Population ecology, growth, and physico-chemical habitat of anadromous European perch Perca fluviatilis

E.A.F. Christensen *, M.B.S. Svendsen, J.F. Steffensen

Marine Biological Section, Department of Biology, University of Copenhagen, Strandpromenaden 5, 3000, Helsingør, Denmark

ARTICLE INFO

Keywords:
Brackish water
Citizen science
Mark-recapture
Oxygen level
Salinity tolerance
Temperature

ABSTRACT

Anadromous sub-populations of stenohaline freshwater fish are vastly understudied in the estuarine environment. The purpose of the present study was therefore to study the population ecology, growth rate, and physico-chemical environment of an anadromous sub-population of European perch (Perca fluviatilis) from the western Baltic Sea. Fish (301) were marked with external identification tags, and anglers and fishermen reported recaptures in a citizen science set-up over three years. In addition, scale samples were collected for population growth rate determination. Furthermore, water temperature, salinity, and oxygen concentration were monitored in the area. The fish showed a consistent annual migration pattern over the three years residing in a bay during summer while being in a delta during autumn, winter, and spring. The population had a high growth rate, but a meta-analysis showed that growth of European perch is not distinctly different between estuarine and freshwater populations. The average salinity measured in the area was around 10, but increased on multiple occasions to salinity levels known for being physiologically challenging for European perch. We argue that high growth rates of estuarine European perch is more likely due to high food availability and low interspecific competition in this environment, rather than due to physiologically optimal salinities. Furthermore, the European perch in the present study lived on the edge of the species salinity tolerance, and the migration into the delta during winter is likely a combination of avoiding high salinities at low temperatures and a spawning migration. These results are important knowledge for the management of estuaries and coastal areas, especially as climate change is locally altering these environments drastically, and calls for further studies on other anadromous sub-populations of stenohaline freshwater fish.

1. Introduction

Most aquatic animal species are adapted to live in the stable osmotic environments of either freshwater or marine habitats, and their osmotic homeostasis is challenged by changes in environmental salinity (Martino and Able, 2003; Remane, 1934; Whitfield et al., 2012). Their distribution is therefore, to a large extent, limited by changes in ambient salinity, e.g. in estuaries, which constitutes a mixing zone between fresh water run-off from rivers and oceanic seawater, and therefore have a progressive salinity gradient which increases from nearly fresh water at their head, to above 30 at their mouth (Kennish, 1986). Furthermore, estuaries are highly dynamic environments where the salinity varies over time due to tides, stratification, patterns in river run-off, adding to the complexity of the habitat (Fenchel and Sand-Jensen, 2017; Heip, 1988; Ray, 2005).

Due to the osmotic challenging environment, the fauna species diversity is low at intermediate salinities in estuaries, compared to fresh or marine habitats (Martino and Able, 2003; Remane, 1934; Whitfield et al., 2012). However, the rate of primary production is typically high in estuaries (Cloern, 1987; Ray, 2005), making them biologically favourable niches of high resource availability and low inter-specific competition. In fish, the high food availability in estuaries is considered a primary driver in evolution of diadromous species, which are characterized by migrating along the salinity gradient once or more in their lifetime (Gross et al., 1988). In several temperate stenohaline freshwater fish species, such as northern pike (Esox lucius), common roach (Rutilus rutilus), ide (Leuciscus idus), and European perch (Perca fluviatilis), sub-populations have developed anadromous life-styles (Jacobsen et al., 2016; Nesbo et al., 1999; Skovrind et al., 2016). These populations forage in estuaries during the summer months and migrate into lower saline deltas and streams over winter, presumably due to adverse physiological effects of high salinities at low

* Corresponding author.
E-mail address: emilflindt@hotmail.com (E.A.F. Christensen).

https://doi.org/10.1016/j.ecss.2020.107091
Received 15 January 2020; Received in revised form 8 November 2020; Accepted 9 November 2020
Available online 17 November 2020
0272-7714/© 2020 Elsevier Ltd. All rights reserved.
Estuarine populations of stenohaline fish show high growth rates in brackish water (Lind, 1977; Lozys, 2004; Olsen, 2002), which has been hypothesised to be caused by the ambient salinity being close to the internal osmotic pressure of the fish, thereby minimising the energetic cost of osmoregulation (Lind, 1977; Lozys, 2004; Olsen, 2002). Osmoregulation is necessary for the fish to preserve physiological homeostasis (Lutz, 1972), and as an active physiological process it implicates an energetic cost, which is theoretically lowest at iso-osmotic conditions (Evans et al., 2005). However, the hypothesis that growth rate of estuarine sub-populations of stenohaline freshwater fish is high due to the presumed physiologically optimal salinity has never been thoroughly investigated.

