# Phytoplankton Retention Mechanisms in Estuaries: A Case Study of the Elbe Estuary

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**Abstract.** Due to their role as primary producers, phytoplankton are essential to the productivity of estuarine ecosystems. However, it is important to understand how these nearly passive organisms are able to persist within estuaries, when river inflow results in a net outflow to the ocean. Estuaries are also representing challenging habitats due to a strong salinity gradient. So far, little is known about how phytoplankton are able to be retained within estuaries. We present a new individual-based Lagrangian model of the Elbe estuary which examines possible retention mechanisms for phytoplankton. Specifically, we investigated how reproduction, sinking and rising, as well as diel vertical migration may allow for populations to persist within the estuary. We find that vertical migration especially rising favors the retention, fast sinking does not. We further provide first estimates on outwashing losses. Our simulations illustrate that riverbanks and tidal flats are essential for the long-term survival of phytoplankton populations, providing refuges from strong downstream currents. These results contribute to the understanding needed to advance ecosystem-based management of estuaries.

## 1 Introduction

Estuaries are highly productive ecosystems. Their relative small area disproportionally contributes to the global carbon cycle, along with their role as a source of nutrients and hatching grounds for marine ecosystems (Cloern et al., 2014; Arevalo et al., 2023). While they are heavily influenced by anthropogenic stressors such as diking, dredging, and fishing, they are of tremendous importance for anthropogenic usage (Jennerjahn and Mitchell, 2013; Brown et al., 2022; Wilson, 2002). Estuaries present challenging dynamics to their smallest residents, due to strong salinity gradient and a net transport to the ocean. Here, we explore how phytoplankton, drifting small primary producers that form the basis of estuarine food webs, can persist within such dynamic environments.

Like most ecosystems - estuarine ecosystem dynamics are strongly controlled by primary producers, in particular phytoplankton (Chen et al., 2023). Apart from biofilm-forming phytoplankton which are attached to their substrate (Cheah and Chan, 2022), the vast majority of phytoplankton organisms drifts passively in currents, though they may be able to influence their vertical movement. With the estuary having a net outwards flow, we would expect phytoplankton to be moving downstream over time and to be washed out from limnic waters, via brackish into marine waters. Hence, the question arises how phytoplankton, as the drifting base of estuarine food webs, are able to maintain their population size without declining due

25 to the net transport into the open ocean. If we assume that the population is not exclusively maintained by a self maintaining source population upstream, that is washed into the estuary, then there must be some sort of retention mechanism that enables a phytoplankton population to persist within the estuary.

So far, different theories exist on how estuarine phytoplankton populations are able to maintain their position. Previous observational studies suggested several possible mechanisms that could enable retention of phytoplankton populations within 30 estuarine systems - vertical migration in the form of sinking, rising or diel migration, stickiness.

Diel vertical migration is a process where organisms move up and down in the water column in response to the sun. This movement favors retention by allowing plankton to reduce the time in the faster downstream currents at the water surface. However, this has only been demonstrated for larger motile estuarine organisms such as zooplankton (Hall et al., 2015; Kimmerer et al., 2002; Crawford and Purdie, 1991; Hall and Paerl, 2011). Yet, a study by Anderson and Stolzenbach (1985) showed 35 that diel migrating dinoflagellates were able to out compete other non-motile phytoplankton in an embayment environment and even compensate for outwashing losses through reproduction increasing their abundance. However, this also implies that the growing part of the population is somehow retaining their position. If the regrowing population is also continuously drifting downstream they will not able to sustain their population in that area and ultimately die out due to unfavorable salinity conditions in marine waters (Admiraal, 1976; von Alvensleben et al., 2016; Jiang et al., 2020).

40 Estuaries are complex and strongly dynamic systems such that it is still difficult to predict ecosystem dynamics or the effects of anthropogenic impacts due to their complex bathymetry (MacWilliams et al., 2016; Fringer et al., 2019). Nevertheless, previous modelling studies have investigated potential retention mechanisms of phytoplankton in estuaries. In Simons et al. (2006); Kimmerer et al. (2014) they used a Lagrangian model to study zooplankton retention. Simons et al. (2006) examined the dispersal and flushing time of mussel larvae in the St. Lawrence Estuary while() (Kimmerer et al., 2014) examined zoo-45 plankton movement in the San Francisco Estuary. They were able to show that sinking and diel vertical migration slows the outwashing process and might be a beneficial retention strategy. However, they did so by ignoring key processes like reproduction, mortality, and stranding or sedimentation processes. Moreover, both studies were based on low resolution structured grid models, which we suspect to under-represent the complex bathymetry of estuarine systems (Ye et al., 2018).

