**Individual behavioural differences, not body size or sex, structure spatial connectivity in coastal northern pike (*Esox lucius*) in the southern Baltic Sea**

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**Abstract**

Individual variation in movement is fundamental to understanding population structure and dynamics in coastal fish. Here, we examine size- and sex-specific patterns of movement, spatial connectivity, and spawning site fidelity in coastal northern pike (*Esox lucius*) across and within years in a spatially extensive lagoon network in the southern Baltic Sea. We analysed capture-mark-recapture data for 666 tagged pike and acoustic tracking data from 318 individuals, spanning total lengths from 28 cm to 126 cm. Neither mark-recapture nor telemetry data revealed a relationship between individual body length and sex, distance between capture and recapture, connectivity, maximum horizontal displacement, and among-year spawning site fidelity. Instead, spatial connectivity and movement ranges were significantly correlated between years and statistically repeatable, indicating stable inter-individual variation in movement behaviour independent of body size or sex. These patterns point to a population in which movement roles are not structured by size or sex, but rather by stable individual-level differences in behavioural types.

**Keywords**

ecological connectivity, population connectivity, mark-recapture, acoustic telemetry, spawning

## Introduction

Connectivity is an important determinant of population dynamics, resilience, and effective conservation and management in coastal fish, as it affects multiple processes such as migration and dispersal, population growth, gene flow, and local adaptations (Gido et al. 2015; Kool et al. 2013; Schindler et al. 2010). Identifying which individuals contribute to connectivity – and how consistently they do so – is therefore essential for understanding population ecology and managing exploited coastal species. Body size and sex are among the most tractable candidate predictors of individual movement and connectivity. Movement rates tend to increase with body size across fish species (Minns 1995; Tamburello et al. 2015), potentially because larger fish swim faster and more efficiently (Alexander 2003; Ohlberger et al. 2006), are often in better condition (Bernatchez and Dodson 1987), accumulate greater spatial experience in locating optimal spawning or foraging sites (Rose 1993; Reebs 2001; Webster 2017), and may be less constrained in their movements due to lower natural predation risk (Lorenzen 2022). In addition to their substantial contributions to offspring production, recruitment, and population stability (e.g., Barneche et al. 2018; Hixon et al. 2014; Hsieh et al. 2010a; Kopf et al. 2024; Marshall et al. 2021), large fish may also function as keystone connectors among spatially separated spawning grounds (Olsen et al. 2023). Despite its relevance, the movement aspect of size variation and the potential impacts of size-selective mortality typical for fisheries on habitat connectivity remain underexplored, even though these factors may contribute to understanding why size-truncated stocks exhibit greater population fluctuations than those with more natural age and size structure (Anderson et al. 2008; Hsieh et al. 2010).

Northern pike (*Esox lucius;* hereafter, pike) is a phytophilic, large-bodied piscivorous freshwater fish (Craig 1996; Skov and Nilsson 2018), heavily exploited in both commercial and recreational fisheries in a positively size-selective manner (Arlinghaus et al. 2018). The species regularly occurs in coastal areas across the Baltic Sea where salinities average below 10 PSU (Practical Salinity Unit; Jacobsen & Engström-Öst, 2018). Pike are mesothermal and annual single-spawners, i.e., species that reproduce only once during the breeding season each year (also known as total spawners), with timing varying by latitude between February and May (Raat 1988). During spawning, individual females release eggs with groups of a few males over a period of a maximum of few days depending on temperature fluctuations (Svardson 1949; Clark 1950; Raat 1988). Males seem to preferentially spawn with larger, more fecund females (Fabricius and Gustafson 1958), and larger males were found to sire a greater number of offspring in a natural lake (Pagel 2009).

In the southern Baltic, pike has diversified into ecotypes ranging from brackish residents to anadromous and freshwater subpopulations (Möller et al. 2019, 2021; Rittweg et al. 2024). Previous telemetry and mark-recapture studies in the Baltic Sea have shown that pike is largely sedentary with limited home ranges (Karås and Lehtonen 1993; Jacobsen et al. 2017; Flink et al. 2023; Dhellemmes et al. 2023b), forming a spatially structured meta-population across a network of brackish lagoons (Möller et al. 2021; Lukyanova et al. 2024) and interconnected rivers (Tibblin et al. 2016; Nordahl et al. 2019). Dispersal is generally low outside the spawning season but increases significantly prior to and during spring spawning, when pike activity and space use increase (Diana 1980; Raat 1988; Cook and Bergersen 1988; Flink et al. 2023; Dhellemmes et al. 2023b; Lukyanova et al. 2024). Increases in space use during spawning are especially pronounced in coastal sites where multiple ecotypes, such as brackish spawners and anadromous fish (Müller 1986; Tibblin et al. 2016; Sunde et al. 2022), co-exist and spawning migrations are regularly observed (Flink et al. 2023; Lukyanova et al. 2024). Anadromous fish that forage in coastal sites but return to freshwater streams for spawning rely on these migrations to spawn successfully (Tibblin et al. 2015). Yet, fully coastal ecotypes have also been reported to engage in spawning migrations towards enclosed, sheltered bays that are used for spawning (Jacobsen et al. 2017; Flink et al. 2023; Lukyanova et al. 2024). Movement is therefore central to the reproductive ecology of coastal pike, and understanding how it varies with body size and sex – and whether it is consistent across individuals and years – is relevant to understanding population connectivity and the potential consequences of size-selective harvest. Past research from freshwater systems has shown that individual pike vary systematically in behavioural types, sometimes described as personality (Kobler et al. 2009). Therefore, systematic individual differences in long-range movement behaviours can also be expected to occur in coastal pike.

In pike, as in many other fish species (Minns 1995), space use is positively correlated with body size (Rosten et al. 2016; Monk 2019; Monk et al. 2021). However, such a positive relationship between body length and activity or home range size is not universally observed (Jepsen et al. 2001; Koed et al. 2006; Kobler et al. 2008; Dhellemmes et al. 2023b). Discrepancies among studies may stem from differences in the size gradients studied, local environmental conditions, local ecosystem extension, population-specific characteristics, or research methods. Additionally, past fishing pressure may play a role, as larger, faster-growing, and more active pike are selectively harvested by passive fishing gear, such as gill nets or by recreational angling (Carlson et al. 2007; Edeline et al. 2007; Monk et al. 2021). Seasonal context also matters: because pike are generally sedentary ambush predators for much of the year (Diana 1980), size-related differences in movement may be most detectable during the spring, during the spawning season, when activity is elevated (Raat 1988; Lukyanova et al. 2024).

Here, we describe size- and sex-specific patterns of movement, connectivity, and spawning site fidelity in a coastal pike population inhabiting an interconnected lagoon ecosystem of approximately 1200 $km^2$ in the southern Baltic Sea (for a review of the study area, see Arlinghaus *et al.*, 2023a). Drawing on both capture-mark-recapture data and multi-year acoustic telemetry, we examine how body length and sex relate to individual movement ranges, space use, and connectivity, and the consistency of these patterns within and across years.

