

Till Mormor

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"So I started to walk into the water. I won't lie to you boys, I was terrified. But I pressed on, and as I made my way past the breakers a strange calm came over me. I don't know if it was divine intervention or the kinship of all living things, but I tell you Jerry, at that moment I was a marine biologist."

- George, in Seinfeld episode "The Marine Biologist"

LIST OF PAPERS

This thesis is based on the following papers, further on referred in text with their roman character.

- I. Engstedt O, Stenroth P, Larsson P, Ljunggren L, Elfman M. 2010. Assessment of natal origin of pike (*Esox lucius*) in the Baltic Sea using Sr:Ca in otoliths. *Environmental Biology of Fishes* 89:547-555
- II. Engstedt O, Koch-Schmidt P, Larsson P. Experimental validation of Sr uptake in juvenile pike (*Esox Lucius* L.) otoliths – from water and food. Submitted.
- III. Engstedt O, Larsson P, Koch-Schmidt P, Skov C, Tibblin P, Nilsson J, Borger T, Stenroth P. Annual spawning migration of anadromous pike (*Esox lucius* L.) in streams entering the Southern Baltic Sea. Manuscript
- IV. Engstedt O, Engkvist R, Larsson P. Elemental fingerprinting of otoliths reveals natal homing of anadromous Baltic Sea Pike (*Esox lucius* L.). Submitted.
- V. Nilsson J, Engstedt O, Larsson P. Wetlands for northern pike recruitment and nutrient reductions. Submitted.

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ABSTRACT

The pike (*Esox lucius*) is a major predator and top-down regulator in the Baltic Sea where it exists in two sympatric forms. One spawn in streams and rivers and the other one spawn in the sea. During the last decades, the habitats for both of these forms have developed in a negative way. In some freshwater systems, up to 90 % of the water areas have disappeared, mainly through drainage and straightening of watercourses for agricultural purposes. In the sea, reproduction habitats decrease due to construction of harbours and human activities that create disturbances. The perhaps largest single factor negatively affecting recruitment of pike in the sea is the eutrophication. Bottoms are overgrown with filamentous algae and shallow bays are covered with dense *Phragmites* belts decreasing the habitats suitable for spawning. Further on, a predator on egg and fish larvae, the three-spined stickleback (*Gasterosteus aculeatus*) has increased in abundance. It is difficult to restore and enhance pike production in the sea and probably the only economically viable alternative is to make restorations in freshwater. However, there is a limited knowledge about the freshwater spawning pike in the Baltic Sea. Thus in this thesis I, together with my co-authors, set out with an aim to increase the knowledge base regarding anadromous pike behaviour.

We found that pike of natal freshwater origin were common in the Baltic Sea. Through Sr:Ca studies in otoliths, about 45 % of the pike were interpreted to be of freshwater origin. The majority of the pike had emigrated out of freshwater at a length below 6 cm. These results indicate that freshwater recruitment is successful, contrasting the vast areas available for spawning in the sea. This creates incitements that restoration measures in these watercourses could have a significant effect on the pike population in the Baltic Sea.

Further, in four streams running out in the Baltic Sea, more than three thousand pike were marked to study spawning migration. About 30-40 % returned to the same river the subsequent year. Most of the pike used the lower parts of the stream for spawning. The homing of pike to a watercourse indicate that freshwater pike in the Baltic Sea consist of specific populations and this is crucial information when taking decisions on fish restoration measures.

Three wetlands adjacent to streams were restored for pike production. The most successful restoration involved minimal digging, with flooded grasslands providing optimal conditions for spawning. The first spawning season after restoration increased the pike production hundredfold.

In conclusion, the anadromous pike are numerous in the Baltic Sea. To compensate for the decline in pike populations in the sea, “pike-factories” created along the coastline are probably the most justifiable option.

SAMMANFATTNING

Gäddan i Östersjön har två olika reproduktionsstrategier, den ena går ut på att fisken leker i grunda vikar i havet, den andra att de vandrar upp i bäckar och åar för att leka i sötvatten. Under de senaste decennierna har levnadsförhållandena kraftigt försämrats för båda dessa typer av gäddor. I havet har näringstillförsel och mänsklig aktivitet i grunda vikar försvårat för gäddans fortplantning. Övergödningen av Östersjön, det vill säga utsläpp av näringsämnen har medfört att grunda vikar där gäddan lekte nu är igenväxta med vass och bottenarna är täckta med fintrådiga alger. Kuststräckor som tidigare betats av boskap växer igen, vilket förhindrar gäddan att leka i översvämmade gräsmarker i strandkanterna. Vidare har storspiggen ökat markant och detta bidrar till att reproduktionen av gädda i havet blir mindre lyckad. Spiggen äter både rom och yngel i stora mängder. I sötvatten hindras vandrande fisk som gäddan att nå sina reproduktionslokaler på grund av olika hinder. Genom utdikning och rätning av vattendragen svämmar de inte över vid vårfloden på samma sätt som förr, vattnet passerar snabbt genom systemet ut i havet. Detta medför en minskning av arealen översvämmade gräsmarker som är viktiga lek- och uppväxtmiljöer för gäddor. Denna utdikning har främst skett i samband med jordbruk och mänsklig bebyggelse. I kustnära miljöer kan ytan av lämpliga rekryteringsmiljöer för gädda ha minskat så mycket som 50-90 %.

Det är svårt och kostsamt att göra habitatförbättringar och restaureringsåtgärder för gäddan i Östersjön, det mest ekonomiska och mest effektiva sättet bör vara att återskapa tidigare lekområden i vattendrag som mynnar i havet. Dock finns en stor kunskapslucka om gäddor som vandrar upp i sötvatten för att leka. Därför har jag i denna avhandling, tillsammans med mina medförfattare haft som mål att öka kunskapen om denna migration.

För att ta reda på andelen gäddor som leker i sötvatten bidrar till beståndet i Östersjön, undersökte vi strontium-kalciumkvoter i otoliter (öronstenar) från gäddor tagna i havet. Genom att analysera dessa kan man avgöra om gäddan är född i havet eller i sötvatten. Analysen visade att upp till 45 % av gäddorna i havet kan ha sötvattensursprung. Otoliterna avslöjade också att merparten av sötvattensgäddorna vandrat ut i havet när de var 6 cm eller mindre. De här resultaten visar att sötvattensreproduktion idag är väldigt framgångsrik, detta trots förstörda lekområden. Ser man till de stora lekområden som finns tillgängliga av havet i kontrast till de relativt små ytor som bäckar och åar utgör, antyder mina data att sötvatten är väldigt produktiva för gädda.

