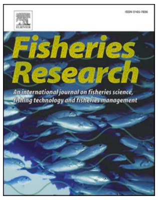
Fisheries Research 263 (2023) 106670

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres



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

Phillip Roser[a,b,*], Félicie Dhellemmes[a], Timo Rittweg[a,b], Sören Möller[c], Helmut Winkler[c], Olga Lukyanova[a,b], Dominique Niessner[b], Jörg Schütt[d], Carsten Kühn[e], Stefan Dennenmoser[f], Arne W. Nolte[f], Johannes Radinger[a], Dieter Koemle[a], Robert Arlinghaus[a,b]

[a] *Department of Fish Biology, Fisheries and Aquaculture, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany*

[b] *Division of Integrative Fisheries Management, Faculty of Life Sciences, Humboldt, Universität zu Berlin, Philippstrasse 13, 10115 Berlin, Germany*

[c] *Allgemeine und Spezielle Zoologie, Institut für Biowissenschaften, Universität Rostock, Universitätsplatz 2, 18055 Rostock, Germany*

[d] *Boddenfishing Jörg Schütt, Strandstraße 5, 18445 Kinnbackenhagen, Germany*

[e] *Mecklenburg-Vorpommern Research Centre for Agriculture and Fisheries, Institute of Fisheries, Dorfplatz 1, 18276 Rostock, Germany*

[f] *Institute of Biology and Environmental Sciences, University of Oldenburg, Carl von Ossietzky-Str. 9-11, 26129 Oldenburg, Germany*

ARTICLE INFO

Handled by Ulf Bergström

Keywords:
Spawning
Grey literature
Resident interviews
Local ecological knowledge
Habitat loss
Wetland
Acoustic telemetry

ABSTRACT

Pike (*Esox lucius*) populations across the central and southern Baltic Sea have undergone declines in recent decades. The underlying reasons are not fully understood but the loss of access to freshwater habitats in tributaries to brackish lagoons may be one important factor in some localities. Our objective was to synthesize evidence for the presence of historic and contemporary anadromy in pike from the brackish lagoon systems around the Fischland-Darß-Zingst peninsula and the islands of Hiddensee, Rügen and Usedom (Germany) by combining a review of grey literature, interviews with local citizens with knowledge tracing back to the mid-20th century, and field studies based on a range of methods, including telemetry, fyke netting and electrofishing of tributaries during the spawning seasons in the years 2020–2022. Genetic analyses were used to validate the existence of reproductively isolated subpopulations among pike migrating into different streams. The collective findings confirm the existence of freshwater spawning activity and genetic subpopulations across the entire study system in a multitude of tributaries, streams and ditches, but many populations appear to be small. The prevalence of anadromy across tributaries has likely suffered from water management activities in the 1970s and 1980s that blocked access to many rivers, ditches, streams and wetlands. Reduced access to freshwater streams through migration barriers associated with wetland management and agriculture could have fostered selection pressures to fully recruit in brackish environments, at the cost of declines and perhaps even local extinctions of once abundant anadromous subpopulations, most likely reducing stock resilience through the loss of genetic diversity and biocomplexity. Restoration of wetlands and access to freshwater spawning sites to recover subpopulations and anadromy can be recommended.

1. Introduction

Brackish environments constitute a physiological challenge for freshwater organisms. This is true, in particular, when it comes to reproduction and survival of larvae and juveniles (Remane and Schlieper, 1971). In the coastal waters of the Baltic Sea, several freshwater fish species have successfully adapted to live under brackish conditions (Nellen, 1965; Müller and Berg, 1982). One such example is the northern pike (*Esox lucius*), a large-sized piscivorous fish which inhabits the brackish coastal waters of the Baltic Sea (Larsson et al., 2015).

In the Baltic, pike have evolved different reproductive strategies. Two pike ecotypes share the same coastal feeding habitat for most of the year but use geographically distinct areas for spawning (Westin and Limburg, 2002; Engstedt et al., 2010). While one part of the sympatric

---

[*] Corresponding author at: Department of Fish Biology, Fisheries and Aquaculture, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany.

E-mail address: phillip.roser@outlook.com (P. Roser).

https://doi.org/10.1016/j.fishres.2023.106670
Received 1 July 2022; Received in revised form 15 January 2023; Accepted 15 February 2023

population has evolved to successfully reproduce under brackish conditions and resides in the coastal waters of the Baltic Sea in salinities up to 15 PSU (Jacobsen et al., 2017; Jacobsen and Engström-Öst, 2018) throughout the year, the other is anadromous and undertakes regular and seasonally recurring spawning migrations into adjacent freshwater environments, such as streams and tributary-associated wetlands (Müller and Berg, 1982; Engstedt et al., 2010; Tibblin et al., 2015, 2016; Larsson et al., 2015).

Salinities vary across the Baltic Sea in a gradient from southwest (higher salinities) to northeast (lower salinities) (Leppäranta and Myrberg, 2009), such that different subpopulations of brackish and anadromous pike are likely to show fitness peaks towards local salinity conditions. Laboratory experiments conducted with individuals from a population inhabiting the mesohaline waters of the southwestern Baltic, where the major fraction of fish is suspected to spawn in brackish waters (Jacobsen et al., 2017), provided evidence for genetic adaptations to salinity as shown by successful egg development at 8.5 PSU where fry could withstand values as high as 13 PSU (Jørgensen et al., 2010). By contrast, fertilized eggs from a Swedish anadromous population were reported to exhibit hatching failure at salinities of 6.0 PSU and beyond (Westin and Limburg, 2002). Similarly, fertilization failed in freshwater pike spawned in oligohaline conditions (Greszkiewicz et al., 2022). In Poland, local extinction of brackish adapted populations and lack of ability to recruit from freshwater sites after access to these was blocked are suspected to be a root cause of severe population declines (Psuty, 2022; Psuty et al., 2023). Pike populations thus seem to show adaptations to local environmental conditions across different areas of the Baltic (Möller et al. 2019; Sunde et al., 2018, 2022).

Pike population differentiation across salinity gradients has recently been confirmed using high resolution genetic methods by Sunde et al. (2022) and using microsatellites by Möller et al. (2021), Nordahl et al. (2019) and Diaz-Suarez et al. (2022). Local adaptation to freshwater vs. brackish spawning and natal homing (Tibblin et al., 2015; Diaz-Suarez et al. 2022; Flink et al., 2023) creates barriers for gene flow and reinforces population differentiation, further assisted by patterns of isolation-by-distance (Möller et al., 2019). Studies investigating the elemental composition of pike otoliths reported considerable variation in the ratio of anadromous to brackish spawning pike in different areas of the Baltic. While Rothla (2015) found that anadromy is the predominant ecotype in the eastern Baltic at the coast of Estonia, accounting for 89% of all Baltic pike in the region, Engstedt et al. (2010) reported only 46% of Swedish coastal pike to originate from freshwater spawning. The latter figure, however, encompassed a northern and a southern sampling site, separated by several hundred kilometers, where the discovered percentages of anadromous pike were 79% and 20%, respectively (Olof Engstedt, personal communication). The percentage of anadromous pike fell to 7% in a recent study from a high salinity site in Germany by Möller et al. (2019). Given the pronounced salinity gradient across the Baltic, it thus appears that the degree of freshwater origin among coastal pike might be inversely related to local salinities. However, it is equally plausible that lower availability of freshwater tributaries in the more saline southern regions compared to the central and northern Baltic may have constituted an evolutionary pressure, favoring the development of adaptations to spawn in brackish environments (Möller et al., 2021). Moreover, a greater significance of the earlier warming of streams in higher latitudes might play a role in the increased frequency of anadromy in the north-eastern Baltic Sea (Sunde et al., 2018). Although the reasons for different ratios of the two ecotypes in different areas are not fully understood, it is known that the anadromous pike ecotype can contribute substantially to the overall productivity of the pike stock in certain areas of the Baltic, specifically in the less saline environments in the central and northern Baltic (Engstedt et al., 2010).

The Bodden lagoons surrounding the island of Rügen constitute a socio-economically relevant pike fishery, which is co-exploited by commercial and recreational fisheries (Arlinghaus et al., 2021, 2022, 2023). Particularly the high abundance of trophy pike is well known among recreational anglers beyond Germany and laid the foundation for a relevant angling tourism sector in the region (Koemle et al., 2021, 2022). However, stock assessments have found the Rügen pike stock is currently declining and showing signs of growth overfishing and current biomass declines (van Gemert et al., 2022). It is possible that a range of pressures besides elevated predation and harvest mortality contributed to the current negative trend in biomass (Olsson et al., 2023; Arlinghaus et al., 2023).

In contrast to the Scandinavian populations of Baltic pike, scientific knowledge of the population structure and recruitment patterns of Baltic pike inhabiting the German coast of the Baltic Sea is scarce and has only recently emerged as a field of interest (Möller et al., 2019). The brackish lagoon systems surrounding the German island of Rügen stretch over 100 km from east to west (total area roughly 2000 km^2) and consist of a variety of oligohaline to mesohaline lagoons called Bodden, which comprise both sheltered, low saline areas as well as more exposed areas with greater fluctuations in salinity (Remane and Schlieper, 1971; Fig. 1). Large salinity gradients have been shown to function as a physiological dispersal barrier for pike in the area and thus shape the genetic structure of populations (Möller et al., 2021). The low density of larger streams in the area has been put forth as a reason possibly explaining the low share of anadromous pike (Möller et al., 2019), but a systematic assessment as to the degree of anadromy in the region is lacking. While Möller et al. (2019) suggest that anadromy is currently of minor importance in the highly brackish waters of the southwestern Baltic and recruitment is mainly based on brackish spawning populations, the sampling was conducted in brackish waters during spring when anadromous fish may have left already to their spawning grounds and therefore might have remained undetected in the sample. Larvae surveys conducted in brackish lagoons showed low success rates (Winkler et al., 1999 a-d; Neubert, 2011; Möller, 2020) but reports of fertilized pike eggs from brackish waters with salinities up to 9.2 PSU indicate that these areas may be used for spawning (Möller, 2020; Falk, 1965; Hegemann, 1964).

In systems, where scientific biological data are scarce and extensive surveys are not feasible, as it is typical for small-scale fisheries, local ecological knowledge (LEK) has become a promising tool to complement, if not substitute, scientific assessments (Bonney et al., 2009). Stakeholder knowledge may capture ecological processes in a comparable detail to expert assessments (Aminpour et al., 2020; Van Gemert et al., 2022; Silvano and Valbo-Jørgensen, 2008). A decline in the Rügen pike populations in the second half of the 20th century was attributed by stakeholders to deteriorating spawning conditions for anadromous pike in the course of large-scale landscape modifications starting in the 1960s under the German Democratic Republic (GDR) regime when former spawning habitats in wetlands were lost and access to freshwater streams was blocked through water infrastructures installed to drain wetlands and allow agriculture (Falk, 1965; Basan, 1989; Junker, 1988; Rechlin and Fadschild, 1991). Because harvesting of pike during the spawning season was widespread practice in ditches and flooded meadows until the early 1980s (Junker, 1988), elder fishers and local residents very likely can report historic changes in abundance of pike entering coastal wetlands and contribute other knowledge and observations not codified in the literature. LEK can ideally be completed with modern tools, such as acoustic telemetry (Dhellemmes et al., 2023; Flink et al., 2023) and population genetics. Early work from the area suggested that the lagoon pike stock is structured by salinity (Möller et al., 2021), however the study was based on microsatellites and lacked a systematic sampling of fish in tributaries. It is thus uncertain, to what extent freshwater (fish possibly spending the entire life-cycle in tributaries (Birnie-Gauvin et al., 2019)), brackish water or anadromous pike ecotypes in the study area constitute genetically differentiated sub-populations as opposed to a more or less panmictic population in which individuals may switch lifestyles to accommodate their needs. We complement the LEK analysis with genome wide population genetic

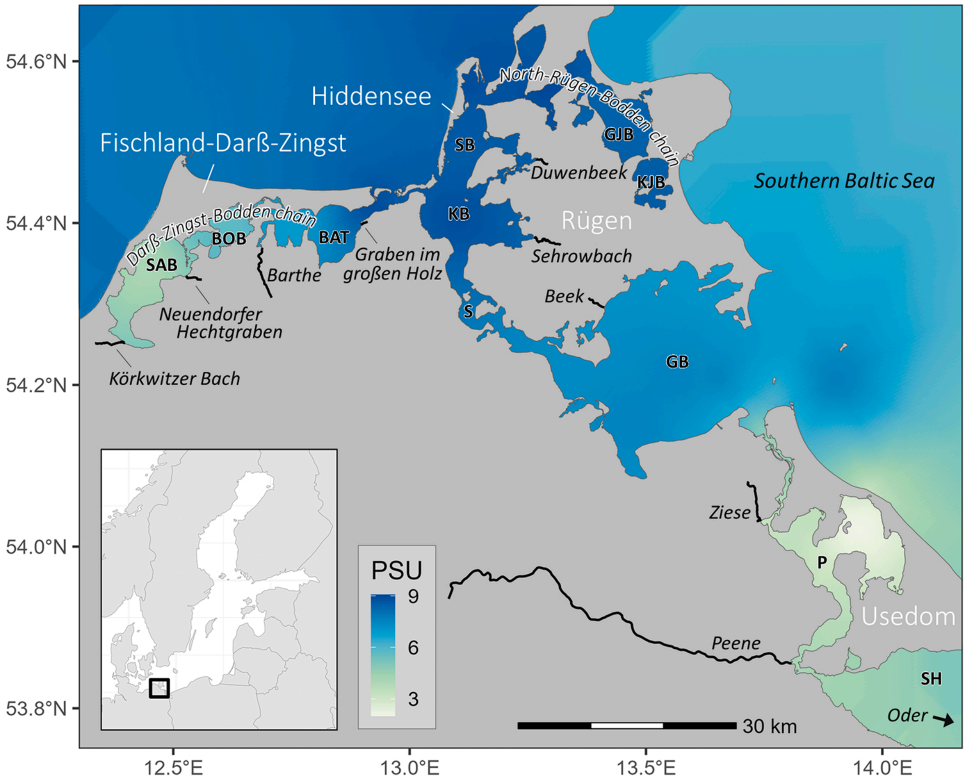


Fig. 1. Overview of the study area. All freshwater bodies sampled for this study are displayed in black with corresponding names (italic). Bodden lagoons are displayed as a colour gradient, denoting average salinity (PSU) in March and April in the years 2017–2022. Salinity data were compiled using official sources (Lung, 2022), fieldwork measurements and data loggers attached to acoustic receivers (Section 2.5.3). Capital letters denote abbreviations for Bodden lagoons: BAT: Barther Bodden (including Grabow); BOB: Bodstedter Bodden; GB: Greifswalder Bodden; GJB: Großer Jasmunder Bodden; KB: Kubitzer Bodden; KJB: Kleiner Jasmunder Bodden; P: Peenestrom (including Achterwasser); S: Strelasund; SAB: Saaler Bodden; SB: Schaproder Bodden; SH: Stettiner Haff.

analysis of pike classified into different ecotypes to test whether the population structure supports the classification into ecotypes and suggests the presence of anadromy, thereby warranting that ecotype designations are considered in management and conservation decisions.

Our paper synthesizes available knowledge about the historic and contemporary extent of anadromy in the Rügen pike stock in the southern Baltic Sea, relying on three types of data: grey literature, citizen observations and field observations through scientific sampling using a variety of gears to measure presence of eggs, larvae and anadromous adults, fish movements with telemetry and genomic data. The study's objectives were:

1. to review the scientific and historic grey literature and search for evidence of anadromy of pike around Rügen;
2. to reveal LEK among coastal residents about the anadromy of pike in our study site and evaluate the possible effect of past landscape engineering efforts on the spawning habits of anadromous pike;
3. to improve understanding on the spatial patterns and extent of freshwater spawning in the Rügen area and thereby corroborate stakeholder knowledge with scientific assessments based on field surveys in streams, marc-recapture and telemetry; and
4. to provide information about genetic structuring between brackish-water, resident and freshwater and anadromous pike in the study area to provide independent evidence for the existence of ecologically and genetically differentiated subgroups.

The key hypothesis tested was that anadromy of pike is present around Rügen and reflected in the pike meta-population structure. We explored whether the degree of anadromy declined over time in conjunction with development of water management infrastructures that block access to stream and ditch networks, similar to report from Puck bay in Poland (Psuty, 2022; Psuty et al., 2023).

