Large female northern pike (*Esox lucius*) do not connect spawning areas across a lagoon network in the southern Baltic Sea

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Abstract

Exceptionally large individuals may serve as keystone connectors among subpopulations and habitats, a role recently demonstrated in large Atlantic cod (*Gadus morhua*) in Norway. To examine whether this pattern extends to other coastal fish species, we analysed capture-mark-recapture data for over 5,800 coastal northern pike (*Esox lucius*) and acoustic tracking data from 317 pike individuals, using a large biotelemetry array covering 1,200 km² in brackish lagoons in the southern Baltic Sea in Germany. The pike in our study spanned a wide size range, with total lengths ranging from 28 cm to 126 cm. In the capture-mark-recapture dataset, we observed a positive relationship between body length and distance between capture and recapture, but this correlation was driven by the presence of two particularly large and mobile individuals in the sample. In the acoustic telemetry dataset, we found no relationship between individual body length, connectivity, and maximum horizontal displacement over two spawning seasons, and separately for spawning and non-spawning periods. These findings suggest that large northern pike may not serve as keystone connectors among spawning sites in brackish lagoons.

Keywords

bet hedging, BOFFFF, site connectivity, spawning, size-selective harvesting

Introduction

The relevance of exceptionally large fish in the conservation of fish populations has gained substantial attention over the past two decades, particularly following the paper by Berkeley *et al.*, (2004) on the positive effect of maternal age on larvae survival in rockfish (*Sebastes melanops*) (Birkeland & Dayton, 2005). This research interest has culminated in the catchy concept of BOFFFF – big old fat fecund female fish (Hixon *et al.*, 2014). Major syntheses have outlined the various mechanisms by which large fish contribute 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). Consequently, stock assessment methods and harvest management strategies are increasingly incorporating measures to conserve large and old fish (Froese, 2004; Griffiths *et al.*, 2024), with growing interest in approaches that protect both small, immature individuals and highly fecund large fish, e.g., through harvest slots (Ahrens *et al.*, 2020; Gwinn *et al.*, 2015) or marine protected areas (Marshall *et al.*, 2021).

The discussion on the relevance of large fish in population dynamics and conservation often centres on two key size-dependent maternal effects: (1) the influence of female size on egg and offspring phenotype and quality (e.g., Berkeley *et al.*, 2004), and (2) size-dependent increases in relative fecundity per female mass, characterized by hyperallometric relationships between body mass and egg number (e.g., Barneche *et al.*, 2018; Hixon *et al.*, 2014a). However, the size-dependent maternal effects on egg and offspring quality regularly reported in laboratory trials (e.g., Berkeley *et al.*, 2004; Hixon *et al.*, 2014a) may not always manifest in the wild and may appear only in studies where environmental influences are controlled (Marshall *et al.*, 2010). Population-level fish recruitment is under strong density-dependent feedback in fishes, diminishing the relevance of spawning stock composition – such as the size or age of spawners and their egg and larval qualities – for population dynamics (Ahrens *et al.*, 2020; Andersen *et al.*, 2019). Similarly, the fecundity advantage of large fish may not be generally impactful for the population as a whole, as large fish are typically in low abundance (Andersen *et al.*, 2019), unless the hyperallometry of the mass-fecundity relationship is exceptionally strong (Ahrens *et al.*, 2020; Marshall *et al.*, 2021). Given that exceptionally large fish are usually rare in most stocks relative to younger and hence smaller spawners, and the degree of hyperallometry in mass-fecundity varies across species and populations (Barneche *et al.*, 2018), the conservation value of protecting large fish similarly varies among fisheries (Marshall *et al.*, 2021). Ultimately, the optimal size limit will also depend on management objectives and hence social values (Ahrens *et al.*, 2020).

Beyond size-dependent impacts on reproductive traits (reviewed by Green, 2008; Hixon *et al.*, 2014; Marshall *et al.*, 2008), body length influences numerous other biological processes that have received less attention from conservation and fisheries management perspectives. Moreover, female size is often given more attention than male size in most exploited stocks, based on the assumption that sperm is rarely limiting (Hixon *et al.*, 2014). Yet, body size in both sexes plays a role in sexual selection, mate choice, and decisions related to spawning and foraging locations (Hixon *et al.*, 2014; Uusi-Heikkilä, 2020). Size variation also affects vulnerability to environmental stressors, such as heat waves or anoxic conditions, and influences dominance hierarchies and trophic interactions in complex ways (Ahti *et al.*, 2020; Roos & Persson, 2013). Importantly, both inter- and intraspecific movement rates and dispersal often increase with body size in fishes (Minns, 1995; Tamburello *et al.*, 2015), and body length reduces natural mortality (Lorenzen, 2022) and increases fecundity of female fish in most species (Barneche *et al.*, 2018). Accordingly, large body size is a key trait under selection in various migratory (e.g., Burns & Bloom, 2020) and non-migratory fishes (e.g., Monk *et al.*, 2021). In Pacific lamprey (*Entosphenus tridentatus*) and herring (*Clupea harengus*), for instance, larger fish migrate greater distances (Hess *et al.*, 2014; Slotte, 1999). Similar patterns have been reported for Atlantic salmon (*Salmo salar*, Jonsson *et al.*, 1991), brown trout (*Salmo trutta*, L'Abée-Lund, 1991), and American shad (*Alosa sapidissima*, Glebe & Leggett, 1981). An inverse relationship between body length and migration distance upstream, however, was reported in Pacific salmon (Crossin *et al.*, 2004). Possible reasons may include differences in life-history (i.e. semelparity v. iteroparity), and selection acting differentially on species that travel only modest distances upriver and ones that must conserve energy for the downriver return to the ocean (Crossin *et al.*, 2004). In another example of a non-migratory species, larger northern pike (*Esox lucius*) exhibited greater movement, larger home ranges, and larger reproductive output in a small lake than smaller, less mobile individuals (Monk *et al.*, 2021). A positive size-movement relationships could be caused by greater swimming speeds at larger body sizes (Ohlberger *et al.*, 2006), reduced cost of swimming (Alexander, 2003), improved condition (Bernatchez & Dodson, 1987), or accumulated experience in locating optimal spawning or foraging sites (Reebs, 2001; Rose, 1993; Webster, 2017). As large fish also face lower natural predation risk (Lorenzen, 2022), they may be less constrained to move and thereby act as keystone connectors, linking distant spawning habitats and thereby facilitating gene flow (Olsen *et al.*, 2023). In social fishes, larger individual fish may also exhibit leadership in locating food patches (Reebs, 2001). Despite its relevance, the social 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 help understand why size-truncated stocks exhibit greater population fluctuations than those with balanced age and size structures (Anderson *et al.*, 2008; Hsieh *et al.*, 2010).

Independent of the ongoing discussion about the conservation value of protecting large fish (reviewed in Kopf *et al.*, 2024), the socio-economical value of large-sized fishes is often substantial. This is especially true for recreational fisheries, where angler satisfaction tends to scale exponentially with increasing capture rates of large fish (Arlinghaus *et al.*, 2014; Beardmore *et al.*, 2015; Birdsong *et al.*, 2022). Therefore, many recreational anglers voluntarily release large trophy fish (Arlinghaus *et al.*, 2007), making their conservation feasible in fisheries where post-release mortality is low (Ahrens *et al.*, 2020).

In a recent study, Olsen et al. (2023) used acoustic telemetry in coastal sites of Norway to demonstrate that large female Atlantic cod (*Gadus morhua*) act as key spawning site connectors. This is an important finding because connectivity among spatially separated spawning sites might provide a major buffering mechanism contributing to population resilience. The authors argue that removing these keystone individuals through fisheries could isolate meta-populations, increasing the risk of local extinctions. The work by Olsen et al. (2023) motivated us to investigate whether similar size-dependent connectivity exists in a coastal population of northern pike in the southern Baltic Sea, an extreme brackish environment for this freshwater species (Arlinghaus *et al.*, 2023a; Rittweg *et al.*, 2024).

Northern pike is a phytophilic, large-bodied piscivorous freshwater fish (Craig, 1996; Skov & Nilsson, 2018), heavily exploited in both commercial and recreational fisheries in a positively size-selective manner (Arlinghaus *et al.*, 2018). The species 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 (Clark, 1950; Raat, 1988; Svardson, 1949). Males seem to preferentially spawn with larger, more fecund females (Fabricius & Gustafson, 1958), and larger males were found to sire a greater number of offspring in a natural lake (Pagel, 2009).

