

Numerical simulations of tidally cued vertical migrations of flatfish larvae in the North Sea

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Abstract

A coupled Eulerian–Lagrangian Hybrid Ecological Model was applied to model the transport of flatfish larvae at different scenarios of tidally cued activity. Hydrodynamic data were supplied by a two-dimensional hydrodynamic model of the southern North Sea and were used as input in a Lagrangian particle model in which the flatfish larvae were represented by particles, which responded differently to tidal cues—in this case, hydrostatic pressure. It was used to investigate the interference of vertical migration, in phase with the tidal rhythm, with the specific circulation pattern of the North Sea, by comparison with passive particle advection and diffusion. Instead of what was anticipated after tests in a simple one-dimensional tidal flow, the horizontal advection was not increased, which would allow a greater distance between spawning ground and nursery area. Rather, tidally cued vertical migration turns the direction of transport towards the nearest coast in the North Sea. This is caused by the phase difference between the onshore component of the water velocity and the along-shore component in this area. Tidally cued vertical migration would also be a very efficient mechanism to enter the Wadden Sea through a tidal inlet. The application of the present model looks promising but needs fine-tuning and calibration with real larval distributions and behaviour during the transport phase.

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1. Introduction

Since the beginning of the last century many hypotheses have been put forward to explain the recruitment variability in fish-populations. For species with pelagic larvae and using estuarine nursery areas, among which are many commercially valuable fishes and shrimps, the early life stages have been found to be most critical in determining the year–class strength (e.g. Rothlisberg et al., 1983; Rijnsdorp et al., 1985; Boehlert and Mundy, 1988; Van der Veer et al., 1998). Many factors have been suggested to be important during the pelagic stage of the larvae. The influence of hydrography on the distributions of larvae has been well established (e.g. Talbot,

1977, 1978; Rijnsdorp et al., 1985; Van der Veer et al., 1998; Brown et al., 2000), which is ultimately controlled by astronomical forcing and climatology. Another important aspect in larval advection is the behaviour of the larvae, which are believed to actively modulate their transport process by vertical migration through a sheared flow field, influenced by factors including light, temperature, pressure, salinity, speed and direction of the flow, availability of food and food odour, turbidity and turbulence. For a review see Norcross and Shaw (1984) and Boehlert and Mundy (1988). The relative contribution of vertical migration to hydrodynamic effects on interannual recruitment variability remains an open question to date. Furthermore, the relative contributions of various factors controlling the vertical migration are also unknown. In situ measurements of larvae and their behavioural responses to changes in their habitat are extremely difficult because it is not easy to make estimates of larval abundances as it

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is, but it would also mean monitoring of possible physical factors for a long enough period. In order to isolate some of the factors that potentially influence the larvae, laboratory experiments have been conducted in which larvae were observed under controlled circumstances. Their responses to various changes in physical parameters were then extrapolated to behaviour in their natural habitats (e.g. Yin and Blaxter, 1987; Burke et al., 1995). Another way to test hypotheses on vertical migration cues is the use of numerical models. A Lagrangian advection model, fed with circulation data of a hydrodynamic model in which the important aspects for a certain migration cue have been accounted for, can be used to study changes in the description of the transport of larvae from spawning ground to the nursery areas relative to, for instance, passive transport. In this way, one could test several cues and see which cue or combination of cues describe best the transport of larvae from the spawning areas to the nursery areas. In this way, Rothlisberg et al. (1983) found that diurnal vertical migration, interacting with wind-forced and tidal currents in the Gulf of Carpentaria, could increase the horizontal advection of shrimp larvae. Bartsch (1988) found diurnal migration schemes, reflecting behaviour of herring larvae in the North Sea, to have great influence on the transport paths. Hill (1994) investigated the potential of diurnal migration on horizontal transport, considering the interference of the migration with the S_2 (principal solar semi diurnal) tidal constituent. In a study of passive tracers, Van der Veer et al. (1998) found interannual variability of circulation patterns to be as large as interannual variability of recruitment of

plaice in the Wadden Sea. Here the effect of vertical migration in larvae of the plaice (*Pleuronectes platessa* L.) and flounder (*Platichthys flesus* L.) triggered by a tidal signal in the southern part of the North Sea is investigated.

The North Sea (Fig. 1) is an important spawning area for plaice and flounder. These flatfish species spawn offshore and the larvae subsequently enter the nursery areas as late larvae or early juveniles. Plaice spawn from December to March, with a well distinguishable peak in late January and early February (e.g. Harding et al., 1978; Van Beek et al., 1989). The main spawning areas for plaice (e.g. Simpson, 1959; Talbot, 1978; Hovenkamp, 1991) and flounder (e.g. Van der Land, 1991) in the North Sea area are depicted in Fig. 1; the named dots in the North Sea refer to the centres of these spawning areas. The most important nursery areas for plaice and flounder are the Wadden Sea and the Scheldt and Thames estuaries. The effect of larval activity on transport paths of the plaice and flounder under the influence of external factors is poorly understood. Moreover, the transport paths themselves are largely unknown. Many studies (e.g. Simpson, 1959; Harding et al., 1978; Talbot, 1978; Van Beek et al., 1989) performed repeated monitoring of larval and post-larval distributions, but detailed information on trajectories from the spawning grounds in the North Sea to nurseries in the Dutch coastal areas is lacking. Hovenkamp (1991) tried to determine the origin of plaice larvae immigrating into the Wadden Sea by linking their age to spawning peaks from different spawning areas. He concluded that plaice immigrating into the western

