



Variation among bays in spatiotemporal aggregation of Baltic Sea pike highlights management complexity

Henrik Flink^{a,*}, Petter Tibblin^a, Marcus Hall^a, Gustav Hellström^b, Oscar Nordahl^a

^a Centre for Ecology and Evolution in Microbial Model Systems (EEMiS), Department of Biology and Environmental Science, Faculty of Health and Life Sciences, Linnaeus University, SE-39231 Kalmar, Sweden

^b Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, Skogsmarksgränd, SE-90736 Umeå, Sweden

ARTICLE INFO

Handled by B. Morales-Nin

Keywords:

Movement ecology
Ecosystem-based management
Fisheries
Protected areas
Habitat restoration
Acoustic telemetry

ABSTRACT

Understanding the movement ecology of fish communities is necessary to take effective management actions that aim to reverse population declines, especially in fish stocks containing sympatric subpopulations with local adaptations, such as Northern pike (*Esox lucius*) in the Baltic Sea. We followed the movement and survival of adult pike for one year by tagging 198 individuals in an estuary (an anadromous subpopulation) as well as in two neighbouring bays (individuals of unknown origin) with acoustic transmitters. We found that the estuary was vital in sustaining the local coastal pike stock, that anadromous pike mainly inhabited a coastal area with a radius of 3 km and aggregated in large numbers in the estuary several months prior to spawning. Management should thus prioritise to identify, restore, and protect estuaries from exploitation. The two neighbouring bays demonstrated distinct differences in spatiotemporal aggregations of pike with no aggregations prior to, and during, spawning in the bay without estuaries. The habitat choice during spawning season suggests that 92% of pike sampled in the bay adjacent to the estuary belong to the anadromous subpopulation, while 94% of pike sampled in the neighbouring bay belong to unknown subpopulation(s) of resident brackish spawners. Survival of tagged pike was 84% and suggest low mortality from fisheries and top predators, which have been proposed as threats to pike populations in other areas of the Baltic Sea. Together, these results call for management of high resolution and highlight the importance of detailed movement data.

1. Introduction

A central challenge to the management of wildlife populations is to correctly identify how animals are distributed in space and time relative to life history, abiotic, biotic, and anthropogenic factors (Erisman et al., 2012, 2017). The effectiveness of management actions, such as a spatially limited seasonal closure of a fishery (Dunn et al., 2011), will be highly dependent on correct information on the movement ecology of the managed stock. Poor information could lead to sub-optimally designed protected areas and the implementation of management actions which may favour certain phenotypes/strategies at the cost of others (Dunn et al., 2011). Obtaining appropriate data of spatiotemporal distributions require cost-effective tools for long-term monitoring of habitat utilisation at the levels of species, populations, and management units. One such solution is acoustic telemetry, a highly modular aquatic tracking technology which allows for large-scale collaborations within and among the scientific community and fisheries management

(reviewed by Brownscombe et al., 2019; Crossin et al., 2017; Nathan et al., 2022). Acoustic telemetry enables detailed spatiotemporal tracking on the seasonal movement patterns, mortality events, and habitat use of individuals and populations.

Coastal ecosystems are under immense anthropogenic pressure world-wide, and despite positive reports on reversed abundance trends of fish stocks in large parts of the world (Hilborn et al., 2020), a considerable share of global stocks are still in poor shape due to recent or historical overfishing (Hilborn et al., 2020; Jackson et al., 2001; Pauly et al., 1998). The coastal ecosystem in the semi-enclosed Baltic Sea has seen drastic ecosystem shifts from dominance of the predatory perch (*Perca fluviatilis*) and pike (*Esox lucius*) to dominance of the meso-predator three-spined stickleback (*Gasterosteus aculeatus*) (Bergström et al., 2015; Donadi et al., 2020; Eklöf et al., 2020; Eriksson et al., 2011; Ljunggren et al., 2010; Nilsson et al., 2019, 2004). Since the first reports of low recruitment of coastal predators along the Swedish coast (e.g., Ljunggren et al., 2010; Nilsson et al., 2004), efforts have been devoted to

* Corresponding author.

E-mail address: henrik.flink@lnu.se (H. Flink).

act against the negative trends. Pike populations have generally not rebounded and data from monitoring programs, although limited, indicate continued negative trends in the central Baltic Sea and a need for further management actions (Bergström et al., 2022; Nilsson et al., 2019; Olsson, 2019). The identification of fine scale genetic structuring (Nordahl et al., 2019; Sunde et al., 2022) and local adaptations (Berggren et al., 2016; Tibblin et al., 2015) in Baltic Sea pike suggest that management will benefit from acknowledging coastal pike as mixed assemblages of sympatric subpopulations.

Fish stocks containing sympatric subpopulations with local adaptations require well-informed small-scale ecosystem-based management (Reiss et al., 2009). Many migratory species show a philopatry to their spawning sites, a behaviour that reduces gene flow among spawning areas and enables the formation of genetic population structures akin to those observed for pike (Nordahl et al., 2019; Sunde et al., 2022). Subpopulations that are isolated during spawning may still mix outside the spawning season when they reside in areas where they can be exploited and managed as a common stock. In such systems, identifying and protecting the assortment of spawning areas can preserve diversity and ensure stock stability and resilience to perturbations (i.e., portfolio effects; Brennan et al., 2019; Schindler et al., 2010). Populations are especially vulnerable to fishery mortality and other stressors during periods of aggregation, most notably associated with spawning (Erisman et al., 2017). Protecting areas in and around spawning areas are thus intuitive management tools to protect recruitment and safeguard local spawning stocks from over-exploitations. Yet, complete closure of fisheries is not always desirable nor required, as the extent of regulations need to be balanced against its effects on local fisheries. Finding a favourable trade-off requires that the distribution of local spawning stocks is known and how these contribute to local fish stocks.

In this study, we focus on pike populations on the south-eastern coast of Sweden, a region that has been in focus of pike management due to early reports of pike recruitment failures followed by fisheries regulations and habitat restoration projects as a mean of reversing the trend. Currently, pike exploitation and harvest rates along the southeast coast of Sweden are mainly from recreational fisheries and are assumed to be low due to an increased popularity and partly mandatory use of catch and release (harvest is limited to 3 pike between 40 and 75 cm per person per day) (Swedish Agency for Marine and Water Management, 2020; Wennerström, 2020). The rapid establishment of cormorants along the Swedish Baltic coast together with increasing numbers of seals, is perceived as a threat to pike stocks, and actions to decimate these populations are often requested by local stakeholders (Bergström et al., 2022; Hansson et al., 2018). Pike has indeed been found in the diet of great cormorants (*Phalacrocorax carbo*) and grey seals (*Halichoerus grypus*) (Hansson et al., 2018; Östman et al., 2013) but their direct effect on mortality rates and their indirect effects on habitat utilisation have yet to be reliably quantified (Bergström et al., 2022; Heikinheimo et al., 2018). With an increased demand for management actions to rebound pike populations comes an increased need for understanding important mortality factors, population structures, and habitat use so that mitigation strategies stand accurate.

Here, we utilise acoustic telemetry to follow movements of adult individuals from an estuary that house an anadromous subpopulation as well as from the recipient coastal pike stock residing within the study area. By tagging individuals in the coastal bays and monitor their habitat choice, we aimed to identify the relative importance of freshwater and coastal spawning habitats for the overall stock of pike in the study area. For one year of movement, we describe the dynamics around geographical distribution within the coastal area and report on mortality events. To that end, we first identified how far individuals from the anadromous subpopulation move from spawning grounds in the estuary to their foraging areas and how the distribution of the subpopulation varies with season. We then investigated the mixing of the anadromous pike subpopulation with coastal resident pike and their migration between bays. Finally, we identified when and where individuals are lost

due to mortality and emigration, as well as when and where aggregations occur.

