Thermosaline niche, resource use and growth of a stenohaline freshwater predator (northern pike, *Esox lucius*) in brackish ecosystems and adjacent tributaries of the southern Baltic Sea

Dissertation

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Title picture „Release“, female pike Artemis being released back into the Grabow in the national park Vorpommernsche Boddenlandschaft after transmitter implantation and standard sampling. Big thanks to Phillip Roser for taking this magnificent photo and allowing me to use it in my thesis. Copyright: Phillip Roser.

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Paper V: **TR (large)**, CT and RA developed the concept; **TR (large)**, CT and MW collected the data; **TR (predominant)** and EE analyzed the data; **TR (large)**, RA and CT wrote the paper; CT, EE, MW and RA provided edits on the manuscript; all authors helped revising the manuscript.

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Paper VII: **TR (large)**, CT and RA developed the concept; **TR (predominant)**, TG, MB and FD collected the data; **TR (entire)** analyzed the data; **TR (large)**, CT and RA wrote the paper; CT, TG, MB, FD and RA provided edits on the manuscript

Abstract (English)

Niche variation and subsequent eco-evolutionary adaptations to different habitats, environmental conditions and resources drive intraspecific diversification and speciation. While niche variations have been documented in multiple different taxa, most studies have focused on only a few specific axes of a species' ecological niche. Much less is known about the interactions between niche axes, and how multidimensional niche variations relate to intrapopulation diversification. I used a stenohaline freshwater predator, northern pike (*Esox lucius*), inhabiting interconnected brackish lagoons and freshwater tributaries around Rügen island in the southern Baltic Sea of Germany, as a model. I studied multidimensional niche variation and intraspecific diversification patterns, leveraging individual-level data on thermal, saline and dietary niche use in combination with telemetry, genetics and growth data as a fitness surrogate. Pike displayed variation along multiple niche axes, corresponding with genetic differentiation, forming three ecotypes with distinct thermosaline and feeding niches. I detected a habitat-specialized ecotype each in freshwater and brackish environments, which were connected by an intermediary migratory ecotype. Reproductive isolation is likely facilitated by environmental factors, specifically salinity, geographical distance, and anthropogenic habitat blockage. Niche overlap and differences in individual-level and subpopulation-level specialization suggested intraspecific competition in parts of the pike metapopulation, likely contributing to niche differentiation and diversification. I detected growth benefits through specialization on marine resources, in particular pulses of Atlantic herring (*Clupea harengus*), especially in large brackish-adapted individuals. However, the absence of differences in lifelong growth indicated similar lifelong fitness among pike ecotypes. Reasons for this are likely tradeoffs between osmoregulatory costs in brackish habitats and growth benefits through marine resource use. Equal growth, as well as resource partitioning, are likely important mechanisms for the coexistence of the pike ecotypes. My results indicate a behaviorally and genetically highly diversified metapopulation that displays strong local adaptation and specialization, which has important consequences for conservation and management. To increase general abundance and resilience of the pike metapopulation against environmental change, habitat connectivity in the system should be increased. Furthermore, protecting large fish that are able to profit most from marine resources may increase the growth performance of trophy pike. The coexistence of multiple discrete ecotypes with distinct habitat and resource specialization in the pike metapopulation highlights the need to integrate individual life histories and intraspecific diversity into adaptive management approaches, which holds the key for healthy pike stocks in the future.

Zusammenfassung (deutsch)

Nischenvariationen und öko-evolutionäre Anpassungen an verschiedene Lebensräume, Umweltbedingungen und Ressourcen treiben intraspezifische Diversifikation und Speziation. Während Nischenvariationen bei verschiedenen Taxa dokumentiert wurden, haben sich bisherige Arbeiten meist auf wenige spezifische Achsen der ökologischen Nische einer Art konzentriert. Weniger ist bekannt über Interaktionen zwischen Nischenachsen und darüber, wie multidimensionale Nischenvariationen zur Intrapopulationsdiversifikation beitragen. Ich nutzte einen stenohalinen Süßwasser-Raubfisch, den europäischen Hecht (*Esox lucius*), in Brackwasser-Lagunen und Süßwasser-Zuflüssen rund um die Insel Rügen in der südlichen Ostsee Deutschlands, als Modell. Ich untersuchte multidimensionale Nischenvariationen und intraspezifische Diversifikationsmuster, indem ich individuelle Daten zur thermosalinen Nischennutzung und Ernährung in Kombination mit Telemetrie, Genetik und Wachstumsdaten als Fitness-Proxy heranzog. Variationen entlang mehrerer Nischenachsen, die mit genetischer Differenzierung korrespondierten, wiesen auf drei Ökotypen mit unterschiedlichen thermo-salinen und Nahrungsnischen hin. Ich entdeckte habitat-spezialisierte Ökotypen in Süßwasser- und Brackwasser, die durch einen intermediären, wandernden Ökotyp verbunden sind. Reproduktive Isolation der Ökotypen ist wahrscheinlich durch Umweltfaktoren wie Salinität, geografische Entfernung und anthropogene Habitatblockaden gegeben. Nischenüberlappungen und Unterschiede in Spezialisierung deuteten auf intraspezifische Konkurrenz in Teilen der Hechtmetapopulation hin, die wahrscheinlich zur Nischendifferenzierung und Diversifikation beiträgt. Ich stellte Wachstumvorteile von mariner Ressourcenspezialisierung fest, insbesondere durch Atlantische Heringspulse (*Clupea harengus*), insbesondere bei großen, brackwasseradaptierten Individuen. Gleiches lebenslanges Wachstum deutete jedoch auf eine vergleichbare Fitness zwischen den Hechtökotypen hin. Gründe hierfür sind wahrscheinlich Kompromisse zwischen osmoregulatorischen Kosten im Brackwasser und Wachstumsvorteile durch marine Ressourcen. Gleiches Wachstum und Ressourcenaufteilung sind wahrscheinlich wichtige Mechanismen für Koexistenz der Ökotypen. Meine Ergebnisse zeigen eine diversifizierte Metapopulation, die lokale Anpassung und Spezialisierung aufweist, mit Konsequenzen für Schutz und Management. Um Abundanz und Resilienz der Hechtmetapopulation zu erhöhen, sollte die Habitatkonnektivität im System verbessert werden. Der Schutz großer Fische, die am meisten von marinen Ressourcen profitieren, würde vorraussichtlich die Wachstumsleistung von Großhechten steigern. Die Koexistenz mehrerer Ökotypen mit spezifischen Habitat- und Ressourcenspezialisierungen innerhalb der Population unterstreicht die Notwendigkeit, individuelle Lebensgeschichten und intraspezifische Diversität in adaptive Managementansätze zu integrieren, was der Schlüssel für gesunde Hechtbestände in der Zukunft ist.

Background

pike on the horizon, copyright: Falk Weiß

Since the beginning of the field of ecology, researchers have wondered why individuals belonging to the same species sometimes vary significantly in their appearance, behavior and physiological characteristics (Bell, 2010). Most species display some degree of phenotypic variation, and determining the underlying mechanisms has occupied and driven ecologists worldwide for the better part of two centuries, since Darwin first published his origin of species (Darwin, 1859). The first authors tackling the variation among and within species back in the 19th and early 20th century, including Darwin (1859), Weismann (1909), Haldane & Huxley (1927) and Wells et al. (1934), predominantly assessed natural variation from a species level, concluding that the evolutionary process of variation must be gradual and over time spans of millennia or millions of years. A notable exception was Wallace (1889), who observed intraspecific variation also across small geographic scales and within species, hypothesizing selection may be stronger and acting on shorter time periods than most contemporary researchers suspected. The predominant view of gradual selection was slowly replaced in the mid-20th century by a growing conscience that diversity may evolve rapidly, spearheaded by studies such as Dobzhansky (1948), Cain & Shepherd (1954), and Clayton & Robertson (1957), who concluded that natural selection is often strong and can act on short time scales (Endler, 1986). With the introduction of studies on discrete morph frequencies to estimate the relationships between continuous characters and fitness components (Hendry & Kinnison 1999), the groundwork was laid for today's evolutionary ecology of individuals (Araújo et al., 2011; Bolnick et al., 2003; Costa-Pereira & Shaner, 2025).

Individuals diverge in the environmental conditions they experience, their movement, reproductive strategy, and the resources they use, in summary, they differ in their ecological niche (Hutchinson, 1957). This is further influenced by environmental stochasticity, competition, and resource availability (Costa-Pereira & Shaner, 2025; White et al., 2022). Within their ecological niches, natural selection drives individuals to strive for optimal energy allocation to growth, survival, and reproduction to maximize their lifetime fitness (White et al., 2022), which fosters dispersal along fitness gradients (Bell, 2010; Brown, 1990; Fretwell & Lucas, 1969; Rosenzweig, 1974). This leads to local adaptations in, for example, behavior, morphology, and physiology, which, combined with sufficient reproductive isolation, are prerequisites for ecological speciation (Doebeli & Dieckmann, 2003). Reproductive isolation may be facilitated simply by distance, time, or physical barriers preventing gene flow, but many natural populations also show sympatric diversification in absence of such barriers, the mechanisms of which are poorly understood (Doebeli & Dieckmann, 2003). Discrete groups of individuals within a population that differ both in their expressed phenotype and their underlying genetic structure are referred to as ecotypes (Stronen et al., 2022). Ecotypes form distinct reproductive contingents within a population, which is then a metapopulation (Hanski & Simberloff, 1997). Therefore, intraspecific diversity, in particular ecotype evolution, drives metapopulation dynamics and, ultimately, speciation in animals (Bell, 2010; Doebeli & Dieckmann, 2003).

Ecotype evolution has important implications for management and conservation of a species, mainly through portfolio effects. Figge (2004) was the first to adapt portfolio theory from economics to population ecology and conservation. Much like asset diversity can stabilize a financial portfolio against stock market crashes and boom-bust dynamics (Markowitz, 1991), a population with a high diversity of different genotypes and phenotypes is more resilient to disturbances (Campana et al., 2022; Šargač et al., 2022; Schindler et al., 2010). However, conserving this diversity is challenging, in particular when distinct reproductively isolated ecotypes coexist in a metapopulation (Hanski & Simberloff, 1997). One way to manage such a metapopulation is localized adaptive management (Westgate et al., 2013), in particular when it is combined with evidence-based approaches (Gillson et al., 2019). However, applying these management approaches requires detailed knowledge about the ecology of different ecotypes, such as reproductive strategy, habitat use, resource specializations, metapopulation connectivity, and ecotype-specific age and growth information (Campana et al., 2022; Lukyanova et al., 2024; Šargač et al., 2022; Schindler et al., 2010). Therefore, research on intraspecific diversity can inform conservation of threatened species as well as management of exploited species.

The northern pike (*Esox lucius*) presents an ideal model for studies of niche use and intraspecific diversification. Its high phenotypic variability, potential for rapid genetic adaptation and wide distribution range across a multitude of habitats established pike as an important model species in studies on ecology and evolution (Forsman et al., 2015). Despite being considered a primarily freshwater species of limited salinity tolerance (Jacobsen and Engström-Öst, 2018), pike have colonized brackish coastal habitats in the Baltic Sea (Jacobsen & Engström-Öst, 2018), including the shallow coastal lagoons (referred to as “Bodden lagoons” in the rest of this thesis) around Rügen island in the Southern Baltic Sea in Germany (Figure 1) (**paper I**). Pike inhabiting these coastal waters are exposed to the strong environmental gradients present in this system, in particular high and fluctuating salinity levels (**paper I**). The Bodden lagoons host a diverse assemblage of both marine and freshwater species along the salinity gradient, and experience pulses of marine resources through migratory marine fish, such as herring, which offers a wide prey range for pike (**paper I**). The environmental variability of a challenging habitat, combined with the potential benefits of connected freshwater and marine food webs, makes the Bodden lagoons an ideal system to investigate the mechanisms behind intraspecific diversification and adaptation processes in a suitable model species, which led to the first main motivation of this thesis.

Pike are a socio-economically important species, for a variety of reasons, including cultural significance (Burnakov, 2019; Shepherd, 1995), commercial use (van Gemert et al., 2022), and in particular as an important target species for recreational fisheries (Arlinghaus et al., 2018). In the Bodden lagoons, pike are historically known for large terminal size and high abundance, drawing recreational anglers from across Europe to the lagoons, in search for trophy-sized pike (**paper I**). However, the population has declined in recent decades, in both overall abundance and in the abundance of large pike (> 100 cm total length), which are prime targets for recreational anglers (Arlinghaus et al., 2018; Koemle et al. 2022, 2024; **paper I**). The inter- and transdisciplinary project Boddenhecht (funded by the state of Mecklenburg-Vorpommern, grant MV- I.18- LM- 004, and European Maritime Fisheries Fund EMFF, grant B 730117000069) was funded with the objectives of describing the socio-economic importance and ecology of Bodden pike, and co-developing a management plan in cooperation stakeholders, containing recommendations for future fisheries management and conservation. My thesis was embedded into this project, which led to the second main motivation of my thesis, the development of ecologically informed management recommendations for the pike stock in the Bodden lagoons. Using the insights I generated on niche use, individual specialization and intraspecific diversification in the pike metapopulation, along with identifying the ecological drivers of growth and size-at-age in Bodden pike, I aimed to identify management recommendations for a sustainable pike fishery and improve resilience of the pike metapopulation in the future.

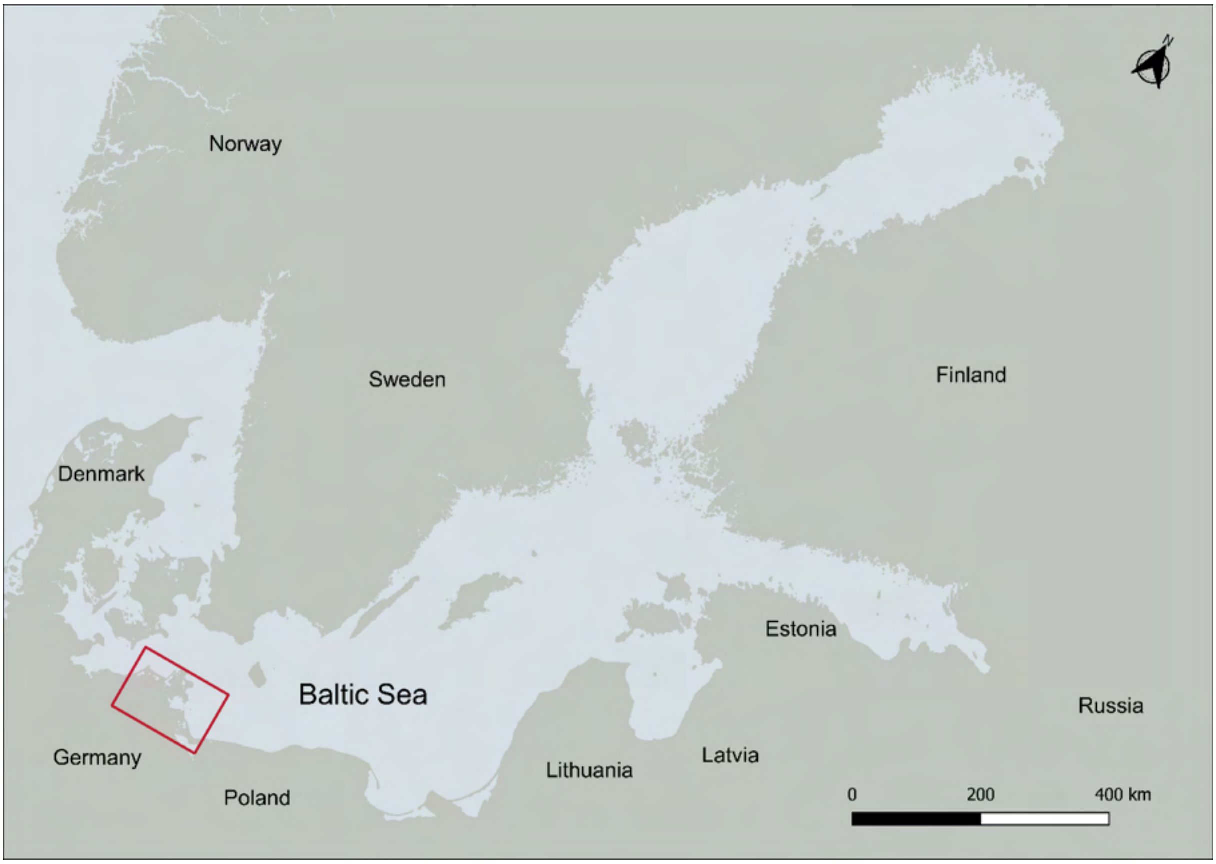


Figure 1. Map of Northern Europe and the Baltic Sea. The study area is marked with a red rectangle.

1. The mechanistic basis of intraspecific diversification

size divergence, copyright: Phillip Roser

1.1. Environmental stochasticity and the n-dimensional niche

Natural environments vary in a multitude of factors, such as environmental conditions and food availability, as well as anthropogenic disturbance and habitat alterations, both in time and in space (Bell 2010; Pörtner *et al.* 2010; Stearns 2000). This creates fitness landscapes for organisms inhabiting these environments (Fretwell & Lucas, 1969), as they vary in physiology, mobility, body size and evolutionary history (i.e., phylogeny), leading to different species-specific preferences and habitat requirements (Istock 1967). Hutchinson (1957) formalized the theory of interacting factors shaping the given environments in which an organism can theoretically survive and maintain stable populations in his concept of the n-dimensional fundamental niche. Organisms of a given species have a set of basic requirements to their environment that allow them to survive and maintain a stable population, termed the 'fundamental niche' by Hutchinson (1957). However, for each individual of a species, there exists another set of requirements that represent the practical subset of the fundamental niche occupied by that specific individual, which Hutchinson (1957) called the 'realized niche'. Each individual of a population will strive to occupy an optimal version of its realized niche in its current environment, in order to maximize its lifetime fitness (Booth *et al.* 1988; Matthiopoulos 2022; Roughgarden 1972). Both these niche volumes represent eco-evolutionary adaptations to fluctuating environments and are shaped by multiple interacting selection pressures (Costa-Pereira & Shaner 2024; Pörtner *et al.* 2010).

Within an ecosystem, variations in environmental factors create a multitude of differing habitats, varying in suitability for individual organisms (Bell, 2010), offering different benefits and challenges for a given combination of traits (Haugen *et al.* 2006). Species inhabiting variable environments therefore often evolve complex life cycles consisting of multiple ontogenetic stages, with each stage evolving adaptations to a specific environment (Istock 1967; Roff 2002; Werner 1988). Ontogenetic changes during individual life histories then generate different ecological scenarios to which individuals have to react by moving habitats, switching diets or changing their behavior (Claessen *et al.* 2000; Werner 1988; Werner & Gilliam 1984). For example, in fishes, body size determines vulnerability to predators (Werner *et al.* 1983), environmental requirements and tolerances (Pörtner *et al.* 2010; Lindmark *et al.* 2018; Varsamos *et al.* 2005), fecundity (Bagenal 1978), metabolic rate (Brown *et al.* 2004), foraging efficiency and assimilative capacity (Armstrong & Schindler 2011; Mittelbach & Persson 1998). As fish grow indeterminately, individuals therefore often navigate a landscape of ecological niches, where selection acts on individual life histories, creating trade-offs between life history traits and adaptations (Bell 2010; Robert *et al.* 2023; Roff 1993; Stearns 1989).

One important consequence of varying fitness landscapes is the ideal free distribution (Fretwell 1969), where individuals disperse within a system according to their preferred realized niche to maximize lifelong fitness prospects. Ideal free distribution is particularly important in mobile species, and has been observed in pike populations before (Haugen *et al.* 2006). Similarly, within an ideal despotic distribution, individuals will disperse along fitness gradients in response to their competitive ability in territorial animals, such as pike (Calsbeek & Sinervo, 2002; Craig, 1996; Raat, 1988). Individuals track variable fitness landscapes throughout their life history in accordance with their ontogenetic stage, but also with general adaptations, knowledge through experience and preferences in respect to their ecological niche (Brown, 1990; Rosenzweig, 1974). This can result in ideal free distribution patterns (Fretwell & Lucas, 1969), as well as different migration behaviors between individuals that move in between nursery, foraging and reproduction habitats (Brodersen et al., 2015; Cagnacci et al., 2011), such as anadromous, catadromous and amphidromous fishes (Dingle, 2014), and individuals that complete their entire life in one habitat (Brown, 1990). However, such behavioral variation in migration patterns often does not occur along such discrete categories, but rather along a behavioral continuum between different points of the fitness landscape, such as different habitat types, that are connected by a gradient of differently migratory individuals (Cagnacci et al., 2011). Such a behavioral gradient is known as partial migration (Chapman et al., 2011 a, b), and appears to be common in fishes (Brodersen et al., 2008, 2015; Chapman et al., 2011 a, b; Rohtla et al., 2020). Partial migration may have strong impacts on population- community- and ecosystem-level (Brodersen et al., 2008; Hansen et al., 2019), and resulting differences in spatial distribution, ecological opportunity (e.g. different food availability), and selective pressures further enhance phenotypic variance and limit gene flow (Brodersen et al., 2008, Hansen et al., 2019), contributing to reproductive isolation, which is a prerequisite to diversification and speciation processes (Bell, 2010).

1.2. Biotic and abiotic ecological factors

Ecological niche axes can be characterized into two primary sets (Hutchinson, 1957). Firstly, niche axes that influence the resource use of an organism, known as bionomic niche axes. Secondly, niche axes that influence the bioclimatic stage of an organism, known as scenopoetic niche axes. One example of a bionomic niche axis would be the diet of an organism (Newsome *et al.* 2007). Examples of scenopoetic niche axes in fish would be temperature, salinity, or water oxygen content (Magnuson, 1979). Bionomic and scenopoetic niche axes were commonly distinguished by assuming that bionomic resources can be depleted (Costa-Pereira & Shaner 2024; MacArthur & Pianka 1966), whereas scenopoetic conditions were assumed to stay constant within the boundaries of the average environmental fluctuations in the system (Costa-Pereira & Shaner 2024; Newsome *et al.* 2007). However, several researchers have challenged this classical view of scenopoetic niche axes. While scenopoetic factors are not directly used up by the organisms inhabiting a patch, favorable conditions may be monopolized by aggressive individuals in territorial species, which may lead to ideal despotic distribution (Calsbeek & Sinervo, 2002), or simply by individuals taking up space (Magnuson *et al.* 1979). Therefore, abiotic factors can be envisioned as resources in much the same way as biotic resources, such as food. Magnuson *et al.* (1979) found that cost/benefit models for thermal and dietary resources led to similar predictions, leading to recommendations to view temperature and other scenopoetic niche axes in the same way as bionomic axes (see also Costa-Pereira & Shaner 2025 for a comprehensive review of this issue).

1.3. Scenopoetic niche axes

In fishes, temperature, salinity (i.e., water osmolality, Bœuf & Payan, 2001) and water oxygen content constitute major ecological factors (Kültz 2015; Lindmark *et al.* 2022a), and represent central scenopoetic niche axes. In this thesis, I mostly focused on temperature and salinity, however, some of my results also briefly touch on the subject of oxygen content, which is why I will discuss all three niche axes in some detail here. All three of these niche dimensions scale with body size in fishes, meaning that they change throughout life and with individual ontogeny as the individual ages (Werner & Gilliam, 1984).

Thermal niches of ectotherm organisms often become colder with age. Maximum consumption in ectotherms increases more slowly with size than metabolic rates, leading to the prediction of declining optimum growth temperatures with body size (Lindmark et al., 2022b). In addition, larger individuals face higher metabolic costs at warm temperatures (Lindmark *et al.* 2022b; White *et al.* 2022), and experience oxygen limitations at their upper thermal limit due to lower aerobic capacity (Pörtner & Knust 2007). Small individuals (juveniles) may therefore experience accelerated growth in warm, shallow water (Bry et al., 1991), along with decreased predation risks (Pursiainen et al., 2021), leading to increased survival at this vulnerable stage. However, metabolic costs and resource limitations in such habitats decrease growth in larger, adult conspecifics (Lindmark et al., 2022b). Therefore, both the fundamental (maximum thermal tolerance) and the realized (thermal preference) thermal niche decrease throughout life (Lindmark *et al.* 2022b). In times of climate change, where ambient water temperatures increase, warmer water consequently leads to increased growth, but reduced maximal size in ectotherms, such as fishes. This phenomenon is also known as the temperature-size rule (Angilletta & Dunham 2003; Arendt 2011; Atkinson 1994). The thermal niche of fishes is therefore a major selective agent during all ontogenetic stages, where different stages will shift in both fundamental and realized thermal niche throughout their life, with a general pattern towards colder temperatures in later life (Atkinson 1994; Dahlke *et al.* 2020; Lindmark *et al.* 2022b).

The second major scenopoetic niche axis to consider in fishes is water osmolality, i.e., salinity. Salinity influences fishes at multiple stages, such as egg fertilization, incubation, yolk sac resorption, early embryogenesis, swimbladder inflation and growth (Bœuf & Payan 2001). Osmoregulatory capacity in aquatic ectotherms also scales with size. Ion loss or uptake from the body is proportional to the volume, which scales quadratically with the body surface, so doubling bodysize leads to a fourfold increase in volume, and consequently, osmoregulatory capacity (Bœuf & Payan 2001). In addition, higher metabolism at larger body sizes enables more efficient osmoregulation due to greater activity and a higher number of ion transport mechanisms, such as chloride cells (Pörtner *et al.* 2010). This enables larger individuals in estuarine habitats to explore saline habitats and exploit a wider spectrum of food (Varsamos *et al.* 2001; Varsamos *et al.* 2005). Fishes are commonly classified as stenohaline or euryhaline, corresponding to experimentally determined fundamental saline niches (Altinok & Grizzle 2001; Altinok & Grizzle 2003; Varsamos *et al.* 2005). Euryhaline species may tolerate up to two times seawater salinity (i.e., ~70 Practical Salinity Units, PSU, Lewis, 1982), whereas stenohaline species can only tolerate fluctuations of ~15 PSU around their salinity optimum, irrespective of whether they are freshwater or marine species (Kültz 2015). However, this categorization is mostly based on adults, ignoring differences in ontogeny and phenotypic plasticity, leading to some authors questioning its general applicability and usefulness (Barnes 1989; Snickars *et al.* 2009; Varsamos *et al.* 2005). In general, it would be expected for the saline niche breadth to increase during ontogeny in fishes (Varsamos *et al.* 2005). However, osmoregulation in salinities above the isoosmotic point (~9 PSU, Kültz, 2015) is energetically more costly than osmoregulation in freshwater (hypo- and hyperosmotic regulation, respectively), in particular in systems where salinities fluctuate around this point, necessitating individuals to regularly switch between hypoosmotic and hyperosmotic regulation (Bœuf & Payan 2001, Pörtner et al., 2010). Therefore, within the context of life history optimization, individuals would only be expected to seek out habitats of high and fluctuating salinity when the energetic benefits, such as through higher food availability, outweigh the energetic costs.

Unlike thermal and saline niches, oxygen requirements scale non-linearly in fishes. This is due to interactions of temperature and metabolism, and the ontogeny of the respiratory system. Early stages without a respiratory system (i.e., eggs and larvae) have low tolerance to low oxygen levels. Juveniles with fully developed respiratory and cardiovascular systems have a high respiratory scope and tolerance of low oxygen levels, as well as low metabolic demands throughout their thermal range (Pörtner & Farrell 2008). This allows for fast growth in oxygen-limited habitats when resources are abundant, and enables survival under resource and oxygen limitation by maintaining basal metabolic rate and trading off growth rate (Pörtner & Farrell 2008). The higher metabolic demands of adult fish then limit respiratory scope, leading to stress and growth depression at low oxygen conditions (Dahlke *et al.* 2020; Limburg & Casini 2019; Pörtner & Farrell 2008). Therefore, while all life stages of fishes can be expected to adapt their habitat utilization to avoid low-oxygen habitats, this is particularly critical for the earliest stages and larger adult fishes.

All three scenopoetic niche axes introduced here scale with individual metabolism, which leads to covariation between them. For instance, metabolic rate in fish increases with temperature (Pörtner et al., 2010), and osmoregulatory capacity increases with metabolic rate (Bœuf & Payan, 2001). At the same time, oxygen demand increases with metabolic rate, but water oxygen content decreases with temperature (Pörtner et al., 2010). This means a smaller individual with lower oxygen demand may use higher saline habitats at warm temperatures, whereas larger individuals may avoid warmer water due to respiratory constraints (Pörtner & Farell 2008). Similar, cold temperatures can impose osmoregulatory constraints, in particular for smaller individuals, but allow larger individuals to increase their activity due to higher water oxygen content (Pörtner et al., 2010). The complex interactions between these niche dimensions can therefore lead to trade-offs between habitats that depend on an individual's life history traits, which are then further exacerbated by an individual's bionomic niche.

1.4. Bionomic niche axes

Foraging niche, predation, parasitism and disease are central bionomic niche axes in fishes. Diet directly influences growth and metabolism via energy acquisition and essential nutrient uptake (Enberg et al., 2012). The other niche axes exert direct influence on survival and metabolism, and may indirectly influence growth (Haugen et al., 2007). In this thesis, I focused on the foraging niche, i.e., biotic resource use, as this is a central niche axis in any organism, governing energy acquisition and building the basis of most biotic interactions between species (Rosenzweig, 1974). Foraging in mobile animals with complex life histories is influenced by multiple interacting factors, such as body size (Mittelbach & Persson 1998), behavior (Brownscombe et al., 2022), personality (Biro & Stamps 2008) and phenotypic plasticity (Bolnick *et al.* 2003). Resource use of an individual is dependent on all these factors, and is also moderated by ecological opportunity, such as habitat type and -quality (Bolnick *et al.* 2003; MacArthur & Pianka, 1966). For example, body size in fishes determines which food items may be ingested by scaling directly with gape width (Mittelbach & Persson 1998). In addition, larger body size affects the amount of resources that can be ingested through larger intestines, which also leads to increased assimilative capacity (Armstrong & Schindler 2011). Ontogenetic shifts in diet, such as from a plankton-based diet to piscivory (Mittelbach & Persson 1998), can therefore be expected in fishes, along with coinciding shifts in habitat use (Werner 1988).

1.5. Interactions between scenopoetic and bionomic niche axes

Scenopoetic and bionomic niche axes often covary and interact, making their quantification challenging (Costa-Pereira & Shaner 2024). For example, resource use in predatory fishes is jointly influenced by the scenopoetic niche of individual predators and that of their respective prey items (Costa-Pereira & Shaner 2024). On the one hand, specific prey items may only be available in a habitat patch with certain scenopoetic conditions, limiting their accessibility to predators that occupy a similar scenopoetic niche (Costa-Pereira et al., 2018). Similarly, systems with high environmental heterogeneity often feature higher biodiversity due to species sorting along environmental gradients (Barnes 1989). An individual predator that is adapted to a wide range of scenopoetic niches can use a wide range of prey items in such system, whereas an individual that is specialized to a specific combination of scenopoetic factors will also restrict its prey range (Costa-Pereira & Shaner 2024). On the other hand, an individual predator that is specialized to one specific prey type is expected to have a scenopoetic niche constrained to that of the prey type, whereas an individual with opportunistic foraging may forage across multiple habitats, expanding its scenopoetic niche (Brodersen et al., 2015; Costa-Pereira & Shaner 2024). This is particularly true in in strongly fluctuating habitats, such as brackish estuarine systems (Altinok & Grizzle 2001). These systems host organisms from both freshwater, brackish and marine fauna, offering a wide range of biotic resources to predators adapted to integrate across multiple habitat patches (coupling across food webs, Rezek et al., 2020). Further, brackish systems may receive allochthonous resource pulses by migratory marine species (Garman & Macko 1998; MacAvoy *et al.* 2000; Winkler 1990), offering short-term high energy subsidies for individuals adapted to capitalize on them (Furey *et al.* 2016, 2018).

Bionomic and scenopoetic niche axes are thus shaped by individual life history traits, environmental opportunity, and stochasticity, and usually covary and interact (Costa-Pereira & Shaner 2024). This further underscores the similarities between these niche axes, indicating both abiotic and biotic factors shape the n-dimensional niche in similar ways, and thus have to be considered simultaneously to be fully understood (Costa-Pereira & Shaner 2024).

1.6. Competition and niche variation

Besides individual-level variation and environmental chance, there are multiple external factors that shape the ecological niche of organisms in the wild. One of the most central amongst these factors is competition, in particular intraspecific competition (Araújo et al., 2011; MacArthur & Levins, 1964). High densities of individuals of the same species and low resource density lead to lower per capita resource availability, where individuals then compete for the same resources and favorable conditions, leading to partitioning of habitat and patch use (Macarthur & Levins 1964; MacArthur & Pianka 1966). There often are several optimal strategies, where individuals may either specialize on a particular narrow subset of the species' niche or generalize across a large range of the niche axes (Brown, 1990; Rosenzweig 1974). Generalizing over all available habitats and resources would in theory yield the highest fitness prospects, but trade-offs between conflicting scenopoetic and bionomic niche axes, life-history traits and adaptations limit an individual's ability to generalize (Bolnick *et al.* 2003; Bolnick *et al.* 2007, 2010). Even if generalization is achieved, it is usually accompanied by compromises between optimization pathways, leading to a "jack-of-all-trades, master of none", that may use all habitats and resources to some degree, but will not excel at any of them (Rosenzweig 1974). The inability of populations to evolve a single "optimal phenotype" is a prerequisite of individual niche variation and enables coexistence of different phenotypes in a population (Brown 1990), and higher population numbers than would be predicted by classical habitat selection theory (Rosenzweig 1974). This concept was formalized by van Valen (1965) in the niche variation hypothesis.

The niche variation hypothesis stated that “populations with wider niches are more variable than populations with narrower niches”, and suggested that animal populations, once released from stabilizing selection imposed by interspecific competition, evolve to use a wider diversity of resources (van Valen, 1965). Intraspecific competition is hypothesized to be the major driver of this niche variation and the resulting phenotypic variance (van Valen, 1965). Favorable scenopoetic and bionomic niches in a system are limited, and preferred resources and habitats are consumed or occupied first (Costa-Pereira & Shaner, 2025; Magnuson et al., 1979; Svanbäck & Bolnick, 2005). As preferred resources and habitats become scarce, individuals switch to different alternatives, leading to individual specialization (Bolnick et al., 2010; Svanbäck & Bolnick, 2005). Bionomic competition, in particular resource competition, has received most attention in past studies (Bolnick *et al.* 2003, 2007; Colwell & Futuyma 1971; Kobler *et al.* 2009; Macarthur & Levins 1964; Ojaveer *et al.* 2018; Svanbäck *et al.* 2008). Competition along scenopoetic niche axes is more difficult to conceptualize, as they are not depletable (Costa-Pereira & Shaner 2024). However, behavioral interactions (e.g., social hierarchy, territoriality, predation) can lead to favorable habitats and environmental conditions becoming unavailable to individuals, similar to interference competition for resources (Calsbeek & Sinervo, 2002; Costa-Pereira & Shaner, 2025; Eklöv & Svanbäk, 2006; Magnuson *et al.* 1979). Furthermore, in cannibalistic species, larger individuals generate predation risks for smaller individuals in favorable habitats, excluding them from preferred environmental conditions (Haugen *et al.* 2007). Competition with other species, i.e., interspecific competition, can also decrease niche variation in a species, so individual specialization is determined by a balance of intraspecific and interspecific competition (Bonick et al., 2010; Costa-Pereira et al., 2018), although results for this in the literature are mixed (Araújo et al., 2011; Shaner & Ke, 2022).

In summary, the interplay of niche variation and competition leads to seemingly generalized populations from a species- or population-level that are highly heterogenous on a phenotypic or individual level (Bolnick *et al.* 2007). This has important implications on population-, metapopulation- and community-level (Bolnick et al., 2010; Costa-Pereira et al., 2018), emphasizing the importance of assessing specialization and adaptations from higher levels of organization down to the ecology of the individual (Bolnick et al., 2003).

1.7. Plastic vs. evolutionary diversification

As the previous sections outlined, life history optimization during ontogeny in variable environments leads to strong phenotypic variation (Bell 2010; Bolnick *et al.* 2003; Bolnick *et al.* 2007; Brown 1990;

Rosenzweig 1974). However, intrapopulation ecological diversity may be many times higher than evolutionary diversity due to phenotypic plasticity, which can be described and quantified within reaction norms, showing how specific traits change across environments (Heino *et al.* 2002; Kawecki & Stearns 1993; Rubin *et al.* 2023; Stearns 1998; Stearns & Koella 1986). Within a reaction norm, every individual of a population may express a multitude of phenotypes, depending on environmental and physiological state (Kawecki & Stearns 1993). For example, in migratory brown trout, some researchers found the phenotypic expression of migratory or non-migratory phenotypes to be linked to environmental and physiological factors, independent of individual evolutionary history (Olsson *et al.* 2006). However, other work found an important role of genetic components for the development of migration behavior in brown trout (Vainikka *et al.* 2023). This indicates that both genetic and plastic components jointly influence the phenotypic expression in brown trout (Ferguson et al., 2019). A theoretical "ideal" plastic genotype, able to express optimal phenotypes for all habitats and life strategies, could become the singular evolutionary optimum (Kawecki & Ebert 2004), and adaptive phenotypic differentiation would occur without underlying genetic differentiation (Kawecki & Ebert 2004). However, similar to individual generalists and specialists before, trade-offs and environmental stochasticity impair costs and restraints on phenotypic plasticity, inhibiting a population from evolving an ideal plastic type (Kawecki & Ebert 2004).

Consequentially, most populations display a degree of genetic variation underlying a larger phenotypic variation, where the difference in variation is due to phenotypic plasticity (Rubin *et al.* 2023). In the brown trout example, phenotypic expression likely depends on a liability trait or cue (controlled by environmental signals or physiological condition), and a genetically determined threshold for that condition (Ferguson et al., 2019). For evolutionary divergence to occur, the underlying genetic variability needs to have an effect on the lifelong fitness of the expressed phenotypes, so selection may act on heritable phenotypes, leading to local adaptation and reproductive isolation (Kawecki & Ebert 2004). Environmental stochasticity and negative frequency-dependent selection may allow multiple genotypes and phenotype expressions to achieve similar lifelong fitness, fostering sympatric coexistence and ecotype evolution (Bell 2010; Brown 1990; Christie & McNickle 2023; Doebeli & Dieckmann 2003; Rosenzweig 1974; Rubin *et al.* 2023).

1.8. Reproductive isolation and ecotype evolution

Heritable phenotypes that are specialized and adapted to a certain n-dimensional niche within a system are predicted to survive in the population as ecotypes (Brown 1990; Rosenzweig 1974). Ecotype evolution occurs under two conditions. Firstly, each ecotype needs to either be specialized on a subsection of the species n-dimensional niche, or be able to generalize along a sufficiently large subsection of the species niche to enable opportunism (see previous sections). Secondly, ecotypes need to be reproductively isolated for adaptive genetic differentiation to occur (Blain *et al.* 2023; Dennenmoser *et al.* 2017; Felmy *et al.* 2022; Kusakabe *et al.* 2017; Nordahl *et al.* 2019a; Stronen *et al.* 2022).

In species with low dispersal capacity or in sufficiently large systems, reproductive isolation may result from geographic distance and reduced gene flow over larger distances, that is, isolation by distance (Wright 1943). Another form of reproductive isolation, which often occurs in conjunction with isolation by distance is isolation by resistance (McRae 2006), where physical or environmental barriers, e.g., environmental conditions outside of a species fundamental niche, prevent gene flow in a system. Isolation by resistance may also result from anthropogenic factors, for example water management facilities causing connectivity barriers (Eschbach *et al.* 2021; Franklin *et al.* 2024). Isolation by time (Hendry & Day 2005), may occur when sympatric phenotypes within a population differ in reproductive timing, e.g., migration times or differences in spawning activity between day/night cycles. Lastly, isolation by environment (Wang & Bradburd 2014), occurs when individuals of a species differ strongly in their specialization and/or adaptation to n-dimensional niches, and use different habitats for reproduction. These habitats may be geographically close, but differ in scenopoetic or bionomic niche components, so only adapted and specialized phenotypes can successfully use a given habitat for reproduction (Sunde *et al.* 2018, 2019, 2022). Isolation by environment is more likely in systems with strong gradients in scenopoetic and bionomic niche axes, leading to segregation of differently adapted individuals along these gradients (Wang & Bradburd 2014). In many cases, multiple isolation mechanisms jointly drive the evolution of ecotypes (Hall *et al.* 2022; Nordahl *et al.* 2019a; Stronen *et al.* 2022; Sunde *et al.* 2022).

As ecotypes are characterized both phenotypic divergence traits as well as genetic differentiation, describing them requires simultaneous assessment of both phenotypic and genetic variation of the same individuals (Clemens & Schreck 2021; Stronen *et al.* 2022). As individual phenotypic and genetic assessments are high in effort and cost, most previous research on ecotypes focused on the description of selected phenotypic traits and niche axes (Blain et al., 2023; Sunde et al., 2018, 2019, 2022), combined with screens for genetic differentiation. Much of the existing literature on ecotypes seems to support dichotomous distinctions, e.g., benthic vs. pelagic salmonids in lakes (arctic charr *Salvelinus alpinus*, whitefish *Coregonus spp.*, e.g., Blain et al., 2023), limnetic vs. marine three-spined sticklebacks (*Gasterosteus aculeatus*, e.g., Kusakabe et al., 2017) or migratory vs. resident brown trout (e.g., Ferguson et al., 2019). This may be the result of limited descriptive capabilities along low numbers of niche axes, which could also influence the sampling designs genetic assays are based on. For example, sampling genetic variability along a set of phenotypes that only differ along one niche axis would likely underestimate both the phenotypic and the genetic variability of the population (Costa-Pereira &

Shaner 2024). Indeed, recent studies using multiple indicators for niche use consistently report unexpectedly high phenotypic diversity in fishes, in particular for estuarine brackish systems (Almeida et al., 2023; Kerr et al., 2007, 2009; Limburg et al., 2001; Rohtla et al., 2020, 2023; Russell et al., 2022). These findings hint at high ecotype diversity that could be revealed by multidimensional niche assessments combined with high-resolution genetics (Stronen *et al.* 2022). The mechanistic basis of this widespread variation in phenotypic variation and ecotype evolution is largely unknown, as inference on coexistence would require data on the fitness of distinct ecotypes. One possible solution could be the combination of ecotype assessments with individual and ecotype level growth assessments as a fitness surrogate.

1.9. The process of growth

Whether an ecotype survives within a metapopulation and achieves stable coexistence with other ecotypes depends on its lifelong fitness (Brown, 1990; Rosenzweig, 1974). Lifelong fitness is determined by trade-offs between growth, fecundity, and survival (Charlesworth 1994; Roff 2002; Stearns 2000). As growth correlates positively with both survival, (by outgrowing gape-limited predators, Werner, 1988), and fecundity (by increasing the amount of eggs females can carry, Barneche et al., 2018) in most fishes, it offers a useful fitness surrogate (Haugen et al., 2007; Roff, 1983), and can be easily measured compared to reproductive investment and survivorship. Growth rates are intricately related to multiple scenopoetic and bionomic niche components in aquatic ectotherms. For example, temperature and water osmolality can impose constraints on growth rate through environmental stress (Arendt 1997), but warm temperatures within the thermal window (Pörtner et al., 2010), and isosmotic conditions (Bœuf & Payan, 2001) can also have a positive influence on stage-specific growth (Atkinson, 1994). Similarly, bionomic niche axes like resource availability and quality have a strong influence on growth rates (Hart & Connellan, 1984). Predation rate and social stress may additionally influence growth rates in fish, in particular for cannibalistic species (Edeline *et al.* 2010; Haugen *et al.* 2007). Werner's (1988) growth-mortality tradeoff (μ/g) offers a framework that integrates the trade-offs along complex life histories in fishes. Growing fast with high resource acquisition requires risk-taking at small sizes but, at later stages, provides lowered mortality by outgrowing gape-limited predators and improved potential for resource acquisition (Smith & Blumstein 2008; Stamps 2007). In this context, Ahrens et al. (2012) developed the concept of foraging arenas, which partition the prey in each predator-prey relationship into vulnerable and invulnerable components. Risk-taking individuals decrease their refuge use and enter the vulnerable compartment of a foraging arena (Ahrens *et al.* 2012), achieving fast growth. Invulnerable individuals will have lower risk but also grow slower, trading off instantaneous fitness benefits through fast growth with increased survival to older age and long-term fitness. As fecundity is related to body size, particularly for female fish (Bagenal 1978; Barneche *et al.* 2018; Koops *et al.* 2004), and larger males may be seen as more attractive mating partners (Sutter *et al.* 2012), factors affecting growth may also indirectly regulate recruitment and population size (Tomcko & Pierce 2005; VanSickle 1977). Another trade-off of fast growth can be elevated tissue aging (Arendt 1997; Saunders *et al.* 1992), so that most fish exhibit evolutionary optimized rather than maximized growth (Enberg et al., 2012). Trade-offs between growth, fecundity, and survival determine lifelong fitness of an organism and are at the heart of the life-history evolution theory (Charlesworth 1994; Roff 2002; Stearns 2000). In populations exploited by fisheries, where the harvest mortality often exceeds natural mortality by large margins, fishes often trade off fast early growth and maturation with later growth, leading to populations dominated by medium-sized, fast-growing individuals with shorter lifespans, a phenomenon also known as fisheries induced evolution (Enberg et al., 2012). To study how niche use interacts with phenotypic diversity and adaptive differentiation in fishes, and potential effects of harvest and fisheries, a focus on somatic growth as a fitness surrogate is therefore useful (Haugen et al., 2007; Monk et al.,2021; Roff 1983; Werner 1988). Further, growth can be easily measured compared to other fitness surrogates, (e.g., reproductive investment, survivorship and metabolism, Vindenes *et al.* 2014).

The two central adaptive mechanisms governing somatic growth are energy acquisition and energy allocation, which are influenced by a complex set of physiological and behavioral traits (Enberg *et al.* 2012, White et al., 2022). Resource acquisition and allocation into somatic growth, survival and reproduction throughout life are evolutionarily optimized in a way that maximizes the expected reproductive output over the lifetime (Charlesworth 1994; Kozłowski *et al.* 2004). As selection pressures fluctuate due to variable fitness landscapes and intraspecific competition, individuals diverge towards different fitness optima, maintaining phenotypic divergence within a population (Bolnick *et al.* 2003; Stearns 2000). A summary of factors influencing multiniche specialization, fitness-related life history optimization and adaptive divergence into ecotypes is provided in Figure 2.

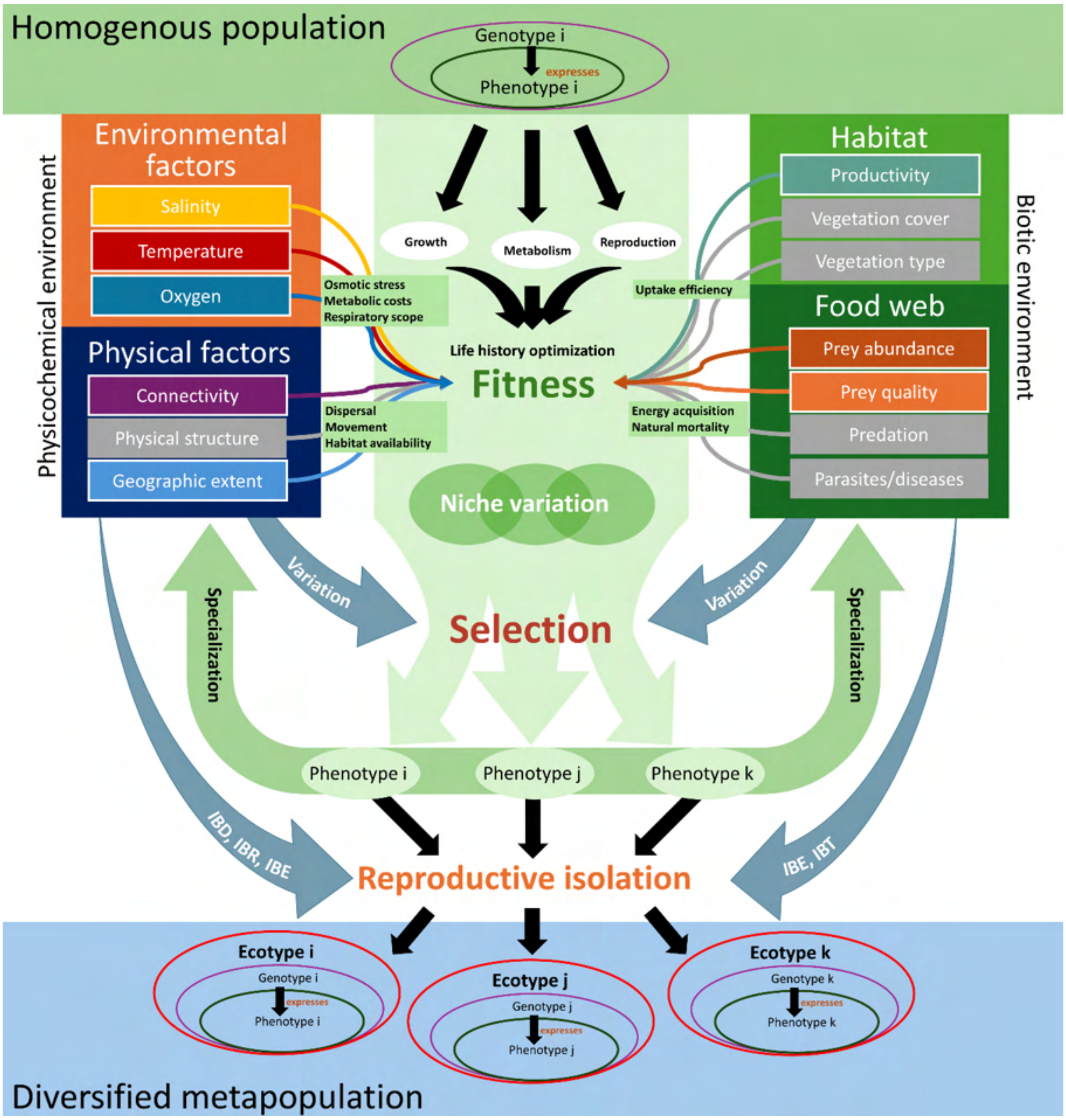


Figure 2. Factors driving life history optimization and intrapopulation diversification in fishes. Colored boxes highlighted in white indicate ecological factors that were part of this thesis. Optimization of life history is facilitated by specialization and adaptation to the n-dimensional niche of an individual and subsequent optimization of energy allocation towards growth, metabolism and reproduction. Variation in selection pressures and trade-offs between different life history traits then leads first to phenotypic variation, which, under reproductive isolation, leads to the evolution of distinct ecotypes. Fluctuations in both abiotic and biotic environment jointly drive the selection pressures and may interact antagonistically, synergistically, or independently. IBD: Isolation by distance; IBR: Isolation by resistance; IBE: Isolation by environment; IBT: Isolation by time. For simplicity, reaction norms (the ability of a genotype to express multiple phenotypes) are not considered in this conceptual figure.

1.10. Ecology of northern pike in freshwater and brackish systems

My doctoral research used northern pike (*Esox lucius*) as a model species to investigate adaptive diversification in response to niche variation, and examine the consequences of diversification and niche variation for individual growth. My study area consists of interconnected brackish lagoons and freshwater tributaries around Rügen island in the southern Baltic Sea of northern Germany, which allow me to study niche use along strong gradients of abiotic and biotic factors.

Pike (Figure 3) is a primarily freshwater-associated species with a wide distributional range in the northern hemisphere (Skog et al., 2014), from 24° to 69° latitude (Forsman et al., 2015). They occur in North America and Eurasia in nearly every type of waterbody, from small ponds through lakes to rivers, creeks, and coastal waters (Craig 1996). Pike are visual ambush predators, and have a binocular vision due to anteriorly directed eye axes (Kottelat & Freyhof 2007). Their dorsal, anal and caudal fins form a “paddle”, which enables rapid acceleration bursts to catch their prey (up to 95.9 m/s^2 acceleration to a top speed of 3.1 m/s, Harper & Blake, 1991). Pike spawn in spring, usually between February and May, but this may vary between systems and latitudes (Raat, 1988). Pike larvae and early juveniles feed on plankton, before they transition to a predominantly piscivorous diet at around 5 cm total length (Bry et al., 1995; Craig, 1996; Raat, 1988). Pike are known for fast growth, in particular at early age, with a short maturation time and a moderate maximum longevity of 30 years (Bry et al., 1991, 1995; Craig 1996). They can reach maximum sizes up to 150 cm total length and maximum weights up to 28 kg (Froese & Pauly, 2024). Pike are cannibalistic, and exhibit strong density-dependence (Haugen et al. 2007). Therefore, fast growth increases survival in juvenile pike, as they outgrow the gape size limitation of their conspecifics and other predators (Haugen et al., 2007). Further, egg counts increase with size in female pike (Haugen et al., 2007) and females show preference for larger males during spawning (Pagel, 2009). This makes growth a good proxy for fitness in pike (Haugen et al., 2007; Monk et al., 2021).

Figure 3. The northern pike (*Esox lucius*). Illustration © DAFV/Eric Otten

Pike are a mesothermal cold-water species, but can tolerate a relatively wide thermal range from 0.1°C to 29.4°C (Casselman, 1978, 1996). Optimum temperatures vary between different life stages in pike, with juvenile pike preferring higher temperatures than adults (Bry et al., 1991; Casselman & Lewis, 1996). Pike display behavioral thermoregulation, and have been shown to seek out thermal refugia at temperatures exceeding 20°C as adults, e.g., thermocline layers in deeper lakes (Pierce et al., 2013; Říha et al., 2021). Further, in the Baltic Sea, active thermoregulation by adult pike through sunbathing during winter has been observed (Nordahl et al., 2019b). Warmer temperatures within the optimal range have been found to positively affect egg and larval development, juvenile and adult growth as well as activity rates (Bry et al., 1991; Casselman, 1978, 1996; Haugen et al., 2006; Pagel et al., 2015; Rypel, 2012). However, warm temperatures above the optimal thermal range increase natural mortality (Berggren et al., 2022; Haugen et al., 2007), and reduce maximum terminal length (Vindenes et al., 2014). Indeed, Berggren et al. (2022) showed warming waters over five decades increased early body growth in pike in the Swedish Baltic Sea coast, but higher mortality ultimately led to reduced body sizes. The consistent decreases in recruitment and stock size across the central and southern Baltic Sea (Olsson, 2019; Olsson et al., 2023) suggests a common environmental factor may drive these patterns at a superregional scale, which could be increasing temperatures. In the Baltic lagoons around Rügen, warming water during the last decades likely led to increased growth, in particular for juvenile stages, but reduced terminal lengths and increased natural mortality in adults, similar to findings in Swedisch brackish habitats (Berggren et al., 2022). Ontogenetic shifts from warmer towards colder habitats would be expected for pike in the brackish lagoons, along with positive effects of warm temperatures on juvenile growth.

Pike is a stenohaline freshwater species, i.e., can tolerate up to 15 PSU (Practical Salinity Units) of salinity fluctuations while maintaining normal body functions (Kültz et al., 2015), but cannot survive marine salinities (Jacobsen and Engström-Öst, 2018). However, pike are capable of osmoregulation in brackish systems, such as the Baltic and Caspian Seas (Casselman and Lewis, 1996; Stolyarov and Abusheva, 1997). Pike have been documented in the Baltic Sea up to salinities of 15 PSU, but mass mortalities have been observed above 18 PSU, indicating an upper tolerance limit (Dahl, 1961). To colonize brackish coastal zones, pike had to overcome two challenges: survival at higher salinities, and reproduction in saline waters. While low salinities up to 2 PSU have been shown to increase egg development, larval survival and growth in freshwater pike (Kuznetsov et al., 2016), salinities exceeding 10 PSU have negative effects on eggs and larvae (Jørgensen et al., 2010). One solution for this issue for pike would be the evolution of anadromy, where reproduction and early nursery occurs in freshwater and later stages forage in brackish water, which has been observed in multiple coastal pike populations (Engstedt et al., 2010, 2011; Larsson et al, 2015; Möller et al., 2019; Müller, 1986; Nordahl et al., 2019a). Alternatively, pike could adapt to complete their entire lifecycle in brackish water, which has also been documented in coastal pike in the Baltic Sea (Möller et al., 2019; **paper II**; Sunde et al. 2022). Maximum tolerances depend on local salinities, indicating patterns of local adaptation (Jørgensen et al., 2010; Möller et al., 2020; Sunde et al., 2018). Swedish coastal pike showed high hatching rates between 6.9 and 9 PSU in a study by Westin & Limburg (2002), while breeding experiments from different parts of the Swedish Baltic coast, where salinities reach up to 10 PSU, showed successful hatching and larval development up to 8.5 PSU (Jørgensen et al., 2010). For the Bodden lagoons around Rügen, breeding experiments showed a general decrease in hatching rates for brackish adapted as well as freshwater adapted pike with increasing salinity (**paper I**). However, 30% of brackish-adapted pike hatched even at salinities of 10 PSU, and survival rates of juvenile brackish pike even increased with salinity up until 10 PSU, after which survival rates dropped, but not to 0. Both hatching rate and survival of freshwater pike steadily decreased with increasing salinity, and dropped to 0% at 7.5 PSU. Observations of spawning activities in high-saline brackish water and tributaries (**paper II**) suggest the lagoons around Rügen harbor a brackish phenotype adapted to complete its whole life cycle in brackish habitats, alongside a migratory anadromous phenotype. Given observations on freshwater resident populations from other parts of the Baltic Sea (Birnie-Gauvin et a, 2018), a freshwater-adapted phenotype in the larger tributaries also seems likely.

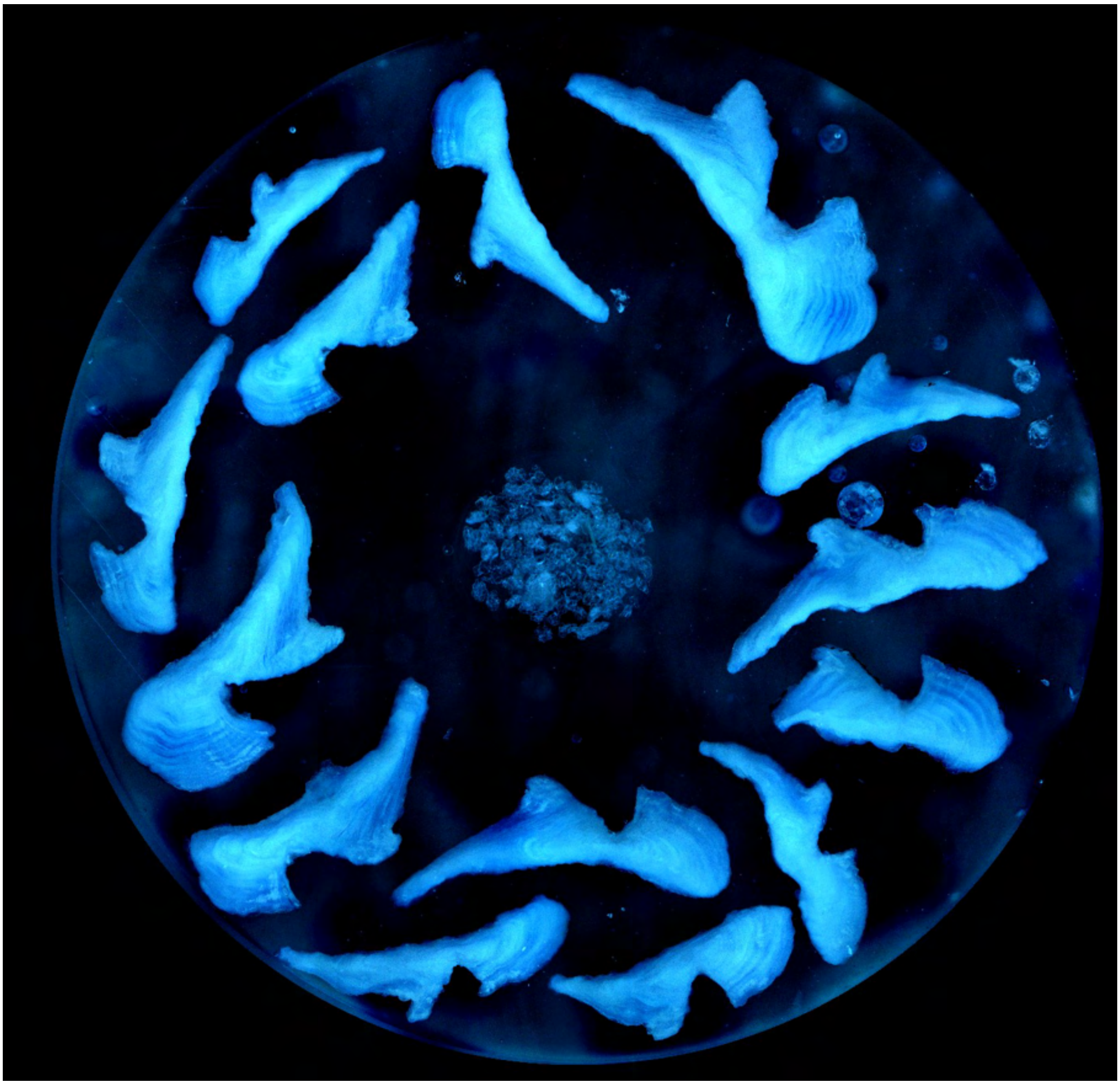
Pike are considered opportunistic fish predators (piscivores), where diet use is mainly predicted by ecological opportunity (Cathcart et al., 2019; Chapman & Mackay, 1989; Pedreschi et al., 2015). However, Beaudoin et al. (1999) found high individual diet specialization in pike in Canadian lakes, where pike were either dominant in terms of abundance, or the only fish species present. In these pike-only lakes, pike displayed strong individual specialization, either on invertebrates, mainly dragonfly (Odonata) larvae, or on other pike (specialist cannibalism). This led to the hypothesis that pike show individual resource specialization when faced with either resource limitation or intraspecific competition (Beaudoin et al., 1999). Pike generally prefer slender-bodied, medium-sized prey over deep-bodied, large-sized prey when resources are abundant (Hart & Connellan, 1984; Nilsson & Brönmark, 2000), but show preference for large-bodied prey in resource-poor systems (Diana, 1979; Gaeta et al., 2018). In systems offering pulsed resource subsidies of marine prey, Nolan et al. (2019) detected strong resource specialization on marine prey, in particular by large pike. Similar specialization was also suggested for the Bodden lagoons by Winkler (1978). Marine prey often has higher energy content compared with freshwater prey (Gross et al., 1988), and in both cases, the marine subsidy was constituted of clupeids (*Alosa spp.* in the study of Nolan et al., 2019; Atlantic herring *Clupea harengus* in the study of Winkler, 1978). Slender-bodied adult clupeids appear to be a particularly valuable resource for pike and can foster individual resource specialization. It would therefore be expected for pike in the Bodden lagoons to specialize on abundant marine resources, in particular marine resource pulses provided by migratory herring (**paper I**), which may boost individual growth through increased energy acquisition. In addition, pike densities are high in parts of the lagoons (**paper I**), likely resulting in intraspecific competition and individual specialization (Beaudoin et al., 1999).

Pike are phytophilic and show preference for submerged vegetation for spawning, as a hiding place for juvenile stages, and as cover when stalking prey (Grimm & Klinge, 1996). Therefore, pike biomass in a system depends not only on density and environmental factors like temperature, oxygen content and prey availability, but also on coverage and types of submerged macrophytes (Grimm, 1981, 1989; Grimm & Klinge, 1996). As visual predators, pike prefer clear waterbodies with mesotrophic conditions (Pierce & Tomcko, 2005), and are less successful in high turbidity (Skov & Nilsson, 2018; Winkler & Debus, 2006). In the Baltic Sea, consistent declines in submerged macrophytes and increasing water turbidity caused by strong eutrophication during the 1960s through to the 1980s (Reusch et al., 2018), likely contributed to the decline in pike populations (Lehtonen et al., 2009; Winkler, 2002). In particular in the innermost oligohaline Bodden lagoons, high eutrophication has led to a shift in predator dominance from pike towards pikeperch (*Sander lucioperca*) dominance (Winkler & Debus, 2006).

Pike show high phenotypic variation along scenopoetic (such as the thermosaline niche, Nordahl et al., 2019b; Sunde et al., 2018, 2019, 2022) and bionomic niche axes (such as morphology, Tibblin et al., 2015; reproductive timing, Tibblin et al., 2016; resource use, Beaudoin et al., 1999). Three phenotypes of pike have been described in the Baltic Sea, with evidence confirming two of them as ecotypes (Nordahl et al., 2019a; Sunde et al., 2022). The first is a freshwater resident form, which spends its entire life in freshwater tributaries, but had not been confirmed as an ecotype due to a lack of genetic evidence (Birnie-Gauvin et al., 2018). The second is an anadromous form that is born in freshwater tributaries, forages in brackish coastal habitats, and returns to the natal tributary each year for spawning, which has been confirmed as an ecotype in Sweden (Engstedt et al., 2011; Larsson, 2015;

Müller, 1986; Möller, 2019; Nordahl, 2019a). The third is a brackish form that completes its entire life cycle in brackish waters, which was confirmed as an ecotype in Swedish, German, and Polish coastal waters (Nordahl et al., 2019a; Möller et al., 2019; Sunde et al., 2022, Wąs-Barcz et al., 2023).

Pike display high site-fidelity, natal homing behavior and limited dispersal capacity (Diana, 1980; Dhellemmes et al., 2023a; Karås & Lehtonen, 1993; Lukyanova et al., 2024; Miller et al., 2001). This may lead to strong patterns of isolation by distance, that are likely reinforced by the phytophily exhibited by pike (Grimm, 1981), as large stretches of water with low vegetation cover in open waters might prevent gene flow between Baltic populations (Wennerström et al., 2017). Indeed, several studies, including Wennerström et al (2017), Maes et al.(2003) and Laikre et al. (2005), found weak genetic structuring on local scales for pike in the Baltic Sea, but strong patterns of isolation by distance on larger scales. However, more recent findings, such as Sunde et al. (2018, 2019, 2022), Nordahl et al. (2019a), and Diaz-Suarez et al. (2022) in Sweden, Möller et al. (2020) in the Bodden lagoons, and Wąs-Barcz et al. (2023) in Polish coastal waters, detected small-scale genetic differentiation in several Baltic populations, which were attributed to isolation by environment and local adaptation (Berggren et al., 2016; Sunde et al., 2022), in addition to isolation by distance (Möller et al., 2020). The key abiotic factors driving this fine-scale divergence included salinity (Jørgensen et al., 2010; Sunde et al., 2018, 2022), and temperature (e.g., Sunde et al., 2019). Tibblin et al. (2016) also revealed phenotypic differences in migratory timing in coastal pike, suggesting isolation by time, while Eschbach et al. (2021) found genetic differentiation in freshwater pike in response to anthropogenic habitat alteration, which would indicate isolation by resistance. Fine-scaled genetic structuring and ecotype evolution may therefore be expected for pike in coastal habitats, with potential for several mechanisms of reproductive isolation.



2. Methodological issues

data in epoxy, copyright: Timo Rittweg

2.1. Evaluation of water isotope variability

Elemental tracers in fish tissues allow inference of both scenopoetic and bionomic niche use along the entire life of individuals (Reis-Santos et al., 2022; Tzadik et al., 2017). Otoliths and other incrementally grown tissues like eye lenses, represent temporally resolved chemical archives that allow reconstruction of niche dimensions back in time (Reis-Santos et al., 2022; Tzadik et al., 2017). For example, measuring the relative abundance of ^{18}O relative to ^{16}O isotopes (expressed as δ^{18}O values) enables back-calculation of experienced temperatures (Morissette et al., 2018; Patterson et al., 1993). Determining the concentration of otolith strontium (Sr), usually relative to calcium (Ca), Sr:Ca, allows inference of experienced salinities, particularly in estuarine brackish systems (Kafemann et al., 2000). The isotopic composition of carbon (expressed as δ^{13}C values) allows inferences about littoral and pelagic resource use, as well as terrestrial and marine resource use. Nitrogen isotopic composition (expressed as δ^{15}N values), indicates trophic level, anthropogenic nutrient inputs, and in many cases varies between freshwater and marine sources. Sulfur isotopic composition (expressed as δ^{34}S values), varies strongly between marine and terrestrial sources, and benthic vs. pelagic habitats in marine habitats (Cobain et al., 2022; Michener & Laijtha, 2008; Newsome et al., 2007, Rogers et al., 2023).

Elemental and isotopic tracers are often influenced by multiple confounding factors, necessitating validation on a species-specific and system-specific level (Reis-Santos et al., 2022; Tzadik et al., 2017). For example, otolith δ^{18}O values are strongly influenced by fluctuations in water δ^{18}O values (Darnaude et al., 2014). Water δ^{18}O values in brackish systems are often linearly related to salinity (e.g., Chamberlayne et al., 2021; Ingram et al., 1996; Mohan & Walther, 2015; Price et al., 2012; Swart & Price, 2002). Indeed, the mixture proportions of oceanic water (enriched in ^{18}O) and freshwater, (depleted in ^{18}O), can be inferred from salinity (Ingram et al., 1996). In systems with variable water salinities and complex hydrographic structure, such as the Bodden lagoons (Schubert & Telesh, 2017), short-term fluctuations in salinity and small-scale mixing dynamics may alter otolith δ^{18}O values. In order to use δ^{18}O from otoliths as thermal proxy, evaluation of environmental confounding factors is a prerequisite (Campana & Thorrold, 2001).

2.2. Environmental tracer validation

Apart from environmental factors, elemental ratios in fish tissues strongly depend on individual physiological processes (e.g., Guiguer et al., 20023; Michener & Laijtha, 2008; Newsome et al., 2007). While many of these processes are well-studied for dietary tracers in tissues such as muscle tissue and eye lenses (Michener & Laijtha, 2008; Newsome et al., 2007), much less is known about physiological controls in biogenic carbonates, such as otoliths (Guiguer et al., 2003; Hane et al., 2020). Otoliths are composed largely of crystalline calcium carbonate precipitated from endolymphatic fluid within the inner ear of fishes (Stevenson & Campana, 1992). Precipitation is facilitated by an organic scaffolding of largely acidic glycoproteins, referred to as otolin (Degens, 1969), making otoliths a composite material with an organic and an inorganic fraction. Analytical challenges introduced by the physiological processes of the fish affecting the organic fraction have been anticipated by Campana & Thorrold (2001), and were confirmed in multiple studies since (Guiguer et al., 2003; Hane et al., 2020; Helser et al., 2018; Matta et al.; 2013; Wycech et al., 2018), which attributed large amounts of unexplained variation in otolith isotope ratios to varying otolin contents. While multiple correction approaches and methods to remove the organic fraction from otolith carbonates have been proposed (such as Guiguer et al., 2003; Hane et al., 2020; Matta et al., 2013), the underlying physiological drivers remain largely unexplained. Further, as Hane et al. (2020) pointed out, most of the correction or removal methods proposed either produced ambiguous results (such as roasting procedures, Guiguer et al., 2003), or were not universally applicable (such as offset corrections between species, Hane et al., 2020). Therefore, otolith proxies for niche utilization need to be validated on a species- and system-specific level. As a fast-growing species with high phenotypic variance (Forsman et al., 2015), the contributions of physiological processes on intra-otolith elemental ratios may be strong for pike, warranting further validation studies.

2.3. Validation of age estimates in fishes

Most life-history traits of fish have a time dimension (Campana, 2001). For example, to estimate growth rates, which I used as a fitness surrogate in my doctoral research, changes in body size (or size of a structure where dimensions correlate with body size) need to be quantified over time (Campana et al., 1995; Denechaud et al., 2020). In temperate fishes, such as pike, this is usually achieved by counting growth rings that form on calcified hard structures in response to seasonal differences in growth, as most temperate fish grow slower in winter, forming translucent growth bands, and faster in spring/summer, forming opaque rings (Campana & Thorrold, 2001). However, the accuracy of age counts may be affected by process errors caused by calcified structures forming false or unreadable annual marks (Casselman, 1996), biasing age estimation towards under- or overaging (Beamish & McFarlane, 1995; Campana, 2001; Maceina et al., 2007). Further, interpretation errors resulting from age reader subjectivity may result in poor precision, and may also introduce directional bias due to learning effects (Beamish & McFarlane, 1995; Campana, 2001; Maceina et al., 2007). Differences in readability of structures can have multiple explanations, such as environmental effects in different habitats (Hüssy et al., 2016a), ontogenetic transitions (such as change in prey type, Casselman, 1996), disease, or slow growth rates forming subannual checks that are misinterpreted as annual marks (annuli: Weyl & Booth, 1999). Additionally, some structures, e.g., scales, may be resorbed during starvation periods (Maceina et al., 2007), rendering age estimates inaccurate and possibly imprecise in resource-limited systems (Spurgeon et al., 2015).

Aging errors can lead to biased estimates of growth and productivity of a fish stock, which can affect ecological interpretations (Campana, 1990; Yule et al., 2008) as well as models used to estimate harvest resilience and reference points for fisheries management (Beamish & McFarlane, 1987; Bertignac & De Pontual, 2007). In particular systematic underaging can lead to mismanagement of fish stocks, by overestimating productivity and growth potential (Beamish & McFarlane, 1995; Lai & Gunderson, 1987; Smith et al., 1995). Overaging may be less problematic, but has also led to biased management advice in some studies (Bertignac & de Pontual, 2007). From an ecological perspective, biased ages and growth estimates are problematic for comparisons between systems and populations, as well as for meta-analyses (Quist et al., 2003; Tyszko & Pritt, 2017). To reduce errors in age estimation, validation studies should be conducted on a per-species basis, ideally followed up by a comparison between systems to rule out effects introduced by systematic differences in environmental factors (Beamish & McFarlane, 1995; Campana, 2001; Maceina et al., 2007, Spurgeon et al., 2015). However, as Beamish & MacFarlane (1983), Campana (2001), Maceina et al. (2007), and, lastly, Spurgeon et al. (2015) noted, age validation studies continue to be the exception rather than the rule.

There have been only few age validations conducted on pike over the years, and significant debate exists on the accuracy of different structures for aging pike. For my doctoral research, I focused on scales as a non-lethal structure and otoliths as a lethal alternative. Pike age estimates have been conducted using scales by e.g., Anwand (1969), Berggren et al. (2022), Dorow (2004), Hegemann (1958), Juncker (1988), Pagel et al. (2015), and Monk et al. (2021), while otoliths have been used by e.g., Oele et al. (2015, 2019) and Blackwell et al. (2016). Otoliths produced accurate and precise age estimates in most studies, and are also known as accurate structures from other fishes (e.g., Blackwell et al., 2016; Hoie & Folkvord, 2006; Kimura & Anderl, 2005; Oele et al., 2015; Terwilliger et al., 2023). However, there is considerable debate on the use of scales for age estimation in pike and other species (Harris, 2020; Tyszko & Pritt, 2017; Van Oosten, 1923, 1929, 1941), due to the strong correlation of scale dimensions with body size, which compresses year rings in older fish and can lead to underaging (Van Oosten, 1923). Scale age estimates in pike were found to be accurate up to an age of 10 years by Laine (1991), and for aging juvenile pike by Pagel et al. (2015), but other studies found scales to be both inaccurate and imprecise (e.g., Blackwell et al., 2016; Mann & Beaumont, 1990; Oele et al., 2015). However, scales continue to be used for age estimation in pike (Monk et al., 2021), and have commonly been used to estimate ages in pike in the Baltic Sea in the past (Berggren et al., 2022; Dorow, 2004; Hegemann, 1958; Juncker, 1988). Combined with the possibility of habitat-induced variability (similar to Baltic Sea cod *Gadus morhua*, Hüssy et al., 2016a, b), a species- and system specific age corroboration for pike inhabiting the Bodden lagoons was necessary to establish a methodological basis for age- and growth determinations in my doctoral research.

3. Objectives and thesis structure

open wide, photo credit: Dirk Vegelahn

My doctoral thesis aimed to disentangle the n-dimensional niche use of pike and its consequences for intraspecific diversity and growth, and identify drivers of phenotypic diversity and growth relevant for management and conservation. I used northern pike (*Esox lucius*) as a model, in an interconnected system of brackish lagoons (Bodden lagoons) and freshwater tributaries featuring strong environmental gradients in temperature and salinity, along with large pulses of marine resources (Atlantic herring *Clupea harengus*). My specific objectives were: i) to develop a methodological basis for niche use and growth assessments using incrementally grown tissues in pike from the Bodden lagoons and adjacent tributaries, ii) to describe habitat use and migration patterns of pike from the Bodden lagoons and adjacent tributaries, and test their correlates on intraspecific diversification and growth performance, iii) to quantify the biotic resource use and assess individual- and phenotype-level specialization, particularly on marine resource pulses, and identify relevant biotic correlates of growth, and iv) to assess multidimensional niche specialization and its consequences for intraspecific diversification. My thesis has five main components: 1) identify relevant knowledge gaps and potential research avenues, 2) develop a methodological basis for the assessment of scenopoetic and bionomic niche use and growth performance, 3) examine the scenopoetic niche use of pike along the thermosaline niche axis and its consequences for intraspecific diversification and growth, 4) assess the bionomic niche use of pike in terms of resource use and individual specialization, especially on marine resources, and its consequences for intraspecific diversification and growth, and lastly, 5) quantify multidimensional niche use along both scenopoetic (thermosaline) and bionomic (resources) niche axes, assess interactions between scenopoetic and bionomic niche axes and identify the drivers of intraspecific diversification and sympatric coexistence in Bodden pike. Most of the findings are published or the corresponding manuscripts are submitted to scientific journals. Some preliminary results, namely the multidimensional niche analysis in **chapter 6.4.**, are presented without being published or submitted yet.

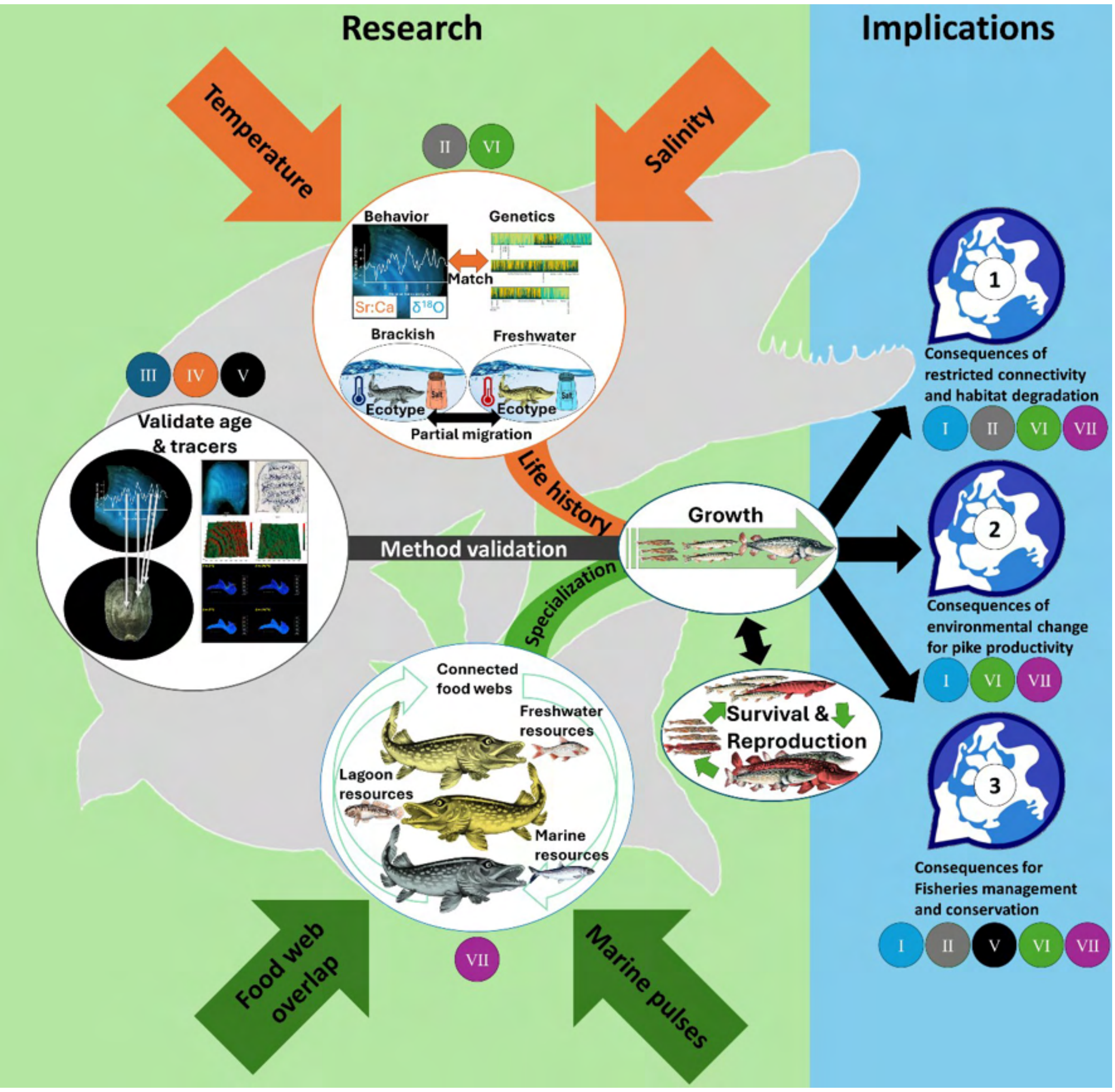


Figure 4. Structure of my thesis aiming to identify the mechanisms governing phenotypic variance, intraspecific diversifications and growth performance in Bodden pike, along with the corresponding papers in roman numerals.

My thesis addressed the following research questions:

What are the knowledge gaps and relevant research questions for ecology and management of pike in the Bodden lagoons? (**Paper I, paper II**)

Methodological issues:

- How reliable are niche assessments from otoliths? (**Paper III, Paper IV**)
- How reliable are age estimates derived from scales as a non-lethal structure compared to age estimation using otoliths as a lethal structure? (**Paper V**)

Scenopoetic niche use and intraspecific diversification of pike:

- How does the thermosaline niche and habitat use of Bodden pike change during ontogeny, and which scenopoetic factors drive age-specific growth in pike? (**Paper VI**)
- Is there relevant phenotypic variation in niche and habitat use along the thermosaline gradients in the study system? (**Paper VI**)
- Is the phenotypic variance between individual pike in the system associated with genetic differentiation and ecotype evolution? (**Paper VI**)
- What are the drivers of intraspecific diversity of pike in the study system, and how do they relate to individual- and phenotype-level growth performance? (**Paper VI, chapter 6.4.**)

Bionomic niche use and individual resource specialization of pike:

- What are the main prey species for pike in the study system, and are there relevant differences in prey quality between them? (**Paper VII**)
- What are the resource contributions from the different food webs present in the system, and what are the main drivers of resource use in Bodden pike? (**Paper VII**)
- Is there evidence for intraspecific competition and individual specialization in Bodden pike, and how does this relate to phenotypic diversity? (**Paper VII**)
- Does individual specialization on marine resources, in particular migratory herring, benefit growth performance in Bodden pike? (**Paper VII**)

Multidimensional niche use and specialization

- How does individual specialization along scenopoetic and bionomic niche axes interact with phenotypic variation, intraspecific competition and growth? (**chapter 6.4.**)
- What are the drivers of intraspecific diversification in Bodden pike from a multiniche perspective? (**chapter 6.4.**)

4. Knowledge gaps and relevant research questions

deep thoughts, photo credit: Philipp Czapla

To identify research gaps and possible management solutions for the declining stock, **Paper I** collected a large amount of peer-reviewed research, grey literature and novel data analyses about the pike fishery and ecology in the study area. It was confirmed that pike in the Bodden lagoons recruit successfully in mesohaline lagoons, up to salinities of 10 PSU, but migratory and freshwater-resident subpopulations also seem to exist in the system, forming a weakly connected metapopulation. **Paper II** assessed the phenotypic divergence in the population by targeted electrofishing of selected streams during the spawning-season in 2021 and a comprehensive citizen-science campaign of questionnaires on spawning activity and migration behavior. It supported the notion of multiple subpopulations that differ in migration behavior, and also found first evidence for genetic differentiation on subpopulation-level. This suggested that pike in the Bodden lagoons diverged into different migratory phenotypes that also display a certain degree of genetic divergence, giving rise to questions about potential ecotype evolution. Among several other stressors identified by **paper I**, a potential loss of stock structure due to past large-scale blockage of freshwater spawning habitat used by subpopulations was indicated. **Paper II** supported this, as many local subpopulations of migratory phenotypes were small, hinting at local extinctions due to largely blocked and heavily modified tributaries, which begs the question of how the pike population responded to the anthropogenic disturbances of the past. To investigate potential ecotype evolution, individual-level phenotypic and genetic assessments were needed for a closer inspection of the metapopulation structure. To evaluate potential impacts of past anthropogenic disturbances, analyzing the growth of the potential ecotypes may provide insight into possible bottlenecks during ontogeny. **Paper II** also hinted at potential intermediary phenotypes, which gather in front of blocked tributaries at shutters and pump sheds, likely using the still-present freshwater influence at these locations for spawning. This bears similarities to intermediary phenotypes with flexible habitat use in research on estuarine brackish fish populations elsewhere (Almeida *et al.* 2023; Kerr *et al.* 2007; Limburg *et al.* 2001; Rohtla *et al.* 2020, 2023; Russell *et al.* 2022). Such intermediary phenotypes may also have evolved in the Bodden as a response to anthropogenic habitat alterations, warranting further investigation into intermediary habitat use in Bodden pike.

In **Paper I**, we hypothesized that the decline in migratory herring stocks (Western Baltic Spring Spawn herring, Polte et al., 2021) may be partially responsible for the reduced growth and productivity of the pike stock. However, no current assessment of resource use existed for Bodden pike, and the degree to which pike specialize on herring and other marine resources was unknown. An assessment of whether pike specialize on pulsed resource subsidies by migratory herring or other marine prey, and examination of the effects on growth performance and productivity was needed to test this hypothesis. In addition, diet and specialization assessments may provide further insights on potential diversification mechanisms, such as intraspecific competition and resource partitioning. Lastly, **paper I** emphasized the currently poor understanding of the effects of climate change and other abiotic drivers of pike growth and productivity. Research on coastal pike populations in Sweden (Berggren et al., 2022) indicated a positive effect of warming on growth in pike, especially at juvenile stages, but a reduction in terminal length due to elevated natural mortality. The question remains whether this is also the case in Bodden pike, which, if so, may suggest rising temperatures as a common regional factor driving the stock declines across the central and southern Baltic Sea (Olsson et al., 2023). Further, breeding experiments in **paper I** hinted at potential reductions in offspring fitness at salinities above 10 PSU, in addition to the potential intermediary phenotypes detected in **paper II**. Therefore, the effects of temperature and salinity, in particular salinities approaching or even exceeding 10 PSU, on pike growth and phenotype variation, needed further investigation.

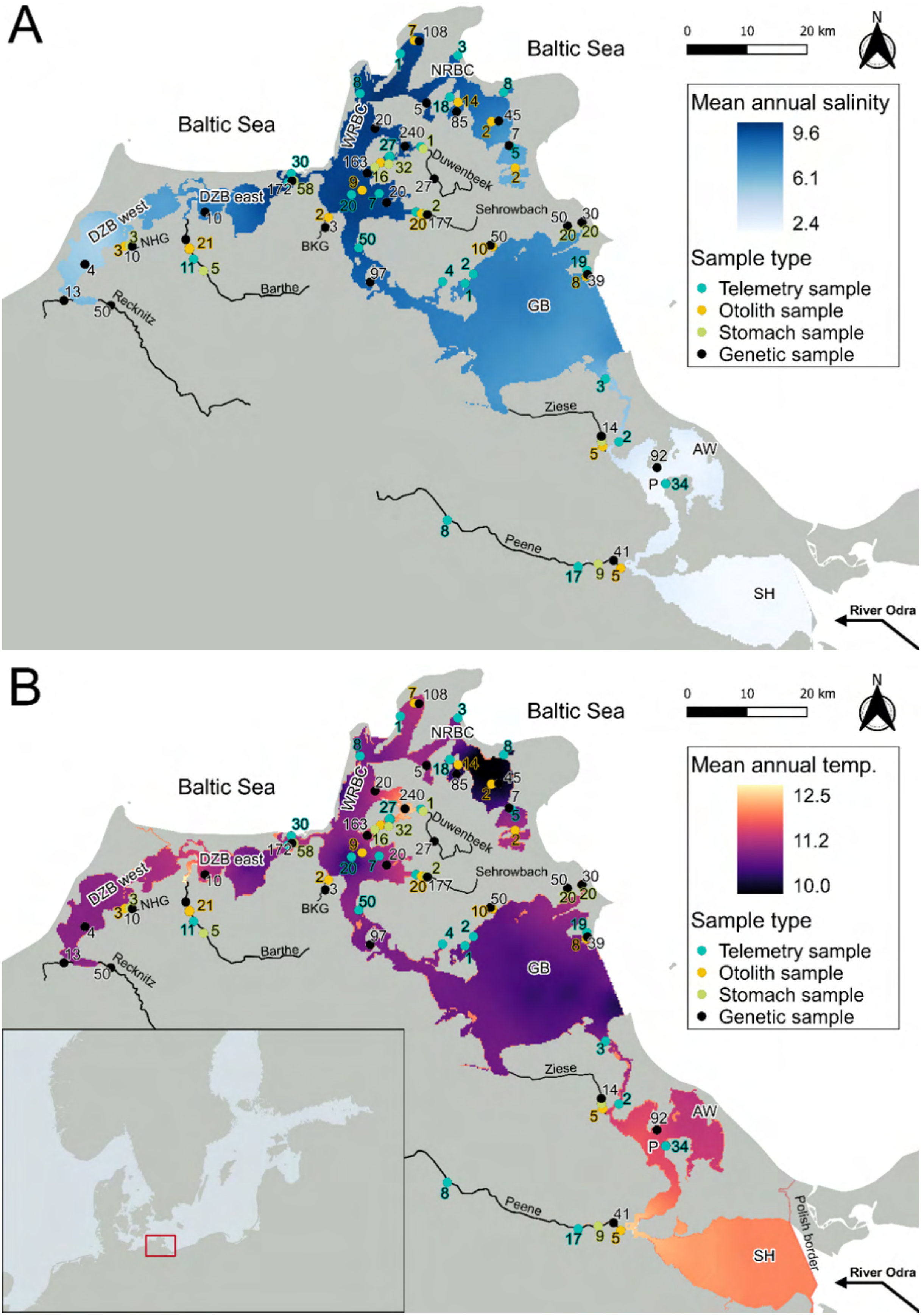
In summary, the findings of **paper I** and **II** suggest that analyzing multidimensional niche use of the different phenotypes found in the system, along with individual-level genetic differentiation and growth, could identify drivers of intraspecific diversification. Such insights may prove invaluable in developing management advice for conserving biocomplexity, growth performance and productivity of the pike metapopulation.

5. Methods

fishing Sehrowbach, photo credit: Dominique Niessner

5.1. Model system

Systems with high environmental stochasticity and diverse food webs, such as brackish estuaries, offer ideal conditions to answer questions about niche variation and diversification (Bell 2010; Costa-Pereira & Shaner 2024). I chose the brackish lagoons in the Southern Baltic sea around the island of Rügen (Bodden lagoons) as the model system for my doctoral research. These interconnected brackish lagoons and freshwater tributaries feature strong environmental gradients of salinity and temperature and a diverse species inventory from both marine and freshwater realms (**paper I**). Several marine species spawn in the lagoons, most notably western Baltic spring spawning herring (WBSS herring, *Clupea harengus*), which enters the lagoons in large abundances, representing a significant energy subsidy of large-bodied, energy dense prey (Von Dorrien et al., 2013, Winkler, 1987). Salinities in the Bodden increase from an annual average of 3-5 PSU in the western oligohaline lagoons to 8-10 PSU in the northwestern mesohaline lagoons, and from 2-3 PSU in the southeastern oligohaline lagoons to 6.5 PSU in the northeastern mesohaline lagoon (Figure 3 A). A temperature gradient spans from warmer average annual temperatures in the eutrophic lagoons in the southwest and southeast, towards colder, mesotrophic lagoons in the north (Figure 3B). Additionally, numerous smaller creeks and drainage ditches, many of which were obstructed by pump sheds and shutters during melioration measures in the 1970s (**paper II**), drain into the lagoons.