Knowledge of the ambient environment and population ecology is instrumental in ecological modelling as well as in management and conservation of species (Kearney and Porter, 2009; Zimmermann et al., 2010). Despite the fact that the biology of anadromous sub-populations of stenohaline freshwater fish is diverging from their freshwater living conspecific in several ways, little is often known about their ecology in the estuaries, such as the population ecology and usage of ambient microhabitat of the species. Climate change is currently affecting local dynamics in river-runoff, wind patterns, and evaporation patterns, which can alter physico-chemical parameters in the already dynamic estuarine environments (Harley et al., 2006; Mohrholz et al., 2015; Vuorinen et al., 2015). This potentially change ecosystem functioning and species dispersal. Therefore, knowledge on ambient microhabitat usage and species ecology in estuaries is particularly important to improve predictability of the effect of climate change on estuarine fish.

The European perch is an ecological key species due to its predatory lifestyle and has a significant top-down regulating effect on the ecosystem (Jeppesen et al., 2000; Ljunggren et al., 2010). Anadromous sub-populations of the species are abundant in the Baltic Sea (Craig, 2000; Hansson et al., 2019; Thorpe, 1977), which can be considered as one the world’s largest estuaries (Kraufvelin et al., 2018; Tzeng et al., 2000; Westerberg, 1998). Here, European perch is a target for a substantial commercial and recreational fishery (Couture and Pyle, 2015; Craig, 2000), yet its abundance has declined substantially over the last few decades (Adgers et al., 2006; Ljunggren et al., 2010; Nilsson et al., 2004), which constitutes ecological, conservation, and societal concerns. Anadromous sub-populations of European perch are physiologically adapted to withstand higher salinities than freshwater conspecifics (Christensen et al., 2019a), which enables them to extend their distribution in brackish water. In the western Baltic Sea, European perch live on the edge of their salinity tolerance (17.5), as this area forms a steep transition zone between low salinity water in the Baltic Proper (salinities of around 5) and oceanic sea water from Kattegat (salinities of around 30) (Fig. 1) (Jacobson et al., 2016; Schiewer, 2008). The European perch populations in the western Baltic Sea are therefore ideal candidates for studying the ecology of estuarine sub-populations of stenohaline freshwater fish, and thus provide valuable insight on the ultimate effects of altered salinities with climate change.

The purpose of the present study was to study the population ecology (population size, survival rate, and migratory behaviour), growth rate, and determine the physico-chemical environment (temperature, salinity, and oxygen level) of an anadromous sub-population of European perch in the western Baltic Sea. We expected to see a consistent annual migration pattern with summer residence in the western Baltic Sea, and overwintering in an adjacent delta. Furthermore, we hypothesised population to have a high growth rate, and conducted meta-analyses of growth rates of freshwater and brackish water European perch populations to test if brackish water is physiologically favourable for estuarine living populations of stenohaline freshwater fish.

Fig. 1. The study area (large map, red rectangle in insert map) is located in the western Baltic Sea (insert map). The delta consists of the lower part of a stream and a harbour basin, which feeds into a bay. The water salinity, temperature, depth, and oxygen level was measured in the delta (CTD; red dot). Baltic Sea salinity data are mean surface salinities for the period 1999–2009. North Sea salinity data are mean surface salinity for the period 2007–2008 (Skovrind et al., 2016). Drogden Sill is indicated by a black dashed line in the small insert map. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2. Materials and methods

2.1. Study area

The study took place over a three-year period (2016–2019) in the Danish part of the western Baltic Sea (55°36’32"N, 12°22’44"E) (Fig. 1). The study area consisted of a delta where the lower reach of a stream, Store Vejle Å, feeds into a man-made harbour basin, Ishøj Harbour (Skovrind et al., 2016; Valgren and Front, 1986). This delta is connected to the adjacent bay, Koge Bugt. Since the 1980’s, local anglers have been aware of a European perch population overwintering in the delta (D. Rasmussen, Ishøj Sport Fishing Club, pers. comm.). The fish enter the delta around September and leave again in April (Skovrind et al., 2013), and are presumed to migrate into the bay to forage during summer months, yet the latter has never been systematically verified. The angling pressure increased substantially during the 2000’s, and consequently, the local management (Ishøj Sport Fishing Club) has voluntarily implemented an unconditional catch-and-release policy concerning angling in the harbour and stream (S. Lyngsø, Ishøj Sport Fishing Club, pers. comm.).