2. Material and methods

2.1. Study area and the acoustic telemetry array

The study area encompasses a 20 km coastal stretch in the Baltic Sea along the southeast part of Sweden centred around the mouth of the creek Lerviksbacken (<0.5 m/s mean annual discharge, N 57° 04.200'; E 16° 32.260') that leads up to the wetland Lervik (1.3 km from coast). The wetland, the creek Lerviksbacken, and its mouth constitute an estuary and are hence referred to as the estuary. The wetland was restored in 2007 and 2008 to improve pike spawning success and has since then served as a study area in several projects aiming to evaluate the usefulness of wetland restorations as a tool for management of pike (e.g., Nilsson et al., 2014). The coastal habitat outside Lervik is a shallow archipelago with a strongly indented coastline that form environmental gradients from sheltered bays in the innermost parts to wave-exposed islands in the outer areas. A 4 km long peninsula separate the study area in two main bays, here called the adjacent bay and the distant bay (Fig. 1). The estuary is in the innermost parts of the adjacent bay, while there are no freshwater creeks or wetlands connected to the distant bay. The entire area is included in a seasonal fishery closure for pike and perch during April to May, a fishery restriction that has been in place since 1998 to protect fish during spawning. The closed season was extended in April 2021 to include March and the area in the immediate vicinity (~500 m) of the estuary received an additional protection by a seasonal closure of all fishing during January to May. But note that these new restrictions were not in place during the data gathering in this study.

A total of 48 acoustic receivers were deployed in the study area forming a receiver array that extended approximately 10 km in water distance to the north and south of the estuary. The array was designed to track movements of pike within the shallow archipelago (<10 m depth)

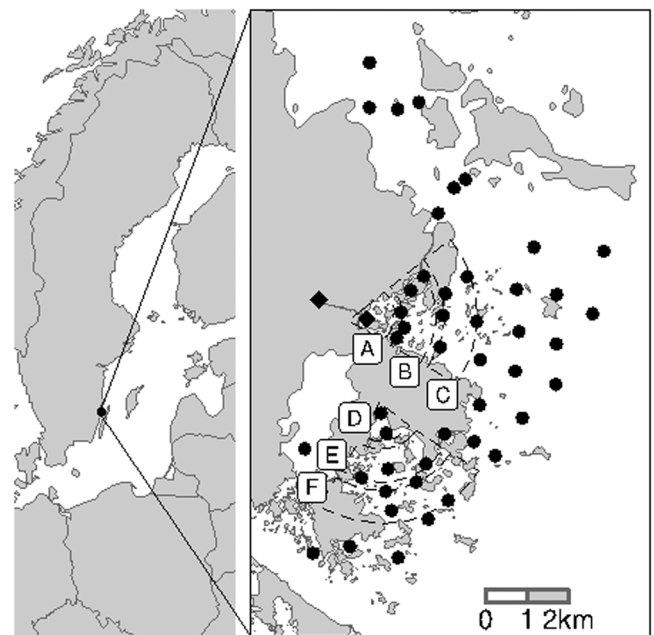


Fig. 1. Study site. Map of the study area in the south-eastern part of Sweden. The map includes the two bays in which pike were sampled in predefined zones illustrated as dashed polygons (adjacent bay: A-C and distant bay: D-F). Points display acoustic receiver locations, diamonds for receivers at the estuary (the mouth of the creek and the wetland in which anadromous pike were sampled) and circles for remaining receivers.

where individuals were assumed to spend most of the time. Two types of receivers were used, Thelma Biotel TBR 700 L ($n = 33$) and Vemco VR2tx ($n = 19$), both operating at 69 kHz with configurations that allow for decoding signals from tags utilising the R64K-protocol. Most of the array (46 receivers) was deployed in February to June 2020, and the remaining 2 receivers were deployed July 16, 2020. Receivers were moored to the bottom with concrete blocks ($35 \times 35 \times 5$ cm, 14 kg) and erected vertically either by being strapped to a steel rod bolted to the centre of the block, or by the lift of two buoys fastened on the sides of the receiver and attached to the block by a line. Receivers located in shallow areas (1–3 m) were marked by a surface buoy while receivers in deeper waters were connected to a second mooring block via a 10- to 30-meter-long mooring line that was used to retrieve the receivers.

2.2. Fish sampling

To maximise sample size in analyses of seasonal movement patterns and spatiotemporal aggregations while avoiding confounding effects caused by sex differences in movement behaviour, we sampled primarily female pike. However, we sampled 20 male pike in the estuary to evaluate sex differences in movement behaviour in the anadromous subpopulation. Captured individuals were sexed by examining the urogenital tract. To reduce the risk of complications due to tagging, we selected only fish larger than 45 cm in total length that had no critical injuries. The tag-to-body mass ratio in air ranged from 0.2% to 1.7% (pike body mass was estimated from length-mass relationship of caught pike in earlier studies in the area).

Anadromous pike from the Lervik estuary were caught with fyke-nets in the wetland during the spawning period at 12 sampling events between March 31 to April 20, 2020 (Fig. 1). We assessed maturity stage for females by applying a gentle pressure on the abdomen and only females that were spent or semi-spent were selected to reduce the risk of jeopardising the reproduction by damaging reproductive organs during tag insertion. Individuals were kept in retainer slings, sorted into keepnets and selected to cover a size distribution from 45 to 85 + cm (details of individual fish in supplemental Tab. s1).

Pike of unknown origins were sampled at the coast by rod and reel angling with artificial lures from boat in six predefined zones (A to F), distributed in the adjacent and the distant bay (Fig. 1). Fish were caught at 24 sampling events between June 8 to October 1, 2020. However, no sampling was conducted during the warmest summer weeks (July 16 to September 1) to minimise thermal stress during and after the capture and tagging procedure. In rare cases of hooking related injuries, fish were not tagged but released or, if severely injured, euthanised. We kept caught pike in retainer slings secured to the boat until tagging of an accumulated catch to make sampling more effective.

The tagging procedure of fish from the estuary was performed at land just at the edge of the wetland, while tagging of fish sampled at the coast was performed in the boat. All pike were tagged and released the same day as they were captured. Each fish was anaesthetised in 40–60 ppm clove oil (concentration depending on water temperature, clove oil was first emulsified in ethanol in a 1:9 ratio) in a well aerated tank with water from the sampling location until they reached complete immobilisation and did not react to handling (Zaikov et al., 2008). Fish were then placed in a standard orientation on a photo-board with a scale bar and photographed on the left side with consistent camera distance and angle. Pictures were used for accurate standard length (from the most anterior tip of the body to the posterior end of the hypural plate) measurements. The sedated fish were transferred to a V shaped cradle and recirculating water was pumped over the gills during the rest of the procedure.

2.3. Tagging

In total, we tagged 198 individuals with acoustic transmitters of which 80 females (standard length 67.3 ± 12.1 cm, mean \pm s.d.) and 20

males (standard length 55.7 ± 7.3 cm) were from the estuary, 53 females from the adjacent bay (standard length 62.3 ± 8.5 cm) and 45 females from the distant bay (standard length 64.4 ± 9.8 cm). Tagging was conducted by surgically implanting an acoustic transmitter (Thelma Biotel ID-MP13: diameter 12.7 mm, length 33.3 mm, weight in water 7.1 g, power output 153 dB, random signal delay of 90–150 s at 69 kHz, expected battery life minimum of 35 months). An additional passive integrated transponder (PIT) tag (Biomark HDX23, diameter 3.85 mm, length 23.1 mm) was implanted so that tagged individuals could be identified with a handheld PIT-tag reader in case of subsequent recaptures. Surgical instruments and tags were cleaned before each surgery by immersion in a 70% solution of ethanol. Tags were inserted in the abdominal cavity ventrally and posterior of the left pectoral fin, at the same incision site, and the incision was closed using two separate single sutures (Monocryl suture 4–0, FS-2 needle, undyed). After surgery, fish were kept in retainer slings and released following their recovery and return to normal locomotor activity.

2.4. Data analyses

Receiver data were downloaded onto a laptop between June 8 to July 17, 2021. The software R 4.1.1 (R Core Team, 2021) through RStudio 2021.9.0.351 (RStudio Team, 2021) was used for all analyses. Figures were prepared in R using the ggplot2 package (Wickham, 2016). One female sampled in the estuary and one female sampled in the adjacent bay, were not detected after their release likely due to prompt mortality, and subsequently not included in any analysis, tables, or figures. Raw acoustic data were initially explored and filtered using the actel package (Flávio, 2020) to identify and exclude influential and obvious false detections, i.e., single detections spatially and temporally isolated at the end of the detection period, and isolated detections which constituted large jumps over the study area without detections in between. Not all false detections are apparent, thus telemetry data filtering require some decision-making and defined thresholds that include a risk of misidentifying behaviour as false positives and vice versa (Klinard and Matley, 2020; Villegas-Ríos et al., 2020). For example, a continuous detection pattern can result from stationary behaviour or from a tag being stationary at the seabed due to mortality (Klinard and Matley, 2020). To distinguish between such outcomes, we assumed fish to be dead when a tag at the end of its detection period had been stationary on a single receiver for more than 20 days without being absent longer than 6 h ($n = 4$). Consequently, identified mortality detections for these fish were removed back to the day when the continuous detections started (a conservative approach recommended by e.g. Klinard and Matley, 2020). Fish that die might also cease being detected, for example if removed from the receiver array due to harvest or predation (Klinard and Matley, 2020). We defined a mortality event to have occurred if the fish had no detection during the last 10 weeks of study period ($n = 31$), except for if the last detection occurred at the edge of the array, then we defined it as an emigration event, i.e., that the fish left the area covered by the receiver array ($n = 6$, information of individual fate in supplemental Tab. s1). Such discrimination between mortality and emigration might be biased if fish die at the edge of the receiver array but is still a recommended method (Villegas-Ríos et al., 2020). These definitions assume that the study area was sufficiently covered by acoustic receivers so that the risk of individuals residing in the area for a longer period undetected is low. To test this assumption, we analysed the trajectories of individuals that moved between the two bays and recorded if the transitions were detected by receivers located between bays. We found that 40 out of 45 transitions (89 %) between bays were detected by at least two receivers, indicating adequate receiver coverage.

