Combining movement ecology and genetics to understand the ecology and evolution of a freshwater top predator (northern pike, Esox lucius) that has colonized brackish lagoons in the southern Baltic Sea: implications for management and conservation of weakly connected metapopulations

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Abstract

To inform management and conservation of fishes, understanding both ecological connectivity of habitat patches, apparent at the year-to-year scale, and genetic connectivity, emerging at the long-term evolutionary scale, is equally important. Ecological connectivity provides an indication of the potential for rapid recolonization upon local depletion, while genetic connectivity informs about the conservation needs related to genetically differentiated subpopulations. We combined acoustic biotelemetry and pooled-genome sequencing to study a northern pike (*Esox lucius*) population as a model of a freshwater top predator that inhabits a network of shallow brackish lagoons in the southern Baltic Sea. We found limited ecological connectivity among genetically similar subpopulations of pike, suggesting a metapopulation structure characterized by discrete local subpopulations with infrequent migrations between them. Connectivity increased during spawning, suggesting directed spawning migrations to either freshwater in tributaries or low salinity patches in connected lake-like bays. Pronounced spawning site fidelity to either brackish or freshwater spawning sites was observed, contributing to reproductive isolation. Genetic population structure aligned with salinity gradients and geographical distance but was unrelated to ecological connectivity. The results collectively suggest that local subpopulations may not rapidly replenish upon local depletion, yet even weak connectivity among them was sufficient to erode genetic differences over time. Effective management and conservation of species forming metapopulations, such as the northern pike studied here, necessitate localized approaches that adapt fishing mortality to local abundance and promote access to specific habitats during spawning to conserve the entire genetic biodiversity and foster resilience of the metapopulation.

1. Introduction

Connectivity is an important determinant of population dynamics, genetic differentiation, and biodiversity conservation because it affects key processes such as migration and dispersal, population growth, gene flow, and ultimately population resilience (Luque et al. 2012; Kool et al. 2013). Although high connectivity can also lead to negative demographic consequences in some circumstances, such as through the rapid spread of disease (e.g., Borg et al. 2017) or the facilitation of natural predation affecting source-sink dynamics (e.g., Olin et al. 2023), in general, it has been shown to mitigate local and regional ecological perturbations and/or overexploitation, e.g., by increasing overall population resilience and allowing negatively affected areas to be repopulated in cases of localised extinction (Hilborn et al. 2003; Gido et al. 2015).

In large aquatic systems, subpopulations of fish are connected either via the passive dispersal of eggs and larvae or via the active movement of juvenile and adult individuals (Brown et al. 2016). While passive dispersal is often studied using hydrodynamic models predicting particle movement (Palmas et al. 2017), for monitoring the active movement of juveniles or adults, telemetry offers a suitable toolbox to determine exchange processes, provided that the spatial scale of study is tractable (Matley et al. 2022). The ultimate outcome of dispersal can also be inferred from genetic techniques that assess the differentiation or relatedness among subpopulations and reveal the heritable consequences of dispersal (Riginos et al. 2014).

Population genetic approaches, however, primarily give an insight into genetic population structure resulting from past gene flow. This depends on the total number of dispersers between subpopulations over intergenerational time scales (Lowe and Allendorf 2010) as well as patterns of adaptive evolution and the related selective removal or enhancement of specific genotypes (Freeland et al. 2011). Although patterns of genetic connectivity emerging from population genetic analyses are fundamental for delimiting the stocks and identifying evolutionarily significant management units (Hawkins et al. 2016), such techniques are not always well aligned to capture ecological connectivity among habitats at year-to-year scale (Lowe and Allendorf 2010; Hawkins et al. 2016). In other words, whereas genetic connectivity provides information on the degree to which gene flow affects evolutionary processes over generational scales (Lowe and Allendorf 2010), ecological connectivity is of central importance for shorter-term ecological and fishery dynamics, such as population growth and vital rates influenced by dispersal as well as local abundance (Nichols et al. 2000; Runge et al. 2006). Decrease or interruption in ecological connectivity may not have an immediate effect on population genetic structure (Marandel et al. 2018), yet, it is highly relevant to local management decisions because it affects, for instance, the risk of localised overfishing, which may be overlooked when solely long-term evolutionary outcomes are considered (Hawkins et al. 2016). That is because even very small levels of exchange may contribute enough gene flow so that the subpopulations in different habitats remain genetically homogenous (Lowe and Allendorf 2010; Hawkins et al. 2016). For example, in a metapopulation, defined as an assemblage of discrete local groups with limited dispersal between them (Hanski and Simberloff 1997), ecological connectivity may be sufficient to maintain genetic panmixia, but low enough to inhibit the rapid recovery of subpopulations when a local mortality event occurs (Hawkins et al. 2016). Furthermore, safeguarding biocomplexity in such populations, which incorporates the diversity of spawning strategies and other behavioural adjustments in animals living in complex ecological systems, has been shown to be critical for achieving long-term stability and high productivity (Hilborn et al. 2003; Schindler et al. 2010).

Only by combining methods that track ecological (on year-to-year time scales) and genetic connectivity (on long-term evolutionary time scales) can the degree of population connectivity be fully characterised and appropriate management and conservation recommendations be tailored to different objectives (Lowe and Allendorf 2010; Hawkins et al. 2016). Over time, telemetry researchers and evolutionary geneticists have independently developed increasingly fine-tuned methods (see Matley et al. (2022); Nathan et al. (2022) for telemetry; and Benestan (2020); Hohenlohe et al. (2021) for genetics) but both communities remain largely siloed (for exceptions, see, e.g., Moore et al. (2017); Hahn et al. (2019); Finlay et al. (2020)). Our work combines these two toolsets by integrating and linking behavioural and genetic data to analyse population structure and understand the complex role of dispersal and connectivity on ecological and evolutionary time scales in a coastal population of northern pike (*Esox lucius*, hereafter ‘pike’) population in the southern Baltic Sea. Based on an improved understanding of the behaviour and genetic population structure, we derive implications for management and conservation of pike in brackish lagoons in the Southern Baltic Sea.

The Baltic Sea is one of the world's largest brackish water bodies, characterized by a strong salinity gradient from sea salinity (30 Practical Salinity Units, PSU) in its western part, connected to the North Sea, to almost fresh water (2 PSU) in the northeast (Schubert et al. 2017). Also, on local levels salinity gradients are pronounced, especially in the coastal areas, such as, for example, the lagoon network in the southern Baltic Sea, where salinities can range from almost freshwater oligohaline (< 5 PSU) to mesohaline conditions (< 18 PSU) (Arlinghaus et al. 2023b). These regional and local ecological gradients in salinity shaped a unique species assemblage, comprising both marine and freshwater species (Wennerström et al. 2013). Pike, a large-sized predator typical of freshwaters in the northern hemisphere (Craig 2008), is widely distributed throughout the coastal waters of the Baltic Sea where salinity does not exceed 18 PSU (Dahl 1961), taking advantage of an abundant foraging environment that provides access to energy-rich marine prey like herring (*Clupea harengus*) (Winkler 1987).

For freshwater fishes, successful survival at these salinity levels requires either evolutionary physiological adaptations allowing them to complete their life cycle in brackish water or development of behavioural traits, such as anadromy, that allow them to forage in brackish areas while continuing to spawn in the adjacent freshwater habitats (Engstedt et al. 2010; Ferguson et al. 2019; Aguirre et al. 2022). Resulting migration during the spawning time can contribute to reproductive isolation of subpopulations, for example, by affecting the timing of spawning among different groups (isolation by time, e.g., Brannon et al. (2004)) or their spawning site preferences (isolation by location, e.g., Neville et al. (2006)) (Kawecki and Ebert 2004; Engstedt et al. 2014). Such spatiotemporal processes may lead to intraspecific differentiation along the ecological gradients, such as salinity, or various habitat patches, where in some species and particular situations, a continuum of ecotypes and/or life-history pathways will be expressed and co-exist (Clemens and Schreck 2021).

