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RESEARCH ARTICLE

Assessing the potential for introducing resident brackish-water pike (*Esox lucius*) to restore depleted Baltic Sea populations

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Abstract. The northern pike (*Esox lucius* L.) inhabits the Baltic Sea and has two reproductive strategies: spawning in freshwater wetlands (anadromous populations) and direct spawning in coastal marine waters (resident brackish populations). Resident brackish populations do not occur in Polish marine waters, and anadromous pike populations in Puck Bay are virtually extinct. This study assessed whether reproductive material from resident brackish pike populations could be used to obtain larvae under hatchery conditions for population restoration. Eggs were collected from resident brackish pike spawners in the coastal waters of Rügen (Germany) and transported 600 km (9 h) to a hatchery in Poland. The eggs were incubated in artificially prepared saline water at 0, 5, 7, and 8.5 PSU. In the 2023 trial, hatching success was 0% at 0 PSU, 0.7% at 5 PSU, 8.3% at 7 PSU, and 8.0% at 8.5 PSU. Larval survival to 18 days post hatching in salinities of 5–8.5 PSU was high (approximately 90%), and growth rates at 14°C ranged from 0.26 to 0.31 mm d^{-1}. No eggs hatched in 2024. The results indicate that this strategy is feasible, particularly given the high larval survival; however, the low and variable hatching success requires further optimization before application in restoration programs.

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Introduction

The northern pike (*Esox lucius* L.) is a species with a wide distribution range that includes both freshwater habitats (Craig 1996) and saline waters, such as the Baltic Sea and the Caspian Sea (Crossman 1996, Skov and Nilsson 2018). Two spawning strategies can be distinguished in the Baltic Sea: anadromous and resident brackish-water populations. Anadromous pike migrate to freshwater environments in spring, where rivers and wetlands provide suitable spawning and nursery habitats. Early life stages remain there for several weeks, after which juveniles migrate to the sea, where they remain until they reach full maturity (Craig 1996, Horbowa and Fey 2013, Greszkiewicz et al. 2022).

The second strategy is represented by resident brackish-water pike populations, which do not require freshwater floodplains for reproduction. These populations not only feed in the sea but also reproduce successfully in coastal waters, as shown for Sweden (Andersson et al. 2000, Westin and Limburg 2002, Engstedt et al. 2010), Finland (Lappalainen et al. 2008, Lehtonen et al. 2009), Denmark (Jørgensen et al. 2010, Jacobsen et al. 2017), Estonia (Rohtla et al. 2012), and Germany (Möller et al. 2019, 2020). However, no such population exists in Polish coastal waters, including Puck Bay (Greszkiewicz et al. 2022). According to Lehtonen and Toivonen (1981), resident saltwater pike populations can reproduce throughout the Baltic Sea in shallow waters, although typically at slightly greater depths than in the inland waters. They are adapted to marine spawning substrates and usually select seaweed (*Fucus* spp.) at depths of approximately 0.5–2 m. After spawning, individuals from both population types – anadromous and resident – mix again in coastal waters, where they feed intensively (Engstedt et al. 2014). Areas where resident brackish populations not only occur but also dominate include coastal bays in Denmark (e.g. Stege Bay and Præstø Bay) and Germany, particularly around the island of Rügen. Salinity levels in these areas typically range from 7 to 10 PSU (Nilsson 2006, Engstedt et al. 2010, Nilsson et al. 2014, Skov and Nilsson 2018).

Unfortunately, both anadromous and resident pike populations in the Baltic Sea have declined markedly over the past four decades (Olsson 2019, Arlinghaus et al. 2023, Olsson et al. 2023). While this decline has not been equally pronounced in all regions, there are areas where current population sizes represent only a small fraction of those recorded in the 1970s (Andersson et al. 2000, Almesjö and Hansson 2001, Westin and Limburg 2002). In some locations, such as Puck Bay (Poland), a severe population collapse has been documented, with catches decreasing from approximately 40–50 tons per year in the 1960s to only tens or hundreds of kilograms per year from the late 1970s to the present (Greszkiewicz et al. 2022).

