Recruitment of the European smelt in a changing estuary: An Individual-based modelling assessment of environmental driver, climate change and management implication in the Elbe estuary

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Abstract

Estuarine environments are highly productive transition zones between freshwater and marine habitats and play an important role as nursery grounds and migration corridors for diadromous fish species. At the same time, they are subject to intense anthropogenic modification and accelerating climate change, altering hydrodynamics, water quality and habitat connectivity. This thesis examines how interacting environmental drivers control early life stage development and recruitment of the European smelt (*Osmerus eperlanus*) in the Elbe estuary and evaluates how future climate change and estuarine management decisions may impact recruitment dynamics and ecosystem functioning.

Using a multi-stage individual-based model (IBM), explicitly developed for the European smelt, the development of eggs, yolk-sac larvae and exogenous feeding larvae was determined by linked of extrinsic environmental drivers (temperature, oxygen availability, prey biomass, currents, turbidity and salinity) to intrinsic physiological processes governing development, growth and mortality. The thesis includes the model's parameterisation, validation and extensive sensitivity analysis as well as the use case application using both a one-dimensional observation based forcing setup and a three-dimensional configuration coupled offline to a Lagrangian particle-tracking framework. The latter framework was used using high-resolution hydrodynamic and biogeochemical forcing provided by a coupled SCHISM-ECOSMO modelling system setup of the Elbe estuary.

IBM results demonstrate that temperature and oxygen availability consistently emerge as the dominant drivers of successful development and survival. Yet significance varied across life stages. During endogenous development, increasing temperatures accelerate development rates thereby shortening vulnerable life stages and advancing the onset of first feeding, all of which can enhance individual survival. However, during the exogenous feeding stage, development is governed by the balance between prey intake and the individual metabolic energy demand, which both are heavily impacted by local temperatures. Once thermal optima are exceeded, metabolic rates increase disproportionately, reducing individual growth and an increased risk of starvation and ultimately mortality. Oxygen limitations impose an additional and often decisive constraint, with sharply increasing mortality if concentrations fall below the individual's critical threshold and are often connected to a temperature-driven component further decreasing survival chances.

Simulations using a RCP8.5-type climate scenario reveal substantial changes in habitat suitability within the estuary. Increased warming, decreased oxygen concentrations and changes in the salinity gradients drive a downstream shift of favourable nursery habitats and a contraction of suitable habitats in the central estuary. This shift results in an increasing exposure of early life stages to combined thermal and hypoxic stress. Although moderate warming may temporarily result in enhanced development conditions during spring, warmer summer temperatures result in increased mortality and vulnerability to frequent hypoxic events. The models result further indicate that future recruitment is even more shaped by a combination of interacting stressors, making the prediction of recruitment variability even more challenging.

Beyond climate driven changes, this thesis highlights the importance of estuarine management decisions for the smelt's recruitment success. Using scenario analysis of potential flood-adaptation measures reveal significant contrasts between hard-engineered structures and nature-based solutions. Barriers such as flood gates severely reduce longitudinal connectivity by restricting access to spawning habitats and promote aggregation affects that could further increase the individual's mortality, especially for migratory species. In contrast, nature-based solutions such as controlled flood polders and channel reconstruction can enhance spawning habitat availability, partially restore connectivity and provide local growth benefits. These results demonstrate that recruitment dynamics of a key species such as the European smelt can be used as a sensitive indicator for the ecological impact of large-scale engineering projects.

Overall, this thesis demonstrates that mechanistic, spatially explicit individual-based model provide a powerful framework for integrating multiple stressors across life stages and habitats. By linking physiological processes to environmental drivers, the developed smelt IBM offers insights that extend beyond correlative analysis and enables robust assessment of climate change impacts and management trade-offs. The findings emphasise that sustainable estuarine management, especially under the increasing influence of climate change should be using key-species based assessments to improve the measures ecological benefit.

Zusammenfassung

Ästuarine Lebensräume sind hochproduktive Übergangsregionen zwischen Süßwasser und marinen Lebensräumen und spielen eine wichtige Rolle als Kinderstuben und Migrationskorridore für diadrome Fischarten. Gleichzeitig stehe sie unter dem ständigen Einfluss anthropogener Veränderungen und des stärker werdenden globalen Klimawandels, was zu Veränderungen des hydrodynamischen Zustands, einer verringerten Wassergüte und schlechterer Habitatqualität führt. Ziel dieser Dissertation ist es zu untersuchen, wie Wechselwirkungen von Umweltfaktoren die Entwicklung und das Überleben von frühen Entwicklungsstufen des Europäischen Stints (*Osmerus eperlanus*) im Elbeästuar steuern und darauf basierend zu beurteilen, welche Folgen die ansteigende Belastung durch den globalen Klimawandel und zunehmende anthropogene Nutzung der Elbe auf die Populationsdynamik des Stints und die allgemeine Habitatualität haben.

Mit Hilfe eines speziell für den Europäischen Stint entwickelten Individual-basierten Modells (IBM), wurde die Entwicklung von Eiern, Dottersacklarven und aktiv jagenden Larven simuliert, indem äußere Umweltfaktoren (Temperatur, Sauerstoffgehalt, Beutebiomasse, Strömung, Trübung und Salzgehalt) mit intrinsischen physiologischen Prozessen der Entwicklung, des Wachstums und der Mortalität verknüpft wurden. Im Zuge der Arbeit wurde das Modell parametrisiert, validiert und mit Hilfe einer Sensitivitätsanalyse getestet. Angewandt wurde das Modell danach in zwei Konfigurationen: einer eindimensionalen, messwertbasierten Forcing-Variante und einer dreidimensionalen Konfiguration, welche offline an ein Lagrange'sches Verdriftungsmodell gekoppelt wurde. Letzteres wurde in Kombination mit hochaufgelösten hydrodynamischen und biogeochemischen Daten aus einem Elbe Setup des gekoppeltem Modells SCHISM-ECOSMO genutzt.

Die Ergebnisse des IBMs zeigen, das Temperatur und Sauerstoffverfügbarkeit als dominierende Einflussfaktoren für die erfolgreiche Entwicklung und das Überleben gesehen werden können, deren Bedeutung jedoch in Abhängigkeit zum Lebensstadium variiert. Während der endogenen Entwicklung beschleunigen steigende Temperaturen die Entwicklungsraten, was zu einem Früheren einsetzen der ersten Nahrungsaufnahme führen kann, wodurch allgemein erhöhte Überlebenschancen zu erwarten sind. Nach dem Übergang zu einer exogenen Nahrungsaufnahme wird die Entwicklung hingegen durch das Gleichgewicht zwischen erfolgreicher Beuteaufnahme und metabolischem Energiebedarf bestimmt, wobei beide Prozesse jeweils eine hohe Temperatur Abhängigkeit aufweisen. Werden artspezifische thermische Optima überschritten, steigen die metabolischen Kosten stark, was zu einem verminderten Wachstum und

schlussendlich einer erhöhten Sterblichkeit führen kann. Sauerstofflimitierungen stellen dabei eine zusätzliche und häufig entscheidende Einschränkung dar, da bei Unterschreitung der spezies-spezifischen Sauerstoffgrenzwerte die Mortalitätsraten stark ansteigen. Besonders gefördert wird dies, wenn sowohl Sauerstoff als auch Temperatur außerhalb der Grenzbereiche liegen und somit eine höhere Stressbelastung des Individuums vorliegt.

Simulationen, welche ein RCP8.5 Szenario als Grundlage nutzen, zeigen deutliche Veränderungen der Habitatqualität innerhalb des Elbeästuars. Erhöhte Temperaturen, abnehmende Sauerstoffkonzentrationen und Veränderungen des Salzgehaltes führen zu einer stromabwärts gerichteten Verlagerung günstiger Aufwuchs Habitate sowie einer allgemeinen Verschlechterung der Aufwuchs Bedingungen im zentralen Ästuar. Besonders während früheren Leben Stadien, steigt dadurch die Exposition gegenüber thermischen und hypoxischen Extremkonditionen. Während moderate Temperatur Anstiege im Frühjahr temporär verbesserte Entwicklungsbedingungen bedeuten, führen erhöhte Sommertemperaturen zu erhöhter Mortalität und einer größeren Anfälligkeit gegenüber der häufiger auftretenden hypoxischen Ereignisse. Die Ergebnisse zeigen, dass zukünftige Rekrutierung weiter durch eine Kombination von Umweltfaktoren beeinträchtig werden könnte, wodurch sich sichere Vorhersagen nur erschwert treffen lassen.

Über klimabedingte Veränderungen hinaus, unterstreicht diese Arbeit die Bedeutung estuariner Managmententscheidungen für die erfolgreiche Entwicklung des Stints. Mithilfe von Modellanalysen potenzieller Hochwasseranpassungsmaßnahmen werden deutliche Unterschiede zwischen hartbaulichen Strukturen und naturbasierten Lösungen deutlich. Barrieren wie Flutstromwerke reduzieren die longitudinale Konnektivität erheblich, indem sie den Zugang zu Laichgebieten einschränken und weiter die lokale Ansammlung von Fischen fördern, wodurch erhöhte Sterblichkeitsrisiken entstehen. All dies betrifft besonders die diadromen Fischarten. Naturbasierte Ansätze wie kontrollierte Flutpolder oder die Wiederverbindung von Nebenarmen können hingegen das Angebot geeigneter Laichhabitate erhöhe, Konnektivität wiederherstellen und lokale Wachstumsbedingungen verbessern. Diese Ergebnisse zeigen, dass die Rekrutierungsdynamik einer Schlüsselspezies wie dem Stint als sensitiver Indikator für den ökologischen Einfluss von wasserbaulichen Maßnahmen dienen kann.

Insgesamt zeigt diese Dissertation, dass die mechanistische, räumlich explizite Individuen-basierte Modellierung ein leistungsfähiges Werkzeug zur Integration multipler Stressoren über verschiedene Lebensstadien und Habitate hinweg

darstellen. Durch die Verknüpfung physiologischer Prozesse mit Umweltbedingungen liefert das entwickelte IBM Erkenntnisse, die überkorrelative Ansätze hinausgehen, und ermöglicht robuste Bewertungen klimabedingter Veränderungen und Management Konflikten. Die Ergebnisse unterstreichen, dass eine nachhaltige Bewirtschaftung von Ästuaren, besonders unter immer weiter steigendem Einfluss des globalen Klimawandels. Die Berücksichtigung schlüsselartbasierter Bewertungen erfordert, um den ökologischen Nutzen von möglichen Anpassungsmaßnahmen zu maximieren.

List of Publications

Study 1

Drewes, D., Schrum, C., Pein, J., Benkort, D., & Daewel, U. (2025). Environmental controls on the development of early life stages of European smelt in the Elbe estuary. *Ecological Modelling*, *510*, 111313. https://doi.org/https://doi.org/10.1016/j.ecolmodel.2025.111313

Study 2

Drewes, D., Schrum, C., Pein, J., & Daewel, U. (2025). Hydrodynamic retention and environmental stressors shape the recruitment of the European Smelt in the Elbe estuary: an individual-based modelling study. (under review in *Estuarine, Coastal and Shelf Science*)
https://ssrn.com/abstract=5899748

Study 3

Drewes, D., Schrum, C., Pein, J., & Daewel, U. (2025). Understanding the consequence of flood adaptation scenarios on migratory key species in the estuarine environment of the Elbe estuary – the European Smelt as a benchmark for future decision making. (to be submitted)

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Introduction

Estuaries as Nurseries and Migration Corridors for diadromous species

Estuarine environments form the transition zone between freshwater and marine ecosystems and play a central role in linking these two domains (Pritchard, 1967). Although estuaries account for only around 5.7% of the global coastal area, they support exceptionally high biological productivity (Whittaker & Likens, 1973). Primary production rates are comparable to those of tropical rainforests (Whittaker & Likens, 1973), and an estimated 5.2% of global fish originates from estuarine systems (Houde & Rutherford, 1993). This significant ecological importance results from a unique combination of nutrient-rich conditions, tidal reallocation of available resources and pronounced spatial heterogeneity along salinity gradients. Together, these factors create a wide range of ecological niches that can be exploited by organisms with different habitat requirements and life history strategies (Pihl et al., 2002; Thiel et al., 1996).

Beyond productivity, estuaries are characterised by strong longitudinal and lateral connectivity, allowing a bidirectional movement of individuals between the oceanic and freshwater regimes via their hydrological connection. Further, connectivity describes the opportunity of individuals to move in between available subhabitats within the estuarine environment (Pringle, 2001). This connectivity supports biodiversity and facilitates the exchange of nutrients and sediments between freshwater, marine and terrestrial ecosystems (Martinetto et al., 2020; Paalvast & van der Velde, 2014). At the same time, estuaries are focal points of human activity (Holzwarth & Wirtz, 2018; Lonsdale et al., 2022; Paalvast & van der Velde, 2014). Their connectivity supports ports, optimal shipping routes and coastal settlements and therefore results in intense socioeconomic pressure on the estuarine environment. The coexistence of ecological importance and socioeconomic value makes estuaries systems of inherent conflict, where conservation goals and human demands often directly oppose each other.

One of the most important ecological functions of estuaries is their role as nursery grounds and migration corridors for diadromous fish species (Guerreiro et al., 2021; Martinho et al., 2007; Tulp et al., 2022). Diadromous species migrate between freshwater and marine environments to complete their life cycles and rely on estuarine habitats especially during critical developmental phases (McDowall, 1988; Thiel, 2001). Early life stages, in particular, benefit from the high productivity

and shelter provided by estuaries, making these habitats central to recruitment success (Thiel et al., 1995).

Depending on the direction of migration relative to salinity gradients, diadromous fishes can be classified into three groups:

(i) **Anadromous species:** Adult spawners enter the freshwater domain for spawning purposes and early life stages utilise the estuarine environment for enhanced development success and continue their foraging in the coastal and open ocean
Example: Atlantic salmon (*Salmo salar*) (Jonsson & Jonsson, 2009)

(ii) **Catadromous species:** Adult spawners use the saline regions for reproduction and the early life stages are drifted into regions dominated by less saline conditions. After foraging in the freshwater domain, the adult individuals migrate back to the saline domain for reproductive purposes
Example: European Eel (*Anguilla anguilla*) (Aarestrup et al., 2009)

(iii) **Amphidromous species:** Species frequently migrate between the two regimes and spend most of their lives under brackish water conditions
Example: Common Flounder (*Platichthys flesus*) (Köhler & Hölzel, 1980)

Despite differences in migration strategies, all groups depend on estuarine nursery habitats where early development is supported by favourable environmental conditions.

The estuaries nursery function is closely linked to a combination of characteristic features. As previously reported, high phytoplankton and zooplankton productivity ensures sufficient prey availability for exogenous feeding early life individuals (Eick & Thiel, 2014; Thiel, 2001; Thiel et al., 1995). Shallow intertidal flats and nearshore areas provide suitable refuge habitats, especially during low tide (Cattrijsse & Hampel, 2006; Nicolas et al., 2010; van der Veer et al., 2011) and often offer warmer conditions resulting in faster development of early life stages (Arula et al., 2015; Guerreiro et al., 2021; Martinho et al., 2007). In addition, tidal-driven sediment dynamics create zones of elevated turbidity that reduce visibility for visual predators while still allowing feeding, especially by larvae adapted to such turbid conditions (Illing et al., 2024; Meager et al., 2005; Tigan et al., 2020). Together, these mechanisms highlight why estuaries function as effective nursery grounds across a wide range of species.

A mentionable side effect of the migration of diadromous species is the bidirectional transport of nutrients and biomass between ecosystems. Especially

anadromous species transport marine-derived nutrients upstream during spawning migration, where carcasses and early life stages provide food resources for aquatic and terrestrial consumers (Bilby et al., 2003; Cederholm et al., 1999; Mitchell & Lamberti, 2005; Reimchen, 1994; Willson & Halupka, 1995). Conversely, the downstream export of juveniles and organic matter links estuarine productivity to coastal marine ecosystems and can enhance primary production under nutrient-limited conditions (Johnston et al., 2004; Moore & Schindler, 2004).

Natural and Anthropogenic Controls on Estuarine Ecosystem Function

Throughout their life cycle, fish are exposed to a complex combination of extrinsic drivers that influence survival, growth and development. Key stressors include temperature, oxygen availability and prey abundance, all of which directly affect physiological performance and energetic balance (Arula et al., 2017; Ban et al., 2022; Blaxter, 1992; Elshout et al., 2013; Kuparinen et al., 2011; Möller & Scholz, 1991; Pörtner et al., 2017; M. Power & Attrill, 2007; Sirois & Dodson, 2000). Additional factors such as salinity, turbidity, current dynamics and pollution further shape habitat suitability and species distribution within estuarine systems (Chen et al., 1997; Hasenbein et al., 2013; Illing et al., 2024; Pohl, 1990; Theilen et al., 2025; Thiel et al., 1995). In natural systems, these drivers vary strongly in space and time, creating dynamic habitats that organisms must continuously respond to. However, anthropogenic modification has intensified and altered many of these gradients (Ahlhorn, 2009; Bindoff et al., 2019; Ducrotoy et al., 2019). Channel deepening, dredging, land reclamation and wastewater discharge modify hydrodynamics, sediment transport and nutrient regimes, often resulting in habitat degradation and reduced connectivity (Courrat et al., 2009; Ducrotoy et al., 2019; Kappenberg & Fanger, 2007; Möller & Scholz, 1991; Thiel & Pezenburg, 2001; Weilbeer, 2014; Winterwerp et al., 2013).

Climate change further amplifies these pressures (Bindoff et al., 2019). Rising water temperatures directly influence metabolic rates, growth and survival of fish, particularly during early life stages (Dahlke et al., 2020; Gillooly et al., 2001; Keskinen et al., 2012). Moderate warming may accelerate development and shorten vulnerable life stages, potentially reducing predation risk (Bailey & Houde, 1989; Cowan et al., 1996; Dahlke et al., 2020; Kuparinen et al., 2011; Vennell et al., 2021). However, when temperatures exceed species-specific optima, metabolic demands increase beyond what can be compensated by food intake, resulting in reduced growth and increased mortality (Blaxter, 1992; Dahlke et al., 2020; Gillooly et al., 2001; Pörtner & Knust, 2007).

Warming also interacts with biogeochemical processes, exacerbating eutrophication and oxygen depletion in many estuarine systems. Increased stratification, reduced river discharge and altered sediment dynamics enhance the frequency, duration and spatial extent of hypoxic events (Biederbick et al., 2025; Hein et al., 2018; Rabalais et al., 2009; Seiffert & Hesser, 2014). Low oxygen conditions impose strong physiological constraints on early life stages by limiting aerobic scope, further reducing growth efficiency and increasing mortality risk (Elshout et al., 2013; Möller & Scholz, 1991; Pörtner et al., 2017; Pörtner & Knust, 2007). In this way, hypoxia can act as a functional barrier, restricting access to suitable habitats or even result in events of mass mortality if nursery grounds become impacted (Ali & Mishra, 2022; Möller & Scholz, 1991; Pörtner et al., 2017; Pörtner & Knust, 2007).

Phenological shifts represent a less visible but potentially critical climate impact on diadromous species. Warming advances spawning timing in temperature-sensitive species through accelerated gonad maturation, while zooplankton phenology shifts independently based on spring temperature and photoperiod cues (Brodersen et al., 2011; Nicholson et al., 2008). Temporal mismatches between larval emergence and prey availability can dramatically reduce recruitment even when absolute abundances of both predator and prey remain stable (Cushing, 1990; Hjort, 1914; Sirois & Dodson, 2000). The magnitude and direction of phenological shifts vary by species, trophic level and geographic region, creating complex and often hard to predict recruitment consequences.

At the same time, the increasing frequency of extreme flood and storm events has driven extensive investments in flood-protection infrastructure (Ahlhorn, 2009; Valente & Veloso-Gomes, 2019). While dams, tidal barriers and river regulation reduce flood risk, they often fragment longitudinal and lateral connectivity within estuaries, restricting access to critical spawning and nursery habitats (Hall et al., 2012; M. E. Power et al., 1996; C. Pringle, 2006). Global projections suggest that reduced connectivity due to dam construction will affect estuarine systems globally within the coming decades (Grill et al., 2019; Zarfl et al., 2015). Even where fish passage structures are implemented, effective accessibility and usage remain uncertain, especially for early life stages and weaker swimmers (Zarri et al., 2022).

Nature-based adaptation measures, such as the construction of controlled flood polders and creation of artificial wetlands, are increasingly promoted as alternatives to hard infrastructure (Warachowska et al., 2025). These systems can provide valuable habitat and partially restore lateral connectivity, but they also modify the hydrodynamic exchange and may alter existing habitat distributions at the estuary scale (Cox et al., 2006). Consequently, climate adaptation strategies

may simultaneously mitigate and intensify ecological stressors, emphasizing the need for system-specific assessments of cumulative impacts on estuarine ecosystem functioning.

Critical Knowledge Gaps

Despite substantial progress in documenting anthropogenic and climatic pressures on estuarine ecosystem, the following gaps formed the foundation of this thesis:

First, the **relative importance and interactive effects** of multiple stressors on early life stage recruitment remain poorly quantified, especially on a species-specific level of estuarine fish. Temperature, oxygen availability, prey abundance, salinity, turbidity and hydrodynamic conditions are known to influence individual survival and growth, but their relative contribution varies across life stages, seasons and spatial context. Observational studies struggle to disentangle these co-varying drivers, particularly when effects manifest at fine temporal scales (hours to days) or through threshold responses rather than linear relationships. Without a concise understanding of how individual stressors combine, management interventions remain speculative

Second, **mechanistic models linking environmental drivers to individual level outcomes** are lacking for many key species in European estuaries. While long-term monitoring trends document population trends and correlative relationships with environmental variables, these approaches can only to a limited amount help to project species level responses to novel future conditions outside the range of previous observations. Mechanistical models that explicitly represent physiological processes (e.g. growth, metabolism, mortality) and their environmental dependencies offer potential to understand future recruitment variability under climate change scenarios and evaluate management alternatives. However, development, parameterisation and validation of such species-specific models require intensive knowledge of the individual life cycle and data and computational resources, limiting their application.

Third, **evaluation of climate adaptation measures** is often only to a certain amount quantifying the impact on local key species and rather focuses on their target specific engineering performance (e.g. flood risk reduction). While the general impact of interrupted estuarine connectivity has been studied, key-species based studies based on current projects in European estuaries remain less prominent. Studying how adaptation measures impact local key-species can help to understand synergetic benefits for both flood protection and population

conservation. Ultimately such understanding can help to create well-suited, system-specific frameworks that allow for the mitigation of future problems on a longer scale.

These gaps are particularly acute for diadromous species, whose complex life histories involving migrations across ecosystem boundaries make them simultaneously sensitive indicators of estuarine health and challenging subjects for predictive modelling. Understanding recruitment drivers of such species requires integration of processes across spatial scales (spawning grounds to coastal feeding grounds), temporal scales (daily physiological responses to multi-year climate trends) and level of biological organisation (individual energetics to population dynamics).

The European smelt in the Elbe estuary: a case study

The Elbe estuary provides an ideal system to address these knowledge gaps. Extending approximately 140 km from the Geesthacht weir to the North Sea near Cuxhaven, the tidally influenced Elbe has experienced pronounced anthropogenic modification over the past (Kerner, 2007; Pein et al., 2023). A map of the model domain is shown in Figure 1. The main driver of these modifications is the increasing economic demand of the Port of Hamburg, Germany's largest port and a critical node in European trade networks (Köster & Thies, 2015). Intensive dredging is necessary to maintain navigational channels, resulting in altered tidal ranges, particularly amplified around Hamburg, modified sediment dynamics increasing turbidity levels and more frequent hypoxic events in the Port region (Kappenberg & Fanger, 2007b; Köster & Thies, 2015; Weilbeer, 2014). These changes have been linked to declining abundances and spatial redistribution of fish species, raising concerns about long-term ecosystem health (Möller & Scholz, 1991).

Within this system, the European smelt (*Osmerus eperlanus*) plays a key ecological role (Eick & Thiel, 2014). This small-bodied anadromous fish dominates the estuarine fish community by biomass, contributing 54-74% of total fish biomass across different time periods (Theilen et al., 2025). Adult smelt migrate upstream from coastal feeding grounds during late winter to spawn in freshwater an oligohaline reaches (Eick & Thiel, 2014; Lillelund, 1961; Sepulveda et al., 1993; Theilen et al., 2025; Thiel, 2001; Thiel et al., 1995). Reported cues for the migration onset are warming

temperatures and increasing discharge that guide the spawners into the estuarine domain.

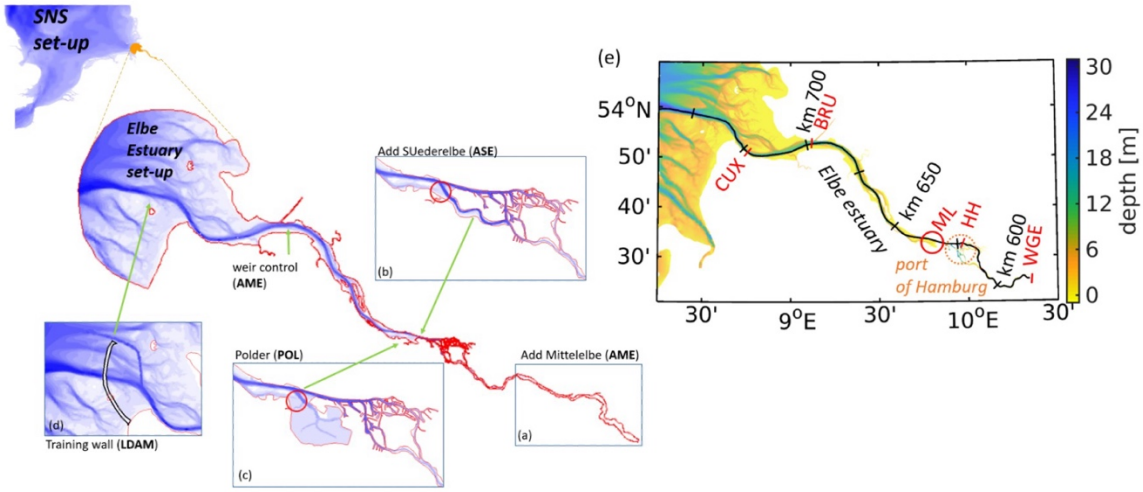


Figure 1: Maps of the Elbe model domain featuring topographical shading of the depth. A)-D) on the left side show the adaptation scenarios that are later used in the course of the estuarine management discussion. E) shows the general domain of the Elbe with a red circle indicating the shallow area commonly named as Mühlenberger Loch, recognized as an important nursery ground for the European smelt in the Elbe. Pictures are adapted from Pein et al. (2025).

Eggs attach to hard substrates in shallow, fast-flowing areas, where early development proceeds through temperature-dependent endogenous stages (Eick & Thiel, 2014; Lillelund, 1961; Thiel et al., 1995). After the transition to exogenous feeding strategies, larvae typically remain in their estuarine nursery grounds exploiting high zooplankton productivity before recruiting to juvenile and adult populations in the North Sea (Lillelund, 1961).

Smelt abundance in the Elbe exhibits pronounced interannual variability, with recent monitoring data documenting sustained declines across all life stages (Bioconsult, 2025; Scholle & Schuchardt, 2019; Thiel, 2011) and monitoring-based catch per unit effort data is presented in Figure 2. Historical reconstruction based on landing records reveals periods of low abundance often associated with degraded water quality, with stock recoveries following significant improvements in environmental conditions such as those observed in the early 1990s after the implementation of strict wastewater treatments (Thiel, 2011). Contemporary declines have been attributed variously to habitat loss, as seen in case of the partial filling of the Mühlenberger Loch, a dedicated shallow-water spawning and nursery area (Bioconsult, 2025; Thiel & Pezenburg, 2001). Further, the increased frequency and spatial extent of hypoxic conditions coupled with elevated turbidity levels were discussed as potential drivers for the recent declines.

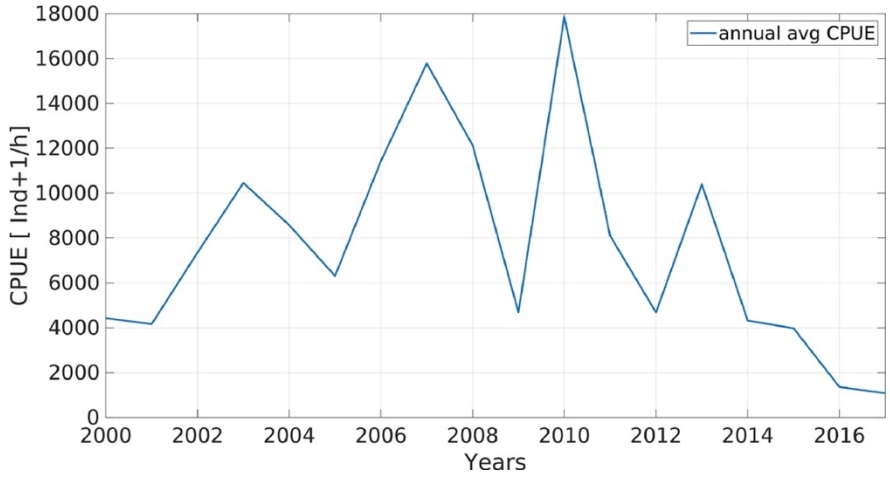


Figure 2: Catch-per-unit-effort (CPUE) as calculated from the available monitoring data covering the years 2000-2017. Figure is taken from Drewes et al. (2025)

The sensitivity of smelt populations to environmental variability makes them vulnerable indicators of ecosystem health (McCarthy et al., 2020). Their ecological role as a trophic link between lower (planktonic) and higher (piscivorous fish, birds, mammals) trophic levels means that smelt population dynamics have the potential to cascade through the estuarine food web, affecting predator populations and energy flow pathways (Dänhardt et al., 2011; Eick & Thiel, 2014). Understanding the mechanism underlying smelt recruitment variability therefore has implications beyond the species itself, providing insights into how estuarine fish communities will respond to the intensifying climate and anthropogenic pressures.

Research Objectives

Against this background, this thesis aims to advance mechanistic understanding of how environmental drivers shape early life stage recruitment in the European smelt and to apply this understanding to assess climate change impacts and evaluate alternative management strategies. Specifically, this research addresses three overarching questions:

Q1: What are the dominant environmental drivers of early life stage recruitment in European smelt and how do their relative importance vary across developmental stages?

Extrinsic drivers including temperature, oxygen availability, salinity, prey abundance, turbidity and hydrodynamic conditions all potentially influence smelt growth and survival. However, their relative importance likely differs between endogenous (eggs, yolk-sac larvae) and exogenous feeding stages and may interact synergistically rather than operate independently. Critical bottlenecks and

threshold effects shall be identified using the stage-specific response of the modelled individuals to multiple environmental drivers simultaneously.

Q2: How will projected climate change and anthropogenic pressure affect smelt recruitment?

Using model results based on RCP 8.5 scenarios the impact of a mean temperature increase of 3.2 °C and a 1 m increase of sea level by 2100 is provided as forcing for the smelt model. The resulting changes in habitat suitability, shifts in phenological timing of spawning and prey availability potentially create novel combinations of extrinsic stressors outside the range of historical experience. The question aims to answer how future climate scenarios and resulting recruitment trajectories change and to identify emerging risks (phenological mismatch, combined thermal-oxygen stress) due to the projected changes.

Q3: What are the ecological consequences of flood adaptation measures for smelt recruitment and how can adaptive management balance flood protection with ecosystem function?

Recently, model-based assessments of the impact of different adaptation strategies aiming at an increased flood protection were discussed. The proposed strategies included hard-engineered solutions (tidal barriers, storm surge gates) and nature-based approaches (polder construction, channel reconnections). These measures will alter estuarine hydrodynamics, habitat connectivity, salinity structures and nursery ground availability with differential consequences for smelt populations. Using the model smelt model, we aim to investigate how these changes affect recruitment of the smelt. The results shall help to understand how effective construction plans could consider ecological co-benefits and trade-offs alongside engineering performance metrics.

Approach

In the following, the approaches and methods used are presented. Further, the key messages of the included studies shall be listed and put into context for an easier understanding of their meaning and role for the overall aim of the thesis. The chapter is therefore structured into two main parts: an introduction into individual-based modelling, where the concept behind the modelling approach as well as the model that was developed in the course of this thesis are described and a second part that covers the summaries of included studies in the frame of the thesis.

The method of individual-based modelling

The concept of individual-based modelling (IBM) has become a widely applied approach in ecological and biological research. Following the study by Huston et al. (1988), the use of this modelling framework increased substantially (Grimm, 1999). One of the first fish related IBMs was presented by DeAngelis et al. (1980) and already incorporated individual-levelled calculations of mortality, growth, feeding and even cannibalism. In subsequent years, the applications of IBMs in population and ecosystem modelling continued to expand (Grimm, 1999).

Using single individuals as the fundamental modelling unit allows for a mechanistic understanding of how changes in extrinsic environmental conditions translate into intrinsic physiological responses. This approach improves the identification of potential stressors and thresholds that may remain obscured in averaged cohort-based or population-level approaches relying on single environmental drivers such as temperature or salinity. An additional advantage of IBMs is the explicit representation of individual life histories within the model domain, enabling the investigation of local processes at fine temporal and spatial scales and their linkage to population-level dynamics. This framework facilitates the inclusion of individual variability, a key property that is typically neglected in traditional cohort-based approaches (Grimm, 1999; Van Winkle et al., 1993).

An important aspect of IBMs is their inherent complexity. As additional processes are included, computational demands increase accordingly. However, higher model complexity can also improve the realism of simulated dynamics and enhance agreement with observed species behaviour and population patterns.

The smelt IBM

A central objective of this thesis was the development and application of an IBM for the European smelt. The model incorporates three different life stages: eggs, yolk-sac larvae and actively feeding larvae. A fourth class was introduced to track deceased individuals. During the analysis, life stages were often classified based on their main energy source. Endogenous stages included the egg and yolk-sac individuals as energy is gained from internal reservoirs (e.g. yolk absorption) and exogenous stages describe the active feeding individuals as their energy intake depends on external sources. In the following we present a brief overview of the main processes and parameterisations of our IBM, a schematic is included in Figure 3 below. A detailed model description and sensitivity analysis of intrinsic and extrinsic parameters is provided in **Study 1**.

Spawning represents the starting point of individual development. In the model, the size of the spawning stock is not explicitly parameterised. Gonad development is the main driver of the time of spawning. As with many fish species, gamete development in smelt accelerates under warmer thermal conditions (Lillelund, 1961). Based on observations by Lillelund (1961), we implemented the averaged February temperature as a proxy for the onset of spawning in our IBM. Warmer conditions result in earlier spawning, with the earliest possible spawning being constrained to occur no earlier than the 1st of March. This approach was used in **Studies 1 and 2**, due to the idea of testing the local differences in earlier spawning across the estuarine domain, the onset of development was manually chosen in **Study 3**.

