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

Large individuals may serve as keystone connectors, a role recently demonstrated in Atlantic cod (*Gadus morhua*). To examine whether this pattern extends to other coastal fish species, we analysed capture-mark-recapture data for 666 individuals out of 4597 tagged coastal northern pike (*Esox lucius*) and acoustic tracking data from 318 individuals in the southern Baltic Sea, with total lengths of the individuals ranging 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, connectivity and movement ranges were correlated between years and repeatable, suggesting consistent inter-individual variation unrelated to body length. These findings suggest that large pike do not serve as keystone connectors, likely due to their reproductive biology as total spawners. In total spawners, spatial bet hedging might be realised through mechanisms other than the use of variable spawning sites by individuals within a season, including ecotype evolution of different spawning phenotypes and variable spawning times or locations across years.

Keywords

mark-recapture, acoustic telemetry, BOFFFF, site connectivity, spawning

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 – and the supposed relevance of large and old fish for population dynamics and stock recovery (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.*, 2014) may not manifest in the wild and may appear only in studies where environmental influences are controlled (Marshall *et al.*, 2010). Further, population-level fish recruitment is under strong density-dependent feedback in fishes, potentially diminishing the relevance of spawning stock composition and the importance of size-dependent effects for population dynamics and fisheries yield (Ahrens *et al.*, 2020; Cooper *et al.*, 2013). 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, or more generally, optimal size-selectivity in fisheries exploitation, 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 salmonid 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 typically 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 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).

Independent of the ongoing discussion about the conservation value of protecting large fish (most recently reviewed in Kopf *et al.*, 2024), the socio-economic 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, 2024; 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) in batch spawning cod 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 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 (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; Flink *et al.*, 2023; Jacobsen *et al.*, 2017; Karås & Lehtonen, 1993), forming a spatially structured meta-population across a network of brackish lagoons (Lukyanova *et al.*, 2024) and interconnected rivers (Nordahl *et al.*, 2019; Tibblin *et al.*, 2016). 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; Jacobsen *et al.*, 2017; 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). Most importantly, as the reproductive biology of northern pike as total spawner strongly differs from Atlantic cod as batch spawner, spawning site connectivity as a function of length might emerge more across years than within a spawning season.

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). Across generations, 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 1200 km² with an acoustic telemetry system, offering a suitable setting 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 across multiple years (for a review of the study area, 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 and especially between 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).