In the southern Baltic, northern pike has diversified into ecotypes ranging from brackish residents to anadromous and freshwater subpopulations (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 (Dhellemmes *et al.*, 2023a; Jacobsen *et al.*, 2017; Karås & Lehtonen, 1993), forming a spatially structured meta-population across a network of brackish lagoons (Lukyanova *et al.*, 2024). Population connectivity is generally low outside the spawning season but increases significantly prior to and during spring spawning, when pike activity and space use increase (Cook & Bergersen, 1988; Dhellemmes *et al.*, 2023a; Diana, 1980; Flink *et al.*, 2023; Lukyanova *et al.*, 2024; Raat, 1988). Increases in space use during spawning are especially pronounced in coastal sites where multiple ecotypes, such as brackish spawners and anadromous fish (Müller, 1986; Sunde *et al.*, 2022; Tibblin *et al.*, 2016), 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 also fully coastal ecotypes have been reported to engage in spawning migrations towards enclosed, sheltered bays that are used for spawning (Flink *et al.*, 2023; Lukyanova *et al.*, 2024). Therefore, movement is a key contributor to successful spawning in coastal pike, and like the case of Atlantic cod (Olsen *et al.*, 2023), larger pike might serve as key connectors among different areas and lagoons. However, it remains unclear whether and to what extent the largest individuals act as key connectors among spawning sites, which are located in tributaries, nearshore areas, and bays within the lagoons (Flink *et al.*, 2023; Roser *et al.*, 2023).

In pike, as in many other fish species (Minns, 1995), space use is positively correlated with body size (Monk, 2019; Monk *et al.*, 2021; Rosten *et al.*, 2016). However, such positive relationship between body length and activity or home range size is not universally observed in pike (Dhellemmes *et al.*, 2023a; Jepsen *et al.*, 2001; Kobler *et al.*, 2008; Koed *et al.*, 2006). Discrepancies among studies may stem from differences in the size gradients studied, local environmental conditions, local ecosystem extension or population-specific characteristics. 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). Such selective harvesting could favour smaller, less active phenotypes, potentially eroding the positive body length-movement relationship over evolutionary time. Also, the timing and duration of sampling and behavioural observation may influence findings, as pike are generally sedentary ambush predators for much of the year (Diana, 1980), with elevated activity primarily occurring before and during the spring spawning season (Lukyanova *et al.*, 2024; Raat, 1988). Therefore, size-related behavioural differences may be more pronounced prior to and during the spawning season and less evident in other seasons. No study so far has examined whether body length, in either males or females, enhances connectivity among spawning sites or whether larger individuals indeed act as key connectors, as observed in Atlantic cod (Olsen *et al.*, 2023). Collecting such data requires studying a large sample of differently sized fish in widespread coastal areas or very large lakes where long-range movements can be detected.

We equipped a coastal lagoon area of 1,200 km^2 with an acoustic telemetry system, offering a suitable arena to examine the size and sex-dependency of spawning site connectivity in pike and assessed whether body length plays a key role in connecting different areas during the spring spawning period and outside spawning in a coastal pike population inhabiting a vast, interconnected lagoon ecosystem in the southern Baltic Sea (for a review, see Arlinghaus *et al.*, 2023a). Following Olsen *et al.* (2023), we hypothesized that the largest individuals of both males and females would act as keystone connectors, linking spawning and foraging sites over large distances, resulting in positive relationships of body length and network connectivity both during and outside spring spawning time.

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 1,200 km² of the total 1,600 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, 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).

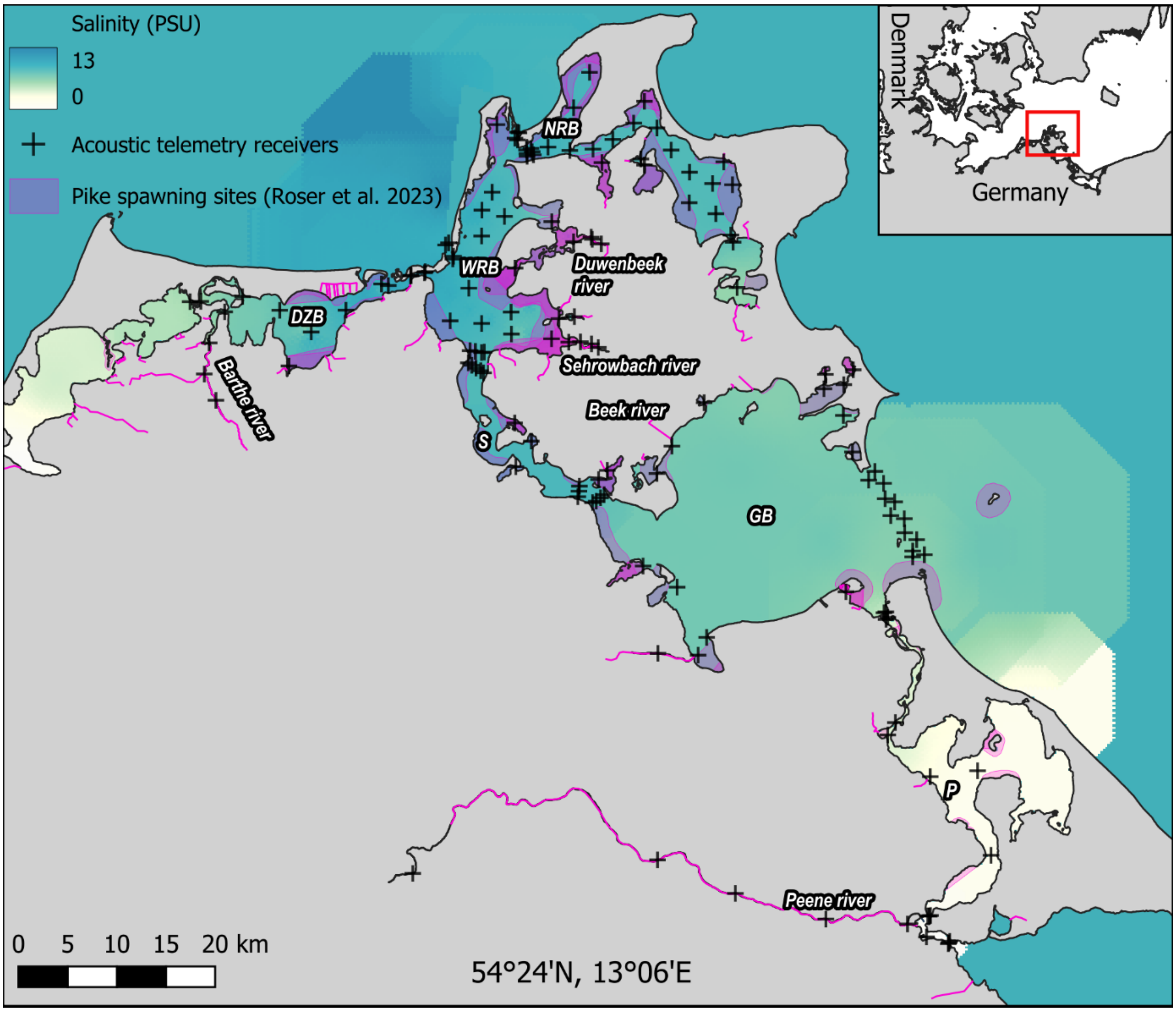


Figure 1. Map of the study area, including receiver locations, the average salinity gradient and the pike's spawning sites. Pike spawning site data are taken from Roser et al., (2023)*, where spawning sites are aggregated from different sources, which may agree on the location of a spawning site, leading 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 freshwater sites to observe year-round behaviour, with a particular focus on the period before and during the spring spawning season.

Between January 2020 and January 2023, we captured 5,836 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.*, 2023b). Capture methods included rod and reel fishing, fyke nets, gillnets (in cool and cold water where fish are still alive), 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 = 2,664, males = 2,509, unknown = 66; Casselman, 1974), weighed to the nearest gram (mean ± standard deviation (SD) = 3,037 ± 1,958 g, min = 2.3, max = 17,000), and measured to the nearest millimetre (total length in cm; mean ± SD = 74.1 ± 15.9, min = 12.6, max = 126.2). The health of all captured pike was assessed visually (i.e., colour, liveliness); healthy individuals measuring more than 28 cm received one or two orange external ID tags (N = 5,239, females = 2,664, males = 2,509, unknown=66; mean total length = 75.7 ± 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) 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.

