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Numerical modelling of physical processes governing larval transport in the Southern North Sea

M. C. H. Tiessen[1], L. Fernard[2], T. Gerkema[1], J. van der Molen[2], P. Ruardij[1], and H. W. van der Veer[1]

[1]Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, Texel, the Netherlands
[2]Centre for Environment, Fisheries and Aquaculture Science (CEFAS), Pakefield Road, Lowestoft, Suffolk NR33 0HT, UK

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Correspondence to: M. C. H. Tiessen (meinard.tiessen@nioz.nl)

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Abstract

A three-dimensional hydrodynamic model (GETM) was coupled with a particle tracking routine (GITM) to study the inter-annual variability in transport paths of particles in the North Sea and English Channel. For validation, a comparison with observed drifter trajectories was made. The aim was to investigate to what extent variability in the hydrodynamic conditions alone (reflecting passive particle transport) contributed to inter-annual variability in transport of eggs and larvae. In this idealized study, no a-priori selection of spawning grounds or periods was made and no active behaviour (vertical migration) or mortality were included. Egg and larval development towards coastal nursery areas was based solely on sea water temperature, while settlement areas were defined by a threshold water depth. Results showed strong inter-annual variability in drift direction and distance, caused by a combination of wind speed and direction. Strong inter-annual variability was observed both in absolute amount of settlement in coastal areas, as well as in the relative importance of the different areas. Settlement in the western Dutch Wadden Sea not only showed inter-annual variability, but patterns were also variable within each year and revealed seasonal changes in the origin of particles.

1 Introduction

The pelagic phase is a characteristic component of the life cycle of the majority of marine species. Within the range from holoplankton to holobenthos species a variety of different life strategies occur including benthic resting stages in plankton species (such as a.o. dinoflagellates, Dale, 1985, and cnidaria, Boero et al., 1991) and pelagic egg and larval stages in benthic bivalves and demersal fish species. Marine species can only exist in geographic locations within which there can be continuity in the life cycle; i.e. "in a geographical setting within which retention (membership) of the population exceeds losses (vagrancy) in some integrated sense for the life cycle as a whole" (cf.

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Sinclair, 1988). The importance of life cycle closure is continuously topical since at any stage of the life cycle an individual can become separated from its population either by spatial (losses from distributional areas) or by energetic (predation, starvation, disease) processes. The variety of all these complex life stages can be viewed as species-specific and/or local adaptations to ultimately achieve life cycle closure.

During the pelagic phase physical factors such as advection and temperature are acting on and potentially resulting in the dispersal of individuals, depending on strength and duration of the physical forcing. Especially for species with a pelagic egg and larval stage, this period of egg and larval drift is considered to be an important factor in year-class strength regulation (bivalves: Thorson, 1966; fishes: Leggett and Deblois, 1994; flatfishes: Van der Veer, 1986; Van der Veer et al., 2000; Van der Veer and Leggett, 2005). As a consequence, the impact of inter-annual variability in hydrodynamic conditions on egg and larval transport has been studied since large-scale 2-D and later 3-D hydrodynamic transport models have become available. For the North Sea area this has resulted in a number of detailed studies on egg and larval drift and transport of fish larvae, especially flatfishes (Van der Veer et al., 1998; de Graaf et al., 2004; Bolle et al., 2009; Dickey-Collas et al., 2009; Savina et al., 2010; Hufnagl et al., 2013) and all these studies stress the importance of drift and transport during the pelagic phase.

Passive transport is the only agent during egg development but from hatching onwards also larval behaviour such as active vertical migration may become into play (Rijnsdorp et al., 1985). In the recent 3-D hydrodynamic modelling studies by van der Molen et al. (2007), Dickey-Collas et al. (2009), Bolle et al. (2009), Savina et al. (2010), and Hufnagl et al. (2013) both passive transport and active behaviour components were included thereby preventing an analysis of their relative importance. In particular, it remains unclear to what extent physical factors alone can be responsible for inter-annual variability.

The aim of the present paper is to determine the importance of passive transport by advection in the dispersal of particles in the southern North Sea, whereby we used plaice *Pleuronectes platessa* as model species. Instead of a focussing on a limited

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number of plaice spawning grounds and periods (cf. de Graaf et al., 2004; Bolle et al., 2009), in our approach particles were released at random over latitude, longitude, depth and time (cf. Hufnagl et al., 2013). By way of validation, we start with a comparison of simulated model trajectories with observed drifter paths. Particle tracking was introduced by means of a three dimensional Lagrangian tracer model in combination with a hydrodynamic model. Instead of selecting specific release areas (reflecting spawning grounds) and time periods (reflecting spawning periods), as was done by de Graaf et al. (2004) and Bolle et al. (2009), no a priori selection was made; the entire southern side of the North Sea and the English Channel were selected as potential starting points for particles over a 4 month period in spring, reflecting the most important period for egg and larval drift in plaice larvae (Talbot, 1977; Harding et al., 1978). Particles were released at random over latitude, longitude, depth and time. With a view to the transport of larvae (such as of plaice *Pleuronectes platessa*), we adopt a dependence on sea water temperature to define a life span. Settling is assumed to take place when encountering an area with a certain minimum threshold depth. In this way, the success of settling can be defined and mapped.