The decline in pike populations in the Baltic waters may result from different factors, depending on whether the populations are anadromous or resident. One of the most important causes of the decline in anadromous Baltic pike is the loss of access to freshwater spawning grounds. River regulation, levee and pumping station construction, and floodplain drainage have led to the disappearance of spring spillways that were common in the past (Hoffman et al. 2000). For example, in some areas of Sweden, approximately 90% of freshwater habitats have disappeared (Hagerberg et al. 2004). These changes were also the main reason for the loss of spawning grounds for the anadromous pike population in Puck Bay (Greszkiewicz et al. 2022). Fishing pressure from both commercial fisheries and recreational angling is also relevant, although it is usually not considered the primary driver of population decline. Other important factors influencing pike populations in the Baltic region include changes in the structure of coastal fish communities, characterized by a decrease in predatory fish and a simultaneous increase in small planktivorous species, particularly stickleback (*Gasterosteus aculeatus* L.) (Nilsson 2006, Nilsson et al. 2019, Donadi et al. 2020). This factor is especially important for resident pike during egg deposition and larval development in the coastal waters. In addition, increased predation pressure from growing populations of cormorants and seals has become an important factor affecting pike abundance (Olsson 2019, Bergström et al. 2022). The relative importance of these factors varies by geographical area.

Given the collapse of the pike population in Polish coastal waters, including Puck Bay (Greszkiewicz et al. 2022, Sapota et al. 2022), the introduction of a resident brackish-water population, for which the lack of freshwater spawning habitats does not represent a limiting factor, may be considered. Although a resident population is currently absent from Puck Bay, environmental conditions in this area – such as salinity (approximately 7 PSU), temperature (approximately 12°C in early spring), shallow depth, and a seabed covered by various forms of vegetation – are similar to those in other Baltic regions where resident pike populations occur and reproduce successfully. From the perspective of salinity, Puck Bay may provide a more stable environment than areas of the western Baltic Sea because it is not exposed to inflows of highly saline water. Such inflows through the Danish Straits have been associated with increased salinity levels of up to 20 PSU and have caused significant mortality in both early developmental stages and adult pike (Dahl 1961). An additional advantage of Puck Bay is its enclosed character, which results in more rapid water warming during spring (Fey et al. 2025). This may promote fast larval growth rates and, consequently, higher survival (Anderson 1988). The main disadvantage of Puck Bay is its relatively small area compared to the extensive coastal waters and numerous bays found along the Danish, German, and Swedish coasts.

The key question when considering the introduction of a resident pike population into Puck Bay, or other regions, is whether such an action is technically feasible. This raises several issues, including: (1) the possibility of obtaining resident spawners from other regions for egg collection; (2) the time required to collect and transport eggs to a hatchery, in the present work in Poland; (3) the efficiency of egg incubation and larval hatching under hatchery conditions using artificially prepared saline water; and (4) the survival and growth of the hatched larvae. Fry obtained through such procedures could potentially be used for stocking the areas of interest. At this stage, the primary concern is technical and logistical feasibility, whereas regulatory aspects, such as obtaining appropriate permits, should be considered once feasibility has been demonstrated.

The objectives of this study were (1) to evaluate the feasibility of introducing a resident brackish-water pike population as a potential tool for rebuilding local pike stocks in environments similar to Puck Bay, and (2) to assess the feasibility of long-distance transport and incubation of eggs from a brackish-water pike population. Eggs were obtained from spawners collected off the coast of Rügen (Germany) and transported to a hatchery in Poland, where incubation was conducted during two breeding seasons (2023–2024). Rügen was selected as the egg source because of its relatively short distance to the hatchery and the logistical possibility of obtaining spawners from a resident brackish-water pike population. The eggs were incubated at four salinity levels: 0 PSU (freshwater conditions typical of anadromous spawning), 5 PSU (low-salinity tolerance), 7 PSU (conditions typical of Puck Bay), and 8.5 PSU (salinity at the spawning grounds near Rügen at the time of egg collection). Hatched larvae were subsequently reared under controlled hatchery conditions for 18 days.