A
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Baltic Sea
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Mean annual salinity
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Sample type
Telemetry sample
Otolith sample
Stomach sample
Genetic sample
NRBC
WRBC
DZB west
DZB east
NHG
BKG
GB
AW
P
SH
Recknitz
Barthe
Duwenbeek
Sehrowbach
Ziese
Peene
River Odra
B
Mean annual temp.
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11.2
10.0
Polish border

Figure 5. Map of the study area from which pike were sampled along A: the salinity gradient; B: along the temperature gradient of the system. Salinity and temperature were interpolated with an inverse path distance weighted algorithm that accounted for land masses and other physical barriers in the system. Pike were captured between March 2020 and May 2022. Green circles: sampling locations for pike stomach content analysis; blue circles: pike for passive acoustic telemetry; orange circles: pike sampled for otolith microchemistry; black circles: Pike sampled for genetics. Number labels indicate the sample size for each method per location. DZB west: Darß-Zingst Bodden Chain west; DZB east: Darß-Zingst Bodden Chain east; WRBC: Western Rügen Bodden Chain; NRBC: Northern Rügen Bodden Chain; GB Greifswalder Bodden; P: Peenestrom; AW: Achterwasser; SH: Stettiner Haff; NHG: Drainage ditch Neuendorfer Hechtsgraben; BKG: Drainage ditch Badendycksgraben.

Table 1. Hydrochemical parameters (annual mean ± standard deviation) from 2005 to 2022 from monthly monitoring stations for major Bodden lagoons and the two tributaries sampled at depth for this thesis (data from LUNG MV). DZB west = Darß-Zingst Bodden Chain west; DZB east: Darß-Zingst Bodden Chain east; WRBC: Western Rügen Bodden Chain; NRBC: Northern Rügen Bodden Chain; GB: Greifswalder Bodden; P: Peenestrom including Achterwasser (AW in Figure 5).

Parameter	**DZB west**	**DZB east**	**WRBC**	**NRBC**	**GB**	**P**	**Barthe**	**Sehrowbach**
Area (km2)	119.4	77.4	231.0	159.4	540.1	181.9	NA	NA
Mean depth (m)	2.0	2.0	1.8	3.5	5.8	2.6	NA	NA
Max depth (m)	10.1	16.5	7.6	10.3	13.5	16.0	NA	NA
Catchment (km^2)	1,578	1,578	238	312	665	5,772	292	NA
Mean temp (°C)	11.6±6.6	11.5±6.6	11.6±6.7	9.9±6.5	11.7±6.8	11.9±6.7	10.6±7.0	10.3±6.5
Salinity (PSU)	5.4±1.8	8.3±1.6	8.7±1.1	8.3±1.0	6.5±0.6	3.2±2.1	0.7±0.01	0.9±0.01
Secchi depth (m)	0.4±0.3	1.0±0.8	1.9±0.8	1.2±0.8	1.7±0.8	0.7±05	NA	NA
Total P (µg/l)	97.4±28.8	55.9±23.1	40±19.6	64.2±39.1	45.8±21.1	98.3±58.1	223.7± 194.6	169.4± 132.6
Trophic state (LAWA 1998)	polytroph.	eutrophic	meso- to eutrophic	eutrophic	eutrophic	polytroph	eutrophic	eutrophic
Habitat quality EU Water Framework Directive	poor to bad	bad	poor	poor	poor	poor to bad	poor	poor

My thesis was embedded in the EU-funded Boddenhecht project, which assessed stock status, socio-economic relevance and ecology of Bodden pike to derive management advice for the pike fishery. This enabled me to participate in the comprehensive sampling campaigns of the project, leverage synergies with other researchers within the project, and allowed me to integrate my research on pike into applied management (Arlinghaus et al., 2023).

Pike were sampled by the research team, and in cooperation with local guides and contracted fishers. To mitigate gear-induced biases on age and size structure (Wilson *et al.* 2015), pike were captured using multiple gears, i.e., gill nets, fyke nets, angling, and electrofishing in tributaries. Unless stated otherwise, all fish were measured for total length (mm), internally sex-determined (visual examination of gonads on dead individuals or through the incision made for acoustic transmitter implantation), fin clipped for genetic analyses, and a dorsal muscle biopsy was taken for isotope analysis.

For inferences on eco-evolutionary dynamics, factors that may influence between-individual variation need to be carefully anticipated in the sampling design (Marshall 2024). Therefore, to capture phenotypic diversity across different life stages and sexes and along the spatial and environmental gradients in the lagoons, I stratified sampling by size, collecting equal numbers of individuals along 5 cm size classes for each major lagoon chain along the environmental gradients and in two tributaries that were sampled in depth, the rivers Barthe and Sehrowbach. I complemented the tributary sample with smaller samples of individuals from other tributaries to cover a larger geographic gradient. In the case of individuals used for **paper IV**, **V**, **VI**, (except for the larger genetics sample in **paper VI**), and the eye lens analyses in **paper VII**, pike were sacrificed, and heads were taken to the lab at IGB Berlin for otolith and eye lens extraction. I sampled the brackish lagoons outside spawning season (March and April), when all potential phenotypes, including individuals that migrate into tributaries for spawning, would be present in this habitat. I termed this the “mixed situation”. In contrast to the lagoons, I assumed the mixed situation in tributaries would occur during the spawning season, when both freshwater residents and migratory individuals would reside in this habitat. Therefore, tributaries were sampled in the months March and April (**Paper II**). To ensure salinity differences between habitats were sufficient to be measured via otolith microchemistry, I excluded oligohaline lagoons from the sampling for **paper VI**. Due to limited sample pools at several locations, and variable capture rates of different gear, I was not able to collect a fully randomized sample (in terms of location, season and gear). Sampling limitations and sex-dimorphic growth (Casselman, 1995) did ultimately not allow for an equal sex ratio. Low capture rates did not allow for length-stratified sampling in all tributaries, so tributary samples were pooled for some analyses in **paper VI** and **VII**.

Habitat use across different habitat types and associated differences in growth rate can impact on age estimation (Hüssy et a., 2016a). Similarly, the age range over which age estimates are compared may influence results from age validations (Maceina *et al.* 2007). Therefore, in **paper V** 86 pike were captured across all different habitats (Bodden lagoons and several tributaries) and along the entire length gradient considered in my doctoral research (Figure 5, Table 2).

Small sample sizes are problematic for growth analyses (Pardo et al., 2013), therefore I complemented the sample used for **paper V** with additional fish from freshwater tributaries for **paper VI** to boost sample sizes. I selected additional individuals sampled in spring 2022 in Barthe and Sehrowbach rivers (Figure 5, Table 2), along with five individuals (three females, two males, 43.4 – 75.1 cm length range, mean ± SD = 60.6 ± 11.6 cm, age rage 2 – 8 years) from a freshwater lake around 150 km from the study area with no in- or outflows, to acquire a sample of fish unaffected by environmental fluctuations of the Bodden.

To capture the full range of phenotypic variation in the system for **paper VI**, I complemented the sample again with additional pike sampled in spring 2022 (Figure 5, Table 2). To capture genetic diversity across all lagoons and tributaries, 1,514 individuals were sampled non-lethally for fin clip samples via cooperating fishers, angling guides, anglers and the research team across the entire salinity gradient (including oligohaline lagoons) and all major tributaries (Figure 5).

For the stomach content analysis in **paper VII**, 696 pike were sampled across the study area between 2019 and 2022. Stomach contents in fish often vary seasonally (Baker *et al.* 2014). Therefore, to capture seasonal differences in diet, we sampled pike stomachs in spring (March - May), summer (June - August), fall (September - November) and winter (December - February) 2022. Stomach contents were retrieved by gastric lavage in living fish, or by excising the stomach in dead fish. Prey items were identified to species level, when possible, measured for total length (mm), and biomass (fresh weight, g) was calculated via species-specific length-weight regressions that were calculated from the prey fish data. As expected for a piscivore (Baker et al., 2014), a large fraction (N = 525) of pike had empty stomachs, leaving 171 individuals for the analysis of major prey items in **paper VII** (Figure 5, Table 2). Only one pike in winter had ingested prey, so winter was excluded from analysis (spring N = 125, summer N = 19, autumn N = 28).

Individual behavior has a large influence on resource use (Brownscombe *et al.* 2022). Therefore, for the analysis of resource use in **paper VII**, I combined a sample of 98 individuals for which muscle isotope values were available and behavioral phenotypes had been characterized in **paper VI**, with a sample of 204 pike for which behavioral phenotypes had been characterized via passive acoustic telemetry (Dhellemmes et al., 2023b). This resulted in a final sample of 302 pike (Figure 5, Table 2). Most individuals were captured in spring (N = 205 between March and May), and winter (N = 76 between December and February), with fewer samples in autumn (N = 23 between September and November) and summer (one individual in July).

To infer individual specialization in resource use, repeated measurements on the individual level, ideally from the same tissue, are needed to account for temporal variation in resource use (Newsome et al., 2007, 2012). Therefore, I sampled sequential eye lens laminae of pike in **paper VII**. First, to capture variation in resource use across the ontogeny, I took a random length-stratified subsample of 50 pike from the sample pool outlined for **paper VI**, with 5 individuals per 5 cm size class between 50 and 100 cm. However, preliminary results indicated significant differences in lifelong isotope values between behavioral phenotypes, so I complemented the sample with an additional 31 pike to enhance sample size in previously underrepresented behavioral phenotypes. This resulted in a final sample of 81 pike (Figure 5, Table 2). This sample included 17 freshwater resident pike, 10 anadromous pike, 21 cross-habitat pike and 33 brackish resident pike.

Table 2. Sampling overview of the papers presented in this thesis. **Paper I** and **II** were excluded as they present syntheses of multiple analyses. No fish were sampled for **Paper III**. The table shows total sample size (N), sex distribution (female: f; male: m; unknown: u), size range, mean size and standard deviation (SD), sampling period (calendar year), age range. Samples for **paper VII** were split into stomach content analysis (SCA), stable isotope mixing models (SIM) and eye lens lamina analysis (ELA). Samples for **chapter 6.4**. were split into samples for scenopoetic niche and samples for bionomic niche.

Paper	**Total N (f, m, u)**	**Size range (cm)**	**Mean size ± SD (cm)**	**Period**	**Age (years)**
IV	112 (74, 38, 0)	40.4 – 126.2	72.9 ± 17.1	2019 - 2022	1 - 13
V	86 (53, 32, 0)	40.4 – 126.2	80.0 ± 14.0	2019 - 2021	1 - 12
VI	120 (79, 41, 0)	40.4 – 126.2	73.6 ± 16.9	2019 - 2022	1 - 13
VII					
SCA	171 (35, 25, 111)	12.9 – 115.2	73.2 ± 18.1	2019 - 2022	Not determined
SIM	302 (163, 138, 1)	40.4 – 126.2	74.8 ± 13.3	2019 - 2022	1 - 13
ELA	83 (60, 23, 0)	40.4 – 126.2	76.4 ± 18.3	2019 - 2022	1 - 13
chapter 6.4.					
Scenopoetic	120 (79, 41, 0)	40.4 – 126.2	73.6 ± 16.9	2019 - 2022	1 - 13
Bionomic	83 (60, 23, 0)	40.4 – 126.2	76.4 ± 18.3	2019 - 2022	1 - 13

5.2. Environmental tracers

Variability in water chemistry propagates to otolith chemistry (Campana 1999), and biases inferences about habitat use and migration (Darnaude *et al.* 2014). To validate $\delta^{18}O$ values as a thermal tracer, I therefore assessed the variation in water salinity and water $\delta^{18}O$ values across the study system, both temporally and spatially in **paper III**. To test the correlation of water $\delta^{18}O$ values and salinity across a larger geographic gradient, water samples were taken across three transects covering all major lagoons and tributaries in June 2019, March 2020 and July 2020. To test for seasonal dynamics of water salinity and $\delta^{18}O$ values, biweekly time-series of water samples were taken at 1 location in the WRBC (Vitter Bodden), and six locations in the DZBC. Water salinity values were derived from the monthly monitoring carried out by local authorities (Landesamt für Umwelt, Naturschutz und Geologie of the German state Mecklenburg-Vorpommern, LUNG MV), or from own measurements using handheld multiparameter devices (Multi 3630 IDS WTW, Weilheim, Germany, equipped with a TetraCon 925 electrical conductivity measuring cell), as well as from HOBO U2-002-C salinity loggers (Onset, Bourne, USA) installed on acoustic receivers of the Boddenhecht telemetry array across the lagoons. Water samples were filtered and measured for $\delta^{18}O$ values at IGB Berlin using a Picarro L2130-I cavity ring-down spectrometer (Santa Clara, Ca, USA). The correlation between water salinity and water $\delta^{18}O$ values was assessed for both seasonal signals using the time series measurements as well as for spatial variation using the transect data. Seasonal differences in spatial correlation were assessed by comparing the summer transects with spring transects.

Variation in otolith elemental composition unrelated to environmental factors, in particular organic content, can strongly bias otolith $\delta^{18}O$ values (Chang & Geffen 2013; Degens *et al.* 1969; Guiguer *et al.* 2003). I therefore analyzed the spatial distributions of potential organic tracers and the correlation of otolith $\delta^{18}O$ values and organic content in **paper IV.** Otoliths were extracted, embedded into Crystalbond glue and cut into thin sections of 100 µm thickness. The Crystalbond glue was dissolved in LC-MS grade Acetone, otolith sections polished and sent to the secondary ion mass spectrometry (SIMS) facility at the GeoForschungsZentrum (GFZ) Potsdam, Germany. There, otolith sections were embedded in round, 1-inch (2.54 cm) thick epoxy mounts, coated with a high-purity gold film to assure electrical conductivity and analyzed for $\delta^{18}O$ values via SIMS, the results of which were also used in **paper V** and **VI** (see below). $\delta^{18}O$ values were determined along point transects (distances between points ~ 35 µm) covering a straight line through the otolith core to the outer margin across the longest axis crossing all visible year rings. To test a potential proxy for otolith organics, $OH^-/^{16}O$ ion count ratio values were determined in a multicollection approach for each $\delta^{18}O$ determination. To examine spatial patterns in environmental and organic tracers, I selected three specimens out of the initial 113 individuals measured with SIMS for electron microprobe scans (EMS) covering the entire surface of the otolith. Otolith thin sections were cleaned and coated with high-purity carbon, to ensure electrical conductivity, and EMS scans of strontium (Sr), magnesium (Mg), manganese (Mn), sulfur (S), phosphorus (P) and calcium (Ca) were conducted at the GEOMAR Helmholtz Center for Ocean Research in Kiel, Germany. After observing a pattern of decreasing organic contents (assessed via S and P concentrations), I checked for spatial correlation with $\delta^{18}O$ values. Consequently, one specimen was chosen for an additional SIMS analysis, where a high-resolution (~ 35 µm) spatial grid of $\delta^{18}O$ and $OH^-/^{16}O$ ion count ratio values was determined across the entire surface of the otolith. I assessed the validity of $OH^-/^{16}O$ ion count ratio values as an organic proxy by comparing the spatial correlation of

$OH^-/^{16}O$ ion count ratio values with the EMS scans of S and P from that otolith specimen. To estimate the covariance between otolith organic contents (otolin) and $\delta^{18}O$ values in otoliths and assess potential ontogenetic or physiological confounding factors, I modelled otolith $\delta^{18}O$ values with linear mixed effects models. $OH^-/^{16}O$ ion count ratio was the response variable, growth rate, sex and age were fixed predictors, individual fish ID was a random predictor to account for multiple measurements on the same individual (Zuur *et al.* 2009). I used the resulting correlation coefficients to develop a pairwise correction approach for intraotolith organics.

5.3. Age validation

Errors in age estimation have major impacts on growth assessments and population models used to generate management advice (Reeves 2003; Tyszko & Pritt 2017; Yule *et al.* 2008). Therefore, to generate a methodic basis for age estimation and develop a quality control routine, I corroborated age estimates of Bodden pike and compared them with visual age estimates in **paper V**. Pike otoliths used for this analysis were an earlier subset of the otoliths used for **paper VI**. After SIMS $\delta^{18}O$ determinations, otoliths were cleaned of the gold coating and high-resolution images were taken under darkfield using a Nikon Eclipse motorized optical microscope. I tested otolith $\delta^{18}O$ values as an age corroboration tool by comparing observed fluctuations in otolith $\delta^{18}O$ with theoretical otolith $\delta^{18}O$ values calculated from seasonal water temperatures and $\delta^{18}O$ values (**paper III**) using two fractionation equations for freshwater (Patterson et al., 1993) and marine (Geffen, 2012) fish otoliths. After comparing age estimates of two expert readers on images of $\delta^{18}O$ transects mapped over otolith thin sections with an automated age counter, I decided on the automated age as the least biased estimate for the corroborated age. Scales from each individual were mounted on object slides, and high-resolution images were taken using a Leica MZ8 stereo microscope. One experienced reader (> 2000 structures over more than 2 years) and one inexperienced reader (no prior experience in age estimation) estimated ages using otolith and scale images. Images were randomized prior to aging and did not contain information about the individual fish. Aging was done in imageJ, using the OtoJ macro (Fischer et al., 2018).

To assess how biased age estimates impact growth models, I used the three different age estimates (corroborated age, scale age and otolith age), to fit three-parameter von Bertalanffy growth curves (Pardo et al., 2013), and compared growth curves and von Bertalanffy parameters L_∞, k and t_0 between structures. To estimate consequences of biased growth parameters for fisheries management, age-structured population models were estimated for each of the different sets of parameters. The models estimated the commonly used management reference points MSY, B_{MSY} and F_{MSY}, and, using a log-utility function to find suitable compromises in a mixed fishery with multiple management objectives (Ahrens *et al.* 2020), also gave estimates for optimal minimum and maximum size limits based on the different growth parameters.

5.4. Thermosaline niche assessment

Environmental stochasticity along the thermosaline niche axis fosters local evolutionary adaptations and population diversification, and can have direct consequences on individual physiology and growth in fishes (Bœuf & Payan 2001; Pörtner *et al.* 2010; Rypel 2012). I therefore quantified individual thermosaline niche variation and consequences for intraspecific diversity and growth of Bodden pike in **paper VI**. I used high-resolution transects of $\delta^{18}O$ values as a proxy for experienced temperature in conjunction with strontium calcium ratios (Sr:Ca ratios) as a proxy for experienced salinity. Both chemical proxies were determined along the same transects in pike otoliths. Following the results of **paper IV**, I corrected the otolith $\delta^{18}O$ values for correlation with otolin. Otolith Sr:Ca ratios were determined at the GEOMAR Helmholtz Center for Ocean Research in Kiel using Laser Ablation Inductively Coupled Plasma Mass Spectrometry (LA-ICPMS) with NewWave UP193fx 193 excimer laser ablation system coupled with a NuInstruments AttoM HR-ICP-MS spectrometer. Due to significant covariance between $\delta^{18}O$ values and Sr:Ca ratio, I transformed otolith $\delta^{18}O$ values into residuals from a linear regression of $\delta^{18}O$ on Sr:Ca, generating a relative thermal proxy. I used a multivariate time-series clustering approach (dynamic time warp; DTW) to identify groups of fish with similar lifelong thermosaline niche use. Some groups only differed in lifelong mean values but not in shape, likely a result of systematic variance in environmental parameters between lagoons. I therefore used a decision framework to evaluate differences in mean lifelong niche patterns of the clusters, to condense the fine-grained clustering solution from the DTW algorithm into ecologically similar groups with similar lifelong habitat use (similar to Hegg & Kennedy, 2021), and reduce the effects of systematic between-lagoon environmental variance. I interpreted these groups as behavioral phenotypes, and tested their reproducibility in a jackknife resampling test. To assess the distribution of behavioral phenotypes along thermosaline gradients, I tested phenotype frequency across capture locations with a χ^2-test.

5.5. Resource use and individual specialization

Stable isotope values allow long-term inference on diet and resource use, however, contributions by specific species to a target organisms diet are difficult to assess, due to the inability to sample the entire isotopic variance in a system (Post 2002). Similarly, stomach content analysis is limited to snapshots of the diet and may be biased by short-term fluctuations in resource availability (Baker *et al.* 2014). Combining both methods is recommended for thorough assessments of resource use and specialization (Beaudoin *et al.* 1999). Therefore, I analyzed diet and resource use of pike using both quantitative stomach content analysis and tissue stable isotope values in **paper VII**. To assess the isotopic variability within prey species and food webs they represent in the system, fish and invertebrate prey were collected opportunistically across the Bodden between 2019 and 2022. Additionally, targeted sampling was carried out with gill nets in spring 2021 at two locations (one freshwater-influenced bay and one marine-influenced open lagoon location), electrofishing in several tributaries (Barthe, Peene, Sehrowbach, Ziese), and dredge net transects at three locations (three repeated transects per location) in the WRBC, The NRBC and the DZBC. To represent the marine food web across all lagoons, marine prey fish, such as herring, were collected from all lagoon chains, as well as bottom trawl samples from the open Baltic, carried out by the Thünen-Institute for Baltic Fisheries, Rostock, Germany. Invertebrate samples were additionally collected using a bottom grab at three locations in the WRBC, the NRBC and the DZBC (three repeated samples per area). Muscle tissue was excised dorsally for prey fish, except for very small fish (such as three-spined stickleback), which were analyzed whole. Invertebrate samples were used whole, or, in case of crustaceans, the carapace and guts were removed prior to analysis. Pike muscle samples (N = 302), pike eye lens laminae (N = 81 individuals, 3 - 18 laminae per individual), prey fish muscle samples and invertebrate samples were freeze-dried, homogenized, and analyzed for the stable isotope ratios of $^{13}C/^{12}C$, $^{15}N/^{14}N$, $^{34}S/^{32}S$, and C/N ratio at the isotope lab at IGB Berlin using Elemental Analyzer Isotope Ratio Mass Spectrometry (EA-IRMS). Isotope values were reported as $\delta^{13}C$ VPDB, $\delta^{15}N$ atm, $\delta^{34}S$ CTD. $\delta^{13}C$ values in fish were mathematically corrected for lipids using the method of Kiljunen et al (2006), if $\delta^{13}C$-C/N ratio plots indicated an influence of lipids on the results, and CN ratio exceeded 3.5. Lipid contents of invertebrates did not exceed CN ratios of 3.5 and were therefore not corrected in any way. For simplicity, I will refer to the combined isotope values as CNS isotope values for the rest of this thesis.

To assess seasonal and interannual diet changes, I compared biomass proportions in pike stomachs and pike CNS isotope values across years and seasons. I used total biomass proportions across all individuals to identify major prey items in the diet of Bodden pike for isotope mixing models, where I defined a species as major prey item if it exceeded 1% total biomass contribution in stomachs. Using a subsample of muscle tissue from those major prey species, I quantified the energy density of the prey items via calorimetry.

To estimate resource use of pike, I assessed the isotopic variability of different prey fish based on capture location and grouped them into resource groups they represented: freshwater resources, lagoon resources and marine resources. Using these resource groups as a priori end members in Bayesian stable isotope mixing models, I calculated relative contributions of each resource group to individual pike diets. These models convert the isotopic data of consumers and resources into proportional estimates, also referred to as proportional space (p-space) metrics (Newsome et al., 2009). I ran several separate Bayesian tracer mixing models within the MixSIAR package (v 3.1.12, Stock et al., 2018), using adjusted trophic discrimination factors from Canseco et al. (2023). I compared models with different combinations of continuous predictors, including body size (total length, mm), extended and core home range estimates from passive acoustic telemetry (HR95 and HR50, respectively, Dhellemmes et al., 2023a), and fixed predictors, including behavioral phenotype, genotype, and capture area. To identify drivers of resource use in Bodden pike, I compared the models against each other and against a null model (no continuous or fixed predictors) using leave-one-out cross validation information criterion (LOOIC).

Using CNS isotope values from sequential eye lens laminae, I described the long-term isotopic niche of pike from birth up until 87 cm of back-calculated length. I back-calculated the length at each consecutive eye lens laminae using Fraser-Lee back-calculation (Lee, 1920). I estimated the between-individual component (BIC), within-individual component (WIC), and the total isotopic niche width (TINW) in isotopic niche (δ-space) of pike at population and phenotype level using variance component analysis, employing Bayesian multiple-response linear mixed effects models at the population and phenotype level. I calculated population-level and phenotype-level specialization by dividing the size (eigenvalue) of the WIC matrix by the size of the TINW matrix. I estimated individual-level specialization by dividing the sizes of individual variance-covariance matrices by the size of the TINW matrix (Ingram et al., 2018). To assess intraspecific competition, I calculated overlap in core (40%) three-dimensional niche area between behavioral phenotypes (Rossman *et al.* 2016), and between individuals and the population niche (Grainger et al., 2023).

5.6. Genetic variability and genotyping

Adaptive evolution may cause increased genomic divergence for adaptive genetic traits (Wu 2001). Therefore, to develop a panel of diagnostic single nucleotide polymorphism (SNP) markers for individual genotyping in **paper VI**, whole genomes of 1514 pike from 20 locations were screened for regions of maximum between-population divergence, in cooperation with the working group for Ecological Genomics at Carl von Ossietzky university in Oldenburg, Germany. Sampling locations included brackish lagoons likely inhabited by high numbers of brackish-resident fish (WRBC, NRBC, GB, DZB east, Figure 5), larger rivers likely inhabited by freshwater-resident pike (Barthe, Peene, Recknitz, Figure 5), oligohaline brackish environments (Peenestrom, DZB west, Figure 5), and putative anadromous populations (Sehrowbach, Duwenbeek, Ziese, Körkwitzer Bach, Neuendorfer Hechtsgraben, Figure 5). Sequence data were mapped against an annotated reference genome (GCF_011004845.1_fEsoLuc1.pri_genomic.gtf, downloaded from NCBI), to identify the functions of genes involved in population divergence (Wu, 2001). SNPs were chosen based on the difference between among-group genetic variance and the range of allele frequency differentials between groups. Following visual inspections for mapping artifacts, a panel of 33 loci was developed for individual-level genotyping.

Using these diagnostic markers, individual pike were genotyped using STRUCTURE, which identified k = 4 clusters as ideal solution based on Evanno´s delta k (Evanno et al., 2005). We tentatively defined these clusters as putative brackish 1 and brackish 2, putative anadromous and putative freshwater genotypes, and derived individual assignment probabilities to the clusters. For 101 fish in **paper VI**, both behavioral phenotype data and genotype were available, which I used for phenotype-genotype matching. To assign discrete individual genotypes from the individual probability distributions, I applied an assignment probability threshold of 0.7 (Austrich *et al.* 2020; Skey *et al.* 2023), which offered a compromise between keeping individuals in the sample (individuals below the threshold were "unassigned") and a conservative threshold. To examine potential geographic patterns of genetic variability, I tested the spatial distribution of the discrete putative genotypes across the lagoons with a χ^2-test.

5.7. Phenotype - genotype matching

To test whether the behavioral phenotypes characterized in **paper VI** were ecotypes in the sense of Stronen et al. (2022), behavioral genotypes identified from lifelong thermosaline niche use were matched with their individual assignment probabilities to the four putative genotypes. To test whether behavioral phenotypes differed in their individual-level assignment probabilities to the genotypes, I ran a PERMANOVA with assignment probabilities to the four genotypes as response variables and behavioral phenotype as predictor, followed by pairwise PERMANOVA tests to screen for significant differences in genetic assignment probabilities between pairs of behavioral phenotypes.

5.8. Multidimensional niche metrics

Variation along, as well as covariation between, scenopoetic and bionomic niche axes need to be understood to accurately describe the environmental associations and resource use of a species (Costa-Pereira & Shaner 2024). Therefore, to test how these niche axes interact on an individual and phenotype level in Bodden pike, I adapted the variance component analysis employed in **paper VII** to combine both abiotic thermosaline niche and biotic resource use data in a common framework. To that end, I transformed niche proxy values (otolith transects of Sr:Ca and δ^{18}O and CNS isotope values) into units standard deviation (z-scores), and combined them in a multi-response Bayesian generalized linear modelling framework with individual ID as random predictor. Similar to **paper VII**, I estimated population-level between individual (BIC) and population-level within individual (WIC) variance and calculated the total population niche width along the condition and resource niche axes. I estimated population-level specialization by dividing the size (eigenvalue) of the within individual variance component matrix by the size of the total niche width matrix. To assess phenotype-level niche width along condition and resource niches, I repeated the analysis on a phenotype level. I also estimated individual-level specialization along the combined niche axes. Resulting condition and resource specialization indices were compared in a multi-response Bayesian generalized linear mixed effects model, with scenopoetic and bionomic specialization index as response variables, and behavioral phenotype, capture location, sex, age and total length as predictors. Phenotype-level multiniche between individual, within individual, and total niche width components were plotted together with the population multiniche between individual, within individual, and total niche width components. This allowed to assess the shape and size of the phenotype niches and compare them with the simulated niches generated by Costa-Pereira & Shaner (2025).

5.9. Consequences for growth

To test for potential fitness differences between behavioral phenotypes, putative genotypes, or ecotypes, I used age-specific and lifelong growth as fitness surrogates. To identify relevant abiotic or biotic drivers of growth in Bodden pike, I also tested for the effects of thermosaline proxies and CNS isotope values on age-specific growth.

To test for differences in age-specific growth in **paper VI**, I ran linear mixed effects models on annual otolith increments, which were measured from high-resolution images of otoliths in imageJ, following the methodology outlined in **paper V**. I used different combinations of fixed predictors, including behavioral phenotype, putative genotype, ecotype, age (growth slows down with age in fish, Lee, 1920), sex (pike grow sex-dimorphic, Casselman, 1996), annual mean $\delta^{18}O$ residuals, and annual mean Sr:Ca values in a common model-comparison framework. Individual ID was a random predictor to account for the repeated otolith increment measurements per individual. Fixed effects were sequentially dropped from the model, and significant differences between models were identified with log-likelihood ratio tests. Marginal and conditional R^2 were used as indicators for goodness of fit. Model assumptions were assessed graphically.

To test for differences in lifelong growth in **paper VI**, I fit individual level von Bertalanffy growth curves separately for behavioral phenotypes, genotypes and ecotypes in a hierarchical Bayesian approach. I estimated otolith radii at age from the parameters R_∞ (equivalent of L_∞ on otolith scale), Brody growth coefficient k and t_0, where radii at ages were nested within individuals, and individuals were nested within phenotypes/genotypes/ecotypes. Convergence problems and autocorrelation were assessed graphically, and non-overlapping outer credibility intervals were interpreted as significant differences in lifetime growth performance.

To test for growth effects of resource use in **paper VII**, I used sizes-at-ages backcalculated from otoliths via Fraser-Lee backcalculation using the intercept from a regression of body size on otolith radius, in conjunction with yearly averaged CNS isotope values from eye lens laminae. Years were assigned to eye lens laminae based on Fraser-Lee backcalculated lengths at laminae (**chapter 4.5.**). If two or more eye lens CNS isotope values were assigned to the same year, values were averaged for that year. I used the mean CNS isotope values at specific years, along with age, sex, and behavioral phenotype as fixed predictors of annual growth (i.e., the increment in total length from year i-1 to year i), with individual ID as random predictor (similar to **paper VI**). Significant effects were identified by comparing models with consecutively removed fixed predictors based on log-likelihood ratio tests.

To test whether lifelong individual specialization along scenopoetic and bionomic niche axes had a significant effect on growth in pike, the individual specialization indices were used as fixed predictors of annual otolith increment in a Bayesian generalized linear mixed effects model, along with age, sex (male/female), and behavioral phenotype. As before, individual ID was used as a random predictor. Significant effects were tested using Bayesian p-values, i.e., which test whether the posterior 95% credibility interval of a given parameter overlaps with 0.

6. Main findings and discussion

diving for pike, photo credit: Fritz Feldhege

6.1. Reliability of age readings and environmental tracers

I showed in **paper V** that seasonal temperature amplitude is the main driver of intraotolith $\delta^{18}O$ fluctuations in pike otoliths, consistent with the study of Gerdeaux & Dufour (2012) on pike from Lake Annecié, France. Strong seasonality in otolith $\delta^{18}O$ values was detected despite the seasonality of water $\delta^{18}O$ values found in **paper III**, which pointed in the opposite direction of the expected seasonality in otolith $\delta^{18}O$. This shows that the effects of seasonally varying temperature on otolith $\delta^{18}O$ values mask the effects of less systematic variations in water $\delta^{18}O$ values, confirming intraotolith $\delta^{18}O$ chronologies as a reliable tool to corroborate fish ages in estuarine brackish systems. Measured $\delta^{18}O$ values in otoliths differed from theoretical $\delta^{18}O$ values predicted from ambient water temperatures and water $\delta^{18}O$ values by approximately 1‰, particularly in juvenile stages (first two years of life). I speculated this discrepancy may be due to environmental fluctuations and active thermoregulation (Nordahl *et al.* 2019b) in **paper V**. However, considering the findings of **paper IV**, high organic content in the otolith carbonate, particularly in the near-core areas, likely contributed towards the observed isotopic mismatch (see below).

Using the corroborated age as a reference age, I assessed accuracy and bias of otolith age estimates (lethal method) and scale age estimates (nonlethal method) in **paper V**. I found a clear bias towards underestimating age using scales after ages older than 6 years. This bias translated into significantly different von Bertalanffy growth parameters, namely overestimation of the mean terminal length L_∞ and underestimation of the Brody growth coefficient k. Several prior studies found similar biases in scale age estimates (Blackwell *et al.* 2016; Mann & Beaumont, 1990; Oele *et al.* 2015), but some researchers also found scales to be accurate (Laine *et al.* 1991; Pagel et al., 2015). I attribute these differences of readability of scales to differences in growth rates and environmental factors between systems, which could not be accounted for in **paper V** or other previous studies. Age-structured population models using scale age estimates overestimated MSY and B_{MSY}, but underestimated F_{MSY}, which could lead to overly conservative management, if the fishery is managed based on $F_{MSY,}$, or overharvest if the fishery is managed based on MSY directly (Martell & Froese 2013). Similarly, in a multi-objective utility model, the predicted optimum minimum-length limit of scales (86 and 87 cm for reader 1 and reader 2 scale age estimates, respectively) was also more conservative than the optimum minimum-length limit calculated for the pooled otolith age estimates (68 cm). **Paper V** thus showed the aging bias of scales to result in more conservative management advice, which, under a cautionary approach, would limit the impact of the aging bias. However, biased growth parameters are a critical problem for ecological inference, in particular for comparisons between systems or populations (Quist *et al.* 2003). **Paper V** therefore confirms scales as a challenging and potentially problematic structure for age estimations, and underlines that age validation efforts are not only recommendable on a species-by-species base, but also for each new system where ages are to be estimated, consistent with work in Baltic cod by Hüssy *et al.* (2016a). Following the recommendations developed in **paper V**, which suggested otoliths as an accurate aging structure in pike, I used otolith age estimates and yearly increment measurements to describe growth rates and size-at-age in **paper IV**, **paper VI** and **paper VII**. I also developed a reference collection of age-corroborated pike otoliths and scale images for training and quality assurance in my subsequent papers and other working packages of the Boddenhecht project.

I described the thermosaline niche of pike in **paper VI** and the analysis outlined in **chapter 6.4.** using high-resolution lifelong transects of Sr:Ca ratios as a proxy for salinity and $\delta^{18}O$ values as a thermal proxy. Sr:Ca is a widely used proxy for salinity in estuarine brackish systems (Kafemann *et al.* 2000), but multiple confounding factors can influence $\delta^{18}O$ values in otoliths, e.g. varying water $\delta^{18}O$ values (Darnaude *et al.* 2014) and intra-otolith organic contents, i.e., otolin (Hane *et al.* 2020). **Paper III** demonstrated significant variation in water $\delta^{18}O$ values in the study system, not all of which could be attributed to changes in salinity. Water $\delta^{18}O$ values showed a linear correlation with salinity during spring, but we detected reversals and deviations from this correlation in summer in several areas (**paper III**). This contrasted with findings from other estuarine systems, where constant linear relationships between salinity and water $\delta^{18}O$ were found (e.g. Chamberlayne et al., 2021; Ingram et al., 1996; Mohan & Walther, 2015; Price et al., 2012; Swart & Price, 2002). Unexpectedly high $\delta^{18}O$ values in oligohaline lagoons and tributaries were likely due to evaporation-induced effects in the shallow inner lagoons, as well as complex mixing processes with the open Baltic in the outermost lagoons, similar to findings by Barrie *et al.* (2015). While the seasonality of water $\delta^{18}O$ was overwritten by the seasonal temperature amplitude in **paper V**, these findings nevertheless prevented me from backcalculating absolute temperatures for **Paper VI**. I therefore used salinity-corrected $\delta^{18}O$ values as a relative temperature proxy to enable individual-level comparisons of relative thermal habitat and thermal history in Bodden pike in **paper VI** and **chapter 6.4.**

Simultaneous $\delta^{18}O$ determinations in mixed phases of anorganic carbonates and organic otolin can result in biased $\delta^{18}O$ values (Guiguer *et al.* 2003; Hane *et al.* 2020; Matta *et al.* 2013). I addressed this concern in **paper IV**, where I validated $OH^-/^{16}O$ ion count ratios, determined simultaneously with the $\delta^{18}O$ values, as a proxy for otolin content in a sample of 113 pike otoliths. I showed $OH^-/^{16}OH$ ion count ratios to be a reliable proxy for intraotolith organic contents, due to the fact that most of the organic-bound oxygen in proteins is bound as hydroxy (OH^-) groups. I found a significant negative correlation between otolith $\delta^{18}O$ values and organic content, which was due to the simultaneous sputtering of anorganic carbonate and the organic otolin lattice in the otolith thin section by SIMS. This led to a bias of $\delta^{18}O$ values towards more negative values when both phases are reported on the same reference scale. I further found a significant positive association of age with otolith $\delta^{18}O$ values, which is partially explained by the negative association of $\delta^{18}O$ values with otolin. Relative otolin content decreases with growth, which in turn scales allometrically with age (Von Bertalanffy 1957). However, **paper VI** also showed older pike prefer colder habitats, which likely contributed strongly to the positive association of age with otolith $\delta^{18}O$. Growth rate and sex (female) were also negatively correlated with otolith $\delta^{18}O$, owing to higher organic contents in areas of fast growth (Hüssy et al.,2004) and sex-dimorphic growth in pike (Craig 1996). Otolin contents were highest in early life, as was expected, as pike tend to grow fast in the first years (Bry *et al.* 1991; Pagel *et al.* 2015, **paper VI**; **paper VII**), necessitating high amounts of otolin to maintain otolith growth (Hüssy *et al.* 2004). I therefore proposed a pairwise correction based on the slope coefficient of a linear regression between $OH^-/^{16}O$ and $\delta^{18}O$ to account for ontogenetically changing otolin contents. Using this correction, I detected strong organic-induced offsets of approximately 1.1‰, in particular in the first 500 µm of the otoliths, owing to fast juvenile growth rates. This offset is consistent with the findings of **paper V**, where the difference between predicted and observed otolith $\delta^{18}O$ values was around 1‰, and was strongest in the first two years. The correction therefore aligned the $\delta^{18}O$ values in pike otoliths with the otolith $\delta^{18}O$ values predicted from environmental temperature and water $\delta^{18}O$ values in **paper V**, strengthening the inferences made by both **paper III** and **paper IV**.

Therefore, I used the findings from **paper V** to validate otoliths for age estimation, and **paper III** and **paper IV** to develop a correction for the effects of mixing processes (i.e., salinity) on otolith $\delta^{18}O$ values, and a correction for the effect of ontogenetically varying otolin contents. While it was not possible to account for effects of different water evaporation rates between lagoons (**paper III**), I generated a thermal proxy that is comparable between brackish and freshwater habitats as well as between pike of different age and growth rates. Along with the ability to reliably estimate age and growth, these results build the foundation for **papers VI** and **VII**. As none of the methods used in **paper III**, **IV**, or **V** are exclusively developed for coastal pike, and the used proxies are likely present in any given fish otolith (Reis-Santos *et al.* 2022), my findings from these papers are easily transferrable to other systems and species. I recommend future studies use otolith $\delta^{18}O$ as thermal proxy to consider the variability of water isotopes in a given study system and test for correlations between different otolith proxies (e.g., $\delta^{18}O$ and Sr:Ca), to account for covariance between environmental factors. Further, otolith composition needs to be accounted for, in particular otolin concentrations, and, if possible, species-, and system-specific corrections should be developed.

6.2. Thermosaline niche use

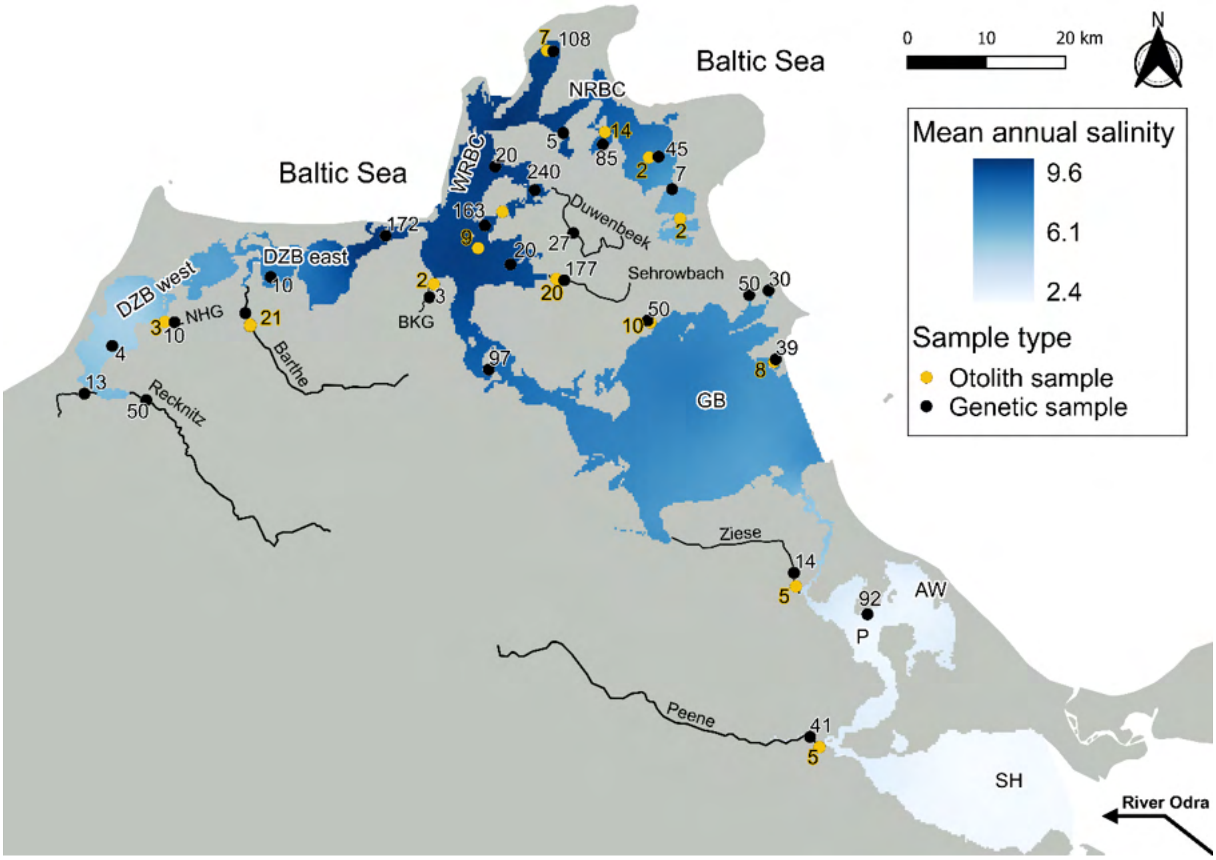

Figure 6. Map of the pike sampled across the salinity gradient of the Bodden lagoons and adjacent freshwater tributaries for thermosaline niche assessments and genetic analyses in **paper VI**. Orange circles: pike sampled for otolith microchemistry; black circles: Pike sampled for genetics. Number labels indicate the sample size for each method per location. DZB west: Darß-Zingst Bodden Chain west; DZB east: Darß-Zingst Bodden Chain east; WRBC: Western Rügen Bodden Chain; NRBC: Northern Rügen Bodden Chain; GB Greifswalder Bodden; P: Peenestrom; AW: Achterwasser; SH: Stettiner Haff; NHG: Drainage ditch Neuendorfer Hechtsgraben; BKG: Drainage ditch Badendycksgraben.

In **paper VI**, I detected strong thermosaline niche variation in the pike metapopulation, and identified four highly reproducible behavioral phenotypes (82% correct reclassification in jackknife resampling), which also differed significantly in bionomic niche use, as **paper VII** showed (see below). The behavioral phenotypes were characterized as follows:

- **Freshwater resident pike (N = 27)**: These individuals displayed lifelong Sr:Ca values below 3 mg/g (upper freshwater threshold, see **paper VI**), indicating full residency in freshwater tributaries. A thermal shift from juvenile warm water habitats towards colder adult habitats in this behavioral phenotype likely coincided with a shift from sheltered but hypoxic juvenile habitats to well-oxygenated open stream adult habitats, which was further confirmed by shifts in $\delta^{13}C$ and $\delta^{34}S$ isotope values of sequential eye lens laminae in **paper VII.**

- **Anadromous pike (N = 21)**: These individuals showed a transition from freshwater Sr:Ca at birth and during early juvenile stages (first 300 - 500 µm of the otolith transect) towards brackish Sr:Ca values in later life, but with regular fluctuations below 3 mg/g Sr:Ca in adult stages, marking return movements to freshwater spawning habitats. A strong thermal shift in from warm juvenile habitats towards colder adult habitats marked the shift from tributaries towards brackish lagoons, confirmed by shifts in eye lens $\delta^{13}C$ and $\delta^{34}S$ values (**paper VII**).
- **Cross-habitat pike (N = 28)**: These individuals showed no clear freshwater or brackish origin in their Sr:Ca values, despite several (15 out of 28 pike) having been captured in lower parts of freshwater tributaries. Lifelong Sr:Ca values lay in between anadromous and brackish resident pike, with some fluctuations below the freshwater threshold, possibly indicating short-term residency in freshwater-influenced areas, such as river mouths and sheltered bays adjacent to blocked tributary outlets. A strong shift in thermal niche at around 500 µm distance from the otolith core likely marked an ontogenetic habitat shift from sheltered freshwater-influenced bays and river mouths towards open lagoon habitats in which the adults forage, confirmed by shifts in eye lens $\delta^{13}C$ and $\delta^{34}S$ values (**paper VII**).
- **Brackish resident pike (N = 44)**: These individuals, like freshwater residents, showed little fluctuation in lifelong Sr:Ca values, which lay well above 3 mg/g Sr:Ca, implying residency and natal origin in brackish lagoons. Slight increases in lifelong Sr:Ca suggested movements towards more saline habitats with increasing age and size, which was further corroborated by eye lens $\delta^{34}S$ isotope values in **paper VII**. This behavioral phenotype showed no strong shifts in thermal niche, but mean lifelong otolith $\delta^{18}O$ values varied between individuals, likely indicating temperature variability between different lagoons. Nevertheless, the absence of an ontogenetic thermal shift and implied these individuals hatched, nursed and foraged in similar thermal habitats throughout their life. This was again confirmed by eye lens $\delta^{13}C$ and $\delta^{34}S$ values in **paper VII**, which remained constant throughout early life for this behavioral phenotype.

Notably, following my classification based on otolith elemental transects in **paper VI**, Dhellemmes et al. (2023b) detected similar behavioral types using passive acoustic telemetry, validating my findings and allowing me to use a larger sample of behaviorally phenotyped pike in the diet analysis of **paper VII**. Frequency distribution of the behavioral phenotypes followed the salinity gradient of the system ($\chi 2 = 9.54$, df = 2, $p = 0.008$). Brackish residents were more frequent in the high-salinity, high-variability WRBC (**paper VI**). The relative frequency of cross-habitat and anadromous pike increased in lagoons with lower salinity and environmental stochasticity, such as the NRBC and GB (**paper VI**). However, while anadromous pike were abundant in the pooled tributary sample (37% anadromous, compared to 26% cross-habitat pike and 37% freshwater residents), they were rare in lagoons (total of 7% out of 66 pike), and did not occur at all in WRBC (**paper VI**). The phenotypic divergence of Bodden pike resembled a behavioral continuum of migratory strategies connecting two behavioral endpoints, i.e., residency in either freshwater or brackish lagoons, which correlate with the extremes of the salinity gradient and also with individual resource use (**paper VI**, **paper VII**), indicating partial migration patterns (Cagnacci *et al.* 2011; Chapman *et al.* 2011a; Chapman *et al.* 2011b; Kerr *et al.* 2009). My findings add to a growing body of evidence for multi-phenotype assemblages in fishes inhabiting transitional habitats in coastal areas (Almeida *et al.* 2023; Kerr *et al.* 2007; Limburg *et al.* 2001; Rohtla *et al.* 2020, 2023; Russell *et al.* 2022), indicating partial migration and intrapopulation diversification between two habitat extremes are commonplace in fishes.

Behavioral diversification in fish, in particular migratory behavior, may be the result of evolution (Vainikka *et al.* 2023), but can also result from phenotypic plasticity (Olsson *et al.* 2006). I found evidence for both these mechanisms in **paper VI**. Brackish residents and cross habitat pike were genetically differentiated (PERMANOVA $p < 0.0001$) from all other phenotypes, confirming them as ecotypes in the sense of Stronen et al. (2022). However, freshwater residents and anadromous pike were closely related (PERMANOVA $p > 0.05$), indicating they are one ecotype performing facultative migrations (i.e., migratory flexible). Five out of 33 diagnostic SNP markers were associated with genes involved in osmoregulation, indicating salinity as a major factor driving intrapopulation divergence, pointing at isolation by environment (IBE), consistent with Sunde et al. (2018, 2019, 2022). Isolation by distance was evidenced by the strong correlation between relative genotype frequency and capture location ($\chi2 = 81.84$, $df = 12$, $p < 0.0001$). The weak differentiation between freshwater resident and anadromous behavioral phenotypes was likely explained by spawning site fidelity and natal homing of freshwater and anadromous pike in tributaries along a spatial gradient (Engstedt *et al.* 2014; Miller *et al.* 2001), inducing patterns of isolation by distance. Isolation by distance may also have contributed to the genetic differentiation of pike within the lagoons, which are only weakly connected by individual movements (Lukyanova *et al.* 2024), consistent with findings by Möller *et al.* (2020). Isolation by resistance (McRae, 2006), caused by the large-scale blockage of freshwater tributaries with shutters and pump sheds during the 1960s and 1970s (**paper II**) may have contributed to the evolution of the cross-habitat ecotype as a genetic mixture between anadromous and brackish resident pike. This phenotype likely selected freshwater-adjacent areas (e.g. outlets of pump sheds) for spawning rather than undertake lengthy migrations, compete for habitat with already present brackish resident pike, or risk reproductive failure through high salinity inflows in fully brackish habitats (**paper I**).

My results challenge the notion of the dichotomous categorization of pike into two ecotypes (e.g., Möller et al., 2019; Nordahl et al., 2019a; Sunde et al., 2022) and reveal the potential of multi-niche approaches to describe intrapopulation diversification. From an evolutionary perspective, the results from **paper VI** point towards a strong diversification effect of salinity gradients within coastal pike, possibly leading to partial migration patterns along behavioral continua (Chapman et al., 2011 a,b). This effect may additionally be reinforced by anthropogenic habitat alteration in my study system, which may have given rise to an additional ecotype, the cross-habitat pike. Alternatively, this ecotype could represent formerly anadromous pike that adapt to a brackish lifestyle, and might therefore be an intermediary step. My results highlight the need to integrate niche variation, behavior and genetic diversity in future research to better capture the large individual variability in coastal estuarine fish communities. Increased biocomplexity and individual variation can act as a safeguard against environmental fluctuations and disturbances through the portfolio effect, for example when a reproductive failure of one subpopulation or ecotype in any given year may be compensated by increased survival of a different ecotype (Šargač et al., 2022; Schindler et al., 2010). Robust characterization and quantification of both represents the first step in developing management actions aimed to conserve this variability and improve stock resilience. However, three of the behavioral phenotypes expressed by the pike ecotypes, namely anadromous pike, cross-habitat pike and brackish resident pike, share a common foraging habitat in the brackish lagoons for most of the year, which leads to the potential of resource competition and raises questions about dietary specializations, which are addressed in the next chapter.

6.3. Dietary niche use

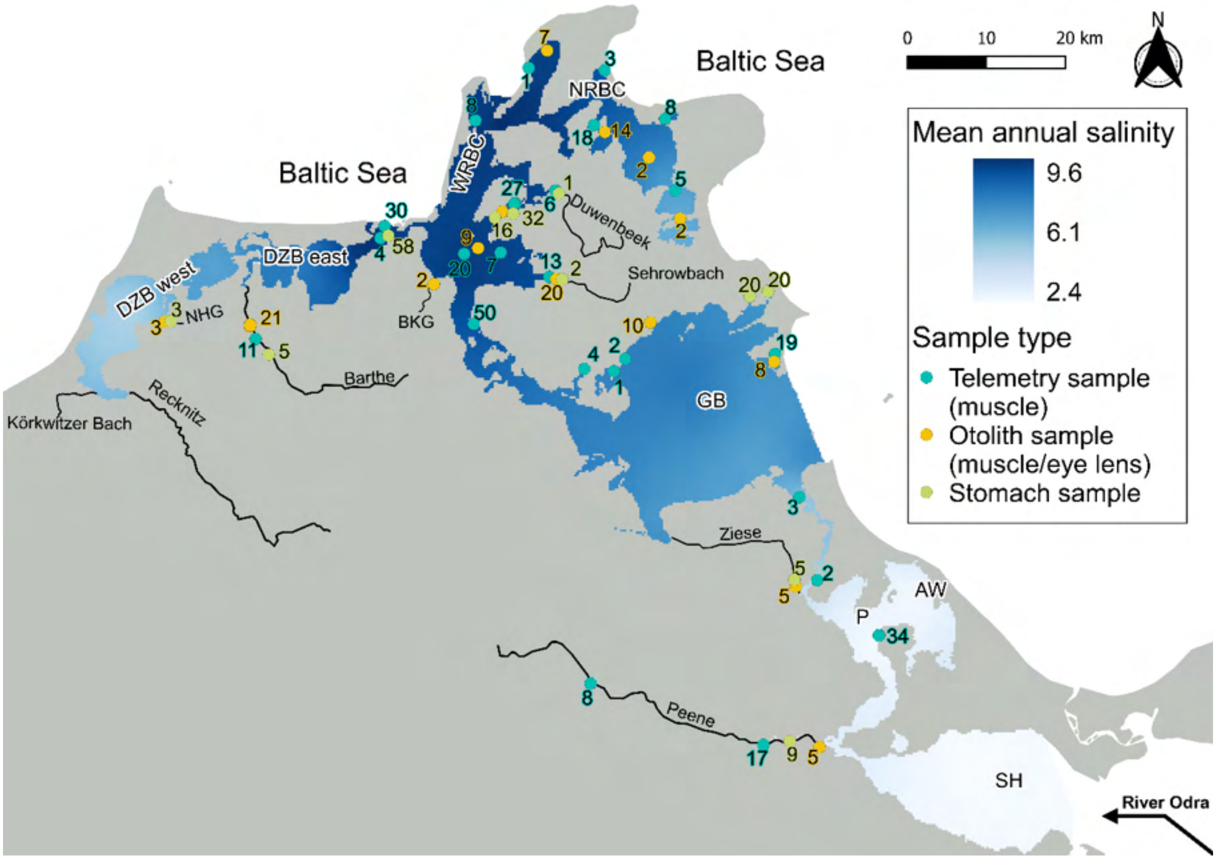

Figure 7. Map of the pike sampled across the salinity gradient of the Bodden lagoons and adjacent freshwater tributaries for stomach content and stable isotope analyses in **paper VII**. Blue circles: Pike sampled for passive acoustic telemetry for which muscle biopsy samples were available; orange circles: Pike sampled for **paper VI**, which were also sampled for muscle biopsies and eye lens delamination; green circles: Pike sampled for stomach content analyses. Number labels indicate the sample size for each method per location. DZB west: Darß-Zingst Bodden Chain west; DZB east: Darß-Zingst Bodden Chain east; WRBC: Western Rügen Bodden Chain; NRBC: Northern Rügen Bodden Chain; GB Greifswalder Bodden; P: Peenestrom; AW: Achterwasser; SH: Stettiner Haff; NHG: Drainage ditch Neuendorfer Hechtsgraben; BKG: Drainage ditch Badendycksgraben.

Paper VI suggested that anadromous pike, cross-habitat pike and brackish resident pike coexist sympatrically in shared foraging habitat for large parts of the year (outside of the spawning season from March until May), which may lead to intraspecific competition fostering individual foraging specialization (Beaudoin *et al.* 1999; Bolnick *et al.* 2007; Costa-Pereira & Shaner 2024). In **paper VII**, I investigated resource use of the behavioral phenotypes found in the pike metapopulation using stomach content analysis in combination with stable isotope analysis of multiple tissues, energy content assessment of prey fish, and growth assessment as proxy for fitness. Stomach content analysis from 171 individuals sampled across all four seasons showed that, despite foraging on a large range of species (15 species: 12 fishes and 3 invertebrate species), pike mostly relied on five main prey items, namely herring, flounder, roach, perch and invasive round goby. This is largely consistent with Winkler (1987), who found herring, flounder, roach and perch to be major prey items, but did not detect invasive round goby, as the species has only recently established in relevant abundances in the lagoons (Lewin *et al.* 2023). Similar to Winkler (1987), I detected strong seasonality in stomach contents, with migratory herring being prevalent in pike stomachs in spring time (38.3 % in March - May), but absent during the rest of the year. Similarly, roach was also predominantly detected during spring (30.5% from March-May), but rarely detected in summer and autumn. In summer, pike switched to a more opportunistic diet, consuming many different species, including sand eel, eel, needlefish, and gammarid shrimp (*Gammarus sp.*), none of which reached more than 1% biomass contribution. In fall, biomass proportion in pike stomachs was dominated by perch (38.0%) and invasive round goby (45%). These results indicated that pike predate on different species at different times of the year, which may be facilitated by spatial overlap of differently adapted phenotypes (Bolnick *et al.* 2003; Saavedra *et al.* 2022; Svanbäck *et al.* 2008), but also through different individual foraging specializations (Bolnick et al., 2003).

Stable isotope mixing models on data from 302 individuals revealed body length to be a significant predictor of short-term resource use (muscle tissue isotopic half-life = 3 - 6 months). Larger pike, with the exception of freshwater residents, relied more on marine resources than smaller conspecifics (**paper VII**). Body length interacted with behavioral phenotype, as brackish residents and cross-habitat pike switched from lagoon resources to marine resources as their dominant food source when they reached greater lengths (after 80 cm for brackish residents and 95 cm for cross-habitat pike). Out of all behavioral phenotypes, brackish residents relied most on marine resources. Anadromous pike increased marine resource use with increasing body length, but lagoon resources remained the dominant source also in larger size classes. Freshwater residents showed no marine resource use, but moderate contributions of lagoon resources at smaller size classes. This indicated resource fluxes from lagoons towards tributaries by prey items that forage in the lagoons but migrate into the tributaries, such as three-spined stickleback (*Gasterosteus aculeatus*), a species known to also form migratory phenotypes (Kusakabe et al., 2017), and a known prey item for Bodden pike (Winkler, 1987). My findings agree with the results of Nolan *et al.* (2019), who detected increasing dietary contributions of marine derived resources (migratory clupeids, *Alosa spp.*) with increasing body size in pike in the River Severn, UK. A lack of seasonality found in the data from muscle isotopes as compared to stomach contents in **paper VII** could be attributable to feast-or-dynamics driven by consumption of migratory herring during parts of the year, when energy stores for pike somatic growth are generated (similar to Armstrong & Bond 2013; Armstrong & Schindler 2011). Alternatively, pike may switch to other marine prey that is available in the lagoons in the absence of herring, such as flounder. Further, dietary contributions by the less-abundant, but still present autumn-spawning herring (Von Dorrien *et al.* 2013) cannot be ruled out. On the one hand, these results may be the outcome of spatial sorting between the ecotypes leading to the dietary differences in a strongly opportunistic species (Beaudoin et al., 1999; Pedreschi et al., 2015). On the other hand, the strong differences in biotic resource use between the behavioral phenotypes may suggest resource partitioning as a potential mechanism to reduce competition and facilitate coexistence of the behavioral phenotypes.

In **Paper VII**, I found strong stage-specific differences in isotopic niche between the behavioral phenotypes. CNS isotope values indicated oxygen limitations in early nursery habitats for freshwater resident and anadromous pike (Alp & Cucherousset 2022; Newsome *et al.* 2007), potentially caused by anthropogenic nutrient input (e.g. fertilizers, Rogers *et al.* 2023). Strong increases in $\delta^{13}C$ and $\delta^{15}N$ values in later life likely marked shifts from freshwater nursery habitats to brackish lagoons for anadromous pike, and shifts to better oxygenated open stream habitat for freshwater residents. The transition between nursery habitat and brackish lagoons in anadromous pike in our study area occurred at a total length of approximately 20 cm, confirming the findings of **paper VI**. Pike therefore outmigrated at larger sizes than in Swedish coastal pike (2.4 - 3.1 cm TL, Tibblin et al., 2015) and Estonian coastal pike (8.1 ± 4 cm TL, Rohtla et al., 2012). This may be attributable to the higher salinities in the Bodden lagoons (8 - 10 PSU compared with 7 PSU in Tibblin et al., 2015 and 5 - 6 PSU in Rohtla et al., 2012), which require juveniles to grow to larger sizes and higher osmoregulatory capacity (Varsamos *et al.* 2005) before outmigration. However, other environmental factors, such as vegetation cover, prey abundance and differences in predation pressure between Bodden lagoons and tributaries may also have contributed to the late outmigration. Brackish residents and cross-habitat pike showed high marine resource use from early life to the maximum size that I was able to reconstruct with eye lens layers (67 cm for cross-habitat and 87 cm for brackish residents). This was consistent with the results from stable isotope mixing models in **paper VI**. However, only the largest brackish residents showed increased $\delta^{34}S$ values (proxy for marine resource use), confirming the increase in marine resource use of larger brackish residents indicated by the stable isotope mixing models on an individual level (**paper VII**). While the oxygen limitations indicated for some habitats by eye lens CNS values could be interpreted as a scenopoetic niche component, the isotopic differences were still propagated through the food web and were also reflected in prey CNS isotope values (**paper VII**). Therefore, I interpreted the individual eye lens CNS isotopic niche as a bionomic niche indicator in **chapter 6.4.**

Pike from different behavioral phenotypes differed in their levels of individual foraging specialization in **paper VII** (GLM, F = 3.26, p = 0.031). Greater within-individual than between-individual variance ($BIC_{Pop}/TINW_{Pop} = 0.21$), suggested a generalist population in terms of resource use, consistent with previous findings on pike (Cathcart *et al.* 2019; Chapman *et al.* 1989; Pedreschi *et al.* 2015). However, individual specialization indices varied strongly between and within the behavioral phenotype groups, with a variety of true specialists, true generalists and intermediary behaviors that suggested high heterogeneity at an individual level. Cross-habitat and brackish resident pike were highly specialized, while anadromous and freshwater resident pike were more generalized. Lifelong isotopic niche overlapped strongly between cross-habitat and brackish resident pike (57% of core isotopic niche). These results suggest resource competition between the two behavioral phenotypes may have fostered individual specialization and resource partitioning along bionomic niche axes. Low individual overlap and high displacement of individual core niches with the population niche further suggested resource partitioning on an individual level, in particular between the competing phenotypes cross-habitat and brackish resident. As **chapter 6.4.** showed, this was also consistent with scenopoetic niche specialization. Beaudoin *et al.* (1999) found both overall resource limitation (for example, all resources are equally scarce in a low productive system) and intraspecific resource competition may drive individual specialization in pike. Estuarine systems are usually highly productive (Garman & Macko 1998; Gross et al., 1988; MacAvoy *et al.* 2000; Winkler 1987), which makes an overall resource limitation in the system less likely as an explanation for the high individual specialization found in brackish residents and cross-habitat pike. Therefore, intraspecific competition between these two behavioral phenotypes in shared foraging grounds, either for locally limited high-quality resources, or for specific habitats, was the most plausible mechanism behind the observed patterns.

I calculated individual foraging specialization and overlap with a common population-level niche for all pike in the analysis (Grainger *et al.* 2023; Ingram *et al.* 2018; Newsome *et al.* 2009). However, considering the spatiotemporal differences between resource surfaces and environmental factors detected in **paper VI** and **paper VII**, it is questionable whether a shared resource surface is a valid assumption for the behavioral phenotypes. Recalculating the individual niche metrics using phenotype-specific resource surfaces showed differences in individual specialization in freshwater residents, which now consisted of a gradient from true specialists to true generalists. Additionally, the differences between phenotypes were less pronounced using phenotype-specific niches. However, cross-habitat and brackish residents were still strongly specialized and anadromous pike were more generalist (**paper VII**). The issue of different individuals and phenotypes integrating over different resource surfaces is well-known in studies of migratory birds (Eyres *et al.* 2017; Laube *et al.* 2015), but seems to be less acknowledged in fishes. Comparing individuals that use different resource surfaces with different isotopic variation under the assumption of a shared resource surface can bias estimates of resource specialization. Individuals integrating over a more variable resource surface would always appear generalist, and individuals integrating over a less variable resource surface would appear as specialists. I therefore recommend future studies to carefully test the assumption that all individuals are likely to share the same resource surface, particularly for partially migratory species. My results also underline the importance of combining multiple niche metrics, e.g., δ-space metrics and p-space metrics, as has previously been recommended (Newsome et al., 2007).

Complementing the multiniche approach of **paper VI**, I demonstrated a similar niche differentiation along bionomic niche axes in **paper VII** and provided insights into possible mechanisms of sympatric coexistence. Consistent with the niche variation hypothesis (van Valen 1965; Bolnick *et al.* 2007), my results suggest a seemingly generalized population that is highly heterogenous at an individual level (**paper VI**, **paper VII**). Generalization in anadromous pike may hint at opportunistic habitat use and foraging across food webs (**paper VI**, **paper VII**). Variable specialization in freshwater residents suggests differences between freshwater tributaries, e.g., in density, habitat quality (e.g., oxygen, **paper VII**) and productivity, which could not be resolved in my work. Adding bionomic niche analyses (**paper VII**) to scenopoetic niche analyses (**paper VI**) hinted at multidimensional specialization patterns contributing to diversification and sympatric coexistence. The separation of analysis frameworks for scenopoetic niches I have outlined in my results so far allowed for a detailed characterization of habitat use and diet specialization in Bodden pike. However, in order to explore questions about interactions and covariance structure between those central niche axes, I combined my results into a common analysis framework in the following chapter.

6.4. Multidimensional niche variation, adaptation and ecotype differentiation

Combining the data from **paper VI** and **paper VII** in a common analytical framework, I quantified scenopoetic niche specialization in salinity (via intraotolith Sr:Ca ratios) and temperature, (via intraotolith $\delta^{18}O$ values) alongside bionomic niche specialization (CNS values from sequential eye lens layers) for the same individuals (N = 81 for bionomic niche axis, **paper VII**, N = 120 for scenopoetic niche axis, **paper VI**). I found significant variations along both niche axes between and within individuals, which were strongly associated with behavioral phenotypes (Figure 8 A, B, Table 3). Consistent with **paper VI** and **paper VII**, brackish residents and cross-habitat individuals specialized strongly in both bionomic (brackish = 0.83; cross-habitat = 0.90) and scenopoetic (brackish = 0.65; cross-habitat = 0.67) niche axes (Figure 8 C, D). Anadromous pike showed low individual specialization in both bionomic (0.52) and scenopoetic niche axes (0.49), while freshwater residents displayed moderate bionomic (0.74), and high scenopoetic specialization (0.74)(Figure 8 C, D). Total length and capture area were also significant drivers of individual multidimensional niche specialization, however, effect sizes for these predictors were one level of magnitude smaller than the effects of behavioral phenotypes (Table 3). On the subpopulation level, brackish residents and cross-habitat pike overlapped in their niche axes (Figure 8 E). Both are moderately displaced from the total population niche (overall niche width across all individuals), and have the largest between individual niche component, indicating stronger specialization on the phenotype level, compared with freshwater residents and anadromous pike (Figure 8 E). Anadromous pike show a large niche space in both total niche width and within individual niche components, along with a small between individual component, suggesting strong generalization in multidimensional niches (Figure 8 E). Freshwater residents were constrained in both niche axes, with some overlap with anadromous pike, but a larger between individual niche component, suggesting moderate specialization (Figure 8). The multidimensional niche of freshwater residents is highly displaced from the total population niche, suggesting this phenotype may be strongly isolated in both axes.

These results confirm the notion of **paper VI** and **VII**, that the behavioral phenotypes use distinct subsections on the scenopoetic and bionomic niche axis of the metapopulation and show specialization both in habitat as well as in diet. High overlap of brackish residents and cross-habitat pike in bionomic and scenopoetic niche axes suggest potential for intraspecific competition, which likely led to high individual specialization. Anadromous pike and freshwater residents show low overlaps relative to their niche widths (Figure 8 E, Figure 9 E), indicating low potential for competition. My results also indicates a strong covariance between these two niche axes. There are two possible explanations: First, resource specialization (bionomic niche axis) may be facilitated by habitat specialization. For example, pike individuals adapted to reproduce in brackish habitats, which could be referred to as brackish “habitat specialists” (sensu Rosenzweig, 1974), gain access to marine resources and abundant marine prey. This would drive divergence and specialization in bionomic niche. Second, the scenopoetic specialization may be driven by the bionomic specialization. Using the same example of brackish resident pike, individuals that are specialized to exploit marine resources pulses would have to seek out habitats where those resources occur, typically higher saline open lagoons. Adaptating to the high and fluctuating salinity of such habitats would then drive divergence in scenopoetic niche. This presents a “chicken or the egg” dilemma, where the direction of the interaction cannot be easily determined (Costa-Pereira & Shaner, 2025). Given the negative effects of higher salinity on individual growth of pike across all behavioral phenotypes, it appears more likely that pike are not entirely specialized on high-saline, and rather trade off the foraging specialization on energy-rich marine prey against the osmoregulatory costs. However, disentangling these two mechanisms lay outside the scope of the thesis, as it would require common-garden or lab-controlled experiments. However, since they are not mutually exclusive (Costa-Pereira & Shaner, 2025), it seems plausible that a combination of both led to the observed patterns. Further, the interaction and covariance between scenopoetic and bionomic niche of the pike metapopulation agrees with the theoretic predictions by Costa-Pereira & Shaner (2025), further underlining the importance of an integrative view of multidimensional niches to approach the quantification and understanding of n-dimensional niches as idealized by Hutchinson (1957).

Table 3. Effect sizes of fixed predictors on combined scenopoetic and bionomic resource specialization. SE: Standard error; SD: Standard deviation; Significant effects are shown in bold. Naïve SE refers to the standard error calculated without accounting for the autocorrelation of the Markov chains. Time series SE is the standard error calculated with considering the autocorrelation in Markov chains. Effective sample size refers to the number of accepted draws from the joint posterior distribution

Individual scenopoetic specialization index + Individual bionomic specialization index

Predictors	**Posterior mean estimate (± SD)**	**Naive SE**	**Time-series SE**	**Effective sample size**	**p-value**
Intercept	**0.42 (0.03)**	**0.0009**	**0.0009**	**910.7**	**< 0.001 *****
Phenotype [freshwater resident]	**-0.25 (0.01)**	**0.0004**	**0.0004**	**1000.0**	**< 0.001 *****
Phenotype [brackish resident]	**-0.26 (0.03)**	**0.0007**	**0.0007**	**1000.0**	**< 0.001 *****
Phenotype [cross-habitat]	**-0.23 (0.02)**	**0.0005**	**0.0005**	**907.1**	**< 0.001 *****
Waterbody [NRBC]	**-0.04 (0.01)**	**0.0005**	**0.0005**	**801.9**	**0.008 ****
Waterbody [WRBC]	**-0.05 (0.02)**	**0.0005**	**0.0005**	**837.6**	**< 0.001 *****
Waterbody [Tributary]	-0.01 (0.02)	0.0006	0.0006	1000.0	0.714
sex [male]	0.02 (0.01)	0.0003	0.0003	1000.0	0.086 .
lifeyear	-0.00 (0.00)	0.0000	0.0000	1484.0	0.368
Total length (mm)	**-0.00 (0.00)**	**0.0000**	**0.0000**	**1008.3**	**0.002 ****

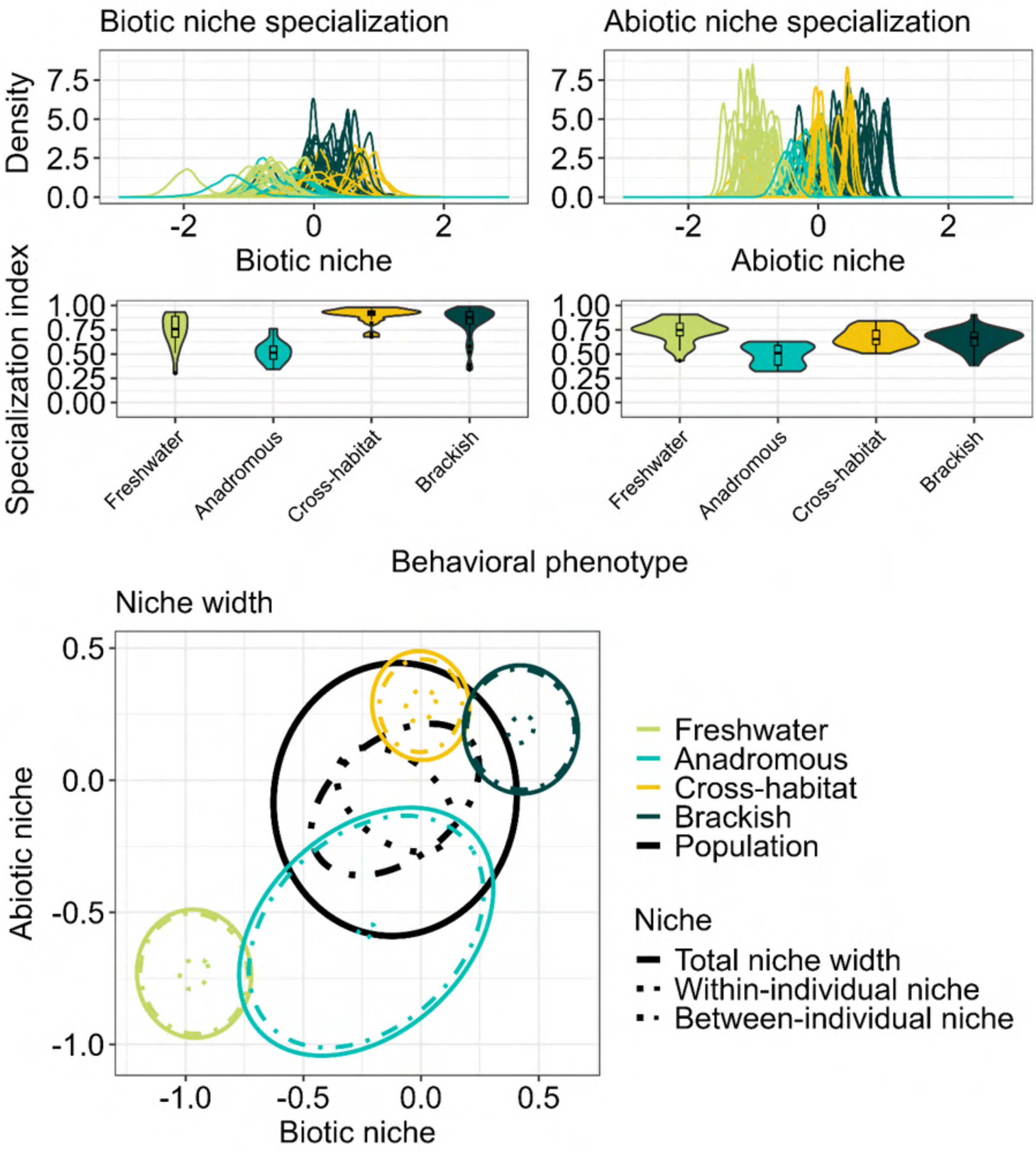

Figure 8. Niche components of pike sampled in the Bodden lagoons and adjacent tributaries between July 2019 and May 2022. Upper two panels: Individual phenotypic distribution along bionomic (A, N = 83 pike) and scenopoetic (B, N = 120 pike) niche axes. Mid two panels: Mean individual specialization index of the behavioral phenotypes for (C) Bionomic niche axes, and (D) scenopoetic niche axes. Lower panel (E) Total niche width (TNW), within-individual niche variance (WIC) and between-individual niche variance (BIC) along combined bionomic and scenopoetic niche axes on population-level (black-colored circles, and behavioral phenotype level (multicolored circles).

Similar to the question of shared resource surfaces in **paper VII**, resources and environmental factors vary stochastically in space and time. Not all individuals from a population may have access to the same subsections of the total n-dimensional population niche, in particular in spatiotemporally complex metapopulations, as is the case for Bodden pike (**paper VII**, Newsome et al., 2007). Systematic differences between subpopulations (in body size, environmental conditions, resource availability) from different lagoons in my study system may bias inferences on drivers of niche variation (Marshall 2024). It is therefore crucial to account for differences in spatiotemporal distribution of the analyzed individuals (Costa-Pereira & Shaner 2024). I therefore repeated the multidimensional niche analysis with a subset of pike where I accounted for these confounding factors. Results from **paper VI** and **VII** indicated significant effects of both total length and capture area, suggesting these variables need to be accounted for. I therefore constrained the second analysis to one Bodden lagoon (WRBC) and one tributary (Sehrowbach, which drains into the WRBC), complementing this with pike from Barthe river to represent freshwater residents, which were not present in river Sehrowbach. The analysis was then conducted with 20 freshwater resident individuals, 12 anadromous pike, 14 cross-habitat pike and 21 brackish residents. I constrained my sample to the same length range across all phenotypes. The results remained largely unchanged by these constraints (Figure 9). Brackish residents and cross-habitat pike still showed the highest individual bionomic niche specialization and, alongside freshwater residents, the highest individual scenopoetic specialization (Figure 9 C, D). On a phenotype level, niche shape and displacement are similar to the first analysis, however, the brackish residents were more displaced from the population niche, suggesting stronger specialization of WBRC brackish residents (Figure 9 E). Niches of brackish residents and cross-habitat pike show similar overlap and are constrained compared to the other phenotypes. Freshwater residents show a displaced and moderately constrained niche in both dimensions. Anadromous pike appear as true generalists, with a wide niche space along both resource and condition axes (Figure 9 E). These results, and the low effect sizes of the confounding factors in multi-response GLMMs (Table 3), indicate that the patterns found in the analysis of the whole sample are robust against confounding effects of capture location and differences in body size.

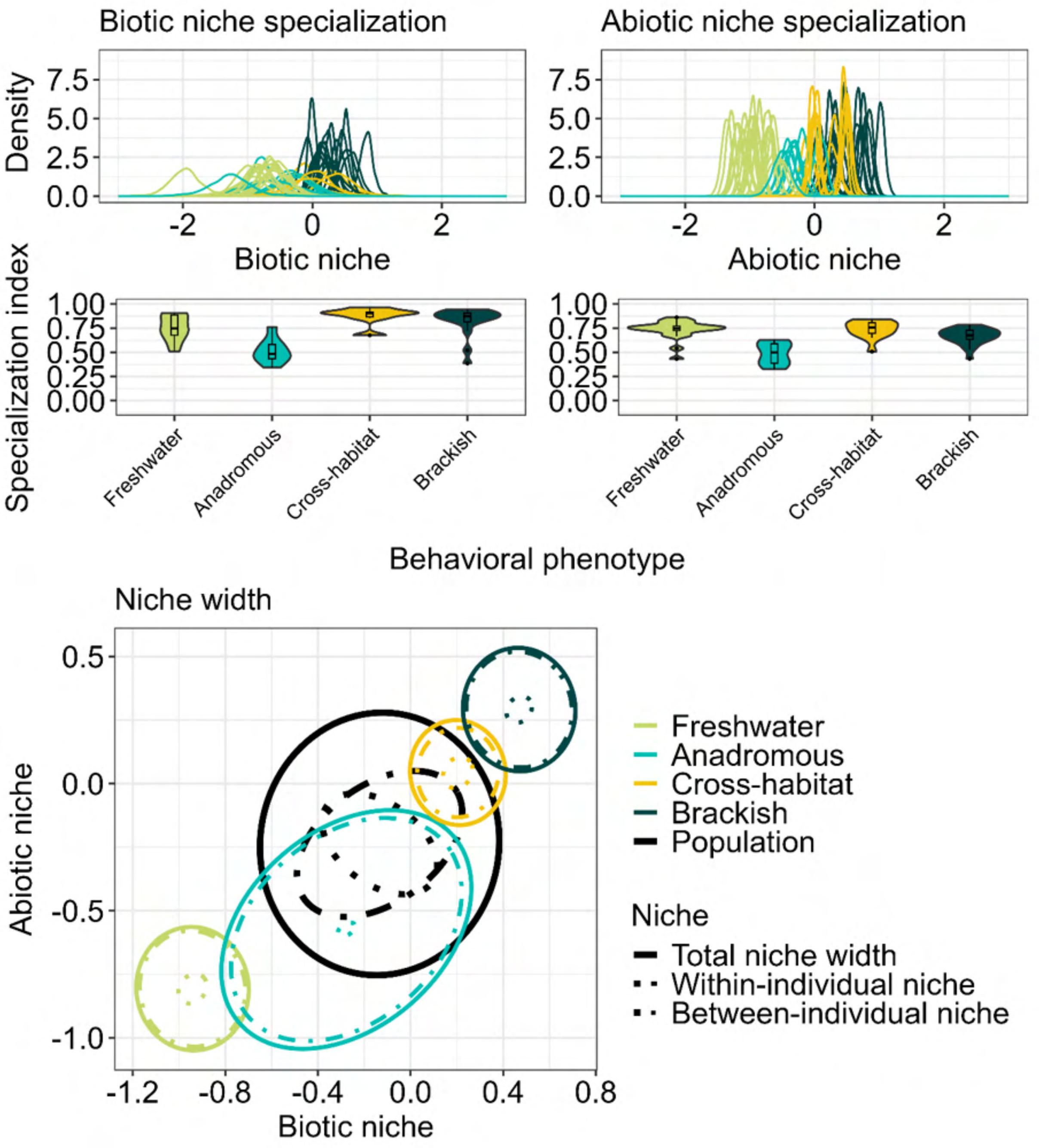

Figure 9. Niche components of pike sampled in the WRBC (N = 26), Sehrowbach (N = 17) and river Barthe (N = 23) between July 2019 and May 2022. Upper two panels: Individual phenotypic distribution along bionomic (A, N = 45) and scenopoetic (B, N = 66) niche axes. Mid two panels: Mean individual specialization index of the behavioral phenotypes for (C) Bionomic niche axes, and (D) scenopoetic niche axes. Lower panel (E) Total niche width (TNW), within-individual niche variance (WIC) and between-individual niche variance (BIC) along combined bionomic and scenopoetic niche axes on population-level (black-colored circles, and behavioral phenotype level (multicolored circles).

Cross-habitat pike displayed the strongest individual resource and condition specialization amongst all behavioral phenotypes (**paper VII**, Figure 8, Figure 9). This strong divergence in both central niche axes, and resulting isolation by environment likely explains the divergence of this ecotype. My results suggest the niche divergence and evolution of the cross-habitat ecotype are likely due to intraspecific competition in combination with large-scale anthropogenic interference. Cross-habitat pike show limited freshwater reliance and consist of a genetic mixture of brackish and anadromous genotypes, suggesting that this phenotype may be a response to the large-scale habitat blockage in the 1960s and 70s (**paper VI**). The loss of a large part of their spawning habitat may have driven formerly anadromous pike to use the still present freshwater influence at the blocked tributaries, presenting a spawning habitat that necessitates adaptations to spawning in intermediate salinities. Resource and habitat competition from spatiotemporally overlapping brackish residents then likely led to the high individual specialization and constrained niche space of this phenotype. Similarly, the presence and competition by a potentially newly developed cross-habitat ecotype may have constrained the niche of brackish residents, explaining the high multidimensional specialization of this phenotype. Anadromous pike, meanwhile, only experience partial spatiotemporal overlap with other phenotypes, which explains their wide resource and condition niche, as well as the low individual specialization. Freshwater residents show little overlap in space or time with any other behavioral phenotype, and would therefore be expected to have a wide niche. However, the constrained niche I found for this phenotype, and the unexpectedly high individual bionomic and scenopoetic specialization, suggests some mechanism may have constrained the multidimensional niche of freshwater residents (Costa-Pereira & Shaner, 2025).. This might be competition within tributaries, however, given the findings on habitat quality, in particular the potential of hypoxia (**paper VII**), resource limitations seem more plausible as mechanism to constrain the niche of this phenotype (Beaudoin et al., 1999). Confirming the results of **paper VII**, my results indicate a population that is generalized along both bionomic and scenopoetic niche axes, but is highly heterogenous on individual level, providing strong empirical support for the niche variation hypothesis (Valen 1965; Bolnick *et al.* 2007).

6.5. Consequences for growth on individual and population level

I modelled growth on phenotype-, genotype-, and ecotype-level in both **paper VI** and **paper VII**. I will focus on the findings on phenotype-level in this thesis, as behavioral phenotypes are the level at which individuals interact with their environment, so growth effects are expected to be strongest (Goodrich & Clark 2023). I detected significant differences in age-specific growth between the behavioral phenotypes in **paper VI** and **paper VII**. Cross-habitat pike, and to a lesser extent, anadromous pike, grew faster in juvenile stages, compared to freshwater and brackish residents in **paper VI**, a result also seen in **paper VII**. However, both freshwater and brackish resident growth increased in later years, likely owing to habitat shifts and resource specialization (**paper VII**) fostering compensatory growth. The age-specific growth effects were also related to temperature, (positive effect), in particular in early life, and high salinity (negative effect), at all life stages (**paper VI**). I further detected significant positive effects of $\delta^{34}S$ on growth rates of pike in **paper VII**, which are likely attributable to marine resource specialization. Pike foraging in brackish habitats, especially individuals specialized on migratory herring, likely benefitted from the higher energy density of herring compared to other prey fish (herring = 24.4 MJ/kg, compared to next highest, roach = 20.8 MJ/kg). However, the positive effect of $\delta^{34}S$ on growth was likely also influenced by scenopoetic components. For freshwater residents and anadromous pike, increases in $\delta^{34}S$ marked habitat transitions from oxygen-limited to well-oxygenated habitats, potentially inducing compensatory growth (Ali *et al.* 2003). This might explain why I was not able to detect any differences in lifelong growth between the behavioral phenotypes (**paper VI**), which suggests roughly equal fitness potential between phenotypes (Haugen *et al.* 2006). Similar lifelong growth in spite of different age-specific growth indicated fundamental phenotype-specific trade-offs that are associated with individual specialization (**paper VI**, **IV**, **chapter 6.4.**). Similar lifelong growth performance and lifelong fitness may be an important mechanism for coexistence of the behavioral phenotypes (Kobler *et al.* 2009), and ultimately, the ecotypes that express them (Brown, 1990).

Freshwater residents grow up in osmotically stable and warm habitats, but may experience periods of low water levels, anthropogenic nutrient inputs and oxygen limitation (**paper VII**), along with potential resource limitation in heavily modified tributaries (Rohtla et al., 2012; **paper II**, **chapter 6.4.**). This leads to slow early growth, however, upon the habitat switch into well-oxygenated habitats, freshwater residents likely show compensatory growth, and are not affected by high osmoregulatory costs in brackish habitats (**paper VI**).

Anadromous pike share the warm and stable low oxygen tributary habitat, but shift to brackish habitats at small size (~ 20 cm TL), inducing compensatory growth, while also gaining access to the productive lagoons, leading to fast early growth (**paper VII**). This would be consistent with results from other fishes expressing migratory phenotypes (Chapman et al., 2011 a,b; Ferguson et al., 2019). However, anadromous pike, as part of the migratory flexible freshwater ecotype (**paper VI**), are likely less adapted to high salinities (**paper VI**), explaining the slower adult growth. Additionally, anadromous migrations to the few tributaries that are still open may prove energetically costly and bear heightened risk of predation and harvest (Haugen et al., 2006), reducing growth and removing fast-growing individuals (Biro & Post 2008).

Cross-habitat pike likely hatch in sheltered freshwater-adjacent bays and lower reaches, offering a warm, low saline nursery habitat (**paper VI**), with full access to marine resources (**paper VII**), leading to fast early growth (**paper VI**, **paper VII**). This phenotype likely also avoids the energetic cost of long migrations into tributaries by spawning in river mouths or adjacent sheltered bays (**paper VI**). This explains the high juvenile growth rates, however, it is not immediately clear why growth levels out with those of other phenotypes later in life. There are two possible explanations for this observation. The first is hinted at by the low number of older cross-habitat individuals in **paper VI**, suggesting a phenotype with fast life-history and high adult mortality (Robert *et al.* 2023). The second is indicated in **paper VII**, as cross-habitat individuals show a lower reliance on the marine food web in adult stages adults than brackish residents. Cross habitat pike might therefore benefit less from growth benefits through marine resources, but are also affected by the negative effects of high salinity, diminishing adult growth performance. It is possible that both these mechanisms work synergistically, reducing the adult growth of cross-habitat pike, thus enabling the other phenotypes to compensate for growth deficits in early life.

Lastly, slow early-growth of brackish residents may be explained by juveniles growing up in high salinity brackish habitats that do not offer significantly warmer temperatures and impose high osmoregulatory costs (**paper VI**), thereby limiting juvenile growth, despite access to the productive lagoons and evident use of marine resources (**paper VII**). Adult growth of brackish residents is likely also limited by high energetic demands in habitats of fluctuating salinity (**paper VI**). However, being adapted to high salinity brackish habitats, this phenotype shows the strongest specialization on marine resources, in particular herring (**paper VII**). As brackish residents become older and grow larger, osmoregulatory capacity increases simultaneously with assimilative capacity (Varsamos *et al.* 2005; Werner 1988; Werner & Gilliam 1984), enabling stronger specialization on energy-rich marine resources, such as the resource pulses offered by migratory herring (**paper VII**). This may lead to consistently high adult growth rates, enabling this phenotype to compensate for the early growth deficits. This, along with the fact that the oldest and largest individuals in my sample were brackish residents, also hints at a slower life history, where early life fitness is traded off against benefits in later life. This can lead to larger terminal size than individuals with faster pace of life and lower life expectancy, even if growth rates are similar (Robert *et al.* 2023).

Multidimensional individual niche specialization (**chapter 5.4**) had no significant effects on individual growth performance, consistent with **paper VI**, which also showed no difference in lifelong growth of the behavioral phenotypes. This adds to the evidence for the hypothesis that the similar lifelong growth detected in **paper VI** may be a mechanism of coexistence, where niche variation and specialization along both bionomic and scenopoetic niches axes enable similar lifetime growth and fitness.

7. Methodical limitations

The limitation of non-random sampling of behavioral phenotypes across the region may have introduced a confounding factor of systematic variance between the studied Bodden lagoons and subpopulations. I addressed this limitation in a number of ways. In **paper VI**, I condensed the multiple clusters identified by the DTW algorithm based on capture location and transect shape, to reduce the number of clusters and adjoin clusters with similar lifelong thermosaline patterns that were only separated due to differences in mean temperature or salinity between locations. I further demonstrated that the same set of behavioral phenotypes exist sympatrically in lagoons with different environmental conditions, and detected a strong structuring of behavioral phenotypes along the salinity gradient. I was able to show that resource use differed between phenotypes on the level of lagoons and tributaries used by different phenotypes as shared foraging grounds, and that effects of phenotype on resource use in p-space was much stronger than the effect of capture location (**paper VII**). Furthermore, despite having a significant influence on individual multidimensional niche specialization, the effect size estimated for capture location was one order of magnitude smaller than the effect of behavioral phenotype. Lastly, the analysis outlined in **chapter 6.4.**, demonstrated that the patterns in individual specialization and behavioral phenotype-level niche components along bionomic and scenopoetic niche axes remained unchanged when only fish from a specific region (WRBC and Sehrowbach, which drains into the WRBC) were considered along the same length gradient. These findings suggests that the differences between individual niches are mainly driven by the behavioral phenotypes expressed by the three pike ecotypes in my study system.

8. Management implications

From a management perspective, my results underline the necessity of quality assurance and control in deriving life-history parameters and niche metrics in fish, and the importance of accurate age estimation for fisheries management. I identified the promotion and retention of behavioral and genetic diversity in the system as a promising avenue to increase the productivity of pike stocks. The finding of multiple distinct ecotype subpopulations with different ecological niches has important implications for management and conservation of pike in the region. The conservation of phenotypic diversity within fish populations can increase the resilience of a species to environmental disturbances through the portfolio effect (Kerr et al., 2010; Schindler *et al.* 2010). However, conservation of the ecotype subpopulations may necessitate adaptive localized management interventions (Lukyanova et al., 2024). Habitat restoration and improved connectivity between lagoons and freshwater tributaries would likely benefit the freshwater ecotype, in particular the rare anadromous phenotype. The cross-habitat ecotype would likely also benefit from increased connectivity between lagoon and freshwater habitats, as some individuals from this ecotype used lower reaches of tributaries for spawning. However, increasing spawning habitat for these two ecotypes may lead to negative density-dependent feedback through increased competition and cannibalism, so increasing the foraging habitats in the lagoons by restoring historical wetlands may be a necessary complementary measure to ensure higher productivity. This may also benefit brackish resident pike, as coastal wetlands are productive, high quality spawning areas for pike (Nilsson et al., 2013), and have been shown to increase pike abundance in adjacent coastal areas (Tibblin et al., 2023). The increase in shoreline complexity introduced by such restoration projects would likely additionally increase pike productivity, as sheltered coastal bays have been shown to be an important reproduction habitat for brackish-spawning pike in Finland (Pursiainen et al., 2021).