2 Material and methods

2.1 Hydrodynamic model

The hydrodynamic model used in this research is the three-dimensional General Estuarine Transport Model (GETM). GETM incorporates the General Ocean Turbulence Model (GOTM), which is a one-dimensional model over the vertical that provides a variety of turbulence closure schemes. The combined 3-D hydrodynamic model suite was developed by (Burchard and Bolding, 2002). It has been applied to coastal seas such as the North Sea and Baltic Sea before (Ruardij et al., 2005; Lenhart et al., 2010; Gräwe and Burchard, 2011; Leeuwen, van et al., 2012; Aldridge et al., 2012). The model can implement the inflow of fresh water and describes the development of stratification in the domain, both as a result of salinity and temperature gradients. The vertical tides and meteo-forcing are prescribed at the open boundaries.

In the present study, the model runs were based on GETM-ERSEM (Leeuwen, van et al., 2012; Ruardij et al., 2005) and were set up to describe the North Sea and part of the Baltic (48.2–60.1° N; −7–16.9° E). The model grid was 6 nautical mile (approximately 10 km) in the horizontal, and 26 sigma-layers were used over the vertical. Open model boundaries were located at the English Channel and between the North Sea and North Atlantic. At these boundaries the surface elevation and currents were forced by data from a barotropic shelf-wide model, which in turn was forced with the Topex Poseidon altimetry data ("Topex Poseidon", n.d.). Monthly sea water temperature and salinity values according to Janssen et al. (1999) were introduced at each grid-point as initial conditions. Both the volume and salinity effects of the various rivers flowing into the North Sea were provided by local agencies (see Acknowledgements). The ECMWF-reanalysis provided the meteorological forcing ("ECMWF", n.d.). The hydrodynamic model was run for the entire duration between 1993 and 2005. From December to July of each year, the hydrodynamic conditions were stored at 45 min intervals to provide a high enough temporal resolution to describe currents during the M2 tidal cycle, which is the main tidal component in the Central and Southern North Sea.

2.2 Particle tracking module

The three dimensional Lagrangian tracer model (GITM) used in combination with the GETM hydrodynamic model was originally developed by Wolk (2003). A re-programmed version has recently been expanded upon by Van der Molen (unpubl.) with modules to allow for egg and larval development and vertical migration behaviour in similarity to the work presented in Van der Molen et al. (2007). The model describes the motion of a number of discrete particles through a 3-D velocity field. This velocity field is provided by the hydrodynamic model. The model divides the motion into an advective and a diffusive component. The advection equation is solved analytically. Turbulence is accounted for by the random walk model where the vertical diffusivity

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is calculated by the turbulence model in GETM using the Kolmogorov-Prandtl relation (Burchard and Bolding, 2002). Horizontal diffusion is here excluded from the particle drift, and the displacement of particles is therefore governed by the output of current velocities from the model. The internal time-step of 10 s is chosen to ensure accuracy of the tracer model.

2.3 Set-up of plaice model runs

Instead of selecting specific spawning grounds and periods (as was done by: Van der Veer et al., 1998; de Graaf et al., 2004; Van der Molen et al., 2007; Bolle et al., 2009), here no a priori selection has been made. This allows for more flexibility in the interpretation. The entire southern side of the North Sea and the English Channel were selected as starting points for particles. Particles were released at random over latitude, longitude, depth and time. 1 000 000 particles were released between 48.5–56° N and −5–9.5° E, between 1 December (of the preceding year) and 31 March (Fig. 1). For instance, for the Southern Bight of the North Sea, this roughly translates in approximately 5800 particles being released every week. Development rates of particles (simulating plaice larvae) were derived from Bolle et al. (2009), but no biological behaviour or active vertical migration was included in the latter stages of the particle evolution. After the final development stage, particles went into a settlement stage lasting up to 30 days. During this stage, a particle would settle if it would encounter favourable conditions. The only perquisite for a suitable settlement location was a predefined threshold water depth: when particles would flow through a grid-cell whose minimum depth (at one of the corners) was less than 10 m, then it was assumed this particle would settle. The duration of the pelagic life span of particles depends on the water temperature, as this determines the duration of the different life stages (as was the case in Bolle et al., 2009). A maximum pelagic life span (which included the settlement stage) of 120 days was imposed, at which point model runs were truncated. No mortality was incorporated.