2. Material and methods

2.1. Study Area

The German Bodden lagoon system is located in the southern Baltic Sea (Fig. 1). The fragmented system of islands and peninsulas creates diverse water conditions due to strong differences in the degree of exposure to the open Baltic waters and the quantity of freshwater inflow from tributaries among the different Bodden lagoons. The different lagoons are characterized by large salinity gradients with average values ranging from 3.2 to 8.2 PSU (Fig. 1, Table A1), but values of over 14 PSU are regularly recorded in lagoons west of Rügen. Major tributaries comprise the rivers Oder, Peene, Barthe and Sehrowbach, with lowest PSU values found in the southeastern part of the study area (Peenestrom and Stettiner Haff, estuaries of rivers Oder and Peene) and in the western part of the Darß-Zingst-Bodden chain where the Barthe River drains (Fig. 1). Besides these larger waterbodies, a network of smaller streams and ditches is found across the entire system, many of which are today equipped with regulated outflow mechanisms to control water levels for water management purposes, so called pump sheds (see Section 3.2).

2.2. Search for scientific and grey literature

We conducted a search of peer-reviewed and grey literature using Google scholar and Web of Science, following the keyword string “pike AND *Esox lucius* AND Baltic Sea AND Germany” as well as a search in German using “Hecht UND Ostsee UND Bodden”. Only a handful of scientific sources containing relevant information relating to reproduction of pike in Germany were identified and available online, while relevant references were directed at unpublished grey sources published in German. To locate these sources, we contacted key informants with a history of research in the German lagoons providing us with German (grey) literature, such as reports and theses. We subsequently used a snowball technique, searching for references in the German literature and examining the literature sources of unpublished reports and student theses mainly from the Universities of Rostock and Greifswald - the main organizations conducting studies in the lagoons in the 20th century. For a literature background on the landscape transformations in the study area through water management, we also searched for German literature on water management and landscape melioration in the 1970s and 1980s via Google and Google Scholar using the keywords “DDR UND melioration UND Mecklenburg Vorpommern”. Besides, we received also internal historic reports summarizing the water management history around the study area from the administration of the national park Nationalpark Vorpommersche Boddenlandschaft upon request.

2.3. *Citizen observations*

Semi-structured interviews, where participants were asked a set of predefined questions, but topics were allowed to evolve over the interview, were conducted with 13 local residents in 2021. Key questions in the survey were: Which waterbodies serving as pike spawning habitat do you know of and what is your source of information? Are pike found in these waterbodies during springtime exclusively? During which month does pike spawning usually start? What is the duration of spawning? Has the extent of pike spawning migrations into freshwater changed over time? How has the melioration period and associated water regulation measures affected the extent and accessibility of spawning areas? Have you pursued fishing and hunting techniques for pike during spawning at one point in your life and which methods have you applied? Have you observed pike spawning in the brackish Bodden lagoons?

We choose a snow-ball technique to identify key informants (fishers, fishing guides, local residents), aiming for at least one representative from each of the different lagoons around Rügen (Fig. 1). An initial set of people who were thought to possess valuable knowledge on the topic were recommended by anglers and fishers participating in a current project studying the Baltic pike at Rügen (www.boddenhecht-forschung.de). Further participants were then recruited via recommendations by the interviewees. Prior to the interviews, participants signed an agreement in which the voluntary participation and consent to recording, transcription and (anonymous) use and publication of the data were declared.

Interviews lasted between 10 and 120 min and were audio recorded. Interviews were transcribed and information was subsequently aggregated by topic, whereby interview sections that were found to be representative or particularly informative were translated into English and are presented as citations in the results to illustrate stakeholders’ memories and thoughts in relation to the topic.

The spatial extent of expertise of the 13 interviewees comprised all Bodden lagoons in the area (Darß-Zingst-Bodden chain (n = 6), Kubitzer Bodden (n = 3), North-Rügen-Bodden chain (n = 2), Strelasund (n = 1), Greifswalder Bodden (n = 4), Peenestrom/Achterwasser (n = 1) and Stettiner Haff (n = 1).

Besides the aforementioned interviews focusing on observations from freshwater, spatial data derived from previous interviews (n = 49) conducted in 2020 were used to complement suspected (mainly brackish) spawning sites. These interviews included the same legal procedures described earlier in this section. For details, see Vogt (2020).

2.4. *Approximation of spawning habitat loss through water management*

To obtain quantitative estimates on the extent of coastal freshwater habitats that could be used for spawning, spatial data of waterbodies from OpenStreetMap, covering also smaller waterbodies like drainage ditches, were used. In accordance with results obtained from electrofishing surveys described in Section 2.5.1, a threshold of 2 km inland from the Bodden shoreline was chosen to define which parts of a waterbody were potentially accessed by anadromous pike. After the exclusion of all waterbody data exceeding this threshold, only the sections of waterbodies found within 2 km proximity to the coast remained (i.e. we only considered the downstream section of all waterbodies). To categorize between accessible and inaccessible habitats (as a relic of blocked access into a waterbody by means of pump sheds, i.e. electrical pumping stations), data on pump shed locations were used. These data were obtained from local water management authorities (Wasser- und Bodenverband of the island of Rügen and the districts of Barthe and Recknitz). From areas without official data, pump sheds were visually identified via Google Maps. For each pump shed, the catchment area (defined as connected waterbodies whose only connection to the Bodden lagoons was interrupted by a pump shed) was manually defined for the freshwater bodies. It is important to note that pump sheds are only one possible obstruction for waterbodies and other obstacles can exist that we did not map (see Section 3.1.1). Therefore, our estimate of blocked access is certainly an underestimate. For quantitative data, the cumulative length of waterbodies (blocked and not blocked) was calculated for each Bodden lagoon.

2.5. *Scientific assessment of current anadromy of adult coastal pike at Rügen*

2.5.1. *Electrofishing and data analysis*

To assess the current degree of anadromy, five selected streams (Beek, Duwenbeek, Sehrowbach, Neuendorfer Hechtgraben and Körkwitzer Bach, see Fig. 1) were sampled over one spawning season. Stream selection aimed to cover the variation of different lagoons of the region, and was based on preliminary indications of anadromy (Sehrowbach and Duwenbeek), recommendations by residents (e.g. Neuendorfer Hechtgraben) and the feasibility of sampling (i.e. accessibility by boat). Weekly sampling was conducted by standardized electrofishing throughout a 7-week study period between March 02, 2021 and April 15, 2021.

Sampling was conducted starting at the river mouth, i.e. outflow into the lagoon. Total sampled stream length varied between the waterbodies (maximum distance from river mouth: Körkwitzer Bach: 3.5 km, Sehrowbach: 3.3 km, Beek: 2.8 km, Neuendorfer Hechtgraben: 2.0 km, Duwenbeek 1.3 km), it was determined under consideration of local conditions such as stream length, width and accessibility. We additionally sampled a 1.8 km stretch of Ziese River draining into Peenestrom on three occasions (March 18, April 01 and April 08, 2021) to complement our systematic field survey in five streams, but logistical constraints prevented us from a weekly sampling campaign in this stream.

To standardize the electrofishing effort across streams, each stream was partitioned into transects of 100 m, where the total number of transects per stream was determined by the sampled stream length mentioned earlier in this section. At each sampling event 600 m stream length, i.e. six transects per stream were sampled. Of the six transects per stream, three of the transects were fixed and subject to repeated sampling during each sampling event, while the other three transects were chosen according to a stratified random sampling design differentiating the mouth, middle and upper sections of the stream with one random transect in each respective section. Fixed transects were placed at the beginning of the lower-, middle- and upper- sections of the study area starting from the river mouth. This design assured coverage of the full range of selected stream length, while allowing for some randomization.

Fishing from boat was conducted using a generator-powered 8 KW pulsed DC electrofishing unit (EFKO FEG 800) with a 500 mm diameter ring anode. In those waterbodies where the channel dimensions did not allow for boating (Neuendorfer Hechtgraben and Beek) a battery-powered 650 W pulsed DC backpack-device (Jürgen Bretschneider Spezialelektronik BSE EFGI 650) with a 300 mm ring anode was used. Captured pike were stored in a live well until all transects were fished, then brought to shore for processing. Each captured individual was measured to the nearest millimeter, weighed to the nearest 0.2 g and sexed by examination of the urogenital tract (Casselman, 1974). Because the latter sex-determination method is not appropriate for immature small pike, some fish were stunned and killed for examination of the

Fig. 2. Fyke net setup at the outflow of a ditch entering Barther Bodden/Grabow at 54.3982° N, 12.8970° E.

Table 1
Numbers of pike externally tagged for mark-recapture per area.

Area	Females	Males	Unknown
Barthe	12	15	0
Barther Bodden/Grabow	526	254	7
Beek	0	3	0
Duwenbeek	4	15	0
Greifswalder Bodden	41	53	0
Kubitzer/Schaproder Bodden	579	880	9
Körkwitzer Bach	7	6	0
Neuendorfer Hechtgraben	12	8	0
North-Rügen-Bodden chain	399	265	2
Peene	2	10	0
Peenestrom/Achterwasser	94	15	29
Strelasund	15	25	1
Sehrowbach	29	132	0
Ziese	8	18	0

presence of internal sexual organs. Fin clips were taken from the pectoral fin for the subsequent genetic analysis and stored in ethanol. All fish larger than 30 cm received external Floy-tags (Floy T-bar anchor, Floy Tag & Mfg. Inc., NE, U.S.A.) near the dorsal fin and were released in their stream of origin.

For the five regularly sampled streams, channel depth- and width were determined every 50 m along the investigated area of each stream using a pole with 5 cm tick marks. For the larger streams (Sehrowbach and Körkwitzer Bach) we used Google Maps to determine stream width at the same 50 m intervals. Water temperatures were recorded via Hobo (HOBO, UA-002–064) pendant data loggers which were set at a recording interval of 30 min and placed in the streams in March 2021. Salinity was determined on each sampling event using a WTW Multi 3630 IDS and a conductivity sensor WTW TetraCon 325 (Xylem Analytics Germany Sales GmbH & Co. KG, Germany).

To test for significant differences in CPUE (catch per unit effort, i.e. individuals per 100 m) between the sampling weeks (alpha = 0.05), we calculated generalized linear models (GLMM) using the software R (R Core Team, 2022). Data comprised 210 observations, each representing a sample of a 100 m transect (nested within stream). Captures of pike > 30 cm per transect were used as a response variable, as we expected predominantly adult size classes to move into the waterbodies for spawning. Data exploration showed heterogeneity in variances in catches between the sampling weeks and non-normal distribution of the response variable (catch) as well as a high percentage of zeros (69%). To accommodate the positively skewed structure of count data and the high share of zeros, we fitted GLMMs for Poisson distributions using the R-package glmmTMB (Brooks et al., 2017). GLMMs were fitted with one fixed effect (weeks, categorical, 7 levels) and two random effect terms (stream and transect:stream to account for spatial nestedness of the data). Because sampling effort was equal across all observations, effort was not included as an offset term in the model. All models were checked for appropriate residual patterns and zero inflation using the R-package DharmA (Hartig, 2022). To test whether the sampling weeks were a significant predictor of the catch, we compared the full fitted model with a model with the week term dropped using the likelihood-ratio test via the anova() command. For a post-hoc comparison between the individual weeks, we used the Tukey-HSD test with a Bonferroni-correction to control the family-wide error rate.

2.5.2. *Fyke net*

Additionally, in the spawning season of 2022, a ditch locally called “Graben im großen Holz” (Fig. 1), known to host spawning pike as witnessed by video material of an interviewee, was fully blocked by a fyke net from March, 9 to May, 1, 2022 to provide a full enumeration of the local pike spawning migration (Fig. 2). The fyke net was checked daily, all captured pike were measured and tagged with Floy-tags. Subsequently, fish were released upstream of the fyke net to allow for spawning. A gap of 20 cm was included between the shore and the fyke net to allow for emigration.

2.5.3. *Mark-recapture and telemetry*

As part of other sampling efforts to estimate fisheries mortality based on mark-recapture with external tags, from 2020 to 2022, a total of 3433 fish were externally tagged with Floy-tags, the majority in brackish lagoons (Table 1).

Fishers and anglers from the area could report any recaptures (along with the capture location) at a web address (www.boddenhecht-forschung.de) or via a telephone number which were both indicated on the external tags, along with the fish’s unique ID. To motivate reports, a lottery chance was given to anyone who reported a recapture, and if the pike carried an acoustic transmitter (see below) and was reported for the first time, a reward of 100 € was given. We added the animals that we recaptured while scientific angling for the project to this data. Recaptures of marked fish tagged outside the spawning season in lagoons within the tributaries or outmigration of externally tagged fish tagged during spawning in tributaries (Table 1) were interpreted as suggestive to be anadromous pike.

Additionally, we deployed an array of 140 acoustic receivers (VR2Tx, Innovasea Systems Inc. DE, U.S.A) which covered the brackish water lagoons (Dhellemmes et al., 2023) around Fischland-Darß-Zingst, Rügen and Usedom as well as key freshwater tributaries (Peene, Barthe, Sehrowbach and Duwenbeek, Fig. 3). 305 pike were tagged with acoustic transmitters (MM-R-16–50 HP, random pulse rate: 60–180 s, 69 kHz, Lotek Wireless Inc., ON, Canada) before and during the 2020 spawning season (Table A2). When a pike swam in proximity of a receiver, the date, time and unique ID of the animal was recorded. The receivers were downloaded yearly in winter, in collaboration with Institut für Fisch und Umwelt (FIUM), Rostock. Further details on the deployments and data processing can be found elsewhere (Dhellemmes et al., 2023).

The acoustic telemetry setup allowed us to collect evidence for anadromy by quantifying the monthly ratio of individuals detected in freshwater on the number of individuals tagged for each area (Fig. 3). This allowed to scrutinize the movements of pike captured and released in the tributaries during the spawning period (especially rivers Barthe, Peene and Sehrowbach) into the brackish lagoons, as well as movements from lagoon-tagged pike tagged outside the spawning period into the rivers during the spawning period. We interpreted the data at the stream level as anadromy when at least one fish showed the respective behavior

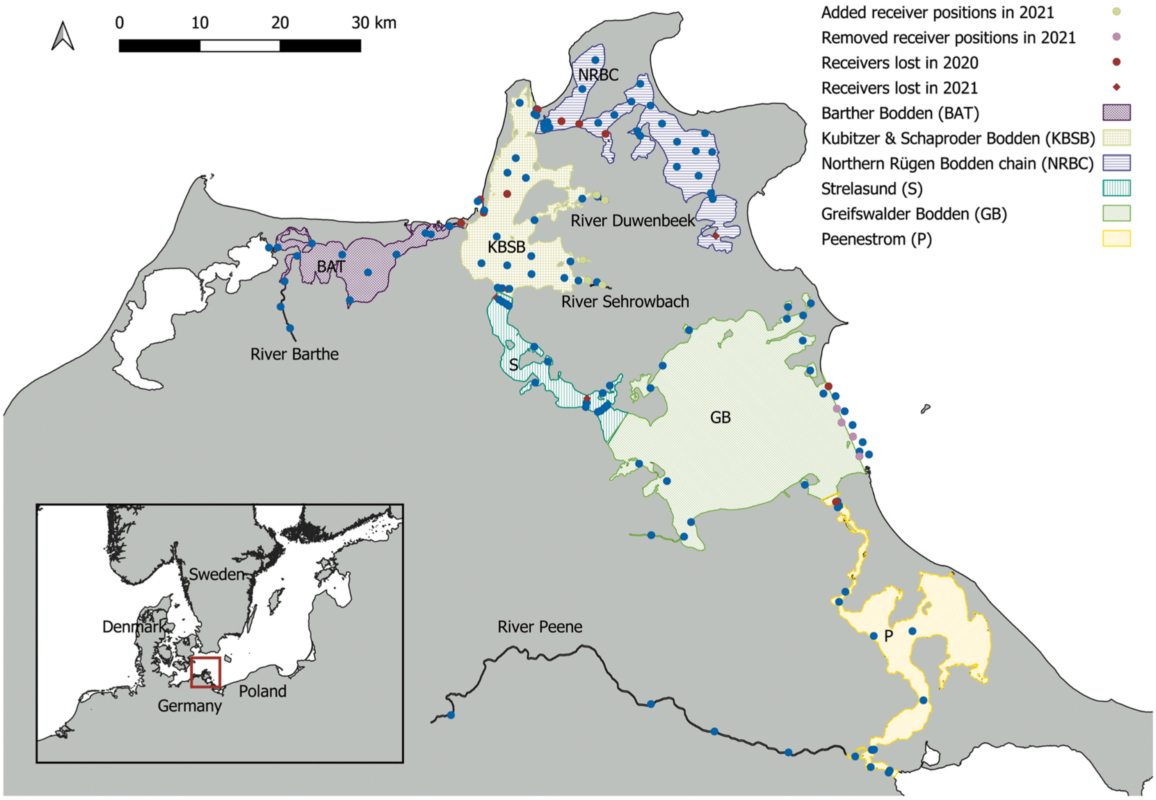


Fig. 3. Map of the study area displaying the position of the acoustic telemetry receivers.