The findings on resource specialization of the different phenotypes also has important consequences for the management of Bodden pike. Strong individual specialization on particular resources may allow a population to maintain larger population sizes and phenotypic diversity than a generalist population (Bolnick et al., 2007; van Valen 1965), but this also implies that the specialized individuals and phenotypes are vulnerable to changes in the abundance of their preferred prey (Bolnick et al., 2003). Resource pulses from migratory herring were shown to be a major resource for pike growth and productivity, alongside other marine resources. Therefore, conservation of Bodden pike needs to consider the food web interactions identified in my thesis. The current decline of migratory herring (Polte et al., 2021) could have negative consequences on the productivity and diversity of the pike population. To increase the amount of trophy pike in the population in order to increase angler satisfaction, a potential management option would be to ensure that pike consistently reach sizes at which they can specialize on marine resources (approximately 85 cm in brackish residents). This may be achieved by installing a harvest slot for the pike fishery, to reduce mortality at larger sizes. In addition, any management measures that increase the abundance of migratory herring in the lagoons would likely also benefit the growth and terminal size of the pike in the Bodden. Lastly, reducing fishing mortality of migrating pike, both on spawning migrations as well as for potential foraging migrations, such as seasonal or permanent marine protected areas as well as net-free corridors could be an important step to increase productivity and growth of Bodden pike. In summary, improving the abundance and size of Bodden pike calls for adaptive, localized management approaches that explicitly consider the genetic and phenotypic diversity of the pike metapopulation and its various ecological specializations.

9. Conclusion

Beek flowing into the Bodden, photo credit: Dominique Niessner

The objective of my doctoral research was to assess the abiotic and biotic niche variations in coastal pike inhabiting the Bodden lagoons in the Southern Baltic sea around Rügen island, and disentangle their effects on growth as an indicator of fitness. I evaluated methods to assess growth and infer niche use in my specific study system, and used a combination of environmental proxies measured in pike otoliths and dietary tracers measured in muscle tissue and sequential eye lens laminae to assess habitat and resource use. I found higher phenotypic and genetic divergence in pike than was expected from previous research. I confirmed a previously described freshwater phenotype as an ecotype and described a new, so far undetected ecotype, the cross-habitat pike. I identified salinity and anthropogenic habitat alteration as important drivers behind the ecotype evolution, structuring the metapopulation along the salinity gradient of the Bodden lagoons. Differences in age-specific growth but similar lifelong growth suggested fundamental tradeoffs associated with specific life histories of the ecotypes, which, along with habitat and resource partitioning, likely facilitated their coexistence. I detected strong individual specialization in a seemingly generalist population of pike, which are commonly described as opportunistic, providing further empirical support for the niche variation hypothesis. Marine resources, in particular migratory herring, were a major driver of specialization along the bionomic niche axis, likely boosting growth through higher energy contents compared with other prey. I assessed population- and individual-level specialization of pike along both scenopoetic and bionomic niche axes, providing one of the first in-situ assessments of a true n-dimensional niche. The main conclusions of my research can be summarized as follows:

1. The validity of age estimation and environmental proxies for growth and niche analysis must be assessed for each new species and system, alongside individual-level ontogenetic and physiological confounding factors, otherwise results will be biased.
2. The pike population around Rügen island can be divided into four behavioral phenotypes that show different abiotic and biotic niche use. Genetic differentiation between three of the four behavioral phenotypes indicated evolution of three distinct, reproductively isolated ecotypes, namely brackish residents, cross-habitat, and a freshwater ecotype that displays facultative anadromy.
3. The four behavioral phenotypes expressed by the three ecotypes differ in their individual specialization along bionomic and scenopoetic niche axes, but not in their lifelong growth performance, suggesting similar growth and fitness potential through resource and habitat partitioning as mechanism for sympatric coexistence.
4. The emergence of the cross-habitat ecotype and the low abundance of the anadromous behavioral phenotype, along with the indications of oxygen limitation in tributaries point towards a significant influence by anthropogenic habitat alteration. The cross-habitat phenotype is likely an evolutionary response to strongly reduced connectivity between lagoon

and freshwater habitats, which likely led to the low abundance of anadromous pike through local extinction. Further, juvenile growth of tributary-reliant behavioral phenotypes is likely hampered by low habitat quality in heavily modified streams.

5. Pulsed marine resource subsidies, in particular by migratory herring, play an important role for growth and coexistence of pike ecotypes in the region, and generate energetic links between the marine, lagoon and freshwater food webs in the Bodden lagoons.

The finding of multiple distinct ecotypes which differentiate in abiotic and biotic niche use, life history strategies, and migration tendencies is a finding both relevant for fundamental science and management. On the fundamental side, this further strengthens ecological theories on niche variation and specialization driving diversification and, ultimately, speciation. It offers a case study of multidimensional niche use of an animal population in the wild, where the findings on individual specialization and competition match up with ecological theory. Populations of fish contain high levels of individual variation, which need to be acknowledged and considered when managing a species. Findings from other fishes all over the world indicate that this phenomenon is likely ubiquitous. The presence of distinct subpopulations that are starkly different in their migration and feeding ecology has far-reaching implications for management. It indicates that we need a paradigm shift in how management thinks about fish populations and metapopulation structuring. Further, my results challenge the dichotomous categorizations that are prevalent in fish science. There is more to fish phenotypic diversity than migratory or non-migratory, benthic or pelagic, freshwater or marine. It is more likely that each individual in a fish population inhabiting a variable environment falls on a continuum of different behaviors, adaptations and specializations. Therefore, we need to rethink how we assess fish populations, and make the individual count.

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11. References

the battle of Mursewiek, photo credit: Phillip Roser

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Declaration of authorship

I hereby declare that I have written this dissertation independently and have used only the sources and aids indicated, and that the dissertation has not been submitted to any other institution for the purpose of obtaining a doctoral degree. Additionally, I confirm that when using AI-based tools, I have listed these tools in the section "Overview of Tools Used" below, including the product name and version number, my source of access, and details on usage. In preparing this work, I have consistently worked independently and exercised control when using AI-based writing tools. I acknowledge having read the doctoral regulations of the Faculty of Life Sciences at Humboldt University of Berlin that underlie this process.

Ich versichere, dass ich die vorliegende Dissertation selbständig verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel verwendet habe, und die Dissertation an keiner anderen Institution zur Erlangung des Doktorgrades eingereicht wurde. Zusätzlich versichere ich, dass ich beim Einsatz von KI-gestützten Werkzeugen diese Werkzeuge in der unten genannten „Übersicht verwendeter Hilfsmittel“ mit ihrem Produktnamen und der Versionsnummer, meiner Bezugsquelle und Angaben zur Nutzung vollständig aufgeführt habe. Bei der Erstellung dieser Arbeit habe ich durchgehend eigenständig und beim Einsatz KI-gestützter Schreibwerkzeuge steuernd gearbeitet. Ich erkläre die Kenntnisnahme der dem Verfahren zugrunde liegenden
Promotionsordnung der Lebenswissenschaftlichen Fakultät der Humboldt-Universität zu
Berlin.

Berlin, 07.10.2024

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Timo Dustin Rittweg

Overview of Tools Used:

- Product name: ChatGPT (GPT-4)
    - version GPT-4 (October 2023 version)
    - Source of access: https://chat.openai.com
    - Usage: Translation of English abstract into German, followed by manual overhaul, translation of the template text for the declaration of KI usage of the Albrecht Daniel Thaer-Institute of Humboldt-Universität zu Berlin into English

Übersicht verwendeter Hilfsmittel:

- Produktname: ChatGPT (GPT-4)
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    - Bezugsquelle: https://chat.openai.com
    - Anwendung: Übersetzung des englischen Abstracts in die deutsche Sprache, mit nachgehender manueller Überarbeitung, Übersetzung des deutschen Vorlagetextes zur Eigenständigkeitserlärung KI des Albrecht Daniel Thaer-Instituts der Humboldt-Universität zu Berlin in die englische Sprache

Appendices

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Paper I

I

Robert Arlinghaus, Timo Rittweg, Félicie Dhellemmes, Dieter Koemle, Rob van Gemert, Hendrik Schubert, Dominique Niessner, Sören Möller, Jan Droll, René Friedland, Wolf-Christian Lewin, Malte Drow, Linda Westphal, Elias Ehrlich, Harry V. Strehlow, Marc Simon Weltersbach, Phillip Roser, Marlon Braun, Fritz Feldhege, Helmut Winkler, 2023, A synthesis of a coastal northern pike (*Esox lucius*) fishery and its social-ecological environment in the southern Baltic Sea: Implications for the management of mixed commercial-recreational fisheries, Fisheries Research, 263: 106663.

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A synthesis of a coastal northern pike *(Esox lucius)* fishery and its social-ecological environment in the southern Baltic Sea: Implications for the management of mixed commercial-recreational fisheries

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ABSTRACT

We synthesize a large body of literature involving peer-reviewed work, grey literature and novel data analyses about the small-scale northern pike (*Esox lucius*) fishery in lagoon ecosystems in the southern Baltic Sea. Based on our comprehensive review that synthesizes ecological as well as social, economic and governance-related literature we derive implications for the management of mixed commercial-recreational fisheries in coastal areas. The interconnected shallow and biologically highly productive meso- to polytrophic lagoons (extension about 2000 km^2) bordered by the peninsula of Fischland-Darß and the islands of Hiddensee, Rügen and Usedom in the southern Baltic Sea of Germany constitute an oligo- to mesohaline transitional habitat suitable for colonization by a range of freshwater fishes, including pike. In the Rügen area, pike successfully recruits in the mesohaline lagoons, but anadromous subpopulations and freshwater residents also exist in tributaries, forming a connected meta-population. The stock is co-exploited by a small-scale commercial fishery and a largely tourism-dominated recreational fishing sector that, depending on the angler type, values the pike for both consumption as well as for its trophy size. The recreational sector has risen in economic and social relevance since the German reunification in 1990 and today removes similar amounts of biomass than commercial fisheries. Pike is a prime target species of anglers, and recreational pike angling in the lagoons today generates a larger economic impact in terms of jobs created compared to the commercial pike fishing, where pike is typically one target among many freshwater fish. Stock assessments and stakeholder reports have revealed that the stock size and size of pike in the catch have been falling since 2010, fueling conflicts among fishers and anglers for space and fish. Reasons for the current decline of the pike stock involve multiple pressures operating jointly and possibly synergistically, such as local overharvest, loss of stock structure through past blocking of freshwater streams, eutrophication and macrophyte loss, predation mortality by natural predators, reduced availability of marine prey through declines of western Baltic spring-spawning herring (*Clupea harengus*), and poorly understood impacts of climate change. The

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assessment of current fishing mortality suggests a the stock stock is size/quality-overfished from the perspective of anglers, and fully exploited to slightly growth-overfished when judged against the reference point of maximum sustainable yield. The current biomass trend is negative. The current instantaneous fishing mortality rate, F, is estimated to range between 0.2 and 0.4 yr^{-1}. Hence, fishing cannot be the sole culprit of the current stock decline because the current fishing mortality rates are too high for the underlying productivity, but not excessive. Because the current fishery no longer meets the expectations of recreational anglers, and angler numbers have recently declined, if the aim is to also suit anglers, reductions of fishing mortality would be useful in recovering the stock and fishing quality, coupled with restoration of access to flooded wetlands as spawning and nursery grounds, and control of other mortality sources of pike (e.g., cormorants). However, whether such actions indeed rebuild the fishery remains uncertain because of the potential for compensatory natural and fisheries mortality and other environmental changes affecting recruitment and abundance negatively. Policy makers may want to solve the allocation problem among commercial and recreational fisheries, install a robust monitoring system and a management framework that is inclusive of multiple perspectives and objectives and adaptive to novel productivity regimes and further structural changes in the mixed fishery. Further research on climate change impacts, food web changes, impacts of natural predators such as seals, cormorants or stickleback, and the behavioral and socio-economic aspects of commercial and recreational fisheries is warranted.

1. Introduction

Coastal fisheries are globally relevant, making important contributions to food security and recreation (Palomares and Pauly, 2019). Coastal ecosystems integrate a range of anthropogenic influences related to coastal development, tourism, mining of terrestrial and marine resources, recreational activities, navigation, pollution, eutrophication, climate change, invasive species and fisheries exploitation (Cheung et al., 2010; O'Higgins and O'Dwyer, 2019; Duarte et al., 2020; Jackson et al., 2001). Given their vulnerabilities to a range of anthropogenic activities and the poor state of aquatic biodiversity, coastal ecosystems are key targets for conservation (Jackson et al., 2001; Hilborn, 2016).

One marine ecosystem that is affected by multiple anthropogenic pressures is the Baltic Sea (Reusch et al., 2018), a semi-enclosed post-glacial sea with a surface of 415,000 km^2 that is characterized by a strong salinity gradient from marine salinity (35 Practical Salinity Units, PSU) in the entrance in the west to near freshwater (< 2 PSU) in the innermost parts in the northeast (Snoeijs-Leijonmalm and Schubert, 2017; Bäck et al., 2020). The Baltic Sea originates from a freshwater lake; the now brackish environment is only 8.000 years old (see Box 1 in Reusch et al., 2018). Along the salinity gradient of the Baltic Sea marine species drop out and are progressively replaced by freshwater species (Ojaveer et al., 2010). One of the freshwater species that is common within lagoons, bays and estuaries along the entire Baltic coast is the northern pike (*Esox lucius*) – a circumpolarly distributed top predator in freshwater systems (Raat, 1988; Craig, 1996; Skov and Nilsson, 2018) that occurs either as a mesopredator (when mammals and fish-eating birds are present) or as a top predator also in coastal zones of brackish ecosystems of North America and Eurasia with upper salinity levels for adult survival of about 18 PSU (Dahl, 1961). Across its distributional range, the species has high fisheries value, particularly for recreational anglers (Crane et al., 2015; Arlinghaus et al., 2018) and regionally for commercial fisheries (Kuparinen and Lehtonen, 2018).

The Baltic Sea and associated inshore areas and lagoons have historically experienced overfishing (Reusch et al., 2018; Opitz and Froese, 2019; Möllmann et al., 2021). Together with multiple other stressors related to warming, eutrophication, oxygen depletion, and acidification, anthropogenic pressures have reduced the abundance of many once abundant commercially relevant species, in some cases resulting in collapses and regime shifts towards low productivity states as in the case of Baltic cod (*Gadus morhua*) (Sguotti et al., 2019; Möllmann et al., 2021) and Western Baltic spring-spawning herring (*Clupea harengus*) (Polte et al., 2021). Similar developments have been reported for several freshwater species in the Baltic Sea coast (Olsson, 2019; Olsson et al., 2023). Discourses about the recent decline of marine demersal and pelagic fish in the Baltic Sea, specifically cod and herring, dominate the scientific and public attention due to their high economic importance. Largely unnoticed by many, there are also increasing reports of declines of the freshwater fishes that inhabit brackish coastal ecosystems and other oligo- to mesohaline estuarine ecosystems in the Baltic Sea, including Eurasian perch (*Perca fluviatilis*), pike-perch (*Sander lucioperca*) and pike (Olsson, 2019; Olsson et al., 2023). Specifically for pike, multiple causes underlying the decline in the central and southern Baltic Sea (Olsson et al., 2023) are discussed, including predation of eggs and larvae by small-bodied mesopredators (Nilsson et al., 2014, 2019; Eklöf et al., 2020), predation losses by cormorants and seals (Bergström et al., 2022), loss of spawning habitats in freshwater streams (Engstedt et al., 2018; Psuty, 2022; Psuty et al., 2023), vegetation loss in lagoons through eutrophication (Lehtonen et al., 2009; Winkler and Debus, 2006), warming (Berggren et al., 2022) and overfishing (Larsson et al., 2015). For many areas and species, however, the lack of long-term monitoring precludes precise status assessments of freshwater piscivores striving in inshore brackish areas and the underlying reasons of population declines (Olsson, 2019; Olsson et al., 2023).

In most economically developed countries, where subsistence fisheries are rare or absent, key conflicts over access to coastal fish stocks revolve around joint exploitation of stocks by commercial and recreational fisheries (Kearney, 2002; Boucquey, 2017; Arlinghaus et al., 2022). Freshwater top predators in coastal ecosystems of the Baltic Sea have traditionally been exploited by commercial fisheries (e.g., Schlumpberger et al., 1966). Yet, freshwater fish targeted in oligo- to mesohaline brackish areas never had the same social and economic importance as other coastal and marine fish species, such as herring or cod, that co-occur in the same ecoregion (Henking, 1923; Rechlin and Fadschild, 1991; Döring, 2001). Recreational anglers also exploit freshwater fish stocks in brackish inshore ecosystems in the Baltic Sea (Basan 1988; Winkler, 1989; Döring, 2001; Larsson et al., 2015; Koemle et al., 2021). Depending on local culture, norms, and target species, recreational fishers may have strong harvest motives (Cooke et al., 2018; Nyboer et al., 2022) and compete with commercial fishers over access to the extraction of resources and space (Kearney, 2002; Arlinghaus et al., 2021, 2022). Some recreational fisher types receive high welfare from the catch of large fish or simply from high catch rates independent of harvest (Beardmore et al., 2015; Birdsong et al., 2021), a large portion of which might be voluntarily released (Arlinghaus et al., 2017a, 2021; Koemle et al., 2021). Yet, the practice of catch-and-release is not without its fair share of issues, including lethal and sublethal impacts (Arlinghaus et al., 2007a), or modification of fish behavior post release that reduce reactivity to fishing (Arlinghaus et al., 2017b; c). A characteristic pattern of high fishing mortality is the reduction in abundance, average size and catchability of the fish, which is why the optimal fishing mortality to please anglers is often smaller than the one that optimally accommodates commercial fisheries (Ahrens et al., 2020). Fishers and anglers may also overlap in space, which can induce mutual accusations of stealing or damaging gear, and generally cause interference competition among anglers and fishers (Arlinghaus, 2005). Importantly, if the combined harvesting pressure of anglers and fishers is sufficiently high, the average size of fish in the stock, the abundance and in turn the catches decline (Ahrens et al., 2020), which fuels further conflicts among recreational anglers and commercial fishers in discourses about optimal fishing mortality, including who to blame for stock declines and debates about the allocation of scarce fish among the two sectors (Arlinghaus et al., 2022). However, many stock declines are at least in part (e.g., Möllmann et al., 2021) and often also predominantly caused by environmental changes that are outside of control of the fisheries manager (e.g., Dekker, 2016; Carpenter et al., 2017). Even purely environmentally driven stock declines contribute to stakeholder conflicts especially when stock dynamics are poorly understood due to lack of monitoring or poor communication among scientists, agencies and stakeholders (Arlinghaus, 2005; Dedual et al., 2013; Arlinghaus et al., 2022). A decline of the stock sizes and of the average size of freshwater species in lagoon systems, such as pike, may aggravate the traditional conflicts with coastal commercial fisheries, particularly when the high-revenue or high-abundance marine species cod, herring or European eel (*Anguilla anguilla*) are declining in parallel or fishers suffer from large quota cuts (e.g., Dekker, 2016; Sugotti et al., 2019) within the Common Fisheries Policy of the European Union, as is presently the case in the southern Baltic Sea.

The present paper aims at synthesizing the historic and contemporary literature and unpublished data revolving around the ecology and exploitation of pike in the southern Baltic Sea, specifically in lagoon ecosystems bordered by the islands of Hiddensee, Rügen and Usedom in north-eastern Germany. We choose pike as a model for a freshwater fish that has colonized brackish ecosystems and that is a prime target for recreational fishers in North America, Europe and parts of Russia (Arlinghaus et al., 2018). At the same time, the species is targeted by commercial fisheries in the Baltic Sea and specifically around the German island of Rügen (Schlumpberger et al., 1966; Winkler, 1989; Arlinghaus et al., 2021). The fishery is considered data-poor due to the widespread lack of fish stock monitoring (van Gemert et al., 2022), and conflicts in the fishery are in part caused by knowledge gaps about the drivers affecting the pike stock (Arlinghaus et al., 2022). With our synthesis, we want to fill some knowledge gaps on the fishery for pike along the German Baltic coast. Although our review is focused on one species in one area, we think it has important lessons for other data-poor coastal and inland fisheries where multiple user groups co-exploit a joint stock. Importantly, we place our comprehensive synthesis in the ecological context of brackish lagoon ecosystems, review historical literature to describe fishery developments and synthesize ecological questions driving the dynamics of pike living “at the edge” of its osmoregulatory tolerance (Jacobsen et al., 2017a). Therefore, our multidisciplinary review advances our understanding not only about how coastal fisheries unfold, but also sheds light on the evolutionary potential of pike as an important model species in ecology and evolution (Forsman et al., 2015).

We had three objectives: 1) to present the state of knowledge from all available sources of information (peer-reviewed, grey literature, unpublished data) on the ecology and historical and present fisheries exploitation of northern pike living in lagoon ecosystems of Germany; 2) to evaluate the relative impact of various ecological and social drivers in directions that may stress northern pike in the future in the lagoons of the southern Baltic Sea, and 3) to derive policy and management recommendations as well as research gaps for the northern pike fisheries in lagoon ecosystems of the southern Baltic Sea.

2. General ecological features of the lagoon ecosystems in the southern Baltic Sea

Coastal brackish lagoons, and estuaries more generally, are transitional zones between marine and terrestrial ecosystems, occupying about 13% of the world’s coastline (Caumette et al., 1996; Kjerve, 1994). They host a rich native fauna and flora and serve as spawning and nursery grounds for migratory organisms of ecological and economic importance, including stenohaline freshwater fishes (Thiel, 1990). Along the southern Baltic Sea coast of Germany, the transitional brackish water bodies are named by a large variety of terms including Förde, Bodden, Haff, Wieck and Bucht, suggesting a classification behind each of them, but in fact most of these terms are just local names. Schlungbaum and Baudler (2001) presented a regional classification differentiating Förde (fjords), Bodden (a specific lagoon type, where the word “Bodden” originates from “Boden”, meaning ground, indicating the shallowness of the ecosystem) and Haff (a specific form of an estuary). Here we deal with the Bodden ecosystems (for a review of the ecology of such systems, see Schiewer, 2008), which are shallow brackish lagoons in the southern Baltic Sea in north-eastern Germany bordered by the peninsula of Fischland-Darss, and the islands Hiddensee, Rügen and Usedom (Fig. 1, Schiewer, 2008). All Bodden ecosystems (inner coastal areas) have a restricted connection to the Baltic Sea and therefore the salinity is lower than in the surrounding open coastline (outer or open coastal area) (Table 1). The sediments of the Boddens are typically soft, and the littoral zone is densely vegetated by emergent vegetation, specifically reed (*Phragmites australis*).

All Bodden ecosystems receive freshwater inflow from connected streams and rivers (Fig. 1). However, they are not typical estuaries (Schiewer, 2008) but rather ”choked”, ”restricted” or ”leaky” systems (Bird, 1982) with limited hydrodynamic exchange to the adjacent open sea (Kjerve, 1986; Schubert and Telesh, 2017). This is caused by the various islands and other land barriers that limit the direct connection of most Bodden lagoons to the open Baltic Sea (Fig. 1). Where a vast connection to the Baltic Sea exists, such as the Greifswalder Bodden, the inflow of the large River Oder contributes substantial freshwater inflow, keeping salinity levels below 8 PSU on average across the year. Coastal lagoon systems around the globe are often influenced by regular tidal regimes, creating a rhythmic variation of salinity, but the Bodden lagoons are different; they are characterized by microtides that are barely noticeable and result in stochastic salinity fluctuations at a very low amplitude (Oertl and Birr, 1995; Sagert et al., 2008). Thus, the seasonal variation in salinity are limited (often < 2–4 PSU) compared to the much more dynamic marine locations in the Baltic Sea (Oertl and Birr, 1995; Sagert et al., 2008; Schubert et al., 2017; Schiewer, 2008). However, a few lagoons with a close connection to the Baltic Sea and limited freshwater inflow (e.g., lagoons east in the Darß-Zingst-Bodden chain, DZBC, Fig. 1), offer more dynamic situations. There, salinity can fluctuate more strongly across the year due to inflow of water from the Baltic Sea through wind-induced hydrodynamics (see the standard deviations for salinity by lagoon area in Table 1).

The German Bodden lagoons addressed in the present paper cover about 2000 km^2 including and about 1300 km^2 excluding Stettiner Haff, which is the Oder estuary (Fig. 1). The lagoons are generally shallow, productive in terms of primary productivity (eutrophic to hypertrophic), polymictic brackish ecosystems with soft sediments and low to medium macrophyte coverage, depending on turbidity and hydrodynamical influences (Table 1). Most lagoons around Rügen have suffered intensive eutrophication through nutrient run-off from agriculture for decades, and internal nutrient cycling is contributing to maintenance of highly eutrophied states of many lagoons (e.g., west Darss-Zingst-Bodden chain or Peenestrom, Schiewer, 2008; Paar et al., 2021). Depending on the degree of separation from the Baltic Sea and the degree of exposure to river run-off, one can differentiate between two broad categories of lagoons: 1. hypertrophic and turbid (with Secchi-depths on average below 40 cm and mean annual total phosphorus values > 100 μg/l), shallow (mean water depth of 2 m or less), oligo- to mesohaline lagoons that are dominated by pike-perch (e.g., western lagoons of the DZBC, the Kleiner Jasmunder Bodden and the Peenestrom/Achterwasser in the Oder estuary, Figs. 1), and 2. meso- to eutrophic, mesohaline, somewhat deeper, less turbid and thus more macrophyte-rich lagoons that often are dominated by pike and perch as freshwater predators and have lower pike-perch stocks (lagoons west, north, south and southeast of Rügen,

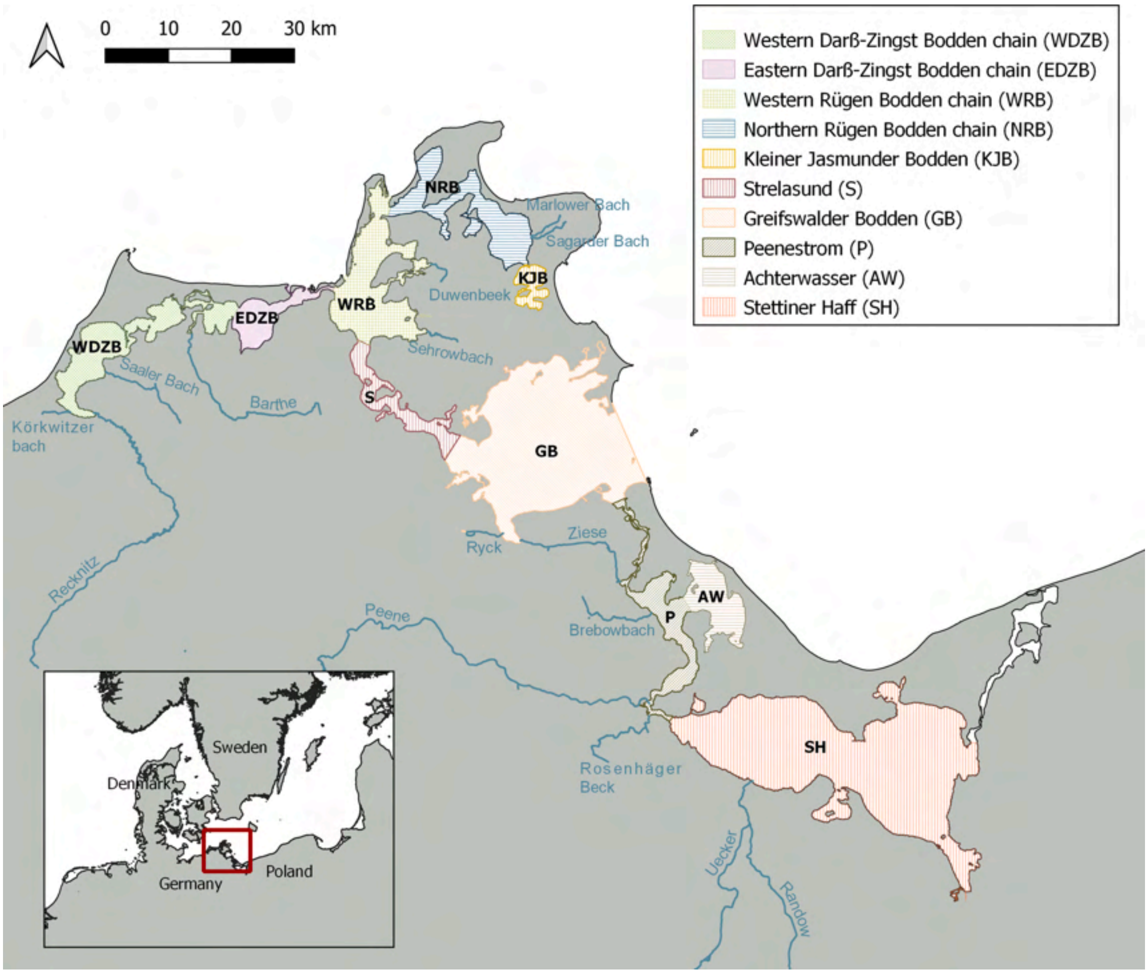


Fig. 1. Map of the lagoon ecosystems in the southern Baltic Sea in Mecklenburg-Western Pomerania, Germany. The different lagoons are differentiated by local names, which mostly, but not always (e.g., Strelasund = S or Peenestrom = P) include the term "Bodden". With few exceptions (such as Greifswalder Bodden = GB or S), the different smaller Boddens have been clustered into sets of lagoons that share similar hydrochemical or morphological features (Table 1) and are associated in space around the largest island of Rügen. Note that only a few smaller rivers exist in the region, the largest of which (the Rivers Oder and Peene) drain into the Peenestrom and from there into Greifswalder Bodden. Accordingly, there is a salinity gradient from higher mesohaline values in the lagoons west and north of Rügen towards lower mesohaline values to the southeast Greifswalder Bodden, and oligohaline conditions in the Peenestrom and the most western, more enclosed part of the Darß-Zingst-Bodden chain (WDZB). A general characterization of hydrochemical features of the different lagoon areas is provided in Table 1.

Table 1
Basic hydrochemical conditions estimated as annual means from 2010 to 2020 from multiple stations with monthly measures (data source: LUNG). DZBC = Darß-Zingst-Bodden chain, WRFB = West-Rügen-Boddens chain, NRB = North-Rügen-Bodden chains (including Grosser Jasmunder Bodden), KJB = Kleiner Jasmunder Bodden, S = Strelasund, GB = Greifswalder Bodden, P = Peenestrom (including Achterwasser, AW, see Fig. 1). Submerged macrophytes represents a best expert judgement of today's situation. The catchment areas of the DZBC represents the catchment of both regions combined.

Parameter	Western DZBC	Eastern DZBC	WRBC	NRBC	KJB	S	GB	P
Area (km^2)	213.2	59.8	231	132.9	26.5	47.6	540.1	181.9
Mean depth (m)	2.0	2.0	1.8	3.5	2.8	3.9	5.8	2.6
Max depth (m)	10.1	16.5	7.6	10.3	5.2	16.0	13.5	16.0
Catchment area (km^2)	1578	1578	238	312	104	238	665	5772
Water temperature (°C)	11.6 ± 6.6	11.5 ± 6.6	11.6 ± 6.7	12.5 ± 6.5	11.9 ± 6.8	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	8.3 ± 1	5.1 ± 1.1	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	1.4 ± 0.7	0.4 ± 0.1	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	56.1 ± 35.1	102.6 ± 34.6	49.1 ± 18.7	45.8 ± 21.1	98.3 ± 58.1
Chlorophyll a (mg/m^3)	83.2 ± 46.3	27.7 ± 19.6	7.9 ± 6.9	16.8 ± 12	82.7 ± 40.7	15 ± 9.1	14.6 ± 13.6	63.6 ± 48.1
Submerged macrophytes	Low-absent	Medium	Medium	Medium-high	Low-absent	Low-medium	Low-medium	Low-absent

including West-Rügen-Bodden WRB, Großer Jasmunder Bodden in North-Rügen-Bodden NRB, Strealsund S and Greifswalder Bodden GB, Fig. 1) (Winkler, 1990). The salinity gradient in the lagoons ranges from highest mean annual values of 6–9 PSU in the north-western lagoons to lower values of 5–7 PSU in southwest lagoons. Within the DZBC there is also a salinity gradient from west (almost freshwater at <2 PSU in the Saaler Bodden, west DZBC) to east (annual mean of 6–8 PSU in the Grabow, east DZBC, Table 1, Fig. 1).

The average salinities in all lagoons around Rügen are below 9 PSU across the year (Table 1) and therefore offer viable conditions for pike survival year-round. However, stochastic spikes in Baltic water inflow specifically in the eastern part of the DZBC and WRB can lead to values exceeding 10 PSU for short periods of time repeatedly throughout the year (Möller et al., 2019), which in turn can limit the occurrence and survival of freshwater species. The key role salinity plays for species occurrence has first been summarized by Remane (1934), showing that species richness of macrozoobenthos exhibits a pronounced minimum at around 5–8 PSU, the so called “horohalinikum” (Telesh et al., 2011, 2015). Large parts of the lagoon systems discussed here are located in this salinity range (Table 1), where small changes in salinity are causing large effects with respect to species richness in the benthos. However, the pattern exhibited by macrozoobenthos cannot easily be transferred to other organism groups (Telesh et al., 2013). Bacterioplankton diversity, for instance, displays little salinity-dependency whereas protists seem to peak exactly at the horohalinkum, and macroalgae exhibit a constant decline in species diversity with decreasing salinity (Telesh et al., 2013; Schubert et al., 2011). For macrozoobenthos and submerged macrophytes, the availability of suitable sediment is another factor restricting the species inventory, resulting in a complicated network of impact of salinity, wave exposition, sediment type and trophic state decisive for the occurrence of species and communities across the Bodden lagoons (Selig et al., 2006, 2007; Schiewer, 2008; Blindow et al., 2015).

With respect to vertebrates, the usually applied scheme of discrimination between freshwater, marine and migratory species is hard to apply in the oligo- to mesohaline brackish lagoons as discussed here. The salinity ranges (Table 1) for most of the Baltic lagoons are just around the critical salinity for recruitment and survival of both freshwater and marine fish (Remmert, 1969; Klinkhardt and Winkler, 1989; Schubert et al., 2017). The fish assemblages in the brackish coastal areas of Rügen are thus a mixture of marine, freshwater, estuarine and migrating fish species that are tolerant of oligo- to mesohaline conditions and are able to osmoregulate within a certain range or migrate into the lagoons seasonally after recruitment elsewhere in either marine or fully freshwater habitats (Winkler and Schröder, 2003). Several freshwater species, including pike, have evolutionarily adapted to brackish salinity and thus colonized the lagoons (described as inner coastal waters in Mecklenburg-Western Pomerania, MWP) shown in Fig. 1, with occasional migration to the outer open coastline around Rügen, but these species avoid areas exceeding 10–12 PSU (Henking, 1923). Large fractions of the stocks of cyprinids and percids migrate from their spawning grounds in oligohaline regions ($<$ 5 PSU) to graze in mesohaline areas ($>$ 5 PSU, Henking, 1923). The extension of the feeding grounds allows them to build high abundances in the productive lagoon ecosystems. This applies in particular to the populations of roach (*Rutilus rutilus*), bream (*Abramis brama*), perch, and pike-perch (Henking, 1923, 1978), with pike having low abundances relative to the other freshwater fish (Falk, 1966). The number of native fish species in the different lagoons varies between 50 and 60. For example, there are about 61 fish species in the Stettiner Haff (Winkler and Joisten, 2021) and the Greifswalder Bodden (Winkler, 1989), 54 in the DZBC (Winkler, 2001), and 65 in the Kubitzer Bodden (area WRB) and Strelasund (Thiel et al., 2005). In the Bodden lagoons, freshwater and migratory marine species (e.g., herring or garfish, *Belone belone*) dominate in terms of biomass over fully marine species (e.g., cod).

Despite the large number of species, only a few species form the bulk of the fish biomass and thus determine the productivity in the food chain. There is no regular fishery-independent survey time series for the lagoons and only snapshot studies on the fish community composition exist (e.g., Fredrich, 1975; Löser, 2004). Therefore, time series of commercial landings have been used in previous studies to indicate fish assemblage shifts in conjunction with environmental change, specifically eutrophication effects in the 1970 s and 1980 s (Winkler, 1990, 1991; Winkler and Debus, 2006). For example, in the western part of the DZBC a pronounced shift from pike to pike-perch dominance was documented in response to increasing nutrient inputs in the 1970 s and 1980 s, which was associated with a collapse of underwater vegetation and a rise in turbidity as consequence of an excessive nutrient input (Winkler and Debus, 2006). Focusing on commercial landings to indicate species composition risks missing the detection of important links in food webs and does not allow inferences about the population sizes of smaller-bodied freshwater species, such as ruffe (*Gymnocephalus cernua*), several commercially less relevant cyprinids, smelt (*Osmerus eperlanus*), marine gobies (*Pomatoschistus microps* and *P. minutus)* and sticklebacks (*Gasterosteus aculeatus, Pungitius pungitius*) that regularly occur in the lagoons (Subklew, 1983; Löser, 2004; Winkler and Schröder, 2003). Beyond the knowledge that these species exist and that abundance fluctuates over time (e.g. Subklew, 1983), there is no standardized time series available that would allow quantitative inferences about population trends of these species.

Standardized surveys of the entire adult fish community in different habitat types over multiple years has only been conducted in the eastern part (mesohaline region) of the DZBC (Winkler et al., 1995). Over a period of three years, it was found that bream, perch, pikeperch, herring, roach and three-spined stickleback always accounted for more than 90% of the total fish biomass. Seven other rare species each represented 0.5%– 2% of the biomass: pike, eel, smelt, nine-spined sticklebacks, two species of gobies and flounder (*Platichthys flesus*). Spring spawning herring was found in large quantities only during the spawning season in spring (March-May), and the offspring used the nutrient-rich lagoons as a nursery in the first summer before migrating into the Baltic Sea. The general species composition in the oligohaline lagoons was found to be rather similar to the more mesohaline areas, but with significantly less herring biomass and more freshwater species in lower salinity areas (Winkler et al., 1995). Here, the ruffe occurred in larger quantities and may therefore has been an important part of the food web for predators such as pike (Winkler, 1987). Since about 2005, the round goby (*Neogobius melanostomus*) has established in increasing quantities in all coastal waters in Germany, and has now become an important part of the lagoon food web (Winkler et al., 2014; Österwind et al., 2017; Rothe et al., 2016).

The age-0 fish community in different lagoons were investigated in various studies in the past (e.g. Fredrich, 1975; Pribbernow et al., 1985; Thiel, 1990). An exemplary study is Löser (2004) who studied the age-0 community with beach seines in two depth strata in the Strelasund (S). A total of 17 estuarine, marine, diadromous and freshwater species were detected as larvae and juveniles, whose distribution was strongly affected by wind exposure and turbidity. Three-spined stickleback was the species with the highest presence, abundance and biomass in the very shallow littoral, and herring in the sublittoral. Age-0 northern pike were found at low abundances and mainly in areas with very low wind exposition (Löser, 2004). Overall, the shallow littoral of the lagoons constitutes a key habitat for the reproduction of a range of freshwater, estuarine and some euryhaline marine fish species (Thiel, 1990), although the majority of freshwater fish successfully reproduce only in oligohaline conditions (Klinkhardt and Winkler, 1989). Generally, the fish community along the lagoons varies alongside salinity, access to the Baltic Sea, influx of species through spawning migrations (e.g., spring and autumn spawning herring), wind exposure, degree of eutrophication, and vegetation abundance and coverage (Pribbernow et al., 1985; Thiel, 1990; Löser, 2004; Winkler et al., 1995). Pike is a regular species in this community and occurs in varied abundance in all lagoons,

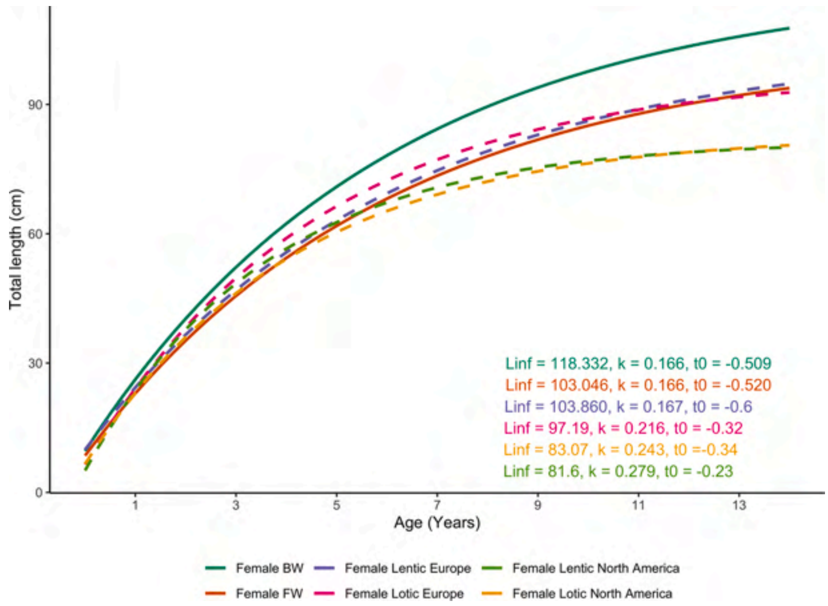


Fig. 2. Comparison of von Bertalanffy growth models of female pike coming from brackish water (BW) around the island of Rügen and the connecting freshwater (FW) streams with growth information of female pike coming from lotic and lentic habitats from North America and Europe (dashed lines) (German data from Droll, 2022, comparison data from the meta-analysis of Rypel, 2012, only average size-at-age is plotted for illustrative purpose).

although it does not build up as high biomasses as species at lower trophic levels (Falk, 1966; Löser, 2004). Identification of the exact recruitment locations for pike in the lagoons has been a continued challenge (Möller et al., 2019; Möller, 2020).

3. Pike ecology in brackish waters

The northern pike is one of the freshwater species with the widest distribution range in the northern hemisphere (Skog et al., 2014), spanning from 24 to 69 decimal degrees in latitude (Forsman et al., 2015). Despite being considered a stenohaline freshwater fish that cannot survive marine conditions (Jacobsen and Engström-Öst, 2018), pike is capable of osmoregulation under brackish conditions and has thus colonized brackish ecosystems, such as the Baltic Sea or the Caspian Sea (Casselman and Lewis, 1996; Stolyarov and Abusheva, 1997). As the general pike biology and ecology is intensively covered elsewhere (Raat, 1988; Craig, 1996; Skov and Nilsson, 2018), here we provide only a brief account of the state of knowledge on pike ecology in particular for the southern Baltic Sea and other brackish areas.

3.1. Growing and surviving in brackish water

Naturally recruiting pike are known from the Baltic Sea in areas with year-long salinities not exceeding on average 10 PSU (Jørgensen et al., 2010; Jacobsen and Engström-Öst, 2018; Möller et al., 2019). Adapted adult pike are able to temporarily survive salinities of up to 15 PSU (Jacobsen et al., 2017), with reported mass mortalities and a collapse following a transient increase in salinity to 18 PSU (Dahl, 1961). Thus, too high salinities constitute a substantial stressor for pike (Kuznetsov et al., 2016; Jacobsen et al., 2007; Greszkiewicz et al., 2022), which limits its occurrence in the open coast of the more saline western and southern Baltic Sea (relative to the northeast Baltic Sea). There is abundant evidence, however, that natural selection has allowed adaptation to brackish conditions and pike can fully recruit in brackish water up to a salinity of about 8–10 PSU depending on the degree of adaptation of the local substock and local salinities (Möller et al., 2019; Sunde et al., 2018, 2022).

Weakly saline brackish environments, like those in lagoons of the southern Baltic Sea, may offer pike certain benefits over living entirely in freshwater environments (Morita et al., 2001). For example, the access to marine-derived food sources that periodically enter the lagoons can foster growth (Winkler, 1987), which is a critical component of pike fitness as fecundity scales positively with mass and natural mortality declines with size (Haugen et al., 2006). Freshwater species such as roach and perch contribute most to the pike's diet in the lagoons of Rügen outside of the herring's spawning season, but also ruffe and stickleback play a role (Winkler, 1987, 1989). In recent years also round goby (personal observations) regularly occur in the pike diet. Generally, living in brackish environments can produce fitness benefits by allowing access to an abundant and energetically rich marine-derived food resource that would not be available in smaller freshwater systems, such as tributaries to the lagoons.

Beyond the egg stage, juvenile and adult pike in the Baltic Sea may also benefit from living under isotonic conditions (~ 9 PSU), as it requires a lower energy investment toward osmoregulation than living in freshwater (Altinok and Grizzle, 2001). Perhaps thanks to this osmoregulatory advantage and the generally high biological productivity of the lagoon ecosystems covered here (Winkler, 1987, 1989; Olsson et al., 2012), pike in the Baltic Sea grow faster than many freshwater populations (Fig. 2, Droll, 2022). Indeed, female pike collected in the brackish Bodden around the island of Rügen were found to have higher average growth rates, and on average larger terminal lengths than typical freshwater pike, while female pike collected in freshwater tributaries around Rügen did not differ in growth and length from pike in other lentic habitats in Europe (Fig. 2).

But living in brackish water can also have drawbacks. Besides the possibility of salinity-induced stress and death, pike is typically the top predator in many freshwater systems. In coastal environments, in contrast, pike are often mesopredators and larger natural predators exert relevant predation risk. Specifically, grey seal (*Halichoerus grypus*) and great cormorant (*Phalacrocorax carbo sinensis*) prey on pike in the Baltic Sea (Arlinghaus et al., 2021; Hansson et al., 2018; Östman et al., 2013;

Svensson, 2021). In areas with high seal abundance, such as the central Baltic Sea in Sweden, seals have been found to constitute a key mortality source, specifically for adult pike (Bergström et al., 2022), while cormorants typically consume juveniles (i.e., pre-recruits) (Österwind et al., 2017; Winkler et al., 2014). Although cormorant predation is of course also an issue in freshwater environments, the local abundances of cormorants in the Baltic Sea are particularly high in recent years and may thereby strongly affect pike survival (Österwind et al., 2017) (see below for an intensified discussion).

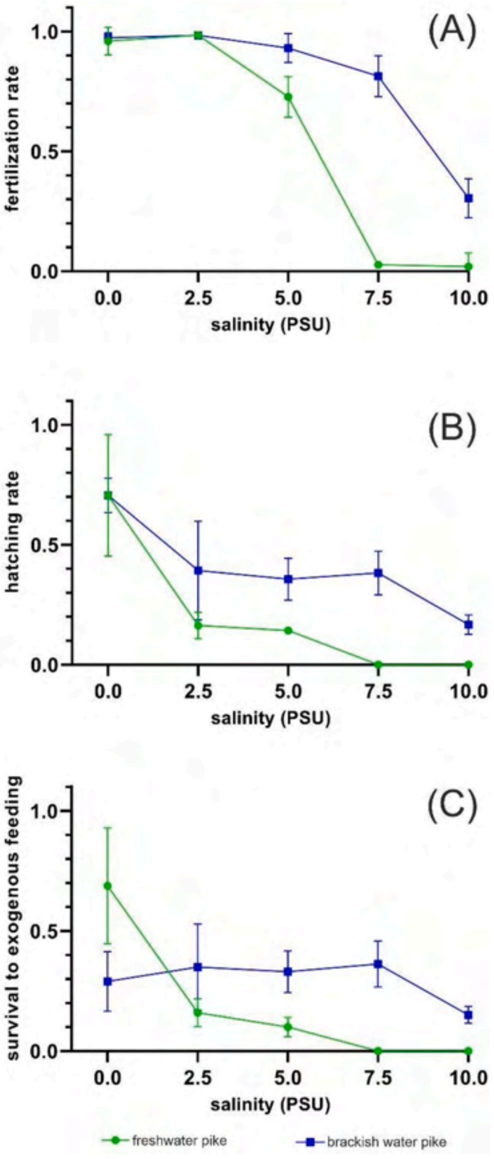


Fig. 3. Fertilization rate of brackish water pike originating from western Rügen and a freshwater control population at different salinities when held under controlled conditions. B. Hatching rates and C. Survival to exogenous feeding (Möller et al. unpublished data).

3.2. *Recruiting in brackish water*

The above described benefits and drawbacks of living in isotonic conditions and accessing seasonally available marine prey mainly apply to pre-recruit and recruited pike. However, also the egg and larval stages are affected by salinity. Indeed, salinity negatively affects and often inhibits fertilization and development of eggs in freshwater-adapted pike (Holliday, 1969; Jacobsen and Engström-Öst, 2018), such that recruitment in brackish lagoons must either happen through emigration of larval and young pike from connected freshwaters/wetlands or be facilitated through local adaptation to brackish conditions. There is evidence for both. In coastal Baltic pike, the influence of salinity on fertilization success varies by population, likely reflecting different substocks with different degrees of adaptation to local salinity conditions (Sunde et al., 2018). Using egg swelling as an indicator of successful fertilization and fish from a population adapted to salinities of 8–10 PSU, Jørgensen et al. (2010) found no relevant differences in fertilization rates at different salinities up to 8.5 PSU (see also Raat, 1988; Westin and Limburg, 2002 for similar results). By contrast, experimental fertilization studies from a brackish population around Rügen, similarly adapted to reasonably high local salinities, showed reduced fertilization with increasing salinities up to 10 PSU, but this effect was significantly stronger for pike of freshwater origin, indicating local adaptation to salinity by the brackish subpopulation (Fig. 3A, Neubert, 2011; Möller, 2020). Relatedly, the hatching rate to the free swimming fry stage of the same brackish pike declined with salinity, but did not drop to zero even at 10 PSU (Fig. 3B,C), indicating that the saline-adapted lagoon pike could successfully recruit along the entire salinity range of the region around Rügen (Table 1). By contrast, the freshwater adapted control population showed zero survival to exogenous feeding when salinities exceeded 7.5 PSU. It is interesting to note that the saline-adapted pike stock showed the highest fertilization and hatching rates at freshwater conditions (Fig. 3A, B), while survival to exogenous feeding was similar at freshwater and salinities up to 7.5 PSU, indicating a selection-induced ability to deal with mesohaline salinities in terms of egg and larval development among the saline-adapted substock (Fig. 3C). However, the study covered only two populations and it is unclear if the results hold for other saline-adapted substocks.

Using both freshwater and brackish adapted pike, Lindroth (1946) found that sperm mobility in pike decreased with increasing salinity, and at 10 PSU only weak swimming movements of sperm were observable. This could explain the trend of decreasing fertilization rates with increasing salinities reported from a brackish adapted stock around Rügen and a freshwater control group (Fig. 3A). Other studies on freshwater pike showed that while fertilization was impossible in brackish water, transferring eggs fertilized in freshwater to brackish conditions resulted in successful development, suggesting that occasional brackish inflow may not harm pike that have laid eggs under freshwater conditions (e.g., in tributaries that receive inflow of brackish water, Greszkiewicz et al., 2022). In another study, eggs and fry from two (anadromous) pike populations had different tolerances to salinity, depending on the presence or absence of regular brackish water incursions in their spawning habitat (Sunde et al., 2018). Relatedly, offspring of an anadromous population forced to spawn early (due to early drying of their spawning habitat) performed better at lower temperatures than offspring of another, later spawning anadromous population (Sunde et al., 2019). Experiments exposing freshwater pike fry to a series of increasing salinity treatments (9–14 PSU) suggested that mortality was faster at warmer water than at cooler water (Jacobsen et al., 2007), implying decreased tolerance of higher salinity values at higher temperature. Whether this increased mortality is indeed indicative of lower salinity tolerance or simply caused by elevated metabolism at higher temperatures is less clear. Laboratory experiments in brackish adapted perch showed that the fish had reduced salinity tolerances at lower temperatures (Christensen et al., 2017), implying that species such as perch may be less tolerant to salinity stress in the winter.

However, no such study exists for brackish adapted pike.

Successful reproduction also depends on other local habitat features, especially hydrological stress and wave action, which can be substantial in open coastlines. The importance of sheltered, low salinity sites for pike recruitment has been confirmed mainly through field-studies from Finland and Sweden, which demonstrated that the occurrence of pike larvae was strongly associated with reed stands in bays with high protection from wind and wave actions (Pursiainen et al., 2021; Niemi et al. 2023). In other Finnish studies, juvenile pike were found almost exclusively in the inner- and middle archipelago of the study areas, which were influenced by freshwater inflows, while larvae were lacking in the outer archipelago exhibiting higher salinities (Kallasvuo et al., 2010; Lappalainen et al., 2008) and greater exposure to wind and waves (Pursiainen et al., 2021). Similar results were found by Sundblad et al. (2009) in central Sweden who moreover found a strong overlap between pike larvae and older young-of-the-year (hereafter YOY) pike. It is possible that pike has a general preference for spawning and early recruitment in sheltered vegetated bays (as documented along the northeastern Baltic in Finland and in Sweden, Flink et al. 2023; Niemi et al. 2023), but natural selection could have altered this fitness optimum in areas where such sites are rare, such as in Germany. Here, there is anecdotal evidence that in the lagoons pike might also spawn in deep water of 4–6 m on seagrass meadows in open water areas (Hegemann, 1964; Falk, 1966), and YOY pike were also reported from more wind- and wave exposed shorelines (Löser, 2004), but there is also evidence of spawning migrations into tributaries and more sheltered brackish bays around Rügen during spawning (Falk, 1966; Möller, 2020; Roser, 2021; Dhellemmes et al., 2023; Lukyanova, 2022).

After hatching in lagoon ecosystems, pike larvae must avoid predation to successfully recruit into older age classes. Other fish species can coincide in their spawning time or location with pike eggs or fry, and may then exert predation pressure on larval pike or pike eggs. Specifically, the three-spined stickleback, an efficient predator (and potential competitor) of eggs and larvae of pike reduced pike recruitment in Swedish coast of the Baltic Sea, specifically in tributaries and flooded wetlands (Byström et al., 2015; Nilsson et al., 2004, 2019). Indeed, in Sweden a steady increase of three-spined stickleback abundances in the inner coastal zones of the Baltic Sea ("stickleback wave") over the last four decades correlated negatively with local pike and perch abundances in the central Baltic Sea (Eriksson et al., 2009; Eklöf et al., 2020; Olin et al., 2022). This suggests a negative effect on recruitment whenever pike larvae and high abundances of stickleback coincide spatially and temporally on or near spawning grounds (Bergström et al., 2015). In Sweden, three-spined stickleback today occur in littoral sites or bays in very high numbers, perhaps due to the loss of top-down control from predators in the open Baltic or due to a combined effect of climate warming and eutrophication (Candolin et al., 2008; Ljunggren et al., 2010; Nilsson et al., 2014, 2019; Eklöf et al., 2020). Although so far only speculative, it is possible that warming has also changed the phenology of spawning timing (Fernandes et al., 2022) of both pike and stickleback, possibly increasing the spatio-temporal overlap in the shorelines of the lagoons. Such mismatch could perhaps contribute to the decline in stock size of lagoon pike in Germany in recent years (van Gemert et al., 2022, for further discussion, see Section 8).

Evolutionarily speaking, pike populations have adapted to variable environments in linked freshwater-brackish ecosystems, with salinity adaptations being particularly well documented (Sunde et al., 2022). Stochastic environmental variation in turn allows different physiological and behavioral strategies to co-exist (Kobler et al., 2009). Human factors such as blocking of freshwater access through land management will reduce the options available to the pike, and induce selection gradients to which pike populations have to adapt through evolution. Psuty (2022) reported a case from Poland where the blocking of freshwater access led to local extinction of lagoon pike, suggesting no evolution to recruitment in saline conditions happened. Around Rügen, local adaptation to recruitment in brackish environments has been reported, allowing multiple substocks to exist in the area (Möller et al., 2019). Broadly speaking, three reproductive strategies have been reported from the Baltic Sea, each navigating the possible benefits (e.g., elevated growth in brackish environments, Fig. 2, which can increase fecundity and egg quality, Kotakorpi et al., 2013; Marshall et al., 2021, Fig. 2) and possible costs (e.g., elevated mortality, osmoregulatory stress, Fig. 3) as best as possible when evolutionarily "deciding" to either stay in freshwater, fully adapt to coastal living, or develop some intermediate form of anadromy: one anadromous and two resident spawning strategies (with residence either in brackish or in freshwater systems). Two of the sympatrically co-occurring subpopulations overlap during the feeding phase in the brackish water as mixed stocks, but are reproductively isolated from each other given their preference for different spawning grounds (Westin and Limburg, 2002). This pattern was first described in Swedish waters of the Baltic Sea (Müller, 1986; Engstedt et al., 2010; Westin and Limburg, 2002), but has since been confirmed also in populations inhabiting the low salinity Baltic coastal waters of Estonia (Rohtla et al., 2012) and the high salinity waters of Denmark (Jacobsen et al., 2017; Birnie-Gauvin et al., 2019) and Germany (Möller et al., 2019), confirming the existence of three sympatric pike populations across vast coastal areas of the Baltic Sea. While the anadromous subpopulation undertakes seasonal spawning migrations into coastal freshwater inflows or wetlands, the residential pike evolved to complete their entire lifecycle under brackish conditions. Successful reproduction in elevated salinities can thus be maintained by genetic adaptations and population sorting in space and time during spawning, which in turn foster divergence of subpopulations of pike through restricted gene flow (Tibblin et al., 2015; Sunde et al., 2022).

Because the anadromous and resident pike ecotypes are subjected to different evolutionary pressures due to contrasting spawning strategies adapted to salinity variation (and possibly also other local pressures, such as stream temperature, Sunde et al., 2018, 2019), strong genetic differences are evident between the two components of the sympatric pike populations even on short geographic scales (Nordahl et al., 2019; Sunde et al., 2022; Diaz-Suarez et al., 2022; Roser et al., 2023). In this context, genetic differentiation is more pronounced among anadromous pike spawning in different streams that maybe only a few kilometers apart than among fish from different coastal areas (Nordahl et al., 2019; Sunde et al., 2018, 2019, 2022; Diaz-Suarez et al., 2022), with a general pattern of isolation by distance across wide geographic scales along the Baltic coast (Wennerström et al., 2017, 2018; Möller et al., 2021; Sunde et al., 2022). Key mechanisms contributing to restricted gene flow may be natal homing, where individuals return to the same streams over consecutive years (Engstedt et al., 2014; Tibblin et al., 2016a), or isolation by time where substocks arrive at spawning places at different times of the year. The inter-population differences are manifested in deviating life-history traits like growth, adult size, and reproductive investment (Berggren et al., 2016; Tibblin et al., 2015, 2016a) as well as in different morphological adaptations, i.e., the vertebrae count (Tibblin et al., 2016b).

Estimates of the relative contributions of the anadromous pike ecotype to the sympatric population vary between studies and locations. Figures of anadromy (or generally freshwater origin fish among coastal stocks) reached 98% in Estonia (Rohtla et al., 2012; Rohtla, 2015), 45% in Sweden (Engstedt et al., 2010) and < 7% in Germany (Möller et al., 2019). These findings suggest that the ratio of brackish to anadromous spawning individuals maybe negatively correlated with the abundance of accessible freshwater habitats in a given region (which is higher in the central and north-eastern Baltic Sea, Möller et al., 2019; Rohtla, 2015) and positively correlated with average local salinity (which is higher in the southern Baltic Sea). Also other factors such as variation in local temperatures in spring (e.g., stream temperature relative to lagoon/-coastal temperature early in the year, which might be higher or more important in the generally colder northern Baltic Sea) might contribute to the broad spatial pattern of a decrease of anadromy with rising local salinities from north-east to south-west across the Baltic Sea. More research in this area is warranted, especially because unpublished work by Rittweg et al. suggests that the degree of freshwater-associated spawning may have been underestimated in the pike stock of Rügen and maybe as high as 25% (Rittweg et al. unpublished data).

4. Other key pike habitat requirements of relevance to the Baltic Sea

Besides salinity, temperature and underwater vegetation affect the biology of pike, which has been well summarized in the pike ecology literature in past reviews and textbooks (Raat, 1988; Craig 1996; Skov and Nilsson, 2018). Therefore, only a very brief account will be given here. Although pike are described as mesothermal or cool-water fish, they can tolerate a broad range of temperatures from 0.1 °C (Casselman, 1978) to 29.4 °C (lethal temperature in captivity, Casselman, 1978). Optimal temperatures vary between life stages but also populations (Casselman and Lewis, 1996). Through its joint influence on egg and larval development and juvenile growth rate (Raat, 1988; Haugen et al., 2006; Pagel et al., 2015) as well as activity and adult growth (Casselman, 1978; Haugen et al., 2006; Rypel, 2012), water temperature can positively influence pike recruitment (Edeline et al., 2008; Paxton et al., 2009; Langangen et al., 2011) and population growth rate (Vindenes et al., 2014), but can also increase adult mortality in the Baltic Sea (Berggren et al., 2022). In the Baltic Sea, spawning has been observed to start at a minimum temperature of 4.3 °C ± 1.1 (Sunde et al., 2019), with the onset of spawning occurring at different temperatures in different areas (Nilsson, 2006a; Sunde et al., 2019). Pike movement activity is also known to peak during spring associated with migration (Dhellemmes et al., 2023), where they tend to seek out bays and wetlands for spawning (Lukyanova, 2022; Flink et al., 2023). In particular the largest fish seek thermal refugia when summer temperature exceed 20 °C, often seeking cool water refuges near the thermocline in deep lakes and reservoirs (Pierce et al., 2013; Říha et al., 2021). In the Baltic, pronounced winter activity during daytime despite ambient water temperatures below 6 °C suggests pike can actively regulate their body temperature via sun-basking (Nordahl et al., 2019). Ultimately, temperature effects on population dynamics of pike are complex and hard to predict due to the joint influence on growth, survival, recruitment (Vindenes et al., 2014), moderated by complex effects in food webs (Haugen et al., 2007; Winfield et al., 2012). As a species, pike has been considered as not overly vulnerable to impacts of climate warming (Jarić et al., 2019; Nyboer et al., 2021). However, extreme thermal events may impose changes in the population dynamics, depending on how other prey or predator species (e.g., perch or stickleback) respond to the same events (Haugen et al., 2007). Recent work from the Great Lakes showed that warming can cause disruptions of gonad development in yellow perch (*Perca flavescens*) and delay, rather than speed up, spawning timing, which can lead to recruitment failures (Farmer et al., 2015). Whether these effects also affect pike in the Baltic Sea are currently unknown, but the winter period is decisive for building the gonads through active foraging (Diana and Mackay, 1979). Shifts in the phenology of spawning timing in relation to possible brood or YOY predators (e.g., stickleback or perch) could, however, substantially affect recruitment of pike, in particular if the fitness advantage of early spawning relative to its prey is altered through climate effects. Due to lack of long-term monitoring data there is no opportunity to robustly examine these and other climate effects on the lagoon pike stock. They should be studied further because the current patterns of consistent declines in stocks across the central and southern Baltic Sea (Olsson, 2019; Olsson et al., 2023) could suggest that a common regional factor (such as temperature rises) might be at play.

Besides temperature and salinity, underwater vegetation is a final key environmental factor that has considerable influences across all life stages of the pike. Submerged macrophytes are spawning habitats for adult pike (Kobler et al., 2008) and provide shelter to larval and juvenile pike (up until roughly 50 cm total length, Bry, 1996; Grimm and Klinge, 1996), including safety from intercohort cannibalism. Detailed studies in ponds and shallow lakes (e.g. Grimm, 1981b, 1981a,; summarized in Grimm and Klinge, 1996) have provided convincing evidence that the survival of juveniles and the carrying capacity for juvenile and adult pike biomass is strongly regulated by availability of submerged and emergent macrophytes. Phytophilia is maintained by adult pike also outside of spawning season (Chapman and Mackay, 1984a; Cook and Bergersen, 1988; Kobler et al., 2008), despite larger pike increasingly losing their attachment to plants (Chapman and Mackay, 1984b; Vøllestad et al., 1986). Besides serving as key spawning habitat for pike, the life-long affinity to macrophytes and other structures (e.g., dead wood) is related to the foraging strategy of pike, which are ambush predators (Diana, 1980), a behavior already observed in young pike (Hunt and Carbine, 1951). Because pike is a primarily visual predator, water clarity affects its habitat use (Skov and Nilsson, 2018) as well as its movements and foraging behavior (Vøllestad et al., 1986). For instance, young pike in turbid water were found to have a shorter reaction distance when turning towards their prey (Jönsson et al., 2012), and pike in turbid water were described to change from ambush to active pursuit (Vøllestad et al., 1986). As turbidity may also act as a refuge, larval and juvenile pike disperse more outside refuges as water clarity declines (Skov and Nilsson, 2018), and pike larger than 50 cm in total length may be entirely be found in pelagic areas (i.e. away from the safety of macrophyte cover, Andersen et al., 2008; Kobler et al., 2009) in turbid systems (Vøllestad et al., 1986, but see Jepsen et al., 2001 for an alternative finding). Turbidity also may enhance the heterogeneity in behavior expressed by individual pike (Andersen et al., 2008). Consequently, variation in standing pike biomass and also pike behavior can be expected as a function of macrophyte coverage and turbidity. Overall, pike should move more extensively and should be found regularly outside the littoral zone in the more eutrophied, turbid lagoons (compare Říha et al., 2021), while the recruitment should be strongly impaired due to loss of underwater vegetation (Winkler and Debus, 2006). The most turbid and macrophyte-poor lagoons (e.g., west DZBC where Secchi-depth is below 0.8 m on average, Table 1) thus might be particularly dependent on dispersal of recruits from other areas or from freshwater streams. As pike are able to track fitness gradients and disperse over wide distances (Haugen et al., 2006), recruitment through dispersal from clear to turbid lagoons is possible, but no data exist on this topic from the German lagoons. What is known, however, is that in the adult stages connectivity of different lagoons is small as pike engage in rather stationary behavioural patterns with extended home ranges only being about 600 ha on average in German lagoons (Dhellemmes et al., 2023). The core home ranges are even smaller with only about 100 ha on average (Dhellemmes et al., 2023). Movements beyond 10 km in maximum distance occur (Lukyanova, 2022), but they are rare (Kåras and Lehtonen, 1993).

Eutrophication generally affect pike abundance negatively (Lehtonen et al., 2009; Jeppesen et al., 2000), but impacts seem to be less caused by turbidity-impaired foraging behavior but rather by the loss of underwater vegetation (Haugen and Vøllestad, 2018). The negative impacts of eutrophication depend on water depths and happen at lower nutrient levels in shallow systems compared to deep systems (Haugen and Vøllestad, 2018). Overall, eutrophication creates trade-offs for pike: it increases prey availability by favoring abundant cyprinid stocks (Persson et al., 1991), but also reduces macrophyte abundance, which constraints stock sizes through high mortality of juvenile pike (Minns et al., 1996; Haugen and Vøllestad, 2018). However, as long as the recruitment is not impaired, nutrient inputs may increase stock biomass of pike through the improved forage bases. Overall, meso- to slightly eutrophic conditions in ecosystems with abundant underwater vegetation seems to be optimal for pike abundance (Casselman and Lewis,

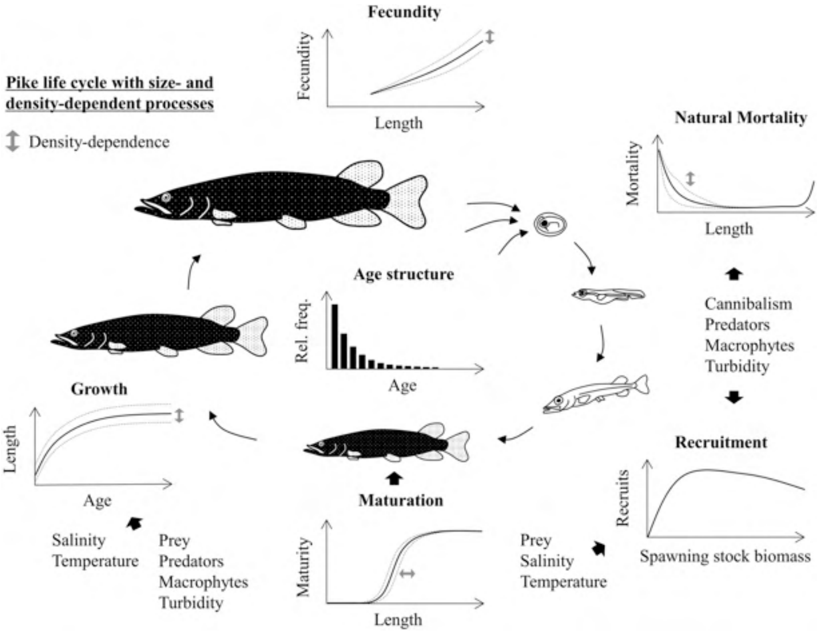


Fig. 4. Representation of the pike life-cycle and the associated size- and density-dependent mechanisms as well as main abiotic and biotic environmental factors affecting them.

1996). The high eutrophication of the German lagoons is thus a challenge to pike recruitment and has led to a shift from pike to pike-perch dominance in some lagoons in the past (Winkler and Debus, 2006). Although pike might contribute to maintaining a clear-water state through top-down control, experimental manipulations of pike abundance in lakes have found that a trophic cascade from pike to affecting water clarity is unlikely and cannot be sustained if nutrient levels remain excessive (Bernes et al., 2015).

5. A synthesis of pike population regulation through size and density dependent processes

Within the general constraints set by the environmental conditions reviewed above a range of size- and density-dependent processes regulate pike stocks, both in freshwater systems and the Baltic Sea (Fig. 4).

Because of the large gape size of pike and the strong overlap of different cohorts in the littoral zone, size-dependent cannibalism, controlled by habitat and refuge availability, constitutes a key regulatory mechanism affecting pike recruitment (Haugen et al., 2007). Cannibalism in pike can lead to overcompensation in recruitment, leading to a Ricker-type stock-recruitment relationship (Ricker, 1954), i. e. the number of recruits starts to decrease with increasing spawning stock biomass (Fig. 4) (Edeline et al., 2008; Langangen et al., 2011; Haugen and Vøllestad, 2018). Cannibalistic control is predominant in the juvenile and small adult stages up until a size of roughly 50 cm total length (Grimm and Klinge, 1996; Eklöv, 1997; Nilsson, 2006b; Nilsson et al., 2009; Skov et al., 2003; Skov and Koed, 2004; Haugen et al., 2007; Haugen and Vøllestad, 2018). Population responses to reduced cannibalism control are substantial (Edeline et al., 2010). For example, Sharma and Borgstrøm (2008) removed a large proportion (55%−65%) of large (> 65 cm) pike from a lake, which led to an immediate abundance increase of medium sized, age-3 individuals who were released from agonistic interactions and cannibalistic control by larger conspecifics. Despite adults being less vulnerable to cannibalism, density feedback on growth (Pierce et al., 2003) and mortality occurs in the adult life-stage, which can involve predation but may also relate to elevated risk of disease or death after reproduction (Haugen et al., 2007) or to social stress (Edeline et al., 2010). Ultimately the interplay of density, prey availability and the structure of refuge interacts to affect survival of young pike and hence recruitment into a fishery (Haugen et al., 2007, Fig. 5).

Size, a state outcome of growth (or the balance of energy acquisition and allocation), is a master trait governing several fitness-related outcomes in pike, specifically survival and fecundity (Figs. 4, 5). Survival is positively size-dependent in most situations (e.g. Grønkjær et al., 2004; Haugen et al., 2007; Pagel et al., 2015). Similarly, fecundity scales positively with length and mass in pike (Frost and Kipling, 1967). While Frost and Kipling (1967) documented isometry in the mass-fecundity relationship of pike, Droll (2022) showed that in southern Baltic lagoons around Rügen pike have hyperallometric mass-fecundity scaling with an exponent linking mass to egg numbers of about 1.1. Thus, larger fish can have higher reproductive success, which is supported by some work in freshwater systems that tracked offspring numbers as a function of length in the wild (Monk et al., 2021). Density-dependence in terms of food availability can negatively affect condition, and in turn lower relative fecundity (Craig and Kipling, 1983). Relatedly, release of density-dependence through exploitation can foster growth and condition and generate positive size-dependent maternal effects on egg quality (Kotakorpi et al., 2013).

Collectively, moderated via environmental conditions (e.g., temperature, nutrient availability, salinity, vegetation, prey availability), there is substantial evidence that several size- and density-dependent processes collectively regulate pike stocks, specifically recruitment (Fig. 5). Despite cannibalism being relevant across almost the entire life-cycle in pike, the current body of literature thus supports the broad generalization that density-dependent survival is the main compensatory mechanism in the larval and juvenile stages of pike, while density-dependent growth (Margenau et al., 1998; Pierce et al., 2003; Lorenzen and Enberg, 2002) is the predominant density-dependent process affecting the large juvenile and adult stages (Johnston et al., 2018),

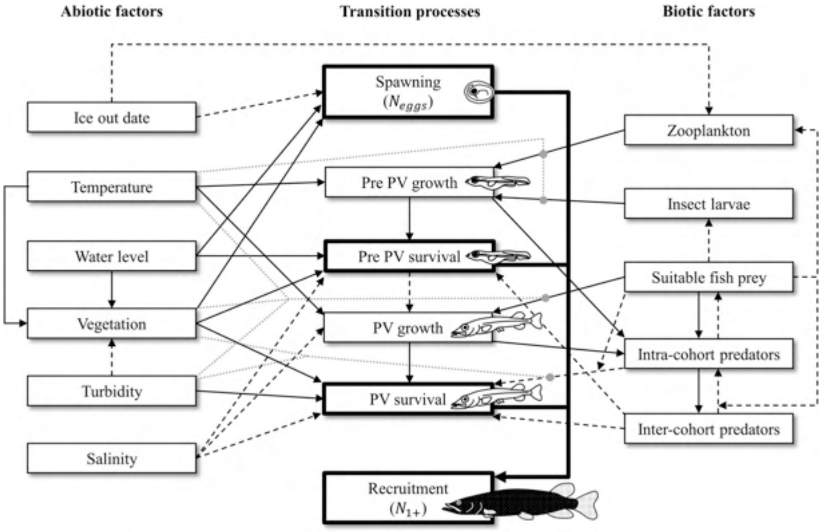


Fig. 5. Density-dependent and independent factors influencing pike recruitment. PV = Piscivorous, Solid black arrows illustrate positive effects and dashed black arrows represent negative effects. Grey lines show modifying effects or interactions (modified from Haugen and Vøllestad, 2018).

similar to other species (Lorenzen, 2005). There is no reason to believe that the lagoon ecosystems function fundamentally different to shallow lake ecosystems, with the most relevant difference being the presence of weakly saline water (Fig. 5). Moreover, the pulse of energy from marine-derived nutrients entering the lagoons may elevate the productivity and standing stock biomass beyond levels that would be expected from the autochthonous primary productivity, which could in turn lower the density-dependence of growth and mortality and increase pike production in lagoons.

6. Exploitation of pike by commercial fisheries

The fish stocks in the lagoon ecosystems around Rügen have been commercially exploited since at least the Middle Ages (Lampen, 2000; Porada, 2009), with written documentation ranging back to 1124 (Münter, 1863). Early settlements, villages and port infrastructures were founded around fisheries along the coastline around the island of Rügen and in other areas of the Baltic coast (Peesch, 1961; Wegner, 2012). In the 18th and 19th century, the lagoon fishery of Rügen was nationally and internationally well-known for its lucrative fishery for spring- and autumn-spawning herring (Münter, 1863; Biester, 1979, 1989; Porada, 2009; Raillard, 2012), which not only provided food, but also drove developments in vessel technology for trade or military (Münter, 1863). The herring was targeted mainly with gillnets, seines and different types of fyke nets, the catch processed in various forms (e.g., salted) and traded over long distances (Henking, 1929; Biester, 1979; Porada, 2009). Fisheries harvest were also used for personal consumption and to supply fish to the dukedom and other landlords (Porada, 2009). A multitude of other freshwater and marine species were caught while targeting herring or additionally, including pike in night-based seining conducted under ice during the wintertime (Henking, 1929; Porada, 2009). Although the dominant fishing gears used in the lagoons have typically been passive gear types (Schlieker 2009), since the second half of the 19th century, fish were also targeted using wind-propelled trawling vessels („Zeesenboote“) (Henking, 1929; Koy, 1990; Schliecker 2009; Mäuslein, 2012). In the off-herring-season, Zeesen--boats were also used to target freshwater species such as roach, perch or pike (Henking, 1929). Fishing with motorized trawls was formally prohibited in the lagoons and within the three-mile coastal zone of MWP in 1908 (Porada, 2009; Raillard, 2012), based on recommendations developed by Paulus Schiemenz (1920) - a leading fisheries scientist of the time based in Berlin whose scientific assessments were in retrospect considered somewhat inaccurate (Weicker, 1924; Porada, 2009). Nevertheless, wind-propelled trawls operated through the Zeesen-boats continued until the 1980 s (Schlieker 2009) and were only prohibited in 2000. Today, Zeesen-boats are occasionally operated for demonstration purposes with a special permission.

Another traditionally important gear type in the commercial fishery in the region has been long-lines and other forms of angling, which were and today occasionally are still used to target high-priced species such as eel, but also pike with baitfish under ice (Henking, 1923). Eel was targeted via fyke nets and eel-spears, and a similar fate awaited for migrating pike on wetlands and in ditches and tributaries around Rügen (Roser, 2021). Up until present day, in the lagoon fisheries commercial fishers have exemptions for using live baitfish on angling gear, which is otherwise prohibited to use in Germany for animal welfare reasons.

Information on the historical role and landings of pike is sparse and mostly anecdotal, but landings of freshwater fish in the lagoons have been repeatedly mentioned, e.g., by Marcard (1870) or Neuhaus (1933); summarized in Winkler (1989, 1991, 2000). The earliest systematic records of commercial pike landings were from the end of the 19th century (Fig. 6). While pike likely has always been targeted as part of the multi-species fisheries of the lagoon fisheries, it became a target species in the early 20th century in some lagoons. For example, in 1913, a fishing cooperative was founded that specifically targeted pike in the Saaler Bodden (west DZBC) (Henking, 1929). Prior to 1990, although freshwater and diadromous fish were regularly exploited in the multi-species fishery and have always generated a high price, given their lower absolute yield the total economic value of freshwater fish did not reach the dimension of the herring fishery (Schlumpberger et al., 1966; Porada, 2009). Already in the late 18th and early 19th century, anthropogenic alterations of lagoon ecosystems were reported to negatively affect the freshwater fish, including pike. For example, road and railway constructions around 1868 reduced the connectivity between the Großer and Kleiner Jasmunder Bodden (Fig. 1), leading to decreases in the landings of pike, perch, bream and roach in the Kleiner Jasmunder

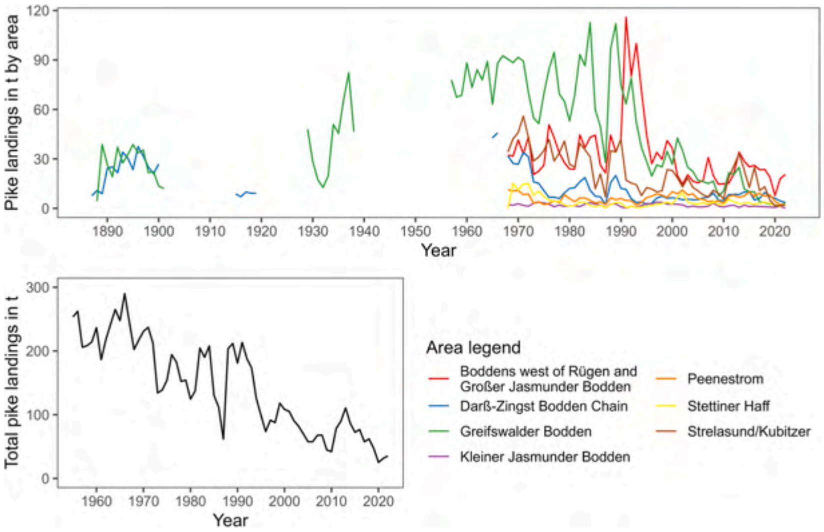


Fig. 6. Commercial pike landings by area and total in the Bodden 1929–2022 (data sources: LALLF, Winkler, 1989, 1990 and Subklew, 1955a; b).

Bodden (Henking, 1929). Fish kills in response to heavy eutrophication were also described from Kleiner Jasmunder Bodden (Kell and Noack, 1991). Pollution of the lagoons has been suspected to cause significant bacterial diseases in pike (Schäperclaus, 1928), which were later identified as being tumors (Esocid lymphosarcoma) caused by viral infections (Wundsch, 1931; Mulcahy and O'Leary, 1970; Papas et al., 1976). Subklew (1955a); b) suggested that the skin tumor was responsible for a heavy decline in pike yield in Greifswalder Bodden in the past.

Typical passive gear types used until the present day in the multispecies small-scale commercial fishery of the lagoons involve gillnets, long-lines, and fyke nets (Meyer and Krumme, 2021). Gillnets dominate by far in the lagoons and are the main gear type targeting pike, perch and pike-perch, while many of the licensed fyke net positions have remained unused in recent years. Long-lines have declined, partly because of the workload involved but also due to concerns with by-catch and public acceptance of live bait fish. Pike become vulnerable to passive fishing gear when they actively swim (Casselman, 1978; Arlinghaus et al., 2017b), which involves the period prior and during to spawning in spring (Cook and Bergersen, 1988; Diana, 1980; Kobler et al., 2008; Říha et al., 2022; Lukyanova, 2022; Dhellemmes et al., 2023). Accordingly, Subklew (1955a) found that fishing for pike in the Greifswalder Bodden was mainly conducted in the cold season, in that time mainly using long-lines. Relatedly, Schlumpberger et al. (1966) reported that in the mid 20th century large fractions (c. 80%) of the total annual pike yield was captured during the spring period from March to May (with a peak in April). Today, due to the presence of a pike protected season in March and April and altered demand for pike, the fishery is less concentrated on just the pre-spawn period and operates throughout the entire year (Meyer and Krumme, 2021).

Total commercial pike landings in the Boddens have strongly varied over time and across the different lagoons throughout history, but the overall trend is a steep decline since 1955 (Fig. 6). From among 200–300 t of pike landed per year as an average of the period 1921–1931 (Porada, 2009) as well as during the GDR period until 1965 (Schlumpberger et al., 1966), commercial pike landings have decreased strongly after the German reunification in 1990, fluctuating between 100 t and a recent (2020) low value of just 59 t (Fig. 6). In the 1960–1990 s, the highest landings were produced in the GDR from Greifswalder Bodden and since the German reunification in the Boddens west of Rügen/Großer Jasmunder Bodden areas (Fig. 6), but landings strongly dropped after 1990 after the transition to the market economy (Figs. 6 and 7).

6.1. The commercial fishery during the socialist period in the German Democratic Republic (GDR)

Fisheries landings were used in the former GDR for food production as well as to generate foreign income through trade. The GDR organized fishers in large cooperatives and installed a system of fixed market prices and target quantities that commercial operations were supposed to deliver to serve the goals of society. Landings up to the target quantities had to be delivered to state-owned delivery stations (= "peoples-owned enterprises", Volkseigene Betriebe, VEB) and cooperations according to quarterly plans. Any quantity above the target quantity could be sold directly on fish markets at unregulated market prices (which required a permit by the district council). Surplus quantities could also be sold to the national bodies. It was the role of the district council to monitor production of the cooperatives (Produktionsgenossenschaften) and individual fishers. Fish that did not meet the minimum-size limits were to be either released or, if damaged or dead, could be used for private consumption of the fisher.

In 1955, the GDR government aimed at increasing fishers' income by (1) creating state-owned enterprises in the cities of Warnemünde, Wolgast, Stralsund, and Wismar (Fischerei-Fahrzeug-und-Geräte-Stationen), (2) requiring fishers to deliver at least 10.5% of higher value "game" fish ("Edelfische", including eel, pike, pikeperch and flatfish species), and (3) requiring that prices for surplus fish were to be 45% higher than prices for the target quantity (Gesetzblatt der D.D.R. Teil I, 1955). To keep producer prices for fish high, the fishery was heavily subsidized (Deutscher Bundestag, 1993; Döring et al., 2020). Thereby, the capacity of the fishing fleet was kept artificially high, resulting in a large number of enterprises. For example, for MWP as a whole, Raillard (2012) reported around 1632 coastal fishing businesses in 1952 in addition to 220 fyke net fishers and 132 cutter fishers.

During the GDR, to meet state goals and delivery quantities, the lagoon pike were heavily targeted, generating high yield levels of among 150 and 200 t of pike per year (Fig. 6, Schlumpberger et al., 1966). In 1965, the per hectar yield of pike ranged from 1.0 to 2.1 kg/ha and year in the different lagoons, with the DZBC (before peak eutrophication) and Strelasund offering the highest yield per hectar and the Westrügen

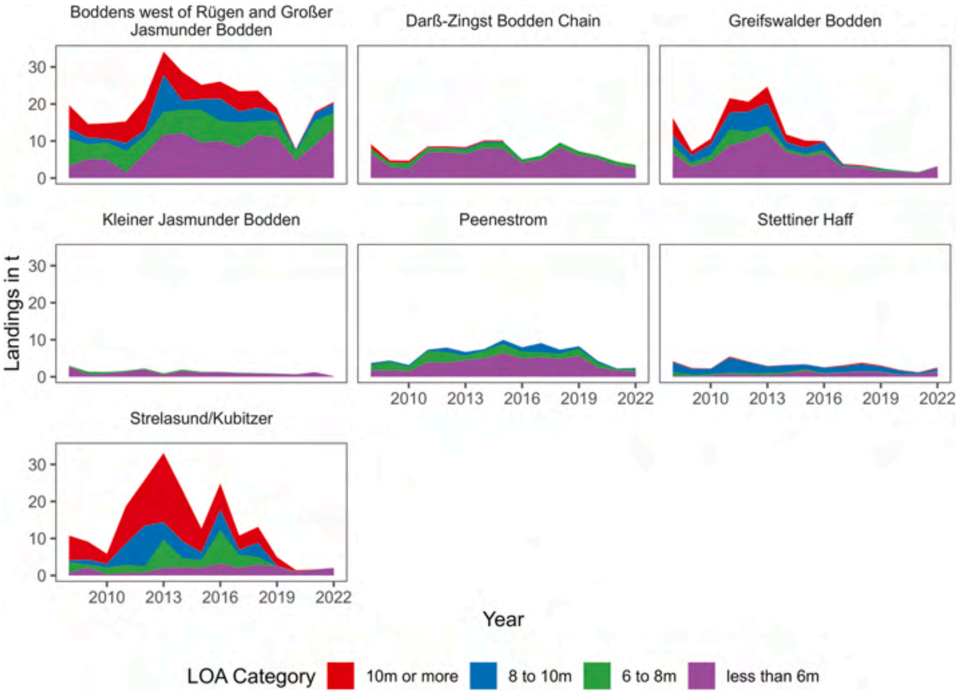


Fig. 7. Annual pike landings by vessel size category and Bodden lagoon, 2008 – 2022 (data source: LALLF).

lagoons Boddens the lowest. In 1965, among the freshwater fish pike represented 4% of the yield and 7.8% of the revenue. Eel (8.1% of yield, 21.2% of revenue), pike-perch (6.2% of yield, 15.6% of revenue) and roach (18.3% of yield, 8.3% of revenue) were economically more important species than pike, but the single most important target species continued to be herring (45.6% of yield, 34% of revenue) (Schlumpberger et al., 1966). Pike were marketed in two size classes (sorting I and II), with the larger sizes classes being economically more relevant. To increase the yield of pike, research projects were developed, minimum-length limits increased and stocking operations with saline-adapted pike started (Falk, 1965, 1966), which were later discontinued to the lack of obvious relationships of stocking rates and pike yield.

6.2. The commercial fishery after the collapse of the GDR

Although historically a regionally important fishery, the number of coastal fishing enterprises has been strongly declining over time and specifically since the German reunification in 1989, sharply reducing the fishing capacity and the number of full time and part-time fishers operating in the region (Arlinghaus et al., 2021). Currently, coastal fishers around the entire coastline of MWP face diminishing fishing opportunities and drastically shrunk quotas for their economically dominant marine species herring and cod, putting pressures on the livelihood of commercial fishing in the region. However, so far these developments have not strongly reduced the total landings of freshwater fish in the lagoons, which have been relatively stable despite the strong reduction in the number of fishing businesses since the 1990 s (Arlinghaus et al., 2021). As we describe below in more detail, lagoon pike currently plays a minor role in the income of the average coastal commercial fisher. The commercial fishery is presently regulated through a licensing system, a minimum mesh size for pike gill nets (100 mm, stretched mesh size), a minimum landing size of 50 cm and a protected season in March and April as well as several fisheries and spawning protection zones that limit access fully (fisheries protection zone) or partly (April and May, spawning protection zones) to commercial fisheries. Commercial fisheries regularly have exceptions to access nature conservation areas or areas with otherwise strict boating regulations, including the areas of the National Park Vorpommernsche Boddenlandschaft, but maximum fishing gear a fisher is allowed to use (e.g. total gill net meters or number of hooks) is capped, and licenses provided to individual fishers relate to selected lagoons (fishing areas). Enforcement of regulations is conducted by the state fisheries authorities and the water police.

Reasons for the demise of commercial fisheries after the reunification are first and foremost related to the changed market dynamics. After the collapse of the GDR in 1989, the fish market was reorganized and transitioned into a free market economy, where state-owned processing factories and fisher cooperatives were privatized. Prices and quantities were now determined by the market, and the coastal fishery, including quotas and vessel regulations and safety standards, was merged into the Common Fisheries Policy (CFP) of the European Union. The state of MWP retained the fisheries rights for the lagoons and today manages that fishery through the state-level fisheries legislation and the state-level coastal fisheries bylaw in addition to the governance within the CFP for quota-regulated marine fishes and the structural aids provided by EU policies. The transition to a market economy revealed the disbalance between supply and demand, particularly for herring, and coastal fishers had difficulties finding buyers for their fish. To soften the impact of the reunification, fishers were offered subsidies for reducing capacity by e.g. scrapping existing vessels, for temporary laying-up (Koemle et al. 2023), but also for investment into new capacity, restoration of vessels, and the foundation producer organizations (Deutscher Bundestag, 1993). Even though the German government did not see the Baltic coastal fishery to be strictly necessary for national food security, the goal was formulated to maintain the fishery as a component of the regional economy, and as an integral component for an attractive tourist destination.

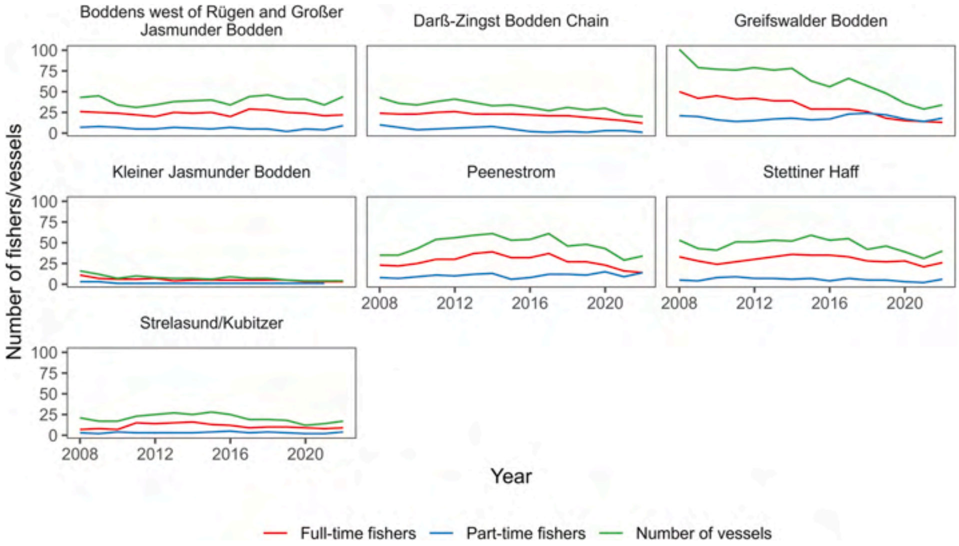


Fig. 8. Number of full-time, part time fishers and boats that have fished for pike in any year between 2008 and 2022, by Bodden area. Note that a single fisher can fish in several Bodden lagoons, i.e. adding up values from individual Bodden will lead to double counting (data source: LALLF).

