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Consequences on population dynamics following regained connectivity in pike (*Esox lucius*) spawning location

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Abstract

Distributional movements of subpopulations may act as a buffer to prevent the loss of a species in a certain area. However, within subpopulations adaptations may evolve that makes the inhabitants of a certain habitat to better cope with prevailing environmental conditions. If such traits are related to reproduction, they may reduce the opportunity of gene exchange between other subpopulations. Also, a lack of adaptations to a specific habitat may be what prevents a group of individuals, arriving from an adjacent habitat, to successfully colonize an area where a previous subpopulation has been lost.

This is the report from a field study conducted in the wetland Lake Långsjön, that in 2018 was restored in order to promote the recruitment of anadromous pike (*Esox lucius*) to the Baltic Sea. Commonly, wetlands that are restored to promote anadromous pike recruitment, are constructed so that they enable spawning migration from the sea towards the wetland and juvenile emigration towards the sea only. In that sense Lake Långsjön is different, from other wetlands restored for the same purpose, due to that it is connected to both the Baltic Sea and an upstream located freshwater lake. By quantifying the migration of pike (spawners and juveniles) in both directions I explore the consequences that the regained connectivity between the Lake Långsjön and the coast may have on the population dynamics within this wetland; (i) whether it is potentially influenced by allowing mixture between pike with different migratory strategies for spawning (anadromous and potamodromous), (ii) what drivers there are of pike fry emigration and how they may influence the pike fry emigration route and (iii) whether or not the pike of potamodromous origin, resident in the upstream located lake, may work as a source, providing the Baltic Sea with pike juveniles. Pike spawners arriving in the wetland were caught in traps between March - April. Pike fry were caught withing the wetland with fyke nets and by netting. Emigrating pike fry were caught in fyke nets. Findings suggest that spawning migration patterns do not differ between anadromous and potamodromous pike. However, the spawners arriving from the Baltic Sea I suggested are to be composed by offspring of potamodromous origin, possibly hatched during the previous season, and that they as juveniles swam downstream. This, in turn, indicates that the potamodromous stock can help establish an anadromous stock in the Baltic Sea. Still, due to the observation of pike fry displaying an emigration behaviour upstream, origin is identified as a factor that may influence the pike fry emigration route. Also, this emigration pattern seems to indicate a heritable trait that has not been described before among pike, that of downstream spawning. The restoration of the wetland and the regained connectivity is key, both for the ability to restock the Baltic Sea with pike juveniles but also to ensure the conservation of a fascinating stock of pike exhibiting a unique spawning strategy.

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Key words

Admixture, emigration, downstream spawning, pike-factory, restoration, source-sink dynamics, spawning strategy,

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Table of contents

1 Introduction

A habitat of low quality (a sink) for a certain organism may lead to that a population living there goes extinct. However, a high-quality habitat (a source) can allow a population to increase leading to a surplus. If individuals of the surplus population move into the sink, the sink population may sustain (Holt.,1985). The understanding of such source-sink dynamics within species have been addressed as a key in conservation management (Berumen et al., 2012; Jones et al., 2005). The movements of populations between habitats have been addressed as a factor that may buffer against extinctions due to environmental changes (Cure et al., 2017). But for that to happen it requires that populations are allowed to disperse and that plasticity allow individuals to cope with the different local environmental conditions that may prevail in the dfferent habitats (Thomas et al., 2001). Disrupted connectivity may lead to that a subpopulation becomes isolated (Fukushima et al., 2007). If the diversity within the subpopulation is not high enough it will reduce population resilience and can be a contributing factor to extinction (Hellmair & Kinziger., 2014). On the other hand, if the subpopulation persists, it may lead to the evolution of novel traits (Sturmbauer, C., 1998; Seehausen, O., 2006).

Fish species may exist as discrete adult populations, connected via a dispersive larval stage (Cowen et al., 2007) or as sub-populations that use strictly separated recruitment strategies (Engstedt et al., 2010). Adults of different origin might utilize forage habitats that overlap one another, while spawning in different areas and evolving unique traits to cope with the characteristics of the spawning habitat (Berggren et al., 2016; Nordahl et al., 2019; Sunde etal., 2018; Tibblin et al., 2015). In discussions regarding fish-population-management, depending on the case and the species of interest, lights could therefore be put either on measures promoting connectivity (Greenberg and Calles, 2010; Nyqvist et al., 2018; Park et al., 2008) allowing former subpopulations to once again meet and interbreed as well as on conservation and/or restoration of fragmented habitats that are of use for specific subpopulations (Engstedt et al., 2010).

In the Baltic sea, habitat degradation, attributed to exploitation and overfishing, has led to cascading effects and vast changes in the composition of the coastal fish communities. A species that has undergone substantial declines during the past decades is the dominating predator northern pike (Esox lucius) (Ljunggren et al., 2010; Olsson, 2019).). From previously being a very abundant species in the coastal habitat, pike are now relatively rare with the fish community experiencing a dramatic increase of meso predatory species, notably the three-spined stickleback (*Gasterosteus aculeatus*)(Eriksson et al., 2009.; Eklöf et al., 2020). Along with an increase in interspecific resource competition among pike fry (Larsson et al., 2015), the three-spined sticklebacks are predating on pike fry larvae and are suggested to prevent pike populations to recover (Bergström et al., 2015.; Nilsson et al., 2019). Thus, a regime-shift has taken place from the top-down controlled ecosystem, with pike and other predators suppressing sticklebacks to a bottom-up controlled food-web where sticklebacks seem to control the ecosystem function (Eklöf et al., 2020). The extent of the different factors impacting the decline of pike abundance may vary but all in all, recruitment problems are established as an overall explanation to the negative trend (Larsson et al., 2015; Ljunggren et al., 2010).

Sympatric pike populations, in the Baltic sea, use different spawning strategies. Either pike spawn in coastal shallow bays (residents) or migrate to spawn in rivers and wetlands (anadromous) (Engstedt et al., 2010; Müller, 1986; Westin and Limburg, 2002). In general, species that exhibit seasonal migrations have evolved such patterns to time environmental conditions in order to maximize fitness (Miller et al., 2005; Saino et al., 2010). Adaptions to the respective spawning area are well documented among fish species that exhibit anadromous life cycles (*Kovach et al., 2012;* Lura, H. & Sægrov, H. 1993). Recent research has shown that anadromous pike populations in the Baltic Sea repeatedly return to their place (stream/wetland) of birth in order to spawn, more known as natal homing (Engstedt et al., 2014). In turn, this have contributed to restrict the genetic exchange (gene flow) resulting in genetic differentiation among pike from different streams such that the Baltic Sea pike population consists of several subpopulations even within confided geographic areas (Nordahl, et al., 2019). By being exposed to different environments (selective regimes) during reproduction, the different pike subpopulations have evolved adaptations to cope with the local environment in their respective spawning habitats such as differences in larval traits (Tibblin, Forsman et al., 2016); and salinity tolerance (Sunde et al., 2018a). Due to the local adaptations of different sub-populations to their recruitment environments, management actions are suggested to *not* include mixing of individuals of different origin (Larsson et al., 2015). However, interbreeding by previously separated populations, referred to as admixture, can affect populations in different degrees (Lynch, 1991, Sunde et al., 2018b). When two populations are genetically divergent, they receive novel alleles from one another when interbreeding thus enabling an increase in genetic diversity (Harpur et al., 2012). This may prevent inbreeding depression and conceal harmful recessive alleles and result in heterosis (Lynch, 1991; Weeks et al., 2011)**.** Such outcomes are beneficial since more diverse populations show higher resilience, better abilities to adapt to new environmental conditions as well as higher colonization success than more uniform populations (Forsman, 2014.; Forsman & Wennersten, 2016). On the other hand, admixture may influence fitness negatively by diminishing favourable alleles and the effects of coadapted genes developing from local adaption (Lynch, 1991) Also, admixture might impair fertility and viability of young life-stages (Sunde & Forsman, 2016).