Earlier studies have shown that Baltic pike have developed three distinct reproductive strategies to successfully spawn in varying salinity levels. Part of the population has undergone local adaptation and can carry out their complete life cycle, including reproduction, in brackish conditions up to 10 PSU (Sunde et al. 2022). Other individuals undertake anadromous spawning migrations from brackish feeding grounds to freshwater tributaries and wetlands (Engstedt et al. 2010; Sunde et al. 2019; Roser et al. 2023), while some fully reside in freshwater throughout the year, making only occasional forays into brackish areas (Birnie-Gauvin et al. 2019). In addition, natal homing and spawning-site fidelity, mechanisms that contribute to reproductive isolation, are common in pike (Miller et al. 2001; Bosworth and Farrell 2006), and both have been reported in Baltic pike (Diaz-Suarez et al. 2022; Engstedt et al. 2014; Nordahl et al. 2019).

The presence of ecotypes with different reproductive strategies may have a strong influence on both genetic and ecological connectivity within pike population. As there is no wide potential for dispersal in pike during the adhesive egg and larval stages (Bry 1996), pike dispersal is based solely on the movements of juveniles and adults. However, pike is a classically described as a sedentary ambush predator that has a rather small home range outside spawning time (Diana et al. 1977; Kobler et al. 2008; Craig 2008), although some studies in freshwater lakes showed that some individuals can be quite mobile and utilize all available habitats (Haugen et al. 2006). In the Baltic Sea, mark-recapture (Karås and Lehtonen 1993) and acoustic telemetry (Flink et al. 2023; Dhellemmes et al. 2023b) studies showed relatively stationary behaviour and rather small home ranges in coastal pike. However, during the spawning period, which usually takes place from March to May, Baltic pike exhibit increased mobility as they seek to reach the spawning grounds either in freshwater tributaries (Tibblin et al. 2016) or in brackish lagoons (Flink et al. 2023). This suggests that subpopulations mix in various combinations throughout the year: brackish water residents and anadromous fish intermingle in foraging habitats but separate during spawning as anadromous fish move to freshwater habitats where they, in turn, share space with resident freshwater pike.

Thus, on the one hand, the general sedentary lifestyle of pike suggests that ecological connectivity between parts of the population may be low, potentially fostering adaptive divergence on small geographic scales of a few km due to limited exchange between groups residing in different areas (Nordahl et al. 2019). But on the other hand, the occasional bursts of movements during spawning, may connect sites that are otherwise disconnected and potentially contribute to a gene flow among the subpopulations (Möller et al. 2021).

Genetic research on pike across the Baltic Sea showed population structuring shaped by pattern of isolation by distance, where geographically close subpopulations are more similar than geographically distant ones (Laikre et al. 2005; Wennerström et al. 2017). There is also genetic evidence for differences between sympatric anadromous and brackish pike ecotypes, likely in response to physiological salinity adaptations and/or natal homing and site fidelity (Nordahl et al. 2019; Sunde et al. 2022), which was also supported by otolith microchemical analyses (Engstedt et al. 2010; Möller et al. 2019). Similarly, studies in the coastal lagoons of the southern Baltic Sea, our study area, showed the influence of salinity on genetic structure, with pike in certain oligohaline lagoons differenting from pike in nearby mesohaline lagoons, which, in the absence of physical barriers between these areas, suggests that physiological reasons, i.e., salinity difference, may be limiting gene flow between them (Möller et al. 2021; Roser et al. 2023). Furthermore, Roser et al. (2023) demonstrated the occurrence of freshwater spawning activity in our study system and showed that putative anadromous subpopulation appears to be genetically intermediate between mesohaline brackish and freshwater or oligohaline brackish stocks.

Substantial declines in pike abundances were documented in many Baltic coastal areas in recent decades (van Gemert et al. 2022; Bergström et al. 2022; Olsson et al. 2023), calling for a well-informed management actions. To contribute to the understanding and conservation of these declining stocks, our study focused on addressing the following key questions:

1. Does the sedentary lifestyle of lagoon pike cause low ecological connectivity between parts of the population, increasing the potential for local overfishing?
2. Do spawning migrations enhance both ecological and genetic connectivity, or do they rather promote reproductive isolation and population differentiation through fostering behaviourally differentiated ecotypes such as brackish residents, freshwater residents, and anadromous fish?

3. Do patterns of space use and reproductive behaviour of pike align with the overall genetic structure of the population, or do environmental factors such as salinity gradients and geographic distances have a greater influence on current genetic differentiation patterns?

We hypothesized that the pike population in the study area is (H1) composed of several subpopulations with relatively stationary space use and low ecological connectivity among them, (H2) shows spawning site fidelity and behaviourally differentiated ecotypes, and (H3) its genetic structure is driven both by limited ecological connectivity and by environmental factors such as salinity gradients and geographic distances.

2. Methods

2.1. Study area

The study area comprises the network of interconnected coastal lagoons (locally known as 'Bodden') bordered by the islands of Fischland-Darß-Zingst, Hiddensee, Rügen and Usedom in the southern Baltic Sea (54.41N, 13.37E; area ca. 1,200 km²; Fig. 1). As a result of geographical characteristics of the region (e.g. varying patterns of land barriers between lagoons and open Baltic Sea and freshwater discharge from rivers), these lagoons exhibit significant hydrochemical variability, including salinity, water temperature, Secchi depth, and nutrient concentrations (Supplementary materials, Table S1) (Arlinghaus et al. 2023b). The most pronounced is the salinity gradient, with higher salinity levels in the northwest mesohaline areas (e.g., in Vitter, Schaproder, and Kubitzer Bodden) and lower salinity levels in the southeast oligohaline lagoons (Peenestrom and Stettiner Haff). Our study site also comprises of several freshwater tributaries, the most important of which are the Barthe and Peene rivers, as well as several small streams such as the Sehrowbach and Duwenbeek (Fig. 1).

2.2. Acoustic telemetry

To study ecological connectivity via pike migration and dispersal across the study area, a total of 389 adult pike (mean total length = 76.9 ± SD 12.4 cm; female = 226, male = 162, unknown = 1) were tagged in February – March 2020 (N = 301), November – December 2020 (N = 17), March – April 2021 (N = 63), and February 2022 (N = 8) (tagging locations on Fig. 1). The sampling methods included rod and reel fishing, fyke nets, gillnets, and electrofishing. Pike were fitted with Lotek 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, Lotek Wireless Inc., ON, Canada). Tagging locations covered all large lagoons, specifically Grabow, Schaproder and Kubitzer Bodden, Grosser Jasmunder Bodden, Strelasund, Greifwalder Bodden and Peenestrom (Fig. 1). Some fish were tagged just before to the spawning time in rivers and streams (Barthe, Peene, Duwenbeck and Sehrowbach; Fig. 1) assuming these represented migratory ecotypes moving to brackish feeding grounds and potentially returning to freshwater bodies during the next spawning (i.e., anadromous ecotype) (Roser et al. 2023).