Movement and coastal distribution of pike sampled in the estuary was examined by calculating the in-water distance between each receiver and the receiver at the river mouth in the estuary, using the distancesMatrix() function in the actel package (Flávio, 2020). First, a shapefile with a land polygon of the study area was modified to increase

the width of narrow water channels. Then, the shapefile was converted into a raster which was used together with coordinates of receivers to create a transition layer (directions were set to 8, allowing fish to swim in intercardinal direction) by estimating the least cost paths in water between receivers.

Maximum migration distance was assessed for individual fish by taking the in-water distance between the estuary and the receiver each fish had been detected at that was furthest from the estuary. To test for differences between sexes in maximum migration distance we used an ANCOVA model including maximum migration distance as the dependent variable, sex as fixed factor, standard length as a covariate, and the interaction between sex and length. The Anova() function in car package (Fox and Weisberg, 2019) was used to assess TYPE III Sums of squares at an alpha level of 0.05. Seasonal distances between female pike sampled in the estuary (locations of the receiver that individuals had most detection at each day) and the estuary were descriptively presented as weekly (ISO week date, ISO 8601) boxplots with medians, 25th and 75th percentiles in Fig. 2, and as monthly means and standard deviations (s. d.) for both sexes in supplemental Tab. s2.

Movement between bays was assessed by identifying the number of individuals that were detected in the two bays respectively, grouped by sampling location (Table 1). Further, we assessed the degree of mixing of the anadromous subpopulation with the coastal resident pike by identifying the number of individuals from each sampling location that were detected in the estuary during spawning period 2021, as indicative of pike originating from the anadromous subpopulation.

Spatiotemporal aggregations were examined bimonthly by identifying the maximum number of female pike detected on a single day at acoustic receivers in the study area. Analyses were separated for pike sampled in the estuary (Fig. 3a), adjacent bay (Fig. 3b), and distant bay (Fig. 3c). Aggregations at the estuary were reported monthly in Table 2 for female pike sampled in the estuary and the adjacent bay.

Disappearances, i.e., interpreted mortality and emigration events, between the start of the study until the last 10 weeks of the study period were illustrated on a map by the location of the last appearance in Fig. 4a. The monthly mortality was calculated as the percentage of sampled fish that died each month per number of sampled fish alive at the start of respective month and reported in Fig. 4b. The monthly

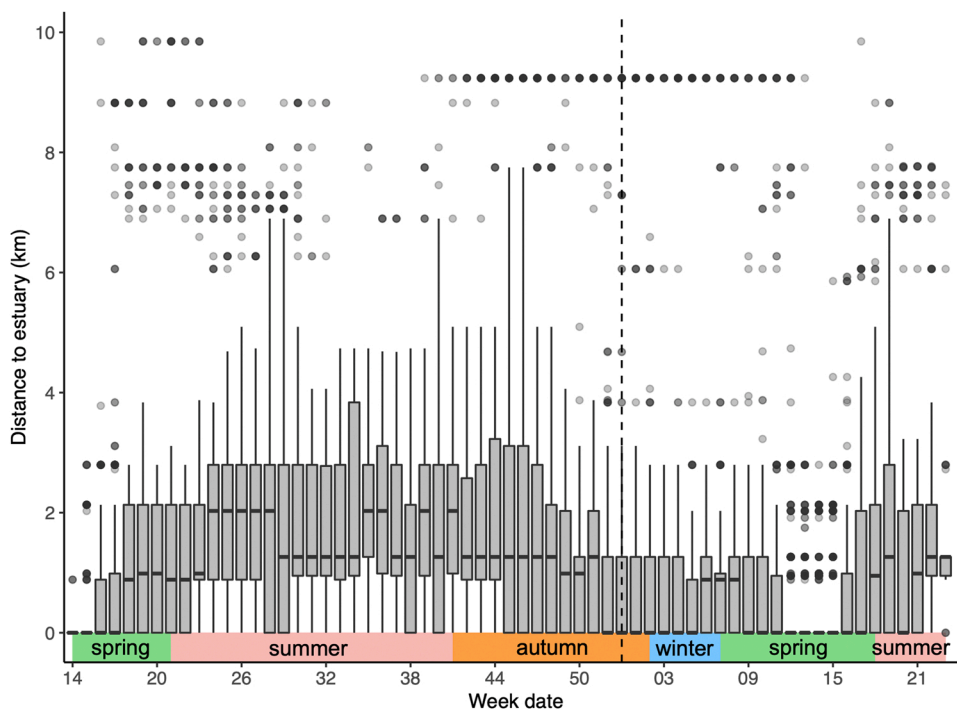


Fig. 2. Coastal distribution of female pike sampled in the estuary. Weekly distribution of the distance to the estuary for female pike sampled in the estuary. The solid lines within the boxes indicate medians, the boundaries of the box indicate 25th and 75th percentiles, and the whiskers below and above extends from the box to the lowest or largest value no further than 1.5 * the inter-quartile range, respectively. Data beyond the end of the whiskers are plotted individually as point outliers with transparency to visualise overlapping data. Coloured background and annotation illustrate seasons of the year for the actual area and period of interest, as defined afterward based on periodic average daily temperatures by the Swedish Meteorological and Hydrological Institute (2022). Dashed vertical line illustrates the shift between year 2020–2021.

Table 1

Movement between bays and mixing of the anadromous subpopulation with the coastal resident pike. Number of pike that were detected in each bay grouped by sampling location. Also, number of pike detected in the estuary during spawning period 2021 and percentages calculated based on the ratio of individuals alive at start of spawning period.

Sampling location	n	n	n	n	n
	initially sampled	detected at adjacent bay	detected at distant bay	alive during spawning period	detected at estuary during spawning period
<i>Adjacent bay</i>					
♀ zone A	12	12	0	11	11 (100 %)
♀ zone B	21	21	2	10	10 (100 %)
♀ zone C	19	19	2	16	13 (81 %)
<i>Distant bay</i>					
♀ zone A	15	3	15	11	2 (18 %)
♀ zone B	16	0	16	14	0 (0 %)
♀ zone C	14	1	14	10	0 (0 %)
<i>Estuary</i>					
♀	79	76	5	74	71 (96 %)
♂	20	20	5	19	18 (95 %)

mortality parameter was thus adjusted for mortality, as well as the addition of fish sampled in August, September, and October. Number of pike alive at the start of spawning season was reported in Table 1.