During the last centuries a consistent drainage of wetlands has been ongoing to promote agriculture in Sweden. This exploitation has resulted in an estimated 90 % loss of wetlands in some areas (Alström & Krook 2008). As a consequence, much of the spawning habitats for anadromous pike have been altered if not erased, yet a considerable proportion of the Baltic Sea pike have an anadromous life cycle which indicates that freshwater spawning habitats are important in contributing recruits to the Baltic Sea pike stock (Larsson et al., 2015). To compensate for the general decline of pike in coastal waters, Engstedt (2010) and Nilsson et al., (2014) proposed that restoration of such wetlands, i.e. creation of so called “pike-factories”, is a cost-effective management effort to improve pike abundances and restoring the coastal ecosystem functioning through increased top-down effects.

Prevailing environmental conditions during spawning and early life-stages are known to impact fish recruitment processes and even subtle variation thereof may influence the recruitment success (Hjort 1914). As an example, the hatching success of pike might vary depending on the temperature during incubation (Sunde et al., 2019). Also, early larvae stages are strongly influenced by environmental conditions, for instance the resource availability at the onset of exogenous feeding have been suggested to be a main driver regarding dynamics of fish recruitment (Cushing, 1975). The idea is that a pike factory should meet such requirements and to be optimized as a nursery habitat it is suggested to contain terrestrial vegetation that is temporarily flooded with a mean depth of 0.2 - 0.5 meters creating an environment that offers both favourable temperature conditions, shelter and food resources in the form of zooplankton and invertebrates (Nilsson et al., 2014). The timing of water level fluctuations within the wetland is crucial due to that it, in various ways, affect pike fry dynamics. As for example, pike fry cannibalism increases with increased density (Wright and Giles, 1987). The cannibalism, together with increasing competition, due to sinking water levels, is suggested to initiate increased pike fry emigration from the nursery habitat (Nilsson et al., 2014). Fry tend to leave the wetland within one month after hatch (Engstedt, 2010) but spawning may last for several weeks (Nilsson et al., 2014) and hatching is dependent on degree days resulting in a continuous recruitment of fry. Thus, pike fry emigrates at different times and sizes (Skov and Nilsson, 2018) and the timing of larvae emigration is size dependent such that early hatched or fast-growing individuals will migrate first (Skov and Nilsson 2018). However, the effects of cannibalism could conceivably also affect emigration so that smaller pike fry are forced to emigrate earlier to avoid predation by larger individuals.

One recently created pike factory along the Swedish coast is the restoration of the earlier drained and overgrown Lake Långsjön in the county of Sörmland. The area has gone through several drainages in the past. After the last lowering Lake Långsjön was constituted by meadow land that was mowed annually. The meadow areas were flooded during spring, thus exhibiting favourable conditions for pike spawning. However, the annual mowing has ceased since the mid 1970s, why the wetland was allowed to overgrow by common reed (*Phragmites australis*). This prevented pike to use the area as a spawning habitat in that extent as it was done prior to the alteration of the habitat.

Nowadays Lake Långsjön consists of meadow and is allowed to flood during spring. This pike factory is unique due to the fact that it in addition to be connected to the coastal habitat, also is connected to the upstream located lake Mellsjön. This allows both anadromous pike from the Baltic sea and potamodromous pike to migrate downstream to spawn in Lake Långsjön. Pike arriving from Lake Mellsjön have been able to reach the wetland also after the overgrowth. A small field in the southern part of the wetland has been mowed as well as flooded annually (**Figure 1**). Here, pike spawning has been observed also prior to the restoration. The stream that connects the wetland to the Baltic Sea (Ålebäcken) has been blocked during half a century in various ways; from the mid 1950s until mid 1970s by a permanent fishing installation, allowing fish to pass only during high water levels, and by a metal slab between mid 1980s to 2015 that completely prevented upstream migrating fish (i.e. that arrived from the sea) to enter the wetland. However, pike may have been able to swim downstream past the impediment during high flow *(Franzén Rolf – personal communication 2020*). Thereby, potential interbreeding between anadromous and potamodromous pike that have utilized Lake Långsjön to spawn, have been prohibited for a considerable amount of years. It is uncertain however, if and to what extent pike have been spawning in the stream during these years. Adult pike have been observed migrating from the Baltic Sea towards the wetland during spring after that the restoration was completed (Ljunggren Nils 2019 - unpublished). Therefore, it could be that a remnant anadromous population still exist that are about to recolonize the wetland as spawning location. Also, observations suggest that pike fry migrate in both directions (upstream to Mellsjön, downstream to the Baltic) during spring and summer (Ljunggren Nils 2019 – personal communication). However, there is still a lack of more detailed knowledge about these alternative migratory strategies including quantifications thereof. Also, behavioural and morphological differences between individuals with different strategies remain unstudied. It is also uncertain how the regained connectivity, enabling anadromous pike to interbreed with a potamodromous stock, do affect the population dynamics and productivity of the pike factory i.e. to what extent the pike factory supplies the Baltic sea with juveniles.

Local spawning adaptations may evolve in fish populations exposed to a new environment within just a few generations (i.e decades) (Hendry et al., 2000). Such adaptation will probably reinforce the reproductive separation between stocks (Nosil et al. 2003) and in turn launch a feed-back loop that accelerates the differentiation process between the stocks- known as Isolation By Adaptation (IBA) (Nosil. 2008). Also, differences in timing of reproduction among individuals may lead to reproductive isolation, known as Isolation By Time (IBT; Hendry & Day 2005). This raises questions as; to what degree the anadromous and potamodromous pike have been interbreeding formerly, as well as whether two nowadays *potentially* interbreeding stocks actually do interbreed. An answer would help understand whether the anadromous and the potamodromous strategy is inherent from adult to offspring. From a management view the final question to be asked is whether his mixture of pike with different life history strategies (anadromous and potamodromous) influences the recruit of pike juveniles from the pike factory to the Baltic Sea.

Both general and habitat-specific investigations are important to shape future successful management. This study aims to get a better understanding of the dynamics influencing pike recruitment in Lake Långsjön. Information about whether there is any temporal mismatch in the arrival of anadromous and potamodromous spawners to the wetland would give an indication whether the spawning of the two stocks is separated. Also, by quantifying the emigration of pike juveniles from the wetland in each direction and compare that to the number of spawners arriving from each direction, one would get a better understanding whether and how other factors rather than origin might affect the emigration towards each of the two forage habitats. In turn, this could give valuable information for future management and whether Lake Långsjön, with the regained connectivity that the restoration has entailed, should be seen as a role model for future pike factory restorations.

2 Addressed questions and hypothesis

2.1 Are the spawning migrations of the two stocks separated in time?

Functional genetic differences may have evolved between the stocks of pike that formerly were spawning in Lake Långsjön, leading to divergent spawning behaviour that may restrict gene flow between anadromous and potamodromous pike, despite that they nowadays have access to the same spawning area. This could be attributed geographic separation (thus, within the wetland) , IBA or IBT. A combination of the three would likely reinforce the reproductive separation. Based on previous studies on fish (Hendry and Day, 2005) and since all spawners have access to the same spawning ground, IBT is considered as the most likely factor that could prevent gene flow nowadays. Hence, the question evaluated is whether individuals from the two populations actually migrate to the wetland during the same period of the spawning season.

2.2 Does the proportion of pike juveniles emigrating down- and upstream correspond to the number of spawners arriving from each direction?

If the spawning migratory strategy (upstream anadromous or downstream potadromous) involves genetic heritable components, the direction of emigration in the offspring should mirror their parental strategy, i.e. they should emigrate the same direction out of the wetland as their parents did arrive. Here, the proportion of fry emigrating from Lake Långsjön in each adjacent creek (downstream vs upstream) is used as a proxy of produced offspring of each strategy. This to see whether that proportion do correspond to the proportion and size distribution (to be used to estimate fecundity) of parental fish migrating to Långsjön in the same creek from both directions. i.e. is the number of migrating fry proportional to the number adults migrating in each creek?