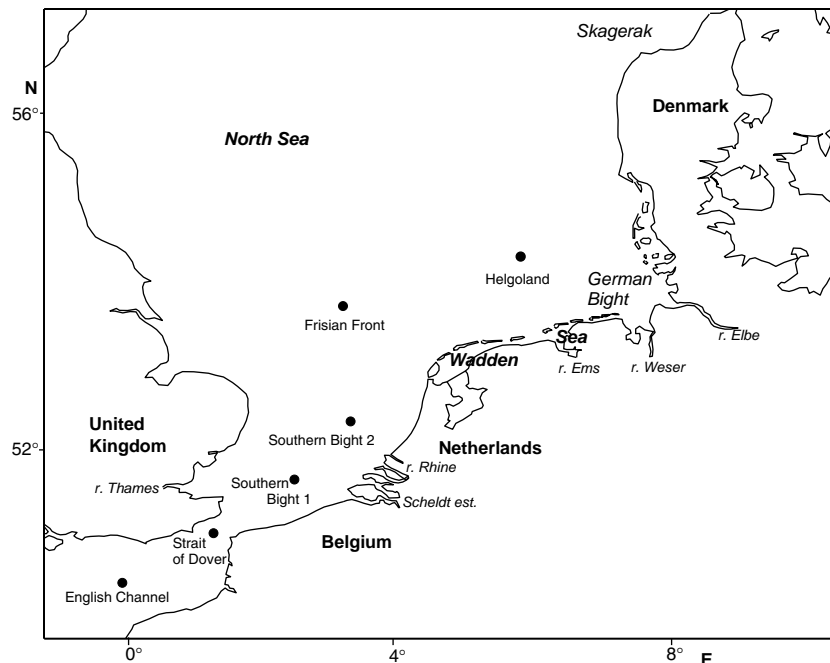


Fig. 1. The North Sea and Wadden Sea area, with relevant names.

Wadden Sea originated from spawning grounds as far away as the Western Channel.

Several studies have investigated the behaviour of plaice and flounder larvae during settlement (Rijnsdorp et al., 1985; Jager, 1999; Jager and Mulder, 1999). These studies show that the larval activity within the nursery areas is in phase with the tide, most larvae being found near the bottom during ebb and larvae moving upwards during flood (Selective Tidal Stream Transport, STST). Day and night cycles seemed of minor importance in triggering the vertical motion of these larvae (Rijnsdorp et al., 1985; Burke et al., 1998; Jager, 1999). This behaviour was extrapolated to the pelagic phase. A numerical model was constructed in which particles were allowed to change their vertical position according to hydrostatic pressure, or water depth, which changes in phase with the tide. This was used to investigate the effect of the tidal signal, as a cue for vertical migration, on the transport paths of pelagic larvae.

First the model assumptions and the various migration schemes will be described. Then the various simulation set-ups and results of the simulations will be presented. Finally some conclusions are drawn from the results and discussed.

2. Materials and methods

2.1. Hydrodynamic model of the southern North Sea

The velocity, pressure and salinity fields of the North Sea area were simulated using a two-dimensional hydrodynamic model called WAQUA (Vollebregt et al., 2003). It is part of the SIMONA suite of numerical models that is used by the Dutch government to simulate the hydrodynamics of the Dutch coastal waters, estuaries, lakes and rivers and the spreading of dissolved and floating matter therein. It is extensively tested, while continuously developed and maintained by the Dutch ministry of Public Works and Water Management. WAQUA describes the hydrodynamic circulation (advection and diffusion) in the southern part of the North Sea, based on the depth-averaged shallow water equations (e.g. Vreugdenhil, 1994). It uses a staggered curvilinear (smoothly following the horizontal geometry) grid of 88×220 numerical grid points (Fig. 2) and is forced by 49 harmonic components of the dominant tides. The modelled area encloses the southern part of the North Sea including the English Channel to about 57°N . A realistic bottom profile is used and river discharges create a salinity field, which influences the flow field. At closed boundaries, full slip conditions are imposed, while at open boundaries tidal frequencies for water level and velocity are prescribed. Boundary condition for the stresses along the free surface and the bottom is coupled with wind stress and the bottom

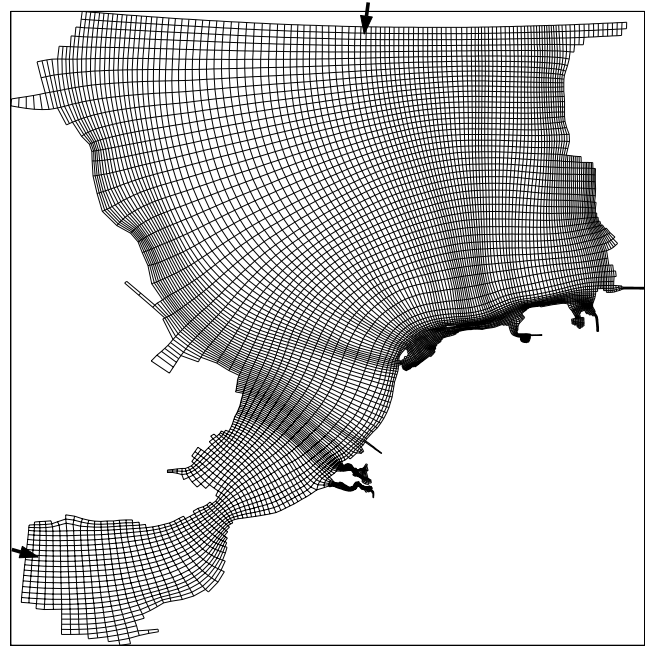


Fig. 2. Extension and resolution of the hydrodynamic model of the southern North Sea. The arrows indicate the open boundaries.