3. Results

3.1. Movement and seasonal distribution of the anadromous subpopulation

Pike sampled in the estuary were detected at the edge of the receiver array, both north and south. In total, five females and two males migrated more than 8 km from the estuary and by that more than 10 km from the sampling location in the wetland. On the contrary, three females never left the estuary. The maximum distance from the estuary that pike were detected differed depending on sex and body size (ANCOVA, effect of sex: $F_{1,94} = 5.23$, $P = 0.024$; effect of body length:

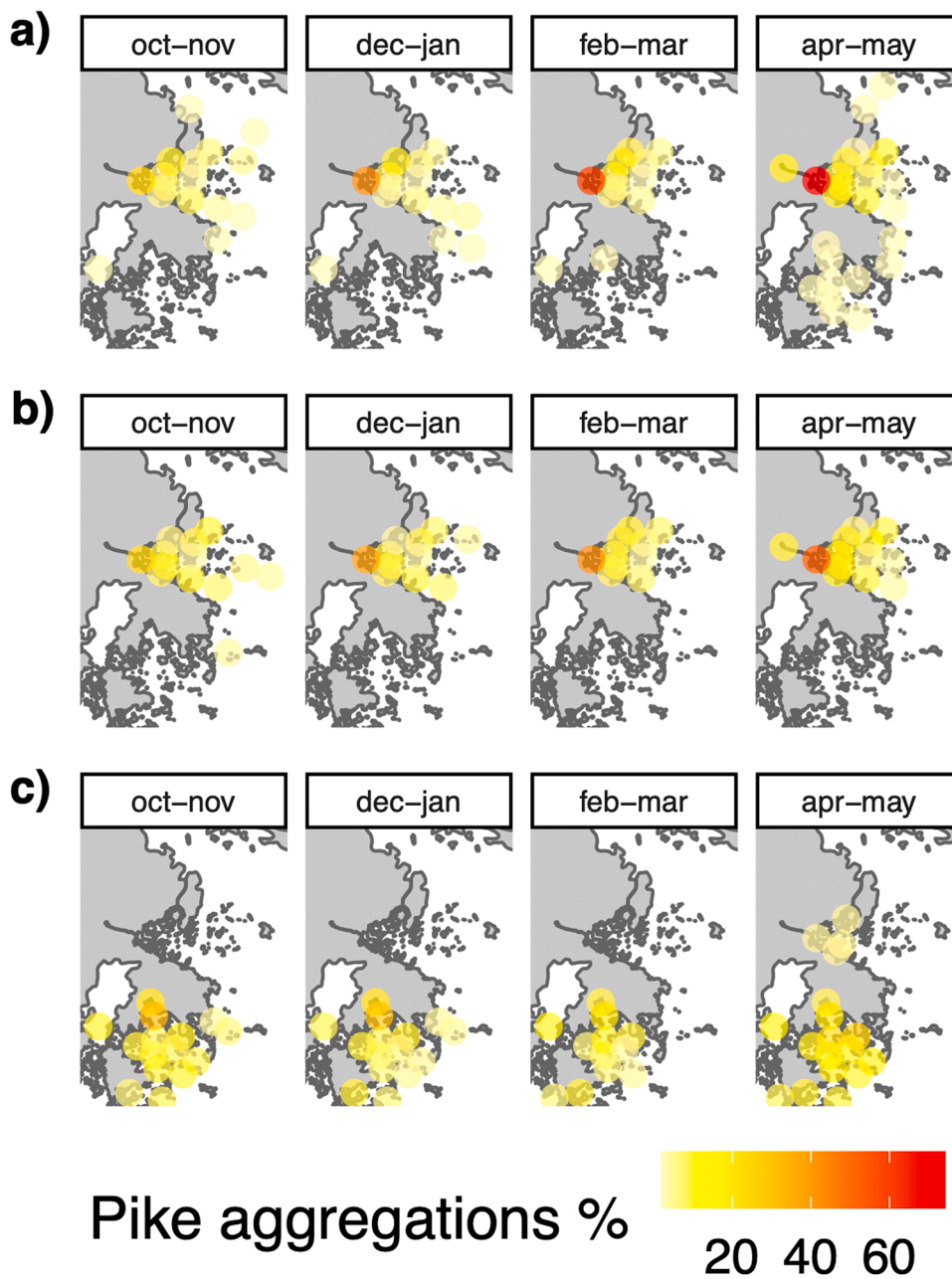


Fig. 3. Spatiotemporal aggregations of female pike. Bimonthly maps of maximum number of female pike detected on a single day at acoustic receivers in the study area as a percentage of initially sampled pike in each sampling location. Analyses are separated for pike sampled in the estuary (a), adjacent bay (b), and distant bay (c). Yellow to red colours indicate aggregations of fish. The radius of the circles is set to 500 m to show estimated detection ranges under ideal conditions without physical boundaries (as reported by acoustic telemetry manufacturers). Receivers is displayed only if a minimum of two fish have been detected on a single day and the map is cropped according to displayed receivers.

Table 2

Seasonal aggregations at the estuary. Monthly minimum, maximum and median number of unique female pike detected per day at the receiver located at the mouth of the Lervik creek in the estuary grouped by sampling location.

Sampling location	2020						2021					
	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
<i>Estuary (n = 79)</i>												
min	6	2	0	0	1	5	7	9	5	11	15	12
median	9	7	2	3	4	10	14	24	16	40	42	16
max	13	14	8	10	10	18	25	33	32	49	58	22
<i>Adjacent bay (n = 52)</i>												
min					2	2	3	4	2	4	15	8
median					3	4	7	12	9	17	22	12
max					6	12	13	19	17	22	28	19

$F_{1,94} = 2.57, P = 0.112$; effect of interaction: $F_{1,94} = 6.29, P = 0.014$. Females migrated in average 3.6 ± 1.9 km (mean \pm s.d.) whereas males migrated 3.9 ± 2.6 km. Male body size had a positive effect on

migration distance while female size was less influential (supplemental Fig. s1).

Weekly distributions of the distance between anadromous pike

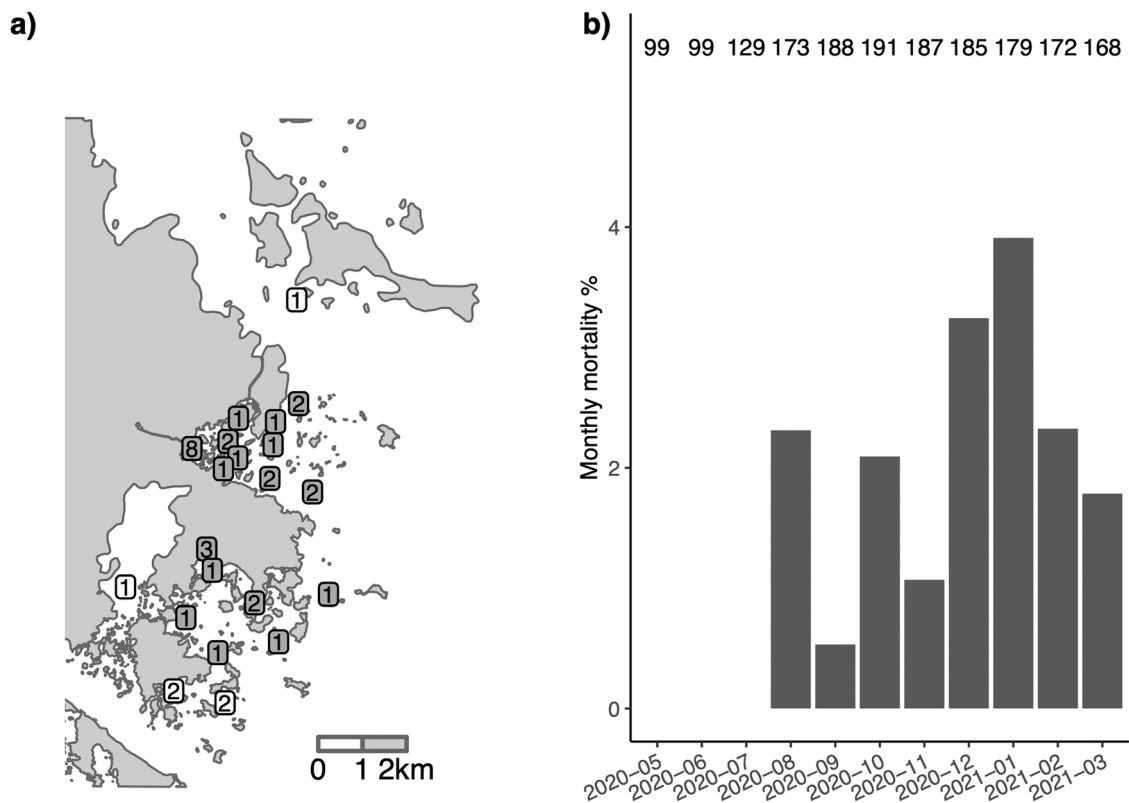


Fig. 4. a) Mortality and emigration map. Map of the study area showing the location of acoustic receivers that was last to detect one or more disappeared pike. Number of disappearances in the outskirts of the array is interpreted as emigration events and reported on white background, while disappearances inside the array is interpreted as deaths and reported on grey background. b) Monthly mortality rate. Bar plot showing monthly mortality as the percentage of sampled fish that died each month per number of sampled fish alive at the start of respective month (this number is shown for respective month on top of the figure).

individuals and the estuary reveal that females from the subpopulation was most dispersed during summer and early autumn, more specifically between week 23–44, 2020 (Fig. 2). During most of this period, 50% of the tagged females resided 1–3 km from the estuary, while 75% of females resided less than 1 km from the estuary throughout large parts of late autumn, winter, and spring. Both female and male pike resided furthest away from the estuary during June to November (supplemental Tab. s2). Females were on average closest to the estuary during April (0.4 ± 1.0 km) while males were closest in March (0.5 ± 1.8 km) and May (0.5 ± 1.5 km).