I hypothesize that the potamodromous pike is working as a source, contributing pike fry to the Baltic Sea. Also I expect that there will be a higher proportion of fry emigrating downstream into the Baltic sea than upstream to a lake at a higher altitude compared to the proportion of adult pike entering the spawning area from each creek. The less demanding emigration downstream ought to make pike more prone to choose that way.

2.3 What are the drivers of emigration?

Abiotic factors such as water temperature and barometric pressure are known to affect fish activity and migration behaviour (Peterson, 1972; Zamorov et al. 2018). In previous studies of pike factories, pike fry has shown to be more prone to emigrate during days with clear skies (Johansson Erik 2019 - unpublished).

Also, size distribution, pike fry density and water level, that all are potential drivers of migration, will be examined. The main question above, is divided into several sub-questions:

- What influence does pike fry size have on the time for emigration and emigration route?
- Are there differences in size distribution (mean ± variance) between emigrating fry (henceforth emigrators) and fry dwelling in the nursery site (henceforth stayers) at a given instant?
- Does the proportion of fry emigrating downstream (henceforth downstream emigrators) and fry emigrating upstream (henceforth upstream emigrators) change across the season?

I hypothesize that cannibalism is a main driver of emigration and as water level drops smaller individuals, who likely would be more exposed to cannibalism (*Craig 1987)*, also would be prone to leave the nursery site to reduce the risk of predation. The timing of leaving the nursery ground has been suggested to be a mechanism for avoiding cannibalism (*Nilsson et al., 2014*). Therefore, it is likely that differences in size will be found between emigrators and stayers at a given instant. Bigger fish are assumed to have a better swimming ability (*Bainbridge, 1957*) which may work as a selecting agent allowing only bigger individuals to swim upstream. Therefore, I hypothesize that downstream emigrators, by average, will be smaller than upstream emigrators. Also, a pike fry emigrating in order to avoid competition and predation might chose the less demanding and likely faster way out of the wetland, thus swimming downstream. Therefore, when cannibalism is as most perceptible, not only the the difference between stayers and emigrators are expected to be found but also the biggest differences between downstream and upstream emigrators.

3 Methods

3.1 Study area

A field study was conducted in the recently restored wetland Lake Långsjön (58°37'56.0"N 16°59'29.4"E) (**Figure 1**). The area stretches over 30 ha and consists of meadow land. Into the wetland a creek (Påldiket) is flowing. Påldiket connects the wetland to the upstream located Lake Mellsjön. The outlet, connecting the wetland to the Baltic sea via the downstream creek (Ålebäcken), is dammed to be able to control the water levels. Between March - mid June the meadow is flooded, whereafter the dam is gradually dismantled in order to mimic a natural flux. The connectivity between the wetland, and the Baltic sea is ensured via a bypass channel during the period when the outlet is dammed. Through the wetland a ditch (approximately 3 meters deep), is running. Also, there is a deeper area (on average approximately 4 meters deep). Considering what is typically preferred by pike as spawning and nursery habitat (*Nilsson et al., 2014*) no part of either the ditches or the deep hole is assumed to be utilized as spawning- / nursery-sites by pike.

Prior to the restoration, the ditches and a small field in the southern end, that was prevented from overgrowth, were the only areas where there was open water. The previous meadow land was left dry (**Figure 1**). Here is where pike spawning most often has been observed prior to the restoration (*Franzén Rolf and Hansson Gunnar., 2020 - personal communication*). The first spawning event after the restoration was completed, took place in 2019 (Gustafsson Rickard., 2020 - personal communication).

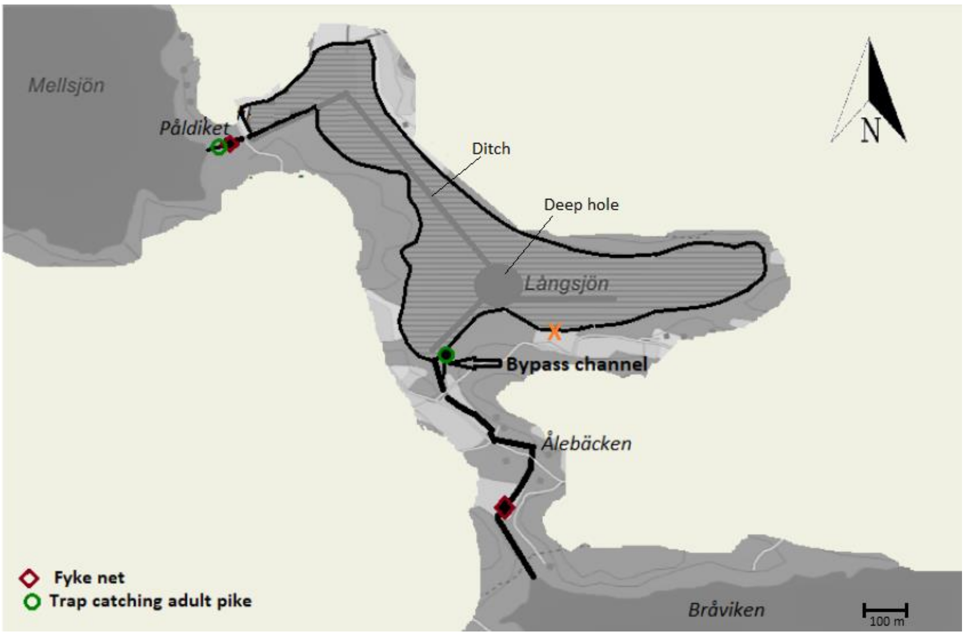

Figure 1. Lake långsjön and the two creeks Påldiket and Ålebäck connecting the spawning area with Lake Mellsjön and Bråviken (Baltic sea). The locations where fyke nets (◊) catching emigrating pike fry were placed as well as the locations of the traps (**O**) catching adult pike entering Lake långsjön are marked (note that the placements of the trap catching adults arriving from Lake Mellsjön and the fyke net catching upstream emigrators in Påldiket overlap). The field next to the southern bay marked by X, has been prevented from overgrowth also after the drainage. Here is where pike spawning has been observed most frequently prior the restoration.

3.1.1 Dismantling of the dam

The dismantling of the dam was done so that sections of the dam (slabs of aproximately 20 x 200 cm) was removed one by one. When the first section was removed the water level was allowed to drop to just a few centimetres above the next section after which that section was removed. By the last lowering two sections were removed at the same time. Thereby the lowering went faster during the last weeks of the project

3.2 Data collection

3.2.1 Adult pike data

Adult pike entering the wetland from Bråviken and Lake Mellsjön were caught and counted throughout the migratory period (March - late April). All pike were measured, weighed and sexed and date of arrival was noted. To monitor the spawning migration to the pike factory from both directions, custom built traps were used. The traps were blocking the creeks thereby making sure all adult pike entering the pike factory were caught and counted. Also, spawners were tagged with Passive

Integrated Transponder (PIT) (32mm, HDX+, Animal, TARIC:), thus making sure that no doubble counts were made.

3.2.2 Pike fry data

To follow the relative densities, progression of growth and migration behaviour over time, pike fry data collection went on from May 18th (when free-swimming fry was expected to be found) to July 8th (when no pike more pike fry was caught and there was indications that pike fry migration was over). Within the wetland, pike fry were captured by a combination of active sampling pushing a landing net along transects (daytime) and passive sampling using four fyke nets. During the first weeks of sampling, fry were only caught with the landing net whereas fyke-nets became more efficient later in the season when fry were larger and more mobile. At this time, the active sampling method became inefficient (no fry captured) and all efforts were instead done using fyke-nets. The fyke-nets were moved within the wetland to obtain a representative sample of the size distribution. Also, attempts to actively force fry into fyke nets were done by splashing and pushing water in front while walking towards the fyke nets. However, this “splash-fishing” method turned out fruitless.