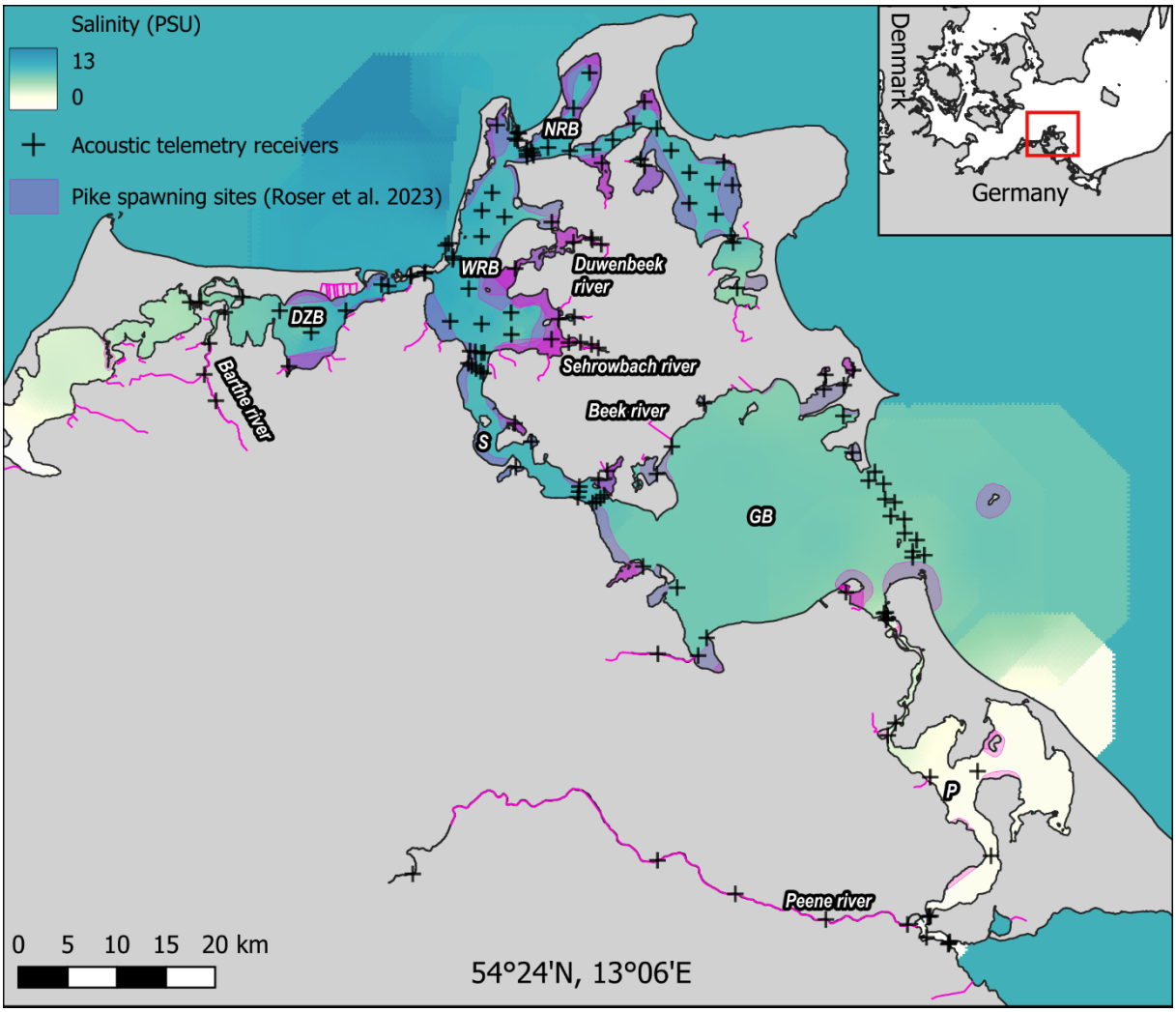

Figure 1. Map of the study area, including receiver locations, the average salinity gradient and the pike's spawning sites. Pike spawning site data are taken from Roser *et al.* (2023)*, where spawning sites are aggregated from different sources, which may agree on the location of a spawning site, leading 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.*, 2023b). 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.

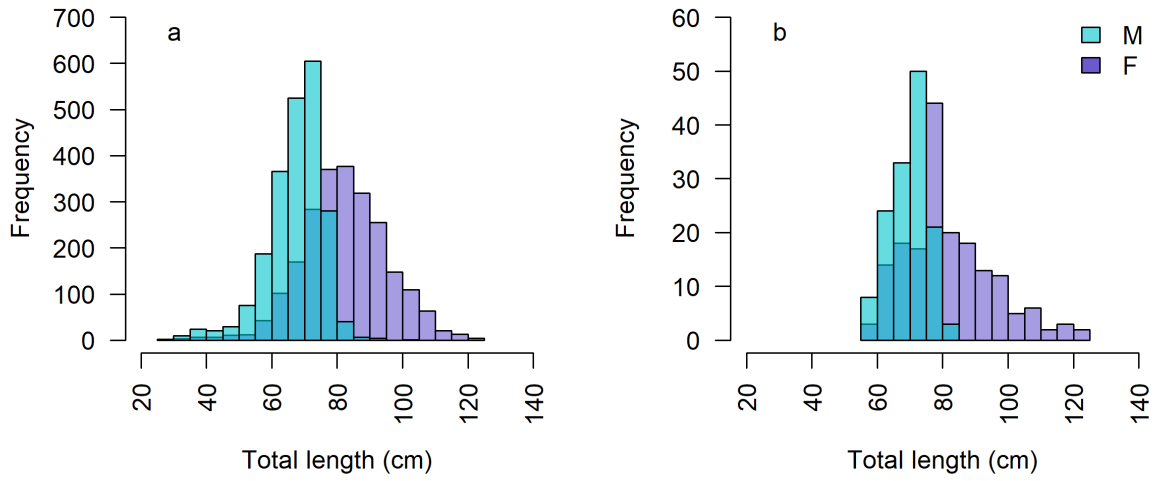

Figure 2. Frequency distribution of total length (mm) in our sample. a) All pike captured for the study and b) pike equipped with acoustic tags. Males (M) and females (F) are represented in blue and purple respectively.

Between February and December 2020, we selected 317 pike (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.*, 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 (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

265 independently of the capture and recapture dates, encompassing the entire study period. The
266 average time between capture and recapture was 250 days (± 229 days).

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

268 We used the telemetry data to calculate connectivity and maximum horizontal displacement (i.e.,
269 maximum in-water distance between all detections of an individual pike, MHD) for February, March,
270 April, and May to focus on the prime spawning season for pike. For comparison, we also calculated
271 connectivity and MHD for each pike outside of the spawning period. MHD was computed in water
272 using the same technique as described above for recapture distance. To assess connectivity, we
273 constructed movement networks as unipartite undirected networks in the *igraph* package (Csàrdi *et*
274 *al.*, 2025; Csàrdi & Nepusz, 2006), with nodes representing the acoustic receiver locations, and edges
275 reflecting subsequent detections of individuals moving between these locations. Following the
276 method in Olsen et al. (2023), each fish was assigned a connectivity score based on the number of
277 unique edges detected within the time window of interest.