3.2. Migration between bays and mixing of the anadromous subpopulation with coastal resident pike

There were migration events between bays performed by pike from all sampling locations (Table 1). Approximately 10 % of pike sampled in the estuary and 8 % of pike sampled in the adjacent bay visited the distant bay at some point during the study period. Comparably, 9 % of pike sampled in the distant bay visited the adjacent bay. Spawning in the estuary 2021 occurred between March 30 to May 27, according to the earliest and latest detection at the receiver inside the wetland. Percentages of fish detected in the estuary during this period differ considerably between sampling locations (Table 1). 96 % of survived females and 95 % of males sampled while spawning in the estuary 2020 was detected in the estuary during spawning 2021, indicating very high site fidelity. 92 % (81–100 % depending on zone) of pike sampled in the adjacent bay was detected in the estuary at this time, suggesting that the bay during sampling period was inhabited by pike originating predominantly from the anadromous subpopulation. On the contrary, only 6 % (0–18 % depending on zone) of pike sampled in the distant bay was detected in the estuary at spawning time which suggest that the bay was

inhabited largely by fish of other origin.

3.3. Spatiotemporal aggregations

Female pike tagged in the estuary and the adjacent bay exhibited analogous movement dynamics and aggregated primarily in the estuary at the mouth of the creek (Fig. 3ab). Aggregations at the estuary started long before spawning period, in November, and was at largest in April (Table 2). The dynamics of spatiotemporal aggregations of female pike differed considerably between the adjacent and the distant bays. In the former, pike aggregated in winter and spring in the estuary located in the innermost bay whereas in the distant bay aggregations of pike were generally less clear and the distribution of individuals more fragmented throughout the bay also during spawning season in spring (Fig. 3c). If anything, the largest aggregation of pike in the distant bay was during autumn, when individuals aggregated in the innermost parts of the bay, rather than spring.

3.4. Mortality and emigration

A total of 37 pike were considered lost during the study period since they ceased being detected at least 10 weeks earlier than the end of the study. A few ($n = 6$) pike were last detected at the edge of the receiver array and were categorised as emigrated (Fig. 4a). However, most ($n = 31$) lost pike were last detected inside the array and thus categorised as deceased. Both female and male pike sampled at the estuary had an annual survival estimate of 94 %, while females sampled at the coast had an estimated survival of 74% over the study period (tracked for 8–10 months). Monthly mortality rates varied between 0 % and 4 % (Fig. 4b).

4. Discussion

National and regional fisheries management have been struggling for 30 years to understand and reverse population declines of pike along the southeast coast of Sweden. Implemented fisheries regulations and habitat restorations has been ambitious but still not successful (Nilsson et al., 2019). For evaluation and improvement of ongoing pike management, information on population distributions and key life-history events is required (Larsson et al., 2015). We followed the movement pattern of Baltic Sea pike by tagging adult pike both in an estuary during spawning (i.e., from an anadromous subpopulation) as well as in adjacent coastal areas (from unknown origin) with acoustic transmitters. This demonstrated how an anadromous pike subpopulation distribute and contribute to the coastal stock of pike, and that the two adjacent bays diverge in spatiotemporal dynamics. We also show that anadromous pike aggregate in large numbers in the estuary several months prior to the spawning, and that the annual survival of adult pike is surprisingly high and suggest low mortality from fishery and top predators. These results and the following discussion highlight how management of ecologically complex Baltic Sea pike stocks need to be dynamic and with high resolution.

To mitigate the negative development of Baltic Sea pike there is an ongoing trend to restore anadromous spawning habitats by reconstructing vegetated wetlands, often referred to as pike factories (Larsson et al., 2015). Such management has proven locally successful by boosting reproduction and emergence of juveniles (Nilsson et al., 2014) and by increasing adult pike abundances nearby (Tibblin et al., unpublished results). However, the ability to produce a significant result on larger scale depends on how the improved populations distribute and mix with the coastal pike stock. Previously studied Baltic Sea pike generally disperse less than 3–5 km, and the dispersal distance is believed to depend on the distances between spawning and feeding areas (Karås and Lehtonen, 1993). Maximum dispersal distances at 10 km in our study demonstrate that a single wetland restoration may, if successful, positively influence 20 km of coastal fish community. However, like previously shown, most pike from the anadromous subpopulation generally inhabited a smaller area, 75% of sampled females resided within 3 km from the estuary during summer when dispersal was greatest (Fig. 2). This suggests the effects of specific population improvements to be primarily local and calls for widespread restoration programs to counter pike declines in a Baltic perspective.

The coastal pike stock along the southeast coast of Sweden are composed of locally adapted subpopulations, both anadromous and resident brackish spawners, with strong genetic differences (Berggren et al., 2016; Engstedt et al., 2010, 2014; Nordahl et al., 2019; Sunde et al., 2018a, 2018b, 2019; Tibblin et al., 2016). Managing such complex fish communities is challenging and knowledge about the fine scale dynamics of the systems is needed to accurately understand population distributions for identification of management units and to preserve adaptive diversity. We found that the bay outside the estuary (i.e., the adjacent bay) was inhabited almost exclusively (92 %) by pike that later visited the estuary during spawning season (Table 1). This result indicates that the bay, approximately 15 km² in size, mainly consist of individuals from the anadromous subpopulation and stress how vital the estuary is in sustaining the adjacent coastal fish community. Conversely, the distant bay was with few exceptions (6 %) inhabited by pike from unknown subpopulation(s) (Table 1). The ecotype of these fish is uncertain, but they are likely to be resident brackish spawners since there are no nearby freshwater habitats and most pike stayed in the distant bay during spawning period (Fig. 3c). The ratio of migrating freshwater to resident brackish spawners is known to differ considerably between coastal areas in the Baltic Sea and is likely to depend on the characteristics of nearby spawning areas. Otolith microchemistry studies on Baltic Sea pike have reported freshwater origin from 6 % around the island of Rügen, Germany (Möller et al., 2019) to 82 % in Matsalu bay, Estonia (Rothla et al., 2012). Our results suggest similar distinct differences in

ratio between ecotypes, however in this study on a very fine spatial scale.

Movement behaviour of pike varies with season and monitoring studies have reported diverse and unpredictable seasonal patterns between pike populations from different habitats (e.g., Baktoft et al., 2012; Kobler et al., 2008a, 2008b; Nordahl et al., 2020). For example, a recent study on Baltic Sea pike found a continued activity pattern in winter during daytime but reduced activity during nights compared to summer (Nordahl et al., 2020). Pike in a small temperate lake reduced their swimming activity during winter (Kobler et al., 2008b) but at the same time dispersed over greater areas and utilised larger home ranges compared to summer (Kobler et al., 2008a). Our study shows distinct seasonal coastal distribution of the anadromous subpopulation. Individuals were spatially most distributed during summer and autumn, while throughout winter and spring fish aggregated within 1 km from the estuary (Fig. 2 and supplemental Tab. s2). This behaviour was also apparent in analysis of seasonal aggregations in which females sampled in the estuary and in the adjacent bay accumulated at the receiver located in the innermost bay at the mouth of the creek in the estuary during winter and spring (Fig. 3ab and Table 2). Strikingly, females from the distant bay had completely different seasonal dynamics and became less aggregated in the innermost bay during the same period (Fig. 3c). The cause of such diverse movement behaviour and phenology among pike residing in two neighbouring bays is important for generalisation but for us unfortunately unknown. It is unlikely that predation pressure or food availability differ significantly between bays and if fish seeks less exposed environment during winter there are plenty of sheltered areas in both bays. However, it is plausible that the diverse dynamics is caused by an attraction to the estuary, for example due to lower salinity or distinct reproductive behaviour as hypothesised for pike performing overwintering in a Western Baltic lagoon (Jacobsen et al., 2017). Whilst the adjacent bay is inhabited by anadromous pike that aggregates over winter around the estuary that serves as spawning ground for thousands of adult pike, it appears like resident brackish spawners are dispersed all over the distant bay during both winter and spawning season, suggesting not one but several coastal spawning areas. Regardless of the cause for the differences, detailed knowledge about spatiotemporal distributions is essential for accurate and effective local management and our results highlight how diverse such dynamics are in coastal pike.