Över tre tusen vuxna gäddor fångades och märktes i fyra bäckar som mynnar i Östersjön. Återvandringensprocenten följande år var i genomsnitt 36 %, vilket indikerar ett homing (hem)-beteende. Merparten av fiskarna stannade för lek i de nedre delarna av bäckarna men en del av fiskarna vandrade långt om möjligheten fanns. Noterbart är att vissa individer som vandrade långt ett år, även gjorde det kommande år. Detta homingbeteende till specifika bäckar indikerar att gäddor i dessa system består av enskilda skyddsvärda populationer.

Tre våtmarker i anslutning till kustmynnande bäckar byggdes eller rekonstruerades i syfte att öka gäddproduktionen till Östersjön. Den våtmark som var mest produktiv var när vatten fick svämma över befintlig gräsmark. Redan första året efter restaureringen ökade yngelproduktionen från ca tretusen till över hundratusen. Sammanfattningsvis, gäddor med sötvattensursprung är vanliga i Östersjön. För att kompensera för nedgången i gäddbestånd i havet är skapandet av *gäddfabriker* (översvämningstvåtmärker) längs kusten det mest ekonomiskt försvarbara och effektivaste sättet.



Pike on spawning migration up in a small freshwater ditch (Photo: Hans Hästbacka and Janne Widjeskog).

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INTRODUCTION

Northern pike in the Baltic Sea

Ecology

The pike (*Esox Lucius* L.) is a common fish in the coastal areas of the brackish Baltic Sea, from the north to the southern parts where salinity seems to be the limiting factor for the distribution area. Being a top predator, it plays an important role in regulating fish communities in the ecosystem (Craig, 2008). Prey species in the Baltic sea are e.g. roach (*Rutilus rutilus*), ide (*Leuciscus idus*), bream (*Abramis brama*), clupeids (*Clupea harengus*, *Sprattus sprattus*), perch (*Perca fluviatilis*) and sticklebacks (e. g. *Gasterosteus aculeatus*). Carpenter (2001) showed that lakes can exhibit alternative stable states, depending on what impact the top-down predators have. At low abundance of predators such as pike, zooplankton-feeding fish such as cyprinids will increase and zooplankton will decrease, which may lead to high density of phytoplankton (Carpenter, et al., 2001; Persson, et al., 1999). Lowered light conditions in the lake create disadvantages in search of prey for top predators such as pike (Turesson, Bronmark, 2007). The other alternative state is when predators are numerous, these lakes often have clearer water and less algal blooms. Studies of lakes in northern Europe have showed that the presence of the top predator pike is an important factor in regulating lakes fish communities (Spens, Ball, 2008). Studies have suggested that similar top-down relationships could be applied in marine environments (Frank, et al., 2005; Scheffer, et al., 2001). If so, the decrease of pike and other predators in the Baltic Sea may contribute to an increase in eutrophication (Eriksson, et al., 2009).

The northern pike have a commercial value and have become a popular target for sportfishing during the last decades (Pierce, et al., 1995).

Reproduction and migration

Northern pike in the Baltic Sea have two strategies for reproduction. They spawn either in shallow brackish waters or in coastal freshwater streams (Muller, 1986; Westin, Limburg, 2002). During springtime (March-May) all sexually mature pike migrate from foraging areas into shallow water. The anadromous pike find their way to rivers, streams and ditches to continue their migration upstream to the spawning areas. The spawning areas in freshwater could be shallow areas of the stream, adjacent wetlands or grass meadows temporarily submersed by water from the spring flood. Ideal spawning conditions for pike are shallow sheltered areas with flooded vegetation such as grass and sedges (Casselman, Lewis, 1996, FIG. 1). The spawning may last for a month and the adult fish then return to the sea (Muller, 1986). The eggs adhere to vegetation and hatch after approximately 120 degree days. The shallow water that quickly

heats up after the ice coverage is melted, provide fast hatching of the eggs and also development of zooplankton which is the main food base for pike larvae (Raaf, 1988). After hatching, the yolk sac larvae remain attached to vegetation. When the yolk sac is almost absorbed, exogenous feeding starts (Craig, 1996; Raaf, 1988). Initially pike are feeding on zooplankton, then on insects and finally shifts over to a piscivorous diet (Raaf, 1988). Proper nursery areas are also of importance, Casselman and Lewis (1996) states that optimal size of nursery habitat for young-of-the-year pike (0+) should exceed ten times the size of spawning habitat. Further on, vegetation should be dense and cover 40-90 % of the habitat. A variation in depth also increases the optimality of the nursery habitat. Juvenile pike are cannibalistic, and a reduced nursery area or low food availability means that cannibalism increases (Giles, et al., 1986; Skov, et al., 2003). However, the majority of juveniles in freshwater habitats migrate to the sea within the first month after hatching, choosing the sea as feeding habitat (Johnson, Muller, 1978). The reasons for the early emigration are several; from threat of being caught in nursery areas when water decreases to intense competition and risk of predation (Forney, 1968; Le Cren, 1965).



FIG. 1 Several spawning pike in emergent vegetation in shallow waters, habitats that show optimal conditions for pike reproduction (Photo: Erik Walmann)

Recruitment problems

Pike populations have generally decreased in the Baltic Sea during the last decades (Nilsson, et al., 2004). Data indicating this decrease have mostly been landings of pike from fisheries without proper effort calculations. However, Lehtonen (2009) showed a unique time series over 69 years with declining CPUE-data of pike from the coast of Finland (Fig 2). Areas that seem to be most affected are Kalmar Sound, Stockholm outer archipelago, Åland and Finland (Andersson, et al., 2000). Studies have suggested that the decline in pike populations is due to recruitment problems (Lehtonen, et al., 2009; Ljunggren, et al., 2010; Nilsson, et al., 2004).

The Baltic Sea is affected by eutrophication caused by human impact (Jansson, Dahlberg, 1999) and the loss of predators such as pike could actually increase the eutrophication effects. The release of predation pressure on

zooplanktivorous species such as roach, sticklebacks and clupeids, cause exploitation of zooplankton and in the end less grazing of phytoplankton (Casini, et al., 2009). This process has been suggested to promote bloom-forming macroalgae and enhance eutrophication (Eriksson, et al., 2009; Sieben, et al., 2011). The eutrophication has direct effect on pike reproduction with filamentous algae covering spawning habitats, with a low hatching rate as an effect. However, effects such as less abundance of zooplankton, may contribute to starving effects of pike larvae with recruitment failure as consequence (Ljunggren, 2002). Such relationship has been suggested for the predator cod (*Gadus morhua*) and zooplankton grazer sprat in the Baltic Proper (Casini, et al., 2008). The decrease in cod abundance (recruitment problems, overfishing) increases the biomass of sprat and the zooplankton exploitation. A recent study suggests a linkage between these offshore processes and weakened coastal predatory fish recruitment (Ljunggren, et al., 2010).