2.2. Population ecology

Fishing and tagging were approved by the Danish AgriFish Agency (reference number: 12-7410-000008 and 17-7520-000001). Tagging took place in over five months, from October 2016 through March 2017. European perch were caught during recreational fishery by local anglers in the delta, and marked with external identification (ID) tags (FD-94 Anchor Tags, Floy Tag Inc., Seattle, WA, USA) inserted in the dorsal musculature on the left side of the fish ventral to the second dorsal fin (Appendix A, Fig. A1). Each tag held a unique ID number as well as a webpage address (www.salmtfish.dk). A total of 301 fish were tagged. The fish were landed, their body mass (BM) determined and their length measured (total length (TL); cm) before being tagged. The fish had a median length of 40 cm, ranging from 26 to 47 cm and a median BM of 0.94 kg, ranging from 0.25 to 1.65 kg (Supplementary material). The time from the fish was hooked to landing was less than 3 min, and the fish were air exposed less than 2 min during the tagging procedure. Twenty-three of the individuals over the full size range had two tags.
inserted ca. 5 cm apart to enable evaluation of tag expulsion rate.

Recaptures of already tagged individuals during the tagging period were used to estimate the population size ($N^\ast$) with a multiple marking–multiple recapture model (Schnabel, 1938):

$$\hat{N} = \frac{\sum C_M}{\sum R_I + 1}$$

(1)

where $C_M$ is the number of individuals caught in sample t (always 1, as fish were caught by angling, one at a time), $M_I$ is the number of marked individuals before sample t, $R_I$ is the number of individuals already marked before sample t, and 1 is applied as the proportion of $N$ caught and marked was expected to be below 0.1 (Krebs, 2016). As the total number of recaptures were lower than 50, 95% confidence intervals (C.I.) for the population size estimate were obtained from a Poisson distribution, according to Krebs (2016).

Anglers and fishermen registered recaptures on the web pagekk over a three-year period along with the respective BM and TL at recapture, and place of the recapture (the delta or the bay). The effect of time on the catchability of the fish was tested with a Spearman Ranks Correlation test on the ID ratio (consecutive ID of the reported fish divided by the total number of fish tagged on the given occasion) and the time from tagging to recapture. The survival rate was estimated as number of recaptured unique individuals during the third year of the study, divided by the number of recaptured unique individuals during the second year of the study.

An occurrence model was constructed to describe the recapture rate over space (delta or bay) and season, as autumn (September to November), winter (December to February), spring (March to May), and summer (June to August) (McGarvey and Feenstra, 2002). The number of recaptures during the first year were corrected for the average numbers of tagged fish during each season, as tagging took place throughout the first year. During the second and third year, the number of recaptures were corrected for the survival rate (year$^{-1}$) and tag expulsion rate (year$^{-1}$). The occurrence was expressed as recapture rate in % $N$ year$^{-1}$. As sampling by citizen science can be affected by spatial bias (Geldmann et al., 2016), occurrence was also expressed as recapture rate according to the population density (recaptures year$^{-1}$ km$^{-2}$) to consider the difference in size between the delta and the bay (Gonsamo and D’Odorico, 2014). The area of the delta was measured using the information of the spatial distribution of the population in the delta from an earlier tagging study (Skovrind et al., 2013), while the area of the bay inhabited by the population was estimated from the squared median distance from the delta to the point of recapture of the individuals caught in the bay. A full factorial general linear model (GLM) was conducted in SPSS (version 25, IBM, Armonk NY, USA) to describe the recapture rate (in both % $N$ year$^{-1}$ and year$^{-1}$ km$^{-2}$) from the place of recapture and time of year (season).