The fishing within the wetland was made in three regions, defined as northern, southern and western region (**Figure 2)**. The areas were different regarding their vegetative character. The western region were much more sparsely covered than the other two. The northern region was dominated by floating-leaved plants *(Potamogeton*) while sedges (*Carex* and *Schoenoplectus*) were dominating the southern region. No fishing was performed in areas that was considered non-wadeable. During the period when pike fry were caught with the landing net (first 4 weeks of the project), equal fishing effort was made in the three regions with both active sampling and the passive fyke-nets. As catches was greater in the southern part of the wetland, a larger proportion of the fishing effort was put in the southern area from the 5th week of the project.

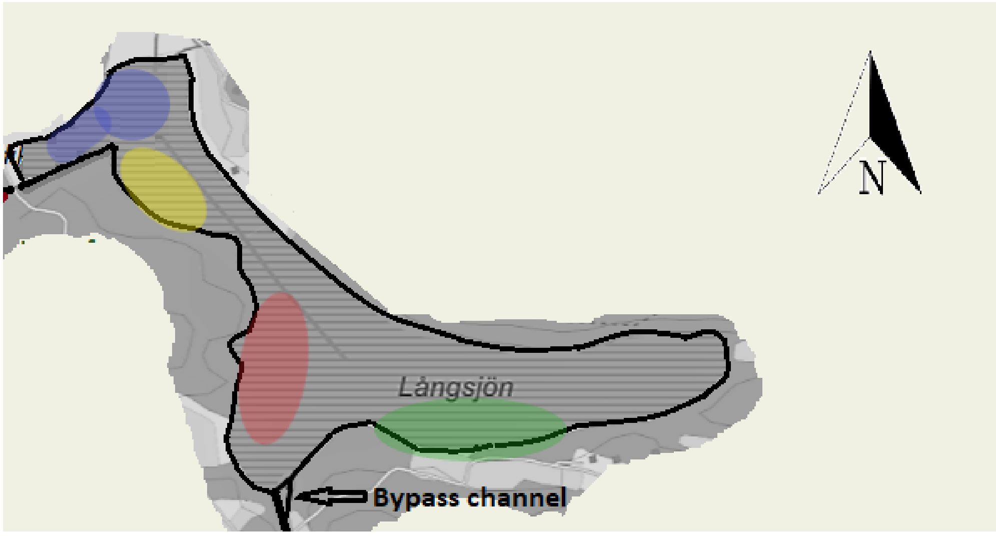

Figure 2. Blue, green and red areas mark the northern, southern and western region respectively, were both landing net (active method) and passive fishing fyke nets (passive method) were used. As the catches were larger in the southern region, a greater part of the total fishing effort was put in that area from the 5th week. The yellow area marks a region where fishing efforts, by using landing net, made during the first 2 weeks of the project. Areas that were considered non-wadeable were left unfished.

To catch pike fry emigrating out of the wetland (henceforth emigrators) fyke nets were placed in each of the two adjacent creeks. The fyke-nets covered the creeks from shore to shore and were placed in areas close to the destination of emigration (Lake Mellsjön upstream, The Baltic Sea downstream) to accurately estimate the proportions reaching each forage habitat. One potential issue with this design is that it may not entirely reflect the numbers of juveniles that initiated the migration each of the directions (i.e. to compare with the adult proportions) since there could be differences in survival throughout the routes.

A double layer of fine meshed net (6 mm mesh size) was sewn on the already existing net covering the fyke nets. The landing net was covered with a net from a weigh sling (mesh size approx 3 mm). The smallest fish caught by both netting and fyke nets were cyprinid fry with a length < 3 mm. Therefore, the different sampling methods were considered comparable and no pike fry were assumed to escape by slipping through the nets. The time for when fyke nets were put in use was noted each day. The fishing went on at a minimum of two days and nights per week. Caught emigrators and stayers were counted and measured for length.

3.2.3 Abiotic factors

Four devices (HOBO, Pendant® Temperature/Light 64K Data Logger), two logging temperature and LUX (Lumen per m^2) and two logging temperature only, were placed in the wetland. Due to the lowering of the wetland the two devices logging LUX were located above the water surface during the second half of the project and only one of the devices logging temperature only lasted throughout the whole project. Thereby no complete data of LUX were obtained but instead retrieved from Swedish Meteorological and Hydrological Institute (SMHI) station in Kolmården (58°68'92.0"N 16°30'69.0"E) approximately 39 kilometers away. Also, data on barometric pressure were retrieved from the SMHI station in Kolmården (SMHI 2020). The lowering of the wetland started June 8th followed by three more lowerings with the last occurring June 25th.

3.3 Statistics

3.3.1 Adult pike data

3.3.1.1 Females

Pike female size is documented positively correlated to absolute fecundity (Craig J.F, 1996). Putative differences in size between anadromous and potamodromous female spawners could give a hint about the recruitment ability among female individuals of the different origins. Data on female length and absolute fecundity (total number of eggs per individual) from twelve different pike populations (Craig J.F, 1996) was used to calculate the relationship between absolute fecundity (AF) and length (L). The function of best fit to describe this relationship was $AF = 0{,}002 * L^{2{,}6597}$; $R^2 = 0.96$, $n = 12$). The length data on adult females entering Långsjön were put into the function to estimate the contribution of eggs per each female. On the assumption that all adult males entering Långsjön are equally successful at fertilizing eggs, an estimation was done of the likeliness that a fry would either be a result of admixture or an offspring with both parents originating either from the anadromous stock or the potamodromous stock. Fry with parents from different populations were assumed to be equally prone to emigrate either way out of the wetland i.e. behave as down- or upstream migrators. Thus, one half of fry with mixed origin, was expected to emigrate downstream and one half were assumed to emigrate upstream.

It is unknown if and if so to what extent, pike male size matters in terms of recruitment ability. Pike has a similarity with species that exhibit male-intrasexual competition where males tend to arrive before females to the spawning grounds (Frost and Kipling 1967; Fleming & Gross, 1994; Petersson et al., 1999). Often, size is correlated to dominance (Dickerson et al., 2002 Jacob et al., 2007; Järvi, 1990). A competitive situation among pike males to be fathering offspring, where larger size is advantageous, cannot be eluded. A- t-test was therefore computed in R-studio (Version 0.99.879–2009–2016 RStudio, Inc), using the rt.package, to compare the size of anadromous and potamodromous males. This was performed to examine *potential* competitive differences that could be due to size differences.

3.3.2 Pike fry data

A X^2 test, computed in SPSS, was used to test how well the proportion of *caught* downstream and upstream emigrators corresponded to the *expected* proportion of pike fry emigrating in each direction.

Further analyses were all computed in R studio (Version 0.99.879–2009–2016 RStudio, Inc).

3.3.2.1 Differences in size composition

Due to small sample size of downstream emigrators and few upstream emigrators caught during the first two weeks after first pike-fry-catch (Figure 3), the size comparison was considered impracticable to conduct with data from the entire duration of the project. Therefore, a one-way analysis of variance (ANOVA) with size-data from 17th of June to 1st of July (Figure 4) was conducted to compare size differences in size composition (total length) between stayers as well as upstream- and downstream emigrators. A Tukey's test was used to determine statistical differences. Statistical differences were considered at $p < 0.05$.

Also, a t-test was conducted to test for differences in size compsition between stayers and emigrators with downstream- and upstream emigrators pooled as one group.

The intention was to conduct a linear mixed model to test for differences in size composition (total length), with each fishing day (sampling occasion) used as a random effect to control for repeated measures while sampling site (three levels: upstream, wetland and downstream) used as a fixed effect. Interaction effect between sampling sites and sampling occasion would have been examined to evaluate temporal dynamics thereof.

3.3.2.2 Linear mixed model – Abiotic factors

To investigate effects of the abiotic factors barometric pressure, lux and temperature (Peterson, 1972; Zamorov et al.2018) on the tendency by fry to emigrate (= number emigrators caught), a linear mixed model was computed with barometric pressure, lux and temperature as fixed effects. The time fyke nets were put in water varied among fishing days. Thus, the effort that was put in varied from week to week, why fishing time (hours per week) was treated as a random factor. Fixed factor significance level and interaction effects between explanatory variables were estimated via an ANOVA, by using the lmer.Test package.