Sticklebacks have dramatically increased during the last decade (Ljunggren, et al., 2010). Observations of up to 100 individuals per m² have been made (ref Jonas Nilsson, personal observations) in coastal areas of the Baltic Sea.

Sticklebacks are also shown to have direct negative effects on pike reproduction, by predation on egg and larvae. Nilsson (2006) showed that pike eggs can be totally depleted by sticklebacks within hours after spawning.

The perhaps most plausible explanation to the decline in pike populations is loss of spawning habitats (Casselman, Lewis, 1996; Lehtonen, 1986; Threinen, 1969). As previously described, pike in the Baltic Sea reproduce in both freshwater streams and shallow bays in the sea. During the last century many of these environments have suffered negative impact caused by human activity. Marinas are constructed around populated areas with increasing boating activity as a consequence. Studies have shown that such activity could have large negative influence on fish recruitment in the Baltic Sea (Sandstrom, et al., 2005). Eutrophication has caused changes in vegetation in spawning habitats in shallow bays of the Baltic, creating poor conditions for pike recruitment (Lehtonen, et al., 2009; Ojaveer, Lehtonen, 2001; Sandstrom, Karas, 2002). However, the perhaps most important factor has been the changes made in the coastal landscape during the last centuries. Large resources have been put in to drain the land to improve conditions for agriculture (Hoffman, et al., 1999). In fact, during the last two centuries, the Swedish government have compensated farmers with over 7 Billion SEK (Hoffman, et al., 1999). In the most affected areas, such as Skåne and Mälardalen, as much as 90 % of the freshwater surface have disappeared (Hagerberg, et al., 2004). In the last 20 years, effort has been put in to restore parts of what has been destroyed, in order to control nutrient emissions. However, these wetlands are optimized for nutrient removal and not for fish reproduction. Often various dam constructions in the outlets from the wetland effectively prevent anadromous fish to continue their migration to spawning areas. However, the depth and vegetation cover of constructed

wetlands for nutrient removal are often functional habitats for pike reproduction (Casselman, Lewis, 1996).

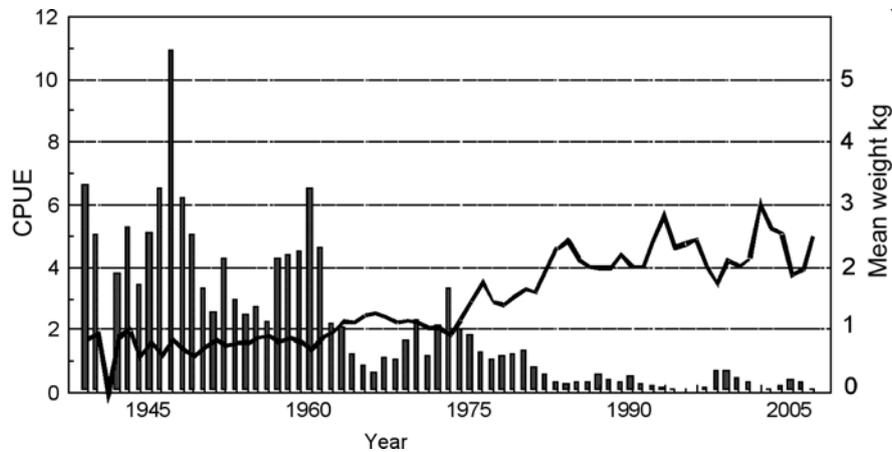


FIG. 2 The bars show decreasing catch per unit effort (CPUE) of pike over time, while the line show increasing mean weight in the western Gulf of Finland during 1939-2007 (Printed with permission from Lehtonen, et al., 2009).

Homing and population structure

How has the anadromous behaviour in pike in the Baltic Sea evolved? The spawning migration to freshwater should increase lifetime reproductive success (fitness) otherwise the fish should be resident in the sea (Gross, 1987). The sea offers good foraging resources and a large variation in litoral and pelagic habitats (Gross, et al., 1988). Freshwater streams are used for spawning during a period of weeks in springtime. There are several benefits for pike to spawn in freshwater. First, shallow flooded areas heat up quickly, providing a fast hatching and a rich food base for pike larvae (Casselman, Lewis, 1996; Nilsson, 2006). Second, predation on eggs and larvae are less intense in freshwater (Nilsson, 2006). Müller (1986) proposed that the primary reason for anadromous migration of pike is higher temperatures in the streams compared to the sea, creating an attraction stimuli for pike to migrate. However, recent studies show the opposite, with lower temperatures in streams compared to coastal bays (Ljunggren, et al., 2011). Despite water temperatures spawning takes place about one month earlier in freshwater (Nilsson, 2006). It seems that anadromous pike have developed an adaption when and where to migrate, probably to match the spring flood in rivers and streams. The earlier spawning means an advantage in size for the juveniles compared with conspecifics born in the sea. It has been suggested that the genetic patch size of pike (for management) in the Baltic Sea is 100-150 km and that it consists of one single

panmictic population (Laikre, et al., 2005a; Laikre, et al., 2005b). The genetic differences in these fishes were proposed to be a function of geographical distance. However, it is not clear if the analysed pike were born in fresh – or marine waters. Preliminary studies of pike from adjacent rivers reveal genetical differences (Ljunggren, et al., 2011). Assuming that homing behaviour creates distinct anadromous populations, management of these populations have to be attended separately. Westin and Limburg (2002) showed reproductive barriers between anadromous pike and pike born in the sea, indicating sympatric populations with genetical adaptations. Size at maturity is larger for several anadromous salmonid species compared with non-anadromous forms (Gross, 1987). Larger fish have a higher reproductive success since quality and amount of roe increase with body size (Gross, et al., 1988). With anadromous pike, life history traits as individual growth rate, size at maturity and overall body size may differ between populations, which provide incentives for fishery management (FIG. 3). If pike return to former utilized spawning grounds in freshwater (homing) or even to their natal spawning ground (natal homing), the dispersal of these pike will be limited (Miller, et al., 2001). This means that small populations with local adaptations in behaviour and physical properties in a stream have an imminent risk of total extinction.