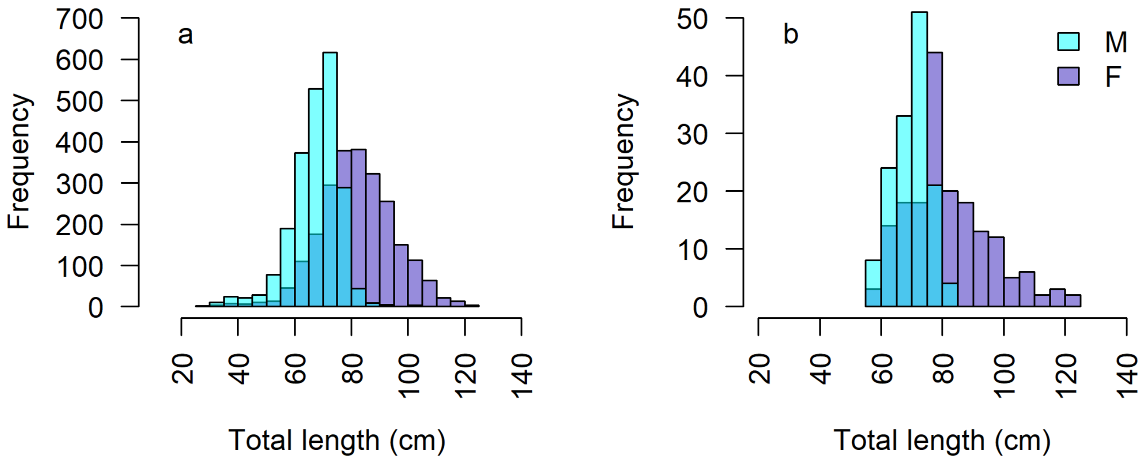


Figure 2. Frequency distribution of total length (mm) in our sample. a) All pike captured for the study and b) pike equipped with acoustic tags. Males (M) and females (F) are represented in blue and purple respectively.

Between February and December 2020, we selected 317 pike 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). 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 (± 12.3 SD; min = 55.7, max = 121.0; Figure 2) and 3,760 g in weight (± 2,114 SD; min = 1,388, max = 15,000). 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 each pike to generate up to three years of data (Dhellemmes *et al.*, 2023a). Upon download, the data was filtered for false detections using *ATfiltR* (Dhellemmes *et al.*, 2023a, 2023b).

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.

	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 (773)	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 because recapture rates by fishers or anglers could not be observed during the spawning period due to official closures during March and April each year. 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 (i.e., maximum in-water distance between all detections of an individual pike, MHD) for February, March, April, and May to focus on the prime spawning season for pike. If an individual pike generated data for multiple years, we averaged the connectivity and MHD metrics across the years. For comparison, we also calculated connectivity and MHD for each pike outside of the spawning period. 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 *et al.*, 2025; Csàrdi & Nepusz, 2006), with nodes representing the acoustic receiver locations, and edges reflecting subsequent detections of individuals moving between these locations. Following the method in Olsen et al. (2023), each fish was assigned a connectivity score based on the number of unique edges detected within the time window of interest.

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 analysis in R version 4.3.1 (R Core Team, 2021). We compared metrics within and outside of the spawning season using t-tests. All of our models were constructed in *brms* (Bürkner, 2017), using 3 chains of 120,000 iterations each, with a thinning interval of 100 and a burn-in of 20,000. 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. 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. All models were fitted using Gaussian distribution, and the connectivity score was log-transformed (base 10) to fit normality assumptions. We used leave-one-out cross-validations based on expected log pointwise predictive density (ELPD) based on the loo criterion in the *loo* package (Magnusson *et al.*, 2019; Vehtari *et al.*, 2017) 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. Results were considered significant if the 95% confidence interval did not overlap zero. Pike of unknown sex (n = 14 for mark-recapture, and n = 2 for telemetry) were removed from the analysis.

Results

Mark-recapture

Out of our 5,836 captures, 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 and a median of 2.6 km (Figure 3, A). Leave-one-out cross-validations suggested that the sex by total length interaction was not improving model fit (difference in expected log pointwise predictive density (ELPD) = -1.1, standard error (SE) = 0.3). We found males and females to be similar in their intercept, and total length to have a significant positive effect on the distance between capture and recapture (Table 2). The latter suggested that larger fish, independent of sex, showed greater minimal movement distance based on mark-recapture data. Upon inspection of the scatterplot (Figure 3, b) we re-ran the model, removing the two pike that travelled more than 40 km, and found the length-recapture distance model to no longer be significant (estimate = 40.76, estimated error = 24.28, lower 95% CI = -5.35, upper 95% CI = 88.15, Table 2). This indicated that the initially positive relationship among body length and recapture distance was driven by the presence of two particularly large and mobile individuals in the sample.

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% Confidence interval**	**Upper 95% Confidence interval**
Full sample	*Intercept (taken as Sex:Female)*	256.13	2390.22	-4344.19	4865.49
	Sex:Male	186.36	707.38	-1224.41	1585.22
	Total Length	**58.19**	**27.90**	**2.96**	**111.85**
Excluding the two most mobile fish	*Intercept (taken as Sex:Female)*	1444.06	2098.48	-2662.91	5450.62
	Sex:Male	169.48	616.31	-1059.94	1345.48
	Total Length	40.76	24.28	-5.35	88.15

Connectivity and maximum horizontal displacement based on biotelemetry

Out of 317 tagged fish, 292 generated data for an average duration of 439 days (time between first and last detection, min = 0, max = 1,065). 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). In total, we analysed 1,649,010 detections. Connectivity (taken as the number of network edges per pike during a given period) was on average 12.8 (± 14.3 SD, min = 1, max = 62.5) during the spawning period (February, March, April, May) and 10.1 (± 11.6 SD, min = 1, max = 44) outside of spawning (Figure 3, B). MHD was on average 11.3 km (± 8.6 SD, min = 0.7, max = 52.7) during spawning and 11.4 km (±7.7 SD, min = 0.7, max = 37.7) outside of the spawning period (Figure 3, C). T-tests indicated that connectivity was higher during spawning (t = -2, p = 0.04), but MHD was not (t = 0.08, p = 0.93). The interaction between body length and sex did not improve model fit and was therefore excluded (connectivity out of spawning ELPD = -0.7, SE = 1.8; connectivity spawning ELPD = -0.6, SE = 0.4; MHD out of spawning ELPD = -0.1, SE = 1.9, MHD spawning ELPD = -1.3, SE = 0.2). Higher connectivity and MHD during the spawning time and the rest of the year were not explained by body size (Table 3), rejecting the hypotheses of a positive size-dependency of spawning site connectivity (for example of 10 smallest and largest fish individuals, see Figure 5, C-D). In the case of MHD out of the spawning period, males exhibited higher MHD than females (Table 3), indicating a sex effect only, independent of body length.

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 (out of spawning)	*Intercept (taken as Sex:Female)*	0.72	0.33	0.07	1.35
	Sex:Male	-0.09	0.09	-0.26	0.09
	Total Length	-0.00	0.00	-0.01	0.01
Connectivity (spawning)	*Intercept*	0.56	0.26	0.04	1.06
	Sex:Male	-0.05	0.07	-0.19	0.08
	Total Length	0.00	0.00	-0.00	0.01
MHD (out of spawning)	*Intercept*	12,565.47	4,895.40	2,963.63	22,194.82
	Sex:Male	**2,779.89**	**1,333.94**	**107.00**	**5357.74**
	Total Length	-37.19	57.34	-149.43	74.55
MHD (spawning)	*Intercept*	11,307.72	4,881.12	1,995.50	21,128.75
	Sex:Male	1,547.37	1,416.09	-1,173.18	4,327.18
	Total Length	-17.31	56.25	-130.61	88.13