4 Results

4.1 Adult pike data - average length and estimated contribution of eggs

Adult pike were caught in each creek during a period from March 1st to April 20th. Among anadromous adults, only one female was caught with a length of f480 millimetres. The length of potamodromous females (n=51) averaged 687.5 ± 120.4 mm. There was a significant difference in size between anadromous and potamodromous males according to the t-test ($t_{39} = 3.6$, $p < 0.001$ **Table 1**). The potamodromous males (*M*=514.8 mm, *SD*=117.2 mm) were on average larger than the anadromous males (*M*=346.9 mm, *SD* = 63.8 mm). Two of the anadromous spawners escaped during measuring and were therefore removed from further calculations. One potamodromous female was slender and considered to have spawned before entering the wetland and was removed from the calculations of estimated absolute fecundity.

Table 1. Total mean length ± standard deviation of female and male spawners of each strategy (anadromous and ptamodromous) entering Lake Långsjön during spring 2020. Also denoted are the estimated contribution of eggs to the spawning event per each stock.

Adult population	Female average length (mm)	Estimated egg contribution	Male average length
Anadromous adults	(n=1) 480	29766	(n=17) 346,9 ± 63.8 range 24 - 55 mm
Potamodromous adults	(n=51) 688 ± 120,4 range 225 – 940 mm	4113262	(n=24) 514.8 ± 117.2 range 290 – 660 mm

4.2 Pike fry data

In total 243 pike fry were measured during the project of which stayers accounted for 102 individuals between may 18th and July 1st. Emigration started two weeks after that the dismantling of the dam was started. 141 upstream emigrators (out of which 130 were measured for length) were caught between June 2nd and July 6th. 8 downstream emigrators were caught between June 30th and July 1st (**Figure 3**).

128 stayers were caught within the area (southern shore of Lake Långsjön) where pike spawning activity was most commonly observed during the years before the restoration and the mid 1900s **(Figure 2).** 6 pike fry were caught in the northern end and one in the west end of the wetland. During the last week, neither emigrators nor stayers were caught and emigration was assumed to be over.

4.2.1 Fry proportions corresponding to adult pike

Based on the estimated egg contribution and the number of males of anadromous and potamodromous spawners (**Table 1**) 0.3 percent were expected to be of pure anadromous origin, 58.1 percent of pure potamodromous origin and 41.6 percent of mixed origin. This leads to an estimation where 21.1 % of the pike fry is expected to swim downstream and 78.9 % expected to swim upstream. The proportion of caught downstream emigrators (N 6 = 4.3 %) and upstream emigrators (N 141 = 95.9 %) differed from expected values = 21.4, $X^{2,1} = 21.4$, df = 1, N = 147, $p < 0.001$, with a higher proportion of fry than expected migrating upstream toward Lake Mellsjön.

4.2.2 Size composition of emigrators and stayers

The total length of stayers increased during the season and averaged 93.4 ± 35.2 mm (mean ± *SD*, N = 135). Upstream emigrators averaged (n=130) 119.9 ± 13.8 mm and downstream emigrators total length averaged (n=8) 125.75 ± 11.05 mm. (**Figure 3**).

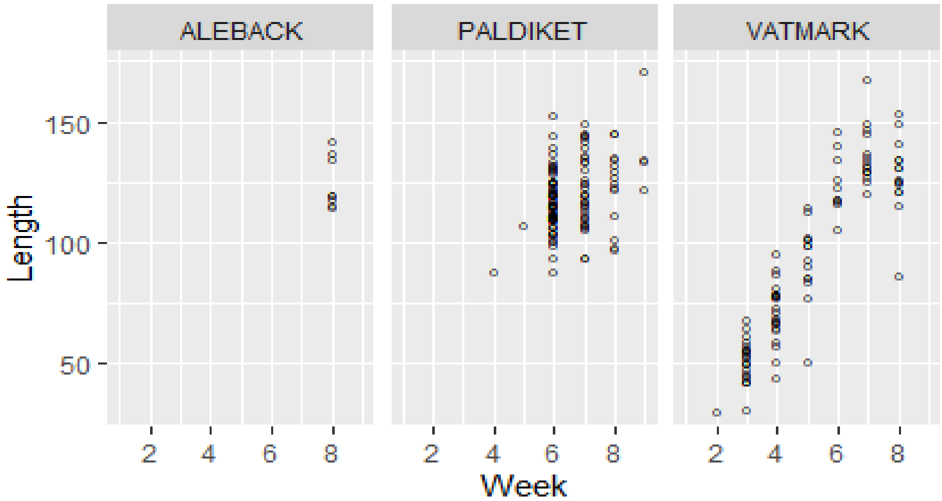

Figure 3. Total length of pike fry caught in the three different locations (Ålebäck, Påldiket and Wetland). The 1st upstream emigrator were caught during week 4. Emigration then went on for 5 weeks. The downstream emigrators were solely caught during the 8th week of the project. No difference was found between downstream and upstream emigrators. Nor were there any size differences between emigrators and stayers when pike fry were present on all three locations (week 8).

4.2.2.1 Differences in size composition

There was a significant difference in size between pike fry caught at different locations (ANOVA, $F_{2,174} = 11.69$, $p < 0.001$). Stayers was on average 11.323 mm longer than upstream emigrators, a significant difference (Tukey’s test $p < 0.001$). However, there were no significant differences between Stayers and Downstream emigrators (Tukey's test, $p = 0.56$), nor between Downstream emigrators and Upstream emigrators (Tukey's test, $p = 0.379$, **Figure 4)**

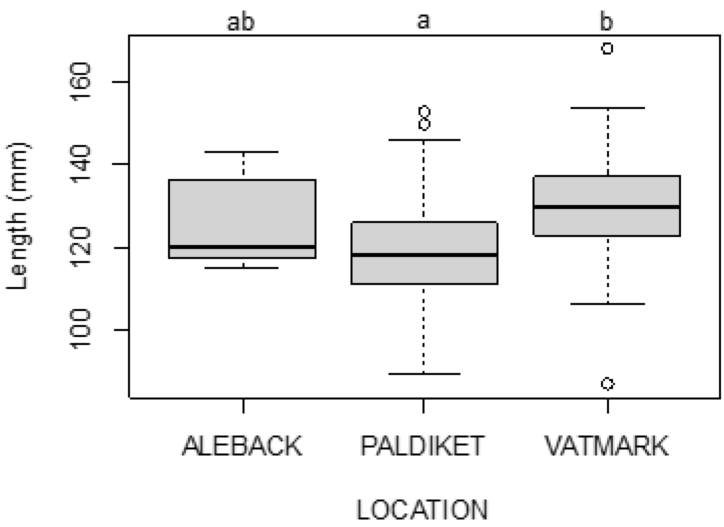

Figure 4. Boxplot over size distribution of Downstream emigrators (ALEBACK), Upstream emigrators (PALDIKET) and Stayers (VATMARK) with median total length marked and box limits indicating upper and lower quartile. Lowercase letters indicate significant differences between groups.