2.3. Growth

Four scales were taken for age determination from just below the second dorsal fin of 18 tagged individuals of various sizes, as well as 5 small individuals caught in the area by cast netting. Scale samples were examined under a stereomicroscope (Laborlux S, Leica Microsystems, Wetzlar, Germany), connected to a digital camera (SD Mk II, Canon, Tokyo, Japan). Age was determined by counting the number of dark bands in the scales (Bagenal, 1978). The first dark band was assigned age 0, and the scale edge the fish’s ultimate age, as the fish were caught during October to March, in which period the dark bands are formed due to slower growth. The maximum TL ($TL_{\infty}$) and growth coefficient ($k$) were determined by fitting age determined from the scales (t; years) to the TL of the fish using a modified von Bertalanffy equation (von Bertalanffy, 1934) (Table Curve 2D v4, Systat Software Inc, San Jose, CA, USA):

$$TL = TL_{\infty} \cdot \left(1 - e^{-kt}ight) + TL_0$$

(2)

where the TL at age 0 ($TL_0$) was set to 2 cm as this is the length at which the scales are formed in European perch (Craig, 2000). The age/length relationship was also obtained for eight other populations from the literature, six from freshwater populations and two from estuarine populations (Ali and Jones, 1978; Bay, 1985; Olsen, 2002; Willemensen, 1977), using the von Bertalanffy curve fit in equation (2). Mann-Whitney U-tests were performed in SPSS on $TL_{\infty}$ and $k$ between the 6 freshwater populations and the three brackish water populations (the two literature populations and the population from the present study).

2.4. Physico-chemical environment

The temperature, conductivity (salinity), and oxygen level (CTD; YSI 6920V2, YSI Inc., Yellow Springs, OH, USA) were measured every 15 min in the delta (Fig. 1), at a water depth of 1.5 m. The CTD was connected online to a PC and internet in the local sport fishing club house, which made the data publicly available in real time on a webpage (www.salmfish.dk) (Appendix B, Fig. B1). Temperature and salinity from the bay were accessed from E.U. Copernicus Marine Service Information. Environmental data from the bay was divided into seasons, defined as above, and a Nested ANOVAs were used to test the effect of season, with year as a nested term, on temperature and salinity. Tukey’s $t$ test were used as post hoc tests. The statistical tests were performed in in SPSS using a significance level of 5%.

3. Results

The data from the present study is available in the supplementary material.

3.1. Population ecology

The population size was estimated to 2872 individuals (95% C.I.: 1850 to 4607) within the tagged size range. Anglers and fishermen reported a total of 112 recaptures over the three year study period. There was no correlation between the ID ratio and the time from tagging to recapture (Spearman Rank Correlation, $r_s = -0.106$, n = 104, $p = 0.285$), and two fish were recapture within the same day as they were tagged. Eight recapture reports had no ID. Twelve of the identified recaptured individuals were recaptured twice and three of the identified recaptured individuals were recaptured three times. The number of recaptured identified individuals was 86 out of 301 (29%) (Appendix C, Table C1). The longest time from tagging to recapture was 887 days. Twelve of the recaptured individuals were double tagged and on all occasions with both tags still attached. Tag expulsion ratio was therefore calculated to 0% year$^{-1}$. The survival rate was estimated to 70.1% year$^{-1}$.

Most recaptures occurred in the delta, with 109 recaptures in total, and the fish resided here in autumn, winter and spring (Fig. 2). During summer, the fish were only caught in the bay, where 3 recaptures were reported 3 to 18 km from the delta. Intriguingly, no tagged fish were caught in any of the other nearby deltas where anadromous European perch occurs (3–25 km from the tagging site). The population density was estimated to 3755 fish km$^{-2}$ in the delta, and 45 fish km$^{-2}$ in the bay. The occurrence models were significantly explained by the interaction between time of year and place of recapture both when occurrence was expressed as recaptures in % $N$ year$^{-1}$ (GLM, $F(3,23) = 4.118$, $p = 0.024$) as well as when standardised for population density (recapture year$^{-1}$ m$^{-2}$; GLM, $F(3,23) = 5.120$, $p = 0.011$). Time of year and place of recapture had significant effects on the recapture rate in % $N$ year$^{-1}$ (GLM, $F(3,23) = 3.686$, $p = 0.034$ and GLM, $F(1,23) = 22.517$, $p = 2.2 \cdot 10^{-5}$, respectively), but not when the recaptures...
were standardised for population density.