(i.e., moving from the brackish lagoons into a stream during spawning time).

To further evaluate the site fidelity of acoustically tagged pike released in the tributaries, a residency index (RI) was calculated. Only the fish for which data was available, i.e. they were detected on the receiver array, were considered for the indices. RI was defined as the ratio of the number of days each individual was detected at the release area to the total number of days it was detected. RI ranged from 0 to 1, where values close to 0 indicate low residency and values close to 1 indicate high residency in tributaries (Bond et al., 2012; Espinoza et al., 2015).

2.6. *Assessment of eggs and larvae*

To evaluate the occurrence of pike eggs and larvae in ditches and streams and adjacent coastal areas and thereby verify reproduction in these habitats, we sampled freshwater streams and their brackish estuaries with salinities in a range of 0–4 PSU as well as small man-made drainage ditches that showed reduced salinities compared to the adjacent lagoons (0–7 PSU) and therefore could be a suitable spawning habitat for anadromous pike. The eggs and larvae encountered were visually identified. Given the size and colour of the eggs and distinct morphological larvae characteristics, species identity of pike was mostly identified in the field. Most of the larvae were measured and released, few specimens were anaesthetized, killed and fixed in 70% ethanol. The eggs that were found were transported in location-specific water to an experimental hatchery setup in the laboratory. The eggs were transferred into two 1.5 l aquaria within the respective location water. The eggs continued developing, and larvae hatched and grew to 120 mm total length, serving as a proof of pike identity and successful hatch. Overall, we sampled a total of 55 different areas in the southern part of the Island of Rügen using six different methods over three consecutive spawning seasons from 2015 to 2017. Based on the maturity level of adult pike captured and the prevailing water temperature, the hatching time was approximated. Sampling methods were adapted to the respective life stage of pike as follows:

A white disc (diameter: 185 mm) was attached to a wooden handle 1200 mm in length. The disc was moved cautiously over the seafloor and between aquatic plants, especially reeds, to detect small fish larvae. Each search transect covered 100 m of shoreline along the reed belt. This method had been used successfully in previous studies (Kallasvuo et al., 2010, 2011) as the disc supplies a strongly contrasting background against which to identify fish larvae. This method is suited during the first 8 – 10 days after hatching in the eleutheroembryonic life stage. Additionally, the search transects were sampled using a dip net with an opening of 60 cm and a square mesh size of 1 mm (measured knot-to-knot).

For sampling of the larval and early juvenile stages of pike we designed Quatrefoil plexiglass light traps. Larvae are known to be positively phototactic (Zigler and Dewey, 1995) and this method has been successfully used in previous studies on northern pike (Pierce et al., 2006; Timm and Pierce, 2015). We deployed 14–21 traps per sampling site at sunset. Chemical light sticks with different colors known to attract 0 + pike for at least six weeks after hatching (Zigler and Dewey, 1995) were inserted in the four chambers of the traps and traps were emptied the next morning. Traps were mainly placed in reed belts in approximately 50 m distance to each other and attached to bamboo sticks (2 m in length).

Beach seining was performed adjacent to reed belts, as reed belts function as nursery habitats for pike larvae and juvenile pike. A beach seine of 8 × 1.2 m with a square mesh size of 20 mm at the wings and 5 mm square mesh size at the cod end was used. It was deployed at depths of 0.5–1.0 m. Every haul was carried out 100 m along the reed belt line and lifted to shore to identify and measure the captured fish.

Electrofishing was carried out at 350–700 V with two different devices (Hans Grassl GmbH, IG200 and FEG5000) and 100–200 m transects in freshwater streams and ditches. This method is suitable for catching adult as well as larval and juvenile pike.

A beam trawl was used in the open lagoon area to collect water plants at depths between 1 and 2 m. The beam trawl we used was 2 × 0.35 m with a square mesh size of 4.5 mm. It was used to sample plant material from the seafloor which was then searched manually for attached eggs or eleutheroembryos. We used this method in the 2017 post-spawning season based on observations of spawning pike by local fishing guides.

The methods were not used in a quantitative manner but as a way to achieve detections of either eggs or larvae as evidence of successful reproduction.

2.7. Genetic structuring of pike populations

To assess population structuring of pike in the Rügen area, we employed a pool-sequencing approach that allows a cost-effective estimation of genome-wide differentiation between pike populations (Schlötterer et al., 2014). In total, 11 locations were included, which at the time of sampling, were assumed to reflect either resident mesohaline brackish-water (Barther Bodden, Kubitzer/Schaproder Bodden, Großer Jasmunder Bodden, Greifswalder Bodden, Fig. 1), possibly resident/anadromous freshwater (rivers Barthe and Peene) or oligohaline brackish environments (Peenestrom, Stettiner Haff) or putative anadromous populations given the rather small size of the stream and the low likelihood to find fully resident freshwater populations (Sehrowbach, Neuendorfer Hechtgraben, Ziese River). The percentage of fish sampled during the spawning months March and April for each waterbody can be found in Table A3.

Tissue samples (fin-clips) were taken from 45-50 individuals per location and stored in ethanol. DNA extraction followed a standard phenol-chloroform protocol (Sambrook et al., 2001). For each location, DNA of 45-50 individuals were pooled (Table A3) and sent for Illumina 150-bp paired-end sequencing to CeGaT (Tuebingen, Germany). All sequence reads were archived at the European Nucleotide Archive under Accession nos ERR10795327 to ERR10795337 (study accession nr PRJEB59012) (http://www.ebi.ac.uk/ena/). Sequence reads were trimmed for a minimum length of 50 bp and a minimum quality score of 20 across 5 bp sliding windows using the Trimmomatic software (Bolger et al., 2014). We used NextGenMap (Sedlazeck et al., 2013) to map the trimmed reads against an annotated genome of *Esox lucius*, available at NCBI (GCF_011004845.1). The SAMtools software (Li et al., 2009) was used for converting the resulting files into a binary (bam) format and to check for average coverage. For calling single nucleotide polymorphisms (SNPs), we combined all bam files into a single mpileup file using SAMtools v.1.3.1. For subsequent analyses in popoolation2 (Kofler et al., 2011), the mpileup was simplified into a sync-file format. We kept only biallelic, chromosomal SNPs with a minimum count of five of the minor allele, a minimum allele frequency of 10% of the minor allele, a minimum coverage of 20 and a maximum coverage corresponding to the average plus two times the standard deviation of the pool with the largest coverage. Next, allele frequencies and FSTs for every SNP were estimated in popoolation2, using the sliding-windows option with a window size of one in order to take pool sizes into account. Average genomic differentiation, measured as FST, was calculated for all pairwise comparisons using a custom perl script. To visualize genetic sub-structuring, we built a Neighbor-Joining tree from the pairwise FSTs using the PHYLIP/NEIGHBOR v. 3.695 (Felsenstein, 2005) and FIGTREE v.1.4.4 (Rambaut, 2011) software. Finally, we used popoolation v.1.2.2 (Kofler et al., 2011) to calculate genome-wide estimates of nucleotide diversity (pi, Nei and Li, 1979) for each chromosome separately, using window sizes corresponding to chromosome sizes and averaging chromosomal pi values at the end.

3. Results

3.1. Literature synthesis

3.1.1. Historical background of water management and agriculture

Human attempts to drain bogs in the Rügen area date back to the 17th century (Wiemers and Fischer, 1998). While occasional drainage ditches are depicted on historic maps from the early 19th century (Fig. 4, Holz, 1991), the ditch network intensified around the end of the 19th century when polders were built, which could be drained using windmills. The construction of ditches continued throughout the first half of the 20th century, however, the most significant changes occurred in the second half of the 20th century (Holz, 1991). Between 1949 and 1990 the study area was part of the GDR in socialist Germany. During the 1950s, agricultural productivity was low and did not meet the requirements laid down in the planned economy of the GDR. Subsequently, the collectivization of the agricultural sector was enforced. Water infrastructure management - called “melioration” - was seen as a crucial prerequisite for the planned transformation of agriculture, heavily impacting also the wetlands along the brackish lagoons (Fig. 4, Van der Wall and Kraemer, 1991), many of which were drained to gain farmland (Holjewilken, 1960). Electrical pumping stations (referred to as pump sheds) were installed within the drainage ditch networks by which groundwater levels could be controlled throughout the year to meet agricultural demands (Holz, 1991). Areas which were previously subjected to regular floodings (thereby providing suitable pike habitat for spawning) were now artificially drained. Only a few decades after the initiation of these major efforts, most wetlands of the GDR had been artificially decoupled from the coastal dynamics and were modified to farmland suitable for the deployment of heavy agricultural machinery (Hermann and Sieglerschmidt, 2017).

Until today, different permanent systems for directed water flow can be found in the area and are present at many freshwater outflows in the region (Fig. 5). While pump sheds are equipped with electric pumps to regulate the water levels in the drainage canal systems inland, flap gates function mechanically and allow for outflow of excess freshwater into the Bodden at high stream discharge rates while closing when water levels in the Bodden increase. The latter system constitutes a less sophisticated approach to avoid flooding of adjacent meadows and can be

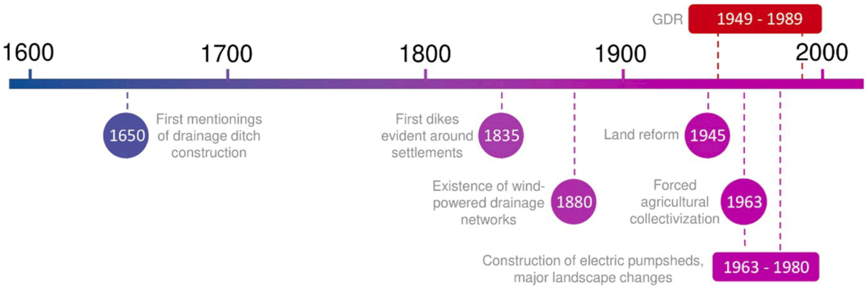


Fig. 4. Conceptual timeline displaying the temporal development of agricultural drainage systems around Rügen in the historical context.

Fig. 5. Examples of barriers for directed water flow between fresh- and brackish waterbodies: Outlet of a pump shed with the main facility building in the background (left) and different types of flap gates (middle, right).

found at the outlet of many smaller ditches. Pump sheds are impermissible gates blocking access into freshwater entirely while flap gates are in theory allowing for limited entry under certain conditions (Fig. 5). Besides that, also other systems are present, such as manual weirs.

Despite ongoing progress in the renaturation of bogs in the federal state of Mecklenburg-Western Pomerania since the reunification in 1990, currently about 65% of the coastal bogs in the Rügen area remain drained (Schiefelbein, 2018). These large-scale transformations substantially reduced access to freshwater bodies for pike feeding in the lagoons and minimized access to temporarily flooded saltmarshes, likely intensifying selection pressures to adapt to spawn in brackish conditions (Möller et al., 2019; Möller, 2020).

3.1.2. *Anadromy of lagoon pike in scientific and grey literature*

The occurrence of spawning migrations of Bodden pike into freshwater habitats for spawning is mentioned in different literature sources, mainly grey literature (Junker, 1988; Winkler, 1989; Rechlin and Fadschild, 1991) or anecdotal reports in angling media (Basan, 1989). In his elaborate summary on the ecology and use of pike in the coastal lagoons around Rügen, Falk (1965) states that among other habitats, tributaries and flood plains are the destinations of the spawning migrations for lagoon pike and constitute a prerequisite for the high catches of commercial fisheries with passive gear in spring at that time. Similarly, Juncker (1988) describes the practice of pike stabbing with customized pitch forks during pike migrations into shallow habitats like ditches and flooded meadows during spawning time. These forks are also mentioned as an illegal but common gear for pike in a summary on German Baltic fisheries from Deutscher Seefischerei-Verein (1905). Moreover, Juncker (1988) and Winkler (1989) refer to potential limitations on the extent of pike spawning habitat as a consequence of melioration and dike construction. Rechlin and Fadschild (1991) report that tributaries of the Bodden lagoons are a meaningful reproduction habitat for the freshwater fishes inhabiting the brackish systems. They also argue that high catch rates of pike in Greifswalder Bodden at the time are evidence of sufficient functional spawning habitat, which was also described by Winkler (1989) and Biester (1991). By contrast, in a statement issued from the fisheries surveillance authority of the city of Lauterbach (Vierck, 1980), pump sheds and weirs were claimed to have blocked access to many natural spawning habitats (i.e. ditches) of pike in Greifswalder Bodden, which was suspected to be a detrimental development. Similar, in a popular angling book describing fishing in the Bodden lagoons, Basan (1989) argues that only a minor share of Bodden pike must swim into freshwater for spawning because the few freshwater inflows would otherwise be stacked with pike in spring. At this time melioration was already completed, perhaps representing an already impacted situation.

Although the above cited sources have expressed concerns that blocking access to the freshwaters might have reduced the recruitment and in turn productivity of the pike stock, evidence for strong stock declines of the Rügen pike stock only emerged in the 2000s (Van Gemert et al., 2022). As the key impacts of the melioration were in the 1970–1990s, either effects on the total stock were delayed or the pike stock has managed to adapt to brackish spawning and has maintained recruitment despite the lost access to freshwater networks through water infrastructure management. In the more eutrophied lagoons (e.g., Darß-Zingst-Bodden chain), pike stocks have likely suffered from loss of underwater vegetation and pikeperch (*Sander lucioperca*) has increased alongside eutrophication. In these areas, eutrophication has likely had a greater impact on stock productivity and recruitment than blocked access to freshwater streams (Winkler, 1991; Winkler and Debus, 2006), although pressures caused by reduced access to flooded wetlands perhaps also played a role by reducing genetic and stock biocomplexity, possibly leading to loss of resilience.

3.2. *Approximation of spawning habitat loss through water management*

The total length of coastal waterbodies currently found within 2 km inland of the Bodden-coastline across all lagoons was determined > 1560 km. Just under 1000 km were found to be drained by pumping stations, corresponding to a share of 63%. An overview of all waterbodies considered for this approximation and the respective Bodden area they were assigned to can be seen in Fig. 6, indicating that the impacts of water management have been widespread and extensive across the region. Note that this is an underestimation as we lacked geographic information on other barriers to migration present in the system (Section 3.1.1).

The highest ratio of blocked freshwater habitats was found in eastern part of the study area (Darß-Zingst-Bodden chain), where about three quarters of the waterbodies considered are today blocked by pumpsheds and only one quarter is freely accessible (Fig. 7). Similarly, a higher share of blocked waterbodies when compared to accessible ones were found in the Bodden-regions of Kubitzer/Schaproder Bodden, Peenestrom/Achterwasser, Oderhaff and the North-Rügen-Bodden chain. At Strelasund the ratio between the two categories was about equal, while only in Greifswalder Bodden the share of freely accessible waterbodies exceeded that of the blocked ones. The absolute figures, split up by Bodden-region, are provided in Fig. 7.

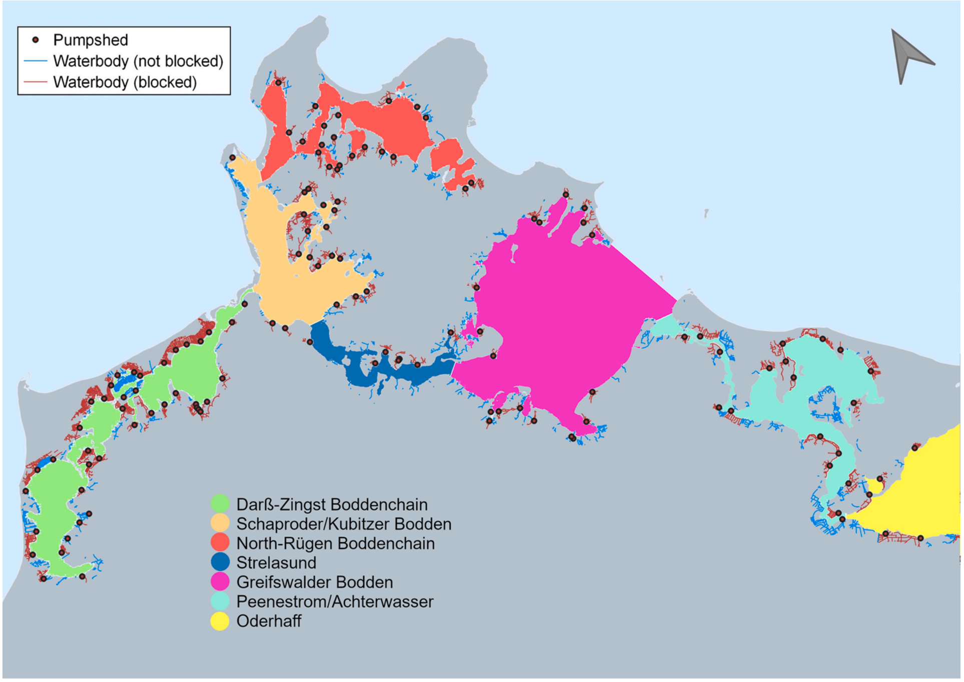


Fig. 6. Depiction of the main Bodden areas around the Island of Rügen. Coastal freshwater bodies (within a 2 km strip inland of the Bodden coastline) are displayed in red and blue along the coastline where colour indicates the existence/lack of connectivity with the Bodden lagoons. Black dots display the locations of pumpsheds blocking access into waterbodies.