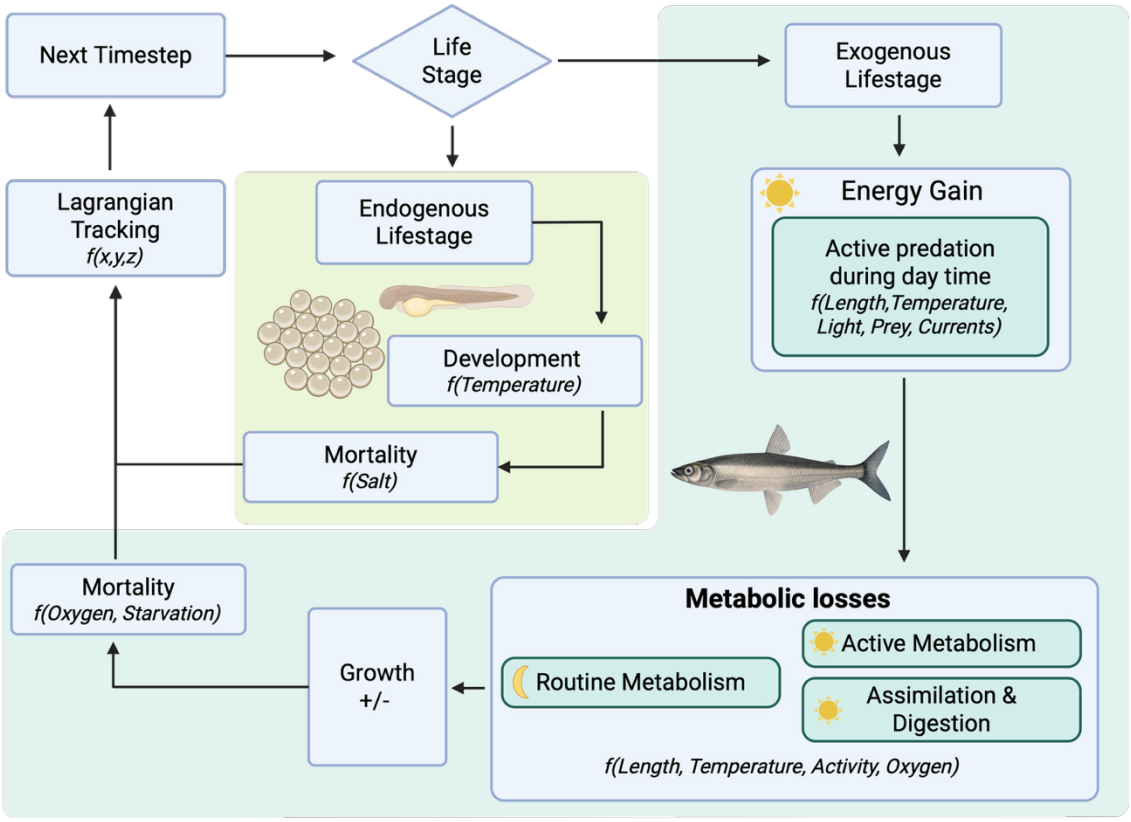


Figure 3: Schematic description of the smelt IBM. Both life stages are included, the endogenous one that describes the development during egg and yolk-sac phase and the exogenous stage that includes the active predation and calculation of growth based on the individual's energy budget. Figure has been adapted based on the model description in Daewel, Peck, Kühn, et al. (2008).

Following spawning, individuals pass through both endogenous life stages during which development rates are exclusively controlled by local temperature. Warmer conditions result in faster completion of these life stages. As smelt eggs are typically attached to hard substrates such as rocks or groynes, individual movement during

endogenous development is restricted. This constraint allows for the differentiation of development conditions among selected spawning grounds (**Studies 2 and 3**), as individuals remain fixed at their initially selected spawning location.

Upon completion of endogenous development, larvae transition into the active feeding stage. Growth and survival during this stage depend on the ability of individuals to successfully capture and assimilate suitable prey. Prey availability is derived from available zooplankton biomass and was prescribed to the IBM as an extrinsic forcing. Conversion of the available zooplankton biomass followed the approach described in Daewel, Peck, Schrum, et al. (2008).

Development of actively preying individuals is described by a simplified energy conservation approach. The individual energy balance is calculated using a Wisconsin-type bioenergetic model (Kitchell et al., 1974), in which growth (G) is calculated as:

$$G = C\rho(1 - \Phi_{SDA}) - R$$

Individual growth reflects the balance between energy intake through consumption (C) and different energy losses. Energy losses arise from the assimilation efficiency (ρ, Buckley and Dillmann 1982), the specific dynamic action (Φ_{SDA}, Lantry and Stewart 1993) and due to metabolic processes (R). Both, assimilation efficiency and the metabolic losses are functions of individual body size. Metabolic loss is further impacted by extrinsic factors such as temperature (Gillooly et al., 2001) and oxygen availability (Domenici et al., 2013). Increasing temperatures increase metabolic demands, resulting in decreased growth as soon as temperature exceeds the species optimal thermal range (Gillooly et al., 2001). Recruitment in the context of this study is referred to as the moment the individuals reach a size of 25 mm. As individuals above such a body size acquire increasing swimming capacities as well as develop further metabolic demands, the simulations were stopped once such lengths are reached.

Individual consumption is governed by both intrinsic and extrinsic drivers. Intrinsic drivers include physiological traits such as swimming speed, optimal prey size in relation to the individual body length, and a maximum daily consumption limit. Extrinsic drivers include temperature, current velocity, prey availability, oxygen concentration and light conditions. In **Study 2**, the influence of turbidity on the prey capture success was parameterised following the study by Illing et al. (2024).

Mortality is included in the model using a superindividual approach (Scheffer et al., 1995). Each individual is represented as a superindividual describing the life history of an initially defined number of subindividuals. All subindividuals share the same

development history, while extrinsic forcing conditions may differ between superindividuals. During the endogenous stages, stage-specific constant mortality rates are applied, reducing the number of subindividuals per superindividual. During later development stages, mortality is derived from the individual energy balance and the Fulton Life Quality Index. Under conditions of starvation or reduced life quality, mortality rates increase and may ultimately result in the loss of the superindividual. During the yolk-sac and exogenous stage, oxygen concentrations below a predefined hypoxic threshold (5 mg L^{-1}) trigger an immediate increase in mortality rates, which are superimposed to the baseline mortality. Under anoxic conditions ($\leq$ 2 mg L^{-1}), the individual dies immediately as no likelihood of survival is reported for smelt larvae under such conditions.

The IBM was designed to allow for flexible forcing configurations. Environmental input can be derived from observational data (**Study 1**), resulting in a one-dimensional modelling setup suitable for testing isolated effects of environmental variability on individual development. In **Studies 2** and **3**, the IBM was coupled to a Lagrangian particle tracking framework, enabling a three-dimensional representation of individual trajectories and development. This coupling allowed the use of high-resolution hydrodynamic and biogeochemical output from the SCHISM-ECOSMO modelling system for the Elbe system as (Pein et al., 2023, 2025). We followed an offline coupling approach, meaning that simulations of the model study were purely used as forcing without potential feedback of the IBM to the model results.

During coupling, individual movement was extended by an additional term representing active vertical migration. Migration capacity was linked to individual swimming speed and therefore increased with body size. Such migration patterns are often observed in early life stages in tidally driven domains and is considered an important mechanism for retention in favourable habitats (Gregory Lough & Manning, 2001; Laprise & Dodson, 1989).

Overview of the included studies

After broadly introducing the IBM system employed in this thesis, the studies forming the base for the subsequent discussion are summarized according to their main objectives and findings.

Model development and validation are an essential component of this thesis, particularly as a novel IBM was developed and required thorough evaluation. **Study 1** therefore provides a comprehensive model description, validation, and sensitivity analysis of both intrinsic and extrinsic parameters. The primary objective was to

demonstrate the model's ability to reproduce previously observed development patterns across all life stages. Parameter sensitivity was assessed using a Latin-Hypercube sampling approach following Megrey & Hinckley (2001). After successfully validating the model, the model's capability to reproduce year-to-year recruitment based on forcing timeseries from the Elbe ranging from 2000-2017 was made. Model development was compared to different extrinsic forcing variables and monitoring based smelt catches.

Study 2 represents the transition of the initial one-dimensional setup to a fully three-dimensional IBM coupled to the SCHISM particle-tracking framework. A key sub-objective of this study was further model evaluation, with a particular focus on the IBM's ability to reproduce favorable spawning ground dynamics observed for example in the Mühlenberger Loch. In addition, the influence of active tidal retention and varying turbidity conditions during the exogenous feeding stage was tested and evaluated based on individual growth responses. All simulations were forced using environmental conditions representative of the state of the Elbe estuary around the year 2012, and the results were used as a reference state, thereafter, setting the base for future comparison. The main objective of **Study 2** was subsequently to assess the impact of global warming and sea-level rise on smelt development. Using forcing representative of an RCP 8.5 scenario, the effects of an average temperature increase of 3.2°C and a mean sea-level rise of 1 m within the estuarine environment were investigated and compared to the reference state.

Finally, **Study 3** represents the next step towards an integrated socio-ecological assessment of environmental change in the Elbe estuary. This study examines how large-scale flood-adaptation measures may influence the life cycle of European smelt in the Elbe. The measures are shown in Figure 1 above. The results focus on potential losses of estuarine connectivity, changes in tidal dynamics affecting individual distribution, and possible positive feedback arising from enhanced spawning opportunities due to the artificial creation of wetlands, warmer conditions during the endogenous development or reduced salinity across the estuarine domain. The overarching goal in this last study is to transfer the species-specific knowledge into a management-concerning framework to show how important the consideration of key species is in case of large-scale adaptation scenarios.

Study 1: Sensitivity of the smelt IBM to extrinsic and intrinsic parameters

Drewes, D., Schrum, C., Pein, J., Benkort, D., & Daewel, U. (2025). Environmental controls on the development of early life stages of European smelt in the Elbe estuary. *Ecological Modelling*, *510*, 111313.
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Authors Contributions:

DD developed the smelt IBM, conducted the data analysis and wrote the manuscript. CS, UD, DB contributed to the data analysis, discussion and design of the study, JP contributed to the model development and provided forcing data. CS initiated the study. All authors revised and approved the manuscript.

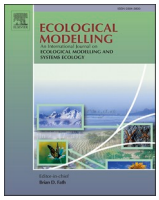
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Environmental controls on the development of early life stages of European smelt in the Elbe estuary☆

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ABSTRACT

The anadromous European smelt (*Osmerus eperlanus*) is a commonly observed fish in the German estuaries of Elbe, Ems and Weser. Their substantial contribution to local biomass and its ecological role as a "wasp-waist" species, show their importance as a key species in estuarine ecosystems. However, recent studies indicate a rapid decrease in smelt populations across all German estuaries. Potential extrinsic drivers of the decrease include climate change driven temperature increase, shifts in food availability and increasing anthropogenic pressures across the estuarine environment. To investigate possible drivers of mortality of early life stages we present an individual-based model (IBM) for the European smelt, applied in a 1D setup. The model includes development during endogenous life stages, the transition to first feeding and growth-related bioenergetic calculations of 0+ larvae. The sensitivity of the model to changes of intrinsic coefficients and extrinsic drivers was tested using ensemble simulations. Ensembles input data was randomly sampled using a Latin Hypercube Sampling routine (LHS). The model's ability to reproduce interannual development variability is tested using a combined input dataset including field measurements and bioecological model output. The model allows us to determine important processes that impact the individual survival throughout its lifetime. We present the model validation along with a dedicated parameter sensitivity study on the individual survival. Using field data, the interannual variability of development rates in the model are compared to available monitoring datasets.

1. Introduction

The European smelt (*Osmerus eperlanus*) is an important contributor to local fish populations of many northern European coastal and estuarine regions. The species is considered a key species in the local environment, as it serves as valuable food source for larger predators such as sea birds along the Wadden sea (Dänhardt et al., 2011; Hennig et al., 2016). Studies focusing on the European smelt describe two populations throughout Northern Europe: the land-locked population (Karjalainen and Sarvala, 1997; Lilja et al., 2012; Keller et al., 2020) and the anadromous population (Lillelund, 1961; Belyanina, 1969; Power and Attrill, 2007; Taal et al., 2014). The latter is known to populate the estuarine environments of Elbe, Ems, Weser and Eider (Lillelund, 1961; Scheffel and Schirmer, 1991; Tulp et al., 2022). Over the years, extensive research has been done on the smelt population in the Elbe Estuary (Lillelund, 1961; Sepulveda et al., 1993; Thiel et al., 1995). It has been demonstrated that during late winter, the adult individuals migrate into the Elbe Estuary to spawn before returning to the coastal regions of the Wadden sea (Lillelund, 1961; Sepulveda et al., 1993). Typically, early life stages of the European smelt spend the first year inside the estuarine environment before leaving towards the coastal regions of the southern North Sea (Lillelund, 1961).

In the past, the population of the European smelt served as a good indicator for the success of restoration measures aiming for improvement of the water quality in the Elbe estuary (Sepulveda et al., 1993). Unfavourable conditions, such as hypoxia (Möller and Scholz, 1991) or enhanced heavy metal concentrations around the spawning grounds (Pohl, 1990) have led to a decline in the overall smelt population. Conversely, improvements in these conditions have contributed to population stability in the Elbe. However, recent reports from local fishers indicate that the smelt population in the Elbe estuary is shrinking, as catch rates have steadily decreased throughout the Elbe (Scholle and Schuchardt, 2020) and Ems (Scholle and Schuchardt, 2019) estuary. This decline may reflect a rise in unfavourable conditions along the

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estuary.

The estuarine environment is predicted to be substantially impacted by anthropogenic climate change. Long-term model-based projections predict major changes in driving forces, such as river run-off, tidal currents and the overall dynamics in the estuary (Seiffert and Hesser, 2014), especially influencing the local temperature and oxygen concentration. Both are critical drivers for successful larvae development and recruitment. These future projections show an increasing trend of seasonal summer mean temperatures in the estuary (Hein et al., 2014). Increased sea levels lead to changes in the tidal regime, resulting in a flood driven, upstream directed, sediment transport (Seiffert and Hesser, 2014). Trend-based analyses in both studies indicate a decline in freshwater runoff due to reduced precipitation. Low riverine runoff increases the residence time and promotes phytoplankton growth, enhancing eutrophication (Hein et al., 2018). This increase in biomass results in greater oxygen consumption during decomposition. Additionally, rising water temperatures reduce oxygen solubility, leading to lower oxygen concentrations year-round. The combined effect of increased oxygen demand and decreased solubility is likely to intensify hypoxic, or even anoxic, conditions in the future (Rabalais et al., 2009; Holzwarth and Wirtz, 2018), creating increasingly unfavourable conditions for smelt larvae.

Nevertheless, anthropogenic climate change is not the only factor influencing the ecosystem of the Elbe estuary. With the port of Hamburg located in the inner estuary, intensive dredging operations were conducted, decreasing the mean water depth of the main channel from 1 m to 14.5 m in recent years (Kappenberg and Fanger, 2007; Winterwerp et al., 2013) to allow large cargo vessels continuous access to the port (Köster and Thies, 2015). Active dredging takes place along the entire main channel spanning over 140 km in length (Kerner, 2007). Due to dredging, changes in the tidal velocities were observed (Kerner, 2007). Outflow velocities during low tide decreased, leading to increase retention of sediment and planktonic biomass. Therefore, oxygen deficiency events occurred more frequently and over larger areas (Kerner, 2007). In addition to the overall effects of oxygen depletion in and around the main channel, dredging was also conducted in shallower regions such as the Mühlenberger Loch (Kerner, 2007). These areas are known as important spawning and nursing grounds for many species, including the European smelt (Sepulveda et al., 1993). Consequently, increased sedimentation due to decreased flow velocities (Kerner, 2007), can influence the development of young individuals due to partial or complete coverage or prevent spawning as adults are not able to reach the spawning locations in time (Lillelund, 1961).

Environmental conditions during early life stage development can vastly impact the individuals later growth and determine their recruitment success. Jonsson and Jonsson (2014) in their table 1 provides a general overview of the potential impact of early life experiences on the later development. Commonly discussed factors are the water temperature and available prey concentrations around the spawning locations (Peck et al., 2012). Both factors are likely to be affected by future changes due to the impact of climate change (Hein et al., 2018) directly altering the likelihood of successful recruitment for early life stages of migratory species such as the European smelt (Kangur et al., 2007; Power and Attrill, 2007; Keskinen et al., 2012; Arula et al., 2017). In his study Lillelund (1961) shows the increased development rates during endogenous life stages under warmer conditions reducing the risk of fungal development and sedimentation related mortality but increasing the risk of a predator-prey mismatch situation (Hjort, 1914; Cushing, 1990; Peck et al., 2012). Further, warmer temperatures during the exogenous stages would induce a larger energy need due to increased metabolic demands, increasing both the need for active movement for active predation and the general prey intake (Peck et al., 2012). Especially during the very early days of exogenous feeding such an increased prey demand can be counteracted by physiological prey limitations such as the larvae's mouth size or stomach capacity (Peck and Daewel, 2007) which would result in starvation induced mortality. The impact of top-down factors determining the recruitment success mainly focusses on predation (Bailey and Houde, 1989; Houde, 2008) and fishing induced mortality (Hixon et al., 2014). While the predator-prey relation between sea birds and the European smelt has been studied in the past years (Dänhardt et al., 2011; Hennig et al., 2016), the impact of fishing especially on the recruitment variability has not been investigated.

Understanding the impact of a changes in the bottom-up limitations and underlying conditions can therefore help to analyse the recruitment variability. A powerful tool for such purposes is the individual-based modelling (IBM) approach. Such models simulate the life history of an individual across life stages. The complexity of IBMs can vary significantly depending on the study's aim. When used to model fish larvae, IBMs generally include egg and yolk-sac development, as well as basic consumption-based growth calculations for exogenously feeding larvae (e.g. Letcher et al., 1996). Similar studies have already been conducted for other species such as sprat (*Spratus spratus*) (Daewel et al., 2008a) and herring (*Clupea harengus*) (Akimova et al., 2023). However, no comparable model has yet been developed for the European smelt.

The aim of the study is to answer: How do extrinsic and intrinsic drivers influence the recruitment success of the European smelt in the Elbe estuary? To address this, we present the first implementation of an IBM for European smelt in the Elbe and apply it to investigate bottom-up driven population dynamics covering the years 2000–2017. The goal of this paper is to (i) introduce the first European smelt IBM's development, (ii) assess the sensitivity of the individual's weight development on internal model parameters using the error analysis approach, (iii) test the impact of extrinsic variables on individual development, (iv) present the impact of realistic forcing fields on the individuals. By achieving these objectives, we aim to understand the complex interplay of physiological processes and external variability affecting recruitment success.

2. Methods

2.1. Model description

The description of the model and conducted analysis follows the ODD protocol (Grimm et al., 2006, 2010, 2020), a standard tool to describe agent-based models to a broader audience. All calculations and the model development was made using the MATLAB software. The model routine as well as the nominal variable values of constant values are publicly available (Drewes et al., 2025). Code used for the analysis can be shared on request.

2.1.1. Purpose

We designed the model with the purpose to investigate the impact of changing extrinsic drivers on the development and recruitment success on an individual level. Determining the impact of such drivers on the physiological state, the optimal foraging, and survivability is achieved by modelling the individual energy balance in relation to the individual's life history. The potential to use both constant and realistic observation-based forcing datasets to run the IBM opens the floor for a detailed analysis of individual sensitivity to a changing ecosystem.

2.1.2. Entities, state variables and scale

Smelt individual development includes 3 life stages: egg, yolk-sac and exogenous feeding individuals. We included the superindividual approach (Scheffer et al., 1995) , to reduce the computational complexity of our model. At spawning each particle is assigned a predefined number of particles that it represents throughout their development. All following calculations are conducted on the superindividual level. Throughout the endogenous life stages, individual development is based on a percentwise stage completion depending on the local temperature. During exogenous feeding, the individual's weight (m_s, μg) and length (L_s,mm) are used to describe their development. Mortality is represented as a decrease of subindividuals per superindividual.

Our model was designed as a 1-dimensional setup using timeseries of

temperature, oxygen, prey availability and a constant day-night cycle as forcing. The model was run using an hourly timestep. Input data was either provided as a range of constant values to test the model's sensitivity or based on measurement timeseries from the Elbe estuary.

The output of our model is available in an hourly resolution including values for development (depending on stage) and the parameters used during the energy balance calculation for exogenous feeding individuals.

2.1.3. Process overview and scheduling

Preprocessing based on the input forcing is necessary to successfully run the model. We therefore introduce both the processes and schedules involved in the preprocessing and the actual model calculation in the following segment.

During the preprocessing two major processes are considered: the conversion of the available zooplankton biomass into size-structured prey data as described in Daewel et al. (2008b) and the determination of the spawning onset based on the provided forcing. Further the preprocessing includes some necessary unit conversions, depending on the input data that is used for each simulation.

The IBM itself was based on the concept proposed by Letcher et al. (1996). At each hourly timestep the input data is updated. While the complexity and number of necessary sub models vary depending on the current life stage, the general structure is equal for all three included stages. After updating the input data, a development is calculated. During egg and yolk-sac stage this is done using a temperature based cumulative sum of hourly development rates. For exogenous feeding individuals' development is described using calculated growth rates using a simple energy conservation approach based on the Wisconsin Energy Conservation model for early marine life stages (Kitchell et al., 1974). Following the development processes, life stage specific mortality rates are calculated and applied as a reduction of the total number of sub-individuals per superindividual. In case of a stage completion, the individuals stage identifier is updated after the mortality rates were calculated. We conclude the model's routine by creating the timestep-wise output of all variables.

2.2. Model design

2.2.1. Submodules

Our model is structured in 4 overarching submodules. Three for the included life stages (egg, yolk-sac and exogenous feeding) and one combining the stagewise calculation of the mortality rates. One further submodule includes the pre-processing routines, but that is not explicitly added to the model routine but calculated beforehand. In the following, we want to introduce the modules, their theoretical background and the mathematical implementation into our modelling system. As underlying basic principles might change depending on the life stage, we decided to introduce the submodules chronologically based on their appearance in the model itself. Equations used in all four submodules are chronologically listed in Table 1, constant parameters in Table 2 and variables are listed in Table 3.

2.2.1.1. Spawning and prey biomass conversion. The first submodule includes the pre-processing routines for the calculation of the spawning onset as well as the conversion from available prey biomass into size-structured datasets that are later used in the optimal foraging module.

Spawning activity of the smelt stock in the Elbe estuary is strongly linked to extrinsic drivers such as water temperature, variations in the day-night cycle and freshwater runoff (Lillelund, 1961). A key driver determining the spawning onset is the temperature driven gonad development (Lillelund, 1961; Sepulveda, 1994). As stated by Lillelund

Table 1
IBM mathematical equations for endogenous and exogenous physiological processes. Fixed values are denoted by lower script numbers (e.g.: a_1, b_1) while other subscripts indicate relations (p_i, m_i: prey length and mass per size class i), L_S: individual length.

	Process	Equation	Unit	Source
1	Egg Development	$D_{Egg} = \frac{a_1 \times T^{-a_2}}{T}$	[% day^{-1}]	(Lillelund, 1961)
2	Yolk-Sac Development	$D_{yolk} = b_1 \times T^{b_2}$	[% day^{-1}]	(Alshuth, 1988)
3	Consumption	$C = \frac{\sum_i m_{i,wet} \times \varepsilon_{L_s,i} \times \eta_{L_s,i}}{1 + \sum_i \varepsilon_{L_s,i} \times \sigma_{L_s,i}} \times \Delta t$	[µg dry weight]	(Letcher et al., 1996)
4	Allometric Relation	$m_{s,wet} = (w_1 \times L_S^{w_2}) \times 10^6$	[µg wet weight]	(Kapusta et al., 2021)
5	Maximum prey length	$p_{i,max} = \frac{p_1}{\left(1 + (L_s/p_2)^{-2}\right)}$	[mm]	(Daewel et al., 2008a; Hufnagl and Peck, 2011)
6	Capture Success	$\eta_{L_s,i} = 1.1 - (a \times p_i / L_S)$	"	(Munk, 1992)
7		$a = \frac{1,1 \times L_S}{p_{i,max}}$	"	(Daewel et al., 2008a)
8	Encounter rate	$\varepsilon_{L_s,i} = \frac{1}{2} \times \pi \times D_i^2 \times p_i \times V$	[# s^{-1}]	(Letcher et al., 1996)
9	Velocity of contact rate	$V = \sqrt{S_{prey}^2 \times S_{L_s}^2 \times w^2}$	[mm s^{-1}]	(Evans, 1989)
10	Swimming speed	$S_{L_s} = \frac{S_1}{(1 + \exp(-L_S - 29.52/5.52))} \times S_{oxy}$	[mm s^{-1}]	(Akimova et al., 2023)
11	Oxygen impact Swimming capactiy	$S_{oxy} = (S_{1,oxy} \times O_2) - S_{2,oxy}$	"	
12	Swimming speed prey	$S_{prey} = 3 \times p_i$	[mm s^{-1}]	(Mauchline, 1998)
13	Reactive Distance	$D_i = \frac{p_i}{(2 \times \tan(\alpha_{L_s}/2))}$	[mm]	(Breck and Gitter, 1983) (Breck and Gitter, 1983)
14	Angle of visual acuity	$\alpha_{L_s} = 0.01667 \times (\alpha_1 + \alpha_2 / L_s)$	[°]	(Miller et al., 1993)
15	Handling Time	$\sigma_{L_s,i} = \exp\left(\sigma_1 \times 10^{\sigma_2 \times (p_i/L_S)}\right)$	[s]	(Walton et al., 1992)
16	Assimilation efficiency	$\rho = \rho_1 \times (1 - \rho_2 \times \exp(-\rho_3 \times (m_{s,dry} - 196)))$	"	(Buckley and Dillmann, 1982)
17	Daily maximum consumption	$C_{max} = ((\tau_1 \times (10^6 \times m_{s,wet})^{-\tau_2}) \times F_T) \times (10^6 \times m_{s,wet})$	[g day^{-1}]	(Lantry and Stewart, 1993)
18	Daily maximum consumption Temperature-dependency	$F_T = \begin{cases} 0.0466 \times T + 0.2662 \text{ for } 3°C < T < 16°C \\ 0.98 \text{ for } 16°C < T < 21°C \\ -0.194 \times T + 5.045 \text{ for } 21°C < T \end{cases}$	"	(Lantry and Stewart, 1993)
19	Basal metabolism	$R_r = r_1 \times (10^6 \times m_{s,wet})^{r_2} \times \exp(r_3 \times T)$	[g O_2 g^{-1} day^{-1}]	(Karjalainen and Sarvala, 1997)
20	Active metabolism	$R_a = k_1 \times R_r$	[g O_2 g^{-1} day^{-1}]	(Beyer and Laurence, 1980)
21	Daily Mortality rate(Exogenous larvae)	$M_p = 5.3 \times 10^{-3} \times m_{s,dry}^{-0.25}$	[day^{-1}]	(Peterson and Wroblewski, 1984)
22	Conversion to probability of survival	$P_{s_i} = \exp(-M_p \times \Delta t)$	"	(Tian et al., 2007)

Table 2
Overview of the fixed values used in the smelt IBM. Sources and units are presented in the major Table 1.

Parameter	Name	Value	Range during LHS	Unit	Used in	Source
a_1	Egg Thermal scaling coefficient	624.0	561.0 – 686.4	days	Eq. 1	(Lillelund, 1961)
a_2	Egg Thermal exponent	0.5994	0.5395 - 0.6593	"	Eq. 1	(Lillelund, 1961)
b_1	Yolk-sac temperature scaling coefficient	0.420	0.3780 – 0.462	(% day^{-1}) $°C^{-1}$	Eq. 2	(Alshuth, 1988)
b_2	Yolk-sac temperature sensitivity exponent	1.4950	1.3455 - 1.6455	"	Eq. 2	(Alshuth, 1988)
L_{ini}	Initial length	7	6.3 – 7.7	mm		(Lillelund, 1961)
w_1	Allometric relation coefficient	0.0022	0.002 – 0.0024	g mm^{-1}	Eq. 4	(Kapusta et al., 2021)
w_2	Allometric relation exponent	3.321	2.9889 - 3.6531	"	Eq. 4	(Kapusta et al., 2021)
p_1	Maximum prey length baseline	2200.0	1980.0 - 2420.0	"	Eq. 5	(Hufnagl and Peck, 2011)
p_2	Maximum prey length scaling	14.0	12.6 –15.4	"	Eq. 5	(Hufnagl and Peck, 2011)
S_1	Swimming speed Reference value	181.15	163.035 – 199.265	mm s^{-1}	Eq.10	(Akimova et al., 2023)
$S_{1,oxy}$	Oxygen scaling Decrease rate	0.0132	"	O_2^{-1}	Eq. 11	
$S_{2,oxy}$	Oxygen scaling Maximum value	0.99	"		Eq. 11	
α_1	Visual acuity baseline	1.25	1.125 – 1.375	min of arc	Eq. 14	(Miller et al., 1993)
α_2	Visual acuity scaling	2657.0	2391.3 – 2922.7	min of arc mm	Eq. 14	(Miller et al., 1993)
σ_1	Handling time coefficient	0.264	0.2376 - 0.2904	"	Eq. 15	(Walton et al., 1992)
σ_2	Handling time exponent	7.0151	6.3136 - 7.7166	"	Eq. 15	(Walton et al., 1992)
ρ_1	Assimilation efficiency maximum value	0.7	0.63 - 0.77	"	Eq. 16	(Buckley and Dillmann, 1982)
ρ_2	Assimilation efficiency coefficient 1	0.3	0.27 - 0.33	"	Eq. 16	(Buckley and Dillmann, 1982)
ρ_3	Assimilation efficiency coefficient 2	0.003	0.0027 - 0.0033	"	Eq. 16	(Buckley and Dillmann, 1982)
τ_1	Maximum consumption coefficient	0.029	0.0261 – 0.0319	g $g^{-1}day^{-1}$	Eq. 17	(Lantry and Stewart, 1993)
τ_2	Maximum consumption Mass exponent	0.275	0.2475 - 0.3025	"	Eq. 17	(Lantry and Stewart, 1993)
r_1	Metabolism respiration coefficient	0.0019	0.0017 – 0.0021	g O_2 $g^{-1}day^{-1}$	Eq. 19	(Karjalainen and Sarvala, 1997)
r_2	Metabolism mass exponent	0.1057	0.0951 - 0.1163	"	Eq. 19	(Karjalainen and Sarvala, 1997)
r_3	Metabolism Thermal coefficient	0.073	0.0657 – 0.0803	$°C^{-1}$	Eq. 19	(Karjalainen and Sarvala, 1997)
k_1	Active metabolism multiplier	2.5	2.25 - 2.75	"	Eq. 20	(Lantry and Stewart, 1993)
Φ_{SDA}	Specific Dynamic Action	0.19	0.171 - 0.209	"	Eq. (0)	(Lantry and Stewart, 1993)

Table 3
Variables used in the IBM and pre-processing.

Variable	Name	Unit	Range in the LHS	Used in
T	Water temperature	°C	6.0–25.0	Eq. 1,2,18,19
m_i	Prey mass	µg	"	Eq. 3
L_s	Individual length	mm	"	Eq. 4,5,6,7,10,14,15
m_s	Individual mass (dry/wet)	µg	"	Eq. 4,16,17,19,21
O_2	Oxygen concentration	$mmol/m^3$	62.502 – 187.507	Eq. 11
	Prey concentration	mg C m^{-3}	30 - 250	"
	Turbulent dissipation	W kg^{-1}	10^{-8} – 10^{-3}	"

(1961), spawning activity can be observed in early March often following a sudden increase of water temperatures at the spawning locations. Warmer winter conditions enhance the gonad development resulting in earlier onset of spawning due to a lower spawning temperature threshold. Conversely, after a colder February, spawning will require higher water temperatures, delaying it to early March or even later particularly in very cold years.

In our IBM model, spawning is therefore limited by two thresholds: time of year and water temperature. As February water temperature is used as a proxy, we do not consider the onset of spawning before the 61st day of the simulation (early march). The spawning temperature threshold is calculated based on the climatological mean of February water temperature at the pre-defined spawning location. The thresholds are based on the study results of Lillelund (1961). Between 1992 and 2021, the climatological February temperature at our selected spawning site was 3.16 °C. If the February temperature in the forcing is warmer than the climatological mean, accelerated gonad development lowers the spawning threshold to 3.8 °C. This can result in earlier spawning, as gonads reach maturity sooner. Conversely, after a colder February, spawning will only commence once temperatures reach 5.9 °C.

Beside the spawning determination, the pre-processing module also contains the transformation of the total available biomass into size-structured prey concentrations as presented in Daewel et al. (2008b). This approach allows for improved optimal foraging due to the consideration of potentially available prey-size classes based on modelled abundance. Predefined prey length, following the suggested distribution in (Daewel et al., 2008b), ranged from 150 to 1600 µm. The resulting prey timeseries are then handed over into the IBM core model.

2.2.1.2. Endogenous feeding lifestages. The second module includes endogenous feeding individuals during their egg and yolk-sac stage. It starts the individual development as soon as both pre-calculated spawning thresholds are matched. At this timestep the individuals stage identifier is changed to 1, denoting the beginning of the egg phase.

Development of the newly spawned eggs is solely depending on the local temperature (T_s) at the spawning location. The daily development rate during the egg stage is calculated using the equation D_{EGG} (Table 1 Eq.1). The end of the egg development is reached when the cumulative sum of the daily rates equals or exceeds 1 ($\sum 1/D_{Egg} \geq 1$). Thereafter, the particles enter the yolk-sac stage.

As for the egg stage, yolk-sac larvae development is a function of water temperature. Daily development D_{Yolk} (Table 1 Eq.2) is calculated using a modified version of the equation for sprat larvae defined by (Daewel et al., 2008a) (Table 1 Eq.2). As previously defined, the transition to the exogenous feeding larvae stage is reached when the cumulative sum of the daily yolk-sac development rates equals or exceeds 1 ($\sum 1/D_{yolk} \geq 1$).

2.2.1.3. Exogenous feeding lifestages. The complete consumption of the yolk sac reservoir marks the shift from endogenous feeding, which relies on internal energy reserves, to exogenous feeding, where the larvae depend on external food sources. During this exogenous feeding larval stage, growth is calculated using a simple energy conservation approach based on the Wisconsin Energy Conservation model for early marine life

stages (Kitchell et al., 1974)

$$G = C\rho(1 - \Phi_{SDA}) - R \quad \text{(Eq. 0)}$$

This type of formulation uses estimates of consumption (C, µg dry weight), assimilation efficiency (ρ), specific dynamic action (Φ_{SDA}) to calculate individual growth (G, µg dry weight) and respiratory costs (R, µg dry weight) at each timestep.

Calculation of the consumption (C) is based on the locally available zooplankton concentration (mg C m^{-3}). The calculation of the total consumption per timestep (C, Table 1 Eq. 3) follows the optimal foraging approach as described in Letcher et al. (1996). Conversion of wet and dry weight were based on findings of the Rainbow smelt (*Osmerus mordax*) (Dai 2018). Their results were obtained for individuals with a minimum length of 32 mm. In their results they propose that the relation DW:WW decreases for smaller individuals. We therefore assumed a reduced DW:WW ratio of 9 % as we deal with comparably smaller individuals in our model.