## Materials and Methods

### ***Study area and telemetry array***

Our study was conducted in the southwestern Baltic Sea, in the lagoons and freshwater tributaries bordering the islands of Rügen, Hiddensee, Fischland-Darß-Zingst, and Usedom in northeastern Germany (Figure 1). Like the rest of the Baltic Sea, the interconnected lagoons of the study area are brackish but exhibit substantial inter-lagoon variation in average salinity, ranging from 2 (oligohaline) to 9 PSU (mesohaline) along a northeast-to-southwest gradient, with the most isolated lagoons being the least saline (Arlinghaus et al. 2023a; Figure 1).

In March 2020, we deployed an array of 140 acoustic telemetry receivers (VR2Tx, Frequency: 69 kHz, MAP-113, Innovasea Systems Inc. DE, U.S.A) across the study area covering 1200 km² of the total 1600 km² lagoon area on German territory (Dhellemmes et al. 2023a, Figure 1). The telemetry array was developed to gather data on area connectivity over a broad spatial scale rather than detect fine-scale movements. The array comprised the most important documented or suspected spawning sites of pike (Roser et al. 2023), both within the lagoons and in major inflowing streams and rivers (Figure 1). Receivers were retrieved, downloaded, and redeployed with a fresh battery in the winters of 2021, 2022, and 2023, in partnership with the Institut für Fisch und Umwelt (FIUM), Rostock, Germany. Over the course of the study, 13 receivers were lost, and 6 were relocated to enhance coverage in areas of interest. More details on receiver deployment are provided in Dhellemmes et al. (2023a).

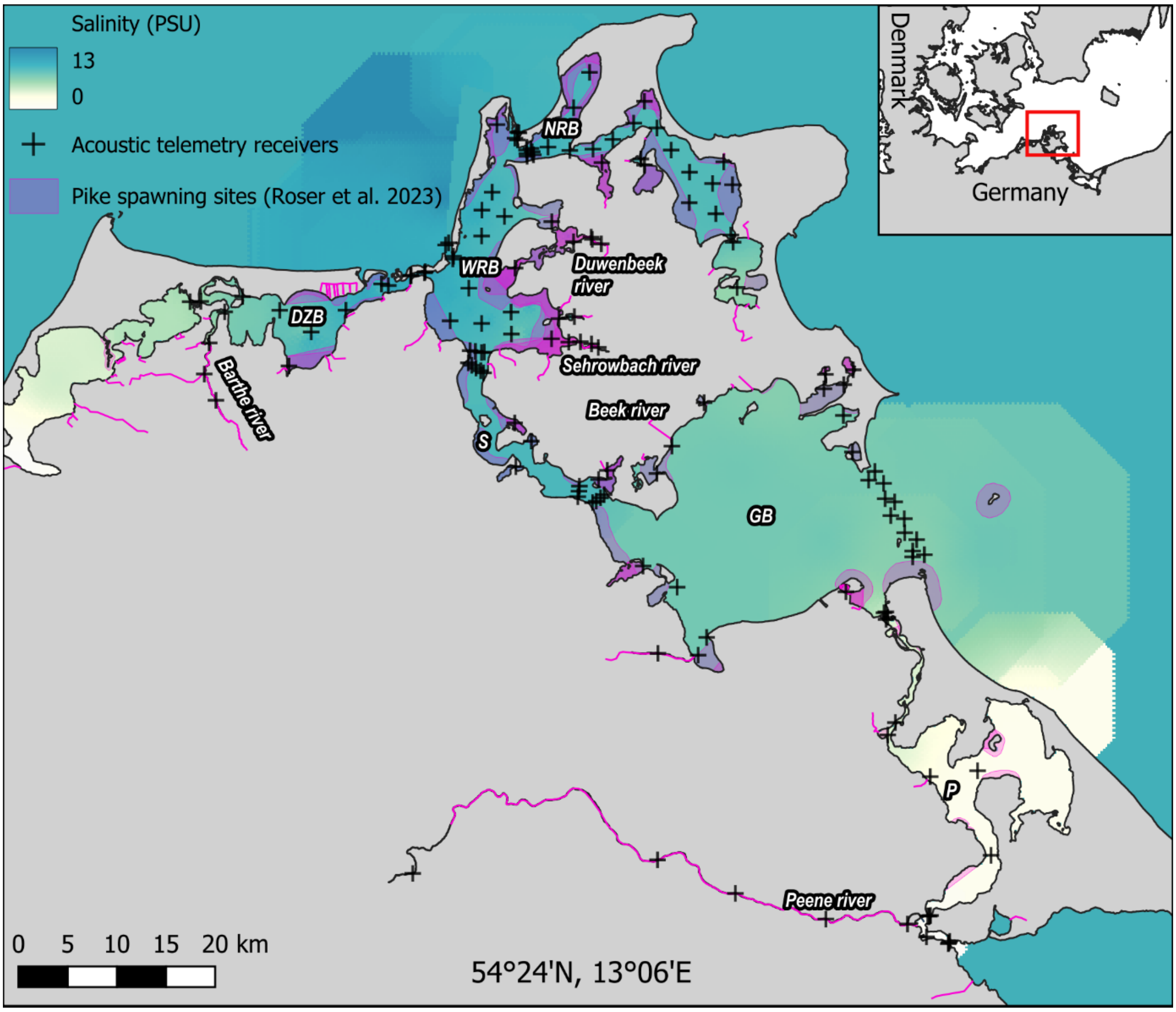
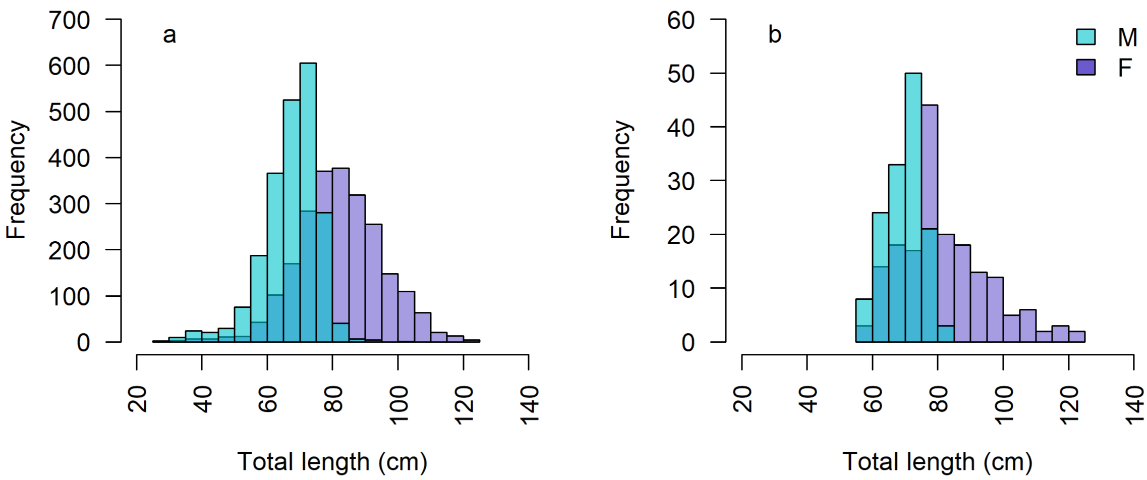



*Figure 1. Map of the study area, including receiver locations, the average salinity gradient and the pike's spawning sites. Pike spawning site data are taken from* Roser et al. (2023), *where spawning sites are aggregated from different sources, which may agree on the location of a spawning site, leading to an overlap in the polygons and a brighter pink colour on the map. Italicised black and white labels indicate the different areas. DZB: Darß-Zingst Bodden; WRB: Western Rügen Bodden; NRB: Northern Rügen Bodden; S: Strelasund; GB: Greifswalder Bodden; P: Peenestrom.*