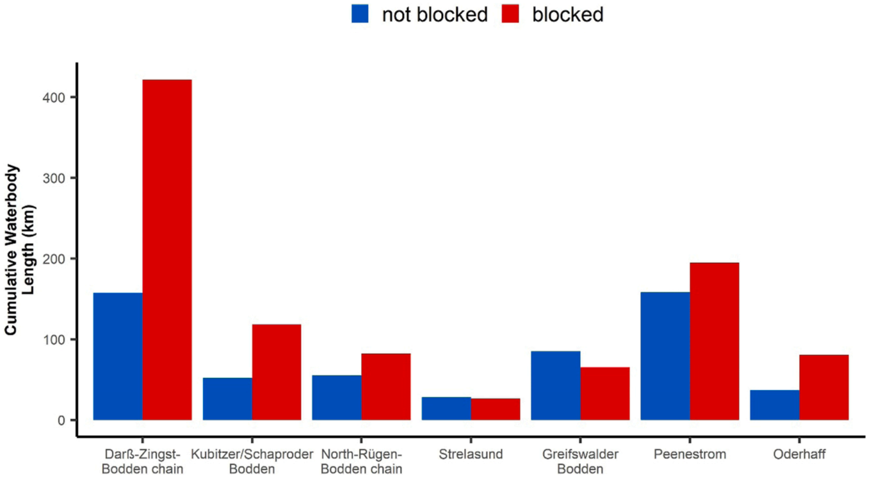


Fig. 7. Cumulative waterbody length of coastal freshwater bodies within 2 km of Bodden coastline, categorized by the presence or absence of pump sheds at the entrance to the Bodden-lagoons.

3.3. *Indications for anadromy from interviews and scientific assessments*

By combining data derived from interviews (Section 3.3.1) and scientific methods (Section 3.3.2 and 3.3.3) we were able to compile a total of 52 freshwater bodies from our study site that are likely to host/having hosted anadromous pike populations or where anadromy has been confirmed (Fig. 8, Table 2).

3.3.1. *Citizen observations*

Interviewees identified 50 waterbodies (streams, ditches and wetlands) hosting anadromous pike (Ryck and Körkwitzer Bach thereof derived from interviews in 2020). In addition, 50 suspected brackish spawning sites were identified (48 thereof derived from interviews in 2020). A map containing all waterbodies mentioned by interviewees is displayed in Fig. 8. Additional information for each waterbody is provided in Table 2. A summary of interview contents for each participant is provided in Table 3.

The in-depth knowledge of pike biology held by 13 participants originated from intense occupation with the waterbodies - due to backgrounds as fishers (n = 4), as (former) employees in water-management (n = 3) and/or by confrontation with the topic through angling and guiding (n = 7). In one interviewee the expertise was derived from intergenerational knowledge exchange exclusively (n = 1). Notwithstanding their professions, all respondents grew up near the lagoons. Many could thus contribute observations and stories they had heard from their family or other members of their community, also dating back to the decades before the GDR melioration period.

Twelve of the thirteen interviewees reported having witnessed

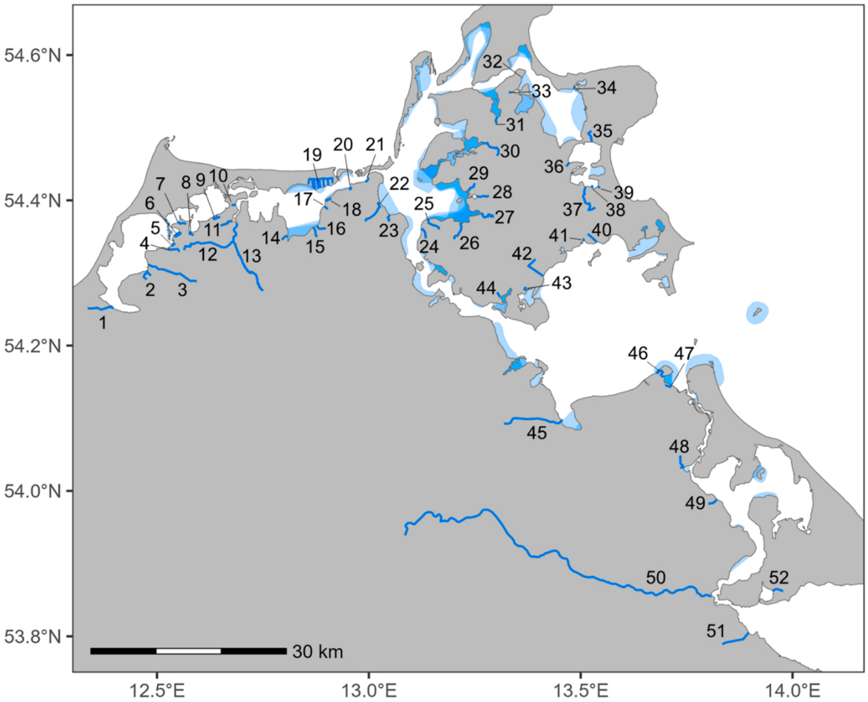


Fig. 8. Overview of freshwater bodies from interviews and field sampling. Suspected brackish spawning sites from interviews are displayed as blue areas in the lagoons with areas more frequently mentioned displayed in higher color intensity. Complementary information for each freshwater body is displayed in Table 2.

spawning aggregations of pike in freshwater tributaries of the Bodden lagoons themselves. Besides their own personal observations, participants were able to name specific waterbodies which they had heard to be functioning as spawning habitat for anadromous pike.

According to the interviewees, the exploitation of pike aggregations during the spawning periods was common practice in former times (Fig. 9). Nine participants reported on their own past experiences in this field. Two different techniques were mentioned: 1: forged pike-forks with barbs (similar to pitchforks) with which fish were then bayonetted, or 2: self-made sling constructions using a wooden stick with a wire which was then patiently guided over the pikes' body until the wire was eventually tightened and the unsuspecting fish could be abruptly scooped on land (Fig. 9). While "*Hechtstechen*" (German colloquial speech for the practice, engl. *"Pike stabbing"*) was not legal and local policemen were aware of its occurrence, most participants described the act as having been a *"youthful folly"* during their childhood and teenage years. Interviewees described these hunting techniques as suited for the spawning season firstly because pike were then perfectly accessible in the shallow waters and secondly because they were distracted during their spawning act: *"You need the pike spawning so they don't get it. Only when they are spawning you can stand right next to them and they won't notice you."* (interviewee G). Still, these techniques required skill: *„You have to be careful - every minor detail! And [there must be] no shadow on the water!"* (interviewee B).

While the most frequently mentioned waterbodies for this type of pike hunting were ditches and streams, also coastal wetlands (which may have had reduced salinities but were not pure freshwater) were indicated as spawning habitats of pike. Examples included Günzer See and Prohner Wiek, both coastal wetlands formerly connected with Barther Bodden and Kubitzer Bodden, respectively. Also flooded meadows along the shores of the lagoons were described to host spawning pike that have formerly been exploited in this way. Participants memories from pike observations on flooded meadows, however, referred back to an era prior to the melioration period after which flooding of meadows did no longer take place in most areas. Interviewee A recalled his past impressions on meadows adjacent to Barther Bodden/Grabow, saying: *"The meadows were generally flooded, every year. [...] Salmon spawning migration in Canada, you know, when they are wagging, the salmon? That's what it looks like too on the meadow. [...] You see them, they come through the surface."*. The responded further reported to have engaged in pike stabbing on these meadows until the area was meliorated and a dike and pump shed was built in the 1970s. Interviewee G stated: *"When the meadows were flooded back in the days, this I only know from my father, I didn't experience this anymore because through all these dikes and so on it didn't happen anymore, [...] then there were also pike on the meadows."*. Similarly, participant B reported of his fathers' stories when pike were found on flooded meadows prior to the construction of dikes.

Owing to the hunting activities, participants were able to report on ecological details they remembered having observed. One interviewee talked about the phenology of spawning: *„When there is ice until April [...] all pike go into the ditches for about two weeks. Then you could catch good numbers. The ditch was filled up [with pike] then. If there is no ice and it happens over a long period then there are no days where you catch a lot."* (Interviewee G). The same person reported that pike would stay no longer than 24 h in the smaller ditches, entering at night while resting during the day and leaving the same channel after spawning in the evening, according to his observations.

All 13 participants were aware of the detrimental consequences of the landscape transformation due to water management (Table 3), having rendered numerous former spawning habitats inaccessible or physically eliminating them through drainage. An observed decrease of anadromous spawning activity, as witnessed by the majority of participants (Table 3), was exclusively related to the construction of impediments, restricting or blocking movement in and out of the freshwater bodies. Freshwater spawning was reported to occur only in waterbodies with unimpeded connection to the lagoons. Reflecting also other participants opinion on the issue, one participant stated: *"All ditches which were once accessible and where there was freshwater flowing into the Bodden, were used for spawning. Fish is moving in everywhere around here. There are few muddy ditches they don't use but into all the larger ones they did migrate."* (Interviewee B), subsequently further arguing *"This is the disaster. All these closed flap gates and things"*, with reference to other types of blockages commonly found in the area. Another interviewee

Table 2

Supplementary information to freshwater bodies displayed in Fig. 8, where the numbers displayed correspond to column “ID”. Column descriptions: *Column 3: Information type available (E1: Systematic electrofishing, E2: Non-systematic electrofishing, I: Interviews, T: Telemetry, F: Fyke net, M: Mark-Recapture), Column 4: the certainty of prevalent anadromy (C: Confirmed with scientific sampling, S: Suspected, N: Not confirmed), Column 5: type of interview knowledge (S: Self-witness, H: Hearsay), Column 6: number of interviewees mentioning a waterbody as hosting/having hosted anadromous pike populations, Column 7: Whether an observation relates to the period before 1970 when access to many waterbodies was blocked. Ditches with unknown names were termed “Graben_x” and consecutively numbered.*

1 ID	2 Name	3 Information Type	4 Confirmed Anadromy	5 Interview Knowledge	6 # n Interviewees	7 Observations before melioration
1	Körkwitzer Bach	I, E1, M	C	H	1	No
2	Graben_x3	I	-	S	1	No
3	Saaler Bach	I	-	S	1	No
4	Neuendorfer Hechtgraben	I, E1, M	C	S	1	No
5	Schulweggraben	I	-	S	1	No
6	Lorsch	I	-	S, H	2	Yes
7	Graben_x4	I	-	H	1	Yes, hearsay
8	Graben_x2	I	-	H	1	No
9	Hechtgraben	I	-	S	1	Yes
10	Grote Ry	I	-	S	1	Yes
11	Steudengraben	I	-	S	1	Yes
12	Plaubeck	I	-	S	1	Yes
13	Barthe	I, T, M	C	S	1	Yes
14	Flemdorfer Beek	I	-	S	1	Yes
15	Graben bei Neu-Bartelshagen	I	-	S	1	No
16	Günzer See	I	-	S	3	Yes
17	Graben_x1	I	-	S	1	Yes
18	Graben im großen Holz	I, F, M	C	S	3	Yes
19	Gräben in den Sundischen Wiesen	I	-	H	1	Yes, hearsay
20	Zahnziehen	I	-	S	2	Yes
21	Wendisch Langendorf	I	-	S	2	Yes
22	Graben 13	I	-	S	1	Yes
23	Badendycksgraben	I	-	S	1	Yes
24	L119	I	-	H	1	No
25	Graben L1	I	-	H	1	No
26	Klostergraben	I	-	H	1	No
27	Sehrowbach	T, E1, M	C	-	0	No
28	Z7	I	-	S	1	No
29	L8	I	-	S	1	No
30	Duwenbeek	I, E1, M	C	H	1	No
31	Venzer Graben	I	-	H	1	No
32	Graben_x8	I	-	H	1	No
33	Graben_x7	I	-	H	1	No
34	Graben zum Mittelsee	I	-	H	1	No
35	Seiser Bach	I	-	S	1	No
36	Der Ossen	I	-	S	1	No
37	Karower Bach	I	-	S	2	No
38	Pumpwerk Streu	I	-	S	1	No
39	Graben_x6	I	-	H	1	No
40	Freetzer Graben	I	-	S, H	2	No
41	3280	I	-	S	1	No
42	Beek	I, T, E1	C	S, H	2	Yes
43	1701	I	-	H	1	No
44	Mellnitz	I	-	S	1	No
45	Ryck	I	-	H	1	No
46	Freesendorfer See	I	-	S	1	No
47	Graben_x5	I	-	H	1	No
48	Ziese	I, E2	S	S	1	No
49	Brebowbach	I	-	S	1	No
50	Peene	T	C	-	0	No
51	Mühlgraben	I	-	H	1	Yes, hearsay
52	Hechtgraben	I	-	H	1	Yes, hearsay

said *“By this closing of access they have lost an immense amount of spawning habitat”* (Interviewee G).

Elaborating on the different types of blockages between brackish- and freshwater that are found in the area, interviewees mentioned different systems acting as barriers for migrating fishes. While most Interviewees were convinced that pump sheds do not allow for any movement of pike in either direction, some respondents thought that flap gates do allow for migrations when stream discharge is high enough so that the gates open up enough for pike to enter. Interviewee F said: *“That is why these snowmelts are nice, so that some life can enter. Then the flap gates stay open wide enough.”*. It was furthermore reported that occasionally locals who are aware of the impediment that these structures impose on fish, manipulate them during spawning time to allow for an unimpeded migration of anadromous fish: *“There are some anglers and when they know that the flooding season is over, they go there and open up the flaps so that they [the pike] can move in and out freely.”* (Interviewee F).

Some respondents (n = 4) reported having seen pike leaping out of the water in front of the freshwater outflow of pumping stations during spawning time in spring where the spawning route is blocked, attempting to bypass these obstacles. All mentionings were referring to different situations and across different Bodden lagoons. Interviewee F remembered: *“The pike jumped all over the place, landing on the shore, when we had the pumps running”*, referring to an instance he had witnessed some years ago at an inflow of Kleiner Jasmunder Bodden. He

Table 3

Stakeholder knowledge of the 13 participants from interviews in 2021. Self-witness refers to personal visual observations of pike in shallow habitats during spawning time. A spatial reference to the waterbodies mentioned can be found in Fig. 1 and Fig. 8. Ditches with unknown names were termed "Graben_x" and then consecutively numbered. Abbreviations for lagoons: BAT: Barther Bodden/Grabow; BOB: Bodstedter Bodden; GB: Greifswalder Bodden; GJB: Großer Jasmunder Bodden; KB: Kubitzer Bodden; KJB: Kleiner Jasmunder Bodden; P: Peenestrom/Achterwasser; S: Strelasund; SAB: Saaler Bodden; SB: Schaproder Bodden; SH: Stettiner Haff. Waterbody types: S: Streams; D: Ditches; M: Flooded meadows; W: Wetlands.