Diatoms or benthic microalgae in particular have been observed to be strongly negatively buoyant, hence sinking to the 50 riverbed and remaining there for a long time (Passow, 1991; Thomas Anderson, 1998). Studies also found sticky compounds in phytoplankton aggregates that are suspected to allow them stick to suspended particles, enabling them to sink to the riverbed or sticking to their surroundings aiding retention (Kiørboe and Hansen, 1993; van der Lee, 2000).

In summary, different retention mechanisms have been observed or examined in modeling studies. However, they did so either in isolation in the case of observational studies or with major simplifications in the modeling studies. There is cur-55 rently a lack of theoretical studies that allow for a more comprehensive overview into the interplay of vertical migration and reproduction in combination with settling and stranding as retention mechanisms.

Here, we explore possible retention mechanisms of phytoplankton using the Elbe estuary as a case study. It is located in the north of Germany and flows into the North Sea. Like most alluvial estuaries, it is relatively shallow, with most of it averaging only a few meters in average depth. Similar to other European estuaries it experienced a strong anthropogenic pressure over the
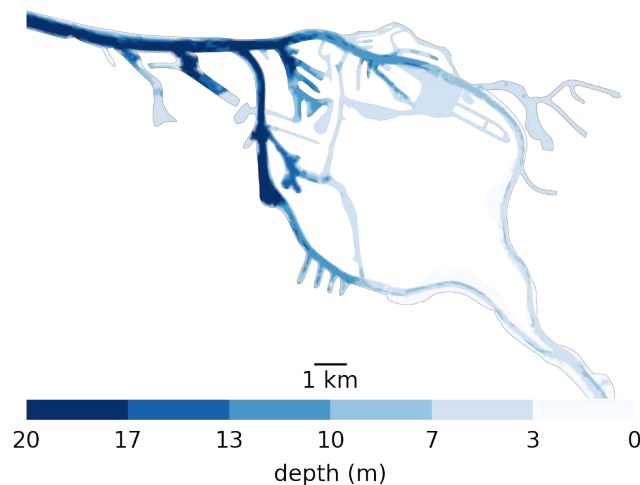
**Figure 1.** Bathymetry of the Elbe model around Hamburg. Note the bathymetric jumps from 5 m on the right, upstream side to a short 10 m step in the upper harbor area to the 20 m in the lower harbor area all the way to the North Sea. Also note that there exists no channel that does not pass through the 10 km of exclusively 20 m deep channel.

60   last centuries. Most notably diking to restrain it to a narrow channel and dredging to improve access to the Hamburg harbor. Unlike other major European harbors, the Hamburg harbor is located far inwards roughly 100 km away from the coast. To create port access the main channel experience a sudden jump in bathymetry from approximately 5 m at border of the city to up to 20 m in the harbor and downstream (see fig. 1). This bathymetric jump is suspected to be the cause of a collapse of the phytoplankton, resulting in an increase in oxygen depletion and high ammonium remineralization downstream of the

65   bathymetric jump (Schroeder, 1997; Holzwarth and Wirtz, 2018; Sanders et al., 2018). Ongoing dredging is being carried out to maintain the depth of the navigational channel causing high turbidity (Kappenberg and Grabemann, 2001). While important aspects of the along-channel biochemical dynamics have been studied, little is known about their vertical and shore-to-shore dynamics (Goosen et al., 1999; Dähnke et al., 2008; Sanders et al., 2018).

For this purpose, we further developed the individual-based Lagrangian model OceanTracker (Vennell et al., 2021) and