Seasonal spring aggregations linked to spawning is well known in Baltic Sea pike (e.g., Karås and Lehtonen, 1993; Larsson et al., 2015), here we demonstrate continuous seasonal accumulation with high resolution. We found apparent aggregation at the estuary already in November, four months prior to spawning and just before arrival of meteorological winter (Fig. 2, Fig. 3ab and Table 2). There were days in November when 25–30 % of individuals sampled in the estuary were detected at the receiver at the mouth of the creek and the proportion detected on the location gradually increased each month until spawning (Table 2). This demonstrate that the estuary is exceptionally important to a very large proportion of the pike that reside in the archipelago of this coastal area during summer and autumn. Pike fishing in Sweden is popular during late winter and spring since large numbers of pike aggregate in shallow waters and thereby become easily accessible. However, it is during periods of such aggregation that the risk of over-exploitation of local stocks is greatest, especially when aggregations are related to spawning. The entire Kalmar Sound, southeast of Sweden, has been included in a seasonal fishery closure for pike and perch during April to May since 1998 to protect fish while spawning and the closure was extended in 2021 to include March. Temporary protection of fish aggregations has been highlighted as particularly meaningful to help rebuild declining stocks, this is partly because the spatial limitation of such protection allows monitoring and management actions to be scaled down, while benefits can apply to entire stocks (Erisman et al., 2017). On April 1, 2021, numerous smaller areas, mainly estuaries, along the southeast coast of Sweden, became complete or seasonally protected to safeguard fish stocks of various species (Swedish

Agency for Marine and Water Management, 2021). The estuary of our study is one of these areas and the coast in the immediate vicinity (~500 m) of the mouth of the creek is currently protected between January 1 to May 31 from all fishing activity to protect perch and pike. The data presented here support the importance of protecting estuaries that house anadromous pike and suggest that seasonal protections could be extended to capture also overwintering fish. However, management actions discussed here concern only fishing activities, management would gain from also considering stressors such as other types of exploitation, eutrophication, boat traffic, and natural predation in estuaries and other hotspots.

We evaluated the fate of sampled individuals to estimate annual and seasonal mortality rates. Unfortunately, the study design did not allow differentiating between natural mortality, fishing mortality or predation events. The estimated mortality rate during the study period was however low compared to Baltic Sea pike (Berggren et al., 2022), only 6% for both female and male pike sampled in the estuary and 26 % for female pike sampled in the bays. This suggests that the current mortality pressure on adult pike from fisheries and natural predators in the area is minor, although the pattern of pike that rarely utilised foraging habitats in the outer archipelago may point to a behavioural response to altered predation pressure from seals (Bergström et al., 2022). The observed differences in mortality rate between pike sampled in the estuary and at the coast is somewhat puzzling considering that they shared a common coastal habitat (Fig. 3abc) and as pike sampled in the adjacent bay likely stem from the same subpopulation as fish sampled in the estuary. The result may be due to differences in site-specific sampling methods and water temperatures, i.e. pike sampled in the estuary were caught in spring using fyke-nets, while pike sampled at the coast were caught by rod and reel during summer and early autumn, which may have impacted long term survival rates. Alternatively, angling may have specifically targeted individuals with certain phenotypes, such as proactive pike (Monk et al., 2021), that are more vulnerable to predation and thus suffered higher mortality rates. Or the observed differences between the two groups may, simply, be due to chance. Monthly mortality rates fluctuated between 0 % and 4 %, with none to low mortality during summer and a small peak in January (Fig. 4b). By comparing the location of aggregations with the position of mortality events (Fig. 3abc and Fig. 4a) it appears like mortality followed the distribution of individuals without being overrepresented in any area. A large cormorant nesting colony inhabits the adjacent bay in our study area. Whilst cormorants rarely eat adult pike, predation on smaller individuals have been proposed to locally reduce adult stocks (Östman et al., 2013). Nevertheless, the anadromous pike subpopulation in our area is thriving and the estimated population census size has increased from less than 1000 individuals during the period 2006–2009 (Tibblin et al., 2016) to approximately 3000 individuals in 2020 and 2021 (unpublished data) indicating that the colony do not constrain the subpopulation to any major degree. Recent studies on declining Baltic Sea pike populations estimate substantial pike removals, by seals in Stockholm archipelago (Bergström et al., 2022) and by commercial and recreational fishers in the Rügen area (van Gemert et al., 2022). The variation between areas in key mortality factors and mortality rate emphasises the complexity and need of high-resolution management.

In conclusion, our results demonstrate the importance of an estuary for the local fish community as the main spawning area for almost the entire pike stock in the adjacent bay, but also as a habitat with dense aggregations of overwintering pike, a dynamic not observed in the distant, but neighbouring, bay without an estuary. These results emphasise the importance of detailed knowledge about spatiotemporal movement and life-history events for accurate management of coastal fish stocks. Acoustic telemetry can, as demonstrated here, provide such information with high-resolution. Management should prioritise to identify, protect, and restore estuaries housing anadromous pike. The significant differences in movement dynamics and population structures on fine spatial scale for Baltic Sea pike, calls for local, but widespread,

adaptive management plans to reverse population declines. However, acoustic studies spanning environmental gradients and different habitats would be required to determine causes for diverging dynamics and mortality factors across Baltic Sea, and thereby allow for effective ecosystem-based management also on larger scale.

Ethical approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. The study was granted ethical approvals (Dnr 168677–2018; Dnr 19359–2019) by the Ethical Committee on Animal Experiments, Swedish Board of Agriculture, in Linköping and Stockholm respectively.

CRedit authorship contribution statement

Henrik Flink: Conceptualization, Methodology, Writing – original draft, Formal analysis, Visualisation, Investigation. **Petter Tibblin:** Conceptualization, Methodology, Writing – review & editing, Funding acquisition, Supervision, Investigation. **Marcus Hall:** Investigation, Writing – review & editing. **Gustav Hellström:** Investigation, Writing – review & editing, Funding acquisition. **Oscar Nordahl:** Conceptualization, Methodology, Writing – original draft, Funding acquisition, Supervision, Investigation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

Acknowledgements

We thank Per Larsson and Tobias Borger for significant support in conceptualisation, field work and research infrastructure. We also thank Per Koch-Schmidt, Kristofer Bergström, Jasper Münnich, Johanna Sunde, Jonas Jakobsson, Peter Söderling, Anton Rarysson, Yannick Francioli, Håkan Johansson, and Christofer Osbeck for excellent help in the field, and three anonymous reviewers for their constructive and helpful review of an earlier draft. We are grateful to the landowners granting us access to the spawning pike sampling site. This work was supported by funds kindly provided by the Swedish Research Council FORMAS (Dnr 2018-00605 to PT), the Crafoord Foundation (Dnr 20210648 to PT) and the Administrative County Board of Kalmar County (Dnr 511-4685-20 and 623-4688-20 to PT and ON).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.fishres.2022.106579](https://doi.org/10.1016/j.fishres.2022.106579).

References

- Baktoft, H., Aarestrup, K., Berg, S., Boel, M., Jacobsen, L., Jepsen, N., Koed, A., Svendsen, J.C., Skov, C., 2012. Seasonal and diel effects on the activity of northern pike studied by high-resolution positional telemetry. *Ecol. Freshw. Fish* 21, 386–394. <https://doi.org/10.1111/j.1600-0633.2012.00558.x>.
- Berggren, H., Nordahl, O., Tibblin, P., Larsson, P., Forsman, A., 2016. Testing for local adaptation to spawning habitat in sympatric subpopulations of pike by reciprocal translocation of embryos. *PLoS One* 11, e0154488. <https://doi.org/10.1371/journal.pone.0154488>.
- Berggren, T., Bergström, U., Sundblad, G., Östman, Ö., 2022. Warmer water increases early body growth of northern pike (*Esox lucius*), but mortality has larger impact on