3.2. Growth

The fish for which age was determined were between 1 and 10 years, with a median of 7 years (Appendix E, Table E1; Fig. 3). The age/length analyses showed a growth coefficient of 0.26 TL year\(^{-1}\) and an estimated TL\(^{\infty}\) of 45.7 cm (Appendix D, Table D2). TL\(^{\infty}\) in the brackish water populations was on average 40.6 ± 3.7 (SE) while it was on average 40.8 ± 6.3 in the freshwater populations and not significantly different between the two habitats (Mann-Whitney \(U\) test, \(p = 1.000\)). The growth coefficients in the brackish water populations was on average 0.295 ± 0.080 while it was on average 0.220 ± 0.016 in the freshwater populations and not significantly different between the two habitats (Mann-Whitney \(U\) test, \(p = 0.548\)).

3.3. Physico-chemical environment

The water parameters were measured in the delta from 8 October 2016 until 14 March 2017, where the CTD malfunctioned due to water leakage. The temperature during this period decreased from 12 °C during October 2016, to just above 0 °C in February 2017, and rose to 6 °C in March before the CTD was flooded (Fig. 4). The median salinity was 11 and ranged between 0 and 22. Five times, the salinity exceeded the hitherto considered maximum salinity tolerance of brackish water living perch (17.5; Christensen et al., 2019a), the longest event lasting five days. The oxygen content varied between 1 and 14 mg O\(_2\) L\(^{-1}\), and three hypoxic events of up to 14 h (oxygen content < 4 mg O\(_2\) L\(^{-1}\)) occurred over the period.

The temperature in the bay varied considerably over time, and was statistically different both between seasons (Nested ANOVA, \(F(3,8.039) = 174.315, p < 0.001\)) and over the years (Nested ANOVA, \(F(8,17544) = 93.468, p < 0.001\)) (Fig. 5). The temperature was in the bay was generally highest in the summer, and lowest during winter, but on occasions, the temperature was also low in the early spring (Fig. 5; Appendix E, Fig. E1). The salinity in the bay also varied significantly over time (Fig. 5), and was significantly different between seasons (Nested ANOVA, \(F(3,8.000) = 4.720, p = 0.035\)) and over the years (Nested ANOVA, \(F(8,7116) = 101.093, p < 0.001\)). The salinity in the bay was, on average, lowest during spring, and highest during winter.

---

**Fig. 2.** Recaptures of tagged European perch over a three year period relative to seasons and place (delta or bay). Recapture rate is given relative to population size estimate (\(\hat{N}\)), and as recapture rate standardised per m\(^{-2}\). The seasons cover autumn (September to November), winter (December to February), spring (March to May) and summer (June to August). Error bars represents standard error over the three consecutive years of the study.

**Fig. 3.** Age and growth of European perch. Panel A: age determined by scales in relation to total length (TL) of the present study (full circles). Solid line represents a von Bertalanffy growth curve. Panel B: von Bertalanffy growth curves of European perch from the present study (solid line) and European perch from the literature (dashed lines; Ali and Jones, 1978; Bay, 1985; Olsen, 2002; Willemsen, 1977), with grey lines being freshwater populations, and black lines being brackish water populations.
4. Discussion

4.1. Population ecology

Tag expulsion and tagging effects on behaviour and mortality can have severe implications on the results of tagging studies (Livings et al., 2007). For instance, tag expulsion can lead to overestimation of population size and underestimation of survival rate and spatial abundance as it infers a faulty proportion of non-tagged fish to be recaptured. In the present study, we found no evidence for tag expulsion, which is supported by earlier studies on both short term and long-term tag expulsion rate and effects of tagging have shown negligible tag loss and mortality in yellow perch (Perca flavescens) (Livings et al., 2007; Scholten et al., 2002), a closely related sister species of the European perch (Couture and Pyle, 2015). Behavioural disturbance and tagging related mortality can also affect the probability of recapture, and thus change metrics iterated from mark-recapture data. In the present study, some of the tagged fish were recaptured within the same day as the tagging occurred and we furthermore found no significant correlation between time and the recaptured fish ID. This showed that tagging had little effect, if any, on the catchability of the tagged fish, neither on the short nor on the long term.

The survival rate of 70.1% year$^{-1}$ found in the present study is high compared to many other species (Pauly, 1980), but comparable to what has previously been found for European perch (71 and 84% (Beverton and Holt, 1959)). The contribution of fishery induced mortality to the survival rate was not estimated from the present study, yet the multiple recaptures of the same individuals and the unconditional catch and release policy by local anglers indicate that it probably was low.