70   applied it to the Elbe estuary using the hydrodynamics calculated by a recent model SCHISM (Pein et al., 2021). While the Lagrangian model simulated the movement of the inanimate organism, we included key phytoplankton features such as reproduction and mortality, sinking and rising, as well as diel vertical migration. Using this model, we investigate under which conditions phytoplankton retention can be reproduced.
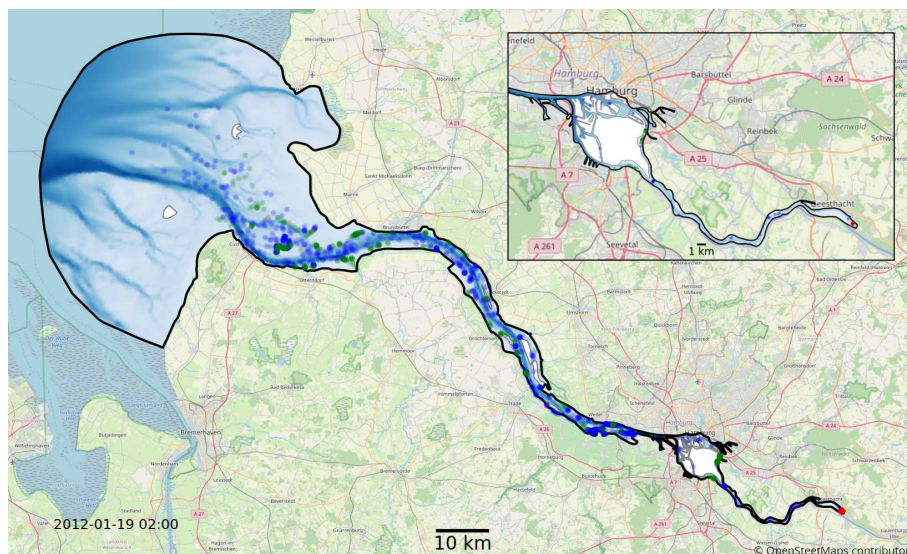
**Figure 2.** Map of the full model domain, with Geesthacht being the upstream boarder on the right and the North-sea being the downstream border on the left. The black outline marks the edge of the model domain. Blue and green dots show an example snapshot of a fraction of the phytoplankton in the model. The location of the initial release is shown in red. Blue represents floating, green particles stranded by the receding tide. The red area is the initial release location. The background map has been provided by © OpenStreetMap contributors 2023. Distributed under the Open Data Commons Open Database License (ODbL) v1.0.

## 2 Methods

### 2.1 Model description

In our study we use a Lagrangian approach with the particle tracking model OceanTracker (Vennell et al., 2021). While off-line particle tracking on unstructured grids has been relatively computationally expensive until recently (Vennell et al., 2021), it offers several advantages. Firstly, it allows us to reuse computationally expensive hydrodynamic models to model tracer-like objects. This is overall much faster than recalculating the advection-diffusion-equation in an Eularian model. Secondly, because we are simulating individually particles we are able to observe their tracks. This makes the interpretation of our results more intuitive and allows us to include individual based properties and processes that can not or only indirectly be represented in Eulerian models.

We use the hydrodynamics data of the most recent SCHISM model of the Elbe (Pein et al., 2021). This model uses a three-dimensional unstructured grid to represent the full Elbe estuary from the weir at Geesthacht to the North Sea, including several side-channels and the harbor area (see fig. 2). The model provides us with a node-based mesh containing a range of information such as water velocity, salinity, water level and dispersion. The year represented in that dataset is 2012 with a temporal resolution of 1 hour and a dynamically varying spacial resolution with distance between nodes ranging from 5 to 1400 m with a median distance of approximately 75 m.

We add a set of biological features on top of the otherwise inanimate organism. These features include reproduction and
90 mortality, vertical movement in form of sinking, rising or diel vertical migration, stranding, and settling on the riverbed.

Reproduction is represented as a chance of creating copies of themselves. This is a novel feature applied in OceanTracker
that has not been included in any previous Lagrangian model of this kind. OceanTrackers recent advances in computational
efficiency (Vennell et al., 2021) and buffer handling make it possible to simulate a large number of particles over a long period
of time for the first time on unstructured grids. We perform several simulations for a range of reproduction rates that are
95 constant over the lifetime of the particle and the chance to reproduce is evaluated every minute. While a fixed reproduction rate
is a simplification that does not allow for more realistic simulation of the population dynamics of a particular species, it does
allow us to investigate the general mechanisms that enable plankton retention.

Mortality is induced either by high salinity, when they dry-out while stranded, or due to long term light limitation. When
particles are exposed to high salinity water above 20PSU, a mortality probability of $0.5\%$ per minute is imposed. This threshold
100 is chosen based on a range of the salinity tolerances of estuarine phytoplankton species presented in (von Alvensleben et al.,
2016). This is only an approximation and salinity tolerances many estuarine phytoplankton species deviate from this. However,
the main motivation for this choice is that most of the particles that die through this process have passed the isohaline for
more than 12 hours, one tidal cycle, and are assumed not to return again through this isohaline. Anything outside the 20 PSU
isohaline is not considered part of the estuary for the purposes of this study. Therefore, we are not tailoring our salinity tolerance
105 to a specific species, but rather testing whether they can retain themselves within this isohaline. We consider particles that are
stranded outside the water by the receding tide, and lie dry for more than 7 consecutive days to be dead and remove them.
Particles also die if they are light-limited for 28 days (Walter et al., 2017). They are considered light-limited at a depth of 1m
based on turbidity data presented in (Pein et al., 2021). A particle starts its life with a light budget of 28 days, and each minute
below 1m reduces this budget by one minute, while the opposite applies when they are above 1m. Children of light-limited
110 parents inherit the remaining light budget of their parents.