	Decade of birth	Knowledge on waterbodies used for anadromous pike spawning (bold = selfwitness / italic = hearsay)	Lagoons covered	Self-witnessed	Type of waterbody	Beginning of spawning	Duration of spawning (Weeks)	Hunt on spawners	Decrease of freshwater spawning apparent	Observations of spawning in Boddens
Interviewee A	60s	**Günzer See**, **Graben im großen Holz**, **Meadows at Wendisch Langendorf**, **Badendycksgraben**	BAT, KB	Yes	M, D	Weather dependent	-	Childhood experience (Fork)	Yes	-
Interviewee B	50s	**Günzer See**, **Zahnziehen**, **Graben 13**	BAT, KB	Yes	W, S, D	March	-	Childhood experience (Sling)	Yes	-
Interviewee C	40s	**Lorsch**, **Grote Ry**, **Steudengraben**, **Hechtgraben**, **Felemdorfer Beek**, **Plaubeck**, **Barthe**	SAB, BAT, BOB	Yes	W, S, D	Mid-March - end-April, depending on length of winter	-	Childhood experience (Fork)	-	No direct observation but suspicion
Interviewee D	70s	**Karower Bach**, **Günzer See**, **Graben im großen Holz**, *Gräben in den Sundischen Wiesen*	BAT, KJB	Yes	D, M, W	Late March - Beginning of April	4	Childhood experience (Fork)	Yes	Yes, in reeds
Interviewee E	70s	**Graben im großen Holz**, **Günzer See**	BAT	Yes	D	March	-	Well-known	Yes	Yes, in reeds
Interviewee F	70s	**Beek**, **Freetzer Graben**, **Klostergraben**, **L119**, **Mellnitz**, **Graben_x6**, **Der Ossen**, **Seiser Bach**, **Graben zum Mittelsee**, **Graben_x8**, **Venzer Graben**, **L8**, **Z7**, **Karower Bach**, *Duwenbeek*, *1701*, *3280*, *Graben_x7, L1*	GB, KB, S, KJB, GJB, WB, SB	Yes	S, D	March, depending on weather	-	No	-	-
Interviewee G	70s	**Schulweggraben**, **Neuendorfer Hechtgraben**, **Graben_x2**, **Saaler Bach**, **Graben_x3**, *Graben_x4, Lorsch*	SAB, BOB	Yes	D, M	Starting in late February	2–8	Childhood experience (Fork)	Yes	Yes, likewise hunting experiences with fork
Interviewee H	30s	**Graben im großen Holz**, **Graben_x1**, **Zahnziehen**, **Meadows at Wendisch Langendorf**	BAT	Yes	M, D	March - May, weather-dependent	-	Yes	Yes	-
Interviewee I	60s	*Hechtgraben, Mühlgraben*	SH	No	M, D	-	-	Well-known	Yes	-
Interviewee J	70s	**Ziese**, **Brebowbach**, **Freesendorfer See**, *Graben_x5*	P, GB	Yes	S, D	February - April, earlier spawning after mild winters	-	Well-known	Yes	-
Interviewee K	60s	**Beek**, **Freetzer Graben**, **Pumpwerk Streu**	GB, KJB	Yes	S, D	April	-	Childhood experience (Sling)	Yes	-
Interviewee L	40s	**Prohner Bach**, **Badendycksgraben**	KB	Yes	S, D	-	-	Only outside spawning season	Yes	-
Interviewee M	40s	**Beek**	GB	Yes	S, D	Mid-March	4	Childhood experience (Fork)	-	No

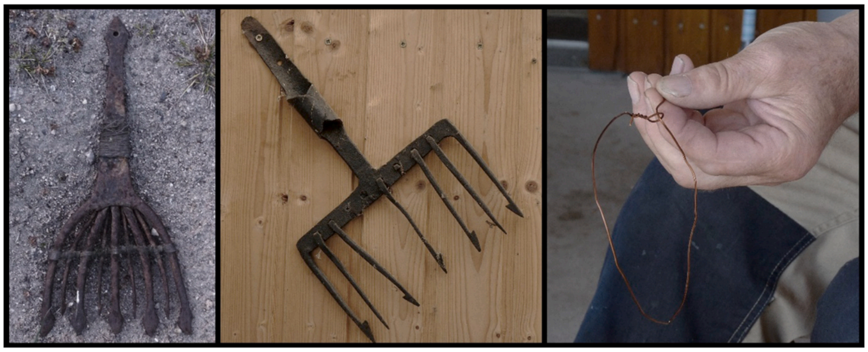


Fig. 9. Tools formerly used to capture spawning pike: Pike-forks (left, middle) and reconstruction of a pike-sling (right) as shown from the participants.

continued: *"Yes, that's almost one meter above the water level [the outlet] and then they want into that tube. And they don't manage and always land on the shore [...]. Masses of pike."*. Interviewee K remembered: *"We heard the stories from anglers. So, we went there, arrived at the pumpshed, the water was flowing and the pike were jumping in front of our feet. Some of them managed to get back into the water themselves, others we had to throw back in."*. Besides personal observations, further participants had heard about this kind of behavior in pike from the area.

When hypothesizing on the potential reasons for the spawning migrations into freshwater habitat, respondents were putting forth different theories. Reduced salinity was mentioned in several contexts. Interviewees said *"Pike want freshwater for spawning, that stimulates them in spring."* (Interviewee B) or *"The pike is a freshwater fish and nothing but it."* (Interviewee D). However, also higher temperatures were mentioned as one potential reason: *"Because it warms more rapidly there"* (Interviewee G). Also, the mixed effect of both factors was discussed: *"When the sun is shining and the temperature increases as well as higher freshwater discharge. This is what stimulates them."* (Interviewee B). The same interviewee also reported: *"They are really sunbathing I have observed."*. Interviewee G referred to natal homing as a potential reason for the spawning migrations: *"Maybe also because they were born there. I think that also plays a role."*.

Two of the participants were themselves engaged in the melioration works taking place during the GDR period (1960s-1980s) and could thus contribute to the technical background. Especially interviewee G had been involved in the proceedings of the "Komplexmelioration". He remembered: *"Previously this was all opened, it was all flowing in and out. But since the drainage didn't work when the tide was high, one created the pumping stations. [...] In the GDR-times everything was supposed to be used, every square meter and that's why they did it. One could now use the meadows at all times"*. An additional benefit of the meadows being constantly drained was seen in the possibility to work on them with new, heavier technology at all times of the year while previously this was possible *"only sometimes, when it dried up"*, according to interviewee G. The largest modifications had been finished until the mid-1980s: *"In the 1990s no big drainage pipes were constructed anymore. [...] The last ones we knew were laid in the beginning of the 1980s."* (Interviewee G).

Interviewees perceived the development in the area with regard to the melioration as regretful. This was expressed even by those participating in the melioration woks at the time: *"It is important that this is going to be changed with the pump sheds and flap gates."* (Interviewee H). One interviewee called the current situation *"a disaster"* (Interviewee B). However, statements like *"This has to be changed real quick. It is possible!"* (Interviewee E) also showed that stakeholders are hopeful for future improvements to come.

3.3.2. Scientific assessment of contemporary anadromy

The five studied streams subject to standardised electrofishing were characterized by scarce but emerging aquatic vegetation during the sampling period in spring 2021. The substrate was predominantly muddy in all streams. Shorelines showed varying degrees of common reed (*Phragmites australis*) and were usually adjacent to agriculturally used surfaces (drained fen soils) in the absence of reed. Stream parameters can be found in Table A4.

A total of 110 pike individuals were captured during the weekly standardised transect sampling between March 01, 2021 and April 15, 2021 (Table 4). There was clear evidence for a significant increase in abundance in April, when the water temperature rose (Fig. 10).

Overall, catches of pike > 30 cm in the five streams subject to regular, standardised sampling were relatively low throughout most of March, with mean catch per unit effort (CPUE) calculated as n/100 m being below 0.5 for most streams in all four initial sampling weeks (Fig. 10). Towards the end of March catches increased markedly and remained high in the beginning of April (CPUE >= 0.5 for all streams except Beek and Duwenbeek in week five and six) and decreased again during the last week of sampling. The increase in CPUE at the end of March took place while water temperatures in the streams had risen above 7 °C on average. Pike catches > 30 cm significantly differed over time as indicated by a significant factor 'week' in the GLMM ($p < 0.001$). More specifically, post-hoc comparisons revealed significant differences ($p < 0.05$) in captures of pike > 30 cm between each of the first three sampling weeks compared to week five.

When looking at individual streams, the pattern described for the overall temporal trend of CPUE was driven by Neuendorfer Hechtgraben, Sehrowbach and Körkwitzer Bach in particular (Fig. 10). At Duwenbeek, the peak in CPUE occurred during the last sampling week

Table 4
Absolute numbers of pike captured by electrofishing during fieldwork in Spring 2021. Recaptures refer to fish being captured more than once within the sampling period 2021. A lack of sampling is denoted by NA.

	Standardized sampling			Additional sampling	
Waterbody	Total Number Individuals	Pike > 30 cm	Recaptures	Total Number Individuals	Recaptures
Beek	4	2	1	NA	NA
Duwenbeek	9	8	1	NA	NA
Neuendorfer Hechtgraben	62	16	4	NA	NA
Körkwitzer Bach	16	14	1	NA	NA
Sehrowbach	19	17	-	113	11
Ziese	NA	NA	NA	55	1

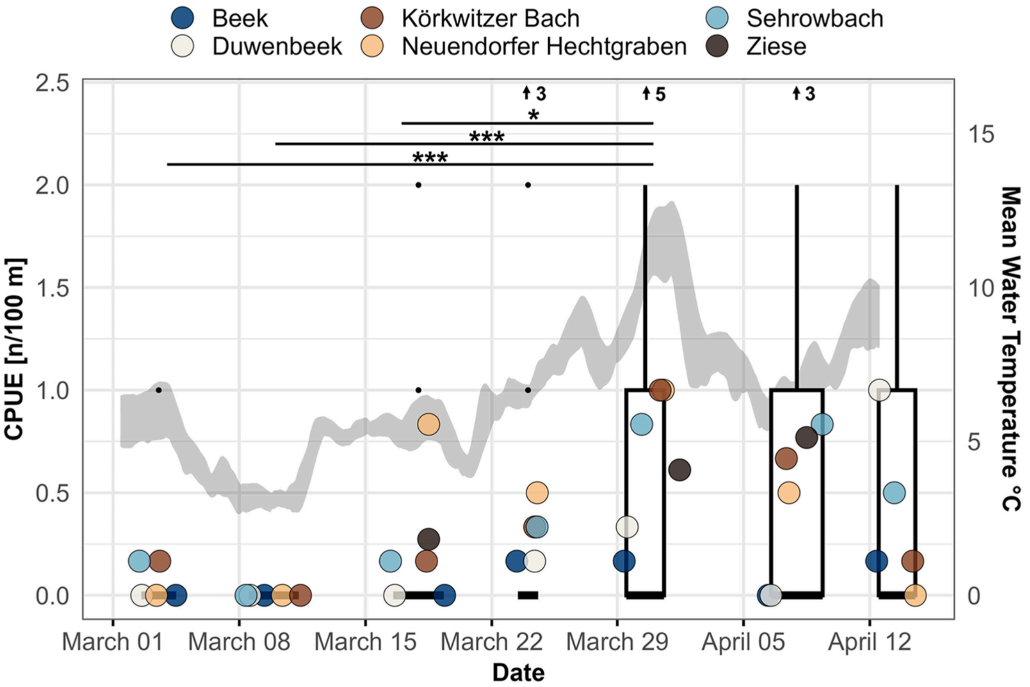


Fig. 10. Boxplots (median, box = 25 and 75 percentile, whiskers = 1.5 * interquartile range) display the temporal progression of CPUE (Pike > 30 cm * 100 m^{-1}) for all 100 m transects from electrofishing of all five streams with standardised sampling in spring 2021, grouped by sampling week (30 data points per boxplot). Outliers outside of plot limits are indicated using arrows with respective y-values in the upper plot margin. Significant differences between weeks revealed by Tukey HSD post-hoc comparisons are indicated by asterisks (* < 0.05 and *** < 0.0001). Coloured dots display the mean adult pike CPUE from each weekly sampling of a stream. Data for Ziese River are displayed despite non-standardised sampling and were excluded for the boxplots and statistical analysis. The range of mean water temperatures (24 h) from all five streams is plotted as a grey line. Ticks on the x-axis display the first day of the calendar weeks 09–15 of the year 2021.

when catch rates had already started to drop in all other streams. In Beek catches remained low and only two individuals > 30 cm were captured throughout the sampling period, one of which was captured twice. CPUE development at Ziese River showed an apparent increase in CPUE in the beginning of April, however, sampling was only conducted in week 3, 5 and 6. In spring 2022, Sehrowbach was sampled on two occasions, largely confirming the patterns seen in 2021 (results not plotted).

Deployment of the fyke net in the ditch “Graben im großen Holz” revealed a small run of nine pike individuals (mean total length 67 cm ± 11 cm SD) entering the waterbody between March 13, 2022 and April 26, 2022. One individual was marked in the brackish lagoons in September 2021 about 1.5 km from the ditch and was recaptured a second time in May 2022 outside the ditch, indicating this fish being anadromous. Water levels were unfavourably low throughout the deployment period of the fyke net in March and April 2022 and did likely not allow for entrance of pike into the ditch for extended periods. Salinities in this waterbody were around 0.4 and 1.0 PSU, however, peaks of > 3 PSU were recorded.

3.3.3. *Further evidence of anadromy through mark-recapture and telemetry*

A total of 15 out of 415 pike individuals marked in freshwater during the spawning season with external Floy-tags were reported as recaptures from the open Bodden lagoons outside the spawning season by anglers and fishers via an online form. This was true for fish marked in Sehrowbach, Neuendorfer Hechtgraben, Duwenbeek, Körkwitzer Bach, Graben im großen Holz and Barthe River (Table 5). Conversely, four individuals marked in lagoons outside spawning were reported as recaptures in freshwater streams including Sehrowbach, Barthe and Graben im großen Holz (Table 5). Return movements into freshwater as indicated by electrofishing recaptures during the spawning season in freshwater over consecutive years were found in Sehrowbach, Barthe and Duwenbeek with a total of 15 individuals, twelve of which were captured in

Table 5
Evidence for anadromy from the external Floy-tag recaptures. A lack of sampling is indicated by NA.

Stream	Evidence of Anadromy	# fish tagged in stream during spawning season and recaptured in brackish lagoons outside spawning	# fish tagged in brackish lagoons and recaptured within tributary during spawning season	# fish recaptured in freshwater over consecutive years during electrofishing in spawning season
Barthe	Yes	1	1	2
Beek	No	0	0	NA
Duwenbeek	Yes	2	0	1
Graben im großen Holz	Yes	1	1	NA
Neuendorfer Hechtgraben	Yes	1	0	0
Körkwitzer Bach	Yes	1	0	NA
Peene	No	0	0	0
Sehrowbach	Yes	9	2	12
Total		15	4	15

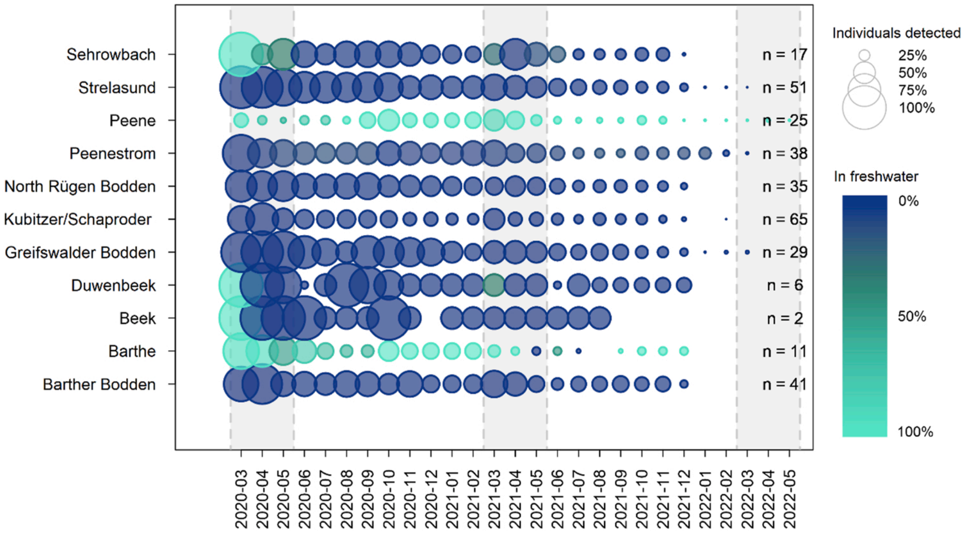


Fig. 11. Proportion of tagged fish that visited a freshwater stream for each month, derived from acoustic telemetry data (i.e. ratio of the number of individuals detected in freshwater on the number of individuals tagged). The number of fish tagged is indicated on the right side of the plotting area and the spawning season is highlighted in grey.

Table 6
N = number of tagged pike released in the area; N* = number of individuals that were detected on the receiver array; DD = number of days detected; DD RA = number of days detected in the release area; NO = number of individuals ever detected outside of the release area; RI = residency index, proportion of days an individual was detected in the release area relative to the total number of days it was detected (DD).

Release Area	N	N*	DD, median (Q1-Q3)	DD RA, median (Q1-Q3)	NO (% on N*)	RI, median (Q1-Q3)
Duwenbeek	6	6	76.5 (34–155.8)	0 (0–0)	6 (100%)	0 (0–0)
Sehrowbach	17	17	74 (19–160)	0 (0–4)	17 (100%)	0 (0–0.03)
Peene	25	15	68 (10.5–198)	57 (10.5–197.5)	1 (7%)	1 (1–1)
Barthe	11	9	78 (24–173)	78 (23–147)	4 (44%)	1 (0.85–1)

Sehrowbach (Table 5). The low figures seen for other streams are at least in part attributable to substantially lower sampling efforts.

Using the acoustic telemetry data, we were able to gather additional indications for anadromy. Some of the fish we tagged in Sehrowbach, Barthe and Duwenbeek during spawning 2020 were detected in brackish water lagoons during the rest of the year (Fig. 11, Table 6).