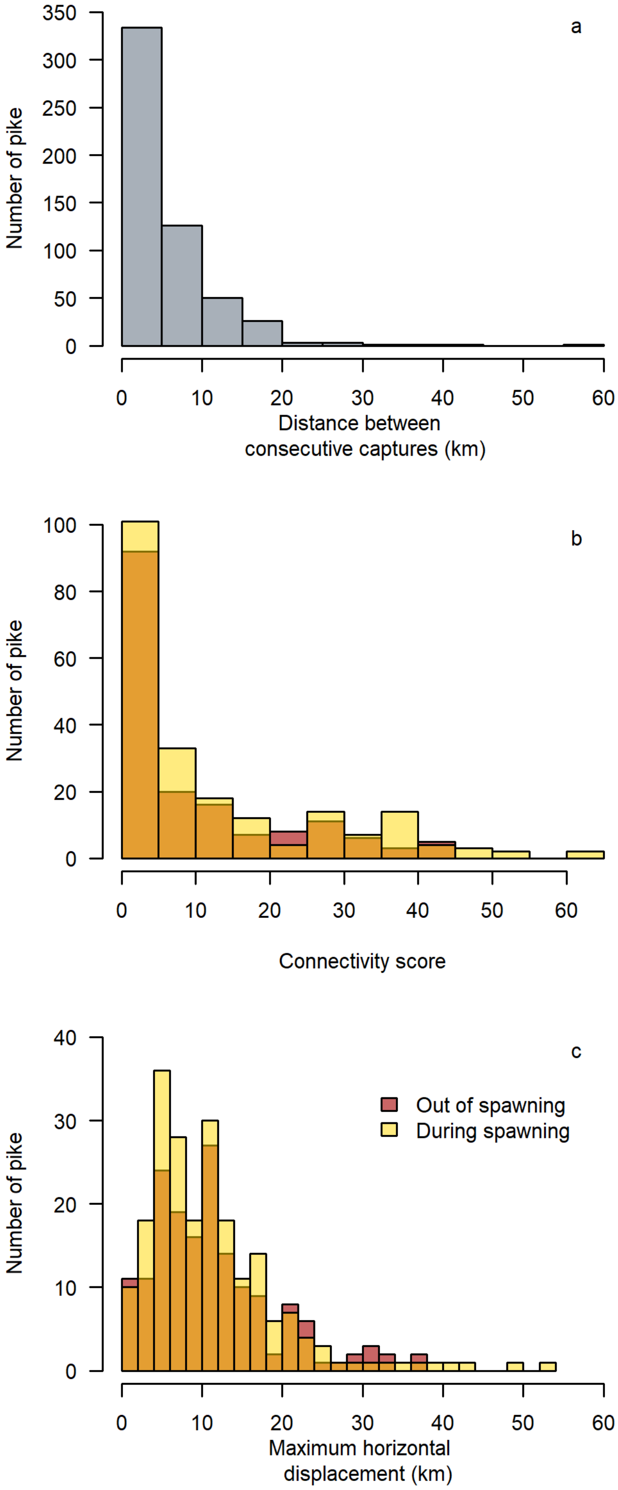


Figure 3. Frequency distribution of the response variables. (a) Distance between capture and recapture of individual pike. (b) Connectivity score during spawning season (February to May) and out of spawning. (c) Maximum horizontal displacement during spawning season and out of spawning.

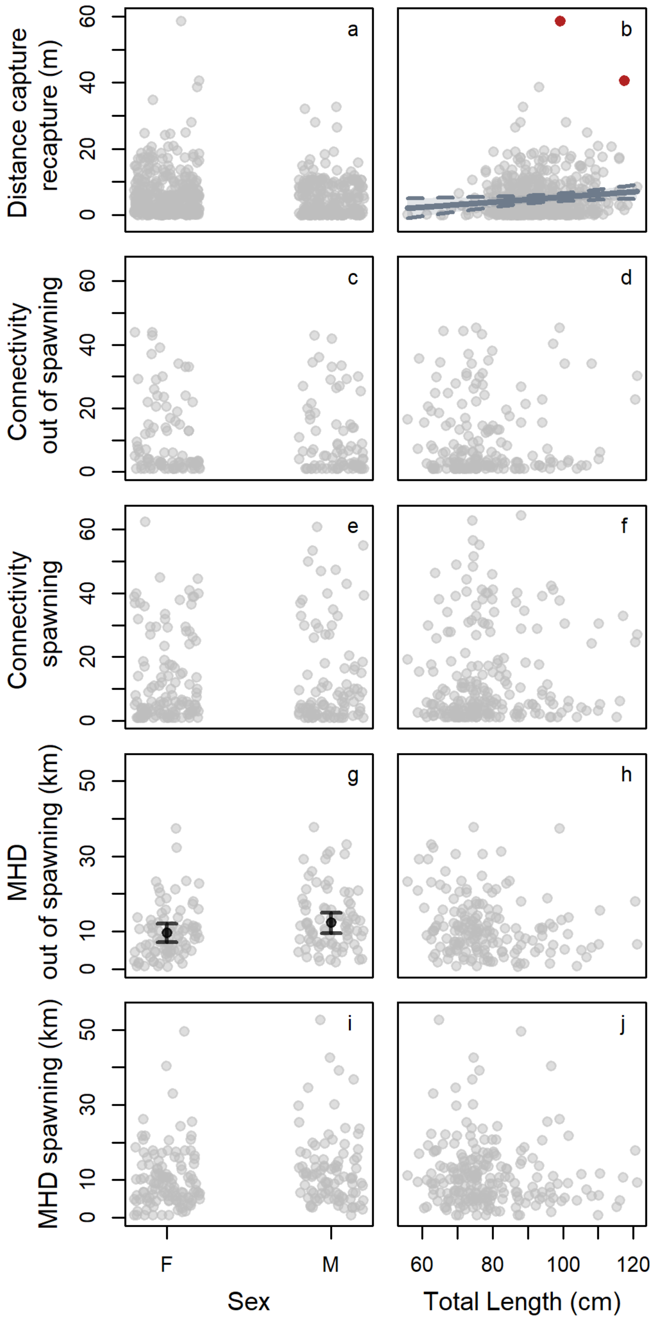
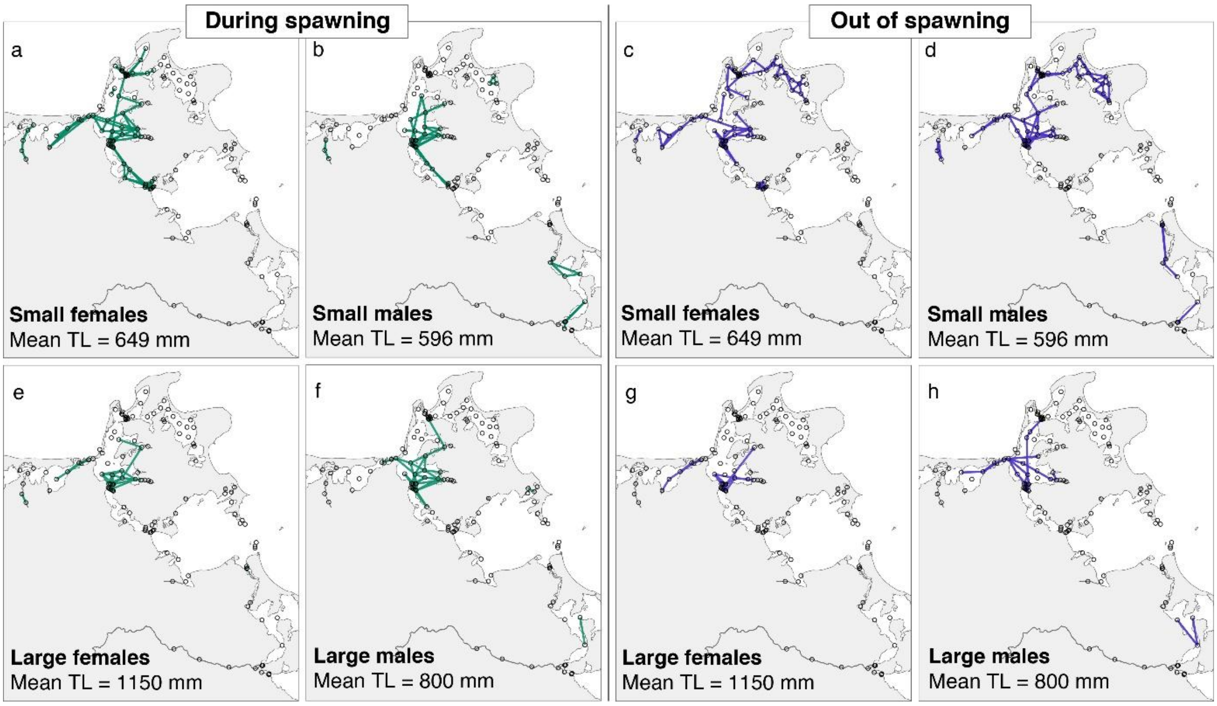


Figure 4. Scatter plot of the raw data for our response variables as a function of sex and total length. Significant slopes and intercepts in the models are displayed on the corresponding plots. (b) Larger fish have higher distances between captures and recaptures than smaller fish, regardless of sex effects. This result, however, seems driven by the two most mobile individuals (in red). (g) Males have higher Maximum Horizontal Displacement than females outside of spawning time. In all other cases (a, c, d, e, f, h, i, j), no relationship between the response and the explanatory variable was detected.



<u>Figure 5. Combined movement networks based on telemetry data.</u> (a) The 10 smallest females, (b) the 10 smallest males, (e) the 10 largest females, and (f) the 10 largest males during the spawning season (February to May). And (c) the 10 smallest females, (d) the 10 smallest males, (g) the 10 largest females, and (h) the 10 largest males outside of the spawning season (June to January).

