Movement of pike (*Esox lucius*) in a large Swedish lake

Julian Horstmann

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Supervisor:	**Daniel Palm, Department of Wildlife, Fish and Environmental Studies**
Assistant supervisor:	Georgia Macaulay, SLU, Department of Wildlife, Fish and Environmental Studies, University of Sydney
Assistant supervisor:	Lo Persson, SLU, Department of Wildlife, Fish and Environmental Studies
Examiner:	Thomas Brodin, SLU, Department of Wildlife, Fish and Environmental Studies

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Swedish University of Agricultural Sciences

Faculty of Forest Sciences

Department of Wildlife, Fish and Environmental Studies

Abstract

Northern pike (*Esox lucius*) play a crucial role in freshwater ecosystems, yet knowledge about their movement remains limited. With the increasing availability of telemetry technology, the traditional image of pike as sedentary ambush predators with limited migratory tendencies is being challenged, revealing more complex movement strategies with implications for ecology and management. In view of the particularly sparse data on large inland lakes, this study investigated the spatial and temporal movement patterns of pike in Lake Siljan, Sweden's sixth-largest lake, using acoustic telemetry. Forty-five large adult pike were tagged at a wetland spawning site (Limsjön) and in the open lake (Storsiljan) in 2022 and 2023, and monitored over two years with a network of 28 receivers.

Movement patterns were highly variable across individuals, with maximum ranges spanning from less than 3 km to nearly 47 km, but mean ranges consistent across tagging groups (~26 km). Many pike used almost the entire system, although despite connectivity, none entered the northern basin, suggesting ecological avoidance rather than physical limitation. Seasonal dynamics were pronounced, pike expanded their ranges in autumn and winter and contracted them in spring when returning to spawning areas in some cases traversing almost the entire lake. Spawning behaviour showed strong site fidelity to Limsjön across years, with individuals returning in spring within a narrow thermal window of about 7 °C. While fish from the Storsiljan group mixed in the open lake outside the spawning season, only a small fraction used Limsjön which suggests that the Siljan population is composed of multiple spawning groups that remain largely distinct during reproduction but intermingle for the rest of the year.

Together, these results show that pike in large lakes can display the same ecological traits known from coastal systems, including spawning-site fidelity and subpopulation structuring. To safeguard population diversity and resilience, effective management will therefore require identifying and protecting multiple spawning habitats and recognizing the population as a mixed-stock fishery.

Keywords: Esox lucius, Acoustic telemetry, Movement ecology, Seasonal dynamics, Spawning-site fidelity, Freshwater connectivity

Table of contents

List of tables **6**

List of figures **7**

1. Introduction **8**

2. Material and methods **10**
2.1 Study area and receiver array 10
2.2 Tagging procedure 11
2.2.1 Limsjön 11
2.2.2 Storsiljan 12
2.3 Data preparation and filtering 12
2.4 Movement strategies and seasonal habitat use 14
2.5 Spawning migration, timing and temperature 15

3. Results **17**
3.1 Individual movement profiles 17
3.2 Spatial and temporal movement patterns 20
3.2.1 Maximum range 20
3.2.2 Distance from Insjön (southern lake outlet) 20
3.2.3 Weekly swimming distances 21
3.3 Spawning migration and timing 23

4. Discussion **26**
4.1 Movement strategies and seasonal habitat use 26
4.2 The role of size and sex 28
4.3 Spawning migration, timing and temperature 29
4.4 Management implications and future directions 30

5. Conclusion **31**

6. References **32**

Popular science summary **37**

Acknowledgements **38**

Appendix **39**

List of tables

Table 1. Proportion of Siljan pike (2022-2024) detected until the end of the study period by tagging group. A fish was considered detected until the end if it was still being recorded at least 60 days prior to the final receiver downloads in spring 2024. 17

Table 2. Linear models testing the effect of body length and release group on maximum migration distance. Full model (including non-movers). 39

Table 3. Linear models testing the effect of body length and release group on maximum migration distance. Filtered model (non-movers removed). 39

Table 4. Linear mixed-effects model testing seasonal effects on weekly swimming distance. 39

Table 5. Correlations between weekly mean acceleration and weekly movement distance. 39

List of figures

Figure 1. Map of Lake Siljan. Dots represent individual acoustic receivers, colour-coded by sub-basin, with additional dashed-line separators. The black rectangle highlights the location of the wetland Limsjön. 10

Figure 2. Left: Aerial view of the spawning site Limsjön. Right: Close-up of the stream-entry to Limsjön, with the fyke net used to capture study animals. 12

Figure 3. Abacus plot depicting cleaned detections of each tagged individual (Tag ID), over the entire study-period. Each row represents an individual, and each point a discrete detection event, colour-coded by lake section (see Figure 1). Hollow dots indicate detections that were invalidated according to the criteria described in Section 2.3.1. 14

Figure 4. Contrasting movement profiles of two pike tagged in Limsjön. **A**, a 750 mm long individual tagged in 2022; **B,** a 960 mm long individual tagged in 2023. Coloured points represent detections at different receiver sections; vertical dashed lines indicate the tagging date. The right panel provides spatial reference of receiver locations, with the Limsjön release site highlighted by a black box. 18

Figure 5. Contrasting movement profiles of two pike tagged in Storsiljan 2022. **C**, a 910 mm long individual; **D,** a 940 mm long individual. Coloured points represent detections at different receiver sections; vertical dashed lines indicate the tagging date. The right panel provides spatial reference of receiver locations, with the Storsiljan release site highlighted by a black box. 19

Figure 6. **A** Maximum spatial range by release group (in-water distance between furthest detections). **B** Predicted range from linear model including body length and release group. Shaded areas indicate 95% confidence intervals. 20

Figure 7. Monthly mean distances (km) from the lake outlet (Insjön) for each pike, grouped by release. Thermal seasons highlighted by background shading, dashed horizontal line indicating position of Limsjön spawning area, as a reference point. 21

Figure 8. Mean weekly distance swam by pike of each release group: Top: Limsjön 2022, Middle: Storsiljan 2022, Bottom: Limsjön 2023. Points show raw weekly group means, lines denote LOESS-smoothed trends (span = 0.3), and shaded ribbons represent 95 % confidence intervals around the smooth. Seasonal background shading reflects thermal periods defined by the Swedish Meteorological and Hydrological Institute (SMHI). 23

Figure 9. Gantt-style plot of individual pike arrival and departure dates at Limsjön by release group and year during the spawning period (April–July). Solid bars indicate observed residency; hatched bars mark inferred residency for the Limsjön 2022 cohort, based on the interval between tagging and the first detection outside Limsjön. Light grey bars denote individuals not detected during a given season. 24

Figure 10. Mean water temperature (± SD) at Limsjön within ±30 days of spawning site arrival, shown separately for 2023 (blue) and 2024 (orange). The dashed vertical line indicates the mean arrival day for each year. 25

1. Introduction

Predators play a fundamental role in maintaining the structure and function of ecosystems. By exerting top-down control on lower trophic levels, they can regulate population and community dynamics (Diz-Pita & Otero-Espinar 2021), contribute to biodiversity (Natsukawa & Sergio 2022) and even mediate disease transmission (Lopez & Duffy 2021). Removal of top predators and the loss of their ecosystem services can have catastrophic effects, disrupting trophic cascades (Nowicki et al. 2021) and facilitating the invasion of non-native species (Sih et al. 2010). These effects are so ubiquitous that according to Estes et al., 2011: "the loss of apex consumers is arguably humankind's most pervasive influence on the natural world." Pressure on aquatic top predators is particularly acute due to overexploitation, habitat degradation, and the accelerating impacts of climate change on freshwater and marine habitats (Gozlan et al. 2019). Given the importance of aquatic top-predators, knowledge of their ecology is crucial for understanding ecosystem functioning and informing conservation strategies.

One important aquatic predator is pike *(Esox lucius)*, a large predatory fish found in fresh and brackish waters throughout the Northern Hemisphere. Along with growing importance in both recreational and commercial fisheries (Lehtonen & Kuparinen 2018; Arlinghaus et al. 2023), pike is gaining attention as model organism for exploring the complexities of predator ecology (Craig 2008; Forsman et al. 2015), genetics, and evolutionary processes in freshwater and brackish environments (Tibblin et al. 2015; Berggren et al. 2016; Nordahl et al. 2019; Sunde et al. 2022).

Local monitoring programs and reports from fishers indicate Swedish pike populations, especially along the Baltic coast, have been in decline for the past few decades (Bergström et al. 2022; Olsson et al. 2023). Various factors have been identified as potential drivers for decrease in pike numbers, including overfishing (Van Gemert et al. 2022; Arlinghaus et al. 2023), predation by seals and cormorants (Bergström et al. 2022) and the loss of wetland spawning sites (Nilsson et al. 2014; J. P. Hansen et al. 2020). The progressive decline in Baltic pike populations has favoured the explosive increase of the three-spined stickleback, *Gasterosteus aculeatus*, a small-bodied mesopredator that predates on the early life-stages of pike and impairs the population's ability to recover (Nilsson et al. 2019; Donadi et al. 2020). Numerous projects and research initiatives have been launched to better understand and attempt to reverse pike declines, offering valuable insights such as the identification of key spawning habitats, the timing and routes of spawning migrations, and the effectiveness of wetland restoration in supporting recruitment, which can guide more sustainable management efforts (Sportfiskarna 2012; Engstedt et al. 2018; J. P. Hansen et al. 2020).