We investigate the effect of different patterns of vertical motion. The first is monodirectional upward or downward vertical
motion, representing either positively or negatively buoyant phytoplankton. This buoyancy can be interpreted either as an active
choice of buoyancy by the organism through adaptation, or as governed by the suspended matter aggregate on which they live.
For monodirectional vertical motion, we assign each particle a vertical velocity, which remains constant throughout its lifetime.
115 The second mode of vertical motion is diel vertical migration. Here the particles change their direction of motion based on the
current phase of the sun, creating a motion pattern where they rise during the day and sink during the night within the same
velocity range.

We include a settling and resuspension model to represent tidal stranding and particles settling on the bed of the estuary.
Particles become stranded when the current grid cell becomes dry. They are not allowed to move from wet cells to dry cells,
120 by the random walk dispersion applied to all particles. A grid cell is considered dry based on the flag given in the SCHISM
hydrodynamic model output. Once this cell is rewetted all stranded particles resuspend and are able to move again. Particles
settle on the bed once they attempt to move below the bottom model boundary and are resuspended based on a critical sheer

velocity of $0.009\ \mathrm{ms^{-1}}$ (see appendix for details). The velocity profile in the bottom layer, or log layer, is calculated by

$$U(z) = \frac{u_*}{\kappa} ln \frac{z}{z_0}, \tag{1}$$

125  where U is the friction velocity representing the drag at height z above the seabed, $\kappa$ is the van Karman constant, $z_0$ is a length

scale reflecting the bottom roughness, and $u^*$ is the critical friction velocity. If the friction velocity is above the critical friction

velocity the particle is resuspended. Particles that are stranded or settled on the bed are allowed to reproduce. Particles are

not only advected but also dispersed based on eddy diffusivity. This allows us implement a dynamic dispersion that is crucial

to represent tidal-pumping processes. Dispersion was modeled using a random walk using a random number generator with

130  a normal distribution. Horizontally the standard distribution of the random walk was set to $0.1\ \mathrm{ms^{-1}}$. The displacement by

vertical dispersion $\partial z$ of particle $i$ is calculated by

$$\partial z_i = K_v^{'}(z_i(n))\partial t + N(0, 2K_v(z_i)) \tag{2}$$

based on Yamazaki et al. (2014) where $z_i$ is the vertical position of the particle, $K_v^{'}$ is the vertical eddy diffusivity gradient, $K_v$

is the vertical eddy diffusivity and $N$ is the normal distribution. The term based $K_v^{'}$ is needed to avoid particle accumulation

135  on the top and bottom of the water column from the hydrodynamic model output.

For each particle we log their distance traveled, age, water depth, and status (whether they are drifting or settled on the river

bank or bottom). This allows us for example to compare successfully retained particles (older than three months) unsuccessfully

retained particles (dead after less than three months). These observables are recorded every 12 hours starting at midnight.

Model simulations and visualizations were performed in Python making heavy use of Numba, a LLVM-based Python JIT

140  compiler (Lam et al., 2015) to significantly speed up the simulations (Vennell et al., 2021). Trajectories were calculated using

a second order Runge-Kutta scheme with a fixed time step of 60 s. Flow velocities, like any other hydrodynamic data, were

interpolated linearly in time and space using barycentric coordinates, with the exception of water velocity in the bottom model

cell, where logarithmic vertical interpolation is used.

## 2.2 Experimental configurations

145  We perform two sets of experiments to test the influence of different vertical movements on the retention success of phyto-

plankton in the Elbe estuary.

In the first experiment, we examine a range of different monodirectional upward or downward particle velocities from $-10$

to $+10\ \mathrm{mm\,s^{-1}}$ in $2\ \mathrm{mm\,s^{-1}}$ steps representing sinking or rising phytoplankton organisms (Fennessy and Dyer, 1996). Each

vertical velocity is examined for a range of different reproduction rates, expressed as population doubling times in idealized

150  conditions ranging from 40 to 404 days with a logarithmic scaling. In the following, we will use reproduction rate to refer to

the prescribed population growth rate under ideal conditions and use growth rate whenever we describe population growth in

nature. Hence, a total of 187 different scenarios are tested. In the second set of model experiments, we study the influence of

possible diel vertical migration patterns for the same vertical velocities and reproduction rates.