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3 Results

3.1 Validation

Validation of the model was done by a comparison with a number of trajectories made by drifter-buoys. During the spring and summer of 2000, CEFAS (UK) released over 30 drifters in the Central and Southern North Sea. These drifters were equipped with a drogue floating at a pre-prescribed depth, which was attached to a floating buoy providing the communication with a satellite. The drogue consisted of a large cylindrical shape with a diameter of 1 m and a length of approximately 5 m. The drogue was kept at a depth of 10 m. Drifter paths lasted up to 60 days, but were all eventually truncated. This was generally due to fishing activities accidentally cutting the wire between the drogue and the surface buoy. The subsequent drift of the surface buoy was (although recorded) not included in the comparison here, as the ensuing (rapid) drift was driven by surface waves and wind, which are not included in the numerical simulations.

The present validation comparison focussed on 6 drifters released in the Southern Bight, since this formed the target area for plaice larvae drift. Additionally, only drift durations of more than twenty days were included. Certain drifter-buoys were also excluded as they drifted shoreward into areas with a water depth of less than 15 m, which would mean that the drogue might be touching the bed, affecting the drift direction and speed.

The drift trajectories were reproduced by releasing particles in the numerical model at the same time and location and at a depth of 10 m. This depth was chosen to cover both the drag-effect of the drogue and that of the surface buoy. For these runs vertical diffusion was excluded to ensure that the modelled particles remained at the same depth as the drifter-buoys.

A comparison between the drift of the actual buoys and their modelled counterparts shows that the model reproduces the general trend of the drifters reasonably well (Fig. 2). At the end of the drift, buoy positions and modelled particle locations have diverged, as can be seen by the distance between the final dot for each colour,

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and the end of the colour-corresponding line. However, there is no general trend in this divergence, suggesting that the model does not over- or under-predict the overall residual current patterns. To put the discrepancy between modelled and actual trajectories into perspective, this divergence is compared to the modelled spread of particles released in the proximity of the drifter release point (Fig. 3) Along with the single modelled particle being released at the same position and time as each of the drifter-buoys, additional modelled particles are positioned in a 10 km-wide circle around the drifter release-point. The initial distance between the central particle and the particles in the circle is chosen to roughly correspond to the tidal excursion as is displayed by the drifter-buoys. With time, the circle gets deformed, and the distance between particles in the circle and the central particle increases (Fig. 3). Significant differences between the different drifter-buoys and their modelled equivalents exist. For the buoys that cover the longest distance (blue and purple, see Fig. 2), the particles in the circle show the smallest deformation to develop over time, with the circle of particles remaining close to 0. On the other hand, the buoys that show a more complicated drift pattern (in particular red, yellow and dark blue) show a much bigger spread of the circle of particles to develop over time. Overall, however, the accuracy of the model predictions is fairly reasonable, in the sense that the maximum spread of the particles originally released in a circle is of the same size as the difference between the drifter-buoys and the corresponding modelled central particle.

3.2 Particle drift and settlement success

In the following sections, an in-depth investigation into the hydrodynamic causes of inter-annual variability in larval transport and settlement success is presented. The analysis will first be applied to the numerical runs of plaice eggs and larvae for a single year (2001), followed by a comparison between the different years. The year 2001 was chosen as this year seems to be a very moderate year, not only considering hydrodynamic conditions (for a comparison with SST values for other years, see: Van der Veer

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and Witte, 1999), but also with respect to settlement success rates, as shown in data of the Balgzand area (Van der Veer et al., 2009).

In Fig. 4, the final position of particles is shown at the end of their pelagic life span (up to 120 days). Particles were released from 25 December to 6 January, in total 100 000. Particles that "settled" (i.e., reached an area shallower than the threshold depth of 10 m in their final pelagic stage) are not included in this figure as their drift was truncated prematurely. The particles showed a significant displacement over this period of time. Especially particles released in the Southern Bight (black) and the English Channel (red) showed drift over a large distance. The particles drifted in an anti-clockwise fashion, especially in the Central North Sea. This conformed with the typical circulation pattern (Otto et al., 1990; Sündermann and Pohlmann, 2011). Just South-West of Dover Straight, particles showed the largest drift distance (towards NE), whereas drift distances around Doggerbank were smallest.

Particle drift directions corresponded with the residual current patterns in the North Sea according to Sündermann and Pohlmann (2011) (Fig. 4). With strong currents along the Eastern shores, particles were propelled further along that side of the North Sea, than for instance North of Doggerbank, where current patterns and particle drift distances were both close to zero.

Settlement success was not only dependent on the particle drift direction, but also on the particle development (Fig. 5). Settling particles mainly occurred along the coastlines of the North Sea, but also in the central parts of the Southern Bight and the English Channel. Additionally, pie charts show the percentages of different outcomes of the numerical simulations: Prolonged development inhibiting particles to reach settlement stage (red), only occurred in the German Bight. However, also large parts of the Central North Sea (for at least a period of time) contained particles with reduced development rates, as these only reach the beginning of the settlement stage (orange), limiting the duration over which a particle could drift into a suitable settlement location. The geographic variation in the success rate of a particle reaching the settlement stage closely corresponded to the water temperature (van der Veer and Witte, 1999). The

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lowest temperatures were occurring in the German Bight and along the Danish Coast, the same area where particles did not reach settling stage due to their prolonged development. The highest water temperatures occurred in the same area (English Channel) where all released particles reach the end of the settling stage before the 120 day model-run duration ends. Note, however, that the particle development took place during the entire particle drift, and that therefore particles may pass through a range of water temperatures in space and time.