***Fish captures and tagging***

The research strategy involved tagging pike across as much of the size range of the species as possible (minimum total length for external ID tag = 28.0 cm; minimum total length for internal acoustic tag = 55.7 cm) and throughout all lagoons and most larger freshwater streams to observe year-round behaviour, with a particular focus on the period before and during the spring spawning season and across a minimum of two spawning seasons. Between January 2020 and January 2023, we captured 5836 individual pike in collaboration with local fishers, angling guides, and through our own sampling. Sampling was non-random across the study sites, instead reflecting preferred fishing grounds by cooperating fishers and specific lagoons aligned with other project objectives (Arlinghaus et al. 2023a). Capture methods included rod and reel fishing, fyke nets, gillnets (in cool and cold water where fish can be released alive after capture), and electrofishing in the freshwater tributaries. Upon capture, pike were externally sex determined (cloacal shape or spilling of gametes upon gently pressing the body cavity; females = 2664, males = 2509, unknown = 663; Casselman, 1974), measured to the nearest millimetre (total length in cm; mean ± SD = 73.6 ± 16.1, min = 12.6, max = 126.2; Figure 2, a) and weighed to the nearest gram (mean ± standard deviation (SD) = 2983 ± 1979 g, min = 11.3, max = 17000). The health of all captured pike was assessed visually (i.e., colour, liveliness); healthy individuals that had not yet been tagged and measured more than 28 cm received external ID tags (N = 4597; females = 2319, males = 2183, unknown = 95; mean total length = 75.2 ± 13.6 SD, min = 28.0, max= 121.0; Figure 2; Floy T-bar anchor, Floy Tag & Mfg. Inc., NE, U.S.A.). Each tag indicated the web address and phone number of the recapture database (www.boddenhecht-forschung.de), through which anglers and fishers could report their catch (date, ID, length, gear, and location, i.e., a lagoon name) to enter a raffle for fishing-related prizes. Overall, 17 % of the fish were captured and tagged by the research team and 83 % by cooperating guides and fishers.



*<u>Figure 2. Frequency distribution of total length (mm) in our sample.</u> a) All pike captured for the study and b) pike equipped with acoustic tags. Males (M) and females (F) are represented in blue and purple respectively.*

Between February and December 2020, we selected 317 pike (males = 139, females = 177, unknown = 1) to receive internal acoustic transmitters (N = 120, MM-R-16 50 HP, approx. 6-year battery life, dry weight = 35 g, in-water weight = 18.9 g; N = 196, MM-R-16 33 HP, approx. 3.5-year battery life, dry weight = 26.7 g, in-water weight = 13.6 g, random pulse rate: 60–180 s, Frequency = 69 kHz, MAP-113, Lotek Wireless Inc., ON, Canada), with 300 individuals tagged in the beginning of spawning season (February-March). Selection criteria included body weight (ensuring that in-water tag weight was always below 2 % of the pike's body mass; Jepsen *et al.*, 2005), visual assessment of their health (lethargic or otherwise damaged pike were excluded), and capture location (Table 1). Pike selected for telemetry were spread widely across the study area in capture locations both in lagoons and freshwater tributaries. They averaged 76.4 cm in total length (± 12.4 SD; min = 55.7, max = 121.0; Figure 2, b) and 3761 g in weight (± 2111 SD; min = 1388, max = 15000). To further motivate reports of captures of telemetry pike in the database, these pike received a white external ID tag, indicating a € 100 reward for the first report of each individual via our website or phone number. The acoustic receivers remained operational until the end of February 2023, allowing for the generation of up to three years of data per individual (Dhellemmes et al. 2023b). Upon download, the data was filtered for false detections using *ATfiltR* (Dhellemmes et al. 2023a, b).

*<u>Table 1. Capture locations, sex, and total length (in cm) of pike selected for transmitter implantation in 2020. Capture locations can be seen in Figure 1.</u>*

| | **Female (Mean ± SD; min; max)** | **Male (Mean ± SD; min; max)** | **Unknown (Mean ± SD; min; max)** |
|---|---|---|---|
| **Barthe river** | 6 (83.1 ± 17.3; 63.6; 115.2) | 5 (62.1 ± 1.7; 61.2; 65.1) | 0 |

| | | | |
|---|---|---|---|
| **Beek river** | 0 | 2 (67.4 ± 6.0; 63.1; 71.6) | 0 |
| **Duwenbeek river** | 1 (77.3) | 6 (68.8 ± 4.9; 60.1; 73.0) | 0 |
| **Darß-Zingster Bodden (DZB)** | 31 (88.5 ± 10.4; 69.6; 110.5) | 9 (72.9 ± 2.9; 68.9; 77.4) | 1 (84.1) |
| **Greifswalder Bodden (GB)** | 17 (70.6 ± 12.9; 58.9; 106.5) | 12 (68.3 ± 4.6; 59.1; 74.8) | 0 |
| **North Rügen Bodden (NRB)** | 27 (81.0 ± 8.5; 65.6; 96.6) | 9 (69.7 ± 6.0; 60.5; 76.2) | 0 |
| **Peenestrom (P)** | 26 (81.9 ± 11.7; 67.5; 110.0) | 12 (66.7 ± 6.1; 58.6; 79.1) | 0 |
| **Peene river** | 14 (73.4 ± 14.1; 56.4; 106.4) | 11 (64.3 ± 5.9; 56.3; 73.5) | 0 |
| **Strelasund (S)** | 27 (87.9 ± 14.3; 64.0; 121.0) | 24 (73.5 ± 4.4; 61.6; 81.5) | 0 |
| **Sehrowbach river** | 5 (83.1 ± 3.5; 79.0; 87.0) | 8 (67.6 ± 4.7; 61.5; 76.1) | 0 |
| **Western Rügen Bodden (WRB)** | 22 (78.3 ± 16.4; 55.7; 120.6) | 42 (71.1 ± 5.3; 58.2; 82.4) | 1 (74.1) |

***Recapture distance***

In the event of a recapture of a tagged pike (from our own sampling or via reports in our participatory mark-recapture database by fishers, guides, and anglers), we calculated the in-water distance between each pike's initial capture and recapture locations. This included recaptures of both externally tagged and telemetry-tagged pike. The calculations were done using the *gdistance* package (Etten 2017), which involved creating a transition layer from a shapefile of the land masses around our study area and then calculating the shortest path through this layer. This was done independently of the capture and recapture dates, encompassing the entire study period. The average time between capture and recapture was 250 days (± 229 days).

***Connectivity and maximum horizontal displacement based on biotelemetry***

We used the telemetry data to calculate connectivity and maximum horizontal displacement (MHD; maximum in-water distance between all detections of an individual pike) across two seasonal periods: a spring period ("Spawning period", February–May) encompassing the broad spawning window observed for pike in our study area (Roser et al. 2023), and the remainder of the year ("Outside of spawning"). Actual spawning activity at any given site typically occurs over a much shorter window than the full spring period but using a broad temporal range allows us to assume that any increase in movement metrics due to spawning activity will be captured in this time window in the absence of information regarding the exact timing of spawning. We therefore treat our movement estimates during the spring period as indicative of spawning-associated movements while acknowledging that they are not exact measures. Choosing this temporal split effectively allows us to compare a period in which spawning likely happened with a period in which it did not and draw conclusions regarding spawning migrations when a lack of fine-scale data prevents us from precisely documenting them.