Discussion

In our study of coastal northern pike in the Baltic Sea, we found ambiguous evidence that larger individuals move larger distances than smaller ones. Mark-recapture data initially indicated higher distances between captures and recaptures for larger individuals across the entire year, but this effect was driven by the presence of two very mobile pike in the sample and thus overall was weak. Importantly, larger fish of either sex monitored via acoustic telemetry did not exhibit higher connectivity or movement ranges during and outside the spawning season. As telemetry data show unconstrained movements independent of a possible location bias of the mark-recapture reports, we conclude that larger pike in the studied population do not serve as key connectors among spawning areas. This finding does not agree with a similar telemetry-based study by Olsen et al. (2023), which demonstrated that larger female and male Atlantic cod were more important connectors among spawning sites compared to smaller individuals.

Besides the potential for “outliers” to be driving significant relationships, the discrepancy between the results obtained using the mark-recapture data and the telemetry data can be due to methodological biases. Compared to the telemetry data, the mark-recapture data lacks two important characteristics: an unbiased sampling of sizes and locations and a near-continuous sampling of movements. Importantly, the mark-recapture database, which relied on voluntary contributions from fishers and anglers in reporting recaptured fish, is more likely to suffer from size and location biases. A very large fraction of the marked pike were tagged through cooperating guides and fishers in preferred fishing grounds, which then likely motivated preferential recapture in the same sites. This, in turn, could have resulted in the mark-recapture data likely representing mainly localized movements. Besides, the fishers and guides were more likely to report larger animals (t_{417} = 9.72, $p < 0.0001$, average size captured by the researchers = 736, average size reported in the online mark-recapture database = 804), and reporting rates of the participating guides, anglers and fishers varied depending on their engagement with the project (Radinger & Arlinghaus, 2023). Further, where telemetry continuously monitors the pike’s location, the mark-recapture database is dependent on fishers, guides and anglers being at the right place at the right time to capture animals. As a result, time between consecutive captures varied between 48 days and 988 days (mean = 249 days). Additionally, around 40% of the captures reported on the web-based database were made using fyke nets and gillnets and 60% while recreational angling, which are known to target particularly mobile fish and be less efficient on passive individuals (Carlson *et al.*, 2007; Edeline *et al.*, 2007; Monk *et al.*, 2021). Taken together, these methodological limitations tend to reduce the reliability of mark-recapture data for testing our hypothesis, whereas telemetry data, with its continuous and unbiased sampling, provides a more robust foundation for analysis. There was no evidence for larger pike being stronger habitat connectors in the telemetry data set.

Our results collectively suggest that larger pike are unlikely to be key connectors among spawning (in the spawning time) or foraging areas (outside spawning time), contrary to what was found in the Atlantic cod in Norwegian fjords (Olsen *et al.*, 2023). The disagreement between the two studies may stem from differences in reproductive biology and behaviour in Atlantic cod and coastal northern pike. Atlantic cod exhibit a lek-based reproductive system with pelagic eggs (Nordeide & Folstad, 2000), where females arrive at spawning territories previously established by larger, dominant males (Brawn, 1961; Dean *et al.*, 2014). Cod are determinate batch spawners, typically engaging in size-dependent batch spawning over multiple weeks to months across several sites (Kjesbu, 1989; Roney *et al.*, 2018). Cod also show strong patterns of spawning site fidelity, as they are presumed to return to high-quality sites year after year (Skjæraasen *et al.*, 2011). In contrast, while spawning and natal site fidelity have also been reported for northern pike (Miller *et al.*, 2001; Tibblin *et al.*, 2015), this species is characterised as total spawners, with females, often surrounded by multiple males who arrive earlier to spawning sites, releasing small batches of adhesive eggs onto underwater vegetation typically within a single day over several hours (Billard, 1996; Fabricius & Gustafson, 1958; Lindroth, 1946; Svardson, 1949). In rare exceptions, individual females release eggs over up to three days, but not involving long-range changes in spawning locations (Clark, 1950). There are reports that older and longer females predominate in the first days of the reproductive periods on spawning sites, and younger females seem to more frequent at the end of the spawning period (Sukhanova, 1979; Wright & Shoesmith, 1988). Male pike have more extended movements during spawning and occupy slightly larger territories than females, exhibiting intrasexual aggression in fights over access to females (Billard, 1996; Fabricius & Gustafson, 1958; Vostradovsky, 1983). In marine coastal areas, pike typically spawn in sheltered, vegetated bays, or in freshwater tributaries at traditional spawning grounds (Flink *et al.*, 2023; Roser *et al.*, 2023; Tibblin *et al.*, 2016). Because pike eggs and larvae are adhesive to underwater vegetation, recruitment is localized (Billard, 1996) as there is no long-range movements of pelagic eggs, unlike in cod. The lek mating characteristic of Atlantic cod, combined with strong intrasexual selection (particularly among males), pelagic eggs, spatial bet-hedging (i.e., releasing eggs by large fish in different spawning sites, Olsen et al., 2023), and highly biased reproductive success in the wild (Hutchings et al., 1999; Roney et al., 2018; Rowe et al., 2008) may render the species more prone to show size-dependency in long-range movements so that the larger, more fecund or competitively superior female cod have an advantage in migrating to optimal spawning sites and can use multiple locations as a bet-hedging strategy to distribute egg production across space and time. This is facilitated by their ability to release pelagic eggs over multiple days or even weeks (Kjesbu, 1989; Roney *et al.*, 2018), allowing them to adapt to temporal environmental variability (Rogers *et al.*, 2017). Such spatial bed-hedging has not been observed in pike, possibly reducing any fitness benefit of long-range movements across multiple spawning sites.

Figure 6. A ca. 95cm pike captured in a ditch during our sampling effort (Photo: P. Roser).

In the study area, pike have evolved four ecotypes: brackish residents, a cross-habitat ecotype favouring low-salinity areas, an anadromous ecotype that forages in brackish water but migrates into streams to spawn and freshwater residents that live and spawn in tributaries to the lagoons (Rittweg *et al.*, 2024; Roser *et al.*, 2023). The evolution of ecotype diversity may represent a pike's own bet-hedging strategy, but one that does not rely on large pike acting as spawning site connectors and instead relies on population differentiation into ecotypes with different migratory tendencies. That said, depending on local conditions, while migrations are adaptive for the anadromous ecotype, large body size may be disadvantageous in small, shallow streams, potentially leading to selection against large body size in this ecotype (Figure 6). Previous studies have indeed failed to record very large and old anadromous individuals migrating into shallow streams draining into the lagoons (Rittweg *et al.*, 2024; Roser *et al.*, 2023). Furthermore, the lack of size-dependent relationships in the long-range migration distance and connectivity in the coastal pike revealed by telemetry and the only weakly, at best, positive relationships of body length and recapture in mark-recapture data suggest that these ecotypes increase activity and space use during spawning time, but do so primarily through localized movements within specific lagoons (Lukyanova *et al.*, 2024). This aligns with previous findings in the study area, which also reported no strong relationship between space use and body length (Dhellemmes *et al.*, 2023a), contrasting with other studies in pike (e.g., Rosten *et al.*, 2016). However, size-dependent space use in pike has not been consistently reported in freshwater systems (e.g., Jepsen *et al.*, 2001; Kobler *et al.*, 2008; Koed *et al.*, 2006a). While the lack of size-dependency in empirical data in past research could be related to low contrast in the size range or limitations in the studied ecosystem dimension (e.g., small lake), these factors are unlikely to apply in our research, given the large size range (50– 126 cm) of our tagged pike and extensive study area (ca. 1,200 km²).

We speculate that the lack of size-dependency both in overall space use (Dhellemmes *et al.*, 2023a) and spawning site connectivity (this study) in the coastal pike population of Rügen, Germany, is related to the specific reproductive biology of pike. In addition, the result may in part stem from 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 (Arlinghaus *et al.*, 2023a; van Gemert *et al.*, 2022), 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.*, 2023a), 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, 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 spawning-related movements to be revealed in current time.

Male pike were found to display higher displacement 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 and disagreeing with Koed *et al.*, (2006) in a river population. The difference between the sexes, did not apply, however, to the spawning season, suggesting that both males and females travel similar long-range distances to reach their spawning grounds. Earlier work had revealed that males appear more active during the spawning season than females (Lucas, 1992), but this study only looked at localized movements and not long-range movements. The observation that males may use more space than females is in agreement with studies conducted in our study area, but also in freshwater (Dhellemmes *et al.*, 2023a; Jepsen *et al.*, 2001). Such differences between the sexes may be due to the cost of gamete production being lower for males than 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 prey items or foraging strategies, or due to sex dimorphism in size, which could mean that smaller males are under greater risk of cannibalistic or other types of predation, motivating displacements through movement (Haugen *et al.*, 2006, 2007; Li & Kokko, 2021).