The geographic origin of particles that settled in the different coastal zones can be seen in Fig. 6. The coastlines around the Southern North Sea and the English Channel are divided into different zones. Particles settling in the Western part of the Wadden Sea (the red part) originated for a large part from the Southern Bight. A clear divide can be seen between the origin of particles settling in the Western Wadden Sea and the North Eastern Wadden Sea (light blue). Particles released in the Dutch coastal zone generally settle in the Western Wadden Sea, whereas particles released only slightly further offshore, drifted into the German Bight before settling. This principle also applied to the other continental coastal areas.

4 Inter-annual variability

Numerical runs were carried out for the years 1994 to 2005. Some characteristic values for all the different years will be compared, but initially a comparison between two extreme years (1996 and 1998) and the "moderate" year (2001) presented previously will be discussed.

The overall displacement of the particles released around 1 January 1996 and 1998 showed significant differences (Fig. 7). The particle drift direction of 1998 was roughly the same as that presented for 2001, mainly towards the North East along the Eastern shores of the North Sea and in the English Channel. In 1996, no clear overall drift direction could be observed. There was only a very small portion that showed a similar trend to that of 1998 and 2001, located around the Dover Strait. Particles released in

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the Central North Sea seemed to drift towards the West and North West, instead of towards the North East (as occurred for 1998 and 2001). Drift distance was also very different for both years, with 1998 showing bigger drift distances than 2001, while these were significantly reduced for 1996. Both the changes in drift direction and distance were the result of significantly different residual current patterns for 1996 in comparison with 1998 (with 2001 being similar to 1998) (Fig. 8), with a reversal in 1996 of the residual currents around Doggerbank and East of Denmark (not shown).

The different drift directions in 1996 resulted in very different settlement success levels (Fig. 9). A very large portion of particles across the Southern and Eastern parts of the North Sea did not reach the settlement stage (within 120 days), and particles did not reach the end of the settling stage in the entire North Sea. Much smaller numbers of particles released from the Southern and German Bights settled compared to both 2001 and 1998. Not only were the currents in 1996 very different from 2001 and 1998, also the water temperature was much lower. The inflow of warm English Channel water was significantly reduced while the cold water patch in the German Bight and along the Danish coast was chilled and expanded across the Central North Sea, resulting in the slow development experienced by particles released in these areas. The SST distribution in 1998 was similar to that of 2001, with only a slightly increased SST across the model domain. The result was that almost all (except in the most Easterly parts of the German Bight) particles reached both the start and end of the settlement stage. In comparison with 2001, 1998 showed a very similar distribution of successful settlement of particles.

The intern-annual variability in currents and water temperature caused not only changes in settlement success but also in location of settlement (Fig. 10). Along the Eastern coast of the UK and in the English Channel, the settlement locations of particles was similar for 1996, 1998 and 2001. However, the origin of particles settling in for instance the Western part of the Wadden Sea (red) changed significantly over the years. In 1998, particles released from the Eastern part of the English Channel reached this settlement area (similar to 2001), whereas in 1996 the origin of particles settling

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here was restricted to the settlement area itself and along the Holland coast. Additionally, the increased currents experienced in 1998 (compared to 2001), increased the number of particles settling along the Northern shores of Denmark and along Norway: in 2001, a collection of particles released just North of the Dutch Wadden Isles would settle in the German Bight and along the Danish Coast; in 1998 such a plume could not be seen and particles released only slightly further offshore, now reached the Norwegian Trench (shown in orange).

The final status of each particle was grouped in different outcomes for each year separately in Fig. 11. The total number of settling particles showed only limited variability, while the number of particles with truncated development (shown in orange and red) showed a strong variability over the years, which could be linked with hydrodynamic conditions. Lower sea surface temperatures (Fig. 13) generally coincided with increased numbers of particles that do not reach (the end of) their settlement stage.

Closer inspection of the number of particles that settled in the different zones (as shown in Fig. 6), showed that the largest number of settling particles did so in the English Channel (Fig. 12). As the particles were released at random over space (including depth), a significantly large portion of particles was released in the (relatively deep) English Channel. The inter-annual trends in settling numbers for each zone illustrated that the number of settling particles along the North Sea coast of the UK (dark blue) and the English Channel (black) was reasonably constant, with the majority of the variability originating from the particles settling along the Eastern shores of the North Sea (yellow, red, light blue and orange). These settlement zone characteristics roughly coincided with increased numbers of particles that show truncated development, as shown in Fig. 11.