The calculated consumption is based on the prey types mass (m_i, Table 1 Eq. 3), the capture success ($\eta_{L_s,I}$, Table 1 Eq. 6), the encounter rate ($\varepsilon_{L_s,I}$, Table 1 Eq. 7) and the handling time ($\sigma_{L_s,I}$, Table 1 Eq. 12). Capture success, handling time and the individual's mass were used to create a ranking of the available prey length classes, based on the foraging routine described by Letcher et al. (1996). Length composition of the consumed prey items is selected based on these ranks to ensure optimal foraging due to size-matched prey item selection (Letcher et al., 1996; Daewel et al., 2008a). Energy intake due to prey consumption cannot be fully utilised for growth. Therefore, the total consumption is decreased using the assimilation efficiency (Table 1 Eq. 13). The efficiency increases as larvae grow. Values range from 0.7 for smaller larvae to 0.8 for larger larvae (Govoni et al., 1986). The relationship between assimilation efficiency and dry body weight is based on data collected for larvae of summer flounder (*Paralichthys dentatus)* presented by Buckley and Dillmann (1982).

The chance of successful prey capture is described using the capture success (Table 1 Eq. 6) parameterisation as described by (Munk 1992). It relates the predator's body length (L_s) to successful predation events based on the prey's body length (p_i). The parameter a (Table 1 Eq. 7) includes the maximum prey length ($p_{i,max}$, Table 1 Eq. 5) into the capture success. The encounter rate (Table 1 Eq. 8), describing the number of potential prey encounters per timestep, is directly linked to larvae's visual ability and indirectly to the impact of turbulence and movement of both the larvae and prey item. The visual ability is expressed using the reactive distance (Table 1 Eq. 13) which is based on the angle of visual acuity (Table 1 Eq.14). The relation is based on the findings for other species like alewife, bloater, and yellow perch (Miller et al., 1993). During growth, the individual's ability to visually track prey items increases, therefore enabling larger larvae to encounter more prey compared to smaller individuals. It is considered in the calculation of the velocity of the contact rate (Table 1 Eq. 9). The velocity component includes the individual's swimming speed (S_{L_S}, Table 1 Eq. 10), the prey's swimming speed (S_{prey}, Table 1 Eq. 12), and the turbulence induced velocity difference (w) as calculated in (Rothschild and Osborn, 1988). Prey swimming speed is assumed to be 3 body lengths per second as found in (Mauchline 1998). Based on the work of MacKenzie et al. (1994), the encounter rate is multiplied by a dome-shaped turbulence-dependant ingestion probability. Due to the 1D nature of our model, constant values of turbulent dissipation are prescribed, following results of the sensitivity analysis done by (Daewel et al., 2008a) .

To prevent unrealistic growth rates in larvae due to potential overfeeding, a daily maximum consumption (C_{max}, Table 1 Eq. 17) limit was incorporated into the model (Peck and Daewel, 2007). This constraint was established using the maximum consumption rates observed in Rainbow Smelt by (Lantry and Stewart, 1993) and were adapted for the European smelt. These values were previously applied by Karjalainen and Sarvala (1997) for landlocked smelt populations. C_{max} is a function of both larval weight and water temperature: larger larvae exhibit higher consumption limits, and consumption is optimized within a species-specific temperature range. Exact measurements of the optimal thermal window were not available. However, studies such as Lillelund (1961) mention a lethal upper temperature limit of 21 to 24 °C for eggs and early life stages. Rearing experiments showed a preference for survival under colder temperatures (≤10 °C). Karjalainen and Sarvala (1997), used a similar temperature dependency in their model approach for a landlocked population of the European smelt. We decided to adapt their values but are aware that fine-tuning, especially due to the differences in land-locked and migratory species might be needed in the future.

The influence of temperature on feeding behavior is modeled by scaling the weight-based maximum consumption with a factor ranging from 0 to 0.98 (Lantry and Stewart, 1993). As temperature rises from 3 to 16 °C, consumption gradually increases, reaching a peak value of 0.98 within the optimal temperature window. When temperatures exceed 21 °C, daily maximum consumption decreases due to adverse conditions. In between these values, the temperature-wise limitation of the daily maximum consumption (F_T, Table 1 Eq. 18) is estimated using linear regressions.

Specific Dynamic Action (Φ_{SDA}) describes the portion of energy that is lost due to digestive processes (Lantry and Stewart, 1993). In their study, Lantry and Stewart (1993) present a constant value of 0.19 for Delta smelt larvae (*Osmerus mordax*) in the Laurentian Great Lakes. As stated by Lillelund (1961), Delta smelts as well as European smelts share a lot of similarities, especially in the early life stages. Therefore, we decided to use the same value to prescribe the SDA in our IBM.

The metabolic loss (R, µg dry weight) is represented using two components: basal (R_s) and active (R_a), defined in Table 1 Eq.19 and Eq.20 respectively. R_s represents the energy costs required for basic survival under unfed conditions to maintain routine activity. The parameter values used in R_s were adopted from Karjalainen and Sarvala (1997), who examined the energy balance of landlocked smelt, and these values align with those reported for Delta smelt (Lantry and Stewart, 1993). R_s is directly related to the larval body length and the local water temperature. Larger individuals therefore feature higher respiration rates (Chabot et al., 2016) while warmer temperatures (Gillooly et al., 2001) increase the metabolic losses for individuals at every size equally. Reported metabolic rates were converted from g O_2 $g^{-1}day^{-1}$ to µg dry weight h^{-1} using the oxycaloric equivalent γ and calorie-to-microgram mass conversion factor χ (Megrey and Hinckley, 2001). R_a accounts for active swimming activity of the larvae and increase during times of active predation. We assumed that active predation is only happening during daytime and prescribed a constant day-night cycle to our model consisting of 10 h of night and 14 h of daytime. To account for activity during daytime the standard metabolism R_s is increased by a constant factor (k_1) of 2.5, which is a ratio between active and basal metabolic rates as measured for herring larvae (Beyer and Laurence, 1980).

Calculation of individuals length at weight is done assuming an allometric relation between both parameters based on reported values for various smelt populations Kapusta et al. (2021). Throughout their life larvae's weight can vary, however length cannot decrease once the individual grew. Thinner individuals are more prone for starvation and generally feature a decreased life quality. Commonly, the Fulton's condition factor $\phi = 1000 \times \frac{w_i}{L_i^3}$ is used to indicate unhealthy weight to length proportions. During phases of weight loss, the factor decreases and indicates unfavourable conditions for individual development.

2.2.1.4. Mortality. The final module includes the stagewise calculation per superindividual. During the endogenous life stages a constant mortality rate is applied. This constant rate included various potential threats such as predation, damage due to enhanced sedimentation or fungal development (Lillelund, 1961). The chance of survival increases

in case of faster development and vice versa in case of too cold temperatures the individuals would die during the endogenous feeding stages. This implementation includes the idea of a stage duration related chance of survival (Chambers and Leggett, 1987; Houde, 1987, 1989).

Calculation of mortality rates is based on the decrease of the subindividuals introduced in the superindividual approach earlier. Daily mortality rates are calculated using a weight dependant relation (M_i; Table 1 Eq. 21) as presented in (Peterson and Wroblewski, 1984). Conversion of mortality rates into the number of dying subindividuals per superindividual is done using Table 1 Eq. 22 (Tian et al., 2007). The first measure of mortality is the earlier introduced condition factor as a mismatch in the proportions of length and weight would only occur during unfavourable conditions. Starvation is also defined to occur if the condition factor (ϕ) persistently decreases below 0.6 leading to an increase of mortality rates resulting in a decreased likelihood of survival of the individual.

Smelt larvae are highly sensitive to low oxygen levels, which frequently occur in the Elbe Estuary, particularly in spawning areas (Möller and Scholz, 1991). Their survey showed that the number of individuals decreased for oxygen concentrations below 5 mg l^{-1}. Further studies found that under low oxygen conditions ($O_2 < 5$ mg l^{-1} (150 mmol m^{-3})), larvae reduce their energy consumption by decreasing movement (Domenici et al., 2013; Abdel-Tawwab et al., 2019). However, anaerobic conditions increase energy demand for internal processes like digestion (Domenici et al., 2013). To account for these effects, an oxygen sensitivity factor (Table 1 Eq. 11) is applied which reduces swimming speed while increasing both the standard metabolic rate and the active metabolism multiplier. Reduced swimming velocity decreases prey encounter rates in hypoxic areas, leading to insufficient food intake to meet energy demands. The decreased energy intake, reducing individuals' growth would lead to a decreased condition factor. Low oxygen levels therefore just enhance probability of starvation induced mortality. A second mortality cause is only considered for oxygen concentrations below 2 mg l^{-1}. If such anoxic conditions would vastly impact the early life stages, immediate death would be the consequence of suffering such conditions. Under these circumstances any other mortality driving factor is neglected.

2.2.2. Initialisation

Most of the initialisation happens before starting the models timestep routine. Each superindividuals is assigned the initial number of subindividuals ($N_{ini} = 1.000.000$). Of further importance during the initialisation is the selection of the starting life stage. If the stage identifier is 0 at the beginning the calculation of spawning based on the forcings averaged February temperature. For any of the endogenous feeding life stages we assume that at the first timestep the individual's development starts, and the respective development is initialised as 0. If the individual completes the endogenous life stages and transitions to exogenous feeding the individuals length is initialised using the initial length ($L_{ini} =$ 7 mm (Lillelund, 1961)). The initial length is afterwards used to compute the individual weight after transitioning.

All other state variables and output variables are initialised as zero, and output is generated after the start of any life stage dependant development.

2.2.3. Input data/forcing/scenarios

2.2.3.1. Input data/forcing. The forcing that is necessary for the model setup consists of physical variables (temperature, Day-Night cycle, turbulent dissipation) and biogeochemical variables (oxygen, zooplankton biomass). The input data can be provided in two ways: as constant values or as timeseries with values matching the IBMs timestep. In our study the timestep of the IBM is always set to one hour. Throughout all simulations a constant day-night cycle was assumed, consisting of 10 h of nighttime and 14 h of daylight conditions. We do not consider seasonal changes in the day-night cycle such as longer daylight conditions during summer or night conditions during winter.

2.2.3.2. Simulation design and output analysis. The following section describes the simulations conducted, their specific purposes, and the methodology used to analyse their output. We performed three main types of analyses: (i) a sensitivity analysis based on individual growth rates to verify the functionality of our energy conservation approach, (ii) an extensive random-sampling simulation set to investigate the impact of variability of both extrinsic and intrinsic parameters and forcings; and (iii) a series of simulations focussing on interannual variability in development speed, using observational timeseries from the Elbe estuary.

The sensitivity analysis started with a general test of the energy balance calculation for exogenous feeding individuals. Using simulations driven by constant input data, the sensitivity of the individual's growth rates to different prey concentrations was tested. While keeping temperature and oxygen constant (9 °C, 6 mg l^{-1}) the available prey concentration was tested over a range of 0–250 mg C m^{-3} Growth rates were averaged over the first 10 days after transitioning to exogenous feeding. The aim of this simulation set is to prove functionality of the energy conservation equations. By comparing our resulting growth rates to literature based estimates the feasibility of our results should be discussed. Further, by decreasing the available oxygen the mortality implementation is tested for exogenous life stages, and the potential survival time is compared to available literature.

We further want to assess the impact of changing intrinsic and extrinsic parameters on the individual's growth. We decided to use a combination of random sampling and Monte Carlo simulations, which follows the study design proposed in Megrey and Hinckley (2001). Random sampling of parameters values was done using the Latin Hypercube Sampling (LHS) method. For each tested parameter a triangular distribution was constructed by applying a 10 % variability to the baseline value. Tested were the constant components as shown in Table 2 and in a second step the input data (see Table 3) as described earlier. For the extrinsic forcing, upper and lower ranges were used to construct the distributions rather than the 10 % variation from the mean value. In preparation of the sampling, these distributions were split into equally spaced intervals. During the sampling a unique interval is chosen per variable, ensuring no doubling of intervals per sample. This approach allows for a comparably cost-efficient random sampling across large datasets (Huntington and Lyrintzis, 1998). The sampled coefficients were then used in Monte Carlo simulations using IBM to assess their impact on the individual growth. We focused on the impact of changes on freshly hatched (50 days past spawning) and exogenous feeding (200 days past spawning) individuals. The selection of these two stages allowed us to investigate how importance of the coefficients on individual development changes with the individuals age. The LHS sampling was conducted using a slightly modified version of the lhsdesign matlab function. The function was modified to allow for the consideration of minimum and maximum values in the generation of the triangular distributions.

A crucial part of the design of the LHS method is to find the necessary of samples and intervals to ensure statistical stability. The IBM presented in this paper consist of various equations and in total 28 parameters were included into the different equations and the intrinsic parameter testing. Based on the procedure described in (Megrey and Hinckley, 2001) where they used 300 samples for 114 variables, we decided to use 280 samples. However, repetition of the sampling can help to increase statistical stability (Matala, 2008). In total a set of 7 parameter ensembles is created, each having 280 variations per parameter included. For the testing of the extrinsic forcings impact on growth we decided to use 2 ensembles with 500 variations included.

For analysis, the corresponding correlation coefficients (r^2) between input parameter value and output variable were calculated for each

ensemble. The total correlation was obtained by averaging the ensemble correlations into total correlations with respect to each input parameter. Significancy of the correlations was determined using a two-tailed *t*-test.

Finally, using observation based forcing we wanted to assess the model's performance in reproducing interannual recruitment success in the Elbe estuary. Here we used a combination of observation and model based timeseries as forcing. The latter were generated using the hydrodynamical model SCHISM (Semi-implicit Cross-scale Hydroscience Integrated System Model) (Zhang et al., 2016) coupled to the lower trophic level ecosystem model ECOSMO (Schrum et al., 2006; Daewel and Schrum, 2013a), via the coupling interface FABM (Bruggeman and Bolding, 2014). A validation and detailed description of the setup and model system is presented in (Pein et al., 2021). Due to the lack of zooplankton measurements in the Elbe Estuary, model-derived hourly zooplankton values were extracted from the closest grid point to the measurement site. Data for meso- and micro zooplankton were combined and included as the available prey concentration for the optimal foraging routine.

Daily temperature and oxygen data from 2000 to 2017 were obtained from the Seemanshöft station (53,54023° N, 9,87970° O), located at the downstream end of the Port of Hamburg. These data were interpolated to an hourly resolution to match the IBM time step used in simulations. Selected years (2002, 2005, 2007, 2009, and 2017) were tested with the IBM, representing a range of winter conditions (cold: 2005, 2009, 2017; warm: 2002) and varying summer temperature and oxygen patterns. Fig. 1 shows the temperature and oxygen time series for these years and the climatological mean of all these years

To assess the model's results, we compare the development time to available monitoring data from the Elbe estuary. This comparison aims to answer the question if suitable conditions in our model resulting in faster development would be matched by higher numbers of smelt catches in the interannual monitoring. The results of the monitoring, conducted between 2000 and 2016, were available at the data system of the FGG Elbe (accessed 01.10.2024) and were converted to CPUE (catch per unit effort) for better comparison. As continuous measurements of water volume per catch was missing (47 of 365 reports), we estimated the effort based on the duration of each reported catch: CPUE = = $Ind_{juvenile}/hours_{fishing}$. In Fig. 2, the available measurements, the resulting number of juvenile individuals and the calculated CPUE are presented. A schematic overview of the coupled setup is presented in Fig. 3.

Using these forcing data the impact of temperature, oxygen and available prey concentration on the survival, growth and development speed is investigated. We focus on the impact of spawning-onset, and winter and summer temperatures on individual growth. Since the IBM is specifically designed to represent larvae stages of the European smelt, its accuracy decreases as individuals grow beyond a certain size. Based on Sepulveda et al. (1993), we set a threshold length of 20 mm. Beyond this size, individuals can position themselves in the water column according to the tidal cycle and exhibit advanced swimming capacities. Therefore, the development time is defined as the time from hatching until this length is reached.

3. Results and discussion

3.1. Growth of individuals

Growth of individuals is highly related to the available prey concentration. Starvation occurs if concentrations are below the minimum threshold leading to an imbalance in the bioenergetic budget resulting in decreased growth rates. On the contrary, the physiological limitation of consumption via C_{max} prevents unrealistically high growth rates under high prey concentrations. Therefore, it is a crucial to investigate how growth is impacted at different prey concentrations. In the following, constant prey concentrations ranging from 10 to 250 mg C m^{-3} were tested. Only prey concentration of 40 mg C m^{-3}or higher, allow for larval growth and prevent starvation induced mortality (see Fig. 4a,b). Further, growth rates at prey concentration higher than 75 mg C m^{-3}showed a maximum averaged growth rate of 0.362 mm day^{-1}. This was caused by the definition of a daily maximum consumption limit (C_{max}) at ad libitum feeding conditions. Prey concentrations below 30

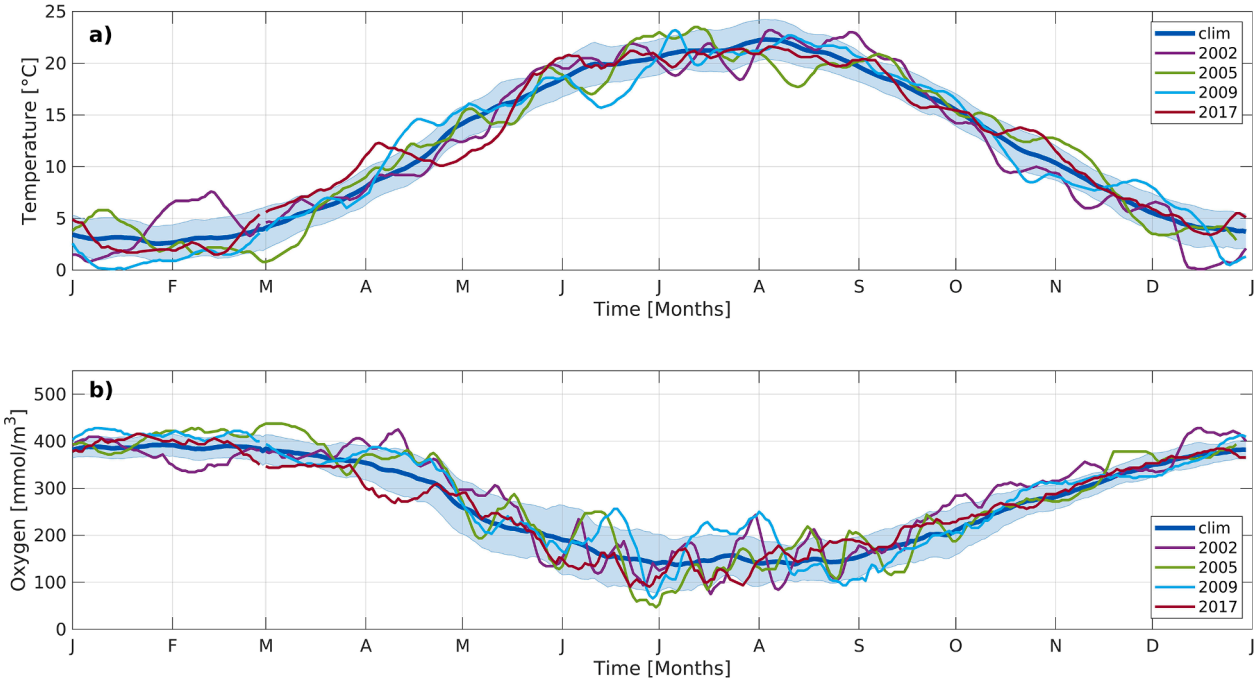


Fig. 1. Timeseries of the observation-based forcing used in this study. Measurements were taken at the Seemanshöft measurement station located in the port of Hamburg. Measurements were available as daily averaged values only.
Top: Temperature for the selected years (2002, 2005, 2009 and 2017) as well as the climatological mean averaged over the time span of 1992–2021. Shaded areas are the standard deviation based on the averaged climatology.
Bottom: Oxygen concentrations for the selected years.

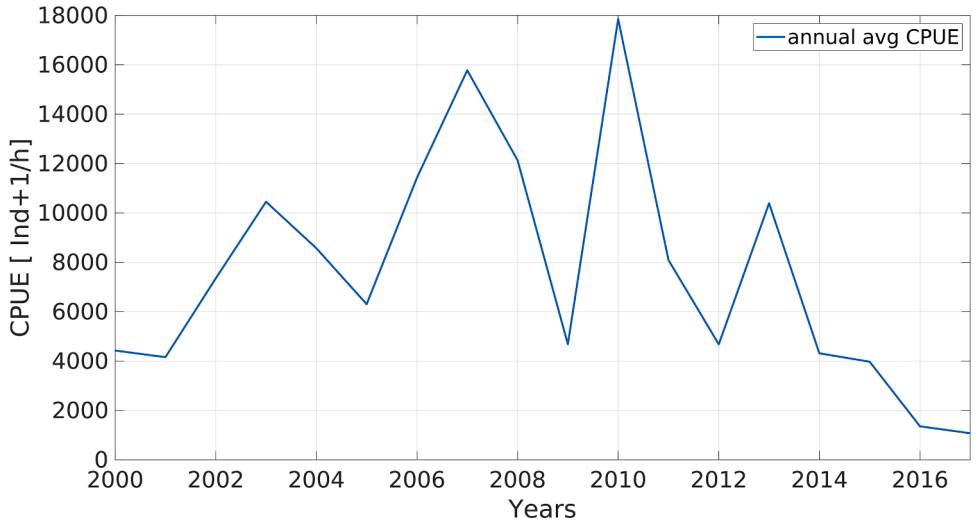


Fig. 2. Monitoring based Catch per unit effort (CPUE) for the juvenile individuals sampled from 2000 to 2017.

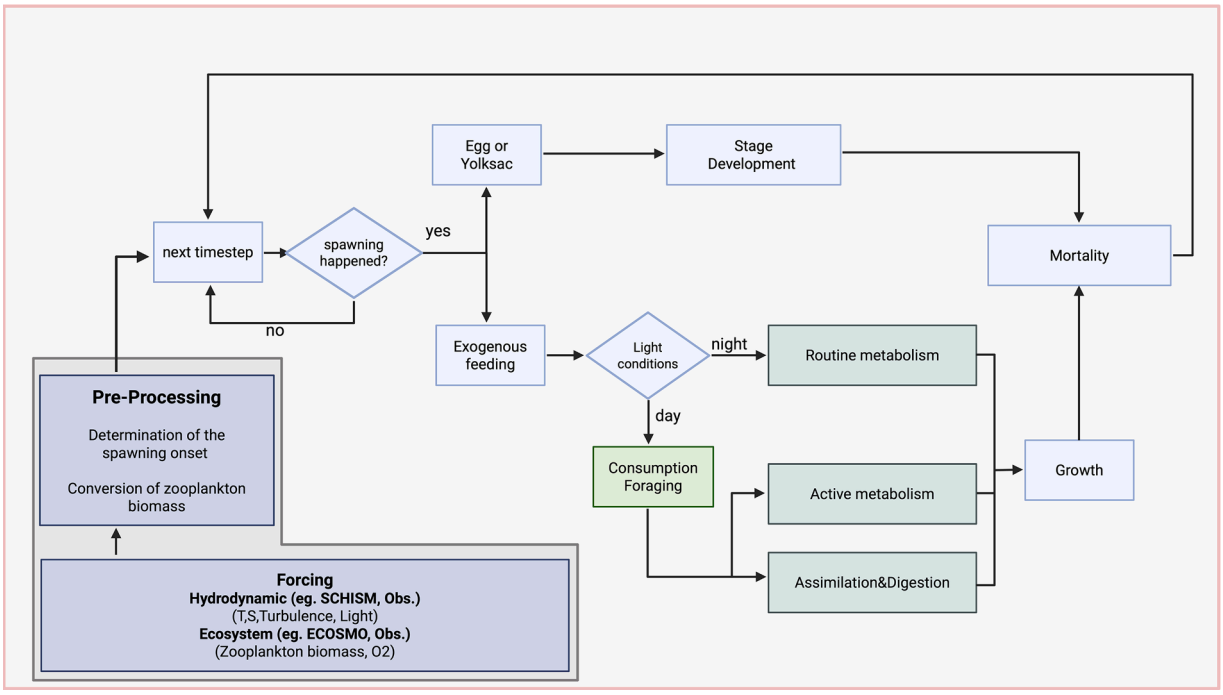


Fig. 3. Schematic overview of the coupled individual based model system and the included forcing. Green boxes show the energy intake in the energy balance, while energy losses are marked with red boxes. Created in BioRender. Drewes (2025) https://BioRender.com/yfdxqrh.

mg C m^{-3} resulted in weight loss and increased the risk of starvation. At concentrations between 30–35 mg C m^{-3} the energy of the consumed prey partially balances the metabolic losses leading to a decreased weight losses and a chance to survive in case food availability increases. We further tested larval survival under insufficient prey conditions ($\leq$30 mg C m^{-3}). Depending on the still available prey concentration, individuals were able to survive for up to 18 days. In contrast, under complete prey deprivation, larvae survived on average only 8.5 days before the critical threshold of mortality is reached, leading to the individual's death. The time until death due to prey deprivation is smaller compared to the one reported in Lillelund (1961) where individuals were able to survive for up to 10–14 days. Their study suggested that increasing temperature can decrease the time until death as the metabolic demand would surpass the possible energy intake. As both, the metabolic rate and maximum daily consumption, are related to the water temperature we should be able to reproduce such a relationship especially under warming conditions.

Our results are in good agreement with the theory of the critical period introduced by (Hjort, 1914). The idea of the theory is, that the amount of available prey during first feeding is inevitably connected to the individual's survival. The onset of first feeding in case of insufficient prey concentrations could therefore result in increased mortalities due to starvation of the vulnerable individuals. The results of simulations under insufficient prey concentrations showed that our model formulation would be capable of detecting prey driven bottlenecks in the development of individuals.

Growth rates during the transition to exogenous feeding ranged from 0.118 to 0.348 mm day^{-1} (Fig. 4a). Table 4 presents an overview of growth rates based on rearing or field studies for individuals in a similar development stage. These results include both landlocked and migratory

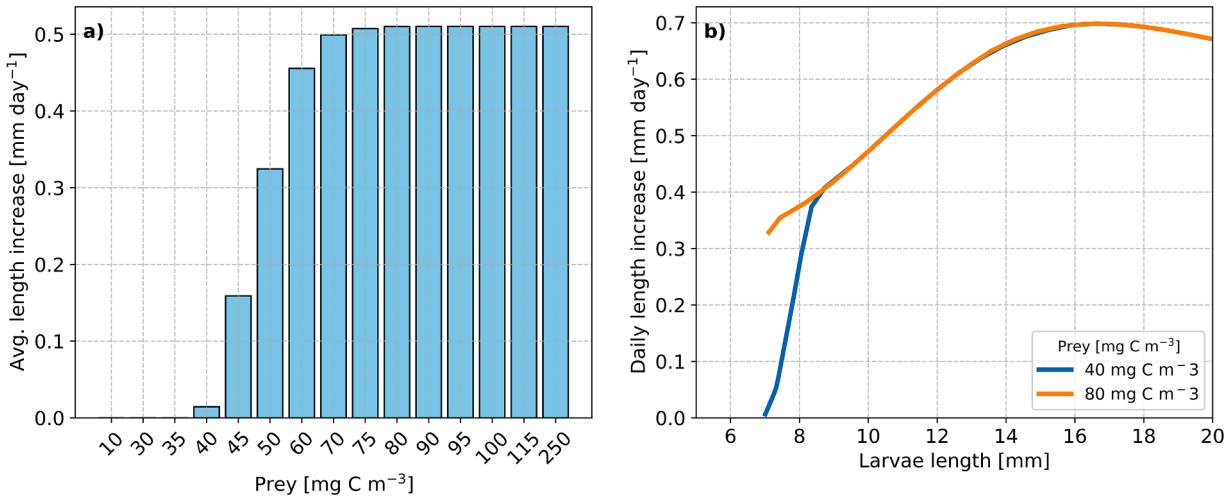


Fig. 4. Growth under changing prey concentrations. a) 10-day averaged length increase after the transition to exogenous feeding for prey concentrations from 10 – 250 mg C m^{-3}. b) Averaged daily growth rates during growth of the individual for 2 prey regimes. Showing accelerated growth of smaller individuals and a decrease after reaching 17 mm body length.

Table 4
Growth rates observed for different populations of European smelt.

Species and location	Growth rate [mm day^{-1}]	Type of study	Source
Osmerus eperlanus (River Cree)	0.37	Rearing	(McCarthy et al., 2020)
Osmerus eperlanus (Weser Estuary)	0.15	Rearing	(Reiser et al., 2023)
Osmerus eperlanus (Elbe Estuary)	0.556	Sampling & Otoliths analysis	(Sepulveda, 1994)
Osmerus eperlanus (land locked)	0.098 – 0.432	Sampling & statistical modelling	(Margonski, 2000)
Osmerus eperlanus (River Thames)	0.29 – 0.34	Sampling & statistical modelling	(Power and Attrill, 2007)

stocks of smelt as well as various spawning locations. Our modelled growth is in good agreement with the measured ones in the two rearing studies (McCarthy et al., 2020; Reiser et al., 2023) but are smaller compared to the observation-based study conducted in the Elbe estuary (Sepulveda, 1994).

In their study on land-locked smelt individuals, Margonski (2000) reported on substantial fluctuations of the individuals growth rates depending on their current development stage. Highest growth rates were reported in the weeks after the transition to exogeonous feeding stage. Enhanced prey availability increased the growth rates even further. A similar growth pattern is found in our model (Fig. 4b), where small larvae reach their maximum growth rate at a size of 14 mm. The dome-shaped relation between growth rates and individual length is often observed for freshly exogenously feeding individuals (Robert et al., 2023). Thereafter, growth rates under different prey concentrations align. This alignment of growth rates is evident for all simulations performed under ad libitum prey concentrations, where food is not limiting. In contrast, under realistic environmental conditions, temporal variability in temperatures, oxygen and prey availability would result in variable growth rates. The timing of the fast growth happens during late spring/early summer, where increasing temperatures result in warmer local water temperatures, which again would increase the individual's ability to grow and mitigate the larger metabolic losses via the increased maximum daily consumption.

Under medium prey concentrations (40 mg C m^{-3}), growth rates decreased and maximum growth at 14 mm is reached after 39 days. Under ad libitum feeding conditions ($\geq$ 80 mg C m^{-3}) the development is accelerated and highest growth rates were reached after 19 days. The following reduced growth is related to the increased metabolic demand in larger individuals. Larger food items and concentrations would be needed to maintain fast growth.

The observed "fast growth"- pattern during the early larvae stage is commonly observed in various fish species as it enhances the individual's survival (Cushing, 1990). Several aspects of such a beneficial growth are included in our model: larger individuals have an increased daily consumption limit and can utilize larger prey items. Especially the increased daily consumption limitation would be beneficial for individuals as increased prey intake allows for even faster growth. Further, larvae size is directly linked to the potential consumption of larger prey items, having a higher encounter speed ultimately leading to more frequent prey encounters. While we do not include any inter-individual competition impact in our model, the ability of preying earlier on larger prey items increases the individual survival in comparison to smaller larvae that still share the same pool of available smaller sized prey items. Increased prey intake allows the individuals to be more resistant to unfavourable conditions (Miller et al., 1988). As we implemented most potential mortality drivers via an increase of the individuals' metabolic demand such a resistance is included in our simulations as it takes heavier individuals longer to reach the critical threshold of the Fultons life quality indicator. Further, increased size and swimming potential decreases the risk of predation (Takasuka and Mitani, 2003; Takasuka and Oozeki, 2007). Therefore, fast growth rates at the early life stage directly supports recruitment and survivability of the individuals.

3.2. Sensitivity of growth to intrinsic variability

Successful development of the early life stages depends on several parameters. Small changes in intrinsic and extrinsic drivers can have a strong impact on the individual. Throughout their development, different intrinsic parameters can play a dominant role for the individual. Disentangling lifetime specific development drivers is therefore crucial for the interpretation of development variability throughout the years. We conducted a sensitivity analysis of the IBM physiological parameters to identify those most sensitive to change. This analysis is performed for each life stage, providing evidence of the model's robustness and highlighting potential uncertainties in its formulation, as intrinsic parameters were tested across a wide range of values. For this purpose, we applied a Monte-Carlo method to apply a range of parameter settings. In Fig. 5, correlations between simulated growth rates and the tested parameter range are shown for both younger and older larvae.

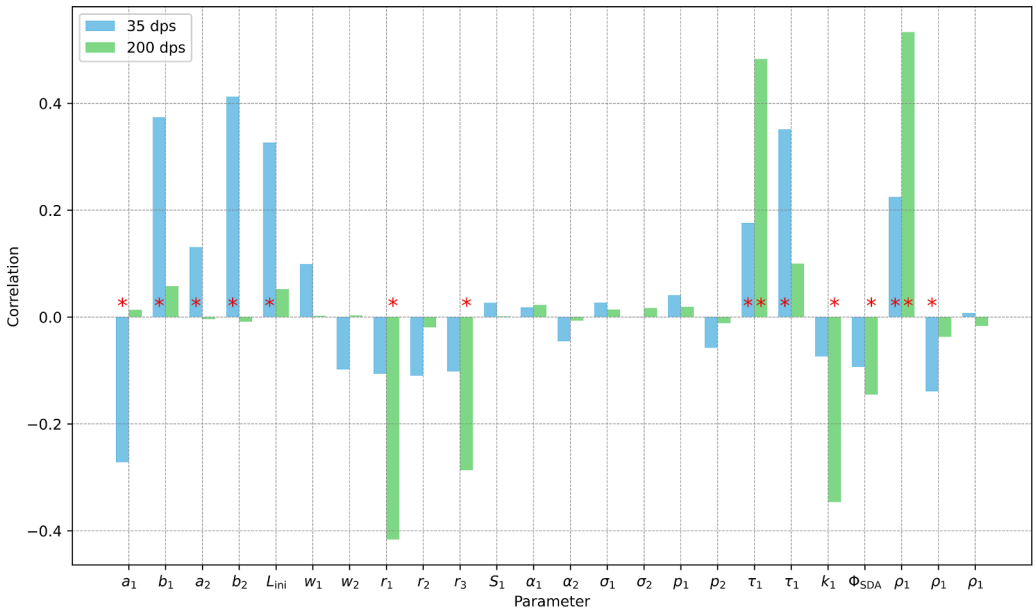


Fig. 5. Correlation of larvae weight and parameter value based on the results of the error analysis. Bars indicate larvae at two different development stages (35 days past spawning (dps) and 200 dps). Stars indicate significant results.

Significant correlations imply positive feedback of a high parameter value on the individual's weight at the selected life stage.

In detail the results reveal that 4 out of 24 tested parameters (b_1, b_2, τ_2, L_{ini}) can significantly influence larval growth at an early stage. For older larvae we found 4 parameters significantly impacting larval growth (ρ_1,τ_1,k_1, r_1). Table 5 displays the significant parameters and their correlation values. However, the set of relevant parameters for the early phase differs from the set of sensitive parameters for older larvae growth. For the early staged larvae (blue bar Fig. 5), we found high sensitivities associated to parameters determining the development during the egg (a_1, a_2) and yolk-sac (b_1, b_2) phase as well as initial length of the larvae (L_{ini}) at first feeding. Both make sense, as larger initial length also increases the weight due to the allometric relation between length and weight. Especially in the first days of development a larger weight and length has a large benefit on the individual's overall growth. Faster development during egg and yolk-sac stages results in a faster transition from endogenous to exogenous feeding, allowing for faster growth. Of the parameters determining the energy balance during the exogenous feeding phase, daily maximum prey consumption intercept (τ_1) and the maximum of the assimilation efficiency (ae_a) show the highest correlation for younger individuals. Both values are limiting factors of the prey intake or digestion. Increasing the possible daily consumption using a higher maximum consumption would lead to a higher individual weight and length. Similarly, increasing the percentage of efficiently usable prey after digestion using a higher assimilation efficiency, would favour increasing growth of the individual.