Materials and Methods

Egg acquisition and transport

Eggs and milt from a resident brackish-water pike population were obtained from spawners caught in the coastal waters of Rügen (Germany) (Fig. 1) in April 2023 (seven females and four males) and April 2024 (six females and five males). Most fish captured

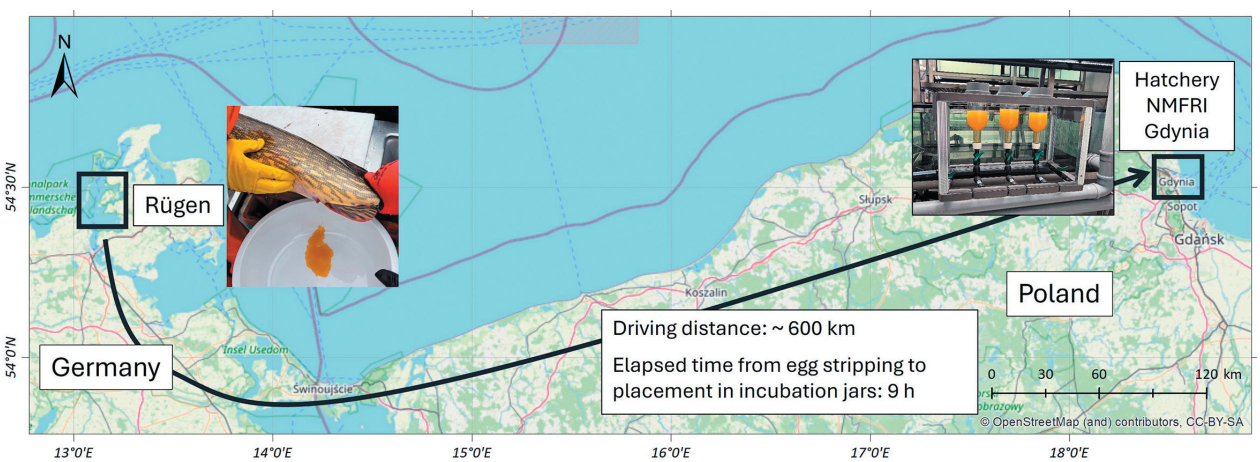

Figure 1. Sampling locations of pike (*Esox lucius*) spawners from a resident brackish-water population (Mursewiek, Rügen, Germany) and the location of the hatchery where eggs were incubated and larvae reared (National Marine Fisheries Research Institute, Gdynia, Poland). Road transport distance was approximately 600 km, and the elapsed time from the beginning of egg stripping to egg placement in incubation jars was ca. 9 h.

by the fishermen were ready to spawn, and only a small number were released without egg extraction. The total length (TL) ranged from approximately 60 to 110 cm. The egg collection and handling procedures were identical in both years. The eggs were collected in a bowl, and milt was added, and the mixture was gently stirred. Bay water was then added to initiate the fertilization process. Fertilized eggs were transferred to four 5-L buckets, with 1 L of the egg mixture placed in each bucket. The remaining volume (4 L) consisted of bay water (salinity: 8.5 PSU; temperature: 10.2°C). The buckets were placed in a passive portable refrigerator (80 × 50 × 40 cm; 80 L) with thick, insulated walls (Cool-Ice, Dometic, Sweden). Eggs were transferred to transport containers approximately 1 h after collection and transported (ca. 600 km) by passenger car to the Experimental and Breeding Center of the National Marine Fisheries Research Institute (NMFRI), Poland. The elapsed time from the beginning of egg stripping to egg placement in the incubation jars was approximately 9 h. The water temperature at the time of arrival at the hatchery was 10.5°C.

Egg incubation

At the hatchery, fertilized eggs were incubated in a recirculating water system comprising four independent circulation systems. Each system consisted of three mini Weiss jars (0.5 L each; replicates) connected to glass tanks with attached net breeder boxes. Each circulation system was equipped with a 70-L polyvinyl chloride (PVC) filtration–sedimentation tank containing 20 L of biological filter media (Bioceramax Pro 600, Aquael) and a UV lamp installed in the water flow. In total, 12 incubation jars were used for the experiment.