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

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

287 ***Statistical analysis***

288 We primarily focused on the size-dependency of movement metrics and connectivity, with a positive
289 size-dependency supporting the assumption that the largest individuals act as key connectors
290 between spawning sites and lagoon areas. We conducted all our analyses in R version 4.3.1 (R Core

291 Team, 2021). We compared metrics within and outside of the spawning season using t-tests.
292 Distance between capture and recapture, MHD, and connectivity score (both for the spawning
293 season and the rest of the year) were each fitted as response variables, with sex and total length as
294 fixed effects in an interaction. For distance between capture and recapture, we added the time (in
295 days) between each capture as a fixed effect. The capture area of each pike was added as a random
296 effect to account for differences in receiver coverage and pike captures between the areas. We also
297 added individual ID as a random intercept to MHD and connectivity models to account for repeated
298 measures of the same individuals across years. Connectivity models were fitted using Poisson
299 distribution, while MHD and recapture distance models were fitted using Gaussian distribution.

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

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

309 All of our models were constructed in *brms* (Bürkner, 2017), using 4 chains of 120000 iterations each,
310 with a thinning interval of 100 and a burn-in of 20000. We used leave-one-out cross-validations
311 based on expected log pointwise predictive density (ELPD) based on the loo criterion in the *loo*
312 package (Magnusson *et al.*, 2019; Vehtari *et al.*, 2017) to test whether or not the interaction between
313 sex and total length should be left in the models. If the difference in ELPD between the models was
314 >4, we estimated their predictive performance to differ and used the model with the highest ELPD
315 for the analysis. If the difference in ELPD was <4, models were considered similar in their predictive
316 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 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 (Dhellemmes *et al.*, 2023a; Karås & Lehtonen, 1993). 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 behaviors in greater depth.

Results

Mark-recapture

Out of our 4597 tagged fish, 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 had an effect on the distance between captures (Table 2, Figure 4).

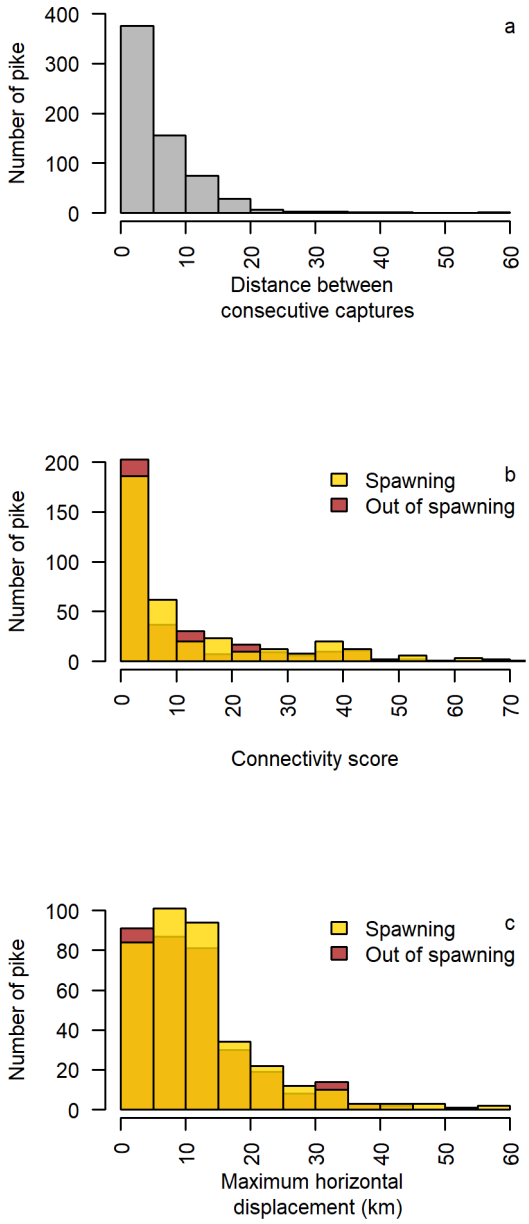

Figure 3. Frequency distribution of the response variables. (a) Distance between capture and recapture of individual pike. (b) Connectivity score during spawning season (February to May) and out of spawning. (c) Maximum horizontal displacement during spawning season and out of spawning.