Pike movements were monitored for three years (March 2020 – March 2023), using an array of 140 acoustic receivers (Vemco VR2Tx, frequency: 69kHz, MAP-113, Innovasea Systems Inc., Massachusetts, U.S.A.) deployed at 146 different locations across the study area. The receiver array covered the areas important to pike fisheries (Arlinghaus et al. 2023a), with higher receiver density in the western and northern lagoons and lower density in the Greifswalder Bodden and Peenestrom (Fig. 1). The receivers had mostly non-overlapping detection ranges, as the array was designed to monitor the broad movement ranges and connectivity between the areas of interest. In narrow links between the lagoons, “gate” format with denser receiver deployment allowed for more focused monitoring of pike transits (Fig. 1). The receiver data was downloaded, processed, and filtered once a year in winter (using R package *ATfiltR* (Dhellemmes et al. 2023a), see Supplementary materials for details). The detection data were aggregated at the daily level so that it provided records of each fish’s daily presence or absence on the array and the list of receivers where they were detected on a given day. Additionally, the dataset was completed with tagging, recapture, and opportunistic active tracking (using a manual VR100 receiver, Innovasea Systems Inc., Massachusetts, U.S.A.) locations and dates, which were attributed to specific geographical sections as described below.

We divided the study area into 29 sections, encompassing freshwater tributaries (e.g., Peene), individual lagoons (e.g., Grabow), and ‘gates’ (e.g., Gate between Grabow and Kubitzer Bodden), and clustered the receivers in these sections into corresponding groups (Fig. 1). The choice of sections was based on environmental differences, particularly in salinity (Supplementary materials, Table S1), and on geographical designations commonly used by locals for better stakeholder relevance and interpretation. We treated ‘gates’ as separate sections due to their higher receiver density, allowing to minimize bias in relevant metrics and analyses.

2.3. Movement networks: movement and ecological connectivity

To evaluate movement-based ecological connectivity, we constructed networks as unipartite undirected networks in which nodes represented the distinct geographic sections (i.e., with sets of receivers grouped according to their section Fig. 1), and edges reflected subsequent detections between the sections. Only apparent movements, i.e., consecutive detections of an individual on two different receivers, were considered to create the network. Hence, the resulting maps with spatially explicit networks represented aggregated pike movement within and between the defined sections represented by nodes. To test whether the observed patterns of movement differed from random, the observed individual networks were compared to those generated from null models (based on the method by Lea et al. (2016); see Supplementary materials for details).

To quantify the networks, three metrics were used: (1) *node strength* reflected the number of movements within each node and provided a measure of occupancy (Barrat et al. 2004; Lea et al. 2016); (2) *edge weight* showed local connectivity and the strength of connections between node pairs, calculated as the total number of internodal transits (Barrat et al. 2004; Jacoby et al. 2012); and (3) *edge density* described the overall connectivity within the network, representing a proportion of edges present in a network out of the total edges possible (Jacoby et al. 2012). Networks were created and analysed using packages *igraph* (Csárdi and Nepusz 2006) and *circlize* (Gu et al. 2014).

To ensure comparability across different sections with varying receiver coverage and unequal tagged pike (Fig. 1), we adjusted node and edge metrics. Node strength was weighted by receiver density and mean distances between receivers (in water, calculated using *actel* (Flávio and Baktoft 2021)), and by the number of fish tagged in each section. Edge weight was adjusted by distance (in water) between connected nodes to give higher value to longer transits. The network was computed monthly for the entire population, and the adjustments were applied to monthly metrics, accounting for new receiver deployments, additional pike tagging, and reported fish mortalities. Lastly, three-year average values were calculated annually and seasonally (winter = Dec to Feb, spring = March to May, etc.).

2.4. Pike movement between brackish and freshwater habitats

We conducted an analysis of pike movement between different habitats within our study area to investigate potential differences in their habitat preferences and habitat exchange behaviours, particularly between brackish and freshwater environments. This was done to investigate whether pike originating from these different habitats show preferences for staying in native habitats or moving to other habitats. Variations in dominant preferences per habitat type would shed light on the presence of behaviourally differentiated ecotypes in the studied pike population, in particular the presence of an anadromous ecotype. To do this we categorized the receiver stations, as well as tagging, recapture, and active tracking locations into the habitat types: *Brackish* for lagoon areas, *Estuary* for the lagoonal areas within 1 km of a river mouth, *Freshwater downstream* for river sections up to 1 km from a river mouth, *Freshwater upstream* for river sections beyond 1 km from a river mouth. For each pike, the location of the first capture/tagging was taken as the starting point and all transitions within and between different habitats were tracked. If no data were available for an individual after a previous observation, it was categorised as moving to the 'No Data' category. We then summarised all documented transits to represent the movements of the entire population between habitats throughout the study period. This was visualised in R using circular plots from *circlize* (Gu et al. 2014).

2.5. Spawning site fidelity

To assess pike spawning site fidelity, we examined whether they were observed in the same areas during the spawning seasons (March to May) in different years (2020–2022) by checking for repeated logging at the same receiver/s. Further, we examined whether pike were tagged, recaptured, or detected by active tracking in the same area, which also indicates a return to the same spawning grounds, but more punctually.

2.6. Population genetics and its link to ecological connectivity, geographical distance, and salinity gradients

We took advantage of already available whole-genome (pool-sequencing) data published in Roser et al. (2023), who genotyped the entire genome of N = 50 animals from 11 study locations in the study area (see details in Supplementary materials, Fig. S1). This genomic investigation focused on pike sampled from lagoons and tributaries, aiming to fully characterize the genetic diversity within the study region and discern patterns of population differentiation. To assess genetic differentiation among the study locations, FST was employed, a metric quantifying genetic variance among populations (Holsinger and Weir 2009). The resulting pairwise FST values indicated a distinct separation between mesohaline brackish-water sites in Bodden (e.g., Greifswalder Bodden, Barther Bodden, Schaproder/Kubitzer Bodden) and larger freshwater rivers (Barthe and Peene), as well as oligohaline lagoons (e.g., Peenestrom). Within this differentiation, putative anadromous populations in smaller streams (e.g., Sehrowbach) exhibited a more intermediate genetic position (see Roser et al. (2023) for details; Fig. S1).

The locations with both genetic and telemetry data available included mesohaline brackish-water (Barther Bodden, Kubitzer/Schaproder Bodden, Großer Jasmunder Bodden, Greifswalder Bodden), possibly resident freshwater (Barthe and Peene river), oligohaline brackish (Peenestrom) and a putative anadromous population (Sehrowbach). Another network analysis was conducted using each of these areas instead of the original, finer-scale (29 sections, Fig. 1) to align it to the genetic sampling locations (Supplementary materials, Fig. S2), with edge weight used as ecological connectivity measure.

To determine the extent to which ecological connectivity and the environmental factors such as geographic distance and salinity difference correlate with the estimated levels of genetic differentiation among the key lagoons and rivers, we used partial Mantel tests using the package *vegan* (Oksanen et al. 2022) which allow to control for one variable. We ran three partial Mantel tests: (1) between pairwise linear FST (i.e., $FST/(1-FST)$, (Rousset 1997)) and pairwise ecological connectivity while controlling for geographic distance in water; (2) between pairwise linear FST and pairwise average salinity difference while controlling for geographic distance in water; and (3) between pairwise linear FST and geographic distance in water while controlling for pairwise average salinity differences.

Further, we fit a generalized linear model (GLM) using the package *glmmTMB* (Brooks et al. 2023) to compare the relative effect of each of the following variables: ecological connectivity (continuous: edge weight), salinity, presence of a freshwater habitat in a pair (categorical: none, one, or both), and geographic distance (continuous: km). Linear FST was used as the response variable, and a beta distribution was used as FST values ranged between 0 and 1 (Nurbaev and Balanovskaia 1998). We identified the explanatory variables that improved model fit by comparing the AIC of the full model with the AIC of stepwise simplified models using the *MASS* package with a 2 units difference of AIC indicating significantly different fit between the models (Venables and Ripley 2002; Burnham and Anderson 2004). The fit of the obtained most parsimonious model was assessed using the uniformity, dispersion and outliers tests in the *DHARMa* package (Hartig and Lohse 2022). Fit was considered appropriate if no tests were significant.