Despite these support policies, the coastal fishery of MWP underwent substantial structural changes since the German reunification (Döring et al., 2020). While a total of 950 full-time fishers were operating in the Baltic coast of MWP in 1990, numbers have steadily decreased to about 202 in 2020, along with 144 part-time fishers, which are mostly former full-time fishers who took up additional labor outside fishing. In 2020, 150 full-time and 76 part-time fishers were using the lagoon fisheries of Rügen at least once (Arlinghaus et al., 2021). The overall decrease in coastal commercial fisher numbers was mainly related to declines in those operating full time (Arlinghaus et al., 2021); many fishers retired and did not find successors (Döring et al., 2020).

Coastal fishers in MWP typically segregate into coastal, beach and lagoon fishers, some have licenses and quotas for selected fishes to be captured both in the outer coast and the lagoons, such as herring. The freshwater fish in the lagoon fisheries have never seen any enterprise-level quota systems and thus remain indirectly managed through a range of input and output rules to be described in more detail in Section 8. The fishery is currently divided into several statistical areas for which licenses are provided and landings are mandatorily reported by fishers to the public fishery authority of MWP. For 2008–2020, detailed public socio-economic and landings data held by the fisheries authority (LALLF) exist that we analyzed for this synthesis (Figs. 7,8). For this period, pike landings and revenue data were available by one of the following fishing districts: (1) Stettiner Haff, (2) Peenestrom and Achterwasser, (3) Greifswalder Bodden, (4) Strelasund including Kubitzer Bodden, (5) western Rügen Bodden chain and Großer Jasmunder Bodden, (6) Kleiner Jasmunder Bodden, and (8) Darß-Zingst Bodden chain. From 2008–2020, the number of fishers who have fished for pike has remained relatively stable, with the exception of Greifswalder Bodden, where this number has decreased (Fig. 8). The number of boats fishing for pike generally followed the trend of the number of fishers, and have particularly decreased in Greifswalder Bodden as well, which historically has been a prominent pike fishing area (Subklew, 1955a; b) but today plays a minor role.

The characteristics of boats fishing for pike differ between the lagoons and have changed over the recent years. Average horse power in the period 2008–2020 was 23.6 (sd=24 min = 0, max = 162), while the average length over all (LOA) was 6.43 m (sd = 2.10, min = 3.8, max = 12.6). In the year 2012, the on average strongest and longest boats were fishing in the Strelasund area (Fig. 7), which goes along with an increase in pike landings from vessels above LOA 10 m in the same area, culminating in a peak of pike landings in 2013 (Fig. 7). The vessels fishing in the Greifswalder Bodden have remained at the same average length in 2012 and after, but the share of larger vessels has steadily decreased along with landings of pike (Fig. 7). Note, however, that the historically most important species in Greifswalder Bodden is Western Baltic spring-spawning herring, which has suffered substantial stock declines and associated quota reductions in recent years (Polte et al., 2021). The vessel structure in the Boddens west of Rügen and in the Greifswalder Bodden have remained relatively stable; however, pike landings here have been increasingly realized with vessels of less than 6 m LOA, particularly after 2011/12 (Fig. 7).

Compared to other species, pike is playing a minor role as a share of revenue since 2008 (Table 2), fluctuating between less than 1% and 3.25% of industry revenue throughout the years and ranging from 61,000 € in 2020 to 210,000 € in 2013 in absolute numbers. In recent years (2020 - 2022) the revenue shares have been rising, indicating price increases in years withlower absolute supply (which could contribute to keeping harvesting pressures high also in years with low stock sizes, Dao et al., 2023) The highest revenues from pike have been produced in the

Table 2
Total revenues from pike and other species in the coastal fishery of MWP including the Bodden in 1000 €, years 2008–2022.

Year	Pike	Other species	Share of pike in %
2008	134	11,956	1.11
2009	105	10,070	1.03
2010	101	10,249	0.98
2011	173	10,046	1.69
2012	173	10,971	1.55
2013	209	10,586	1.94
2014	159	8,891	1.76
2015	134	9,951	1.33
2016	142	9,925	1.41
2017	108	10,028	1.07
2018	131	9,009	1.43
2019	105	6,918	1.50
2020	62	4,650	1.32
2021	88	3,712	2.32
2022	112	3,331	3.25

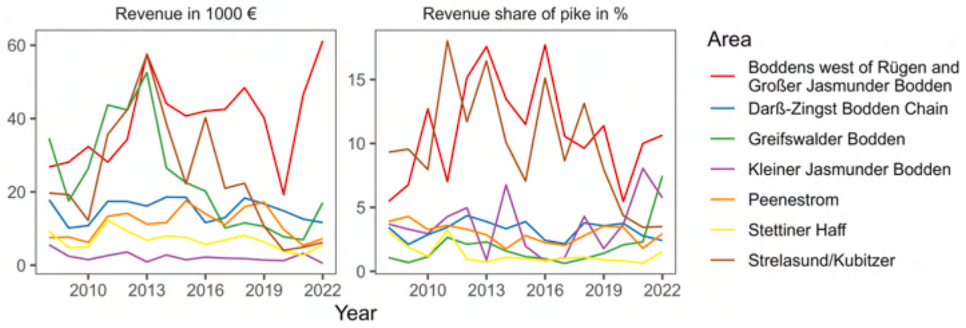


Fig. 9. Revenue from pike in 1000 € and revenue share of pike in %, per Bodden (data source: LALLF).

Boddens west of Rügen/Großer Jasmunder Bodden, where revenues have sharply decreased after 2018 (Fig. 9). Similarly high revenues have been produced from pike in Greifswalder Bodden and Strelasund, where revenues peaked in 2013 and steadily decreased thereafter (Fig. 9). The price per kg of pike varies inversely with the local supply, typically ranging among 1 and 4 €/kg for fresh unprocessed pike sold to wholesalers (Dao et al., 2023). Fishers that process pike and engage in direct marketing can generate a much larger price, depending on demand.

6.3. Future outlook for commercial fisheries

In terms of the future, the outlook for coastal commercial fisheries has been questioned by some (Döring et al., 2020). By contrast, despite substantial restructuring and loss of fisher enterprises the total landings of the lagoon fishery, particularly of the freshwater fish as a whole, have remained stable for a long time (Arlinghaus et al., 2021), suggesting the lagoon fishery maybe more resilient to shocks than the quota-regulated offshore coastal fishery for marine fish. Declines in pike yield – a species with rather local market demand in Germany – have been compensated by increased yields in other species with greater market demand (e.g., perch, pike-perch) or in species with large harvest volume (e.g., bream, roach). The next couple of years will show how the restructuring will continue in light of strong quota cuts of herring and cod in recent years. Döring (2001) suggested that allocating pike away from commercial to recreational angling in the Rügen fishery might induce higher economic impact to the region, but no thorough economic analysis was presented. Prices for freshwater fish in the lagoons have always been relatively high relative to marine species such as herring (often generating a per kg price around 1 €), and the small-scale commercial fishery can find creative ways of marketing their catch and remain viable, even if stock productivity of selected fishes such as pike decline. One reason for the buffering capacity of the fishery maybe the multi-species nature, which can allow portfolio effects, similar to the case in many inland fisheries (Matsuzaki et al., 2019).

7. Recreational fisheries

The productive fish stocks in the shallow lagoon systems around Rügen have attracted recreational fishing since the popularization of recreational angling as leisure activity in Germany in the late 19th and early 20th century (Winkler, 1989, 1990, 2000). Along with increases in leisure time and wealth since World War II there has been a steady increase in the use of the lagoon systems for recreational pike angling (Basan, 1988; Winkler, 1989; Biester, 1991; Dorow, 2004; Arlinghaus et al., 2021, Weltersbach et al., 2021). In this context, the pike stock in the Greifswalder Bodden has been highlighted as particularly sought-after resource for recreational fishing in the GDR prior to the German reunification in 1990 (Basan 1988; Winkler, 1989). However, during the GDR times, constraints on who were allowed to fish for recreation as well as limited availability of boats, motors, and angling gear constrained which areas of the lagoons could be accessed by recreational anglers. For example, as ruled by law in 1955 recreational fishing in lagoons bordering Poland was only allowed from shore and confined to residents living within 10 km of the lagoon waters (Ministerium des Innern 1955). These and other limitations are now overcome as recreational fishing and the associated technology and infrastructure is fully developed in the region.

Recreational angling activity in the coastal waters of Germany, and in the Bodden waters specifically, has sharply increased after the German reunification in 1990 (Arlinghaus et al., 2021; Weltersbach et al., 2021). In particular pike fishing in the Bodden areas using lures from boats and from shore has acquired quite some reputation nationally and internationally as evidenced by non-scientific angling books about the Bodden (Basan 1988; Schroeter, 2006; Fuhrmann and Balkow, 2013), where both residents and international tourists (for example from Sweden, Switzerland or Poland) regularly visit the Bodden waters. Surveys have shown that German anglers choose Bodden sites over freshwater sites specifically to catch trophy pike (Koemle et al., 2022) from boats in the colder season of the year (October to February and also in May, Koemle et al., 2021, Weltersbach et al., 2021). Most of the fishing activity is from small boats, but there is also shoreline bound fishing using waders for pike, including a small segment of pike fly fishers.

A recreational fishing license is obligatory in the state of MWP. In addition, anglers require a valid coastal fishing permit to fish in the lagoons around Rügen or any other area of the Baltic Sea in MWP (Küstenfischereiverordnung MV 2006). Available records of the coastal fishing license sales indicate an increase since the German reunification in 1990 (Fig. 10). From 1990–2015 the total permit numbers rose from 40,000 to roughly 130,0000 (Arlinghaus et al., 2021). Most of this growth arose from non-resident anglers participating in the lagoon fishery (Arlinghaus et al., 2021; Weltersbach et al., 2021). Recently, the numbers have again declined (Fig. 10), likely in response to declining fish stocks, changes in regulations for some fisheries (e.g., introduction of a daily bag limit for Western Baltic cod) and due to the COVID-19 pandemic in 2020 and 2021, which constrained domestic travel (Pita et al., 2021).

As one measure to attract non-resident anglers to the coastline, including the Bodden, in 2005 the state of MWP implemented a fixed-term tourist fishing license that entitles the license holder to fish for 28 days in the state without the need to pass a German angling examination. The tourist fishing license sales rose from 4,000 at the introduction of the license in 2005 to close to 22,000 in recent years, mainly encompassing tourists that are not resident to the state (Arlinghaus et al., 2021). In recent years, both the numbers of tourist angling licenses and also the general coastal fishing permit have plateaued and recently declined, suggesting that the growth of the fishing interest has vanished (Fig. 10). In 2020 and 2022 also two large boat rentals in the region have gone out of business due to declining demand associated with the demise of the lagoon pike stock.

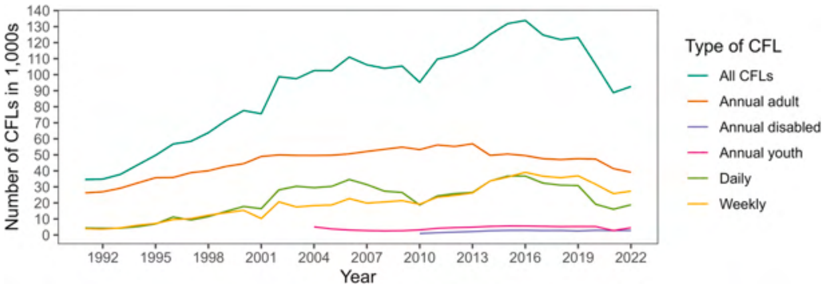


Fig. 10. Sales of coastal fishing licenses (CFL) (including the Bodden) of Mecklenburg-Western Pomerania (MWP). The general fishing license only covers residents of MWP who want to fish anywhere in MWP, while the coastal fishing permit may be bought by any angler who wants to fish in coastal waters of MWP, no matter from which federal state she or he originates. (data source: LALLF, updated from Arlinghaus et al. (2021)).

There are no exact annual records on the total number of Bodden anglers as the coastal fishing license holders in Fig. 10 can also fish in the outer coastline (e.g., for cod), but a telephone-diary study conducted in 2014/2015 estimated about 50,000 Bodden anglers exerting roughly 200,000 angling days just for pike (Weltersbach et al., 2021). These Bodden anglers can be partitioned into residents and non-residents. Non-residents encompass people that travel to the coastline of MWP from other federal states in Germany and from abroad to fish. Out of a total of about 50,000 anglers only 15,000 (30%) were residents from Mecklenburg-Western Pomerania, while 35,000 (70%) anglers came from other federal states to fish at the lagoons (Weltersbach et al., 2021). In terms of total effort (measured in angling days), resident angling at the Bodden accounted for 47% of the total effort of about 390,000 angling days (185,000 resident angler days, 205,000 non-resident angler days), which encompass day trips or multiple-day trips of either short (a weekend) or long (a holiday week) duration. Of these days, about 50% of total effort was directed at pike in the lagoon fisheries (Arlinghaus et al., 2021; Weltersbach et al., 2021).

Since the German reunification, angling media and selected guiding enterprises have advertised trophy pike fishing in the Bodden (Schroeter, 2006; Fuhrmann and Balkow, 2013), which is attracting both non-residents and international anglers (Holgate, 2007). To serve mainly the non-resident angling effort, a commercial angling sector has therefore developed that offers guided fishing trips in the Bodden area, specifically for pike (Fuhrmann and Balkow, 2013; Drossel, 2015). Own analyses revealed that 39 guides operate in the area today offering trips for pike, 49% are full-time and 38% part-time guides, and the rest (13%) are unknown. Anglers alone are responsible for an economic impact of 42 million € (direct and indirect expenses) in the lagoon fishery, creating 420 full time jobs (Strehlow et al., in prep.), particularly outside the peak tourism season in autumn and winter where the fishing effort is concentrated (Ehrchen, 2015; Drossel, 2015; Weltersbach et al., 2021). Roughly half of his economic activity can be attributed to pike recreational angling. For comparison, using similar input-output methods, the total economic impact of coastal commercial fishing in MWP can be approximated by a volume of 10 million € per year, supporting 180 full time jobs. If one takes the revenue shares from Table 2, about 2 - 3 % of the total economic output of commercial fishing can be expected to be directly pike-related (about 140,000 € production volume, supporting 2 - 3 full time jobs). However, there are substantial conceptual and ethical issues in using economic impact measures to motivate allocation decisions among fishers and anglers, which should be avoided following economic theory (Edwards 1991).

What distinguishes the lagoon fisheries from other freshwater sites in the region and beyond where pike also occur? Two key reasons play a role (Koemle et al., 2021, 2022). First, fishing in the lagoon fisheries is thought to be an adventure that taps into the desires of specific angler types that seek challenges. Second, the chances to catch a trophy pike well beyond 100 cm or 10 kg is comparatively high in the lagoon fisheries around Rügen compared to other freshwaters in Germany (Fig. 11).

Fig. 11. Trophy pike are desired targets in the lagoon fishery around Rügen.

The possibility to catch large pike beyond 100 cm in length has also been described in the scientific literature (Winkler, 1989) and is mentioned in the international angling press (Holgate 2017) (Fig. 11). Analyses by Koemle et al. (2021) showed that the expectation to catch a trophy pike and to master angling-related challenges indeed constitute prime motives by anglers targeting pike in the Bodden waters, and Koemle et al. (2022) showed that a large likelihood to catch trophy fish increased utility of fishing to four different angler types, both consumptive and non-consumptive anglers. By contrast, catch rates of pike showed diminishing marginal utility returns to anglers, where each additional pike up to a maximum of 3 per day raised utility, but additional fish did not substantially (Koemle et al., 2022). It is possible that the increased media attention devoted to the Rügen pike angling after the reunification, and the increase in local-level availability of rental boats and other infrastructure including guiding were two reasons that promoted the increase in interest of recreational angling in the lagoons (Fig. 10). Many of these tourist anglers fish for pike, which is also a key target for German anglers in general (Arlinghaus and Mehner, 2004; Ensinger et al., 2016), but there are also avid resident anglers that target pike in the lagoons (Koemle et al., 2022). Given the high catch expectations of pike anglers targeting lagoon pike (Koemle et al., 2022), substantial declines in pike sizes and catch rates of the Bodden pike are bound to negatively affect satisfaction (Arlinghaus et al., 2014; Beardmore et al., 2015). A recent study also showed that lagoon pike anglers preferred ambiguous catch rates (i.e., not knowing exactly the odds of catching pike) over knowing that the catch likelihood was low (Koemle et al., 2022). Therefore, the media attention recently devoted to scientific evidence supporting a decline in the lagoon pike stock in Germany (van Gemert et al., 2022) likely resulted in reduced participation by anglers.

The reduced catch of pike and increasing media attention spreading in angler circles has reinforced the traditional conflicts of recreational anglers and fishers (Arlinghaus et al., 2022). Vogt (2020) conducted qualitative interviews with N = 46 stakeholders in the region, revealing that the two dominant conflicts in the region were among fisheries and conservation and among commercial fishers and recreational anglers. The key conflict among anglers and fishers revolves mainly around exploitative and interference competition for resources such as space and pike (Arlinghaus et al., 2022). The conflict is further fueled by varying norms and beliefs about the causes of pike declines and the erosion of catches. While fishers perceive that catching fish for consumption is an acceptable moral reason for engaging in fishing, many recreational anglers today practice voluntary catch-and-release (Arlinghaus et al., 2021) – a practice heavily resented by commercial fishers on ethical grounds (Arlinghaus et al., 2022). Commercial fishers also sometimes perceive non-resident tourist anglers are infringing in traditional fishing areas where they do not belong (Vogt, 2020). Some anglers and particularly guides on the other hand devalue commercial fisheries based on economic arguments that a pike captured is worth much more when fished recreationally than when traded on food markets (Arlinghaus et al., 2022). Both fishers and anglers want to see greater regulation of the other sector (Arlinghaus et al. unpublished data), but this perspective varies with angler type, demographics and education (Slaton, 2022; Slaton et al., 2023). The conflict among anglers and fishers is today quite heated, with instances of violence and damages of gear being reported (Arlinghaus et al., 2022).

Scientifically it is not clear which sector is contributing most to the harvest of pike. Already prior to the German reunification, Winkler (1989) noted that “anglers catch a non-negligible amount of pike that do not occur in the official landing statistics”. In a different publication Winkler and Debus (2006) speculated that the combined pike harvest by commercial and recreational fishing may affect population abundance negatively, and Dorow (2004) estimated that the recreational harvest exceeded commercial harvest of pike in the Peenestrom. Although in 2014/2015 on average every angler in the Bodden only harvested roughly 1 pike per year (Weltersbach et al., 2021) and despite over the time period from 2005 to 2015 the release rate of pike increasing from 30% to 60% (Arlinghaus et al., 2021), the total biomass of pike harvested by anglers increased parallel to the increase in coastal angling permit sales after the German reunification (Arlinghaus et al., 2021). Although fraught with uncertainties and likely representing the upper bound of harvest that could be expected (likely due to biased sampling of more active and more skillful fishers in the angling diaries underlying the estimates by Weltersbach et al., 2021, Dorow and Arlinghaus, 2011; Lewin et al., 2023), in 2014 anglers’ harvest was estimated to be two to three times higher than the harvest of pike by commercial fisheries (Arlinghaus et al., 2021; Weltersbach et al., 2021). Underreporting of pike by commercial fisheries might contribute to this apparent dominance of recreational fishing harvest for pike (Arlinghaus et al., 2021). In more recent years, equal harvest rates of commercial and recreational fisheries are more likely, based on mark-recapture data (Radinger et al., unpublished data). In spite of the substantial among-year variability, catch reconstructions based on extrapolations of angler numbers suggest that since the early 2000 s the harvest of anglers may have surpassed the pike harvest by commercial fishers (van Gemert et al., 2022, Fig. 12), indicating a shift in dominance of recreational pike harvest over commercial fishing for pike. In recent years, however, a drop in total landings is visible, which coincides with a declining biomass trend following data-poor stock assessment models (van Gemert et al., 2022). Relatedly, since 2010, angling media have started to describe a decline in the abundance of large trophy pike and in the general catch rates of pike in the lagoons (see for an example Ehrchen, 2015; Fuhrmann, 2021). The development around Rügen coincides with other pike stock

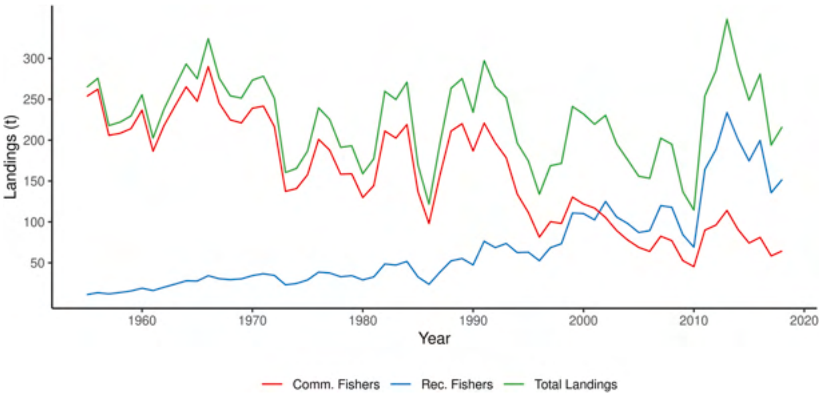


Fig. 12. Reconstructed pike landings in commercial and recreational fisheries around the Island of Rügen from 1955 to 2018. Modified from van Gemert et al. (2022).

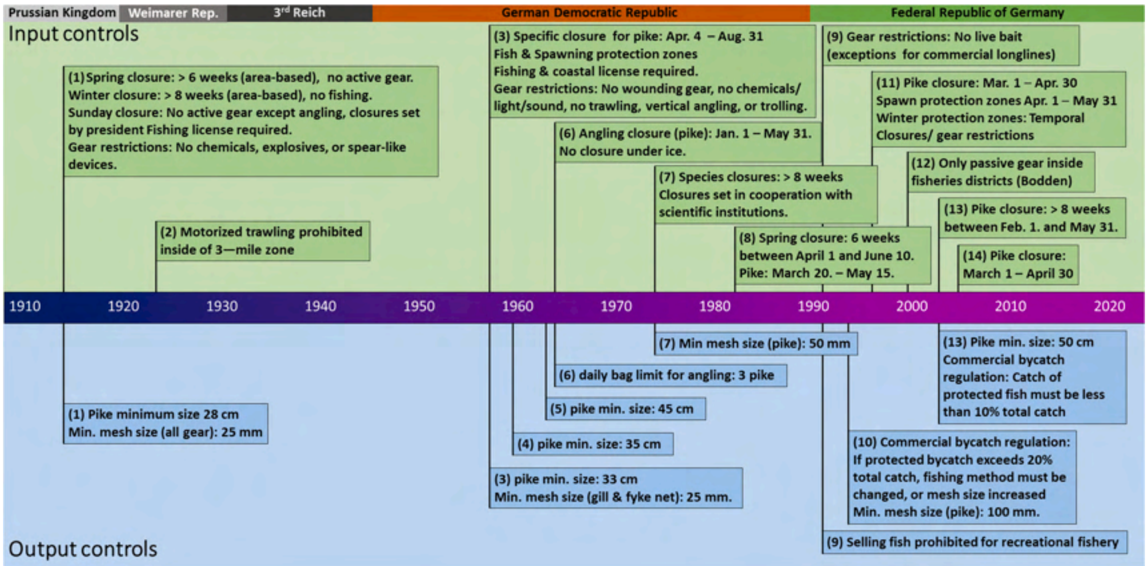


Fig. 13. Timeline of management changes in pike fishery within the time period 1900–2022. Cited law paragraphs are denoted numerically: (1) Prussian fishery law, May 11, 1916; (2) Republic of Weimar order on coastal fishery, April 4, 125; (3) GDR order coastal fishery, Dec. 12, 1959; (4) GDR order on fishery in coastal waters, May 16, 1960; (5) GDR order 3 on fishery in coastal waters, May 24, 1964; (6) GDR order 4 on fishery in coastal waters, Jan. 13, 1965; (7) GDR order coastal fishery, March 3, 1976; (8) GDR order coastal fishery, Jan. 14, 1985; (9) MV state law on fishery in coastal waters, Dec. 6, 1993; (10) MV state order coastal fishery, Oct. 5, 1994; (11) MV second state order concerning amendment of coastal fishery law, March 18, 1998; (12) MV state order coastal fishery, June 5, 2000; (13) MV state order coastal fishery, Jan. 31, 2003; (14) MV state order coastal fishery, Aug. 31, 2005.

developments in the Baltic region, particularly in some areas of Scandinavia, where strong declines in the biomass and size of pike have been reported (Lehtonen et al., 2009; Olsson, 2019; Bergström et al., 2022; Olsson et al., 2023).

8. Fisheries governance and management of lagoon pike

The pike, and more generally the lagoon fishery, has traditionally been managed based on variants of input (measures affecting effort) and output (measures affecting removal of pike) regulations (see Arlinghaus et al., 2016 for categorization) (Fig. 13). Since the Middle ages, lords and later governors appointed by the state have regulated coastal fisheries through various licenses and gear limits and limits on allowed fishing times/spaces (Porada, 2009). However, these regulations tended not to be pike-specific. The Prussian fisheries law of 1916 was the first formal fisheries law in Germany in which specific harvest regulations of pike were enacted for the coastline of MWP (Fig. 13). However, fishing mortality acting on lagoon pike has always been indirectly controlled rather than managed directly through pike-specific annual landing quotas as is typical in marine fisheries in developed nations. The governance and management system for the lagoons thus mirrors the state-specific German inland fisheries system, but within a state-controlled fishing rights system for the coastline; it relies on a mix of measures that provide indirect controls of total fishing mortality and which are decided by the Minister of Fisheries and Agriculture of MWP within a political process involving interest groups and where the fisheries authorities can also implement additional restoration and conservation measures in the short-term to complement the basic provisions as specified by state-specific fisheries legislation. The licensing for both commercial and recreational fisheries in the coastline of MWP (which include the lagoons) is also dealt with at the state level. Interest groups representing fishers or anglers may be involved in decision processes to alter regulations, usually through publicly-registered fisher or angler associations who are given the possibility to comment on draft regulations. Yet, the formal decision-making power to decide on rules and regulations and specifically to change the coastal fisheries bylaw for the coastline lies with political actors at the fisheries ministry level and in relation to pike is rarely or never informed by regular stock assessments, similar to the case in inland fisheries in Germany. The governance system for the lagoons thus largely contrasts with the top-down marine fisheries-management approach of the European CFP that is characterized by regular stock assessments that inform annual quotas decided by the Council of Fisheries Ministers based on recommendation by the European Commission that are distributed to commercial fishing enterprises at the member state level of the EU. That said, also EU's CFP affects the lagoon fishery, e.g., through structural aids or decisions on quota-regulated marine species that can affect the targeting behavior of freshwater fish such as pike (Koemle et al. 2023). However, it is important for the following discussion that the concrete managerial provisions for the lagoon pike are decided at the state level of MWP and not at the EU level.

Input regulations in the form of licenses and gear limits (e.g. bans on the use of explosives, bans on motorized trawling), including regular exemptions for certain gear types for private consumption by casual or household fishers, have been present since the Middle Ages and throughout the 18th and 19th century (Porada, 2009), ultimately codified in the Prussian fisheries law of 1916 (Fig. 13). General temporal closures, e.g., during spawning time, were enacted in 1916 as well, but initially these protected seasons were not species-specific. Since 1916 and specifically during the GDR regime after World War II, spawning closures could be systematically implemented by the local fisheries authorities, also for pike specifically (Fig. 13). However, because of the socio-economically exposed role of commercial fisheries to safeguard national supply of fish, these spawning closures in the lagoons typically only applied to recreational fisheries. For example, during the GDR regime, spawning closures to protect spawning pike in 1959 and 1965 only related to recreational fisheries (Fig. 13). A pike-specific temporal closure during the spawning time that also encompassed commercial

Table 3
Current regulations for lagoon pike fisheries, categorized into commercial and recreational fisheries and input/output regulations.

Type	Regulation	Commercial fishery	Recreational fishery
Input	**Protected season**	1st of March - 30th of April	
	Gear limit	Limited per fishery district (limit on overall gear use, but not in fishing days)	Limited per person (no limit on overall fishing day)
	Gear restrictions	**Only** passive gear	3 rods & 1 baitfish rod, 6 baited hooks per rod
		Mesh size (stretched) for gill nets (for pike) ≥ 100 mm	Trolling not allowed within fisheries districts in lagoon
		Minimum mesh size fyke net 25 mm	
		Fyke net restriction to area ≤ 1/3 of water width	
		General prohibition of snagging gear	
		Minimum distance between gear types 50 m (300 m to fyke nets)	
		Persons fishing with mobile gear (e.g. angling) have to stay way from passive gear (e.g. gill nets, fyke nets)	
	Area with permanent closure (Fischereischonbezirk)	13.56 km^2	13.56 km^2
	Area with seasonal closure (Laichschonbezirk)	99.66 km^2 (01. April - 31. May)	99.66 km^2 (01. April - 31. May)
	Area requiring special permit	0 km^2	24.5 km^2
	Area with restricted access	139.2 km^2	388.9 km^2
Output	**Minimum-size limit**	50 cm	50 cm
	Bag limit/quota	None	3 pike per angler and day
other	**Reporting obligation**	Yes	No
	Labeling **obligation**	Yes	No
	Market approval	Yes	No

fisheries was firstly enacted in 1985 (Fig. 13). Subsequently, the specific time frames where pike was not allowed to be harvested have varied, but often encompassed the months of March and April in each year (Fig. 13). Today, during the pike spawning closure of March-April, commercial fisheries are only allowed to have 10% of pike in terms of biomass as by-catch, but if this happens they have to change location and are not allowed to market the catch.

Spatial fisheries closures where all forms of fishing was prohibited year-round and closures during the spawning period (typically only bans on harvest during two months in the spawning period) have become part of the input regulatory mix since the 1960 s and apply to all forms of fishing (Fig. 13). Note that there are different spatial closure types in the fisheries legislation for the coast: one that bans access and take to both anglers and fishers year-round (Table 3, Fischereischonbezirk, 13.56 km^2 or 1% total extension) and one limiting access and fishing activity for two months, supposed to protect spawning fish more generally (Table 3, Laichschonbezirk, 99 km^2). The latter typically apply to bay-like extensions (Lauterbach, 2001) and may cover a portion of the pike spawning time (e.g., April and May). Only the fisheries closures are fully closed to all forms of fishing, which represent a negligible portion of the entire lagoon area of 1,433 km^2 (13.4 km^2 or 0.9%). Another 7% of the area of the lagoons is fully protected from fishing during two months in the spring spawning season and as such may also protect pike, who happens to be a spring-spawning species. All other area-based conservation areas in the region and those littoral areas that are not well accessible to recreational anglers (e.g., due to bans on motor boating, Table 3, Fig. 14) have been motivated by nature conservation more generally and carry important exemptions to access for commercial fisheries, and in some cases also exemptions to anglers are possible (11% of all lagoons are areas with potential exemptions, Table 3, see Tab. S1a,b in the appendix for details). Other area-based regulations, specifically boating regulations that limit access of motorboats to selected areas, selectively target recreational fisheries as commercial fisheries have exemptions. As the no-take areas are spatially very limited, we can thus conclude that most conservation areas are effectively open to some form of fishing, specifically commercial fishing, and are hence partially protected areas or even paper parks. Enforcement of regulations is mainly organized through the police as well as dedicated fisheries officers, but the control frequency is low and people complaint about regular rule breaking (e.g., in areas without permission to be accessed by anglers, Vogt, 2020), some of which maybe due to the complexity of regulation leading to low awareness of the local rules.

Most spatial input regulations other than Fischschonbezirke and Laichschonbezirke were directed at protection of certain habitats and other species than pike, first established in 1922 and 1925 during the Weimarer Republic (Klafs, 1989; Ostermann et al., 2015; Jeschke and Sporns, 2012). Most non-fisheries related conservation measures of that time were related to bird conservation, which has become increasingly important after the German reunification associated with various conservation laws at the EU level. Over time, the degree of space fully or partially protected from fishing for conservation reasons has increased in the lagoons, and bird protection continues to feature high in the political priority of conservation agencies (Fig. 14). In terms of nature conservation areas, the Nationalpark Vorpommersche Boddenlandschaft and the Biosphere Reserve Südost-Rügen, both formed in 1990 after the German reunification (Jeschke and Sporns, 2012) encompass the largest conservation areas of the region (Fig. 14). Regulations concerning commercial fishing and recreational angling in the national park, the biosphere reserve and the various smaller protection areas managed by the Staatliches Landesamt für Landwirtschaft und Umwelt (STALU) vary depending on conservation goals of the respective area or subarea (see Supplementary Material). Regulations also vary depending on the whether the area belongs to the core or extended areas of the national park or the biosphere reserve. In many cases, such as the biosphere reserve, fishing and angling is not prohibited per se, but strict boating regulations like prohibition of combustion motors or restricted access to shoreline impose effective restrictions for the recreational fishing effort. A comprehensive list of individual protection areas and their specific regulations concerning recreational and commercial fishing is given in the Supplementary Material.

In terms of output regulations, the first minimum-landing sizes to maintain the pike stock around Rügen were implemented during the German Empire in the first decades of the 20th century (Walter, 1927). The first size limit of pike as specified in the Prussian Fisheries Law (Fig. 13) was only 28 cm, which is smaller than the size-at-first-maturation in this species for females (Raat, 1988). Over time, minimum-length limits for pike rose from initially 28–33 cm, then 35 cm and later to 45 cm in the 1960s (Falk, 1965) and 50 cm today (Fig. 13). In 1965, the GDR also enacted a daily bag limit of 3 pike per recreational angler and day, which is in effect until today. No maximum or daily limits on pike removals have existed or do exist today for the commercial fishery. Early harvest regulations enacted specifically for pike in the first half of the 20th century were not backed up by local ecological studies, and it was not until the first scientific studies directed at pike emerged during the GDR regime in the 1950 s and 1960 (e.g., Hegemann, 1958; Subklew, 1955a; b; Falk, 1965, 1966) that management took a step towards biologically informed measures, such as the spawning protection seasons being scheduled according to the actual spawning season of pike (Hegemann, 1958), and the implementation of size limits informed by size-at-maturation and yield maximization principles in the 1960 s (Falk, 1965). More recently, further studies on lagoon pike were completed in the region, but most were unpublished master theses (Junker, 1988; Korich, 1993; Neubert, 2011), unpublished reports (Lauterbach, 2001) and more recently a dissertation (Möller, 2020).

The current management regulations for pike (Table 3) were largely implemented shortly after the reunification by the first legislation of the Coastal Fisheries Act (Küstenfischereiverordnung, KüFVO M-V, 6th of December 1993). Regulation of the fishery in the current legislation is that of a state-regulated open-access (Homans and Wilen, 1997) system, in which the state authorities give out licenses and permissions enabling access to the fishery to commercial (both full time and part-time) and recreational fisheries (typically recreational anglers, but also recreational fishers who fish for own consumption with other gear than angling). Additional regulations such as gear and area restrictions, minimum-size limits, protected seasons and areas and daily bag limits (for recreational anglers only) are installed by the state ministry for fisheries, occasionally informed by local scientific studies. Recreational anglers are not allowed to sell fish, including pike, and there is a small sector of recreational fisheries that are allowed to use non-angling gear for acquiring fish for personal consumption. Only part-time and full-time fishers are allowed to sell pike in markets. Enforcement is organized by the public authorities and assisted by volunteer officers from recreational fisheries who control recreational anglers, but there is no study on the effectiveness of the enforcement. Nature conservation regulations are decided by the same ministry and assisted by the upper and lower nature conservation authorities and the two independent authorities governing the national park Vorpommersche Boddenlandschaft and the biosphere reserve Südost-Rügen as well as other conservation areas. When examined in detail, up to the present day, key objectives, at least those found in formal policy documents, to develop fisheries or for conservation are merely ecological in orientation and lack socio-economic objectives as well as explicit objectives designed for recreational fisheries. Some anglers and angling guides thus lament that public policies are often directed at either maintaining commercial fisheries or for conservation, while the policy system disregards or devalues recreational fisheries objectives (Vogt, 2020; Arlinghaus et al., 2022).

In addition to input and output controls and various gear-related regulations, the pike stocks have also been supported by stocking both in the 1930 s (Subklew, 1955b) and later in the GDR (Falk, 1966), partly relying on offspring from saline-adapted stocks (Falk, 1966) raised in two hatcheries in Born and Gager. However, outcomes were not satisfying and stocking discontinued by the mid 1970 s. A new attempt for assessing stocking outcomes was made after the reunification with the release of freshwater raised fingerlings released in the Peenestrom, but results were again negative and stocking not recommended to be pursued further (Dorow and Lemcke, 2004).

Since the 1970 s, water infrastructure management in the area resulted in the loss of wetlands through dikes and the loss of access to tributaries (see Section 10 and Roser, 2021; Roser et al., 2023). Water pumping systems and dikes were widely installed in the so called “Great melioration” in the 1970 s and 1980 s during the GDR, which blocked access to flooded wetlands and tributaries for pike around Rügen (see Roser, 2021 for more details). In recent years, for nature conservation reasons several dike removals and rewetting projects have been completed (see Section 10 for details). None of them were planned with pike rebuilding as an objective. No monitoring data exist on the outcomes of these restoration activities.

9. Stock status of the Rügen Pike

Insufficient data is available for the completion of standard stock assessments typically performed for data-rich stocks because there has never been a systematic coastal monitoring for Rügen pike. However, several data-poor assessments are available that shed light on the stock status of the pike stock around Rügen.

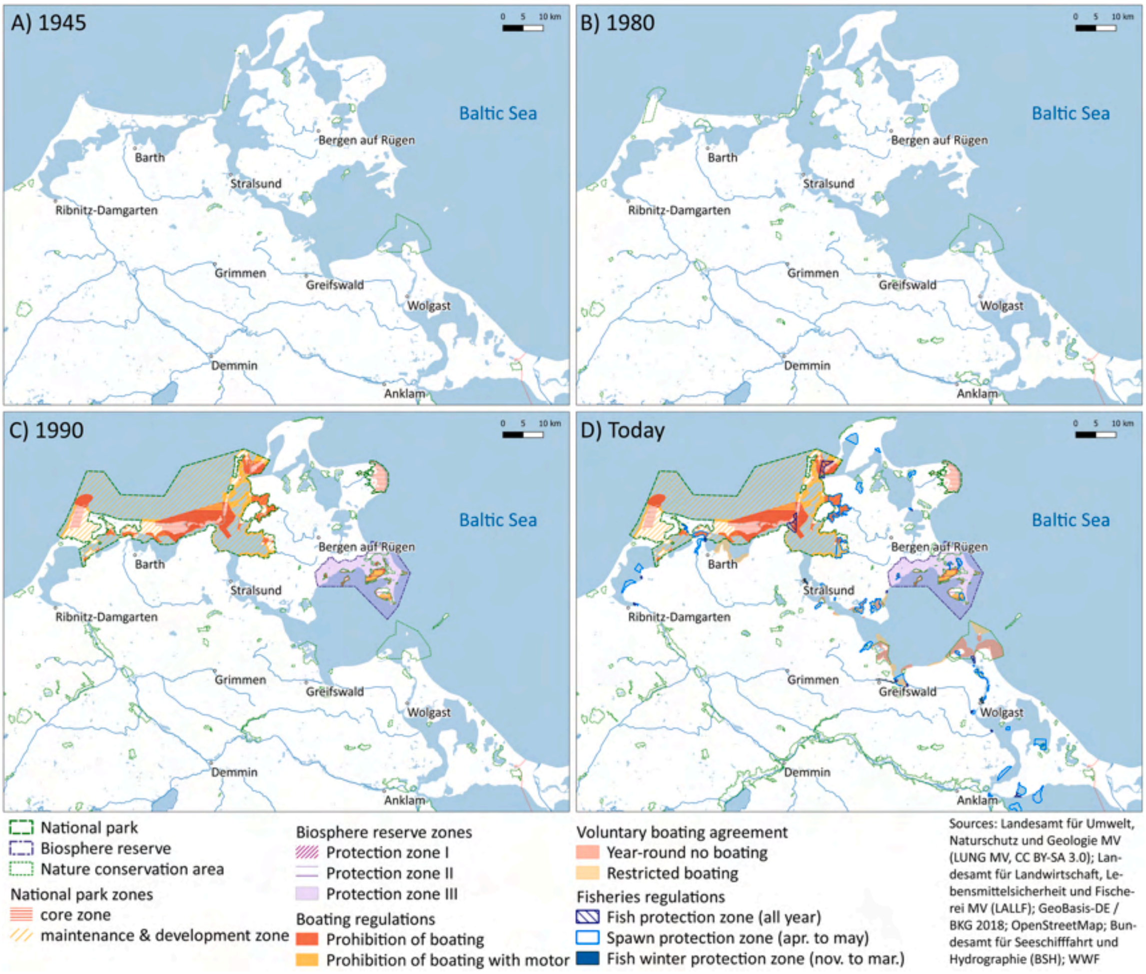
9.1. Trends in commercial landings

There is a long time-series available on commercial landings of pike in the Bodden area, which is available back to 1955 (Fig. 6). It would be convenient if the trend in these landings would also indicate the trend in stock status. Unfortunately, raw landings data are not a reliable indicator of stock status, because that trend does not consider the changes in fishing effort or catchability over time (Ovando et al., 2022). However, fishing effort is unknown for the pike fisheries in the lagoons. Fortunately, perhaps, several predatory freshwater fish are captured in the leading commercial gear, typically gill nets, and some of these species, such as pike-perch, have consistently had a high market value over time and thus were always in demand. Thus, it can be assumed that the commercial fishery in the lagoons has consistently operated with a reasonable gill net effort, and pike could have been captured as by-catch, even when fishers were targeting other freshwater fish. Therefore, it might still be possible to infer some information on the trends in the pike stock by looking at pike landings if we also look at concurrent landings of pike-perch. Waters that contain an abundance of pike often contain fewer pike-perch (Winkler and Debus, 2006), and vice-versa. A likely cause of this is that pike-perch favor turbid, macrophyte-less eutrophic waters, whereas pike reproductive success and stock biomass depends crucially on submerged macrophytes and other underwater structures, which often disappear with eutrophication (Winkler and Debus, 2006). Assuming that pike and pike-perch are caught with the same fishing gear (e.g., gill nets of similar mesh sizes), there should be no difference in the effort trend experienced by pike and pike-perch in the Bodden around Rügen. Thus, by looking at how trends in pike landings compare with trends in pike-perch landings for individual Bodden, it may be possible to deduce changes over time in the suitability of a given Bodden for pike, at least in terms of trophic state.

Results show that the combined area of lagoons west of Rügen and Grosser Jasmunder Bodden has consistently produced greater pike than pike-perch landings, whereas the reverse is true for the more eutrophied Peenestrom and the DZBC (Fig. 15). The highly eutrophied Kleiner Jasmunder Bodden has had a brief period where pike-perch landings decreased in levels toward those of pike, but has otherwise largely been dominated by pike-perch landings in line with its strongly hypertrophic state (Table 1, Fig. 15). Lastly, Greifswalder Bodden and the combined area of Strelasund and Kubitzer Bodden have historically generated more pike than pike-perch landings, but over time this difference has been reduced to roughly equal landings of both species, suggesting a decline of pike as both areas are rather meso-trophic to weakly eutrophic with reasonable vegetation densities (Fig. 15). Overall, if these trends in landings can be seen as trends in habitat quality for pike and pike-perch, then it would seem that habitat quality for pike (or stock abundance more generally) has been declining around Rügen (Olsen et al., 2023), with only the combined area of the Westrügen/Hiddensee and Grosser Jasmunder Bodden maintaining landings of pike that consistently exceed those of pike-perch. Overall, there is also a strong decline in pike landings in all major lagoons that traditionally generated high pike yield (e.g., Greifswalder Bodden, Boddens west of Rügen, Strelasund, Figs. 7, 15). Clearly, changes in landings can and will also reflect changing consumer demands, changed harvesting incentives (e.g., alteration of fixed price policy after the reunification), changes in gear catchability and reductions in effort, so that our analysis only offers tentative suggestions in line with other area-specific analysis in the past (especially for the DZBC, Winkler, 1991; Winkler and Debus, 2006).

9.2. CPUE index of pike abundance

Combining a time-series of landings with a time-series of effort into a CPUE time-series allows for more reliable deductions on stock status trends (Ovando et al., 2022). For the Bodden pike, high-resolution data



Sources: Landesamt für Umwelt, Naturschutz und Geologie MV (LUNG MV, CC BY-SA 3.0); Landesamt für Landwirtschaft, Lebensmittelsicherheit und Fischerei MV (LALLF); GeoBasis-DE / BKG 2018; OpenStreetMap; Bundesamt für Seeschifffahrt und Hydrographie (BSH); WWF

Fig. 14. Fisheries and nature conservation-related areal-based conservation zones of the Bodden lagoons during WWII (upper left panel), during the GDR regime (upper right panel), at the end of the GDR regime (lower left panel) and after the reunification of Germany (lower right panel). The size of the individual nature conservation areas may have changed over the years due to area expansions. The sizes of the nature conservation areas are shown in their current size at the respective points in time, unless the respective areas were available elsewhere.

in commercial effort (e.g., effort in gill net nights or fyke net nights per fisher per day/month) is unavailable. However, from 2008-onward, there exists data that allow a rough index of effort (i.e., number of boats landing at least some pike), which can be used to estimate pike fisher-boat specific landings per Bodden per month as a CPUE index. However, since the boat data are only available from 2008-onwards, it represents a relatively short effort time-series, probably too short to be able to make any meaningful conclusions about long-term trends in stock status. Also, there is a limitation that pike boat numbers do not necessarily indicate the amount of gear used, such that the boat index can only be a rough CPUE index that remains uncertain. However, as the lagoon fishery for predatory freshwater fish is a multi-gear fishery and species with higher commercial demand, such as pike-perch and perch, are targeted with a similar gear, pike boat numbers are perhaps not a completely unrealistic effort index. Additional lower-resolution commercial boat effort for the Bodden area is available from 1992 onwards, obtained from the EU Fleet Register. This register gives an overview of all fishing vessels registered to any member state of the EU over time, including the port they are registered to and some of their characteristics such as length and power. Filtering out the boats registered to ports in the Bodden area, matching those ports to specific Boddens, and removing boats greater than 20 m in length (which are assumed to fish on the Baltic Sea) gives Bodden-specific time-series of commercial effort from 1992 onwards. For the time before 1992, the GDR had detailed boat registers for boats below and above 12 m in length, and these data were available back to 1955 and also used to express pike landings per lagoon boat.

The analysis on pike landings per registered lagoon boat from 1955 to 2019 show that, aggregated across all lagoons, the pike CPUE has been strongly decreasing since the early 1960 s (Fig. 16). When looking at disaggregated data at lagoon levels for the shorter time series from 2008 to 2020 and relating the pike landings to the number of active fisher boats landing at least some pike (Fig. 17), it is revealed that the stocks have been stable in the historically less dominant and more eutrophied DZBC, the Peenestrom, and Kleiner Jasmunder Bodden, there is a weakly negative but statistically significant CPUE trend in Greifswalder Bodden and a strongly negative, but statistically not-significant trend for Strelasund/Kubitzer Bodden as well as the lagoons west of Rügen and north of Rügen (including Grosser Jasmunder Bodden) –the three historically dominant pike fishing lagoons (Schlumpberger et al., 1966). Clearly, above-mentioned limitations as to the effort index apply.

9.3. Formal data-poor stock assessments: catch-only and length-based models

There is not enough data available on pike in the Bodden for a standard catch-at-age stock assessment. This is a problem faced by many fisheries worldwide, especially those of relatively low economic importance (Ovando et al., 2022). Data-poor stock assessment methods have been developed to try and obtain information about stock status when there is not enough data available for a standard stock assessment (Free et al., 2020). One type of data-poor stock assessment methods are catch-only models (COM). Given their data-poor nature, the results of individual COMs can be prone to bias and inaccuracy (Free et al., 2020). Combining the results of multiple COMs in an ensemble approach has been found to increase accuracy and reduce bias in the estimate of stock status (Anderson et al., 2017; Free et al., 2020). This approach was used for the lagoon pike stock in Germany by van Gemert et al. (2022) (Fig. 18).

The landings time-series of van Gemert et al. (2022) consisted of commercial landings and reconstructed recreational removals of Bodden pike from 1955 to 2018. The authors then fitted seven different COMs to this fishery-dependent catch time-series. They in turn fitted results to three ensemble models trained with simulated data, thereby getting an estimate of the mean and slope of B/B_{MSY} over the past 5 years. The results indicated that the Bodden pike was close to or already being growth-overfished ($B<B_{MSY}$), that its biomass was declining below the level that would produce maximum sustainable yield (MSY) (Fig. 18), and that the fishing mortality rate was rising in the last ten years (Fig. 19). Length-based assessments fitted to length structure data collected from 2019 to 2021 supported the results of the catch-only models, revealing that the current spawning potential ratio is slightly above the target reference point of 0.4 (Droll, 2022; Fitzgerald et al. 2023) and the recent fishing mortality is about 0.2 – 0.4 per year (Fitzgerald et al. 2023). Collectively, the results indicated a fully exploited to slightly growth overfished stock, with the current fishing mortality being larger than target fishing mortality rates, and the current stock biomass declining. The total fishing mortality rate is rising and biomass falling (Fig. 19), suggesting that the underlying recruitment is declining or non-fishing mortality is affecting abundance (e.g., natural predation on adult pike), perhaps due to the joint influence of environmental change and a fishing mortality rate that is too high relative to the current productivity of the stock (van Gemert et al., 2022).

9.4. Stakeholder-based stock assessment

Knowledge of local stakeholders can help increase confidence in the assessment results. Although individual perceptions of stock status can be prone to biases, multiple studies have found that local stakeholder knowledge and model results can match (Aswani and Hamilton, 2004; Neis et al., 1999), and that local stakeholders can have a good understanding of local ecological dynamics of pike (Aminpour et al., 2020). We asked fishers and anglers about the perceived trends in recent stock status of the Bodden pike (see Fig. 20 for sample size). The majority of respondents (> 69%), both anglers and fishers, indicated they perceived a strong or very strong decline of the stock in recent years, as well as a perceived decline in the abundance of large (> 1 m) individuals. Anglers perceived a more negative trend than fishers (Fig. 20). These results matched the results of the formal stock assessments, increasing confidence in the estimate that the Bodden pike stock is currently declining in abundance (and therefore catch rate and size of fish in the catch) and approaching or has even already undergone growth overfishing. The stock has clearly experienced size and quality overfishing, which

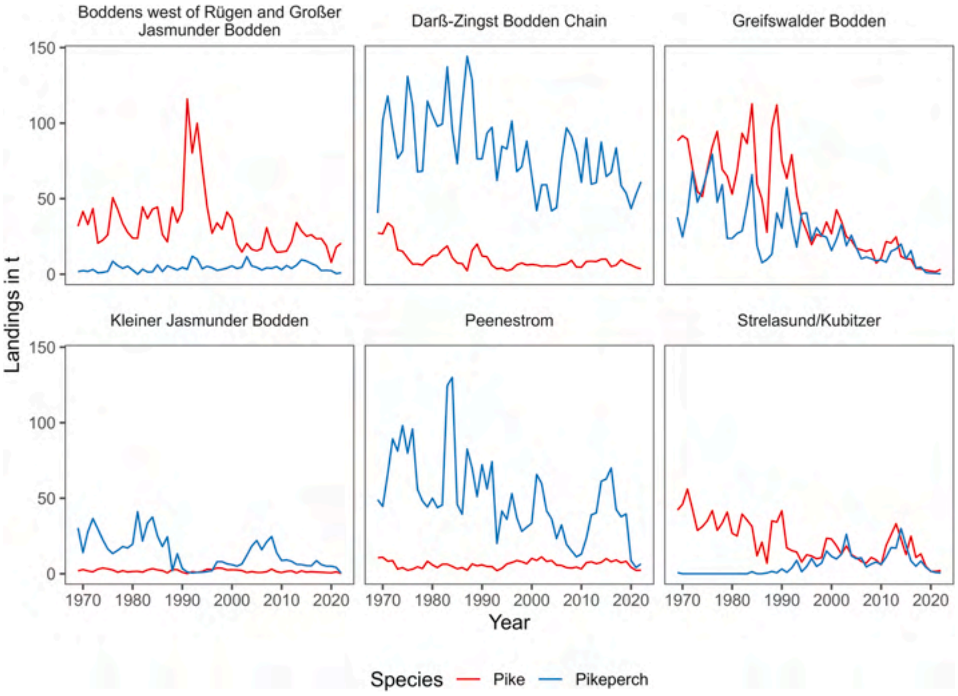


Fig. 15. Commercial landings of pike (red) and pikeperch (blue) in the various Bodden around Rügen since 1969 to 2022. See also Fig. 7 for area specific pike landings by boat type. (data source: LALLF).

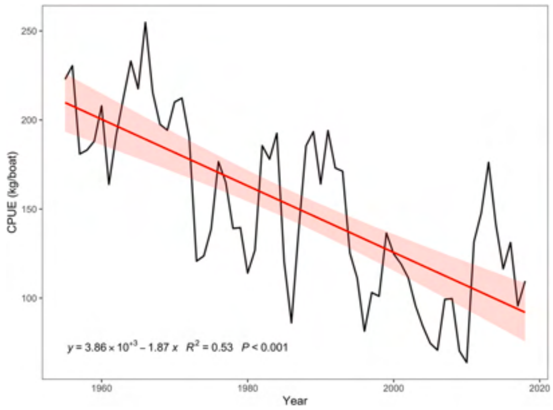


Fig. 16. Landings of pike (in kg) per fisher boat fishing in or being registered in ports in the lagoons from 1955 to 2019.
Modified from Droll (2022).

jeopardizes particularly the fishing quality of anglers (Ahrens et al., 2020; van Gemert et al., 2022). It is possible that the catch rates further decline in response to the high catch-and-release rates of 60% (Arlinghaus et al., 2021), which can induce timid, hook-shy pike (Arlinghaus et al., 2017b).

10. Assessment of contemporary environmental drivers affecting the lagoon pike stock

To understand the possible reasons underlying the recent decline in pike abundance and biomass in the lagoons in the southern Baltic Sea, we compiled data and literature emphasizing possible environmental trends, including those related to anthropogenic factors, in the last 10–20 years since about 2000. We focused on this time period because changes during this time would best explain the contemporary status and the decline in pike biomass since 2010. We assume that environmental changes happening in previous decades, e.g., 1970–1990, could be excluded as primary reasons to explain the current trends.

10.1. Fishing pressure

As mentioned before, the current biomass trends of adult pike is declining, suggesting either recruitment is impaired or adult mortality excessive. Although absolute commercial pike landings have been falling since 1990 (Fig. 6), the combined fishing mortality rate is increasing since 2010 and is now above F_{MSY} (van Gemert et al., 2022). While the recreational fishing mortality rate was likely dominating the harvest in 2014/2014 (Arlinghaus et al., 2021), unpublished mark-recapture data for 2019–2021 suggest that the commercial and recreational fishing mortality was roughly equal in 2020 and 2021, perhaps because recreational anglers increasingly release pike rather than harvest them and angler numbers have been falling in recent years (Arlinghaus et al., 2021). Notably, during the COVID pandemic angling pressure in the lagoons has been low (Britton et al. manuscript in review). Nevertheless, given the negative biomass trend and the current fishing mortality rate exceeding F_{MSY}, both recreational and commercial fishing mortality combined are likely affecting the adult pike stock and pressures are rising, despite lower absolute landings in recent years in the commercial fishery. Moreover, it is well possible that local overfishing occurs where local stocks in selected lagoons or bays are heavily targeted by either commercial or recreational fisheries, which can affect local abundance negatively (Jansen et al., 2013). Importantly, angling catch-rates were found to be substantially greater in no-take protected areas compared to open areas (Roser, unpublished data; Eklöf et al. 2023), collectively suggesting that fishing pressure is affecting the abundance of pike. Further impacts on angler catch rate could emerge from fisheries-induced timidity effects affecting the catchability of pike particularly to lures (Beukema, 1970; Arlinghaus et al., 2017b,c, Monk et al., 2021), which are heavily used in the lagoon fishery.

10.2. Natural predators

Although a range of natural predators, including seals, cormorants, otters (*Lutra lutra*) and white-tailed eagle (*Haliaeetus albicilla*) predate on pike (Fig. 22, for eagle, see Nadjafzadeh et al., 2015), in terms of predator abundance only cormorants and seals matter in the lagoons. We will therefore focus on these two species.

Seals: Seals, in particular the grey seal, have been shown to incorporate northern pike as important prey (among 11% and 20% of biomass in diets) in coastal systems in Sweden (Svensson, 2021; Bergström et al., 2022). The total Baltic Sea population of grey seals has strongly declined from the 1950 s onwards due to intensive hunting and environmental pollution by organochlorines, which caused infertility of females (Bäcklin et al., 2010). The Baltic subspecies (*Halichoerus grypus grypus*) was on the brink of extinction. Due to the implementation of consistent protection measures in the 1980 s, grey seal numbers increased steadily from a few thousands in the early 1990 s to 42,000 in 2021 (ICES, 2019, 2020; HELCOM, 2021). These numbers are still far below the historically documented population size of 88,000 - 100,000 individuals at the beginning of the 20th century (Galatius et al., 2020; Wendt, 2018). About 90% of the Baltic grey seal population can be found in the northern Baltic Sea, less than 10% occur south of the island of Gotland in the southern Baltic Sea (Galatius et al., 2020; HELCOM, 2021). Even though grey seal numbers in the southern Baltic Sea are still comparatively small, there is a high population growth rate in recent years: in 2003, only 146 grey seals were counted (1% of the total Baltic Sea population). By 2015 the numbers have increased to 2,600 (7% of total population) (Galatius et al., 2020). This rapid growth was also reflected in an increase of carcasses found at the coasts of MWP, from less than 10 carcasses per year until 2007 up to more than 50 carcasses in 2020 (Herrmann et al., 2016; Maschner et al., 2014; Reif et al., 2021). Fig. 23 shows the development of abundance of seals in Greifswalder Bodden between 2007 and 2021, revealing a rising trend in the Greifswalder Bodden area but also strong seasonal fluctuations. The median abundance recorded across all months in a year has risen from close to zero in 2007 to about 120 in 2020, with peak numbers close to 500 in certain months of the year (Fig. 23). Highest sighting frequencies occur between February and May during the herring spawning season around the island Greifswalder Oie east of Greifswalder Bodden (Buschhaus and von Rönn, 2022; von Nordheim et al., 2019).

The daily food requirement for adult grey seals varies between 4 and 8 kg of prey fish (Wendt, 2018; Nestmann and Harder, 2014). Studies on stomach content in the Baltic Sea confirmed opportunistic feeding behavior depending on region and prey availability (Lundström et al., 2007, 2010; Winkler et al. 2011; Olsen et al., 2018; Mehtonen, 2019; Hoffmann, 2019). In early Swedish studies, pike has been found to account for less than 5% of the biomass in the diet of grey seals in the outer archipelago (Lundström et al., 2007; Strömberg et al., 2012; Hansson et al., 2018). In a recent study for the inner and central parts of the archipelago by Svensson (2021), pike was found as an important prey species for grey seal contributing 20% of the diet biomass, third in ranking after perch (46%) and herring (24%). Recalculations from otoliths estimated lengths of prey between 28 and 73 cm with a mean length of 44 cm for pike, i.e., seals predate on comparative large recruited pike. Bergström et al. (2022) and Bergström et al. (2023) suggested a relationship between the increasing grey seal population and a declining pike population in the archipelagos of the Swedish east coast.

A critical aspect of morphological stomach content analyses is the underestimation of smaller prey fish. In-vitro digestion experiments

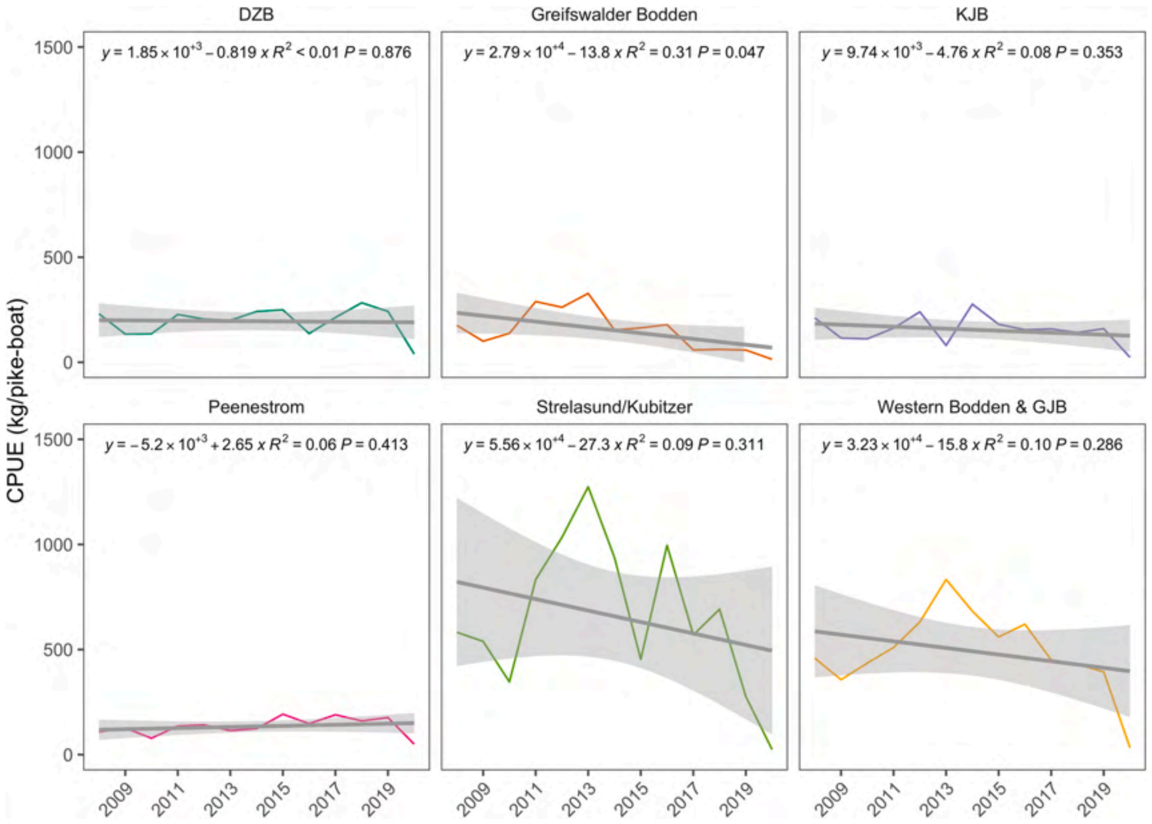


Fig. 17. CPUE trends in terms of commercial pike landings per pike-fisher boat for each Bodden from 2008 to 2020, including a linear model fit (red) to test for an increasing or decreasing trend in CPUE in pike landings (kg) per active pike fishing boat registered by Bodden.
Modified from Olsson et al. (2023).

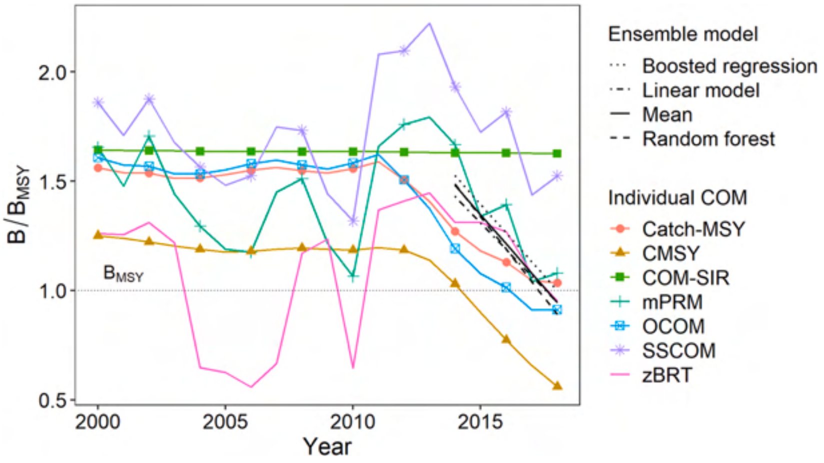


Fig. 18. Estimates of B/B_{MSY} for the Bodden pike from seven different COMs (coloured lines), and from three different ensemble models (black lines) which take these COM results as input and are trained on simulated data. The horizontal dotted line indicates B_{MSY} (from van Gemert et al., 2022).

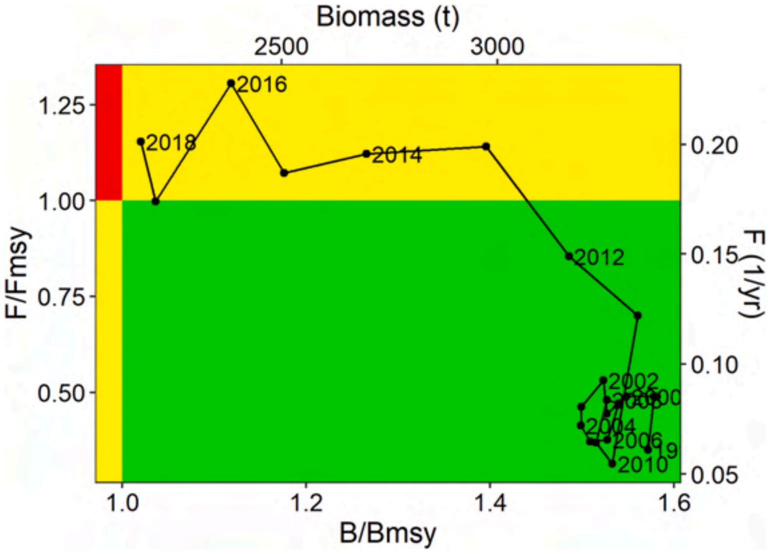


Fig. 19. Kobe plot showing the weighted means of B, B/B_{MSY}, and F/F_{MSY} for the years 2000–2018. The green area indicates healthy stock status, the yellow areas indicate that the stock is either overfished (B/B_{MSY} <1) or subject to overfishing (F/F_{MSY} > 1), and the red area indicates that the stock is both overfished and subject to overfishing (from van Gemert et al., 2022).

showed that the digestion of smaller fish in artificial seal and porpoise stomachs was faster than larger fish (Hoffmann, 2019; Klemens, 2019). However, pike may equally be underestimated as seals often do not ingest the heads and thus otoliths and other hard structure may be lacking for identification (Bergström et al., 2022, Fig. 22). Also the area of sampling matters, as seals in inner coastal lagoons will very likely differ in diet composition from seals sampled in outer coastal sites. In the only study to date on grey seal stomach contents from the Bodden lagoons and the coastal waters of Western Pomerania, no pike was recorded, but the sample size was small (Hoffmann, 2019). Grey seals in the coastline of MWP were found to prey on herring (45.7–62.8%), roach (24.7–35.7%), cod (8.1–14.6%), flounder (2.7–3.7%), sprat (Sprattus sprattus) (1%), sand eel (Ammodytes tobianus) (<1%) and garfish (<1%) (Hoffmann, 2019). In that study, 22 intact stomachs and 10 stomach contents of carcasses from 2016 to 2019 from the entire Baltic coast of MWP were processed (Hoffmann, 2019). In 50 further grey seal stomachs from MWP no structures of pike were found. Although there is so far no scientific evidence that seals living around Rügen prey on pike, there remains the limitation that the samples currently analyzed were mainly from dead seals found on the outer coast. Anecdotal evidence by anglers and fishers, including photo reports made available to the authors, do indeed show that seal predation on pike does exist in the German lagoons and that seals also eat and damage pike from gill nets in the lagoons (Fig. 22). Further work is needed to examine the impact of seals on lagoon pike.

10.2.1. Cormorants

The cormorant is another fish predator that is often assumed to have an influence on pike populations by fishers and anglers (Arlinghaus et al., 2021). Similar to the case of seals, as a perceived fisheries pest cormorants were hunted to very low levels in the 20th century (Rauschmayer and Weiss, 2013). Through EU level bird conservation regulations, the species has seen a massive recovery in recent years. After a phase of rapid rises in abundance (Fig. 24), the cormorant population in the south-western Baltic Sea region (Denmark, MWP, Schleswig-Holstein) has stabilized over the last decades. In 2020, the breeding population in the southern Baltic Sea was 47,794 breeding pairs (BP). In the northeastern parts of the Baltic Sea (Finland and

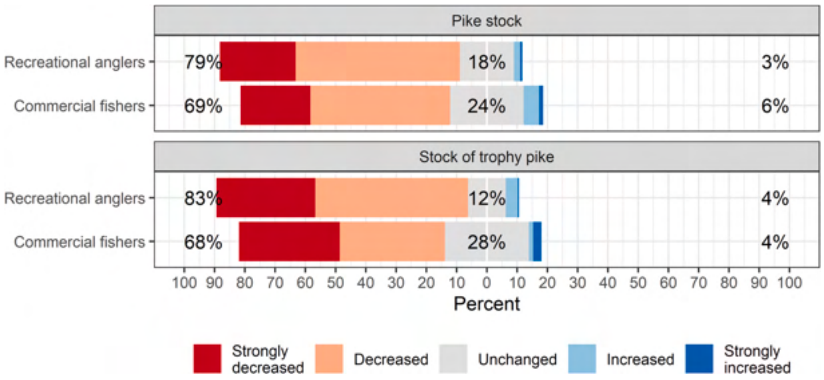


Fig. 20. Perceptions of pike stock decline by anglers (N = 704) and fishers (N = 75) around Rügen, Germany.

Fig. 21. Fish from commercial gear with bite marks from mammals (picture credit Steffen Schnorrenberg).

Estonia), the population has stabilized as well at around 50,000 BP since 2016. Today, there are around 20,000–26,500 BP in Germany alone, 60% of which breed in MWP. Additionally, substantial numbers of migratory birds visit the area of MWP and the lagoons, especially during winter. Fig. 24 shows the number of breeding pairs around the Island of Rügen and per Bodden lagoon during the last 70 years, revealing the strong rise in abundance from 1990 to today and a stabilization in recent years. The figure does not include non-breeding and migratory birds. Using monthly count data from 2018 (LUNG M-V and OAMV (unpublished data), Herrmann and Zimmermann, 2019), which included also non-breeding and migratory cormorants and were corrected by counting errors, we calculated the annual mean number of cormorants in the total Bodden area in 2018. The estimate was around 29,800 individuals, i.e. 38% above the number of cormorants derived from breeding data in the same year. In 2018 as in other years, the number of cormorants varied strongly seasonally (Herrmann and Zimmermann, 2019) with a maximum in September (ca. 54,000 individuals) and a minimum in January (ca. 11,800 individuals).

In light of its strong recovery (Arlinghaus et al., 2021) and due to the consumption of roughly 500 g of fish per cormorant and day (Ridgway, 2010), the species has become the source of a ritualized conflict between nature conservation, species protection and fisheries (Dierschke and Helbig, 2008; Rauschmayer and Weiss, 2013). According to Arlinghaus et al. (2021) the calculated removals by cormorants for the Bodden lagoons around Island of Rügen (without Peenestrom and Achterwasser) ranged in-between the removals by commercial and recreational fisheries with an average estimated total fish consumption of only the resident cormorant population of 2394 t of fish per year for the years 2011 and 2012. The most important consumed fishes were perch (26%) and roach (24%), besides other smaller-bodied non-game species (stickleback, gobiids and ruffe, Winkler et al., 2014). In that study, pike was rare in terms of biomass (0.3%) in the diet of cormorants. As a result of the different species that each forager consumed, the overlap of the foraging niche of commercial and recreational fisheries with cormorants was low (Arlinghaus et al., 2021). However, in specific locations (e.g., colony Heuwiese in the Kubitzer Bodden), diet contributions up to 11.4% were reported in other studies (Müller, 2014). Updated calculations assuming a diet contribution of 1% (see supplementary information) revealed that cormorant predation could be more than 50 t of pike, exceeding commercial landings in recent years (Fig. 25) and vastly exceeding the previous estimate of 8.2 t of pike consumption by cormorants in the lagoons (Arlinghaus et al., 2021). Given that cormorants consume much smaller pike (mainly 20–40 cm, Östmann et al., 2013) than the ones taken by commercial fishing (≥ 50 cm), the number of pike consumed by cormorants can be expected to substantially exceed the numbers of pike taken by commercial fishers in recent years. Full life-cycle modeling that accounts for density-dependent population feedback is needed to judge whether cormorant predation negatively affects the stock or yield, but first analyses suggest that the pike stock could be increased by 60% in the absence of cormorant predation

Fig. 22. Documented pike predation events of otters in a small creek draining into Grabow in the DZBC (picture credit Jörg Schütt) (left) and by otters or grey seal in Kubitzer Bodden in December 2020 (picture credit Tommy Tiegs) (right).

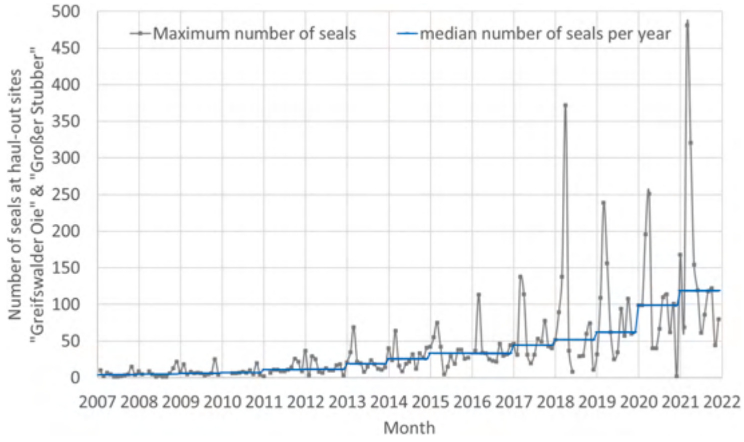


Fig. 23. Median monthly number of seal present in the area (blue line) and maximum monthly number of grey seal at the two haul out sites "Großer Stubber" in Greifswalder Bodden and "Greifswalder Oie" east of Greifswalder Bodden since 2007 (data sources: monitoring data by several institutions, Verein Jordsand, Weisse Flotte, Bundesamt für Naturschutz, Biosphärenreservatsamt Südost-Rügen and Deutsches Meeresmuseum).

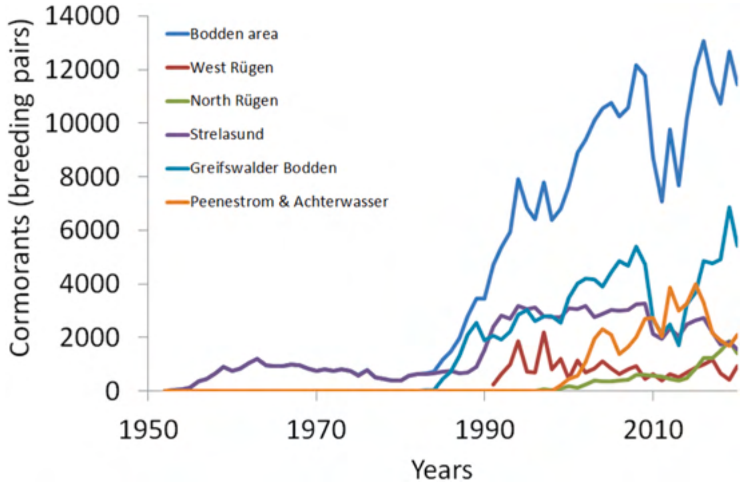


Fig. 24. Breeding pairs of great cormorants in Rügen, total number and aggregated per lagoon (data source: LUNG M-V). Modified from Arlinghaus et al. (2021).

(Ehrlich et al., unpublished data). Also other studies from the Baltic Sea suggest that cormorant predation on pike and other freshwater predators could generate socio-economically relevant impacts on commercial and recreational fisheries (Östman et al., 2013; Bergström et al., 2022).

10.3. Food web and fish community changes

Fish assemblages in the time between 2009 and 2020 in five Bodden lagoons were sampled with enclosure fyke nets (detailed description in Ubl and Dorow, 2015 and supplementary information). These enclosures capture a representative set of demersal species, but undersample small-bodied pelagic fishes like sprat or three-spined stickleback and very large species such as pike. Yet, this is the best available data to examine fish community changes that might affect the pike stock and is thus reported here as an unpublished analysis (for details, see Tables S2–6 and Figs. S1–7 in the appendix). The fish catch in the sampled lagoons was predominantly composed of the nine species ruffe, perch, pikeperch, stickleback, round goby, and roach (Fig. 26). Catches varied substantially between lagoons and years, and therefore fish assemblages did not differ statistically among lagoons and over time (see appendix). Concerning fish species able to impact pike negatively, specifically egg predators such as stickleback and round goby, no clear temporal trends in dominance were found over the years. This finding is in contrast with the results from the Swedish Baltic Sea (Donadi et al., 2020; Eklöf et al., 2020), which showed a strong correlation between a temporally stable increase in three-spined stickleback abundance and a subsequent decrease in pike recruitment abundance. However, for Greifswalder Bodden specifically, there has been a strong increase in the total abundance of stickleback and a moderate increase in the total abundance of round goby over all years combined (Fig. 26). Due to their small body size, stickleback were unlikely to be representatively sampled by the eel enclosures, which limits quantitative inferences. Yet, it is interesting to

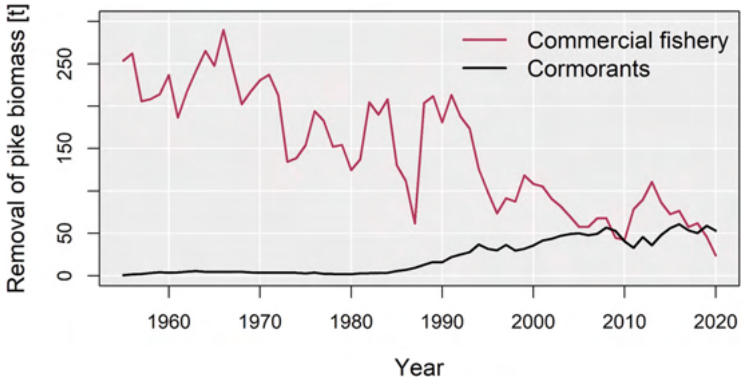


Fig. 25. Estimated consumption of cormorants in terms of pike biomass relative to the pike biomass harvested by commercial fisheries over time in German lagoons around Rügen (see supplement for methods).

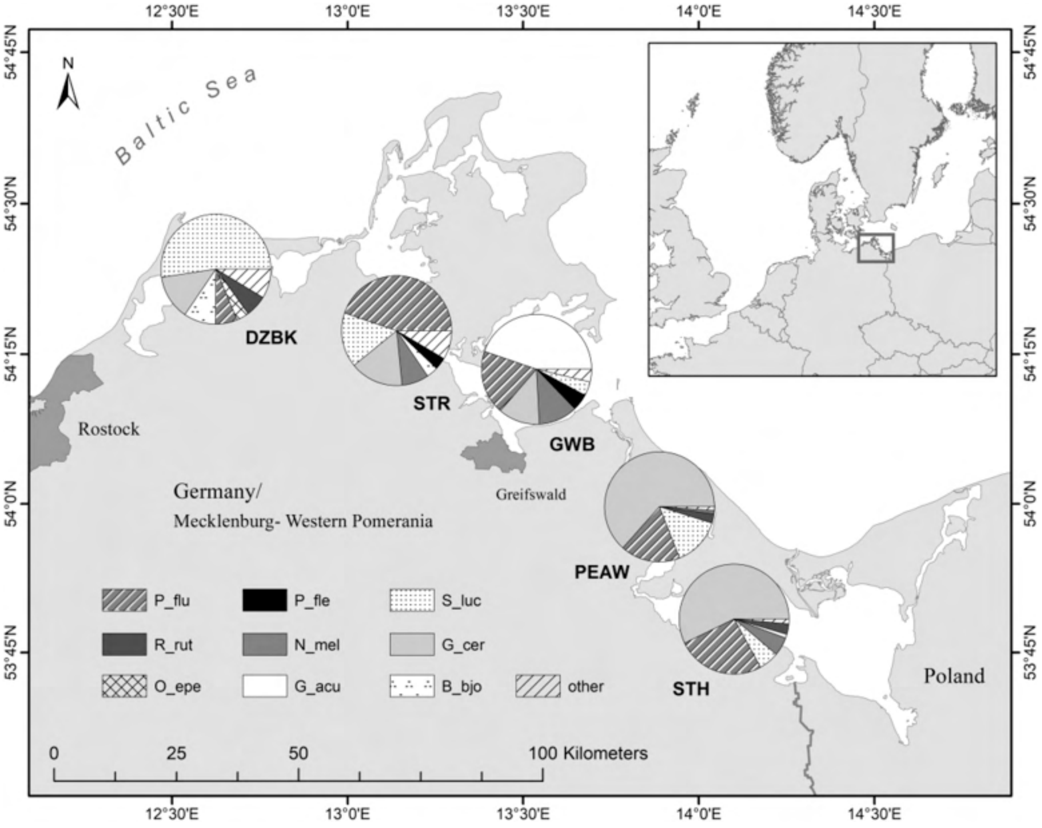


Fig. 26. Fish assemblage composition of the inner coastal waters (“Bodden”) of the German Baltic Sea. The pie charts show the six most frequent species per Bodden from west to east, pooled across the years 2009–2020: DZBK: Darß-Zingst Bodden chain (*n* = 1.537), STR: Strelasund (*n* = 2.118), GWB: Greifswalder Bodden (*n* = 6.327), PEAW: Peenestrom and Achterwasser (*n* = 28.000), STH: Stettiner Haff (*n* = 36.598); *n*: mean total number of fish caught during the study period; P_flu: *Perca fluviatilis*, R_rut: *Rutilus rutilus*, O_epe: *Osmerus eperlanus*, P_fle: *Platichthys flesus*, N_mel: *Neogobius melanostomus*, G_acu: *Gasterosteus aculeatus*, S_luc: *Sander lucioperca*, G_cer: *Gymnocephalus cernuus*, B_bjo: *Blicca bjoerkna,* other: other species.

note that Subklew (1983) reported threespined stickleback to be either rare or absent in Greifswalder Bodden around 1980, so that we might indeed today witness a recent stickleback "boom" in Greifswalder Bodden and perhaps in other lagoons. Visual inspections of many lagoons show that stickleback is highly abundant, e.g., in Kubitzer Bodden or Grabow. However, the lack of fishery-independent monitoring data for the phase prior to 2009 does not allow to substantiate this speculation.

It should further be noted that the enclosure samplings took place mainly from May to July. The marine species herring and garfish, which use the lagoons for spawning and nursery and constitute a large fraction of the fish biomass in the Bodden when they are present (Winkler, 1987, 1990), were thus not represented in the fish community assessment in the years 2009–2020. Stock assessment of spring spawning herring indicated this species is strongly declining in stock size, which includes reductions in herring abundance in the Greifswalder Bodden (Polte et al., 2021). Climate change and specifically the mismatch of egg development and zooplankton abundance peak are proposed as a main reason for reducing the herring stock in the lagoons (Polte et al., 2021). As herring is a major prey source of lagoon pike (Winkler, 1987), the recent demise in herring can reduce the growth, productivity and generally the prey base of lagoon pike. Also other food web changes might contribute to affect pike, e.g., changes in prey or possible predators (e.g., invertebrate predators of pike larvae), but no detailed monitoring data are available.

10.4. Land use and water management

Engineering efforts and building of coastal infrastructure regulating water flows have severely modified the coastal landscapes of the Baltic Sea (Gibson et al., 2007; Sundblad and Bergström, 2014). In the lagoons around Rügen, already over the course of the 19th century intensive drainage-ditch networks were developed and windmills built to pump water from agricultural fields into the sea, while dikes prevented the flooding of near-sea settlements (Holz, 1991; Wiemers and Fischer, 1998). The activities intensified further in the early 20th century (Mehl and Thiele, 1998 after Marcinek and Nitz, 1973; Jeschke et al., 2003) and specifically during the GDR, whose policies for land reform demanded to intensive agricultural production also around Rügen (Holz, 1991; Jeschke et al., 2003). Since the 1960 s and early 1970 s especially peatlands (fens, coastal floodplains, etc.), which accounted for 16.9% of the area in Western Pomerania (12,138 ha), were systematically drained for agriculture (Hirschelmann et al., 2020). During the following three decades, the most pronounced changes in the landscape took place within the program of the "Great Melioration", whose aim was to maximize agricultural yields (Holz, 1991). To that end, drainage ditches and streams draining nearshore wetlands were deepened and equipped with automated electrical pumps in many areas to lower water levels by more than 0.5 m below natural levels, thereby draining wetlands to allow year-round agriculture and blocking access to streams and ditches for migrating pike and other species (Holz, 1991, Figs. 27, 28). Pump sheds and other structures today block access to at least 60% of all tributaries and ditches and have thus strongly reduced the possibility for spawning of pike and other fish in freshwater systems (Figs. 27, 28, Roser, 2021). However, most structures were in place by the German reunification in 1989 and have not increased in intensity thereafter. Thus, while water management has certainly reduced access to flooded wetlands and freshwater tributaries, these stressors have not increased over the last 20 years. Instead, in more recent years since 2006 at least 19 renaturation projects for a total area of 4000 ha have removed dikes and restored saltmarshes (Schiefelbein et al., 2011; Schiefelbein, 2018), but access to freshwater tributaries has not substantially improved

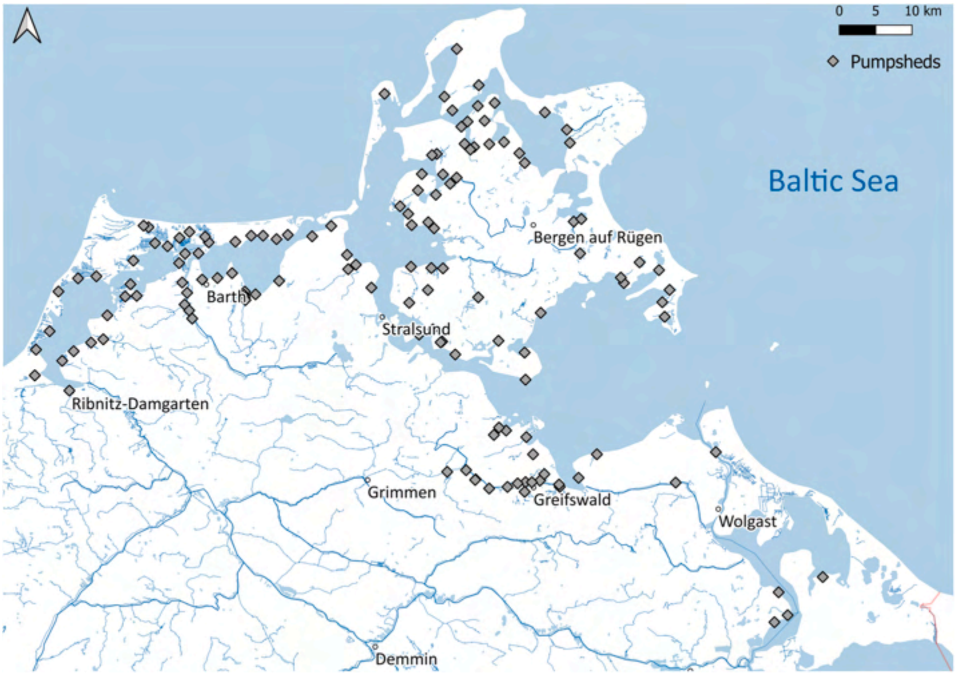


Fig. 27. Overview of pump sheds across different watersheds in the lagoon system of Rügen.

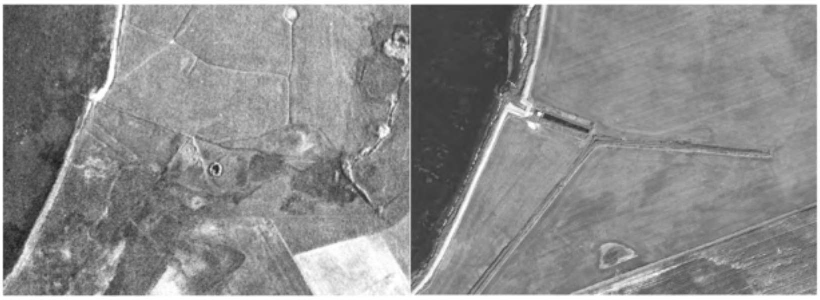


Fig. 28. Coastal strip near Wendisch Langendorf, Barther Bodden, known by local informants to formerly harbor spawning pike during spring floodings, before (1953, left) and after (today, right) melioration. Left: The floodmarks left by the sea are clearly visible. Right: Nowadays a dam prevents flooding with seawater, drainage ditches were created and a pumping station pumps excess water into the Bodden. Sources: GeoBasis-DE/M-V (left), Bing Virtual Earth (right). (from Roser, 2021).

(Roser, 2021). Whether the improved availability of brackish wetlands is helping recruitment is not known due to lack of monitoring.

10.5. Trophic state, macrophytes, temperature and salinity

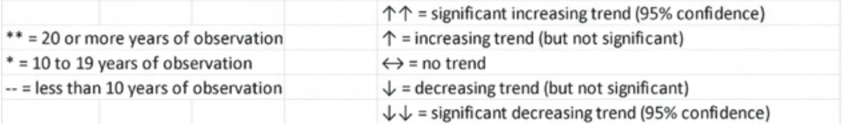
The intensified agricultural land use in the early and mid-20th century in Germany contributed to heavy eutrophication of the Baltic Sea, which was particularly pronounced in coastal bays and lagoons with limited water exchange with the open Baltic, such as the Bodden lagoons (Nehring, 1992; Nausch et al., 1999; Schubert et al., 2007; Munkes 2005; Schubert and Müller, 2023). Eutrophication-induced impacts on pike in the lagoons were particularly pronounced in the 1970 s and 1980 s (Schubert and Schories, 2008; Winkler and Debus, 2006) and led to strong declines of pike and rises of pike-perch in the more enclosed and turbid lagoons as elaborated before (e.g., DZBC, Winkler and Debus, 2006). While nutrient levels gradually decreased in the outer coastline of Rügen since the 1980s, over the last 20 years they have remained high in the lagoons, which have very limited water exchange with the open Baltic and receive substantial nutrient input through river run-off and via internal remobilization of nutrients (Blindow and Meyer, 2015). Thus, despite in principle reduced nutrient loadings in the lagoons, in the last 20 years macrophyte coverage has not responded strongly (Blindow and Meyer, 2015), such that the reduced nutrient levels might further reduce prey availability, without positively affecting the spawning and refuge habitat quality for pike in the lagoons. For example in Greifswalder Bodden, macrophyte coverage was 90% in the 1938, dropping to 3% in 1988 (Buchwald et al., 1996; Messner and v. Oertzen, 1991), and has remained at low levels (6%) until present time (Kanstinger et al., 2018). Another example is the well-documented collapse of macrophytes indicating a shift from a clearwater, macrophyte rich to a turbid, algae dominated state in the western part of the DZBC where loss of macrophyte dominance happened around 1980 (Schiewer, 2001), followed by a long period of phytoplankton dominance that continued throughout the 1990 s (Schiewer et al., 1994) until today, interrupted by a brief phase in the mid 1990 s where macrophytes partly recovered (Yousef, 1999; Yousef and Schubert, 2001). Although macrophytes can react strongly to reduced nutrient loads (Blümel et al., 2004), a widespread recovery of macrophyte coverage has not happened in the eutrophied lagoons in the last 20 years (Blindow and Meyer, 2015; Blindow et al., 2016). Possible reasons relate to continuously high impacts of high internal loading, waves resuspending sediments and impacts of pesticides and herbicides in interaction with climate change (Schiewer, 2001; Selig et al., 2007; Vijayaraj et al., 2022). Similar regime shifts from clear to turbid conditions are known from the Swedish coast (Eriksson et al., 2009), and pike alone cannot control trophic effects to maintain clear-water status, even after heavy biomanipulation to increase standing biomasses of pike (Bernes et al., 2015). Thus, we have to conclude that in the lagoons the pike habitat quality for spawning and recruitment has not substantially improved in the recent decades despite lower nutrient loadings.

Other indicators reinforce that eutrophication continues to affect the lagoon ecosystems, and also rising impacts of climate warming are detectable. Using long term environmental data provided by the state agency for environment, nature conservation and geology Mecklenburg-Western Pomerania (LUNG), time series trend analysis were performed for four major Bodden chains to analyze which hydrochemical indicators of trophic state, temperature and salinity have seen changes in recent years. Only data since 1990 were used to represent the last 30 years. On average and not considering interannual fluctuations, most lagoons showed no clear change in chlorophyll-a, salinities and Secchi-depth, while water temperatures increased in some stations (specifically in Greifswalder Bodden and in the boddens west of Rügen) 1990 to today (Table 4). During spring seasons, some lagoons are, on average, getting more turbid, warmer and less saline. Sometimes opposing trends can be observed, e.g. in Großer Jasmunder Bodden or Peenestrom, where the annual average chlorophyll-a concentration decreased and water clarity increased, suggesting reduced trophic state (Table 4).