According to the t-test the difference in size between emigrators and stayers was significant $t(179) = 4.24$, $p < 0.001$. Stayers were significantly larger 130.85 ± 13.52 mm, n = 41 than emigrators 119.89 ± 14.65 mm **(Figure 5).**

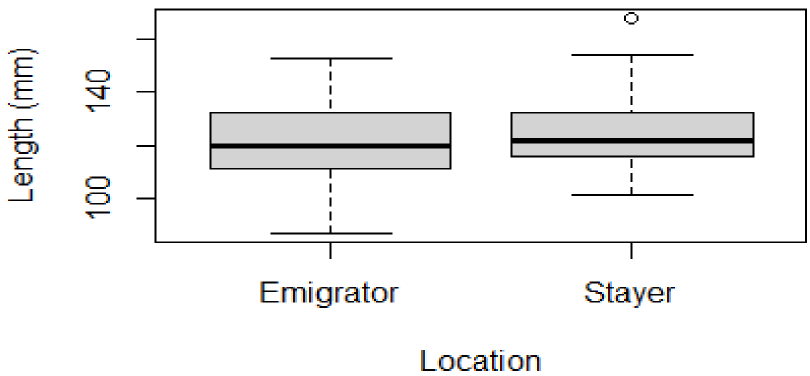

Figure 5. Boxplot over size distribution of emigrators (Downstream emigrators and Upstream emigrators pooled) and Stayers with bold line indicating median values and the box limits indicating upper and lower quartiles. Stayers are on average 10.96 mm longer than emigrators

4.2.3 Influence of abiotic factors on emigration

There was no pattern indicative of a high emigration tendency (associated with water run off) within the very next days after a piece of the dam was removed (**Figure 6**) and little variation of the number of caught emigrators could be explained by the other abiotic factors tested for (**Table 2**). According to the ANOVA, no factor was significantly associated to the number of caught emigrators (Barometric pressure, p = 0.945) (Lux, p = 0.741) (Mid temperature, p = 0.288)

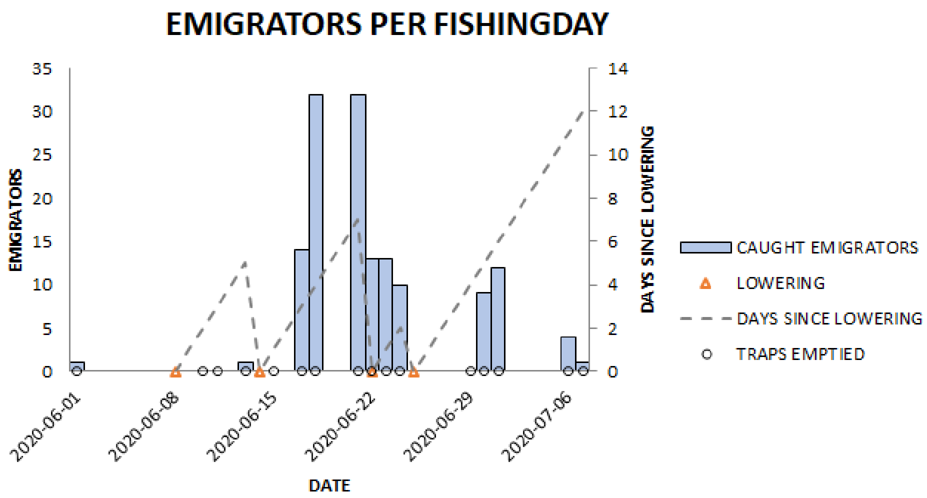

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Figure 6. The number of emigrators (both upstream and downstream), since first catch, at each of the dates where the fyke nets were fishing. The wetland was lowered (**Δ**) stepwise by dismantling the dam piece by piece, starting at June 8th.

Table 32 The estimated average amount of caught emigrators during each fishing occasion (Constant) and the variation explained by each of the abiotic factors tested for. Standard error (SE) within parentheses.

	Dependent variable
ABIOTIC FACTOR	CAUGHT PIKE
Barometric pressure	-0.035 (0.439)
Lux	0.003 (0.00.7)
Mid temp	1.767 (1.488)
Constant	3.272 (429.219)
Observations	16

Log Likelihood	-60.773
Akaike Inf. Crit.	133.546
Bayesian Inf. Crit.	138.182

4.2.4 Capture of additional fish species

All species caught in the wetland and the creeks are listed below (**Table 3)**. Notable were large amounts (>30) of large bodied three-spined sticklebacks and nine-spined sticklebacks (*Pungitius pungitius*) continuously caught during every week except on the last one, in Ålebäcken. Also, one nine-spined stickleback were caught in Påldiket and both nine-spined and three-spined sticklebacks were caught within the wetland.

Table 3. All species (except pike) caught in the wetland and the two adjacent creeks during the project. Trivial names followed by binomial names within parenthesis. "x" marks whether the species were found within the above-mentioned location.

	Sampling site		
Species	Långsjön	Påldiket	Ålebäck
Bleak (*Alburnus alburnus*)	x	x	x
Bream (*Abramis brama*)		x	x
European eel (*Anguilla anguilla*)			x
Nine spined stickleback (*Pungitius pungitius*)	x	x	x
Three spined stickleback (*Gasterosteus*	x	x	x
aculeatus)	x	x	x
Perch (*Perca fluviatilis*)	x	x	x
Roach (*Rutilus rutilus*)	x	x	x
Tench (*Tinca tinca*)	x		
Rud (*Scardinius erytropthalmus*)	x		
White bream (*Blicca bjoerkna*)			

5 Discussion

The Number of pike fry caught was much smaller than expected based on earlier observations and test fishing (*Gustafsson Rickard and Johansson Erik - Personal communication*). However, the fact that both anadromous and potamodromous spawners were migrating *towards* and dwelling *within* the wetland during the spawning period, does not give any support for any temporal mismatch restricting gene flow between anadromous and potamodromous spawners. The considerable share of pike fry that exhibited an upstream emigration pattern, indicates that the parental strategy is heritable. It is evident that *origin*, rather than other factors, determined the emigration route of pike fry. However, this should not be interpreted as if the potamodromous spawners arriving from Lake Mellsjön, would never be able to act as a source providing the Baltic Sea with juvenile pike. Pike females mature earlier than pike males (*Bondarenko et al., 2018; Billard., 1996*). Thus, the sex distribution, with only one female found among anadromous spawners, as well as the small average size implies that they are young. This combined with what was reported from qualitative studies from the previous season, with numerous pike fry found in the outlet of the wetland as well as further down in the Ålebäcken stream (Gustafsson Rickard and Johansson Erik - Personal communication) implies that a large fraction of the anadromous spawners could be made up of pike of potamodromous origin but that they as pike fry swam downstream towards the Baltic Sea.

The very small share of pike fry emigrating downstream this season, I suggest is to be due to the low abundances of pike fry and thereby low concurrence and predation pressure within this season's pike fry cohort. Cannibalism has been suggested to initiate emigration (Nilsson et al., 2014). Reduced space increases cannibalism among juvenile pike (Wright and Giles, 1987). The larger size among stayers than emigrating pike fry gives support for the hypothesis that smaller pike fry emigrates earlier in order to avoid predation and or concurrence from larger pike fry. During a year with greater pike fry abundance and thereby higher predation pressure and concurrence, a share of emigrating pike fry may be forced to swim downstream towards the Baltic Sea, regardless of origin.

To be able draw further conclusions about the source–sink dynamics influencing juvenile pike dispersal in Lake Långsjön, a larger sample size of pike fry would be needed and geneti. The low number of caught pike fry compared to what was expected after last year's observations, I consider as a recruitment failure. In turn, this is suggested to be due to stickleback-mediated predation. Therefore, I suggest that a part of the future administration f Lake Långsjön should include prevention of sticklebacks of reaching the wetland. However, the positive effect that pike factories have proven to be able to have on juvenile pike recruitment (Nilsson et al., 2014) together with the observations of large amounts of pike fry from previous season (Gustavsson Rickard and Johansson Erik - Personal communication)**,** suggests that the restoration of Lake Långsjön and the regained connectivity could be important for the ability to restock the Baltic Sea with pike juveniles. Maybe more important is the restoration to ensure the conservation of a completely unique stock of pike. The most novel finding from this project, is precisely, that revealed by spawners arriving *from* and pike fry displaying a highly purposive emigration back *towards* Lake Mellsjön; a stock of downstream spawning pike. As far as I am concerned this has never been described previously.