MHD was computed in water using the same technique as described above for recapture distance. To assess connectivity, we constructed movement networks as unipartite undirected networks in the *igraph* package (Csàrdi and Nepusz 2006; Csàrdi et al. 2025), with nodes representing the acoustic receiver locations, and edges reflecting subsequent detections of individuals moving between these locations. Each fish was assigned a connectivity score based on the number of unique edges detected within the time window of interest.

***Among-year spawning site fidelity***

To assess whether individuals change spawning sites among years, we estimated site fidelity in two ways. First, we used a binary variable indicating whether a pike was detected at the exact same location during spawning time across years (yes = 1, no = 0). Second, we calculated the Sørensen index (Sørensen 1948), a metric commonly used in community ecology, which describes the overlap between a set of data points (here, areas) and can be used to assess site fidelity (Lenormand et al. 2021). Sørensen values of 1 indicate identical area use and values <1 indicate increasing dissimilarity. Both metrics were calculated at two spatial scales: a broad area scale and a finer receiver scale (Figure 1).

***Statistical analysis***

We primarily focused on the size-dependency of movement metrics and connectivity, with a positive size-dependency supporting the assumption that the largest individuals act as key connectors between spawning sites and lagoon areas. We conducted all our analyses in R version 4.3.1 (R Core Team 2021). We compared metrics within and outside of the spawning season using t-tests. Distance between capture and recapture, MHD, and connectivity score (both for the spawning season and the rest of the year) were each fitted as response variables, with sex and total length as fixed effects in an interaction. For the distance between capture and recapture, we added the time (in days) between each capture as a fixed effect. The capture area of each pike was added as a random effect to account for differences in receiver coverage and pike captures between the areas. We also added individual ID as a random intercept to MHD and connectivity models to account for repeated measures of the same individuals across years. Connectivity models were fitted using Poisson distribution, while MHD and recapture distance models were fitted using Gaussian distribution.

To assess whether pike behaved in similar ways across years, we assessed the consistency and repeatability of pike behaviour by estimating Pearson's correlations between metrics in one year and the next, and adjusted repeatability (i.e., controlling for the effects of area, total length and sex) for each model using the *rptR* package (Stoffel et al. 2017) with 1000 bootstraps.

To further our analysis of among-year variation in space use, we modelled site fidelity (binary: 0 or 1, at both area and receiver levels) and the Sørensen index (continuous: 0 to 1, at both area and receiver levels) as functions of total length interacting with sex while accounting for area and pike ID as random effects. Site fidelity was modelled using a Bernoulli distribution, while the Sørensen index was modelled using a beta distribution.

All of our models were constructed in *brms* (Bürkner 2017), using 4 chains of 120000 iterations each, with a thinning interval of 100 and a burn-in of 20000. We used leave-one-out cross-validations based on expected log pointwise predictive density (ELPD) based on the loo criterion in the *loo* package (Vehtari et al. 2017; Magnusson et al. 2019) to test whether or not the interaction between sex and total length should be left in the models. If the difference in ELPD between the models was >4, we estimated their predictive performance to differ and used the model with the highest ELPD for the analysis. If the difference in ELPD was <4, models were considered similar in their predictive performance, and we used the simplest model in our analysis. We assessed model fit by visually inspecting the posterior chains and considered fit to be satisfactory if no patterns could be observed. We interpreted effects as meaningful when their 95% credible intervals excluded zero. Pike of unknown sex (n = 14 for mark-recapture, and n = 2 for telemetry) were removed from the analysis.

***Visual assessment of spawning season movement and site use***

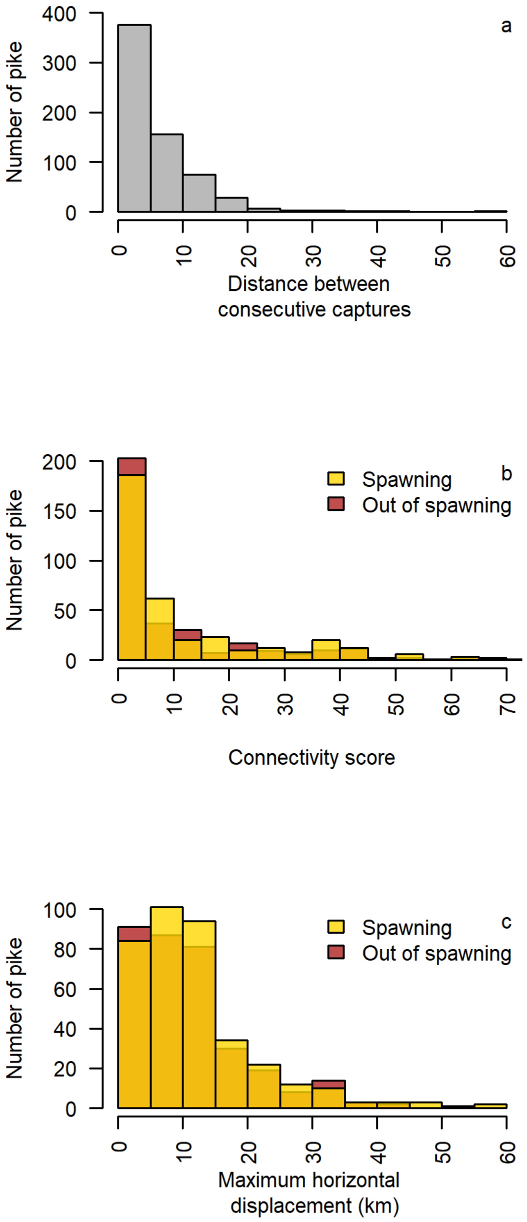
For all telemetry pike with an MHD greater than 10 km during the spawning season, we conducted an additional visual inspection of movement patterns. This included examining spatial maps of their displacements and plots showing the distance to their first detection during the spawning period (see Figure 6 for an example). We focused on the most mobile fish, i.e., individuals with broad-scale movements (MHD > 10 km), as the spatial resolution of our telemetry array was insufficient to detect finer-scale movement patterns, and because Baltic pike have been observed to undertake spawning-related movements of this magnitude (Karås and Lehtonen 1993; Dhellemmes et al. 2023b). Within each year, we assessed whether individuals may have visited multiple spawning sites by identifying distinct peaks in the distance-from-first-detection plots (see Figure 6). For individuals with data spanning multiple years, we also examined whether they returned to the same areas across years. This analysis did not aim to rigorously test hypotheses regarding multi-site spawning, but rather to provide additional descriptive observations that could inform and guide future studies seeking to investigate these behaviours in greater depth.

## Results

### *Mark-recapture*

Out of our 4597 tagged fish, 14% (N = 666) individuals were recaptured at least once (with 51 pikes having multiple recaptures). We were able to calculate the distance between capture and recapture and had total length and sex data for 546 of these. The minimum recorded distance was 0 km, and the maximum was 58.6 km, with a mean of 5 km (±6.2 SD) and a median of 2.6 km (Figure 3, a).