Several limitations should be noted for our work. First, we inferred the connectivity among spawning sites by analysing movement metrics during the key spawning period known for pike, without observing exactly where 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, we cannot rule out the possibility of missing fine-scale behaviours during spawning site selection, and size-dependent micro-level site selection may still occur on local scales, as perhaps indicated by the mark-recapture data. The telemetry system we used was not designed to detect fine-scale movement resolution, which is why we cannot conclusively answer this question. Future studies focusing on specific lagoons will be necessary to determine whether pike of different lengths choose particular spawning sites and connect them through localized movements within specific lagoons.

To conclude, we found no strong evidence that larger pike serve as key connectors of different spawning and foraging sites. The lack of size-dependent connectivity suggests that spatial bet-hedging may not confer fitness advantages for pike, likely due to their specific reproductive biology as total spawner that releases adhesive gametes typically within a day once a year. In addition, we speculate that historical harvest pressure may have evolutionarily favoured reduced movement rates during spawning that are independent of body length in pike. Our findings do not diminish the importance of conserving large fish given their social value (e.g., high angler preference for catching large fish; Koemle *et al.*, 2022) and fecundity-related benefits. As we did not find evidence that exceptionally large pike are important connectors among spawning sites, the findings by Olsen *et al.* (2023) do not generally apply across other coastal fish species that vary in reproductive biology from cod.

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

The data are available in the European Tracking Network repository: Dhellemmes F, Arlinghaus R (2021) Boddenhecht telemetry dataset. https://marineinfo.org/id/dataset/7859

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References

Ahrens, R. N. M., Allen, M. S., Walters, C., & Arlinghaus, R. (2020). Saving large fish through harvest slots outperforms the classical minimum-length limit when the aim is to achieve multiple harvest and catch-related fisheries objectives. *Fish and Fisheries*, *21*, 483–510.

Ahti, P. A., Kuparinen, A., & Uusi-Heikkilä, S. (2020). Size does matter — the eco-evolutionary effects of changing body size in fish. *Environmental Reviews*, *28*, 311–324.

Alexander, R. M. (2003). *Principles of Animal Locomotion*, STU-Student edition. Princeton University Press.

Andersen, K. H., Jacobsen, N. S., & van Denderen, P. D. (2019). Limited impact of big fish mothers for population replenishment. *Canadian Journal of Fisheries and Aquatic Sciences*, *76*, 347–349.

Anderson, C. N. K., Hsieh, C., Sandin, S. A., Hewitt, R., Hollowed, A., Beddington, J., … Sugihara, G. (2008). Why fishing magnifies fluctuations in fish abundance. *Nature*, *452*, 835–839.

Arlinghaus, R., Beardmore, B., Riepe, C., Meyerhoff, J., & Pagel, T. (2014). Species-specific preferences of German recreational anglers for freshwater fishing experiences, with emphasis on the intrinsic utilities of fish stocking and wild fishes. *Journal of Fish Biology*, *85*, 1843–1867.

Arlinghaus, R., Alós, J., Beardmore, B., Díaz, Á. M., Hühn, D., Johnston, F., … Riepe, C. (2018). Recreational piking – sustainably managing pike in recreational fisheries. *Biology and Ecology of Pike* (pp. 288–336). CRC Press.

Arlinghaus, R., Cooke, S. J., Lyman, J., Policansky, D., Schwab, A., Suski, C., … Thorstad, E. B. (2007). Understanding the complexity of catch-and-release in recreational fishing: an integrative synthesis of global knowledge from historical, ethical, social, and biological perspectives. *Reviews in Fisheries Science*, *15*, 75–167.

Arlinghaus, R., Rittweg, T., Dhellemmes, F., Koemle, D., van Gemert, R., Schubert, H., … Winkler, H. (2023a). A synthesis of a coastal northern pike (*Esox lucius*) fishery and its social-ecological environment in the southern Baltic Sea: Implications for the management of mixed commercial-recreational fisheries. *Fisheries Research*, *263*, 106663.

Arlinghaus, R., Braun, M., Dhellemmes, F., Ehrlich, E., Feldhege, F., Koemle, D., … Winkler, H. (2023b). *BODDENHECHT: Ökologie, Nutzung und Schutz von Hechten in den Küstengewässern Mecklenburg-Vorpommerns*. Berichte des IGB. Vol. 33.

Barneche, D. R., Robertson, D. R., White, C. R., & Marshall, D. J. (2018). Fish reproductive-energy output increases disproportionately with body size. *Science*, *360*, 642–645.

Beardmore, B., Hunt, L. M., Haider, W., Dorow, M., & Arlinghaus, R. (2015). Effectively managing angler satisfaction in recreational fisheries requires understanding the fish species and the anglers. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*, 500–513.

Berkeley, S. A., Chapman, C., & Sogard, S. M. (2004). Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology*, *85*, 1258–1264.

Bernatchez, L., & Dodson, J. J. (1987). Relationship between Bioenergetics and Behavior in Anadromous Fish Migrations. *Canadian Journal of Fisheries and Aquatic Sciences*, *44*, 399–407.

Billard, R. (1996). Reproduction of pike: gametogenesis, gamete biology and early development. In J. F. Craig (Ed.), *Pike: Biology and Exploitation* (pp. 13–43). London: Chapman & Hall.

Birdsong, M., Hunt, L. M., Beardmore, B., Dorow, M., Pagel, T., & Arlinghaus, R. (2022). Does the relevance of catch for angler satisfaction vary with social-ecological context? A study involving angler cultures from West and East Germany. *Fisheries Research*, *254*, 106414.

Birkeland, C., & Dayton, P. (2005). The importance in fishery management of leaving the big ones. *Trends in Ecology & Evolution*, *20*, 356–358.

Brawn, V. M. (1961). Reproductive Behaviour of the Cod (*Gadus callarias* L.). *Behaviour*, *18*, 177–198.

Bürkner, P.-C. (2017). brms : An R Package for Bayesian Multilevel Models Using Stan. *Journal of Statistical Software*, *80*.

Burns, M. D., & Bloom, D. D. (2020). Migratory lineages rapidly evolve larger body sizes than non-migratory relatives in ray-finned fishes. *Proceedings of the Royal Society B: Biological Sciences*, *287*, 20192615.

Carlson, S. M., Edeline, E., Asbjørn Vøllestad, L., Haugen, Thrond. O., Winfield, I. J., Fletcher, J. M., … Stenseth, N. Chr. (2007). Four decades of opposing natural and human-induced artificial selection acting on Windermere pike (*Esox lucius*). *Ecology Letters*, *10*, 512–521.

Casselman, J. (1974). External Sex Determination of Northern Pike, *Esox lucius* Linnaeus. *Transactions of The American Fisheries Society*, *103*, 343–347.

Clark, C. F. (1950). Observations on the Spawning Habits of the Northern Pike, *Esox lucius*, in Northwestern Ohio. *Copeia*, *1950*, 285.

Cook, M. F., & Bergersen, E. P. (1988). Movements, habitat selection, and activity periods of northern pike in Eleven Mile Reservoir, Colorado. *Transactions of the American Fisheries Society*, *117*, 495–502.

Craig, J. F. (Ed.). (1996). *Pike: Biology and exploitation*, First Edition. Fish & Fisheries Series. London: Chapman & Hall.

Crossin, G. T., Hinch, S. G., Farrell, A. P., Higgs, D. A., Lotto, A. G., Oakes, J. D., & Healey, M. C. (2004). Energetics and morphology of sockeye salmon: effects of upriver migratory distance and elevation. *Journal of Fish Biology*, *65*, 788–810.

Csàrdi, G., Nepusz, T., Traag, V., Horvat, S., Zanini, F., Noom, D., & Muller, K. (2025). *igraph: Network analysis and visualization in R*.

Csàrdi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal*, *Complex Systems*, 1695.

Dean, M. J., Hoffman, W. S., Zemeckis, D. R., & Armstrong, M. P. (2014). Fine-scale diel and gender-based patterns in behaviour of Atlantic cod (*Gadus morhua*) on a spawning ground in the Western Gulf of Maine. *ICES Journal of Marine Science*, *71*, 1474–1489.