For older larvae (green bars Fig. 5), the highest correlations are related to parameters influencing the bioenergetic balance. The strongest positive correlation occurs for maximum daily consumption ($\tau_{1,2}$) and the maximum value for assimilation efficiency. These results are in good agreement with the findings of other studies using individual based models. Lough et al. (2005), found that growth of cod was largely impacted by parameters determining the energy demand and uptake such as the assimilation efficiency or SDA. In contrast to their results our model showed a comparably small impact of the visual acuity parameters ($\alpha_{1,2}$). However, due to the differing predation behaviour of smelt compared to cod larvae, this distinction is of no concern for our subsequent results. Additionally, Letcher et al. (1996) emphasized that growth in generalised IBMs is particularly influenced by the daily maximum consumption limit (C_{max}) making it a key parameter of such a model. This is again well represented in our system as well, with C_{max} being significant for both younger and older individuals.

Table 5
Significant parameters for younger (50 dps) and older (200 dps) individuals as calculated by the correlations of the random sampling.

50 days past spawning		200 days past spawning	
Parameter	Correlation coefficient	Parameter	Correlation coefficient
b_2	0.412492	ρ_1	0.533392
b_1	0.374005	τ_1	0.482989
τ_2	0.351378	k_1	-0.416289
L_{ini}	0.326440	r_1	-0.346383

3.3. Sensitivity to extrinsic forcing variability

One important variable throughout all life stages of the larvae is the water temperature (Blaxter, 1992). Both egg and yolk-sac development were defined as functions of water temperature. Here the difference between low and high temperatures can be rather large. At 8 °C, eggs hatch after 22.5 days, while temperatures of 18 °C decreases the time until hatching by 72.2 % to 6.25 days. For yolk-sac larvae the stage duration at 8 °C is 10.6 days and at 18 °C 3.1 days, which is 70.3 % less. Both the longer as well as the faster yolk-sac consumption is well within the values reported in the literature. Reiser et al. (2023) for example report that at an incubation temperature of 12.1 °C the yolk-sac at most larvae were depleted after 6 days past hatching. A change in the onset of spawning or development during the early life stages can have huge consequences for the further growth of the individuals. Faster development and earlier spawning under warmer conditions might increase the risk of a mismatch between first feeding and optimal feeding conditions (Cushing, 1990) as has been discussed for example for cod in the North Sea (Daewel et al., 2011; Daewel and Schrum, 2013b). This however depends on the phyto- and zooplankton phenology at the place of first feeding. The impact of temperature on mortality during egg stage specifically should be discussed further. In our model we assume constant hourly mortality rates. Especially in the egg stage those are comparably high as the risk fungal development, predation or unsuccessful fertilisation is high. If, due to colder temperatures the development of the egg takes longer this would induce a higher risk of the

superindividual dying during the egg stage. On the other hand, to warm temperatures would also induce a risk of increased mortality as, similar to older life stages, these individuals are also having a lethal temperature limit which does not allow survival of the egg.

Moreover, water temperature affects the bioenergetic equilibrium of larvae that feed externally. Elevated water temperatures accelerate metabolic rates and enhance maximum daily food intake. The concept of an optimal temperature is crucial in this context; it denotes the temperature at which food consumption is maximised. Exceeding this optimal temperature results in decreased prey utilisation by the organism. Consequently, the likelihood of starvation increases in larvae during periods of elevated water temperatures in the summer. In this case optimal growth is determined using higher weight at each of the two timesteps. For younger larvae optimal growth conditions can be observed at temperatures around 15 °C. At this temperature the metabolic losses are still fully compensated by the consumption. The optimum of the maximum daily consumption is reached in a temperature window between 16–21 °C. However, our analysis shows that the temperature driven increase of the metabolic rates decreases the capability of the individual to compensate those losses via the increased consumption. Therefore, a decreased wet weight can be observed under these conditions. Colder temperatures however also show decreased growth of the individuals. The reason for that is, that the possible daily consumption decreases for lower temperatures. Although the metabolic rates are also smaller the consumption cannot balance the losses. The older individuals show a completely different window of optimal growth in terms of temperature. Larger individuals were simulated at temperatures between 8–14 °C. This likely has to do with the increased metabolic rates for larger individuals. The weight increases the metabolic rates so much, that under higher temperatures the consumption cannot compensate those losses. This result is supported by the results of (Lantry and Stewart, 1993) that showed that older and larger rainbow smelt individuals rather prefer colder water temperatures and that especially warm temperatures can have a huge impact on the spawning activity and stock survival. In their case juvenile and adult individuals were modelled using a different optimum temperature range for the maximum daily consumption to account for the change of preferences.

The results further show the impact of decreasing oxygen concentrations on development and survival. Especially the combination of low oxygen concentrations and higher temperatures decrease the survival of the individual in both age groups. Individuals encountering lower oxygen concentrations at lower temperatures are still able to survive, but their growth is reduced as stress reactions increase the metabolic losses while simultaneously decreasing the ability to successfully capture prey. If temperatures increase the additional increase of metabolic losses decreases the chance of survival for the individual. This is clearly visible in the remaining percent of individuals per superindividual. Tests were conducted to estimate the time an individual can survive under decreased oxygen conditions. At oxygen concentrations of 3.5 mg O_2 l^{-1} larvae can survive for 4.5 days with the survival increasing to 19 days at oxygen concentrations of 4.5 mg O_2 l^{-1}. In case of nearly anoxic conditions (<2 mg O_2 l^{-1}) no survival is reported in the literature and therefore individuals die as soon as such conditions occur. As the larvae cannot escape the areas due to their lack of excessive movement capabilities, oxygen is assumed to be a major environmental factor determining overall survival of the population. As previously stated for the temperature, the time at which oxygen deficiencies occur can result in another critical timespan during the larvae due to their missing ability to capture prey.

Turbulence is an important driver of the hydrodynamics in an estuarine system such as the Elbe Estuary (Thiel et al., 1995). The interaction between tidal currents, density differences and other processes can lead to local increases of turbulence. In our IBM turbulence is included in the calculation of the capture success. Testing of different turbulence regimes showed that increasing the turbulent dissipation would result in only a small decrease of growth rates and overall survival. However, studies suggest that an optimum level of turbulence can be beneficial for growth of the individuals (Sirois and Dodson, 2000). But as values within the expected range of the Elbe estuary were tested and the impact compared to that of changing oxygen or temperature values is rather small, we rule out turbulence as a main driver of recruitment success in our IBM. This might change in the future as more data on successful foraging under various turbulence conditions would be necessary to refine the implementation in our model. However, such data is not available at this point.

In summary, the external forcing does play an important role throughout all development stages of the individual. Each important variable was analysed, and their impact varies depending on the life stage that was investigated. While temperature and oxygen concentrations tend to be the dominant drivers throughout all life stages included in our mode, prey concentrations and turbulence levels can only limit the survival and development in rare extreme cases

3.4. Smelt in the Elbe Estuary

Interannual variability of the smelt stock has been continuously reported over the past few years (Scholle and Schuchardt, 2020). As stated by Lillelund (1961) variations in the water quality as well as the interannual variability of extrinsic parameters such as the water temperature can vastly impact the recruitment success over the years. To investigate such impact, we used measured timeseries of oxygen and temperature covering the timespan 2000 to 2017. Due to missing measurements of local zooplankton concentrations we prescribed a constant model based timeseries equally to all the conducted runs. To investigate the influence of temperature on the development during egg and yolk-sac stages, development speed during 4 years (2002, 2005, 2009, 2017). While smelt monitoring data was limited to the mentioned period, temperature and salinity measurements were available for a much longer timeframe. From these records, we constructed a climatological year (1992–2021 average), which was subsequently used as an environmental forcing for our model.

An important driver of the spawning process is the temperature threshold determining the onset of spawning activity. Warmer winters allow for a faster development of the gonads leading to an earlier onset of spawning and vice versa for years featuring a colder winter (Lillelund, 1961). Comparing the onset of spawning between the selected years reveals two distinct groups. The first group, comprising the years 2002, 2017, and the climatological average, show early spawning within the initial days of March. Notably, only 2002 features February temperatures at or above the climatological mean. The early onset of spawning in 2017, despite lower February temperatures, is attributed to a steep temperature increase starting at the end of the month. Conversely, colder February temperatures in 2005 and 2009 delayed the spawning onset by increasing the necessary spawning threshold temperature (Lillelund, 1961).

Development during egg and yolk-sac stage is governed by the water temperature. Interannual variability of the spring water temperature as well as year-specific temperature increases can vastly enhance the development speed during these two life stages. The fastest hatching of individuals is observed in 2005 (21.33 days, green line Fig. 6a) followed by 2009 (24.13 days, blue line Fig. 6a) and 2017 (24.75 days, yellow line Fig. 6a). Although earliest spawning (dashed line in Fig. 6b) is observed for 2002 and for the climatology year, the rather cold temperatures after spawning lead to a prolonged egg development phase and later hatching. Similar results are found for the development during the yolk-sac stage. Modelled duration of the stage lasted between 5.29 – 8.7 days. Fastest development is again found in years that previously featured high egg development speeds. These reported timespans are well within the range previously reported in different studies and ensure survival and a successful transition into the exogenous feeding life stages (McCarthy et al., 2020).

The different durations of development in both life stages are also

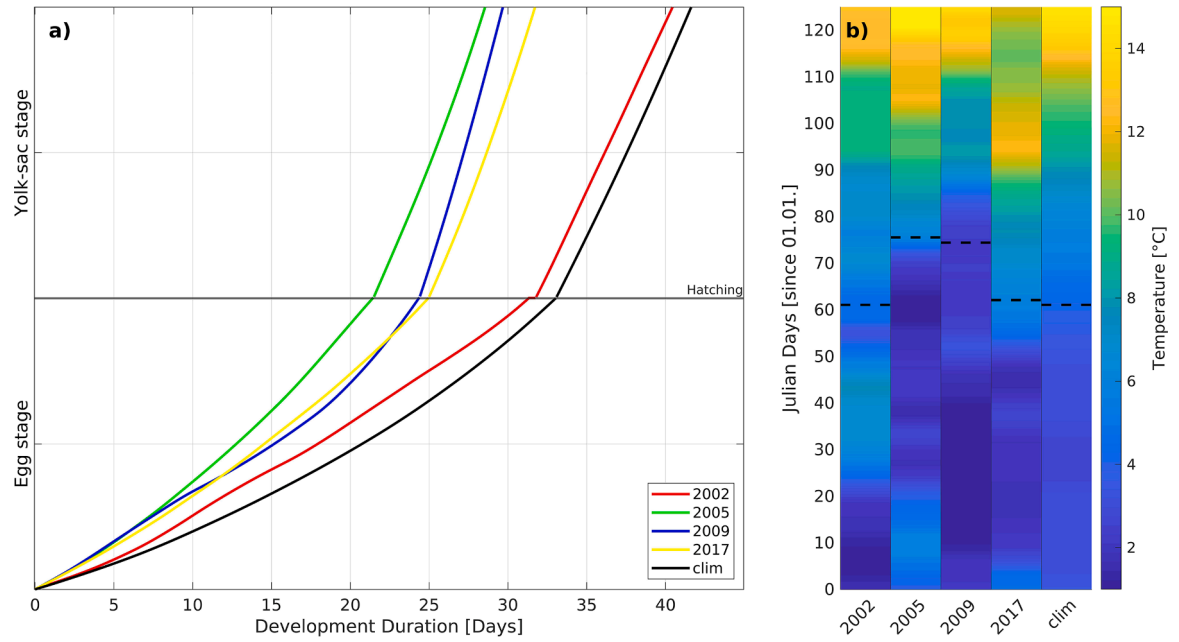


Fig. 6. a) Impact of temperature on the spawning process and the development during the early life stages. Using the observation based forcing the development during the egg stage as well as the development towards yolk sac depletion is presented. b) Temperature development during the development period. Black dashed lines mark the time of spawning.

important for the potential survival of the individual. Two aspects should be mentioned here. The first is related to the concept of a stage duration related mortality (Chambers and Leggett, 1987; Houde, 1987, 1989). This concept suggests that the risk of mortality increases if an individual stays in the same life stage for longer times. Consequently, a faster development during endogenous feeding stages could increase the chances of reaching the exogenous feeding stages. Especially during the egg stage, increased sedimentation or fungal infections can lead high mortality events, as the eggs are largely stationary due to their attachment to the substrate. The second aspect is the decreased potential of a predator-prey mismatch situation (Robert et al., 2023). Later spawning, as seen in 2005 and 2009, is counteracted by faster development due to fast rising water temperatures. Time between earliest and latest spawning differed by 14.75 days. The faster development during years featuring later spawning decreases the overall difference between earliest and latest hatching to 11.08 days. At the time of first feeding the

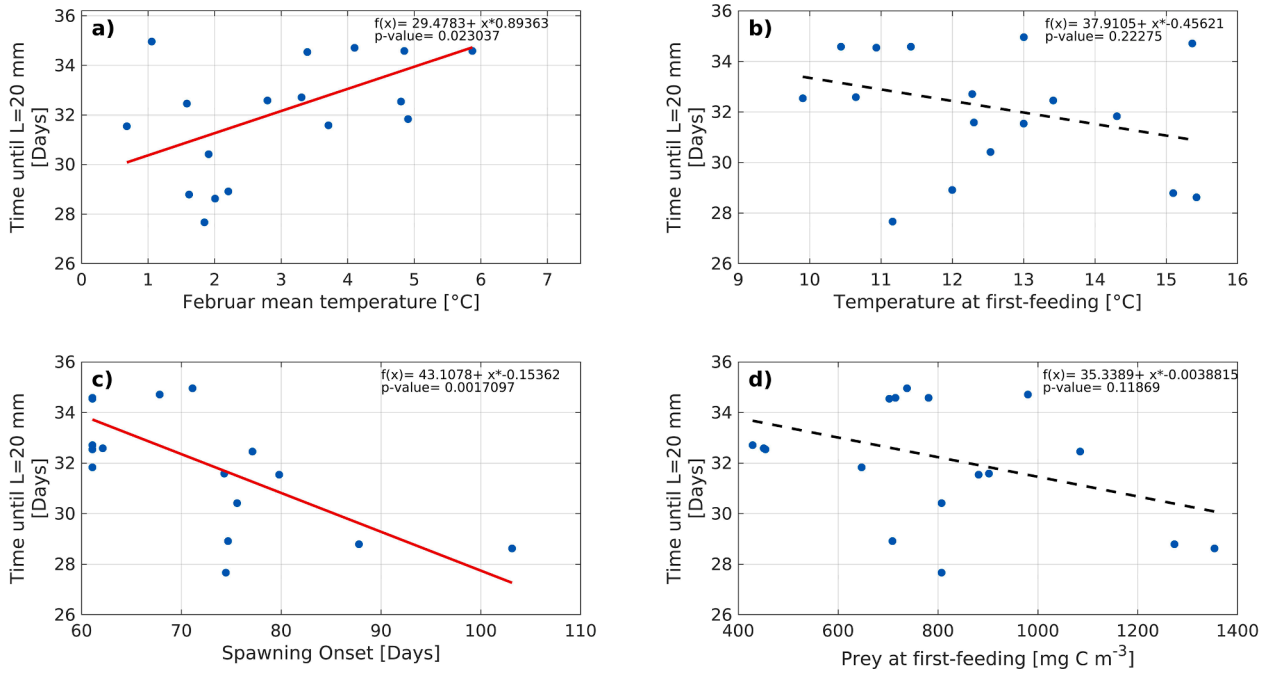


Fig. 7. Impact of 4 drivers on the development time duration of the individual. Simulations are based on daily forcing for the years 2000–2017. Development time in days is calculated as the time from spawning until reaching a length of 20 mm. Tested is the relation between development time and (a) February mean temperatures as estimated based on the available forcing, (b) Temperature at first feeding, (c) Onset of spawning and (d) the available prey concentration at first feeding. Linear regressions were conducted for each of the 4 tested parameters and are included in the figures. Significant regressions are shown in solid red, while non-significant relations were included as dashed lines.

difference between all presented years is only 9.833 days. Especially during years including comparably late spawning this helps to prevent a possible mismatch as suitable prey concentrations might already start to decrease in case of longer development and later first feeding.

Further, we investigated the impact of temperature and available prey concentration at the individuals transition to exogenous feeding. The results (Fig. 7b&d) indicate faster development under higher prey concentrations and warmer temperatures. As the individual's length at first feeding is equal throughout all years the increased maximum daily consumption due to increased temperatures is the main driver of the faster development. In none of the investigated years the temperatures exceeded the optimal temperature window (13–17 °C). Neither was a potential mismatch due to insufficient prey concentrations found in the model results.

In summary, our results demonstrate how interannual variability in extrinsic factors affects individual development. By using observation-based forcings and model-derived prey fields, we assessed the influence of spawning timing, winter and spring temperatures, and prey availability on all modelled life stages. The spawning process significantly affects subsequent development stages. However, assessing the impacts of climate change was limited due to the absence of extreme temperature and low oxygen conditions in the provided data, particularly during the critical first feeding period. The potential impact of extreme summer temperatures on the population dynamic of smelt was studied by (Keskinen et al., 2012) and is briefly discussed in the following. Their study focused on land-locked populations in Lake Pepsi. Strong temperature increases during summer led to increased mortality rates in the local population.

The mixture of temperature driven stratification, limiting the vertical migration potential and therefore decreasing the available prey, as well as eutrophication-based oxygen depletion led to large interannual variations in the population. However, following years of a reduced recruitment success, were years in which the population was able to reestablish itself. An important aspect in this context is the comparison between negative and positive feedback to temperature increases. It was already shown that warmer temperatures can be beneficial during the egg and yolk-sac development. During exogenous feeding the individuals metabolism is strongly dependent on the temperature with increasing energy demands under warmer conditions. Balancing of the increased energy demand is possible due to an increased daily maximum consumption. Only if temperatures surpass the favourable thermal window (Munday et al., 2009), the increased energy demand cannot be balanced by increased daily consumption. However, during first feeding all temperatures were well within the thermal window.

The final part of our study tries to connect the variability of the reported CPUE based on the available monitoring data and the development speed of the individuals in our IBM. Overall the monitoring data (Fig. 8a) shows a large interannual variability as well as a possible decrease in the populations towards the end of the measurement period. Some years (2002-4,2006-8,2010-11,2013) feature above average catch numbers and are often followed by years with decreasing catches (2005,2009,2012,2014). For each of the years, the time required for individuals to reach a body length of 20 mm was compared to the number of caught individuals during the monitoring. The comparison in shown in Fig. 8b). The results indicate a mixed predictive success of our simplified model. Generally, the model is able to reproduce the impact of extreme changes in the extrinsic forcing. Years with high reported CPUE correlate to faster development in our IBM, while years with low CPUE are matched with longer development times as calculated by the IBM.

In the following we want to briefly discuss potential reasons for the lack of a significant relationship between the CPUE and our modelled development time. The monitoring data itself should be mentioned first as a major source of uncertainity in this relation. Only a limited amount of data was collected per year and quality of reports varied based on the reporting fisher. From these reports a preselection was needed as the effort (time spent fishing) has not been properly document in every report. The impact changing gear, fishing routine or bait can have on the

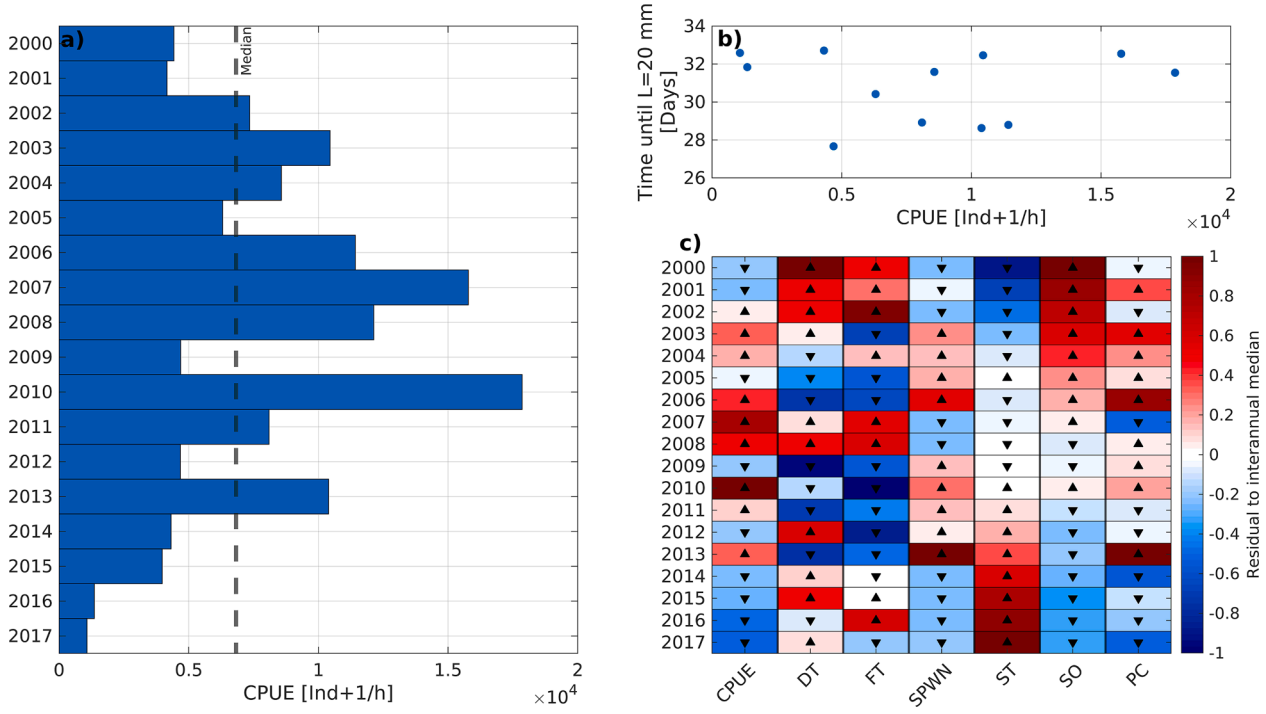


Fig. 8. (a) Yearly monitoring data summed up over the entire area of the Elbe estuary. Dashed line marks the interannual median over (2000–2017). (b) Relation between the previously described development time and the measured juvenile smelt numbers for each year. (c) Summary of possible driving factors for the interannual variation of the smelt population (CPUE = monitoring based CPUE of smelt, DT= Development time, FT= mean February temperature, SPWN= onset of spawning, SU= Averaged summer temperatures, SO= averaged summer oxygen concentrations, PC= Prey availability at first feeding). Arrows and colours indicate if the value for that year is below or above the interannual median (calculated over the years 2000–2017).

CPUE is nicely summarised in Hoyle et al. (2024). Often CPUE and length or individual size are sampled simultanously but never compared. The results of Chifamba (2000) nicely proved that CPUE and individual development are both highly related to the local water temperatures as well as other extrinsic variables. While these are automaticaly included in the CPUE presented in our study as sampling of early life stages requires them to reach a certain saize within a few months to be accounted for in the annual monitoring, a lot of variablity of extrinsic drivers is missing due to the reduced complexity of our model. We compare the development time as calculated based on the forcing that was extracted from a singular measurement site with a spatially conducted monitoring that included fish from different sites of the Elbe estuary. While including more forcing could potentially increase the models predictive skill on recruitment, but would also include further insecurities based on the input forcing and data availability. The 3D implementation of our model is a work in progress and is beyond the scope of this study. As it is a sensitivity study the underperformance in terms of predicting the CPUE and linking recruitment to the catch per year is of smaller importance compared to the previously reported matching growth, mortality and development aspects. Changes in these variables is again highly realted to changes in the extrinsic forcing and a matter of our sensitivity study of the model.

We therefore want to focus on the variablity of key drivers in our model setup in comparison to the available monitoring data. Interannual variabilities were compared by calculating the deviation from the interannual mean. The resulting data is shown in Fig. 8c). For each year the table indicates wheather the value of each parameter is below of above the averaged value over all years. Many of the years featuring a high abundance of juvenile smelt also feature an onset of spawning that is later then the interannual average and winter temperatures below the average. Another interesting aspect is the clearly visible shift in the forcing in terms of summer temperatures and oxygen concentrations. Averaged summer temperatures after 2010 were always above the interannual mean, while oxygen concentrations after 2006 tend to be below the mean. This trend is presumably continuous and is one prominent feature of the anthropogenic impact of climate change on the ecosystem of the Elbe Estuary (Seiffert and Hesser, 2014). While showing the decreasing trend of oxygen concentrations, the forcing data seldom featured hypoxic events. This could be due to the measurments being taken in surface areas close to the shore, where mixing processes would most likely always increase the measured concentrations. Noticeably, the number of years with higher CPUE decreased in the same timerange as the shift in the summer temperature and oxygen conditions. This further strengthens the assumption that changes in the exogenous forcing decreases the recruitment success of smelt larvae.

Overall the presented potential drivers and their combination with respect to the smelt abundance show that a single parameter alone can hardly explain the interannual variation or the successful recruitment. Although some similarities can be seen for years with stronger smelt populations (faster development, later spawning or larger availability of prey). Some years show an increased population without featuring the entire set of these factors making predicitons of recruitment variablity and population dynamics rather complicated. Determining single drivers of a successful or failed recruitment on a yearly scale is therefore nearly impossible. But assessing the impact of various drivers on shorter timescales such as the duration of single lifestages can give us a better understanding of the dynamics that are later on, in a combined matter, determining the interannual recruitment success.

4. Conclusion

Using the newly developed individual-based model for the European smelt, we assessed the impact of intrinsic and extrinsic drivers on the interannual recruitment variability observed in the Elbe Estuary. By applying idealised constant forcing, we isolated the effects of singular external and internal factors to better understand the fundamental dynamics involved in the successful development of the early life stages. A comparison of our results with other previous studies showed that the growth patterns reproduced by our model fall within the range of plausible values. Based on these results, we identified minimum threshold values for prey availabilities as well as optimal temperature and oxygen ranges, which were further compared to the existing literature.

Assessing the impact of extrinsic drivers such as temperature and prey availability revealed that only a combined analysis can adequately capture their effect on individual growth and development. Both factors play a critical role in the context of anthropogenic usage and climate change in the Elbe Estuary. Our study proved that increasing temperatures combined with decreasing oxygen conditions limit individual development and growth for both younger and older individuals. Due to the ongoing warming and reported more frequent occurrence of hypoxic events around the port of Hamburg (Kerner, 2007), we assume that the extrinsic driver's potential to harm the local smelt population in the Elbe estuary will increase in future years. The presence of such a shift in summer conditions has also been included in our model forcing as from 2011 on the oxygen concentrations decreased, while water temperatures during summer increased in our forcing. While hypoxic conditions were not found at the measuring location, our sensitivity tests toward decreasing oxygen concentration showed the model capability to reproduce decreased growth and ultimately individual death under severe hypoxic conditions.

We concluded our study with the comparison of the model results to the available monitoring datasets for juvenile smelt in the estuary. Although both the monitoring dataset as well as the observation-based forcing contain uncertainties, the model is reasonably able to reproduce higher and faster development time in years with a higher abundance of juvenile smelt. However, the development speed can only be used as one possible indicator for a successful recruitment, especially since our IBM does not fully account for internal processes influencing the transition from early life stages to the juvenile phase. Therefore, mortality risk or successful growth after reaching the threshold of 20 mm length and developing enhanced swimming capabilities cannot be guaranteed.

We will use this study as a baseline model refinement. Next, we will couple this IBM to a 3D general circulation model further coupled to a biogeochemical modelling system via an Lagrangian tracking approach to represent spatial dynamics and individual drift. This fully 3D biophysical coupled framework would allow us to overcome the problem with the limited data availability. Further, due to the high spatial resolution of our modelling system, the impact of small-scale changes on the individual can be assessed and used to investigate the recruitment success in time and space, considering the meaning of nursery grounds for individual development. Due to the increased data availability in the model, we also want to incorporate new mechanism to the IBM itself. Currently we are working on an active vertical retention scheme, that allows the individual to vertically position itself in the water column to prevent drifting into the open sea as well as including turbidity as another driver that impacts the individual's ability to find suitable prey items.

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Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) used ChatGPT and DeepL in order to check for spelling mistakes and major gramatically

mistakes. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

CRediT authorship contribution statement

David Drewes: Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Conceptualization. **Corinna Schrum:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Johannes Pein:** Writing – review & editing, Resources, Methodology. **Déborah Benkort:** Writing – review & editing, Methodology. **Ute Daewel:** Writing – review & editing, Validation, Supervision, Software, Methodology, Funding acquisition, Formal analysis, Conceptualization.

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.

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Data availability

The data underlying this article will be shared on reasonable request to the corresponding author.

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Study 2: Impact of climate change on smelt development in the Elbe estuary

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Author Contributions:

DD conducted the IBM simulations, performed the data analysis and wrote the manuscript. CS, UD contributed to the study design, data analysis and discussion. JP provided and developed the model-based forcing and model setup of SCHISM. All authors revised and approved the manuscript.

Comment:

Due to a communication problem, the figure captions were missing in the pre-print version of this paper. As the coordination and final fixing of the prepublished version took too much time to be included into this study, the draft version that is identical to the submitted one is included instead. Text, Story and Results of the paper remain unchanged, the decision was purely based on a complete representation of the study, including the missing figure captions.

Hydrodynamic retention and environmental stressors shape the recruitment of the European Smelt in the Elbe estuary: an individual-based modelling study

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Abstract

Estuarine environments like the Elbe in Germany are known hotspots of fish early life stages due to their function as nursery grounds. Anadromous species such as the European smelt (*Osmerus eperlanus*) migrate into the estuarine environment and spend nearly their first year there to benefit from the local growth conditions. Here we assess the recruitment success of this species in the estuary with respect to a) spatial and interannual variations in environmental conditions; b) behavior to support retention in favorable areas; and c) proxies for climate and anthropogenic stressors. We use a three-dimensional Individual-based model (IBM) together with high-resolved input data from a coupled physical-biogeochemical model. We examine how environmental driver such as temperature, oxygen, prey availability and turbidity impact the individual development, growth and recruitment success. Our model reproduces observed spatial variability of egg and larval development, especially within hotspot regions of larval development such as the Mühlenberger Loch. Passive drift of larvae resulted in substantial export out of the less saline estuarine environment. By implementing a selective tidal-stream transport, individual retention improved significantly. While larvae remain in the estuary increased summer temperatures become a limiting factor for successful development and survival. To assess climate and human-induces stressors we examined the impact of warming and turbidity-driven development constraints. Increasing temperatures further reduce the suitability of the estuarine environment, while decreased prey consumption due to unsuitable turbidity conditions results in a higher risk of starvation driven mortality. Overall, our study aims to increase the

understanding of the linkage between early life stage development of the European smelt and recruitment and the continuously changing environment of the Elbe estuary.

Introduction

Estuarine environments are known to be a hotspot of biological development (Barbier et al., 2011) and play a key role as nursery grounds for many marine species (Able et al., 2005; J. Baptista et al., 2019; Borges et al., 2007; Cabral, 2022; Primo et al., 2013). The unique conditions feature highly turbid areas combined with increased prey conditions throughout the year, making it the perfect area for development of early life stages of fishes (Arevalo et al., 2023). Worldwide anadromous species are impacted by increasing human pressure and climate change as they rely on estuarine environments as nursery grounds protecting their larvae until successful recruitment (Anderson et al., 2013; Brian, n.d.; Jonsson & Jonsson, 2009; Lassalle & Rochard, 2009; Nicholson et al., 2008; Robinson et al., 2009).

A key species in the Elbe estuary is the European Smelt (*Osmerus eperlanus*) (Lillelund 1961, Möller and Dieckwisch 1991, Sepulveda Aquiles, Thiel, and Nellen 1993, Thiel et al. 1995, Eick and Thiel 2014). This anadromous spawning species utilize the inner parts of the Elbe around the harbour of Hamburg, the shallow areas of the Mühlenberger Loch as well as the coastal areas towards the weir in Geesthacht as potential spawning areas (Gerkens & Thiel, 2001; Möller & Dieckwisch, 1991; Thiel et al., 1995). Migration of the adult individuals is based on temperature differences of the riverine outflow during winter months (Belyanina, 1969; Lillelund, 1961). Adults accumulate in the mouth of the estuary and migrate upstream towards the potential spawning grounds (Lillelund, 1961). The onset of spawning is driven by natural cues such as freshwater runoff or temperature increase in early spring (Arevalo et al., 2023; Lillelund, 1961). Spawning activity of the European smelt is reported to happen during March (Belyanina, 1969; Lillelund, 1961). The duration of the spawning season is clearly defined by temperature changes (Belyanina, 1969; Lillelund, 1961). Freshly spawned eggs are attached at the ground or rocks using their adhesive eggshell (Lillelund, 1961; McCarthy et al., 2020) keeping them in place in the rapidly moving tidally driven environment. Normally spawning grounds are chosen strategically around larger structures like rocks or groynes, utilizing the reduced current velocities in their vicinity (Lillelund, 1961). While eggs are rather stationary, freshly hatched larvae are heavily relying on their potential to remain in the chosen spawning locations. Their success to stay there impacts their recruitment success and future development (Bailey et al., 2008; Martinho et al., 2007). Using the tidal currents is a comparably energy conserving method of

retention (Chen et al., 1997). To utilize the tidally driven circulations the young larvae need to move vertically through the water column. In general, the swimming ability of fish larvae increases with body size (V. Baptista et al., 2020; Teodósio et al., 2016), allowing larger individuals to improve their ability to remain in beneficial conditions. Studies on other osmeridae species (Laprise & Dodson, 1989) showed that retention in the estuary improves growth conditions as prey availability increases and predation risk decreases significantly.

Climate change is expected to alter the estuarine environment in ways that may shift the dominant factors affecting especially early life stages. Sea level rise can significantly affect tidal circulations and current dynamics in coastal and estuarine systems. As shown in previous studies (Hein et al., 2018; Kerner, 2007; Thiel et al., 1995), increased current velocities may enhance dispersal of early life stages out of their preferred nursery grounds out into the coastal regions. Earlier studies indicate that climate change and anthropogenic use of the estuarine environment can negatively impact fish early life stages (Arula et al., 2017) through e.g. increasing temperatures and the enhanced occurrence of hypoxia (Möller & Scholz, 1991; Thiel et al., 1995). Further, the continuous dredging work to maintain the necessary depth especially in the port of Hamburg led to an increase of turbidity levels throughout the estuary (De Jonge et al., 2014). Increasing turbidity levels can impact individuals in both a positive and negative way, like the thermal window (Munday et al., 2009; Pörtner & Knust, 2007). Species tend to prefer certain turbidity levels. The results of Illing et al. (2024) showed that anadromous living smelts show a bell-shaped reaction to increasing turbidity with a maximum of growth around values of 200 FTU. Due to their visual feeding strategy (Belyanina, 1969; Illing et al., 2024; Reiser et al., 2023; Taal et al., 2014), turbid conditions enhance their potential to detect prey items. However, if the optimal conditions are surpassed, growth decreases while mortality rates increased. Studies showed, that due to their fragile body conditions especially very young individuals can be harmed by highly turbid conditions due to damages on their gills as well as clogging of their internal digestive organs (Illing et al., 2024; Lowe et al., 2015; Rodrigues et al., 2023; Salonen & Engström-Öst, 2013; Swenson & Matson, 1976; Tigan et al., 2020).