In both sets of experiments, we release 10,000 individuals representing the studied phytoplankton population at the beginning

155  of the year. This results in over 1 billion individual particles simulated for each case with approximately 1 million particles

active simultaneously counted over all cases over 500,000 time steps. The initial population is homogeneously distributed in a volume covering the full water column at the weir in Geesthacht (see fig. 2) and examine how the population distributes itself over the estuary and whether it is able to maintain its population size over time. Conceptually, we consider a population to be successfully retained if it is showing long term growth. Practically, this is evaluated by comparing the population size at the

160 end of the year to the size after release. The first three months of the simulations are considered as initial model spin-up time during which the initial population is dispersed downstream throughout the estuary. Population size changes are measured at the end of the year relative to the population size after this initial spin-up time.

Computations were performed on the supercomputer Mistral at the German Climate Computing Center (DKRZ) in Hamburg, Germany. The simulations were performed on a compute node with two Intel Xeon E5-2680 v3 12-core processor (Haswell)

165 and 128 GB of RAM with a total run time of approximately 4.5 hours.

## 3 Results

### 3.1 Retentions success in different scenarios

The results of the retention experiments are visualized as heatmap in fig. 3. Fig. 3a shows the results for the monodirectional vertical migration scenarios i.e. constant sinking or rising. Fig. 3b shows the results for the diel vertical migration scenarios.

170 Each pixel in the heatmap represents a simulation with a specific combination of vertical velocity and reproduction rate. The coloring indicates the relative population change after one year. White pixels and the boundary between green and brown pixels represent net-zero growth rate simulations. In this case, the losses are equal to the growth. Therefore, we can use the reproduction rate as an estimate for the total relative losses due to downstream transport, drying out while being stranded, and light starvation.

175 Our simulations show that the population is able to successfully retains itself under certain conditions. Passively drifting particles are able to sustain themselves in the estuary if they have a reproduction rate that doubles their population size within approximately 3 months. Note that the growth rates realized in nature may vary from this value due to e.g. nutrient or temperature limitations. The reproduction thresholds should be interpreted as an upper bound rather than an accurate estimate of the growth rate.

180 For the case of the monodirectional movement we see that a higher positive velocity (representing buoyancy) and higher reproduction rates are more beneficial for retention success than a downward oriented velocity (sinking) and lower reproduction rates. As expected, simulations in which the reproduction is set to zero do not show any retention success. While it is easy to understand that high reproduction rates aid retention, we were surprised that buoyant phytoplankton particles are more successful in maintaining their growth in an estuary than sinking ones.

185 For the case of the diel vertical migration in the velocity range of 4 to 10 $\mathrm{mm\,s^{-1}}$ we see an equal or higher retention success compared to the case with no vertical migration. A diel velocity of 2 $\mathrm{mm\,s^{-1}}$ is less successful than no migration. Most importantly, none of the diel migration scenarios improve the retention success, when compared to passively drifting organisms.
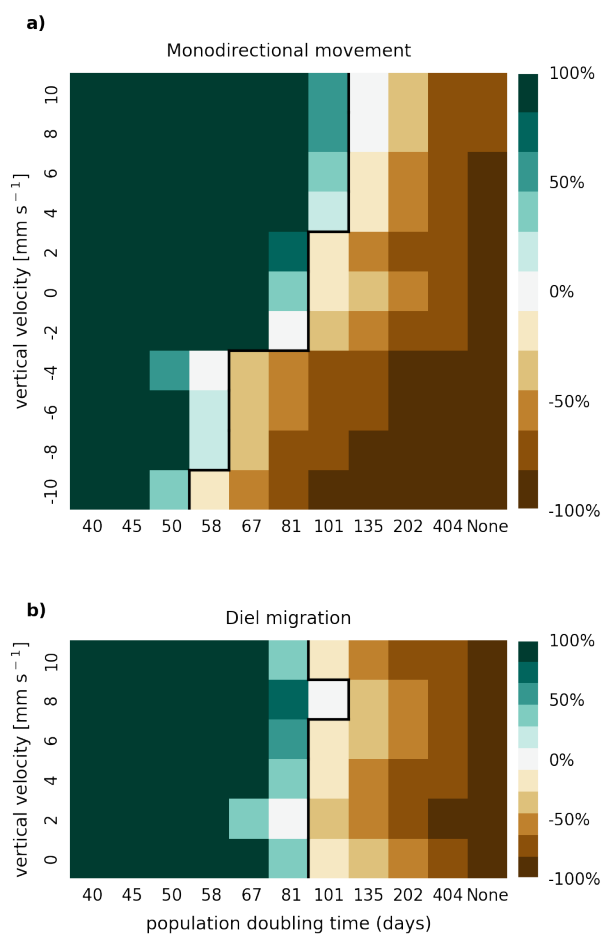
**Figure 3.** Relative population changes for the monodirectional movement (a) and diel migration (b) scenarios. Positive vertical velocities indicate an upwards drift. Positive population changes represent a retention success (green) while negative population changes represent a loss of the population (brown). The vertical black lines indicate the boundary between successfully and unsuccessfully retained scenarios.
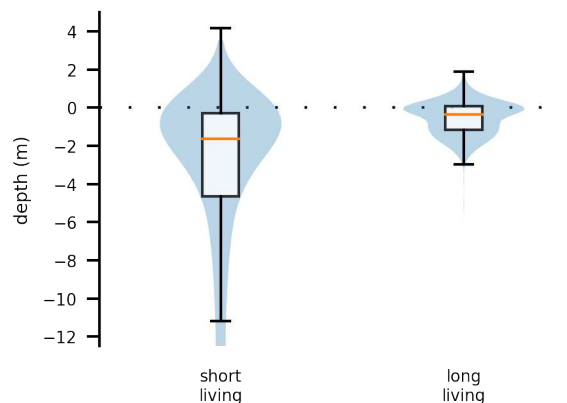
**Figure 4.** Box and violin plot showing the vertical distribution of particles that are passively drifting. Short-living are those younger than 3 months and long-living all those older than that. Depth is measured relative to the current water surface with positive numbers being above the water surface i.e. stranded on shore.