The population showed a clear annual migration pattern over three years in the present study, spending the summer in the bay and overwintering in the delta. Occurrence in the bay during the summer most likely reflects the high availability of food in estuaries (Cloern, 1987; Ray, 2005), as well as a lower competition for food resources with other species (Martino and Able, 2003; Remane, 1934; Whitfield et al., 2012), from which the fish may benefit largely from during the growth season. Furthermore, lower intra-specific competition may also be a contributing factor, as the population density was markedly lower in the bay than in the delta.

Natal homing has earlier been shown for other anadromous populations of European perch (Jarv, 2000; Müller and Berg, 1983; Siddaka and Lehtonen, 2004; ). Interestingly, no apparent emigration from the population was registered in the present study, as no tagged fish were caught in adjacent deltas in connection with the bay, which indicates strong natal homing in the population. As natal homing has also been shown in anadromous northern pike, common roach, ide, and pikeperch (Sander lucioperca) (Aro, 2002; Larsson et al., 2015; Müller and Berg, 1983), it seems a common trait for populations of anadromous stenohaline freshwater species. In the present study, we took the difference in size between the delta and the bay into account in the occurrence model (Gonsamo and D’Odorico, 2014) to minimise spatial bias for the recapture reporting (Geldmann et al., 2016). However, annual variations in fishing effort by anglers and fishermen could potentially have affected the occurrence model, a bias known as the “recorder effort problem” in citizen science studies (Hill, 2012). As there is no close
6

season for fishing on European perch in the study area, there was no obvious driver of such recorder effort problem in the present study. Speculatively, a potential limitation on reporting rate could have been that the occurrence of European perch in the delta during summer, and in the bay during winter, was too low to induce regular fishing in the areas during these periods, in turn, creating a small probability of marked individuals to be recaptured. Assuming that this has been the case, the present study have at least described the migration pattern of the majority of the population.

4.2. Growth

Although the estuarine population of European perch from the present study had high growth rates and large maximum length, the growth metrics were not distinctly higher than for fast-growing freshwater populations reported in the literature (Ali and Jones, 1978; Willemsen, 1977). It has previously been suggested that high growth rate of brackish water living freshwater fish in the Baltic Sea was due to the ambient salinity being close to the internal osmotic pressure of the fish, thereby minimising the energetic cost of osmoregulation (Lind, 1977; Lozys, 2004; Olsen, 2002). Osmoregulation is necessary for the fish to preserve physiological homeostasis (Jütz, 1972), and as an active physiological process it implicates an energetic cost, which is theoretically lowest at iso-osmotic conditions (Evans et al., 2005). However, the cost of osmoregulation of European perch is hardly measurable on whole animal metabolism (Christensen et al., 2017; Christensen et al., 2019b), and is probably only approximately 5% of the standard metabolic rate (Kirschner, 1995). The high growth rate of estuarine European perch is thus more likely a question of high food availability (Cloern, 1987; Ray, 2005) and low inter- and intra-specific competition (Martino and Able, 2003; Remane, 1934; Whitfield et al., 2012) in estuarine environments rather than a reduced cost of osmoregulation.

4.3. Physico-chemical environment

The salinity in the bay was highest during winter, during which period the fish resided in the delta. However, the salinity in the delta was occasionally lower than the bay (Appendix E, Fig. E1), the fish still experienced incidents of high salinity in the delta over the winter. Indeed, the ambient environment in the delta fluctuated considerably, and on multiple occasions, the salinity increased above the hitherto considered maximum salinity tolerance of European perch (Christensen et al., 2019a). While the salinity is lower higher up in the stream that feeds into the delta, an earlier study showed that the fish do not migrate further upstream than the lower reach of the stream, which in this study was considered a part of the delta (Skovrind et al., 2013). In the lower reach of the stream, the salinity may be lower than at the mouth of the delta, but at occasions of high delta salinity and high tide, the salinity in the lower reach of the stream is equally high. It is therefore likely that the fish indeed experienced the measured water conditions, and the ambient salinity of up to 22 is, to our knowledge, the highest ever reported in an area that are inhabited by estuarine living European perch.