How do anadromous pike find their way home? In species of salmon, theories about different navigational “tools” have been proposed. Imprinted geomagnetic cues are suggested to assist the fish when navigating over longer distances in the sea on its way to the spawning region. When close to its natal river, the fish locates the migration route by sensing chemical cues from the river water (Lohmann, et al., 2008). It is possible that pike use both of these methods for their navigation to the spawning grounds.



FIG. 3 Why do pike from certain rivers become larger than others? An historical catch in River Lödde 1997-03-23. From left, Dick Persson with 19.9 kg (127 cm), 16.5 kg and Mikael Paulsson with 15.9 kg. Photo: Peter Gråhn

Using otolith chemistry in research

Earstones of fish, or otoliths, are calcified structures situated in three pairs in the head of the fish (Campana, 1999, FIG. 5b). The chemical composition can be used in reconstructing life histories of fish, since several elements from surrounding water are incorporated in the earstone. The otolith itself is considered to be metabolically inert, which makes it a recording device of events in the life of the fish (Campana, 1999). To analyse them, they are ground down to the core, revealing increments from birth to death of the fish (FIG. 5a). Natural tags such as otoliths are useful tools and have advantages compared with conventional tags. It involves no handling of the fish affecting its behaviour, requires no recapture of fish, and it constantly records data (Elsdon, et al., 2008). However, using otoliths in combination with other markings of the fish (such as dart-tags, pit-tags), could create more certainty in the sampling (Elsdon, et al., 2008). Otoliths can answer questions about natal origin (Thorrold, et al., 1998), early life-history strategies (Bradbury, et al., 2008b) and fish stock assessment (Campana, et al., 2000). The most common use of otoliths is to study fish migrations between fresh- and marine waters (Gillanders, 2005; Kafemann, et al., 2000; Limburg, 1995; Secor, Rooker, 2000). The fish that undergo such migrations are called *diadromous*.

Diadromous fish can be divided in three categories:

- *anadromous* – live in the sea during most of the year, migrate to spawn in freshwater.
- *catadromous* – live in freshwater, migrate to spawn in the sea.
- *amphidromous* – migrate between the sea and freshwater, but not for spawning.

The concentration of strontium (Sr) is considerably higher in seawater compared with freshwater, and correlates positively with salinity (Ingram, Sloan, 1992; Zimmerman, 2005). Often a ratio between strontium and calcium is used (Sr:Ca) and it has been shown in studies that Sr:Ca deposited in otoliths is in proportion with Sr:Ca of the surrounding water (Bath, et al., 2000; Milton, Chenery, 2001). Figure 4 shows a simplified example of how Sr:Ca in otoliths can detect movements between freshwater and marine waters.

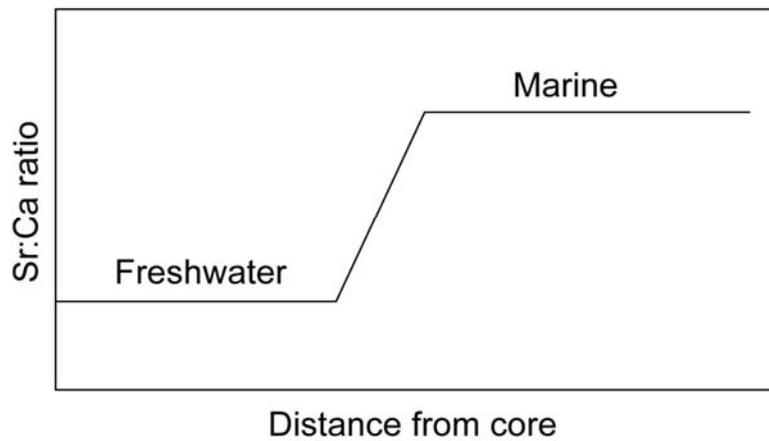


FIG. 4. *A conceptual figure of how Sr:Ca ratio changes in otoliths of diadromous fish when moving from freshwater to saltwater.*

An elemental fingerprint can be established by analysing several elements incorporated in the otolith. The theory is that e.g. rivers have different water chemistry, that it can be reflected in the otoliths and used to identify spawning fish to a specific river (homing behaviour and natal origin) (Bradbury, et al., 2008a; Clarke, et al., 2007; Nishimoto, et al., 2010).



FIG. 5a *The inner core of an otolith* **b)** *The three pairs of pike otoliths. From above the sagittae, asteriscii and lapilli. (Photo: Olof Engstedt)*

AIMS

The aim of this thesis was to extend the knowledge about pike with freshwater origin in the Baltic Sea through the following objectives:

- To investigate how common freshwater origin is for pike inhabiting the Baltic Sea (Paper I).
- To investigate if otolith strontium in pike can be used as a tool to reconstruct life histories in the Baltic Sea (Paper II).
- To obtain an understanding of the seasonal spawning migration of pike to rivers and if the pike return to the river they were born in (natal homing) (Paper III and IV).
- To use the collected knowledge and reconstruct former wetlands with the aim to increase pike production to the Baltic Sea (Paper V).

STUDY AREA

The study area comprises the Baltic Sea and five streams leading out in the sea. Most of the surveys in the sea were carried out in Kalmar Sound, southeast of Sweden (enlarged picture in FIG. 6). The investigated streams were:

Törnebybäcken

A small stream with an average flow of less than $0.5 \text{ m}^3 \text{ s}^{-1}$. It is considerably nutrient enriched from adjacent airport and agriculture. In 1996 a wetland system of 8 ponds was constructed in the lower parts of the stream. The last pond was accessible for anadromous pike but heavily overgrown by *Phragmites* belts reducing the spawning area. During spring 2007 a restoration measure for fish was performed in the last pond before the outlet into the stream. The *Phragmites* was dugged up and the water surface was increased 3 times to 3.5 ha. The dominating fish species are pike, roach, tench (*Tinca tinca*) and ide.

Kronobäck/Oknebäck

Kronobäck and Oknebäck are two branches of the brook Koverhultsbäcken. The two small streams lead out in the Baltic close to each other. It passes mainly through woodland, but in the lower parts it is surrounded by agriculture. The average flow is below $0.5 \text{ m}^3 \text{ s}^{-1}$. Like many other of these coastal streams the watercourse have been straightened and barriers have been built, especially in the lower parts, decreasing the frequency for flooded water on grassland. In beginning of 2008, a habitat restoration for pike reproduction was carried out. It consisted of widening by digging the riverbed in Oknebäck, creating depths from 0.3-1.5 m. Very little vegetation was left. In Kronobäck, the straightened watercourse was reconstructed to meandering. Close to its river mouth a dam was constructed, flooding the water to about 40 cm over 3 ha grassland (grasses and sedges). To secure water levels, a small ditch from Oknebäck was led in. The dam could regulate the water level. The dominating fish species are pike, ide and roach.