## 3.2 Spatial factors

190 We are now taking a closer look at spacial factors that allow phytoplankton particles to maintain net growth in the estuary. For this analysis we used data from both sets of experiments. Fig. 4 compares two box plots showing the average water depth at the location of each particle between particles that remained alive for less than three months (short-living) and for more than three months (long-living). Depth is measured relative to the current water surface. Hence, a value above zero indicate that the particle is stranded on the river bank. These analyses demonstrate that long-living particles predominantly live close to the

195 river banks in shallower waters or on tidal flats.

We moreover analyzed the horizontal spacial distribution of long and short-living particles in fig. 5. To do this, we divide the model domain into equally sized hexagons. The color of each hexagon indicates the average age of the particles within it. Hexagons with a yellow color indicate an average age of over three months. These yellow areas are mainly found along the river banks in shallow waters or tidal flats.

200 To further investigate the reasons for the positive effect of buoyancy and the importance of shallow waters and tidal flats, we repeated the first set of simulations and disabled the reproduction of settled and stranded particles. Under these conditions, populations were unable to retain themselves in the estuary, regardless of their vertical velocity and reproduction rate indicating that tidal flats are essential for the survival of the population.

## 3.3 Interpretation and contextualization of Results

205 In this study, we investigated different strategies to explain how phytoplankton populations are able to maintain their population growth in estuaries while constantly being at risk to be transported into the open ocean.
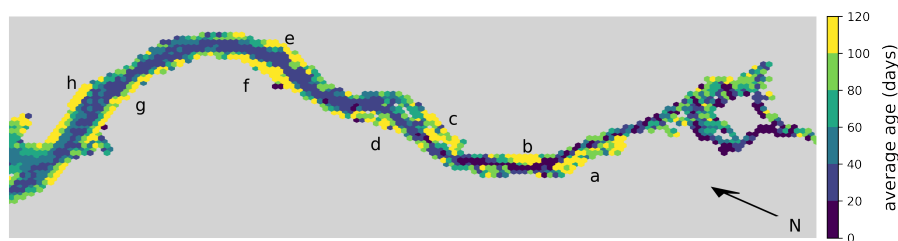
**Figure 5.** Hex-bin heatmap of the Elbe with Hamburg in the bottom right showing average particle age per bin. Colors indicate the age of the particles, with yellowish colors indicating an average age of over three months. Yellow areas are mainly found along the river banks in shallow waters or tidal flats. The important areas are Mühlenberger Loch (a), Wedeler Marsch (b) Haseldorfer Binnenelbe (c), Asseler- and Schwarztonnensand (d), at the mouth of Wischhafener Süderelbe (f), , and Stör (e), and at Nordkedding (g) and Neufelder Marsch (h).