In Sehrowbach and Duwenbeek, residency index (RI) was close to zero suggesting a very low fidelity among the individuals captured, tagged and released there during the spawning period, all of whom were mainly detected outside the streams throughout the year outside the spawning period (Fig. 11, Table 6). In Barthe, only four out of nine individuals were detected in brackish lagoons, and residency to the river was high with fish visiting freshwater throughout the study period regardless of the season (Fig. 11, Table 6). We also collected evidence for return in freshwater for the following spawning season (2021) for 3 fish in Sehrowbach, 1 in Duwenbeek, and 3 in Barthe (Fig. 11). In Peene River a majority of fish was detected in freshwater during the spawning season, with one individual visiting brackish water at that moment (Table 6, Fig. 11). Out of spawning season, fish from Peene were mostly detected in freshwater (Fig. 11) and their relative residency to their capture site was the highest (Table 6) with only one individual leaving the river (Fig. 11). In Beek, individuals left the river after the spawning period but the absence of receivers in the stream did not allow us to quantify potential returns in freshwater (Fig. 11). Overall, a pattern emerged that fully resident freshwater fish were more common in the larger rivers Peene and Barthe, while the smaller streams mainly hosted anadromous fish that left the stream after spawning, some of which returned in the second observational year.

In all brackish water lagoons, fish tagged there remained mainly in brackish water during and outside the spawning season (Fig. 11), apart from Peenestrom/Achterwasser where a handful of fish (4 in 2020 and 2 in 2021) entered the river Peene during spawning time and in Kubitzer Bodden where one fish was found to enter Sehrowbach during spawning season 2020. Therefore, fish tagged in the lagoons were mainly brackish residents with little evidence of anadromy to freshwater sites.

3.4. Evidence for successful reproduction via detection of eggs and larvae

We found no eleutheroembryonic life stages in any of the sampling locations during the three spawning seasons 2015–2017. Overall, we found 34 young-of-the-year (YOY) pike between 15 and 128 mm in five different locations (Fig. 12, Table 7). Specifically, we identified Sehrowbach, Klostergraben and ditch L8 as nursery sites for pike. However, no pike egg or larvae was recorded in Duwenbeek. Most of the larval pike were caught under freshwater conditions between 0.1 and 1.5 PSU in the mouth of Sehrowbach and the smaller freshwater ditches. Therefore, evidence of successful recruitment in some sites where we also recorded anadromy was provided, but overall numbers of fry or YOY captured in streams were small.

The only juvenile pike we caught in brackish water far from freshwater streams was a 128 mm long YOY specimen. However, YOY were regularly reported from eel fyke nets by commercial fishers and we personally collected YOY pike from brackish sites that fell dry due to strong currents.

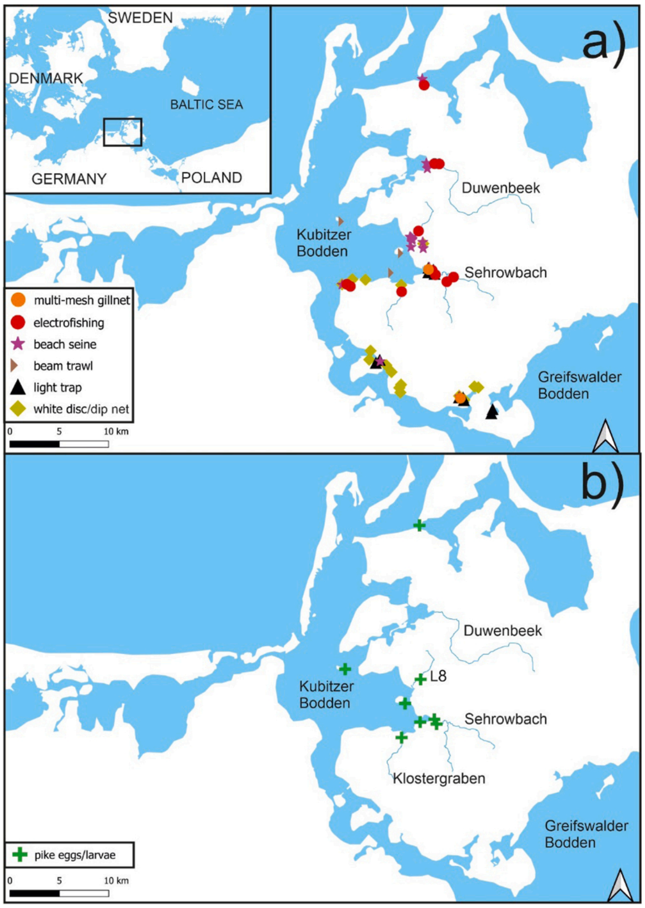


Fig. 12. Locations in which sampling for early pike life was conducted with different gears (a) and locations in which early pike life stages were detected (b).

Pike eggs were found in two different brackish locations using the beam trawl method (Fig. 12, Table 7). These eggs were found in water depths > 1 m and distant from freshwater tributaries (Salinities 9.0–9.2 PSU), proving successful spawning of brackish-adapted pike.

3.5. Genetic structuring

The Pool-sequencing approach assessed genome-wide differentiation among different pike populations from different oligo- and meshaline brackish capture lagoons and several larger (e.g., Barthe, Peene) and smaller streams (e.g. Neuendorfer Hechtgraben, Sehrowbach). On average, 98.9% (range: 98.6–99.1%) of sequence reads were mapped to the reference genome, corresponding to an average of 679.248.716 reads per pool (range: 333.821.794 – 1.210.480.472 mapped reads) and a coverage ranging between 51x and 192x (average 108x). SNP calling resulted in 1.190.970 SNPs after filtering. Pairwise FST values ranged from 0.0128 (Greifswalder Bodden vs. Kubitzer/Schaproder Bodden) to 0.0547 (Greifswalder Bodden vs. Stettiner Haff) and were generally highest in Bodden vs. Peene River and Stettiner Haff comparisons (range: 0.036–0.0547). Accordingly, an NJ-tree visualizing genetic distances between pike populations revealed a clear separation of mesohaline brackish-water Bodden sites (e.g., Greifswalder Bodden, Barther Bodden, Schaproder/Kubitzer Bodden, Großer Jasmunder Bodden) from larger freshwater streams (river Barthe and river Peene) and oligohaline lagoons (Peenestrom and Settiner Haff), with putative anadromous populations Sehrowbach, Neuendorfer Hechtgraben, and Ziese River showing a more intermediate position (Fig. 13). It is also very likely that

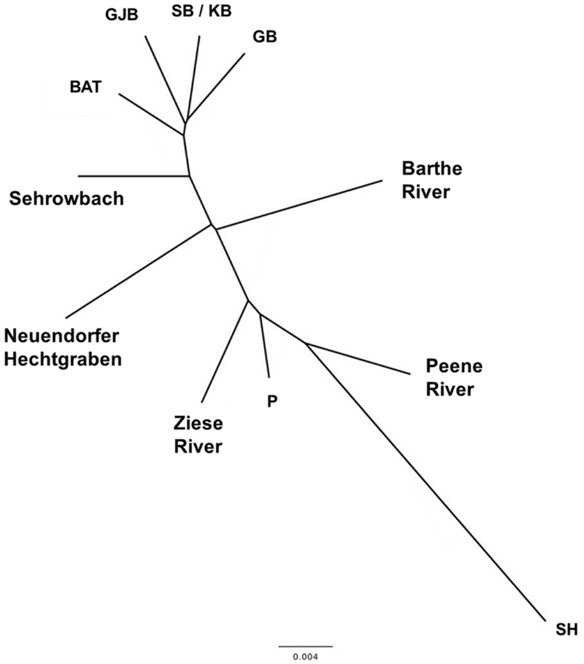


Fig. 13. Neighbor-Joining distance tree based on 1.190.970 SNPs from whole-genome sequences of pooled individuals from different study sites. In the tree, pike populations from brackish-water Bodden areas form one cluster including Barther Bodden, Schaproder/Kubitzer Bodden (SB/KB), Großer Jasmunder Bodden (GJB) and Greifswalder Bodden (GB). Freshwater populations from rivers Barthe and Peene and the oligohaline lagoons Peenestrom (P), and Stettiner Haff form a cluster with a notably higher among-population divergence than the mesohaline brackish water populations (BAT, GJB, SB/KB, GB). Putative anadromous populations are given by Sehrowbach, Neuendorfer Hechtgraben, and Ziese River. River Ziese is however part of the cluster including freshwater populations and oligohaline lagoons (SH, P) of the river Oder estuary. Importantly, Neuendorfer Hechtgraben and Sehrowbach show less divergence from the brackish-water populations than pure freshwater populations (rivers Barthe and Peene). Taken together, the tree demonstrates divergence of putative anadromous population samples at a level that is comparable with what is observed among pure freshwater populations and suggests genetic divergence of anadromous pike from brackish water pike as well as from populations from different freshwater sites.

Table 7
Occurrence of pike eggs, larvae and juveniles and respective salinities of the ambient water.

Waterbody type	Date	Sample location	GPS coordinates	Sampling method	Salinity (PSU)	n (pike total length)
freshwater stream, mouth	18.05.2015	Sehrowbach	N 54.38175, E 13.26702	light traps	1.5	5 (15 – 41 mm)
freshwater stream, mouth	03.06.2016	Sehrowbach	N 54.37977, E 13.25753	beach seine	3.8	1 (43 mm)
freshwater stream	08.06.2017	Sehrowbach	N 54.38053, E 13.26736	Electro-fishing	0.5	3 (52 – 81 mm)
drainage ditch	16.06.2015	Klostergraben	N 54.36739, E 13.21588	Electro-fishing	0.8	20 (42 – 95 mm)
drainage ditch	23.06.2015	L8	N 54.41831, E 13.24652	Electro-fishing	0.1	4 (75 – 110 mm)
lagoon, littoral zone	23.06.2015	North-Rügen- Bodden chain	N 54.55305, E 13.25011	beach seine	9.1	1 (128 mm)
lagoon, pelagic zone	20.04.2017	Kubitzer Bodden	N 54.42602, E 13.13535	beam trawl	9.0	2 eggs
lagoon, pelagic zone	20.04.2017	Kubitzer Bodden	N 54.39585, E 13.21964	beam trawl	9.2	3 eggs

Barthe River is a mixed population that inhabits some anadromous fish but also freshwater residents, justifying an intermediate position among the mesohaline brackish lagoons and more freshwater influenced genetic branch. Since sampling took place outside the spawning season in the rivers Barthe and Peene (Table A3), the samples are unlikely to be comprised by a high share of anadromous fish. Note that the geographically close Peenestrom and Greifswalder Bodden are genetically speaking diverged, where the mesohaline Greifswalder Bodden structures more closely with other mesohaline lagoons than with the oligohaline Peenestrom, similar to previous microsatellite studies (Möller et al., 2021), suggesting structure by salinity gradients. Genome-wide nucleotide diversity (pi) estimates ranged from 0.0018 to 0.0023 (average: 0.0019) and tended to be higher in the area of Stettiner Haff/Peenestrom/Peene River (pi = 0.0023/0.0019/0.0020) as compared to other areas (Barther Bodden: 0.0018; Neuendorfer Hechtgraben: 0.0018; Großer Jasmunder Bodden: 0.00183; Greifswalder Bodden: 0.00184; Sehrowbach: 0.00184; Ziese River: 0.00184; Kubitzer/Schaproder Bodden: 0.00185; Barthe River: 0.0018.

3.6. Synthesis

For eight freshwater bodies out of nine in which we conducted field sampling, we were able to identify anadromous spawning runs to a high degree of certainty either by means of systematic electrofishing, telemetry, marc-recapture or captures of fish marked in lagoons with fyke net during migration into a stream (Table 2, Fig. 8). We also reported genetic structuring by salinity gradients, suggesting local adaptation to salinity as a pressure and the presence of stream-specific genetic diversity. For the majority of waterbodies suggested by the interviewees as putative sites for anadromy (Fig. 8), no sampling was undertaken to confirm the contemporary presence of anadromous or freshwater spawning subpopulations. However, in our field surveys in only in one waterbody suggested by stakeholders we failed to find indications of directional migration to freshwater during the spawning time while we could confirm stakeholder knowledge by finding pike during spawning time in six waterbodies. Although anadromy cannot be proven with certainty by repeated return movements to freshwater streams and successful reproduction in freshwater, the collective body of evidence is strong to suggest that anadromy was and continues to be present in the Rügen pike stock to some degree, particularly in the intermediate to smaller streams and ditches. The genetic structure analyses further confirmed the presence of genetic structure by salinity and putative anadromous fish in smaller streams to be genetically intermediate between mesohaline brackish and freshwater or oligohaline brackish stocks.

4. Discussion

We found migrations into freshwater streams during spawning are a common phenomenon in coastal pike inhabiting the German brackish Bodden lagoon systems around Fischland-Darß-Zingst peninsula and the islands of Hiddensee, Rügen and Usedom and occur throughout the entire region in all lagoons to some degree. It is very likely that this represents anadromy as reported for other areas of the Baltic using tagging and telemetry studies (Tibblin et al., 2015; Flink et al., 2023). However, not all streams and ditches that continue to be accessible are used for spawning to the same degree. Run sizes vary and especially the larger streams (Barthe and Peene) show high levels of freshwater residents and limited anadromy. By contrast, the smaller streams seem to have a higher prevalence of seasonal spawning migrations and thus anadromy. Many of these populations are small relative to the entire lagoon area. The data presented in this paper therefore suggest that anadromy and freshwater recruitment are unlikely to constitute a major recruitment pathway for the total Rügen stock, which is in line with studies from the region (Möller et al., 2019). However, the typically small local populations in streams represent genetic substocks and as such contribute to the total genetic diversity present in Rügen pike. Importantly, despite the melioration dating back to the 1970–1990s, it is important to note that the Rügen stock maintains at least three ecotypes, brackish residents, freshwater residents and anadromous substocks. This contrasts sharply with the situation in Puck bay in Poland, a brackish lagoon where brackish recruitment seems to be zero, suggesting the local extinction of lagoon pike after water infrastructure blocked access to freshwater streams (Psuty, 2022; Psuty et al., 2023). Similar to the case in Puck bay, for the Rügen stock, interviewees indicated that the prevalence of anadromy has declined in association with the installation of migration barriers since the 1970s - the degree to which we cannot quantify. Given the temporal offset between citizen reports (past) and scientific surveys (present), a verification of citizen observations for individual streams was not possible. However, aggregated data from both sources confirm the overall existence of anadromy, and LEK allowed us to assess a period for which scientific data is lacking, therefore complementing our scientific understanding.

Our work suggested the presence of three ecotypes of pike, freshwater and brackish residents as well as anadromous fish, which agrees with reports from other Baltic countries. We also identified one of the larger tributaries, the Peene River, to almost exclusively host freshwater residents, similar to a case study from River Tryggevælde in Denmark (Birnie-Gauvin et al., 2019). Therefore, the size of the stream may be inversely related to the degree of freshwater residency. It is possible that larger streams offer pike enough resources after the spawning season and the fish may continue to live in the stream and not move to feeding grounds in the lagoons. By contrast, in smaller streams with possibly fluctuating water levels and low food resource availability, adult pike might be forced to migrate towards the lagoons, maintaining anadromy as the only viable strategy.

A study along the Baltic has shown that the population differentiation among subpopulations in geographically closely related tributaries can overwhelm the population differentiation in brackish adapted subpopulations (Sunde et al., 2022). In line with this, the Fst values reported here for Rügen pike suggest larger population level divergence among freshwater and putative anadromous populations than among the mesohaline brackish-water Bodden areas that are genetically more similar to each other. Our analysis suggests for pike that natal homing and processes of local adaptation, even in small streams, structure the pike meta-population in coastal areas. Therefore, even small ditches and streams contribute to the genetic biodiversity of populations and may help to sustain the productivity of the stock as a whole, similar to the case reported from Pacific salmon stocks in Alaska (Schindler et al., 2010).