Traditionally, pike have mostly been viewed as a sedentary ambush predator confined to shallow, vegetated habitats and their movement ecology thought to be relatively restricted (Craig 1995; Skov & Nilsson 2018). Recent studies are reshaping this narrative and reveal wide variations in pike behavioural ecology between populations, subpopulations and individuals (Flink et al. 2023; Cittadino et al. 2024). Such differences in pike movement ecology lead to fine scale genetic variation and local adaptations between populations (Berggren et al. 2016; Nordahl

et al. 2019; Sunde et al. 2022; Flink et al. 2023). A well described aspect of pike behaviour is their spawning site fidelity, where adults use the same spawning site over the course of their lives, returning to their place of birth to spawn (Miller et al. 2001; Engstedt et al. 2014; Larsson et al. 2015). In brackish environments, differences in pike spawning migrations have led to the formation of different ecotypes that largely inhabit the same habitats during the year, but just through the short separation during the spawning period show signs of adaptive divergence (Berggren et al. 2016). The effectiveness of conservation measures such as stocking and spatiotemporal fishing closures depends on detailed knowledge of the movement ecology of the population in question, to avoid localized overfishing and conserve the genetic diversity (Dunn et al. 2011; Flink et al. 2023). Due to variations in life history and spawning behaviour between and within populations, pike should be managed on a fine spatial scale.

Like in the Baltics, pike stocks in the large Swedish lakes (Vättern, Vänern, Malären, Hjälmaren) show signs of decline, but data on pike populations in Swedish freshwater lakes is even more sparse and thus, no clear course of management has been taken (Bryhn 2021). The amount of telemetry studies covering fish-movement in large lakes is generally limited and studies on pike even more so (Abecasis et al. 2018; Brignone et al. 2024). Threats of overfishing, predation and loss of spawning habitat are however not exclusive to coastal habitats. It is important to gain management-oriented insight about lake pike to effectively manage them. Within these populations, large individuals are of particular importance. As with other fish species, bigger females produce disproportionally many eggs of higher quality than smaller individuals, therefore increasing overall offspring survival and recruitment of the whole year-class (Edeline et al. 2007; Hixon et al. 2014; Barneche et al. 2018). In addition to their reproductive contribution, large pike occupy the dominant position in the trophic network, and through their wide prey-size range and high consumption rate regulate prey populations and species composition (Byström et al. 2007; Skov & Nilsson 2018)

This study addresses part of this knowledge gap by investigating the movement ecology of large pike in Siljan, a large (352 km^2) and deep lake (max. 134 m) in central Sweden, using acoustic telemetry. The study aims were to: (i) Determine the size tagged pikes' home ranges and analyze their movement within these home ranges, (ii) Assess the importance of Limsjön, a wetland in the southern part of the system, as a spawning site for the pike population of Siljan and explore movement patterns associated to the spawning period, and (iii) Explore the ecological implications of these findings for sustainable management. By addressing these aims, this research will contribute to a growing body of knowledge on pike ecology, with particular relevance to fisheries management and conservation in large, deep lakes.

2. Material and methods

2.1 Study area and receiver array

The study was conducted in Lake Siljan, a large (total 352.4 km²) and deep (mean: 28 m, max: 134 m) lake system in central Sweden (discharge point: 60.72865° N, 14.99820° E) (Figure 1). The system comprises the main basin Siljan (292.5 km²), Orsasjön to the north (52.3 km²), and Insjön to the south (7.6 km²) (SMHI 2025). For simplicity, the term "Lake Siljan" is used throughout this study to refer to the entire connected system. The lake is located in the catchment area of the River Dalälven, fed by two major tributaries in the northwest, upper Österdalälven (90 $m^3 s^{-1}$) and Oreälven (22 $m^3 s^{-1}$), and drained in the southeast by Österdalälven (155 $m^3 s^{-1}$). A pike spawning wetland, Lake Limsjön (0.3 km²) (Figure 2), is situated near the lake outlet in the river connection between Siljan and Insjön.

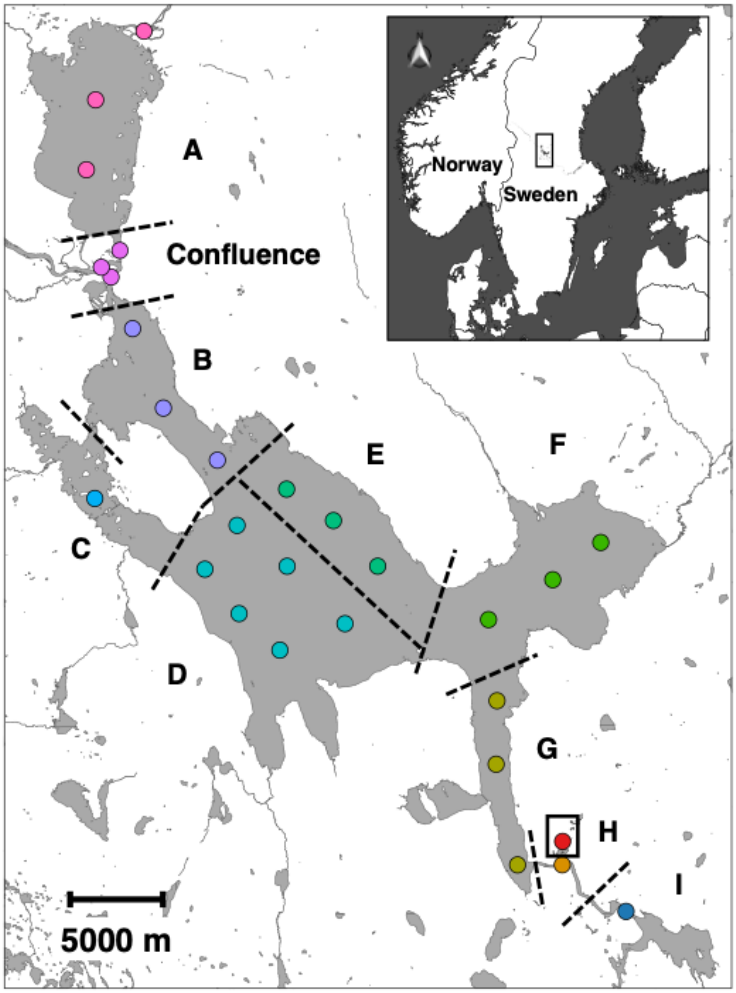

Figure 1. Map of Lake Siljan. Dots represent individual acoustic receivers, colour-coded by sub-basin, with additional dashed-line separators. The black rectangle highlights the location of the wetland Limsjön.

The receiver array consisted of 28 acoustic receivers (69 kHz), including 9 VR2Tx, 9 VR2AR, and 10 VR2W units (Innovasea, Bedford, Canada). In late May 2022, receivers were strategically deployed across 10 sections of the study area to monitor fish movements in different lake habitats and connected water bodies. Nineteen receivers were deployed in the main lake at depths ranging from 20 to 80 m, with additional placements in associated rivers and tributaries (Figure 1). The receivers were distributed within 9 predefined sub-basins (A–I) and the confluence area where upper Österdalälven meets the lake. The boundaries between sub-basins were defined based on bathymetric and geographic differences. Sub-basins A, D, and F consist of an open lake habitat predominated by depths between 20–40 m, only extending below 50 m in a few locations. Sub-basins B and G consist of a narrow strait habitat predominated by depths between 40–60 m, with areas exceeding 100 m depth at a few locations. Sub-basin C is dominated by shallow areas (2–3 m) with abundant scattered islands and margins with plentiful vegetation, whereas sub-basin E has an open lake habitat predominated by depths between 60–90 m that occasionally extends down to 130 m. Sub-basin I consists of the shallow, vegetation-rich lake Insjön to the south of Siljan, which is connected to the main basin through sub-basin H, a narrow river section that also contains the spawning site Limsjön.

The receivers were suspended roughly 5 meters above the lake bottom using submerged buoys. In shallower locations, VR2Tx and VR2W receivers were anchored with two interconnected weights, to allow retrieval by dragging an anchor across and catching a retrieval rope. In deeper locations, VR2AR receivers were used, equipped with an integrated release mechanism for remote retrieval. In spring 2023, the receivers were collected for data download and battery replacement and then redeployed. Four receivers were lost during the first sampling season and were replaced for the second: Two receivers in sub-basin F and two in sub-basin D.

2.2 Tagging procedure

Over the course of the study, a total of 45 pike (mean length: 878 mm, range: 550–1210 mm) were caught and tagged during the following tagging events: 19 pike at Limsjön in spring 2022 (mean: 823 mm, range: 550–1130 mm); 5 pike in Storsiljan_Shallow in summer 2022 (mean: 902 mm, range: 680–1210 mm); 8 pike in Storsiljan_Deep in summer 2022 (mean: 844 mm, range: 780–940 mm); 13 pike at Limsjön in spring 2023 (mean: 966 mm, range: 690–1180 mm).

2.2.1 Limsjön

A fyke net was installed at the entrance to Limsjön on April 15th and emptied every day between April 23 and May 1, 2022 (Figure 2). Pike below 500 mm body length were transported and released into Limsjön directly, as the study focused on the movement ecology of large, adult female pike whose home-range shifts and migratory behaviour drive population-level connectivity in the lake. During the spawning period at Limsjön, individuals could be externally sexed with relatively high certainty, and all tagged fish were classified as females. Following anaesthesia (0.067 mL L^{-1} clove-oil solution) the pike were examined for injuries, measured and implanted with V13 (diameter: 13 mm, length: 30.5 mm, weight: 5.1 g in water) or V16 (16 mm, 68 mm, 10.3 g) 69 kHz coded transmitters (Innovasea, Bedford,

Canada). After recovery for 20 minutes in a holding net, tagged pike were transported and released into Limsjön to complete spawning. The same procedure was used between April 24 and 28, 2023, for the second batch of Limsjön pike. Two pike were tagged with V13TP transmitters, equipped with temperature and pressure sensors (13 mm, 41.5 mm, 5.5 g) on April 24 and five pike with V13AP transmitters, equipped with acceleration and pressure sensors (13 mm, 36 mm, 5.4 g) on April 24 and April 28.