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

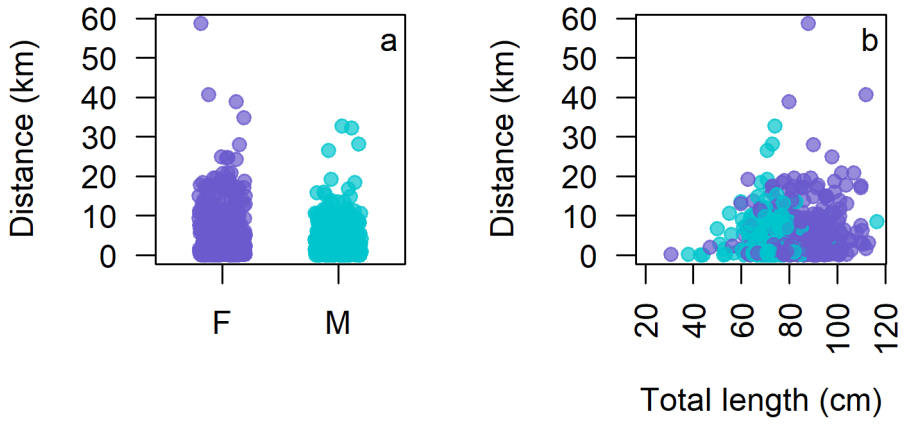

Figure 4. Distance between consecutive captures as a function of sex (a) and total length (b).

Connectivity and maximum horizontal displacement based on biotelemetry

Out of 318 tagged fish, 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, N = 128 individuals produced data in two distinct years, and 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 $r_{(143)}$ =

383 0.44, p <0.0001; out of spawning Pearson's $r_{(134)}$ = 0.43, p <0.0001; Figure 5, i, l) and was strongly

384 repeatable at the individual pike level (intra class correlation = 0.35 [0.2, 0.48], p < 0.0001; out of

385 spawning intra class correlation = 0.26 [0.1, 0.39], p < 0.001).

386 *Table 3. Model output for the connectivity and maximum horizontal displacement based on acoustic*

387 *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

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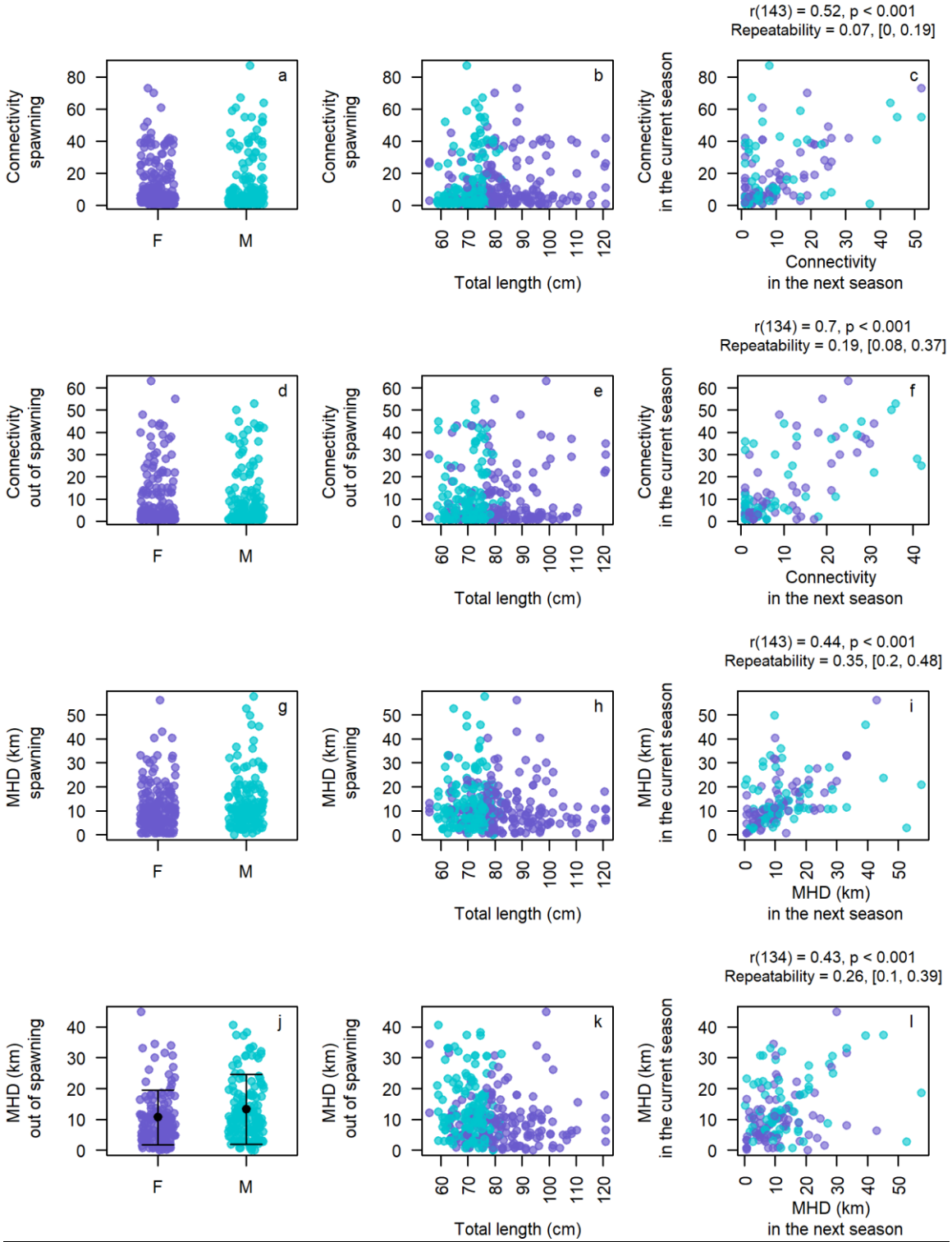