- decreasing body sizes. *Can. J. Fish. Aquat. Sci.* 79, 771–781. <https://doi.org/10.1139/cjfas-2020-0386>.
- Bergström, U., Olsson, J., Casini, M., Eriksson, B.K., Fredriksson, R., Wennhage, H., Appelberg, M., 2015. Stickleback increase in the Baltic Sea – a thorny issue for coastal predatory fish. *Estuar. Coast. Shelf Sci.* 163, 134–142. <https://doi.org/10.1016/j.ecss.2015.06.017>.
- Bergström, U., Larsson, S., Erlandsson, M., Ovegård, M., Ragnarsson Stabo, H., Östman, Ö., Sundblad, G., 2022. Long-term decline in northern pike (*Esox lucius* L.) populations in the Baltic Sea revealed by recreational angling data. *Fish. Res.* 251, 106307. <https://doi.org/10.1016/j.fishres.2022.106307>.
- Brennan, S.R., Schindler, D.E., Cline, T.J., Walsworth, T.E., Buck, G., Fernandez, D.P., 2019. Shifting habitat mosaics and fish production across river basins. *Science* 364, 783–786. <https://doi.org/10.1126/science.aav4313>.
- Brownscombe, J.W., Lédée, E.J.I., Raby, G.D., Struthers, D.P., Gutowsky, L.F.G., Nguyen, V.M., Young, N., Stokesbury, M.J.W., Holbrook, C.M., Brenden, T.O., Vandergoot, C.S., Murchie, K.J., Whoriskey, K., Flemming, J.M., Kessel, S.T., Krueger, C.C., Cooke, S.J., 2019. Conducting and interpreting fish telemetry studies: considerations for researchers and resource managers. *Rev. Fish Biol. Fish.* 29, 369–400. <https://doi.org/10.1007/s11160-019-09560-4>.
- Crossin, G.T., Heupel, M.R., Holbrook, C.M., Hussey, N.E., Lowerre-Barbieri, S.K., Nguyen, V.M., Raby, G.D., Cooke, S.J., 2017. Acoustic telemetry and fisheries management. *Ecol. Appl.* 27, 1031–1049. <https://doi.org/10.1002/eap.1533>.
- Donadi, S., Bergström, L., Berglund, J.M.B., Bäck, A., Mikkola, R., Saarinen, A., Bergström, U., 2020. Perch and pike recruitment in coastal bays limited by stickleback predation and environmental forcing. *Estuar. Coast. Shelf Sci.* 246, 107052. <https://doi.org/10.1016/j.ecss.2020.107052>.
- Dunn, D.C., Boustany, A.M., Halpin, P.N., 2011. Spatio-temporal management of fisheries to reduce by-catch and increase fishing selectivity. *Fish. Fish.* 12, 110–119. <https://doi.org/10.1111/j.1467-2979.2010.00388.x>.
- Eklöf, J.S., Sundblad, G., Erlandsson, M., Donadi, S., Hansen, J.P., Klemens Eriksson, B., Bergström, U., 2020. A spatial regime shift from predator to prey dominance in a large coastal ecosystem. *Commun. Biol.* 3, 1–9. <https://doi.org/10.1038/s42003-020-01180-0>.
- Engstedt, O., Stenroth, P., Larsson, P., Ljunggren, L., Elfman, M., 2010. Assessment of natal origin of pike (*Esox lucius*) in the Baltic Sea using Sr:Ca in otoliths. *Environ. Biol. Fish.* 89, 547–555. <https://doi.org/10.1007/s10641-010-9686-x>.
- Engstedt, O., Engkvist, R., Larsson, P., 2014. Elemental fingerprinting in otoliths reveals natal homing of anadromous Baltic Sea pike (*Esox lucius* L.). *Ecol. Freshw. Fish.* 23, 313–321. <https://doi.org/10.1111/eff.12082>.
- Eriksson, B.K., Sieben, K., Eklöf, J., Ljunggren, L., Olsson, J., Casini, M., Bergström, U., 2011. Effects of altered offshore food webs on coastal ecosystems emphasize the need for cross-ecosystem management. *Ambio* 40, 786–797. <https://doi.org/10.1007/s13280-011-0158-0>.
- Erisman, B., Aburto-Oropeza, O., Gonzalez-Abraham, C., Mascareñas-Osorio, I., Moreno-Báez, M., Hastings, P.A., 2012. Spatio-temporal dynamics of a fish spawning aggregations and its fishery in the Gulf of California. *Sci. Rep.* 2, 284. <https://doi.org/10.1038/srep00284>.
- Erisman, B., Heyman, W., Kobara, S., Ezer, T., Pittman, S., Aburto-Oropeza, O., Nemeth, R.S., 2017. Fish spawning aggregations: where well-placed management actions can yield big benefits for fisheries and conservation. *Fish. Fish.* 18, 128–144. <https://doi.org/10.1111/faf.12132>.
- Flávio, H., Baktoft, H., 2020. actel: Standardised analysis of acoustic telemetry data from animals moving through receiver arrays. *Methods Ecol. Evol.* 12, 196–203. <https://doi.org/10.1111/2041-210X.13503>.
- Fox, J., Weisberg, S., 2019. An R Companion to Applied Regression. Third edition. Sage, Thousand Oaks CA. (<https://socialscisearch.com/master.ca/jfox/Books/Companion/>).
- Hansson, S., Bergström, U., Bonsohoff, E., Härkönen, T., Jepsen, N., Kaustky, L., Lundström, K., Lunneryd, S.-G., Ovegård, M., Salmi, J., Sendek, D., Vetemaa, M., 2018. Competition for fish – fish extraction from the Baltic Sea by humans, aquatic mammals and birds. *ICES Mar. Sci. Symp.* 75, 999–1008. <https://doi.org/10.1093/icesjms/fsx207>.
- Heikinheimo, O., Lehtonen, H., Lehikoinen, A., 2018. Comment to Hansson, S. et al. (2017): “Competition for the fish – fish extraction from the Baltic Sea by humans, aquatic mammals, and birds”, with special reference to cormorants, perch, and pikeperch. *ICES Mar. Sci. Symp.* 75, 1832–1836. <https://doi.org/10.1093/icesjms/fsy054>.
- Hilborn, R., Amorosa, R.O., Anderson, C.M., Baum, J.K., Branch, T.A., Costello, C., de Moor, C.L., Faraj, A., Hively, D., Jensen, O.P., Kurota, H., Little, L.R., Mace, P., McClanahan, T., Melnychuk, M.C., Minto, C., Osio, G.C., Parma, A.M., Pons, M., Segurado, S., Szuwalski, C.S., Wilson, J.R., Ye, Y., 2020. Effective fisheries management instrumental in improving fish stock status. *PNAS* 117, 2218–2224. <https://doi.org/10.1073/pnas.1909726116>.
- Jackson, J.B.C., Kirby, M.X., Berger, W.H., Björndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner, R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293, 629–637. <https://doi.org/10.1126/science.1059199>.
- Jacobsen, L., Bekkevold, D., Berg, S., Jepsen, N., Koed, A., Aarestrup, K., Baktoft, H., Skov, C., 2017. Pike (*Esox lucius* L.) on the edge: consistent individual movement patterns in transitional waters of the western Baltic. *Hydrobiologia* 784, 143–154. <https://doi.org/10.1007/s10750-016-2863-y>.
- Karås, P., Lehtonen, H., 1993. Patterns of movement and migration of pike (*Esox lucius* L.) in the Baltic Sea. *Nord. J. Freshw. Res.* 68, 72–79.
- Klinard, N.V., Matley, J.K., 2020. Living until proven dead: addressing mortality in acoustic telemetry research. *Rev. Fish Biol. Fish.* 30, 485–499. <https://doi.org/10.1007/s11160-020-09613-z>.
- Kobler, A., Klefoth, T., Arlinghaus, R., 2008a. Site fidelity and seasonal changes in activity centre size of female pike *Esox lucius* in a small lake. *J. Fish. Biol.* 73, 584–596. <https://doi.org/10.1111/j.1095-8649.2008.01952.x>.
- Kobler, A., Klefoth, T., Wolter, C., Fredrich, F., Arlinghaus, R., 2008b. Contrasting pike (*Esox lucius* L.) movement and habitat choice between summer and winter in a small lake. *Hydrobiologia* 601, 17–27. <https://doi.org/10.1007/s10750-007-9263-2>.
- Larsson, P., Tibblin, P., Koch-Schmidt, P., Engstedt, O., Nilsson, J., Nordahl, O., Forsman, A., 2015. Ecology, evolution, and management strategies of northern pike populations in the Baltic Sea. *Ambio* 44, 451–461. <https://doi.org/10.1007/s13280-015-0664-6>.
- Ljunggren, L., Sandström, A., Bergström, U., Mattila, J., Lappalainen, A., Johansson, G., Sundblad, G., Casini, M., Kaljuste, O., Eriksson, B.K., 2010. Recruitment failure of coastal predatory fish in the Baltic Sea coincident with an offshore ecosystem regime shift. *ICES J. Mar. Sci.* 67, 1587–1595. <https://doi.org/10.1093/icesjms/fsq109>.
- Möller, S., Winkler, H.M., Klügel, A., Richter, S., 2019. Using otolith microchemical analysis to investigate the importance of brackish bays for pike (*Esox lucius* Linnaeus, 1758) reproduction in the southern Baltic Sea. *Ecol. Freshw. Fish.* 28, 602–610. <https://doi.org/10.1111/eff.12478>.
- Monk, C.T., Bekkevold, D., Klefoth, T., Pagel, T., Palmer, M., Arlinghaus, R., 2021. The battle between harvest and natural selection creates small and shy fish. e2009451118 *PNAS* 118. <https://doi.org/10.1073/pnas.2009451118>.
- Nathan, R., Monk, C.T., Arlinghaus, R., Adam, T., Alós, J., Assaf, M., Baktoft, H., Beardsworth, C.E., Bertram, M.G., Bijleveld, A.L., Brodin, T., Brooks, J.L., Campos-Candela, A., Cooke, S.J., Gjelland, K.Ø., Gupte, P.R., Harel, R., Hellström, G., Jeltsch, F., Killen, S.S., Klefoth, T., Langrock, R., Lennox, R.J., Lourie, E., Madden, J. R., Orchan, Y., Pauwels, I.S., Rñha, M., Roeleke, M., Schlägel, U.E., Shohami, D., Signer, J., Toledo, S., Vilik, O., Westrelin, S., Whiteside, M.A., Jarić, I., 2022. Big-data approaches lead to an increased understanding of the ecology of animal movement. *Science*. <https://doi.org/10.1126/science.abg1780>.
- Nilsson, J., Andersson, J., Karås, P., Sandström, O., 2004. Recruitment failure and decreasing catches of perch (*Perca fluviatilis* L.) and pike (*Esox lucius* L.) in the coastal waters of southeast Sweden. *Boreal Environ. Res.* 9, 295–306.
- Nilsson, J., Engstedt, O., Larsson, P., 2014. Wetlands for northern pike (*Esox lucius* L.) recruitment in the Baltic Sea. *Hydrobiologia* 721, 145–154. <https://doi.org/10.1007/s10750-013-1656-9>.
- Nilsson, J., Flink, H., Tibblin, P., 2019. Predator–prey role reversal may impair the recovery of declining pike populations. *J. Anim. Ecol.* 88, 927–939. <https://doi.org/10.1111/1365-2656.12981>.
- Nordahl, O., Koch-Schmidt, P., Sunde, J., Yıldırım, Y., Tibblin, P., Forsman, A., Larsson, P., 2019. Genetic differentiation between and within ecotypes of pike (*Esox lucius*) in the Baltic Sea. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 1923–1935. <https://doi.org/10.1002/aqc.3196>.
- Nordahl, O., Koch-Schmidt, P., Tibblin, P., Forsman, A., Larsson, P., 2020. Vertical movements of coastal pike (*Esox lucius*) - On the role of sun basking. *Ecol. Freshw. Fish.* 29, 18–30. <https://doi.org/10.1111/eff.12484>.
- Olsson, J., 2019. Past and current trends of coastal predatory fish in the Baltic Sea with a focus on perch, pike, and pikeperch. *Fishes* 4, 7. <https://doi.org/10.3390/fishes4010007>.
- Östman, Ö., Boström, M.K., Bergström, U., Andersson, J., Lunneryd, S.-G., 2013. Estimating competition between wildlife and humans - a case of cormorants and coastal fisheries in the Baltic Sea. *PLoS One* 8, e83763. <https://doi.org/10.1371/journal.pone.0083763>.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres Jr., F., 1998. Fishing down marine food webs. *Science* 279, 860–863. <https://doi.org/10.1126/science.279.5352.860>.
- R Core Team, 2021. R: A language and environment for statistical computing. Reiss, H., Hoarai, G., Dickey-Collas, M., Wolff, W.J., 2009. Genetic population structure of marine fish: mismatch between biological and fisheries management units. *Fish. Fish.* 10, 361–395. <https://doi.org/10.1111/j.1467-2979.2008.00324.x>.
- Rothla, M., Vetemaa, M., Soesoo, A., 2012. Early life migration patterns of Baltic Sea pike *Esox lucius*. *J. Fish. Biol.* 80, 886–893. <https://doi.org/10.1111/j.1095-8649.2012.03226.x>.
- RStudio Team, 2021. RStudio: Integrated Development Environment for R. Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., Webster, M.S., 2010. Population diversity and the portfolio effect in an exploited species. *Nature* 465, 609–612. <https://doi.org/10.1038/nature09060>.
- Sunde, J., Tamario, C., Tibblin, P., Larsson, P., Forsman, A., 2018a. Variation in salinity tolerance between and within anadromous sub-populations of pike (*Esox lucius*). *Sci. Rep.* 8, 22. <https://doi.org/10.1038/s41598-017-18413-8>.
- Sunde, J., Tibblin, P., Larsson, P., Forsman, A., 2018b. Sex-specific effects of outbreeding on offspring quality in pike (*Esox lucius*). *Ecol. Evol.* 8, 10448–10459. <https://doi.org/10.1002/ece3.4510>.
- Sunde, J., Larsson, P., Forsman, A., 2019. Adaptations of early development to local spawning temperature in anadromous populations of pike (*Esox lucius*). *BMC Evol. Biol.* 57, 289–300. <https://doi.org/10.1186/s12862-019-1475-3>.
- Sunde, J., Yıldırım, Y., Tibblin, P., Bekkevold, D., Skov, C., Nordahl, O., Larsson, P., Forsman, A., 2022. Drivers of neutral and adaptive differentiation in pike (*Esox lucius*) populations from contrasting environments. *Mol. Ecol.* 31, 1093–1110. <https://doi.org/10.1111/mec.16315>.
- Swedish Agency for Marine and Water Management (Havs- och vattenmyndigheten), 2020. Recreational Fisheries in Sweden 2020. Statistical Report JO 57 SM 2101.
- Swedish Agency for Marine and Water Management (Havs- och vattenmyndigheten), 2021. Havs- och vattenmyndighetens forskrifter om ändring i Fiskeriverkets föreskrifter (FIFS 2004:36) om fiske i Skagerrak, Kattegatt och Östersjön (in Swedish). *HVMFS* 2021:6, 1–48.