For the different Bodden chains, additional to the analysis of annual chlorophyll a, surface temperature and salinity, a second trend analysis was performed to show trends in surface temperature and salinity during the likely spawning season of pike (February to April). The results were comparable for all four major areas, revealing trends for increasing chlorophyll a and temperature values and decreasing salinity (see Figs. S8–17 in the appendix for details). Although reduced salinity may benefit pike, the outlook of warming water is mixed. Specifically for the Swedish Baltic coast, i.e., an area of the Baltic Sea that is on average cooler than around Rügen, Berggren et al. (2022) reported juvenile growth of pike to rise, adult growth of pike to decline and adult mortality to increase with recent warming, in agreement with theoretical predictions (Thunell et al. 2023). As a mesothermal or coolwater species pike particularly responds to heat stress, where temperatures above 20 °C can create severe stress (Casselman, 1978) and motivate behavioral thermoregulation. To find out whether the number of days with critically warm temperature has been rising in recent years, an analysis of satellite data (E.U. E.U. E.U. Copernicus Marine Service Information, 2021) was performed for the central part of Greifswalder Bodden. The analysis revealed an increase of 9 very warm days per decade since the 1970s, suggesting the degree of heat stress may be strongly increasing in

Table 4
Trend analysis in hydrochemical indicators of selected stations (data provided by LUNG) located in the lagoon waters around Rügen. Significant trends drived from sufficiently long time series are highlighted. See footnote for symbol meaning. footnote for symbol meaning. Empty cells mean lack of data.

Bodden	Station of LUNG-MV	Chlorophyll-a			Seechi Dept			Water Temperature (near surface)				Water Temperature (near bottom)				Salinity (near surface)				Salinity (near bottom)			
		annual mean	Feb to Apr	May to Sept	annual mean	Feb to Apr	May to Sept	annual mean	Feb to Apr	annual min	annual max	annual mean	Feb to Apr	annual min	annual max	annual mean	Feb to Apr	annual min	annual max	annual mean	Feb to Apr	annual min	annual max
Kleiner Jasmunder Bodden	RB15	↔**	↔**	↔**	↓↓**	↓**	↓↓**	↔**	↑**	↔**	↔**					↑**	↑**	↑**	↑**				
Großer Jasmunder Bodden	RB10	↓**	↔**	↔**	↑↑**	↑**	↑↑**	↔**	↓**	↔**	↔**	↔**	↓**	↔**	↔**	↓**	↓**	↓↓**	↓**	↓**	↓**	↓↓**	↓**
	RB9	↓↓**	↔**	↓**	↑↑**	↑**	↑↑**	↑**	↓**	↔**	↔**	↔**	↓**	↔**	↑**	↓**	↓**	↓↓**	↓**	↓↓**	↓**	↓↓**	↓**
Greifswalder Bodden	GB19	↑**	↑**	↔**	↑**	↑↑**	↑**	↑**	↔**	↑**	↔**	↑**	↔**	↑↑**	↔**	↔**	↓**	↔**	↓↓**	↓**	↓**	↔**	↓↓**
	GB2	↔**	↑**	↔**	↑**	↔**	↑↑**	↑**	↔**	↑**	↔**	↑**	↔**	↑**	↔**	↔**	↓**	↔**	↓↓**	↓**	↓**	↑**	↓↓**
	GB3	↔**	↔*	↔**	↑**	↔*	↑**	↑**	↔*	↑**	↑**	↑**	↔*	↑**	↑**	↔**	↓*	↔**	↔**	↓**	↓*	↔**	↓↓**
	GB5	↔	↔	↔	↓↓*	↓	↓↓*	↔*	↔	↔*	↔*	↔*	↔	↔*	↔*	↓↓*	↔	↓*	↓↓*	↓↓*	↔	↓↓*	↓↓*
	GB6	↔	↔	↔	↓↓*	↓	↓*	↔*	↓	↔*	↔*	↔*	↓	↔*	↔*	↓*	↔	↔*	↓*	↓*	↔	↓*	↓↓*
	GB7	↑**	↑**	↔**	↔**	↔**	↑**	↑**	↔**	↔**	↔**	↑**	↔**	↑**	↔**	↔**	↓**	↔**	↓↓**	↓**	↓**	↔**	↓↓**
Westrügen	KB90	↑**	↔**	↔**	↓**	↓**	↓↓**	↑**	↔**	↑**	↔**	↑↑**	↔**	↑**	↑**	↔**	↔**	↑**	↔**	↔**	↔**	↔**	↔**
	RB6	↔**	↔**	↔**	↔**	↔**	↓**	↑↑**	↓**	↑**	↑**	↓	↓↓	↓↓	↔	↔**	↔**	↔**	↔**	↔	↔	↓↓	↔
	RB3	↔**	↔**	↔**	↔**	↔**	↔**	↑**	↓**	↔**	↑**	↔**	↓**	↔**	↑**	↔**	↔**	↑**	↔**	↔**	↔**	↔**	↔**
	RB2	↔**	↑↑**	↓**	↑↑**	↑**	↑↑**	↔**	↔**	↓**	↑**					↔**	↓**	↓↓**	↔**				
	RB1	↔**	↑**	↔**	↔**	↔**	↔**	↔**	↔**	↓**	↑**					↔**	↓**	↓**	↑**				
Darss-Zingst-Bodden Chain	DB2	↓↓**	↓**	↓**	↔**	↔**	↓**	↔**	↔**	↔**	↑**					↔**	↔**	↔**	↔**				
	DB1	↓↓**	↔**	↓**	↑↑**	↔**	↔**	↔**	↔**	↔**	↑**					↑**	↔**	↔**	↑**				
	DB6	↓↓**	↓↓**	↓**	↔**	↓**	↓**	↔**	↔**	↔**	↑**					↔**	↔**	↔**	↔**				
	DB10	↔**	↔**	↔**	↓**	↓**	↓**	↑**	↑↑**	↑**	↔**	↔*	↔*	↔*	↔*	↑↑**	↑↑**	↑↑**	↑↑**	↑↑*	↑*	↑*	↑*
	DB16	↔**	↔**	↔**	↓↓**	↓**	↓**	↑**	↑**	↑**	↔**					↑↑**	↑↑**	↑↑**	↑↑**				
Peenestrom	AW1	↓↓**	↔**	↓↓**	↑**	↔**	↔**	↔**	↑**	↓**	↔**	↓	↑	↔	↔	↑**	↔**	↔**	↑↑**	↔	↔	↔	↔
	P20	↔**	↑**	↓**	↑↑**	↑**	↑**	↑**	↑↑**	↔**	↔**	↑**	↑↑**	↔**	↔**	↔**	↓**	↔**	↔**	↔**	↔**	↔**	↓**
	P42	↓**	↑**	↓**	↑↑**	↔**	↑**	↔**	↑**	↔**	↔**	↔**	↑**	↔**	↔**	↔**	↔**	↔**	↔**	↔**	↔**	↔**	↔**
	P48	↔**	↑**	↔**	↑**	↑**	↑**	↔**	↑**	↔**	↔**					↔**	↓**	↔**	↔**				


** = 20 or more years of observation
* = 10 to 19 years of observation
-- = less than 10 years of observation
↑↑ = significant increasing trend (95% confidence)
↑ = increasing trend (but not significant)
↔ = no trend
↓ = decreasing trend (but not significant)
↓↓ = significant decreasing trend (95% confidence)

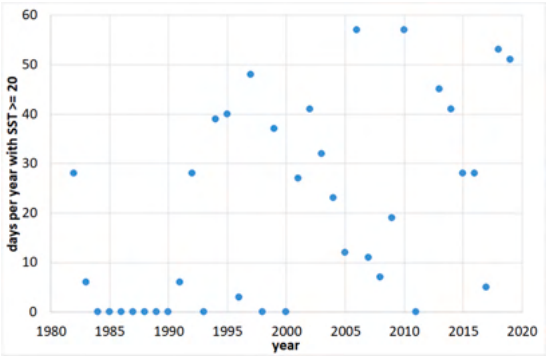


Fig. 29. Number of days with sea surface temperature above 20 °C derived for central Greifswald Bodden using satellite data. (data source: E.U. E.U. E.U. Copernicus Marine Service Information (2021)).

the lagoon ecosystems (Fig. 29).

11. Synthesis of environmental and anthropogenic stressors

As elaborated in the previous sections and summarized in Fig. 30, a range of factors that affect the life-cycle, abundance and size structure of pike have been changing in the lagoon ecosystems. Most of the factors can be considered stressors for the pike stock, such as increasing fishing pressure, loss of recruitment habitat and continuously low access to freshwater habitat for spawning, decline of the marine prey base and in part strong rises in natural predators. As far as we can judge from the review of evidence, none of these factors can be considered of overwhelming importance as a single dominant impact source. Therefore, additive and possibly synergistic effects among multiple factors are more likely to have reduced the resiliency of the Rügen pike stock and impacted recruitment or carrying capacity and adult abundance negatively. It is possible that slowly changing variables (defined as variables that are slow in change but critical for population renewal), such as reduced access to freshwater sites leading to loss of locally adapted substocks and reductions in submerged macrophytes or slowly increasing effects of climate warming, now act in concert with other stressors, such as elevated fishing rates or increased natural predation, reducing the carrying capacity and renewal rate of pike in the lagoon ecosystems. The lack of long time series of fishery-independent monitoring data tracking recruitment and abundance of pike as well the underlying lagoon environment and its food web severely limits our ability to exactly quantify additive and synergistic effects and thereby quantitatively weigh the impacts of different pressures. In the absence of better-quantifiable relationships, we thus assume that the key predation-related factors outlined in Fig. 30 exert their effects on top of an overall decline in resiliency, recruitment and adult abundance caused by reduced herring abundance, continuously low macrophyte abundance, high predation losses (both via natural predation and fisheries), reduction of genetic population biocomplexity and a range of poorly understood climate-induced factors, including heat stress. The dominant factors likely also vary by lagoons, with the large Greifswalder Bodden likely being exposed the largest number of co-occurring threats, such as continuously low degree of underwater vegetation, reduced abundance of spring spawning herring, increased natural mortality (due to seals, cormorants and possibly stickleback) and loss of freshwater access. Perhaps for this reason, the decline of pike has been reported by stakeholders to be particularly strong in the Greifswalder Bodden. Clearly, the decreasing commercial pike landings may also be an indirect cause of the increasing seal abundance reducing the attractiveness of gill netting, thereby contributing to the particularly strong decline in total pike landings reported for the Greifswalder Bodden (Fig. 6).

To further synthesize our insights, we developed a score for the impact strength of various stressors and used the results to rank pressures in terms of priority factors in need of management attention (Table 5). The final score integrated independent assessments of the relevance of a given factor for pike biology, its current state in relation to pike ecology in the region, recent information on trends, the strength of evidence and feasibility of management interventions. Each factor was scored on a five-point scale from 1 to 5 and the scores were first provided for each factor and metric and then summed to create the overall score. Finally, the assessment certainty was qualitatively scored in terms of scientific uncertainty as to the evidence base. Pressures were ranked high that a) have high relevance for pike, b) show a particularly negative trend with a reasonably robust evidence base and c) show high feasibility to be addressed by management.

The ranking exercise in Table 5 revealed that three factors a) fishing mortality, b) access to freshwater and c) macrophyte coverage constituted key areas of immediate managerial concern. Factors of intermediate score involved natural predators of pre-recruits and recruits by cormorants and possibly seals, warming, a reduced forage base and natural predation of eggs/larvae. All these four factors were identified as potentially highly relevant, but with important scientific gaps in understanding for the lagoon fishery at Rügen. Based on the available

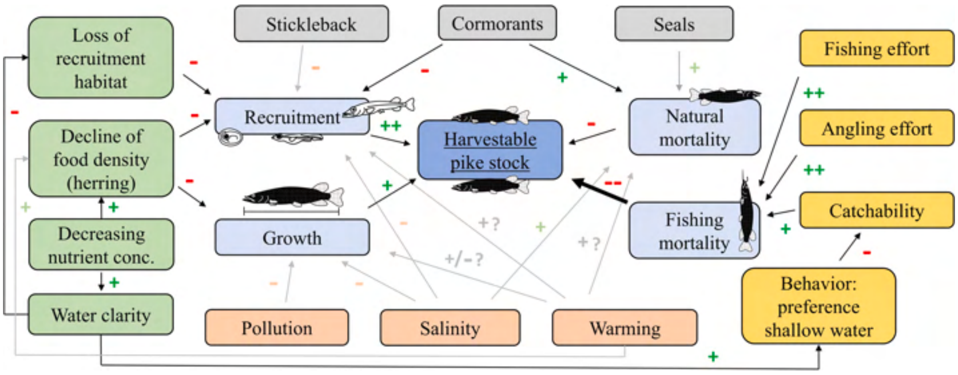


Fig. 30. Synthesis of main drivers of lagoon pike ecology and abundance of the recruited stock. Light blue boxes show the four central population processes governing pike stock size that are affected by local habitat condition (green), abiotic factors and pollutants (orange), natural predators (grey) and factors related to fishing mortality (yellow). Arrows illustrate positive (+) and negative (-) effects where some of them are considered to be of particular importance for the currently decreasing pike stock size (++ and –). Grey arrows indicate effects that are less certain or understood (?) due to lacking local data and studies.

Table 5
Synthesis of impacts on the Rügen pike population.

Pressure	Relevance for pike ecology	Current state of driver	Recent trend	Evidence strength	Feasibility of management intervention	Overall score	Certainty of synthesis result
Fishing mortality	4	3	4	4	5	20	High
Freshwater access	4	5	1	2	4	16	High
Macrophyte coverage	5	3	1	4	2	15	High
Natural predators precruits/recruits	3	2	4	2	2	13	Low
Warming	3	2	4	1	1	11	Low
Forage Base	2	2	3	2	1	10	Medium
Natural predators eggs/ larvae	2	2	3	1	1	9	Low
Salinity	2	1	1	4	1	9	Medium

Scores for relevance were 1 = little relevance to pike ecology to 5 = very high relevance, scores for state was 1 = very positive for the pike to 5 = very negative for the pike, scores for recent trend was 1 = no trend to 5 = strongly negative trend for pike, score for evidence strength 1 = very low evidence to 5 = very strong evidence, score for feasibility was 1 = very low feasibility of management intervention to 5 = very high feasibility of management intervention.

evidence we excluded changes in salinity as a major driver of the currently negative biomass trend.

Fishing mortality: Although current fishing mortality rate, F, of about 0.2 – 0.4 yr^{-1} (Fitzgerald et al., 2023) is not excessively high and thus cannot be the sole cause of the current pike decline, fishing mortality rates on the stock have been rising in relation to the available stock biomass (van Gemert et al., 2022). They might be underestimates due to underreporting of landings and are very likely to exceed target fishing mortality rates given the natural mortality schedule typical for pike (M about 0.2, target F < 0.87 M; Zhou et al., 2012). Importantly, in a fishery with a large recreational sector where high catch rates and large sizes of pike matter, fishing mortality rates of 0.2 – 0.4 yr^{-1} are causing size overfishing as the fish no longer reach maximum age and size (Ahrens et al., 2020; van Gemert et al., 2022), which will affect angling quality negatively (Koemle et al., 2021, 2022). Other effects of fishing could occur due to patterns of local overfishing as the core home range areas of pike in the lagoons were found to on average only 100 ha (Dhellemmes et al., 2023) and coastal pike rarely move more than 10 km (Kåras and Lehtonen, 1993; Dhellemmes et al., 2023). Thus, heavy fishing in a concentrate area could lead to strong local depletion (Bergström et al., 2023; Eklöf et al. 2023; Flink et al., 2023). Moreover, given the strong population differentiation of pike stocks in the Baltic, particularly among the anadromous subpopulation, even on small geographic scales of a few km (Nordahl et al., 2019), local fishing pressure (e.g., in front of tributaries) could strongly reduce the biocomplexity of the entire stock through local depletion of specific genotypes (Schindler et al., 2010). In addition, continuous angling with artificial lures can lead to hook avoidance learning, further reducing catchability (Beukema, 1970; Arlinghaus et al., 2017b; c; Monk et al., 2021). Therefore, heavily targeting specific bays or localities, e.g., prior to spawning, can have substantial impact on local abundance and differentially affect certain localities and reduce pike abundance available to fisheries and anglers (Bergström et al., 2023). Indeed, work from large lakes showed that the specific harvesting pattern of individual commercial fishers can strongly affect the fishing quality and catch rates of anglers (Jansen et al., 2013). We would therefore conclude that further limiting fishing mortality by both anglers and fishers could benefit pike abundance and catchability in the long term, especially in light of currently negative biomass trends (van Gemert et al., 2022).

Access to freshwater and wetlands: It is highly likely that the reduced access to freshwater tributaries through landscape and water management between 1970 s and 1990 s has had substantially negative impacts on the anadromous subpopulations in the region, similar to the case in Poland (Psuty, 2022; Psuty et al., 2023), but the lack of time series data limits our ability to quantitatively assess the degree of the impact. Yet, evidence from salmonids and from Baltic Sea stocks in Sweden point to a large importance of a biocomplexity of substocks within the meta-population, which builds resilience to buffer environmental stochasticity (Schindler et al., 2010; Sunde et al., 2022). Therefore, improving access to freshwater streams and restoration of wetlands is most likely to have positive effects on the lagoon fishery in the long term. However, as the most severe constraints to freshwater access were already happening in the system in the 1970–1980 s, these factors are unlikely to be directly responsible for the current decline of the lagoon pike stock. Most likely, the lagoon pike stock has managed to self-recruit in sufficient numbers through the brackish spawning subpopulation, which were described already in the 1960 s (Falk, 1966) and further documented in recent years (Möller et al., 2019, 2021). It is interesting to note that in a Polish bay such compensation of loss of freshwater access by increased brackish recruitment has not happened, contributing to local extinction of the lagoon pike stock there (Psuty, 2022; Psuty et al., 2023), perhaps due to a fatal combination of heavy pollution in the 1970–1990 s affecting the saline-adapted lagoon stock and reduced recruitment compensation from the freshwater substocks. However, in Germany the lagoon stock has certainly survived, and the lack of access to freshwater streams has perhaps fostered and strengthened selective pressures to adapt to fully recruit under brackish conditions. It is possible, however, that other environmental factors (e.g., natural mortality, food web changes, climate induced changes in maturation rates and timing) have now reduced the recruitment capacity of the lagoon substock in recent years, and now the lack of substantial recruitment from wetlands or freshwater sites may have reduced the total buffering capacity of the stock.

Macrophyte coverage: Due to intensive eutrophication in the 1970 s and 1980 s, declines in submerged macrophytes have been reported across most lagoons. Changes in a key recruitment habitat for pike has reduced the carrying capacity for pike, specifically of the most eutrophied lagoons for pike (e.g., western DZBC), leading to a shift from pike to pike-perch dominance (e.g., Winkler and Debus, 2006). Also in the less eutrophied Greifswalder Bodden a substantial decline of macrophyte coverage from 90% in the 1940 s to only 6% today has happened (Kanstinger et al., 2018), which most likely negatively affected recruitment and standing stock size. However, the most dramatic decline in macrophyte coverage in the lagoons has happened in the 1970–1990 s and can thus be excluded also to be a prime reason for the contemporary stock decline. That said, despite reduced nutrient loadings, macrophyte coverage is also not rising strongly across the lagoons, which will constraint current recruitment and reduce stock resilience similar to the loss of freshwater access in streams and ditches. Management actions that further reduce nutrient inputs and elevate macrophyte coverage will very likely increase recruitment and resilience, but such actions are not easily implemented in shallow water ecosystems where wave action can lead to a stabilization of a turbid, macrophyte poor state despite reduced nutrient loading through hysteresis effects (Scheffer, 1993).

Natural predators of pre-rercuits/recruits and eggs/larvae: In relation to natural predators of pre-recruits and adults, there is strong evidence that the abundance of cormorants and seals has strongly increased in the region. Although diet studies in cormorants did not reveal that pike represent a very large portion of the ingested biomass (Winkler et al., 2014), pike also naturally represents only a small fraction of total fish biomass in the lagoons. Thus, the total consumed biomass scales with the abundance of cormorants. Newer calculations presented in this synthesis suggest that the pike consumption by cormorants in terms of biomass is more than six times larger than assessed in the past, and numerically exceeds the number of pike taken by fisheries. The consumption by seals remains obscure. In a first study of dead grey seals collected from both the outer and inner coastline no pike were found in seal stomachs (Hoffmann, 2019), but anecdotal reports by fishers and anglers and picture documentation suggests that seals also predate on pike. Despite possibilities for density-dependent compensation of mortality losses, the rising total predator numbers in recent years suggest a possibility that selective feeding on small-sized pre-recruits by cormorants and more importantly perhaps predation on recruits by seals could contribute to stock declines (Arlinghaus et al., 2021) and affect yield negatively (Östman et al., 2013). Seals have recently risen in abundance, particularly in Greifswalder Bodden, but they are regularly seen in other lagoons and anglers have documented seal predation on adult pike, which is particularly problematic as mortality is likely additive in the adult stage (Allen et al., 1998). It is thus possible that seal predation could substantially affect pike abundance in areas where seals overlap with pike (Bergström et al., 2022, 2023), e.g., in bays, but scientific work to substantiate this speculation is needed before management actions can be recommended. In relation to three-spined stickleback as possible predator of eggs and larvae, there is no monitoring data information that would allow trends to be derived for the Rügen fishery. Similar to the case in Sweden (Eklöf et al., 2020), however, it is certainly possible that stickleback locally consume large quantities of pike eggs and larvae, especially if climate change fosters increased overlap of pike and stickleback spawning time, but the lack of scientific studies for the region prevent us from reaching thorough conclusions. Thus, before management actions are implemented (e.g., directed fishing of stickleback), further research is necessary.

Warming and forage base: Although there is clear evidence that the lagoons around Rügen are experiencing significant warming, the information base on warming negatively affecting pike is thin. The potential certainly exists, in light of research from the Swedish coasts that reported increases in natural mortality caused by warming (Berggren et al., 2022) and models by Vindenes et al. (2014) reporting warming can alter population growth rate, survival and size structure in pike. Other impacts of climate change are even less understood, but can involve changes in the maturation and egg development processes and phenological timing of spawning (Farmer et al., 2015; Fernandes et al., 2022) that could increase the spatio-temporal overlap of pike spawning with the presence of egg predators in the inshore areas of the lagoons, for example by delaying the spawning activity of pike through alterations of gonadal investment processes or irregular spring temperature and thereby increasing the overlap with three-spined stickleback that move into lagoons for spawning in late spring (Eklöf et al., 2020). Other potential impacts of climate change relate to changes in the forage bases, e.g., alternation of the abundance of spring spawning herring (Polte et al., 2021) as a key forage base of pike in the lagoons (Winkler, 1987). Elevated number of days with extremely high temperature can also substantially reduce body condition and negatively affect pike through metabolic overload. Similar to the case in herring (Polte et al., 2021), there is also the possibility that shifts in zooplankton occurrence might create threats to the prey base for pike fry, or winds and currents can affect the littoral zone in unfavorable ways (e.g., by creating drawdowns in shallow areas or influx of saline water to spawning grounds). The impacts of climate change on the pike stock are complex, involve both intraspecific and interspecific as well as food web effects and must be further studied. However, the fact that pike stocks are currently declining in many areas of the central, western and southern Baltic Sea (Olsson et al., 2023) suggest that a common regionally acting driver might be involved. Climate change and associated effects on the food web, maturation timing and distribution of predators is a likely candidate that should be studied further.

Salinity: Although always a factor of relevance to a freshwater fish such as pike, trend analysis suggested that the salinity levels of the lagoons are on average declining, such that we can exclude salinity as a major negative driver to affect the current biomass. However, it is possible that hydrodynamic effects at a particular spawning site lead to inflow of high saline water close to or above 10 PSU, possibly affecting fertilization and egg development negatively. Although such stochastic effects are possibly and may locally affect recruitment, they have been present in the system for decades and thus do not serve as a suitable explanation for the current negative biomass trend.

12. Management options

In light of the currently declining pike stock and the pervasive and partly heated allocation conflict of pike and fishing space among commercial and recreational fisheries (Arlinghaus et al., 2022), management actions are warranted that acknowledge scientific uncertainty and are flexible to new understanding and novel conditions in the future. Management actions should also represent the perspectives of stakeholders because stakeholder support is typically important for the success of fisheries-management actions. We conducted a participatory stakeholder process in the region of Rügen. Stakeholders identified key issues that are affecting the Rügen pike stock and that need management attention. The resulting list encompasses many aspects identified of key concern in Section 10 (Table 6), e.g., elevated fishing pressure, angling-induced timidity effects or rising natural predators. Other issues identified by the stakeholder related specifically to human aspects, such as non-compliance and the lack of a pike-specific management plan (Table 6). Stakeholders also identified the need to address the decline of both commercial and recreational fisheries for pike, which is an indication of the need to engage in management.

Table 6
Main issues identified by stakeholders in a one day workshop that should be accounted for by future management of the pike fishery in the Rügen lagoons (numbering does not imply any ranking, from Ehrlich et al., 2023). The key issues were mutually agreed by a stakeholder group consisting of representatives from all interest groups (i.e., anglers, guides, fishers, conservation, tourism, fishery agency) who worked together during stakeholder workshops in a participatory process to develop management recommendations for policy makers.

No.	Issues
1	Declining stock and catch/harvest rates of pike as well as lower numbers of large trophy pike
2	High and non-regulated recreational and commercial fishing pressure with an increasing number of tourist anglers
3	Decreasing catchability of pike perceived by anglers due to hooking avoidance and decreasing turbidity of water
4	Decline in commercial fishery and partly decreasing number of anglers in certain areas which threatens the local tourism sector relying on angling
5	Knowledge gap and lack of reliable monitoring data on pike biology, environmental change and fishery development
6	Missing management plans for the lagoon pike
7	Deterioration of environmental conditions for pike (decreasing spawning and rearing habitats due to land use and decline of submerse macrophytes, changing salinity and nutrient conditions, increasing predation pressure by cormorants and seals, and decreasing abundance of prey fish like *Clupea harengus*)
8	Lacking awareness of sustainability issues and conflicts among user groups, non-compliance with rules and regulations

To develop management recommendations for the Rügen pike stock from a scientific perspective, the Resist-Accept-Direct (RAD) framework is useful to think about strategies in a situation where transformative (defined as a shift that radically departs from current state, e.g., prolonged climate warming) and partly inevitable (from a management perspective) ecosystem change is affecting the context in which fisheries management happens (Lynch et al., 2022), also known as the Safe Operating Space (Carpenter et al., 2017). The RAD framework proposes that managers can (Lynch et al., 2022):

- *Resist* social-ecological and ecosystem change and possibly transformations; management actions focus on maintaining current or historical ecosystem structure and function (services);
- *Accept* ecosystem change and transformations; managers yield to ongoing changes and possibly transformations (i.e., by not intervening), accepting ecosystem structure and function that emerge from the change process; and lastly
- *Direct* ecosystem changes and possibly transformation toward a specific alternative outcome; managers accept that change is inevitable but intervene to steer the change process toward an ecosystem and socio-economic state with particular structure and function.

The actions that can be targeted with a *Resist* target aim at restoring pike abundance or changing other features of the current system, e.g., improved allocation of fish among the commercial and recreational sector, reduced fishing mortality or improved habitat structure. In this context feasibility of actions matters, for example, fisheries managers will not be able to affect drivers that are beyond their immediate control, like climate change or eutrophication caused by agricultural run-off, and then have to work within the limits set by the changing ecological environment (Carpenter et al., 2017). The managers then have to focus on those areas they can manipulate to avoid ("Resist") the changes that are happening. In this context, actions that are potentially able to address ongoing pike biomass declines and changing size structures of pike involve various input and output controls of fisheries, habitat management, stocking and control of natural predators (Fig. 31). We in turn assess the success probabilities inherent in each of these strategies and examine stakeholder support for such actions based on survey results.

Biologically, the strong size- and density-dependence in population regulation in pike elaborated in Section 3 has consequences for how the species can be managed and how it responds to both exploitation or stocking (Johnston et al., 2018). Pike management can come in three variants: regulating harvest through input and output controls, adding fish through stocking or improving the stocks through habitat management. In addition, managers can engage in control of excessive natural predation. Depending on which factor primarily constrain pike abundance, it should be targeted. For example, if fishing mortality is excessive, this factfor shall be controlled first rather than trying to solve the issues by stocking or habitat enhancement (FAO, 2012). In some situations, combinations of tools are warranted (see FAO, 2012 for details).

Managing fisheries: The management of pike fishing in the lagoons is currently based on a simple set of harvest regulations that involve a minimum-length limit of 50 cm (and additionally for commercial fisheries a minimum mesh size for pike gill nets of 100 mm stretched), a daily bag limit (only for anglers) of 3 pike per angler, a spawning closure (March and April) and restricted access or full closures of a range of protection zones that are implemented for fisheries protection or general nature conservation reasons. The vast majority (99%) of these protection zones, however, do not fully exclude fishing mortality (Table 3). Moreover, there are gear restrictions limiting the total number of rods or commercial fishing gear used. Managers could further limit fishing mortality by changing these input and output controls further (Fig. 31) and thereby increase abundance (and catch rate) as well as size of pike in the catch (Ahrens et al., 2020).

Direct constraints on fishing mortality rates could be achieved through the implementation of yearly quotas for both individual anglers or commercial fisheries, although this would raise important allocation, assessment and compliance issues that would substantially complicate governance. Improved indirect controls of fishing mortality could be achieved by further strengthening access and removal constraints, such as increased use of protected areas (with access to all fishing sectors controlled), enlargement of protected seasons, spatial zoning of fishers and anglers (e.g., selected lagoons only accessible to one sector group), implementation of rotated closures, changes to the size-limits (including the option to implement harvest slots and maximum upper limits on mesh sizes to save large fish better, Ahrens et al., 2020) and reductions in daily bag limits to anglers. It is also important to improve the public communication of rules and regulations and engage in improved enforcement as we observed in the field that many protected areas and access rules are currently not followed, perhaps due to the lack of

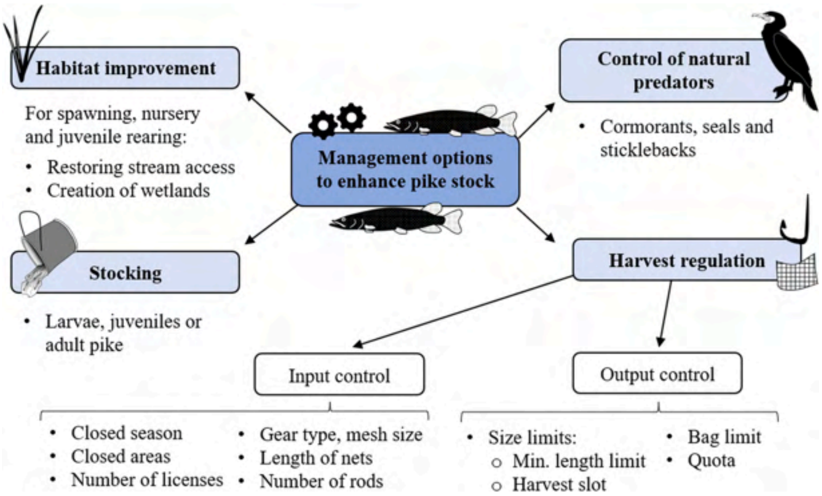


Fig. 31. Actions and tools that managers can realistically target to rebuild pike stocks in lagoon fisheries of Rügen and that are currently discussed among stakeholders and policy makers.

enforcement or lack of understanding of the rules. We would also recommend to consider the fishing mortality of both fisheries sectors as both sectors contribute to total fishing mortality and savings in pike in one sector could easily be compensated by increased harvest by the other sector, especially if annual quotas continue to not be used for pike management. This compensatory nature of fishing mortality is important especially in a mixed exploitation scenario. In the Rügen fishery, conflicts among fishers and anglers are not only exploitative (competition for a shared stock) but also based on interference competition (e.g., competition for space). Interference competition can be managed based on spatial zoning or removal/constraint of certain gear types (e.g., gill nets) in areas that are important for recruitment and for the other fishing sector. Also, any savings in harvest by fisheries may be compensated by increased mortality by natural predators as shown in protected areas in Sweden (Bergström et al., 2023). Therefore, it is recommended to design changes in fishing mortalities in the context of a holistic management plan that also addresses other mortality sources.

To assess the perspective of fishers and anglers on the various options to manage the fishing mortality on pike, two large-scale surveys were recently completed among the two user groups (details on the survey of anglers, see Koemle et al., 2022), and the attitudes towards various management actions were assessed, including attitudes to input and output controls of the fishery. The vast majority of both fishers and anglers (> 60%) agreed that increases in minimum-size limits or implementations of harvest slots for pike (for anglers only) would be highly desired and accepted (Fig. 32). A majority (> 50%) of both user groups also favored the introduction of an annual quota and a reduction of the daily bag limit for anglers. Opposing perspectives were raised as to the reduction of commercial fishing gear allowed for each fisher, the reduction in angler numbers and differential access to protected areas for either anglers or fishers (Fig. 32). In terms of the standard harvest regulations, the majority of fishers and anglers agreed that a reduction of a daily bag limit to either 2 or 1 pike per angler days and installation of a harvest slot of pike among 60 and 85/90 cm would be highly preferred (Koemle et al., 2022). Implementation of these actions will thus unlikely to find much resistance among fisheries stakeholders in the region (Koemle et al., 2022). Scientifically, we cannot exactly predict how these actions would contribute to stock recovery, but they can all help to reduce harvest and thereby increase stock size, catch rate and size of fish in the catch (particularly important to anglers).

The outcomes of input and output controls depend on the management objectives, the recruitment, adult mortality and growth levels and compliance with rules; hence their success cannot be guaranteed or generalized (Ahrens et al., 2020; FAO, 2012). If the aim is to avoid stock collapse while maximizing biomass yield, managing with a minimum-length limits or other tools of size-selectivity that avoid catching the young immature pike, assisted by other protection offered during the fishing season, such as gear constraints and daily bag limits to anglers (Oele et al., 2016), has been proven successful in pike management (reviewed in Arlinghaus et al., 2018). Yet, if management objectives also include a certain size-structure and allowing fish to reach trophy sizes to suit angler expectations, minimum-length limits have shown reduced success and maximum size limits or harvest slots have been found to be superior (Ahrens et al., 2020; Arlinghaus et al., 2010; Gwinn et al., 2015; Tiainen et al., 2017). Larger pike have higher reproductive success (Monk et al., 2021) and are socially extremely valuable, particularly to anglers (Koemle et al., 2021, 2022), which could warrant their increased protection. Protected areas, including temporal restricted protected areas, can increase abundance of fish and of large fish, which can buffer and perhaps even increase recruitment (Marshall et al., 2021; Eklöf et al. 2023), although it less clear whether such areas have also improved fisheries outside the protection zones in the Baltic in pike (Edgren, 2005). Recent work by Eklöf et al. (2023) in bays in Sweden suggest that positive effects for coastal pike can emerge from spawning protection zones. In light of the now dominant sector of recreational fisheries in the lagoon fishery, both in terms of yield in some years as well as economic impact through angling-related tourism, we suggest implementing harvest slots (e.g., 60–90 cm), increasing the protected season to fully cover the reproduction phase and reducing daily bag limits maybe useful strategies, particularly to control fishing mortality by anglers. Control of the fishing mortality of fishers might need the installation of quotas, alterations of protected area networks that limit access and reduce mortality and installation of upper limits to mesh sizes, if the aim is to save large fish from harvest.

Managing habitat: Improving the habitat quality and thereby increasing either recruitment rate or carrying capacity is always important, especially if habitat constraints affect recruitment and production as seems currently to be the case around Rügen. For the lagoon pike improvement of access to freshwater and re-recreation of wetland access during spawning seems to be a natural management objective. Indeed, semi-natural stock-enhancement facilities called “pike-factories”, which mimic regularly flooded natural wetlands under controlled water level conditions, have repeatedly been used to restore Baltic pike stocks in Sweden (Engstedt, 2011). Nilsson et al. (2014) monitored three Swedish coastal streams serving as spawning habitats for anadromous pike populations before and after the implementation of such habitat restoration approaches. While two of the study-systems did not show increased production after restoration, outmigration of juvenile pike into the Baltic Sea was 30 times higher in the third system. Here, absolute figures reached up to 30.000 individuals ha^{-1} 2-years after- and 75.000 individuals ha^{-1} 5-years after the restoration measures were put in place (Engstedt et al., 2018). This difference was explained by the regulated outflow of the pike factory, allowing juveniles to freely out-migrate whereas natural marshes often temporarily trap the fishes and thereby increase cannibalism. The abundance of adult spawners recorded at the wetland more than doubled from 1.400 to 3.100 individuals in the 5 years following restoration (Engstedt et al., 2018). The authors emphasize the importance of shallow areas with temporarily flooded terrestrial vegetation to coastal pike, which provide refuge from cannibalism and high densities of zooplankton-prey for juveniles and can strongly support coastal pike according to recent work (Eklöf et al. 2023). While in the above cases streams were already used for spawning prior to restoration, there is also evidence that pike are able to recolonize former spawning habitats after access has been regained, as well as colonize newly created spawning habitats (Oele et al., 2019), further emphasizing the potential applicability of restoration measures in the littoral of the lagoon ecosystems. Where bottlenecks exist in early life stages, improvement of the natural spawning habitat seems to be of superior importance in anadromous populations of pike (as opposed to e.g. stocking practices, see below) given that local adaptations are manifested between different populations (Berggren et al., 2016; Nordahl et al., 2019; Sunde et al., 2022). Other possibilities to increase the habitat quality for pike are factors that control eutrophication and increase macrophyte coverage, but this will demand constraining nutrient inputs further and attempting to move systems from a turbid-algal dominated state to one that is characterized by clear water and abundant macrophytes (Eriksson et al., 2009). Support among fishers and anglers for habitat enhancement that either generates access to freshwaters or increases vegetation is very high (Fig. 33), very likely because such actions have limited costs to the fishers and anglers.

Managing the pike abundance directly: A majority of anglers and fishers also believe that stocking can increase the lagoon pike stock (Fig. 33). However, decades of research on stocking of pike into self-recruiting populations raises important doubts that this practice is sustainable (Hühn et al., 2014; Johnston et al., 2018; Jansen et al., 2013; review Guillerault et al., 2018). Stocking of brackish adapted pike was once prominent in the lagoon fisheries in the 1970 s (Falk, 1966) and was also tried in the 1930 s (Subklew, 1955b), but the programmes ended in light of limited evidence that catches were increased. A more recent stocking experiment in the Peenestrom (Fig. 1) with marked juvenile pike of 15–25 cm total length also failed to generate additive effects (Dorow and Lemcke, 2004). Relatedly, an assessment of the genetic traces of a

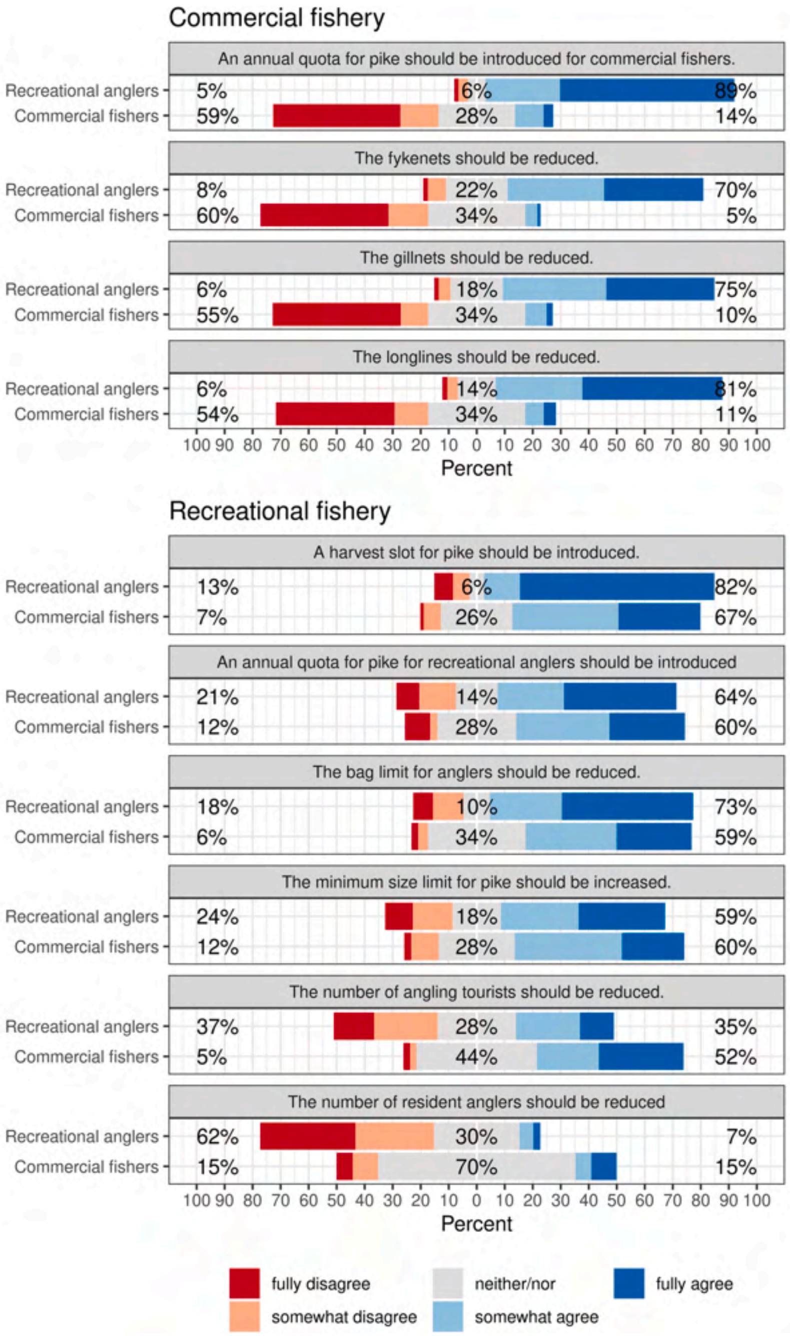


Fig. 32. Attitudes of fishers (N = 80) and anglers (N = 916) in the lagoon fishery of Rügen on various harvest regulations.

long-term stocking program in the coastline of Denmark has shown no introgression of (stocked) freshwater pike into the Baltic population (Larsen et al., 2005). These observations are likely the result of a maladaptation of stocked freshwater pike to the saline environment of the Baltic Sea and are also expected in response to strong density-dependent process of juvenile mortality compensation that quickly removes excess pike from a system (Johnston et al., 2018). We would thus not recommend engaging in stocking to sustain the lagoon pike in the southern Baltic Sea.

Managing natural predators: Controlling natural predators, specifically cormorants, receives very high support by both fishers and anglers, and fishers additionally want to control seals (Fig. 33). Both anglers and fishers wanted to control cormorants, while the attitudes towards seal control were stronger among fishers rather than angler. In

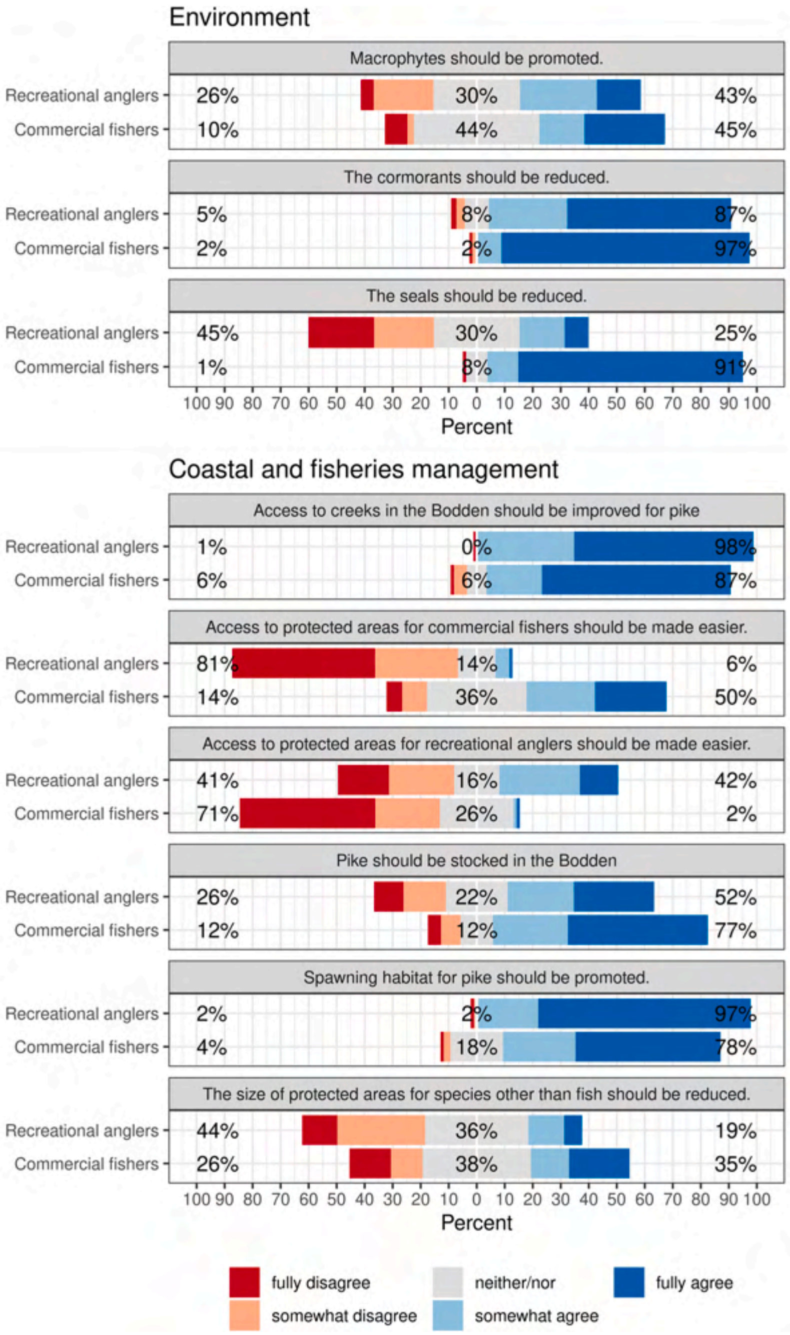


Fig. 33. Attitudes of fishers (N = 80) and anglers (N = 916) in the lagoon fishery of Rügen as related to regulations affecting the environment of pike.

Sweden, seal predation is suggested to affect local pike abundance (Bergström et al., 2022), but we have no hard evidence for this effect in the Rügen fishery. High losses of pike by cormorants is more certain for the Rügen fishery, but we lack research that accounts for density-dependent population feedback to quantify the relevance of cormorant predation for the Rügen pike fishery. However, first models suggest that impacts on the Rügen pike stocks are well possible (Ehrlich et al. unpublished data). Moreover, it is possible that savings of pike through reduced fisheries and angling mortality might be compensated by increased natural predation mortality as was shown in Sweden (Bergström et al., 2023), such that managers are recommended to pay attention to compensatory natural mortality effects in response to harvest regulations of pike. Further studies are needed before management actions to control natural predators can be recommended for the lagoon fishery at Rügen. This recommendation also holds for controlling stickleback or goby abundance on spawning groups of pike, which has been shown to be decisive for recruitment in anadromous pike in Sweden (Nilsson et al., 2019). No such data exist for the Rügen fishery, but the potential is certainly there, particularly in light of the potential for climate change-induced changes in the spatio-temporal overlap of pike eggs/larvae and locally high stickleback abundances.

No matter which path is chosen, implementation uncertainty of all forms of management of lagoon pike will be high. It is plausible that the current negative biomass trend of the lagoon pike is caused by one or multiple poorly understood environmental factors, specifically impacts of climate change interacting with other stressors, and that this trend continues even after further controlling fishing or natural mortality. If environmental change is rapidly, and perhaps permanently reducing the productivity and recruitment regime, managers may want to engage in alternative strategies, including accepting that the stock is moving to a novel low abundance state (*Accept*) or choose to *Direct* the fishery into a new future. Transformative actions can involve permanently reducing the fishing pressure, targeting new species, changing fishery locations, engaging in novel forms of marketing and distribution, diversification of fisheries enterprises, reduction in catch expectations by anglers, increasing the added value of catch for fishers, and supporting fishers to engage in alternatively livelihood or in designing aquaculture operation as alternatives to capture fisheries. Clearly, intensive stakeholder debates are needed to decide on suitable directions that are acceptable within an *Accept* or *Direct* framework. Moreover, installation of a monitoring system to track pike abundance and recruitment is highly recommended to allow managers to adapt strategies and learn from past changes and to be empowered to periodically reassess objectives, states and possible management solutions within an active adaptive management framework (FAO, 2012).

13. Conclusions and further research

The lagoon pike fishery in the southern Baltic Sea is an example of a coastal fishery undergoing rapid social and ecological change and where conflicts among multiple sectors are rising due to increased competition for scarce resources (both fish and space). The fishery has seen a sustained shift from a dominance of commercial fishery towards a situation where recreational pike angling and the associated guiding sector now dominates from an economic impact perspective. The fishery is under pressure from multiple drivers that include both ecological (e.g., rises in natural predators, warming, low macrophyte coverage due to eutrophication) as well as anthropogenic forces (e.g., high fishing mortality, increased area-based protection that limit access to certain areas specifically to anglers, continued blocking of access to freshwater streams due to water infrastructure management). Many of the conflicts among stakeholders have to do with reduced availability of fish, specifically trophy fish, and competition for space that cannot be easily reconciled due to a pervasive knowledge gap as to the key underlying reasons of the current biomass decline and the open-access nature of the fishery (Arlinghaus et al., 2022). A range of management actions could nevertheless be attempted, but it is unclear whether they would rebuild the pike stock or whether ongoing effects of global change are transforming the ecological properties of the underlying ecological system towards a new state that is less productive than in the past. Further research is needed to better understand impacts of climate change and of natural predation on the Rügen pike stock. Socio-economically, more research on the behavioral responses of fishers and anglers and on fostering rule compliance and mutual acceptance of different sectors is needed. Further, a monitoring system to track ecosystem change in the lagoons is important to establish to increase the manager's ability to understand social and ecological dynamics and how they affect both the pike stock and the fishery that depend on it. As a stepping stone toward the future, based on the reviewed evidence in this article, we recommend to further reduce fishing mortality on pike which is currently showing signs of growth overfishing and certainly of size overfishing, and to increase activities that elevate recruitment, e.g., through restoration of access to flooded wetlands. Whether these actions have the intended effect depends strongly on how natural predators respond to the elevated abundance of precruited and recuited pike. Moreover, as the current total fisheries removals are not capped, any savings of removals by one fisheries sector may be compensated by increased removals of the other or by natural predators. To manage conflicts among commercial and recreational fisheries and ease allocation decisions, participatory processes that involve all stakeholder groups in management decisions should be developed to help solve the allocation problem in a fair and Pareto-efficient way to avoid win-lose or lose-lose situations. Further research is needed on the local abundance of pike assessed using fishery-independent methods, recruitment pathways of pike, food web and predator-prey interactions, meta-population structure, and the potential for recreational angling-induced timidity and how this could be managed using novel systems such as rotating closures. Research on the targeting behavior and the economics of commercial fishing in lagoon fisheries is also warranted to help identify economically viable options for co-existence of commercial and recreational fishery for coastal pike in the southern Baltic Sea of Germany.

CRediT authorship contribution statement

Robert Arlinghaus: Conceptualization, Methodology, Investigation, Formal analysis, Writing – original draft, Writing – review and editing, Supervision, Project administration, Funding. **Timo Rittweg:** Validation, Investigation, Visualization, Writing – original draft, Writing – review & editing. **Félicie Dhellemmes:** Validation, Investigation, Visualization, Writing – original draft, Writing – review & editing. **Dieter Koemle:** Methodology, Investigation, Visualization, Software, Formal analysis, Investigation, Data curation, Writing – review & editing. **Rob van Gemert:** Methodology, Investigation, Visualization, Software, Formal analysis, Investigation, Data curation, Writing – review & editing. **Hendrik Schubert:** Investigation, Writing – original draft, Writing – review & editing. **Dominique Niessner:** Validation, Investigation, Visualization, Writing – original draft, Writing – review & editing. **Sören Möller:** Investigation, Visualization, Writing – original draft, Writing – review & editing. **Jan Droll:** Investigation, Visualization, Writing – review & editing. **René Friedland:** Methodology, Investigation, Formal analyses, Visualization, Writing – original draft, Writing – review & editing. **Wolf-Christian Lewin:** Methodology, Investigation, Formal analyses, Visualization, Writing – original draft, Writing – review & editing. **Malte Dorow:** Data curation, Writing – review & editing. **Linda Westphal:** Investigation, Writing – original draft, Writing – review & editing. **Elias Ehrlich:** Methodology, Investigation, Formal analyses, Visualization, Writing – original draft, Writing – review 7 editing. **Harry V. Strehlow:** Writing – original draft, Writing – review & editing. **Marc Simon Weltersbach:** Writing – original draft, Writing – review & editing. **Phillip Roser:** Methodology, Investigation, Visualization, Writing – review & editing. **Marlon Braun:** Writing – review & editing. **Fritz Feldhege:** Writing – review & editing. **Helmut Winkler:** Methodology, Investigation, Writing – review & editing.

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

Non-proprietary data available upon request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2023.106663.

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Paper II

II

Phillip Roser, Félicie Dhellemmes, Timo Rittweg, Sören Möller, Helmut Winkler, Olga Lukyanova, Dominique Niessner, Jörg Schütt, Carsten Kühn, Stefan Dennenmoser, Arne W. Nolte, Johannes Radinger, Dieter Koemle, Robert Arlinghaus, 2023, Synthesizing historic and current evidence for anadromy in a northern pike (*Esox lucius* L.) meta-population inhabiting brackish lagoons of the southern Baltic Sea, with implications for management, Fisheries Research, 263: 106560.

pike spawning run, photo credit: Phillip Roser

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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

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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

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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

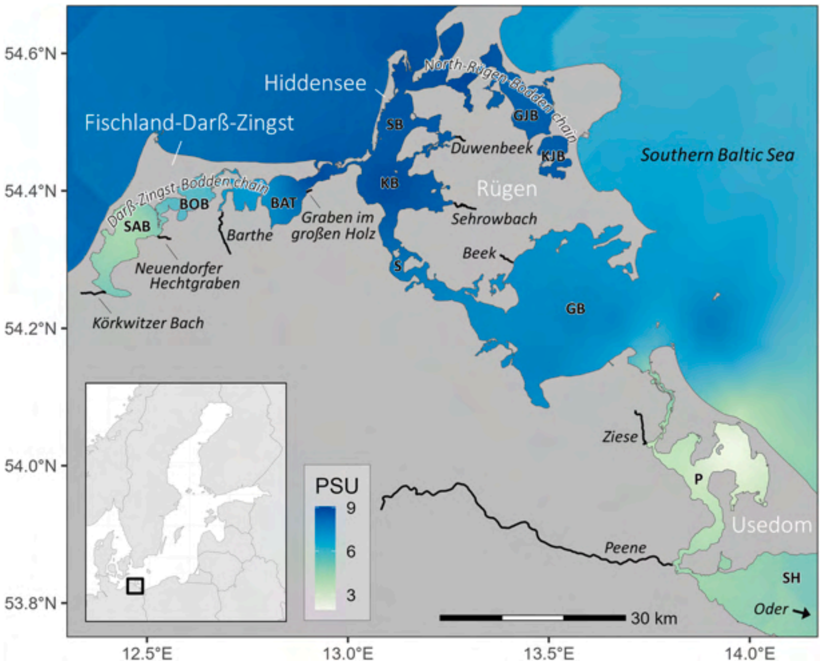

Fig. 1. Overview of the study area. All freshwater bodies sampled for this study are displayed in black with corresponding names (italic). Bodden lagoons are displayed as a colour gradient, denoting average salinity (PSU) in March and April in the years 2017–2022. Salinity data were compiled using official 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

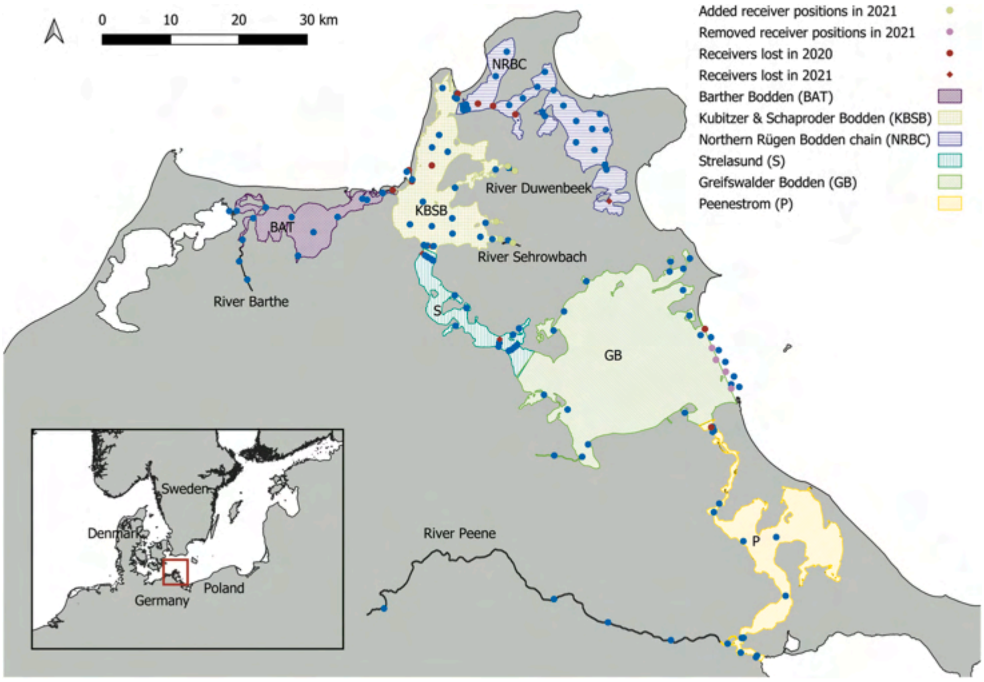

Fig. 3. Map of the study area displaying the position of the acoustic telemetry receivers.

(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

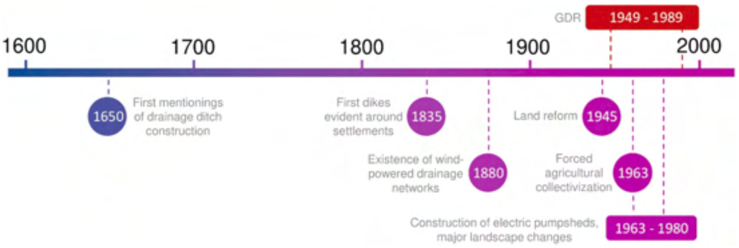

Fig. 4. Conceptual timeline displaying the temporal development of agricultural drainage systems around Rügen in the historical context.

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.

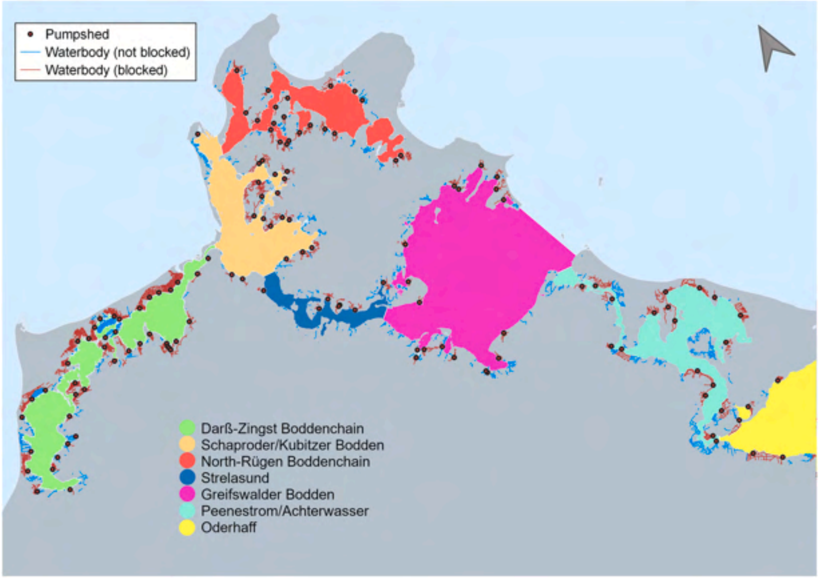

Fig. 6. Depiction of the main Bodden areas around the Island of Rügen. Coastal freshwater bodies (within a 2 km strip inland of the Bodden coastline) are displayed in red and blue along the coastline where colour indicates the existence/lack of connectivity with the Bodden lagoons. Black dots display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

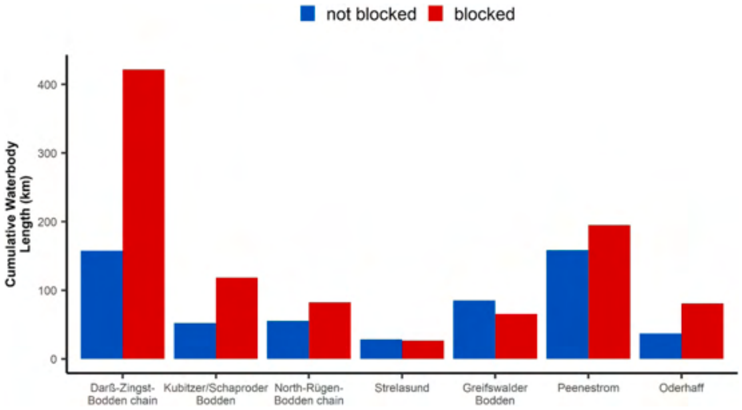

Fig. 7. Cumulative waterbody length of coastal freshwater bodies within 2 km of Bodden coastline, categorized by the presence or absence of pump sheds at the entrance to the Bodden-lagoons.

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

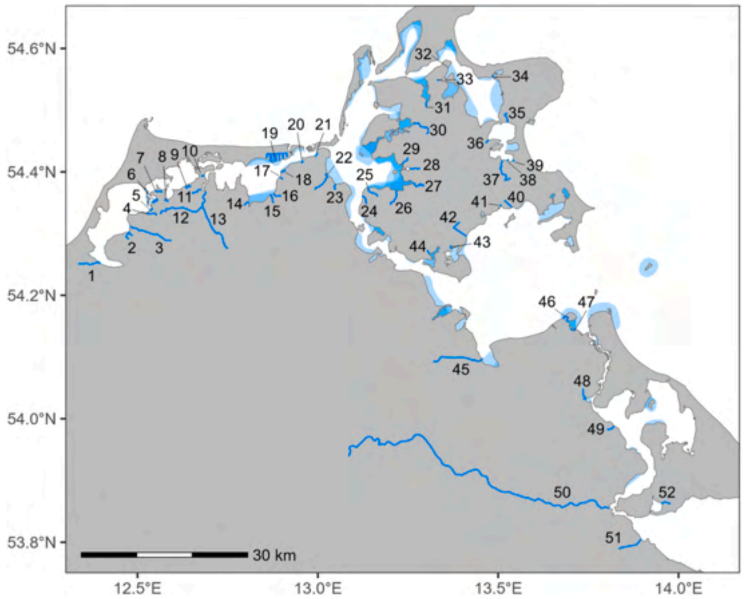

Fig. 8. Overview of freshwater bodies from interviews and field sampling. Suspected brackish spawning sites from interviews are displayed as blue areas in the lagoons with areas more frequently mentioned displayed in higher color intensity. Complementary information for each freshwater body is displayed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

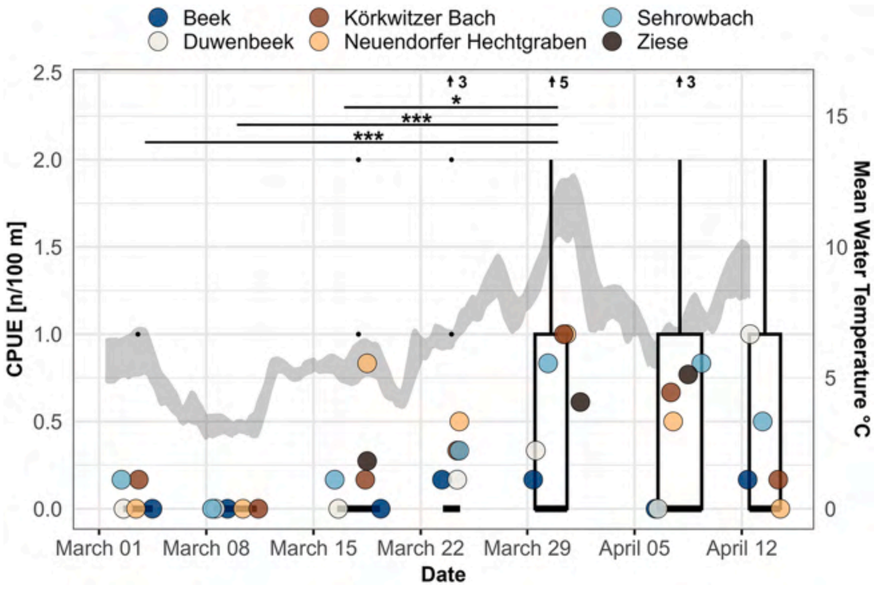

Fig. 10. Boxplots (median, box = 25 and 75 percentile, whiskers = 1.5 * interquartile range) display the temporal progression of CPUE (Pike > 30 cm * 100 m^{-1}) for all 100 m transects from electrofishing of all five streams with standardised sampling in spring 2021, grouped by sampling week (30 data 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

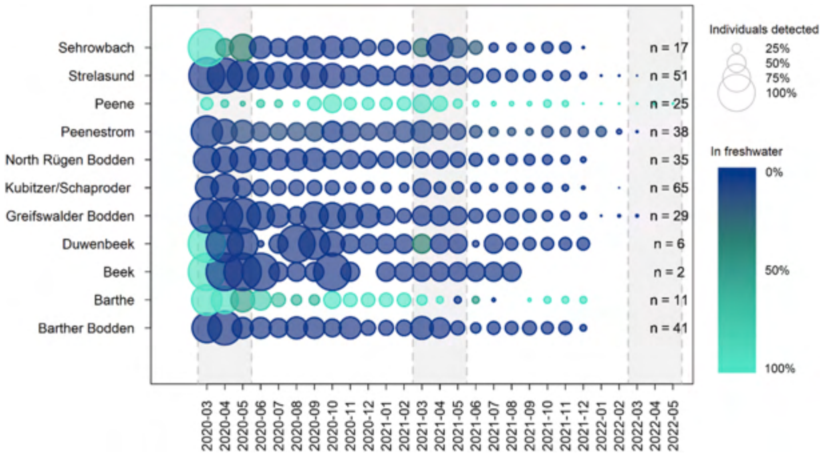

Fig. 11. Proportion of tagged fish that visited a freshwater stream for each month, derived from acoustic telemetry data (i.e. ratio of the number of individuals detected in freshwater on the number of individuals tagged). The number of fish tagged is indicated on the right side of the plotting area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

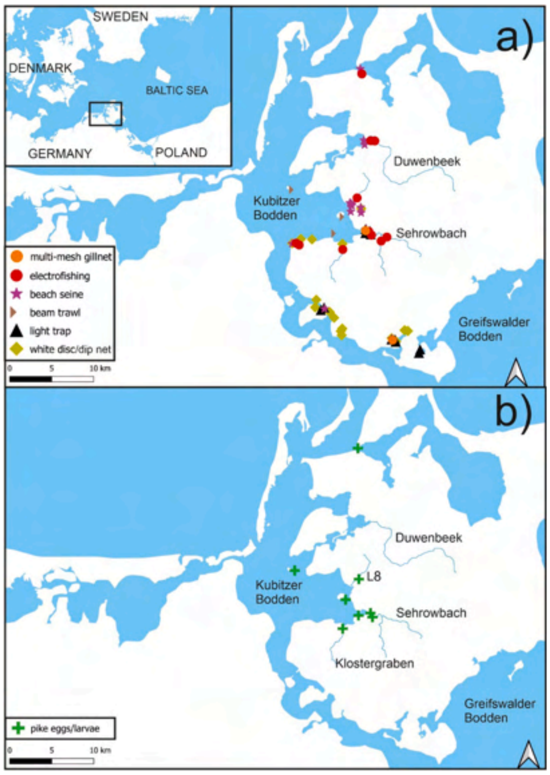

Fig. 12. Locations in which sampling for early pike life was conducted with different gears (a) and locations in which early pike life stages were detected (b).

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

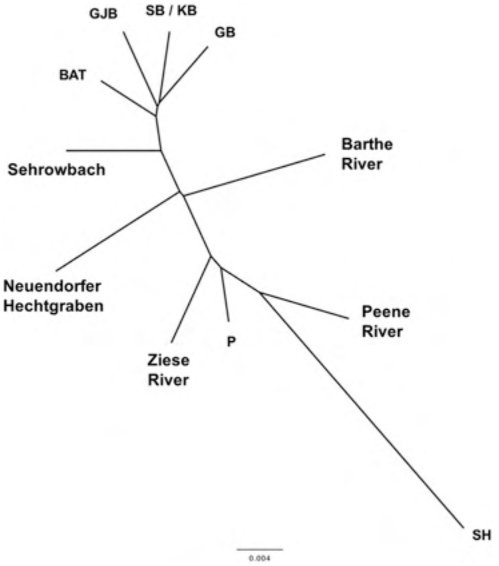

Fig. 13. Neighbor-Joining distance tree based on 1.190.970 SNPs from whole-genome sequences of pooled individuals from different study sites. In the tree, pike populations from brackish-water Bodden areas form one cluster including Barther Bodden, Schaproder/Kubitzer Bodden (SB/KB), Großer Jasmunder 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.

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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

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Paper III

III

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RESEARCH ARTICLE

Spatial and temporal dynamics of water isotopes in the riverine-marine mixing zone along the German Baltic Sea coast

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Abstract

River estuaries are characterized by mixing processes between freshwater discharge and marine water masses. Since the first are depleted in heavier stable isotopes compared with the marine realm, estuaries often show a linear correlation between salinity and water stable isotopes ($\delta^{18}O$ and $\delta^{2}H$ values). In this study, we evaluated spatial and seasonal isotope dynamics along three estuarine lagoon transects, located at the northern German Baltic Sea coast. The data show strong seasonality of isotope values, even at locations located furthest from the river mouths. They further reveal a positive and linear salinity-isotope correlation in spring, but -in two of the three studied transects- hyperbolic and partially reverse correlations in summers. We conclude that additional hydrological processes partially overprint the two-phase mixing correlation during summers: aside from the isotope seasonality of the riverine inflows, the shallow inner lagoons in the studied estuaries are influenced by evaporation processes. In contrast the estuarine outflow regions are under impact of significant salinity and isotope fluctuations of the Baltic Sea. Deciphering those processes is crucial for the understanding of water isotope and salinity dynamics. This is also of relevance in context of ecological studies, for example, when interpreting oxygen and hydrogen isotope data in aquatic organisms that depend on ambient estuarine waters.

KEYWORDS
$\delta^{2}H$, $\delta^{18}O$, Baltic Sea, bodden, Rügen, salinity, Schlei, Zingst

1 | INTRODUCTION

The water cycle, or hydrological cycle, refers to the movement of water molecules throughout the globes geological, biological and ecological compartments. Major constituents of this cycle are water evaporating from the oceans, transportation of vapour to continental realms, re-condensation to rain droplets, and back flow via groundwater and surface flow towards the ocean. The varying physical properties, specifically the different weights of stable oxygen and hydrogen isotopes of the water molecule (^{16}O, ^{17}O, ^{18}O, ^{1}H, ^{2}H), lead to isotope fractionation during all these processes (Craig, 1961; Dansgaard, 1964). As a consequence, the isotopic signature of water in both the liquid and the vapour phase is characterized by spatial and temporal variability, and in principal is depleted of the heavier isotopes in water vapour and continental freshwater, compared with the ocean water (Gat & Gonfiantini, 1981). For this reason, mixing processes in the transitional zone between the riverine/freshwater and marine/saline realm lead to linear relationships between salinity and water isotopes, as observed in multiple river estuaries around the globe (Barrie et al., 2015; Chamberlayne et al., 2021; Ingram et al., 1996; Mohan & Walther, 2015; Price et al., 2012; Swart & Price, 2002).

In precipitation, isotopes exhibit a seasonal signal, with lower/higher values in the cold/warm season, respectively (Bowen & Revenaugh, 2003). Riverine and lacustrine systems reflect this signal (Dutton et al., 2005; Ogrinc et al., 2008; Halder et al., 2015; Orlowski et al., 2016; Reckerth et al., 2017; Aichner et al., 2021), but the seasonal amplitude is attenuated and timing of the signal delayed by 1–3 months (Bittar et al., 2016; Jasechko et al., 2016; Reckerth et al., 2017; Rodgers et al., 2005). The reasons for the time delay between precipitation and river/lake water isotopes, and the smaller seasonal amplitude of the latter, can be attributed to multiple catchment characteristics and processes. Crucial influencing factors on how fast a precipitation isotope signal is transferred into fluvial systems are the flow regime of rivers, and the area, topography and geology of their catchments (Maloszewski et al., 1992; McGuire et al., 2005; Rodgers et al., 2005; Sklash et al., 1976).

In water bodies with high residence time of the water, such as large and/or voluminous lakes or in the marine realm, the seasonal $\delta^{18}O$ and $\delta^{2}H$ variability decreases. Instead, mixing processes of water from different sources with variable isotopic signatures, become more dominant on the actual isotopic signature (Benetti et al., 2017; Craig & Gordon, 1965; Frew et al., 2000). The North Sea, for example, is influenced by both North Atlantic water with high salinity, entering the North Sea basin from the northeast, and inflow of brackish water and freshwater, derived from the Baltic Sea and from rivers, respectively (Harwood et al., 2008). The Baltic Sea, in turn experiences occasional inflow intrusion from the North Sea (higher $\delta^{18}O$ and $\delta^{2}H$ values), but also constantly receives freshwater discharge from rivers (lower δ-values). For these reasons, water isotopes show a strong positive correlation with salinity in both the Baltic Sea and North Sea (Ehhalt, 1969; Frohlich et al., 1988; Jefanova et al., 2020; Richter & Kowski, 1990; Torniainen et al., 2017).

Isotope signatures of the ambient water are mirrored in the local fauna and flora. For example, fish incorporate elements from ambient water into their body structures, (Zanden et al., 2016). These structures form through precipitation from the water the fish currently lives in, and as such mirror the current isotopic profile of the water (Patterson et al., 1993). In recent years, oxygen isotopic ratios of ear bones (otoliths) have been commonly used in studies of migration and geolocation of fish, for example to develop isoscapes, that is predictive surfaces of large-scale water isotope data. Those were used to retrospectively predict the whereabouts of migrating fish (Brennan et al., 2019; Torniainen et al., 2017; Trueman et al., 2012), and to assign fish to discrete, geographically segregated stocks (Matta et al., 2010). With respect to aquatic plants or algae, their cellular lipid compounds have been shown to track the hydrogen isotopic signature of the ambient water, but with a potential additional influence of varying salinity (Aichner et al., 2017; Häggi et al., 2015; He et al., 2020; Ladd & Sachs, 2015, 2017; Sachs & Schwab, 2011; Schouten et al., 2006). These dependencies have frequently been applied in paleoclimatic studies, for reconstruction of past hydrological conditions and salinities (e.g. Aichner et al., 2019; Leduc et al., 2011; Meer et al., 2007).

Knowledge and understanding about water isotopic gradients and the hydrological processes behind, has great potential to facilitate application and interpretation of oxygen and hydrogen isotopic compositions in biogenic carbonates and plant lipids. In this study, we analysed water isotope dynamics in estuarine river and lagoon systems along the northern German Baltic Sea coast. Main questions were: (1) how far are seasonal isotope signals in rivers transmitted into Baltic Sea estuarine systems? (2) what are the major processes behind the observed gradients? (3) are water isotopes a predictor for salinity in the riverine-marine mixing zone? The major aim was to understand how hydrological processes control seasonal and spatial water isotope variability in this study area.

2 | STUDY AREA

The northeastern German coast of the Baltic Sea is basically a flooded glacial moraine landscape. It is characterized by extensive bays, shallow lagoons (the boddens) and marine inlets, which form the mixing zone between rivers and the marine realm (Correns, 1977; Schwarzer et al., 2008). These zones are characterized by hydrologic events which in turn affect biochemical characteristics of the ecosystem. For example they react sensitively both to discharge pulses from rivers and inflow events from the marine side after storms (Gocke et al., 2003). Furthermore, a dense net of water management structures, such as water retention flaps, partially attenuate freshwater flow from creeks into the lagoons. Here, automatic ones will release water from creeks when the lagoons are low while some manual flaps exist, which are operated by hand (Funkel, 2004) .

For this study, water samples were taken along three transects, encompassing salinity gradients (Figures 1 and 2; Tables S1 and S2):

a. The Schlei estuary (Figures 1 and 2a) is a flooded sub-glacial channel, extending ca. 42 km from the major Baltic Sea coast line towards the inlands. The inner Schlei comprises the two larger basins of the 'Kleine Breite' and 'Große Breite', while the outer Schlei at some sections resembles a wider river. Adjacent, several 'noors', that is water bodies similar to lakes, are connected to the main Schlei often by just narrow outlets. The Schlei has one medium sized inflow, the Füsinger Au at Kleine Breite, and several small creeks entering along the whole length of the water body. The salinity gradient is linearly increasing from 0 to 3 psu at the inner Schlei (Burgsee and Kleine Breite) towards values of ca. 15–20 psu near the outflow to the Baltic Sea (Gocke et al., 2003; Grupe et al., 2009; LLUR, 2001; Seiß, 2014). This gradient is seasonally influenced by relatively high freshwater discharge in winter and spring compared with summers. In addition, episodic sea level changes by ±0.5–1.5 m, caused by strong winds, lead to rapid movement of water masses within the Schlei, which superimposes the salinity gradient (Schulz, 1979). Saltwater intrusion events,

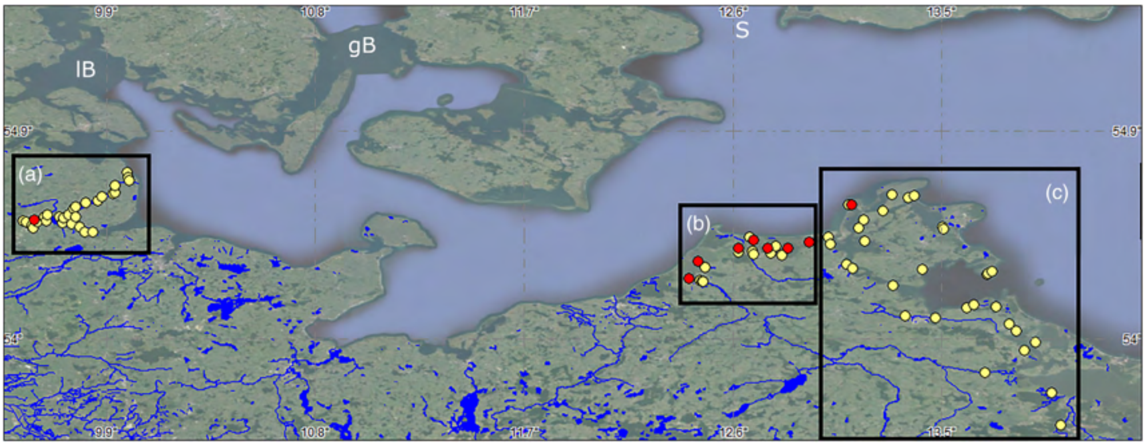

FIGURE 1 Transect sample points at (a) Schlei, (b) Darss-Zingst Bodden chain (DZBC) and (c) East Transect (Stettiner Haff—Peenestream—Greifswalder Bodden—Rügener Boddens). Red circles: Time series sampling March 2020–March 2021. Yellow circles: Seasonal sampling (June 2019, March 2020, July 2020). gB, Great Belt; IB, Little Belt; S, Øresund. Sampling points are listed in Tables S1 and S2.

from the North Sea into the Baltic Sea (Mohrholz, 2018a, 2018b) (Figure 3) similarly have the potential to increase salinity values in the outer Schlei, as visible for March 2020 in contrast to July 2020 (Figure 2a).

b. The Darss-Zingst Bodden chain (DZBC) is a system of several shallow water basins, which mostly do not exceed 2–3 m water depth (Figures 1 and 2b). The rivers Recknitz and Barthe are major inflows and there are two outflows towards the Baltic Sea, which lie close to each other at the easternmost end of the Darss-Zingst peninsula. The salinity gradient is covering the range from almost freshwater conditions near the Recknitz and Barthe inflows to ca. 10 psu near the outflows (Chubarenko et al., 2005). The latter reflect the salinity levels of the adjacent Baltic Sea, which are lower than in the more western Baltic realms (where the Schlei is situated), but likewise influenced by salt water intrusion events (Figure 2b). The DZBC can be divided into an inner/western part (Saaler Bodden and Bodstedter Bodden), which is mainly influenced by riverine inflows, and an outer/eastern part (Barther Bodden and Grabow), which is more susceptible to Baltic water inflow during conditions of east winds (Schumann et al., 2006). The two parts are connected by the Zingster Stream (ZS), a narrow and deep water channel located in the central bodden chain.

c. the easternmost transect reaches from the Stettiner Haff, via the Greifswalder Bodden to the multiple lagoons which form the western and northern bodden chains around the isle Rügen (WRBC and NRBC) (Figures 1 and 2c). While the covered salinity gradient is similar than in the DZBC (i.e. 0 – ca. 10 psu), several inflows and connections to the Baltic Sea create a highly dynamic system in pronounced exchange with marine water (Bachor, 2005; Correns & Jäger, 1979; Hübel et al., 1998; Hübel & Dahlke, 1999). The Stettiner Haff is strongly under influence of the Oder river, which contributes >95% of the riverine discharge along the northeastern German Baltic Sea coastline (Richter & Kowski, 1990). Salinity is gradually increasing between the Stettiner Haff, along the Peenestream towards the Greifswalder bodden (Figure 2c) (Lampe, 1999). The latter is a larger basin of max 13.5 m depth which is separated to the open Baltic Sea by the 'Greifswalder Boddenrandschwelle', a glacial terminal moraine which builds a just 1–2.5 m deep shallow. The Greifswalder Bodden is connected by the Strela Sound to the WRBC, which in turn terminates in the Vitter Bodden next to Hiddensee island. The same bodden can be seen as terminal basin of the inner or northern Rügen bodden chain (NRBC; reaching from Kleiner Jasmunder Bodden via Großer Jasmunder, Breeger and Wieker Bodden), which is characterized by a salinity gradient from 0 to ca. 10 psu, comparable as in the DZBC (Birr, 1997; Schiewer, 2008).

3 | MATERIAL AND METHODS

3.1 | Water sampling

Water samples were taken along transects (yellow dots in Figure 1) in June 2019 (lower spatial density of sampling points), March 2020 and July 2020. They were collected close to shores with a pipette from ca. 40 to 60 cm below water surface and directly transferred into a measurement vial. The vials were instantly closed and stored in a cooling box, before being placed in a fridge until further processing.

At selected spots, time series were sampled every 2–4 weeks (A: Schlei, A. P. Møller Skolen Schleswig; E: Zingster Stream, Biological Station; I: Vitter Bodden, Kloster/Hiddensee) or monthly (B–D, F–G: Zingster Bodden) from March 2020 to March 2021. Samples from A and I were taken accordingly to shore samples, while samples B–H were taken in deep parts of the boddens, close to buoys marking long-term monitoring locations. For the latter, a Limnos water sampler was used to obtain 2 l samples from 0.5 to 1.0 m depth below water surface, of which 1.5 ml were transferred into measurement vials.

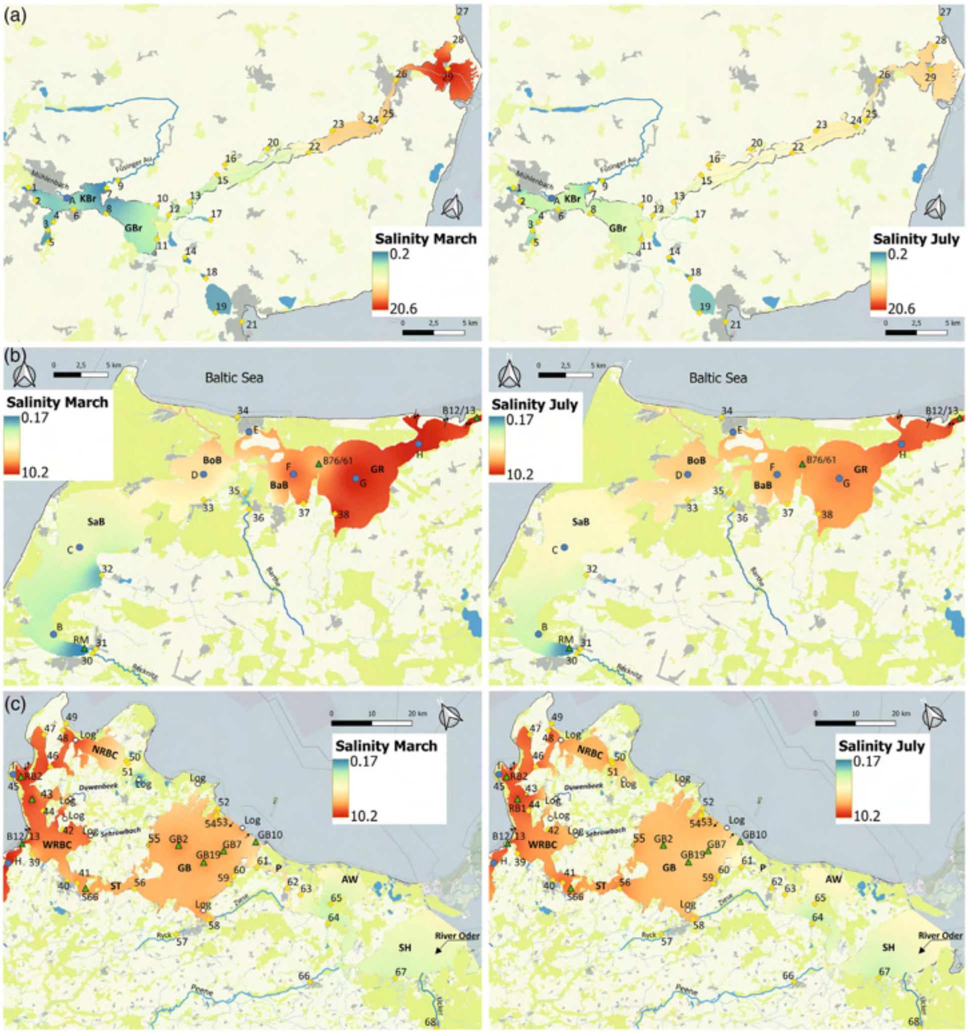

FIGURE 2 Salinity in March (left) and July (right) 2020 in (a) the Schlei; (b) the DZBC; and (c) the East Transect. Panels a–c refer to sub-regions as indicated in Figure 1. Different colour scales are due to different salinity gradients in these sub-regions. Blue circles #A–I: Sampling points for time series. Yellow circles #1–68: Shore samples. Green triangles indicate long-term monitoring points from local authorities, and white circles ('Log') spots with installed salinity loggers, both delivering data included into salinity interpolation. Double arrows indicate exchange points with Baltic Sea water. AW, Achterwasser; BaB, Barther Bodden; BoB, Bodstedter Bodden; GB, Greifswalder Bodden; GBr, Große Breite; GR, Grabow; KBr, Kleine Breite; NRBC, Northern Rügen Bodden chain; P, Peenestream; SaB, Saaler Bodden; SH, Stettiner Haff; ST, Strela sound; WRBC, Western Rügen Bodden chain.

3.2 | Water chemical parameters

Water chemical parameters were measured in situ at shore transect and time series sampling spots A and I, using a Multi 3630 IDS multi-parameter device (WTW, Weilheim, Germany), equipped with a WTW TetraCon 925 electrical conductivity measuring cell. At the A. P. Møller Skolen, salinity and temperature were measured using a modular multi-parameter probe (WTW multimeter 3440), mounted with TetraCon® 925-P and MPP 930 IDS electrical conductivity cells. Before each application the cells were calibrated with E-Set Trace 0.01 M KCl calibration solution based on PTB/NIST. For samples from DZBC-timeseries (spots B–H), a WTW 1970i conductivity meter and TetraCon 325 measuring cell were used to analyse electrical conductivity/salinity in the laboratory.

Salinity maps (Figure 2) were produced in QGIS 3.14, using the inverse distance weighted interpolation tool with a squared weighting coefficient, for the sampling periods March and July 2020. Herefore, the in situ measured salinity values were used for spatial interpolation,

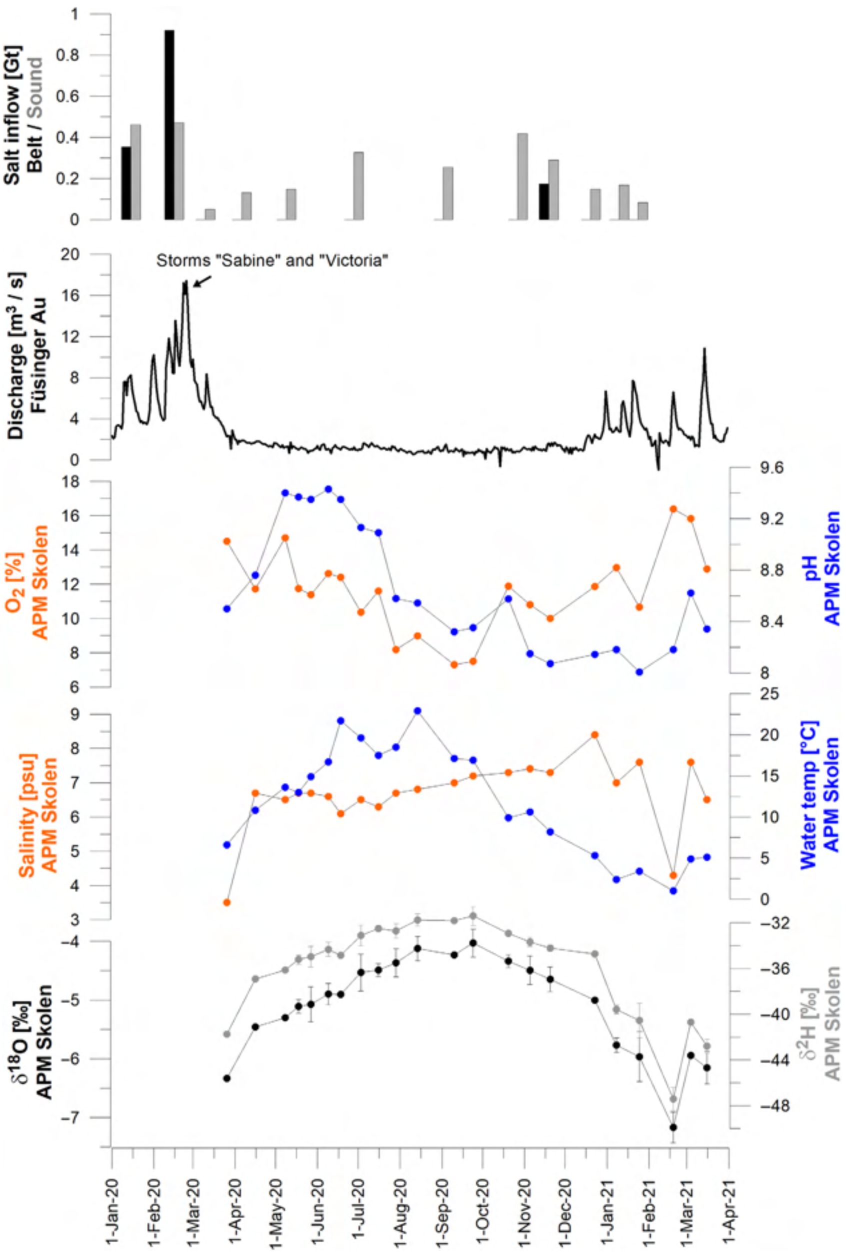

FIGURE 3 Time series of δ^{2}H/δ^{18}O values in water samples collected between 26th March 2020 and 16th March 2021 near A. P. Møller Skolen (APM Skolen), Schleswig (Kleine Breite, Schlei; sampling point #A; Figure 2a). Error bars indicate standard deviation of replicate measurements. Salinity, water temperature, O$_2$-concentration and pH measured in situ during sampling. Data of daily mean values of water discharge derived from the major inflowing river Füsinger Au (LLUR, 2022). Major Baltic Sea salt inflow events at Great Belt and Øresund from (Mohrholz, 2018a, 2018b).

in combination with data derived from monthly monitoring stations of local authorities (LUNG; Landesamt für Umwelt, Naturschutz, Geologie of the German State Mecklenburg-Vorpommern) (Figure 2). Some additional values were derived from HOBO U24-002-C salinity loggers (Onset, Bourne, USA), which were installed at different locations around the Rügener Boddens. Data were only interpolated within the riverine-marine mixing zone, while the open Baltic Sea was excluded.