Figure 2. Left: Aerial view of the spawning site Limsjön. Right: Close-up of the stream-entry to Limsjön, with the fyke net used to capture study animals.

2.2.2 Storsiljan

The pike from Storsiljan were caught by trolling with standard lures between June 15 and July 7, 2022, and tagged following the general protocol outlined in Section 2.2.1. Pike below 500 mm body length were not tagged and were released immediately, as the study focused on large adult female individuals. For pike captured in the open lake later in the season, external sexing was more uncertain due to the absence of clear spawning-related traits. Individuals were sexed to the extent possible, and given their large body size, were assumed to be females. Five pike were tagged with V16TP transmitters, equipped with temperature and pressure sensors (16 mm, 71 mm, 12 g), and eight pike with V13 transmitters, equipped with acceleration and pressure sensors (13 mm, 36 mm, 5.4 g). All fish were monitored and recovered post-surgery in a 100-l flow through tank for 20 minutes before being released at the respective capture site.

2.3 Data preparation and filtering

After download, the receiver detection files were cleaned and visualized in RStudio (version 4.4.1; R Core Team, 2024), using the actel package (Flávio & Baktoft 2021). To visually screen for failed tags, premature tag loss, or early mortality, cleaned detection data were plotted using abacus plots in ggplot2 (Wickham, 2016) (Figure 3). Following Dhellemmes et al., (2023) and Kessel et al., (2014), detections were filtered by invalidating:

1. stray tags not associated with any of the tagged fish,
2. detections outside the deployment window of each receiver,
3. duplicate timestamps,
4. detections within the first 48 hours post-tagging (to exclude behavioural effects of surgery; Baktoft et al. 2013) and
5. detections occurring only once within a 60-minute period at a given receiver.

To focus on long-term movement patterns, only individuals with a detection span of at least 100 days were retained. This threshold, based on Cittadino et al. (2024) helps exclude fish that likely emigrated, experienced tagging failure, or were removed by anglers shortly after tagging. One tag exhibited an abrupt change in pressure readings after January 28, 2023, consistent with detachment or mortality; all detections from this transmitter after that date were excluded. After filtering, 42 individuals were retained for analysis, while three were removed.

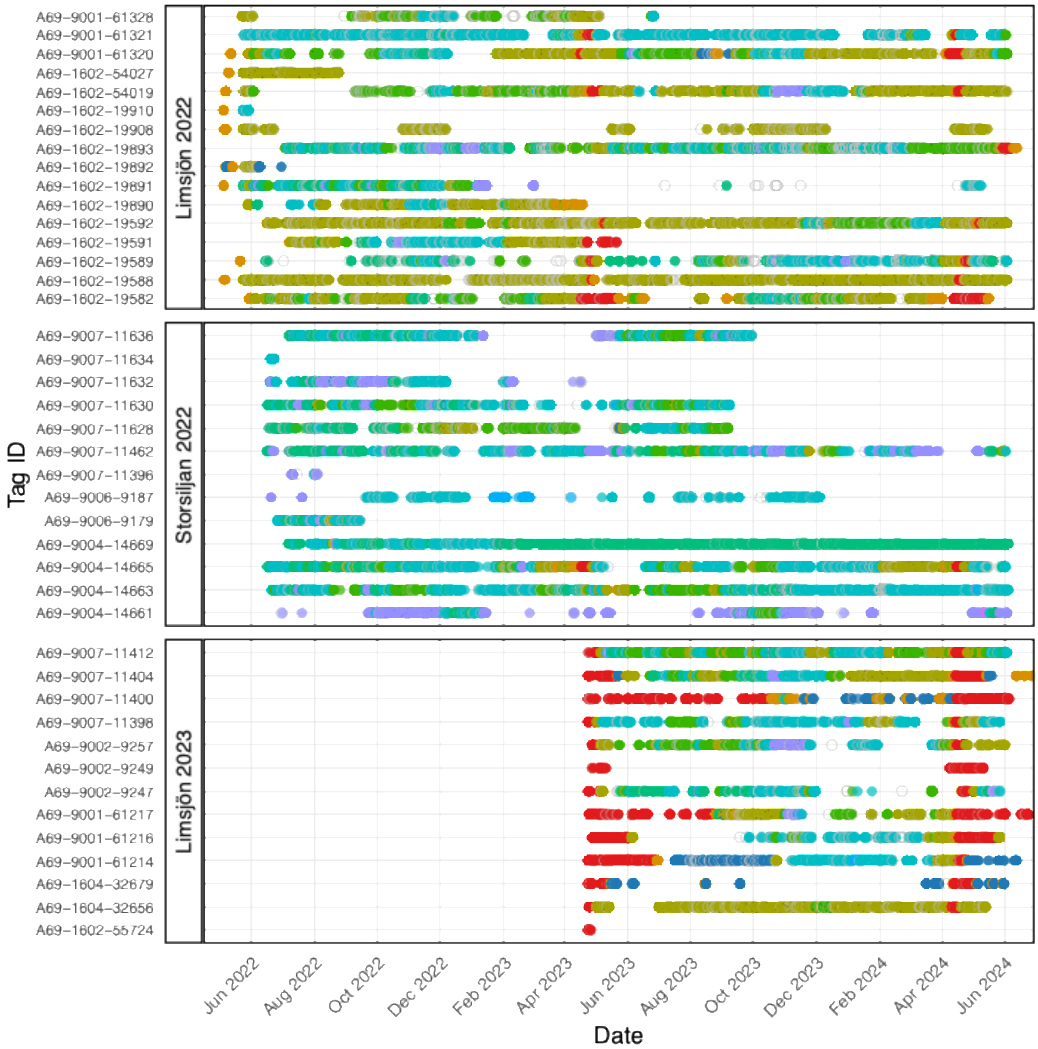

Figure 3. Abacus plot depicting cleaned detections of each tagged individual (Tag ID), over the entire study-period. Each row represents an individual, and each point a discrete detection event, colour-coded by lake section (see Figure 1). Hollow dots indicate detections that were invalidated according to the criteria described in Section 2.3.1.

2.4 Movement strategies and seasonal habitat use

The maximum spatial range was assessed as the in-water distance between the two most distant receivers at which a fish was detected. This provides an estimate of how far each pike moved across the study system. The approach was based on Flink et al. (2023), who calculated maximum migration distance as the distance between the tagging site and the furthest detection. However, with the release site Storsiljan located at the center of the study site, range was considered more appropriate, as it allows for comparison between the tagging locations. To calculate these ranges, a shapefile of the lake was imported, converted into a 10 m resolution raster using shapeToRaster(), and then into a transition layer using transitionLayer(). This transition layer models movement through water-only pathways allowed for estimation of least-cost paths between all receiver locations. A distance matrix was generated using distancesMatrix() from the *actel* package (Flávio & Baktoft 2021),

containing the pairwise in-water distances between all receivers. For each individual, the maximum spatial range (i.e., the largest distance between any two receivers where detections were recorded) was extracted from this matrix. A linear regression model (lm(), R Core Team, 2024) was fitted to test whether maximum range was influenced by body size (length in mm; continuous variable) and release site (categorical variable).

To investigate the temporal dynamics of pike range, the monthly average distance of each fish from the lake outlet Insjön was calculated using the same least-cost distances. Each detection was assigned the distance from its corresponding receiver to Insjön, and monthly averages were calculated per individual. These distances, grouped by release site, were visualized using boxplots with seasonal shading based on thermal season arrival dates from the Swedish Meteorological and Hydrological Institute (SMHI 2025).

Weekly swimming distances were estimated as a proxy for activity levels for all the tagged fish, including individuals without acceleration sensors. To reduce noise in areas with higher receiver coverage, detections were aggregated into hourly Centres of Activity (COAs; Simpfendorfer et al., 2002). COAs were calculated by averaging the latitude and longitude of all detections per individual within each 60-minute time bin. The COAs were projected onto a lake raster to calculate least-cost path distances between consecutive COAs using the previously generated transition layer. To avoid overestimating movement during detection gaps, only steps separated by less than 24 hours were retained. Weekly distances were calculated per individual by summing valid steps. All calculations were implemented manually in R version 4.4.1 with support from the packages sf, terra, raster, gdistance, and dplyr. This approach ensured that movement estimates were based on biologically realistic displacement paths constrained to the lake environment, rather than simple straight-line distances across land or unsuitable habitat. For individuals equipped with acceleration sensors, activity index values were aggregated into matching weekly bins to enable direct comparison. Plots for this section were generated in Python version 3.11 using the packages matplotlib (Hunter 2007) and seaborn (Waskom 2021).

2.5 Spawning migration, timing and temperature

To examine whether pike tagged at Limsjön show fidelity to the spawning site, whether individuals from the open lake migrate to Limsjön during spring, and how consistent the timing of these movements is between years, spawning site residency was calculated. The spawning season was defined as 1 April–31 July. Arrival was the first detection at Limsjön in this period; departure was the last detection before the next detection elsewhere. For Limsjön 2022 fish, arrival was the tagging date and departure date the first detection outside Limsjön. Residency was calculated as the time between arrival and departure dates. Fish present in multiple spawning seasons were classed as repeat spawners. For Storsiljan 2022 fish, any detection at Limsjön during the spawning season was considered immigration. Arrival and residency were summarized by median and range; individual timelines were plotted into a Gantt-style plot.