The water conditions were the same in both years. Salinity levels were set at 0.0, 5.0, 7.0, and 8.5 PSU, with each level assigned to a separate circulation system for the experiment. The water temperature was maintained at 10°C, and constant light was applied during incubation. In 2023, water temperature increased to 13.2°C during the first few hours due to a system malfunction but was gradually reduced to 10°C within the following 24 h. Although this temperature remained within the optimal range for pike reproduction (8–15°C; Raat 1988), a possible negative effect cannot be excluded, particularly given the relatively rapid temperature change. Saline water was prepared by dissolving aquarium-grade sea salt (Aquaforest.eu) in the tap water. The tap water was not chlorinated and was routinely used at the hatchery for egg incubation and larval rearing of other fish species, including pike from local populations. The volume of eggs placed in each incubation jar was 150 mL in both years. Dead eggs were removed daily.

Larval growth

After hatching, a 12 h light : 12 h dark photoperiod was applied, and water temperature was gradually increased from 10 to 14°C over 48 h. During egg incubation and larval rearing, the oxygen concentration (>7 mg L^{-1}) and pH (approximately 7.8) were monitored using an OxyGuard Pacific monitoring system. Ammonia (<0.2 mg L^{-1}) and nitrite (<0.2 mg $L^{-1)}$ concentrations were measured daily using a DR3900 Hach spectrophotometer. All measured parameters remained within the safe limits throughout the experiment.

Newly hatched larvae initially attached to the net of the breeder boxes (Fig. 2b). Once active swimming began, larvae were fed ad libitum every 2 h during the light period using artificial feed: ArtEX 2 (0.15 mm; Aller Aqua, Poland) was provided during the first four days after yolk-sac absorption, and from day 3 after yolk-sac absorption onward, Perla Larva Proactive 4.0 (0.3–0.5 mm; Skretting AS, Norway) was used. The experiment was terminated when the larvae reached 18 days post-hatching (dph).

The larvae were measured to the nearest millimeter using an NIS-Elements image analysis system (Nikon, Japan) shortly after hatching (n = 20) and at the end of the experiment (n = 40). Statistical analyses were performed using analysis of variance