stress, respectively. The horizontal grid size varies from 400 m near the Dutch coast to 36 km away from the coast. This configuration ensures sufficient accuracy in areas relevant to larval transport and reduced data generation in less relevant areas. Diffusion is used to simulate the dispersive effects of small term motions like molecular and turbulent viscosity. The vertical exchange of horizontal momentum, which is lost in depth-averaging, is modelled as an additional dispersion term. In the simulations, a constant value for the diffusion of $10 \text{ m}^2 \text{ s}^{-1}$ was used. Sensitivity analyses showed that the model was most critically dependent on grid size and suggested that both the advection and diffusion rates presented in this paper were lower limits. The time step used in the simulations was 10 min and the model was run for three months, from 01 February to 01 May. This period covered roughly the time from spawning of the flatfish until the time of metamorphosis. A constant southwesterly wind of 4.5 m s^{-1} was applied during the entire period, simulating average atmospheric conditions. The output of the model was stored every 60 min to reduce data storage.

2.2. Transport model

The SIMONA suite of numerical models includes a transport model for the migration of floating and suspended particles. This model was adapted to include active behavioural components and simulate STST of larval fish reacting to tidal rhythms.

The transport model computes particle displacements based on a Lagrangian scheme. It consists of an advection part, determined by the hydrodynamic model, and diffusion to represent the contributions of random molecular and turbulent motions. The diffusion part was modelled with a random flight model, which is a random walk model, adjusted to ensure that the particles are uncorrelated also for small time scales (Heemink, 1990). It had the same constant value as in the hydrodynamic model, i.e. $10 \text{ m}^2 \text{ s}^{-1}$. The transport model uses the same grid as the hydrodynamic model and is run off-line, i.e. after all hydrodynamic data have been generated. The time step of the transport model was 10 min. As the data from the hydrodynamic model were saved only every 60 min, these data were interpolated. Particles were released at several locations in the domain and traced as they drifted through space and time. The release points were point sources; so shortly after release, only the diffusion part of the particles from one source point differed. Only when the distance between the particles was large enough the advection part could be different. All particles were always released at the same moment at a random time. At closed boundaries no-flux conditions were imposed, while particles were able to leave the domain at open boundaries. Once a particle left the domain it could not return.

2.3. Selective tidal stream transport simulation

For effective STST, vertical shear and synchronisation to the tidal frequency are needed (Hill, 1991). In a two-dimensional model only vertical averaged velocities are calculated, so there is no vertical shear. Therefore, a logarithmic current profile was assumed (e.g. Hill, 1991), viz. $u(z) = c_1 U \ln(z/z_0)$, where $u(z)$ is the velocity of the water at a height z above the bottom, U the average velocity as calculated by the hydrodynamic model, z_0 the roughness length where the velocity vanishes and c_1 some constant depending on the water depth and the bottom friction coefficients (Fig. 3).

For synchronisation, a simple one-dimensional tidal wave was assumed, in which the velocity lags the water

level by $\pi/4$. Then STST can be achieved by vertical movement in time with local flood and local ebb. To model this, the water level, or hydrostatic pressure, at a particle position was determined from the hydrodynamic data and compared with the water level at the same position at the previous time step. A rising water level was regarded as local flood, while a descending water level was defined as local ebb. The particles were then forced to be at different vertical levels z_p during ebb and during flood, see Fig. 3. So a particle was displaced with the horizontal velocity corresponding to the vertical level z_p of the particle in the vertical velocity profile, as determined by the local tidal condition.

2.4. Simulations

To study the effect of vertical migration, three scenarios with different particle responses to hydrostatic pressure were studied. The particles were followed for a period of three months as they drifted through the model domain. The position of each particle at each time step during the entire period was stored. The particle properties in the simulations were as follows.

1. Passive particles. These particles did not select tidal currents and drifted with the average tidal velocity as calculated by the hydrodynamic model. This was done by selecting a vertical level $z_p = z_s = H e^{-1}$, where H is the water level, for all particles during both flood and ebb conditions. At this level, the water velocity is equal to the depth-averaged velocity.
2. Particles with maximum responses to hydrostatic pressure differences. These particles rested on the bottom $z_p = z_0$ during ebb, where the velocity is zero, and instantly moved to the surface of the water column $z_p = H$ during flood, where the velocity is higher than the depth-averaged velocity. Note the infinite vertical velocity of these particles. These particles merely simulated the maximum potential of this type of STST.
3. Particles with increasing responses to hydrostatic pressure differences. These particles incorporated

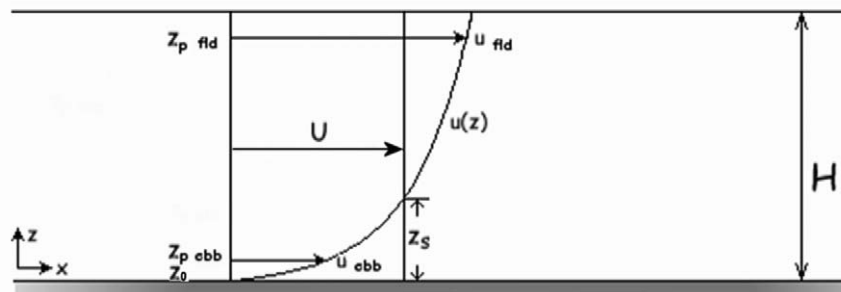


Fig. 3. Logarithmic current profile.

a developmental component of the larvae. The STST effect was split into three parts, each part lasting one month. The first month of simulation, the particles were passive, like type 1, simulating small larvae that were unable to alter their transport. The second month, the vertical level of the particles during flood was linearly increased from $z_p = z_s$ to $z_p = H$ at the end of the month, while the vertical level during ebb was linearly decreased from $z_p = z_s$ to $z_p = z_0$. This reflected the supposedly increasing capacity of the larvae to move with the tide more optimally every day. The last month, the maximum STST conditions were kept constant, like type 2, reflecting well developed larvae that can optimally select tidal currents.