Lerviksbacken

A small ($< 0.5 \text{ m}^3 \text{ s}^{-1}$ average) straightened stream with high barriers on both sides, flowing through agricultural landscape. During the late fall of 2008, measures to improve pike reproduction was made. A widening of the riverbed created a wetland of 1.5 ha about 1 km from the river mouth. The digging resulted in an average water depth of 0.5 m with flat shorelines. The dominating fish species are pike, ide and roach.

Snärjebäcken

A river with an average water discharge of $1.5 \text{ m}^3 \text{ s}^{-1}$ running through woodland and agricultural landscape. A wetland was created late 2008, however the purpose was more for nutrient removal and catchment rather than for fish. In

the lower parts of the river are flat meadows that could easily be transformed to a wetland optimised for pike reproduction. The dominating fish species are pike, perch, roach and tench.

Frösslundabäcken

A small stream ($< 0.5 \text{ m}^3 \text{ s}^{-1}$ average) that frequently dry out during summertime (Leberfinger, Herrmann, 2010). Running on the Great Alvar Plain with some agriculture and deciduous forests in the lower parts close to the Baltic Sea. The dominating fish species are pike and trout (*Salmo trutta trutta*).



FIG. 6 Location of the study streams in this thesis.

RESULTS AND DISCUSSION

Papers I and II

How common is anadromy in pike living in the Baltic Sea?

A few studies have shown that migrations from the sea to freshwater exist for pike in the Baltic Sea (Muller, 1986; Westin, Limburg, 2002). The latter study used Sr:Ca ratios in otoliths to confirm freshwater origin of pike through a limited number of samples (n=10). Their study revealed that freshwater born pike exist in Baltic Sea pike, but not to what extent. We investigated the life history by sampling pike from the Baltic Sea during the summer period, when pike originating from freshwater and marine waters are mixed in the sea, to forage (paper I). Using otolith data from juveniles in rivers as references, a Sr:Ca freshwater signature was developed statistically. In the investigated material (n = 175), a total of 80 pike (45 %) were interpreted to be of freshwater origin (paper I, FIG. 8).

Contrasting the vast marine areas potentially suitable for spawning to the limited freshwater spawning habitats, freshwater recruitment of pike seems to be very successful.

Of the freshwater classified adult pike, 79 % had one or more signs of freshwater imprints in their otoliths besides their natal imprint (paper I, FIG. 7b). The fish classified to be of marine origin, however also had freshwater imprints but to a lower extent, - 45 % (paper I). The results indicated that freshwater is important for pike regardless of origin, either for spawning or foraging. Otolith analyses further revealed that pike in this study had high Sr:Ca values in the centre of the core. This was most obvious in the pike of freshwater origin (FIG 7b). Kalish (1990) showed that salmon juveniles had higher Sr:Ca values if the mother came from the sea (anadromous). The habitat where vitellogenesis takes place seem to be reflected in Sr:Ca values in the otolith core, showing the mother origin in the otoliths of the juvenile (Kalish, 1990). In pike, vitellogenesis (yolk deposition) starts in September-October and continues until spawning occurs in March-May (Billard, 1996). The habitat for the anadromous pike during vitellogenesis is mainly the Baltic Sea (paper III).

Using total length of pike and otolith diameter, a relationship was established to calculate at which length the anadromous pike migrated out of freshwater as juveniles. The back-calculated size at emigration from freshwater in adult otoliths ranged from 1-38 cm (paper I). Juveniles that had reached adulthood were significantly larger at emigration compared with average larvae/juvenile trapped in a river on their way to the sea (paper I). However, both early and late emigrants contributed to the population.

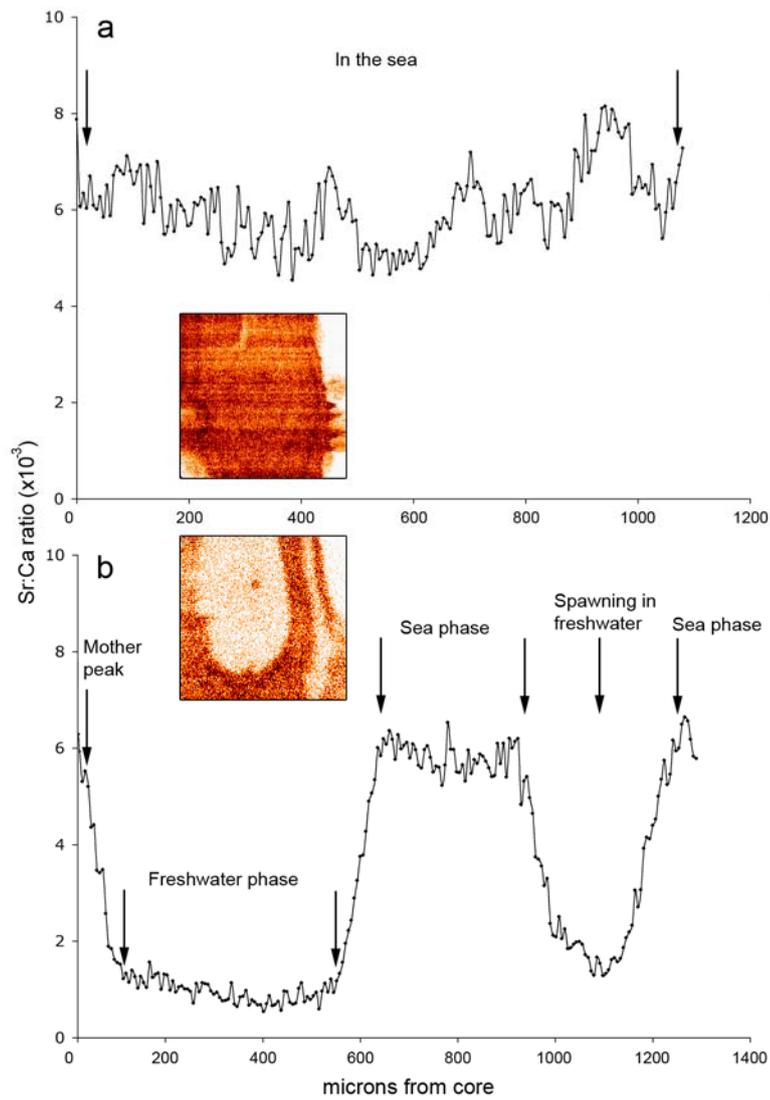


FIG. 7 Sr:Ca quotients in an otolith over the lifetime (distance from otolith core, μm) of **a**) one pike born in the sea shown as a graph and as a Sr PIXE map (inset). The fish stay in the sea for the whole lifetime as shown by the high Sr:Ca signal. **b**) one pike born in freshwater. The Sr:Ca signals start with a "mother peak" (Kalish, 1990) where Sr from the mother has been transferred into the egg, followed by the juvenile growth in the stream (freshwater), migration to the sea and growth in this habitat. The adult fish then migrated back to the stream probably for spawning and then return to the sea.