To examine potential thermal cues for entry into the spawning site, temperature data were analysed from all pike equipped with V13TP or V16TP transmitters that

were detected at Limsjön during the spawning season. For each year, all detections from the arrival day were extracted, and the mean temperature recorded by the transmitter was calculated for each individual. These individual means were then averaged to obtain a yearly mean arrival temperature. To visualize temperature patterns before and after arrival, temperature time series for each fish were aligned by arrival day, and mean values (± SD) were plotted for the period ±30 days from arrival.

Plots for this section were generated in Python version 3.11 using the packages matplotlib (Hunter 2007) and seaborn (Waskom 2021).

3. Results

Following data filtering, a total of 42 fish were retained for analysis, contributing approximately 900,000 detections recorded across 23 receivers. The number of detections per individual varied widely (mean: 24,707; range: 56-127,845), as did detections per receiver (mean: 45,117; range: 24-372,448). Table 1 summarizes the number and proportion of individuals from each tagging group that were still being detected at the end of the study period.

Table 1. Proportion of Siljan pike (2022-2024) detected until the end of the study period by tagging group. A fish was considered detected until the end if it was still being recorded at least 60 days prior to the final receiver downloads in spring 2024.

Tagging Cohort	Fish tagged (n)	Detected until end (n)	Proportion (%)
Limsjön 2022	16	10	63%
Storsiljan 2022	13	5	38%
Limsjön 2023	13	12	92%

Detection statistics also reflected the sparse spatial coverage of the receiver array. Only a small proportion of hourly detection bins contained detections on more than one receiver (median = 0.043; range = 0-0.327), with most multi-detection events occurring in Section D, where receiver density was highest.

3.1 Individual movement profiles

To illustrate the behavioral diversity observed across tagging groups, four individuals, two from Limsjön and two from Storsiljan, were selected to represent contrasting movement strategies in terms of spatial extent, seasonal use, and site fidelity.

The two Limsjön pike displayed distinctly different movement behaviours after tagging (Figure 4). Fish A (750 mm; Figure 4A) showed localized behaviour, remaining predominantly within the southern parts of Section G, about 2.8 km from the tagging site. Without leaving Section G, Fish A undertook only two short excursions beyond its core area, one to Hjortnäs (11 km) in 2022 and another to Sommarland (7.7 km) in 2023, before returning to the southernmost receiver (Figure 4A).

In contrast, Fish B (960 mm; Figure 4B) exhibited broad-scale movements shortly after tagging. It initially moved downstream into Section I, then shifted northward into the main basin. The same pattern repeated after the 2024 spawning period, including a long-range winter excursion to Section G, 39 km from the tagging site. Despite these differences in movement extent and seasonal habitat use, both individuals returned to Limsjön during the spring in consecutive years, indicating consistent spawning site fidelity.

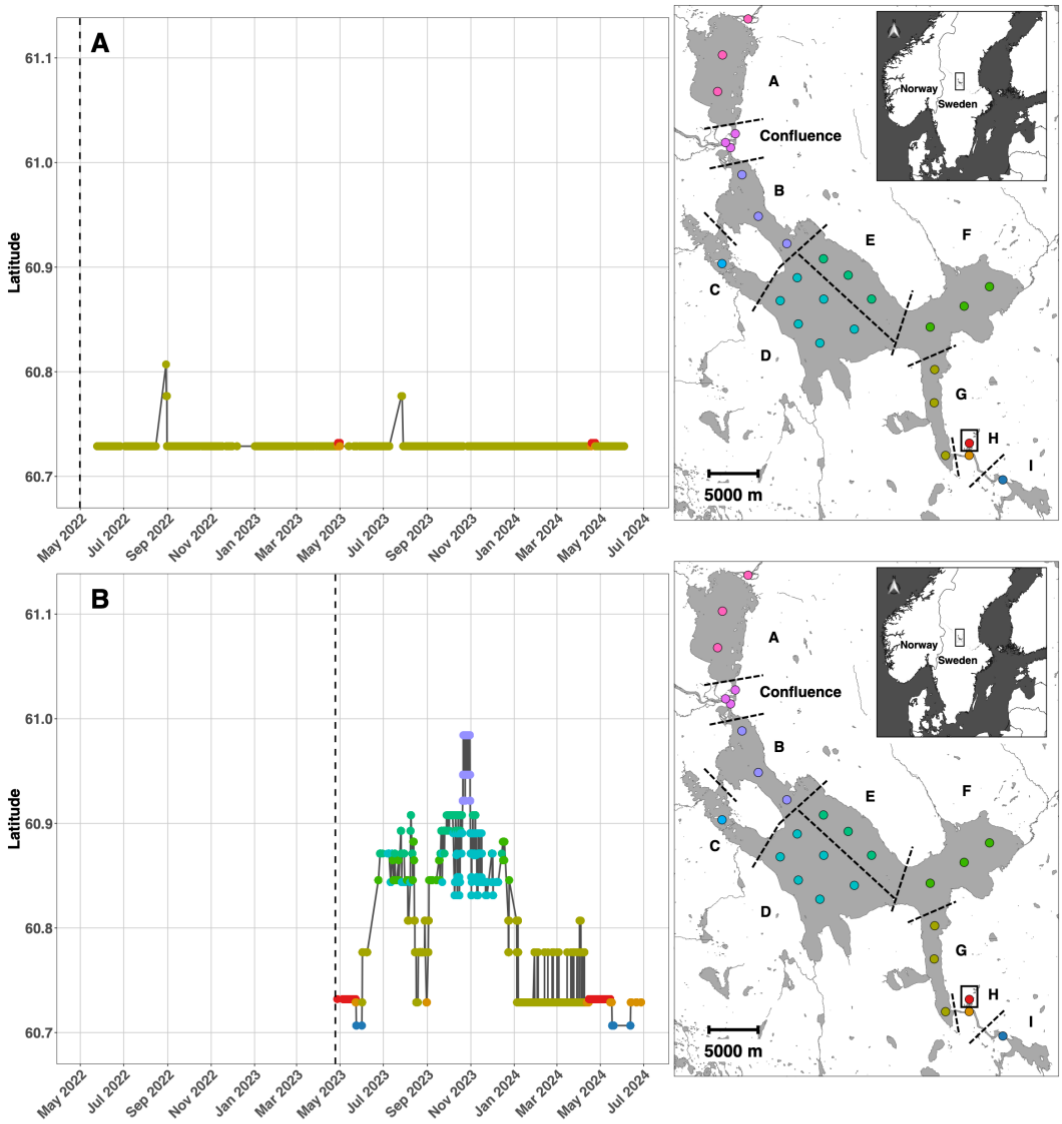

*Figure 4. Contrasting movement profiles of two pike tagged in Limsjön. **A**, a 750 mm long individual tagged in 2022; **B,** a 960 mm long individual tagged in 2023. Coloured points represent detections at different receiver sections; vertical dashed lines indicate the tagging date. The right panel provides spatial reference of receiver locations, with the Limsjön release site highlighted by a black box.*

The individuals from the Storsiljan-Group were caught and tagged in July 2022, after the spawning season, when pike from different subpopulations may already have intermixed. Their movement profiles reflect this potential heterogeneity within the Storsiljan cohort (Figure 5).

Fish C (910 mm; Figure 5C) exhibited extensive spatial use across the main basin, moving frequently between Sections B, D, E and F (Figure 5). In early spring of both 2023 and 2024, Fish C shifted toward the southern basin (Section G) and eventually entered Limsjön to spawn. In each year, it was first detected at the lake outlet approximately 2-3 weeks prior to entering the spawning site. This behaviour mirrors that of the more mobile individuals from the Limsjön tagging cohort.

Fish D (940 mm; Figure 5D) primarily occupied Section B in the northern main lake in the months after tagging. In both years it performed excursions into the southeastern main lake (Section F) during the winter months before returning to Section B. Its detection record has extended gaps, from late winter to early autumn 2022 and again from December 2022 to May 2023, suggesting prolonged residence in nearshore areas, outside of the receiver range.