Six release points were defined in the model, corresponding with the major spawning areas. These release points are depicted in Fig. 4. At each point 100 particles were released. The real number of eggs laid in the North Sea is estimated to be in the order of 10^{12} eggs (Harding et al., 1978), far more than the number of particles that can be tracked and stored in the computer's memory. The natural mortality rate is huge, lying in the order of 99.9% over the total period of spawning to settlement (Talbot, 1977). No attempt was made to simulate accurate absolute numbers of particles and the model ignores mortality. Only the potential of the STST mechanism was investigated and the number of particles was kept small and constant.

A success yield was defined as the percentage of the released particles that reached the Wadden Sea, i.e. when after 90 days they had crossed the imaginary line of the outer contour of the islands that divide the Wadden Sea from the North Sea. This line is shown in Fig. 7a.

To study the effect of the distance from the coast of the release points, 12 new starting points were chosen in the Southern Bight (Fig. 7a) and the experiments were repeated, releasing 100 of each of the three different types of particles at each point and tracking them for 90 days.

3. Results

3.1. Comparison of the spawning areas

First the results of the release of different types of particles in the various release points are presented. Fig. 4 shows the end positions of the passive particles after 90 days. Most particles were transported to the northeast, which is the direction of the residual current in the southern North Sea. The particles originating from the Frisian Front were not transported but only spread over a relatively small area. The particles from the English Channel were spread over a large area of the Southern Bight, between the Dutch and English coast. The particles that originated in the Southern Bight were

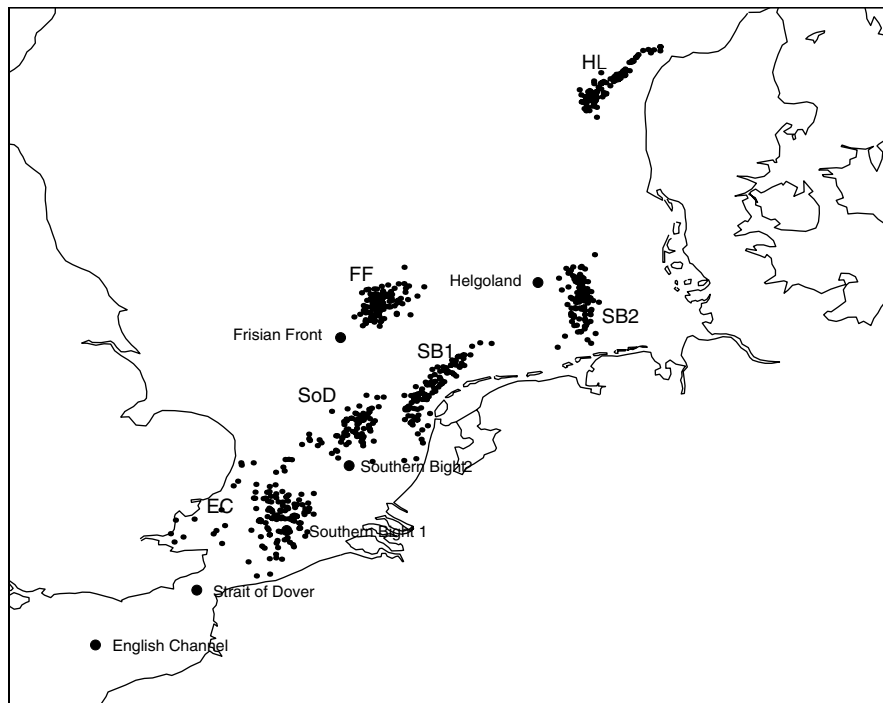


Fig. 4. Positions of the passive particles (type 1) after 90 days (small dots). HL = Helgoland, FF = Frisian Front, SB1 and SB2 = Southern Bight 1 and 2, respectively, SoD = Strait of Dover, EC = English Channel. Large dots with names are the release points.

transported towards the Wadden Sea area. The particles from the Helgoland area drifted towards the Skagerrak, north of Denmark. None of the particles entered the Wadden Sea.

Fig. 5 shows the distribution of the particles of type 2, which executed maximum STST, after 90 days. These particles ended much closer to the coast than the particles of type 1, except for the particles originating from the Frisian Front. The particles from the English Channel and the Dover Straits moved towards either the Dutch or the English coast. The particles from the Southern Bight 1 station now also moved rapidly towards the coast, in contrast to the passive particles, which from this point drifted towards the western Wadden Sea. The particles from Southern Bight 2 ended up in the Wadden Sea.