Water temperature in the Western part of the North Sea (station b) showed less variability over the years (Fig. 13), as the residual current patterns (and therefore also variations in this) generally resulted in temperature effects along the Eastern shores. This was also (partially) the reason for the more constant number of particles settling along the UK's North Sea coast. Similarly, the higher temperatures recorded in the En-

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glish Channel (station d) resulted in all particles reaching the end of their settling stage in this area, therefore also (partially) explaining the reasonably constant settlement numbers in this area over the years. Wind and current conditions also influenced particle settlement success. In general, years with increased numbers of particles settling along the Eastern North Sea shores (specifically 1998, 2000, 2002, 2004 and 2005 see Fig. 12) coincided with strong Eastwards directed winds, similar to those observed for 1998 (shown in Fig. 8). On the other hand, years with small settlement values for the most northerly settlement areas (shown in orange, in particular 1997, 2001 and 2003) generally coincided with smaller than normal residual currents in the north and overall reduced wind speeds.

4.1 Settlement in the Western Wadden Sea

The Western Wadden Sea forms one of the main nursery areas of plaice juveniles in the North Sea basin (Zijlstra, 1972). he characteristics and origin of particles settling in this domain is presented in Figs. 14 and 15. The settlement area that is considered to represent the Western Wadden Sea, geographically roughly encompasses the Marsdiep-Vlie inlet system, although with the coarse model grid used in these runs, neither can be distinguished here. To compensate for this coarseness the settlement domain was chosen to partially encompass the neighbouring North Sea as well (black box in Fig. 14a, c, e). Please note that, as was previously the case, the settlement domain is further limited solely to grid cells where the water depth of at least one grid-point is below 10 m.

In Fig. 14, a link between the origin of particles settling in the Western Wadden Sea, and the relation between the release and arrival times in this area ware investigated for the three specific years already discussed in Sect. 3.3. The variability in origin of particles settling in the Western Wadden Sea was strongly dependent on residual currents, and showed great inter-annual variability, as was discussed in the previous section. However, also the moment of settlement in this area was strongly variable. In 1996, low water temperatures prolonged particle development, and only after day 145, particles

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started to settle in the domain. These particles were released around day 25, meaning that the particle drift duration lasted the 120 day maximum. This was in strong contrast with 1998 and 2001, when particles that were released during the entire simulation period settle. The distributions of release times vs. settling times for 1998 and 2001 showed two edges. The straight edge at the top corresponded with the maximum drift duration of 120 days. The bottom edge was curved, and is linked to the development rate of the particles, and therefore the water temperature. During the early stages of the model simulation, water temperatures dropped, causing the particle development to be prolonged, resulting in a shorter duration over which particles could settle. With the gradual increase of water temperatures in spring, development accelerated, and particles could settle earlier. Under extremely cold conditions (as happened in 1996) the temperature related bottom-curve cut through the 120 day limit, inhibiting any particles to settle for the duration of this colder period. There was a rough sorting through the settle time in the origin of particles: in 1998 and 2001, particles from the Dover Straight and English Channel (shown in different shades of yellow in Fig. 14) generally arrived during the start of the year, whereas particles that originated from close to the settlement domain (purple and blue) mainly arrived in the second half of the modelled period. Another remarkable feature was that the particles released close to the settle area (blue) settled after the shortest drift duration (release time – settle time). Another feature that could be observed in the drift-duration plots (right hand side of Fig. 14) was the grouping of settling particles at certain moments in time. During periods of several days very small numbers of particles settled, whereas at other moments particles released from a broad range of release times settled all at once (for instance just before day 160 in 2001, particles settled that were released from day 40 until day 90). Only occasionally the right conditions seemed to force large numbers of particles to drift into suitable settling areas.

A comparison over all the modelled years of the settle times and drift durations can be seen in Fig. 15 where the maximum drift duration of 120 days is presented as a vertical edge in the distribution, while the diagonal distribution edges at the bottom (clearly

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visible for for instance 1995 and 1998) and top (visible for all years) corresponded with the start and end when particles were released. Using the same colour coding of the dots as in Fig. 14, the features observed for the three years studied above can be recognised for most other years. The arch in drift duration during the colder spring period shifted over the years. This shift corresponded well with the surface water temperatures observed in Fig. 13 (especially for station c and d). The origin of particles also varied over the years, with particles in 1994 and 1995 (dark yellow) originating furthest away, well into the English Channel. The particles originating from the area closest to the settlement domain (in blue) seemed to settle after the shortest drift duration, but only when water temperatures had increased to enable the particles to reach their settle stage early (which generally occurs after around 130 to 140 days). Prior to that, particles released further South, experienced warmer temperatures promoting faster development and earlier settlement.

4.2 Sensitivity analysis

In the previous numerical simulations, various settings were used whose impact on the particle success rate is investigated in the following section.