The salinity in the bay was highest during autumn and winter, supporting the notion that winter migrations of anadromous fishes could be to avoiding negative effects of high salinity and low temperatures during this period (Christensen et al., 2017; Larsen et al., 2008). Interestingly, the salinity in the bay was generally low during spring, but still, the fish resided in the delta. Notably, the delta is the primary spawning site for the population (Christensen et al., 2016; Skovrind et al., 2013), and the migration into the delta can thus be regarded both a winter migration and a spawning migration.

Mass mortality of stenohaline fish species (e.g. northern pike and common roach) in the western Baltic Sea has occurred on many occasions during periods of high water salinity levels (Jacobsen et al., 2016; Pers. Obs.). However, salinity stress is not necessarily instantly lethal. When the salinity tolerance of a fish is exceeded, lethal osmotic distress may take several weeks to establish, depending on the level of homeostatic disturbance (Christensen et al., 2019a). Furthermore, low temperatures may extent survival time at salinities above the tolerance level (Overton et al., 2008). The reason fish kills did not occur during the observed events of high salinity can therefore be due to the short duration of high salinities incidents (5 days at salinities between 17.5 and 22) in combination with the cold temperatures they occurred at. The high water salinity events coincided with low water oxygen content and must therefore have occurred due to infusion of deoxygenated bottom water from Kattegat being forced over the Drogden Sill (Fig. 1), which can happen during stormy events only, typically in autumn and winter (Fenchel and Sand-Jensen, 2017; Fischer and Matthias, 1996; Jacobsen et al., 2016; Mohrholz et al., 2015). On three occasions, the water became hypoxic (oxygen concentration < 4 mgO₂ L⁻¹), which must also have imposed physiological stress in the fish (Richards et al., 2009). However, even the combined stress of high salinity and hypoxia apparently did not cause fish kills.

4.4. Conclusions and perspectives

Our study showed an anadromous sub-population of the stenohaline European perch with a clear annual migration pattern between a delta and a bay, spending the summer in the bay and the colder months in the delta. While the growth parameters were high in the estuarine European perch population of the present study, a meta-analysis showed no difference in growth capacities between brackish water and freshwater populations. This indicates that food availability and competition is more important for growth than a reduced cost of osmoregulation in estuaries. Our results also showed that anadromous European perch may temporarily experience salinities of up to 22, which is higher than the hitherto reported maximum salinity tolerance of the species, indicating that the fish live on the edge of their salinity tolerance in the western Baltic Sea. We conclude that the migration into the delta can be regarded both a winter migration to avoid high salinities in the bay during colder months as well as a spawning migration with the purpose of spawning in the area during spring.

The present study provides important knowledge for ecologists and management of estuarine environments, especially as estuaries and coastal areas are locally affected by climatic changes in river-runoff and evaporation patterns (Harley et al., 2006; Vuorinen et al., 2015). Other stenohaline freshwater fish, such as northern pike and ide are also inhabiting the western Baltic Sea (Jacobsen et al., 2016; Skovrind et al., 2016), and the results of the present study calls for further studies on anadromous populations of freshwater fish in the estuarine environment.

CRediT authorship contribution statement

E.A.F. Christensen: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Data curation, Writing - original draft, Visualization, Funding acquisition. M.B.S. Svendsen: Conceptualization, Methodology, Validation, Software, Formal analysis, Investigation, Data curation, Visualization, Supervision, Project administration. J.F. Steffensen: Conceptualization, Methodology, Validation, Resources, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: E. A.F. Christensen is a private member of Ishøj Sport fishing Club, but holds no board or administrative assignments.
Acknowledgements

Thanks to A. Ruth who helped setting up the CTD, and to H. Carl, M. A. Krag, and M. Skovrind, Natural History Museum of Denmark for help during fish tagging. Also, thanks to all the anglers and fishermen who contributed to this study. E.A.F. Christensen was supported by Elisabeth and Knud Petersens’s Foundation and strategic internal Ph.D. funds from the Department of Biology, University of Copenhagen. Half of the tags used in the present study were provided by Ishøj Sport Fishing Club. E.A.F. Christensen is a private member of Ishøj Sport Fishing Club, but holds no board or administrative assignments. Furthermore, this study has been conducted using E.U. Copernicus Marine Service Information.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2020.107091.

References

Rutilus rutilus
¨Sander lucioperca
¨trade.
¨Kallasvuo, M., Lappalainen, A., Lozus, L., Møller, P.R.
¨¨ Trade.
¨Trade.
¨Economics
¨Trade.
¨Trade.
¨Trade.
¨Trade.