For the Mantel tests and GLM, geographic distances and salinity differences among pairs of sites were calculated as follows: distances were calculated as the mean distance between all pairs of receivers located in different areas, and salinity differences were calculated based on estimates presented in (2023) (Table S1). The obtained values were then mean centred, and their standard deviation set to 1, to allow for direct comparison of effect strength in the models.

All data handling, and analysis was performed in R (R Core Team 2023), with the exception of the random network calculations which were done in in *Python 3.8.10* via the *Anaconda 3 distribution* (2020) (see Supplementary materials for details).

3. Results

3.1. Descriptive information

Out of 389 tagged pike, 342 (88%) were detected on 138 receiver stations (out of the original 146 locations: 13 receivers were lost and five moved in 2021, Fig. 1). 47 individuals (12%) were never detected, with the largest proportion tagged in the Peene river (40%) and Sehrowbach stream (33%). 54 individuals (14%) were detected by only one receiver during the entire study period, and it is not clear whether they resided in the respective areas, were not moving because they have died, or had equipment malfunction. Overall, a total of 8,041,130 detections were recorded between March 2020 – March 2023. After removing duplicates, the dataset comprised 4,318,623 detections. Out of these, 399,337 (9%) indicated movements, regarded as consecutive logs of an individual on distinct receivers, while all other records were at unchanging locations, pointing to the predominantly sedentary behaviour and site fidelity of pike. The testing of the individual pikes' networks against those created with random walks showed that pike's movements were non-random, as the edge density of the data and random networks were significantly different (Wilcoxon one-sample signed rank test, p-value < 0.05).

3.2. Movement and ecological connectivity

The movement network structure showed that pike movement linked most of the lagoons and freshwater tributaries in the study area as far as geography allowed, but all these links as well as overall level of ecological connectivity were weak (Fig. 2, A, B). Most of the movements were local, occurring within selected (mostly original tagging) lagoons and freshwater tributaries, where 75% of the transitions were recorded (Fig. 2, A, B). When exchange levels were higher, they mainly happened between lagoons and nearby "gates", still reflecting rather local movements (e.g., Kubitzer Bodden (KB) and Gate between Kubitzer Bodden and Strelasund (Gate KB-S), Fig. 2, B).

Strong seasonal differences in pike movement and connectivity were observed, with peak connectivity between the sections of the study area in spring, corresponding to the well-known spawning time of pike (Fig. 2, C; Fig. S3). Connectivity was notably lower during other seasons, reaching its minimum in winter, indicating very low movement between the sections during this time (Fig. 2, C; Fig. S3).

In spring, the movement network displayed high connectivity, with most regions linked by pike movement reflecting an increase in movement (Appendix, Fig. S3, B). Some sections, like lagoons Greifswalder Bodden (GB) and Peenestrom (Gate GB-P and P), showed no exchange movements despite being geographically close, and only a small increase in movement was recorded between Rügischer Bodden (RB, northern Greifswalder Bodden) and Peenestrom (Gate GB-P and P) (Fig. S3, B). These two lagoons thus remained weakly connected to each other throughout the year despite their geographic proximity (Fig. S3).

3.3. Pike movement between brackish and freshwater habitats

The analysis of the movement between different habitats revealed distinct behavioural patterns among groups of pike, pointing at their differentiating ecotypes and spawning strategies. Pike tagged in brackish water tended to remain in brackish habitats. Most of their movement occurred either within brackish waters (53%) or between brackish waters and estuaries (40% of all movements to and from brackish habitats, Fig. 3). Correspondingly, movements to and from estuaries were mostly connected to brackish habitats (53%) or happened entirely within estuaries (27% out of all movements to and from estuaries, Fig. 3).

Pike tagged in freshwater rivers and streams showed overall more diversity in habitat use. Individuals originating from upstream sections of larger rivers Barthe and Peene primarily remained in freshwater habitats (40% of movements remained upstream, and 22% happened between upstream and downstream freshwater habitats). Some of these fish ventured to estuaries (24% out of all movements to and from upstream freshwater habitats), but very few entered brackish lagoons (2%, Fig. 3).

In contrast, individuals tagged or observed in downstream sections of rivers and specifically in the small streams Sehrowbach and Duwenbeek were frequently found in estuaries (47% out of all movements to and from downstream freshwater habitats) and brackish lagoons (12%, Fig. 3). This suggests that these pike have a greater tolerance for salinity variations and may represent an ecotype that uses both freshwater and brackish water habitats.

3.4. Spawning site fidelity

A total of 369 (95% of tagged) individuals were observed (tagged, recaptured, recorded by receivers or by active tracking) in at least one spawning season (March-May). Among these, almost half (N = 151, 43%) were only seen in one spawning season (32 of them were known to have died due to fishing harvest or naturally). The remaining half (N = 208, 56%) had records available for two (N = 143) or all three (N = 65) spawning seasons (March-May 2020–2022), which allowed analyses of spawning site fidelity.

Pike showed strong spawning site fidelity: out of the 208 individuals observed over multiple spawning seasons, the vast majority (97%, N = 201) were found in the same section of the study area (lagoon, freshwater tributary, or “gate”) in at least two spawning seasons in three years of observations (Table 1). Among them, only a third (29%, N = 59) were documented to have left the section outside of spawning, indicating a return migration to the spawning site (Table 1). 85% (N = 178) were detected at the same receiver in at least two spawning seasons, meaning that they used the exact geographical locations within the respective section (Table 1). Among those, 80% (N = 142) did not visit exactly the same receivers outside of the spawning season (Table 1).

Table 1

Repeated observations of individuals at the same sections of the study area during three spawning seasons (2020–2022). N fish – number of individuals with available data for 2 or more spawning seasons (tagged, recaptured, recorded by receivers or by active tracking); Same stations 2 years, N – number of individuals detected by the same receiver/s in at least 2 different spawning seasons; Same stations in 3 years, N – number of individuals detected by the same receiver/s in all 3 spawning seasons; Visited other stations outside spawning, N – number of individuals detected by at least one receiver outside of the spawning season that differed from receivers during spawning (% of pike visited same stations in 2 seasons); Same sections in 2 seasons, N – number of individuals observed (tagged, recaptured, recorded by receivers or by active tracking) in the same sections/s of the study area in at least 2 different spawning seasons; Same sections in 3 years, N – number of individuals observed (tagged, recaptured, recorded by receivers or by active tracking) in the same section/s in all 3 spawning seasons; Visited other sections outside spawning, N – number of individuals found outside the spawning season in at least one area different from that during the spawning season (% of pike visited same sections in 2 seasons).

N fish	**Same stations in 2 seasons, N (% of N fish)**	**Same stations in 3 seasons, N (% of N fish)**	**Visited other stations outside spawning, N (% of Same stations in 2 seasons)**	**Same sections in 2 seasons, N (% of N fish)**	**Same sections in 3 seasons, N (% of N fish)**	**Visited other sections outside spawning, N (% of Same sections in 2 seasons)**
208	178 (85%)	59 (28%)	142 (80%)	201 (97%)	59 (28%)	59 (29%)

3.5. Population genetics and its link to ecological connectivity, geographical distance, and salinity gradients

The partial Mantel tests revealed no significant effect of (movement-based) ecological connectivity on pairwise linear FST (r = -0.032; p = 0.56; 9999 permutations, Fig. 4, A) regarded as a measure of genetic connectivity. On the other hand, there were significant effects of salinity differences among sites (r = 0.681; p = 0.004; 9999 permutations, Fig. 4, C), indicating that populations differed more in their genotypes when they were from sites with stronger salinity differences. Both tests were controlled for geographic distance in water. The partial Mantel tests between the linear FST and geographic distance while controlling for salinity differences also showed a significant correlation (r = 0.749; p = 0.008; 9999 permutations), indicating that larger geographic distance was associated with greater degrees of genetic population differentiation (isolation by distance, Fig. 4, B).

