = 0.005$). Eggs were more evenly distributed in the brackish spawning grounds, compared to the streams where eggs were often more aggregated and in some cases even in multiple layers. The highest number of eggs observed in one quadrate in streams was 178 (i.e. 17 800 m^{-2}) compared to 39 (i.e. 3900 m^{-2}) in the brackish areas.

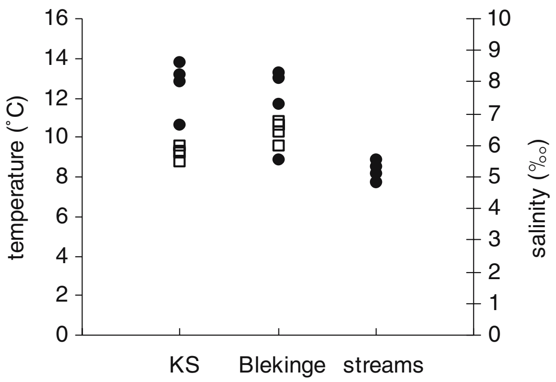

Figure 2. Temperature (●) and salinity (□) recorded within 24 h of observed spawning activity in Kalmar Sound (KS), the Blekinge Archipelago (Blekinge) and coastal freshwater streams (streams).

Estimated egg loss ranged from 25 to 100% among the twelve sites, and there were significant differences between the areas (ANOVA $F_{2.9}$ = 49.81, $p < 0.001$). Approximately 41% of the spawn disappeared in the streams and 67% disappeared in Blekinge, while all the spawn disappeared in Kalmar Sound (Fig. 3).

Three-spined sticklebacks were considerably more abundant in Kalmar Sound, 4.7 ± 1.2 number m^{-2}, than in Blekinge, 0.1 ± 0.05 number m^{-2} (ANOVA $F_{1.14}$ = 15.41, $p < 0.001$). The mean abundance at the visited sites varied between 2 and 11 m^{-2} in Kalmar Sound and 0 and 0.1 m^{-2} in Blekinge. A total of 262 three-spined sticklebacks were collected in Kalmar Sound for diet analysis. Despite considerable efforts with both gill nets and traps, only 15 sticklebacks were collected in Blekinge and none in the streams. The stomach contents were dominated by mysids in both areas, and pike eggs were only found in stomachs from Kalmar Sound. Pike eggs comprised a minor part of the stomach contents, and only 8.4% of sticklebacks had consumed eggs (Table 1).

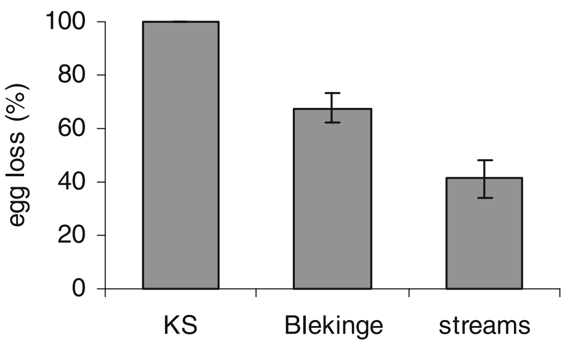

Figure 3. Estimated mean egg loss (in percent, ± 1 SE, $N = 4$) for pike spawning grounds in Kalmar Sound (KS), the Blekinge Archipelago (Blekinge) and coastal freshwater streams (streams).

The transplanted pike eggs were rapidly encountered and detected by several fish species in Blekinge, the most common being perch, rudd (*Scardinius erythrophthalmus* L.) and roach. In 1 h, between 30 and 50% of the eggs were consumed. In Kalmar Sound, the only species that preyed on the eggs was the three-spined stickleback. The stickleback was a very efficient predator and all eggs on the nets were eaten after less than 1 h. Other potential predators such as roach, silver bream (*Blicca bjoerkna* L.), European eel (*Anguilla anguilla* L.) and the common prawn (*Palaemon adspersus* Rathke) were observed during snorkelling but were not observed to consume the transplanted pike eggs.

Daily consumption of pike eggs per square metre by sticklebacks (C) in Kalmar Sound was estimated using the following data. The abundance of sticklebacks (A_s) was 6.4 m^{-2}; the frequency of egg-consuming sticklebacks (F_s) was 8.4%; the mean body weight of sticklebacks (W_s) was 2.1 g; the mean weight of a pike egg (W_{pe}) was 0.01 g, and finally a daily food consumption (C_s) of 11.7% of stickleback body weight was assumed (Ali & Wootton, 2000). This gives a daily egg loss of 13.2 eggs m^{-2} from consumption by sticklebacks, which results in a total removal of 105.6 eggs m^{-2} over an 8-day incubation period, equivalent to a total mortality of 22.5%.