The limit for population doubling times that we found to be necessary for survival for passively drifting plankton is of the order of around 4 months. Doubling times typically realized in natures are of the order of a few days which is two magnitudes small then those that we found necessary in our model (Koch et al., 2004; Wirtz, 2011). The low reproduction rates required for
210  successful retention demonstrate that our model is also meaningful under more realistic environmental conditions, for example if maximum growth rates cannot be reached due to nutrient or temperature limitations.

Our results suggest that shallow areas are very important for maintaining the estuary phytoplankton population. Plankton that consistently finds itself in areas that are dry due to the tides will regularly become stranded and therefore not move for much of the tidal cycle. We further see that positively buoyant plankton are more successful in retaining themselves. This is
215  probably because they are more likely to be transported high up on the river bank where the water is less likely to reach them. This effect is emphasized in flatter regions as the distance between the wash margin and constantly flooded areas is larger, increasing the chance of settlement or them stranding again.

Initially, we expected sinking particles to have a higher retention success than buoyant ones. However, we found that faster sinking particles are less successful in retaining themselves. Sinking velocities of less than $2\,\mathrm{mm\,s^{-1}}$ are common for diatoms
220  (Passow, 1991) while larger velocities have been observed for aggregates in the Elbe estuary (Fennessy and Dyer, 1996). Sinking particles have a reduced downstream velocity because find themselves either settled on the riverbed not moving at all or close to the bed where the average downstream velocity is lower. In addition, the deeper water layers of the Elbe have on average a lower downstream velocity than the upper water column or move upstream due to temperature-induced density stratification (Pein et al., 2021). Nevertheless, buoyant particles were more successful in their retention in our simulations.
225  The low chance of survival in the estuary for sinking particles might be explained by their light limitation in deeper waters. We expected particles to die if they are exposed to dark conditions for more than two weeks. Thus, sinking particles have a disadvantage to buoyant particles since they are more likely to become light limited and eventually die. This suggests that dredging has a negative impact on sinking plankton because it increases both depth and turbidity (de Jonge et al., 2014), which increases the aphotic depth and therefore the volume of dark water relative to the amount of light water.

230  We suspect that the reason for the increased retention success of diel migrating organisms is similar to the monodirectional case. When the upwards diel migration coincides with high tide, particles are more likely to be stranded far out on the shore, reducing their risk of being washed out quickly. The higher the upward velocities, the greater the chance of being at the waterline during high tide. However, because they are sinking for half of the day they also tend to be light limited more frequent than positively buoyant particles. It seems like these favorable and unfavorable processes balance each other out,

235  resulting in a similar retention success as for the monodirectional case.

### 3.4  Model limitations & future perspectives

In this study, we aimed to thoroughly investigate different possible retention mechanisms in a complex Lagrangian model system with a highly resolved bathymetry. Due to this computational and spatial complexity, the complexity of the biological particle properties needed to remain simple to keep computational cost manageable and due to a lack of high resolution

240  validation data.

Our model design does not resolve more complex ecosystem dynamics such as nutrient limitation and grazing by higher trophic levels. The Lagrangian model is performed offline, meaning it is not coupled to the Eulerian model that calculates the hydrodynamics and is performed after the fact. Therefore, modeling the advection and dispersal of changes in concentration fields e.g. nutrients due to growth or remineralization was not easily possible. Future modeling efforts could couple the La-

245  grangian model to a Eulerian model that disperses changes in concentrations fields by biotic activity throughout the model domain. However, this would have drastically increased both, developing and computational time to a point where it would have been infeasible in our time frame and due to the lack of appropriate validation data. The key draw back of this is that growth rates could only be modeled as a constant rate in the current model description, similar to "ad libitum" experiments. This can lead to systematic errors in estimating population growth. In reality, it can happen that nutrient limitation, which slows

250  down the growth of the population, can occur, especially in the most light-saturated areas near the shore. For this reason, we may overestimate the role of shallow areas in our model.

To be consistent with the complexity of the representation of biotic mechanisms, we use a simplistic light limitation. Particles are expected to be light limited below a water depth of $1$ m and not light limited above this threshold. We have not included a more complex light limitation model that takes into account current light availability and attenuation. A more realistic

255  formulation of light limitation could particularly favor particles that exhibit diel vertical migration. A process we mostly ignore in our study is dormancy. Our organisms can survive for 28 days in light limited waters. However, phytoplankton species have life stages in which they can remain dormant for a longer period of time and germinate again when they find themselves in more favorable waters (Thomas Anderson, 1998). In the process of choosing the light limitation threshold, we conducted sensitivity studies testing the effect of higher light budgets. We found that light budgets over 3 months begin to significantly increase the

260  survivability of sinking organisms, when we crudely assume that they could still reproduce under these conditions. Whether dormancy plays a significant role in an environment where the river bed is continuously dredged is unknown.