The most parsimonious generalised linear model also included geographic distance and salinity difference as well as presence of a freshwater site in a pair, all revealing significant associations with genetic distance (pairwise linear FST) except for when only one of the areas in a pair was of freshwater category (Table 2, Fig. 4). Salinity difference had the strongest relative effect on genetic distance, followed by geographic distance, and the differentiation in pairs that contained two freshwater sites. By contrast, including ecological connectivity did not improve the model fit (Supplementary materials, Table S2), suggesting no influence of movement-based ecological connectivity and genetic connectivity in lagoon pike population.

Table 2
Estimates in the most parsimonious models for explaining genetic distance (pairwise linear FST) in northern pike in brackish lagoons and their freshwater tributaries as a function of environmental variables (distance, ecological connectivity, salinity differences)

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	-3.736	0.047	-79.037	0.000
Mean Distance	0.161	0.022	7.330	0.000
Salinity Difference	0.273	0.041	6.615	0.000
One freshwater in a pair	-0.068	0.076	-0.899	0.369
Two freshwaters in a pair	0.426	0.086	4.929	0.000

4. Discussion

A solid understanding of population structure and the complex role of dispersal and connectivity on evolutionary and ecological time scales requires a combination of behavioural and genetic data (Lowe and Allendorf 2010; Hawkins et al. 2016; Marandel et al. 2018). In this study, we combined whole-genome sequencing from individual pike pooled at capture site levels and associated measures of genetic connectivity with behavioural observations over three study years using acoustic telemetry to investigate ecological and genetic connectivity in the northern pike population inhabiting brackish lagoons surrounding the German islands of Fischland-Darß, Hiddensee, Rügen and Usedom in the southern Baltic Sea. We found support for our first hypothesis (H1) that the study population was composed of several subpopulations with relatively stationary space use and low movement-based ecological connectivity among them, resembling a metapopulation structure. We also found support for our second hypothesis (H2) by revealing spawning site fidelity and the presence of behaviourally differentiated ecotypes. In relation to our third hypothesis (H3) we found that the genetic structure of the studied pike populations was affected by salinity differences among study sites and by geographic distances, suggesting that both evolutionary adaptations to local salinities as well as restricted movement in space structured the gene flow in the study area.

The limited movement-based ecological connectivity observed within the study area was in line with earlier studies that have described pike as a rather sedentary species (Diana et al. 1977; Cook and Bergersen 1988; Kobler et al. 2008). Previous studies in our study area reported rather small core home ranges for the lagoon pike (1.5 km² in the lagoons system of over 2,000 km²) (Dhellemmes et al. 2023b), with maximal distances among two farthest recorded positions for an individual being on average 11.7 km, with most individuals having low maximal dispersal and only very few being explorers (Dhellemmes et al. 2023c). Marc-recapture studies on pike in the Baltic showed even smaller dispersal range, with recapture distances of 10 km being exceptional (Karås and Lehtonen 1993). Our network analyses provided further support for within lagoon behavioral lifestyles, which renders the stock vulnerable to local pressures from harvesting or natural predation, similar to findings in Sweden (Olin et al. 2023). Nevertheless, most lagoons and freshwater tributaries in the study area were still connected through occasional adult pike movements as far as geography allowed (Fig. 2), pointing at a metapopulation-like demographic structure, consisting of an assemblage of discrete local groups with limited dispersal between them (Hanski and Simberloff 1997).

Most of the overall movement-based connectivity was gained in spring during the spawning season (March-May) when almost all the areas became connected by pike movement with traffic between some increasing sharply (Fig. A.2). These findings align with earlier research indicating that pike activity peaks during spawning due to migration to spawning grounds (Cook and Bergersen 1988; Skov et al. 2018), behavior also observed in brackish water pike populations (Tibblin et al. 2016; Flink et al. 2023; Dhellemmes et al. 2023b). The observed increased mobility level is likely due to migrations of anadromous pike to freshwater (Tibblin et al. 2015; Roser et al. 2023), but is also due to movements by brackish water adapted individuals to their specific spawning sites (Jacobsen et al. 2017). The pike in the Baltic Sea tend to preferentially aggregate in brackish sheltered bays for spawning (Flink et al. 2023) and if reaching these entails moving from more offshore feeding sites then the fish will engage in a spawning “run”.

Previous studies indicated that pike’s spawning migrations are primarily motivated by their fidelity to specific spawning sites (Miller et al. 2001; Craig 2008), which was also documented in the Baltic Sea (Larsson et al. 2015; Nordahl et al. 2019; Diaz-Suarez et al. 2022). Our findings align with that as most fish (98%) observed in at least two spawning seasons were documented to occupy the same area during spawning (Table 1). However, telemetry tracking cannot definitively confirm that pike spawn where they are located during telemetry, as they may also miss spawning. In fact, it is possible that the inferred spawning site coincides with their year-round habitat, supported by the fact that 71% of pike did not leave their spawning area for the rest of the year. However, previous translocation experiment in the Rügen lagoons reported strong evidence for spawning site fidelity and revealed that brackish pike translocated to freshwater streams returned to brackish sites and freshwater fish translocated to brackish water similarly returned to their streams, suggesting adaptation to specific spawning habitats that vary in salinity (Dhellemmes et al. 2023d). Laboratory experiments further support this, showing that brackish-adapted pike struggle to reproduce successfully in freshwater, while the opposite is true for freshwater-adapted pike (Arlinghaus et al. 2023a, b). Additionally, the genetic differences in pike sampled from different tributaries during spawning point towards natal site fidelity (Roser et al. 2023), although experiments exposing larval pike to different stream odors remain to be done. These findings underscore the importance of physiological adaptation to specific salinities in explaining the movements and spawning site fidelity observed in our tracking study.

Distinct behavioural patterns were evident among groups of pike observed in different habitats, particularly in terms of their movements between fresh and brackish waters. These variations hint at the presence of diverse pike ecotypes and shed light on their spawning strategies. First, the majority of pike tagged in brackish water lagoons remained in the lagoons throughout the year, including spawning season (Fig. 3), implying that they also spawned there and thus had undergone evolutionary adaptation to brackish spawning, similar to reports from a telemetry study in a comparable Danish lagoon (Jacobsen et al. 2017). Pike from freshwater rivers and streams showed more diversity in habitat use. Individuals originating from upstream sections of the larger rivers predominantly stayed in freshwater habitats and rarely ventured into brackish lagoons (Fig. 3). Comparable observations were reported in a study from Denmark by Birnie-Gauvin et al. (2019) who found a freshwater pike stock in a coastal river of the Baltic Sea that only occasionally visited the estuary but were otherwise freshwater residents. By contrast, individuals tagged or observed downstream, particularly in small streams (e.g., Sehrowbach), were seen both in estuaries and brackish lagoons (Fig. 3), suggesting their greater tolerance to salinity variations and pointing to potentially anadromous subpopulations. Anadromy is well documented in pike in many Baltic Sea studies (e.g., Engstedt et al. 2010; Tibblin et al. 2016) including in our study area (Möller et al. 2019; Roser et al. 2023), although here this pike ecotype is rare today (< 6% among brackish samples) (Möller et al. 2019; Arlinghaus et al. 2023a). This is most likely due to extensive blocking of freshwater access since the 1970s (Roser et al. 2023) which might have advanced the selection pressures to adapt to spawning in brackish water.