5.1 Interbreeding between anadromous and potamodromous spawners

Spawners are arriving from both the Baltic Sea and Lake Mellsjön and have access to the same spawning area. There *could* be a possibility that a remnant anadromous stock has been able to spawn in the Ålebäcken creek when not being able to reach the wetland due to the impediments (*Franzén Rolf., 2020 - personal communication*). This could have led to an evolution of different spawning adaptations among anadromous and potamodromous pike respectively. Within just a few generations, fish populations may develop local adaptations, when being exposed to new environmental conditions (Hendry, et al.,2000; Christie et al., 2011; Willoughby et al., 2018). In a study on sockeye salmon (*Oncorhyncus nerka*), Hendry, et al., (2000), observed two populations of common ancestry evolving reproductive barriers within 13 generations. This due to local adaptations to different spawning areas (a lake beach and a river). The time that the anadromous and the potamodromous pike have been separated could have been long enough for them to evolve different spawning adaptations which in turn may restrict interbreeding between spawners of the two stocks. I suggest that the most likely factor to prevent the anadromous and potamodromous pike from interbreeding would be IBT. However, IBT seems not to be serving as an agent that prevents anadromous and potamodromous spawners from interbreeding at present.

The catches of pike fry in the northern, western and southern region (**Figure 2**) indicate that spawning took place in these areas. Juvenile pike often move within only a few meters in their nursery area (Cucherousset et al., 2009). Further, the deeper ditches between the three regions constitutes an environment that are not associated with what is preferred by pike as nursery habitat (Nilsson et., al 2014). Thus, it is reasonable to assume that pike fry have not been swimming from one region to the other, but that spawning likely occurred throughout the wetland. The large proportion of pike fry that was caught within the southern would suggest that a large proportion of the spawning also took place in that area. This is an area of the wetland that has been preserved and where pike spawning most often was observed during the mid-1900s (*Hansson Rolf and Hansson Gunnar, 2019 – personal communication*). This could be interpreted as that the behaviour of today's spawners mirrors that of earlier generations. Such habits could *potentially* be due to an inherited preference.

Even though it cannot be eluded that different preferences regarding spawning area within the wetland do exist between spawners, the habitat quality may vary within the wetland, why more pike fry are found in one area but not the other. It may take time before a wetland reaches its full potential as a pike factory after restoration due to that vegetation must recover before it is suitable as a pike spawning and nursery site (Nilsson et al., 2014). Sparse vegetation may increase the potential spawning area but not favour recruitment (Casselman and Lewis 1996).The fact that one, yet small, part of the southern region has been prevented from overgrowth throughout the years and that this area did not have to go through the same extensive restoration (e.g. excavation of reed root systems), likely does that this particular part of the wetland exhibits a higher quality as nursery and spawning habitat, why it could be preferred by spawners regardless of origin. Also, pike fry survival may be higher in this area. The denser vegetation and the large distribution of sedges in the southern region compared to the others, supports that theory. Yet, the small proportion of pike fry, caught in the western and the northern region of the wetland, coincides with a small proportion of pike fry downstream emigrators as well as with fewer anadromous than potamodromous spawners. However, I think the mere coincidence of few anadromous spawners and few pike fry in discrete areas within the wetland should *not* be interpreted as that the anadromous pike would have evolved dissimilar preferences regarding spawning area from the potamodromous pike and thereby spawn in different areas, thus avoiding interbreeding. One has to bear in mind that the sample size of pike fry was much smaller than expected and that different factors may have caused the low abundance of pike fry throughout the wetland. Another theory about the origin of the anadromous spawners is that they are constituted by strayers from other populations that are spawning in the Baltic Sea. Based on previous research on local adaptations to local spawning habitats (Berggren et al., 2016; Nordahl et al., 2019; Sunde etal., 2018; Tibblin et al., 2015) one would wonder how such strayers would succeed colonizing lake Långsjön. Thus, the contribution of pike from other stocks has to be continuous and large enough to increase the possibility of the evolution of adaptations that enable the establishment of an anadromous stock. The theories about a remnant anadromous stock and / or the contribution of strayers from populations that are spawning in the Baltic Sea should, even though they might be possible, be seen as cautious theories. In fact, the only viable stock of pike in the close proximity that one actually knows of, is the stock resident in Lake Mellsjön.

To me, the most likely theory is that the anadromous spawners are constituted by descendants from the potamodromous stock from Lake Mellsjön but that they as fry choosed to swim towards the sea (due to concurrence and predation as hypothesized to drive emigration), is supported by both the sex- and size distribution obtained among the anadromos spawners. That only one female arrived from the Sea together with the size distribution of the anadromous spawners imply that all individuals among the anadromous spawners are young. The Ålebäcken creek, connecting the wetland to the Baltic Sea has been opened in stages. Upstream migration *may* have been possible since the removal of the metal slab in 2015. Pike have by certainty been able to reach the wetland after the final restoration (excavation of debris causing potential barriers) and the building of the bypass channel in 2018. Thus, the first spawning event after the restoration was completed, took place in 2019 (Gustafsson Rickard., 2020 - personal communication). It is possible for 0+ pike to reach sexual maturity but males tend to mature earlier than females *(Billard., 1996)*. The ability to grow 40 cm within the first year is also observed among several pike populations scattered over the world *(Bondarenko et al., 2018; Billard., 1996)* as well as among pike of Baltic sea origin (Tibblin unpublished 2019). This makes it reasonable to assume that quite a large fraction derives from last year's spawning. Thus, from the first spawning event occurring after the restoration. The probability that anadromous spawners derive from a cohort hatched after 2015, when the metal slab was removed, are even higher. If the anadromous spawners would be of the same origin as the potamodromous spawners they would consequently not contribute with any novel traits to the population that is spawning in Lake Långsjön. Discussions on potential interbreeding between different stocks and the influence it may have on pike fry recruitment would then be a non-issue.

5.2 Source-sink dynamics influencing pike fry emigration patterns

The willingness, exhibited by pike fry, to move towards one specific forage habitat and not towards the other contradicts the theory given above and suggests that the pike of potamodromous origin will not restock the Baltic Sea with any large number of juvenile pike. The behaviour of emigrating upstream, clearly indicates a heritable strategy among potamodromous pike; that of spawning in Lake Långsjön while utilizing Lake Mellsjön as forage habitat. Populations that display a downstream spawning strategy has for example been described among brown trout (*Salmo trutta*) populations (such as that of Lake Sommen (Nydén & Halldén., 2002) and the nowadays extinct large-bodied trout of Lake Vättern (Alm 1929)) but has to be considered as rather rare. As far as the literature, that I have come across, is telling this has never been described before among pike.

The estimation of emigrators calculated on the basis of absolute fecundity where 21,1 % was expected to swim downstream and 78,9 % expected to swim upstream is somewhat rough and should be treated carefully. The estimated proportion of fry emigrating either up- or downstream rests on the assumption that one half of the pike fry of mixed origin should swim downstream and the other upstream. This field has to be further investigated and the uncertainty gives rise for speculations; as if the part of the genome that determines the emigration route consists of dominant and recessive alleles, one allele could dominate the other why that trait is expressed. Further, provided that the anadromous and potamodromous spawners are of different origin, the ability that juvenile pike would be of pure anadromous origin, relies on that the single anadromous female would succeed with this year's spawning. In addition, the similarity that pike show with other species that exhibit male-male competition, that males arrive before females to the spawning grounds (Frost and Kipling 1967; Fleming & Gross, 1994; Petersson et al., 1999) could be used as an argument to suggest that the smaller males arriving from the sea had a competitive disadvantage of fertilizing eggs. These eventualities give some room for a margin of error. To find out if the reproductive ability differs between spawners and how that would affect the dynamics between two interbreeding stocks, future genetic analyses are likely to be necessary. For such studies, Lake Långsjön is *very* suitable and a rare study system due to the uniqueness with both anadromous and potamodromous migrations to the same spawning area.