3.3 | Isotope measurement

Water samples were filtered (0.2 μm cellulose acetate) prior to analysis of stable isotopes (δ^{18}O and δ^{2}H values) in the water isotope lab at IGB Berlin, using a Picarro (Santa Clara, CA, USA) L2130-i cavity ring-down spectrometer. Measurements were routinely checked for organic contamination using the Picarro ChemCorrect software.

Isotope values and standard deviations are based on six replicate measurements of each sample, discarding the first three measurements to account for memory effects. In house criteria excluded all injections with a water SD higher than 400 ppm or water amount deviation greater than 3000 ppm to furthermore improve precision.

For instrument calibration we used three laboratory standards for each group of 24 samples: L (δ^{18}O −17.86 ‰ and δ^{2}H −109.91 ‰), DEL (δ^{18}O −10.03 ‰ and δ^{2}H −72.81 ‰), H (δ^{18}O 2.95 ‰ and δ^{2}H 0.29 ‰). A fourth lab standard, M (δ^{18}O −7.68 ‰ and δ^{2}H −56.70 ‰), was used as quality and drift control after every six samples. All lab standards were referenced against primary measurement standards: VSMOW2 (Vienna Standard Mean Ocean Water 2), GRESP (Greenland Summit Precipitation) and SLAP2 (Standard Light Antarctic Precipitation 2) from the IAEA (International Atomic Energy Agency, Vienna, Austria).

The measurement uncertainty was quantified by error propagation, including the parameters: (a) uncertainties of lab standards; (b) errors of standard calibration; (c) average standard deviation of replicate measurements. Based on this, measurement uncertainty was estimated to account 0.16 ‰ for δ^{18}O and 0.57 ‰ for δ^{2}H.

4 | RESULTS

4.1 | Time series

Water samples collected at the A. P. Møller Skolen (Kleine Breite, Schlei; sampling point #A), Biological Station Zingst (ZS, #E) and Hiddensee/Kloster (Vitter Bodden; #I) all exhibit clear seasonal isotopic trends (Figures 3–6). The seasonal amplitude is in range of ca. 10–15

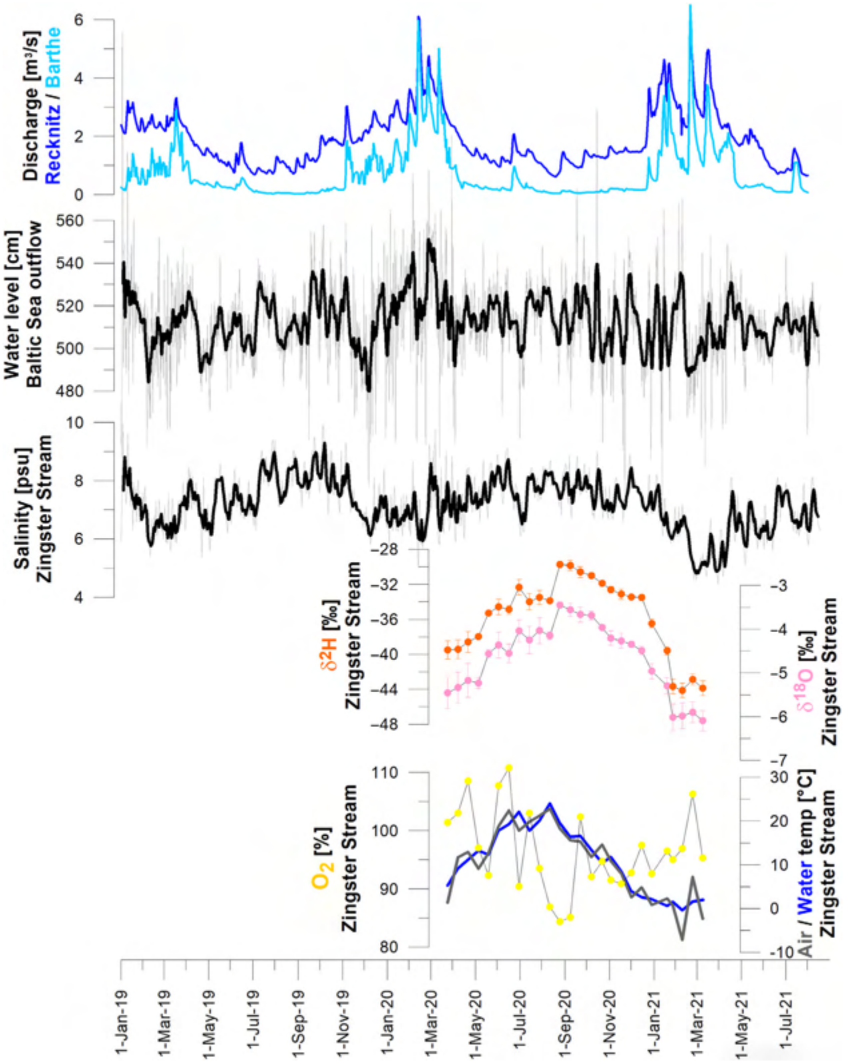

FIGURE 4 Time series of δ^{2}H/δ^{18}O values in water samples collected between 24th March 2020 and 9th March 2021 at Biological Station Zingst (Zingster Stream; sampling point #E; Figure 2b). Error bars: Standard deviation of replicate measurements. Water temperature and salinity derived from long-term daily monitoring program conducted at Biol. Station Zingst. Water levels at the bodden outflow towards the Baltic Sea near Barhöft provided by WSA-WSV (2022): Thick black line indicates 5-point average. Riverine discharge of Recknitz and Barthe from STALU (2022).

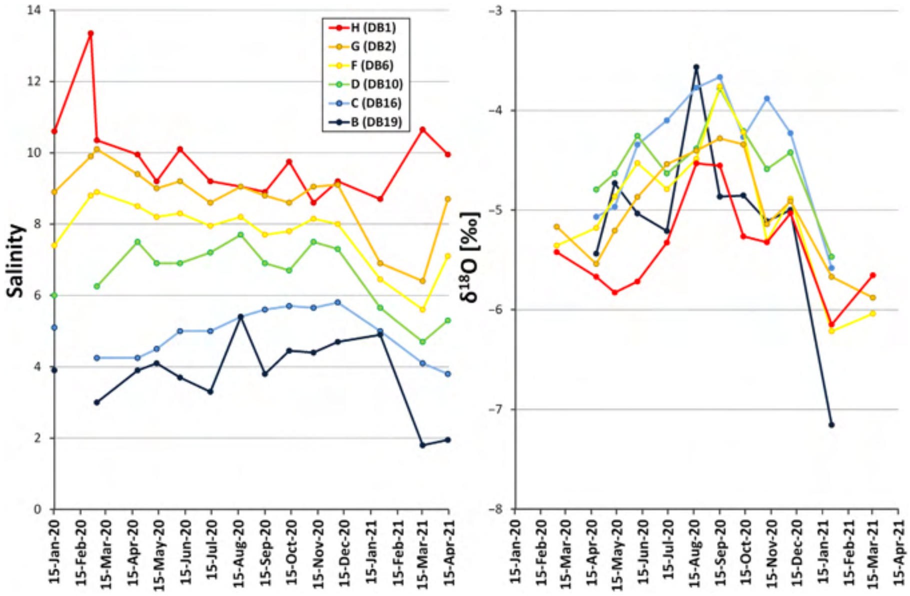

FIGURE 5 Time series of (a) salinity and (b) $\delta^{18}O$ values in water samples collected monthly at a transect along the Zingster Bodden chain. Sample points reaching from buoys located near the inflow of the river Recknitz (sampling spot #B; LUNG monitoring point DB19) to those located close to the outflow towards the Baltic Sea (sampling spot H; LUNG monitoring point DB 1).

‰ (δ^2H) and 2–2.5 ‰ ($\delta^{18}O$), reaching minimum and maximum values in February/March and September/October, respectively.

In contrast to water isotope values, the salinities showed variable trends at the different sampling locations. At the Schlei (point #A), values were relatively constant (ca. 6–7 psu) at most measuring days within the sampling period (26th March 2020 to 16th March 2021) (Figure 3). Exceptions were two samples from 26th March 2020 and 19th February 2021, which showed decreased salinity values of 3.5–4.3 psu. Those are mirrored by lower δ-values in water samples collected at those 2 days.

In the DZBC (sampling points #B–H), the salinity values exhibited pronounced seasonal trends throughout the studied time period (24th March 2020 to 9th March 2021) (Figures 4 and 5). At the ZS (point #E), they show lower values in winter/spring and higher values in summers, hence they resemble the seasonal water isotope trend (Figure 4). This is also true for the sampling spots in the western part of the DZBC (#B, #C, #D), that is close to the inflow of the river Recknitz. In the eastern part (#F, #G, #H), this seasonality becomes less pronounced (Figure 5). Close to the outflow towards the Baltic Sea (point #H), peak salinities up to 14 psu were observed in February 2020 and March 2021.

At Vitter Bodden (Hiddensee/Kloster; sampling point #I), the salinity measurements showed values around 9–10 psu, with a slight decreasing tendency throughout the sampling period (18th March 2020 to 3rd March 2021) (Figure 6). Maximum values up to 11.2 psu were observed in late winters 2020 and 2021. Hence, the seasonal trend in the Vitter Bodden resembles the conditions at the outflow of the DZBC (point H).

4.2 | Transects

Similar to salinity gradients (Figure 2), the water isotope values in March 2020 increase from low to high along all three transects, that is from river inlets to the outflows to the Baltic Sea (exemplarily plotted for $\delta^{18}O$ values in Figure 7). In July 2020, most regions show higher δ-values compared with March (Figure 7; interpolated maps with isotope offsets between the two seasons in Figure S1). Especially, the innermost waterbodies, such as Kleine and Große Breite (Schlei), the Saaler Bodden (DZBC) and the NRBC, exhibit relatively strong increases of isotope values (Figures 7 and S1). Exceptions from these trends are areas under direct influence of Baltic Sea water, such as the outflow regions of the Schlei and DZBC, which show lower δ-values in July compared with March (Figure 7).

These dependencies lead to isotope gradients which are much less pronounced in July 2020, compared with March. Specifically, the DZBC shows almost homogenous isotope values along the whole bodden chain in July 2020, with exception of the areas directly adjacent to river inflows (Figure 7b). In the following, isotope-salinity correlations are closer examined.

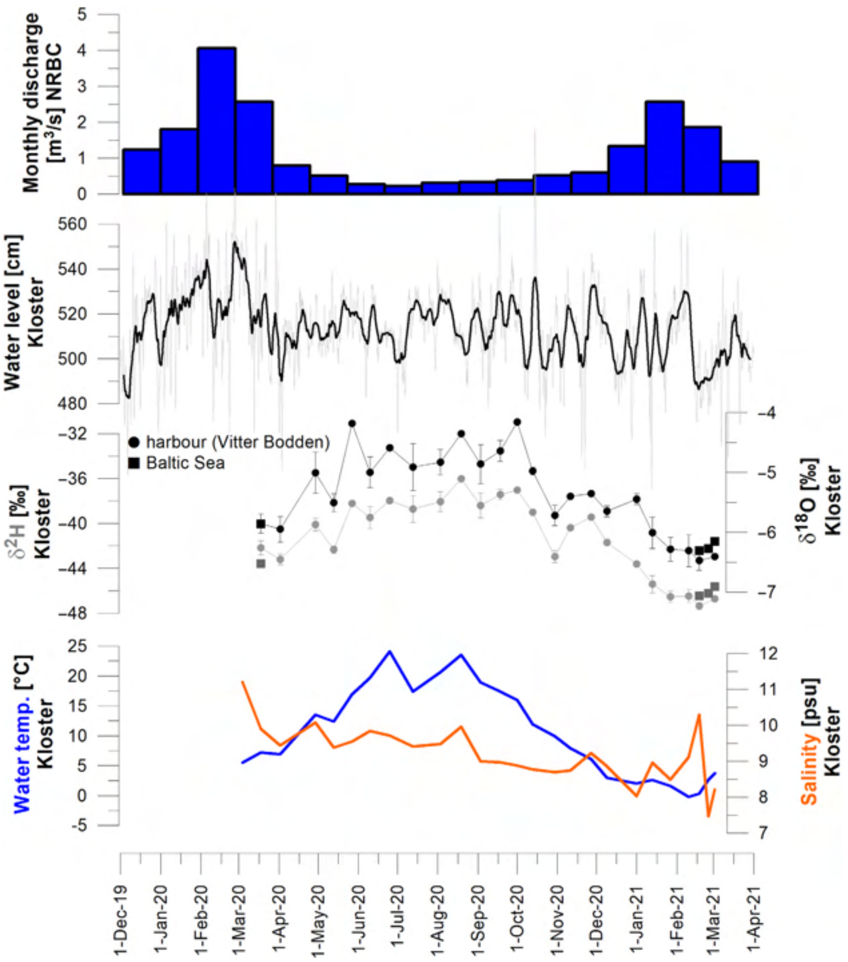

FIGURE 6 Time series of $\delta^2H/\delta^{18}O$ values in water samples collected between 18th March 2020 and 3rd March 2021 at the ferry harbour Kloster, Hiddensee (Vitter Bodden; sampling point #I), in comparison to salinity and water temperature. Error bars indicate standard deviation of replicate isotope measurements. Water levels from Kloster provided by WSA-WSV (2022). Monthly surface flow data from NRBC to Vitter Bodden from STALU (2022).

5 | DISCUSSION

5.1 | Surface runoff and Baltic Sea dynamics drive estuarine salinity

The salinity in Baltic Sea estuarine lagoons is strongly influenced by the seasonal discharge patterns of the inflowing rivers, which in turn is characterized by maximum runoff in the late winter and in spring (Cyberski et al., 2000). During our sampling period, especially the major winter storms 'Sabine' and 'Victoria', lead to increased precipitation and consequently higher surface runoff of rivers and creeks in February 2020 (Figures 3, 4 and 6).

The sampling spot #A is located about 5 km west of the mouth of the Füsinger Au. This river delivers an annual freshwater input of about twice the total water volume of the entire Schlei (Gocke et al., 2003). Furthermore, spot #A is located ca. 100 m eastwards from the inflow of the small creek Mühlenbach (Figure 2a), and therefore susceptible to major freshwater discharge events. Likewise, the decreasing influence of freshwater inflow is clearly visible along the DZBC transect, with stronger impact on the seasonal salinity trends near the inflows of the river Recknitz (#B and #C) (Figures 2a and 5a). Short-term salinity fluctuations in the DZBC can be explained by influence of different water masses from either the eastern or western side of the ZS, which is controlled by wind direction and water level differences (Schumann et al., 2006).

By contrast, the areas close to the estuarine outflows towards the Baltic Sea are more susceptible to marine salinity dynamics. Those in turn are influenced by water intrusion events from the North Sea, via the Little Belt, Great Belt and Øresund (Mohrholz, 2018a, 2018b) (Figure 1). Especially in February 2020 large amounts of North Sea water was driven into the Baltic Sea (Mohrholz, 2018a, 2018b) (Figure 3), probably enforced by the same storms that contributed to enhanced precipitation amounts. These North Sea water masses are characterized by higher salinity and also by higher δ-values, compared with the Baltic Sea water (Harwood et al., 2008; Jefanova et al., 2020).

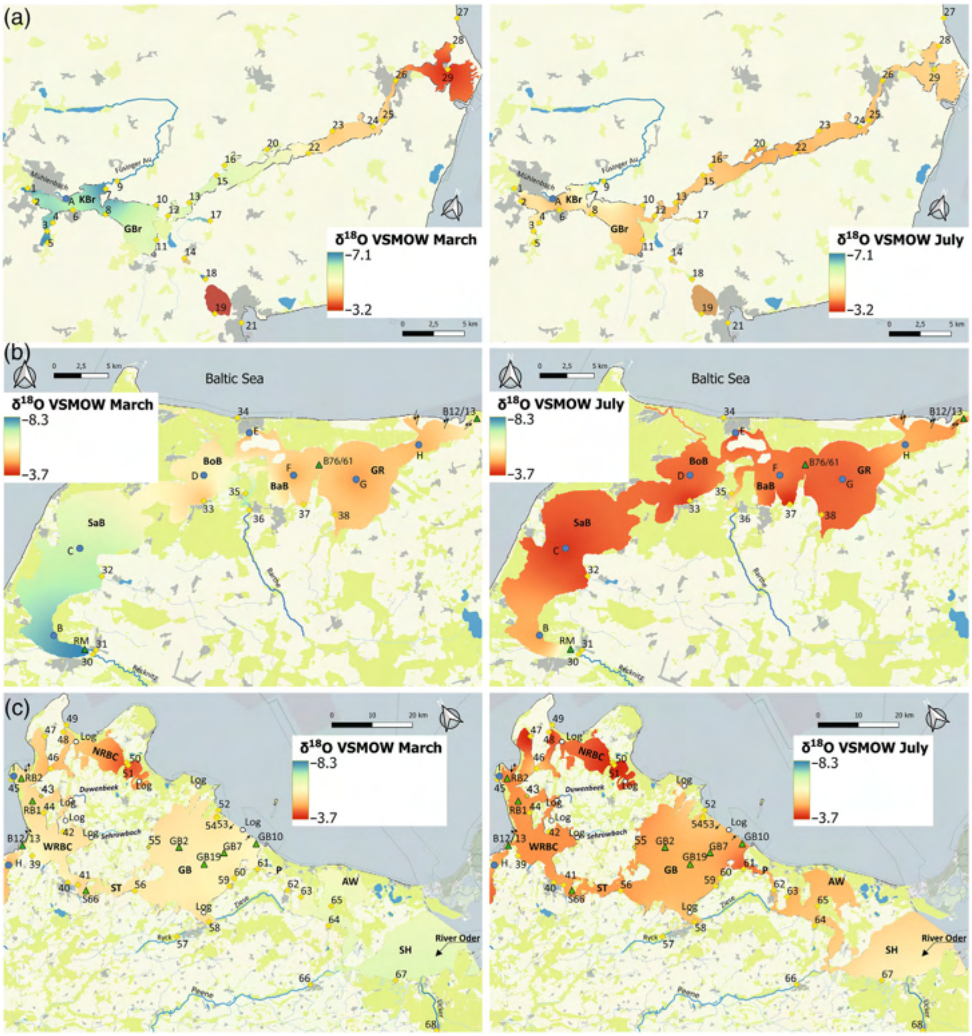

FIGURE 7 Interpolated δ^{18}O values along the three sampled transects for March (left) and July (right) 2020. Baltic Sea excluded from interpolation. Panels a–c refer to sub-regions as indicated in Figure 1. Circles #A–I: Sampling points for time series. Circles #1–68: Shore samples. Arrows indicate exchange points with Baltic Sea water. Abbreviations as in Figure 2.

The outermost Rügener Boddens (e.g. the WRBC including Vitter Bodden) are additionally shaped by complex dynamics within multiple influencing water masses: water is partially intruding from the Baltic Sea, south and northeast of Hiddensee island (Bachor, 2005). Freshwater surface runoff is derived from the NRBC (Hübel et al., 1998) (Figure 6). The boddens are further susceptible to large-scale water exchange with more eastern parts of the bodden coast, via the Strela Sound (Birr, 1988; Schiewer & Gocke, 1996).

In both the Vitter Bodden and the easternmost parts of the DZBC, salt water intrusion events from the North Sea (Figure 3) can explain the maximum salinities in February 2020 and 2021 (Figures 4–6). Strongly fluctuating values in February 2021 are probably influenced by the partial appearance and melting of an ice-cover across the boddens.

5.2 | Control mechanisms on water isotopes

All isotope time series exhibit strong seasonality of δ-values with comparable magnitude (ca. 2–3‰ δ^{18}O; Figure 3–6). This suggests, that even the sampling points most distant from the freshwater inflows reflect a delayed and attenuated precipitation signal, that is a seasonality pattern as previously observed in German rivers (Reckerth et al., 2017) and northern German lakes (Aichner et al., 2022). Those trends in δ^2H and δ^{18}O values are not fully mirrored by seasonal salinity changes, especially in the inner Schlei (#A), the outer Zingster boddens (#F–H) and the Vitter Bodden (#I) (Figures 3–6).

These results give evidence, that other factors than mixing processes between freshwater and marine water masses exhibit additional control on local water isotopes. We hypothesize, that ^{18}O/^{2}H-enrichment due to evaporation from surfaces of the shallow lagoons, such as the Kleine and Große Breite (Schlei) and the inner Zingster boddens, is a potential driver behind higher δ-values in summers. As estimated for the DZBC and the East Transect, the overall contribution of evaporation to the water budget is relatively low (<4%), while the largest contributors are riverine inflow and water exchange with the Baltic Sea (Chubarenko et al., 2005; Correns, 1977; Correns & Jäger, 1979; Lampe, 1994). On the other hand, potential evaporation exhibits a two to four times higher contribution to the overall water budget in the shallow inner lagoons of the DZBC (Saaler, Bodstedter and Barther Bodden), compared with the regions eastwards of the ZS (Grabow), and with the NRBC, the Stettiner Haff, and the Greifswalder Bodden (Lampe, 1994; Mertinkat, 1992). These spatial patterns, intermediated by morphometric factors such as shape and depths of the estuarine lagoon, might contribute to the seasonal isotope variability in these systems.

Furthermore, the correlations between water isotopes and water/air temperature, as well as O_2-saturation cannot rule out effects of these parameters onto δ-values. In winters, lower δ-values were observed in February/March 2021 compared with February/March 2020. This could indeed be explained by temperature control, due to the generally colder conditions with partially ice-cover on all sampling spots in winter/spring 2020/2021, compared with the relatively mild winter/spring 2019/2020 (reflected in water temperatures; Figures 3, 4 and 6).

In summer, the maximum δ-values are reached in September and early October (Figures 3, 4, and 6), that is 1–2 months delayed to maximum air and water temperatures. On the other hand, this timing is synchronous to maximum O_2-depletion (i.e. minimum O_2-concentration) at the sampling spot (Figures 3 and 4). The mechanistic relationship between phytoplankton blooms, local oxygen depletion and oversaturation, carbonate precipitation and pH values and their effects on oxygen isotopes in lacustrine waters have long been debated (e.g. Dietzel et al., 2009; Li et al., 2020; Quay et al., 1995). Likewise, an effect of this parameters on the measured δ^{18}O values cannot be fully excluded, but are considered as unlikely, because they do not explain synchronous trends in δ^2H values.

Near the estuarine outflows, the direct influence of Baltic Sea water onto the δ-values becomes apparent. Following the salt water intrusion events in February/March 2020, marine water with higher salinity and consequently higher δ-values shape the outflow environments of the estuaries. By contrast, lower salinities in July also lead to decreased δ-values in those realms (Figure 7).

We conclude, that specifically evaporation processes during summers are likely factors that lead to additional ^{18}O/^{2}H-enrichment on top of the seasonal signal as delivered by the riverine inflows. Other factors such as photosynthetic processes and related water chemical parameters are most likely of minor importance. Since the Baltic Sea is characterized by pronounced fluctuations in both salinity and isotope values, it shapes the water chemical conditions in its influence zone which include the outer estuarine regions.

5.3 | Salinity—Isotope correlation

The spatial trends in water isotopes as visualized in Figure 7 are illustrated as correlation crossplots between δ-values and salinities in Figure 8. Those reveal an almost linear correlation (R^2 0.99 δ^2H and 0.98 δ^{18}O; $p < 0.0001$) for samples taken along the Schlei in March 2020, and significant correlation (R^2 0.75 δ^2H and 0.77 δ^{18}O; $p < 0.0001$) for DZBC and Rügener Bodden samples. The isotope amplitude over ca. 20 salinity units accounted for ca. 30‰ δ^2H and 5.5‰ δ^{18}O.

By contrast, samples from July 2020 reveal hyperbolic correlations between the two parameters (Figure 8). Here, δ-values reach a plateau of maximum values for salinities >7. For some samples, a reversal towards lower δ-values with increasing salinities is observable. A similar trend is observable in samples from June 2019, which were taken in lower spatial resolution (Figure 8).

When analysing the three transects individually and in more detail, they all show a significant correlation between isotope values and salinity in March 2020 (Figure 9a). Especially in the Schlei, an almost linear correlation between δ-values and salinity is observable. Outliers with significant higher δ-values are samples taken from adjacent lakes and noors, which not or only weakly connected to the Schlei (Bültsee #14, Schnaaper See #18, Ornumer Noor #17 and Windebyer Noor #19) (Figure 7a). Furthermore, a sample from the close-by Baltic Sea location Eckernförde (#21) might be influenced by local mixing process different than in the Schlei system and its adjacent Baltic Sea outflow (e.g. #27, #29). In the DZBC, the March 2020 samples can be assigned to two clusters: (1) low saline samples taken from rivers or close to their outflows (#30/#31, #35/#36) and from Saaler Bodden (#32). (2) samples with salinity >6 psu from all other locations (Figures 7b and 9a). In the East Transect, again a linear salinity—isotope correlation is observed from the Stettiner Haff to Rügener Boddens, with one outlier (#51) derived from the inner NRBC (Figures 7c and 9a).

By contrast, in the Schlei and DZB, the two sampled summers (June 2019 and July 2020), reveal constant isotope values or even a reverse correlation from salinities 4 to 6 psu and higher on (Figure 9a). In the East Transect, however, a positive correlation along the Stettiner Haff—Peenestream—Greifswalder Bodden transect is observable, while samples from the WRBC, NRBC and adjacent Baltic Sea samples show mixed values clustering around −4.9 to −6.2‰ δ^{18}O and salinity values 8.1–9.6 psu (dashed black circles in Figure 9a,b).

These patterns come out more clearly when correlating δ-values to latitude/longitude, following their geographical orientations along the flow direction of the transects (Figure 9b), especially when considering the March–July offset of isotope values ($\Delta\delta$) (Figure 9c). This approach eliminates the influence of larger salinity ranges in March

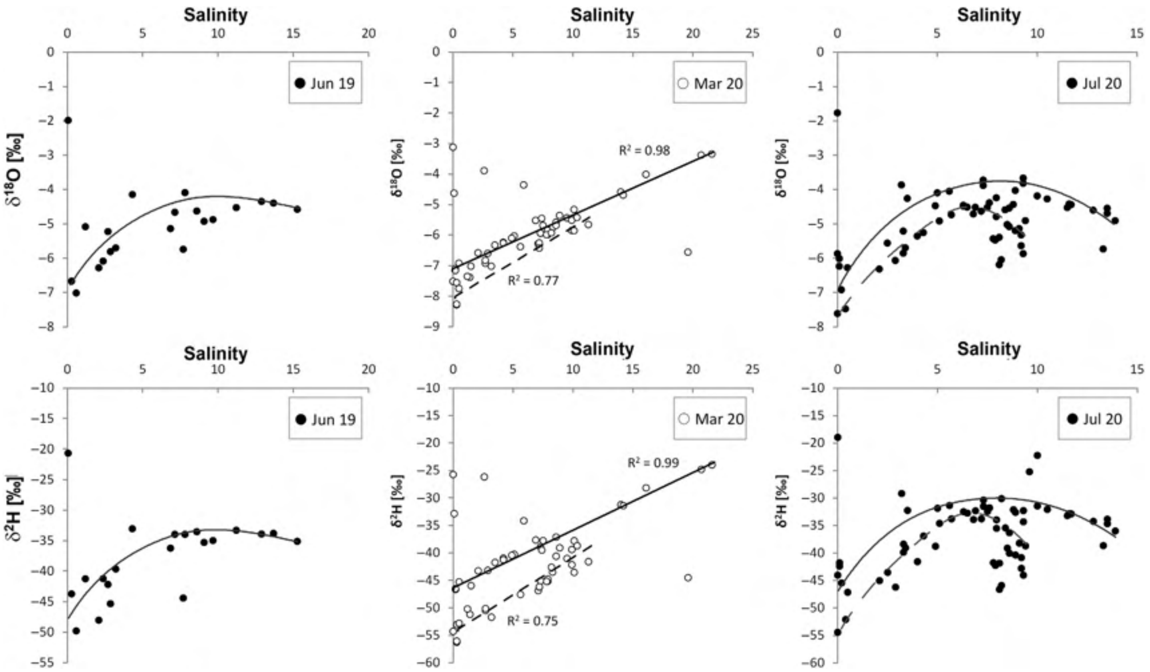

FIGURE 8 Correlation between δ^{18}O and δ^{2}H values and salinity in June 2019, March 2020, and July 2020. Linear and hyperbolic trendlines for Schlei (solid) and combined DZBC and Rügener Bodden (dashed) samples, under exclusion of outliers as derived from lakes and the open Baltic Sea.

compared with July, which is strongest in the Schlei, and makes isotope values from specific spots better comparable.

As noted above, most samples show isotope enrichment in the warmer season (i.e. negative $\Delta\delta$ March–July values) (Figure 7). Exceptions are a number of samples from the Baltic Sea, whose isotope signatures are rather driven by mixing processes than by seasonal trends, or samples under direct influence of Baltic Sea water (e.g. close to the outflows of the Schlei and DZBC). In general, samples show a tendency towards stronger isotope enrichment when located further inlands. Thus, they show increasing $\Delta\delta$ (March–July) values from the river inflows towards the Baltic Sea (Figure 9b,c; Figure 7; interpolated salinity and $\Delta\delta$ maps in Figure S1). Obviously, the shallow lagoons inlands (such as Kleine Breite at the Schlei, and Saaler and Bodstedter Boddens at DZBC) are more susceptible to undergo stronger isotopic enrichment in summers, than locations more adjacent to the Baltic Sea. This is most pronounced in the Schlei, here the $\Delta\delta$ values are balanced (i.e. similar isotope values in March and July) at ca. 75% of the distance between the inner Schlei and the outflow towards the Baltic Sea (Figure 9c). Beyond this place (which lies around the narrow passage aside the town Arnis, #24/#25), $\Delta\delta$ values become even positive due to lower δ-values in July compared with March (Figures 7a and Figure S1a).

The major inference from these data set is, that sampling points that undergo larger salinity changes between the maximum and minimum freshwater inflows in spring and summers (i.e. most negative ΔSal March–July) are also more susceptible to larger isotopic enrichment in the summers (more negative $\Delta\delta$ values March–July). This systematic is most pronounced in the Schlei, which is characterized by the most linear salinity gradient among the studied transects (Figure 9d). A similar trend is visible in the DZBC, but here it is weakened due to outliers as mainly derived from the Barther Bodden and Grabow samples. In the East Transect, no clear systematics between ΔSal and $\Delta\delta$ could be observed. While almost all samples show isotopic enrichment in summers (negative $\Delta\delta$), the stronger influence of mixing processes of multiple water sources (i.e. from rivers, inner Rügen boddens, Baltic Sea water intrusion from both the east and the north-west) can explain the heterogenous isotope values in this study area. Here, increasing sample density along sub-transects could potentially facilitate interpretation of isotope data and the control mechanisms behind.

6 | CONCLUSIONS

The results show that the studied estuarine systems exhibit a clear seasonality within their water isotope values. This is comparable to NE German lakes and rivers in both isotope amplitude and time succession. The data from three transects further reveal complex isotope versus salinity correlations: positive and significant correlations were observed in March 2020 along all transects. By contrast, hyperbolic

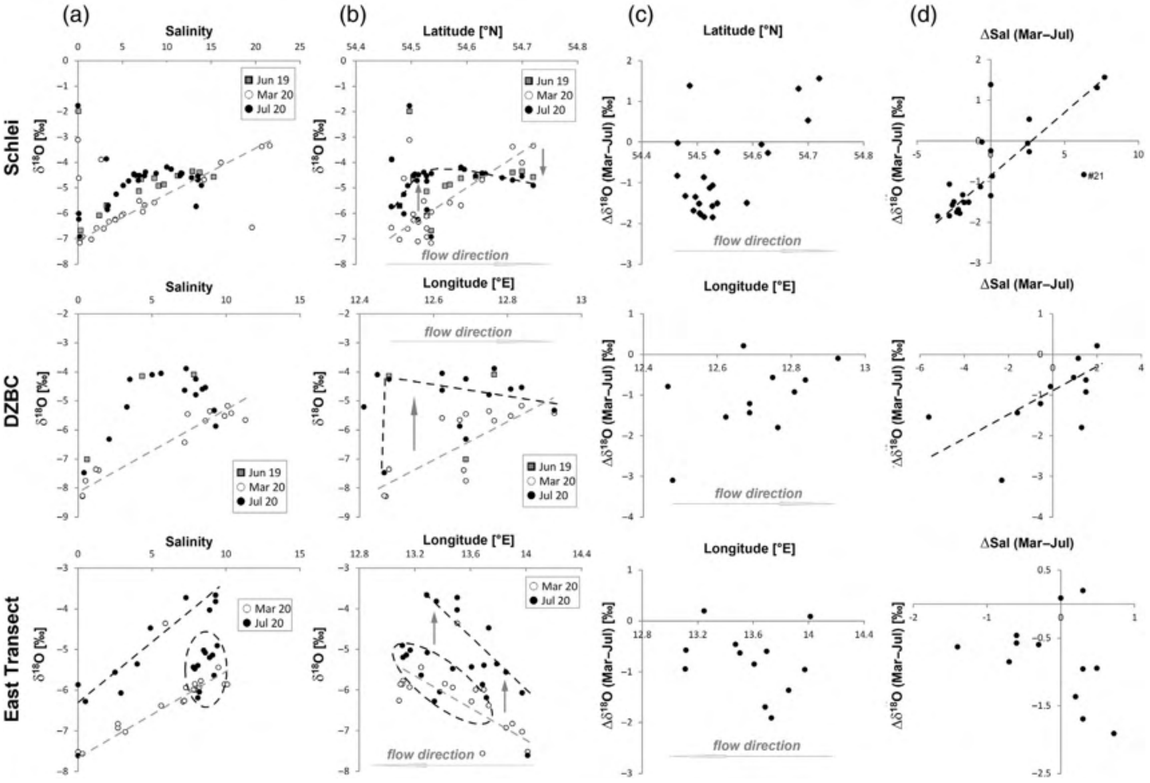

FIGURE 9 Correlations between: (a) δ^{18}O values and salinity. (b) δ^{18}O values and latitude or longitude. Dashed grey/black trendlines for March/July 2020. Vertical grey arrows indicate direction of isotopic change from March to July. Dashed black circle in the East Transect crossplots indicate Rügener Bodden and Baltic Sea samples. (c) $\Delta\delta^{18}$O (March–July) and latitude or longitude. (d) $\Delta\delta^{18}$O and ΔSal (March–July). DZBC: Darss-Zingst Bodden chain. East Transect comprises Stettiner Haff to GW Bodden and Rügener Boddens.

and partially inverse correlations were found in the two sampled summers (June 2019 and July 2020) along the Schlei and DZBC transects, while the spatially more extensive Eastern Transect still showed positive correlation.

We hypothesize that this is triggered by increased susceptibility of the shallow inland water basins to evaporative isotope enrichment in summers, causing higher δ-values. Furthermore, the discharge regime and isotope seasonality of tributary rivers is an important factor, with potentially a stronger impact near the inflows and the inner lagoons. In addition, the influence of water intrusion from the Baltic Sea can profoundly affect the water isotope signature of the outflow regions of the estuaries.

In summary, salinity is a fairly good predictor for water isotopes in winters, and on larger spatial scales in our study area. In summers and on regional scales, local hydrological processes are able to overprint the positive correlation between the two parameters, partly even leading to reverse correlations. This seasonality within the correlation of salinity versus water isotopes needs to be considered when interpreting biogenic isotope data (of plants or animals) because those might be similarly seasonally biased (often towards the warm/growing season).

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in PANGAEA at https://doi.org/10.1594/PANGAEA.937990 (Aichner et al., 2021).

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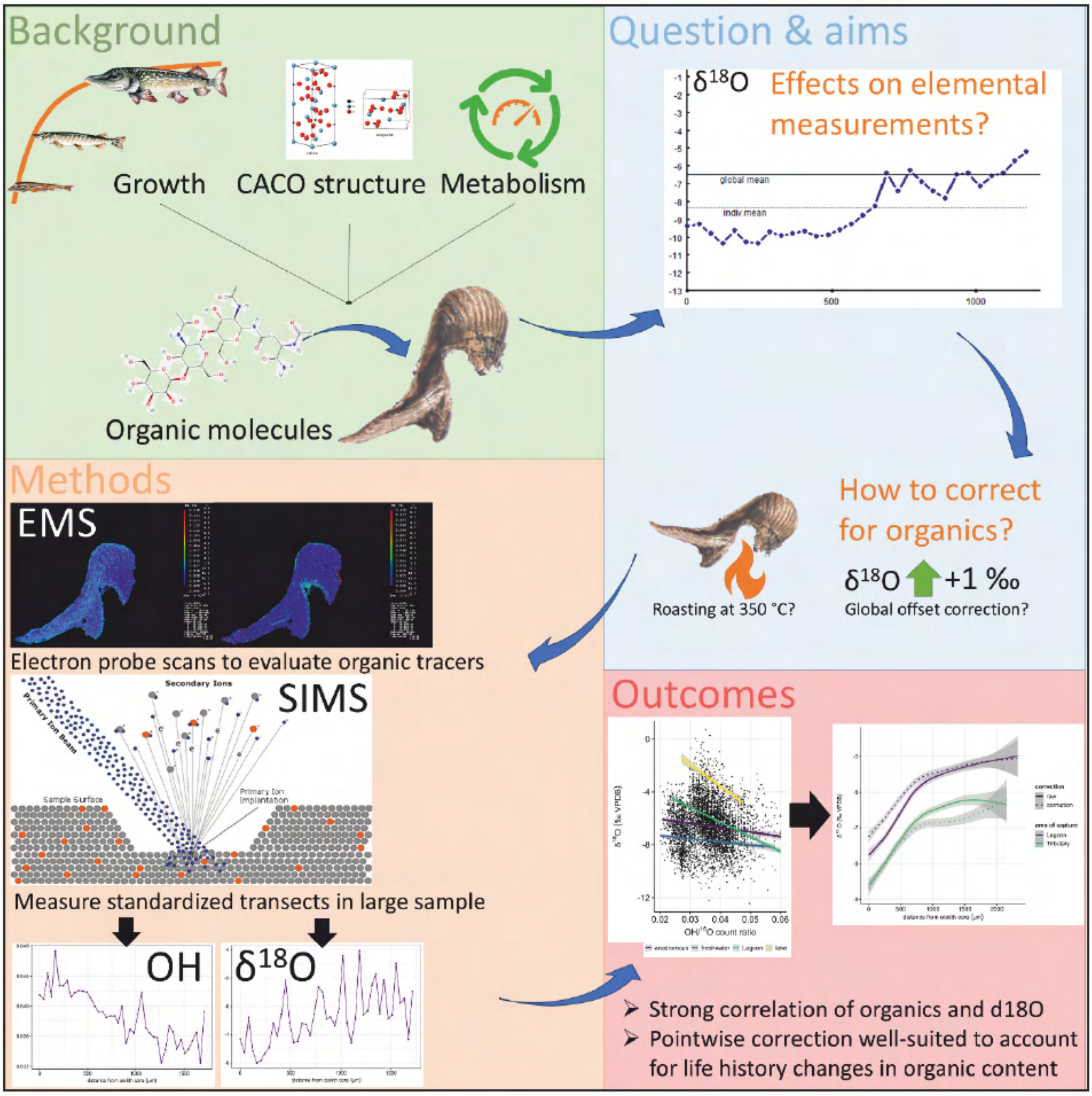
Paper IV



IV

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Varying organic content in fish otoliths: Effects on SIMS-based δ18O measurements and possible corrections

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ABSTRACT

Varying organic contents in otoliths have complex and sometimes counterintuitive effects on intra-otolith $\delta^{18}O$ measurements. This is often addressed by roasting otoliths or applying fixed corrections, however, the underlying chemical and physiological mechanisms involved are poorly understood and have not been tested in a quantitative manner, potentially rendering such corrections unreliable. Using high-resolution secondary ion mass spectrometry (SIMS) measurements of $\delta^{18}O$ values paired with $OH/^{16}O$ ion ratios as organic proxy, we derived quantitative relationships of these measurements over the entire life of a large sample of northern pike (*Esox lucius*) otoliths from freshwater and brackish habitats. We assessed $OH/^{16}O$ ion count ratio as an organic tracer, and estimated its relationship with $\delta^{18}O$ determinations. We developed a pointwise correction approach that accounted for variations in otolith organic contents. $OH/^{16}O$ ion ratio profiles agreed with other organic proxies, confirming them as reliable tracer of organic content. We detected an inverse relationship between $\delta^{18}O$ values and $OH/^{16}O$ ion ratio, with elevated $OH/^{16}O$ ion ratios near otolith cores. $OH/^{16}O$ ratios decreased with distance to the core. Pairwise corrections for the effect of $OH/^{16}O$ ratios on $\delta^{18}O$ values resulted in a mean offset between uncorrected and corrected values of 0.52 ‰, suggesting an approximately 2°C bias towards warmer temperature if uncorrected data were to be used for $\delta^{18}O$ thermometry. Simultaneous determination on organic- and inorganic-bound oxygen resulted in a negative offset of $\delta^{18}O$, which varies with the life history of individual fish. Varying offsets in $\delta^{18}O$ values within individual life histories could be accounted for using our correction. We recommend future SIMS-based $\delta^{18}O$ thermometry studies to estimate the local organic content to assess whether correction is warranted. We further offer more general recommendations on how future studies may assess whether corrections for organics are necessary.

1. Introduction

Otoliths record time-resolved chemical signals from the ambient water, enabling inferences on environmental factors throughout the individual animal's life history (Reis-Santos et al., 2022). Otolith elemental composition reflects environmental as well as physiological conditions, aiding in understanding physiological processes, migration, and population connectivity (Campana and Thorrold, 2001; Heidemann et al., 2012; Kafemann et al., 2000; Chung et al., 2020). For instance, intraotolith $\delta^{18}O$ determinations are commonly used to reconstruct past water temperatures in fishes (Patterson et al., 1993) and to track large-scale migrations and habitat shifts (Darnaude and Hunter, 2018). However, the chemical composition of otoliths can be influenced by multiple physiological factors, which need to be understood (Campana and Thorrold, 2001).

Otoliths are composed mainly of crystalline calcium carbonate precipitated from endolymphatic fluid within the inner ear of fishes (Stevenson and Campana, 1992). Precipitation is facilitated by an organic scaffolding of largely acidic glycoproteins (Degens, 1969). During otolith growth, minor and trace elements within the endolymph are incorporated into the otolith by replacing calcium ions in the crystal lattice, adsorption to surfaces, binding to the organic matrix, or incorporation in interstitial spaces between calcium carbonate crystals (Campana, 1999). In temperate fishes, organic matter concentrations

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fluctuate seasonally, influencing light absorption (organic matter has a higher absorption than carbonate), resulting in visually discernible growth zones (Campana, 1999; Stevenson and Campana, 1992). Fast growth, which in temperate fishes often takes place in summer, leads to higher organic matter content, yielding opaque zones, while slower growth, which often occurs in winter for temperate fishes, produces more translucent zones due to higher proportion of calcium carbonate (Stevenson and Campana, 1992). Critically, otoliths, like many biomineralized tissues, are composite materials. For example, intra-otolith $\delta^{18}O$ values are commonly assumed to reflect only oxygen bound within the calcium carbonate. However, the glycoprotein-rich organic matter, which constitues between 0.2 % and 10 % of total otolith mass (Degens et al., 1969), also contains oxygen in form of hydroxy groups. Measurements of $\delta^{18}O$ in otoliths may therefore be biased by admixing organic and mineral phases (Degens et al., 1969; Guiguer et al., 2003; Hane et al., 2020, 2022).

The impact of oxygen release from organic matter and calcium carbonate on $\delta^{18}O$ values in otoliths has been first noted by Guiguer et al. (2003) and Matta et al. (2013). Removal of organic phases by roasting (Guiguer et al., 2003) resulted in significantly higher $\delta^{18}O$ values as compared to unroasted samples, implying preferential removal of a phase depleted in ^{18}O. Similarly, Matta et al. (2013) observed a roughly 1 ‰ increase for roasted (360 °C for 3.5 h under vacuum) vs. unroasted halves of a yellow sole (*Limanda aspera*). The studies used different analytical methods (acid digestion followed by continuous flow IRMS and SIMS, respectively), but reported similar effects on $\delta^{18}O$ values, likely resulting from the presence of organics. The effect of mixed organic-anorganic matter on isotope measurements was also described more generally by Oehlerich et al. (2013), and therefore seems to be independent of measurement method. More recent research on otoliths (Hane et al., 2020; Helser et al., 2018; Wycech et al., 2018) also found consistent offsets between untreated and roasted otoliths using SIMS and acid digestion. Observed offset were hypothesized to result from organic matter, differences between sample and reference materials, or from water adsorption. Although such offsets appear to be common across species and systems, the underlying mechanism(s) remains unclear.

Reported effects of organic matter on $\delta^{18}O$ values prompted some studies to roast otoliths to reduce or eliminate the organic contents (e.g., Burbank et al., 2020; Geffen, 2012). However, roasting has led to inconsistent outcomes (Guiguer et al., 2003), and questions persist regarding potential heat-induced phase transitions (e.g., aragonite to calcite) in the carbonate matrix (Matta et al., 2013). Other studies, such as Hane et al. (2022) and Morissette et al. (2020), applied mathematical corrections to $\delta^{18}O$ measurements (+0.41 ‰ and +1 ‰ shifts, respectively), but applying such general correction factors across all measurements likely overlooks individual ontogenetic effects and habitat shifts (von Bertalanffy, 1938; Werner, 1988). To understand how individual life history influences intraotolith organic content and $\delta^{18}O$ values, quantification of organics in otoliths are needed. Contributions of hydroxy groups, OH^-, to the overall oxygen content can be measured during SIMS $\delta^{18}O$ determinations by using a multi-collection strategy measuring both the $^{18}O/^{16}O$ and the $OH/^{16}O$ ratios of the emitted secondary ions. This offers a potential proxy for organic content, as oxygen in organic matter glycoproteins can be expected to be primarily bound as hydroxy groups (Degens et al., 1969). Validated by established organic proxies, such as phosphorus and sulfur concentrations, $OH/^{16}O$ ratio might be a promising tool for quantifying the intraotolith organic matter distributions.

Our study asessed the impact of intraotolith organics on $\delta^{18}O$ measurements with SIMS. We had three objectives: 1) To test whether SIMS-determined $OH/^{16}O$ ratios can be used as a proxy for the organic content in otoliths at the ~200 picogam sampling scale provided by SIMS; 2) to assess whether intra-otolith organic content biased $\delta^{18}O$ values measured by SIMS analyses of otoliths from a population of wild fish; and 3) to suggest a possible correction strategy for the organic-derived oxygen component within individual SIMS $\delta^{18}O$ results. We hypothesize that i) the spatial distributions of element ratios indicative of organic materials (P, S and $OH/^{16}O$ ratios) vary similarly and in a predictable way within otoliths, showing banding patterns corresponding to annual growth zones; ii) concentrations of P, S and the $OH/^{16}O$ ratio decrease with increasing age and size of the otolith, covarying with increasing $\delta^{18}O$ values from core to margin; and iii) intraotolith $\delta^{18}O$ values show an inverse relationship with $OH/^{16}O$ values, leading to lower $\delta^{18}O$ values in growth zones containing large amounts of organic matter.

2. Materials and methods

2.1. Study site & sampling

We sampled 113 pike (*Esox lucius*) from three major brackish lagoon chains (n = 54) and freshwater tributaries (n = 53) around Rügen island in the southern Baltic Sea, Germany. (Fig. 1). To represent different habitats and abiotic conditions, pike were sampled along environmental gradients of salinity and temperature (Figure S1). We aimed for equal size and sex distributions, however, equal sex distribution was not achieved due to sex-dimorphic growth in pike (Casselman, 1995, but see also Figure S2, S3). Additionally, we sampled five individuals from Lake Kleiner Döllnsee (4 females, 1 male, Fig. 1), a dimictic lake with 25 ha surface area and a mean depth of 4.1 m, situated around 150 km from the main study area, which we used as a reference site with no connection to the lagoons. To account for gear-dependent size- and growth-selectivity, pike were sampled with different gears, including fyke nets, gill nets, rod and line fishing and electrofishing in tributaries (Table S1). Each fish was euthanized, measured for total length, sex determined, and the head was frozen for processing in the lab. We extracted sagittal otoliths from all 113 pike, and measured each individual otolith for lifelong $\delta^{18}O$ and $OH/^{16}O$ values with SIMS (Table 1). SIMS data of all 113 fish were then used for linear mixed effects modelling and the development of a pairwise correction (Table 1). A subsample of three individuals were chosen for EPMA scans of potential trace elemental proxies of organic content (Table 1). BH-01855, a seven-year-old male pike sampled from WRBC (Fig. 1) in May 2020 at 72.2 cm total length; BH-01588, a 10-year-old female pike sampled from NRBC (Fig. 1) in January 2020 with 105.0 cm total length; and BH-01722, a 13-year-old female pike sampled from NRBC in February 2020 at 95.0 cm total length. Out of these three specimen, BH-01588 was chosen for a SIMS grid measurement and subsequent interpolation of $\delta^{18}O$ across the otolith surface (Table 1). Pike used in this study exhibited three behavioral phenotypes: 55 individuals permanently inhabited brackish lagoons, 32 individuals permanently inhabited freshwater tributaries (or the inland lake), and 26 regularly migrated between brackish and freshwater (for detailed characterization of the behavioral phenotypes, see Rittweg et al., 2024)

2.2. Otolith processing and SIMS analyses

Sagittal otoliths were extracted and cleaned, dried in a desiccator for 48 h, then stored under atmosphere in the laboratory. Otoliths were glued onto glass slides with Crystalbond glue and cut into 100 μm thin sections using an Isomet low-speed saw (BUEHLER Ltd 11–1180). The Crystalbond was then dissolved in acetone, resulting free otolith sections were polished with 3000 and 5000 grit sandpaper and 0.3 μm lapping film, and sent to the SIMS facility at the German Research Center for Geosciences (GFZ), Potsdam. Thin sections were embedded in 1-inch diameter, round epoxy sample mounts using Epofix resin (STRUERS), along with the UWC3 and IAEA603 calcite reference materials (Kozdon et al., 2009, International Atomic Energy Agency, 2016). Resulting mounts were polished until a surface quality of <5 μm was reached, which was verified with white-light profilometry. Mounts were imaged with an optical microscope using both reflected light and dark field modes, then sputter-coated with a 35-nm high-purity gold film to assure

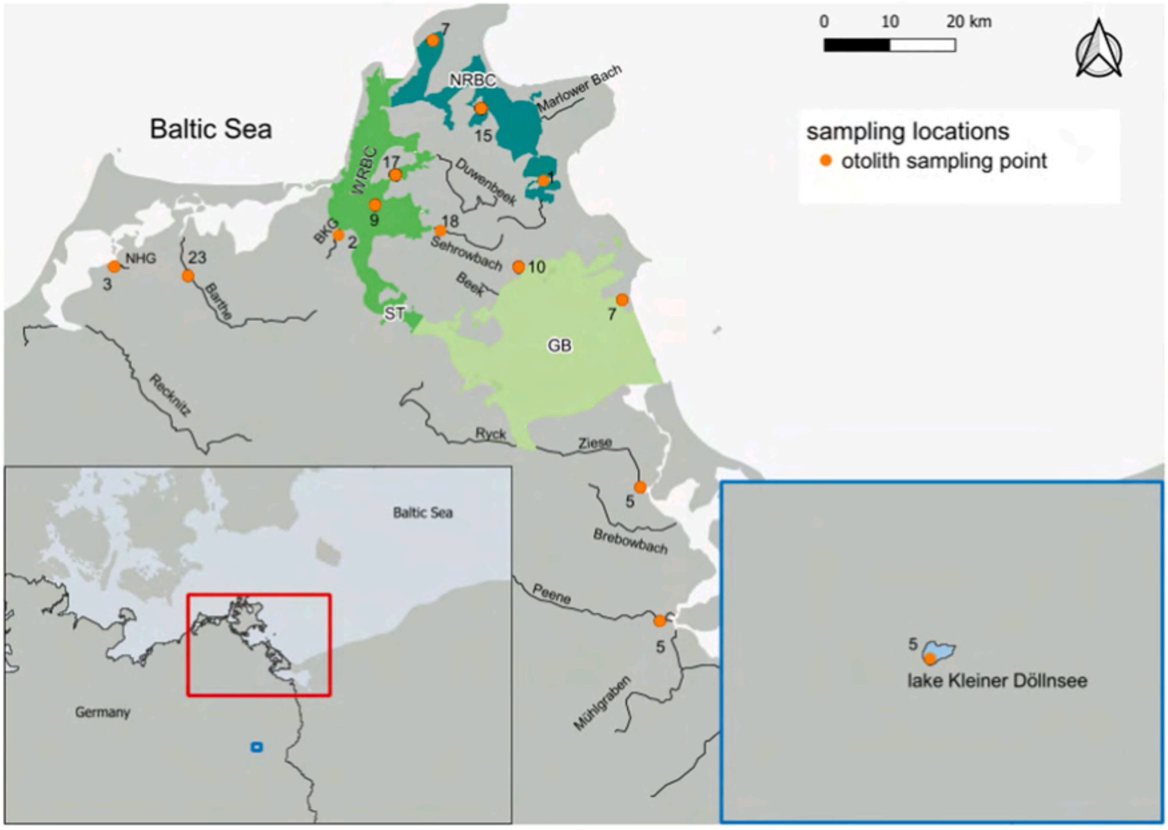

Fig. 1. Sampling Locations for pike captured between July 2019 and April 2022 in brackish lagoons and freshwater tributaries around Rügen island in northern Germany (large map), and in the freshwater lake Kleiner Döllnsee in Brandenburg (right inset map). Numbers beside the sampling points refer to the number of fish captured at a given location. NRBC: North Rügen Bodden chain; WRBC: West Rügen Bodden chain; GB: Greifswalder Bodden; ST: Strelasund; NHG: Neuendorfer Hechtgraben; BKG: Badendycksgraben.

Table 1
Overview of sample sizes, sex ratio (f = female, m = male), size and age range of pike individuals per analysis method.All fish were captured between between July 2019 and May 2022 from brackish lagoons and freshwater tributaries around Rügen island in northern Germany, and the reference freshwater lake Kleiner Döllnsee in northern Germany.

Method	Total N (f, m)	Size (cm)	Mean size ± SD (cm)	Period	Age (years)
SIMS	113 (70, 43)	40.4 – 126.2	72.9 ± 17.1	2019–2022	1–13
Mixed linear models	113 (70, 43)	40.4 – 126.2	72.9 ± 17.1	2019–2022	1–13
$\delta^{18}O$ correction	113 (70, 43)	40.4 – 126.2	72.9 ± 17.1	2019–2022	1–13
EPMA	BH–01855 (m)	72.2	NA	2020	7
	BH–01588 (f)	105.0	NA	2020	10
	BH–01722 (f)	95.0	NA	2020	13
SIMS grid	BH–01588 (f)	105.0	NA	2020	10

electrical conductivity. The mounts were then placed in a specially designed high-vacuum storage chamber of the Cameca 1280-HR secondary-ion mass spectrometer (details in Rittweg et al., 2023). $\delta^{18}O$ and $OH/^{16}O$ values were determined along transects which were marked digitally on otolith sections covering a straight line from otolith core to distal edge along an axis crossing all visible annuli. Transects were determined as point measurements with step distances of ~35 μm, with UWC3 and IAEA603 calcite reference materials determined after each 10th measurement. Results were corrected for instrumental mass fractionation and instrumental drift and the $\delta^{18}O$ values were reported in ‰ relative to Vienna Standard Mean Ocean Water (VSMOW), and converted to ‰ relative to Vienna Pee Dee Belemnite (VPDB) reference scale using the equation of Brandt et al.(2014). In order to determine the relative abundances of hydrogen, which is a proxy for the amount of protein-bound oxygen included in a given analysis, we determined the $OH/^{16}O$-ratios as part of each 80 second integration. Briefly, the OH-intensity was determined using the mono-collection Faraday Cup detector with an e12 Ohm amplifier while the ^{16}O-count rate was determined concurrently using the L2' Faraday cup with an e10 Ohm amplifier. The reported $OH/^{16}O$-values were derived by dividing one count rate by the other without any attempt to calibrate for absolute hydrogen contents - hence the values only provide relative abundances between analytical locations. To assess the spatial distribution of $\delta^{18}O$ and $OH/^{16}O$ values and to validate $OH/^{16}O$ as proxy for organic

Table 2
Effects of fixed and random predictors on linear mixed models of z-transformed $\delta^{18}O$ values measured in transects extending between otolith core and otolith margin in 113 pike otoliths sampled from specimens captured between July 2019 and May 2022 from brackish lagoons and freshwater tributaries around Rügen island in northern Germany, and the reference freshwater lake Kleiner Döllnsee in northern Germany.

scaled $\delta^{18}O$ (marginal $R^2 = 0.52$; conditional $R^2 = 0.68$)[a]				
Predictors	**Estimate (± SE)**	**t-value**	**LLR**	**p-value**
Intercept	−0.47 (0.13)	−3.56		
OH count rate	**−0.36 (0.02)**	**−18.58**	**316.65**	**< 0.001 *****
distance from core	**0.74 (0.20)**	**25.34**	**604.03**	**< 0.001 *****
increment width	**0.18 (0.07)**	**2.50**	**5.71**	**< 0.05 ***
capture location [freshwater]	−0.13 (0.17)	−0.80		
phenotype [freshwater resident]	**−2.92 (0.21)**	**−14.00**	**121.34**	**< 0.001 *****
phenotype [brackish resident]	**−1.83 (0.27)**	**−6.91**	**121.34**	**< 0.001 *****
sex [male]	0.11 (0.09)	1.31		
Random Effects	**Variance (± SD)**		**LLR**	**p-value**
ID	**0.18 (0.42)**		**994.53**	**< 0.001 *****
Residual	0.37 (0.61)			

SE: Standard error; SD: Standard deviation; LLR: Log-likelihood ratio. Significant effects are shown in bold.

[a] Marginal R^2 describes the proportion of the total variance explained by fixed effects in the model; conditional R^2 describes the proportion of total variance explained by fixed and random effects combined in the model.

contributions, 818 SIMS measurements were performed in an evenly spaced grid pattern with a 35 × 35 μm step size covering the distal portion of the otolith thin section of specimen BH-01588, a 10-year-old female pike sampled from NRBC in January 2020 with 105.0 cm total length. To assess the spatial distribution of $\delta^{18}O$ and $OH/^{16}O$, inverse probability weighted (IPW) interpolations were produced from the grid pattern of the otolith specimen BH-01588.

2.3. *EPMA analysis*

Following SIMS analysis, the gold coating was removed from each mount using ethanol and polishing powder (Alpha alumina, 300 nm). The mounts were sent to the electron microprobe facility at GEOMAR Helmholtz Center for Ocean Research, Kiel. The three chosen specimen samples were sputter-coated with high-purity carbon and analyzed using a JEOL JXA 8200 electron microprobe. The microprobe was calibrated with KAN1, VG-2, apatite, sphalerite, strontianite, dolomite, and calcite reference materials. A 10 ×10 μm grid covering each of the three selected otoliths was determined for the elements calcium (Ca), phosphorus (P), sulfur (S), magnesium (Mg), and strontium (Sr). The $\delta^{18}O$ and $OH/^{16}O$ interpolations determined with SIMS for specimen BH-01588 were visually compared to bitmap images from EPMA scans of the same otolith showing the concentrations of the organic proxies P and S.

2.4. *modelling intraotolith $\delta^{18}O$ and $OH/^{16}O$ values*

To assess the impact of organic contributions along $\delta^{18}O$ line transects across the whole sample (n = 113 otoliths), we fitted linear mixed effects models predicting lifelong individual $\delta^{18}O$ values from a set of fixed and random predictors. $OH/^{16}O$ ratios, our proxy for organic content, was included as a fixed predictor. To account for effects of different growth, we included increment width (width of annual rings) as a fixed predictor. To account for effects associated with the body size of individual fish, we included distance from the otolith core as a proxy of body size as fixed predictor. To account for effects associated with differences in salinity between capture locations, capture location was included as fixed predictor. To control for the effect of ontogentic habitat shifts, behavioral phenotype (resident freshwater, resident brackish or migratory) was included as fixed predictor. To test for possible effects of sex, sex was also included as a fixed effect. Individual fish ID was included as a random predictor, to account for the repeated measures design. To correct for differences in scale, $\delta^{18}O$ and $OH/^{16}O$ values were z-scored and mean-centered prior to modeling. Log likelihood ratio (LLR) tests were used to assess the significance of fixed and random effects; we have reported marginal and conditional R^2 estimates as measures of goodness-of-fit. Assumptions of the model were assessed graphically (supplementary material section C).

2.5. *Correcting for the effect of organics on $\delta^{18}O$*

Using the coefficients from a linear best-fit regression of $OH/^{16}O$-ratios vs $\delta^{18}O$, we developed an individual-level correction of $\delta^{18}O$ values. Extracting the calculated regression slope estimate for the effect of $OH/^{16}O$-ratios on measured $\delta^{18}O$ values across all fish, we calculated a corrected $\delta^{18}O$ value for each measurement point using the formula:

$$\delta^{18}O_{corrected} = \delta^{18}O_{otolith} - OH/^{16}O \times \text{population slope coefficient}$$

The results of these corrections were assessed as average offset across the whole sample (n = 113) at the population level, distinguishing capture location and life history strategy. Furthermore, we examined the individual level offsets across the three specimens that were selected for EPMA analysis by plotting them individually with corrected and uncorrected values.

To validate our correction, we used water $\delta^{18}O$ measurements and time series of water temperatures for the lagoons to predict theoretical monthly $\delta^{18}O$ values in pike otoliths between 2008 and 2022 (age range of our sample). Monthly variation in water $\delta^{18}O$ was determined from biweekly samples between March 2020 and March 2021 taken by Aichner et al. (2022), and interpolated for each lagoon region across the time span from 2008 to 2022. We used two fractionation equations to predict $\delta^{18}O$ in pike otoliths, as no species-specific equation exists for pike, and the coastal lagoons cannot be easily classified as fully marine or fully freshwater. Eq. 1 was developed as general fractionation equation for freshwater fish (Patterson et al., 1993), Eq. 2 was developed for a marine species (plaice, *Pleuronectes platessa*, Geffen, 2012). The two equations took the form:

$$1000\ln\alpha = 18.56\left(1000T(K)^{-1}\right) - 33.49 \tag{1}$$

$$\text{where } \alpha = \frac{1000 + \delta^{18}O_{Oto}VSMOW}{1000 + \delta^{18}O_{Water}VSMOW}$$

and

$$1000\ln\alpha = 15.99\left(1000T(K)^{-1}\right) - 24.25 \tag{2}$$

$$\text{where } \alpha = \frac{1000 + \delta^{18}O_{Oto}VSMOW}{1000 + \delta^{18}O_{Water}VSMOW},$$

where T is temperature in Kelvin (K), α is the fractionation factor between water δ^{18}O and otolith δ^{18}O. A linear interpolation of δ^{18}O values measured in pike otoliths was used to interpolate to a period of 12 months within identified annuli to facilitate comparison to predicted values. Predicted, raw and corrected δ^{18}O values were compared graphically. Some error was expected from matching sample locations within otoliths to months and interpolation errors. Incorporating the variance in water temperatures across lagoons and water δ^{18}O values across seasons into the interpolations allowed us to construct upper and lower confidence intervals for predicted otolith δ^{18}O for the two equations.

3. Results

3.1. *Distribution patterns of elemental proxies*

The spatial distribution of phosphorus (P) and sulfur (S) correlated closely with annual bands of slow and fast growth in the three otolith specimen (Figures S4 - S6). P and S were concentrated within summer growth zones, with maximum concentrations of 12.1 % (percent weight) for P and 3.6 % for S (Figures S4 - S6). Concentrations of P and S decreased from the otolith core outwards in all three otoliths (Figures S4 - S6). Concentrations of Mg were low, ranging from 0 % to 1.9 %, leading to no clear banding in the EPMA images (Figures S4 - S6).

The two-dimensional spatial interpolations of δ^{18}O and OH/^{16}O values of otolith BH-01588 showed a clear banding pattern in δ^{18}O values, corresponding to summer and winter growth zones (Fig. 2). The banding in OH/^{16}O ion count ratios was less pronounced, however, higher OH/^{16}O count ratios near the otolith core corresponded to areas with generally lower δ^{18}O (Fig. 2), indicating that the correlation between δ^{18}O values and OH/^{16}O extended across the otolith from core to margin.

3.2. *Correlation between organic proxies*

The organic proxies P and S appeared to broadly corrrelate with SIMS point profiles of both δ^{18}O and OH/^{16}O ratios (Figure S7 – S9). Higher concentrations of P and S in summer growth zones often coincided with higher OH/^{16}O ratio in SIMS point profiles, but more importantly, the overall decrease in P and S from core region towards the otolith margin coincided with an increase in δ^{18}O values and a decrease in OH/^{16}O ratio across all three sample otoliths (Figure S7 – S9). This relationship was also found for the spatial distribution of P, S, δ^{18}O and OH/^{16}O (Fig. 2). This suggests that the OH/^{16}O ratio is a useful proxy for organic content in fish otoliths. We assumed this to hold true for our larger sample ($n = 113$ pike otoliths) and used OH/^{16}O ratio as a predictor for δ^{18}O values in subsequent modelling steps (see below).

3.3. *Modelling intraotolith $\delta^{18}O$ values*

The best-performing model for correcting our δ^{18}O values included OH/^{16}O ratio (continuous, z-transformed), distance from otolith core (continuous) as a measure of age, increment width (continuous) as a measure of yearly growth, behavioral phenotype (factor with three levels, freshwater resident, brackish resident, migratory) capture location (factor with two levels, lagoon/tributary) and sex (factor, two levels male/female) and the random effect of individual ID (1|ID, 112 groups). The model explained 68 % of the variance in intra-otolith δ^{18}O values, where 52 % of the variance was explained by the fixed predictors (Table 2). This indicated a large amount of variation in δ^{18}O values was due to inter-individual variation, reflecting differences in life history between individual pike. Accordingly, the random effect of ID was highly significant (Table 2). Scaled OH/^{16}O ratios had a significant negative effect on scaled δ^{18}O values (Table 2, Fig. 3). Age and body size had a positive effect on δ^{18}O values, as indicated by a highly significant positive correlation between scaled δ^{18}O and distance from the otolith core (Table 2, Fig. 4). Fish growth rate, as inferred by otolith increment widths, also showed a positive effect on δ^{18}O values (Table 2). As expected, behavioral phenotype was a significant predictor of intraotolith δ^{18}O, with freshwater-resident and migratory pike showing lower δ^{18}O values than brackish residents (Table 2). Male and female pike did not differ in intra-otolith δ^{18}O values, indicated by a non-significant fixed effect of sex on scaled δ^{18}O values (Table 2).

3.4. *Correcting for organic effects on SIMS determinations of $\delta^{18}O$*

Applying a mathematical correction based on paired δ^{18}O values and OH/^{16}O ratios resulted in a mean offset of 0.54 ‰ in δ^{18}O values across all 113 pike. Average offsets between the uncorrected δ^{18}O values and the corrected values differed significantly between behavioral phenotypes (One-way ANOVA, $F_{2,4604} = 596.6$, $p < 0.001$), with lagoon-captured pike showing the highest average offset (+ 0.59 ‰, Fig. 4), followed by migratory anadromous individuals (+ 0.52 ‰, Fig. 3), and freshwater-resident pike showing the lowest average offset (+ 0.48 ‰, Fig. 4), suggesting some variance was induced by different habitat use of individual fish. The strongest offsets across all fish were detected in near-core areas of otoliths, with an average offset of + 1.1 ‰ in the first 500 μm of the otolith, which corresponds to larval or juvenile life stages.

The magnitude of the correction differed strongly between individuals, as some individuals exhibited intra-otolith δ^{18}O determinations that were corrected by a maximum of 0.5 ‰, while other individuals showed shifts by up to 1 ‰ (Fig. 6). Of the three pike otoliths chosen for EPMA mapping, the otoliths BH-01588 and BH-01855 showed large differences between raw and corrected δ^{18}O values, in particular in their near-core regions (Fig. 6). This was in accordance with the steep concentration gradient found in P and S for these two specimens (Figure S7, S8). The δ^{18}O values of BH-01722 changed comparatively little after applying the correction (Fig. 6), which can be attributed to the rather low and homogenous P and S contents found in this otolith (Figure S9). Our correction shifted δ^{18}O values in pike otoliths closer to the theoretical prediction intervals calculated from monthly water temperatures and interpolated water δ^{18}O values between 2008 and 2022 (Fig. 5). Corrected δ^{18}O values lay within the confidence intervals of the two predictions from Eqs. 1 and 2 for most of the year, although some offset between corrected and predicted δ^{18}O values remained in the coldest months of the year, where the highest δ^{18}O values were predicted (Fig. 5).

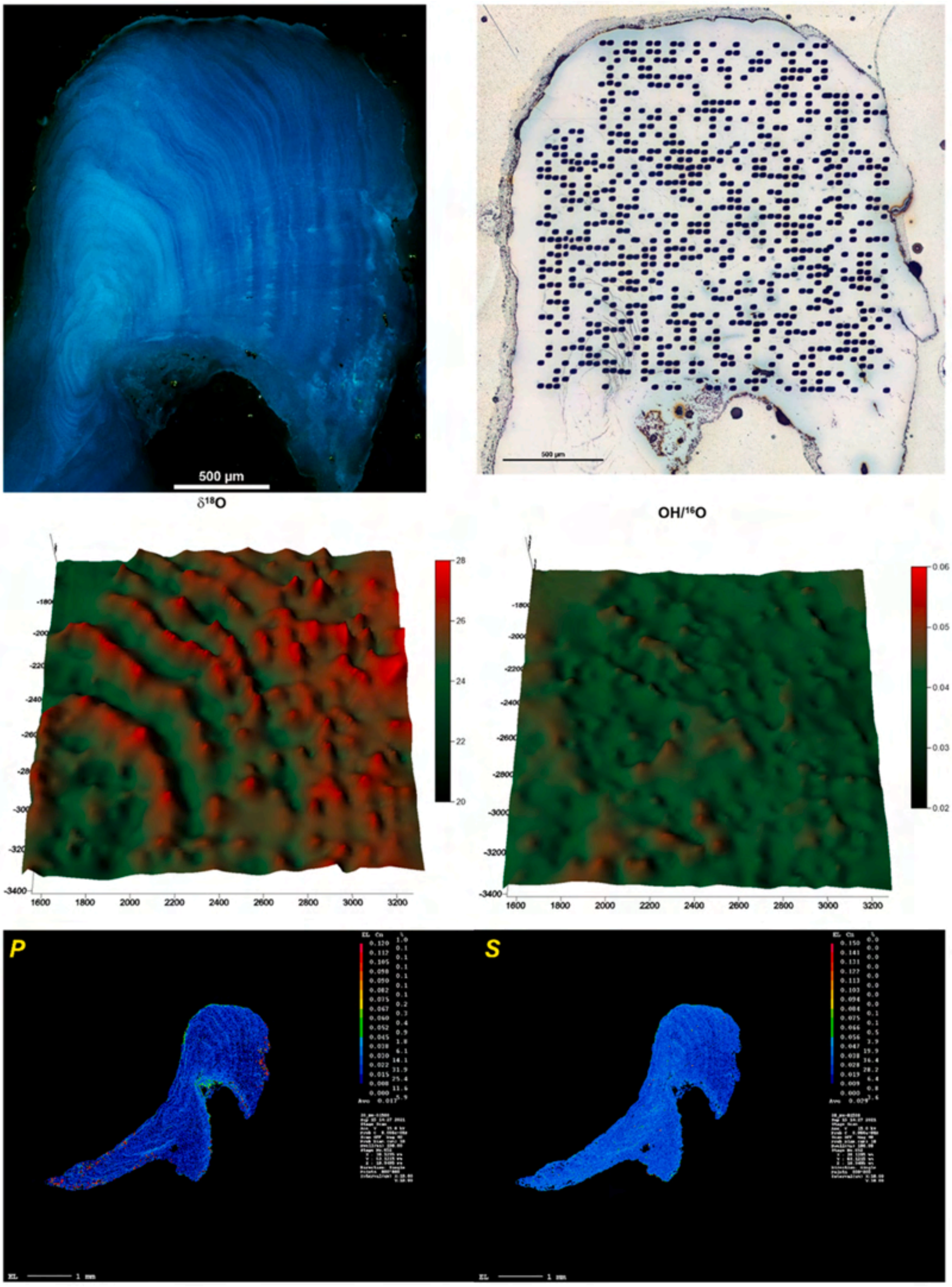

Fig. 2. SIMS interpolation of δ18O values (middle left panel) and OH/16O ion counts (middle right panel) of pike otolith specimen BH-01588, a 10-year-old female pike sampled from NRBC in February 2020 at 105 cm total length. For orientation, we included the optical dark field image of the otolith prior to measuring the SIMS grid pattern (upper left panel), and the bright field image of the otolith taken after the SIMS grid pattern was measured (upper right panel). Lower panels show the EPMA maps of the entirety of the same otolith.

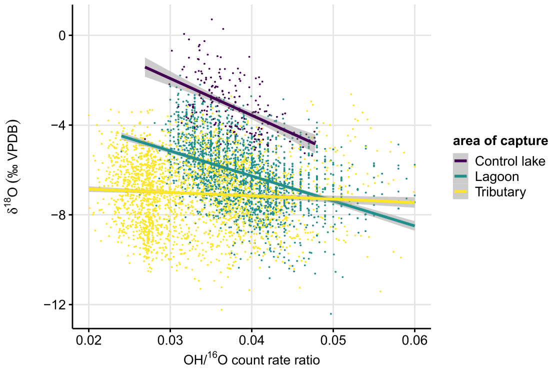

Fig. 3. Correlation between SIMS determined $\delta^{18}O$ values and $OH/^{16}O$ ratios in 113 pike captured between July 2019 and May 2022 from brackish lagoons and freshwater tributaries around Rügen island in northern Germany and a reference freshwater lake 150 km inland.

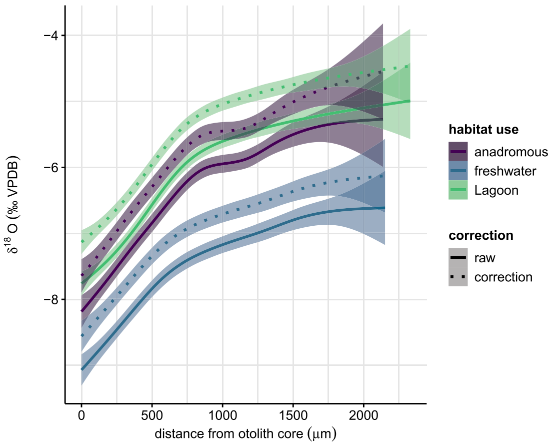

Fig. 4. Corrected vs. uncorrected intraotolith $\delta^{18}O$ values from 113 otoliths from pike sampled between July 2019 and May 2022 in brackish lagoons and several freshwater tributaries around Rügen island in northern Germany and a reference freshwater lake 150 km inland. Individuals were grouped based on their lifelong habitat use behavior, with lagoon-residing pike in green, migratory (anadromous) individuals in purple and freshwater resident pike in blue. Solid lines show the raw $\delta^{18}O$ measurements, dashed lines show the values after applying the correction. Shaded areas represent the 95 % confidence intervals around the smoothing lines.

4. Discussion

We determined the relationship between intraotolith $\delta^{18}O$ values and several organic tracers for pike otoliths and derived a mathematical correction for SIMS $\delta^{18}O$ values using paired measurements of $OH/^{16}O$ and $^{18}O/^{16}O$. We demonstrated the effect of organic components was constant across a variety of habitat use strategies in an ecologically plastic species (Dhellemmes et al., 2023; Rittweg et al., 2024; Sunde et al., 2022). According to our first hypothesis, the organic content in otoliths was associated with seasonal growth zones, with opaque summer growth zones showing higher concentrations of proxies associated with organic phases, such as P and S. While this was the case for the two organic proxies P and S, in support of our hypothesis, we were not able to detect a clear annual banding in $OH/^{16}O$ counts, potentially due to other physiological mechanisms affecting organic content. In general, however, the concentrations of organic proxies decreased from otolith core towards margin across all three samples analyzed by EPMA, which supported our second hypothesis. In response to our third hypothesis, we detected a significant inverse linear relationship between $OH/^{16}O$ and $\delta^{18}O$ values, which was influenced by growth rate, capture location and fish age. Applying a pairwise individual-level correction of $\delta^{18}O$ using $OH/^{16}O$, we determined an average 0.54 ‰ shift in $\delta^{18}O$ values due to the admixture of organic-bound oxygen to otolith carbonate. The correction shifted otolith $\delta^{18}O$ values of pike closer towards theoretically expected values predicted from ambient temperatures and water $\delta^{18}O$, suggesting the offset between measured and expected value was due to intraotolith organics.

The decrease in elements associated with organics, specifically S and P, as well as the trend towards lower $OH/^{16}O$ from core to margin reflect decreasing growth rates and consequentially lower organic content (Hüssy et al., 2004) with increasing age in fishes (von Bertalanffy, 1938). The similar spatial distributions in P, S and $OH/^{16}O$ indicated that $OH/^{16}O$ ratios also record organic content in otoliths, and can be used as a quantitative indicator for the organic content in aragonite. The higher organic contents found in the core regions followed our expectations, as pike are known to grow fast in early life, with growth rates slowing with onset of maturity (Bry et al., 1991; Pagel et al., 2015). Behavioral phenotype was a strong predictor of intra-otolith $\delta^{18}O$ values, which can be explained by freshwater tributaries being depleted in ^{18}O compared to brackish lagoons, which consist of a mixture of isotopically heavy ocean water and isotopically light freshwater (Aichner et al., 2022). Therefore, individuals that spend parts of their life cycle (migratory anadromous), or their whole life cycle (brackish residents) in brackish lagoons were expected to show overall higher $\delta^{18}O$ values. Direction and magnitude of the relationship between $\delta^{18}O$ and $OH/^{16}O$ was consistent between habitats and behavioral phenotypes, indicating the negative correlation did not result from habitat-related effects. However, pike from our reference lake showed much higher $\delta^{18}O$ values than any other fish in the sample, despite it being a pure freshwater lake. A possible explanation for this could be strong evaporation effects on the lake, which has only neglectible in- and outflow, and therefore receives little groundwater input to balance out $\delta^{18}O$ enrichment through evaporation (Horton et al., 2015). This may drive $\delta^{18}O$ values towards more positive values (Aichner et al., 2022), which would also be reflected in fish otoliths.

The inverse relationship between organic matter (approximated by $OH/^{16}O$) and $\delta^{18}O$ values seen in our study agrees with previous work on fish otoliths (Guiguer et al., 2003; Hane et al., 2020, 2022; Matta et al., 2013), and also with more general studies on isotope measurements (Oehlerich et al., 2013). This effect likely results from the scale conversion between reference scales - Standard Mean Ocean Water (SMOW) and Pee Dee Belemnite (PDB) – which have commonly been used to report the small isotopic variations in organic (SMOW) or inorganic (PDB) materials. The conversion between the scales is $\delta^{18}O_{VPDB} = 0.97001 \times \delta^{18}O_{VSMOW} - 29.99$ (Brandt et al., 2014).

Water (and organic-bound oxygen derived from body water) is typically expressed relative to SMOW, and thus, when expressed on the VPDB scale, becomes 29.99 ‰ lighter. Consequently, when organic-bound oxygen with $\delta^{18}O_{VSMOW}$ values close to 0 ‰, but $\delta^{18}O_{VPDB}$ values closer to −30 ‰ are determined together with mineral carbonate, the organic fraction drives the overall $\delta^{18}O$ value lower. However, the extent to which otolith $\delta^{18}O$ values are influenced by organic-bound oxygen appears to be variable, ranging from 3.7 ‰ in Guiguer et al. (2003) to 1 ‰ in Matta et al. (2013), to 0.41 ‰ in Hane et al. (2020). Our results suggested an average shift in $\delta^{18}O$ values of 0.52 ‰, which is close to the offset reported by Hane et al. (2020), but we found the offset values to vary significantly between individuals and across behavioral phenotypes. This variability in offsets might be explained by our correction being based on paired values of an organic proxy that allowed the correction to change across individual otolith transects. The overall differences in mean offsets between studies suggested species-level

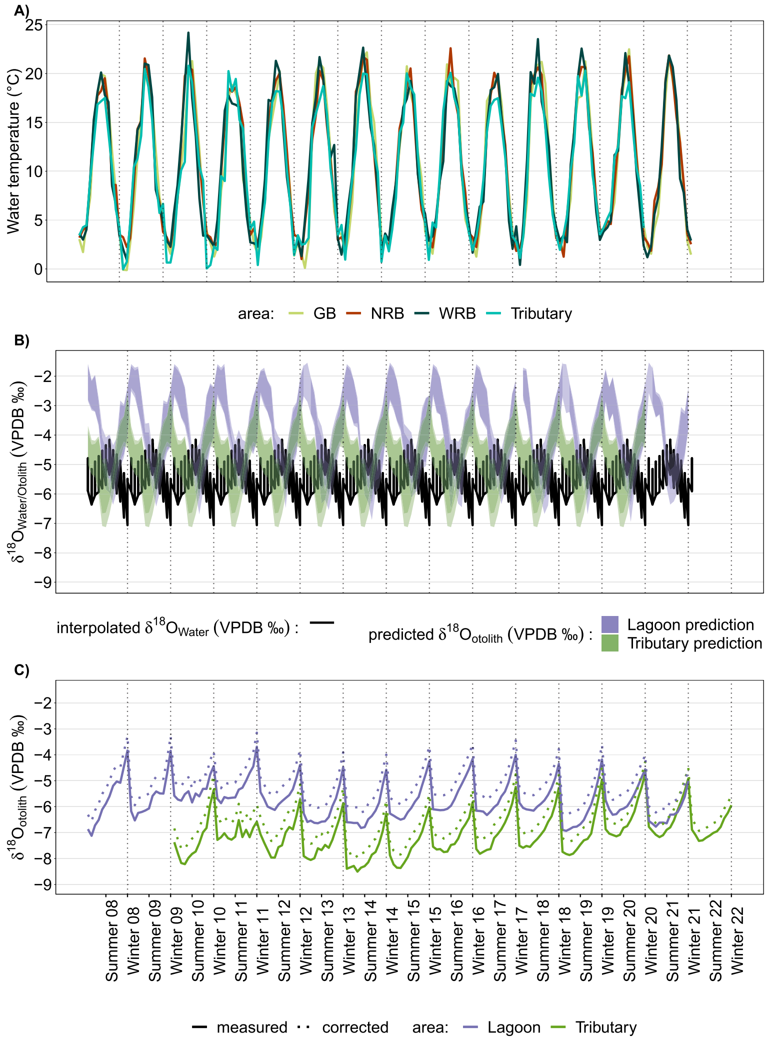

Fig. 5. A) Water temperature between January 2008 and December 2022 for the lagoon chains Greifswalder Bodden (GB), Northern Rügen Bodden Chain (NRB), Western Rügen Bodden Chain (WRB) and several tributaries, averaged across all tributaries (data source: LUNG MV). B) Water $\delta^{18}O$ values interpolated from time series (March 2020 to March 2021) and transect measurements (June 2019, March 2020 and July 2020) by Aichner et al# (2022), along with theoretical otolith $\delta^{18}O$ values calculated via fractionation equations from water $\delta^{18}O$ and temperatures (Geffen, 2012; Patterson et al, 1993). C) Raw (solid lines) and corrected (dotted lines) $\delta^{18}O$ values for 113 otoliths from pike sampled between July 2019 and May 2022 in brackish lagoons and several freshwater tributaries around Rügen island in northern Germany. Individuals were grouped based on capture location brackish lagoon and freshwater tributary. Pike from the reference freshwater lake were excluded as we had no water $\delta^{18}O$ data for the reference lake.

differences in intraotolith organic contents, rendering generalized offset corrections across species potentially unreliable.

In addition to the offsets induced by organic matter, SIMS $\delta^{18}O$ determination may further be influenced by matrix effects. A bias favoring ^{16}O ions has been reported when sputtering an organic matrix as compared to inorganic calcium carbonate during studies employing a nano-SIMS instrument (Oehler et al., 2009). Such an effect could partially explain the difference between species as the mass fraction of organic component would differ systematically between, e.g., species of fast vs slow growth and high vs. low metabolic rate. However, Guiguer et al. (2003) employed micro-drilling followed by phosphoric acid digestion to measure intra-otolith $\delta^{18}O$ values and reported significant effects of organic content (up to 3.7 ‰) on $\delta^{18}O$ values. Acid digestion is free of matrix effects, confirming the offset between organic-rich and organic-poor materials in SIMS $\delta^{18}O$ data cannot solely be due to matrix effects.

A final point to consider is that atmospheric water may be hygroscopically adsorbed onto otoliths when exposed to air. The organic lattice of the otolith consists of glycoproteins, i.e., proteins with covalently bound carbohydrate chains (Morales-Nin, 1986; Stevenson and Campana, 1992). Outer hydroxyl groups offer a site for water molecules to bind via hydrogen bonding. Amino acids, and in particular carbohydrate chains, are likely strongly hygroscopic compared to inorganic carbonates. During atmospheric storage of otoliths, this could result in atmospheric water molecules attaching to the outer OH groups of either the amino acids of the proteins or the carbohydrates through hydrogen

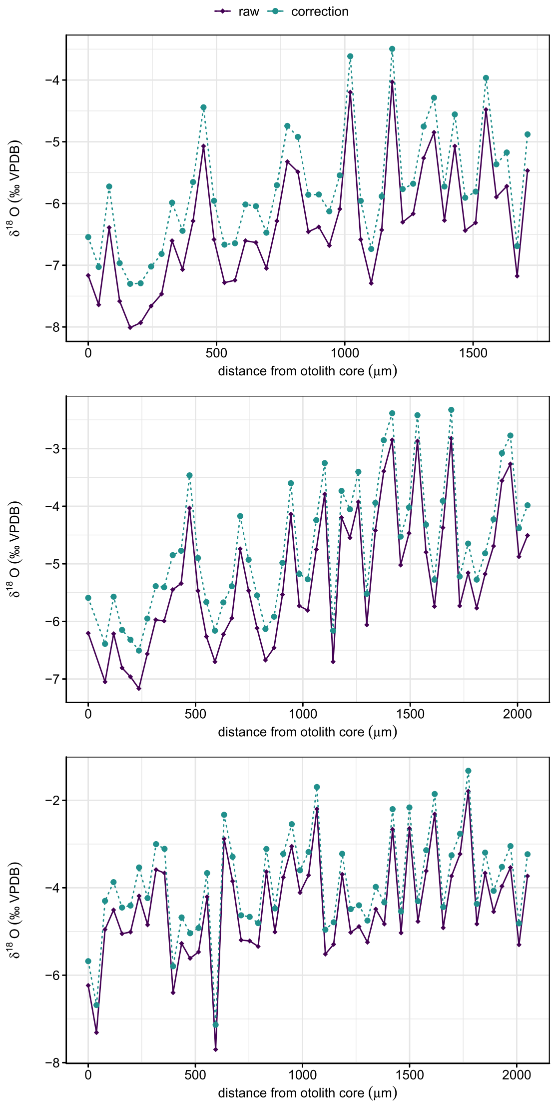

Fig. 6. Intraotolith δ^{18}O values of the three example pike otoliths captured in May 2020 in brackish lagoons around Rügen island in northern Germany before (solid purple lines) and after (dashed green lines) applying the pairwise correction. Upper panel: BH-01855, a seven-year-old male pike sampled from WRBC in May 2020 at 72.2 cm total length; middle panel: BH-01588, a 10-year-old female pike sampled from NRBC in February 2020 at 105 cm total length; low panel: BH-01722, a 13-year-old female pike sampled from NRBC in February 2020 at 95.0 cm total length.

bonding. Additionally, water molecules from the atmosphere could also bind to imperfections in the aragonite crystal structure. Such imperfections are more common in areas of accelerated growth and higher organic content (Stevenson and Campana, 1992), potentially amplifying the effect. Oxygen in atmospheric water vapor is depleted in ^{18}O relative to otolith carbonate, possibly altering δ^{18}O measurements (Bowen et al., 2011). However, given that the upper 70–80 nm of otoliths used for our study were presputtered under vacuum, atmospheric water molecules would have had to diffuse into the otolith matrix down to around 100 nm, which we deemed unlikely. The possibility of otolith water content influencing δ^{18}O was also discussed by Hane et al. (2020), who compared SIMS-derived δ^{18}O values to CF-IRMS, but this was not explicitly tested in Hane et al. (2020), nor in our study, suggesting avenues for further research.

Organic-induced offsets in δ^{18}O may have significant implications for the reconstruction of ambient water temperatures from fish otoliths. Hane et al. (2020) indicated that the offset in δ^{18}O values caused by organic matter content would result in an error in reconstructed temperatures of 1.5 °C in larval bluefin tuna. Other studies (e.g., Guiguer et al., 2003; Helser et al., 2018; Matta et al., 2013) suggest the potential bias in temperature reconstruction induced by varying organic contents might range between 1.5 °C and, in extreme cases, up to 13.5 °C. Using the commonly applied temperature fractionation equation of Patterson et al. (1993), the mean offset in δ^{18}O values reported in our study (0.52 ‰), would result in an overestimation of temperature of ~1.9 °C when applying δ^{18}O thermometry. Furthermore, our results indicate stronger offsets for juvenile and larval stages, likely due to accelerated juvenile growth and higher organic matter cotent, potentially resulting in temperature overestimation of up to 4 °C for these early life stages. Early life stages are particularly vulnerable to environmental perturbations and represent a common bottleneck in recruitment and productivity of fish populations (Dahlke et al., 2020). Given the need to identify suitable spawning and nursery habitats for fisheries management (Reis-Santos et al., 2022), accurate environmental temperature reconstructions for early life stages are critical. Errors induced by offsets in δ^{18}O could therefore lead to erroneous assessments of habitat suitability and resilience to warming.

Correcting SIMS δ^{18}O values using paired OH/^{16}O values and the slope of a linear model of δ^{18}O predicted by OH/^{16}O resulted in a decreasing offset with increasing distance from the otolith core. Applying this correction shifted pike otolith δ^{18}O values closer towards theoretical values predicted by ambient temperatures and water δ^{18}O values, validating the approach. However, differences remained between predicted and corrected values in the colder months of the year, where predicted δ^{18}O was higher than corrected δ^{18}O. This may be due to pike seeking thermal refuges, e.g., sheltered bays that are warmer than the open lagoons where the temperatures for the prediction were measured (Pursiainen et al., 2021), and active thermoregulation through sunbathing in pike (Nordahl et al., 2019), which would lead to lower otolith δ^{18}O values than predicted by ambient water temperature. An alternative explanation could be errors introduced by the linear interpolation of otolith δ^{18}O values over 12 months, as otoliths do not grow isometrically throghout the year (Stevenson and Campana, 1992). The magnitude of the correction varied between behavioral phenotypes, being lowest in freshwater resident pike and pike from the reference lake, likely due to slower juvenile growth of these individuals (Rittweg et al., 2024). Our results suggest that the relationship between organic content and δ^{18}O values are more complex than anticipated previously, and may vary depending on growth dynamics and life history strategies. Unless the organic material can be quantitatively removed from the sample material prior to analysis, both SIMS and IRMS data may require correcting for the organic-derived oxygen (Guiguer et al., 2003; Hane et al., 2020). Roasting otoliths offers one possible solution, however, the effects of roasting on mineral composition (e.g., potential recrystallization of aragonite to calcite through heating) may be a problem for SIMS (Guiguer et al., 2003). We suggest that our correction approach based on paired δ^{18}O values and OH/^{16}O ratios partially resolved the challenge associated with decreases in organic matter content with the increasing age of the fish. However, SIMS analysis is costly, and facilities with the necessary equipment for this method remain rare. Combining laser ablation inductively-coupled plasma mass spectrometry (LA-ICPMS) measurements of organic-bound trace elements, such as P, S, Cu, Zn, or Mn (Izzo et al., 2015), with commonly applied methods of measuring δ^{18}O, such as micromilling (Helser et al., 2018), may present a cheap and more readily available method to assess influences of organic matter if SIMS is not an option. However, more research would be required before such correction methods become widely applicable.

4.1. Limitations

The otoliths we used for our study were sampled from an area experiencing considerable isotopic variation in $\delta^{18}O_{Water}$ over the course of a year due to mixing processes and seasonal differences in evaporation (Aichner et al., 2022). This might have introduced variation in intra-otolith $\delta^{18}O$ which could contribute to the observed large differences between individual fish. Such environmental variation in oxygen isotopic ratio might further complicate our model, although this is unlikely to change the direction of the effects. Possible movements of individuals between habitats featuring different $\delta^{18}O_{Water}$ values could further mask the impact of organics on $\delta^{18}O_{Otolith}$. However, we incorporated behavioral habitat use types described elsewhere (Rittweg et al., 2024) for fish in our model, which likely accounted for this possibility. Applying the correction led to different results for different capture locations and behavioral phenotypes, suggesting also other factors may have contributed to the observed effects, which our study did not fully resolve. Investigating the interaction of analytical and biological effects on SIMS $\delta^{18}O$ determinations thus remains an important research topic that deserves further attention. The absence of clear seasonal bands in $OH/^{16}O$ might indicate factors other than organic matter could contribute to this proxy, however, the negative association between $OH/^{16}O$ and $\delta^{18}O$ was strong across the entire sample, as was the positive associaton between $OH/^{16}O$ and organic proxies across ontogeny, suggesting this proxy to be robust across the life history of an individual.