Firstly, a 10 m depth limit was chosen to define the boundaries of suitable settlement areas (for at least one corner of the grid-cell). The effect of changing this threshold on settlement levels not only show an increase in the total number of settling particles, but also indicate a shift in importance of different settlement areas (Fig. 16). Settlement in the English Channel (black) was relatively constant for different settlement depths. The depth in this region was in general significantly larger than in the other areas. In 1996, the settlement in the Southern and Eastern Bights of the North Sea was non-existent, as the particles were released in a very cold period, truncating their development (see Sect. 3.3). Additionally, the settlement along the English coast (dark blue) showed a (relatively) abrupt increase in settling particles, when the settle depth threshold was increased from 15 to 20 m, which is caused by the Doggerbank coming into play, then also becomes a suitable settlement area. All other areas showed a more constant

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increase in the number of settling particles, with the increasing settlement depth. The increasing settlement depth forces the boundaries of the settlement areas gradually outwards, enabling particles that drift further offshore to settle.

In this research, the hydrodynamic conditions were updated every 45 min. This value was chosen to give a high enough temporal resolution to describe the M2 tidal cycle. However, in other particle tracking publications, larger hydrodynamic update intervals are generally used (Van der Veer et al., 1998; Hufnagl et al., 2013). The impact of larger hydrodynamical time-steps, was evaluated by reproducing the drifter-buoy tracks discussed in Sect. 3.1, whereby the hydrodynamic update interval was varied from 45 min to 24 h (Fig. 17), with all the values above 45 min being averages over the specified periods. In general, tracks that showed large residual currents were reasonably well reproduced for bigger hydrodynamic update intervals (not shown). However, if the residual current was less important, the coarser temporal interval caused significant differences between the different modelled tracks to develop. A low frequency of the hydrodynamic updates could be very computationally advantageous. However, by substituting the tidal motion with tidally averaged motion, even the residual drift patterns could not be well reproduced.

5 Discussion

The aim of this research was to investigate whether changes in hydrodynamic conditions alone can potentially cause significant inter-annual settlement variability of North Sea plaice juveniles whereby the focus was to investigate the influence of hydrodynamic forcing on plaice egg and larval drift patterns and not to reproduce the actual settlement demographics. The reproduction of the paths of the CEFAS drifter-buoys showed that the model reproduces the hydrodynamic conditions reasonably well. No direct comparison between plaice larvae drift patterns and numerical model results is presented here. In fact, such a comparison will face a number of hurdles, placing it beyond the scope of this paper. Comprehensive datasets combining the numbers of

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plaice eggs at spawning locations, the drift of eggs and larvae along the various transport paths, and of juveniles upon arrival nursery areas are non-existent. Quantitative field data from spawning grounds is sparse, while the drift patterns of plaice are even less well known (Talbot, 1977; Taylor et al., 2007). Field data that can be obtained most easily is that of the arrival of plaice juveniles in the nursery areas (Van der Veer et al., 2009). Given the uncertainty about plaice spawning areas, numbers and times, and only very sparse data from the egg and larval drift, the numerical simulations can only be linked with settlement data (as was done by for instance Bolle et al., 2009). However, if structured cruise data of egg and larval abundance are available, presence-absence maps can be compiled and compared (van der Molen et al., 2007). However, assumptions have then to be made about spawning and drift of plaice eggs and larvae.

5.1 Selection of spawning grounds and periods

In the present paper, particles were released across the entire Southern and central North Sea, and also encompassing the English Channel (similar to Hufnagl et al., 2013). Studies of egg abundance in the different parts of the study domain have shown a strong variability in egg abundance over the different areas, as well as over the years (Taylor et al., 2007; Loots et al., 2010). There is some sorting in spawning areas within a year; in the English Channel spawning can already occur in December, whereas the maximum spawning in the German Bight occurs around February and lasts into March (Bergman et al., 1988). In the present set-up, limits could be placed with respect to specific spawning grounds and periods (cf. De Graaf et al., 2004; Bolle et al., 2009). However, the variability over the years as well as the uncertainty in the location, start time and duration of the different spawning periods in the different parts of the North Sea mean that any limits on these cannot be prescribed based solely on hydrodynamic circumstances, which would inhibit the original aim of this research.

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5.2 Vertical migration

To investigate the pre-juvenile drift of fish eggs and larvae, a particle tracking routine may be used that combines hydrodynamic forcing conditions and active behaviour, such as vertical migration, to describe the drift of particles from spawning grounds to nursery areas. With respect to plaice larvae, several studies have been carried out where, during the latter stages of pre-juvenile evolution, it is assumed that plaice show a tendency to migrate vertically over the water column, either in a daily frequency (Rijnsdorp et al., 1985), or over a tidal cycle (de Graaf et al., 2004; Fox et al., 2006; van der Molen et al., 2007; Fox et al., 2009; Bolle et al., 2009; Hufnagl et al., 2013). The latter will cause plaice larvae to be able to drift faster when the tidal current is towards suitable nursery areas and reduce the backward drift, when the tidal flow is opposite. The overall impact of vertical migration on the particle drift might be limited as it only occurs during the brief latter stages of particle development (Bolle et al., 2009). However, the impact on the numbers of juveniles successfully settling in a certain domain can be significant, as particles that would otherwise drift too far offshore of the settling area, will now be able to drift towards it (de Graaf et al., 2004; Fox et al., 2006). The presented results show a very strong short-term variability in the numbers of particles arriving in a nursery area. These intra-annual changes in settling figures are forced by local changes in (residual) current patterns. Residual current patterns are however significantly smaller than the tidal currents, and active vertical migration would most likely result in a reduction of these intra-annual fluctuations and cause a more constant flow of particles to settle in the settling domain.