Figure 5. Scatter plot of the raw data for our response variables during the spawning period (February to May, panels a, b, c, g, h, i) and for the rest of the year (d, e, f, j, k, l) as a function of sex and total length and from one year as a function of the next. *Connectivity during spawning and 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.

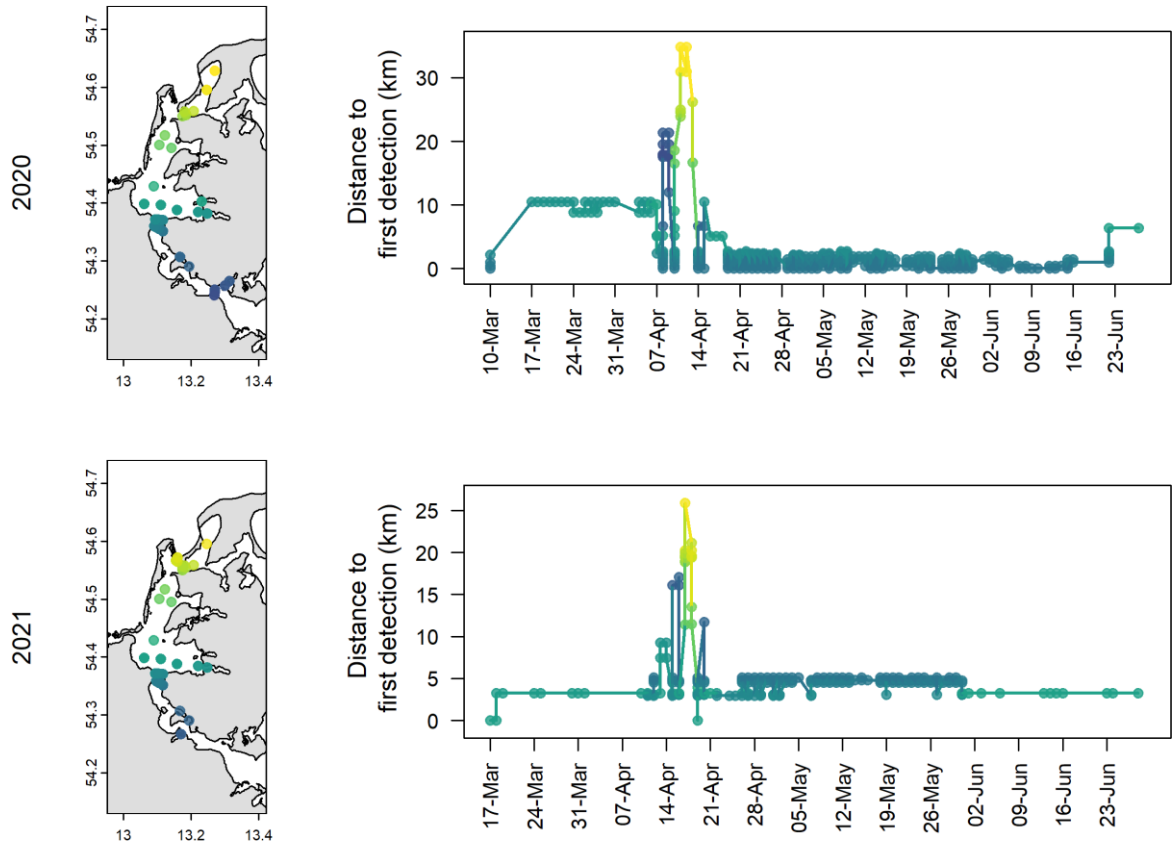
		Estimate	**Estimated error**	**Lower 95% Confidence interval**	**Upper 95% Confidence interval**
Site fidelity (area level)	*Intercept (taken as Sex:Female)*	-0.53	1.77	-3.96	3.05
	Sex:Male	0.07	0.49	-0.87	1.06
	Total Length	0.02	0.02	-0.02	0.06
Site fidelity (receiver level)	*Intercept*	1.27	2.28	-3.20	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 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 in across different years (for example see Figure 6).