- Swedish Meteorological and Hydrological Institute (Sveriges Meteorologiska och Hydrologiska Institut). SMHI. Available online: (<https://www.smhi.se/vader/observationer/ankomst-arstider/>) (accessed on 25 January 2022).
- Tibblin, P., Forsman, A., Koch-Schmidt, P., Nordahl, O., Johannessen, P., Nilsson, J., Larsson, P., 2015. Evolutionary divergence of adult body size and juvenile growth in sympatric subpopulations of a top predator in aquatic ecosystems. *Am. Nat.* 186, 98–110. <https://doi.org/10.1086/681597>.
- Tibblin, P., Forsman, A., Borger, T., Larsson, P., 2016. Causes and consequences of repeatability, flexibility and individual fine-tuning of migratory timing in pike. *J. Anim. Ecol.* 85, 136–145. <https://doi.org/10.1111/1365-2656.12439>.
- van Gemert, R., Koemle, D., Winkler, H., Arlinghaus, R., 2022. Data-poor stock assessment of fish stocks co-exploited by commercial and recreational fisheries: applications to pike *Esox lucius* in the western Baltic Sea. *Fish. Manag. Ecol.* 29, 16–28. <https://doi.org/10.1111/fme.12514>.
- Villegas-Ríos, D., Freitas, C., Moland, E., Huneide Thorbjørnsen, S., Olsen, E.M., 2020. Inferring individual fate from aquatic telemetry data. *Methods Ecol. Evol.* 11, 1186–1198. <https://doi.org/10.1111/2041-210X.13446>.
- Wennerström, L., 2020. Gädda, egentliga östersjön och bottniska viken. SLU – Institutionen för akvatiska resurser. Fisk- och skaldjursbestånd i hav och sötvatten 2020. Resursöversikt, Havs- och vattenmyndigheten, Rapport 2021:6, 76–79.
- Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis.
- Zaikov, A., Iliev, I., Hubenova, T., 2008. Induction and recovery from anaesthesia in pike (*Esox Lucius L.*) exposed to clove oil. *Bulg. J. Agric. Sci.* 14, 165–170.