Despite this roughness in the estimation of juvenile pike origin, the findings suggests that origin, rather than other factors determine the emigration route. That in turn is, though not enough to state that pike of potamodromous origin *never* will emigrate towards the sea. The hypothesis that smaller fry are exposed to higher predation risk (Craig 1987) and that avoidance of predation and concurrence would drive emigration tendency, is based on previous research (Nilsson *et* al., 2014). In the study of Nilsson *et.*, al (2014) a combination of passive drift and active emigration to avoid predation and concurrence is suggested to make pike fry leave their nursery sites. That study is made in smaller pike factories with much higher abundances of juvenile pike per unit area found (>100 000 emigrating pike fry on a couple of hectares of wetland). The cannibalistic behaviour increases with reduced space (Wright & Giles 1987). A fry emigrating mainly to avoid predation might be less fussy in their choice of emigration route. This could lead to a situation where a stressed fry of a certain origin potentially chooses the “wrong” emigration route out of the wetland. The considerably lower abundances of pike juveniles found in Lake Långsjön compared to other pike factories, has likely strong effects on such dynamics. The emigration behaviour induced by cannibalism has most likely been dampened. The few emigrators that were swimming downstream did so at the very end of the project when the water level dropped faster than during previous weeks. Even though the pike juveniles on average were not triggered to follow the flow direction immediately after that a piece of the dam was removed, the downstream emigrators could have chosen that way due to that the amount of pike per unit area (thus the risk of cannibalism and concurrence) increased rapidly at this time.

5.2.1 Potential influence of stickleback predation

There is no doubt about wetlands suitability as spawning and nursery habitat for pike (Nilsson et. *al* 2014). But the results obtained from this study have to be considered as that pike recruitment in Lake Långsjön this season is a failure. A much larger sample size was also expected after what was reported reported from qualitative studies during the previous season, when hundreds of juvenile pike were caught in the outlet of the wetland within only hours of fishing. Numerous juvenile pike were also found in several places of Ålebäcken during electrofishing. (Gustavsson Rickard and Johansson Erik - Personal communication). The amount in combination with the size distribution of fry is somewhat peculiar. It resembles that obtained by Nilsson *et. al* (2019) where the presence of three spined stickleback is suggested to deplete 97 % of fry under 35 mm. The very smallest fry caught during this project falls just within the upper limit of what is suggested as the maximum size that a three spined stickleback could catch (Nilsson et. *al* 2019). The large amounts of both three-spined and nine-spined sticklebacks caught in Ålebäcken each week of sampling, in combination with their presence also in the wetland, could explain the low abundances of pike fry and lack of small individuals (Bergström et al., 2015; Byström et al.; Nilsson et al., 2019). The reason why no pike fry smaller than 30 mm where found may be due to stickleback-mediated predation on pike roe and newly hatched pike fry. If, as observed by Nilsson et al (2019), stickleback predation occurs on newly hatched emigrating pike fry within creeks running from wetlands, this could mask the behaviour of smaller pike fry emigrating early and downstream that was hypothesized. Due to this suspicion of sticklebacks affecting the pike recruitment negatively, an advice of remedial measure is hereby given: The migration of sticklebacks (both three- and nine-spined stickleback) in to the wetland should immediately be monitored and if possible, prevented to protect and improve the prospects for a successful pike recruitment.

The notedly larger size that emigrating pike fry exhibit compared to what has been observed from other wetlands (Nilsson et. al 2014, Nilsson et. *al* 2019), could partly be attributed to the low influence of competition and predation. That emigrators are large-bodied may also to some extent be due to that Lake Långsjön in its character is slightly different from other wetlands due to the ditches and deep holes. Life history traits, such as that of migrating between habitats, are evolved to maximize fitness during different life stages (Kovach *et al.*, 2012), i.e. the benefits of leaving the nursery area has to outweigh those of staying within it. The deeper areas besides the flooded fields differ from those where earlier studies of pike fry emigration behaviour has been made (Nilsson et. al 2014, Nilsson et. *al* 2019), and is more somewhat lake-like. This could be a factor that allows pike juveniles to stay long and grow big before emigrating to their forage habitat. Whether this pattern of large-bodied emigrators will persist in a year where higher pike fry abundances are obtained, remains to be seen. Larger fry may have bigger chances to survive due to less predation risk in their forage habitat. That in turn suggests that quite a large proportion of pike fry has the opportunity to return to the wetland to spawn. All in all, Lake Långsjön seems to possess potential to host far more pike fry than during this season.

5.3 Prospects for future pike recruitment in Lake Långsjön

All in all, above reasoning suggests that despite that pike fry display a strategy (which very likely may be heritable) of emigrating upstream, the potamodromous stock can contribute with juvenile pike to the Baltic Sea. Within a year when spawning succeeds and high pike fry abundances are obtained, the migration patterns may look different from that observed this season i.e. the contribution of pike juveniles to the Baltic sea will be greater. If spawning succeeds within the coming years, there may be a trend with more and more spawners arriving to Lake Långsjön. However, for that to happen, pike must be given the best possible conditions to succeed with recruitment. It is of greatest concern that the suspicion of stickleback predation is taken seriously. Adaptive management and future research is crucial to obtain the desired outcome of the restoration of Lake Långsjön. If possible, immediate actions should be taken to prevent stickleback predation from depleting the pike recruitment. An increase in juvenile production leading to competition-mediated dispersal in combination with that several areas within Lake Långsjön reaches a higher quality as nursery habitat due to vegetative succession, will likely contribute to a bigger production of juvenile pike in future. This underlines the potential that Lake Långsjön has as an important recruitment area for coastal pike.

Future genetical studies and studies where adult pike are tracked and migration routes are revealed would be useful to deepen the understanding of the long-term effects of these source-sink dynamics. The key role that the regained connectivity between the Baltic Sea, Lake Långsjön and Lake Mellsjön plays, for the ability of restocking the Baltic Sea with pike juveniles of potamodromous origin is pretty straitforward. However, it also raises questions, such as: how an individual that ends up in an adult habitat different from that experienced by its ancestors and how well such individuals cope with the situation of ending up in such an environment? It is crucial that plasticity allow individuals to cope with the different local environmental conditions if any benefits are going to be derived of the connectivity (*Thomas et al., 2001*). Also, it leaves room for speculation of how such an individual would behave when it reaches adulthood and return to the wetland to spawn. Will it return to the Sea or adopt the behaviour that I suggest is inherited and swim upstream towards Lake Mellsjön? As long as pike of potamodromous origin end up in the Baltic Sea, they may act as a buffer against a complete loss of pike in these parts of Bråviken. If / when the trait of exhibiting an anadromous strategy becomes hereditary, through introduction from strayers from other populations or through the evolution of a novel trait, there will be an opportunity for a rapid increase of pike displaying an anadromous life cycle. That would be the moment where an anadromous stock gets established in the area.

Similar to how pike fry is suggested to be forced to swim downstream due to competition, the spawners of the potamodromous-stock might be forced due to competition e.g. for spawning sites, to spawn in Lake Långsjön and not in Lake Mellsjön from where they originate. Thus, there could be that the pattern of migrating downstream to spawn is not heritable but simply due to lack of enough spawning areas in Lake Mellsjön. The emigration behaviour of pike *fry* that mirror the parental strategy, however, indicate a trait that is genetically determined. Thereby, the restoration of Lake Långsjön is not only important to restock the Baltic Sea with pike but *crucial* simply due to that it enables the conservation of the highly unique stock of downstream spawning pike in lake Mellsjön.

5.4 Conclusions

- If anadromous spawners arriving in Lake Långsjön are of different origin, the prevailing conditions do allow anadromous and potamodromous spawners to interbreed. Nothing concrete points towards the opposite. However, a large fraction of the spawners arriving from the Baltic Sea this season is suggested to be constituted by descendants of potamodromous origin that as juveniles swam downstream.
- The unique downstream spawning stock indicates that origin is a determining factor for the emigration route. Even though it may seem contradictory, the potamodromous stock is suggested to be able to provide Bråviken and the Baltic Sea with juvenile pike that return to the area to Lake Långsjön to spawn. This despite the purposive behaviour of emigrating upstream. The influences of concurrence and predation is certainly not dismissed as factors affecting pike fry emigration patterns, including emigration route. These factors are though likely dependent on that high pike fry abundances within the wetland are obtained.
- The restoration of Lake Långsjön and the regained connectivity is a key both for the ability to restock the Baltic Sea with pike juveniles through the contribution of pike offspring of potamodromous origin, but also to ensure the conservation of a completely unique stock of pike.

6 References

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