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423 *Figure 6. Map of detections (left) and distance from the first detection for pike BH-90099, an 88 cm*

424 *female, in 2020 and 2021. In both years, the pike makes a brief visit to the south (blue receivers),*

425 *followed immediately by a visit to the north (yellow receivers). This movement pattern may indicate*

426 *visits to different spawning sites, although actual spawning behavior cannot be confirmed with our*

427 *technology. In 2020, the pike travelled both slightly farther south and farther north compared to*

428 *2021, suggesting possible use of different areas between years.*

429

Discussion

In disagreement with the study hypothesis, neither mark-recapture nor telemetry data indicated higher connectivity or broader movement ranges in larger coastal northern pike of either sex during and out of the spawning season, except for males exhibiting higher maximum horizontal displacements (MHD) out of spawning. Site fidelity and repeated area use among years were also independent of size and sex in all analyses. These findings suggest that larger individuals of the total spawner pike do not serve as key spawning site connectors, unlike in the batch spawning cod (Olsen *et al.*, 2023). However, at the individual level and unrelated to body length, we detected that both connectivity and spawning-season movement ranges were highly correlated between years and repeatable, as was connectivity outside the spawning season. This behavioral consistency suggests strong inter-individual variation in adult pike (i.e., the presence of behavioral types or personalities), aligning with prior research on pike in our study area (Dhellemmes *et al.*, 2023a) and in other study systems and life stages in pike (Kobler *et al.*, 2009; Laskowski *et al.*, 2016; McGhee *et al.*, 2013; Monk *et al.*, 2021; Pasquet *et al.*, 2016). Our additional visual assessment of the 93 most active pike (MHD > 10 km; 29% of all tagged fish) also pointed to the consistency in behaviours of these individuals, e.g., return to the same spawning area across the years. Some (13%) of these wide-roaming individuals visited multiple spawning sites within a single season, with no apparent sex- or size-based differences. Agreeing with our results, previous studies have found that behavioral consistency in pike was unrelated to body length (Nyqvist *et al.*, 2012).

Our results 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 is a batch spawner, which exhibits a lek-based reproductive system with pelagic eggs (Nordeide & Folstad, 2000) and 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 release of small egg batches 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 strong 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 weeks (Kjesbu, 1989; Roney *et al.*, 2018), allowing them to adapt to temporal environmental variability (Rogers *et al.*, 2017).

Such spatial bed-hedging within a spawning season by linking multiple spawning sites through movement is apparently not possible in the total spawning pike who mostly releases eggs within a single day, reducing any possibility to reap fitness benefit through long-range movements across multiple spawning sites. 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. However, we also found no evidence for such size-dependent behaviour in our study system, agreeing with previous reports that revealed a high degree of natal site fidelity and high consistency in both lentic and coastal pike across years (Miller *et al.*, 2001; Tibblin *et al.*, 2015, 2016). Therefore, we believe spatial bet hedging at the individual level is far less pronounced in total spawners such as coastal pike compared to batch spawners such as cod, and instead, other mechanisms of spatial bet hedging through individual variation, such as ecotype evolution of brackish residency over anadromy and development of a long spawning season lasting up to two months (Arlinghaus *et al.*, 2023a; Pagel *et al.*, 2015), may provide population resilience in total spawning fish species. That said, the exploratory visual inspection of pike's movement patterns of the most widely roaming individuals suggested that some individuals (13%), both females and males, may visit multiple spawning sites within a single season, with several fish (4%) doing so repeatedly across the years. This could indicate that a small fraction of pike might engage in some form of spatial bed-hedging within a season, where individuals travel substantial distances to visit different spawning sites (Figure 6), but importantly, this pattern was unrelated to body length. Using oviduct transmitters and other tagging technologies could help to gain more precise estimates of

spawning time and location for bony and cartilaginous fish (Gardner & Höök, 2024; Sulikowski & Hammerschlag, 2023), including pike (Pierce, 2004).

Figure 7. A ca. 95cm pike captured in a ditch during our sampling effort (Photo: P. Roser).

In the study area, coastal pike have evolved three reproductively isolated ecotypes that express four behavioural phenotypes: 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 spatial 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 7). 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 (Dhellemmes *et al.*, 2023a) suggests that these ecotypes increase activity and space use during spawning time, but do so primarily through

520 localised movements within specific lagoons (Lukyanova *et al.*, 2024). This aligns with previous
521 findings in the study area, which also reported no strong relationship between space use and body
522 length (Dhellemmes *et al.*, 2023a), contrasting with other studies in pike (e.g., Rosten *et al.*, 2016).
523 However, size-dependent space use in pike has not been consistently reported in freshwater systems
524 (e.g., Jepsen *et al.*, 2001; Kobler *et al.*, 2008; Koed *et al.*, 2006a). While the lack of size-dependency in
525 empirical data in past research could be related to low contrast in the size range or limitations in the
526 studied ecosystem dimension (e.g., small lake), these factors are unlikely to apply in our research,
527 given the large size range (50– 126 cm) of our tagged pike and extensive study area (ca. 1,200 km²).