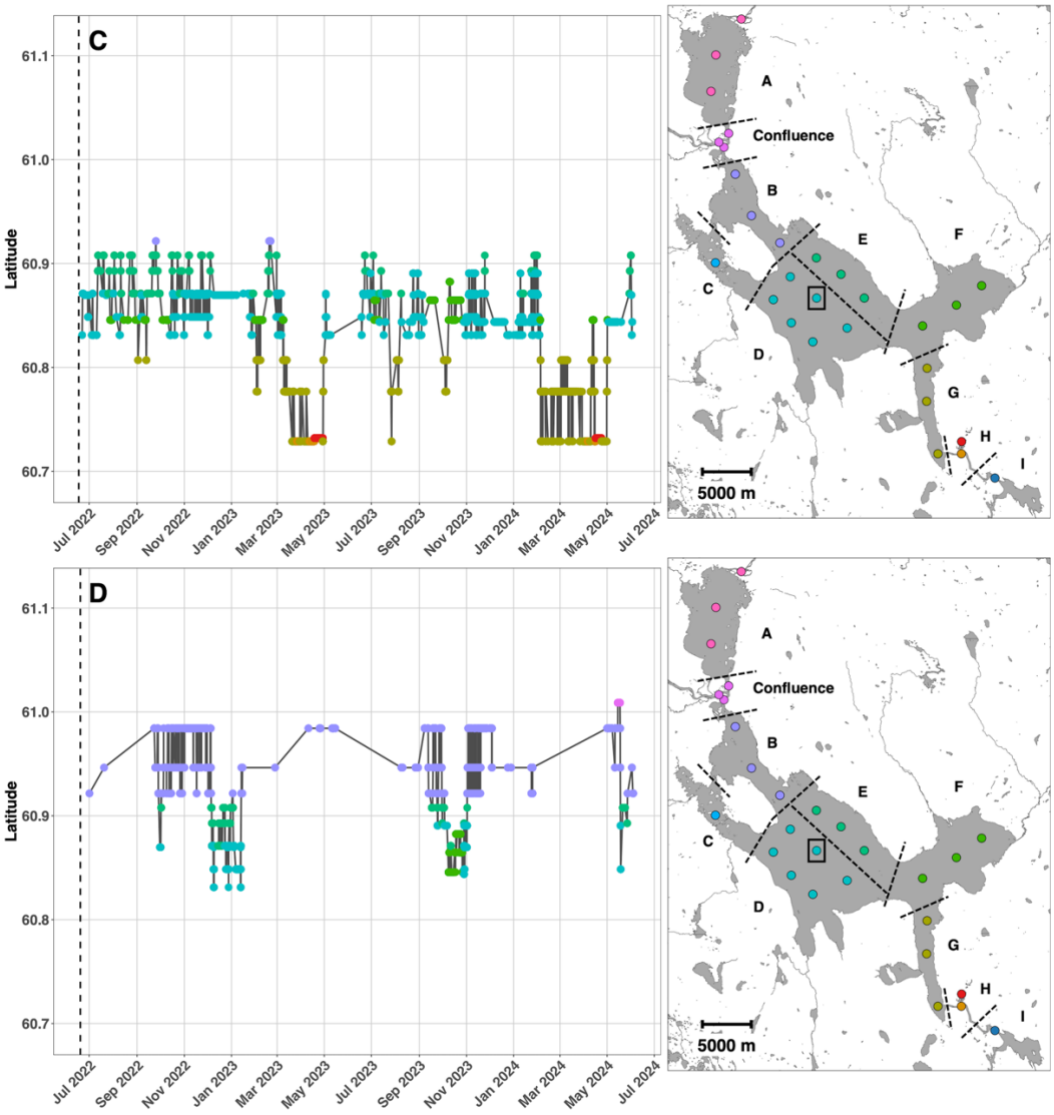

Figure 5. Contrasting movement profiles of two pike tagged in Storsiljan 2022. ***C****, a 910 mm long individual;* ***D,*** *a 940 mm long individual. Coloured points represent detections at different receiver sections; vertical dashed lines indicate the tagging date. The right panel provides spatial reference of receiver locations, with the Storsiljan release site highlighted by a black box.*

In summary, the individual movement profiles reveal wide variability within and across tagging cohorts. The following section examines whether this variability translates into consistent group-level differences in spatial and temporal habitat use.

3.2 Spatial and temporal movement patterns

3.2.1 Maximum range

The maximum range (i.e. the in-water distance between the two most distant receivers at which an individual was detected) varied considerably between individuals but was highly consistent across release groups (Figure 6).

Mean ranges were nearly identical: 26.2 km (2.5-39.0 km; min-max) for Limsjön 2022, 26.9 km (0-46.8 km) for Limsjön 2023, and 25.9 km (5.9-38.7 km) for Storsiljan. A linear model testing for the influence of body length and release group on range did not detect a significant main effect of length ($F(1, 35) = 0.58$, $p = 0.45$) or release group ($F(2, 35) = 0.03$, $p = 0.97$). However, the interaction between length and release group was significant ($F(2, 35) = 5.58$, $p = 0.01$), driven by a positive length–range relationship in the Limsjön 2023 group ($\beta = 73.78$, $p = 0.01$). Removing the two smallest individuals in Limsjön 2023 (800 mm and 930 mm; group mean = 966 mm) that remained at the tagging site slightly reduced the strength of this effect, but the interaction remained statistically significant ($F(2, 33) = 4.34$, $p = 0.03$; $\beta = 58.47$, $p = 0.03$).

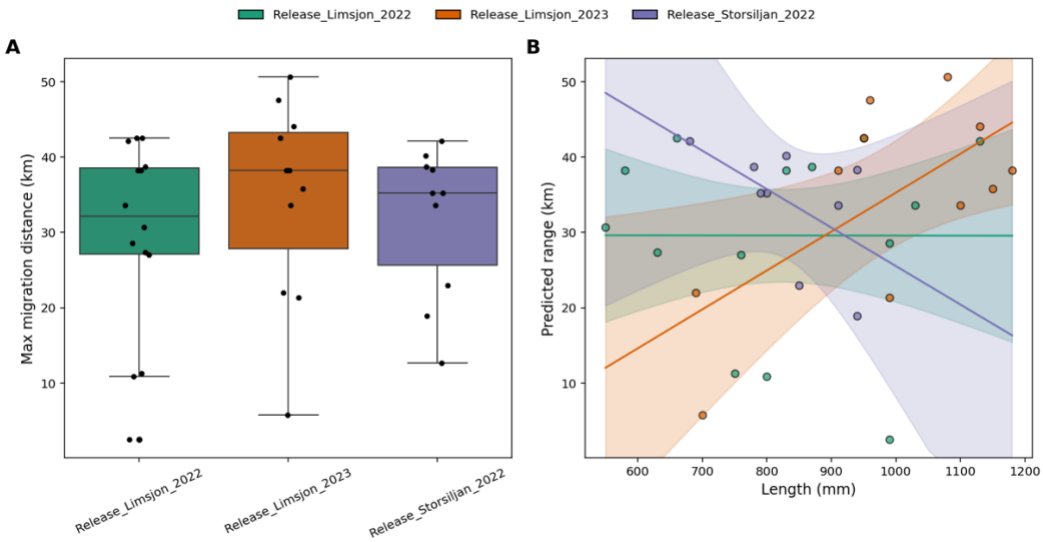

*Figure 6. **A** Maximum spatial range by release group (in-water distance between furthest detections). **B** Predicted range from linear model including body length and release group. Shaded areas indicate 95% confidence intervals.*

3.2.2 Distance from Insjön (southern lake outlet)

The monthly average distances revealed distinct group-level dynamics through the seasons (Figure 7). After leaving the spawning site, fish from Limsjön immediately moved into the main lake, spending most of the summer months at an average 14 to 20 km from the lake outlet (10-15 km from Limsjön). In November and December, both groups reached the maximum extension of 20 to 27 km, followed by a steady contraction towards the next spawning season in April and May. This pattern mirrored the northward excursions in autumn, already described in Chapter 3.1.

Storsiljan fish showed relatively stable spatial behaviour, with most individuals maintaining high distances from Insjön throughout the year, consistent with their central lake release location. During the spring months, standard deviation in the Storsiljan group peaked (SD ~ 11-15 km), as several fish moved north, likely towards an unidentified spawning location and one migrating all the way to Limsjön to spawn.

Notably, despite several individuals venturing into the northernmost part of the main lake in autumn, and two even getting detected on a receiver in the Mora section, none entered Orsasjön (the northernmost basin). Receiver coverage in this section was good, making undetected passage unlikely.

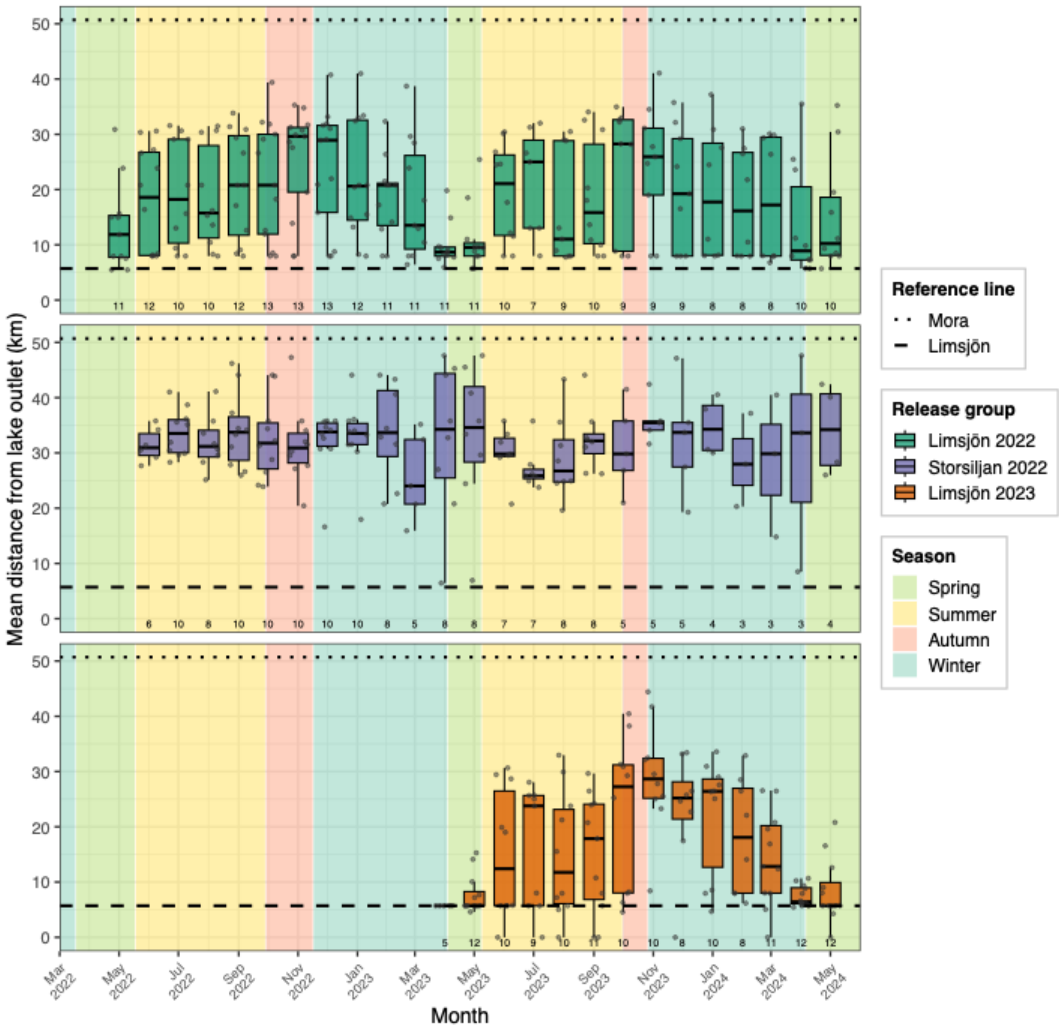

Figure 7. Monthly mean distances (km) from the lake outlet (Insjön) for each pike, grouped by release. Thermal seasons highlighted by background shading, dashed horizontal line indicating position of Limsjön spawning area, as a reference point.