While in-field monitoring programs acquire a lot of effort and funding due to the necessity of chartering fishing vessels, modelling studies using Individual based models can help to understand differences in the development of individuals due to changes in the extrinsic forcing (Daewel et al., 2011; Dudley, 2019; Hinckley et al., 1996; Kimmerer & Rose, 2018; Letcher et al., 1996; Peck & Daewel, 2007; Van Winkle et al., 1993). The method of individual based modelling has already been applied for

several species in estuarine environments (Dudley, 2019; Dur et al., 2009; Höök et al., 2008). Depending on the number of considered external factors such models can be used as an excellent tool for investigating spatial differences in growth and overall development (Daewel et al., 2008; Hinckley et al., 1996; Letcher et al., 1996; Peck & Daewel, 2007; Van Winkle et al., 1993). So far in case of the Elbe estuary, individual based modelling was only used for the development and survival of phytoplankton (Steidle et al., 2024; Steidle & Vennell, 2024). Extending and combining the available modelling systems of the tidally driven Elbe estuary with newly designed routines to model the individual growth of early life stages of the European smelt enables us to investigate how local changes might impact the individual's growth.

Our IBM has previously been validated in a 1-dimensional setting (Drewes et al., 2025), and has now been extended to a 3-dimensional setup allowing for vertical and lateral drift of individuals and has been connected to a coupled ocean model to increase the accuracy of our calculations. We want to use this newly extended setup to answer the following three questions:

What is the role of the spawning location for the individual’s growth and development?

Does active selective tidal stream transport promote the larvae retention in the estuary and how does that effect growth and survival?

How are early life stages of the European smelt influenced by anthropogenic and global warming induced changes of the ecosystem in the Elbe estuary?

These questions are based on previous results that showed the importance of spawning and endogenous development on the recruitment success at later stages. Using a combination of literature-based assumptions and the simple implementation of a retention scheme presumably increases the ability to remain within the estuary. These two questions form a baseline for the latter part of the paper where we focus on the suitability changes due to increased warming and how increasing turbidity is impacting the individual’s consumption potential. Answering these questions allows us to further understand how future changes potentially impact the European smelt in the Elbe estuary.

Methods and Simulations

Model system

Hydrodynamic and biogeochemical model setup

The baseline of our study is the forcing data provided for the offline coupled computation of the IBM. We use a modelling system, containing a hydrodynamic core as well as a one way coupled biogeochemical modelling system. For the hydrodynamical calculation we decided to use the Semi-implicit Cross-scale Hydroscience Integrated System Model (SCHISM) (Zhang et al., 2016). The model solves the Reynolds-averaged Navier Stokes equations on unstructured grids using the semi-implicit finite element formulation reducing numerical dissipation and enhancing numerical stability. The grid setup used in our study is presented in Pein et al. (2021) and is presented in Figure 1. The grid is constructed using 32k nodes and features varying horizontal resolutions ranging from 500 m at the open ocean directed boundaries up to 30 meters in the vicinity of the Port of Hamburg. Vertically, the LSC2-grid allows for a detailed resolution of vertical structures depending on the maximum local depth. A maximum of 20 vertical layers is applied to areas deeper then 5 meters. Shallow regions (<2m) are resolved by a single vertical cell. Model simulations were conducted using a 60s timestep.

Calculation of the biogeochemical forcing was done using the ECOsystem Model (ECOSMO, (Daewel & Schrum, 2013; Schrum et al., 2006)). The ecological routine of ECOSMO was coupled to the SCHISM hydrodynamic system using a one-way coupling provided by the messaging interface FABM (Framework of Aqua Biogeochemical Models, (Bruggeman & Bolding, 2014)). For a detailed description of fine-tuning of parameters in both the hydrodynamical core as well as the biogeochemical module, we refer to the detailed model description and evaluation found in (Fan et al., 2025; Pein et al., 2021)

Forcing and resulting scenarios

Our study includes data obtained from two scenarios: a reference and a warming case. The reference case describes the state of the estuarine environment based on the year 2012 and shows the current conditions. The warming case aligns with an extended climate scenario under 1 m of sea level rise.

For consistent forcing under both the historical hindcast and the climate change experiment, both numerical model runs have been nested into an intermediate model simulation of the southern North Sea (Pein et al., 2023). The one-way-nest between the parent model of the southern North Sea and the child model of the Elbe

estuary includes physical variables such as sea surface elevation, horizontal currents and temperature and salinity. Further, biogeochemical boundary conditions were prescribed at the open boundary using observation based-averaged timeseries from the ICES database representing the conditions of nutrients, oxygen and biomass I the southern North Sea (ICES area IVb).

The river discharge, an important driver of estuarine dynamics, was prescribed at the most western part of the model grid. Discharge forcing was derived based on the daily observations available at the gauge in Neu Darchau, located a bit upstream of the weir of Geesthacht. Small side tributaries were included in the model as point sources that contribute to the freshwater balance of the modelling system. Discharge timeseries were based on the available observations found online at the FGG Database (www.fgg-elbe.de/elbe-datenportal.html). Based on the inflow volume the input concentrations of nutrients, oxygen and organic matter were estimated.

Finally, the atmospherical forcing, including wind, air temperature, precipitation, short- and longwave radiation is based on reanalysis data provided by the COSMO-EU model operated by the German weather service (DWD). A detailed description of the forcing, especially at the air-sea interface can be found in (Stanev et al., 2019).

For the warming scenario, a simplified climate change scenario was applied across the parent model domain increasing sea level by 1 m and temperature forcing by 4°C at the open boundaries and at the ocean surface relative to the reference case, respectively. The dynamic response at the mouth of the Elbe estuary represents an extended RCP8.5 scenario corresponding to global warming and mean sea level rise median trajectories by 2125 (Pein et al., 2025)- For consistent scenario implementation with the estuary, the increased air temperature forcing and the by 4°C increased river water temperature forcing are applied to the Elbe estuary model simulation at the water service and at the tidal weir, respectively. As a result, average mean sea level increases by approximately 1 m and average water temperature increases by 3.2°C in the estuary (Pein et al., 2025).

Lagrangian Particle Tracking

The Lagrangian particle tracking is based on the available tracking routine within the SCHISM framework. The tracking routine itself is available as an offline coupled module relying on the modelling input of the SCHISM model. This tracking was initially created for the modelling of oil spill scenarios (Chiu et al., 2018) and microplastic drift experiments (Summers et al., 2023). We expanded the available

tracking to allow for the inclusion of biological and physical properties in the tracking routine. Further the IBM was included as an additional module into this framework.

Lateral movement of particles is governed by advective and diffusive contributions. Especially the impact of mixing related processes is described by the diffusive transport contribution. Yet the scales on which turbulent movements occur is small and, in most cases, not resolvable by models. The diffusive contribution is therefor included via a random walk (Grimes et al., 2021; Steinbuck et al., 2011). The horizontal displacement ΔX_p for each particle p is calculated as follows:

$$\Delta X_p = \left(U_p + \nabla K_x\right) \times \Delta t + RW \quad (1)$$

With U_p being the advective u-component of the modelled flow field and ∇K_x being the horizontal gradient of the local diffusion. Finally, the random walk (RW) induced turbulent movement is calculated as $RW = R \times \sqrt{6K_X(\frac{\Delta t}{2})}$ (Li et al., 2023). R is a randomly generated number within the range of -1 to 1, K_x being the local turbulent diffusion coefficient.

Vertical displacement of the particles is calculated based on local vertical advection and diffusion and the additional term RT_p that allows for the implementation of vertical migration movements. Based on the study of Laprise & Dodson (1989), we decided for a form of selective tidal stream transport via local changes of the sea surface elevation as a cue for the vertical migration:

$$\Delta Z_p = \left(W_p + \nabla K_x + RT_p\right) \times \Delta t + RW \quad (2)$$

Horizontal gradients of the turbulent diffusion are calculated based on the Smagorinsky algorithm (Smagorinsky, 1963) using the local velocity fields. Calculation of the horizontal and vertical displacement is limited to the exogenous feeding individuals as we assume that egg and yolk-sac larvae remain at the spawning locations. The latter are typically calmer locations at the shallow regions along the shoreline (Lillelund, 1961; Sepulveda et al., 1993).

Wetting and drying of cells is considered in the initial tracking formulation but not further included in our model as we assume that even though a cell is marked as dry small puddles of water remain there enabling survival of early life stages. Accumulation at the model boundaries is prevented by a direct reflection of the individual in case it hits one of the boundaries. The reflection is done by reversing the normal velocity component while keeping the tangential one and updating the particles position accordingly.

All tracking simulations used the hourly output provided by the previously described coupled model system. To meet the requirements of the CFL criterion (Courant et al., 1967) and avoid overshooting an internal timestep of 2 min was used in the particle tracking.

Individual Based Model

The final part of our modelling system is the individual based model (IBM) itself. The IBM was online coupled to the particle tracking routine. Values for the location, temperature, available prey, oxygen and current velocities are calculated in the tracking routine and shared with the IBM module. An extensive description of the IBMs included processes, and a full validation is given in Drewes et al. (2025). We therefore only focus on the major two new additions used for this study.

The first addition to the initial model is the possibility of the individuals to vertically migrate based on the local sea surface elevation (previously named RT_p). In the Elbe estuary tidal forces are presumably the largest contributor to lateral larvae displacements. Active tidal driven retention is observed for other smelt species such as the Rainbow smelt (Osmerus mordax) (Laprise & Dodson, 1989). Vertical displacement of the individuals allows for an optimal utilization of the tidal currents to remain inside of their favourable nursery grounds (selective tidal stream transport). Retention potential increases with individuals' length as it is directly linked to their swimming capabilities (V. Baptista et al., 2020; Teodósio et al., 2016). The total retention contribution to the vertical displacement calculation is calculated as $RT_p = \text{ret}_{\text{fac}} * (SP_s/1000) * \text{ret}_{\text{dir}}$. The ret_{fac} determines how much of the total swimming speed SP_s can be used for the vertical migration. In our cases we decided that half of the swimming capacity can be used to adjust the individual's vertical position. The retention direction ret_{dir} is based on the difference between the sea surface elevation at the current and previous timestep: $\text{ret}_{\text{dir}} = \begin{cases} 1 \text{ if } \text{sse}_{\text{old}} < \text{sse}_{\text{new}} \\ -1 \text{ if } \text{sse}_{\text{old}} > \text{sse}_{\text{new}} \end{cases}$.

The second major addition to the IBM was the inclusion of turbidity as a potential thread for the individual's survival. The impact of a range of turbidity values was just recently published studies by Illing et al. (2024). Their study showed that increasing turbidity values can alter the individuals prey success resulting in fewer larvae with filled guts. Studies proved that enhanced turbidity impacts the ability visual ability to find suitable prey (Hansen et al., 2013; Mazur & Beauchamp, 2003; Meager et al., 2005; Minello & Benfield, 2018). We chose to decrease the individual's visual aquity based on the local turbidity values. Further adjustments were made to the maximum daily consumption as prey intake in general decreased for high turbidity

values as found in (Illing et al., 2024). Turbidity was included using 1D observational based timeseries from the Elbe Estuary. Observations were taken from the measurement station located at Hanskalbsand operated by the Wasserstraßen- und Schifffahrtsamt Elbe-Nordsee (www.kuestendaten.de). Observations were available at bottom and surface level with a timestep of 5 minutes. Years without data gaps were selected and interpolated to match our hourly forcing timestep. Using tidal observations and autocorrelation we modified the resulting observation timeseries to match the tidal cycle in the model. Three turbidity timeseries were created with differing averaged turbidity's: low (trb1), medium (trb2) and high (trb3). Due to the missing spatial resolution of available observation, we assumed spatial homogeneity and particles encounter the same turbidity regardless their location.

IBM initialisation and data analysis

Spawning locations were chosen based on findings from literature (Lillelund, 1961; Möller & Dieckwisch, 1991; Thiel et al., 1995). In total 5 stations were chosen and are presented in Figure 2f). Due to their adhesive nature (Lillelund, 1961; McCarthy et al., 2020), eggs were spawned in the bottom layers at the predefined spawning locations.

Due to the missing active spawning stock in our model, the spawning onset is estimated using the local averaged February temperature (Drewes et al., 2025). The model simulations were initialised with 1500 particles each, equally distributed over the chosen spawning locations. At each location, the spawning period lasts for 20 days with an equal number (300) of particles being released per station. Following the superindividual approach (Scheffer et al., 1995), each of the released particles represented a total of 1 million larvae. A particle is assumed dead if the number of remaining particles surpasses 1% of this initial value.

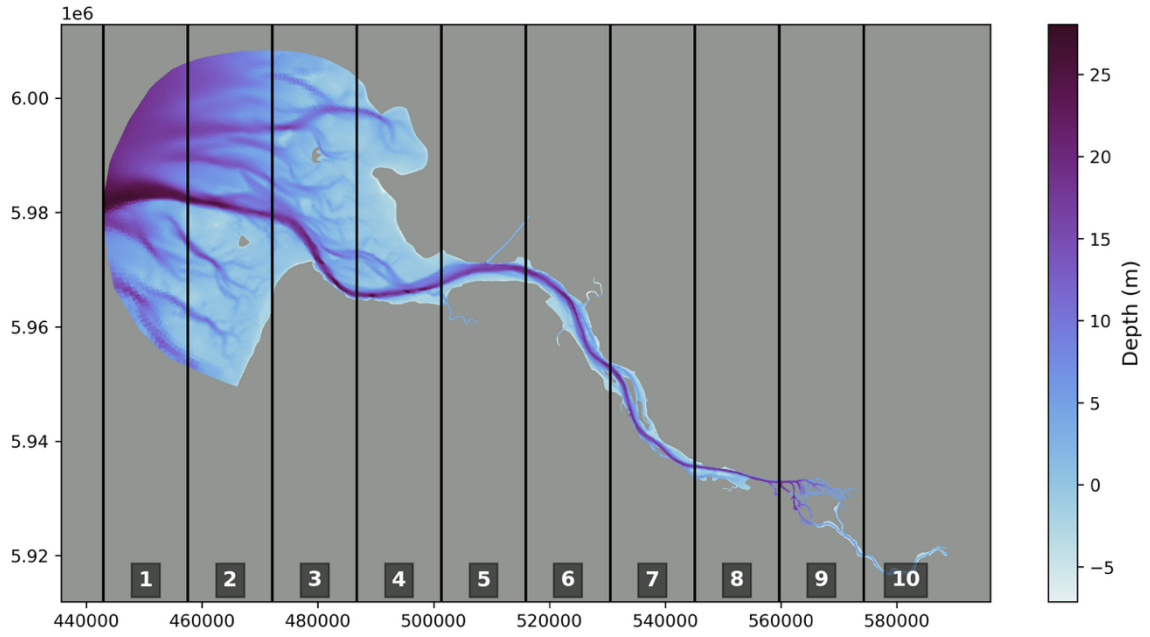


Figure 1: Section wise division of the model domain to assess the suitability over time. Sections were equally spaced, and their numbers are shown in the bottom of the map. The validation of the model grid can be found in Pein et al. (2021).

Like the input timestep of the forcing provided to the tracking, the IBM output is available in an hourly resolution. Important output variables that were used in this study were the stage identifier, body length (mm) and weight (mg). Stage duration is calculated based on the first and last timestep that an individual spends in each life stage. Endogenous development will in the following account for the cumulative development duration during egg- and yolk sac stage. While exogenous development only includes growth and survival of actively preying individuals after first feeding.

Individuals were simulated until they would reach a length of 25 mm. Due to the increasing swimming capacity of larger individuals continuous modelling after surpassing that threshold would need us to incorporate active horizontal movement based on extrinsic ques. Under the assumption of a passive drifting behaviour, we decided to not include older individuals.

Comparison of the development is directly linked to this maximum length via the introduced development time. The development time describes the cumulative hours that an individual's needs to complete the endogenous stages up until reaching the maximum length of 25 mm.

Suitability index

Assessment of suitable conditions was done by creating a nodewise calculated index S_I based on local temperature, oxygen, and salinity. Optimal parameter ranges and thresholds were defined based on previous studies and available

literature for exogenously feeding life stages of smelt. A threshold of 150 mmol m^{-3} was used as it reassembles the upper boundary for hypoxic conditions. Based on McCarthy et al. (2020) growth rates increased under salinity conditions between 0-10 psu. Our previous 1D study showed that growth of younger individuals was highest within temperatures between 13 to 19°C. Using these ranges, variable-wise penalties (P_T, P_S, P_{O2}) are calculated using the following equation:

$$P_T = \begin{pmatrix} 0, \text{ if } T_{min} \leq T \leq T_{max} \\ \min(|T-T_{min}|, |T-T_{max}|), \text{ else} \end{pmatrix} \quad (3)$$

The variables contribution to the suitability index is calculated based on these penalties as follows:

$$S_T = 1 - \frac{P_T}{T_{max} - T_{min}} \quad (4)$$

Finally, using a weighted approach to allow for varying influences of external forcings, the node-based suitability index is calculated as $SI_{total} = w_T \cdot SI_T + w_S \cdot SI_S + w_{O_2} \cdot SI_{O_2}$ with $\sum w_{T,S,O_2} = 1$. We assumed that due to their limited swimming capability oxygen deficiency would have the highest impact on survival. We assigned a slightly increased weight in the calculation ($w_{O_2} = 0.4$). Temperature and salt were both weighted equally with 0.3.

The model domain was split into 10 subsections to indicate the spatial variability of the suitability. Based on vertically averaged input from the coupled model system the suitability index was calculated for each section. Monthly averaging finally used to indicate suitable conditions and their variability over the year.

Results and Discussion

The following sections cover the results of our 3D simulations. We want to focus on the endogenous development as well as the impact of active tidal steered migration as well as enhanced turbidity on the development of exogenous life stages. Based on our results we want to emphasise the importance of already known nursery grounds such as the Mühlenberger Loch. Finally, we want to extend our analysis on the impact of global warming on the individual development and survival.

Spatial variability of development and growth

Endogenous development and first-feeding

For our simulations, 5 spawning locations were selected based on their location within the estuarine environment. In the literature, spawning takes place mostly in

hotspots such as the Mühlenberger Loch (station B) or in the shallow coastal regions east of the port of Hamburg up to Geesthacht (station E). The other stations were distributed over the area of the port.

Conditions during the endogenous life stages are summarised in Figure 2. The cumulative duration of both egg and yolk-sac stage shown in panel a), can be used as a proxy for favourable growth conditions. Faster development during these life stages is generally associated with improved survival and increased recruitment rates (Hinckley et al., 1996). Among the investigated locations, station B exhibits the fastest development with a median of 30.5 days, while the slowest development occurs at station A (38.2 days). The other stations exhibit comparable development durations, falling in between these two extremes.

The sole extrinsic driver of development variability during these life stages is the local water temperature at the predefined spawning locations. Corresponding temperature distribution are shown in Figure 2c. Fast development at station B correlates with highest water temperatures at this location (10.8°C median), while the coldest temperature is found at station A (9.81°C median). The remaining stations show similar median values and range of temperature. Broadest range of temperature is found at station B. This greater variability may reflect the regions shallow depth, which can amplify the impact of local changes in the meteorological forcing leading to increased warming of the water body. In contrast, lowest variability of temperature is found at station A, likely due to its location closer to the tidally driven main channel, enhancing the impact of tidal mixing on the conditions. This is further supported by the bimodal temperature distribution at this station.

To assess the recruitment potential across the selected spawning sites more comprehensively, oxygen and prey availability were further analysed. Station B features the highest median of available prey (median: 1365.69 mg C m^{-3}) and moderately elevated oxygen concentrations (median: 342.06 mmol m^{-3}). At the other extreme, station E exhibits lowest prey (median: 256.22 mg C m^{-3}), but the highest oxygen concentrations (median: 402.14 mmol m^{-3}). While oxygen concentrations are relatively consistent across the selected stations, prey concentrations varied significantly. Station B and D show substantially increased prey availability compared to the other stations. Notably, these two stations were both selected to be in enclosed or semi-enclosed shallow areas such as the Mühlenberger Loch or Polder structures located in the vicinity of the Port of Hamburg. This likely promotes the increased availability of zooplankton biomass as a potential prey source The latter forms the primary food source for early life stages of the European smelt and likely enhances the local recruitment potential.

Finally, growth rates during the first 12 hours of exogenous feeding were used to assess the early development success. Due to the short timeframe, we could ensure that the drifting individuals remain close to their initial location, which allows us to relate their growth variability to local environmental condition in the vicinity of the spawning locations. Like the pattern observed for the duration of the endogenous stages, increased growth rates are found at station B (median: 0.174 mm h^{-1}), followed by station A and D (0.14 and 0.12 mm h^{-1} respectively). Lowest growth is reported at station C (0.06 mm h^{-1}). These results in general match those observed for the available prey concentrations, where lower concentrations were also found at stations C and E.

Interestingly, station A supports relatively high growth rates despite its reduced prey availability. This is explained by the lower local water temperatures, which in our model formulations reduce both the metabolic needs and maximum daily prey intake. Under these colder conditions, individuals therefore require less energy and can balance their energetic demand even under the limited prey availability resulting in stable growth rates. Across all stations, growth rates exhibited a unimodal distribution, though stations C and E included individuals with growth rates near or equal to zero. This highlights the suboptimal feeding conditions at those sites and the impact on local recruitment.

In summary, these results present distinct spatial differences in extrinsic conditions across the predefined spawning locations. Endogenous development is most favourable at station B (Mühlenberger Loch), which is a well-known hotspot for early life development (Eick & Thiel, 2014; Sepulveda et al., 1993). The shallow waters in this polder-like area offer enhanced water temperatures, decreasing the stage duration and are generally linked to faster development across life stages (McCarthy et al., 2020; Power & Attrill, 2007; Reiser et al., 2023). Besides that, high prey availability supports a successful transition to exogenous feeding (Arula et al., 2017). Both conditions are well captured by our model and jointly contribute to enhanced growth and development during endo- and exogenous life stages at station B.

In contrast, while additional spawning habitats were reported along the shallow, freshwater-dominated reaches located west of the Port of Hamburg (Sepulveda et al., 1993; Thiel, 2001), these to not perform equally well in our model. The station located close to Geesthacht, for instance, does not exhibit faster development of endogenous life stages and smaller growth rates compared to the station at the Mühlenberger Loch. Although high oxygen concentrations at this site reduce the risk of hypoxia-induced mortality, elevated temperatures combined with low prey

availability increase the individual's risk of starvation during the transition to exogenous feeding.

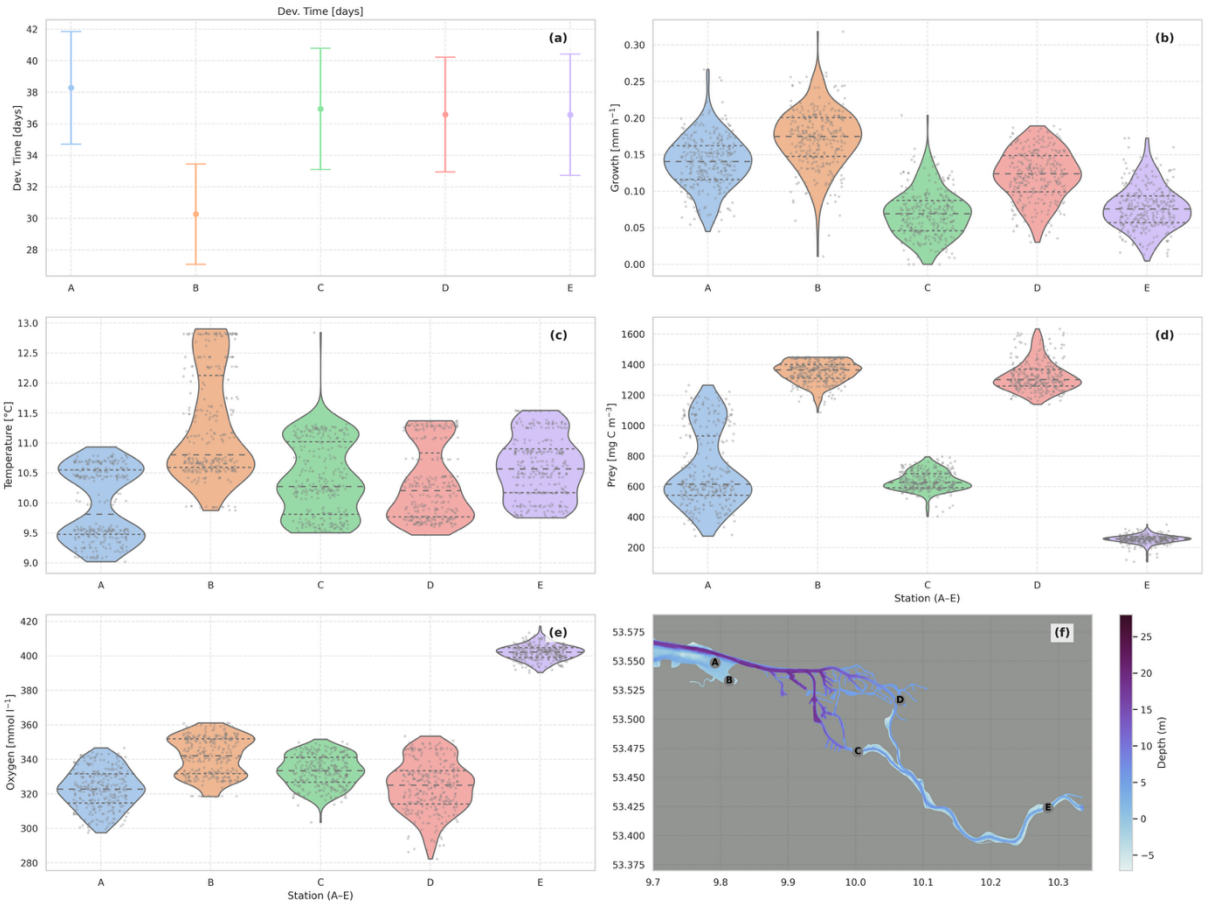


Figure 2: Results for endogenous development and early growth at the 5 selected spawning stations. a) shows barplots indicating the median development duration during endogenous life stages (egg and yolk-sac), b) Violinplots with the distribution of growth during the first 12 hours of exogenous feeding after the first-feeding transition, c-e) Violinplots of the extrinsic conditions during endogenous development, shown are temperature, prey availability and oxygen concentrations. The map in f) shows the 5 preselected spawning locations and their respective letters (A-E) used during our analysis.

Impact of retention and turbidity

The potential number of factors determining the growth variability increases as soon as the individuals start drifting through the environment. Following their life cycle, the early life stages should remain in the protected areas of the estuarine environment. Especially in areas with enhanced tidal currents, the individuals are at high risk to be flushed out into the open ocean. One often observed technique to avoid the flushing out is an active vertical retention behaviour (Chen et al., 1997; Gregory Lough & Manning, 2001; Laprise & Dodson, 1989). The young individuals position themselves in the water column according to the tidal cycle and utilise the strong transport as an energy conserving drifting method. This way, despite their

poor swimming capacity at smaller size, they can stay inside the estuarine environment.

Applying the vertical migration scheme to our individuals shows a change in drift behaviour (Figure 3a). Without an active retention, individuals spend on average 100 hours in the Sections located within the estuarine environment (4-10). Accumulation, described by higher numbers of hours per section, is only observed in the coastal areas of the North Sea and the surrounding southern German Bight (Sections 1-3). In both retention scenarios, particles accumulate in the inner estuary (Sections 5-9). Further, the vertical migration not only increases the accumulation of individuals inside of the estuary but successfully prevents the individuals to drift out of the estuarine environment. In fact, individuals in the retention scenarios gather at locations like the Mühlenberger Loch (Section 8) or inside channels of the port of Hamburg (Section 9).

Conditions there vastly differ from those observed in the simulations without retention. As a result, observed growth rates (Figure 3b) changed due to the variation of extrinsic drivers compared to the other simulations. The general shape of the curves yet remain similar. Growth rates were highest in Sections 4-7 and decreased for the eastern and western located Sections. Simulated growth rates decreased if using the retention mechanism. Averaged hourly growth rates showed a decreased from 0.13 % h^{-1} to 0.05 % h^{-1}. Growth rates in the retention scenario were always below those in the scenario without an active retention. Only Sections 5&6 featured slightly higher growth rates when using the retention.

Reduced growth rates are a good indicator for changes in the extrinsic drivers determining the individual's energy balance. Using the time of reaching a length of 25 mm, we extracted the values of the temperature, oxygen and prey concentration. The results are shown in Figure 3 c,e,g) and show how conditions change due to the vertical retention preventing the individuals from being flushed out into the coastal areas of the North Sea. An increase in median temperature (without retention: 11.37°C, with retention: 15.98°C) and prey (without retention: 680.10 mg C $m^{-}3$, with retention: 2530.49 mg C m^{-3}) is observed, while oxygen concentrations decreased (without retention: 277.63 mmol m-3, with retention: 259.14 mmol m-3). These differences reflect the benefits and risk the estuarine environment offers to early life stages. The combination of increased temperature and prey concentrations results in faster development under optimal feeding conditions, therefore decreasing the risk of starvation.

On the contrary, the decreased oxygen concentrations match the reports of more frequent occurrences of low oxygen or even hypoxic conditions, especially in the areas surrounding the port of Hamburg (Fan et al., 2025; Kerner, 2007; Pein et al., 2021). Studies showed that especially in the context of climate change, conditions in this area potentially changes to the worse, especially for early life stages (Hein et al., 2018; Kerner, 2007; Möller & Scholz, 1991).

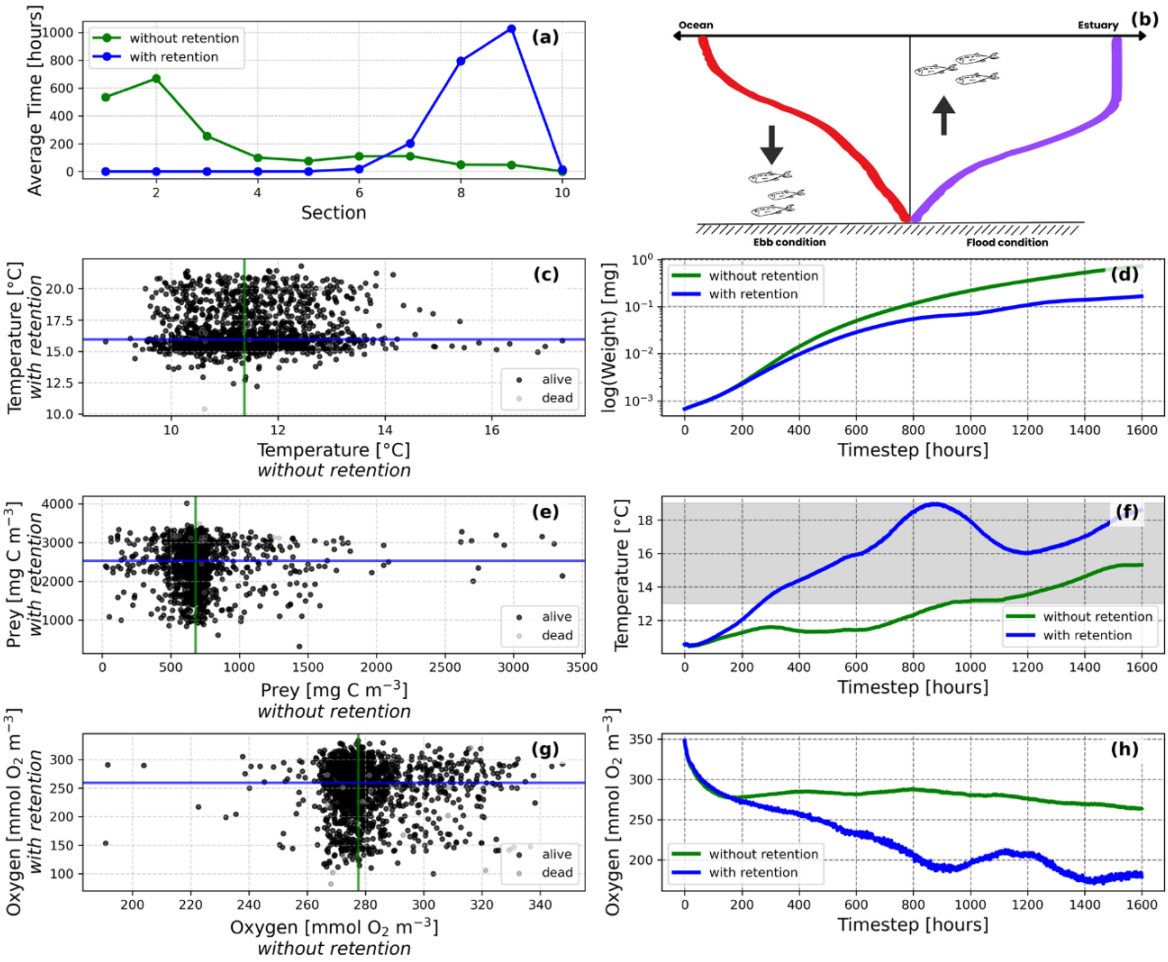


Figure 3: Impact of active tidal retention of larvae development and external conditions. a) Average time (hours) spent per lateral section as well as averaged growth in % per timestep as averaged over the Sections. B) shows a schematic representation of the tidally driven vertical movement of the individuals. c,e,g) Scatter plots comparing extrinsic parameters (Temperature, Prey and Oxygen) at a length of 25 mm. Grey points show individuals that could not reach that size, their maximum length was used to assess the extrinsic drivers. d,f,h) Averaged weight, temperature and oxygen values of all particles during growth. Again, runs with and without active retention were compared.

The scatter of conditions at reaching the maximum length, modelled in our study gave us a first glimpse into how conditions change in the estuarine environment. Yet the development of individuals is rather impacted by the changes in the extrinsic forcing over time. Therefore, we also include the development of weight, temperature and oxygen over time (Figure 3 d,f,h) into this analysis. The timeseries shows again the decreased weight gain due to reduced growth rates in the retention simulations. Only a single period of intense heating occurred after roughly

900 hours, while the rest of the modelled time had temperatures below or just inside the optimal thermal window. Yet the growth is reduced compared to the substantially colder water temperatures in case of no active retention being applied. Unfavourable prey conditions were ruled out as we found in our previous study that even small prey concentrations of up to 20 mg C m^{-3} can result in growth (Drewes et al., 2025). As the weight curves start to divert just after 10 to 12 days, with a temperature increase that can be observed in the same period, we assume that this might be the driving force behind the decreased growth rates. We found two potential reasons for such a result:

(i) The optimal thermal window has been reported with a wide range of values and is mainly determining the efficiency of daily maximum consumption. Lillelund (1961), showed a temperature range of 16-21°C for early life stages of smelt in the Elbe estuary, while our model suggested enhanced growth rates even at colder temperatures and a range of 13-19°C. Further, the constrains of the maximum daily consumption might be even less for very early individuals as they are known for their nearly continuously feeding strategies to support very fast early growth rates. It might be that also the reported thermal windows rather match those of slightly older and already grown individuals and not those of larvae within the first days after the first-feeding onset.

(ii) The warmer temperatures would result in higher metabolic needs for very young individuals that are still restricted to small prey items due to the less developed mouth sizes. As feeding is only possible during nighttime, the individuals might not be able to cover the entire energy demand due to the comparably smaller energy that is consumed while preying on smaller and less energetic planktonic items.