528 We speculate that the lack of size-dependency both in overall space use (Dhellemmes *et al.*, 2023a)
529 and spawning site connectivity (this study) in the coastal pike population of Rügen, Germany, is
530 related to the specific reproductive biology of pike as total spawner as discussed above. In addition,
531 the result may in part stem from behaviour-selective harvesting and corresponding evolutionary
532 adaptations. Far-roaming larger phenotypes and their underlying genotypes may have been
533 systematically removed in decades of intensive harvesting in the study area (Arlinghaus *et al.*, 2023a;
534 van Gemert *et al.*, 2022; Roser *et al.*, 2024), altering the population's phenotypic and genetic
535 composition, and eliminating individuals with a tendency to move a lot before and during spawning.
536 The study area has been intensively harvested by small-scale commercial and recreational fisheries
537 for more than a century (Arlinghaus *et al.*, 2023a), which is sufficient time for the evolutionary
538 impacts of harvesting to manifest in pike (Matsumura *et al.*, 2011). Both gill nets (Carlson *et al.*, 2007;
539 Edeline *et al.*, 2007) and recreational angling gear are known to target not only larger individuals but
540 also those with an elevated space use (Monk *et al.*, 2021), which often have higher fitness in the wild
541 (Monk *et al.*, 2021). In the study region, the so-called pre-spawn gill net fishery actively targets pike
542 in spawning aggregations in bays (Arlinghaus *et al.*, 2023a), exploiting their increased activity levels
543 and migration into sheltered spawning bays (Flink *et al.*, 2023). It is conceivable that the largest
544 individuals and those with the longest migration distance have been selectively removed from the

545 population, erasing the potential for size-dependent spawning-related movements to be revealed in
546 current time.

547 Male pike were found to display higher MHD than females outside of the spawning season, when
548 controlling for body size, in agreement with Jepsen *et al.* (2001) in one of two study lakes, but
549 disagreeing with Koed *et al.*, (2006) in a river population. The difference between the sexes, did not
550 apply, however, to the spawning season, suggesting that both males and females travel similar long-
551 range distances to reach their spawning grounds. Earlier work had revealed that males appear more
552 active during the spawning season than females (Lucas, 1992), but this study only looked at localized
553 movements and not long-range movements. The observation that males may use more space than
554 females is in agreement with past studies conducted in our study area (Dhellemmes *et al.*, 2023a).
555 Movement differences between the sexes may be due to the cost of gamete production being lower
556 for males than females (Jonsson *et al.*, 1997), resulting in males having more residual energy to
557 dedicate to movements. They may also be driven by intersexual competition for resources, with
558 males and females specializing in different foraging strategies, or due to sex dimorphism in size,
559 which could mean that smaller males are under greater risk of cannibalistic or other types of
560 predation, motivating greater displacements in the search for safe refuges (Haugen *et al.*, 2006,
561 2007; Li & Kokko, 2021).

562 Several limitations should be noted. First, we inferred the connectivity among spawning sites by
563 analysing movement metrics during the key spawning period known for pike, without observing
564 exactly where individual pike spawned. However, our receiver array broadly covered the most
565 important known spawning sites (Figure 1), making our study likely robust for assessing long-range
566 movement patterns. Second, given our array design, we were unable to track fine-scale behaviours
567 during spawning site selection, and size-dependent micro-level site selection and associated
568 differences in activity (e.g., Lucas, 1992) may still occur on local scales. The telemetry system we used
569 was not designed to detect fine-scale movement resolution, which is why we cannot conclusively
570 answer this question. Future studies focusing on specific lagoons and using biologgers and micro

571 transmitters inserted into the oviduct, capable of direct spawning site detection, will be necessary to
572 determine whether pike of different lengths choose particular spawning sites and connect them
573 through localised movements within specific lagoons.

574 To conclude, we found no evidence that larger pike of either sex serve as key connectors of different
575 spawning and foraging sites within and across spawning seasons in different years. The lack of size-
576 dependent connectivity suggests that spatial bet-hedging within a spawning season through
577 connecting spawning sites maybe biologically impossible in the total spawner pike, and choosing of
578 different spatially separated spawning sites across years may not confer sufficient fitness advantages
579 for pike for evolution to happen. That said, we found indications that some individuals might still
580 exhibit spatial bet-hedging behaviour during a spawning season by choosing multiple possible
581 spawning sites independently of sex or size, although further research is needed to confirm that the
582 pike indeed release multiple egg batches in different sites and not only visit multiple sites to choose
583 the one to ultimately release their eggs. Our findings do not diminish the importance of conserving
584 large fish, given their high social value (e.g., high angler preference for catching large pike; Koemle *et*
585 *al.*, 2022) and fecundity-related benefits of large-sized pike females (Ahrens *et al.*, 2020). However,
586 the conservation value of large pike cannot be motivated by their key role as spawning site
587 connectors, unlike the case of batch spawning Atlantic cod (Olsen *et al.*, 2023).