Leave-one-out cross-validations suggested that the sex by total length interaction resulted in a poorer model fit (difference in expected log pointwise predictive density (ELPD) = -0.6, standard error (SE) = 0.5). We found males and females to be similar in their intercept (i.e., the average movement distance among captures), and neither time between captures nor total length influenced the distance between captures (Table 2, Figure 4).




*<u>Figure 3. Frequency distribution of the response variables.</u> (a) Distance between capture and recapture of individual pike. (b) Connectivity score during spawning season (February to May) and out of spawning. (c) Maximum horizontal displacement during spawning season and out of spawning.*

*Table 2. Model output for the distance between capture and recapture. Significant slopes and significant differences in intercept are highlighted in bold. Two samples are presented: the full sample, and a sample excluding the two most mobile fish.*

| | | **Estimate** | **Estimated error** | **Lower 95% Credible interval** | **Upper 95% Credible interval** |
|---|---|---|---|---|---|
| ***Full sample*** | *Intercept (taken as Sex:Female)* | 0.5 | 2.39 | -4.22 | 5.28 |
| | *Sex:Male* | 0.06 | 0.7 | -1.29 | 1.42 |
| | *Total Length (cm)* | 0.05 | 0.03 | -0.01 | 0.11 |
| | *Time between captures (days)* | 0.00 | 0.00 | -0.00 | 0.00 |

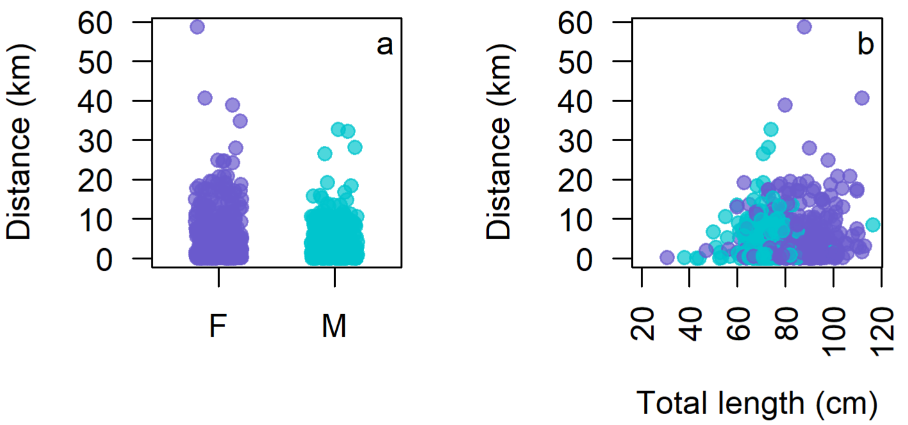



*Figure 4. Distance between consecutive captures as a function of sex (a) and total length (b).*

***Connectivity and maximum horizontal displacement based on biotelemetry***

Out of 318 tagged fish, 92% (N = 292) generated data for an average duration of 439 days (time between first and last detection, min = 0, max = 1065). After removing pike of unknown sex and those detected on only a single receiver, the final sample size was N = 242 (females = 133, males = 109). Of those, 53% (N = 128) produced data in two distinct years, and 20% (N = 48) in three distinct years. In total, we analysed over 1.6 million (1649010) detections.

Connectivity (taken as the number of network edges per pike during a given period) was on average 12.56 (± 15.67 SD, min = 1, max = 87) during the spawning period (February, March, April, May) and 9.45 (± 12.55 SD, min = 1, max = 63) outside of spawning (Figure 3, b). MHD was on average 11.74 km (± 9.61 SD, min = 0.14, max = 57.61) during spawning and 10.85 km (± 8.58 SD, min = 0.14, max = 44.80) outside of the spawning period (Figure 3, c). T-tests indicated that connectivity was higher during spawning ($t = 2.92$, $p = 0.003$), but MHD was not ($t = 1.28$, $p = 0.19$).

The interaction between body length and sex decreased model fit in the case of connectivity during spawning and was therefore excluded (connectivity spawning ELPD = -11.4, SE = 5.6). In all other cases, the inclusion of the interaction did not improve model fit, which also led to the exclusion of the interaction term (connectivity out of spawning ELPD = -1.1, SE =4.1; MHD spawning ELPD = -0.1, SE = 1.5, MHD out of spawning ELPD = -0.2, SE = 1.0). Higher connectivity and MHD during the spawning time and the rest of the year were not explained by body size (Table 3, Figure 5, b, e, h, k), rejecting the hypotheses of a positive size-dependency of spawning site connectivity. Males had higher MHD out of the spawning period (Table 3, Figure 5, j), but we detected no other effect of sex on movement metrics (Figure 5, a, d, g).

Connectivity, both within and outside of spawning season was well correlated between years (within spawning Pearson's $r_{(143)} = 0.52$, $p < 0.0001$; out of spawning $r_{(134)} = 0.7$, $p < 0.0001$; Figure 5, c, f) but had low repeatability at the individual pike level (within-spawning intra class correlation = 0.06 [0, 0.19], p=0.01; out of spawning intra class correlation = 0.19 [0.08, 0.37], $p < 0.0001$). MHD within and outside of spawning time was also highly correlated among years (during spawning Pearson's $r_{(143)}$ =

0.44, $p < 0.0001$; out of spawning Pearson's $r_{(134)} = 0.43$, $p < 0.0001$; Figure 5, i, l) and was strongly repeatable at the individual pike level (intra class correlation = 0.35 [0.2, 0.48], $p < 0.0001$; out of spawning intra class correlation = 0.26 [0.1, 0.39], $p < 0.001$).

*Table 3. Model output for the connectivity and maximum horizontal displacement based on acoustic telemetry. Significant slopes and significant differences in intercept are highlighted in bold.*

| | | **Estimate** | **Estimated error** | **Lower 95% Confidence interval** | **Upper 95% Confidence interval** |
|---|---|---|---|---|---|
| ***Connectivity (spawning)*** | *Intercept (taken as Sex:Female)* | 1.15 | 0.57 | 0.06 | 2.25 |
| | *Sex:Male* | -0.08 | 0.15 | -0.38 | 0.22 |
| | *Total Length* | 0.00 | 0.01 | -0.01 | 0.01 |
| ***Connectivity (out of spawning)*** | *Intercept* | 1.29 | 0.69 | -0.02 | 2.64 |
| | *Sex:Male* | -0.10 | 0.18 | -0.45 | 0.25 |
| | *Total Length* | 0.00 | 0.01 | -0.01 | 0.02 |
| ***MHD (spawning)*** | *Intercept* | 11.47 | 4.71 | 2.17 | 20.60 |
| | *Sex:Male* | 1.28 | 1.40 | -1.45 | 3.96 |
| | *Total Length* | -0.02 | 0.05 | -0.12 | 0.09 |
| ***MHD (out of spawning)*** | *Intercept* | 10.80 | 4.51 | 1.74 | 19.57 |
| | ***Sex:Male*** | **2.61** | **1.25** | **0.2** | **5.02** |
| | *Total Length* | -0.02 | 0.05 | -0.13 | 0.08 |