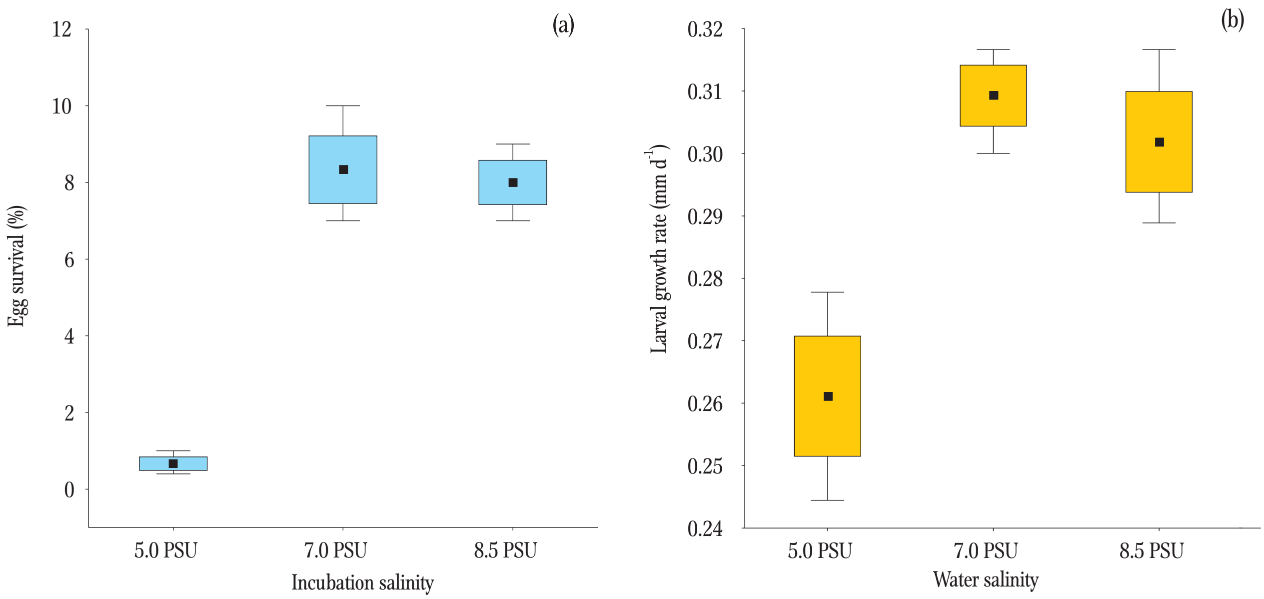

Figure 2. Survival of pike (*Esox lucius*) eggs obtained from spawners of a resident brackish-water population after incubation at 5.0, 7.0, and 8.5 PSU (a). Growth rates of pike larvae hatched and reared at 5.0, 7.0, and 8.5 PSU (b). Points indicate mean values; boxes represent the standard error (SE), and whiskers denote minimum and maximum values.

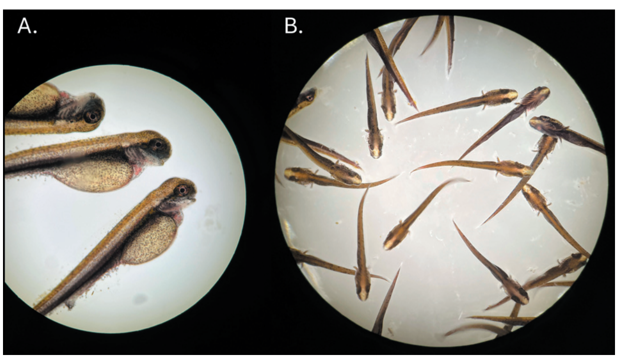

Figure 3. Pike larvae (*Esox lucius*) obtained from spawners of a resident brackish-water population, hatched and reared at 8.5 PSU, shown at the yolk-sac stage (A) and the first-feeding stage (B).

(ANOVA) in Statistica v.10 software. Differences were considered statistically significant at $P < 0.05$.

Results

Egg survival and hatching success

In the first trial conducted in 2023, egg survival during incubation differed significantly among salinity treatments (ANOVA, $P < 0.001$). Survival was 0% at 0 PSU, 0.7% at 5 PSU, 8.3% at 7 PSU, and 8.0% at 8.5 PSU (Fig. 2a). Larvae hatched only at salinities of 5, 7, and 8.5 PSU. The mean larval standard length (SL) at hatching was 7.9 mm (range: 7.1–8.8 mm SL), with no differences among salinities (ANOVA, $P > 0.05$). In the second trial conducted in 2024, no eggs survived incubation, and no larvae hatched. Egg mortality began on day 3 of incubation (30 degree-days, °D), and complete mortality was observed by day 7 (70 °D).

Larval survival and growth

In the 2023 trial, most larvae began active swimming and accepted artificial feed eight days after hatching (Fig. 3). Survival from hatching to 18 days post-hatching (dph) was approximately 90% at all salinity levels. Most mortality occurred immediately after hatching and during the period of first feeding. At the end of the experiment, the mean larval lengths were 12.6 mm at 5 PSU, 13.5 mm at 7 PSU, and 13.3 mm at 8.5 PSU. These values corresponded to growth rates of 0.26, 0.31, and 0.30 mm d^{-1}, respectively (Fig. 2b). Growth rates differed significantly among salinity treatments (ANOVA, $P < 0.001$), with lower growth observed at 5 PSU compared to 7 and 8.5 PSU.

Discussion

Egg and larval survival

In this study, we demonstrated that larvae can be obtained from eggs collected from a resident brackish-water pike population in Rügen and transported within 9 h to a hatchery in Poland. Survival of hatched larvae over 18 days post-hatching was high, and growth rates (approximately 0.3 mm d^{-1}) were comparable to those reported for freshwater populations reared at the same temperature of 14°C (Fey and Greszkiewicz 2021). However, egg survival was low, reaching approximately 8% in the 2023 trial; survival was higher at 7 and 8.5 PSU than at 5 PSU, no eggs survived at 0 PSU, and no hatching occurred in 2024. This low hatching success is disappointing, particularly in the context of potential applications for stocking Puck Bay. These results indicate that once hatching occurs, larvae originating from resident brackish populations can survive and develop normally under hatchery conditions, even after long-distance egg transport.