3.2.3 Weekly swimming distances

Weekly swimming distances were calculated as a proxy for activity levels and significantly varied across the seasons (Figure 8). Activity levels across all tagging groups were lowest during the summer months, began increasing in October and

peaked during late autumn and winter. This pattern was observed in both years but especially pronounced in Winter 2023/2024. A linear mixed-effects model confirmed the significant effect of season on weekly swimming distances ($F(8, 218) = 4.87$, $p < 0.001$). Post-hoc comparisons showed that Winter 2023/2024 was associated with significantly higher movement than all spring and summer periods ($p < 0.01$), and Autumn 2023 also showed elevated movement compared to Spring 2023 and Summer 2023. These trends suggest increased exploratory or migratory activity during colder seasons. Fish released in Storsiljan exhibited higher weekly distances than individuals released in Limsjön, particularly in winter. However, this group-level difference was not statistically significant after accounting for individual and seasonal variation (Release site: $F(2, 33.7) = 4.61$, $p = 0.02$; pairwise contrasts all $p > 0.09$). Substantial variation in activity levels was observed among individuals within each release group (random effect variance = 53.3 km², SD = 7.3), accounting for ~14% of the total variance in weekly distances. Body size had no detectable influence on weekly distance ($F(1, 32.7) = 0.59$, $p = 0.45$).

For the two release groups equipped with acceleration transmitters, the relationship between weekly mean acceleration and weekly movement distance was weak. For the Limsjön 2023 group, the correlation coefficient was ($r = 0.13$), indicating only a slight positive association between higher acceleration values and greater weekly displacement. For the Storsiljan 2022 group, the correlation was slightly negative ($r = –0.07$), suggesting no meaningful relationship. These findings are consistent with the visual inspection of the time series plots, which did not reveal any distinct peaks in acceleration coinciding with periods of increased weekly movement distances.

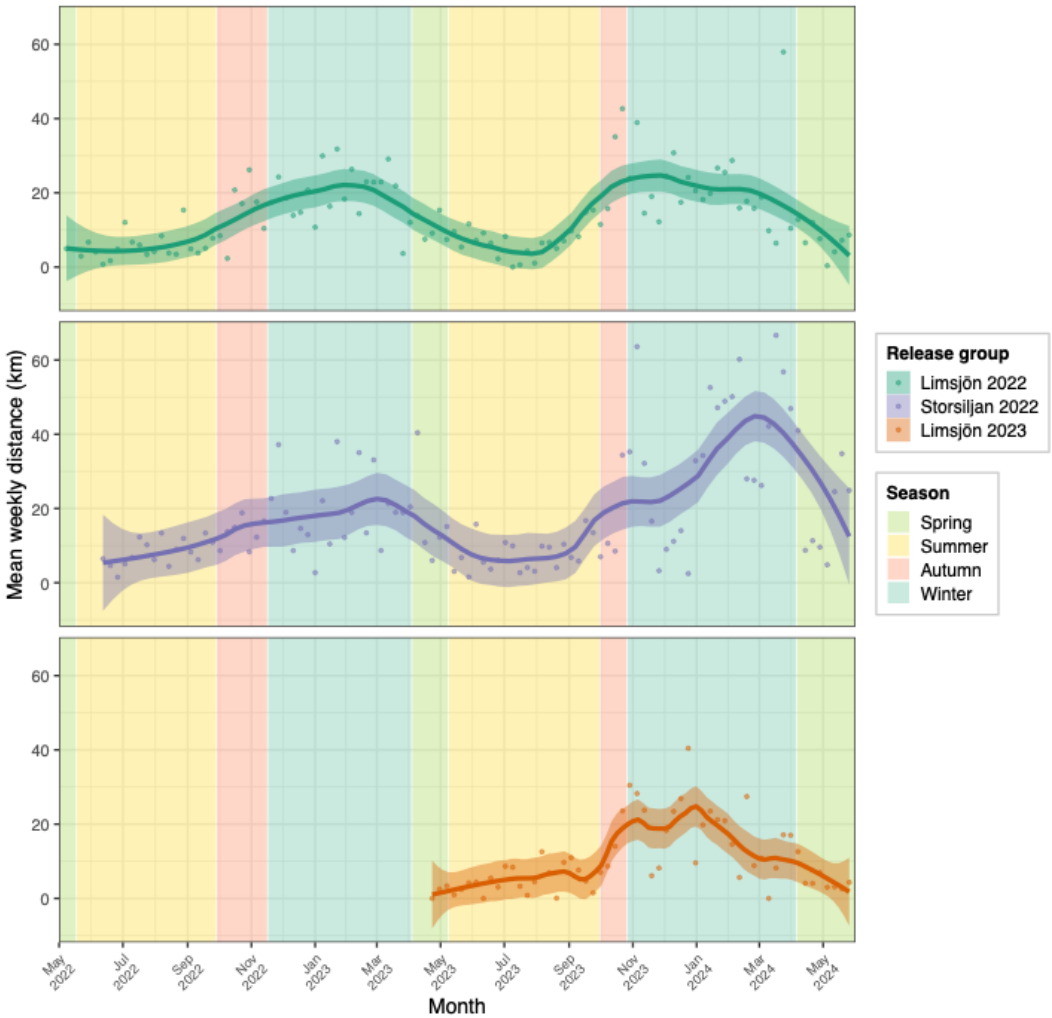

Figure 8. Mean weekly distance swam by pike of each release group: Top: Limsjön 2022, Middle: Storsiljan 2022, Bottom: Limsjön 2023. Points show raw weekly group means, lines denote LOESS-smoothed trends (span = 0.3), and shaded ribbons represent 95 % confidence intervals around the smooth. Seasonal background shading reflects thermal periods defined by the Swedish Meteorological and Hydrological Institute (SMHI).

3.3 Spawning migration and timing

Figure 9 shows individual arrival and departure dates by cohort and spawning season. Solid bars represent observed Limsjön residency, hatched bars indicate inferred first season stays for the Limsjön 2022 cohort, and light grey bars mark seasons without detections. The plot illustrates clustered arrivals within years and multiple cases of return migrations across seasons.

Pike tagged at Limsjön showed strong spawning site fidelity, with most individuals returning in at least one subsequent year, while immigration from the open lake was rare, recorded only for a single Storsiljan-tagged fish that entered Limsjön in both monitored seasons after release. Arrival timing was relatively consistent across years, generally occurring in late April to mid-May., with one distinct exception. After arriving with the cohort in 2022 and 2023, one Limsjon

2022 Individual (A69-9001-61320, 870 mm) arrived in late June of 2024, after all other Individuals from its cohort had already left the spawning site. Across all groups, pike arrived notably earlier in 2024, with median arrival dates about 10 days ahead of 2023 and roughly one week earlier than in 2022 (inferred for the Limsjön 2022 cohort).

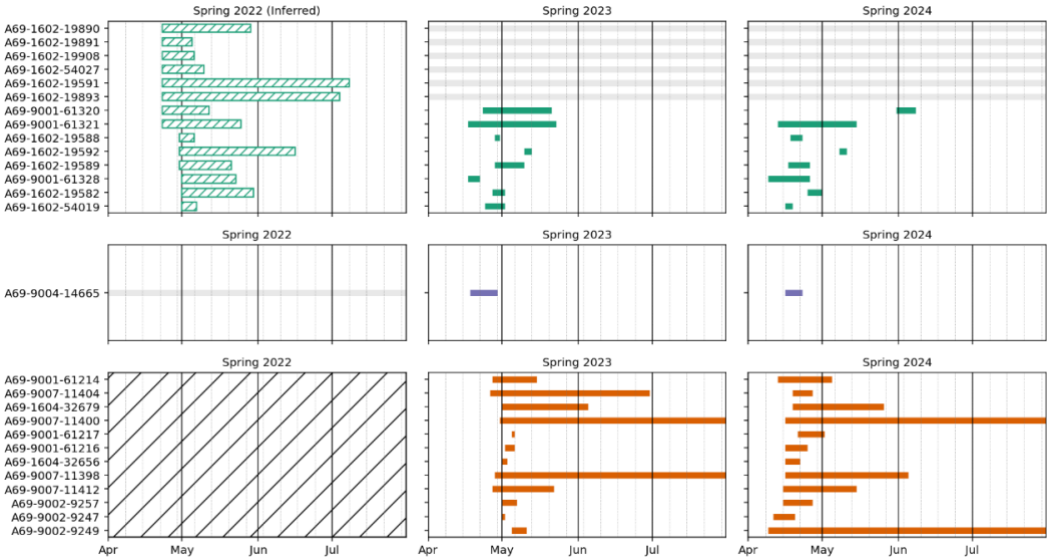

Figure 9. Gantt-style plot of individual pike arrival and departure dates at Limsjön by release group and year during the spawning period (April–July). Solid bars indicate observed residency; hatched bars mark inferred residency for the Limsjön 2022 cohort, based on the interval between tagging and the first detection outside Limsjön. Light grey bars denote individuals not detected during a given season.