4.2. Conclusions

Our study shows that, while the effect of organic contents on otolith $\delta^{18}O$ was consistent with previous work, individual variability in habitat use, age and growth plays an important role, that has gone unrecognized. In our system, failing to account for the effect of organics on otolith $\delta^{18}O$ values would result in overestimation of reconstructed temperatures by $\sim 1.9^{\circ}C$, which is ecologically significant. The ontogenetic effects revealed in our work lead us to advise caution when applying global corrections. If a correction is applied, non-constant, pairwise corrections, such as the equation proposed here, are biologically more realistic. Paired measurements of $OH/^{16}O$ may be acquired without increasing the measuring time or cost during SIMS analyses, and a correction can be readily developed on a case-by-case basis. Where $\delta^{18}O$ values are determined via acid dissolution, it is less clear how such a correction may be applied, although combined LA-ICPMS and micromilling approaches may offer a potential solution, warranting further investigations. In either case it is clear that life history dynamics and habitat use of the target species need to be considered. Last, where it is practically possible, we recommend spatial assessments of different organic tracers on subsamples via EPMA scans or similar methods before analyzing otolith $\delta^{18}O$, to determine whether intraotolith organics may introduce bias.

Ethics approval

Fish were sampled in accordance with permit 7308.2 of the Landesamt für Landwirtschaft, Lebensmittelsicherheit und Fischerei (LALLF MV). Sampling in national park Vorpommernsche Boddenlandschaft was carried out in accordance with permit 21/5320.142, Nationalparkamt Vorpommern, sampling in biosphere reserve Südost-Rügen was carried out in accordance with permit 5321.2/FM/SchnB.Nr.20002, Biosphärenreservatsamt. Sampling in nature reserves was carried out in accordance with permit 5328.1.99/654–19–40–3 of the Staatliches Amt für Landwirtschaft und Umwelt (STALU MV). Sampling of freshwater tributaries was carried out with permission by the Landesanglerverband Mecklenburg-Vorpommern e.V. (LAVB MV).

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CRediT authorship contribution statement

Timo Dustin Rittweg: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Michael Wiedenbeck:** Writing – review & editing, Validation, Software, Resources, Methodology, Data curation, Conceptualization. **Jan Fietzke:** Writing – review & editing, Validation, Software, Resources, Methodology, Data curation, Conceptualization. **Clive Trueman:** Writing – review & editing, Writing – original draft, Supervision, Investigation, Conceptualization

Declaration of Competing Interest

The authors declare no conflicts of interests.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2024.107239.

Data availability

Data used for the analysis are available from doi 10.18728/igb-fred-946.0, R code used for the analysis is available from https://github.com/Traveller-2909/Otoganics.

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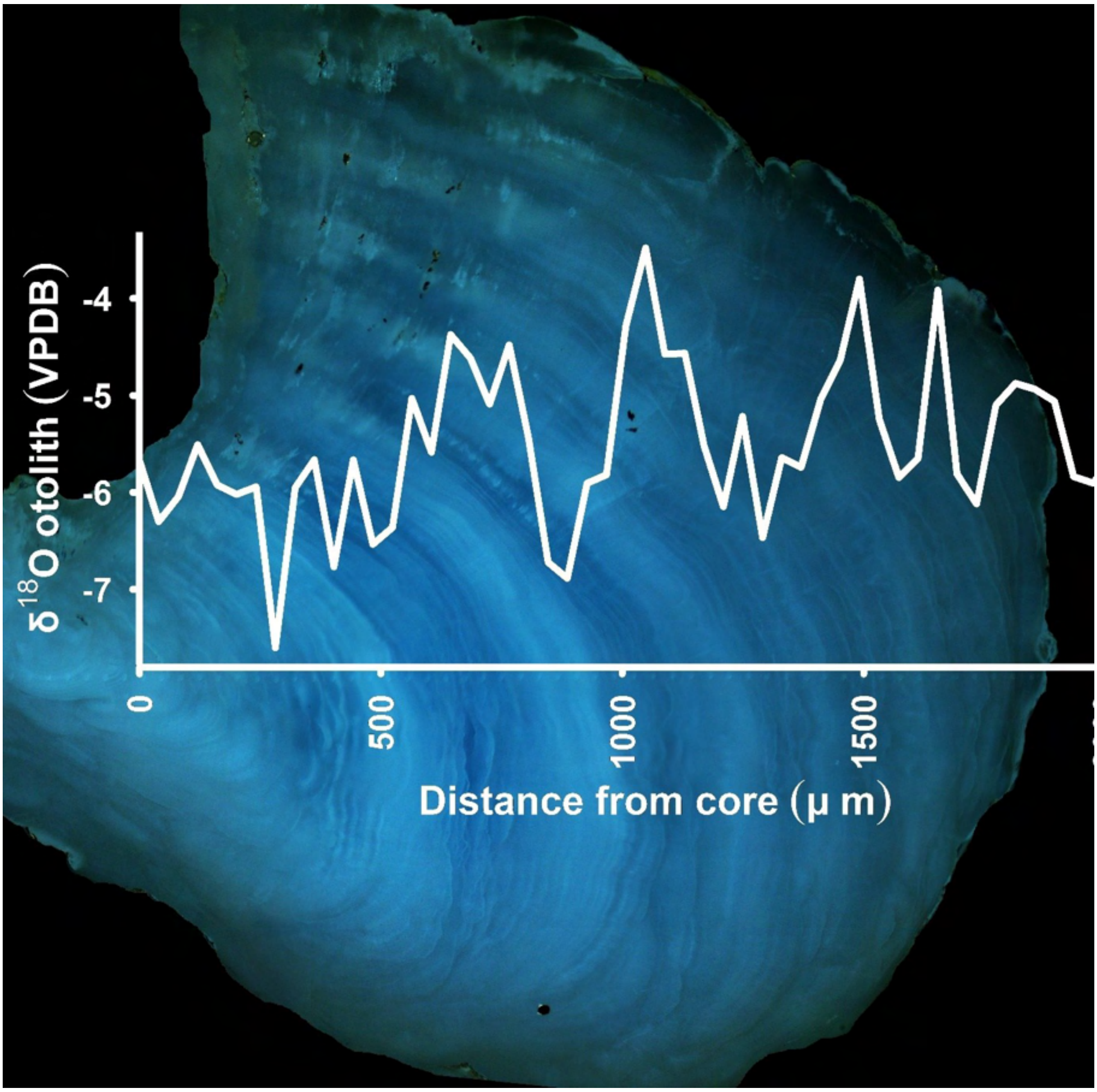
Paper V



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Timo Rittweg, Clive Trueman, Elias Ehrlich, Michael Wiedenbeck, Robert Arlinghaus, 2023, Corroborating otolith age using oxygen isotopes and comparing outcomes to scale age: Consequences for estimation of growth and reference points in northern pike (*Esox lucius*), Fisheries Management and Ecology, 31, e12646.

oxygen in pike otolith, photo credit: Timo Rittweg

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ARTICLE

Fisheries Management and Ecology WILEY

Corroborating otolith age using oxygen isotopes and comparing outcomes to scale age: Consequences for estimation of growth and reference points in northern pike (*Esox lucius*)

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Funding information

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Abstract

management advice, but validation studies are rare for many species. We corroborated

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Esox lucius) from the southern Baltic Sea, compared results with visual age esti

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underestimated the age of pike older than 6 years compared to the corroborated refer

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MSY

MSY B_{MSY} ≥ 100 cm

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in MSY would cause unrealistic expectations of yield potential in commercial fishers.

KEYWORDS

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1 INTRODUCTION

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of a managed fish species. Such information is particularly rare in

nual monitoring (Beard Jr. et al., .

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southern Baltic Sea targeting northern pike (*Esox lucius*

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Coastal pike stocks in the Baltic Sea have traditionally been ex

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nuli) (Weyl & Booth,

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ondary ion mass spectrometry (SIMS) transects on otoliths (Matta

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). While otoliths provide accurate and precise age

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ages of pike were accurate up to an age of 10 years (Anwand,

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Especially in the Baltic Sea, where age estimation from scales has

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lected from brackish lagoons of the southern Baltic Sea in Germany.

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2 METHODS

2.1 Sampling

lagoon chains (called Bodden chains) in the southern Baltic Sea

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Bodden Chain (NRB), the Western Rügen Bodden Chain (WRB), and

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between 7.2 and 9.2 PSU ( ), with extremes up to 14.2 PSU and down to 3.0 PSU. Mean annual temperature ranged from 2.0 to 20.5°C, with extremes from −0.5°C to 25.1°C. Additional fish were sampled from freshwater tributaries Barthe and Peene, Sehrowbach,

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(BKG). Fish were sampled with fyke nets, gill nets, rod and line, and electrofishing. The total length of each fish was measured (mm). We

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lected from a transect of the whole study system in June 2019, March 2020, and July 2020, and biweekly measurements at fixed locations

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2.2 Scale processing

Scales were sampled from above the lateral line just anterior to the

gether. A minimum of three scales per fish were mounted. Slides

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enhanced in the Fiji distribution of ImageJ (Schindelin et al., .

2.3 Otolith processing

Sagittal otoliths were extracted and cleaned in an ultrasonic water

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cator for 48 h. Otoliths were glued to an object slide with Crystalbond,

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Geosciences Potsdam (GFZ). Sections were embedded into SIMS sample mounts with Epofix epoxy resin, along with UWC3 and IAEA603

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Kozdon et al., .

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ensure a complete transect from core to edge. Sample mounts were

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~35 μ

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‰ relative to Vienna Standard Mean Ocean Water (VSMOW). Otolith

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Dee Belemnite (VPDB) reference scale (Kim et al., .

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2.4 Seasonal δ^{18}O values in otoliths

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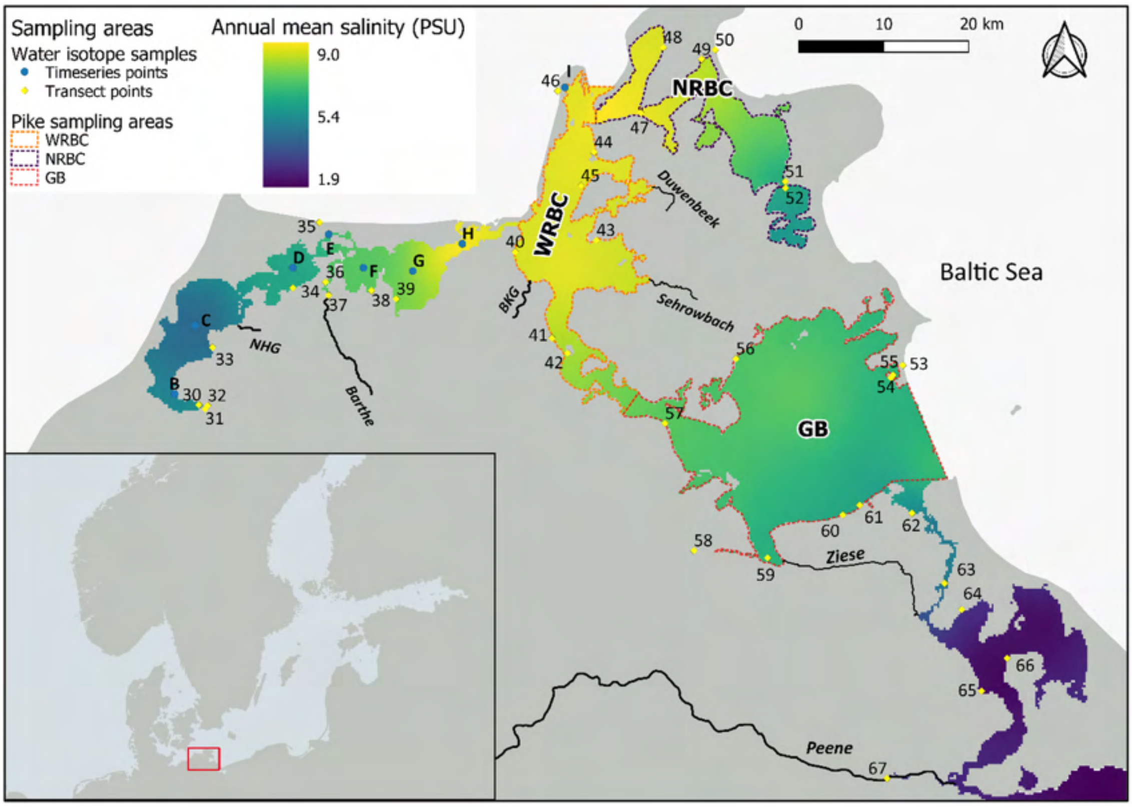

FIGURE 1 Study area around the island of Rügen, Germany, in the southern Baltic Sea, depicting three lagoon chains from which pike were sampled between June 2019 and November 2020. Lagoons are indicated by NRBC (Northern Rügen Bodden Chain), WRBC, (Western Rügen Bodden Chain), and GB (Greifswalder Bodden). Tributary abbreviations are NHG (Neuendorfer Hechtsgraben) and BKG
. δ_{Water} measurement transects in June 2019, March 2020,
and July 2020 (Aichner et al., I δ_{Water}
March 2020 until March 2021. The average monthly salinity between 1 January 2008 and 1 January 2023 is shown as a color gradient.

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$$1000\ln\alpha = 18.56\left(1000T(K)^{-1}\right) - 33.49$$

$$\text{where } \alpha = \frac{1000+\delta^{18}O_{\text{Oto}}\text{VSMOW}}{1000+\delta^{18}O_{\text{Water}}\text{VSMOW}}$$

$$1000\ln\alpha = 15.99\left(1000T(K)^{-1}\right) - 24.25$$

$$\text{where } \alpha = \frac{1000+\delta^{18}O_{\text{Oto}}\text{VSMOW}}{1000+\delta^{18}O_{\text{Water}}\text{VSMOW}},$$

T is temperature in Kelvin (K), α

δ_{Water} δ . δ

period of 12 months within identified annuli to facilitate comparison

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compared using a Spearman rank correlation coefficient. Some error

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2.5 Age estimation

Age was estimated on high-resolution images using the OtoJ macro

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ugin ObjectJ in imageJ. Image names and order were randomized

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>2000 structures over more than 2 years) and reader 2 was

not experienced (no structures read). Scale-age estimates from three

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Each otolith was interpreted once by each reader. Second, to cor

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2.6 Age-estimation accuracy and precision of otoliths and scales

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age. The ageBias function of the FSA package (Ogle et al.,

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multiple comparisons. Wilcoxon's signed rank test, with a continu

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and Evans-Hoenig's pooled test was used to compare the number of

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2.7 Population-level growth from size-at-age

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$L_a = L_\infty\left(1 - e^{(-k(a-t_0))}\right)$.

structure and reader using the rstan package, version 2.21.2 (Stan

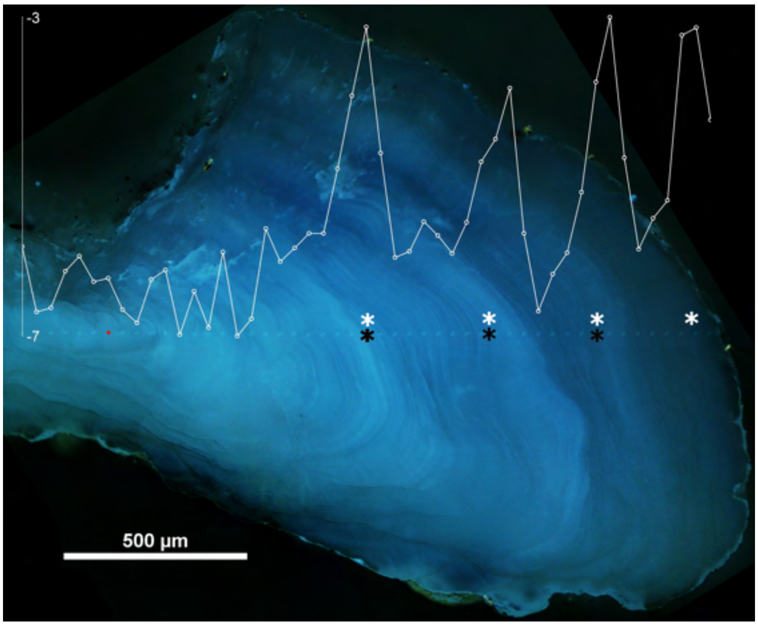

FIGURE 2 Oxygen isotope values in

2020 in the Western Rügen Bodden Chain (WRBC). The oxygen isotope profile is

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development team 2020), a Bayesian approach implemented in Stan

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L_∞ t_0 parameters, as suggested by Smart

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termined by the reported maximum length of pike (150 cm, Froese &

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2.8 Assessing fisheries management reference points and optimal size limits

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We assumed size selectivity of the fishery in capture and retention

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k L_∞ M_{ref}.

Specifically, k

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$L_\infty = C\,k^{-0.33}$ (Jensen, C

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ity at length = 70 cm) of the Lorenzen size-dependent mortality

$M_{ref} = 4.118\,k^{0.73} L_\infty^{-0.33}$ T . . T

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ios, while keeping the current minimum length limit of 50 cm, to esti

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B_{MSY}

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the number of trophy pike longer in total length than 100 cm, L_{trophy}

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catch rate, contributing to angler welfare (Koemle et al.,

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regulation between 50 and 100 cm in steps of 1 cm among model

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length limit (50 cm) and F (0.2 year^{-1}. E

for 1000 years, and model outputs were averaged across the last 200 years to ensure the modeled population reached equilibrium.

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3 RESULTS

32 males. Sampling limitations did not allow for an equal sex ratio.

Therefore, 24 pike (13 females, 11 males) were captured in WRB, 22
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3.1 Seasonality of $\delta^{18}O_{Otolith}$ values

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in winter (−7.1‰) and higher values in summer (−4.2‰,
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E =−6.0‰, E =−6.4‰) and high
est values in January and February (E =−2.0‰, E
=−2.2‰, . δ
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lower values in the first 2 years of individual pike. The Spearman
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$r(86)=0.45$ (S1 .

3.2 Corroborated age estimate

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$\chi^2=0.00$, df = 1, $p=1.00$;
E $\chi^2=4.33$, df = 4, $p=0.36$). Using age estimates by
t
$t=0.00$, df = 8, $p=0.93$). Age estimates from the automated count agreed with those by reader 1 for 40.7% of pike (ACV = 11.8%) and with those by reader 3 for 28.6% of pike (ACV = 18.7%). Estimated
$\chi^2=0.02$, df = 1, $p=0.90$; Evans–Hoenig $\chi^2=2.77$, df = 4, $p=0.60$). Age estimates by reader 1 were also not
$\chi^2=0.30$, df = 1, $p=0.59$; Evans–Hoenig $\chi^2=3.64$, df = 4, $p=0.46$). The mean
t
$t=0.07$, df = 85, $p=0.94$; t-tests for reader 3: $t=0.07$, df = 176.25, $p=0.94$).

3.3 Age-estimation accuracy and bias of otoliths and scales

T
.
. T
. . T). Scale-age
variation (CVs) (Wilcoxon's signed rank test, reader 1: $W=3394.5$, df = 170, $p<0.05$; reader 2: $W=3285.5$, df = 170, $p<0.05$), higher ab
±1 and ±2 years of deviation (T . R
t
$t=-4.40$, df = 85, $p<0.05$; age 11: $t=-9.80$, df = 85, $p<0.05$). Reader
$t=3.92$, df = 85,
$p<0.05$). Bias decreased for ages older than 3 and reversed for the
$t=-8.66$, df = 85, $p<0.05$). Reader 1 gen
$\chi^2=10.20$,
df = 1, $p<0.01$; Evans–Hoenig $\chi^2=15.6$, df = 5, $p<0.01$), while
R
$\chi^2=8.20$, df = 1, $p<0.01$; Evans–Hoenig
$\chi^2=13.70$, df = 6, $p<0.05$). Otolith age estimates were not signifi
$\chi^2=0.16$, df = 1, $p=0.69$; Evans–
$\chi^2=3.09$, df = 5, $p=0.69$; reader 2 McNemar $\chi^2=1.10$, df = 1,
$p=0.29$; Evans–Hoenig $\chi^2=2.91$, df = 4, $p=0.57$), and mean age es
$t=0.15$, df = 85, $p=0.88$).

3.4 Population-level growth of pike using age data from different age estimation structures

G
. G
.
T
significantly smaller sizes at age for pike younger than 8 years, as indi
.
k .
G
T). Scale-age estimates
L_∞

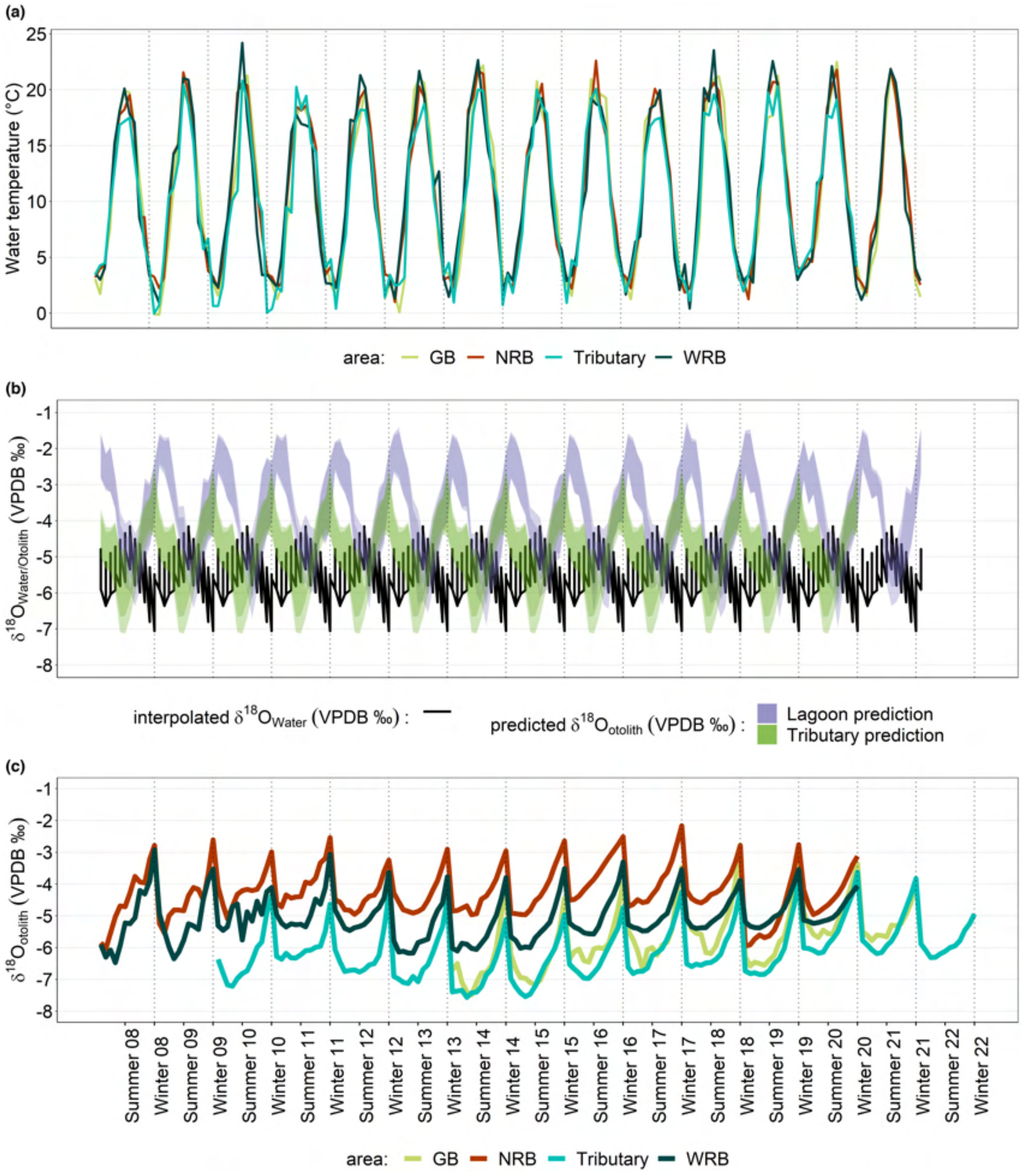

FIGURE 3 (a) Water temperature between January 2008 and December 2022 from the lagoon chains Greifswalder Bodden (GB), Northern Rügen Bodden Chain (NRBC), Western Rügen Bodden Chain (WRBC) and several tributaries, averaged across all tributaries (data G . δ $_{Water}$ values interpolated from time series (March 2020 to March 2021) and transect measurements (in June 2019, March 2020 and July 2020) from Aichner et al. (δ δ $_{Water}$ G . . δ . .

TABLE 1 Summary of age estimation precision and accuracy metrics for visual age estimates on scales and otoliths on 86 pike caught in three coastal lagoon chains and several tributaries around Rügen island in Germany between June 2019 and November 2020.

Structure	N	% agreement	±1 year	±2 years	Average coefficient of variation [%]	Average absolute deviation	Average percent error [%]
R		.	.	.	.	.	.
R		.	.	.	.	.	.
R		.		.	.	.	.
R		.	.	.	.	.	.

Note .

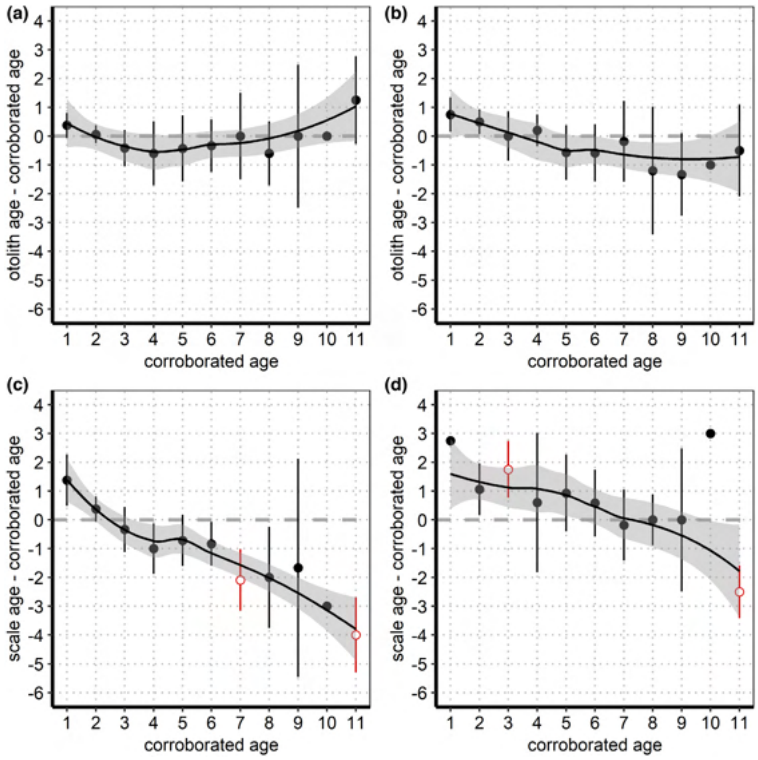

FIGURE 4 Age bias plots showing .

between June 2019 and November 2020

R I

G .

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. R

t

. R

R

R

R .

k T . E t_0

T . T L_∞ *k*

.

S4–S7 .

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MSY), biomass at MSY (B_{MSY}

≥ 100 cm $freq_{trophy}$

.

3.5 Fisheries management reference points and optimal minimum-length limit

F_{MSY}

MSY .

MSY). When using the

F_{MSY} B_{MSY}

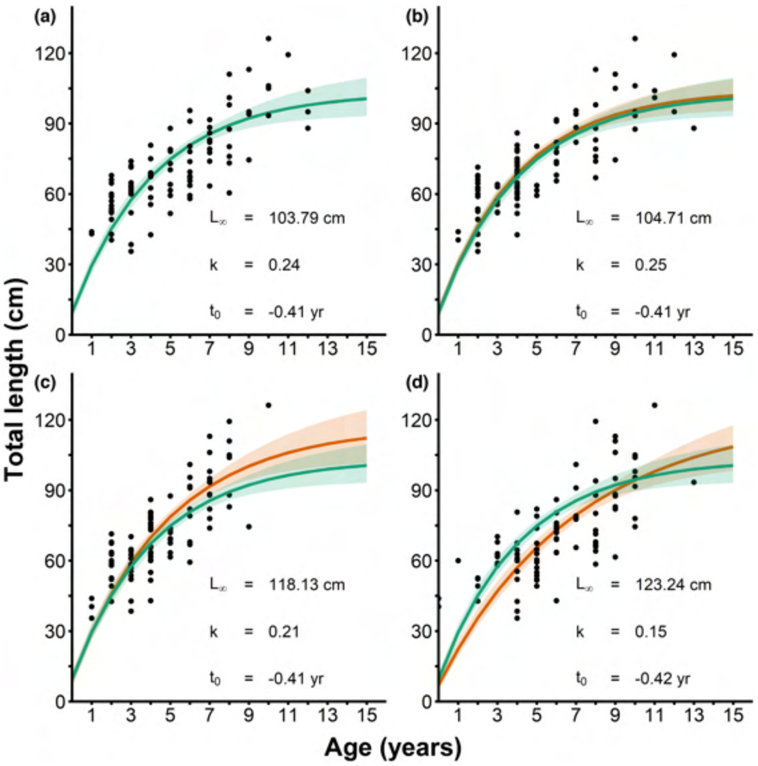

FIGURE 5 Von Bertalanffy growth

R G

June 2019 and November 2020. The

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G

G

G

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TABLE 2 Summary of VBGF

Rügen island in Germany between June

.

Sample	N	L ∞ [cm]	Brody growth coefficient k	Age at size 0 [yr]
I		103.8 ± 11	0.24 ± 0.06	−0.4 ± 0.15
		104.7 ± 8.7	0.25 ± 0.05	−0.4 ± 0.15
Scale age reader 1		118.1 ± 16.4	0.21 ± 0.055	−0.4 ± 0.15
Scale age reader 2		123.2 ± 21.4	0.15 ± 0.045	−0.4 ± 0.15

MSY freq$_{\text{trophy}}$. T

F_{MSY} (−32%) more than

MSY = 26%, B_{MSY} = 55%, freq$_{\text{trophy}}$ = 179%). Overestimation

F_{MSY} MSY

B_{MSY} freq$_{\text{trophy}}$

MSY . I

.

. T

fisheries was 69 cm for the model based on isotope-based ages, 19 cm higher than the current minimum-length limit of the fishery.

similar to the model based on otolith ages (68 cm), the model based

minimum-length limit by 23% (85 cm) and the model based on scale ages by reader 2 by 26% (87 cm). Harvest slot limits that added a

S8 S9 .

4 DISCUSSION

We used high-resolution SIMS data to corroborate ages estimated

δ

studies and the limited sample sizes of past studies (range = 8–40

; Kastelle

. ; Kimura et al., T . ; Weidman

. I

FIGURE 6 Model outputs on fisheries

R

in northern Germany between June

. F_{MSY},

(b) MSY, and (c) B_{MSY}

≥ 100 cm

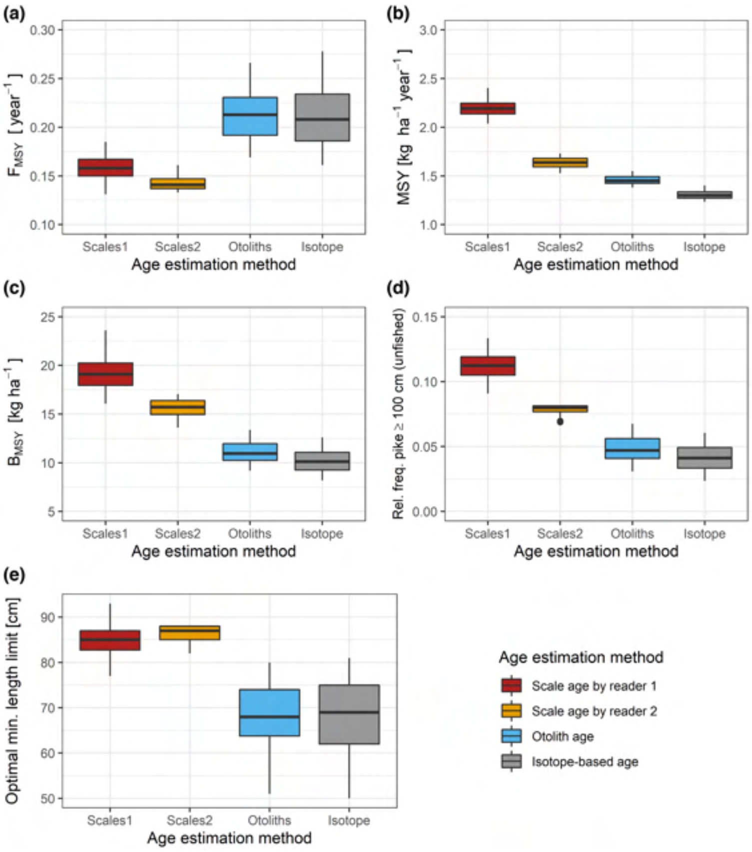
.

T

M_{ref} . . . .

year^{-1}

.



. I

L_∞

. I

MSY

B_{MSY}

F_{MSY}.

4.1 Age corroboration and the value of scales

We conclude that observed cyclic variations in δ

. T

δ Water G

. δ

. .

the Baltic Sea increase their body temperature during winter months

. δ

ture. We found no indication of movement across salinity gradients in

δ

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.

stationary (mean size of extended home range: 6.58 km ± 5.77 km;

. .

.

short periods of less than 14 days (Arlinghaus et al.,

δ .

δ

uous between readers, as was also found by Kastelle et al. (

δ

transects instead of human readers. With only two readers for the

.

. .T

first age of significant underestimation in scales (6 years) agreed

. . .

. ; Frost & Kipling,

. . .

Micropterus salmoides T

Esox masquinongy

. *Leucichthys artedi*

accuracy of pike scales up to an age of 10 years (Laine et al.,

. .

. . G

& Kipling, . T

growth of the local populations (Frost & Kipling,

. I

.

E .). Scales have the obvious

. . T

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4.2 Consequences of age estimation bias for growth and fisheries reference points

L_∞

k

G .

E

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. . R ; Smart & Grammer, . T

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. I

T .

T

F_{MSY} MSY B_{MSY}

. F_{MSY}

k .

k F_{MSY} B_{MSY}

MSY

.

MSY B_{MSY}

. I

T .

T .

F_{MSY} B_{MSY}

MSY

.

MSY

F_{MSY} B_{MSY} MSY (Walters &

). However, if management directly targets MSY,

.

Similarly, for a trophy fishery oriented toward recreational fish

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. I

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4.3 Limitations

δ

exceeded 4 SIMS-points for the oldest individuals, which was sufficient for detecting the seasonal temperature signal (Kastelle . ; Weidman & Millner, . I

E .). Such feedback would

. .

4.4 Management recommendations

$\delta^{18}O$

estimates were of poor accuracy and precision. We also found that

ity assessment of fish. We found the age-estimation bias introduced

.

which the specific structure has been validated. Second, if the aim

.

tive management strategies when based on MSY-related reference

F_{MSY} B_{MSY} . T

.

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G E .
TR I
E I IG
European Maritime Fisheries Fund (EMFF) of the EU and the State
G
MV- I.18- LM- 004) within the Boddenhecht project. We thank Rob
T

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Couffignal at the Potsdam SIMS laboratory contributed vital sample preparation and SIMS analytical work, respectively. Open Access
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CONFLICT OF INTEREST STATEMENT

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DATA AVAILABILITY STATEMENT

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T .

ETHICS STATEMENT

T G

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ORCID

Timo D. Rittweg .
Clive Trueman .
Elias Ehrlich .
Robert Arlinghaus .

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SUPPORTING INFORMATION

Supporting Information section at the end of this article.

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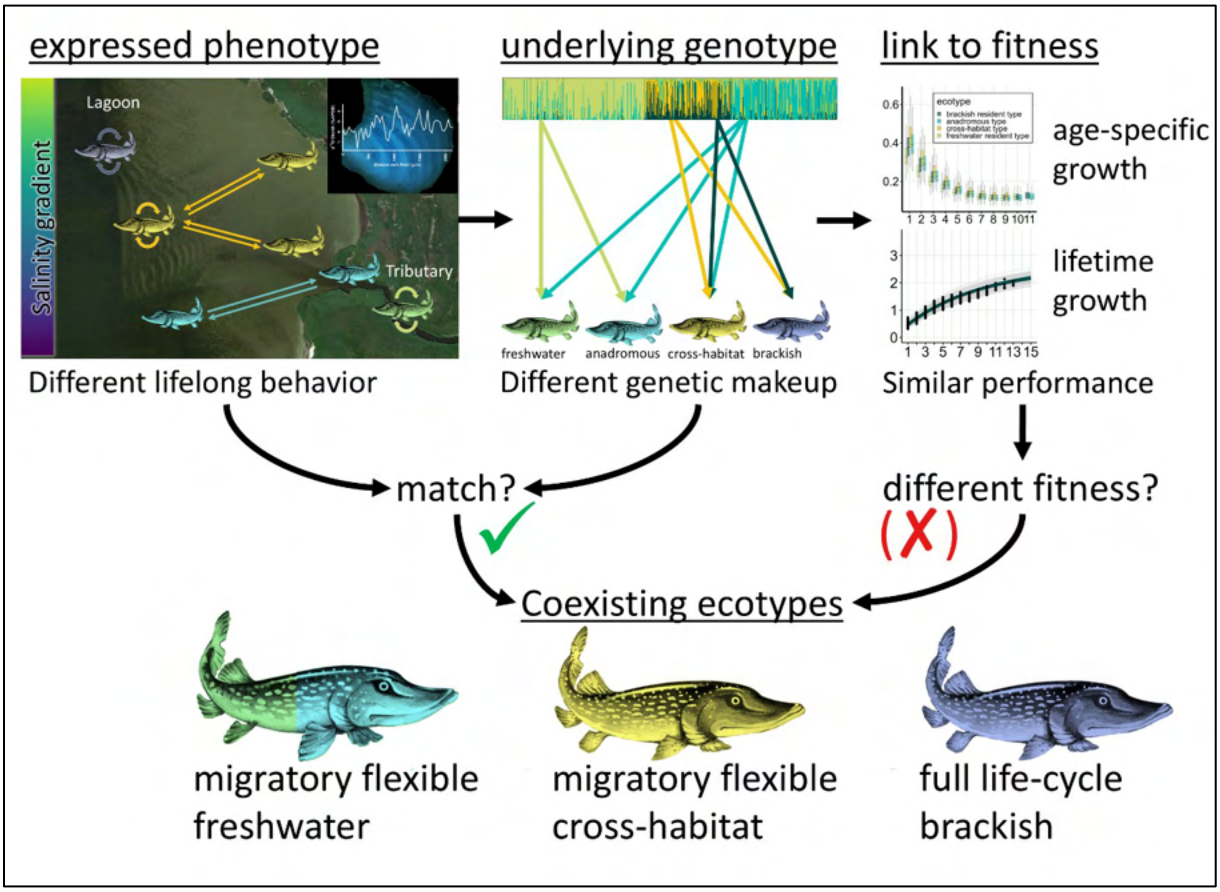
Paper VI



VI

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graphical abstract, Timo Rittweg

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https://doi.org/10.1007/s00442-024-05627-7

ORIGINAL RESEARCH

Variable habitat use supports fine-scale population differentiation of a freshwater piscivore (northern pike, *Esox lucius*) along salinity gradients in brackish lagoons

Timo D. Rittweg[1,7] · **Clive Trueman**[2] · **Michael Wiedenbeck**[3] · **Jan Fietzke**[4] · **Christian Wolter**[1] · **Lauren Talluto**[5] · **Stefan Dennenmoser**[6] · **Arne Nolte**[6] · **Robert Arlinghaus**[1,7]

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Abstract

In mobile animals, selection pressures resulting from spatio-temporally varying ecological factors often drive adaptations in migration behavior and associated physiological phenotypes. These adaptations may manifest in ecologically and genetically distinct ecotypes within populations. We studied a meta-population of northern pike (*Esox lucius*) in brackish environments and examined intrapopulation divergence along environmental gradients. Behavioral phenotypes in habitat use were characterized via otolith microchemistry in 120 individuals sampled from brackish lagoons and adjacent freshwater tributaries. We genotyped 1514 individual pike at 33 highly informative genetic markers. The relationship between behavioral phenotype and genotype was examined in a subset of 101 pikes for which both phenotypic and genomic data were available. Thermosaline differences between juvenile and adult life stages indicated ontogenetic shifts from warm, low-saline early habitats towards colder, higher-saline adult habitats. Four behavioral phenotypes were found: Freshwater residents, anadromous, brackish residents, and cross-habitat individuals, the latter showing intermediary habitat use between brackish and freshwater areas. Underlying the behavioral phenotypes were four genotypes, putative freshwater, putative anadromous, and two putatively brackish genotypes. Through phenotype-genotype matching, three ecotypes were identified: (i) a brackish resident ecotype, (ii) a freshwater ecotype expressing freshwater residency or anadromy, and (iii) a previously undescribed intermediary cross-habitat ecotype adapted to intermediate salinities, showing limited reliance on freshwater. Life-time growth of all ecotypes was similar, suggesting comparable fitness. By combining genetic data with lifelong habitat use and growth as a fitness surrogate, our study revealed strong differentiation in response to abiotic environmental gradients, primarily salinity, indicating ecotype diversity in coastal northern pike is higher than previously believed.

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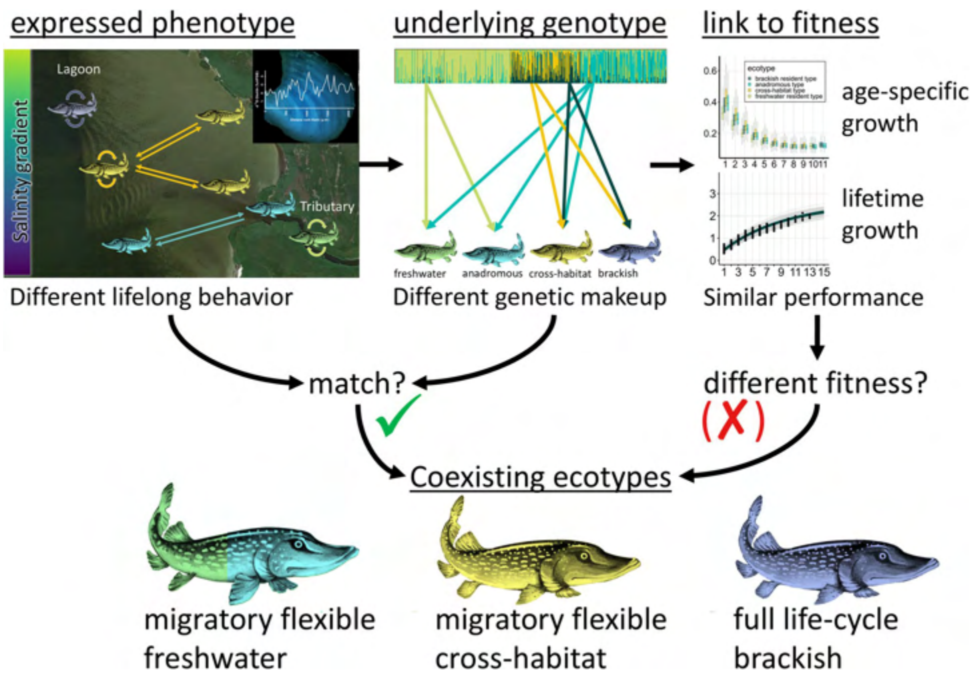
Graphical abstract



Keywords Ecological niche · Evolution · Life histories · Growth · Partial migration

Introduction

Ecological factors like food availability, predation, and abiotic environmental conditions shape niche spaces and the fitness landscape of organisms in the wild (Roff 2002). Selection pressures vary over time and space due to density fluctuations, environmental gradients, and environmental stochasticity (Bell 2010). Organisms adapt to fluctuating selection through various traits and processes, e.g., behavioral shifts in habitat use, migration, physiological adaptation to local environmental factors, or microevolutionary changes in adaptive life history traits (Felmy et al. 2022; Sunde et al. 2022; Tibblin et al. 2015, 2016). Trade-offs between traits and limited ability to generalize (Rosenzweig 1974) cause intraspecific phenotypic and genetic variability, fostering ecotype evolution (Brown 1990) and sympatric speciation (Doebeli and Dieckmann 2003). Although terminology varies (Clemens and Schreck 2021), ecotypes are characterized by both phenotypic (e.g., in morphology, physiology, and behavior) and genetic differentiation (Stronen et al. 2022). Documenting ecotypes therefore requires that phenotypic and genetic data are combined, which is rarely the case (Clemens and Schreck 2021; Stronen et al. 2022). For example, out of 112 publications reviewed by Stronen et al. (2022) that use the term ecotype, only 53% incorporated genetic analyses, which was attributed to limited availability of genomic resources, particularly for nonmodel organisms.

Environmental conditions near the edge of a species tolerance can prompt local evolutionary adaptations and cause population diversification (Pörtner et al. 2010). Brackish estuarine systems pose such challenges, particularly for osmoregulating ectotherms, such as fishes, where salinity and temperature are key ecological factors (Kültz 2015; Magnuson et al. 1979). Spatio-temporal variation in these factors invokes trade-offs among traits and metabolic costs on the individual level (Sokolova 2021), driving adaptive responses, such as the evolution of variable migration strategies (Delgado and Ruzzante 2020). A possible outcome is partial migration, when varying migration behaviors are expressed along a behavioral continuum (Chapman et al. 2011), and behavioral endpoints (such as residency in one habitat) often correlate with the extremes of underlying environmental factors (Cagnacci et al. 2011). Variable migration behaviors, along with genetic differences, have been described in several coastal fish species, indicating ecotype evolution (e.g., Nordahl et al. 2019; Dennenmoser et al. 2017; Kusakabe et al. 2017). Adaptations to environmental factors also occur in less mobile life stages, such as eggs or larvae, as physiological tolerances are often size-specific in fishes (Werner 1988). Larger individuals often exhibit greater osmoregulatory capacity and lower temperature preference (Lindmark et al. 2022; Varsamos et al. 2005). Thus, mobile species in brackish environments can also be expected to adapt behaviorally through ontogenetic habitat shifts, e.g., favoring warmer, less saline juvenile habitats and colder, more saline adult habitats (Casselman and Lewis 1996; Pursiainen et al. 2021).

Genetically, intrapopulation diversification can arise from isolation by environment (IBE), where individuals become reproductively isolated through adaptation to local environmental factors (Wang and Bradburd 2014), and isolation by distance (IBD), where geographic distance limits gene flow (Wright 1943). Additionally, reproductive timing (isolation by time, IBT, Hendry and Day 2005), and natural or anthropogenic barriers (isolation by resistance, IBR, McRae 2006) can limit gene flow among subpopulations. The northern pike (*Esox lucius*), a mesothermal, stenohaline freshwater predator (Jacobsen and Engström-Öst 2018), presents a suitable model to study intrapopulation diversification (Forsman et al. 2015), as it exhibits all these isolation mechanisms and multiple phenotypes across its distribution range in the subarctic northern hemisphere (Bekkevold et al. 2015; Eschbach et al. 2021; Nordahl et al. 2019; Sunde et al. 2022; Tibblin et al. 2016). Pike are strongly phytophilic, relying on macrophytes both for reproduction as well as for foraging and predator avoidance (Grimm 1981). They exhibit limited mobility and dispersal (Dhellemmes et al. 2023a) and show natal homing (Engstedt et al. 2014; Miller et al. 2001; Tibblin et al. 2016). Pike have colonized brackish habitats in the Baltic Sea from glacial freshwater refuges (Maes et al. 2003), inhabiting brackish water up to 15 Practical Salinity Units (PSU) (Jacobsen and Engström-Öst 2018). Previous studies indicated weak genetic differentiation between coastal populations, but large-scale IBD patterns, most likely explained by limited dispersal, as pike prefer shallow vegetated habitats (Laikre et al. 2005; Maes et al. 2003; Wennerström et al. 2017). More recent research, however, identified genetic differentiation at small geographic scales in coastal pike populations (Diaz-Suarez et al. 2022; Möller et al. 2020; Nordahl et al. 2019; Wąs-Barcz et al. 2023). Although IBD patterns were also present on a local scale (e.g., Möller et al. 2020), several studies found strong evidence for IBE through local adaptation (Sunde et al. 2018, 2019, 2022). Key abiotic factors driving fine-scale adaptive population differentiation in pike include salinity (Jørgensen et al. 2010; Sunde et al. 2018, 2022; Arlinghaus et al. 2023), and local temperature (Sunde et al. 2019). Subpopulation-specific variation in early life history traits, growth rates, vertebra number and reproductive investment (Berggren et al. 2016; Tibblin et al. 2015, 2016) indicated the evolution of ecotypes with limited gene flow.

The literature on coastal pike often emphasizes two ecotypes: A brackish resident, adapted to reproduce in salinities up to 10 PSU (Arlinghaus et al. 2023; Jørgensen et al. 2010; Sunde et al. 2018), and an anadromous ecotype that forages in coastal sites but returns to freshwater for reproduction (Arlinghaus et al. 2023; Larsson et al. 2015; Müller et al. 1986). This dichotomy mirrors ecotype literature in various fish species, such as benthic vs. pelagic (e.g., Blain et al. 2023), limnic vs. marine (e.g., Kusakabe et al. 2017) or migratory vs. resident (e.g., Olsson et al. 2006). However, intermediary phenotypes with flexible habitat use between freshwater and brackish water have repeatedly been reported in coastal fishes (Almeida et al. 2023; Kerr et al. 2007, 2009; Limburg et al. 2001; Rohtla et al. 2020, 2023; Russell et al. 2022), challenging the dichotomous perspective and hinting at patterns of partial migration (Chapman et al. 2011). The presence of additional phenotypes has also been proposed in coastal pike populations (such as freshwater residents in tributaries, Birnie-Gauvin et al. 2019), but without genetic evidence to confirm them as ecotypes.

Previous studies on habitat use of coastal pike often focused on specific habitats (coastal habitats only in Engstedt et al. 2010; Jacobsen et al. 2017; or freshwater tributaries only in Engstedt et al. 2014; Tibblin et al. 2015), or specific life stages (natal origin, Möller et al. 2019, or adult movements, Dhellemmes et al. 2023a). Therefore, much of this past research only resolved short periods of individual life cycles, and only for subsets of coastal populations. High-resolution otolith microchemistry offers a powerful complementary tool to purely genetic studies (Trueman et al. 2012) by retrospectively identifying individual-level movements between freshwater and brackish habitats throughout their entire lives, for example through strontium to calcium ratios (Sr:Ca, Kafemann et al. 2000), and by reconstructing thermal environments experienced by individuals through oxygen isotope ratios ($\delta^{18}O$ values, Patterson et al. 1993). Lifelong individual assessments that cover all possible phenotypes, and link habitat use to genetic diversity and fitness surrogates, may reveal crucial aspects of the species' evolutionary history (Durif et al. 2023), and aid in detecting additional ecotypes (Stronen et al. 2022).

The study objective was to identify the full suite of behavioral phenotypes and genotypes present in a coastal pike population along a salinity gradient from freshwater tributaries to mesohaline lagoons, compare subpopulation-level fitness (using growth as a proxy), and identify ecotypes. To assess evolutionary divergence, individual-level thermosaline habitat use was matched to individual-level genotypic information, using genomic markers involved in adaptive divergence along a salinity gradient. We hypothesized that (1) thermosaline habitat use changes with size and age, with smaller pike inhabiting warmer, less saline habitats that become increasingly colder and more saline as individuals grow; (2) pike in brackish lagoons and their tributaries have evolutionarily diverged into multiple phenotypically and genetically distinct ecotypes; and (3) adaptation to salinity is a driver of ecotype evolution of pike in coastal brackish lagoons and adjacent tributaries.

Materials and methods

Study site and sampling

We studied the pike population in brackish lagoons surrounding Rügen island in the southern Baltic Sea, Germany. This interconnected system of lagoons and tributaries features strong environmental gradients in salinity and temperature. Freshwater from rivers (e.g., Recknitz, Barthe, Odra, Peene) mixes with brackish water from the Baltic Sea, forming oligohaline lagoons towards the west (Saaler Bodden, SAB, Bodstedter Bodden, BOB, Fig. 1) and southeast (Peenestrom, P, Achterwasser, AW, and Stettiner Haff, SH, Fig. 1). Additionally, numerous smaller creeks and drainage ditches, many of which were obstructed by pump sheds and shutters during melioration measures in the 1970s (Roser et al. 2023), drain into the lagoons (Fig. 1). Salinity levels increase from an annual average of 3–5 PSU in the western oligohaline lagoons to 8–10 PSU in the northwestern mesohaline lagoons (Western Rügen Bodden chain, WRBC, and Northern Rügen Bodden chain, NRBC, Fig. 1), and from 2 to 3 PSU in the southeastern oligohaline lagoons to 6.5 PSU in the northeastern mesohaline lagoon (Greifswalder Bodden, GB, Fig. 1). A temperature gradient spans from warmer average annual temperatures in the eutrophic lagoons in the southwest (SAB, BOB) and southeast (P), towards colder, mesotrophic lagoons in the north (WRBC and NRBC) (Fig. S1, Table S1).

To assess the full range of phenotypic diversity along the salinity and temperature gradient, we sampled 66 adult pike (> 95% maturation size, Palder et al. 2023) (43 females, 23 males, 40 – 126 cm total length, mean ± standard deviation, 82 ± 17 cm, 1 – 13 years in age) from the three major mesohaline lagoon chains WRBC ($N = 24$), NRBC ($N = 24$) and GB ($N = 18$), and 54 adult pike (36 females, 18 males, 42 – 106 cm, mean total length 77 ± 13 cm, 1 – 11 years in age) from adjacent freshwater tributaries (Fig. 1) over three consecutive years (2019 – 2022) for otolith microchemistry. To capture both resident and migratory phenotypes, we collected fish outside the spawning season (outside March and April) in the brackish lagoons, and during the spawning season (March and April) in the freshwater tributaries, when we assumed all phenotypes were present in a given habitat (Table S2). To ensure salinity differences between habitats were sufficient to be measured via otolith microchemistry, we excluded oligohaline lagoons. To sample the full range of freshwater residents, a small additional set of fish ($N = 11$) was captured in tributaries outside the spawning season in July 2019. To cover variability across larger spatial scales and different habitat types, tributaries of varying size and location were sampled: Larger rivers Barthe ($N = 23$) and Peene ($N = 5$), medium-sized creeks Sehrowbach ($N = 20$) and Ziese ($N = 5$), and two small drainage ditches, Neuendorfer Hechtgraben (NHG, $N = 3$) and Badendycksgraben (BKG, $N = 2$, Fig. 1). To mitigate gear-induced bias on size and age structure, multiple gears were employed (Wilson et al. 2015): Gill nets, fyke nets and angling in brackish lagoons, as well as electrofishing in freshwater tributaries (Table S2). Fish were sampled by the research team and by contracted fishers, measured (total length, mm), internally sex determined, fin clipped for genetic analyses, and sagittal otoliths were retrieved. To represent different age classes for lifelong phenotypic assessments, pike were selected randomly in a length-stratified manner. We aimed for an equal sex ratio at 5 cm size class intervals and equal sample sizes for each lagoon chain and tributary. Sampling limitations and sex-dimorphic growth (Casselman 1995) did ultimately not allow for an equal sex ratio (Figs. S2, S3). Low capture rates did not allow for length-stratified sampling in all tributaries, so tributary samples were pooled for some analyses (Table S2). However, we acquired length-stratified samples in two tributaries draining into two different lagoons (Sehrowbach and Barthe, Table S2), and supplemented samples from the other tributaries to cover the spatial gradient of freshwater tributaries in the region (Fig. 1).

To assess genetic diversity present in the lagoon system at the individual level, we sampled 1514 individuals for which fin clips were collected non-lethally via cooperating fishers and anglers and by the research team across the entire salinity gradient (including oligohaline lagoons) and all major tributaries (Fig. 1). In addition, 6 fish were collected from a freshwater lake (Kleiner Döllnsee) roughly 250 km to the south of the study system. All fish were individually genotyped (see below). For a subset of pike where both otolith microchemistry and genotype information was available ($N = 101$), data were used for phenotype-genotype matching as described below.

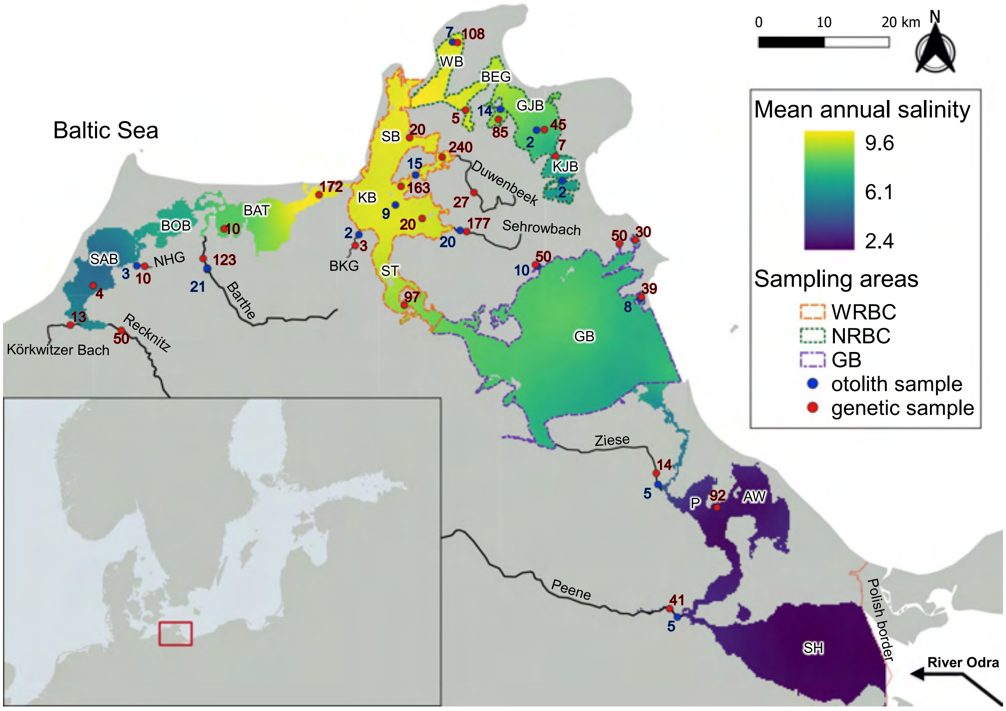


Fig. 1 Capture locations of northern pike (*Esox lucius*) between July 2019 and April 2022 around Rügen island, Germany. Numbers highlighted in blue indicate the number of pike captured for otolith microchemistry (total $N = 120$) at the respective locations, numbers highlighted in red indicate the total number of genetic samples (total $N = 1514$) from a location. Major brackish lagoon chains used for otolith sampling are outlined in color: *WRBC* Western Rügen Bodden Chain, *NRBC* Northern Rügen Bodden Chain, *GB* Greifswalder Bodden. Labels with white text buffer are referring to brackish lagoons, labels without text buffer to freshwater tributaries. Single lagoon abbreviations (from west to east): *SAB* Saaler Bodden, *BOB* Bodstedter Bodden, *BAT* Barther Bodden & Grabow, *KB* Kubitzer Bodden, *SB* Schaproder Bodden, *ST* Strelasund, *WB* Wieker Bodden, *BEG* Breeger Bodden, *GJB* Großer Jasmunder Bodden, *KJB* Kleiner Jasmunder Bodden, *P* Peenestrom, *AW* Achterwasser, *SH* Stettiner Haff. Tributary abbreviations: *NHG* Neuendorfer Hechtgraben, *BKG* Badendycksgraben

Otolith microchemistry

To assess the lifelong thermal environment experienced by each individual fish, intraotolith δ^{18}O (‰ relative to Vienna Pee Dee Belemnite, VPDB) values were determined at 35 µm intervals along transects from the otolith core to the outer edge, covering all visible year rings (annuli) on transverse thin sections of sagittal otoliths with secondary ion mass spectrometry (SIMS) at the GeoForschungsZentrum (GFZ), Potsdam. To resolve the lifelong saline environment, Sr:Ca ratios (mg/g) were determined at GEOMAR Helmholtz Centre for Ocean Research Kiel with laser ablation inductively coupled plasma mass spectrometry (LA-ICPMS), at 5.5 µm intervals within the same core–edge transects used for SIMS. An average of 40 combined elemental determinations per individual otolith equated to an average spatial resolution of 14 values per annulus, achieving sub-monthly temporal resolution. To correct δ^{18}O values for salinity-induced effects (Darnaude et al. 2014), we extracted residuals from a linear regression of δ^{18}O on Sr:Ca values from the same location on the otolith. δ^{18}O residuals were then assumed to reflect lifelong individual variation in the thermal environment. Age, annual otolith growth increments and radius of each otolith were determined to estimate the growth rate as per Rittweg et al. (2024). To avoid back-calculation assumptions, growth analyses were conducted on otolith annual increments (supplement, section B).

Analysis of otolith transects

We used individual-level salinity and thermal metrics to identify habitat use patterns in pike. We applied dynamic time warp (DTW) clustering on individual elemental transects of Sr:Ca and δ^{18}O residuals, pooling samples from brackish lagoons ($N=66$) and tributaries ($N=54$). We performed an agglomerative hierarchical clustering following Hegg and Kennedy (2021), using Wards distance with a 5% slanted band window in the R package dtwclust (v5.5.10, Sarda-Espinosa 2022). A range of clustering solutions (number of clusters $k=2-10$) were tested, with the ideal number of clusters determined by a majority vote from six internal cluster validity indices (Barbour et al. 2023). Dynamic time warp clustering may result in very fine-grained cluster solutions, as both the shape and mean values of a time series are evaluated (Hegg and Kennedy 2021). To account for clusters of fish distinguished solely based on differences in mean values between habitats that were otherwise ecologically similar (such as migratory fish from streams draining into lagoons of different average salinity, or brackish resident fish differing in mean δ^{18}O residuals due to differences in mean temperature between lagoons), we grouped the resulting clusters further into a smaller set of ecologically informative groups, which we interpreted as behavioral phenotypes. To that end, a decision framework, grouping by capture location (e.g., pike captured in tributaries during spawning could not be brackish residents), natal origin (e.g., pike with Sr:Ca values corresponding to brackish water in the otolith core could not be freshwater resident), and lifelong habitat use (e.g., oscillations in Sr:Ca or δ^{18}O residuals indicated habitat shifts), was applied (supplement, section C). To test whether these final behavioral phenotypes accurately represented natal (first year), early (second year) and later life (all remaining years) habitat use, we tested the reproducibility of behavioral phenotype assignments from average values of Sr:Ca and δ^{18}O for the different life stages using jackknife cross-validation (MASS package, v7.3.57, Venables and Ripley 2002). The frequency distribution of behavioral phenotypes across capture locations was then assessed with a X^2-test.

Genetic population structure

To identify genotypes, we developed a genotyping assay based on a panel of 33 single nucleotide polymorphism (SNP) markers, targeting previously identified genomic candidate regions with maximal differentiation. To identify candidate genomic regions of maximal allele frequency difference that were likely involved in adaptive population divergence, we screened sequences of 11 DNA pools, representing samples of putative brackish, putative freshwater and putative anadromous populations by capture location (Roser et al. 2023), using whole-genome sequencing. Genes associated with these regions and their functions were identified based on an annotated pike genome (GCF_011004845.1, NCBI, 2020). Next, we individually genotyped all 1,514 pike, including 101 pike ($N=58$ brackish, $N=43$ tributary) for which both behavioral phenotype and genetic data were available. We used STRUCTURE (Pritchard et al. 2000) to determine the most likely number of genetic clusters and extract individual assignment probabilities to each genetic cluster. A PERMANOVA (vegan package, v2.6–2, Oksanen et al. 2022) tested the association between genotype and behavioral phenotypes, using assignment probabilities to the four genotypes as dependent variables. To assign discrete individual genotypes for frequency testing, an assignment probability threshold of 0.7 (Austrich et al. 2020; Skey et al. 2023) was applied, which offered a compromise between retaining individuals in the sample and applying a conservative threshold. We also tested the association of genotype, phenotype, and capture location with X^2-tests. Behavioral phenotypes that differed significantly in their genotype assignment probability from all others, i.e., represented phenotypically and genetically distinct entities, were interpreted as ecotypes in the sense of Stronen et al. (2022).

Growth analyses

To examine whether behavioral phenotypes and genotypes differed in age-specific growth and in response to thermosaline niche, we fitted linear mixed effect models to annual otolith increments. Behavioral phenotype, genotype, average annual δ^{18}O residual as thermal proxy, average annual Sr:Ca as salinity proxy, age and sex were fixed effects, with a quadratic term for age, as growth slows down with age (von Bertalanffy 1938). Sex is a known predictor for growth in pike, with females growing larger than males (Casselman 1995). Individual ID was a random predictor, to account for the repeated measures design. To test for differences in age-specific growth rate, we included interactions between behavioral phenotype/genotype (run in separate models) and age. The model was run using restricted maximum likelihood estimation (lme4 & lmerTest packages, v. 1.1.30 and 3.1.3, Bates et al. 2015), and log-likelihood ratio (LLR) test for significance. Model assumptions were assessed graphically.

To infer lifelong growth performance, we estimated individual-level von Bertalanffy growth functions (von Bertalanffy 1938) separately for behavioral phenotypes, genotypes, and ecotypes, in a hierarchical Bayesian approach (Stan, version 2.21.0). Otolith radius R at age t was estimated

$$R_{(t,i)} = R_{\infty,i}\left(1 - e^{-k_i(t_i - t_{0,i})}\right),$$

with $R_{t,i}$ as the radius of fish i at age t. $R_{\infty,i}$ is the theoretical maximum radius, k_i is the Brody growth completion coefficient, t_i is the estimated age, and $t_{0,i}$ is the age at which radius was zero for fish i. Radii at ages were nested within individuals, and individuals were nested within phenotypes/genotypes. Parameters of the models were assumed to be gamma-distributed with phenotype/genotype-specific mean and precision. Convergence problems and autocorrelation were assessed graphically (supplement, section F). Non-overlapping credibility intervals (95%) were interpreted as significant differences in lifetime growth among behavioral phenotypes, genotypes, or ecotypes.

Results

Behavioral phenotypes

Time-series clustering identified four clusters as the best solution for the lagoon sample and six clusters for the tributary sample. In the tributary sample, several clusters differed only in later-life Sr:Ca values, while in the lagoon sample, several clusters differed only in mean $\delta^{18}O$ residuals, but not in the shape of their lifelong trajectories (Figs. S4, S5). To discern general habitat use patterns, clusters were further grouped based on natal origin, capture location and thermosaline history (supplement, section C). Through this approach, we identified four distinct behavioral phenotypes (Fig. 2):

(i) Freshwater residents ($N=27$): Born in freshwater, these individuals exhibited low Sr/Ca values throughout life, suggesting freshwater residence, and a shift from warm (lower $\delta^{18}O$ values) to colder (higher $\delta^{18}O$ values) habitats with age (Fig. 2A).

(ii) Anadromous individuals ($N=21$): Born in freshwater, these individuals oscillated between brackish and freshwater habitats in later life, with an ontogenetic shift from warm juvenile to colder adult habitats (Fig. 2B).

(iii) Brackish residents ($N=44$): Born in brackish water, these individuals displayed high lifelong salinity, no freshwater signal and a weak ontogenetic shift from warm juvenile to colder adult habitats (Fig. 2D).

(iv) Cross-habitat phenotype ($N=28$): Comprising pike captured from both freshwater tributaries and brackish lagoons, this phenotype had no clear freshwater or brackish origin. It instead exhibited intermediate lifelong salinity, a distinct ontogenetic shift from warm juvenile to colder adult habitats, and oscillations in salinity above the freshwater threshold (Fig. 2C).

These four behavioral phenotypes accurately reflected habitat use across life stages, with a high reproducibility rate based on life stage-specific Sr:Ca and $\delta^{18}O$ residual values (82% correct jackknife reclassification). The ratio of males to females was constant across the behavioral phenotypes. In the lagoon sample (by capture location), 44 individuals (67%) were identified as brackish residents, 17

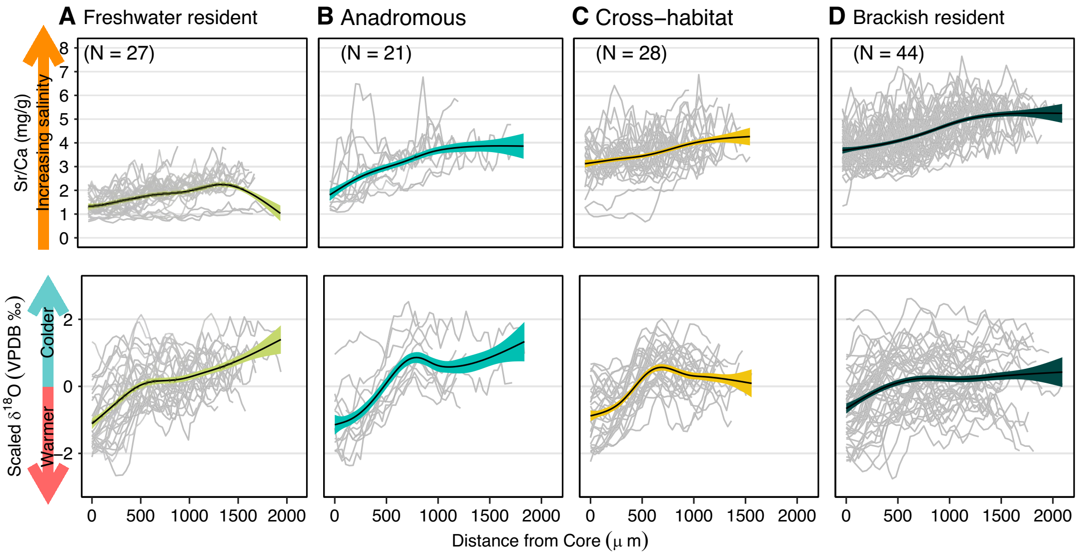


Fig. 2 Behavioral phenotypes identified in northern pike (*Esox lucius*, $N=120$), sampled between July 2019 and April 2022 from brackish lagoons and several freshwater tributaries around Rügen island, Germany. Upper panels show individual lifelong Sr/Ca values in grey in mg/g, fitted with a GAM smoothing Line. Lower panels show individual lifelong $\delta^{18}O$ residuals in transparent grey fitted with a GAM smoothing line. The mean of the GAM smoother is shown as black line, colored areas depict 95% confidence intervals

(26%) as cross-habitat, and 5 (7%) as anadromous. For the tributary sample, the timing of sampling was important. All individuals captured in tributaries outside spawning season (July 2019) were classified as freshwater residents (*N* = 11, Table S2), while those sampled during spawning season (*N* = 43) included relevant proportions of anadromous (N = 16, 37%) and cross-habitat types (*N* = 11, 26%), in addition to freshwater residents (*N* = 16, 37%, Fig. 3). The 11 individuals captured in tributaries outside of spawning season were omitted from frequency distribution tests. Frequency distributions of behavioral phenotypes of the remaining fish (*N* = 109) followed the salinity gradient ($\chi^2 = 9.54$, df = 2, $p = 0.008$): Fish captured from higher salinity lagoons were more likely brackish residents, while frequencies of cross-habitat and anadromous pike significantly increased from higher salinity to lower salinity lagoons and freshwater tributaries (Fig. 3).

Genotypes

A genome-wide screen of 11 pooled sequence samples of pike revealed 33 candidate loci (supplement, section D, Table S4). Five SNP markers with high diagnostic potential between brackish water and freshwater samples were tightly associated with osmoregulatory genes, suggesting salinity contributed to the divergence (Table S4). Known functions of other candidate genes have not been associated with ecotypes in fishes yet (Table S4). STRUCTURE analysis revealed $k = 4$ clusters as the best solution (Fig. 4). We called these clusters putative freshwater genotype, putative anadromous genotype and two putative brackish water genotypes brackish 1 and 2. Distribution of genotypes was correlated with capture location: The two putatively brackish genotypes (*N* = 13 for brackish 1; *N* = 22 for brackish 2) had mostly been captured in brackish lagoons (92%). Putatively freshwater genotypes (*N* = 19) had mostly been captured in the larger rivers Peene and Barthe (84%), and putatively anadromous genotypes (*N* = 17) had mostly been captured in the smaller tributaries Sehrowbach and Ziese (76%) ($\chi^2 = 81.84$, df = 12, $p < 0.0001$, Fig. S12). 28 individuals did not reach the 0.7 assignment threshold and remained unassigned, suggesting they were related to more than one genotype.

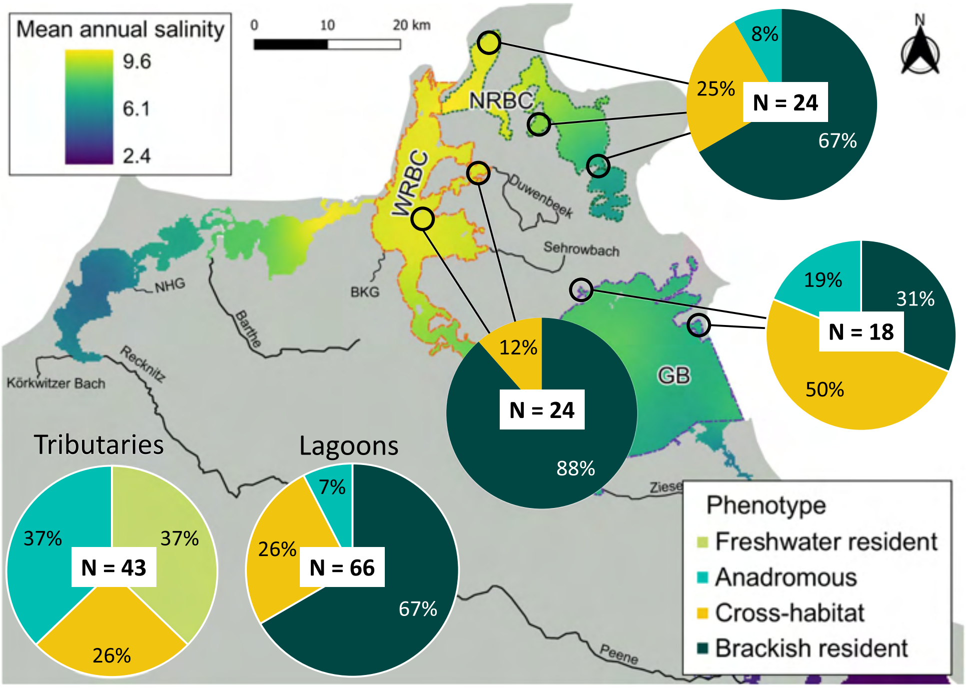


Fig. 3 Distribution of behavioral phenotypes of northern pike (*Esox lucius*, *N* = 120), sampled between July 2019 and April 2022 in brackish lagoons and freshwater tributaries around Rügen island, Germany. *NRBC* North Rügen Bodden chain, *WRBC* West Rügen Bodden chain, *GB* Greifswalder Bodden, *NHG* Neuendorfer Hechtgraben, *BKG* Badendycksgraben. The two lower pie charts on the left represent the pooled samples for freshwater tributaries and brackish lagoons

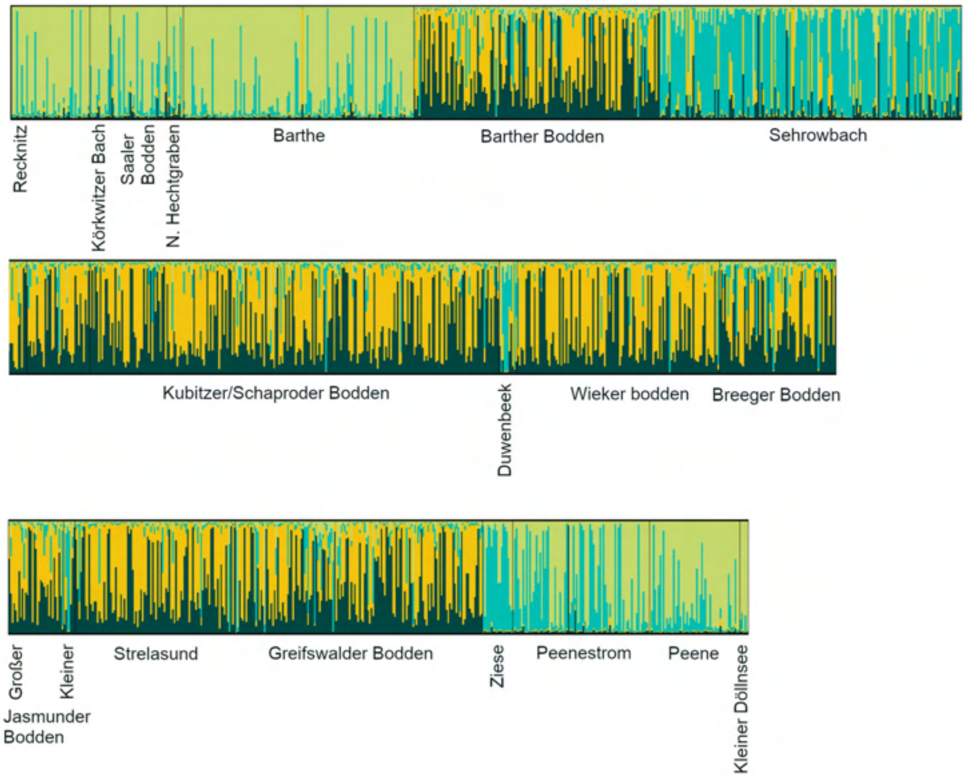


Fig. 4 STRUCTURE plot of individual northern pike (*Esox lucius*, $N = 1514$), sampled between July 2019 and April 2022 in brackish lagoons and freshwater tributaries around Rügen island, Germany. Each vertical segmented line represents an individual pike. Sampling areas are ordered according to geographic location from west to east, and correspond to the sampling areas of Roser et al. (2023), described in detail in supplement, section D. The plot shows the best-fitting solution of $k = 4$ genetic clusters. Yellow and dark green corresponds to the putative brackish clusters brackish 1 and brackish 2, turquoise corresponds to the putative anadromous cluster, light green corresponds to the putative freshwater cluster

Age-specific and lifelong growth performance

The best performing age-specific growth model included *age* (continuous), *sex* (factor, 2 levels male/female), yearly mean δ^{18}O residuals ($\delta^{18}O_{res}$, continuous) as thermal marker, z-scored yearly mean Sr:Ca (Sr, continuous) as salinity marker, an interaction term between *age* and *behavioral phenotype* (factor, 4 levels) and the random effect of individual ID (*1|ID*, 120 groups). Genotype was not a significant predictor of growth (LLR = 12.45, $p = 0.26$, Fig. S13), and was therefore not included in the final model.

The model,

$$\log_{10}\text{Increment} \sim \text{age} + \text{age}^2 + \text{sex} + \delta^{18}O_{res} + Sr + \text{age} \times \text{phenotype} + (1|ID),$$

explained 78.9% of the variance in otolith increments of the 120 pike individuals, 77.3% was explained by fixed predictors (Table 1). Age and sex were significant predictors: As expected, fish grew slower with age, and females grew faster than males (Table 1). Relative temperature ($\delta^{18}O_{res}$) was a significant predictor, where warmer relative temperature led to faster growth (Table 1). This effect appeared to be mainly driven by the early growth phase and diminished as individuals grew older (Fig. 5). Salinities exceeding the population mean, assessed by Sr:Ca z-scores, had a negative effect on pike growth, consistent across the whole age range (Table 1; Fig. 5). Pike behavioral phenotypes showed different growth performance at different ages, as indicated by a significant interaction between phenotype and age. In early life, freshwater residents grew slower, and cross-habitat types grew faster compared to the other phenotypes (Table 1). However, growth differences levelled out in later life (Fig. 6). We found no differences in lifelong growth between behavioral phenotypes, as 95% credibility intervals overlapped between phenotype-specific von Bertalanffy

Table 1 Effects of fixed and random predictors on a linear mixed effects model of $\log_{10}$-transformed otolith increment widths of northern pike ($N = 120$), sampled from brackish lagoons and freshwater tributaries around Rügen island in Germany between July 2019 and April 2022

$\log_{10}$-transformed Increment width (marginal $R^2 = 0.77$; conditional $R^2 = 0.79$)[1]				
Predictors	Estimate (± SE)	*t*-value	LLR	*p*-value
Intercept	2.76 (0.03)	85.67		
Age	−0.15 (0.01)	−15.13		
Age^2	**0.01 (0.00)**	**12.90**	**142.08**	**< 0.001 *****
Mean d18O residuals	**−0.03 (0.01)**	**−4.74**	**20.79**	**< 0.001 *****
Mean Sr/Ca (z-score)	**−0.04 (0.01)**	**−3.19**	**9.72**	**< 0.01 ****
Phenotype [BW resident]	−0.02 (0.03)	−0.68		
Phenotype [FW resident]	−0.08 (0.03)	−2.71		
Phenotype [Cross-habitat]	0.04 (0.03)	1.07		
Sex [male]	**−0.03 (0.01)**	**−2.62**	**6.84**	**< 0.01 ****
Lifeyear * phenotype [BW resident]	**0.01 (0.01)**	**0.63**	**388.13**	**< 0.001 *****
Lifeyear * phenotype [FW resident]	**0.01 (0.01)**	**1.52**	**388.13**	**< 0.001 *****
Lifeyear * phenotype [Cross-habitat]	**0.01 (0.01)**	**0.11**	**388.13**	**< 0.001 *****
Random Effects	Variance (± SD)	t-value	LLR	p-value
ID	**0.001 (0.03)**		**4.20**	**0.04**
Residual	0.012 (0.11)			

SE Standard error, *SD* Standard deviation, *LLR* Log-likelihood ratio. Significant effects are shown in bold

[1] Marginal R^2 describes the proportion of the total variance explained by fixed effects in the model; conditional R^2 describes the proportion of total variance explained by fixed and random effects combined in the model

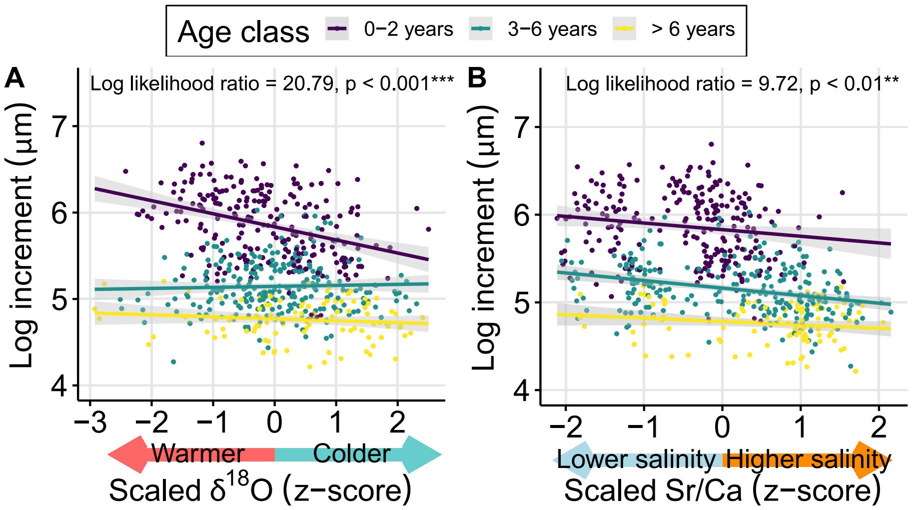


Fig. 5 Effect of relative temperature (**A**, salinity-corrected $\delta^{18}O$ values) and relative salinity (**B**, Sr/Ca values) on growth increments of northern pike (*Esox lucius*, $N = 120$), captured in brackish lagoons and freshwater tributaries around Rügen island between July 2019 and April 2022. Individuals were grouped into age categories: Early life (0–2 years), adult (3–6 years) and late adult (> 6 years), to visualize age- and stage-dependent effects. Colored lines represent the linear regression line between the predictor variable and the growth increments of each subgroup, and shaded areas around the regression lines depict the 95% confidence intervals. Note that no pairwise comparisons were run between discrete age classes in the model

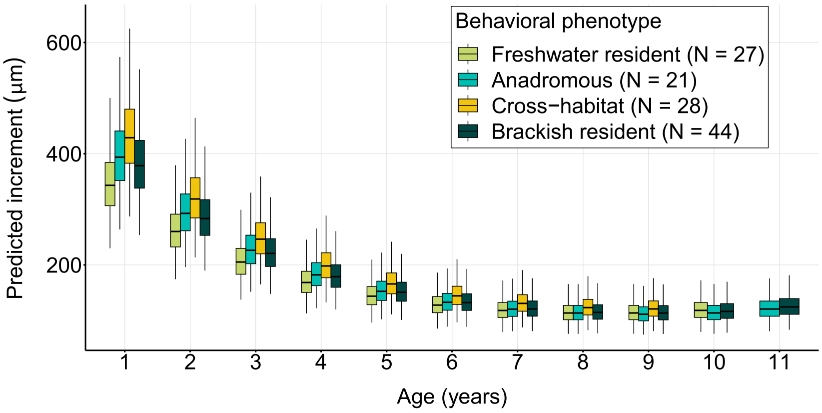


Fig. 6 Predicted otolith increments for four behavioral phenotypes calculated from growth data of northern pike (*Esox lucius*, $N = 120$), sampled between July 2019 and April 2022 in the brackish lagoons and several freshwater tributaries around Rügen island in Germany. Boxes depict the median, lower, and upper quantile of the data, with vertical lines depicting the 95% confidence interval

Table 2 Phenotype-specific von Bertalanffy growth parameters of northern pike (N = 120), sampled between July 2019 and April 2022 from brackish lagoons and freshwater tributaries around Rügen island

Phenotype	L_∞	k	t_0
Freshwater resident	2.61 – 3.18 (2.85)	0.10 – 0.13 (0.12)	−0.77 to −0.46 (−0.62)
Anadromous	2.60 – 3.09 (2.85)	0.11 – 0.14 (0.12)	−0.77 to −0.48 (−0.63)
Cross-habitat	2.61 – 3.31 (2.96)	0.10 – 0.14 (0.12)	−0.76 to −0.52 (−0.64)
Brackish resident	2.52 – 2.87 (2.68)	0.10 – 0.12 (0.11)	−0.93 to −0.69 (−0.81)

Parameter values are given in the interquartile range from 2.5% to 97.5% credible parameter space. Values in brackets denote the median parameter estimate

parameter estimates for all phenotypes (Table 2; Fig. 7). Similarly, average lifelong growth showed no difference between genotypes, or ecotypes (Tables S5, S6; Figs. S14, S15).

Matching behavioral phenotypes with genotypes to infer ecotypes

Behavioral phenotypes exhibited significantly different assignment probability distributions to the four genotypes (PERMANOVA with 9999 permutations, $F = 19.55$, $p < 0.001$), with behavioral phenotype explaining 37.8% of the variance in genotype assignment probabilities. Freshwater residents ($N = 21$) and anadromous phenotypes ($N = 11$) were related to both putative anadromous and freshwater genotypes, with no significant differences in assignment probabilities (pairwise PERMANOVA, fdr-adjusted pairwise Wilks λ tests, $p = 0.20$), but not to the putative brackish water genotypes (pairwise PERMANOVA, $p_{\text{brackish}} = 0.0015$, Fig. 8; S11). In contrast, brackish resident phenotypes (N = 39) were genetically distinct from all other phenotypes and predominantly comprised of the putative brackish genotypes 1 and 2 (pairwise PERMANOVA, $p_{\text{anadromous}} = 0.0015$; $p_{\text{freshwater}} = 0.0015$; $p_{\text{cross-habitat}} = 0.0096$) (Fig. 8; Fig. S11). Cross-habitat phenotypes (N = 28) comprised a mixture of putative anadromous and both brackish genotypes, with little relation to the putative freshwater genotype (Fig. 8; Fig. S11). The genotypic composition of the cross-habitat phenotype was significantly different from all others (pairwise PERMANOVA, $p_{\text{anadromous}} = 0.0015$; $p_{\text{brackish}} = 0.0096$; $p_{\text{freshwater}} = 0.0015$). No obvious patterns in behavioral phenotype expression (Fig. 8; Fig. S11), or capture location (Fig. S12), were evident for the two divergent putative brackish genotypes. Therefore, phenotype-genotype matching suggested the presence of three ecotypes: (i) a brackish ecotype encompassing two genotypes with limited gene flow and life-time residence in brackish areas, (ii) a freshwater ecotype expressing either freshwater residency or anadromy, and (iii) an intermediary cross-habitat ecotype adapted to intermediate salinity and limited reliance on freshwater. Lifelong growth of the three ecotypes was not significantly different (Fig. S15).

Discussion

We integrated otolith microchemistry data on habitat use and migration behavior with genetic differentiation in a freshwater-adapted predatory fish, to test whether environmental gradients in salinity and temperature promote

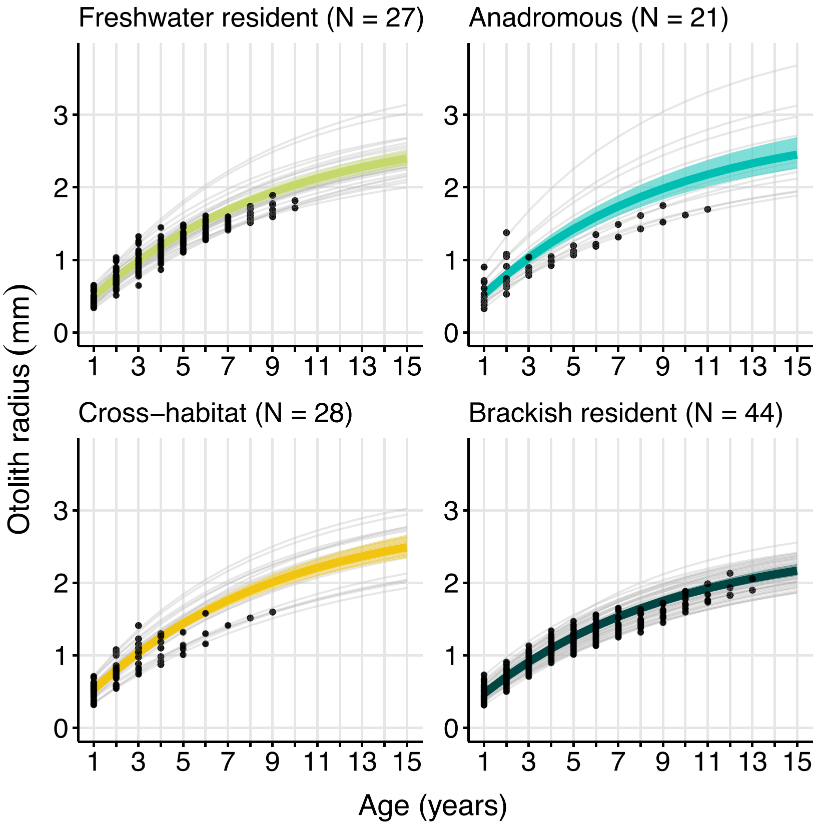


Fig. 7 Von Bertalanffy growth curves of four behavioral phenotypes described in northern pike (*Esox lucius*, $N = 120$), sampled between July 2019 and April 2022 in brackish lagoons and freshwater tributaries around Rügen island, Germany. Grey lines represent individual-level growth curves. Colored lines represent mean radius-at-age of phenotypes, with shaded areas indicating 95% credible intervals

ecotype diversification in a brackish lagoon ecosystem. Our findings supported our first hypothesis, revealing significant ontogenetic variation in thermosaline niches among pike. They showed a preference for warmer and less saline habitats in early life, transitioning to colder, more saline environments as adults. In response to our second hypothesis, we identified four behavioral phenotypes: Freshwater residents, anadromous individuals, brackish residents, and a previously unrecognized cross-habitat phenotype. While phenotype-genotype matching confirmed the evolution of three ecotypes, not all phenotypes exhibited clear genetic differentiation. Freshwater and anadromous phenotypes were genetically similar, and all genotypes expressed more than one behavioral phenotype. Our results imply a split between a freshwater/anadromous and a brackish-adapted ecotype, with a third, intermediary, cross-habitat ecotype connecting them. Supporting our third hypothesis, we found evidence of clear separation in behavioral phenotypes and genotypes along the salinity gradient of the brackish lagoons. Divergent functional candidate genes related to osmoregulation suggested the observed differentiation was, at least in part, driven by adaptation to salinity.