Several factors may have contributed to the reduced egg survival rates observed in this study. One possible explanation for this is the variability in gamete quality among spawners. Gamete quality is a well-recognized factor affecting fertilization success and early egg survival in the northern pike. Differences in egg characteristics, maternal condition, and spawning circumstances can result in substantial variation in hatching success, even within a single population (Raat 1988, Wright and Shoesmith 1988, Craig 1996). In the present study, due to time constraints associated with long-distance transport, gamete quality was not assessed on-site. Therefore, this factor remains a potential contributor to the reduced hatching success. In future studies, the use of eggs obtained from a larger number of females may help reduce the influence of individual variability in gamete quality. However, it should be noted that the number of females used in this study was already relatively high (seven in 2023 and six in 2024).

In addition, the effects of using artificially prepared saline water for egg incubation remain uncertain. Although artificial salt mixtures prepared with tap water are commonly applied in experimental studies, including investigations of pike salinity tolerance (Sunde et al. 2018, Greszkiewicz et al. 2022), their ionic composition may differ from that of natural brackish water, potentially affecting egg activation, embryonic development, and buoyancy (e.g. Sørensen et al. 2016). Sørensen et al. (2016), who examined nine different salt types in European eel (*Anguilla anguilla*), highlighted the importance of considering the ionic composition of incubation media when rearing fish eggs. With respect to the use of tap water, its application at the hatchery in question is likely safe, as it has previously been verified during the incubation of pike eggs from local populations in studies aimed at both the mass production of stocking material (Fey et al. 2022) and small-scale experimental research (Greszkiewicz et al. 2022). Future studies should directly compare egg incubation in artificially prepared saline water and natural bay water. However, transporting and storing sufficient volumes of seawater from the source location poses major logistical constraints, making this approach impractical. As an alternative, Baltic Sea water collected near the hatchery in Poland could be used. Although this would not be technically feasible for large-scale fry rearing, given that the hatchery is not located directly on the coastline, it appears feasible for egg incubation only.

Another factor potentially contributing to egg mortality was the elevated water temperature recorded at the beginning of incubation (13.2°C), caused by a technical malfunction of the cooling system. Although this temperature falls within the range observed during spawning in shallow, sun-heated coastal waters (8.9–13.8°C; Nilsson 2006), sudden temperature increases are known to negatively affect egg survival, particularly during the early developmental stages (Raat 1988). Therefore, the combined effects of temperature fluctuations and salinity conditions may have amplified egg mortality. However, this effect may have been limited to the 2024 trial, in which complete egg mortality was observed. In contrast, during the 2023 trial, when hatching success reached approximately 8% and larval survival was approximately 90%, water temperature remained stable at the correct value of approximately 10°C from egg collection through incubation.

Finally, it cannot be excluded that the low hatching success primarily resulted from long-distance transport itself. Although previous studies have demonstrated that fertilized pike eggs can be successfully transported for more than 12 h (Fey and Greszkiewicz 2023), these results were obtained for freshwater populations, which may limit their direct applicability to brackish-water pike.

Environmental suitability for resident pike

The concept of introducing a resident brackish-water pike population in Puck Bay is supported by environmental conditions that are favorable for successful reproduction. Temperatures in Puck Bay during early spring (5–12°C) are comparable to those observed in other Baltic regions where brackish pike populations occur. With respect to salinity, anadromous populations require freshwater or very low salinity (up to 2 PSU) for effective egg development (Bonisławska 2014, Kuznetsov et al. 2016, Greszkiewicz et al. 2022), whereas resident populations in the Baltic Sea typically reproduce at salinities ranging from 6 to 8 PSU (Westin and Limburg 2002, Jørgensen et al. 2010). Such conditions are present in Puck Bay, while at the same time the area is not exposed to episodic inflows of highly saline water that can be detrimental to pike eggs and larvae, as observed in the western Baltic Sea (Schinke and Matthäus 1998; Jørgensen et al. 2010). Another important factor is the availability of suitable substrates for egg attachment, including emergent vegetation and bottom substrates, such as seagrass (Nilsson 2006, Kallasvuo et al. 2011). Puck Bay provides such conditions (Sokołowski et al. 2021, Zgrundo and Złoch 2022). While vegetation is generally preferred, eggs may also adhere to other substrates, such as stones or sand fragments, as reported for many teleost species with adhesive eggs (Riehl and Patzner 1998). Interestingly, Wright and Shoesmith (1988) reported higher hatching success of pike eggs deposited on sand or silt compared with those laid on aquatic plants.