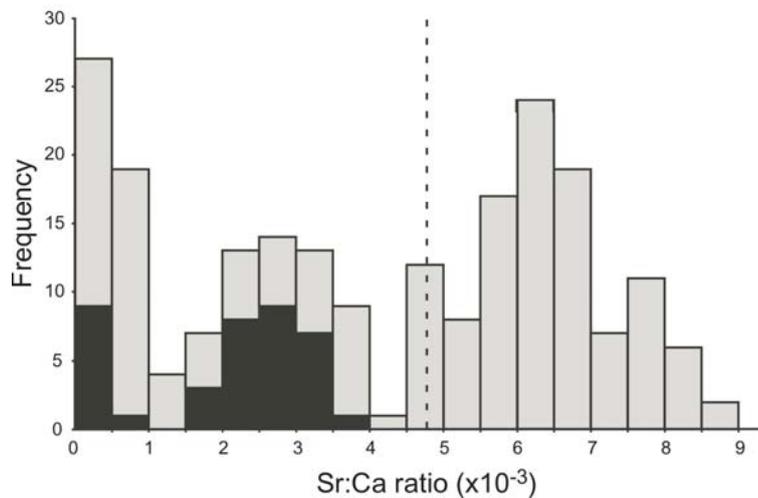


FIG. 8 The frequency of natal Sr:Ca ratios in otoliths from juveniles of known origin and in otoliths from adults of unknown origin. The bars are additive with the adults on top. The dashed line was defined by bootstrapping the juveniles and represents the dividing point between freshwater and saltwater origin (paper I).

Validation of otolith strontium

A positive relationship between Sr:Ca in otoliths and ambient salinity have been shown for several fish species and environments (Bath, et al., 2000; Gillanders, 2005; Secor, et al., 1995; Zimmerman, 2005). However, most studies have focused on fish in true marine waters (> 30 ‰). No verification studies on the process for the brackish water of the Baltic Sea have been published. In a laboratory study, we set out to test responses in pike otoliths with increasing salinity (paper II). The results revealed a positive significant relationship between Sr:Ca and days with increasing salinity. By using a high resolution analysis, proton induced x-ray emission (PIXE), fine scale Sr:Ca increases were recorded (Elfman, et al., 2000; Johansson, Johansson, 1976; Limburg, et al., 2002). Maximum values of Sr:Ca in this experiment was in average 7.9×10^{-3} (paper II). This is comparable to the maximum values observed in adult pike from the Baltic Sea, 8.4×10^{-3} (paper I, FIG. 7a).

The question whether Sr:Ca is influenced by food intake was investigated (paper II). Pike were divided in the experiment into two food treatment groups (freshwater and marine food). The results showed that food contributed to Sr in otoliths of pike. Regressions of the two treatments were statistically different and maximum values differed. Metal analysis of the two food sources revealed a fourfold difference in Sr content (paper II). Whether Sr in food contributes to

Sr in otoliths is debated in many studies. Several have stated that Sr in food has no or little effect (Marohn, et al., 2009; Milton, Chenery, 2001). Other studies have stated the opposite (Buckel, et al., 2004; Limburg, 1995). For example, Buckel (2004) found a difference in otoliths of an eustarine piscivore, when given food with a fourfold difference in Sr concentration. It seems like there are interspecific differences concerning Sr uptake in fish. However, the risk of misinterpreting otolith analysis of pike in the Baltic Sea on account of food uptake of Sr is low, since most of its food originates from marine sources.

Papers III and IV

Homing of anadromous pike

In a long-term study involving four streams running out in the Baltic Sea, pike were marked during spawning season in order to study whether they returned to their spawning grounds. During the years of 2006-2009, 3415 pike were marked, where of 1371 marked with pit-tags. In three streams pike were marked with pit-tags and outer tags; Törnebybäcken, Kronobäck/Okneböck and Snärjebäcken. In Lerviksbacken only outer tags were used (FIG 6, 10a, b). In the watercourses pit-tag stations were built up every spawning season (FIG.9), with exception for Törnebybäcken, where the stations were running constantly during 2006-2010.



FIG. 9 PIT-TAG station powered by solar panels, recording returning pike after a year in the Baltic Sea (Photo: Olof Engstedt)



FIG. 10a Inserting a PIT-TAG in a spawning migrating pike and b) Pike marked with DART-TAG (Photo: Olof Engstedt).

In Törnebybäcken, a total of 317 pikes were marked during 2006-2008. Pit-tag data revealed the percentage of pike that returned the following year after marking. 41 % (2007), 44 % (2008) and 44 % (2009) (paper III). There was a loss of fish following a marked cohort in consecutive years. For example, 41 % of the fish marked 2006 returned 2007, in 2008 27 % of the 2006 fish returned and in 2009 16 % returned (paper III). The loss of fish was high between years, but considering mortality could be as much as 50 % each year, the return rates is high in each consecutive year after marking (Craig, 1996).

Assuming that homing behaviour in anadromous fish create distinct populations, management of these populations have to be attended separately.

In Snärjebäcken 41 % of the 125 marked pike in 2007 returned 2008 past the lower pit-tag station. 16 % of the 2007 fish returned in 2009. In this stream a pit-tag station were built 2.5 km upstream the river mouth. Only 7 out of 125 pike migrated above that station in 2007 (paper III). In 2008, 5 of these long migrators swam past this station. In 2009, 2 of the “long distance migrators” from 2008 returned to the river, and both were recorded at the upper pit-tag station. The results indicated that long migration is a trait, with the purpose of returning to the same spawning grounds each year (Vehanen, et al., 2006). This is in conformity with the behaviour of salmon, that not only return to the same river they were born in to spawn (natal homing), but also to the vicinity of their birth place (natal homing) (Gross, 1987; Miller, et al., 2001).