Our association tests among ecological and genetic connectivity revealed that although movement-based ecological connectivity was generally limited and predominantly observed between directly adjacent lagoons areas, it nevertheless supports sufficient gene flow to homogenize subpopulations. Accordingly, our measures of current movement-based connectivity had no significant effect on genetic divergence. The presence of sufficient gene flow among various brackish lagoons is exemplified by little genetic differentiation among all mesohaline lagoons (Greifswalder Bodden, Großer Jasmunder Bodden, Barther Bodden, Kubitzer and Schaproder Bodden, (Roser et al. 2023), which was also found in an earlier microsatellite-based study in Rügen pike by Möller et al. (2021). Moreover, evaluation of restricted ecological connectivity via telemetry suggests a finer demographic population structure than genetics data would imply, indicating that many local subgroups in different lagoons are genetically related, but spatially disaggregated due to infrequent exchange. Such low levels of ecological connectivity leave the local populations susceptible to local overfishing and other stressors, eroding its overall resilience (Kool et al. 2013; Gido et al. 2015; Olin et al. 2023) – a key finding that an isolated genetic study would not have captured.

Geographic distance still emerged as a significant driver of genetic differentiation, consistent with localised patterns of pike movement (Diana et al. 1977; Craig 2008), so that populations separated by larger distances displayed greater differentiation as they become increasingly reproductively isolated. This is in agreement with previous research in our study area (Möller et al. 2021) and in the Baltic Sea in general (Laikre et al. 2005; Wennerström et al. 2017; Nordahl et al. 2019; Sunde et al. 2022), which all showed that genetic structure is associated with geographic distance along the Baltic coast at both large (e.g., from Denmark to Finland) as well as smaller scales (e.g., within a lagoon system like our study site).

Our association models also showed a significant influence of salinity levels and the presence of freshwater in each pair of sites on genetic differentiation among these sites. This emphasises that, in addition to geography, genetic differentiation is also driven by local adaptation to salinity, consistent with the observed habitat utilisation strategies in the population, which revealed brackish residents as well as more migratory ecotypes. The whole-genome sequencing at the site level also showed a surprisingly high genetic differentiation among a mesohaline and an oligohaline lagoon, namely the Greifswalder Bodden and Peenestrom (Roser et al. 2023). This lagoon pair also exhibited the lowest ecological connectivity of all site pairs, although we might have underestimated the levels of movement here due to low receiver density in the area and considering the number of pike tagged (Fig. 1). Nonetheless, our results align with findings by Möller et al. (2021), who also reported that pike in most adjacent lagoons were genetically similar, except for fish from mesohaline Greifswalder Bodden and oligohaline Peenestrom lagoons, which are geographically adjacent but have very different salinities. This suggests that divergence may be rather driven by physiological dispersal barriers related to reproductive salinity tolerance (Möller et al. 2021; Sunde et al. 2022). Our results support these earlier findings by revealing how the behaviour of pike contributes to reproductive isolation and population differentiation, both in terms of geography but also in terms of salinity adaptation.

4.1. Implications for management and conservation

Understanding both ecological and genetic connectivity is pivotal for effectively managing lagoon pike populations and fish populations in general (Hawkins et al. 2016). Both perspectives offer complementary views on population structure on different timescales, sometimes leading to divergent conclusions on suitable management and conservation strategies. In the case of the lagoon pike, whereas high genetic connectivity implied limited differentiation between the pike subpopulations in different mesohaline lagoons and thus a possibility to manage all lagoon pike as a single large stock, limited movement exchange between individual lagoons results in low ecological connectivity, hindering the recolonisation potential and increasing the vulnerability of local subpopulations to local overfishing or other adverse events. Hence, the effective management and conservation of the metapopulation of pike would require managing units on a more localized spatial scale in ecological time (e.g., year-to-year), so that the population can withstand local stress factors and sustain harvest for both recreational and commercial fisheries that co-exploit the stock (Gido et al. 2015; Hawkins et al. 2016; Olin et al. 2023). At the same time, it is critical to maintain and fostering ecotypic and genetic biocomplexity at the entire met-population level, which is recognized as a critical factor for building resilience and maintaining fisheries productivity (Schindler et al. 2010). To that end, a subpopulation-tailored approach is needed to support different pike ecotypes that are genetically and phenotypically differentiated. Anadromous subpopulations can be directly supported only at the stage when they migrate to freshwater habitats to spawn, e.g., by restoring connectivity between the freshwater and brackish realms though removing the barriers associated with wetland management and agriculture to allow anadromous subpopulations to reach their historical spawning grounds (Roser et al. 2023). Another key action is control of excessive captures via passive gear (e.g., gill nets) prior to spawning as they might preferentially target mobile pike during their spawning migration. Such measures, and especially the restauration of wetlands, were shown effective in enhancing the abundance and size structure of adult pike in Baltic coastal habitats (Larsson et al. 2015; Tibblin et al. 2023) and will also help to maintain a genetic ecotype that is presently rare in Bodden lagoons. For supporting the brackish-adapted subpopulations, it is equally important to maintain connectivity to allow dispersal from foraging sites to spawning bays (Flink et al. 2023). Further research may focus on precisely identifying the lagoon spawning locations that can be seasonally protected to enhance the stock. Until such studies become available, it is safe to assume that enclosed vegetated bays, providing shelter from wave action and allowing freshwater inflow from streams and ditches to reduce local salinity, are important spawning grounds whose protection would favour brackish water adapted pike in the Rügen lagoons.

Declarations

Authorship contribution

OL: Conceptualization, Methodology, Investigation, Formal analysis, Visualization, Writing - original draft. FD: Conceptualization, Data curation, Methodology, Investigation, Formal analysis, Software, Supervision, Writing - review & editing. SD: Formal analysis, Investigation, Writing - review & editing. AN: Formal analysis, Investigation, Writing - review & editing. RA: Conceptualization, Methodology, Funding acquisition, Supervision, Project administration, Validation, Writing - review & editing.

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Ethics statement

The research was completed following German legislation for animal experimentation, approved by Landesamt für Landwirtschaft, Lebensmittelsicherheit und Fischerei Mecklenburg-Vorpommern – Veterinärdienste und Landwirtschaft – under grant number 7221.3-1-052/19.

Competing interests statement

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

Data availability statement

The telemetry data is available in the European Tracking Network repository.