Wetlands undoubtedly provide favorable spawning conditions, including high zooplankton availability, reduced predation pressure during egg and larval development, and strong temperature increases that promote larval growth (Fey and Szczepkowski 2023). These benefits are undeniable. However, although temperature increases in Puck Bay may not reach wetland levels, its shallow and enclosed topography still results in pronounced spring warming compared with more open coastal areas (Fey et al. 2025). Moreover, spawning in coastal waters offers improved access to spawning grounds and reduces the risk of larval mortality associated with the delayed migration from floodplain habitats.

Ecological and genetic consequences

Ecological impacts are an important consideration when evaluating the introduction of a resident brackish-water pike population, in addition to the suitability of environmental conditions for their reproduction. Most importantly, the introduced population would not compete with the virtually non-existent anadromous pike population in Puck Bay and could contribute to long-term ecological and socio-economic benefits compared to repeated fry stocking. Moreover, food availability in the bay appears to be sufficient, with large quantities of round goby (*Neogobius melanostomus* (Pall.)) and other prey species present (Sapota and Skóra 2005, Sokołowska and Fey 2011).

From a genetic perspective, the introduction of a resident brackish-water pike population should be considered in the context of the existing population structure in the Baltic Sea. Recent genetic analyses have shown that the Danish brackish pike population from Stege Nor is not strongly differentiated from several Polish coastal populations, particularly those inhabiting the Gardno and Łebsko coastal lakes along the southern Baltic coast (Wąs-Barcz et al.

2023). Although comparable data are not available for the Rügen population, the results obtained for Danish pike suggest genetic similarity consistent with isolation by distance rather than strict population separation. This interpretation is supported by other studies indicating substantial genetic variability both within and among Baltic pike populations, with evidence of population structure and isolation by distance (Laikre et al. 2005, Wennerström et al. 2017, Möller et al. 2020).

Importantly, the coexistence of anadromous and resident pike populations within the same coastal areas is a natural phenomenon. For example, Engstedt et al. (2010) reported that 55% of pike along the Swedish coast belonged to resident populations, while 45% were anadromous. In Matsalu Bay (Estonia), the proportion of anadromous populations reached 82% (Rohtla et al. 2012). In contrast, Möller et al. (2020) found that 94% of pike in the waters surrounding Rügen Island originated from the saltwater population. Therefore, it can be argued that the potential introduction of a resident brackish-water pike population into areas such as Puck Bay would not represent an artificial or novel population structure, but rather the restoration of a reproductive component that is currently absent or functionally extinct.

Implications and future directions

In conclusion, the present study demonstrates the technical feasibility of obtaining eggs from a resident brackish pike population, transporting them over long distances, and rearing larvae that show high survival and normal growth under hatchery conditions. The main limitation remains low and variable egg survival during incubation. This likely reflects the combined effects of variable gamete quality, unresolved impacts of artificial saline water, temperature instability during early embryogenesis, and transport-related stress. One or more of these factors may be responsible and should be addressed in future studies. Therefore, future work should focus on optimizing incubation conditions, including direct comparisons of artificial and natural brackish water and standardized assessments of gamete quality. Addressing these issues is essential before the introduction of resident brackish pike populations can be implemented as a reliable restoration tool in Puck Bay and similar coastal systems.

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Author contributions. D.F.: conceptualization, fieldwork, methodology, investigation, data analysis, writing – original draft, writing – review & editing, project administration; M.G.: methodology, fieldwork, investigation, visualization; A.L.: methodology, fieldwork, investigation; M.Z.: methodology, fieldwork, investigation; M.B.: fieldwork, investigation.

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