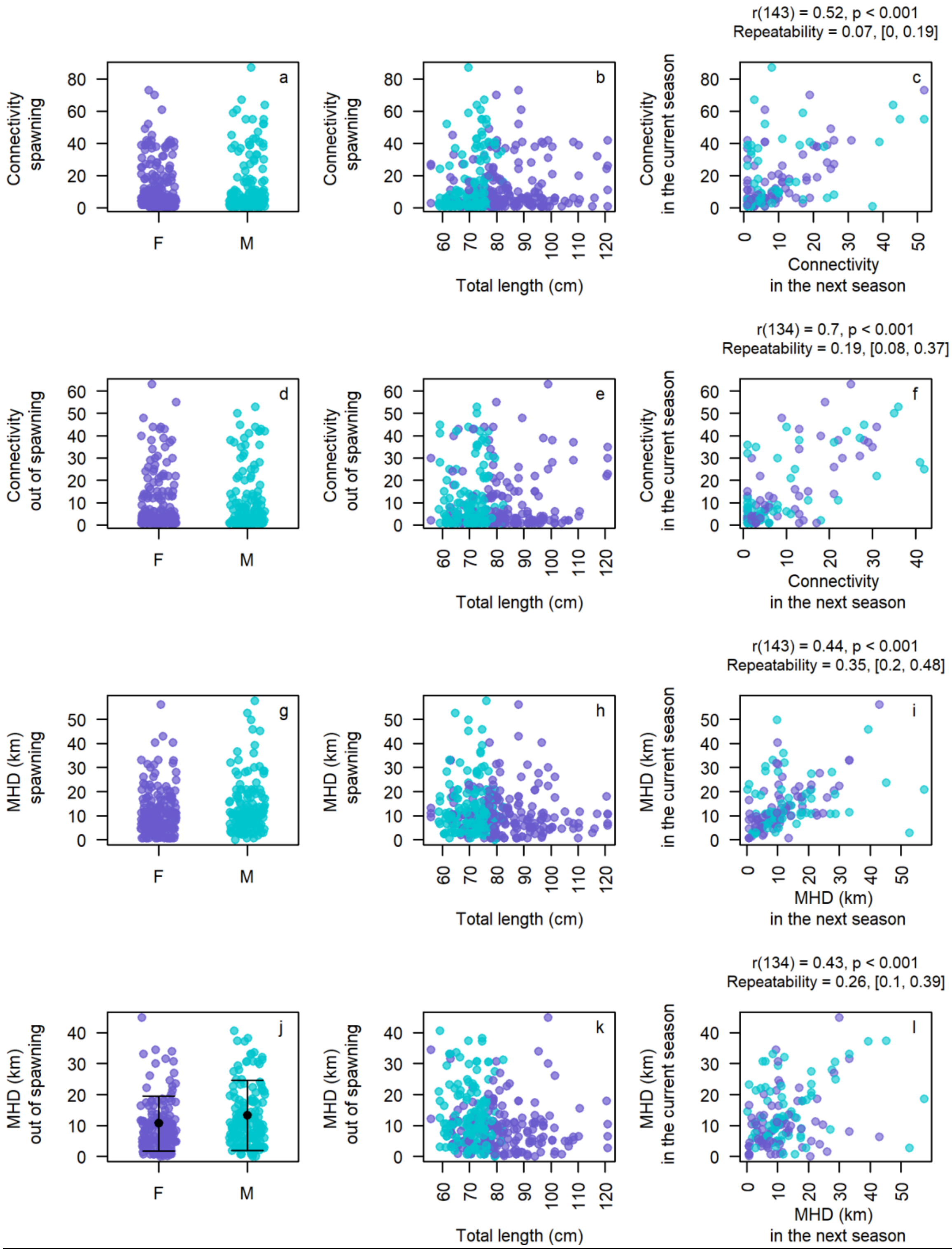



*Figure 5. Scatter plot of the raw data for our response variables during the spawning period (February to May, panels a, b, c, g, h, i) and for the rest of the year (d, e, f, j, k, l) as a function of sex and total length and from one year as a function of the next. Connectivity during spawning and for the rest of the year is not explained by sex (a, d) or size (b, e), but individuals are consistent across years (c, f), although not repeatable during spawning. MHD during spawning is not explained by sex (d) or size*

*(e), but males have higher MHD out of spawning (j). Individuals are consistent and repeatable in MHD across years (i, l). Estimates and credible intervals are shown on panel j.*

***Among-year spawning site fidelity***

In all four among-year analyses, we dropped the sex by total length interaction as it did not improve model fit (site fidelity between area ELPD = -0.8, SE =0.3; site fidelity between receivers ELPD = -1.1, SE =0.6; Sørensen index between areas ELPD = -0.8, SE =0.5; and Sørensen index between receivers ELPD = -0.7, SE =1.1). Across all models, we found no effect of either total length or sex on among-year spawning site fidelity (Table 4). This indicates that although some individuals may change spawning sites across years, such differences were not explained by body size or sex.

*Table 4. Model output for the indices of site connectivity among-year as a function of body size and sex. Significant slopes and significant differences in intercept are highlighted in bold.*

| | | **Estimate** | **Estimated error** | **Lower 95% Confidence interval** | **Upper 95% Confidence interval** |
|---|---|---|---|---|---|
| ***Site fidelity (area level)*** | *Intercept (taken as Sex:Female)* | -0.53 | 1.77 | -3.96 | 3.05 |
| | *Sex:Male* | 0.07 | 0.49 | -0.87 | 1.06 |
| | *Total Length* | 0.02 | 0.02 | -0.02 | 0.06 |
| ***Site fidelity (receiver level)*** | *Intercept* | 1.27 | 2.28 | -3.20 | 5.75 |
| | *Sex:Male* | -0.25 | 0.58 | -1.43 | 0.87 |
| | *Total Length* | -0.04 | 0.03 | -0.10 | 0.02 |
| **Sørensen index (area level)** | *Intercept* | 1.52 | 0.68 | 0.19 | 2.83 |
| | *Sex:Male* | -0.09 | 0.19 | -0.45 | 0.28 |
| | *Total Length* | 0.00 | 0.01 | -0.01 | 0.02 |

| | | | | | |
|---|---|---|---|---|---|
| **Sørensen index (receiver level)** | *Intercept* | 1.25 | 0.79 | -0.31 | 2.80 |
| | *Sex:Male* | -0.21 | 0.23 | -0.66 | 0.26 |
| | *Total Length* | -0.01 | 0.01 | -0.03 | 0.01 |

***Visual assessment of spawning season movement and site use***

Out of the 93 individuals with an MHD greater than 10 km during the spawning season, 83% (N = 77, females = 42, males = 33) exhibited pronounced displacement behaviour in at least one year, i.e., they travelled to areas distinct from their non-spawning residency areas, as indicated by clear peaks in distance-from-first-detection plots (see Figure 6; Supplementary file 2, section 2 B). Among these, 13% (N = 12, females = 5, males = 7; Supplementary file 2, section 2 A) visited two different spawning sites in at least one year.

Of the fish with multi-year data (N = 62), 84% (N = 52) were recorded visiting a location during spawning season distinct from where they resided the rest of the year, indicating migratory behaviour. Among these migrants, 65% (N = 34; 20 females, 14 males; Supplementary file 2, section 1B) returned to the same spawning area for at least two years, with 7% of migrants (N = 4; 2 females, 2 males; Supplementary file 2, section 1A) recorded repeatedly using two distinct spawning sites across different years (for example see Figure 6).