5.3 Mortality based on predation and food abundance

In the present simulations, particles released from very different parts of the North Sea and English Channel drifted into suitable settlement areas. Without food abundance or predation included in the present runs, particle drift is only truncated when a particle settles, or because a particle reaches the end of its pelagic life span, either coming to the end of the 30 day settlement period without settling, or because of reaching the 120 day simulation limit (cf. de Graaf et al., 2004; van der Molen et al., 2007; Bolle et al., 2009; Hufnagl et al., 2013). As a result (along with the lack of spawning-ground and -period selection), most years show continuous settlement of particles for almost the entire modelled duration. A constant mortality (Van der Veer et al., 1998) or mortality based on temperature (Fox et al., 2006, 2009) could give insights into the survival rates during egg and larval stages. However, an intra-annual variability in food abundance could form an extra threshold for particle development, and survival. Expressing the changing particle development rate with regard to the particles dynamic energy budget (DEB) would form a promising way to model more realistic circumstances in which plaice eggs and larvae might evolve. Additionally, intra-annual population dynamics of predator species might give a second input towards seasonal changes in survivability rates of plaice eggs and larvae before settlement.

5.4 Temperature sensitive development

As was mentioned previously, no direct comparison between numerical simulations and field measurements of numbers of arriving plaice juveniles in the western Wadden Sea is presented, as this would involve unverifiable assumptions towards spawning grounds and periods. However, the total lack of arriving plaice juveniles in the early stages of 1996 in the numerical simulations (Fig. 14) is in stark contrast with the peak in plaice juveniles arriving in the western Wadden Sea according to field studies, however this can also partially be due to lower mortality rates in cold years (Van der Veer et al., 2000; van der Veer and Witte, 1999; Bolle et al., 2009). In 1996, the development of many particles is truncated due to low water temperatures resulting in slow particle development. The resulting lack of settlement in the western Wadden Sea is caused by slow development rates in combination with the 120 day numerical simulation limit. This limit was chosen based on limits used in previous studies (Bolle et al., 2009), and a small change (on order of 10 days) would not result in massive increases in particle settlement. However, a change in the relation between sea water temperature and the

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development rate of plaice larvae might result in accelerating the particle development, and therefore result in more realistic settlement figures in 1996.

5.5 Suitability of settlement areas

As already discussed in the sensitivity analysis, settlement areas are probably defined by food abundance (cf. Creutzberg et al., 1978) and lack of predation of plaice juveniles, whereas the boundaries of settlement areas are presently solely defined by a threshold water depth. Similar to the possibility to make a-priori a selection of spawning grounds and periods, also different nursery areas could be pre-defined based on field data. Similarly to the addition of a velocity threshold discussed in Sect. 3.5, this would not only lead to an increase in settling particles in the (more limited) number of nursery areas, but also possibly to shifts in importance of different settlement areas. In this respect the Doggerbank is a puzzling area: settlement does not seem to be successful, however transplantation experiments indicate that it could be a potential nursery area for plaice with goed growth conditions (Borley, 1919).

6 Conclusions

In this study, we demonstrate a substantial effect of physical factors alone on the inter-annual variability in the transport of eggs and larvae and their subsequent success-rate in settling. These idealised studies are not intended to explain or reproduce observations (insofar as they exist, mainly from nursery grounds). This would require that assumptions of spawning grounds and periods, mortality and possibly active behaviour (such as vertical migration) be included in the model. The present study serves therefore to give an indication of the extent of variability that can be attributed to physical factors.

Inter-annual variability in wind speed and direction cause residual current patterns to show significant changes over the years, strongly influencing the direction and distance

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of the particle drift. As a result, different years had a significant variability in the origin of the particles settling in the different nursery areas. In general, an anti-clockwise circulation in the Central and Southern North Sea could be observed, and a north-easterly drift direction when released in the English Channel. However, in years with strong easterly winds there was less drift along coastlines, and more into the central North Sea, limiting settlement chances and also giving rise to different connections between spawning areas and nursery grounds.

In combination with wind-driven current variability, the sea water temperature also varied over the years. Assuming that particle development was dependent on water temperature, differences in experienced water temperature significantly affected their success rate. With higher temperatures in early winter, late spring and summer, particle development was accelerated, and the settlement stage reached earlier, thereby reducing the distance between spawning ground and settlement area. A maximum particle lifespan of 120 days in combination with temperature dependent trajectory, meant that for some years (1996 in particular) large numbers of particles did not reach the settling stage before the end of their pelagic lifespan.