Dhellemmes, F., Aspillaga, E., Rittweg, T., Alós, J., Möller, P., & Arlinghaus, R. (2023a). Body size scaling of space use in coastal pike (*Esox lucius*) in brackish lagoons of the southern Baltic Sea. *Fisheries Research*, *260*, 106560.

Dhellemmes, F., Aspillaga, E., & Monk, C. T. (2023b). ATfiltR: A solution for managing and filtering detections from passive acoustic telemetry data. *MethodsX*, *10*, 102222.

Diana, J. S. (1980). Diel activity pattern and swimming speeds of northern pike (*Esox lucius*) in Lac Ste. Anne, Alberta. *Canadian Journal of Fisheries and Aquatic Sciences*, *37*, 1454–1458.

Edeline, E., Carlson, S. M., Stige, L. C., Winfield, I. J., Fletcher, J. M., James, J. B., … Stenseth, N. C. (2007). Trait changes in a harvested population are driven by a dynamic tug-of-war between natural and harvest selection. *Proceedings of the National Academy of Sciences*, *104*, 15799–15804.

Etten, J. van. (2017). R package gdistance: distances and routes on geographical grids. *Journal of Statistical Software*, *76*, 21.

Fabricius, E., & Gustafson, K. (1958). *Some new observations on the spawning behaviour of the pike, Esox lucius L.* Reports of the Institute of Freshwater Research. 29. Drottningholm: Institute of Freshwater Research. pp. 57–99.

Flink, H., Tibblin, P., Hall, M., Hellström, G., & Nordahl, O. (2023). Variation among bays in spatiotemporal aggregation of Baltic Sea pike highlights management complexity. *Fisheries Research*, *259*, 106579.

Froese, R. (2004). Keep it simple: three indicators to deal with overfishing. *Fish and Fisheries*, *5*, 86–91.

van Gemert, R., Koemle, D., Winkler, H., & Arlinghaus, R. (2022). Data-poor stock assessment of fish stocks co-exploited by commercial and recreational fisheries: Applications to pike Esox lucius in the western Baltic Sea. *Fisheries Management and Ecology*, *29*, 16–28.

Glebe, B. D., & Leggett, W. C. (1981). Latitudinal differences in energy allocation and use during the freshwater migrations of American shad (*Alosa sapidissima*) and their life history consequences. *Canadian Journal of Fisheries and Aquatic Sciences*, *38*, 806–820.

Green, B. S. (2008). Maternal effects in fish populations. *Advances in Marine Biology* (pp. 1–105). Elsevier.

Griffiths, C. A., Winker, H., Bartolino, V., Wennhage, H., Orio, A., & Cardinale, M. (2024). Including older fish in fisheries management: A new age-based indicator and reference point for exploited fish stocks. *Fish and Fisheries*, *25*, 18–37.

Gwinn, D. C., Allen, M. S., Johnston, F. D., Brown, P., Todd, C. R., & Arlinghaus, R. (2015). Rethinking length-based fisheries regulations: the value of protecting old and large fish with harvest slots. *Fish and Fisheries*, *16*, 259–281.

Haugen, T. O., Winfield, I. J., Vøllestad, L. A., Fletcher, J. M., James, J. B., & Stenseth, N. C. (2006). The ideal free pike: 50 Years of fitness-maximizing dispersal in Windermere. *Proceedings of the Royal Society B: Biological Sciences*, *273*, 2917–2924.

Haugen, T. O., Winfield, I. J., Vøllestad, L. A., Fletcher, J. M., James, J. B., & Stenseth, N. C. (2007). Density dependence and density independence in the demography and dispersal of pike over four decades. *Ecological Monographs*, *77*, 483–502.

Hess, J. E., Caudill, C. C., Keefer, M. L., McIlraith, B. J., Moser, M. L., & Narum, S. R. (2014). Genes predict long distance migration and large body size in a migratory fish, Pacific lamprey. *Evolutionary Applications*, *7*, 1192–1208.

Hixon, M. A., Johnson, D. W., & Sogard, S. M. (2014). BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. *ICES Journal of Marine Science*, *71*, 2171–2185.

Hsieh, C., Yamauchi, A., Nakazawa, T., & Wang, W.-F. (2010). Fishing effects on age and spatial structures undermine population stability of fishes. *Aquatic Sciences*, *72*, 165–178.

Jacobsen, L., & Engström-Öst, J. (2018). Coping with environments: vegetation, turbidity and abiotics. In C. Skov & P. A. Nilsson (Eds.), *Biology and Ecology of Pike* (pp. 32–61). Boca Raton, FL: CRC Press.

Jacobsen, L., Bekkevold, D., Berg, S., Jepsen, N., Koed, A., Aarestrup, K., … Skov, C. (2017). Pike (*Esox lucius* L.) on the edge: consistent individual movement patterns in transitional waters of the western Baltic. *Hydrobiologia*, *784*, 143–154.

Jepsen, N., Beck, S., Skov, C., & Koed, A. (2001). Behavior of pike (*Esox lucius* L.) >50 cm in a turbid reservoir and in a clearwater lake. *Ecology of Freshwater Fish*, *10*, 26–34.

Jepsen, N., Schreck, C., Clements, S., & Thorstad, E. (2005). A brief discussion on the 2% tag/bodymass rule of thumb. In M. T. Spedicato, G. Lembo, & G. Marmulla (Eds.), *Aquatic telemetry: advances and applications. Proceedings of the Fifth Conference on Fish Telemetry held in Europe. Ustica, Italy, 9-13 June 2003* (pp. 255–259). Rome: FAO/COISPA.

Jonsson, N., Jonsson, B., & Hansen, L. P. (1997). Changes in proximate composition and estimates of energetic costs during upstream migration and spawning in Atlantic Salmon *Salmo salar*. *The Journal of Animal Ecology*, *66*, 425.

Jonsson, N., Hansen, L. P., & Jonsson, B. (1991). Variation in age, size and repeat spawning of adult Atlantic Salmon in relation to river discharge. *The Journal of Animal Ecology*, *60*, 937.

Karås, P., & Lehtonen, H. (1993). Patterns of movement and migration of pike (*Esox lucius* L.) in the Baltic Sea. *Nordic journal of freshwater research*, *68*.

Kjesbu, O. S. (1989). The spawning activity of cod, *Gadus morhua* L. *Journal of Fish Biology*, *34*, 195–206.

Kobler, A., Klefoth, T., & Arlinghaus, R. (2008). Site fidelity and seasonal changes in activity centre size of female pike *Esox lucius* in a small lake. *Journal of Fish Biology*, *73*, 584–596.

Koed, A., Balleby, K., Mejlhede, P., & Aarestrup, K. (2006). Annual movement of adult pike (*Esox lucius* L.) in a lowland river. *Ecology of Freshwater Fish*, *15*, 191–199.

Koemle, D., Meyerhoff, J., & Arlinghaus, R. (2022). How catch uncertainty and harvest regulations drive anglers' choice for pike (*Esox lucius*) fishing in the Baltic Sea. *Fisheries Research*, *256*, 106480.

Kopf, R. K., Banks, S., Brent, L. J. N., Humphries, P., Jolly, C. J., Lee, P. C., … Winemiller, K. O. (2024). Loss of Earth's old, wise, and large animals. *Science*, *387*, eado2705.

L'Abée-Lund, J. H. (1991). Variation within and between rivers in adult size and sea age at maturity of anadromous Brown Trout, *Salmo trutta*. *Canadian Journal of Fisheries and Aquatic Sciences*, *48*, 1015–1021.

Li, X., & Kokko, H. (2021). Sexual dimorphism driven by intersexual resource competition: Why is it rare, and where to look for it? *Journal of Animal Ecology*, *90*, 1831–1843.

Lindroth, A. (1946). *Zur Biologie der Befruchtung und Entwicklung beim Hecht*. Mitteilungen der Anstalt Binnenfischerei bei Drottningholm. 24. Stockholm. p. 173.

Lorenzen, K. (2022). Size- and age-dependent natural mortality in fish populations: Biology, models, implications, and a generalized length-inverse mortality paradigm. *Fisheries Research*, *255*, 106454.

Lucas, M. C. (1992). Spawning activity of male and female pike, *Esox lucius* L., determined by acoustic tracking. *Canadian Journal of Zoology*, *70*, 191–196.

Lukyanova, O., Dhellemmes, F., Dennenmoser, S., Nolte, A. W., & Arlinghaus, R. (2024). Combining biotelemetry and genetics provides complementary insights relevant to the management and conservation of a freshwater predator (*Esox lucius*) living in brackish lagoons. *Aquatic Sciences*, *86*, 77.