Mean arrival temperatures were highly consistent between years, measuring 6.92 °C in 2023 and 6.85 °C in 2024 (n = 3 each year, Figure 10). Across both years pike entered Limsjön within a narrow thermal window of approximately 7 °C.

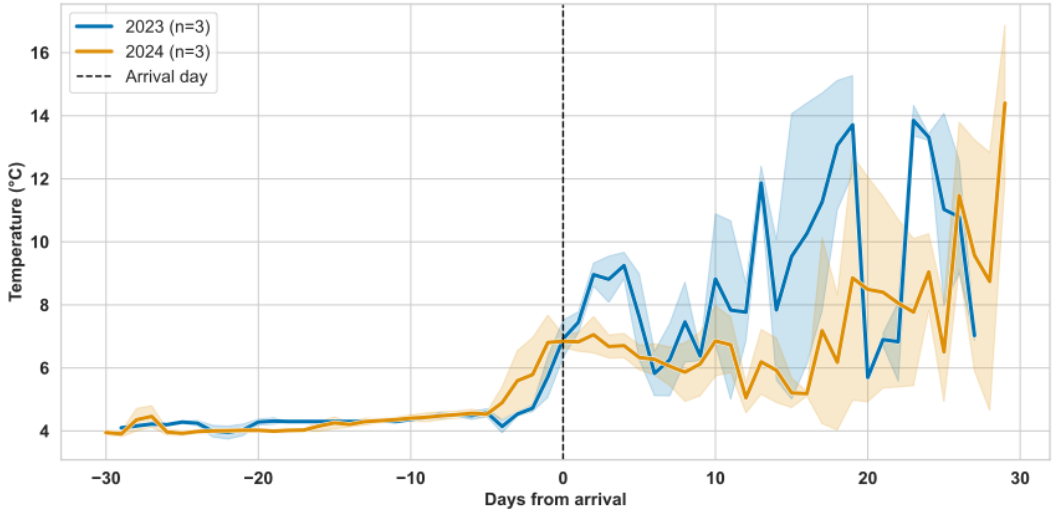

Figure 10. Mean water temperature (± SD) at Limsjön within ±30 days of spawning site arrival, shown separately for 2023 (blue) and 2024 (orange). The dashed vertical line indicates the mean arrival day for each year.

4. Discussion

Driven by continuous technological improvement and availability, acoustic telemetry has in recent years evolved into one of the most prominent methods of studying movement and behaviour of fish in their natural habitat (Matley et al. 2022; Jacoby & Piper 2023). At the forefront are large-scale studies on salmonids, like Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*), flagship species of global conservation efforts carrying large economic and social value (Abecasis et al. 2018). These studies have demonstrated that an understanding of a species' movement ecology is key to designing effective management and protection measures. With broader accessibility, telemetry studies increasingly target species whose movement ecology has in the past been considered more simplistic and for which management actions were considered less urgent. This study used an acoustic telemetry network to investigate the movement ecology of large pike in Sweden's sixth-largest lake, to inform future conservation and management strategies of an understudied and ecologically important species.

Although pike are widespread across Europe, studies on their movement ecology in large inland lakes are scarce. Traditionally, studies on pike, particularly those from small lakes, slow-flowing rivers, or coastal ecosystems, have concluded that individuals remain close to their spawning site throughout the year, with limited dispersal (Craig 1995; Larsson et al. 2015; Skov & Nilsson 2018). However, more recent multi-year telemetry studies with broader spatial coverage (e.g., Engstedt et al., 2014; Flink et al., 2023), have revealed a more complex pattern. While spawning site fidelity remains strong, many individuals range widely during the non-spawning period, sometimes moving to entirely different basins.

4.1 Movement strategies and seasonal habitat use

The results from this study align with these newer findings and showed a wide range of movement strategies within the pike population. While mean maximum ranges were similar across release groups (~26 km), individual movement ranges varied widely across the study population. Maximum distances between the two most distant detections for each fish ranged from less than 3 km to nearly 47 km. This variation was observed within all release groups. In the Limsjön cohorts, some individuals remained within a few kilometres of the release site throughout the study, while others moved through multiple basins and reached the northern limits of the array. A linear model testing the effects of body length and release group on maximum range found no significant main effect of length on maximum range across all individuals. A significant interaction was detected in the Limsjön 2023 group, where larger fish tended to occupy larger spatial ranges, but this pattern was not observed in the other cohorts. This indicates that body size is not a consistent predictor of movement extent in this system and that variation in range is likely shaped by other factors such as individual behavioural tendencies, habitat suitability, or spawning strategy.

Despite this variation, clear seasonal patterns were detected. Individuals released at the Limsjön spawning site consistently moved into the main basin immediately after spawning, expanded their range during autumn and winter, and returned to the

southern part of the lake around March in preparation for the next spawning season. The timing and direction of the northward movements in autumn and winter were consistent across years, suggesting the movements are a regular part of the annual cycle rather than random events. Similar seasonal shifts in pike and other large freshwater predators may be linked to changes in prey distribution and to cooling water temperatures that improve foraging efficiency and expand the range of suitable habitats (Westrelin et al. 2022; Říha et al. 2025). This pattern is evident for both release groups, with distances from the outlet increasing in autumn and winter in line with movements toward deeper, thermally stable habitats, although the Storsiljan group maintained a consistently more northerly distribution reflecting differences in overall habitat use between release groups. Notably, despite good receiver coverage, no individuals from either group were detected moving into Orsasjön via the narrow northern passage at Mora, suggesting that it functions as a permanent ecological barrier. Given that flow conditions here are comparable to the southern passage into Insjön, which was used by individuals from all cohorts, this pattern indicates selective avoidance rather than movement limitation. A thermal barrier caused by colder inflowing water from the Österdalälven cannot be ruled out entirely, but in the absence of temperature data from this area, it remains speculative. The absence of movement into Orsasjön across years and seasons therefore most likely reflects ecological factors that make the area less favourable relative to the other basins of Siljan. Similar patterns of avoidance of accessible basins have been documented for pike in other connected lake systems, driven by differences in prey abundance, vegetation cover, or seasonal habitat suitability (Skov & Nilsson 2018).

Given these broad seasonal patterns in habitat use, the next step was to examine how movement behaviour varied at a finer temporal resolution. Weekly movement distances provided a proxy for spatial activity when precise positioning was not feasible and for fish not equipped with an acceleration sensor. Spatial activity was examined to see whether seasonal shifts in habitat use were accompanied by corresponding changes in movement behaviour that may have reflected ecological processes such as foraging strategy adjustments or pre-spawning migration. Across all cohorts and both years, activity was lowest during the summer months and increased during late autumn and early winter. This was especially pronounced in the Limsjön cohorts, aligning with the movements into the northern main-lake habitats observed in the spatial distribution data. For the Storsiljan cohort, the highest weekly distances were recorded in the weeks preceding the spawning period, consistent with directed migrations towards the spawning sites in Limsjön. The absence of a strong correlation between weekly mean acceleration and weekly swimming distances suggests peaks in weekly distance represent sustained, directed swimming at relatively low acceleration, rather than bursts of high-intensity activity associated with hunting. Such behavioural patterns highlight the importance of distinguishing between movement metrics like spatial relocation and short-term activity, as each provides insight into different aspects of pike ecology. These findings, especially the weekly distances, should be interpreted under consideration of two methodological questions. First, Siljan is ice-covered in winter. The effect of ice on acoustic detection efficiency and range is not well documented and appears system specific. Under some conditions, ice and snow attenuate or scatter transmissions and reduce detection efficiency, especially during formation and

break-up when acoustic noise from cracking or abrasion is high (Klinard et al. 2019). Under other conditions, detection range can increase because noise caused by wind and waves is damped and signals may be reflected downward toward receivers (Klinard et al. 2019). In this study, no seasonal range tests were conducted, so the direction of the ice effect in Siljan is unknown. Second, receiver coverage increased after redeployment in spring 2023, with lost units replaced. Because weekly distance sums least-cost paths between hourly centres of activity (COAs) and includes only steps separated by <24 h, denser receiver coverage raises the probability of consecutive detections and reduces gaps in detections. This effect is most pronounced for the central-basin habitats, where receiver coverage gains were greatest. Absolute weekly distances from the first season should therefore be regarded as conservative given the sparser array. Nonetheless, the winter peaks in weekly movement coincide with the independent monthly redistribution patterns and cohort-specific timing, which supports a biological reason rather than a detection artefact. In the absence of an overlapping telemetry network, weekly movement distances are a useful proxy of activity, while data from acceleration sensors adds complementary information on short-term activity.

4.2 The role of size and sex

The absence of a consistent effect of body length on movement range may partly reflect the sex composition of the tagged fish. Northern pike are strongly sexually dimorphic, with females generally growing to much larger sizes than males, which in most populations rarely exceed 80–90 cm (Craig 2008; Larsson et al. 2015; Skov & Nilsson 2018). As they were caught during the spawning season, the Limsjön cohorts could be externally sexed as female with high certainty, while for the Storsiljan cohort, which was tagged in the open lake after spawning, the sex of individuals could not be verified. Nevertheless, their large size range (up to 121 cm, mean close to 90 cm) suggests that most were also female. When controlled for length, sex-specific differences in space use have been observed in some populations, with males displaying higher activity or broader ranges than females (Raat 1988; Kobler et al. 2008). Similarly, a recent study in Baltic lagoons found that positive body size scaling of space use was only evident in males, suggesting that sex can strongly influence how size translates into spatial behaviour (Dhellemmes et al. 2023b). The underrepresentation of large males in the present dataset could therefore explain why body size did not consistently predict movement extent across cohorts.