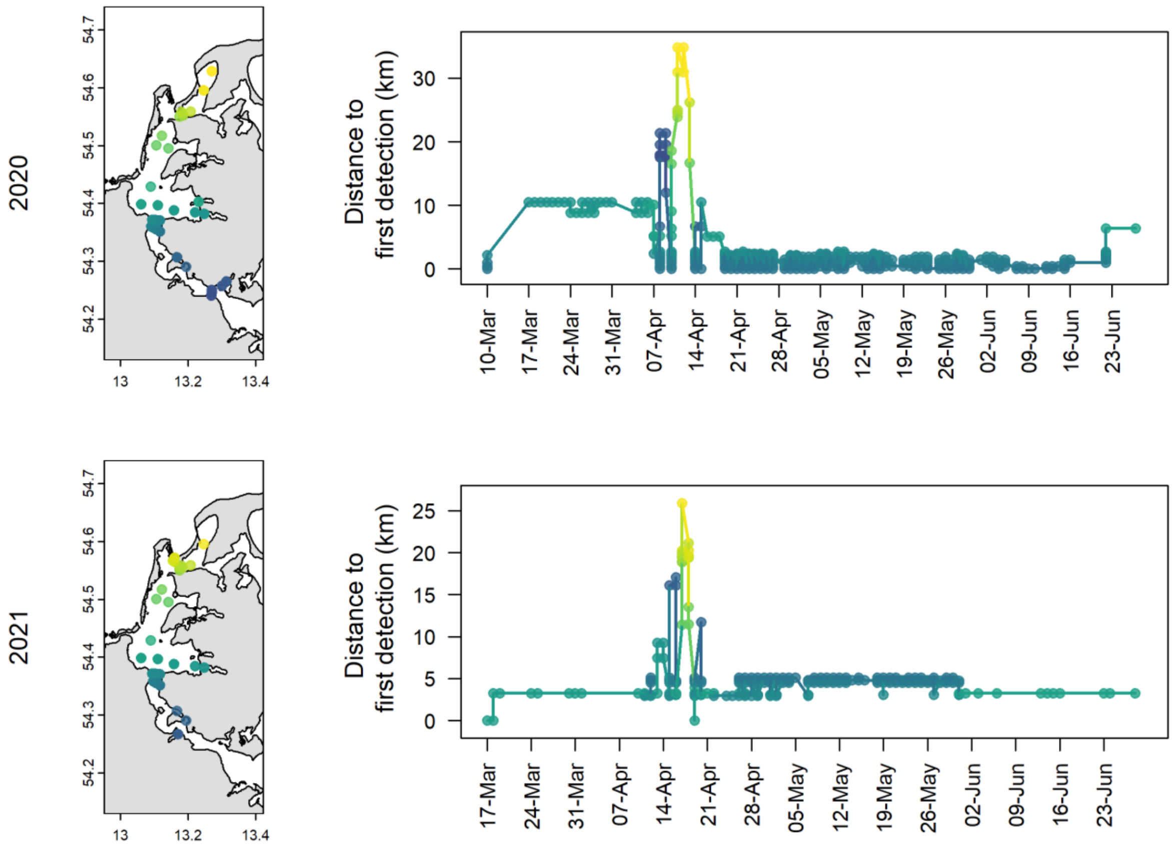



*Figure 6. Map of detections (left) and distance from the first detection for pike BH-90099, an 88 cm female, in 2020 and 2021. In both years, the pike makes a brief visit to the south (blue receivers), followed immediately by a visit to the north (yellow receivers). This movement pattern may indicate visits to different spawning sites, although actual spawning behavior cannot be confirmed with our technology. In 2020, the pike travelled both slightly farther south and farther north compared to 2021, suggesting possible use of different areas between years.*

**Discussion**

In this study, neither mark-recapture nor telemetry data indicated higher connectivity or broader movement ranges in larger coastal northern pike of either sex during or out of the spawning season, with the exception of males exhibiting higher maximum horizontal displacements (MHD) outside spawning. Site fidelity and repeated area use among years were also independent of size and sex in all analyses. At the individual level, however, connectivity and movement ranges during the spawning season were highly correlated between years and repeatable, as was connectivity outside the spawning season. Our additional visual inspection of the 93 most active individuals (MHD > 10 km; 29% of all tagged fish) further supported this consistency, with many returning to the same spawning area across years. Some (13%) of these wide-roaming individuals visited multiple spawning sites within a single season, with no apparent sex- or size-based differences.

The individual consistency in movement behaviour observed in our study suggests strong inter-individual variation (i.e., the presence of behavioural types or personalities) in adult pike independent of body size or sex, aligning with prior research on pike in our study area (Dhellemmes et al. 2023b) and in other study systems and life stages (Kobler et al. 2009; McGhee et al. 2013; Laskowski et al. 2016; Pasquet et al. 2016; Monk et al. 2021; Cittadino et al. 2024). Previous work has shown that the behavioural consistency in pike is unrelated to body length (Nyqvist et al. 2012; Laskowski et al. 2016). More broadly, while some general patterns in pike and other esocids' spatial behaviour have been identified, marked variability in movement ecology persists both within and among populations (Lucas et al. 2018; Hessenauer et al. 2021; Cittadino et al. 2024), pointing at the importance of individual-level differences as one of the sources of this variance.

The absence of size- and sex-dependent movement range and connectivity in coastal pike reported here is in contrast with studies showing the tendency of movement rates and dispersal to increase with body size in multiple species as ecologically diverse as Pacific lamprey, herring (Slotte 1999; Hess et al. 2014), Atlantic salmon (Jonsson et al. 1991), brown trout (L'Abée-Lund 1991), and American shad (Glebe and Leggett 1981). Evidence in pike itself is mixed: some studies document positive size–movement relationships (e.g., Kobler et al. 2008; Monk et al. 2021; Rosten et al. 2016), while others do not (e.g., Dhellemmes et al. 2023a; Jepsen et al. 2001; Koed et al. 2006). Notably, some studies found that the positive size-activity relationships depended on environmental conditions, e.g., turbidity (Andersen et al. 2008) or habitat complexity (Říha et al. 2021). This context-dependency suggests that pike possess considerable behavioural flexibility, allowing them to adapt their behaviour to increase fitness, rather than body size dictating it. Generally, even though pike is traditionally regarded as a sedentary ambush predator (Diana, 1980), they display considerable variability in spatial behaviour, both within and among populations, across the wide range of habitats they occupy (Harvey-Lavoie et al. 2016; Lucas et al. 2018; Somers et al. 2021; Cittadino et al. 2024).

Male pike were found to display higher MHD than females outside of the spawning season, when controlling for body size, in agreement with Jepsen et al. (2001) in one of two study lakes, but disagreeing with Koed et al. (2006) in a river population. Notably, this difference did not extend to the spawning season, suggesting that both sexes travel similar long-range distances to reach spawning grounds. The observation that males may use more space than females is in agreement with past studies conducted in our study area (Dhellemmes et al. 2023b). Movement differences between the sexes may be due to the cost of gamete production being lower for males than for females (Jonsson et al. 1997), resulting in males having more residual energy to dedicate to movements. They may also be driven by intersexual competition for resources, with males and females specializing in different foraging strategies, or due to sexual dimorphism in size, which could mean that smaller males are under greater risk of cannibalistic or other types of predation, motivating greater displacements in the search for safe refuges (Haugen et al. 2006, 2007; Li and Kokko 2021).