Magnusson, M., Andersen, M., Jonasson, J., & Vehtari, A. (2019). Bayesian leave-one-out cross-validation for large data. In K. Chaudhuri & R. Salakhutdinov (Eds.), *Proceedings of the 36th International Conference on Machine Learning* (pp. 4244–4253). PMLRProceedings of Machine Learning Research.

Marshall, D., Allen, R., & Crean, A. (2008). The ecological and evolutionary importance of maternal effects in the sea. In R. Gibson, R. Atkinson, & J. Gordon (Eds.), *Oceanography and Marine Biology* (pp. 203–262). CRC PressOceanography and Marine Biology - An Annual Review.

Marshall, D. J., Bode, M., Mangel, M., Arlinghaus, R., & Dick, E. J. (2021). Reproductive hyperallometry and managing the world’s fisheries. *Proceedings of the National Academy of Sciences*, *118*, e2100695118.

Marshall, D. J., Heppell, S. S., Munch, S. B., & Warner, R. R. (2010). The relationship between maternal phenotype and offspring quality: Do older mothers really produce the best offspring? *Ecology*, *91*, 2862–2873.

Matsumura, S., Arlinghaus, R., & Dieckmann, U. (2011). Assessing evolutionary consequences of size-selective recreational fishing on multiple life-history traits, with an application to northern pike (*Esox lucius*). *Evolutionary Ecology*, *25*, 711–735.

Miller, L. M., Kallemeyn, L., & Senanan, W. (2001). Spawning-site and natal-site fidelity by Northern Pike in a large lake: mark–recapture and genetic evidence. *Transactions of the American Fisheries Society*, *130*, 307–316.

Minns, C. K. (1995). Allometry of home range size in lake and river fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, *52*, 1499–1508.

Monk, C. (2019). Mining the behavioural reality of fish-fisher interactions to understand vulnerability to hook-and-line fishing. Humboldt-Universität zu Berlin. https://edoc.hu-berlin.de/handle/18452/20565.

Monk, C. T., Bekkevold, D., Klefoth, T., Pagel, T., Palmer, M., & Arlinghaus, R. (2021). The battle between harvest and natural selection creates small and shy fish. *Proceedings of the National Academy of Sciences*, *118*, e2009451118.

Müller, K. (1986). Seasonal anadromous migration of the pike (*Esox lucius* L.) in coastal areas of the northern Bothnian sea. *Archiv Fur Hydrobiologie*, *107*, 315–330.

Nordeide & Folstad. (2000). Is cod lekking or a promiscuous group spawner? *Fish and Fisheries*, *1*, 90–93.

Ohlberger, J., Staaks, G., & Hölker, F. (2006). Swimming efficiency and the influence of morphology on swimming costs in fishes. *Journal of Comparative Physiology B*, *176*, 17–25.

Olsen, E. M., Karlsen, Ø., & Skjæraasen, J. E. (2023). Large females connect Atlantic cod spawning sites. *Science*, *382*, 1181–1184.

Pagel, T. (2009). Determinants of individual reproductive success in a natural pike (*Esox lucius* L.) population: a DNA-based parentage assignment approach (Master Thesis). Humboldt-Universität zu Berlin, Lebenswissenschaftliche Fakultät, Leibniz-Institut für Gewässerökologie und Binnenfischerei (IGB) Berlin.

R Core Team. (2021). R: A language and environment for statistical computing, 2021.

Raat, A. J. P. (1988). Synopsis of biological data on the northern pike (*Esox lucius* Linnaeus, 1758). *FAO Fisheries Synopsis 30* (p. 177).

Radinger, J., & Arlinghaus, R. (2023). Fischereiliche Sterblichkeit abgeschätzt aus Fang-MarkierungWiederfang-Daten. *BODDENHECHT: Ökologie, Nutzung und Schutz von Hechten in den Küstengewässern Mecklenburg-Vorpommerns* (pp. 508–528).

Reebs, S. (2001). Influence of body size on leadership in shoals of Golden Shiners, *Notemigonus crysoleucas*. *Behaviour*, *138*, 797–809.

Rittweg, T. D., Trueman, C., Wiedenbeck, M., Fietzke, J., Wolter, C., Talluto, L., … Arlinghaus, R. (2024). Variable habitat use supports fine-scale population differentiation of a freshwater piscivore (northern pike, *Esox lucius*) along salinity gradients in brackish lagoons. *Oecologia*, *206*, 275–292.

Rogers, L. A., Storvik, G. O., Knutsen, H., Olsen, E. M., & Stenseth, N. C. (2017). Fine-scale population dynamics in a marine fish species inferred from dynamic state-space models. *Journal of Animal Ecology*, *86*, 888–898.

Roney, N. E., Oomen, R. A., Knutsen, H., Olsen, E. M., & Hutchings, J. A. (2018). Temporal variability in offspring quality and individual reproductive output in a broadcast-spawning marine fish. *ICES Journal of Marine Science*, *75*, 1353–1361.

Roos, A. M. de, & Persson, L. (2013). *Population and community ecology of ontogenetic development*. Monographs in population biology. Princeton (N. J.): Princeton university press.

Rose, G. A. (1993). Cod spawning on a migration highway in the north-west Atlantic. *Nature*, *366*, 458–461.

Roser, P., Dhellemmes, F., Rittweg, T., Möller, S., Winkler, H., Lukyanova, O., … Arlinghaus, R. (2023). Synthesizing historic and current evidence for anadromy in a northern pike (*Esox lucius* L.) meta-population inhabiting brackish lagoons of the southern Baltic Sea, with implications for management. *Fisheries Research*, *263*, 106670.

Rosten, C. M., Gozlan, R. E., & Lucas, M. C. (2016). Allometric scaling of intraspecific space use. *Biology Letters*, *12*, 20150673.

Skjæraasen, J. E., Meager, J. J., Karlsen, Ø., Hutchings, J. A., & Fernö, A. (2011). Extreme spawning-site fidelity in Atlantic cod. *ICES Journal of Marine Science*, *68*, 1472–1477.

Skov, C., & Nilsson, P. A. (2018). *Biology and Ecology of Pike*. C. Skov & P. A. Nilsson (Eds.). Boca Raton, FL : CRC Press, 2017. | “A Science Publishers book.”: CRC Press.

Slotte, A. (1999). Effects of fish length and condition on spawning migration in Norwegian spring spawning herring (*Clupea harengus* L.). *Sarsia*, *84*, 111–127.

Sukhanova, G. I. (1979). The spawning and fecundity of the pike *Esox lucius* in Vilyuy reservoir. *Journal of Ichthyology*, *19*, 74–79.

Sunde, J., Yıldırım, Y., Tibblin, P., Bekkevold, D., Skov, C., Nordahl, O., … Forsman, A. (2022). Drivers of neutral and adaptive differentiation in pike (*Esox lucius*) populations from contrasting environments. *Molecular Ecology*, *31*, 1093–1110.

Svardson, G. (1949). *Note on the spawning habits of Leuciscus erythrophthalmus L., Abramis brama L. and Esox lucius L.* Mitteilungen der Anstalt für Binnenfischerei in Drottningholm. 29. pp. 102–107.

Tamburello, N., Côté, I. M., & Dulvy, N. K. (2015). Energy and the scaling of animal space use. *The American Naturalist*, *186*, 196–211.

Tibblin, P., Forsman, A., Koch-Schmidt, P., Nordahl, O., Johannessen, P., Nilsson, J., & Larsson, P. (2015). Evolutionary divergence of adult body size and juvenile growth in sympatric subpopulations of a top predator in aquatic ecosystems. *American Naturalist*, *186*, 98–110.

Tibblin, P., Forsman, A., Borger, T., & Larsson, P. (2016). Causes and consequences of repeatability, flexibility and individual fine-tuning of migratory timing in pike. *Journal of Animal Ecology*, *85*, 136–145.

Uusi-Heikkilä, S. (2020). Implications of size-selective fisheries on sexual selection. *Evolutionary Applications*, *13*, 1487–1500.

Vehtari, A., Gelman, A., & Gabry, J. (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing*, *27*, 1413–1432.

Vostradovsky, J. (1983). Techniques et méthodes d’aménagement et d’élevage du brochet en Tchécoslovaquie. *Le Brochet: gestion dans le milieu naturel et élevage, INRA Publ., Paris*, 271–281.

Webster, M. M. (2017). Experience and motivation shape leader–follower interactions in fish shoals. *Behavioral Ecology*, *28*, 77–84.

Wright, R. M., & Shoesmith, E. A. (1988). The reproductive success of pike, *Esox lucius* : aspects of fecundity, egg density and survival. *Journal of Fish Biology*, *33*, 623–636.