The positions of particles of type 3 after 90 days are indicated in Fig. 6. These particles were allowed to increase their selective tidal stream selection after a month of passive movement and drifted to the northeast during their first month, followed by a coastward movement during their STST period. As a result particles from the three southernmost stations moved farther northeast than the particles that were active from the beginning, while particles from Southern Bight 2 and Helgoland did not reach the coast like type 2 particles. The type 3 particles from the English Channel and Strait of Dover do not reach as far northeast as the passive particles, while they were slightly more drawn towards the English and Belgian coast. Type 3 particles from the Southern Bight 2 area ended also slightly closer to the coast than

the passive particles, while for Southern Bight 1 particles the effect was reversed. Type 3 particles from Helgoland and the Frisian Front drifted in the same way as the passive particles. None of the type 3 particles entered the Wadden Sea.

3.2. The Southern Bight area

The simulations were repeated in the Southern Bight area with 12 new release points, as this turned out to be the most important spawning area supplying larvae to the Wadden Sea. In Fig. 7a the new release points and the line that divides the Wadden Sea from the North Sea are shown. In Fig. 7b–d the end points of the particles of type 3, released in stations 1–4, 5–8 and 9–12, respectively, are shown. These particles were again first transported to the northeast and when STST was turned on they started to move towards the coast. The chance to reach an estuary increased with a release point increasingly close to the coast. In Fig. 8 the success yield for the various types of particles is given. It shows that 10–80% of the particles of type 3 released in the stations closest to the coast can reach the Wadden Sea, although all of these particles stay close to the coast and also end up in the Scheldt estuary. Even from a station as far away from the coast as station 12 a few percent of the particles of type 3 reached the Wadden Sea.

Control runs with passive particles (type 1) and active particles (type 2) showed that passive particles only reached the Wadden Sea if they were released very close

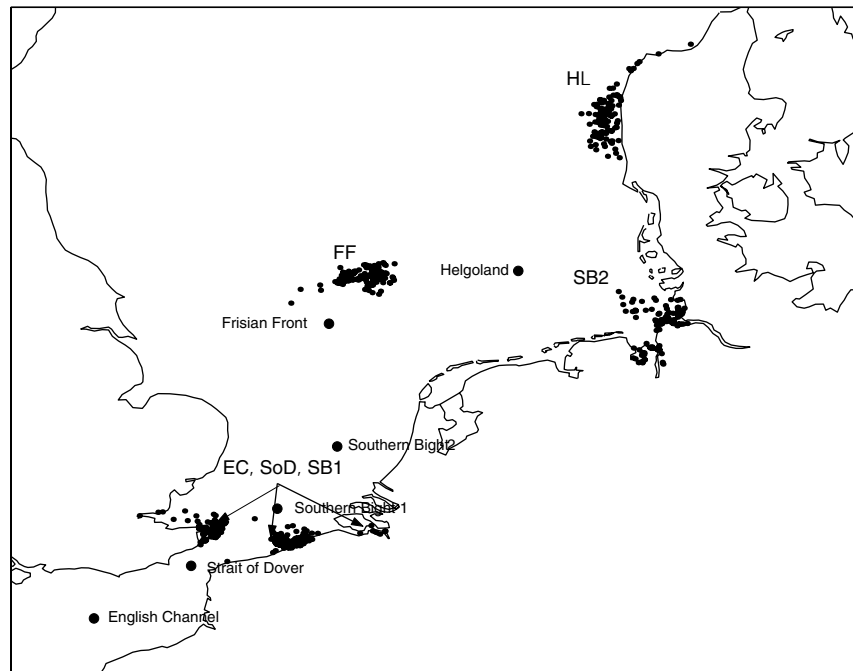


Fig. 5. Positions of the active particles executing maximum STST (type 2) after 90 days.

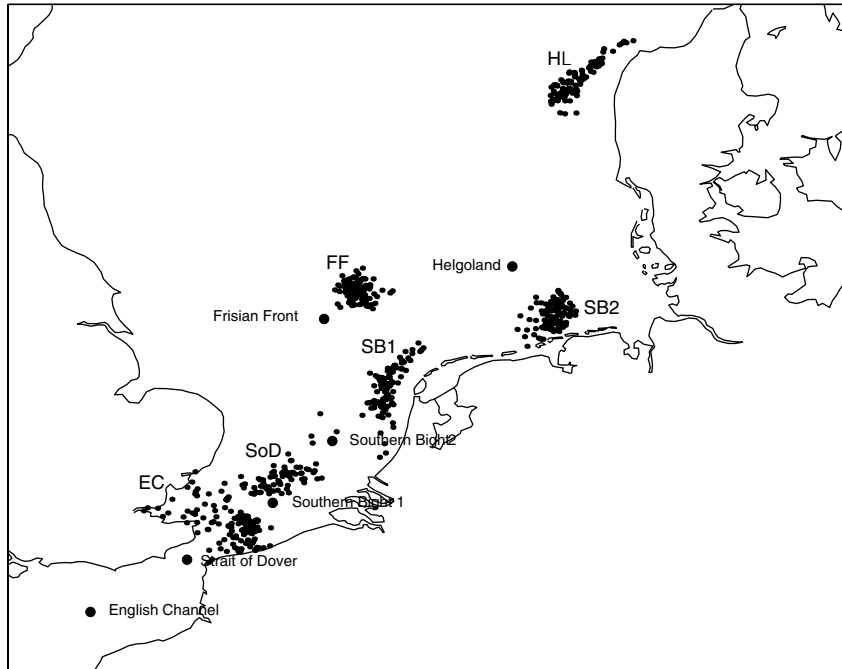


Fig. 6. Positions of the increasingly active particles (type 3) after 90 days.

to the Dutch coast (stations 2–4), but still less than 5% entered the nursery area (Fig. 8). Particles released near the Belgian coast drifted to the Scheldt estuaries. However, passive particles from stations farther offshore (5–12) all drifted to the northeast with the residual currents, similar to the previous experiments, without reaching nurseries. Particles of type 2, that were active from the start, were transported northward if they were released in the northeasterly stations, while type 2 particles released in the other stations were transported southward. All particles reached a coastal area in a relatively short time, except for particles released in stations 11 and 12, which are most distant from the coast. Particles released in half of the stations, the ones closest to the Wadden Sea (stations 2–4, 7, 8 and 12), ended up close to or in the Wadden Sea. Some of the particles from stations 2 and 3 were transported to the northeast, while others from the same stations were transported to the southwest. This was true for all types of particles. The residual currents very near the Scheldt outlet are not unambiguously northeastward, so shortly after release, diffusion determines whether a particle will reach the northeastward flow towards the Wadden Sea or whether it will stay near the Scheldt area.