The absence of size- and sex-dependent connectivity during spawning suggests that larger pike are unlikely to function as key connectors among spawning areas, contrary to what was recently documented for other coastal species, such as the Atlantic cod in Norwegian fjords (Olsen et al. 2023). Both species are characterized by strong spawning site fidelity (see Skjæraasen et al. (2011)

for cod; and Miller et al. (2001); Tibblin et al. (2015) for pike), but this behavioural difference may stem from fundamental contrasts in reproductive biology. Atlantic cod is a batch spawner with a lek-based mating system, pelagic eggs, and size-dependent release of egg batches across multiple sites over weeks to months (Kjesbu 1989; Roney et al. 2018). Larger, more fecund females, therefore, may benefit from visiting multiple spawning locations as a spatial bet-hedging strategy, facilitated by their ability to release eggs repeatedly (Olsen et al. 2023). Pike, on the other hand, are total spawners: females typically deposit adhesive eggs onto submerged vegetation within a single day over several hours (Lindroth 1946; Svardson 1949; Fabricius and Gustafson 1958; Billard 1996). In rare exceptions, individual females release eggs over up to three days, but long-range changes in spawning locations by individuals within a spawning season were never documented in that case (Clark 1950). This reproductive constraint fundamentally limits any within-season fitness benefit of moving among spawning sites, regardless of body size or sex, and likely explains why size-dependent connectivity during and across different spawning seasons was not observed in pike. However, spatial bet hedging in total spawners such as pike may occur through the choice of variable spawning sites or variable timing of reproduction (Tibblin et al. 2016) across different spawning seasons. We found no evidence for size-dependent among-year site switching in our system either, in agreement with previous reports of strong natal site fidelity and high consistency in both lentic and coastal pike (Miller et al. 2001; Tibblin et al. 2015, 2016), further suggesting that individual-level spatial bet hedging is considerably less pronounced in total spawners than in batch-spawning species such as cod. Instead, other mechanisms of spatial bet hedging through individual variation, such as the evolution of reproductively isolated ecotypes (e.g., brackish residents, anadromous individuals, and freshwater residents; Rittweg et al. 2024; Roser et al. 2023), and the development of a long spawning season lasting up to two months (Pagel et al. 2015; Arlinghaus et al. 2023b), may provide population resilience in total spawning fish species.

That said, our exploratory visual inspection of the most widely roaming individuals suggested that some (13%, 5 females and 7 males) visited multiple putative spawning sites within a single season, with several (4%, 2 females and 2 males) doing so repeatedly across years (e.g., Figure 6). While total spawning biology likely constrains within-season spatial bet-hedging in pike, these observations suggest the possibility cannot be entirely excluded. Importantly, though, this behaviour was unrelated to body length, remaining consistent with individual-level rather than size-structured movement. Using oviduct transmitters and other tagging technologies could help to gain more precise estimates of spawning time and location for bony and cartilaginous fish (Sulikowski and Hammerschlag 2023; Gardner and Höök 2024), including pike (Pierce 2004).

Beyond reproductive biology, we speculate that the lack of size-dependent space use (Dhellemmes et al. 2023b) and spawning site connectivity (this study) in the Rügen coastal pike population may also partly reflect past behaviour-selective harvesting. Far-roaming larger phenotypes and their underlying genotypes may have been systematically removed in decades of intensive harvesting in the study area (van Gemert et al. 2022; Arlinghaus et al. 2023b; Roser et al. 2025), gradually altering the population's phenotypic and genetic composition, and eliminating individuals with a tendency to move a lot before and during spawning. The study area has been intensively harvested by small-scale commercial and recreational fisheries for more than a century (Arlinghaus et al. 2023b), which is sufficient time for the evolutionary impacts of harvesting to manifest in pike (Matsumura et al. 2011). Both gill nets (Carlson et al. 2007; Edeline et al. 2007) and recreational angling gear are known to target not only larger individuals but also those with an elevated space use (Monk et al. 2021), which often have higher fitness in the wild (Monk et al. 2021). In the study region, the so-called pre-spawn gill net fishery actively targets pike in spawning aggregations in bays (Arlinghaus et al. 2023b), exploiting their increased activity levels and migration into sheltered spawning bays (Flink *et al.*, 2023). It is conceivable that the largest individuals and those with the longest migration distance have been selectively removed from the population, erasing the potential for size-dependent movements to be revealed in the current time.

Several limitations should be noted. First, we inferred the connectivity among spawning sites by analysing movement metrics during the key spawning period known for pike, without observing exactly where and when individual pike spawned. However, our receiver array broadly covered the most important known spawning sites (Figure 1), making our study likely robust for assessing long-range movement patterns. Second, given our array design, we were unable to track fine-scale behaviours during spawning site selection, and size-dependent micro-level site selection, and associated differences in activity (e.g., Lucas, 1992) may still occur on local scales. The telemetry system we used was not designed to detect fine-scale movement resolution. Future studies focusing on specific lagoons and using biologgers and micro transmitters inserted into the oviduct, capable of direct spawning site detection, will be necessary to determine whether pike of different lengths choose particular spawning sites and connect them through localised movements within specific lagoons.

To conclude, this study demonstrates that individual behavioural consistency, rather than body size or sex, is the primary driver of movement, spatial connectivity, and spawning site fidelity in coastal northern pike across a southern Baltic lagoon network. These findings align with a growing body of evidence that stable individual-level variation, broadly consistent with the concept of animal personalities or behavioural types, is an important feature of pike population ecology. From a conservation and management perspective, this carries meaningful implications: if connectivity is driven by a consistent minority of wide-ranging individuals rather than by a predictable size or sex class, standard harvest regulations, such as size restrictions for harvesting large fish, are unlikely to effectively protect the connectivity processes that underpin metapopulation dynamics and gene flow in coastal pike. This does not diminish the importance of conserving large individuals, given their high social value (e.g., high angler preference for catching trophy-sized pike; Koemle *et al.*, 2022) and fecundity-related benefits of large females (Ahrens et al. 2020). For population resilience and long-term persistence, however, our findings point to a broader set of priorities: protecting and restoring the network of spawning and foraging habitats on which the metapopulation depends, reducing incidental capture of wide-ranging individuals through passive gear such as gill nets in migration corridors, and fostering ecotypic biocomplexity across the full metapopulation and its constituent river and coastal systems – a diversity increasingly recognised as critical for sustaining resilience and long-term fisheries productivity (Schindler et al. 2010).

**Ethics statement**

The research was completed following German legislation for animal experimentation, approved by Landesamt für Landwirtschaft, Lebensmittelsicherheit und Fischerei MecklenburgVorpommern—Veterinärdienste und Landwirtschaft—under grant no. 7221.3-1-052/19.

**Data availability statement**

Telemetry data are available in the European Tracking Network repository: Dhellemmes F, Arlinghaus R (2021) Boddenhecht telemetry dataset. https://marineinfo.org/id/dataset/7859. Mark-recapture data are available from the authors upon reasonable request.

**Declaration of Interest statement**

The authors declare no conflicts of interest related to this work.

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**Author Credits**

**O.L.**: Writing - Original Draft, Writing - Review & Editing, Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data Curation, Visualization. **R.A.**: Writing - Review & Editing, Conceptualization, Methodology, Resources, Supervision, Project administration, Funding acquisition. **F.D.**: Writing - Review & Editing, Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data Curation, Visualization, Supervision.

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