Interindividual variability in habitat use revealed diverse migration and habitat use behaviors in the coastal pike meta-population. While previous studies have described three behavioral phenotypes in coastal pike—brackish residents, anadromous, and freshwater residents (e.g., Birnie-Gauvin et al. 2019; Jacobsen et al. 2017; Möller et al. 2019; Nordahl et al. 2019)—we identified a fourth behavioral phenotype. This cross-habitat phenotype resembled intermediary behaviors connecting freshwater and marine realms reported in other coastal fishes (Almeida et al. 2023; Kerr et al. 2007, 2009; Limburg et al. 2001; Rohtla et al. 2020, 2023; Russell et al. 2022). Each behavioral phenotype likely faces specific trade-offs. Brackish residents avoid energetically costly spawning migrations and benefit from access to marine prey in the brackish lagoons (Winkler 1987). But they face risks of reproductive failure during high saline inflows (Sunde et al. 2018; Arlinghaus et al. 2023), and predation by top predators such as grey seals (*Halichoeres gryphus*) (Bergström et al. 2022; Olin et al. 2024). Freshwater residents also do not migrate and avoid the need for osmoregulatory adaptations. However, they may experience lower prey availability (Rohtla et al.

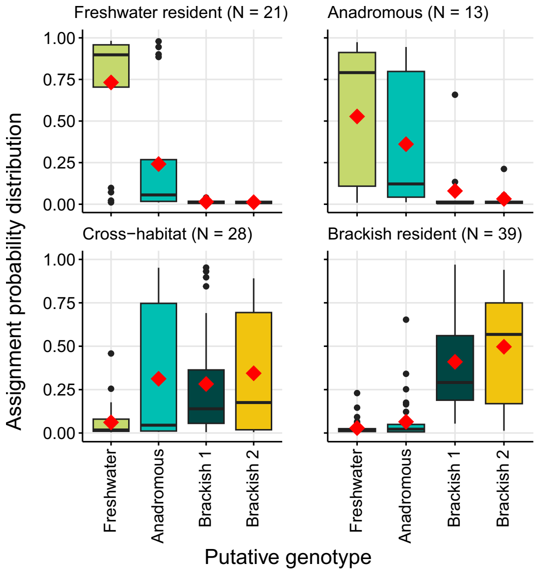


Fig. 8 Assignment probabilities to four genetic clusters identified by STRUCTURE for four behavioral phenotypes described in northern pike (*Esox lucius*, $N = 101$), sampled from brackish lagoons and freshwater tributaries around Rügen island between July 2019 and April 2022. Boxes represent upper and lower quantile along with median assignment probability value per genotype, vertical lines represent the 95% confidence intervals, single points represent outlier values, and red diamonds indicate mean assignment probability per genotype

2012) and local environmental challenges, such as varying water levels and anoxic conditions in highly modified tributaries (Roser et al. 2023), reducing early growth. Anadromous individuals spawn in freshwater and benefit from productive brackish environments after outmigration (Rohtla et al. 2012). In turn, they face energy costs and increased mortality risk during migrations (Haugen et al. 2006). Cross-habitat individuals select intermediary habitats for spawning, such as sheltered bays with freshwater influence (Flink et al. 2023) and river mouths (Dhellemmes et al. 2023b; Lukyanova et al. 2024), potentially avoiding extensive migrations. Their offspring can then benefit from less saline conditions while retaining access to brackish environments, resulting in rapid early growth. However, the absence of old individuals in this phenotype suggests increased adult mortality, potentially offsetting early growth advantages (Roff 1988).

The positive effect of temperature on pike growth, particularly in early life, aligns with previous research (Pagel et al. 2015), suggesting that young pike thrive in sheltered habitats that warm up faster (Pursiainen et al. 2021). All phenotypes except freshwater residents experienced increasing salinities with age, which reflects higher osmoregulatory capacity in adults (Varsamos et al. 2005). This allows older and larger individuals to explore more saline habitats with a wider prey range (Winkler 1987). However, there is an upper limit to salinity adaptation (Jacobsen and Engström-Öst 2018), as higher salinities negatively affect growth, likely due to the energetic costs of osmoregulation in fluctuating salinities (Bœuf and Payan 2001). Our findings collectively suggest that pike undergo ontogenetic habitat shifts from less saline, warm habitats to open, more saline habitats, similar to habitat shifts from shallow to deeper habitats known from pike in lakes (Casselman and Lewis 1996), but also indicate that higher salinities can reduce growth despite evolutionary adaptations to brackish environments.

Our study builds upon prior research on coastal pike (e.g., Engstedt et al. 2010, 2014; Möller et al. 2019, 2020; Tibblin et al. 2015, 2016; Nordahl et al. 2019; Sunde et al. 2018, 2019, 2022) by linking behavioral phenotypes with underlying genotypes along a salinity gradient. Genetic differentiation among behavioral phenotypes suggests evolutionary adaptations to salinity, consistent with earlier findings (Arlinghaus et al. 2023; Jørgensen et al. 2010; Lukyanova et al. 2024; Sunde et al. 2018, 2022). In addition, IBD (Möller et al. 2020; Nordahl et al. 2019), adaptations to other ecological factors, such as temperature (Sunde et al. 2019), and habitat alterations (Eschbach et al. 2021; Roser et al. 2023), i.e., IBR, may all have contributed to the observed patterns. For instance, the blocking of freshwater tributaries since the late 1970s in the study region (Roser et al. 2023) likely increased selection pressure for the evolution of cross-habitat pike. Differences in phenotypic and genotypic frequencies were particularly evident at the extremes of the salinity gradient, indicating salinity adaptation, i.e., IBE, was a major driver of differentiation, consistent with previous studies (Sunde et al. 2022). Unexpectedly, we identified two divergent, spatially overlapping genotypes within the brackish lagoons. The absence of thermosaline niche differentiation among the two brackish genotypes suggests sympatric coexistence. Previous telemetry work in our study area hinted at subtle differences in thermal microhabitat between the two brackish genotypes, but these differences were not statistically significant (Nolte et al. 2023). Mechanisms for the reproductive isolation between the two brackish genotypes remain unclear and may involve other ecological factors not resolved by our work.

Our study did not provide conclusive evidence for lifelong growth advantages between the behavioral phenotypes, genotypes, and ecotypes. Similar growth rates can facilitate coexistence (Kobler et al. 2009), as growth strongly correlates with fitness in pike (Haugen et al. 2006). However, despite comparable growth rates, different phenotypes and genotypes might still vary in reproductive fitness due to different breeding success in fluctuating environments (Bell

2010). Controlled common garden experiments using offspring from wild-captured parents, either pure or hybrids, as well as large-scale tracking and offspring assignments to parents could provide insights into the environment-dependent reproductive fitness variation of the various phenotypes, genotypes and ecotypes.

The presence of two well-defined ecotypes in freshwater and brackish habitats, linked by a third intermediary cross-habitat ecotype, aligns with the theory of habitat selection and ecotype evolution in variable environments (Rosenzweig 1974; Brown 1990). The overlap in behavioral phenotype expression between putatively anadromous and freshwater genotypes suggests a single freshwater-adapted ecotype, expressing migratory or resident behavior, which may depend on both environmental (Olsson et al. 2006) and genetic cues (Vainikka et al. 2023), consistent with predictions from partial migration theory (Chapman et al. 2011). Indeed, telemetry work on putatively anadromous pike in our study area revealed flexibility in migration behavior among years, with some individuals migrating into tributaries in one year, but remaining in estuaries during spawning time in the next (Dhellemmes et al. 2023b). Genetic differentiation between freshwater and putatively anadromous pike likely arose from local adaptation, exacerbated by isolation by distance, natal homing and spawning site fidelity to specific streams (Engstedt et al. 2014; Nordahl et al. 2019). The well-defined brackish resident ecotype has adapted to complete its entire life cycle in brackish habitats, and is known to show the highest reproductive fitness at intermediate salinities (Arlinghaus et al. 2023). The third, less defined cross-habitat ecotype, is an intermediate between freshwater/anadromous and brackish residency. This ecotype might be a response to extensive blockage of freshwater tributaries in the 1970s (Roser et al. 2023). These habitat alterations likely caused selection pressures for intermediate behavioral strategies that seek out low salinity areas for spawning, consistent with previous studies showing rapid adaptive divergence in response to anthropogenic habitat alteration in pike (Bekkevold et al. 2015; Eschbach et al. 2021). Therefore, the cross-habitat ecotype potentially evolved as a hybrid between anadromous and brackish lagoon genotypes that thrives in intermediate salinities. A discrepancy in the proportion of brackish residents (68%) in our work compared to previous studies in the same region (98.7%, Möller et al. 2020) can be explained by our identification of the cross-habitat ecotype.

Our results challenge the dichotomous categorization of pike into just two ecotypes along the Baltic coast, suggesting a range of individual habitat use and migration behaviors connect the two behavioral endpoints of freshwater and brackish residency. Behavioral extremes correspond with the extremes of the salinity gradient, consistent with partial migration theory (Cagnacci et al. 2011; Chapman et al. 2011). Adding to similar observations in other coastal fish species (Almeida et al. 2023; Kerr et al. 2007, 2009; Limburg et al. 2001; Rohtla et al. 2020, 2023), we suggest intermediary behaviors and partial migration patterns are a common and often overlooked occurrence in coastal fish populations. Conservation of the pike population requires protecting the whole suit of intrapopulation diversity, to retain portfolio effects of population productivity in the face of environmental change (Schindler et al. 2010). In light of stressors associated with climate change, eutrophication, flow disruption, and migration barriers in the region (Roser et al. 2023), anadromous phenotypes, already rare in the study region (Möller et al. 2019, 2020; Roser et al. 2023), might eventually go extinct, decreasing phenotypic diversity and resilience of coastal pike populations (Schindler et al. 2010).

Limitations

Our study system showed significant seasonal water δ^{18}O fluctuations due to evaporation during our study period (Aichner et al. 2022). However, these were consistent across the area and unlikely to impact our relative thermal proxy. Our sampling design for the otolith microchemistry did not cover the oligohaline lagoons and only two streams were sampled at depth, potentially underrepresenting freshwater phenotypes. But we found strong genetic similarities between oligohaline lagoons and freshwater tributaries, suggesting our sample likely captured the phenotypic diversity present in the system, despite this limitation. Further, anadromous fish might be in rivers only for restricted periods of times (days or weeks, Dhellemmes et al. 2023b), which might not be sufficient to be detected in otoliths. However, the temporal resolution of otolith transects, particularly in the early years, reached up to 40 combined determinations per annulus, which we deemed sufficient for detecting freshwater excursions even on weekly scales. In addition, the semi-random sampling design of our study prevented us from arriving at unbiased estimates of phenotypic composition at the different capture locations. Nonetheless, the result of phenotype frequency in response to the salinity gradient should be robust. Another limitation was our clustering approach, which might have obscured subtle patterns in juvenile and adult habitat use. However, high jackknife reproducibility (82%) of behavioral phenotypes indicated an accurate representation of habitat use across ontogenetic stages. Finally, a limited within-group sample size may have biased results on age-specific and lifelong growth, so that smaller differences remain undetected. Indeed, other research in the region suggests that the lifetime growth of freshwater residents may be lower than that of brackish residents (Rittweg et al. 2023), but we only detected this effect in the juvenile life stage.

Conclusions and implications

Our study suggests that a salinity gradient in lagoon ecosystems fostered intraspecific diversification of ecotypes with distinct realized thermosaline niches that show similar growth, indicating comparable fitness potential. Flexible migration and habitat use behavior, both across phenotypes but also ontogenetically, constitute an adaptation to variable local ecological factors and contribute to ecotype evolution. The notion of pike as stenohaline freshwater species that can be categorized into only two ecotypes in coastal habitats (anadromous vs. brackish resident) is challenged by our findings, suggesting the species can evolve intermediary migration and habitat use strategies, and complete its life cycle across a wider range of salinities. That said, the negative impact of above-average salinities on growth, as well as laboratory findings of reduced reproductive success at salinities exceeding 10 PSU in brackish-adapted pike (Arlinghaus et al. 2023), indicates an upper threshold for salinity tolerance in this species. From a conservation perspective, our findings highlight the importance of maintaining and, if possible, increasing access to freshwater tributaries through habitat restoration (Roser et al. 2023). This could maintain phenotypic and genotypic diversity and increase the resilience of the pike meta-population through portfolio effects (Schindler et al., 2010). Improving connectivity between brackish lagoons and freshwater tributaries can help sustain and increase the currently rare anadromous fish and would likely also be of use for the conservation and improvement of cross-habitat pike.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00442-024-05627-7.

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Author contribution statement TR, RA, CT, CW and AN conceived the ideas and designed the study; TR, MW, JF and SD collected data; TR, LT and SD analyzed data; TR wrote the manuscript with substantial input by RA; other co-authors edited the manuscript.

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Availability of data and material Data used for the analysis are available from https://doi.org/10.18728/igb-fred-908.0, R and Stan code used are available from https://github.com/Traveller-2909/Ecotype_analysis/.

Declarations

Conflicts of interest The authors declare that they have no conflicts of interest.

Ethics approval All applicable institutional and/or national guidelines for the care and use of animals were followed. Fish were sampled in accordance with permit 7308.2 of the Landesamt für Landwirtschaft, Lebensmittelsicherheit und Fischerei (LALLF MV). Sampling in national park Vorpommernsche Boddenlandschaft was carried out in accordance with permit 21/5320.142, Nationalparkamt Vorpommern, sampling in biosphere reserve Südost-Rügen was carried out in accordance with permit 5321.2/FM/SchnB.Nr.20002, Biosphärenreservatsamt. Sampling in nature reserves was carried out in accordance with permit 5328.1.99/654–19-40–3 of the Staatliches Amt für Landwirtschaft und Umwelt (STALU MV). Sampling of freshwater tributaries was carried out with permission by the Landesanglerverband Mecklenburg-Vorpommern e.V. (LAVB MV).

Consent to participate Not applicable.

Consent for publication Not applicable.

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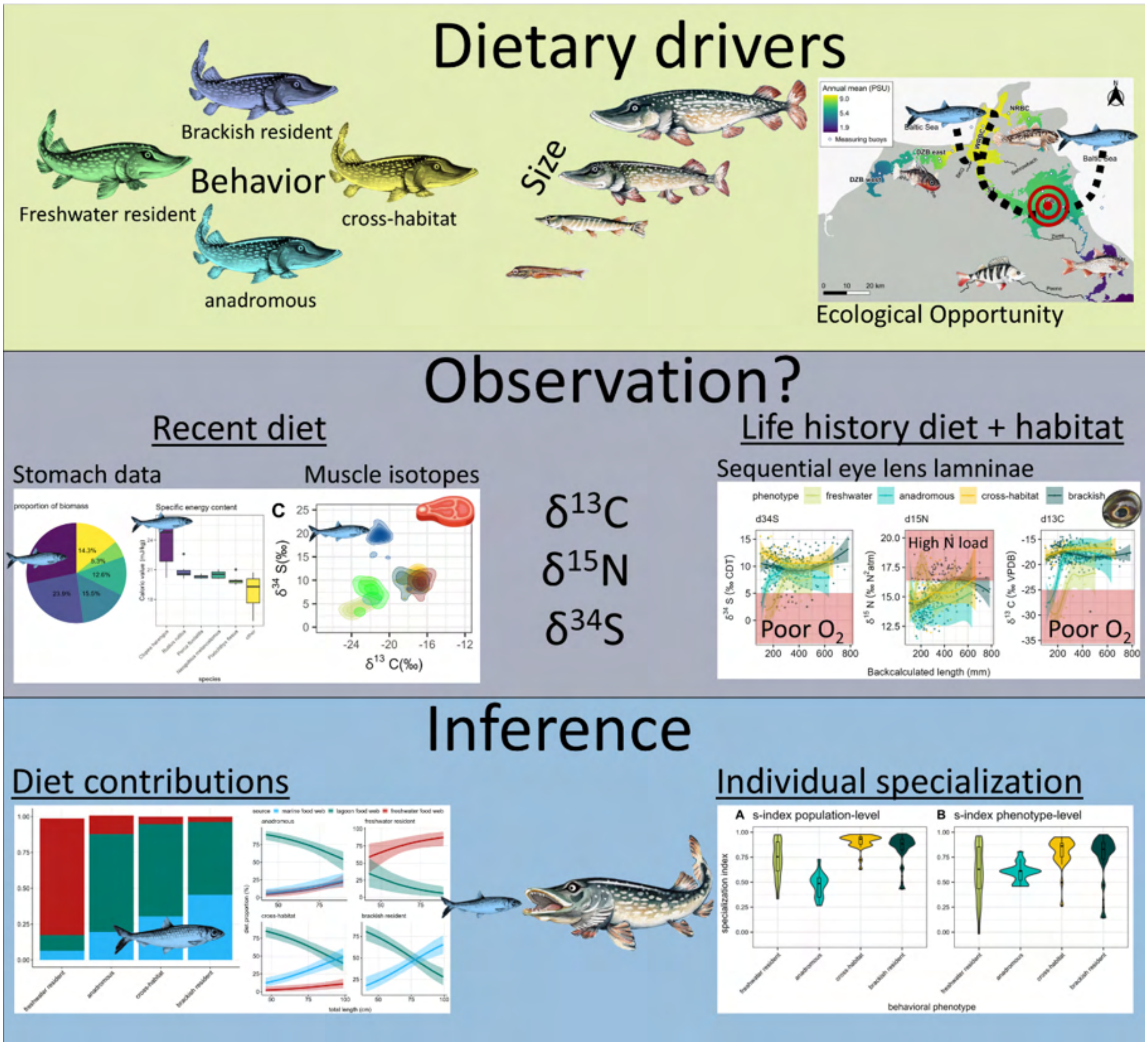

VII

Timo Rittweg, Clive Trueman, Tobias Goldhammer, Marlon Braun, Félicie Dhellemmes, Robert Arlinghaus, 2024, Resource specialization predicted by body size and behavioral phenotype benefits growth of northern pike (/) in coastal habitats, to be resubmitted

graphical abstract, Timo Rittweg

Eating with a grain of salt: Trade-offs and benefits of marine resource specialization for a freshwater predator (northern pike, *l*) in coastal habitats

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stract

1. Freshwater predators adapted to forage in brackish habitats can integrate marine and freshwater food webs, where individual specialization on high-energy marine prey could accelerate growth and thereby yield fitness benefits. Yet, foraging in saline habitats exposes individuals to osmoregulatory challenges, which can negatively affect growth.
2. We used a freshwater predator, northern pike (*l*), as a model to examine how four behavioral phenotypes with different spawning-related migration behavior, habitat use, and salinity adaptation navigate trade-offs between dietary specialization and habitat-associated costs. We identified prey items and resource use using stomach contents in 171 pike and stable isotope mixing models on muscle δ^{13}C, δ^{15}N and δ^{34}S values in 302 fish, along with calorimetry of prey species as index of prey quality. Consecutive eye lens laminae and their isotope values in 81 pike were used to quantify lifelong individual specialization and growth effects of dietary tracers and environmental co-variates.
3. Atlantic herring (*l ea a e*) constituted a key marine prey in pike stomachs, and this species revealed significantly greater energy content than lagoon or freshwater prey types. Body length and pike behavioral phenotype were important predictors of resource use, with larger and brackish-associated individuals showing higher marine resource use. Brackish-adapted individuals were also more specialized, while migratory (anadromous) and freshwater resident pike foraged more generalist across food webs. Despite specializations on energy-rich marine prey, brackish residents, on average, showed lower annual growth rates than migratory behavioral phenotypes up to an age of 6 and approximately 85 cm total length. High individual marine prey reliance correlated positively with individual growth rate, while exposure to high salinity levels, indicated by strontium-calcium ratios in otoliths, had a negative effect on growth rate.
4. Evolution of different habitat use patterns, along with adaptation to salinity, enabled a part of the pike population access to an energy-rich marine food web. However, spatiotemporal

variability of marine prey and osmoregulatory costs in brackish habitats suggest fundamental trade-offs associated with a brackish lifestyle.

5. Our study provides insights into the drivers of niche variation and individual specialization using high-resolution data of individual resource use. By coupling our findings to growth as a fitness surrogate, we elucidate life history tradeoffs associated with individual specialization of predatory freshwater fish in brackish habitats. We further demonstrate how a freshwater predator couples freshwater, lagoon, and marine food web in an estuarine system, implying successful management needs to adopt an ecosystem-based approach that considers food web interactions.

I. Introduction

Variation in diet and foraging niche is a common mechanism to reduce intraspecific competition in natural animal populations, which can foster intraspecific phenotypic diversification and ecotype evolution (Bolnick et al., 2003; van Valen, 1965). In mobile animals with complex life histories, such as fishes, dietary specialization is modulated by multiple interacting traits and is additionally affected by local environmental conditions (Felmy et al., 2022). For example, in most fishes, body size is positively associated with gape size, which decides what prey items can be ingested; therefore, changes in body size affect habitat choice, resource utilization and susceptibility to other gape-limited predators, resulting in growth/mortality tradeoffs (Werner et al., 1983, Werner & Gilliam, 1984). As fecundity and survival are both positively related to size in most fishes (Haugen et al., 2007; Barneche et al., 2018), fitness can be increased by decreasing mortality costs for each increment in size (Werner & Gilliam, 1984). Growth rates and fitness of fishes are often tightly linked to diet choice and prey quality (Armstrong & Schindler, 2011). Individual variation in foraging and habitat use behavior provides spatio-temporal overlap with different prey items, modulating dietary specialization through ecological opportunity (Mittelbach & Persson, 1998, Brodersen et al., 2015).

In variable environments like brackish estuarine systems, specialization and adaptation along multiple niche axes (e.g., diet, salinity and temperature) fosters intraspecific phenotypic and genotypic differentiation (Bell, 2010; Sunde et al., 2022; Costa-Pereira & Shaner, 2025; Doebeli & Dieckmann, 2003). In estuaries, adapted individuals may exploit a wide range of resources and benefit from temporal resource pulses of migrating marine species (Garman & Macko, 1998; Nolan et al., 2019; Winkler 1987), coupling different food webs (marine, estuarine and freshwater in inflowing rivers (Rezek et al., 2020; Stewart et al. 2022). Specialization on marine resource pulses can benefit growth, especially when prey abundance and quality are high (Armstrong & Bond, 2013; Furey et al., 2016), thereby reducing intraspecific competition (Svanbäck et al., 2008). This can enable coexistence of different phenotypes within a population, resulting in seemingly generalized populations with high individual heterogeneity in diet choice (i.e., niche variation hypothesis, Bolnick et al., 2007, Van Valen, 1965). However, while marine prey can offer a high-energy resource (Gross et al., 1988; MacAvoy et al., 2000), energetic costs of hypoosmotic regulation might counteract possible benefits to growth (Bœuf & Payan, 2001), creating substantial trade-off for freshwater predators in coastal habitats. A key open question addressed in this paper is whether access to marine prey can compensate the osmoregulatory costs freshwater predators with limited osmoregulatory capacity will face.

The brackish lagoons around Rügen island in the southern Baltic Sea, Germany (referred to as Bodden in the following, Figure), are a dynamic system of interconnected lagoons and tributaries (Schubert & Telesh, 2017). Western Baltic spring spawning herring (*l ea a e*) enter these shallow, oligo- to mesohaline lagoons in high abundances for spawning (Biester et al., 1978; Von Dorrien et al., 2013). Smaller abundances of fall-spawning herring (Von Dorrien et al., 2013), and other marine species, (e.g., garfish, *el e el e*, and flounder, *la t e*) also occur in the lagoons (Winkler, 1990). Marine prey items often hold higher nutritional value (Gross et al., 1988), potentially offering an energy-rich subsidy for freshwater predators in coastal sites, such as coastal northern pike (*l*) (Winkler 1987). Pike is a stenohaline, mesothermal freshwater predator that has adapted to brackish coastal habitats along the Baltic Sea (Sunde et al. 2022). Although subpopulations have managed to adapt to mesohaline coastal conditions, fertilization and larval survival drop at salinities exceeding 6-8 PSU (Arlinghaus et al., 2023, J rgensen et al., 2010), and growth rate of adults is also negatively associated with high salinity levels (Rittweg et al., 2024). This shows that despite physiological and behavioral adaptations, salinity constitutes a significant stressor for coastal northern pike . Salinity spikes in Bodden with openings to the Baltic Sea can regularly exceed 10 PSU (Arlinghaus et al. 2023), but these areas might also host a greater abundance of marine prey, which could compensate for osmoregulatory costs. Pike in the Bodden indeed show extremely fast growth and large terminal sizes (Rittweg et al., 2024) and therefore constitute an important target species of recreational and commercial fisheries (Arlinghaus et al., 2023).

The pike meta-population around Rügen comprises four behavioral phenotypes (Dhellemmes et al., 2023a; Roser et al., 2023; Lukyanova et al., 2024; Rittweg et al., 2024): Freshwater residents complete their whole life cycle in freshwater tributaries. Anadromous pike are born in tributaries and return to their natal stream for spawning. Cross-habitat pike display flexible habitat use between brackish and freshwater-adjacent habitats. Brackish residents complete their life cycle in high-saline brackish habitats. Bodden pike have been shown to feed on herring and other marine prey in the past (Winkler 1987), possibly contributing to their fast growth, but it is unknown to what extent different phenotypes rely on marine, lagoon and freshwater resources.

Marine resources are likely only accessible to certain behavioral phenotypes, offering opportunities to study the coupling of food webs and individual diet specialization. Most marine prey items are relatively large sized (e.g. herring or garfish spawners) or have a peculiar shape (e.g., flounder) that might allow mainly larger predators with large gape size ingest the prey (Nilsson & Brönmark, 2000). Migratory herring are predominantly found in open mesohaline habitats (Biester et al., 1978). Pike foraging efficiency on herring thus depends on gape size and osmoregulatory capacity, which should be linked to habitat choice of high saline habitats. Therefore, mainly larger individuals foraging in mesohaline brackish habitats (Mittelbach & Persson, 1998; Varsamos et al., 2005) are expected to specialize on marine prey. Physiological adaptations to differently saline habitats should affect access to marine resources for all behavioural phenotypes, possibly fostering individual specialization in phenotypes adapted to mesohaline conditions, while freshwater residents would be expected to rely more or exclusively on freshwater prey. Migratory pike phenotypes should integrate over multiple habitats, potentially resulting in mixed resource use and opportunistic foraging patterns.

Tissue stable isotopes offer a useful tool to investigate niche variation and dietary specialization (Newsome et al., 2007, Post et al., 2002). Carbon isotope ratio ($\delta^{13}C$) varies between littoral (enriched) and pelagic (depleted) resources, and between freshwater (depleted) and marine (enriched) resources, nitrogen isotope ratio ($\delta^{15}N$) increases with trophic level, while sulfur isotope ratio ($\delta^{34}S$) varies between marine (enriched) and terrestrial (depleted) resources (Michener & Kaufman, 2007, Newsome et al., 2007). Isotope values in isotopic niche space (δ-space) can be converted into estimates of resource contributions (p-space) from sources to consumers through mixing models (Newsome et al., 2007), enabling inferences about drivers of resource use by integrating covariates (Brownscombe et al., 2022). Incrementally grown tissues, such as eye lenses, offer isotopic time-series (Tzadik et al., 2017; Vecchio & Peebles, 2020), allowing inference on long-term diet specialization through variance component analysis in δ-space (Newsome et al., 2012; Ingram et al., 2018). Further, eye lens diameter strongly correlates with body length, enabling the correlation of isotope values with sizes to link age-specific diets to growth rates (Bell-Tilcock et al., 2020).

The objective of this work was to identify drivers of coastal pike resource use and specialization and assess coupling of food webs through predation in a brackish environment. Thereby, we wanted to examine how a freshwater predator navigates trade-offs associated with marine resource specialization. Specifically, we tested whether individual specialization on marine resources leads to increased growth rates in individual pike and pike phenotypes. We hypothesized that 1) energy-rich marine resources, specifically herring, increase individual growth rates in pike; 2) larger pike show stronger reliance on marine resources; 3) pike behavioral phenotypes differ in their life-long individual resource specialization, with brackish-adapted phenotypes with access to marine resource pulses specializing more strongly on marine resources than other phenotypes, and 4) increased salinity has negative impacts on pike growth, an effect that is dampened in phenotypes with greater reliance on marine prey.

II. Methods

Study area

The Bodden lagoons exhibit strong environmental gradients in salinity and temperature, and host a diverse community of freshwater, brackish and marine organisms. Average conditions in specific lagoons vary from oligohaline (2-5 PSU, annual average) with predominantly freshwater species assemblages in the east and west (Figure 1), to mesohaline (6.5-9.6 PSU) in the northwest, north and northeast (Figure 1). Salinity declines from north west of Rügen to south-east, where the large River Odra drains abundant freshwater in the largest lagoon – the Greifswalder Bodden (Figure 1). The

Greifswalder Bodden is a major spawning area for spring spawning herring, but this species occurs in all mesohaline lagoons, especially during spring, which is also the spawning time of pike. Several tributaries, including larger rivers, smaller creeks and drainage ditches hosting freshwater species, drain into the lagoons (Figure 1).

Sampling of pike

All fish in this study were sampled using mixed gears, including gill nets, fyke nets and angling in brackish lagoons, and electrofishing in tributaries. Pike were sampled across seasons over four consecutive years (2019- 2022, Figure 1) in spring (March – May), summer (June – August), fall (September – November) and winter (December – February). All individuals were sexed (internally or based on cloaca shape or running eggs/milt, Caig, 1996), measured (total length, mm), weighed (g), and dorsal muscle tissue was taken for stable isotope analysis. To examine dominant prey species and seasonal variation in short-term diet, we analyzed 171 pike stomachs (155 from brackish lagoons, 16 from tributaries, 13 to 115 cm, mean ± SD = 73.9 ± 17.2 cm, Table S1). Only one pike in winter had ingested prey, and was excluded (spring N = 125, summer N = 19, fall N = 28). Stomach contents were obtained by gastric lavage (nonlethal) or by excising the stomach (lethal). Prey items were identified to species level, and total length (mm), and biomass (fresh weight, g) were calculated (details in supplement, section A). Behavioral phenotypes of pike were characterized using acoustic telemetry in 204 adult pike (see Dhellemmes et al., 2023a for details) and otolith microchemistry in 98 pike (see Rittweg et al., 2024 for details). To assess the effect of home range on resource use (similar to Brownscombe et al., 2023), we calculated individual-level 50% core and 95% extended home range (HR50 and HR95, respectively, see Dhellemmes et al., 2023b for details on calculations) for the 204 pike included in the telemetry dataset. In total, 302 pike of known behavioral phenotype were collected (202 from brackish lagoons, 100 from tributaries, 40 to 126 cm total length, mean ± SD = 74.8 ± 3.3 cm, 1 to 13 years age, median 7 years). To evaluate effects of resource use on pike growth, a subset of 50 pike was selected based on length (5 individuals per 5 cm size class between 50 and 100 cm) for eye lens delamination and isotope analysis. Due to differences among behavioral phenotypes, an additional

31 pike were chosen to enhance sample size in underrepresented phenotypes, resulting in 81 pike (50 from lagoons, 31 from tributaries, 40 cm to 126 cm total length, mean ± SD = 82.7 ± 18.5 cm, 1 to 13 years age, median 7 years).

Sampling of prey organisms

To assess the isotopic variability of different food webs in the system, potential prey species were collected opportunistically during field campaigns, complemented by targeted gill net sampling, bottom dredging, and targeted electrofishing in tributaries (supplement, section A, Figure S1). Offshore marine prey fish were obtained from bottom trawl surveys (Thünen-Institute of Baltic Sea Fisheries, Rostock) in 2020 and 2021 (Figure S1). Prey fish were identified to species level, length measured (total length, mm) and weighed (g). Muscle tissue for stable isotope analysis was excised dorsally.

Isotope analyses and calorimetry

Pike and prey samples were freeze-dried, homogenized, weighed into tin cups, and analyzed for $\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$ and C:N ratios, using elemental analysis isotope ratio mass spectrometry (EA-IRMS) (supplement, section B). Possible effects of lipid content (lipids are depleted in $\delta^{13}C$) were visually examined (linear regression of $\delta^{13}C$ on C/N ratio) and mathematically corrected following Kiljunen et al. (2006). Scaled images of whole eye lenses were used for a linear regression of body length on eye lens diameter to back-calculate length for a given eye lens diameter. The mucosal layer of the eye lenses was removed, and lenses were delaminated until reaching the core. Scaled images were taken after each lamina removal for length back-calculation.

To compare energy content of different prey species, homogenized dry mass samples from selected prey were analyzed for energy density in MJ/kg using a PARR 6400 A1435DDEE calorimeter. Differences in energy content between species were tested using one-way ANOVA and pairwise Tuckey tests.

Isotope mixing models (p-space)

To determine end members for mixing models, species with a stomach biomass contribution of less than 1% were considered opportunistic prey and excluded. Based on isotopic differences between and similarities within capture locations, prey species were grouped into freshwater, lagoon and marine resources, represented by dominant prey species from pike stomachs (Figure 2). Perch and roach from tributaries represented freshwater, perch, roach and invasive round goby from lagoons represented lagoon, herring and flounder from lagoons and offshore represented marine resources (Figure 2).

Relative contributions of resource groups on pike muscle isotope values were estimated with Bayesian stable isotope mixing models (MixSIAR, v 3.1.12, Stock et al., 2018). To identify drivers of resource use, we ran different combinations of continuous and fixed predictors, along with a null model (no predictors). Models were compared based on leave-one-out cross validation (LOOIC, Stock et al., 2018). Continuous predictors included body length, individual home ranges (HR50 and HR95), fixed predictors included behavioral phenotype and capture location. No temporal effects were tested, as we did not observe seasonal patterns in pike muscle isotope values (Figure S3).

Individual specialization and niche overlap (δ-space)

To infer individual specialization in δ-space, we calculated population-level between-individual variance (BIC_{Pop}), and within-individual variance (WIC_{Pop}) with variance component analysis (Ingram et al. 2018), using multiple response linear mixed effects models (MCMCglmm v 2.35, Hadfield, 2010). Individual eye lens laminae isotope values ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) were the response variables, individual ID was a random predictor. The model was specified with a Gaussian error structure and non-informative inverse Wishart priors. BIC_{Pop} and WIC_{Pop} were summed to estimate the population-level total isotopic niche matrix ($TINW_{Pop}$) (Ingram et al. 2018). Mean individual specialization was estimated by dividing the size (sum of eigenvalues) of WIC_{Pop} by the size of the $TINW_{Pop}$ (Newsome et al., 2012). Similar to Grainger et al. (2023), we extracted individual-level covariance matrices to estimate individual-level niche widths (WIC_{Ind}). The degree of individual specialization (s-index from 0, true generalist to 1, true specialist) was inferred by dividing the size of each WIC_{Ind} matrix by the size of the $TINW_{Pop}$ matrix (Grainger et al., 2023).

Individual overlap with the population niche was calculated as individual standard ellipsoid area overlap with the $TINW_{Pop}$ standard ellipsoid, normalized with the $TINW_{Pop}$ ellipsoid volume (Rossman et al., 2016). The resulting overlap index (o-index) ranged from 0 (low overlap with $TINW_{Pop}$) to 1 (high overlap with $TINW_{Pop}$). To test whether intraspecific competition may be driving individual specialization, we also calculated niche overlap between behavioral phenotypes of pike. To test drivers of individual specialization, we fit generalized linear models separately to the s-index and o-index metrics, using size, sex, capture location and behavioral phenotype as fixed effects, and F-tests to test for significance.

Individual-level growth

We back-calculated body length from individual eye lens diameters using the Fraser-Lee equation (Lee, 1920). Age classes were assigned to the backcalculated length-at-diameters using individual-level length-at-age data from otoliths for the same individuals (Rittweg et al., 2023). Backcalculated size ranged from 16.3 to 87.5 cm total length, covering an age range of 1 - 7 years. We averaged isotope values within years and assessed the effects of dietary tracers on age-specific growth with linear mixed effects models (lme4 & lmerTest versions 1.1.30 and 3.1.3, Bates *et al.*, 2015). Yearly growth increment (length at age i - length at age i-1) was modelled with behavioral phenotype, $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$, age and sex as predictors. Intraotolith $\delta^{18}O$ residuals (thermal proxy) and Sr:Ca ratios (saline proxy) measured by Rittweg et al. (2024) for the same individuals and years were also included, as they were significant predictors of growth in a previous study in this area (Rittweg et al., 2024). Age and sex were fixed effects, as growth slows with age in fishes (Von Bertalanffy, 1938), and pike grow sex-dimorphic, with females reaching larger sizes (Casselman, 1995). Individual ID was included as random predictor to account for the repeated measures design. Models were compared based on Akaike´s information criterion (AIC) and log likelihood estimates.

III. Results

Stomach contents

12 fish species were detected in pike stomachs, and 3 invertebrates (Table S2). Five prey species dominated biomass proportions with a combined biomass of 85.7% (Figure 3A). Marine fish herring

and flounder constituted 33.6%, freshwater species perch (*e a a l*) and roach (*l l*) 39.4%, invasive round goby (*e ela t*) accounted for 12.6% of biomass (Figure 3A). All other prey species comprised less than 1% in biomass proportion (other in Figure 3A). Pike diets were highly seasonal, with herring and roach dominating in spring, and perch and round goby being prevalent in fall (Figure3B). Herring was not detected outside of spring. Prey species differed significantly in energy content (one-way ANOVA, df = 58, F = 22.89, p 0.0001), with herring exhibiting the highest energy density (mean 24.4 MJ/kg), while other species ranged from 19.9 MJ/kg (flounder) to 20.8 MJ/kg (roach), differing significantly from herring, but not from each other (pairwise Tukey tests, significance level = 0.05, Figure 3C).

Stable isotope mixing models (p-space)

Body length received the highest statistical support among continuous predictors of resource use. Individual home ranges (HR50 and HR95) received no statistical support (Table 1). Behavioral phenotype and capture location were important predictors, receiving the strongest statistical support among all models when combined with body length (Table 1). Pike captured in freshwater tributaries used more freshwater resources than lagoon-captured pike. Pike captured in mesohaline lagoons used more marine resources than pike from oligohaline lagoons. Behavioral phenotype was a stronger predictor of resource use than capture location (Table 1). Freshwater residents predominantly used freshwater resources (82%), with minor contributions from lagoon (14%) and marine (4%) resources (Figure 4). Anadromous pike primarily used lagoon resources (75%), with smaller contributions from freshwater (15%) and marine (10%) resources (Figure 4). Cross-habitat pike relied mostly on lagoon (70%) and moderately on marine (23%) resources, with minor contributions from freshwater (7%,Figure 4). Brackish residents strongly relied on both lagoon (57%) and marine resources (39%), with minor contributions from freshwater (4%, Figure 4).

Marine resource use increased with body length across all behavioral phenotypes except freshwater residents (Figure 5). In brackish residents, marine resource use surpassed that of lagoon resources after reaching approximately 80 cm in body length (Figure 5). For cross-habitat pike, a shift from lagoon to marine resources occurred much later, at about 95 cm body length (Figure 5). In anadromous pike, lagoon resources remained the major food source along the entire length gradient, but both marine and freshwater contributions increased with body length (Figure 5). In freshwater residents, freshwater resources continued to be the primary dietary source throughout the size range considered, but smaller-sized individuals showed some use of lagoon resources (Figure 5).

Individual specialization (δ-space)

Early life $\delta^{13}C$ and $\delta^{34}S$ values of freshwater resident and anadromous pike were unexpectedly low, indicating a contribution of C and S sources influenced by microbial processes associated with oxygen limitation in early habitats (e.g. sulfate reduction and methanogenesis, Alp & Coucherousset, 2022; Newsome et al., 2007). In anadromous pike, the values of both isotopes increased sharply with size, stabilizing after backcalculated body lengths of approximately 20 cm (Figure 6). Freshwater residents also increased in $\delta^{13}C$ and $\delta^{34}S$ values with size, reaching constant levels at around 30 cm (Figure 6). Cross-habitat and brackish resident pike showed high average $\delta^{34}S$ values, suggesting marine resource use, but only brackish residents increased in $\delta^{34}S$ with size (Figure 6). As expected for gape-limited predators (Beaudoin et al., 1999), we detected steady increases in $\delta^{15}N$ values with size across all behavioral phenotypes. Additionally, we observed strong fluctuations of $\delta^{15}N$ during early life stages of freshwater residents (Figure 6).

Within-individual components (WIC_{Pop}) explained a greater proportion of variance in isotopic niche ($WIC_{Pop}/TINW_{Pop} = 0.79$) than between-individual components ($BIC_{Pop}/TINW_{Pop} = 0.21$), indicating a generalist population. However, individual specialization, assessed by s-indices ($WIC_{Ind}/TINW_{Pop}$) varied strongly (Figure 6). Behavioral phenotype was the only significant predictor of s-indices, with cross-habitat and brackish resident pike exhibiting higher s-indices compared to freshwater resident and anadromous pike (GLM, $F = 3.26$, $p = 0.031$, Figure 7, Table S3). Following these results, we recalculated s-indices using phenotype-level total isotopic niche widths ($TINW_{pheno}$) as population niche for the calculation of individual specialization. Considered separately, pike still appeared generalist on subpopulation-level ($WIC_{freshwater}/TINW_{freshwater} = 0.88$; $WIC_{anadromous}/TINW_{anadromous} = 0.95$; WIC_{cross-}

$_{\text{habitat}}$/TINW$_{\text{cross-habitat}}$ = 0.68; WIC$_{\text{brackish}}$/TINW$_{\text{brackish}}$ = 0.77). Patterns detected for individual specialization on population-level persisted for the phenotype-specific approach (Figure 7B). However, differences were smaller in the phenotype-specific approach, and freshwater residents now showed high variation in their s-index (Figure 7B).

iche overlap (δ-space)

We observed low individual-level overlap with the population 40% core isotopic niche (average o-index = 0.02, Figure 8). There were no consistent patterns in o-indices, as a generalized linear model including length, capture location, sex and behavioral phenotype did not perform better than an intercept only model (GLM, F = 1.04, p = 0.42, Table S3). Despite this, we recalculated the o-index using subpopulation (behavioral phenotype) isotopic niches, similar to the s-indices. However, the result did not change (average phenotype-specific o-index= 0.02), indicating high niche displacement within a large population niche (Figure S4). On a phenotype-level, core niche area of freshwater residents overlapped for 10.3% with anadromous pike, but showed no overlap with brackish resident and cross-habitat pike (Figure 8). The core niche of anadromous pike overlapped with cross-habitat pike for 0.6%, and 4.6% with brackish residents (Figure 8). Cross-habitat pike and brackish residents overlapped for 57.1% core niche area, indicating resource competition (Figure 8).

Individual-level growth

The model containing behavioral phenotypes, thermal (δ^{18}O residual) and saline (Sr:Ca) proxies, in conjunction with δ^{13}C, δ^{15}N, and δ^{34}S performed best for predicting annual growth increments of pike up to 87 cm total length and 7 years of age (Table 2). Out of the environmental and dietary proxies, experienced temperature (positive effect), salinity (negative effect), and δ^{34}S (positive effect) significantly improved AIC score of the model (Table 2). δ^{13}C and δ^{15}N did not improve explanatory power significantly (Table 2). Behavioral phenotype was a significant predictor of pike growth (Table 2). Pairwise contrasts on the most parsimonious model revealed cross-habitat pike, on average, grew faster than the other behavioral phenotypes (on average 86 mm and 119 mm more per year, respectively), and anadromous pike also grew faster, on average, than freshwater residents (on average

40 mm more per year). All other pairwise phenotype comparisons indicated no significant differences. As expected, age had a negative effect on pike growth, and males grew slower than females (Table 2).

I . iscussion

We tested whether allochthonous marine resource subsidies support individual specialization and growth of differently adapted behavioral phenotypes in a pike metapopulation living in a lagoon network in the southern Baltic Sea. In agreement with our first hypothesis, we found evidence for positive effects of marine resource use on growth rates of individual pike. Supporting our second hypothesis, pike increased marine resource use with increasing body size, except for freshwater residents that did not use marine resources. In response to our third hypothesis, pike behavioral phenotypes, on average, differed significantly in marine resource use, consistent with their main habitat use patterns. Brackish-adapted phenotypes relied more strongly on marine resources compared to freshwater-adapted phenotypes, and showed stronger individual specialization. Key reasons are likely spatiotemporal overlap among lagoon and marine food web that are only accessible to physiologically or behaviorally adapted phenotypes, along with the elevated intraspecific competition experienced by brackish-adapted phenotypes. However, individual-level growth benefits of marine resource specialization were counteracted by negative average effects of high salinity exposure on growth. Thus, increased marine resource use of brackish-adapted pike did not fully compensate the increased osmoregulatory costs of foraging in saline habitats.

The main prey species in pike stomachs were Atlantic herring, roach, perch, flounder, and invasive round goby, the latter occurring in high abundances across all lagoons since 2017 (Lewin et al., 2023). Consistent with Winkler (1987), herring and roach were most abundant. The high proportion of round goby aligns with several recent studies reporting increased consumption of round goby by predators in the Baltic Sea, suggesting the species induced new trophic interactions across the Baltic Sea (Herlevi et al., 2023; Oesterwind et al., 2017; Wallin et al., 2023). The seasonal signals in stomach contents that we found broadly agreed with Winkler (1987), e.g., Atlantic herring were only detected during their spring spawning migration and not in autumn. Pike foraged more opportunistically in summer, indicated by high amounts of other prey, and relied more on lagoon prey (perch and round goby) in fall. This suggests pike specialize on certain prey items only during specific times of the year, driven by availability and habitat overlap (Armstrong & Bond, 2013; Bolnick et al., 2003; Nolan et al., 2019), highlighting the importance of cross-seasonal sampling when interpreting stomach-content data to infer diet specialization.

As expected, marine resource use was positively associated with body size in pike. Our findings align with Nolan et al. (2019), who found increased consumption of large-bodied anadromous clupeids (*l* *a* .) with larger size in pike in river Severn, UK. Body size-dependent gape width influences the ability of pike to ingest larger and deeper-bodied prey (Hart & Connellan, 1984; Nilsson & Brönmark, 2000). Larger individuals can consume larger quantities of prey within limited time frames, potentially engaging in feast-and-famine dynamics during large aggregations of suitable prey (e.g, herring in spring) (Armstrong & Schindler, 2011). This could potentially explain the lack of seasonal signal in pike stable isotopes compared to stomach contents, as energy stores from herring could be used for somatic growth throughout the growing season, similar to findings in other fish (Armstrong & Schindler, 2011). Alternatively, pike may shift towards other, isotopically similar marine prey in the absence of spawning herring, such as flounder, which are available year-round (Winkler, 1989), and which also constituted a relevant prey item in our study. Also, despite lower abundances (Von Dorrien et al., 2013), fall-spawning herring could be an important resource that perhaps went undetected in pike stomachs due to limited sample sizes in fall (our study N = 28; Winkler, 1987 N = 18).

Potential energy gains from migratory herring may be traded off against increased predation risk in mesohaline habitats, e.g., by cormorants (*ala* *a* *a*) and grey seal (*al* *e*) (Arlinghaus et al. 2021; Bergström et al. 2022), and increased osmoregulatory cost (Bœuf & Payan, 2001). Our findings show that the increased reliance on marine prey by brackish residents did not fully compensate the negative growth effects of high salinity exposure. This might not hold for the largest individuals, which are less vulnerable to predation (Werner & Gilliam, 1984), and have higher osmoregulatory capacity (Varsamos et al., 2015). Previous work in Rügen indicated that larger and older

(6 years) brackish resident individuals show compensatory growth and higher adult growth compared with other behavioral phenotypes (Rittweg et al., 2024). These large individuals might thus reap the strongest benefits of marine resource use. Indeed, marine resources constituted the main diet source of brackish residents after a size of approximately 85 cm total length. The outermost eye lens layers are not suitable for isotope analysis (Bell-Tilcock et al., 2020), therefore we were not able to include these largest size classes in the growth models of the present paper. We think the growth/mortality/osmoregulation tradeoffs associated with mesohaline habitats likely favored specialization on marine prey at larger sizes. Conservation of large individuals through harvest regulations (Ahrens et al. 2020) may thus benefit the pike stock.

Behavioral phenotypes of pike differed strongly in resource use, likely due to divergent adaptations to the salinity gradient (Sunde et al. 2022; Lukyanova et al. 2024; Rittweg et al., 2024), and variation in spatio-temporal overlap with resources. Freshwater residents are not adapted to brackish habitats (Birnie-Gauvin et al., 2018; Arlinghaus et al., 2023; Rittweg et al., 2024) and therefore stay in tributaries, in turn using mostly freshwater resources. Anadromous pike, in contrast, are adapted to forage, but not recruit in brackish environments, and undertake seasonal spawning migrations to tributaries in spring (peaking in March to April, Roser et al. 2023; Dhellemmes et al. 2023a; Lukyanova et al., 2024). These migrations temporally coincide with the spring herring migration, potentially limiting access to this resource pulse. A similar pattern may account for the lower-than-expected marine resource use in cross-habitat pike, which migrate to freshwater-adjacent habitats in spring and generally use habitats that are less saline than those used by brackish residents (Dhellemmes et al., 2023a; Rittweg et al., 2024). Only brackish residents, adapted to complete their whole life cycle in high-saline brackish habitats, can exploit the entire period of the marine resource pulse. Brackish residents also use the highest average salinities compared to the other behavioral phenotypes (Rittweg et al., 2024), likely leading to greater spatial overlap with other marine prey, consistent with their greater marine resource use. Findings on similar phenotypic diversity in other coastal pike populations in the Baltic Sea (e.g., Sunde et al., 2022) suggest phenotype-specific resource use might be commonplace, warranting further investigation on niche variation in coastal pike.

Individual resource specialization of pike very likely reduced competition among brackish resident and cross-habitat behavioral phenotypes in shared foraging habitats, possibly contributing to intrapopulation differentiation. Pike are known to be opportunistic foragers (Cathcart et al., 2019; Chapman & Mackay, 1990; Pedreschi et al., 2015). However, Beaudoin et al. (1999) observed high degrees of individual specialization in lentic pike, possibly induced by resource limitation or intraspecific competition. In our study, intraspecific competition is a plausible pathway explaining diet specialization, given the significant overlap in isotopic niche of brackish residents and cross-habitat pike (Rossman et al., 2016). High individual-level specialization in these behavioral phenotypes may be a mechanism to decrease competition in shared foraging grounds (Saavedra et al., 2022; Svanbäck et al., 2008), where brackish residents specialize on marine resources and cross-habitat individuals specialize on lagoon resources. Consistency in p-space and δ-space metrics suggests that specialization persisted from juvenile to adult stages, promoting coexistence through resource partitioning (Bolnick et al., 2007; Knudsen et al., 2010; Kobler et al., 2009). Anadromous pike, in contrast, were more generalist, foraging opportunistically across freshwater and lagoon resources. Freshwater residents were a mix of specialists and generalists, possibly reflecting varying degrees of resource limitation and intraspecific competition in tributaries of different habitat quality. However, we lacked detailed information on productivity and food density in individual tributaries, such that our explanation remains speculative. Our findings are however consistent with the niche variation hypothesis (Bolnick et al., 2007; Van Valen, 1995), i.e., more generalized populations are also more heterogenous on an individual level, underlining the crucial importance of considering individual and phenotypic variation in ecological studies.

Behavioural phenotype-specific growth in our study diverged from previous findings (Rittweg et al., 2024), despite using a subsample of the same individuals. In contrast to Rittweg et al. (2024), we did not detect compensatory growth of freshwater and brackish residents in later life, which can be explained by truncation of the size and age range (87.5 cm total length and 6 years) over which we made comparisons in this study. By contrast, Rittweg et al. (2024) modelled pike growth for pike up to 126 cm total length and 13 years of age, which were particularly abundant among brackish residents. However, slower early growth in freshwater and brackish residents in our work is still consistent with the findings of Rittweg et al. (2024). For freshwater residents, this might be explained by oxygen limitations in heavily modified tributaries (Roser et al., 2023), e.g., through anthropogenic nutrient inputs (Rogers et al., 2023). In the case of brackish residents, osmoregulatory costs in high saline habitats had a negative effect on growth (as found in the present study and in Rittweg et al., 2024). These habitat-associated growth depressions can be compensated late in life in very large pike (Rittweg et al., 2024), where freshwater residents shift to well-oxygenated adult habitats and brackish residents increase in osmoregulatory capacity (Varsamos et al., 2005), thereby reaching sizes where they benefit most from large-sized marine prey (~85 cm). Anadromous and cross-habitat pike grow up in sheltered nursery habitats at low salinities (Rittweg et al., 2024), while retaining access to the productive brackish lagoons, boosting early growth. However, these phenotypes lack access to the marine resource pulse offered by the spring spawning herring, likely limiting later growth. Overall, our work showcases the trade-offs involved in different habitat use decisions and adaptations, where variability in local environmental factors and resources (e.g., marine prey), as well as habitat-associated costs (e.g., osmoregulation) limit the consistency in fitness of different strategies, facilitating co-existence (Kobler et al. 2009).

imitations

Stomach contents present snapshots of consumer diets, and are limited by variable digestion times (Baker et al., 2014). However, we used stomach contents mainly to select end members for stable isotope mixing models, sampling across a whole year to ensure robust results on major prey species. Opportunistic sampling hindered estimates of seasonal changes in prey isotope values for some species, but we did not detect seasonal effects in pike and prey species with cross-seasonal isotope values. Functional groups used for the mixing models might not capture the full isotopic range of pike diets, introducing uncertainty in the proportional estimates at the species level, especially for isotopically similar species. However, isotope values of prey chosen to represent different resource groups were consistent with expectations (Newsome et al., 2007; Michener & Kaufmann et al., 2007). Small sample sizes per group could have biased effect sizes in our growth rate analyses, however, model evaluation indicated that detected effects were likely robust (supplement, section E). Lastly, both resource use and habitat influenced the positive effect of δ^{34}S on growth. However, while δ^{34}S had significant effects, δ^{13}C, also influenced by the ontogenetic habitat shifts, had none, indicating marine resource use outweighed ontogenetic habitat shifts in determining individual pike growth. The robustness of our growth analysis is further indicated by finding expected relationships, e.g., faster growth in female pike and a slowing of growth rate with age.

onclusions and implications

We used a freshwater predator that diversified into behavioral phenotypes in brackish coastal habitats to identify drivers of resource use and individual specialization in response to allochthonous marine subsidies. By linking resource use to fitness through growth as a proxy, we found marine resources to significantly benefit individual pike growth, but this was counteracted by osmoregulatory costs in high salinity habitats. Fitness benefits for pike that use high saline brackish water vary with fish size, with only larger individuals benefiting strongly from marine prey, creating variable selection pressures that contribute to maintenance of intrapopulation phenotypic variation. We suggest that physiological and behavioral adaptations and trade-offs, along with intraspecific competition and trophic overlap through habitat choice, synergistically drive resource specialization and individual growth in coastal pike populations. Currently, the spring spawning Atlantic herring population is strongly declining across the Baltic Sea (ICES 2022). No independent assessment of spawning stock biomass of herring is available for the lagoons of Rügen, but recruitment of herring is also declining here (Polte et al., 2021). A decline in marine prey would be particularly consequential for the brackish-adapted pike phenotype and could increase competition among the different ecotypes, suggesting successful management of lagoon pike is intimately linked to ecosystem-based management of Baltic

Sea fishes more generally. Implementing management measures to ensure pike consistently reach sizes where they benefit most from marine subsidies (85 cm), such as harvest slots (Ahrens et al., 2020), would likely enhance growth performance of pike around Rügen. Additionally, reducing anthropogenic nutrient inputs and restoring habitats to mitigate oxygen limitations, as well as improving connectivity between tributaries and lagoons, would benefit the pike population as a whole (Roser et al., 2023; Lukyanova et al., 2024), particularly the freshwater and anadromous pike.

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Ethics approval

Fish were sampled in accordance with permit 7308.2 of the Landesamt für Landwirtschaft, Lebensmittelsicherheit und Fischerei (LALLF MV). Sampling in national park Vorpommernsche Boddenlandschaft was carried out in accordance with permit 21/5320.142, sampling in biosphere reserve Südost-Rügen was carried out in accordance with permit 5321.2/FM/SchnB.Nr.20002. Sampling in nature reserves was carried out in accordance with permit 5328.1.99/654-19-40-3 of the Staatliches Amt für Landwirtschaft und Umwelt (STALU MV). Sampling of freshwater tributaries was carried out with permission by the Landesanglerverband Mecklenburg-Vorpommern e.V. (LAVB MV).

Author contribution statement

Conceptualisation: TR, CT, RA. Developing methods: TR, CT, TG. Conducting the research: TR, FD, MB. Data analysis: TR, FD, MB. Data interpretation: TR, CT, RA. Preparation figures & tables: TR. Writing: TR, RA, CT, FD, TG

Data availability statement

Data are available from https://github.com/Traveller-2909/Pike-diet-analysis

Conflict of interest statement

The authors declare no conflicts of interest.

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Table 1. Comparison of mixing models testing drivers of resource use in 302 individual pike captured between March 2020 and May 2022 in brackish lagoons and adjacent tributaries around Rügen island in Northern Germany. Models are ordered based on LOOIC scores. SE (LOOIC): standard error of LOOIC, LOOIC : difference between a model and the best-performing model.

Comparison of continuous effects (N = 221)	**LOOIC**	**SE (LOOIC)**	**LOOIC**
phenotype + area + body length	602.9	47.9	0.0
null model (only phenotype + area)	642.0	48.1	39.1
phenotype + area + HR95	647.0	47.1	44.1
phenotype + area + HR50	649.1	47.0	46.2
Comparison of fixed effects (N = 316)			
phenotype + capture location + body length	1346.1	66.9	0.0
phenotype + body length	1590.5	69.6	244.4
Capture location + body length	1610.7	71.9	264.6
phenotype	1620.0	67.4	273.9
capture location	1648.3	68.4	302.2
null model (only body length)	2117.5	92.8	771.4

Table 2. Model comparison for linear mixed effects models predicting annual growth increment in 81 northern pike captured from brackish lagoons and several tributaries between March 2020 and May 2022 around Rügen island, northern Germany. Models were compared based on Akaike´s information criterion (AIC) against a Null model. Models that explained significantly more variance in pike growth increments compared to the Null model are shown in bold. The coefficients from the most parsimonious model are shown in the lower half of the table. Note that for $\delta^{18}O$, a higher value corresponds to lower experienced temperature.

Yearly growth increment (mm)

Model	AIC	LogLik	LLR	p-value
(age sex phenotype (I)	2402.3	-1193.2		
age sex phenotype δ δ δ S δ Sr a (I)	**.**	**- .**	**.**	**.**
age sex phenotype δ δ δ S δ (I)	**.**	**- .**	**.**	**.**
age sex phenotype δ δ δ S (I)	**.**	**- .**	**.**	**.**
age sex phenotype δ δ S (I)	**.**	**- .**	**.**	**.**
age sex phenotype δ δ S (I)	**.**	**- .**	**.**	**.**
age sex phenotype δ^{13}C (1 ID)	2400.9	-1191.4	3.5	0.06.
age sex phenotype δ^{13}C δ^{15}N (1 ID)	2400.7	-1190.3	0	
age sex δ^{13}C δ^{15}N δ^{34}S δ^{18}O Sr:Ca (1 ID)	2415.9	-1197.9	0	

Effect sizes (best model marginal R^2 = 0.49; conditional R^2 = 0.61)[1]	Estimate (± SE)
age (years)	**- . (.)**
sex male	**- . (.)**
behavioral phenotype freshwater resident	**- . (.)**
behavioral phenotype brackish resident	**- . (.)**
behavioral phenotype cross-habitat	**. (.)**
δ^{13}C (z-score transformed)	3.27 (4.78)
δ^{15}N (z-score transformed)	-10.23 (5.81)
δ S (z-score transformed)	**. (.)**
δ (z-score transformed)	**- . (.)**
Sr a (z-score transformed)	**- . (.)**

ta a e a e a te l el l el a .
a al e e t e t e t tal a a ee la e e e e t t e el al
e e t e t tal a a ee la e e a a e e t e t e el.

Figure 1. Map of the study area sampled for pike from March 2020 until May 2022. Green circles: sampling for stomach content analysis; blue circles: passive acoustic telemetry; orange circles: otolith microchemistry. Colored labels indicate the sample size of pike for each method per location. D B west: Dar - ingst Bodden Chain west; D B east: Dar - ingst Bodden Chain east; WRBC: Western Rügen Bodden Chain; NRBC: Northern Rügen Bodden Chain; GB: Greifswalder Bodden; P: Peenestrom; AW: Achterwasser; SH: Ste ner Haff; BKG: Badendycksgraben; NHG: Neuendorfer Hechtsgraben.

Figure 2. Isotopic variability of behavioral phenotypes in 302 individual pike (dashed lines) and three functional prey groups representing freshwater, lagoon and marine resources (solid lines), captured between March 2020 and May 2022 in brackish lagoons and several tributaries around Rügen island in northern Germany. Isotopic variability is shown as kernel density plot in two-dimensional isospace for A: $\delta^{13}C/\delta^{15}N$; B: $\delta^{34}S/\delta^{15}N$; C: $\delta^{13}C/\delta^{34}S$.

Figure 3. Total biomass proportions (A), monthly biomass proportions (B) and energy density (C) of prey species found in stomachs of 171 northern pike (/) captured between November 2020 and June 2021 in brackish lagoons and several tributaries around Rügen island in northern Germany.

Figure 4. Proportional contributions of marine, lagoon and freshwater resources on the diet of four behavioral phenotypes of pike, calculated from muscle isotope data of 302 individuals captured between March 2020 and May 2022 in brackish lagoons and adjacent tributaries around Rügen island in Northern Germany.

Figure 5. Relative contribution of marine, lagoon and freshwater resources in response to body length of four behavioral phenotypes in 302 individual pike, captured between March 2020 and May 2022 in brackish lagoons and several tributaries around Rügen island in Northern Germany.

Figure 6. Isotope values against backcalculated total lengths from eye lens laminae depicting early life to adult isotope values for 81 individuals captured between March 2020 and May 2022 in brackish lagoons and several tributaries around Rügen island in Northern Germany. Colored dots depict isotope values of lens layers from individual fish, with color corresponding to behavioral phenotype. Isotope

data for behavioral phenotypes were fitted with GAM smoothing lines following the same color code, shaded areas depict the standard deviation.

Figure 7. Specialization index calculated relative to A: population-level TINW; B: phenotype-specific TINW, across four behavioral phenotypes in 81 pike captured between March 2020 and May 2022 from brackish lagoons and several tributaries around Rügen island, Northern Germany. Boxes depict the median, lower and upper quantile, points depict outlier values. Violin plots depict the relative density of data.

Figure 8. Individual core 40% niche ellipses in A: $\delta^{15}N/\delta^{13}C$; B: $\delta^{15}N/\delta^{34}S$; C: $\delta^{13}C/\delta^{34}S$ of 81 pike captured between March 2020 and May 2022 in brackish lagoons and several tributaries around Rügen island, Northern Germany. Solid ellipses depict core population niche ($TINW_{Pop}$, black), within-individual component (WIC_{Pop}, orange) and between-individual component (BIC_{Pop}, red). Individual ellipsoids are colored corresponding to the behavioral phenotype.

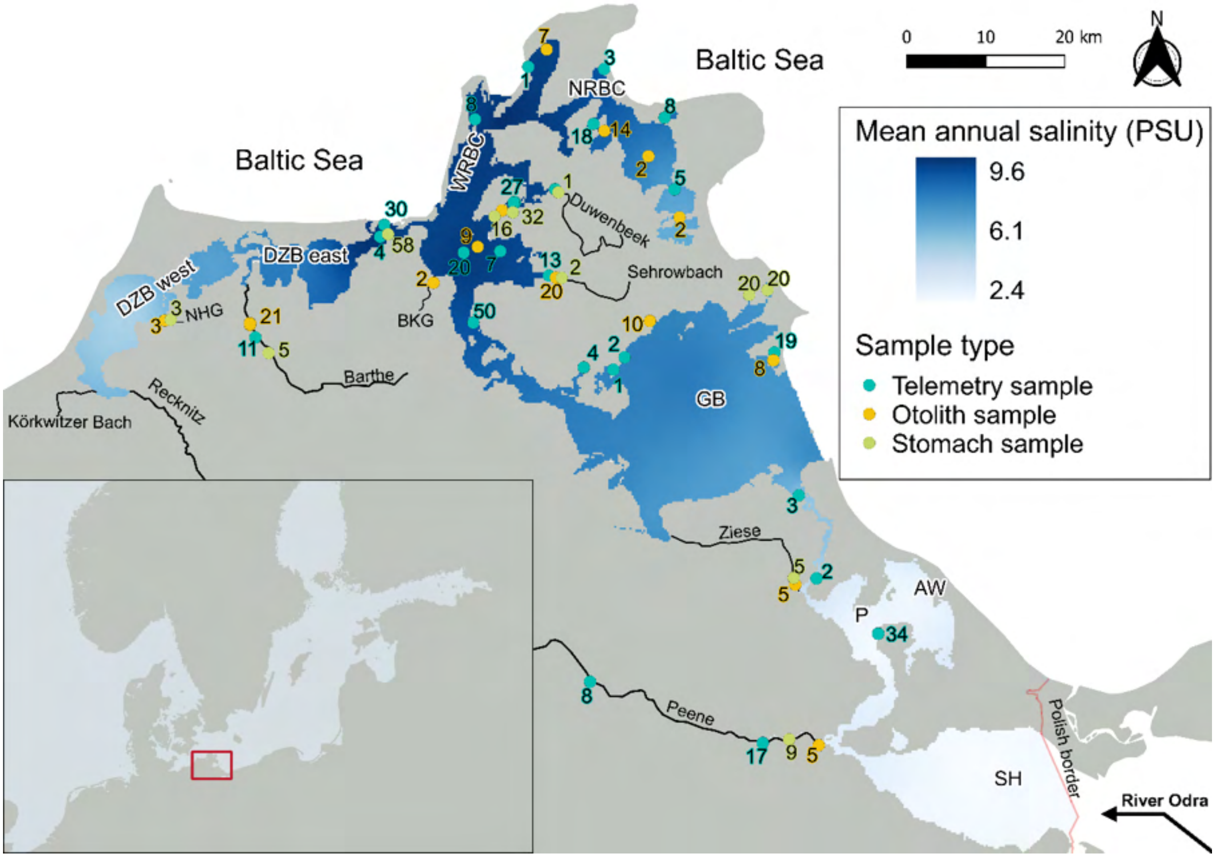
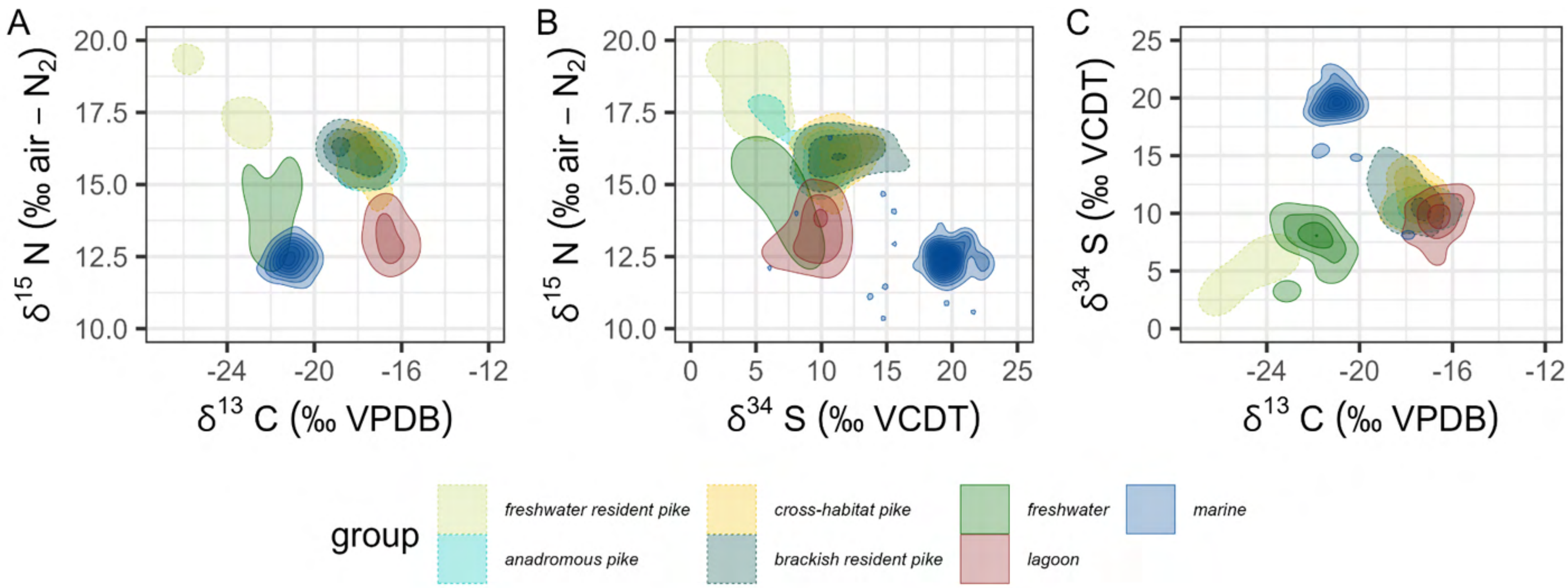

Baltic Sea
Baltic Sea
0 10 20 km
N
Mean annual salinity (PSU)
9.6
6.1
2.4
Sample type
● Telemetry sample
● Otolith sample
● Stomach sample
NRBC
WRBC
DZB west
DZB east
NHG
BKG
Duwenbeek
Sehrowbach
GB
Barthe
Recknitz
Körkwitzer Bach
Ziese
AW
P
Peene
SH
Polish border
River Odra

Figure 1



A
B
C
δ15 N (‰ air – N2)
20.0
17.5
15.0
12.5
10.0
-24
-20
-16
-12
δ13 C (‰ VPDB)
0
5
10
15
20
25
δ34 S (‰ VCDT)
group
freshwater resident pike
anadromous pike
cross-habitat pike
brackish resident pike
freshwater
lagoon
marine

Figure 2

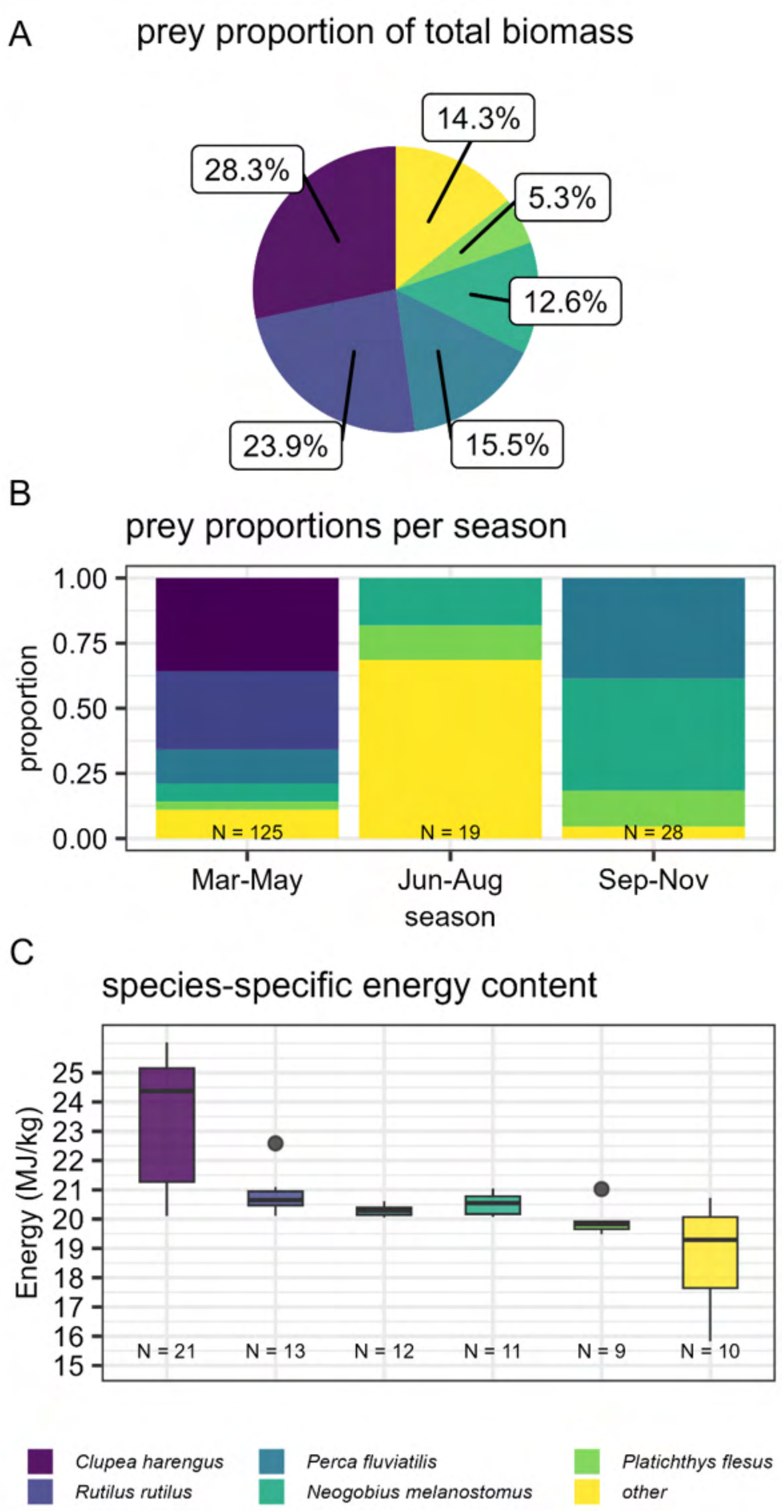

A
prey proportion of total biomass
28.3%
14.3%
5.3%
12.6%
15.5%
23.9%
B
prey proportions per season
proportion
1.00
0.75
0.50
0.25
0.00
N = 125
N = 19
N = 28
Mar-May
Jun-Aug
Sep-Nov
season
C
species-specific energy content
Energy (MJ/kg)
25
24
23
22
21
20
19
18
17
16
15
N = 21
N = 13
N = 12
N = 11
N = 9
N = 10
Clupea harengus
Rutilus rutilus
Perca fluviatilis
Neogobius melanostomus
Platichthys flesus
other

Figure 3

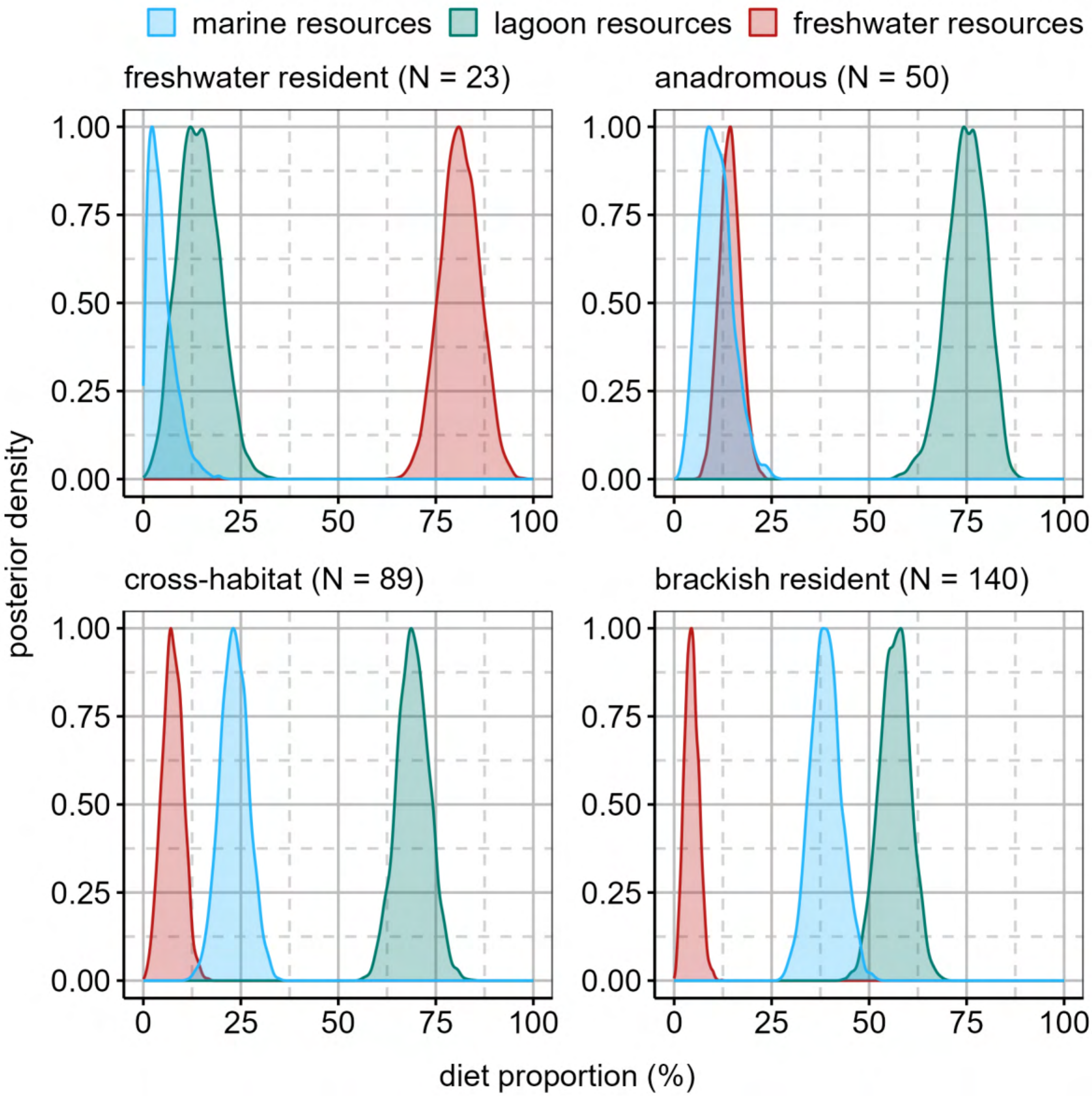

marine resources
lagoon resources
freshwater resources
freshwater resident (N = 23)
anadromous (N = 50)
cross-habitat (N = 89)
brackish resident (N = 140)
posterior density
1.00
0.75
0.50
0.25
0.00
0
25
50
75
100
diet proportion (%)

Figure 4

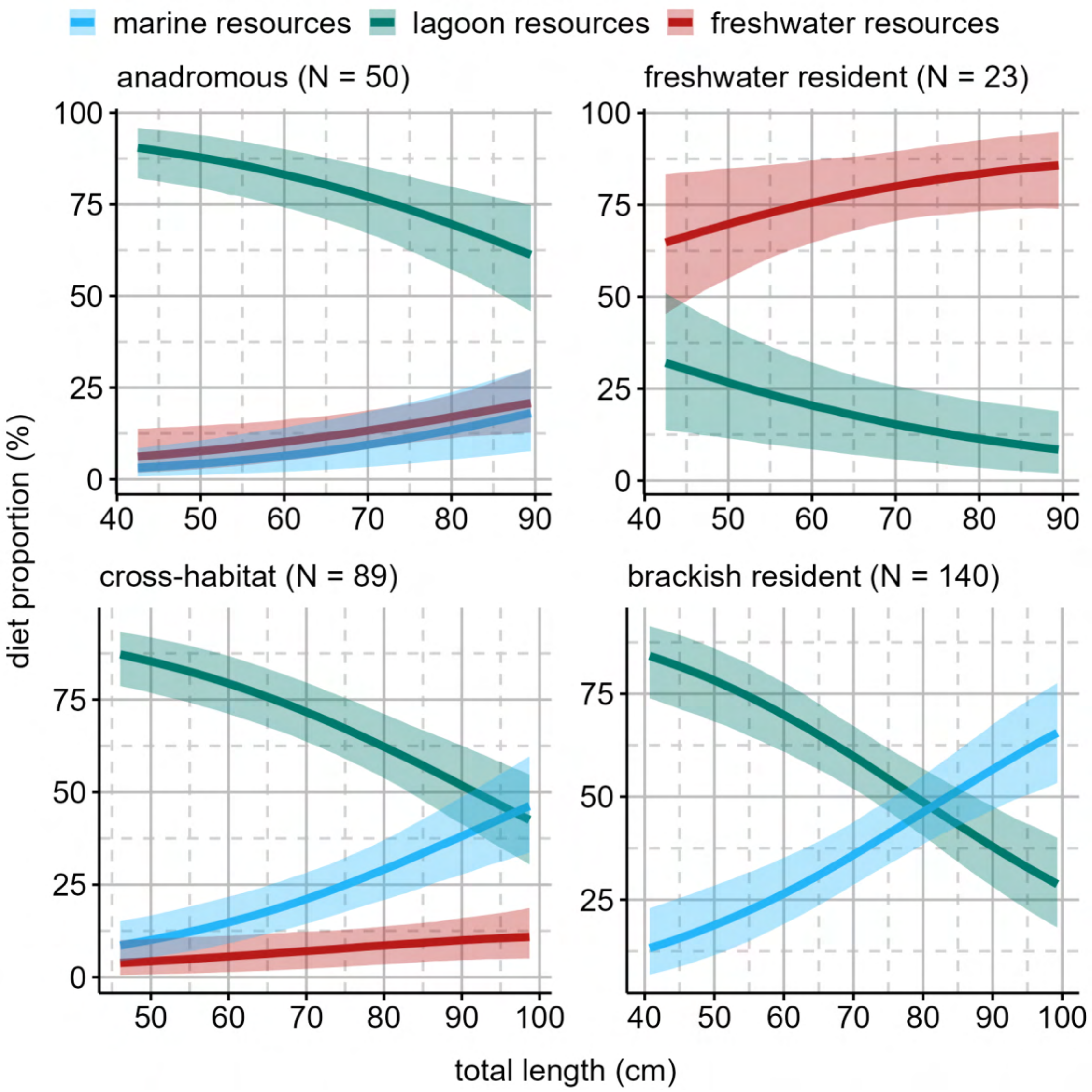

marine resources
lagoon resources
freshwater resources
anadromous (N = 50)
freshwater resident (N = 23)
cross-habitat (N = 89)
brackish resident (N = 140)
diet proportion (%)
total length (cm)
0
25
50
75
100
40
50
60
70
80
90
100

Figure 5

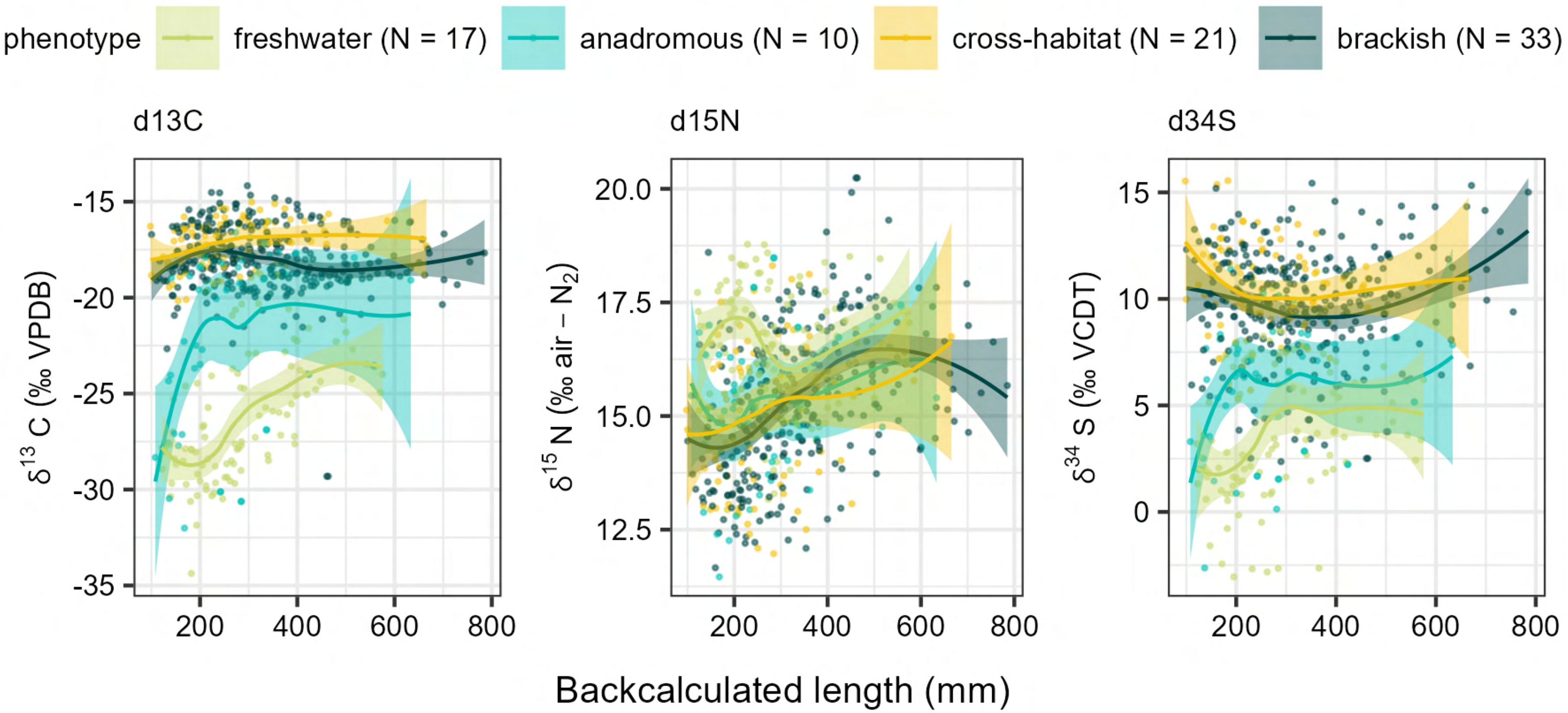

phenotype
freshwater (N = 17)
anadromous (N = 10)
cross-habitat (N = 21)
brackish (N = 33)
d13C
d15N
d34S
δ^{13}C (‰ VPDB)
-15
-20
-25
-30
-35
δ^{15}N (‰ air – N_2)
20.0
17.5
15.0
12.5
δ^{34}S (‰ VCDT)
15
10
5
0
200
400
600
800
Backcalculated length (mm)

Figure 6

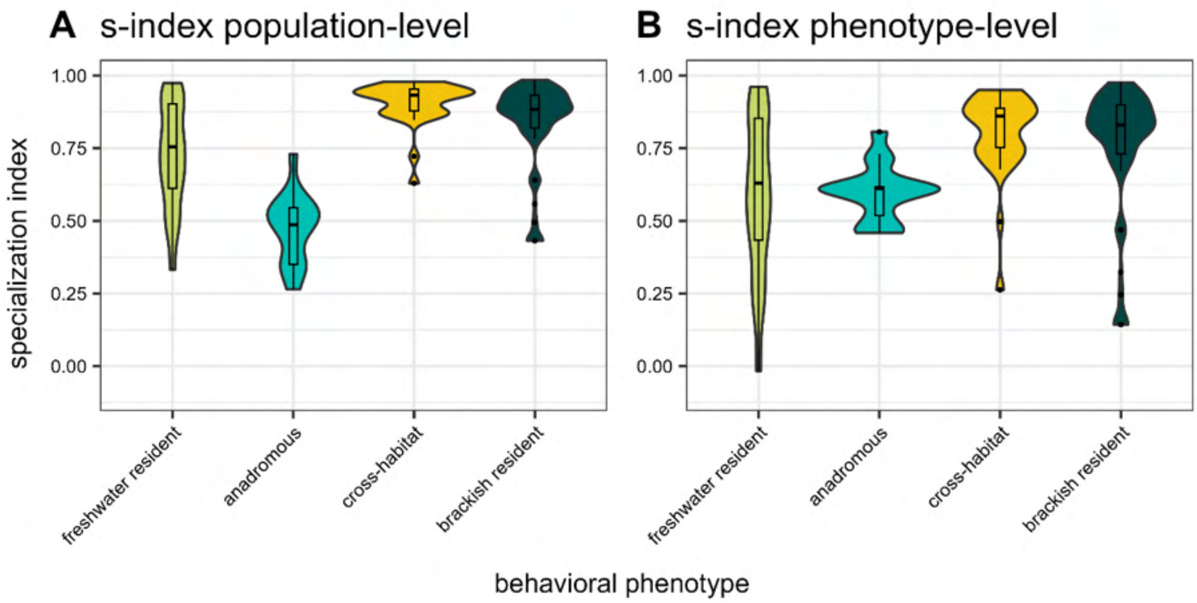

A s-index population-level
B s-index phenotype-level
specialization index
1.00
0.75
0.50
0.25
0.00
freshwater resident
anadromous
cross-habitat
brackish resident
behavioral phenotype

Figure 7

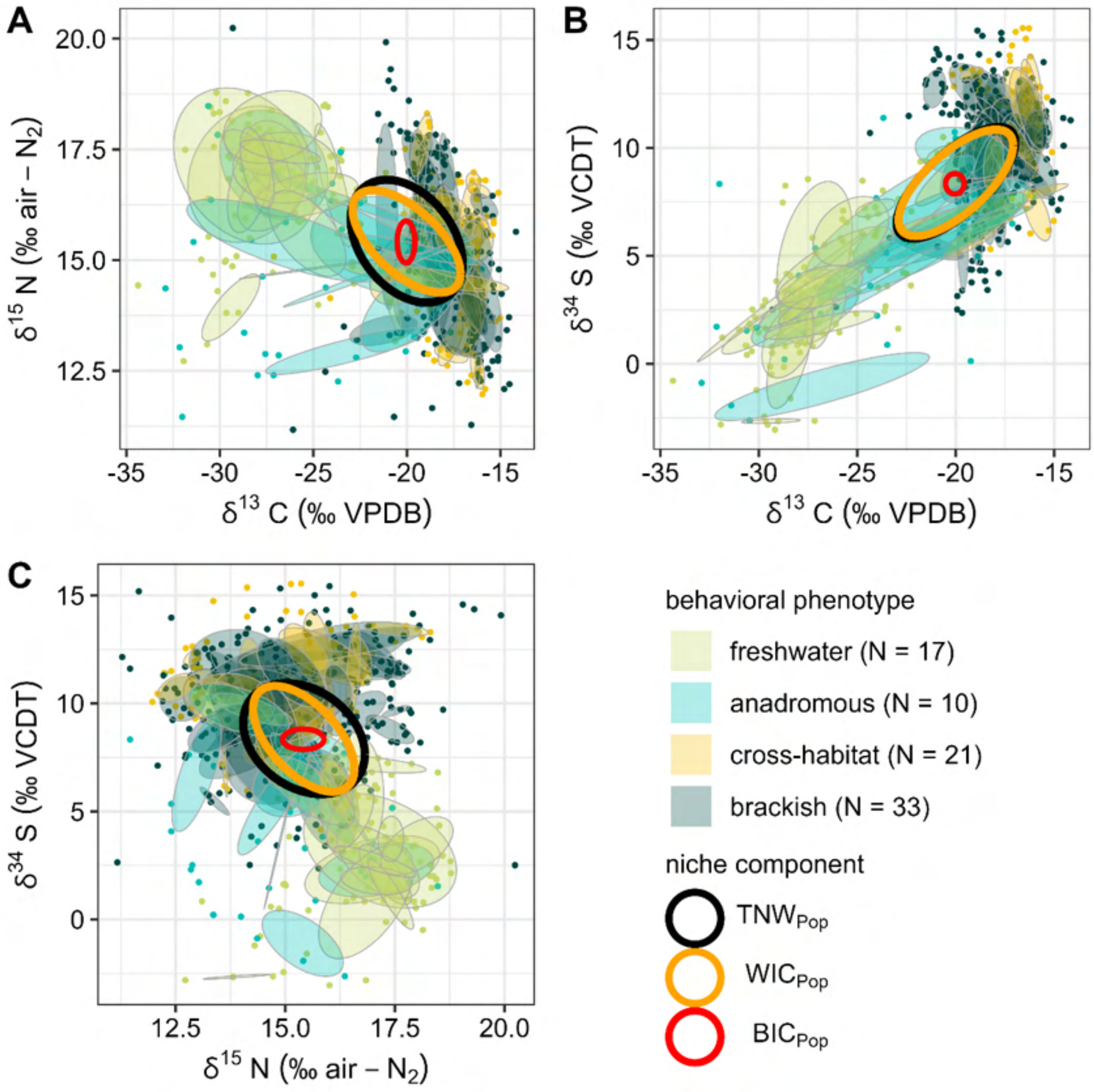

A
δ15 N (‰ air – N2)
20.0
17.5
15.0
12.5
-35
-30
-25
-20
-15
δ13 C (‰ VPDB)
B
δ34 S (‰ VCDT)
15
10
5
0
-35
-30
-25
-20
-15
δ13 C (‰ VPDB)
C
δ34 S (‰ VCDT)
15
10
5
0
12.5
15.0
17.5
20.0
δ15 N (‰ air – N2)
behavioral phenotype
freshwater (N = 17)
anadromous (N = 10)
cross-habitat (N = 21)
brackish (N = 33)
niche component
TNWPop
WICPop
BICPop

Figure 8