Our results show that active retention can have both positive and negative impacts on the individual's development. While the tidal orientated vertical migration successfully prevented flush outs of the individuals, it further increased their vulnerability towards unsuitable conditions, especially during summer. However, key drivers of successful development such as the available prey concentration or overall temperature improved significantly. Most importantly, retention prohibits that the larvae are transported into detrimental salinity regimes. An upper value of suitable salinity was estimated to be around 10 psu (Lillelund, 1961). Leaving the estuarine environment would therefore not only increase the risk of predation (Arevalo et al., 2023) due to other larger species but would also decrease the development speed.

Another extrinsic factor that is often discussed in the context of smelt survival is the local turbidity, especially in an estuarine environment such as the Elbe Estuary. By applying the bell-shaped relation between local turbidity values and the gut-content for the European smelt found by Illing et al. (2024), allowed us to assess the impact of varying turbidity levels on the individual's development. Using the available 1D timeseries of measured turbidity, the resulting weight gain is shown in Figure 4a. Overall growth decreases in comparison to the reference case, that neglected the potential impact of turbidity. Turbidity levels in our simulations ranged from 90-260 FTU and included tidally driven variability. The averaged timeseries are shown in Figure 4b.

The averaged weight development shows the impact of periods of unsuitable conditions. Growth decreases as soon as the turbidity levels leave the optimal window. Both too high and too low turbidity would then result in slower development and higher risk of unsuccessful recruitment. Dominant driver of the decreased growth is the reduction of the maximum daily consumption. The resulting decreased prey intake results in an imbalance between metabolic demands and energy intake leading to periodic weight losses.

The importance of turbidity on the individual's development is however widely discussed in the literature. Especially in the estuarine environment, increased turbidity levels are commonly observed. Combined with the ongoing dredging and industrial usage of the Elbe estuary will increases the turbidity levels in the future (Kerner, 2007). This could result in both beneficial and unsuitable conditions for the European smelt. Especially at the shallow nursery grounds increased turbidity and sedimentation can lead to increased mortality rates and decreased development rates (Thiel & Pezenburg, 2001).

Further, increased turbidity limits the individuals' visual abilities. This reduces the prey intake and can cause enhanced starvation mortality (Rodrigues et al., 2023). General availability of zooplankton relies on the successful survival of phytoplankton. However, in turbid environments, light can become a limiting factor, decreasing the available phytoplankton biomass, which is directly linked to the primary food source of early life stages (De Jonge et al., 2014; Steidle & Vennell, 2024). Especially in the highly populated hotspots such as the Mühlenberger Loch, such decrease can further increase starvation induced mortalities on a larger scale.

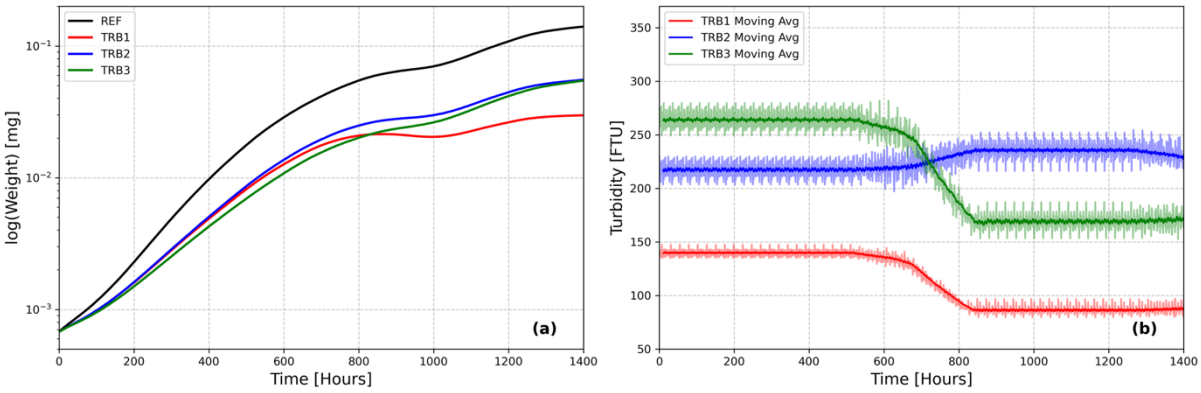


Figure 4: Impact of various turbidity forcings on the development of smelt early life stages. (a) Timeseries of the induvial weight gain for the 4 modelled scenarios. (b) Averaged turbidity values extracted from local measurement station along the Elbe Estuary. Solid line shows the moving 6 hours mean, shaded plots show the unaveraged data.

To conclude the previously presented results, we were able to show that development during endogenous life stages is enhanced at known spawning hotspots such as the Mühlenberger Loch. Further, due to the strong tidal currents the individuals are at high risk to be flushed out of the secure estuarine environment. We applied an active tidally driven vertical retention mechanism, that allowed for an energy sustaining way of staying inside the inner estuary. While our results confirmed that individuals remain inside the expected area, the theoretically suitable conditions did not result in faster growth rates. While a growth limitation based on available prey concentrations was ruled out, the combination of small mouth size, high temperatures and light conditions might be the limiting factors for growth of very early life stages. Yet, no observations of such growth rates were done in the Elbe Estuary and lab-based studies allowed for continuous feeding. Further, the rather simply implementation of turbidity induced growth reduction resulted in reasonable data confirming, that the need of highly resolved turbidity data would help to understand the impact in future scenarios.

Impact of climate change on the development

The overarching goal of this study is to use the previously gained knowledge regarding the impact of extrinsic drivers on early development of smelt and transfer it into the potential scenario including the impact of global warming. We therefore compare our previous runs with those based on a different model input that included the local impact of increased warming and sea level rising trends especially in the Elbe estuary. Both IBM runs used the previously discussed retention scheme and had consistent turbidity forcings applied. The analysis covers two major aspects, a simplified analysis of the suitability for growth covering the entire

estuarine model domain as well as the individual level impact of global warming and implications on the growth and mortality.

Suitability analysis

Optimal suitability for growth and survival in our analysis is determined using Section-wise, vertically averaged values of temperature (12-18°C), salinity (£10 psu) and oxygen concentration (>150 mmol/m³). The results are shown in Figure 5 a,b) for the reference and warming case respectively. Our results indicate that conditions outside the estuarine environment are generally unsuitable, as confirmed by Lillelund (1961). Suitability increases upstream with the highest values observed in the eastern estuarine sections. Shallower regions exhibit slightly elevated temperatures, which enhances the potential maximum daily consumption rates, while maintaining stable prey conditions (Guerreiro et al., 2021; Tulp et al., 2022). This increasing suitability highlights the critical role of estuarine habitats in supporting development and survival of early life stages.

In the upstream sections, however, suitability slightly declines during the summer months (June-August). Elevated temperature exceeding the optimal thermal window, along with recurring hypoxia events, presents significant stressors for the early life stages. As shown in Figure 5c, substantial differences between the reference and warming scenario, especially during summer, were found. Suitability generally increases in the downstream areas and during the colder season (January-March, November-December) due to the elevated water temperatures. During these months, the other two extrinsic factors remain within their optimal range.

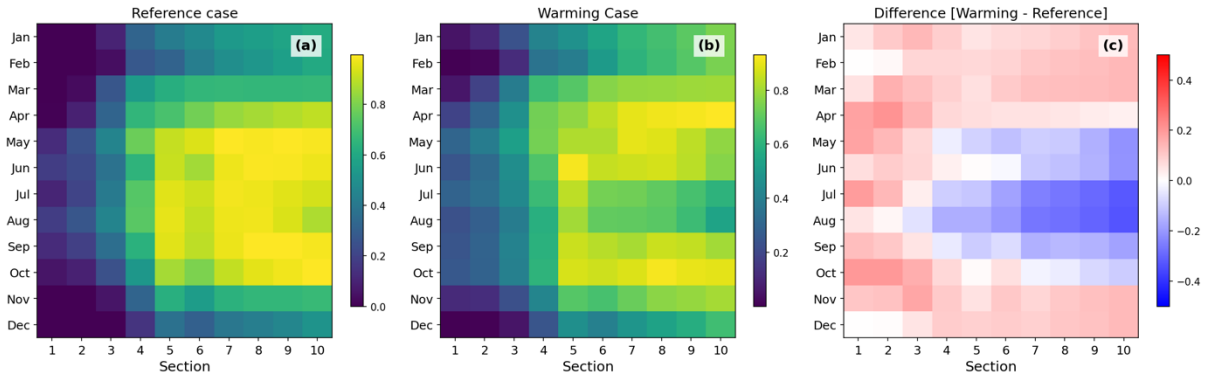


Figure 5: Spatial and temporal changes of the suitability index for early life stages of the European smelt. Shown are the conditions for the reference (a) and warming (b) case. The differences (warming-reference) are shown in c). The calculation of the index includes temperature, oxygen and salinity based on literature findings and testing of the IBM for younger individuals.

Conversely, the reduction in suitability during summer becomes more pronounced under the warming scenario. Suitability decreases by nearly 40%, and the period of

unsuitability extents from 3 to 5 months. Spatially, the decline spans between section 4 to 10, effectively covering nearly the entire estuarine area. These findings suggest that rising temperatures combined with more frequent hypoxia events would substantially reduce the habitat quality. As known spawning hotspots such as the Mühlenberger Loch are severely impacts by these changes, the risk of long-term consequences due to an overall decrease of the recruitment success of estuarine-dependent species increases.

Development of endo- and exogenous individuals under the impact of global warming

In the warming scenario, increased suitability during the spawning season due to elevated temperatures leads to accelerated endogenous development. Median temperatures during the egg and yolk-sac stage increased from 7.63°C to 10.26°C, reducing the total endogenous stage duration by up to 13.2 days. This accelerated development in combination with the earlier spawning onset, leads to a shift of the onset of exogenous feeding from late April (20th April, reference) to early April (05th April, warming scenario).

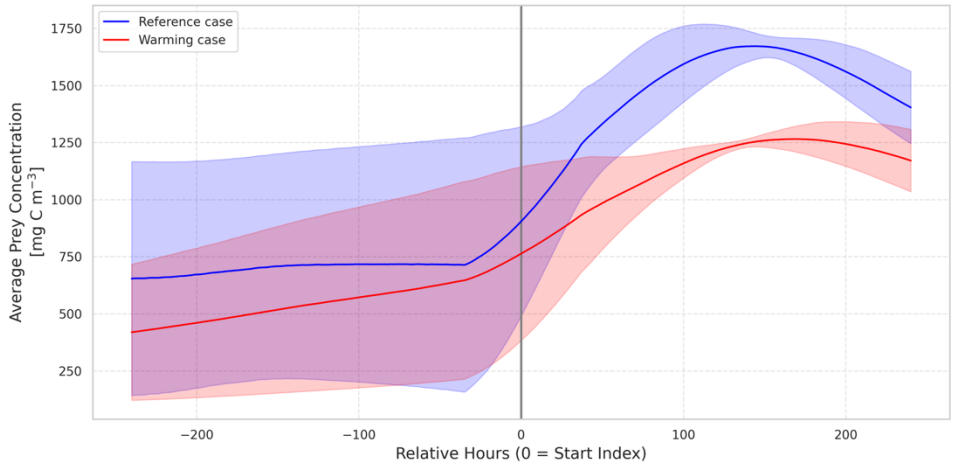


Figure 6: Averaged prey concentrations with respect to a shift in the onset of first feeding. Considered is a 10-day window prior and after the current onset of feeding. Available prey was averaged to daily values using all data from the 5 pre-selected spawning locations. Shaded areas indicate the standard variability based on the daily averaged concentrations.

A central concept in early life stage development is that the transition between endo- to exogenous feeding marks a potential critical period for individual survival and successful recruitment (Hjort, 1914) due to the absence of potential prey items. A mismatch between predator and prey timing (Cushing, 1990), driven by the accelerated endogenous development rates under warmer conditions and earlier spawning, could significantly increase the risk of starvation induced mortality. To investigate the potential of such a mismatch, we analysed averaged prey concentrations withing a 10-day window around the averaged first feeding onset in

both scenarios. Averaged values included data from all 5 predefined spawning locations and are shown in Figure 6.

Comparisons between the reference and warming scenarios show a general decline in prey availability under the warming scenario, though the overall shape of the prey availability curve relative to the current onset remains unchanged. Increased prey concentrations occur for a delayed onset of first feeding with the strongest increase being observed under the reference conditions. Prey availability occurs with a delay of first feeding by approximately 6 days (reference case), and 7 days (warming case) compared to the current onset. However, especially under warming conditions, first feeding is likely to occur even earlier, increasing the threat of a predator-prey mismatch. Prey conditions up to 10 days prior to the current onset remain within suitable conditions, albeit declining. Sensitivity tests of our model indicated that growth is still supported under relatively low prey concentrations (Drewes et al., 2025). However, these tests were made under assumption of the current temperature regime found at the spawning locations and did not consider the impact of increased warming on the metabolic demands of the individuals.

However, our analysis does not account for local predation pressure, which may be elevated in nursery hotspots due to the high densities of early life stages. Arula et al. (2017) presented that increased prey availability during early development stages can enhance the recruitment success. They further highlighted the interplay between elevated temperatures and sufficient prey availability due to the increased metabolic demands under warmer temperatures.

Under warming scenarios, this balance might be interrupted. Elevated temperatures in combination with decreased prey availability, potentially increase starvation-driven mortality and reduced recruitment (Kangur et al., 2007; Keskinen et al., 2012). Our results support this risk: growth rates decline for the warming scenario, and the duration of the exogenous feeding stage on average increased by 8.2%, from 37.56 days under reference conditions to 40.56 days. This indicates a substantial deterioration of growth conditions in a warmer environment.

Using the extrinsic conditions at completed development (reaching 25 mm length) or maximum length changes in key drivers for the exogenous life stages can be assessed. The results are shown in Figure 7 and follow the previously presented scheme from the retention analysis.

Conditions when reaching the maximum length of 25 mm differed significantly under the warming scenario. Median temperature increased by 10.4% from 15.92°C

to 17.59°C, while the available prey concentration decreased by 14.2% from 2530.49 mg C m^{-3} to 2168.93 mg C m^{-3}. While these two factors exhibit significant differences between both scenarios, median oxygen concentration decreases by only 0.4% from 259.1 mmol m-3 to 257.99 mmol m-3. Despite this marginal decrease of available oxygen, the proportion of individuals failing to reach the maximum length of 25 mm increased considerably under the warming scenario, with approximately 40% of released particles not attaining this size. These individuals are visualised using grey dots in the scatter plots, representing their physiological conditions at their largest length. The data indicates that individuals experiencing high temperature (»20°C) combined with low prey concentrations (<1500 mg C m^{-3}) were less likely to sustain continuous growth.

This further confirms our finding that the prey and temperature regime is significantly altered under the warming scenario. Due to the retention behaviour, individuals stay inside of the now vastly unsuitable conditions and studies suggest that such worsen conditions are especially harmful for early life stages (Hein et al., 2018; Kerner, 2007; Möller & Scholz, 1991). Figure 7 d,f,h present growth, temperature and oxygen development as averaged over all particles in our system. The averaged weight shows a bivalent behaviour after 1000 hours for both scenarios. While faster weight gain is observed for the reference forcing, individuals tend to lose weight under the warming conditions. Weight loss in our model is inevitably linked to increased starvation mortality due to a decrease of the Fulton's life-quality factor. Both changes in the weight gain correlate with sudden changes in the temperature regime. While the temperature experienced by the individuals decreases in the reference case, a significant warming is shown for the warming scenario. The averaged temperature even surpasses the optimal thermal window (>19°C) (Lillelund, 1961). Under such conditions the individuals' metabolic needs increase and cannot be balanced anymore due to the bell-shaped temperature dependencies of the maximum daily feeding (Thornton & Lessem, 1978).

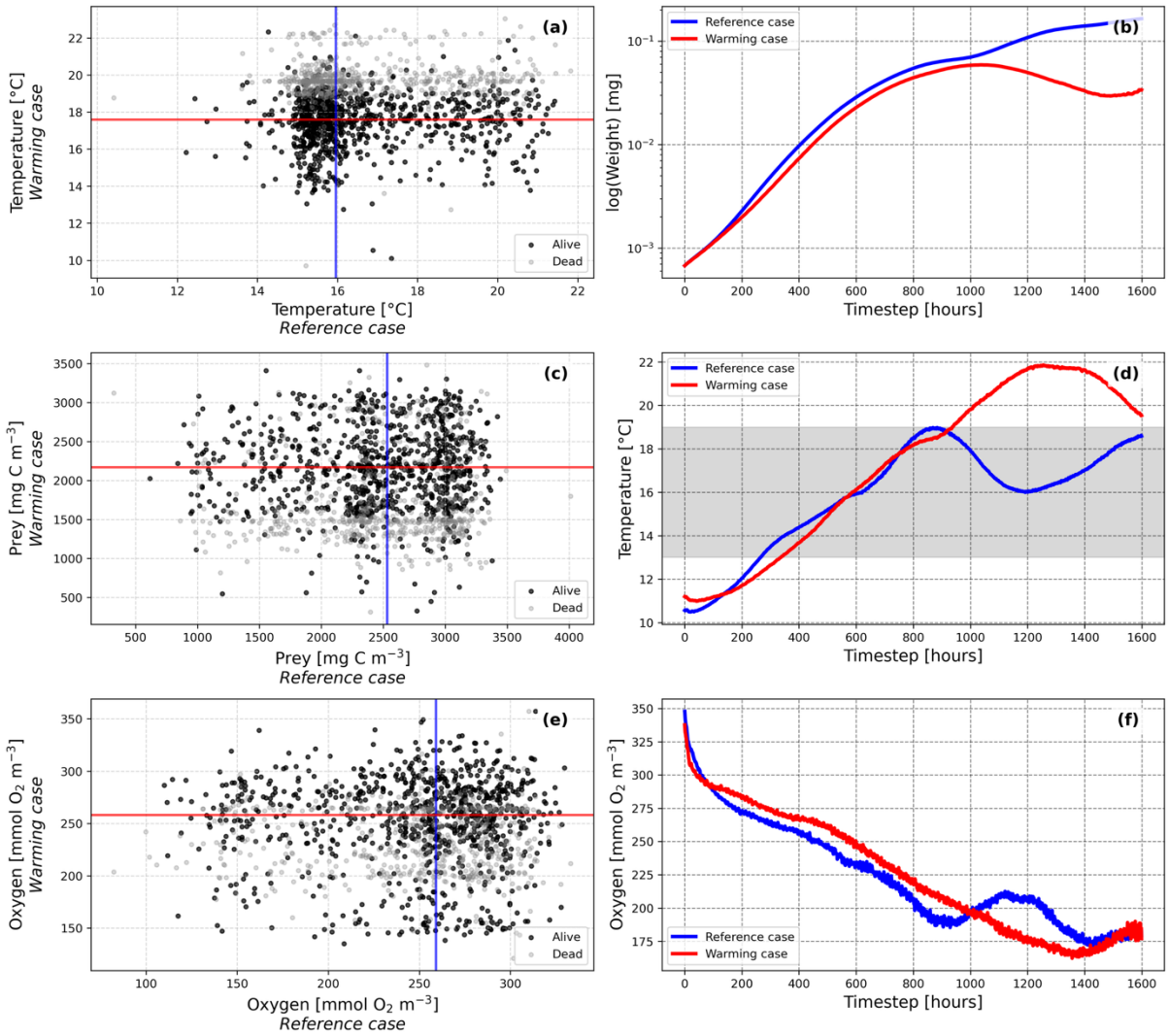


Figure 7: Comparison of the impact of increased temperature in the warming scenario on the individual growth and survival. a,c,e) Scatter plots comparing extrinsic parameters (Temperature, Prey and Oxygen) at a length of 25 mm. Grey points show individuals that could not reach that size. Values indicate the conditions at their largest length. b,d,f) Averaged weight, temperature and oxygen values of all particles during growth. Blue represents the reference scenario, red the warming scenario.

The decreasing energy availability therefore results in starvation and ultimately results in individuals' death as proven prior. Further, the temperature decrease in the reference scenario coincides with a notable increase of oxygen concentrations. Our results show, that only during this period, where extremely warm temperatures in the warming scenario were found, a significant reduction of oxygen in comparison to the reference case can be seen. Yet this condition only holds for approximately 400 hours.

Counting of the timesteps that are associated to hypoxic conditions further confirms these non-intuitive findings. The number of hours that individuals are severely impacted by hypoxia decreases under the warming scenario. However, simultaneously the number of hours under temperatures surpassing the optimal

thermal window increases. Based on these findings, we can conclude that even under current day conditions the threat of hypoxia is well documented in our model. However, the increased energy demand due to these conditions is still balanced due to the lower temperatures in the reference setup. The combination of high temperatures and low oxygen concentrations is set to play the most crucial role in determining the recruitment success of smelt in future years.

Conclusion

Our results for the development variability of endogenous life stages confirmed the critical role of spawning site selection for the later development. Spatial variability of temperature and prey availability resulted in significant differences in the duration of the endogenous stages and early growth rates during the onset of first feeding. From our 5 selected spawning locations the one located in the Mühlenberger Loch (station B) provided the most favourable conditions, resulting in a significantly faster development and high growth rates during the first day of active feeding. On the contrary, despite their known importance as potential spawning grounds, the spawning location close to Geesthacht (station E) showed reduced growth potential due to comparably low prey conditions.

Using the warming case, we were able to determine how increasing temperatures would impact the ecosystem at such important spawning locations. Our results show that recruitment is still benefiting from the increased suitability of the Mühlenberger Loch. This proves the importance of environments such as the Mühlenberger Loch. During the recent years the economic value of these areas as potential construction grounds increased and parts of the Mühlenberger Loch have already been destroyed for economical purposes. Studies like ours can help to understand the long-term meaning of such areas and offer potential maintenance solutions for a future estuary that combines both economic value and ecological conservation. Successful conservation of spawning hotspots and keeping them accessible for migratory and local fish populations can in future scenarios help to support recruitment success.

Using the selective tidal stream transport via an active vertical retention movement allowed the individuals to remain within the estuarine environment. Using the oscillating tidal flow directions prevented major flush-out events into the coastal zones or open North Sea. Our results show that even at smaller sizes the swimming capacity is sufficient to maintain the retention strategy and remain within the estuarine environment. However, such retention included a trade-off as suitability of the inner estuarine environment decreased especially during summer months.

Using the model scenario including the impact of global warming our system predicts decreasing suitability during summer, mainly driven by summer temperatures surpassing the individual upper limit of the optimal thermal window and decreasing prey concentrations. Our model therefor enables us to understand how extrinsic drivers change in a scenario such as our warming case. The scenario is clearly tending toward more drastic changes as RCP8.5 is commonly the most extreme case when modelling the impact of climate change. However, suitability of the habitat and the survival of individuals is also directly impacted by anthropogenic drivers such as the turbidity. Increased construction work, dredging activity and changes in the hydrodynamic system will most likely lead to increased turbidity concentrations within the future. Using the 1-dimensional forcing provided a first insight into how the turbidity dynamics are currently impacting the smelt development via the decreased prey intake. The simplicity of our approach helped to understand the base, but future work is needed to include modelled turbidity as a state variable to distinguish between local turbidity changes. We believe that this would increase the model capacity to predict larval recruitment.

Another theory that is often discussed in the context of climate change, environmental adaptation and recruitment success of early life stages is the well described predator-prey mismatch during the onset of first feeding. We were able to rule out mismatches using the current setup in both scenarios (reference and warming). While prey concentrations varied, none of the selected spawning sites ever had prey concentrations below the minimum threshold for growth. However, in the warming case the risk of a mismatch increased with warmer temperatures resulting in faster development. In the context of spawning and endogenous development another important aspect that should be highlighted here is the onset of spawning. To our knowledge the onset of spawning as well as the onset of spawner migration has not been studied in the Elbe estuary over the last years. Our model shows, that as soon as the onset of spawning could happen earlier due to increased water temperatures the risk of insufficient prey concentrations increases significantly.

Our study nicely presents the capability of our modelling system to reproduce the development dynamics of the European smelt in the Elbe estuary. It can be used as a hands-on tool to understand how changes in the extrinsic forcing are directly impacting the development during the early life stages. For future use this setup allows for the testing of numerous assumptions related to the individual survival. Future work will focus on the impact of structural changes within the estuarine environment to assess the suitability of such adaptation measures on the

development and recruitment on a key species such as the European smelt. Especially in the context of policy making such a tool can vastly help the understanding of the direct consequences of structural changes for the future conservation of the ecosystem.

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Author contributions

D.D, C.S,U.D conceived the manuscript; J.P conducted the model runs with the Elbe estuary model and provided these as forcing data for the IBM; D.D wrote the first draft; D.D,C.S,U.D,D.B and J.P edited, revised, and refined the manuscript

Conflict of interest

The Author(s) declare(s) that there is no conflict of interest.

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Data availability

The data underlying this article will be shared on reasonable request to the corresponding author.

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Study 3: Assessment of flood adaptation measures

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DD conducted the IBM simulations, performed the data analysis and wrote the manuscript. CS, UD contributed to the study design, data analysis and discussion. JP provided and developed the model-based forcing and model setup of SCHISM. All authors revised and approved the manuscript.

Understanding the consequence of flood adaptation scenarios on migratory key species in the estuarine environment of the Elbe estuary – the European Smelt as a benchmark for future decision making

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Abstract

Estuarine environments are often close connectors of economical, ecological and anthropogenic problems. Global warming continuously threatens the estuarine domain due to enhanced flooding risks and storm surges. Maintenance of economical values such as cities along the estuary demand for large scale adaptation measures to decrease the risk of extreme events. However, the impact of such measures should always be analysed by focusing on more than the pure economical value or benefit. Using high-resolved modelling data as an input for our individual-based model (IBM) we assess the impact of four adaptation measures for the Elbe estuary. All aiming to increase the local flood protection. Our IBM simulates the impact of extrinsic drivers such as temperature, prey concentrations and oxygen on early life stages of the European smelt (Osmerus eperlanus), which is considered a key species in the Elbe estuary. Our study shows that the generation of local wetlands in the context of polder formations can help to boost endogenous life stage development and create vital spawning and nursery grounds while improving the local flood protection. We further show how the reallocation of a tidal weir closer to the North Sea can limit spawning migration of the smelt leading to less suitable spawning grounds and a decrease of smelt abundance within the estuary. Other scenarios showed little, yet not dramatic shifts in development and finally likelihood of survival due to extrinsic stressors. Our study helps to understand

how drastic projects can be used to improve both economic and ecological well-being in a changing world.

Introduction

Estuarine environments worldwide are important contributors to local biodiversity (Thiel *et al.* 1995; Barbier *et al.* 2011; Ducrotoy *et al.* 2019). Their role as nursery grounds has been widely acknowledged (Sepulveda *et al.* 1993; Nellen and Thiel 1994; Thiel 2001). In recent years the pressure on estuarine ecosystems enhanced due to the increased demand of space for economic growth. The increasing demand of construction works to enhance flood protection, creation of additional economical grounds or for power generation widely alters the system of the affected estuary (Thiel *et al.* 2003; Kerner 2007; Eick and Thiel 2014). Predictions show that by 2030, 89% of the global river flows are potentially impacted measures such as damming (Zarfl *et al.* 2015; Grill *et al.* 2019; Zarri *et al.* 2022).

The Elbe estuary, located in northern Germany, is a good example for such a heavily modified system (Pein *et al.* 2023). It stretches from the southern North Sea and Wadden Sea areas to the weir at Geesthacht, encompassing the port of Hamburg. Construction work along the estuary mainly targets two purposes: increasing the local flood protection and maintaining the port of Hamburg's accessibility and potential expansion. The work mainly includes continuous dredging of the estuaries main channel (Kerner 2007; Köster and Thies 2015). The dredging resulted in various changes of the hydrodynamic and sediment dynamics (Kerner 2007; Hillebrand *et al.* 2018; Pein *et al.* 2023) as well as the ecosystem as hypoxia occurred more frequently, especially around the Hamburg region (Schroeder 1997; Kerner 2007; Hillebrand *et al.* 2018; Biederbick *et al.* 2025; Fan *et al.* 2025).

Beside their social and economic importance, the Elbe estuary is also a well-known nursery hotspot for many species (Nellen and Thiel 1994; Thiel *et al.* 1995, 1996; Barbier *et al.* 2011). The connection to the southern Wadden sea regions allows anadromous fish to migrate into the estuarine environment and utilise the idea prey conditions as well as the shallow wetlands as optimal spawning grounds that offer enhanced protection to the juvenile individuals (Lillelund 1961; Thiel *et al.* 1995, 1996). One of these migratory species is the European smelt (*Osmerus eperlanus*) (Lillelund 1961). The smelt uses the freshwater dominated areas of the estuary as well as shallow regions like the Mühlenberger Loch as favoured spawning grounds. The early life stages spent their first time in the estuary, profiting from the beneficial local condition at the spawning grounds. (Lillelund 1961; Sepulveda *et al.* 1993; Sepúlveda and Sepûlveda 2021). Over the last years the smelt population showed

large variations, raising concerns regarding the well-being of the stocks. (Matthiesen and Thiel 2019; Reiser *et al.* 2023; Drewes *et al.* 2025a). Studies such as Lillelund (1961), showed that smelt in the Elbe is highly reactive to changes in the ecosystem, making them to a good indicator for ecological well-being and improvement of local conditions. Changes in the abundance of smelt have a direct effect on other species such as sea birds like the Common Terns (*Sterna hirundo)* (Dänhardt *et al.* 2011).

In recent years, the pressure of flooding and changing extrinsic stressors on individual development increased, especially in the context of climate change (Huang *et al.* 2010; Seiffert and Hesser 2014; van Beusekom *et al.* 2018). Increasing temperatures, frequent hypoxia events and decreasing freshwater fluxes directly impact the estuarine ecosystem (Möller and Scholz 1991; Seiffert and Hesser 2014; Hein *et al.* 2018; Fan *et al.* 2025). Similarly, the increased occurrence of extreme flooding events and anticipated future sea level rise pose significant challenges for populations residing along the estuary (Ge *et al.* 2014; Weisse *et al.* 2014; Pein *et al.* 2023). These circumstances underscore the necessity for effective mitigation strategies to provide reliable flood protection (Siefert and Havnoe 1988; Ge *et al.* 2014). Due to the previously mentioned close connection of estuarine ecosystem, zones of economic interest any discussed measure needs to be validated based on the potential impact on both these domains while offering valuable and long-term flood protection. Recently, Pein et al. (2025) published an extensive model study introducing 4 potential adaptation measures to reduce the flood risk by either reducing the marine forcing or by altering the tidal regime. We want to extent the scope of their work by providing an ecological based assessment of the impact such adaptation measures can have on the early life stage of a key species such as the European smelt.

Our study therefore analyses the impact of introducing such measures on spawning, endo- and exogenous development stages. Using an individual-based modelling approach, we want to distinguish the impact of extrinsic factors and link them to resulting changes in growth, survivability of early life stages. We want to investigate how a) the introduction of such adaptation measures alters the availability and suitability of spawning grounds within the estuary, b) how the alteration of the tidal regime in the estuary impacts individual drift and growth during the exogenous lifestages and finally c) how the introduction of solid barrier such as navigational locks, disrupting the estuarine connectivity, impacts individual survival.

Methods

Model system

In our study we use two-parted modelling system, where the first system provides the input for our study, while the second system is used to conduct the Lagrangian tracking experiments and provides the coupling to the Individual-based model (IBM). Using a coupled version of the semi-implicit cross-scale hydroscience integrated system model (SCHISM, Zhang et al. 2016) and the **ECOS**ystem **MO**del (ECOSMO, Schrum et al. 2006; Daewel and Schrum 2013). Both models have been previously used to successfully model the Elbe system (Pein et al. 2021, 2023; Fan et al. 2025). The SCHISM model solves the Reynolds-averaged Navier-Stokes equations under the assumption of hydrostatic conditions on an unstructured horizontal grid.

The resulting output was used as forcing or the offline coupled tracking and IBM modelling system, the second part of the used modelling system. We used the SCHISM provided tracking routine as it has already been designed to conduct particle tracking experiments on unstructured grids. All tracking runs were conducted using an hourly timestep, as this allows for a realistic inclusion of tidal movement effects on the particle's movement. To reduce the total number of particles a superindividual approach was included for the calculation of mortality rates (Scheffer *et al.* 1995). A single tracked particle therefore represents an initially fixed number of subindividuals and mortality is applied as a reduction of subindividuals per superindividual. A particle is considered dead when the number of subindividuals reaches a critical threshold of 1% of the initial number.

Extrinsic factors, including temperature, oxygen concentration, prey availability, and light intensity, are updated at each timestep following particle drift calculations to reflect the new locations. The Individual-based model (IBM) comprises four life stages: egg, yolk-sac, exogenous feeding larvae, and dead individuals. The first two stages: egg and yolk-sac are also referred to as endogenous feeding stages, as they do not require external prey sources. Only exogenous feeding larvae exhibit movement; during endogenous development, individuals remain at their initial spawning site. While eggs are known to be advected by sediment transport, this factor is excluded from our model due to limitations in accurately representing local sediment accumulation, particularly in shallow wetlands.

During endogenous stages, individual development is primarily influenced by water temperature at the spawning location (Blaxter 1992; Keller *et al.* 2020; McCarthy *et*

al. 2020). Research such as (Lillelund 1961; McCarthy *et al.* 2020; Reiser *et al.* 2023) indicates that local salinity levels further affect development rates, with elevated salinities reducing smelt egg survival. This relationship has been incorporated into our model through a linear correlation between local salinity and an increased mortality rate, resulting in higher numbers of dead particles or greater vulnerability in later stages. This is attributed to reduced numbers of sub-individuals stemming from adverse salinity conditions during the egg stage.

Model simulations used in this study were conducted to analyse the impact of artificial adaptation measures on the Elbe estuary and are described in Pein et al. (2025). In total 5 scenarios were developed. These scenarios include a reference setup as well as four adaptation measures implemented via changes in the estuarine geometry. In the following the included measures as well as their mayor impact on the ecosystem are summarised. For a detailed analysis of implications of such adaptation measures on sediment dynamics and the tidal regime is included in Pein et al. (2025).

All 4 adaptation measures were designed with the intention to increase the local flood protection and decrease the risk of storm induced floodings.

Model run configuration

Selection of initial spawning nodes & Run configuration

First step of the run configuration is the selection of suitable spawning nodes where particles are later initialised at. Selection of nodes is based on nodewise averages of temperature and salinity. Based on earlier studies, spawning suitability was defined based on the nodewise averaged values of temperature [4.4°C < $T_{suitable}$ <10°C, (Lillelund 1961; Belyanina 1969; Keller *et al.* 2020; McCarthy *et al.* 2020; Drewes *et al.* 2025a)] and salinity [$S_{suitable}$<10 psu, (Lillelund 1961; Belyanina 1969; McCarthy *et al.* 2020)]. Following the labelling of suitable nodes based on the averaged values, we introduce a third metric. This metric is choosing suitable nodes that have suitable conditions for more than 10 days in a row, this way the "long-term" suitability of chosen areas is ensured.

Due to the large number of suitable nodes per scenario, we decided to only have a single particle spawn per node per run. The large number of spawned particles still allows for meaningful determination of spawning site related development impacts while keeping the computational demand as reasonable as possible.

Another important factor, determining successful development of early life stages is the time of spawning onset. In this study we decided to investigate rather flexible

spawning times by initialising our model with 35 different starting days. Keeping the spatial spawning constant, the changing onset of spawning allows for an analysis of the temporal impact of spawning in our model. Earliest spawning onset is set to the 3rd of January. Following spawning were delayed by 4 days each, with the last spawning onset is happening on the 18th of May. This timespan covers the previously reported main spawning season (Lillelund 1961; Thiel 2001; Eick and Thiel 2014; Matthiesen and Thiel 2019), but allows us to investigate if spatial and temporal changes might arise from the adaptation scenarios.