588

589 **Ethics statement**

590 The research was completed following German legislation for animal experimentation, approved by
591 Landesamt für Landwirtschaft, Lebensmittelsicherheit und Fischerei MecklenburgVorpommern—
592 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. (2024). Catch uncertainty and recreational fishing attraction: Propositions and future research directions. *Fish and Fisheries*, *25*, 761–780.

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.

Cooper, W. T., Barbieri, L. R., Murphy, M. D., & Lowerre-Barbieri, S. K. (2013). Assessing stock reproductive potential in species with indeterminate fecundity: Effects of age truncation and size-dependent reproductive timing. *Fisheries Research*, *138*, 31–41.

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.

Gardner, S. T., & Höök, T. O. (2024). Efficacy of a novel reproductive tag to index spawn timing. *Canadian Journal of Fisheries and Aquatic Sciences*, *81*, 348–353.

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.

Kobler, A., Klefoth, T., Mehner, T., & Arlinghaus, R. (2009). Coexistence of behavioural types in an aquatic top predator: A response to resource limitation? *Oecologia*, *161*, 837–847.

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.
Laskowski, K. L., Monk, C. T., Polverino, G., Alós, J., Nakayama, S., Staaks, G., … Arlinghaus, R. (2016). Behaviour in a standardized assay, but not metabolic or growth rate, predicts behavioural variation in an adult aquatic top predator *Esox lucius* in the wild. *Journal of Fish Biology*, *88*, 1544–1563.
Lenormand, M., Pella, H., & Capra, H. (2021). Animal daily mobility patterns analysis using resting event networks. *Applied Network Science*, *6*, 7.
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.
McGhee, K. E., Pintor, L. M., & Bell, A. M. (2013). Reciprocal Behavioral Plasticity and Behavioral Types during Predator-Prey Interactions. *The American Naturalist*, *182*, 704–717.
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.

Nordahl, O., Koch-Schmidt, P., Sunde, J., Yıldırım, Y., Tibblin, P., Forsman, A., & Larsson, P. (2019). Genetic differentiation between and within ecotypes of pike (Esox lucius) in the Baltic Sea. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *29*, 1923–1935.

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

Nyqvist, M. J., Gozlan, R. E., Cucherousset, J., & Britton, J. R. (2012). Behavioural Syndrome in a Solitary Predator Is Independent of Body Size and Growth Rate. *PLoS ONE*, *7*, e31619.

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.

Pagel, T., Bekkevold, D., Pohlmeier, S., Wolter, C., & Arlinghaus, R. (2015). Thermal and maternal environments shape the value of early hatching in a natural population of a strongly cannibalistic freshwater fish. *Oecologia*, *178*, 951–965.

Pasquet, A., Sebastian, A., Begout, M. L., LeDore, Y., Teletchea, F., & Fontaine, P. (2016). First insight into personality traits in Northern pike (*Esox lucius*) larvae: a basis for behavioural studies of early life stages. *Environmental Biology of Fishes*, *99*, 105–115.

Pierce, R. B. (2004). Oviduct Insertion of Radio Transmitters as a Means of Locating Northern Pike Spawning Habitat. *North American Journal of Fisheries Management*, *24*, 244–248.

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).

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.
Roser, P., Radinger, J., Feldhege, F., Braun, M., & Arlinghaus, R. (2024). Getting Scarce and Lure Shy: Impacts of Recreational Fishing on Coastal Northern Pike (*Esox lucius*) Abundance, Size Structure and Vulnerability to Angling. *Fisheries Management and Ecology*, *32*, e12769.
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.
Sørensen, T. (1948). A method of establishing groups of equal amplitude in plant sociology based on similarity of species and its application to analyses of the vegetation on Danish commons. *Biol Skrifter/Kongelige Danske Videnskabernes Selskab.*, *5*, 1.
Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2017). rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *8*, 1639–1644.
Sukhanova, G. I. (1979). The spawning and fecundity of the pike *Esox lucius* in Vilyuy reservoir. *Journal of Ichthyology*, *19*, 74–79.
Sulikowski, J. A., & Hammerschlag, N. (2023). A novel intrauterine satellite transmitter to identify parturition in large sharks. *Science Advances*, *9*, eadd6340.
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.