Another limitation in our modelling efforts is the lack of sub-grid-resolution structure on the shores. In our representation we assume perfectly flat surfaces with a median distance between nodes of approximately $60$ m. This 'polished' model rep-

resentation can lead to an underestimation of the retention success, since the surface area on which phytoplankton organisms
can settle is underestimated. In reality, vegetation, rocks or other surface irregularities cause a larger surface area on which the
phytoplankton organisms can settle.

Our hydrodynamics data set was limited to the year 2012. Therefore, we were not able to study different release times with
the same methodology. While we do not expect the general dynamics to change, future research could examine the effect of
varying discharge throughout the seasons on retention.

While our model does have a settling and resuspension mechanic based on critical sheer velocities we still assume a static
bathymetry with sediments not able to move or bury particles. This masks potential losses due to particles being buried but
also decreases resuspension times.

Our results clearly suggest the importance of tidal flats and shallow areas along the river banks for the successful maintenance
of primary production in the Elbe estuary. However, their effect can currently not be quantified due to the lack of validation data.
Chlorophyll data with a sufficient temporal and spacial resolution is only gathered in the center of the river. Future monitoring
efforts should therefore also include data along the river shores on tidal flats or shore-to-shore to quantify the effect of potential
future changes by dredging, diking or restoration attempts.

Frequently stranded plankton have been shown to be essential to the survival of populations in our model. However, data on
their ability to survive under these conditions are scarce. Our results suggest that these conditions may be as important as their
ability to quickly regrow under more favorable conditions, and we suggest further research on plankton survivability when
stranded.

For several decades, the annual average chlorophyll concentration in the Elbe estuary has been decreasing (data available at
www.fgg-elbe.de/elbe-datenportal.html or see (Hardenbicker et al., 2014; Schöl et al., 2014)), while upstream concentrations
do not show this effect. The reasons for this are not fully understood, but one possible reason is the increase in dredge activity.
This increases the average turbidity and thus the aphotic depth, reducing the volume of water in which phytoplankton can
grow. A large fraction of the phytoplankton measured upstream of Hamburg harbor consists of diatoms (Muylaert and Sabbe,
1999), which typically have negative buoyancy (Passow, 1991), making them particularly susceptible to sinking in light-limited
waters. Our finding that sinking particles have a harder time surviving in the estuary supports this theory.

Another mechanism that might in part explain the drop in phytoplankton concentration at the bathymetric jump, which
is not yet explored in our model, is the phytoplankton stickiness. Phytoplankton, especially blooming one, has been shown
to be sticky due to exudates (Kiørboe and Hansen, 1993; van der Lee, 2000; Dutz et al., 2005). Some phytoplankton also
produce transparent exopolymer particles, which increase their stickiness to other particles (Windler et al., 2015; De Brouwer
et al., 2005). We suspect that this in combination with higher turbidity induced by dredging results in losses due to plankton
aggregates sticking to negatively buoyant suspended matter and subsequently sinking to the ground where they are starved of
light. A future model study could create estimates on chlorophyll concentration losses caused by this effect.

## 4 Conclusions

In this study, we investigated the role of different possible retention strategies for drifting phytoplankton organisms to remain in an estuarine environment. Our model simulations suggest that realistically high growth rates are sufficient for populations to prevent decline of estuarine populations. Moreover, buoyancy and strong diel vertical migration enhance retention within the estuary. The reason for this is that phytoplankton organisms with strong buoyancy or the potential to move upward in the water column are more likely to be transported to shallow areas near the river banks or tidal flats, where currents are slower and the chances of settlement under sufficiently light conditions to allow reproduction are higher than in deeper waters. These results illustrate the importance of shallow nearshore areas to allowing the productivity of estuarine ecosystems to persist. Our results also highlight the need for informed ecosystem-based management to avoid the degradation of estuarine ecosystems by dredging and diking activities.

*Code and data availability.* Input data can be requested from Johannes Pein (johannes.pein@hereon.de). OceanTracker's source code is available atgithub.com/oceantracker/oceantracker. Model configuration and output is available at doi.org/10.25592/uhhfdm.13235

*Author contributions.* LS and RV contributed to conception of the study. LS designed the studies details and organized the hydrodynamic data. RV provided the source code for OceanTracker. RS,LS improved on the original physical model and LS developed the biological model. LS performed the model simulations, post-processing, and visualization. LS wrote the draft of the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

*Competing interests.* The authors declare that they have no conflict of interest.

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