The chance of entering the Wadden Sea increased if the particles were released increasingly close to the coast and with increasing activity. Near the Wadden Sea, STST is very effective for entering the lagoon through one of the tidal inlets. Particles released south of the Rhine outlet do not reach the Wadden Sea but do reach other estuarine areas when executing STST, where STST

increases the speed with which active particles can reach these coastal areas.

4. Discussion

STST based on tidal signals would be a very effective mechanism in the North Sea for larvae to migrate towards the coast. It was anticipated that an STST mechanism would greatly enhance the northeastward velocity of particles drifting with the tide, thereby increasing the number of larvae that could reach the Wadden Sea area from areas as far as the English Channel or beyond. The specific hydrodynamics of the North Sea however do not increase the northeasterly displacement of particles with this type of STST. Figs. 4–6 show the main impact of the STST in the North Sea area. Instead of moving northeast with the residual tidal current like the passive particles, the particles of type 2 move rapidly towards the coast. This rapid coastward movement is caused by the shape of the tide in this area. Fig. 9 shows the relationship between the water level, the velocity in the direction along the coast (η velocity) and the velocity perpendicular to the coast (ξ velocity) as calculated by the hydrodynamic model. The velocity along the coast is in phase with the water level, while the velocity perpendicular to the coast lags the water level signal by approximately $\pi/4$. This means that the tidal signal in the North Sea is more complicated than assumed in our simple one-dimensional tidal model and only the velocity perpendicular to the coast satisfies the

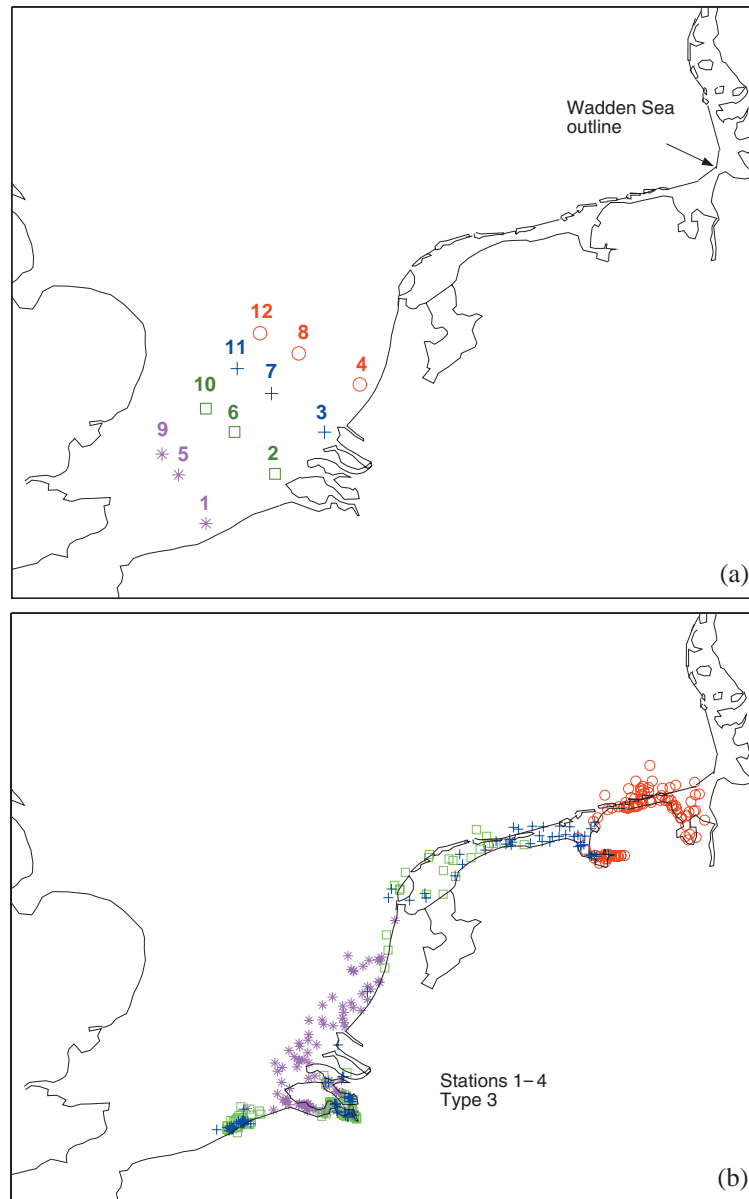


Fig. 7. (a) Release points in the Southern Bight. (b) Positions of type 3 particles after 90 days from stations 1–4. (c) Positions of type 3 particles after 90 days from stations 5–8. (d) Positions of type 3 particles after 90 days from stations 9–12.