In Kronobäck/Okneböck the spawning migration was extensive during the first year (2008), 858 mature pike were recorded and marked (FIG 11). In 2009, 23 % (195 ind.) returned for spawning. In 2010, 10 % of the fish marked 2008 returned for spawning (paper III). The loss of pike between years seems to be consistent between the streams and rivers. The mean weight of pike was lowest in Kronobäck/Okneböck (1.2 kg), followed by Snärjebäcken (1.8 kg) and

Törnebybäcken (2.2 kg). The lower initial homing percentage in Kronobäck/Oknebäck (22 % compared with 41 % in both Törnebybäcken and Snärjebäcken), can be explained by the lower mean weight. A smaller pike are subjected to a wider range of predators that increase the probability of mortality (Craig, 1996; Le Cren, 1965).



FIG. 11 Male and female pike in arriving from the Baltic Sea to spawning grounds in Kronobäck. Notice the red tag marking. (Photo: Adam Bergman).

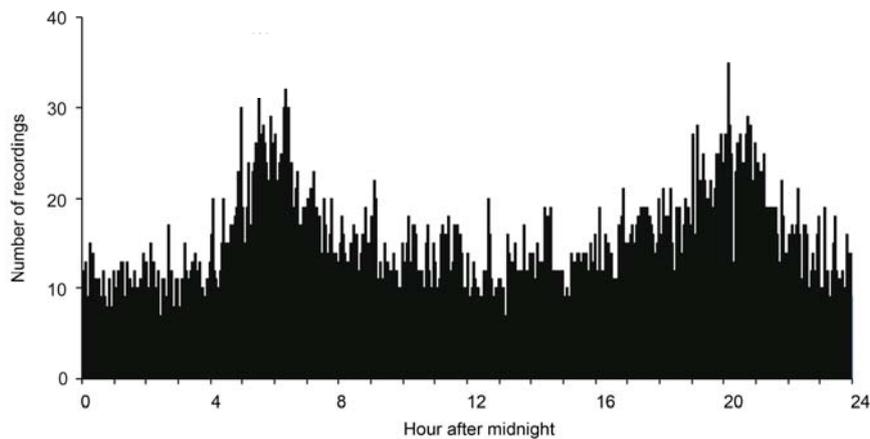


FIG. 12 Diel migration activity of pike during spawning season in Törnebybäcken. The Y-axis represents pit-tag antenna recordings and x-axis hours after midnight (Modified from paper III).

In Lerviksbäcken, only outer tags were used. Using fykenets covering the entire stream, pike were caught and marked. During four years, a total of 2044 pike were marked. Recaptures following years revealed a high return rate, 35 % (2006), 35 % (2007), 38 % (2008) and 42 % (2009) (paper III).

In the study of Hodder et al. (2007), pike exhibited a clear diel migration pattern. The pike showed most frequent movement during dawn and dusk. The results from the three streams with pit-tag stations corroborates Hodders results (paper III). This was especially true in Törnebybäcken, with clear bimodal distribution on antenna recordings during dawn and dusk (FIG. 12).

The homing behaviour of anadromous pike is a key factor to consider when making decisions on restoring wetlands for fish reproduction.

The marking studies showed that pike return to former spawning grounds (homing) to a high extent (paper III). However, the results do not tell whether the pike were born in the stream they later spawned in (natal homing). Studies in lakes have shown that pike do exhibit such behaviour (Miller, et al., 2001), but no evidence of natal homing of the anadromous pike in the Baltic Sea have been presented. Using elemental fingerprinting in otoliths, we set out to investigate this process (paper IV). Sr, Zn, Br, Co and Mn were analysed in the core of juvenile and adult pike otoliths from four streams, Törnebybäcken, Kronobäck, Lerviksbäcken and Frösslundabäcken. Through PCA analysis and ANOSIM analysis, statistical differences were shown between the juveniles from different streams and similarities for fish within streams. The adults were marked individuals that were recaptured in the streams after a year out in the sea. Even though it was years between adult and juvenile recruitment, adults and juveniles within streams grouped together (paper IV). The results indicate natal homing for pike.

Paper V

Pike factories - improving pike production

In 2007-2008, restoration of three wetlands adjacent to streams running out in Baltic Sea were carried out. The restorations were different depending on the physical properties of the wetland. In Törnebybäcken, reed belts were removed by digging and sediments were taken out. In Kronobäck, a dam was built and old spawning grounds were flooded with water (FIG. 13). In the Lervik stream, a widening of the riverbed by digging created new spawning areas for the pike.

A high production of pike in other temporarily flooded areas has previously been described and such areas are referred to as *pike factories* (Threinen, 1966).



FIG. 13 *The Kronobäck wetland after restoration; flooded shallow areas with emergent vegetation (Photo: Jonas Nilsson)*

The juvenile pike production was measured during the spawning season a year before each restoration measure and consecutive years after. The restoration in Kronobäck was the only measure that had a significant effect in increasing pike production. Before restoration about three thousand juveniles emigrated from the wetland each year. After restoration the number increased to over one hundred thousand juveniles annually in the following years (paper V, FIG. 14). This large increase followed directly after restoration, revealing that production was not limited to number of spawning adults, but more likely attributed to increased spawning and nursery habitats (Casselman, Lewis, 1996). In Törnebybäcken and Lervik, the total numbers of emigrating pike were annually below 3100 and 4600 respectively (paper V). After restoration in these wetlands, the total numbers decreased slightly. The reason for the decrease is probably vegetation that was removed during restoration. In Kronobäck, large areas with flooded vegetation were made available, contributing to a large increase in pike production. The sheltered and shallow areas that were created were optimal for

pike reproduction with emergent vegetation in patches such as grasses and sedges (Casselman, Lewis, 1996; Forney, 1968; Threinen, 1966). It is possible that the pike recruitment could increase in Törnebybäcken and Lervik when new vegetation is established.

In Kronobäck, more thorough studies of the juvenile pike were made. Yolk sac larvae were dominant in the shallowest areas with emergent vegetation (grasses and sedges). Free-swimming larvae of 14 and 19 mm were also dominant in this vegetation type. Areas with *Phragmites* showed lower abundance of these length classes of pike, but still considerably higher than areas with submerged or no vegetation (paper V, FIG. 15).

Zooplankton (copepods and cladocerans) were sampled in the four habitat types. The highest densities were found in emergent vegetation and *Phragmites* belts (paper V). Flooded vegetation offers a complex and rich habitat for development of zooplankton suitable as food for juvenile pike (Bry, 1996; Wright, Giles, 1987). Stomach contents of juvenile pike showed that zooplankton was the major food source for pike up to 35 mm. In pike <45 mm, insects were the dominating food source and from 45-68 mm fish became a common prey (paper V, FIG. 16). The fish diet consisted of cyprinid species such as juveniles of roach and ide, but smaller pike were also frequently found. Pike becoming cannibals quickly increase in size (Giles, et al., 1986).