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Figures

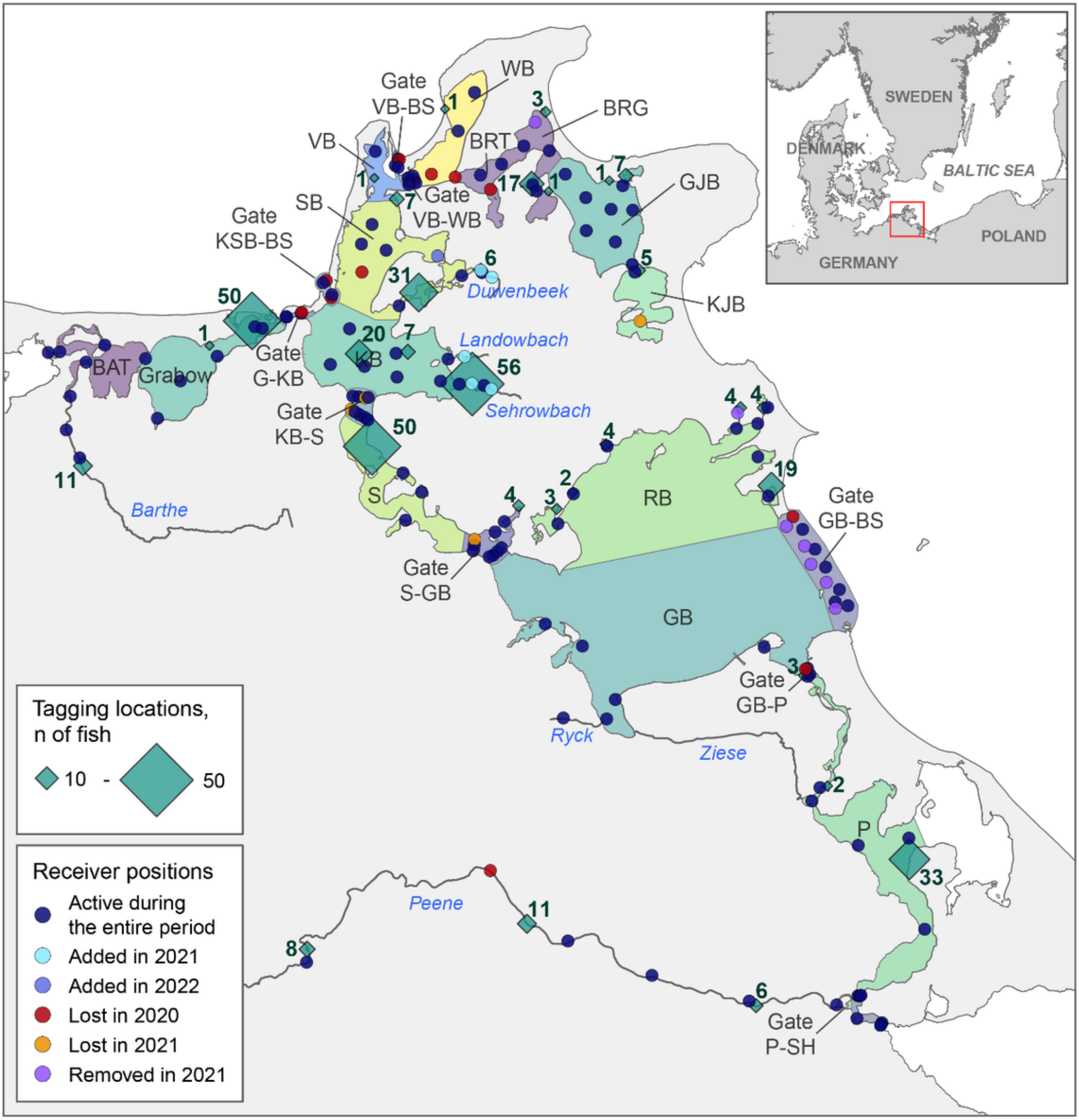

Figure 1

Map of the study area displaying the positions of the acoustic telemetry receivers and fish tagging sites. Full names of the areas (freshwater in blue font): Barthe – Barthe river; BAT – Barther Bodden; BRG – Breeger Bodden; BRT – Breetzer Bodden; Duwenbeek – Duwenbeek stream; Gate GB-BS – Gate between Greifswalder Bodden and open Baltic; Gate GB-P – Gate between Greifswalder Bodden and Peenestrom; Gate G-KB – Gate between Grabow and Kubitzer Bodden; Gate KB-S – Gate between Kubitzer Bodden and

Strelasund; Gate KSB-BS – Gate between Schaproder/Kubitzer Bodden and open Baltic Sea; Gate P-SH – Gate between Peenestrom and Stettiner Haff; Gate S-GB – Gate between Strelasund and Greifswalder Bodden; Gate VB-BS – Gate between Vitter Bodden and open Baltic Sea; Gate VB-WB – Gate between Vitter Bodden and Wieker Bodden; GB – Greifswalder Bodden (South); GJB – Großer Jasmunder Bodden; Grabow – Grabow; KB – Kubitzer Bodden; KJB – Kleiner Jasmunder Bodden; Landowbach – Landowbach stream; P – Peenestrom; Peene – Peene river; RB – Rügischer Bodden; Ryck – Ryck stream; S – Strelasund; SAB – Saaler Bodden; SB – Schaproder Bodden; Sehrowbach – Sehrowbach stream; VB – Vitter Bodden; WB – Wieker Bodden.

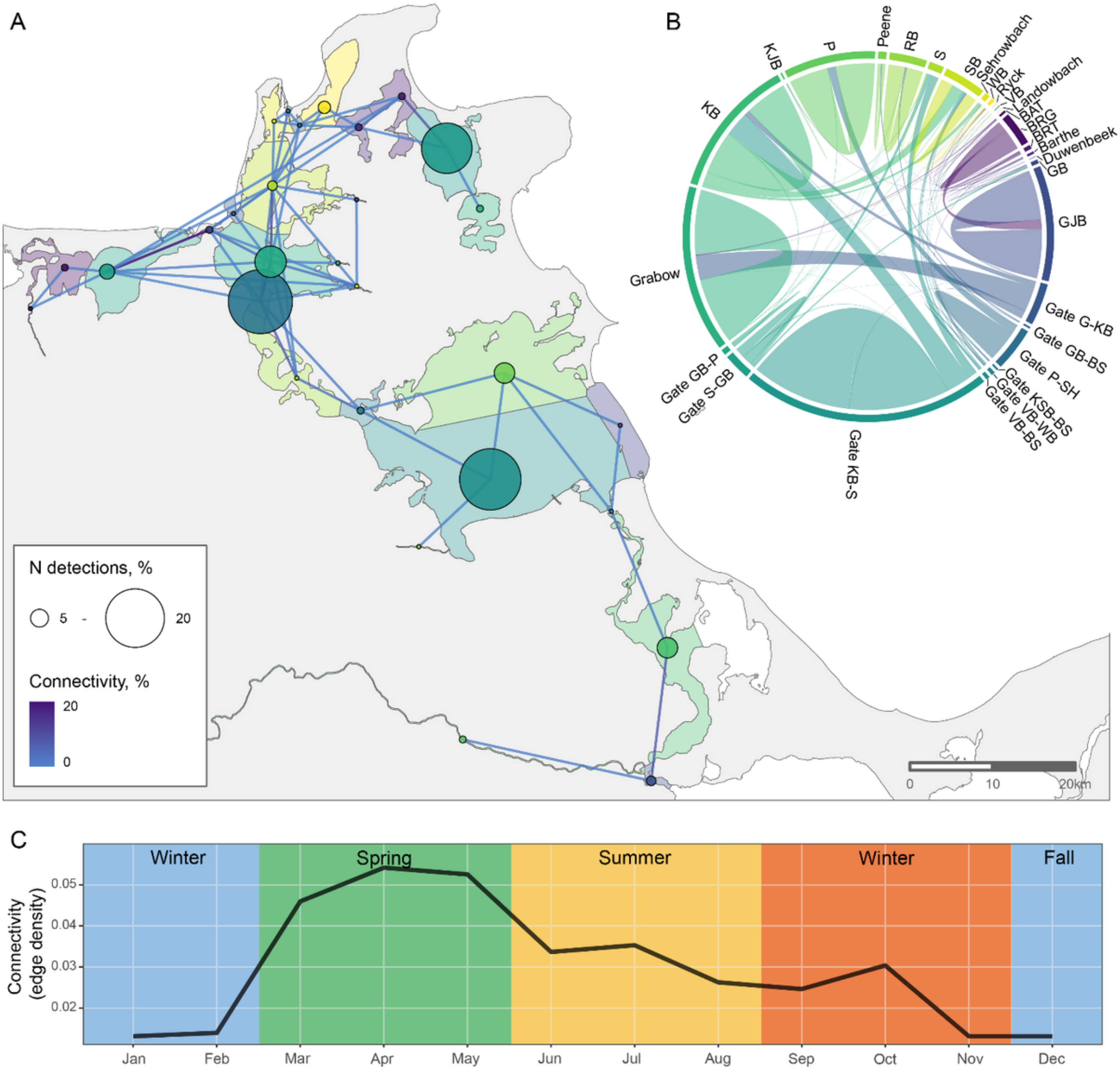

Figure 2

Ecological connectivity. (A) A map displaying the network structure of the pike movements, where node size corresponds to the total number of detections within each area and edge colour represents the frequency of internodal movements. (B) Circular plot displaying proportions of movements within the areas and between the pairs of areas (the graph displays apparent movements, i.e., consecutive detections on two different receivers). (C) Monthly dynamics of overall connectivity withing the study system, represented by edge density network metric. See full names of the areas in Fig. 1.