$\pi/4$ lag condition. Therefore, a net transport will occur mainly in the ξ -direction. This means that tidally cued STST is not able to explain the large advection distances suggested by Hovenkamp (1991) within 90 days.

Van der Veer et al. (1998) showed that the interannual variability of transport from the spawning grounds to nursery areas of plaice in the North Sea is as large as the variability in larval abundance, suggesting it to be a key factor in determining year-class strength in plaice. Bartsch (1988) showed with the same hydrodynamic model that the variability of mass transport in the North Sea is strongly dependent on wind stress and stratification. This study confirms the northeastward advection of passive particles in a model with a finer grid. Bartsch (1988) also found daily vertical migration

schemes, in this case used to simulate behaviour of herring larvae in the North Sea, to be an important factor with which the larvae could influence their horizontal advection. The present study shows that tidally cued vertical migration could play an important role in the advection paths of larvae in the North Sea in the last stage of the pelagic phase. It would be an efficient mechanism for coastward directed advection. Note that there is neither a horizontal directional component in the model nor specific timing in the release of the particles. The rather large grid boxes of the hydrodynamic model used in the studies of Van der Veer et al. (1998) and Bartsch (1988) could not resolve the tidal inlets of the Wadden Sea. The present study shows that tidally cued vertical migration would be

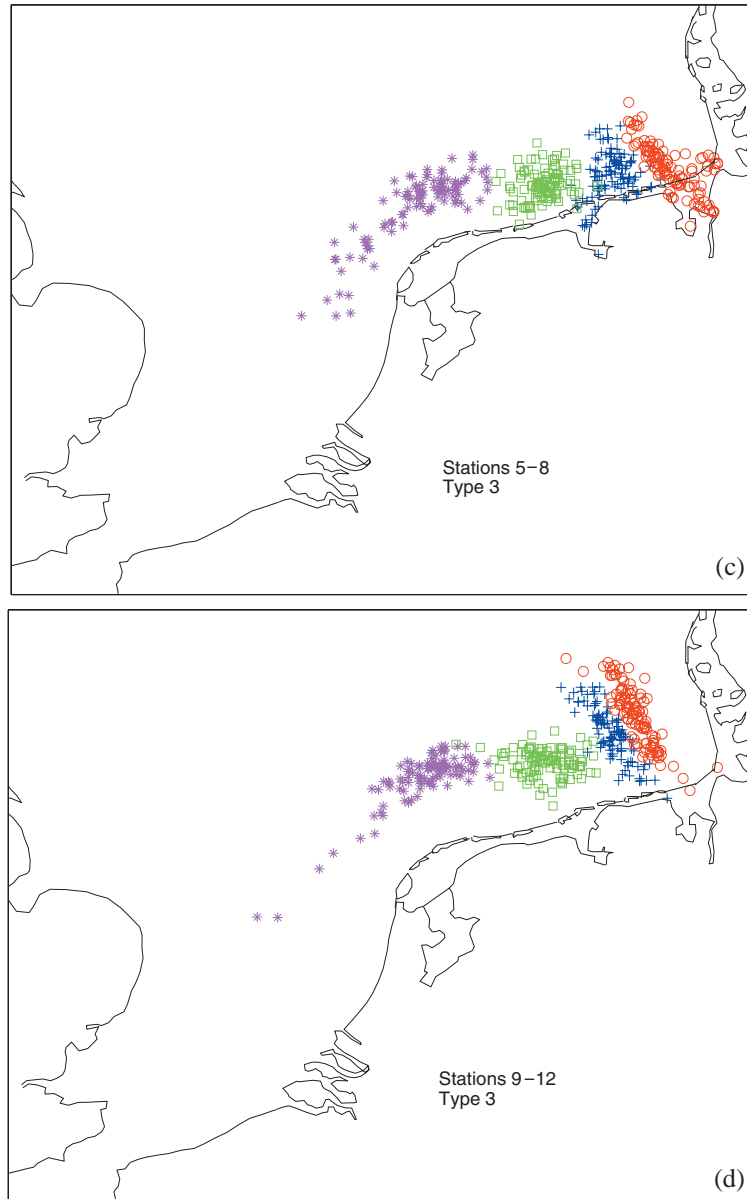


Fig. 7 (continued)

a very effective mechanism to enter the Wadden Sea through these inlets.

The assumed model for vertical migration suggests a cloud of larvae all vigorously swimming or floating towards the surface during flood and sinking during ebb. In reality, the vertical migration is much more diffuse. As Jager (1999) showed for flounder larvae in the Ems estuary, larvae are found throughout the entire water column, but the centre of mass of the larval distribution was distinctly different from that for suspended matter. She generally found highest concentrations near the surface, even when the larvae were negatively buoyant. A well defined layer with active larvae would suggest a smaller value in the transport model for diffusion, as one of the terms it represents is the horizontal dispersion of particles distributed over the water column by vertical

shear in the velocity field. On the other hand, when turbulent mixing would be small, all passive negatively buoyant larvae would be found near the bottom, where active larvae would be spread out over the water column, justifying a greater dispersion value (Smith and Stoner, 1993). In order to keep the model transparent, this effect has not been taken into account and one constant value for the dispersion was chosen for both active and passive particles.