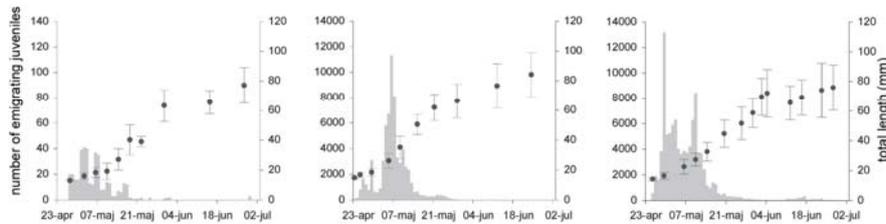


FIG. 14 Number and mean length (\pm SD) of emigrating pike juveniles caught in downstream traps in three successive years: Kronobäck, 2007, 2008 and 2009. Wetland restoration was made in early 2008 and a response in pike production was immediate (Modified from figure 6 in Paper V).

A majority of the juveniles (> 90 %) emigrating from the wetland were less than 6 cm of length (paper V). This information can be used in management of constructed flooded wetlands, by lowering the water level at a suitable time releasing most of the remaining pike juveniles to the sea. The flooded grass can then dry out and the area can be used for grazing cattle to reduce overgrowth of reed and bushes.

Local measures to counteract coastal eutrophication by constructing wetlands could successfully be combined with the recruitment of pike to the Baltic Sea.

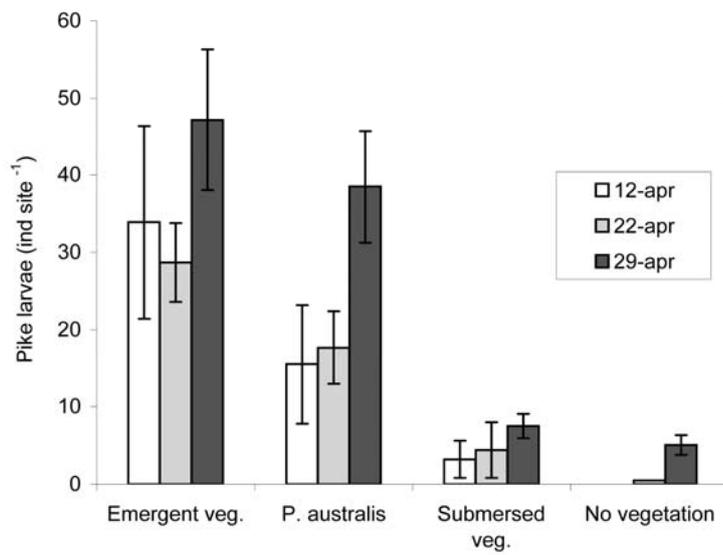


FIG. 15 Number of yolk sac larvae (April 12), 14-mm larvae (April 22), and 19-mm larvae (April 29) in habitats dominated by emergent vegetation (mainly grasses and half grasses), *P. australis*, and submersed vegetation and in non-vegetated areas.



FIG. 16 Juvenile pike around 7 cm in Kronobäck wetland with preyfish, roach and ide. (Photo: Jonas Nilsson)

Wetlands for nutrient removal from rivers running out in the Baltic Sea are often placed near the river mouths to have optimal effects in the drainage area (Paludan, et al., 2002). The wetlands catch phosphorous adsorbed to particles and by microbial processes transforms nitrate to nitrogen gas. The construction of wetlands in rivers entering the Baltic Sea have potential to reduce eutrophication in the Baltic Sea and there is a need to intensify the pace of constructing new wetlands (Jansson, Dahlberg, 1999; Paludan, et al., 2002). A wetland for nutrient removal could in most cases be combined with predatory fish production such as pike. Nutrient reduction and fish recruitment are optimised in shallow areas that heats up quickly, which provides fast hatching of pike larvae and also enhances the nitrification process (Casselman, Lewis, 1996). Nutrients caught in the wetland also provide the base of good food production for the juvenile pike (paper V).

CONCLUSIONS

Research on migration behaviour and spawning success of anadromous pike in the Baltic Sea have been scarce, thus very little is known. The research that has been made has stated that migration from the sea to freshwater behaviour exists, but not to what extent. The findings in my thesis have increased the knowledge base on pike of freshwater origin in the Baltic Sea. This knowledge can be applied when taking decisions on population restoration.

The main results in my thesis are:

- Anadromous pike are common in the Baltic Sea and <45 % of the fish have freshwater origin (**paper I**).
- Sr:Ca in pike otoliths is a useful proxy for salinity in the Baltic Sea, thus the migrations between freshwater and brackish water can be reconstructed in the otoliths (**paper II**).
- Spawning migrations of pike from the Baltic Sea to streams and rivers are extensive, in some watercourses > 1000 individuals gather every year in the springtime (**paper III**).
- Pike return to a high extent to same streams and rivers for spawning (homing behaviour), up to 45 % of marked fish returned the following year after marking (**paper III**).
- Individual migration behaviour such as “long migration” (>2 km) has been observed in individual pike in consecutive years (**paper III**).
- Analysing elemental fingerprints in otoliths, pike were interpreted to be spawning in the same stream as they were born – natal homing (**paper IV**).
- More than 90 % of juvenile pike emigrate from nursery areas to the sea before reaching a size of 60 mm. These size-classes build up the major part of the stock in the sea (**paper V**).
- Pike production to the Baltic Sea in a small stream could with little means increase with a factor of hundred (**paper V**).

Taken together, our results show that anadromous behaviour in pike is common in the Baltic Sea. Spawning migration is extensive, even in small streams. A large part of the pike in the sea have freshwater origin, that reveals a high spawning success in freshwater considering the vast areas available for spawning

in the sea. The fact that pike to a high extent return to the same watercourse year after year to spawn, even to the same stream they were born in, reveals that anadromous pike in the Baltic Sea probably are consisting of separate populations. The fact that pike in the sea are composed of different populations increases the vulnerability and creates incitements for restoration plans on an other scale than the whole Baltic Sea. The focus on management should instead be based on populations in individual streams and rivers. Results from wetland restorations show that pike production to the Baltic Sea could be drastically improved, through creating *pike factories* constituted of flooded grasslands. The results create incitements to restore previously drained and ditched watercourses along the entire coastline, to increase pike abundance in the Baltic Sea.

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FIG. 17. *Back she goes...* Pike from Lödde river 2010, 13,78 kg, 115 cm. Foto: Carl-Johan Andersson.

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