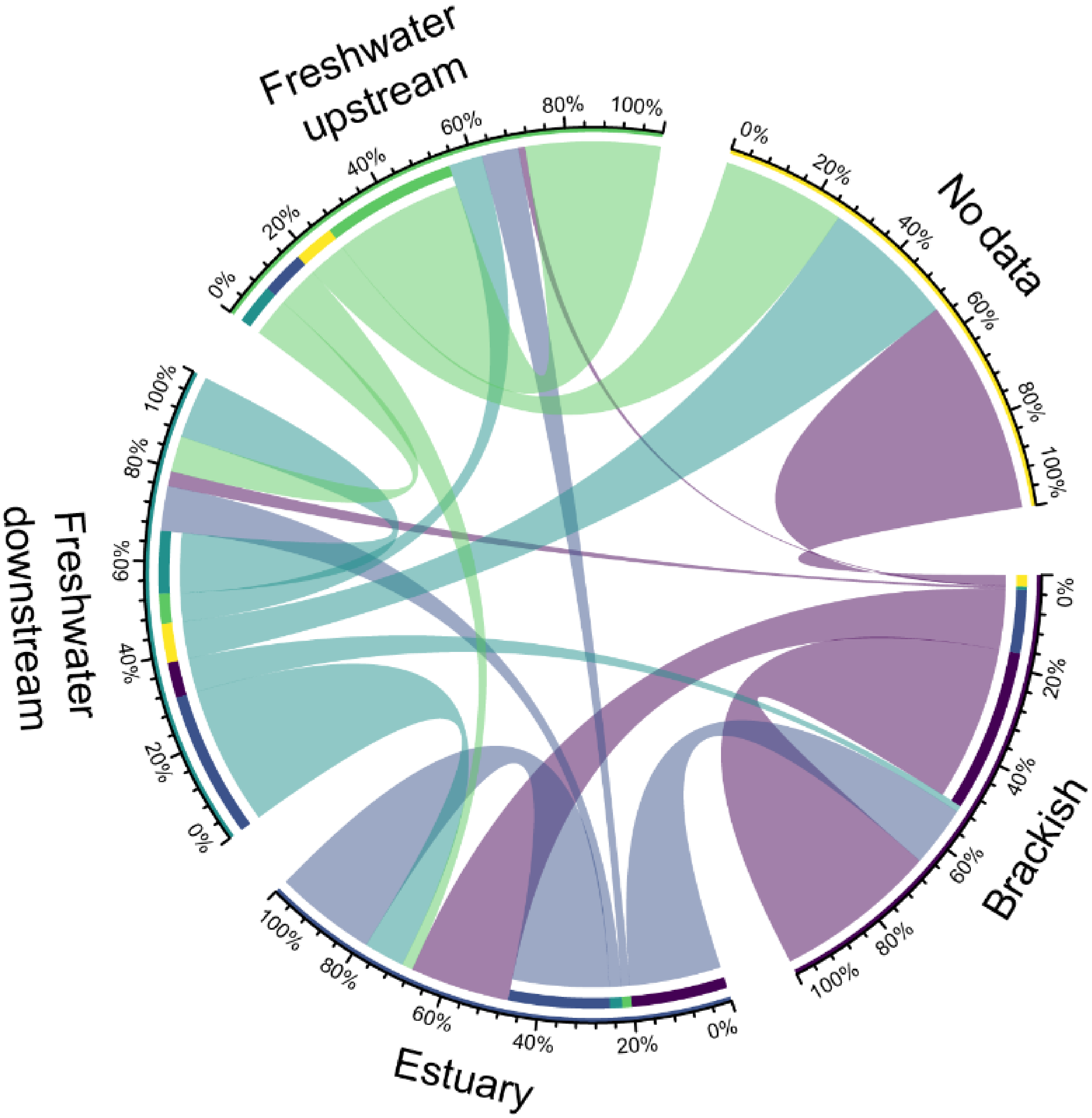

Figure 3

Pike movements between different habitat types: Brackish – lagoon areas, Estuary – lagoonal areas within 1 km of a river mouth, Freshwater downstream – river sections up to 1 km from a river mouth, Freshwater upstream – river sections beyond 1 km from a river mouth. The graph shows observed pike transits from (coloured bars), to, and within the habitats, summarised to represent the entire population's movements. If data on an individual were unavailable after the previous observation, it was categorised as moving to "No data".

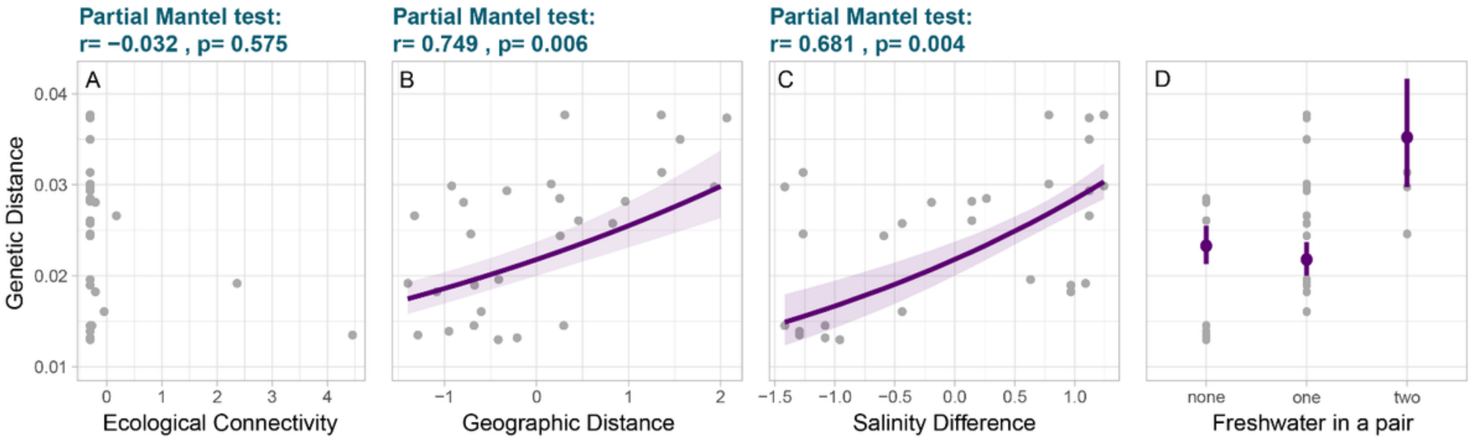

Figure 4

Effects of ecological connectivity, geographic distance, salinity difference, and the presence of the freshwater in a pair on genetic distance (pairwise linear FST). Green titles: results of the partial Mantel tests; in purple: GLM model fit for the predictors included into the most parsimonious model.

Supplementary Files

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- SupplementaryMaterials.docx