Our results add a further case to the scientific literature on anadromous spawning behavior of Baltic pike which has previously been described in Sweden (Tibblin et al., 2016; Engstedt et al., 2014), Finland (Müller and Berg, 1982; Müller, 1986) and Estonia (Rothla, 2015). Similar to our findings, Tibblin et al. (2015) found that streams with varying dimensions between 1 m and > 10 m width were home to anadromous pike along the Swedish coast. Also, agricultural drainage ditches acting as pike spawning grounds have previously been described (Cottrell et al., 2021). Our work thus broadly agrees with literature reports on freshwater spawning in coastal pike. In line with reports from stakeholders, different types of wetlands and lakes have been found to be hosting anadromous pike in other parts of the Baltic (Larsson et al., 2015; Müller, 1986; Nilsson et al., 2014). Flooded meadows, which were reported by some interviewees as formerly omnipresent spawning grounds in the study area, have previously been identified as a productive spawning ground in the context of Baltic pike (Nilsson et al., 2014). However, interviewees reported a strong decline in the availability of wetlands and degree of anadromy, which can be traced back to the installation of dikes and the management of water infrastructures that blocked access to freshwater since the 1970s in the former GDR. It is very likely that this large infrastructure development can be held responsible for the decline of anadromous stocks around Rügen. The degree to which this anadromy has declined cannot be quantified exactly based on our study, but has likely been substantial given our documented loss of accessible streams and ditches around Rügen. The current decline of the Rügen pike stock (van Gemert et al., 2022) cannot be explained by the loss of freshwater populations, which happened several decades earlier. However, the reduced biocomplexity of the stock which results from the degradation of freshwater environments, possibly has negatively affected the stocks ability to buffer other pressures.

Some interviewees reported about pike ecology in great detail. Hypotheses mentioned on the reasons for anadromy were higher temperature and lower salinity in the spawning habitats, both of which have been discussed in scientific literature (Müller, 1986; Jørgensen et al., 2010). One participant moreover referred to natal homing in the context of anadromy, which has been studied in other parts of the Baltic (Tibblin et al., 2016). Similarly, the sunbasking behavior mentioned by one participant has recently been described in the Baltic in Sweden (Nordahl et al., 2020). Another interviewee mentioned shorter but more intense spawning runs following long winters, a phenomenon which likewise has been described previously (Müller, 1986). This suggests that local knowledge can be used to support biological understanding, however, anecdotal evidence naturally comes with cognitive biases, which should be considered when interpreting resident knowledge which may be remembered incorrectly while validation is usually not possible.

Variation in the timing of spawning between different streams, as indicated by a late peak of CPUE in Duwenbeek when compared to other streams sampled, was previously described from two adjacent coastal streams in Sweden where the arrival timing differed consistently between two waterbodies (Larsson et al., 2015; Tibblin et al., 2015). Adaptations of subpopulations to local salinity and temperature conditions are assumed to be driving this phenomenon (Sunde et al., 2018). The stream-specific behavioral variation in arrival timing was hypothesized to be an adaptation of the genetically differentiated subpopulations to differences in water discharge regimes so that unimpeded outmigration of juveniles could happen. It was outside the scope of our study to investigate discharge regimes or to examine exact reasons that initiate or prevent anadromy. We thus conclude our work by outlining that not all streams or ditches around Rügen host abundant pike runs. Some of the larger streams hold very few anadromous fish (e.g., Peene River) or host a mixture of anadromous and resident spawners (e.g., Barthe River), while other streams seem to be fully anadromous (e.g., Neuendorfer Hechtgraben, Sehrowbach, Ziese River). Such variation of run timing and size on small spatial scales can ultimately contribute to buffer environmental variation and stochastic impacts on recruitment and contribute to the maintenance of productive biocomplexes (Schindler et al., 2010).

Recaptures and telemetry from Sehrowbach, Barthe and Duwenbeek show that some pike were returning to the same stream over consecutive years, a pattern that has been found also in Swedish streams (Engstedt et al., 2014; Tibblin et al., 2016). It is possible that pike return to the same stream through experience rather than due to local adaptation to some local environmental factor (Tibblin et al., 2015). If fish are returning to their birth stream for spawning, referred to as natal homing, genetic flow is confined to streams and genetically distinct subpopulations with local adaptations will emerge as reported from Sweden (Sunde et al., 2022). Our population genetic analysis based on whole genome sequencing of pools of pike from around Rügen shows that populations sampled in different tributaries harboring anadromous or freshwater resident pike are differentiated from one another as well as from those in the lagoons. This population structure supports that homing behavior of anadromous pike around Rügen is sufficient to cause genetic differentiation as opposed to a random choice of spawning sites which would erode genetic differences among local populations. The overall pattern of divergence we find also agrees with Möller (2020) who previously found for the Baltic stocks that genetic differentiation happens alongside salinity gradients in the Rügen lagoons. Adaptations may include the specializations in arrival timing or body size but are moreover manifested in other traits like salinity tolerance, growth or reproductive investment (Berggren et al. 2016; Sunde et al. 2018, 2019, 2022).

There are important limitations to our study. Firstly, our electrofishing sampling delivered only a limited temporal resolution and does therefore not allow for detailed insights into temporal patterns at smaller scales. Additionally, there are strong limitations under elevated salinity > 1 PSU sometimes found in the mouth of tributaries and some ditches. We chose electrofishing as a compromise to cover a wider range of water bodies. To get a better understanding of temporal migration patterns and determine absolute population sizes of anadromous populations in future studies we recommend other sampling methods than electrofishing, such as fyke nets, fish traps or camera systems.

Another limitation is that we cannot conclusively differentiate between anadromous and resident freshwater fish in our electrofishing sample. While we argue that in the three smallest sampling waterbodies (Neuendorfer Hechtgraben, Duwenbeek and Beek) the size of the electric field of our sampling gear was extending throughout the water column in most sampling locations and resident fish therefore had a consistent likelihood of being captured throughout the sampling period, for the larger streams it is possible that some of the fish we sampled were indeed resident fish whose likelihood of capture increased in association with a habitat shift in spring. These individuals could potentially blur the population genetic signal that distinguishes anadromous from freshwater resident populations in our analysis. However, in Sehrowbach and Neuendorfer Hechtgraben we were able to additionally confirm the occurrence of anadromy through recapture- and telemetry data. Accordingly, the status of anadromy and the conclusions we draw from the population genetic analysis are unlikely to confounded by the uncertainties associated with distinguishing anadromous and resident freshwater pike. It is possible, however, that fish from Ziese River were in fact resident fish. By contrast, we might have missed anadromous fish in Peene River. We recommended to engage in population genetic studies using markers that distinguish anadromous from freshwater resident and brackish water pike individuals. A third possible limitation is the reduced of comparability of CPUE between the study streams due to the employment of different sampling gears. However, because the gear use was consistent within a stream, we think that this limitation does not affect findings on a stream basis.

We are not able to quantify the total recruitment of anadromous spawners to the stock. The sampling for early life stages of pike yielded only limited traces of pike eggs and larvae, which would be necessary, however, to close the entire life cycle from anadromy to recruitment. One limitation is the difficulty in sampling young, largely immobile pike in saline water. However, we conclude that either most of the tributaries where we found anadromy do not provide excessive numbers of recruits or outmigration after egg development in the larval stage happens within a short period of time and we therefore were not able to detect juveniles.

Lastly, we also want to highlight a limitation to our analysis of spawning habitat loss which does not account for the loss of flooded meadows. We resorted to the more simplistic approach presented here given uncertainties in the interpretation of digital elevation models which would be necessary for such more complex analysis. As large parts of the study area have undergone land sinking in response to drainage, using recent elevation levels would lead to an overestimation of the historic extent of flooded meadows.

4.1. Implications for management

Interviewees consistently reported a human-induced decline in the availability of spawning grounds for anadromous pike through melioration around Rügen. A similar effect of drainage efforts throughout the past century has been reported from Swedish, Polish and Estonian wetlands where increased awareness of the issue has recently resulted in the restoration of wetland access to promote natural recruitment of local anadromous pike stocks (Engstedt et al., 2018; Nilsson et al., 2014). Water management in general, especially those actions that block spawning migrations or access to spawning grounds, constitutes a globally relevant threat to many freshwater fishes (Su et al., 2021), and Baltic pike are no exception. Our analysis implies that divergence among local populations of anadromous, freshwater and brackish water pike is based on genetic differences implying an own evolutionary trajectory and degree of independence from one another. Anadromy is unlikely to be merely the result of a plastic decision to follow one or another lifestyle. Accordingly, anadromous populations may be managed as unique units and management regulations be implemented that allow for free migration into streams and avoid local depletion of typically small stocks by commercial fishing gear (e.g., gill nets). Despite the likely historic decline of anadromy and the assumed extinction of local subpopulations in response to water infrastructure installation, the continued occurrence of reproductively isolated subpopulations in pike meta-populations along the coastline of the Baltic and the continued presence of anadromous pike alongside brackish residents both in Germany and in other areas of the Baltic bears important implications for management (Larsson et al., 2015). It is important to maintain and if possible increase the freshwater-spawning subpopulations, and thereby maintain genetic diversity in the region. To increase the resilience of Baltic pike, it is recommended to reopen and restore as many wetlands and tributaries/ditches as possible and to facilitate the flooding of vegetated meadows during the spring spawning season. While stocks will already benefit from the opening of smaller waterbodies, greater impacts are probably achieved when large and formerly meaningful sites such as Günzer See or Prohner Wiek are reconnected to the lagoons. Given that the Rügen stock still holds freshwater spawning-adapted genotypes, rehabilitation of an extended stock complex through recolonization is possible and will provide buffer to the stock as a whole to deal with environmental stochasticity, thereby maintaining and fostering genetic biodiversity at small spatial scales.

CRediT authorship contribution statement

Phillip Roser: Writing – original draft, Writing – review & editing, Formal analysis, Visualization, Data curation. **Félicie Dhellemmes:** Formal analysis, Software, Visualization, Writing – review & editing, Data curation. **Timo Rittweg:** Investigation, Software, Writing – review & editing, Data curation. **Sören Möller:** Investigation, Visualization, Writing – review & editing. **Helmut Winkler:** Investigation. **Olga Lukyanova:** Formal analysis, Software, Visualization, Writing – review & editing. **Dominique Niessner:** Investigation, Writing – review & editing. **Jörg Schütt:** Investigation. **Carsten Kühn:** Investigation. **Stefan Dennenmoser:** Formal analysis, Investigation, Software, Visualization, Writing – review & editing. **Arne W. Nolte:** Conceptualization, Writing – review & editing. **Johannes Radinger:** Formal analysis, Software, Writing – review & editing. **Dieter Koemle:** Investigation. **Robert Arlinghaus:** Supervision, Conceptualization, Methodology, Writing – original draft, Writing – review & editing, Funding acquisition, Project administration.

Declaration of Competing Interest

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

Data of genetic analysis are linked in section 2.7. All other data will be made available upon request.

Acknowledgements

Financial support was provided by the funding bodies of the Project BODDENHECHT (European Maritime Fisheries Fund (EMFF) and the state of Mecklenburg-Vorpommern, MV-I.18-LM-004, B 730117000 069). We are grateful for the contributions of our interviewees without whom much of the insights gained would not have been available to us. Moreover, has much of the data been gained by catch reports of anglers, fishers and guides whose contribution is a crucial part of the project. We thank Jan Hallermann and Alexander Türck for technical support and Jan Droll for support during electrofishing. We thank the Angler Association of Mecklenburg-Vorpommern for authorizing our electrofishing survey in the freshwater tributaries. The Landesamt für Landwirtschaft, Lebensmittelsicherheit und Fischerei Mecklenburg-Vorpommern (LALLF) is thanked for approving our sampling methods, including the animal care protocol for tagging (Aktenzeichen 7221.3–1-052/19), and facilitating our surveys. The Staatliches Amt für Landwirtschaft und Umwelt Vorpommern (StALU) is thanked for granting us access to Nature Conservation Areas. The Nationalparkamt Vorpommern for temporal access to national parks and Biosphärenreservatsamt Südost-Rügen for access to the biosphere reserves. Map data copyrighted OpenStreetMap contributors and available from https://www.openstreetmap.org. Finally, we thank reviewers for feedback and all team members for many hours of help and discussions.

Appendix

See Tables A1-A4.

Table A1

Summary of annual average parameters of the Bodden lagoons within the study area of this work. DZBC: Darß-Zingst Bodden chain; KB/SB: Kubitzer/Schaproder Bodden; NRBC: North-Rügen- Bodden chain; S: Strelasund; GB: Greifswalder Bodden; P: Peenestrom (including Achterwasser). Data source: Lung, 2022.

Parameter	Western DZBC	Eastern DZBC	KB/SB	NRBC	S	GB	P
Area (km2)	213.2	59.8	231	159.4	47.6	540.1	181.9
Mean depth (m)	2.0	2.0	1.8	3.5	3.9	5.8	2.6
Max depth (m)	10.1	16.5	7.6	10.3	16.0	13.5	16.0
Catchment area (km2)	1578	1578	NA	312	238	665	5772
Water temperature (°C)	11.6 ± 6.6	11.5 ± 6.6	11.6 ± 6.7	12.4 ± 6.5	11.9 ± 7	11.7 ± 6.8	11.9 ± 6.7
Salinity (PSU)	5.4 ± 1.8	8.3 ± 1.6	8.7 ± 1.1	7.8 ± 1.6	7.8 ± 1.1	7.2 ± 0.9	3.2 ± 2.1
Secchi depth (m)	0.4 ± 0.3	1 ± 0.8	1.9 ± 0.8	1.2 ± 0.8	1.4 ± 0.6	1.7 ± 0.8	0.7 ± 0.5
Total phosphorus (µg/l)	97.4 ± 28.8	55.9 ± 23.1	40 ± 19.6	64.2 ± 39.1	49.1 ± 18.7	45.8 ± 21.1	98.3 ± 58.1

Table A2
Overview of the pike acoustically tagged before and during the spawning season of 2020. Lagoon and river locations are displayed in Fig. 1.

Area	01-Feb-2020–1-Mar-2020		2-Mar-2020–31-May-2020		
	Female	Male	Female	Male	Unknown
Barthe	2	0	4	5	0
Sehrowbach	0	0	7	12	0
Duwenbeek	0	0	1	5	0
Peene	14	11	0	0	0
Beek	0	0	0	2	0
Barther Bodden/Grabow	13	1	15	5	0
Kubitzer/Schaproder Bodden	0	0	18	42	1
North-Rügen-Bodden chain	5	3	21	6	0
Strelasund	6	10	21	14	0
Greifswalder Bodden	10	2	4	7	0
Peenestrom/Achterwasser	0	0	26	12	0

Table A3
Absolute numbers of pike sampled for genetic analysis and respective numbers sampled during the spawning months March and April for each waterbody.

Waterbody	Waterbody type (Freshwater/Brackish)	n total	n sampled during March/April	Share sampled during March/April (%)
Barthe River	Freshwater	50	0	0
BAT	Brackish	48	19	40
GB	Brackish	45	28	62
GJB	Brackish	50	0	0
SB/KB	Brackish	48	0	0
Neuendorfer Hechtgraben	Freshwater	48	48	100
P	Brackish	46	21	46
Peene River	Freshwater	50	0	0
Sehrowbach	Freshwater	50	50	100
SH	Brackish	50	NA	NA
Ziese	Freshwater	50	50	100

Table A4
Dimensions and water parameters of the five regularly electrofishing-sampled study streams and water parameters, measured in March and April 2021.

	Mean depth (m) ± SD	*Depth range (m)*	*Mean width (m) ± SD*	*Width range (m)*	*Length studied (km)*	*Mean temperature (°C) ± SD*	*Mean salinity (PSU)*	*Mean O_2 (mg/L)*
Neuendorfer Hechtgraben	0.2 ± 0.1	0.05–0.45	1.8 ± 0.3	0.6–2.6	2.8	5.7 ± 2.3	0.4	14.7
Duwenbeek	0.9 ± 0.3	0.4–1.45	2.0 ± 0.5	1.1–3.4	1.3	6.1 ± 2.0	0.4	12.7
Beek	0.7 ± 0.4	0.25–1.6	3.6 ± 0.4	2.7–4.9	2.0	6.0 ± 2.2	0.4	12.4
Sehrowbach	1.6 ± 0.2	0.95–1.95	6.1 ± 2.8	2.2–14.0	3.5	6.2 ± 2.2	0.4	11.4
Körkwitzer Bach	1.9 ± 0.1	1.4–2.2	10.3 ± 2.4	3.7–19.9	3.3	6.1 ± 2.0	0.3	11.5

References

Aminpour, P., Gray, S.A., Jetter, A.J., Introne, J.E., Singer, A., Arlinghaus, R., 2020. Wisdom of stakeholder crowds in complex social-ecological systems. Nat. Sustain. 3, 191–199.

Arlinghaus, R., Lucas, J., Weltersbach, M.S., Kömle, D., Winkler, H.M., Riepe, C., Kühn, C., Strehlow, H.V., 2021. Niche overlap among anglers, fishers and cormorants and their removals of fish biomass: a case from brackish lagoon ecosystems in the southern Baltic Sea. Fish. Res. 238, 105894.

Arlinghaus, R., Vogt, A., Kömle, D., Niessner, D., Ehrlich, E., Rittweg, T., Droll, J., 2022. Ursachenanalyse von Berufsfischer-Angler Konflikten am Beispiel der Nutzung von Hechten (*Esox lucius*) in den Boddengewässern Mecklenburg-Vorpommerns. Z. Fisch. 2, 27-27.