Discussion

Earlier documentation of pike spawning habitat characteristics (reviewed by Raat, 1988 and Craig,

Table 1. Diet composition (frequency of occurrence and percentage of total volume) of three-spined sticklebacks in Kalmar Sound and Blekinge Archipelago (Blekinge) in spring 2001. N = Number of fish studied

Food item	Frequency of occurrence (%)		Percentage of total volume	
	Kalmar sound	Blekinge	Kalmar sound	Blekinge
Mysidacea	76.0	92.9	66.9	88.0
Amphipoda	19.1	14.3	18.8	5.3
Chironomidae	12.6	0	5.4	0
Pike eggs	8.4	0	4.4	0
Other	9.2	42.8	4.5	6.7
N	262	15		
Empty (%)	24.4	13.3		

1996), such as water temperature at the onset of spawning, localization of spawning to shallow, sheltered and vegetated areas, and no preference of spawning vegetation, seemed to be also valid for the coastal populations of pike in Kalmar Sound and Blekinge. Lindroth (1946) showed that hatching success was negatively affected at salinities of around 7‰. In Blekinge, where spawning took place at salinities of between 6.0‰ and 6.8‰, similar effects were not detectable. Müller (1986) found that coastal pike populations frequently use freshwaters as reproduction sites in the northern Baltic. The main reason appeared to be a more rapid warming of the water compared to adjacent brackish areas. Both coastal freshwater streams and brackish waters are frequently used as spawning areas in Kalmar Sound (J. Nilsson, personal observation). However, in 2001 in Kalmar Sound the main spawning period peaked in streams only one week earlier than in brackish areas and actually at lower water temperatures, indicating that factors other than water temperature could also be important.

Wright & Shoesmith (1988) found egg densities of 729 m^{-2} on flooded grass and Gillet & Dubois (1995) found densities of 2500 m^{-2} on artificial spawning substrates. However, egg densities are usually lower, varying from a few to several hundred per square metre (Craig, 1996). The reason for the comparatively high densities (469–1829 m^{-2}) observed in the current study could be the short time between egg deposition and surveying.

The results of the egg loss survey indicated that a large proportion of the deposited pike eggs were removed before hatching, and that predation was the most obvious factor in egg removal from pike spawning grounds, especially in Kalmar Sound where the entire spawn disappeared. Certainly, many factors such as water quality, oxygen deficit, algal exudates and siltation could negatively affect the survival of demersal fish eggs during incubation (Aneer, 1987; Raat, 1988). However, all these factors would simply increase mortality and not lead to the physical removal of eggs from the spawning site. Heavy wave actions may detach demersal fish eggs or even remove spawning substrates (Rooper et al., 1999); however, the weather in the end of April and beginning of May was calm in 2001 and all spawning along the coast took place in sheltered bays. Other physical forces, such as water currents, could explain some of the egg loss in the streams: unattached eggs were found on the sediment in the mouth area of Kronobäcken and Ryssbyån. Other causes of egg losses are unknown; however, field incubation studies in predation-free enclosures indicated that it was not simply decomposition of dead eggs (Nilsson et al., 2004).

Other studies of pike have found egg survival on hatching to be highly variable. Svärdson (1947) gives a maximum survival of 76%; Franklin & Smith (1963) present values between 64 and 90% for three successive years; Bryan (1967) gives a rate of 90%; and Gillet & Dubois (1995) state that the survival of pike eggs is generally over 70%. Common to these studies, however, is that the survival rates are based on a live egg to dead egg ratio, with no consideration of loss of eggs from predation. Studies that take predation into account indeed report much lower figures; with survival rates between 4 and 30% (Monten, 1948; Forney, 1968; Wright & Shoesmith, 1988). In the current study, the initial egg density was estimated almost immediately after spawning in Kalmar Sound and a half to one day after spawning in the other areas. Consequently, the calculated egg loss could have been underestimated both in Blekinge and the streams, as loss due to predation is probably greatest in the first days after spawning (Wright & Shoesmith, 1988).

The large variation in egg loss between the areas surveyed could probably be explained by differences in predation pressure. The spawning of pike in the brackish waters of Kalmar Sound coincided both temporally and spatially with great abundances of three-spined sticklebacks, a well-documented predator of eggs of both con-and heterospecifics (Whoriskey & FitzGerald, 1985). The sticklebacks return from their winter-feeding areas in the spring and congregate in the vegetated littoral where they spawn later in the season (Lemmetyinen & Mankki, 1975).

The substantial difference between estimated (22.5%) and observed (100%) egg loss in Kalmar Sound might be explained by a strong numerical response to the availability of eggs. When pike eggs were transplanted and observed, the stickleback was the only active predator seen. The visually feeding sticklebacks detected the eggs within a few minutes and foraging began immediately. Within a short while conspecifics were migrating from adjacent areas and aggregating in the area, leading to abundances of hundreds of individuals per square metre. Thus, migration of sticklebacks from adjacent areas without deposited spawn would significantly increase the removal of eggs. High densities of small-sized fish in vegetated habitats are generally explained by availability of food and shelter against predation (Rozas & Odum, 1988). Introducing eggs in such high densities and with no vegetative cover, as in the present consumption experiment, may have resulted in an unnatural foraging behaviour of the three-spined stickleback. However, aggregating sticklebacks were also observed feeding on freshly released spawn in three of the visited spawning sites in Kalmar Sound and in fact the entire spawn disappeared in this area. The role of other fishes and the high egg loss should not, however, be overlooked. In Blekinge, perch, rudd and roach were all seen eating eggs. Another possibility, not investigated by this study, is that avian or other egg predators may have contributed to egg loss (Rooper et al., 1999).