Simulations of the IBM were conducted using an hourly timestep, matching the model derived input data. As the exogenous moving individuals require a large amount of computational time, we decided to cut each simulation the moment that all particles reached the exogenous stage and had growth and survival modelled for 10 days only.

Structure of the analysis

Spatial Differences in Suitable Spawning Nodes and Endogenous Life Stage Development

The initial phase of our study examines the variations in suitable spawning nodes and their influence on spatial development across the different scenarios. Unlike the earlier approach, where spawning nodes were determined uniformly for model initialisation, this section involves calculating monthly averages of suitable nodes for each scenario, based on consistent temperature and salinity criteria. The differences between these averaged values and those of the reference case were computed and evaluated, focusing on both the number of suitable nodes and their temporal progression throughout the scenarios. In case of the AME scenario, that included a reallocation of the weir upstream, we introduced a further limitation to study the impact of connectivity. Spawning grounds were only limited to be found west of the weir, simulating the impact of a non-passable weir. A second set of simulations was done that included migration through the weir into the estuarine environment and was used in the latter to investigate the importance of estuarine connectivity.

Subsequently, our analysis shifts to investigating the spatial development differences of endogenous life stages, specifically the egg and yolk-Sac stages. Here, we assess spatial variations in average development time and the overall sum of spatial survival per simulation run. To facilitate analysis, a spatial hexagonal averaging method was applied across the entire model domain. Survival across the available spawning runs was quantified by identifying hexagons in which

individuals survived through the first two life stages and counting the number of successful runs per hexagon. A similar spatial averaging approach was used to evaluate the average duration of development, measuring the number of days required to complete both the egg and yolk-sac stages. These run-specific values were then averaged to produce a single two-dimensional representation of spatial development dynamics.

Finally, the impact of the artificially constructed polder on endogenous development was examined in greater detail. Particles that spawned within the polder area were specifically flagged and extracted to facilitate focused analysis. These particles were further categorised into those spawning outside and those spawning and developing inside the polder. The analysis concentrated on locally averaged temperature, the rate of development, and the number of surviving subindividuals at the onset of first feeding. Additionally, the standard deviation was calculated for both averages and differences, enabling comparison across the 35 available model runs.

Analysis of growth and survival during exogenous feeding

The second part of our study focuses on the adaptations impact on the development of exogenous feeding life stages. Pein et al. (2025), focused on changes in the tidal regimes throughout the estuary. The tidal regime and dominant forces vary depending on the location within the estuary. We applied a spatial analysis that has previously been described and tested in Drewes et al. (2025b). During this analysis we separated the estuary in 10 equally sized sections, based on the lateral extent of the estuary. A map showing the reference case including the selected sections is shown in Figure 1.

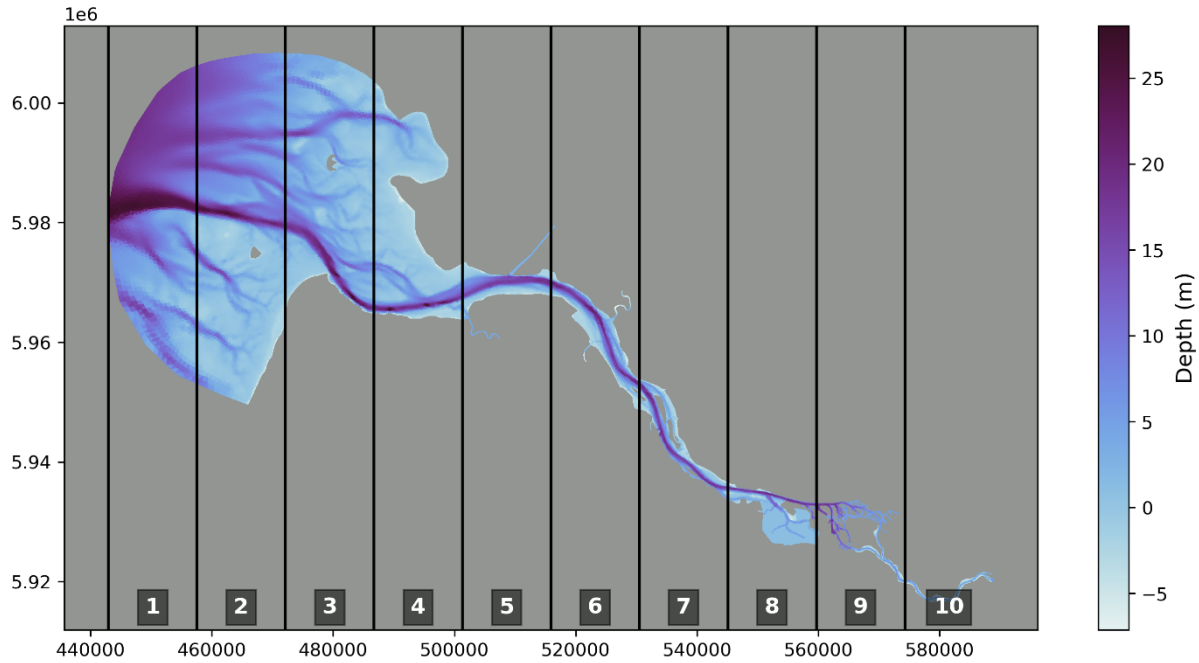


Figure 1: Example of the sections that were used in the analysis of the adaptations impact on the exogenous life stages

After applying the spatial section, we investigated how the 24-hour averaged displacement of particles changed in between scenarios. Using these findings, we were able to understand how the prognosed changes in the tidal regime impact the spatial distribution of individuals. Finally, the impact of the adaptation scenarios on individual growth with respect to the first 10 days of first feeding is analysed. Growth, determined as the weight difference at 10 days of feeding minus the starting weight. Similar comparisons were made for the temperature and available prey and oxygen concentrations. As differences between the runs are expected to be comparably small, we decided to only show the differences between adaptation scenarios and the reference state.

In the last part of our analysis, we focus on the impact of estuarine connectivity on successful development and spawning potential. The two setups for the AME scenario were used and compared in terms of spawning availability and finally averaged residence time per previously described section.

Results and Discussion

Alteration of available spawning grounds due to adaptation scenarios

Temperature and salinity were used to determine overall suitability within the model grid in terms of spawning and development of early life stages. Suitable

nodes were determined and monthly averaging was used to investigate how the spawning success might change over time due to the simulated adaptation measure. The results are shown in Figure 1.

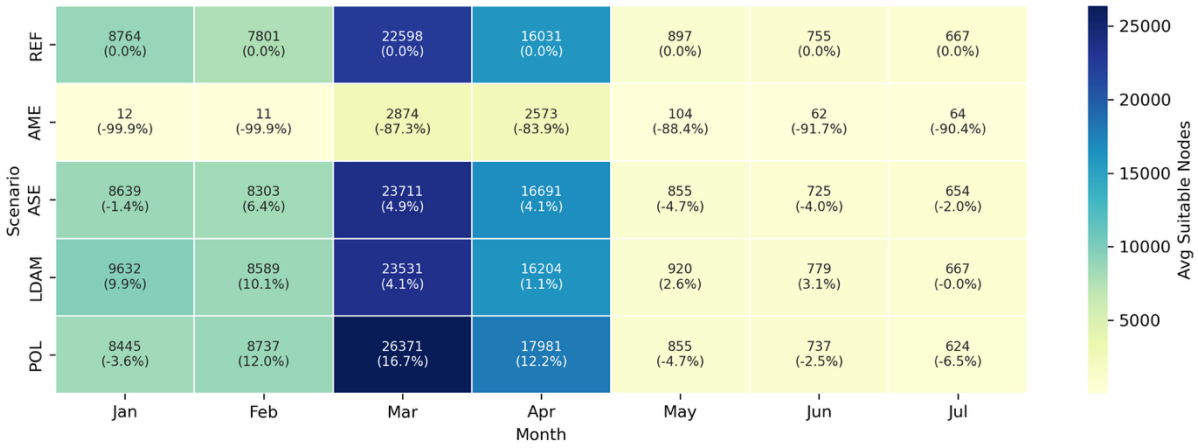


Figure 2: Monthly averaged number of suitable spawning nodes per scenario. Colours indicate the general development of monthly available suitable spawning node. Differences in respect to the reference scenario (REF) are shown per month. Local temperature and salinity values were used to determine spawning suitability, nodes were counted and monthly averaged values were determined.

The simple analysis of the number of available spawning grounds per month per scenario provides us with a first impression of the potential impact of each measure on our target species. Alteration of available spawning areas can vastly impact the overall survival of populations. From 4 scenarios only one features a vast decrease of suitable spawning grounds, while the other show enhanced spawning suitability throughout the analysed months. The vast reduction of spawning grounds in the AME scenario is driven by the construction of a tidal flood gate within the upper estuarine domain. This flood gate is not equipped with fish ladders or gate ways, that would allow for selective migration of species and serves as an example for deprecated estuarine connectivity. The flood gate serves as a permanent barrier for migratory species decreasing the available spawning areas to only those within the mouth of the estuary. Due to the favoured low salinity values, the available spawning areas further decline as the upper estuarine environment is mainly under the influence of the southern North Sea and adjacent Wadden sea areas. These factors lead to the decrease of 87.3-99.9% of previously available spawning nodes in the model domain. The largest increase of available spawning nodes is observed in the POL scenario and can be explained by the addition of the vast polder structure. The structure has been created in the vicinity of a previously known nursery hotspot, the Mühlenberger Loch (Sepulveda *et al.* 1993; Thiel *et al.* 1995; Eick and Thiel 2014). This shallow region is known to boost the recruitment of individuals due to vast availability of light, food and hiding spots to prevent early predation by

larger individuals. Due to the shallow nature, water temperatures increase faster compared to the rest of the estuarine environment further boosting early life development. Both other scenarios featured increases between 4.1-10.1% of suitable nodes compared to the reference case.

The results further show that we cannot expect a temporal shift of the main spawning season of European smelt in the Elbe purely due to changes in the estuarine geometry. As temperature is the dominant factor, especially of endogenous life stages (egg and yolk-sac individuals), the small changes of up to 1°C are not impacting the occurrence of higher spawning suitability throughout March and April. All 4 scenarios feature substantial increases of the number of spawning nodes within these two months.

We therefore rather focus on the spatial impact of early life stage development than to investigate temporal shifts in the spawning onset. Using runs 1-28 each starting at a different day from early January to mid of May, we can investigate how spawning suitability develops spatially and how the spawning location ultimately improves the average development rate. Later runs were excluded as spatial temperature differences were too small, all individuals survived under these conditions. The results are shown in Figure 3.

The upper maps show a spatial gradient in survivability, in this case defined as finishing the endogenous life stage. Higher numbers of days with at least a single individual surviving indicate areas of interest, especially in the context of early development under colder conditions outside of the optimal spawning window. The maps show a distinct east-west gradient with earliest development being observed in the eastern most parts of the estuary. Throughout all four scenarios, the pattern persists. Survivability in the eastern parts is lowest in the POL scenario (72.6%±4.6%) and highest in the reference case (80.2%%±6.1%). Individual survival is mainly determined by two factors: temperature determining the duration of the two life stages and salinities over 10 psu which result in increased mortality during the egg development. The latter can be ruled out in the freshwater dominated eastern reaches of the estuary. Therefore, local differences in temperature impact the development, leading to increased survival.

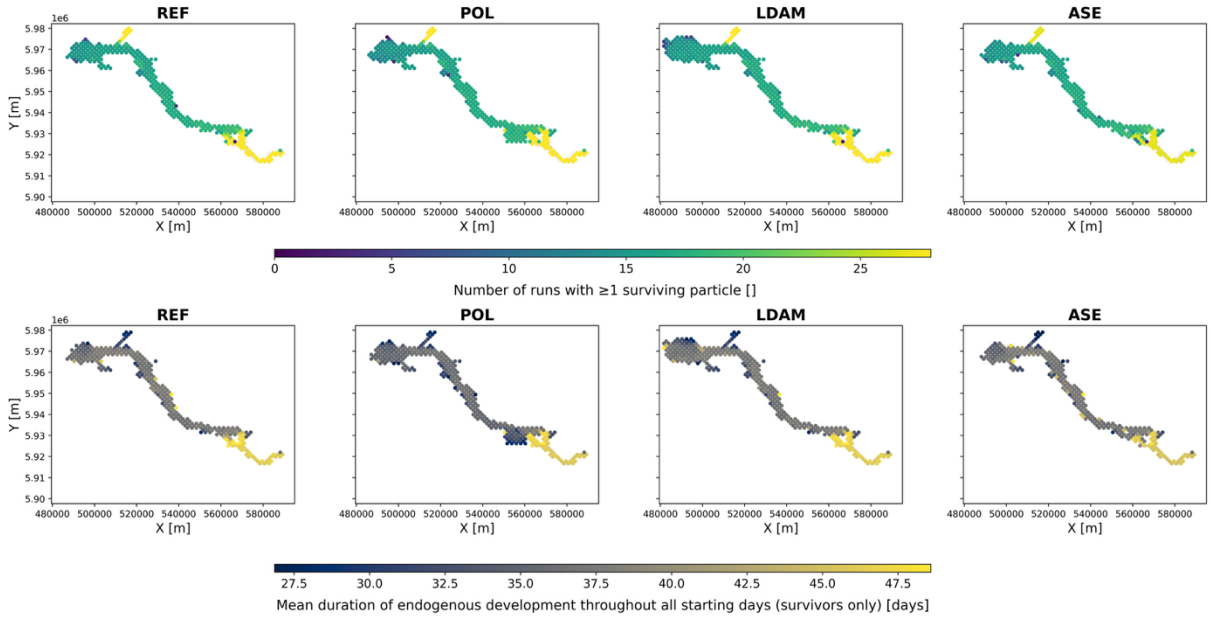


Figure 3: Maps showing survival (upper row) and averaged duration of the endogenous life (lower row). Maps show spatial averages over model runs 1-28. Survival and suitability show in how many of the total included runs, particles successfully finished the endogenous life stages. In this case the number of the respective dot is increased by 1. Average duration is calculated for each run and finally combined in one value. The early spawning in the freshwater domain east (x>560000) leads to longer averaged durations as cold temperatures slow down early life development.

The averaged development duration per scenario is presented in the lower maps in Figure 2. The previously discussed east-west gradient is persisting with longer duration of the endogenous stages in the areas that previously featured earlier spawning. This is not surprising as development at earlier spawning onsets resulted in longer stage durations. While temperatures over 4.2°C persisted egg individuals were able to develop, while colder temperatures would pause the development resulting in increased mortality due to longer stage duration (Chambers and Leggett 1987; Houde 1987, 1989). Particles do survive but the average number of subindividuals per superindividual is drastically reduced for runs featuring earlier spawning onsets. This would result in an increased vulnerability of the population for unfavourable conditions during the transition towards exogenous feeding or during the later drifting stage. Fastest development in all runs is found in the shallow coastal areas or small river inlets along the middle and lower reaches of the estuary. Later spawning in these areas is correlated to warmer water temperatures resulting in faster development, increased survival and a higher number of subindividuals at the transition to exogenous feeding. Differences regarding the reference grid, without the additional spawning grounds, are shown in the Supplementary Figure 1. Observable differences are small (±2-3 days) and follow the temperature changes reported in Pein et al. (2025). Again, these differences mostly impact the domain

west of the port of Hamburg. The POL scenario features an overall decrease in development duration due to the increased water temperatures (≈1°C) averaged across the entire estuarine domain. Differences in the ASE Scenario were neglectable small, while the LDAM Scenario featured an overall increase of the development duration.

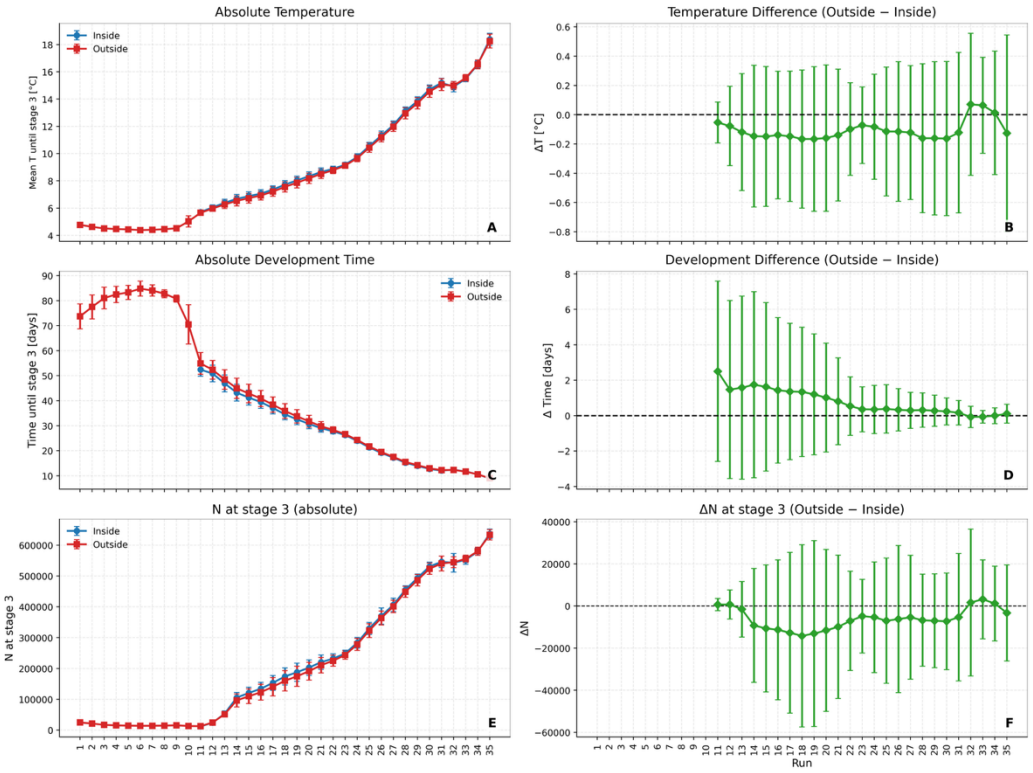


Figure 4: Cross-run comparison of the conditions within and outside of the polder region in the POL scenario. Shown are Temperature (A,B), total development time (C,D) and the number of subindividuals left per superindividual (E,F). Temperature shown is an average including the entire endogenous development. Subindividuals show the averaged remaining number after the transition to the exogenous feeding stage. The right-side features differences between the outside and inside domain for clearer visibility. Error bars indicate the standard deviation of the averaged values.

Throughout all scenarios one area stands out and needs some additional discussion: the inflow into the Kiel Canal located in the western part of the estuary. This area features both, early spawning and fast development. However, the area in our model is resolved without the navigational locks that are located just at the entrance to the canal to maintain a constant water level in the canals system. Reports such as (Kafemann *et al.* 2002; Hegegemeinschaft Gewässersystem Nord-Ostsee-Kanal 2008) show that smelt individuals were abundant around the locks and the western parts of the Kiel Canal. Especially the report from Hegegemeinschaft Gewässersystem Nord-Ostsee-Kanal (2008), showed high numbers of juvenile smelt that passed through the locks into the Elbe estuary. Our

model predicts potential spawning and suitable development conditions both in front of the locks as well as within the canal system. The studies suggest that a lot of measured fish inside of the chambers were impacted by the suction of water during active operations of the lock system. An active migration of adult individuals was not reported in the reports. It is however possible that single spawners enter the canal and contribute to local communities that could result in such an export of larvae into the estuary. Vice versa, intrusion of larvae due to their poor swimming capacities into the lock chambers and the canal is possible and would result in the reported measurements of juvenile smelt.

Finally, in the context of artificial spawning grounds creation, the impact of the polder on the successful development is discussed. Development of individuals within the polder increases in comparison to adjacent areas, especially the main channel at the entrance to the port of Hamburg. The differences in temperature and averaged development time per release date are shown in Figure 4.

Successful spawning and development are reported since runID 10. Until ID 31 averaged temperatures during the endogenous life stages showed slightly warmer conditions inside the polder. These warmer conditions directly result in a faster endogenous development, with higher differences for earlier spawning onsets. Temperature differences increased from run 11, while the differences in duration decreased for runs featuring later spawning dates as temperature differences decrease and development speed in the entire estuary equalises. This equalising of the temperature is also visible in the standard deviation of the averaged temperatures during the development. The spatial differences diminished and the warmer atmospheric forcing dominates the warming due to seasonal changes. The number of subindividuals left at the transition to the exogenous feeding stage is also increased for larvae that developed inside the polder. As for the other two variables, the differences peaked for runs between start number 12-23.

Summarising the results regarding the impact of each adaptation measure on potential spawning grounds and endogenous development we can confirm the result as discussed in Pein et al. (2025). Their analysis of ecological suitability showed that the polder scenario increases ecological well-being of the estuary. We extended the analysis by applying the extrinsic forcing to very early life stage development of a key species such as the smelt. While the polder does not favour significant earlier development yet later featured improved extrinsic development conditions. Our results are also matching in a wider picture. Construction or partial flooding of polder structures is increasingly discussed within estuarine communities (Cox *et al.* 2006; IUCN [International Union for Conservation of Nature] 2021;

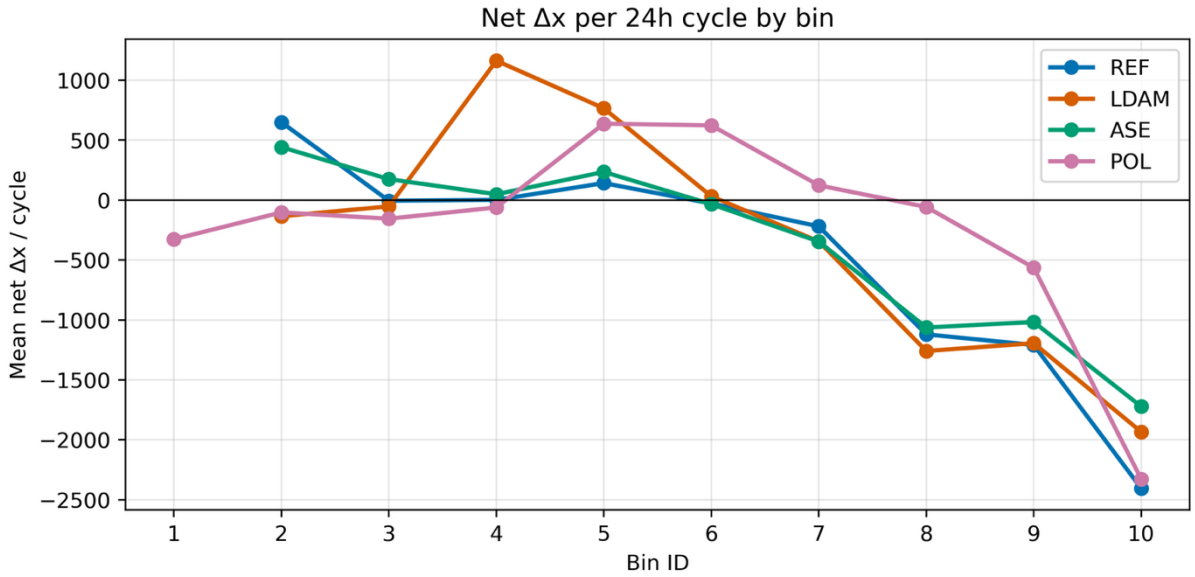
Warachowska *et al.* 2025). Especially partially flooded polders as found along the Scheldte Delta offered suitable spawning and living grounds for a variety of species (Hampel *et al.* 2003; Cox *et al.* 2006). Using our results as an example for a single species, that showed high abundances over the last decades and therefore served as a key-species within the Elbe estuary confirms these results in the presented case of the polder. We would assume that beneficial conditions for larval growth of the smelt, would also result in a boost of aquatic larval development and later also enhance the predator-prey dynamics within the food chain. The importance of successful smelt recruitment on higher trophic level species such as sea birds has been shown in (Dänhardt *et al.* 2011). Overall, the enhanced development speed, increased number of sub individuals proves that the idea of such a polder structure can help to mitigate the risk of storm floods and increasing sea level while maintaining the estuaries ecological value due to the artificial generation of spawning grounds.

Impact of adaptation measures on individual drift and exogenous development conditions

Three-dimensional drift in our model is limited to the exogenous feeding stages. The onset of first feeding therefore not only poses as a critical phase for general recruitment but allows further threats due to the drift of the individuals. Their swimming capacity is relatively limited yet increases when they grow. In our estuarine setup, tidal currents are the main driver for particle movement. All presented adaptation scenarios feature changes in the tidal regime We therefore want to investigate how these changes translate into changes in the exogenous development of the smelt larvae. Figure 4 shows the averaged net displacement of particles over a 24-hour period with respect to the binned x-position. Overall results show a similar shape across all adaptation scenarios featuring a positive eastward displacement of particles in the outer estuary and a westward directed transport of particles in the freshwater dominated reaches of the estuary. Largest import of particles is observed in the LDAM scenario. This agrees with the results presents in Pein et al. (2025) and the implemented retention of individuals only increases the likelihood of individuals being drifted into the estuary as it should mainly prevent a flush out event due to stronger ebb currents. Beside the increased flood pumping in the outer estuary, LDAM like ASE is comparably similar to the reference state. The POL scenario features a prolonged tendency for eastward displacement in bins 5-7, which covers nearly the entire middle reach of

the Elbe estuary from Brunsbüttel to the Port of Hamburg just before the opening of the polder.

The port area and the adjacent inner estuary feature a strong westward net transport. However, the displacement in these areas is comparably small with



respect to the other scenarios. As briefly mentioned before, exogenous feeding individuals can conduct a selective vertical migration to mitigate their displacement by using the tidal flows to avoid being flushed out of the estuarine environment. We calculated the averaged residence time per bin to investigate if the reported changes in the tidal regime might result in a shift in spatial retention. The overall pattern of the residence time remains similar throughout all scenarios. Individuals mainly stay in the middle parts of the estuary with a shared maxima in bin 8, that includes the areas west of the port of Hamburg and the Mühlenberger Loch.

Figure 5: The spatially averaged displacement in x direction per 24-hour cycle across the predefined sections. Positive x displacement would mean an eastward directed transport, while a negative displacement would be a westward directed displacement. All runs were conducted with the tidal retention behaviour turned on that should prevent an outflushing of individuals out of the estuary and would favour positive displacement values.

Solely the ASE scenario shows deviations from this shape by having a significant increase of residence time in bin 9, covering mainly the port area. A possible reason for the "trapping" of individuals within this area might be the reported formation of a secondary tidal current maximum leading to enhanced currents around the newly formed channel of the Süderelbe. Particles tend to be trapped there and need longer to reach the westerly located areas compared to the other scenarios. Finally, we want to use our IBMs potential to connect the variability of extrinsic factors to the

individual growth under the impact of the adaptation measures. We calculated differences of growth (Difference of the 10-day achieved weight gain), available prey and oxygen concentration and temperature between the scenarios and the reference run. The averaged results per runID are presented in Figure 5.

Focusing on the growth differences between the adaptation scenarios shows that enhanced growth through all runIDs is only found in the POL scenario. Largest differences are in general found between IDs 20-30. The LDAM scenario features nearly no growth differences with respect to the reference case, while the ASE scenario results in a sharp increase of enhanced growth after ID 25. All runs show a decrease in growth after ID 30. An important factor that determines the individual growth potential is the available prey.

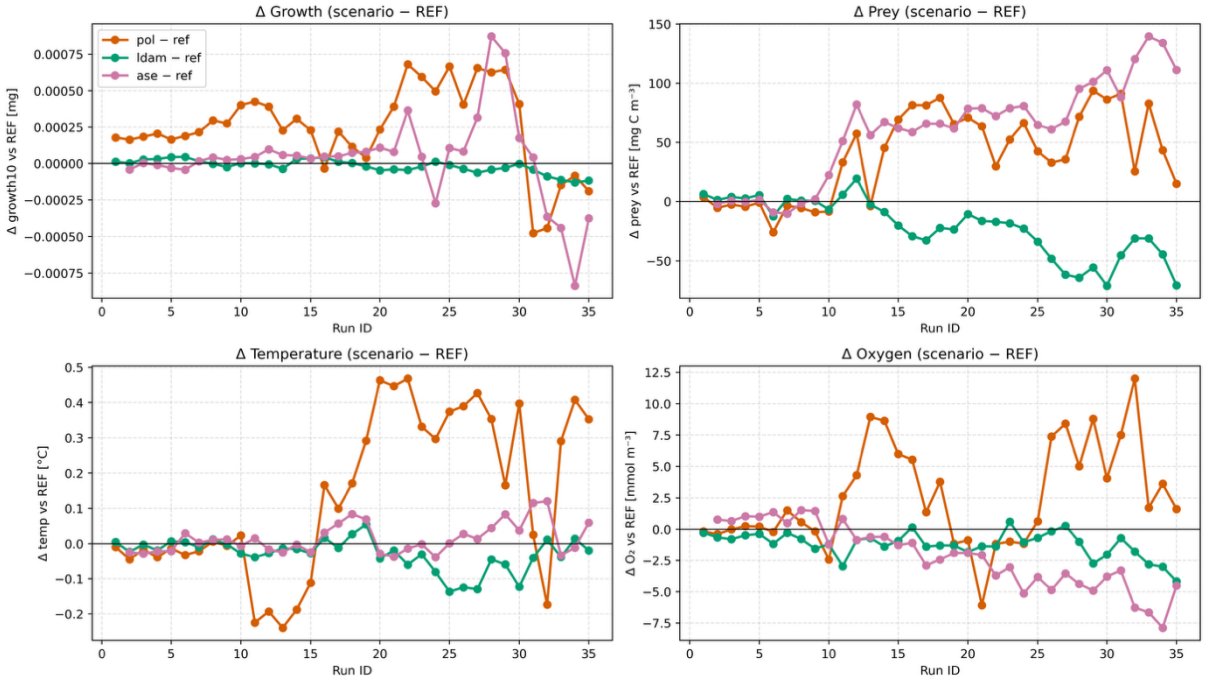


Figure 6: Cross run differences in Growth (A), available prey concentrations (B), temperature (C) and oxygen concentrations (D) during the exogenous drifting stage. Values are all calculated based on the 10-day window after the onset of first feeding as this marks a critical window in the development. As differences between the runs are comparably small, we decided to only show the differences between adaptation scenarios and the reference case.

Differences in prey availability are small during early starting runs (ID 1-10), afterwards POL and ASE show increased averaged prey concentrations with increasing trends towards later runIDs, while a decrease of prey concentrations is found for the LDAM scenario. However, prey concentrations do not surpass below the starvation threshold, which rules out prey induced growth limitations in all scenarios.

Differences in temperature and oxygen availability are rather small throughout all scenarios. Largest differences of both are found in the POL scenario, where temperatures decreased compared to the ref case for runs between ID 10-15 and afterwards significantly increased by up to 0.4°C. Oxygen concentrations in the POL scenarios are generally showing an increase compared to the reference state, with a steep negative difference at IDs 19-21. Both LDAM and ASE show a small, yet clear decreasing trend of oxygen concentration, while the temperature shows no clear trend compared to the reference state. The mixture of slightly increased temperatures, higher prey abundance is driving the development of exogenous individuals. These findings again support the conclusions of Pein et al. (2025) that the POL scenario is the ecological most convincing one.

Dam blockage – AME vs AME_c, excurs on estuarine connectivity

Finally, we want to focus on the topic of estuarine connectivity and the potential of the AME scenario. A relocation of the tidal weir from Geesthacht into the upper estuary close to Brunsbüttel has already been discussed based on the reduction in potential spawning grounds. In an additional model run we allowed for migration through the weir and enabled spawning grounds based on the previously described selection criteria for nodes. Due to the extension of the freshwater reach in the AME Scenario and the missing tidal locks in Geesthacht, the total number of suitable spawning nodes increased by 35-38% during January and February, on average 25% during March and April and remained significantly higher even in the following months. The increased spawning potential in the estuarine environment is a good example for the importance of role of estuarine connectivity. Estuarine connectivity has been a prominent concept in current discussions dealing with ecological conservation (Crooks and Sanjayan 2006; Pringle 2006).

The weir impacts the development of a migratory species in two ways. Directly as it induces a potential limitation for the upstream migration and block of potential spawning grounds from the migratory spawning stock and indirectly by altering the extrinsic conditions within the estuary impacting early life stage development. Similar findings were previously discussed in the context of the enhanced spawning potential of the Kiel Canal, where juvenile smelt individuals were caught in the vicinity of the lock chambers. However, the studies did not include their overall health status or an assessment of vulnerabilities and injuries that could have been explained by the passage of the chambers. Another important factor is the weirs potential to alter the outflow of water out of the Elbe into the Wadden sea. The fresher water from the Elbe estuary serves as a cue for the onset and direction of smelt migration (Lillelund 1961). We calculated the residence time per bin for both

spawning under restricted migration conditions as well as under full migratory potential. The results, including the reference residence data are presented in Figure 6.

The weir, located in Bin 5, clearly increases the time that feeding larvae spend in exactly this area. It however allows for a small exchange through the weir, but the blocking of particle drift inside the estuary remains the significant impact. It does however not block individuals from leaving the estuary, as shown by the residence time of particles spawned under non-limited spawning conditions. The increased time spent in front of the weir introduces new risk factors that could reduce the survival and successful recruitment of early life stages. Studies showed that weir construction significantly changes the species composition on both sides of the weir (Hur *et al.* 2018; Jo *et al.* 2019). Such changes also induce increased feeding pressure as overlapping niches reduce the total available amount of suitable prey items. Another aspect that is closely related to such composition shifts is the increased risk of predation. Combined with the increased residence time of individuals in front of the weird enhances their individual risk of dying due to predation. Similar results were found in Baumgartner (2007), where the gut content of predatory species showed a significant increase after weir construction.

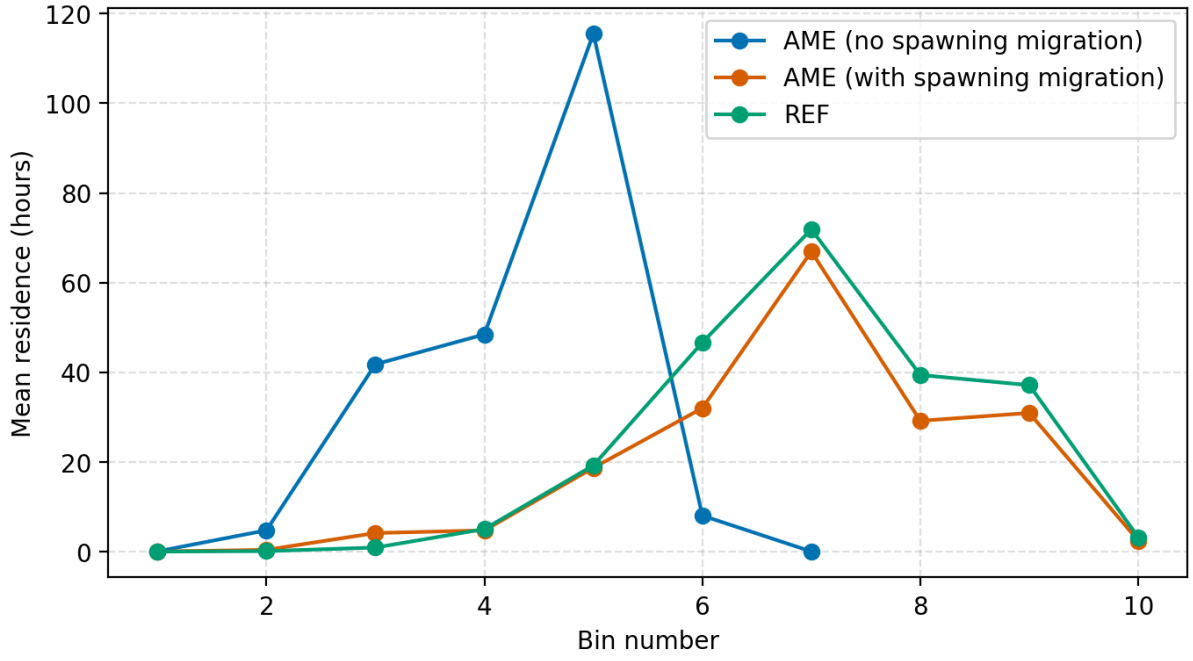


Figure 7: Averaged residence time shows the impact of the tidal weir on the particles potential to move through the estuary. Residence time was calculated based on the average number of timesteps particles spent in each bin. Compared are the runs in which the initial spawning conditions were chosen to simulate a total migration barrier due to the weir and would only allow for spawning in front of the weir, while in the spawning migration setup normal crossing of the weir was assumed. For a better comparison of the changes the reference case is again shown.