Arlinghaus R., Rittweg T., Dhellemmes F., Koemle D., Van Gemert R., Schubert H., Niessner D., Möller S., Droll J., Friedland R., Lewin W.C., Dorow M., Westphal L., Ehrlich E., Strehlow H.V., Weltersbach M.S., Roser P., Braun M., Feldhege F., Winkler H., 2023. A synthesis of a coastal northern pike (*Esox lucius*) fishery and its social-ecological environment: implications for management and research of pike in brackish lagoons in the southern Baltic Sea, Germany. Fish. Res., in press.

Basan U., 1989. Wir angeln in Bodden und Haffen, Sportverlag, ISBN: 3-328-00225-1.

Berggren, H., Nordahl, O., Tibblin, P., Larsson, P., Forsman, A., 2016. Testing for local adaptation to spawning habitat in sympatric subpopulations of pike by reciprocal translocation of embryos. PLoS One 11, e0154488.

Biester E., 1991. Ökologische Veränderungen in Boddengewässern und mögliche Folgen in der Fischerei. Arbeiten des Deutschen Fischerei-Verbandes 52, 1-16.

Birnie-Gauvin, K., Birch Højrup, L., Kragh, T., Jacobsen, L., Aarestrup, K., 2019. Getting cosy in freshwater: assumed to be brackish pike are not so brackish after all. Ecol. Freshw. Fish. 28, 376–384.

Bolger, A.M., Lohse, M., Usadel, B., 2014. Trimmomatic: a flexible trimmer for illumina sequence data. Bioinformatics 30, 2214-2120.

Bond, M.E., Babcock, E.A., Pikitch, E.K., Abercrombie, D.L., Lamb, N.F., Chapman, D.D., 2012. Reef sharks exhibit site-fidelity and higher relative abundance in marine reserves on the Mesoamerican Barrier Reef. PloS One 7, e32983.

Bonney, R., Cooper, C.B., Dickinson, J., Kelling, S., Phillips, T., Rosenberg, K.V., Shirk, J., 2009. Citizen science: a developing tool for expanding science knowledge and scientific literacy. BioScience 59, 977–984.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R. J. 9, 378–400.

Casselman, J.M., 1974. External sex determination of northern pike, *Esox lucius* Linnaeus. Trans. Am. Fish. Soc. 103, 343–347.

Cottrell, A.M., David, S.R., Forsythe, P.S., 2021. Productionand outmigration of young-of-year northern pike *Esox lucius* from natural and modified waterways connected to Lower Green Bay, Wisconsin. J. Fish Biol. 99, 364–372.

Deutscher Seefischerei-Verein, 1905. Übersicht über die seefischerei deutschlands in den gewässern der ostsee. ICES J. Mar. Sci. Volume s1, 61–140.

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

Diaz-Suarez, A., Noreikiene, K., Kisand, V., Burimski, O., Svirgsden, R., Rohtla, M., Vasemägi, A., 2022. Temporally stable small-scale genetic structure of Northern pike (*Esox lucius*) in the coastal Baltic Sea. Fish. Res. 254, 106402.

Engstedt, O., Engkvist, R., Larsson, P., 2014. Elemental fingerprinting in otoliths reveals natal homing of anadromous Baltic Sea pike (*Esox lucius* L.). Ecol. Freshw. Fish. 23, 313–321.

Engstedt, O., Nilsson, J., Larsson, P., 2018. Habitat restoration a sustainable key to management. In Biology and ecology of pike. CRC Press, pp. 250–268.

Engstedt, O., Stenroth, P., Larsson, P., Ljunggren, L., Elfman, M., 2010. Assessment of natal origin of pike (*Esox lucius*) in the Baltic Sea using Sr:Ca in otoliths. Environ. Biol. Fishes 89, 547–555.

Espinoza, M., Lédée, E.J., Simpfendorfer, C.A., Tobin, A.J., Heupel, M.R., 2015. Contrasting movements and connectivity of reef-associated sharks using acoustic telemetry: implications for management. Ecol. Appl. 25, 2101–2118.

Falk, K., 1965. Der Hecht unserer Küstengewässer und seine Bewirtschaftung. Institut für Hochseefischerei und Fischverarbeitung Rostock-Marienehe.

Felsenstein, J., 2005. PHYLIP (Phylogeny Inference Package) version 3.6. Distributed by the author. Department of Genome Sciences, University of Washington, Seattle.

Flink, H., Tibblin, P., Hall, M., Hellström, G., Nordahl, O., 2023. Variation among bays in spatiotemporal aggregation of Baltic Sea pike highlights management complexity. Fish. Res. 259, 106579.

Greszkiewicz, M., Fey, D.P., Lejk, A.M., Zimak, M., 2022. The effect of salinity on the development of freshwater pike (*Esox lucius*) eggs in the context of drastic pike population decline in Puck Lagoon, Baltic Sea. Hydrobiologia 849, 2781–2795.

Hartig F., 2022. DHARMa: Residual Diagnostics for Hierarchial (Multi-Level / Mixed) Regression Models, R package version 0.4.6.

Hegemann, M., 1964. Der Hecht, second ed. VerlagsKG Wolf, Magdeburg.

Hermann, B., Sieglerschmidt, J., 2017. Umweltgeschichte in Beispielen. Springer Verlag. ISBN-10: 658154322.

Holjewilken, H., 1960. Meliorationstechnik: mechanisierung der Entwässerung. Agrartech. Heft 5.

Jacobsen, L., Engström-Öst, J., 2018. Coping with environments; vegetation, turbidity and abiotics. In *Biology and ecology of pike*. CRC Press, pp. 32–61.

Jacobsen, L., Bekkevold, D., Berg, S., Jepsen, N., Koed, A., Aarestrup, K., Baktoft, H., 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.

Jørgensen, A.T., Hansen, B.W., Vismann, B., Jacobsen, L., Skov, C., Berg, S., Bekkevold, D., 2010. High salinity tolerance in eggs and fry of a brackish *Esox lucius* population. Fish. Manag. Ecol. 17, 554–560.

Junker, C., 1988. Vergleichende Studien zur Biologie des Hechtes (*Esox lucius* L.) in Brackgewässern der DDR-Küste (Greifswalder-Bodden, Darß-Zingster Boddenkette, Oderhaff/Peenestrom). W.-Pieck Universität Rostock.

Kallasvuo, M., Salonen, M., Lappalainen, A., 2010. Does the zooplankton prey availability limit the larval habitats of pike in the Baltic Sea? Estuar., Coast. Shelf Sci. 86, 148–156.

Kallasvuo, M., Lappalainen, A., Urho, L., 2011. Coastal reed belts as fish reproduction habitats. Boreal Environ. Res. 16, 1–14.

Koemle, D., Beardmore, B., Dorow, M., Arlinghaus, R., 2021. The human dimensions of recreational anglers targeting freshwater species in coastal ecosystems, with implications for management. North Am. J. Fish. Manag. 41, 1572–1590.

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. Fish. Res. 256, 106480.

Kofler, R., Pandey, R.V., Schlötterer, C., 2011. POPOOLATION2: identifying differentiation be-tween populations using sequencing of pooled DNA samples (Pool-Seq). Bioinformat-ics 27, 3435–3436.

Larsson, P., Tibblin, P., Koch-Schmidt, P., Engstedt, O., Nilsson, J., Nordahl, O., Forsman, A., 2015. Ecology, evolution, and management strategies of northern pike populations in the Baltic Sea. Ambio 44, 451–461.

Leppäranta, M., Myrberg, K., 2009. Physical oceanography of the Baltic Sea. Springer Science. ISBN: 978-3-540-79703-6.

Li, H., Handsaker, B., Wysoker, A., Fennell, T., Ruan, J., Homer, N., Marth, G., Abecasis, G., Durbin, R., 1000 Genome Project Data Processing Subgroup, 2009. The sequence alignment/map format and SAMtoools. Bioinformatics 25, 2078–2079.

Lung, M.V., 2022. Landesamt für Umwelt, Naturschutz und Geologie, Abteilung 3 - Geologie, Wasser und Boden.

Möller, S., Winkler, H.M., Klügel, A., Richter, S., 2019. Using otolith microchemical analysis to investigate the importance of brackish bays for pike (*Esox lucius* Linnaeus, 1758) reproduction in the southern Baltic Sea. Ecol. Freshw. Fish. 28, 602–610.

Möller, S., 2020. Untersuchungen zur Reproduktionsbiologie und Populationsgenetik des Hechtes (*Esox lucius* Linnaeus, 1758) im Brackwasser der südlichen Ostsee, Doctoral thesis. University of Rostock.

Möller, S., Winkler, H.M., Richter, S., Bastrop, R., 2021. Genetic population structure of pike (*Esox lucius* Linnaeus, 1758) in the brackish lagoons of the southern Baltic Sea. Ecol. Freshw. Fish. 30, 140–149.

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

Müller, K., Berg, E., 1982. Spring migration of some anadromous freshwater fish species in the northern Bothnian Sea. Hydrobiologia 96, 161–168.

Nei, M., Li, W.H., 1979. Mathematical model for studying genetic variation in terms of restriction endonucleases. Proc. Natl. Acad. Sci. USA 76, 5269–5273.

Nellen, W., 1965. Beiträge zur Brackwasserökologie der Fische im Ostseeraum. Kiel. Meeresforsch. 21, 192–198.

Neubert, K., 2011. Die Salinität als limitierender Faktor der Reproduktion des Hechtes (*Esox lucius* L., 1758) im Brackwasser der Ostsee, Diploma thesis. University of Rostock.

Nilsson, J., Engstedt, O., Larsson, P., 2014. Wetlands for northern pike (*Esox lucius* L.) recruitment in the Baltic Sea. Hydrobiologia 721, 145–154.

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. Aquat. Conserv. Mar. Freshw. Ecosyst. 29, 1923–1935.

Nordahl, O., Koch-Schmidt, P., Tibblin, P., Forsman, A., Larsson, P., 2020. Vertical movements of coastal pike (*Esox lucius*) - on the role of sun basking. Ecol. Freshw. Fish. 29, 18–30.

Olsson, J., Andersson, M.L., Bergström, U., Arlinghaus, R., Audzijonyte, A., Berg, S., Östman, Ö., 2023. A pan-Baltic assessment of temporal trends in coastal pike populations. Fish. Res. 260, 106594.

Pierce, R.B., Shroyer, S., Pittman, B., Logsdon, D.E., Kolander, T.D., 2006. Catchability of larval and juvenile northern pike in quatrefoil light traps. North Am. J. Fish. Manag. 26, 908–915.

Psuty, I., 2022. Are we ready to implement resist–accept–direct framework thinking? A case study of fish stocks and small-scale fisheries in the Puck Bay (Southern Baltic). Fisheries Management and Ecology 29, 423–438.

Psuty, I., Zaporowski, R., Gaweł, W., 2023. Goodbye to northern pike (*Esox lucius*) in the Polish southern Baltic? Fish. Res. 258, 106549.

R Core Team, 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: ⟨https://www.R-project.org/⟩.

Rambaut A., 2011. FigTree, Version 1.4.4. Available at: ⟨http://tree.bio.ed.ac.uk/software/figtree⟩.

Rechlin, O., Fadschild, K., 1991. Fischereierträge aus den Boddengewässern der Küste Mecklenburg-Vorpommerns, Arbeiten des Deutschen Fischerei-Verbandes Heft 52 - Fragen zur fischereilichen Nutzung küstennaher Flachwassergebiete - Wattenmeer und Boddengewässer.

Remane, A., Schlieper, S., 1971. Biology of brackish water. Verlagsbuchhandlung. ISBN: 978-3-510-40034-8.

Rothla M., 2015. Otolith sclerochronological studies on migrations, spawning habitat preferences and age of freshwater fishes inhabiting the Baltic Sea, Dissertationes biologicae Universitatis Tartuensis 271.

Sambrook, J., MacCallum, P., Russell, D., 2001. Molecular Cloning: A Laboratory Manual. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, New York.

Schiefelbein U., 2018. Was kam nach den Karrendorfer Wiesen? – Über Ausdeichungen an der Ostseeküste Mecklenburg-Vorpommerns, Natur und Naturschutz in Mecklenburg-Vorpommern 46, 19–34.

Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., Webster, M.S., 2010. Population diversity and the portfolio effect in an exploited species. Nature 465, 609–612.

Schlötterer, C., Tobler, R., Kofler, R., Nolte, V., 2014. Sequencing pools of individuals—mining genome-wide polymorphism data without big funding. Nat. Rev. Genet. 15, 749–763.

Sedlazeck, F.J., Rescheneder, P., von Haeseler, A., 2013. NEXTGENMAP: fast and accurate read mapping in highly polymorphic genomes. Bioinformatics 29, 2790–2791.

Silvano, R.A.M., Valbo-Jørgensen, J., 2008. Beyond fishermen's tales: contributions of fishers' local ecological knowledge to fish ecology and fisheries management. Environ. Dev. Sustain 10, 657–675.

Su, G., Logez, M., Xu, J., Tao, S., Villéger, S., Brosse, S., 2021. Human impacts on global freshwater fish biodiversity. Science 371, 835–838.

Sunde, J., Larsson, P., Forsman, A., 2019. Adaptations of early development to local spawning temperature in anadromous populations of pike (*Esox lucius*). BMC Evolut. Biol. 19, 1–13.

Sunde, J., Tamario, C., Tibblin, P., Larsson, P., Forsman, A., 2018. Variation in salinity tolerance between and within anadromous subpopulations of pike (*Esox lucius*). Sci. Rep. 8, 1–11.

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

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. Am. Nat. 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. J. Anim. Ecol. 85, 136–145.

Timm, A.L., Pierce, R.B., 2015. Vegetative substrates used by larval northern pike in Rainy and Kabetogama Lakes, Minnesota. Ecol. Freshw. Fish. 24, 225–233.

Van der Wall H., Kraemer R.A., 1991. Die Wasserwirtschaft in der DDR, Studie im Auftrag der Hans-Böckler Stiftung.

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. Fish. Manag. Ecol. 29, 16–28.

Vierck, 1980. Stellungnahme zur Durchführung der Frühjahrsschonzeit 1980 im Fischereiaufsichtsbereich Lauterbach. Personal statement issued by fisheries supervision Lauterbach.

Vogt, A., 2020. Understanding stakeholder conflicts in coastal fisheries: evidence from the brackish lagoons around Rügen. Master Thesis, Humboldt-Universität zu Berlin, Germany.

Westin, L., Limburg, K.E., 2002. Newly discovered reproductive isolation reveals sympatric populations of *Esox lucius* in the Baltic. J. Fish. Biol. 61, 1647–1652.

Wiemers T., Fischer K., 1998. Darstellung der historischen Entwicklung des Naturraumes Darß-Zingst im Zeitraum 1692 bis 1991, Natur und Naturschutz in Mecklenburg Vorpommern 34, 5-12.

Winkler, H.M., 1989. Fische und Fangerträge im Greifswalder Bodden. MEER UND MUSEUM Band 5 - Greifswalder Bodden, Schriftenreihe.

Winkler, H.M., 1991. Changes of structure and stock in exploited fish communities in estuaries of the southern Baltic coast (Mecklenburg-Vorpommern, Germany). Int. Rev. der Gesamt Hydrobiol. Hydrogr. 76, 413–422.

Winkler H.M., Dumke A. & Schulz N., 1999a. Fischereibezirk Greifswalder Bodden (03), Gutachten aufgetragen durch das Ministerium für Ernährung, Landwirtschaft Forsten und Fischerei Mecklenburg-Vorpommern.

Winkler H.M., Dumke A. & Schulz N., 1999b. Fischereibezirk Strelasund (04), Gutachten aufgetragen durch das Ministerium für Ernährung, Landwirtschaft Forsten und Fischerei Mecklenburg-Vorpommern.

Winkler H.M., Dumke A. & Schulz N., 1999c. Gewässer zwischen Hiddensee und Rügen (05), Gutachten aufgetragen durch das Ministerium für Ernährung, Landwirtschaft Forsten und Fischerei Mecklenburg-Vorpommern.

Winkler H.M., Dumke A. & Schulz N., 1999d. Fischereibezirk Darßer Boddenkette (08), Gutachten aufgetragen durch das Ministerium für Ernährung, Landwirtschaft Forsten und Fischerei Mecklenburg-Vorpommern.

Winkler, H.M., Debus, L., 2006. Auffällige Bestandsveränderungen bei wichtigen Fischarten der Darß-Zingster Boddenkette und mögliche Ursachen. Rostock. Meeresbiol. Beitr. 16, 61–70.

Zigler, S.J., Dewey, M.R., 1995. Phototaxis of larval and juvenile northern pike. North Am. J. Fish. Manag. 15, 651–653.