Smaller individuals may also exhibit different spatial strategies due to energetic demands and predation risk. Juvenile and subadult pike are often closely associated with vegetated littoral habitats, because prey is abundant and cover reduces the risk of predation by their larger conspecifics. In contrast, large adults with higher energetic requirements may rely on more extensive movements across the lake to secure sufficient food. The present findings, which are dominated by large individuals, therefore likely represent a wide-ranging strategy that may not apply to smaller size classes. In Siljan, the wide-ranging behaviour of large females may reflect seasonal tracking of prey such as coregonids, which aggregate in the deeper northern basins during winter.

Future studies that combine simultaneous tracking of prey species, such as coregonids, with telemetry of pike across different size classes and both sexes would be valuable to clarify whether wide-ranging movements of large females are linked to prey dynamics or reflect other factors.

4.3 Spawning migration, timing and temperature

As pronounced as the northern excursions in early winter were, the subsequent range contraction across the Limsjön cohorts in late winter and spring was equally evident, marking the transition into the spawning period. The telemetry data indicate strong spawning-site fidelity to Limsjön across years, with clustered arrivals within seasons and repeated use of the site by many individuals. This pattern is consistent with established evidence for philopatry in *Esox lucius* from Baltic systems, where adults repeatedly return to specific wetlands (Engstedt et al., 2014; Larsson et al., 2015; Miller et al., 2001), and suggests that sub-basin-scale reproductive units may also operate within large inland lakes. Because the Storsiljan fish were tagged post-spawning, after subpopulations had intermixed in the open lake, this cohort represents a mixed assemblage. Within that mixed cohort, only one of 10 individuals that were detectable into the next season used Limsjön as a spawning site in both 2023 and 2024. This suggests Limsjön accounts for only a relatively small share of spawning destinations used by the open-lake pike; most Storsiljan fish likely spawned elsewhere in the system. This should be treated as a lower-bound estimate, given the small sample size and the lack of receivers at other candidate spawning sites. However, detection probability for Limsjön itself was high during 2023 and 2024, so non-detections there are informative.

Arrival temperatures derived from tag-internal sensors were essentially identical between years (2023: 6.92 °C; 2024: 6.85 °C; n = 3 each), indicating a narrow thermal window for site entry around ~7 °C. Because temperatures were recorded only at detections (i.e., when fish were within receiver range), these values index arrival conditions rather than providing continuous ambient records. Nonetheless, the data support temperature as a proximate cue for entry and align with the species' spring spawning at cool littoral temperatures (~5–9 °C) (Craig 2008; Skov & Nilsson 2018).

One individual that had arrived early within the spawning window in earlier years was detected at the Limsjön receiver only later in 2024 (the beginning of June). Given the bulk of pike arrived at Limsjön between late April and early May, this raises the question of whether this entry represents participation in the spawning event. Plausible explanations are non-reproductive visits (foraging or prospecting), after spawning earlier at an unmonitored site, or reproductive skipping. The latter is well documented in many iteroparous fishes and reported or inferred for pike under poor energetic condition (Rideout & Tomkiewicz 2011; Skov & Nilsson 2018). This theory would be supported by the strong spawning site fidelity of all other Limsjön individuals, which makes it unlikely that the late arrival spontaneously changed spawning site, and the improved receiver coverage at Limsjön from spring 2023 onward, which should advance rather than delay first detections. The seasonal movements and spawning patterns observed in Siljan show clear parallels with Baltic pike systems, where repeated use of discrete wetlands and short periods of reproductive segregation can lead to fine-scale genetic

structuring, despite extensive mixing for the remainder of the year (Berggren et al. 2016; Nordahl et al. 2019; Sunde et al. 2022; Flink et al. 2023). The strong multi-year fidelity to Limsjön, combined with the lack of detections from most Storsiljan fish during the spawning period, suggests that the Siljan population is composed of multiple spawning populations that remain largely distinct during spring but mix in the open lake during the rest of the year.

4.4 Management implications and future directions

From a management perspective, these patterns are consistent with a mixed-stock fishery for most of the year, with discrete spawning groups becoming ecologically and reproductively distinct during the spawning season. Limsjön is already recognised as an important ecological habitat, reflected in the existing fishing closure from 1 January to 30 June. This regulation offers protection during a vulnerable life-history stage, but sustaining overall diversity will also require locating and protecting additional spawning habitats within Siljan, particularly those used by the open-lake fish that did not visit Limsjön. Mapping and characterising these sites should be a priority for future work and could be achieved by combining denser receiver coverage in candidate shallow bays with targeted sampling during the spawning season. Collecting genetic samples from future tagged fish would allow testing whether spawning groups in Siljan are genetically differentiated to a similar degree as Baltic pike subpopulations.

Large pike have declined dramatically in Baltic coastal systems, and there are indications that some large Swedish lakes may be experiencing similar pressures. The data basis for inland populations remains much weaker and their future uncertain (Bergström et al. 2022). The movement patterns and spawning structure documented in Siljan show that large-lake pike can exhibit the same ecological traits that underpin subpopulation differentiation in coastal systems. Identifying key spawning habitats, understanding seasonal connectivity, and mapping the extent of mixing between subpopulations are therefore critical steps toward safeguarding population resilience. The present findings, together with future work on additional spawning areas and potential genetic structuring, provide a foundation for proactive management that can be adapted to emerging threats. By building this knowledge base now, management can act before large-lake populations follow the same trajectory as their declining coastal counterparts.

5. Conclusion

Large pike have declined dramatically in Baltic coastal systems, and there are indications that some large Swedish lakes may be experiencing similar pressures. The data basis for inland populations remains much weaker and their future uncertain. The movement patterns and spawning structure documented in Siljan show that large-lake pike can exhibit the same ecological traits that underpin subpopulation differentiation in coastal systems. Identifying key spawning habitats, understanding seasonal connectivity, and mapping the extent of mixing between subpopulations are therefore critical steps toward safeguarding population resilience. The present findings, together with future work on additional spawning areas and potential genetic structuring, provide a foundation for proactive management that can be adapted to emerging threats. By building this knowledge base now, management can act before large-lake populations follow the same trajectory as their declining coastal counterparts. As the tagged individuals were primarily large females, complementary studies on smaller and male pike will be important to complete the picture.

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Popular science summary

Pike are among the most characteristic fish of Swedish lakes, yet surprisingly little is known about how they move and use different parts of large inland waters. Understanding their behaviour is important, since pike are top predators that influence the balance of fish communities and are also a valued species for both recreational and commercial fishing.

In this study, the movements of 45 large pike in Lake Siljan, Sweden's sixth-largest lake, were tracked using small transmitters that sent signals to a network of underwater receivers. The fish were monitored for two years, providing insights into both their everyday movements and their migrations to spawning areas. The results showed that some pike moved much farther than previously believed, in some cases travelling almost the entire length of the lake. They used different parts of the system depending on the season, spreading out during autumn and winter but returning in spring to reproduce. Most pike were loyal to specific spawning areas, such as the wetland of Limsjön, but the study also revealed that other, still unknown, spawning grounds must exist. These patterns suggest that the Lake Siljan population is made up of several groups that reproduce separately but mix for the rest of the year. Protecting multiple spawning areas will therefore be crucial to safeguard the pike population and ensure sustainable fisheries in the future.

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Appendix

Table 2. Linear models testing the effect of body length and release group on maximum migration distance. Full model (including non-movers).

Predictor	Estimate	SE	t	p
Intercept	34,112	14,811	2.30	0.03
Length (mm)	–9.45	17.42	–0.54	0.59
Release group (Limsjön 2023)	–69,436	25,270	–2.75	0.009
Release group (Storsiljan)	26,388	28,150	0.94	0.35
Length × Limsjön 2023	73.78	27.21	2.71	0.01
Length × Storsiljan	–29.06	32.38	–0.90	0.38

Model fit: $F(5, 35) = 2.36$, $p = 0.06$, $R^2 = 0.25$

Table 3. Linear models testing the effect of body length and release group on maximum migration distance. Filtered model (non-movers removed).

Predictor	Estimate	SE	t	p
Intercept	34,112	13,454	2.54	0.02
Length (mm)	–9.45	15.83	–0.60	0.55
Release group (Limsjön 2023)	–50,660	24,129	–2.10	0.04
Release group (Storsiljan)	26,388	25,571	1.03	0.31
Length × Limsjön 2023	58.47	25.55	2.29	0.03
Length × Storsiljan	–29.06	29.41	–0.99	0.33

Model fit: $F(5, 33) = 2.13$, $p = 0.09$, $R^2 = 0.24$

Table 4. Linear mixed-effects model testing seasonal effects on weekly swimming distance.

Predictor	F(df)	p
Season	$F(8, 218) = 4.87$	< 0.001
Release site	$F(2, 33.7) = 4.61$	0.02
Body length	$F(1, 32.7) = 0.59$	0.45

Random effect variance (Fish-ID): 53.3 km² (SD = 7.3), ~14% of total variance.

Table 5. Correlations between weekly mean acceleration and weekly movement distance.

Release group	r	p
Limsjön 2023	0.13	n.s
Storsiljan 2022	-0.07	n.s

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