Conclusion

Our study nicely showed how IBMs and models can help to understand the impact of adaptation scenarios on local key species such as the European smelt. Our results extended the previously gained knowledge on the impacts on the tidal regime, sediment transport and plankton distribution that was presented in Pein et al. (2025). They concluded that the "nature-based" measures (POL and ASE) are performing best in terms of ecological suitability as they improve oxygen concentrations and available prey concentrations. Using our model results of endogenous development as well as exogenous development and conditions fully supports these findings. The increase in available spawning grounds shows that simple solutions such as the polder flooding can create valuable solutions for flood protection for both the ecosystem as well as the humans living in the catchment of the estuary. Overall, differences in development are comparably small, which, as we cover quite drastic changes of the estuarine system of the Elbe, is a good sign for a species such as the smelt. All the scenarios feature increased or similar growth rates within the first 10 days of active feeding compared to the reference case. Throughout all 4 scenarios, the polder creation peaks out as the one with the highest improvements, both in terms of development speed and growth rates. We further discussed the impact of a reallocation of the tidal weir towards the saline regime. Such a weir can impact the individuals during their spawning migration, reducing the effectively usable spawning grounds and decrease the overall population stability. Yet, additional measures such as fish ladders could be used to support migration while improving the storm protection along the estuary. However, as such modelling would require higher spatial resolutions, it is beyond the scope of this study.

In general, our results nicely demonstrate how modelling of drastic adaptation measures as those presented in this study can be used to understand potential impacts on the ecosystem and community within the impacted area. Using a key species allows for a wide transfer of our results across the local food chain. The smelt serves as an important contributor to the local biomass and is a commonly observed prey for larger fish, sea birds or mammals. Stability of such a species should be ensured when large construction projects are planned and monitored during the construction phase. While our model only includes core processes during three early life stages, the results show that based on these conditions in the Elbe might only improve if the proposed adaptation measures would be truly realised. It should however be noted that all the used scenarios are hypothetical and will most likely not be realised in their presented size or shape. But downscaling is often easier

than upscaling, so understanding the potential impact of such large-scale measures shows how capable the ecosystem is to adapt to the resulting system.

More research would be needed to determine the impact of such measures on sub-adult or even adult stocks. Also, the potential interaction with other species (predator-prey interaction) could be a nice future addition as it would further increase the need for suitable spawning grounds that yield protection for early life stages. Such a dynamic interaction would also increase the understanding of the impact of accumulation of individuals due to restricted estuarine connectivity, as it was shown in den AME scenario.

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Author contributions

D.D, C.S,U.D conceived the manuscript; J.P conducted the model runs with the Elbe estuary model and provided these as forcing data for the IBM; D.D wrote the first draft; D.D,C.S,U.D,D.B and J.P edited, revised, and refined the manuscript

Conflict of interest

The Author(s) declare(s) that there is no conflict of interest.

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Data availability

The data underlying this article will be shared on reasonable request to the corresponding author.

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Understanding the consequence of flood adaptation scenarios on migratory key species in the estuarine environment of the Elbe estuary – the European Smelt as a benchmark for future decision making

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Supplementary Figures

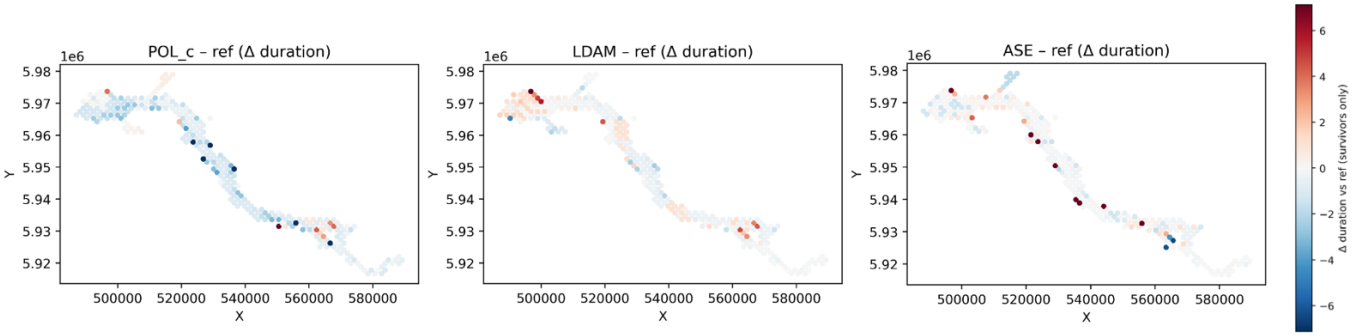


Figure 1: Differences in bin-wise averaged development duration. Differences are calculated as Scen - Ref. Additional areas (Polder and ASE) case were not included in the difference calculation as reference values were missing.

Discussion

Our study, focusing on the European smelt population in the German Elbe estuary, aimed to understand how extrinsic stressors and their coupling to intrinsic processes shape individual development and recruitment success (**Q1**). This process-based understanding further allows an assessment of projected risks under climate change and increasing anthropogenic pressure (**Q2**) and provides a baseline for evaluating potential future adaptation strategies (**Q3**).

Environmental drivers shaping recruitment success

The overarching goal of this study was to determine and interpret the role of extrinsic drivers influencing smelt development and recruitment success. In the final version of the IBM, six extrinsic drivers were considered in the calculation of smelt development: temperature, oxygen concentration, zooplankton prey biomass, currents, turbidity and salinity. Their relative importance varied substantially in magnitude and relevance across life stages. Across all analysis, temperature and oxygen availability consistently emerged as the dominant drivers and therefore form the base of the following discussion.

Our results showed a significant impact of temperature on endogenous and exogenous stages. During endogenous development, increasing water temperatures accelerate the individual stage completion, resulting in an earlier onset of first feeding and ultimately enhanced survivability (**Study 1**). All of these are potential indicators for a suitable nursery habitat. **Study 2, Figure 2**, confirms the model's capacity to reproduce the beneficial impact of such local thermal conditions as faster development was observed at the spawning site located in the Mühlenberger Loch. The shallow nature of these spawning locations resulted in higher water temperatures compared to the other selected spawning grounds. Faster stage completion further resulted in a higher number of remaining subindividuals at the onset of first feeding (**Study 3, Figure 4**). Due to the model's mortality implementation, such a higher number of remaining subindividuals acts as a potential buffer against unfavourable conditions at later development stages, as reaching the lethal threshold takes more time. During the exogenous stage, warmer conditions result in higher metabolic demands while increasing the daily maximum consumption amount, which are the dominant factors in determining individual growth. Using the temperature-dependant variation of growth potential under constant prey availability, the optimal thermal ranges were determined for two classes of individuals. First the thermal range for smaller individuals, just after the onset of first feeding, was determined and highest growth rates were found at

temperatures around 15°C. Larger individuals, close to the maximum threshold of 25 mm, showed optimal growth under cooler conditions between 9-14°C. Temperatures exceeding these optimal ranges led to imbalances between energy intake and losses, promoting starvation and increased mortality rates. These results match the general understanding of temperature being a critical driver of individual development, especially during early life stages (Blaxter, 1992; Kangur et al., 2007; Keller et al., 2020; McCarthy et al., 2020). Studies such as M. Power & Attrill (2007), associate elevated temperatures during early development with increased body size, while colder years were linked to delayed spawning and reduced egg development. Similar results were found for the individuals developing at spawning grounds (**Study 2, Figure 2**). Warmer conditions aligning with further suitable extrinsic conditions allowed for an increased prey intake and resulted in higher growth rates (from 0.14 mm h^{-1} to 0.174 mm h^{-1}, **Study 2**) during the first ten days of active feeding. More generally, summer temperature is considered a critical driver of year-class strength and population variability, with increasing temperatures, above the optimal thermal range, resulting in increased mortality (Arula et al., 2017; Kangur et al., 2007; McCarthy et al., 2020; M. Power & Attrill, 2007).

Oxygen availability represents a fundamental survival constraint in aquatic ecosystems (Möller & Scholz, 1991). Sufficient oxygen concentrations are essential for survival of yolk-sac and exogenously feeding individuals. Unsuitable oxygen levels were directly translated into increased individual mortality rates (Elshout et al., 2013; Möller & Scholz, 1991). Reduced oxygen availability further constrained swimming capacity and increased basal metabolic demands due to stress reactions and the individual attempt to reduce energy losses by decreasing mobility (Pörtner et al., 2017). The threshold for a sensitivity testing of survival in relation of decreasing oxygen concentrations showed a sharply decreased survivability at concentrations below 4.5 mg L^{-1} and instant mortality below 2 mg L^{-1} (**Study 1**). An interesting factor increasing the individual's exposure to unfavourable oxygen concentrations is the tidally driven retention that was implemented in **Study 2**. Comparing the oxygen concentrations showed a significant decrease throughout the exogenous development (**Study 2, Figure 3**). Averaged oxygen concentrations, however, never fell below the critical threshold value (2 mg L^{-1}). These results confirm the enhanced risk of individuals exposure to unsuitable conditions within the region of the Port of Hamburg (Hein et al., 2018).

Overall, the modelled results match well with previous studies addressing extrinsic drivers of smelt development. Temperature-driven recruitment dynamics have been documented for the Elbe estuary (Bioconsult, 2025; Lillelund, 1961; Oesmann,

2025; M. Power & Attrill, 2007; Scholle & Schuchardt, 2020; Sepulveda et al., 1993), Lake Ijssel (Keller et al., 2020) and the Thames estuary (M. Power & Attrill, 2007). These studies consistently emphasise the importance of temperature for larval growth and endogenous development (e.g. Power and Attrill 2007; Keller et al. 2020; McCarthy et al. 2020). Further supported is the avoidance of areas impacted by hypoxic conditions as described by Möller & Scholz (1991)). The implemented handling of such conditions within the IBM represents the observations of Lillelund (1961) underlining the ability to reproduce the impact of increasing hypoxic events under the warming scenario.

In addition to temperature and oxygen availability, salinity is frequently identified as an important driver of spatial species distribution (Thiel et al., 1995). Accordingly, salinity was included as one of three drivers in the habitat suitability analysis (**Study 2**), where reduced suitability in marine-dominated regions was primarily associated with increased salinity values. Further, salinity is an important factor determining individual survival, as early life stages showed high vulnerability for saline conditions over 10 psu (Lillelund, 1961; McCarthy et al., 2020). Salinity as a driver of increased mortality rates was added to the egg stages in the context of **Study 3**, allowing us to analyse potential salt intrusion scenarios due to changes in the tidal regime driven by the proposed flood adaptation measures such as opening polders or adding additional flood gates. As spawning grounds were selected based on the preferred salinity ranges, the impact was only visible on a very small portion of the spawning individuals. Yet it will possibly become more important in future years as marine conditions shifted upstream, resulting in more saline conditions within the estuarine environment (Theilen et al., 2025).

Using catch-per-unit-effort (CPUE), available at the FGG Elbe data portal (https://www.elbe-datenportal.de/), the interannual variability of smelt early life stage abundance was compared to extrinsic drivers such as winter and summer mean temperature and oxygen availability. Ultimately, we tried to compare development speed as an indicator for recruitment to the CPUE. These results from **Study 1** indicated a significant relationship between colder February temperatures and faster development of individuals. Other drivers such as prey availability or temperature at the onset of first feeding showed no significant influence on the individuals development speed (**Study 1, Figure 7**). The comparison of development speed and annual CPUE variability showed that faster development and successful recruitment do not necessarily correlate. Despite the general agreement, observation-based analyses of smelt stock variability in the Elbe demonstrate the difficulty of disentangling the relative importance of individual extrinsic drivers. Two

available reports from Scholle & Schuchardt (2020) and Bioconsult (2025), focusing on juvenile, preadult and adult smelt abundance derived from long-term monitoring data, concluded that habitat loss, intensified estuarine maintenance and turbidity were the dominant drivers of population dynamics, while temperature, salinity and oxygen were of minor importance due to missing trends throughout the covered timespan. Different to the findings of Scholle & Schuchardt (2020), our results showed a significant trend towards higher summer temperatures and decreased oxygen availability during the same period were visible and the calculated CPUE of smelt decreased especially in the last years of the available data (2014-17). It should be noted that the reports presented here did in fact not cover very early larval stages, which a direct comparison of relations between the monitored abundance and the drivers even harder. However, the impact of habitat loss, especially along the known nursery spots has later been covered in **Study 2** and **3**, resulting in similar findings as those in the available reports. These results suggest that the relative importance of extrinsic drivers varies across life stages and may shift over time. These results further show how important the detailed understanding of development processes and their drivers is, as actual monitoring in nature is barely possible, especially if very early life stages are targeted by the monitoring. The mechanistic approach of the IBM allows us to disentangle drivers and their potential impact on development throughout the included life stages based on physiological measurements of the individuals.

Overall, our results show that recruitment of the European smelt in our IBM is primarily governed by temperature and oxygen availability, which jointly constrain individual development, survival and habitat suitability throughout the early life stages. Warmer conditions promote faster development and higher growth rates if temperatures do not exceed the species-specific thermal ranges. Exceeding these would result in increased mortality, especially if combined with reduced oxygen availability. Additional drivers such as salinity, individual retention and habitat availability further modulated individual exposure to favourable or unfavourable conditions. Comparison with observation-based CPUE data underlines that recruitment variability cannot be explained by single drivers alone and that the relative influence of extrinsic factors may shift over time. Based on these findings, the following section builds on this process-based understanding to assess how changes in environmental conditions and habitat accessibility affect recruitment success at the system scale. These results act as a baseline for the later understanding of recruitment variability in the changing system of the Elbe.

Climate change and anthropogenic impacts on recruitment success

Understanding recruitment processes under reference conditions was essential for interpreting individual responses to future climate change and anthropogenic pressure. Simulations under the RCP8.5 scenario revealed a pronounced decline in habitat suitability within the central estuary and a downstream shift of favourable areas (**Study 2, Figure 5**), driven primarily by increasing water temperatures. Such spatial shifts in habitat suitability provide the mechanistic foundation for interpreting broader climate-driven changes in habitat suitability.

Shifts in suitable habitats are widely reported for diadromous species under the emerging pressure of climate change. Lassalle & Rochard (2009) predicted a redistribution of smelt habitat towards colder areas, including Irish and Scottish lakes and Icelandic basins. For cold-adapted species such as the European smelt, a northward shift in abundance is therefore expected as warming progressively degrades former spawning habitats (Sunday et al., 2012). Together, these studies highlight temperature as a dominant climatic driver of large-scale habitat redistribution, with Lassalle & Rochard (2009) identifying summer temperature and precipitation as key forcing factors. Habitat loss associated with such shifts may further increase the system's vulnerability, particularly if key species are affected opening vulnerable ecological niches. In such cases, niche overlaps most certainly result in the extinction of one of the competitors. Such dynamics have, for example, been reported in context of the targeted introduction of anadromous salmonids into ecosystems in New Zealand (McDowall, 1988; Scott & Irvine, 2000).

Warming exerted both positive and negative effects on recruitment success. During endogenous development, elevated temperature accelerated development and significantly shortened stage durations. Faster development is often associated with reduced predation risk and earlier acquisition of swimming capacity (Robert et al., 2023). During the early exogenous development, warmer conditions supported higher daily prey consumption through temperature-dependant prey limitation. However, once thermal optima were exceeded, especially during summer, increased metabolic demands could no longer be compensated by prey consumption, resulting in higher starvation-driven mortality (**Study 2, Figure 7 b and d**).

Another key consequence of increasing temperatures is reduced solubility of oxygen (Diaz & Breitburg, 2009; Seiffert & Hesser, 2014; Walther et al., 2002). Periods of elevated temperatures coincided with decreasing oxygen concentrations,

resulting in increased mortality rates. Model-based projections of the water quality showed an increase in both the frequency and spatial extent of hypoxic events under warming scenarios (Biederbick et al., 2025; Hein et al., 2018; Kerner, 2007; Schroeder, 1997). Further projected factors of increased hypoxic conditions are the decreased freshwater run-off as well the continuous dredging within the port region (Hein et al., 2018; Hillebrand et al., 2018; Kappenberg & Fanger, 2007; Kerner, 2007; Schroeder, 1997). The combined impact of elevated temperatures and reduced oxygen availability substantially increased mortality and reduced growth rates compared to the reference conditions (**Study 2, Figure 7**), indicating a strong synergy between these two stressors. Although the number of timesteps with unsuitable oxygen concentrations decreased in the warming scenario, the overall mortality increased. This suggests that lethal effects were primarily driven by temperatures exceeding the individual thermal optima rather than by hypoxia alone. The temperature-driven increase of metabolic rates is under hypoxic conditions superimposed with the increased energy demand for survival. As a result, even a slight reduction of the available oxygen results in starvation conditions, reducing growth and increasing mortality rates.

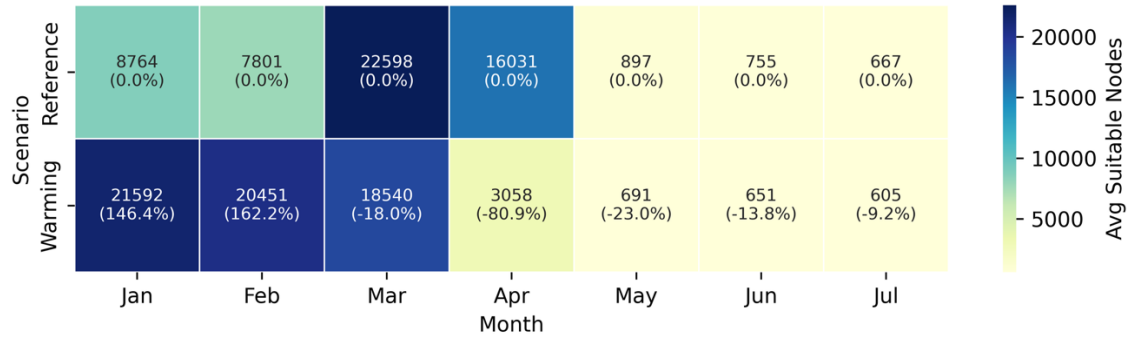


*Figure 4: Monthly averaged numbers of suitable spawning nodes per scenario. Colours indicate the general development of available nodes. Differences (%) are calculated with respect to the reference. Local temperature and salinity values were used to determine spawning suitability, nodes were counted and monthly averaged values were determined. The figure is adapted to from **Study 3, Figure 2** and has been redrawn to show the impact of the warming scenario on spawning phenology.*

Climate change may further affect recruitment through shifts towards an earlier onset of spawning activities. Spawning-related processes of migratory species such as the European smelt are governed by environmental cues including freshwater discharge, temperature and light conditions. Observations of the winter temperature as a spawning cue for smelt stocks in Lake Ijssel showed positive trends with earlier spawning resulting in an earlier onset of first feeding since 1961 (Keller et al., 2020). Such an earlier transition to exogenous feeding can result in a so-called predator-prey mismatch situation, enhancing starvation-induced

mortality at a vulnerable stage-transition (Hjort, 1914; Keller et al., 2020; Peck et al., 2012). In the reference scenario, prey availability at the onset of first feeding consistently exceeded levels indicating a potential mismatch situation (**Study 2, Figure 6**) representing favourable feeding conditions for early life stages. In contrast, reduced prey concentrations under the RCP8.5 scenario suggest an increased vulnerability of larvae to conditions of food limitation. Keller et al. (2020) described a close relation of the onset of first feeding in smelt with the onset of spawning activity. And in general, earlier spawning or faster development advance the time of first feeding increasing the risk of a mismatch situation (Blaxter, 1992; Peck et al., 2012). Spawning onset in the IBM formulation has been constrained to an earlier spawning in early March, thereby limiting the likelihood of a temporal mismatch between larval feeding requirements and prey availability. To assess how warming may alter the spawning conditions, the analysis of suitable spawning nodes was repeated under the warming scenario. The results are shown in Figure 4. Based on temperature, salinity and oxygen availability, the total number of suitable model nodes were counted and averaged into monthly means to quantify temporal variability across scenarios. While spawning suitability in the reference scenario peaked during March and April, the warming scenario showed highest suitability during January and February, representing a 146-162% increase during this time relative to the reference conditions. Thereafter, suitable spawning habitat declined sharply, with a pronounced reduction in April. Such a potential shift towards earlier spawning under warming conditions substantially increases the risk of a mismatch situation. Reduced prey concentrations were already apparent when the onset of first feeding occurred only ten days earlier than the mean timing in the reference scenario (**Study 2, Figure 6**). A projected advance of the spawning onset by one to two months would therefore strongly reduce prey availability during the critical first feeding phase and significantly increase the likelihood of prey limitation and recruitment failure.

While the timing of individual transition to exogenous feeding represents a key determinant of mismatch dynamics, mismatch risk is not governed by larval phenology alone. It is further shaped by concurrent changes in prey production and trophic interactions within the nursery environment. Increased spring temperatures at key nursery grounds (**Study 2, Figure 2**) are expected to alter both phyto- and zooplankton bloom dynamics. In addition, the earlier onset of spawning migration combined with increased biomass of spawners introduces a small yet significant top-down control on lower trophic levels through enhanced predation pressure (Brodersen et al., 2011). The prey-selective consumption of zooplankton by those early arriving spawners reduced grazing pressure on phytoplankton, potentially

advancing the timing of the phytoplankton bloom and thereby increasing the risk of mismatches for later spawning early life stages. Such feedback may further amplify local recruitment variability under future warming scenarios.

In summary, our results demonstrate that climate-driven warming has a huge impact on smelt recruitment, acting across spatial, temporal and trophic scales. Temperature emerged as the dominant driver structuring habitat suitability, developmental rates and physiological stress in a changing ecosystem. Its interaction with oxygen availability, prey dynamics and spawning phenology strongly amplifies mortality risks during critical stages of the early life development. Rather than acting in isolation, these stressors interacted synergistically, reducing both the extent of suitable habitat and the resilience of individuals towards suboptimal conditions. Importantly, indirect effects mediate through altered prey phenology and trophic feedback further increased the likelihood of mismatch situations, especially if we include the potential of earlier spawning due to changes in the migratory driving cues. Together, these findings highlight the need to consider cumulative responses on individual recruitment when assessing the impact of future climate change and anthropogenic usage on key species such as the European smelt.

Estuarine management from a key-species perspective

Over the last decades, the demand for estuarine management in the Elbe increased both to increase local resilience against extreme events such as flooding and for maintaining important economic agents such as the Port of Hamburg. The following section therefore focuses on two aspects of estuarine management relevant to the smelt: the assessment of flood protection adaptation measures and the ongoing land reclamation associated with the Port of Hamburg.

The demand for the construction of flood protection measures increased in recent years as the frequency of heavy floodings during storm events increased significantly (Gönnert, 2003; Von Storch & Reichardt, 1997). Pein et al. (2025) presented the hydrodynamical assessment of the impact of proposed adaption measures, followed by a brief analysis of their impact on the local ecosystem. Using our IBM, we expanded this analysis by investigating how such measures would impact growth and survival of the European smelt as a representative key species in the Elbe. Our analysis primarily focused on the measures impact on spawning grounds availability and connectivity of these, as the latter is crucial for migratory species to reach their destination. Further analysis was then done to determine how the changing extrinsic drivers due to the implemented measure impact

development and survival of smelt individuals throughout the estuary. The proposed measures were broadly separated into two groups: hard-engineered solutions (flood gates, artificial dams) and nature-based solutions (polder construction, reconnection of old branches).

Hard-engineered solutions such as flood gates or artificial dams often act as static barriers, limiting the habitat connectivity and the individual's ability to move between the marine and freshwater domain (Fullerton et al., 2010; Hall et al., 2012; Larinier, 2000; M. E. Power et al., 1996; Zarri et al., 2022). Our results showed a significant decrease of up to 99% of accessible and suitable spawning grounds in the flood-gate scenario compared to the reference scenario (**Study 3, Figure 2**). Acting as an effective migration barrier, the flood gate severely restricts the estuarine connectivity within the Elbe. Over time, such habitat fragmentation can lead to shifts in species composition on both sides of the barrier, ultimately reducing biodiversity and destabilizing the ecosystem functioning (Darimont et al., 2009; Fugère & Hendry, 2018). Analysis of individual residence times further revealed pronounced aggregation of particles in the vicinity of the flood gate (**Study 3, Figure 7**). While only individuals spawned downstream of the barrier were directly affected, the gate not only impeded the upstream migration of spawners but also prevented the passive upstream drift of early life stages into known nursery habitats. This spatial concentration of individuals is likely to increase local predation pressure and competition, reducing individual survival probabilities (M. E. Power et al., 1996). These findings align with the broader consensus that migratory species are particularly sensitive to disruptions in estuarine connectivity, with barriers consistently associated with declines in recruitment success and population resilience (Larinier, 2000; Zarfl et al., 2015; Zarri et al., 2022). These findings show how important the assessment of hard-constructed measures especially in regards of their impact on the connectivity are. A prominent example of the vast underestimation of the impact of decreased habitat connectivity has been the construction of the Afsluitdijk in the Netherlands. Completed in 1932, it had a vast impact on fish migration between marine and freshwater habitats, resulting in extirpation of especially diadromous species (Winter et al., 2014). Since 2011 the Fish Migration River (FMR) is planned and constructed, producing a "hole" in the dike, allowing for beneficial migration conditions while maintaining the dikes capacity of flood protection and prohibiting saltwater intrusion into Lake Ijsselmeer. With a prognosed cost of 80 million euros this project nicely demonstrates that management decisions should include key species as indicators for the potential outcome after completion as modifications to later ensure ecosystem stability are often connected to higher cost and efforts.

Further, nature-based solutions such as flood polders or the reconnection of the Süderelbe, a currently closed side channel of the Elbe, were covered. Contrary to hard-engineered measures discussed previously, these nature-based solutions can enhance local ecosystem services for instance by providing valuable nursery habitat. Even when only partially flooded, these areas offer suitable spawning and growth conditions for many different species (Hampel et al., 2003). Importantly, our results demonstrated that the creation of polders provides a significant benefit by increasing the availability of spawning grounds and improving growth conditions (**Study 3, Figure 4**). Warmer conditions during the endogenous development accelerated stage completion and increased the number of subindividuals reaching the onset of first feeding, which together suggest higher survival potential. Post-first feeding conditions further support these results as temperature, oxygen and prey availabilities clearly improve relative to the reference case, resulting in higher growth rates during the first ten days after first feeding (**Study 3, Figure 5**). Despite these ecological benefits, Warachowska et al. (2025) showed that the implementation of large-scale nature-based projects can be constrained by complicated legal frameworks as well as socioeconomic interests. In our study case, the polder size may be exaggerated compared to what could be realistically implemented. However, our results are promising in terms of suitable habitat and are likely transferable to configurations where the polder structure is divided into several smaller shallow polders located along the estuary. Such a distributed setup might even be more beneficial, as it would increase the habitat availability across the estuary rather than concentrating it in a single location such as the Mühlenberger Loch, which may increase the local risk of habitat degradation and ultimately decrease the likelihood of successful recruitment.

Another important stressor and component of the estuarine management is the increasing demand for economic space, especially around major cities such as Hamburg. (Köster & Thies, 2015; Thiel & Pezenburg, 2001). Land reclamation has a long history within the Port of Hamburg as a method of increasing the usable land but is obviously affecting the adjacent estuarine habitats. The Mühlenberger Loch is again a prominent example, and the local impact of habitat loss in this area has been widely identified as a potential driver of the declining smelt population in the Elbe (Bioconsult, 2025; Scholle & Schuchardt, 2020). Increased land reclamations resulted in a loss of 37% of the former area of the Mühlenberger Loch (Scholle & Schuchardt, 2020), exacerbated by increased sedimentation in the following years (Bioconsult, 2025). Such loss of habitat area will certainly affect the recruitment success and the nursery function of the Mühlenberger Loch, as more individuals compete for a spatially smaller distributed amount of suitable prey items or for

potential shelter in case of predation risk. In addition, the increase of sedimentation may further threaten the freshly spawned eggs, as sand coverage often results in unsuccessful development, reducing the hatching success of entire batches of eggs (Lillelund, 1961). These observations are in good agreement with our results from **Study 3**. In our simulation, the creation of a polder region acting as an artificial extension of the Mühlenberger Loch, resulted in a 16% increase of available spawning grounds and more successful recruitment of the early life stages.

Lastly, the impact of the increasing maintenance demand for the main navigation channel within the Elbe should be mentioned. The continuous dredging of the Elbe resulted in large-scale changes of the hydrodynamic regime over the past decades. Enhanced sedimentation results in a continuous increase of turbidity within the entire tidal-driven estuary. Building on the findings of Illing et al. (2024), the impact of turbidity on exogenous feeding smelt larvae has been implemented in the model (**Study 2, Figure 4**). Unfavourable turbidity conditions decrease the individual's visual capability to detect suitable prey items, resulting in decreased growth rates and, if such conditions prevail, increased starvation driven mortality. Our results show the model's capacity to simulate the impact of unfavourable turbidity conditions. However, the forcing used at the time did not included turbidity as an explicit state variable, which limited our ability to assess its spatial dynamics. Especially in the context of the increased demand of estuarine maintenance, construction work and dredging the spatial gradients of turbidity levels will most likely increase in importance and should be considered as a potentially major driver of recruitment success in the future assessments.

Using the newly developed IBM framework, the role and impact of different flood mitigation strategies were assessed across multiple life stages of a key species such as the European smelt. Explicitly accounting for life-stage-specific responses improves the mechanistic understanding of management impact and support the future development of strategies that balance socioeconomic objectives with ecological system integrity. These results highlight how integrating key species responses at an early planning stage can reduce the need for costly redevelopment or modification of finalised mitigation measures later on, as exemplified by the Dutch Fish Migration River. Compared to observation-based monitoring alone, modelling approaches such as the one presented in the scope of this thesis, allow for a more flexible and integrative assessment of management impacts. This is particularly relevant for migratory species, where habitat modification often led to delayed population-level responses that may remain undetected by conventional monitoring programs. At the same time, the modelling

framework is a valuable tool that can support and refine future monitoring efforts by identifying potential critical habitats, life stages and stressors. Such targeted monitoring would, in turn, improve the model validation and further enhance the accuracy of the system, creating a mutually reinforcing cycle between empirical observation and process-based modelling.

Conclusion and Outlook

The studies presented within the framework of this thesis aimed at deepening the understanding of extrinsic drivers underlying the recruitment variability of the European smelt in the Elbe. We adopted a stepwise approach by first determining potential drivers and including them into the IBM formulations. Using this framework, we investigated their combined effects on early life stage development and survival and identified temperature and oxygen concentration were to most dominant extrinsic drivers. Other drivers such as prey availability were in general considered potentially important, but under both the reference and warming forcing scenario did not show any sign of potential growth limitation.

Building on the identification of these critical drivers, we used climate change projections to assess how recruitment might respond to enhanced warming and increasing anthropogenic pressure. Further model development, including coupling to the three-dimensional Lagrangian tracking routine also opened the opportunity to use it as an assessment tool for spatiotemporal recruitment variability of a key species in the Elbe estuary. Finally, this modelling framework enabled an integrated evaluation of adaptation measures aimed at increasing local resilience to extreme flooding events. Using our model, we were able to highlight the additional importance of habitat connectivity and ecosystem services when selecting and designing effective management measures.

To conclude this study, it can be said that the presented model in its current state is a well-designed tool to understand and project the impact of major drivers of recruitment variability of the smelt. However, as it is a model study, a key aspect of such a conclusion is the future development and the potential to expand the knowledge even further, as a more detailed formulation of the individuals' intrinsic processes would always increase the results accuracy. Especially as this study covered the impact on a key species for the estuary of the Elbe, any further gain of knowledge can potentially help to mitigate the impact of climate change on the local aquatic community.

Model outlook and potential future development

Throughout this thesis, the importance of interactions across trophic levels, as well as density-dependent effects among individuals, were highlighted. In its current configuration, the IBM is coupled to the hydrodynamic–biogeochemical modelling system (SCHISM-ECOSMO) in an offline way, which prevents any feedback of the individuals to ecosystem state variables such as zooplankton biomass or oxygen. A transition to an online-coupled IBM would allow for such feedback and enable a more dynamic representation and a deeper understanding of processes such as prey depletion during first feeding and nutrient recycling through excretion and mortality. These mechanisms may become relevant in densely populated spawning grounds such as the Mühlenberger Loch.

Further developments that are closely linked to an online coupling could address computational efficiency, particularly during three-dimensional tracking of exogenous feeding. While the SCHISM framework is highly parallelised, the current offline tracking routine is not. Incorporating lightweight parallelisation would substantially improve the runtime performance, which would also allow for the consideration of higher individual counts and the implementation of new subroutines and parameters into the IBM.

Among potential model extensions, two priorities emerge from this work: turbidity and predation. Turbidity is currently represented in the IBM using one-dimensional observation based timeseries from the Elbe estuary, which do not capture the spatial variability. The results of **study 3** showed, that changes in the tidal regime will most certainly also impact the sedimentation and therefore also the turbidity within the Elbe. Future parameterisation of turbidity could therefore rely on the light conditions or on three-dimensional sedimentation-related output derived from the hydrodynamic model to better resolve spatial scales. Given its demonstrated influence on smelt development and growth, turbidity is expected to become more relevant under future management and climate scenarios.

The second important improvement that should be consider in future steps is to explicitly include the risk of predation during early life stages. In the current setup, mortality is determined by stage duration and development speed, oxygen availability and starvation linked to temperature and prey availability for the growth calculation. Including predation as an additional mortality term could improve our understanding of the impact of migration barriers or unsuitable conditions resulting in aggregation of individuals within the estuary.

Overall, the structure of the IBM and the tracking routine have been designed over the last years to support modular extensions, allowing additional processes to be integrated. Adding new processes and parameters is therefore straightforward if suitable observations and measurements are available for the European smelt or similar species. While the transition to an online-coupled system will most likely require the greatest development effort, it offers major opportunities to strengthen feedback modelling between fish individuals and ecosystem dynamics, which would improve the robustness of our results and increase the applicability of the approach presented in this thesis to other keys species.

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