The depletion of large dominant species may result in an increase in smaller predators previously suppressed by a combination of direct predation and competition. These small predators then cause an increase in the predation mortality rate for the eggs, or compete for food with the larvae or juveniles of the large dominant species (Walters & Kitchell, 2001). This would cause a depensatory decrease in the recruitment rate per spawner for the large dominant species, slowing or preventing population recovery even if fishing or other repressing factors are removed (Köster & Möllman, 2000; Swain & Sinclair, 2000). A young-of-the-year survey in 1998 showed a dominance of sticklebacks in the central and northern parts of Kalmar Sound and a concurrently low abundance of pike. In an area approximately 20 to 90 km north of Kalmar Sound, same species showed a reversed pattern (Fig. 4). A low adult biomass of pike and a simultaneously high egg predation could result in a low recruitment (Craig, 1996). Today we could have a situation with a pike stock in Kalmar Sound that cannot produce more eggs

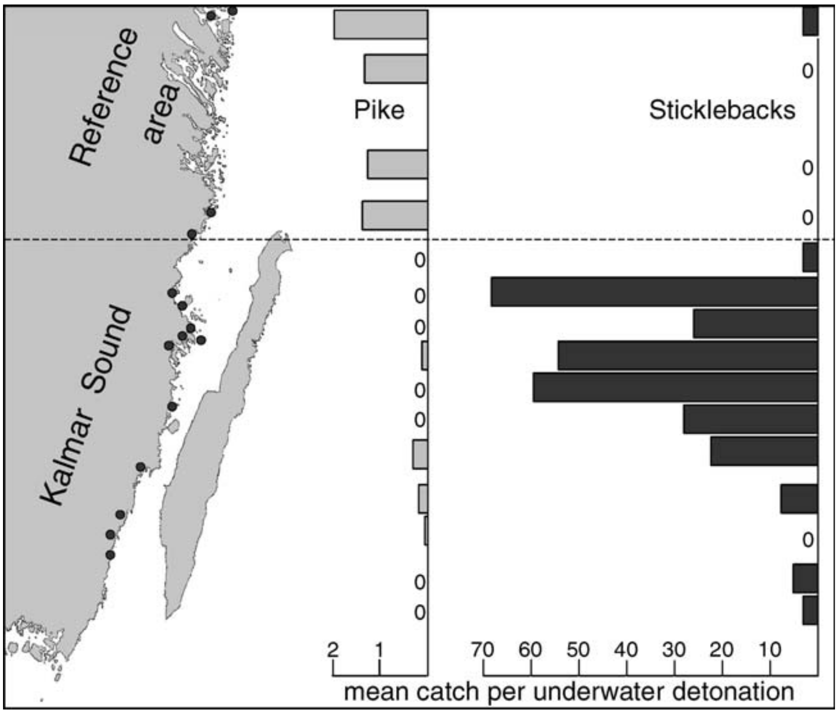

Figure 4. The mean abundance of young-of-the-year pike and sticklebacks in September 1998, registered by underwater detonation, which stunned or killed fish within an area of about 50 m^2. Fifteen samples were collected at each site. Data are taken from (Andersson et al., 2000; Nilsson et al., 2004).

than the sticklebacks and other predators efficiently can eat. Thus, egg predation may have become a bottleneck for pike recruitment in this region.

Westin & Limburg (2002) identified two populations of pike living together in the coastal waters of Baltic. During spawning season they separate into two different populations. One reproduce only in brackish waters and the other is an obligate freshwater spawner. Juvenile pike hatched in the streams migrate to the sea, where they together with the brackish population comprise the coastal stock (Müller, 1986). Egg loss in streams discharging into Kalmar Sound did not exceed 50% in the current study. A mortality rate of this magnitude would probably not be high enough to induce large-scale changes in recruitment. This appears to contradict the earlier statement about egg predation being a major sink for pike recruitment in Kalmar Sound. However, the importance of recruitment to the coastal stock from anadromous pike populations in relation to brackish water spawning populations is not yet understood, and possibly the recruitment from coastal streams is insufficient to supply the large coastal areas with pike.

Acknowledgements

I am grateful to many friends for help with fieldwork and to all the anglers and commercial fishers who generously provided information on pike spawning sites. Many thanks also to Lars-Eric Persson for helping to improve the manuscript and to Johan Carlsson at the County Administrative Board of Blekinge. Financial support was provided by the University of Kalmar.

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