In order to reduce computer costs, a simple logarithmic vertical velocity profile was constructed from two-dimensional hydrodynamic data to create the necessary vertical shear needed for STST. An obvious improvement would be the use of a three-dimensional model and a more realistic vertical migration scheme, but the advantage of these improvements should not be

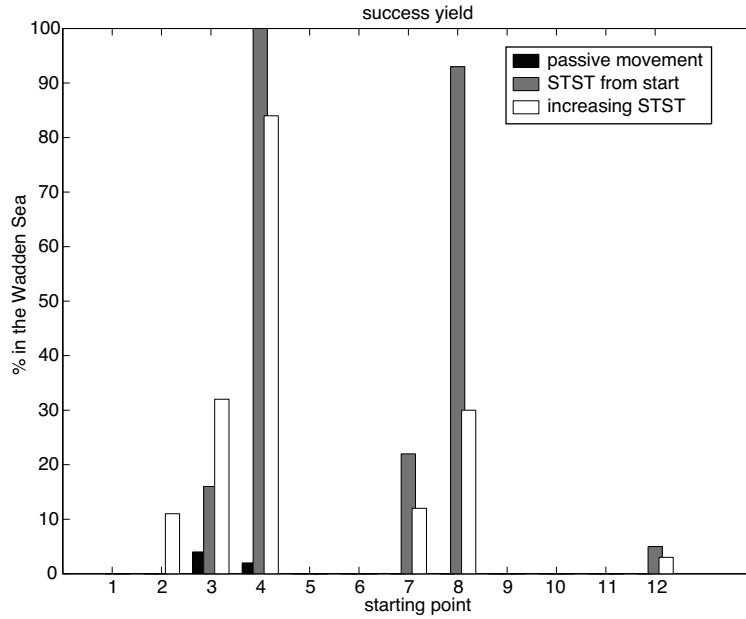


Fig. 8. Success yield.

overestimated. For example, one could incorporate effects of Ekman layers at the bottom and the surface to account for wind stress and bottom friction more accurately, especially with larvae moving to the bottom and top layers in the migration scheme. But these effects are of second order at least and moreover, the larvae are not necessarily found in the extreme layers of the water column for this model to be correct. Type 2 particles merely give an upper estimate of this mechanism of STST

in the sense of increased horizontal advection relative to passive particles. In this study the largest errors result not from hydrodynamic numerics but lack of biological and ecological knowledge. Although the hydrodynamical simulations are not exact, the numerical approximation of these phenomena has a long history and, most importantly, accurate error estimates can be given. Numerical simulation of larval behaviour is relatively young and larval behaviour is complex and evolving with

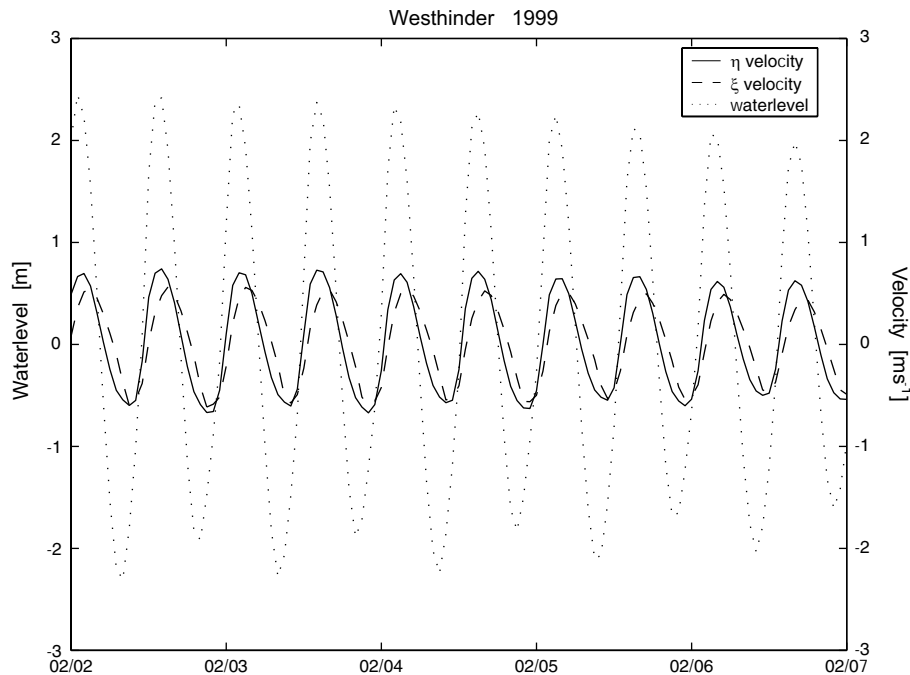


Fig. 9. Water level H and velocity of ‘Westhinder’ station, located near release point SB1, during five days. η -direction is locally directed along the coast and ξ -direction is perpendicular to the coast.

development. Measurements on the behavioural ‘laws’ of larvae would be very valuable for the construction of coupled physical–ecological models. Especially quantification of the relative influences of external stimuli on the behaviour of individuals and sets of individuals could highly improve the construction of numerical models. The Lagrangian scheme used in this model considers individual particles and follows them through space. All relevant properties are stored and movement decisions can be tested against these properties. Generally, physical and chemical properties like position, velocity, size or energy content are stored, but this can easily be extended with biological parameters like age, light and temperature preferences or hunger. Therefore, the Lagrangian scheme can easily be adapted to future insights in ecology or applied to different species.

Despite the large amount of observations available on larval populations, trajectories of larval transport are largely unknown. Such trajectory data would be very valuable for calibration and further development of models on numerical simulation of larval behaviour. In this study a constant southwesterly wind stress was applied during the entire simulation period, reflecting average climatological circumstances. During periods of persistent northeasterly winds however the residual northward currents along the Dutch coast can be slowed significantly and even reversed. When model results are compared to real larval data, the actual climatological conditions during collection of the data should be applied to the model.

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