Settlement in the Western Wadden Sea showed strong inter-annual variability due to changes in the hydrodynamic conditions. Not only did the origin of particles settling in this area vary, but the general arrival time was also influenced by hydrodynamic conditions. Over each season, the origin and drift duration of particles settling in this nursery area changed: during winter, particles generally originated from more distant areas, than particles settling in the western Wadden Sea in spring and summer. The low sea water temperatures during late winter and early spring resulted in slower development rates and longer drift durations. Additionally, stronger wind conditions during winter and early spring, generally force particles to drift further. Settlement success also varies substantially as a result of temporary local conditions: for example, if the right conditions prevail large numbers of particles, whose origin can be widely variable, can be forced into this settlement area over a short period of time.

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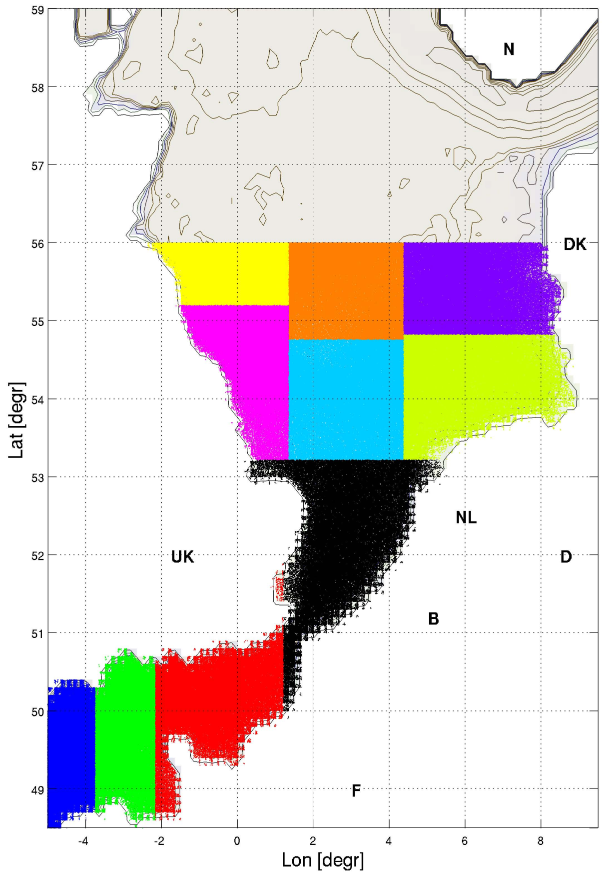

Fig. 1. Release distribution of particles for the numerical runs. Colour of the dots solely indicates the release position. Note that the area shown does not correspond with the domain of the hydrodynamic simulations, which span from 48.2–60.1° N and −7–16.9° E, and included part of the Baltic sea.

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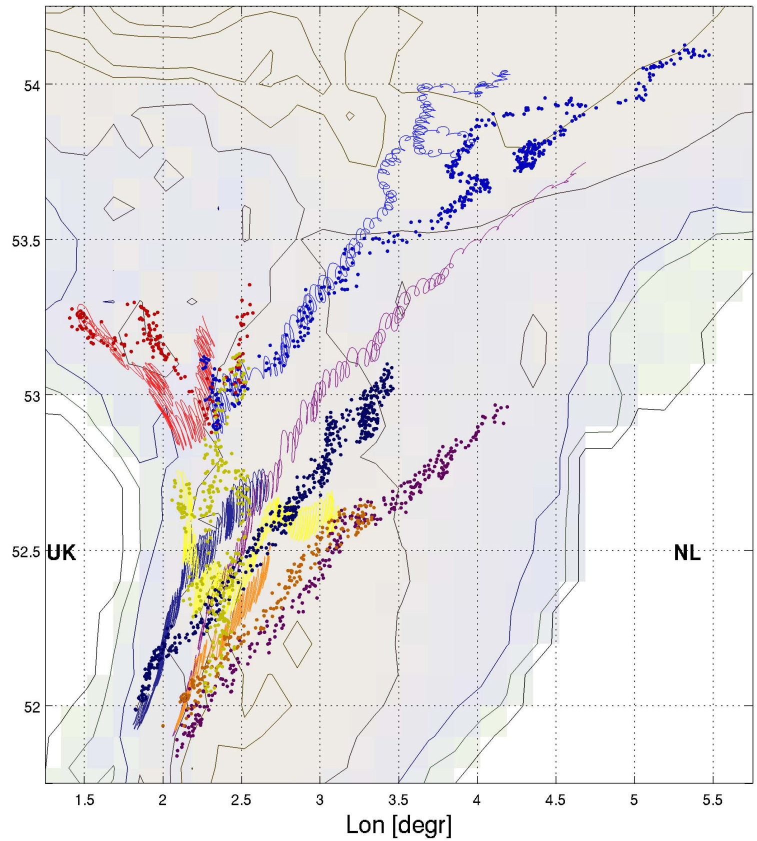

Fig. 2. Comparison between five drifter paths (different coloured dots) and modelled trajectories (shown in differently coloured lines). The starting-point of each of the drifter-buoy pairs is shown as a thicker circle, and is generally located close to the UK coast.

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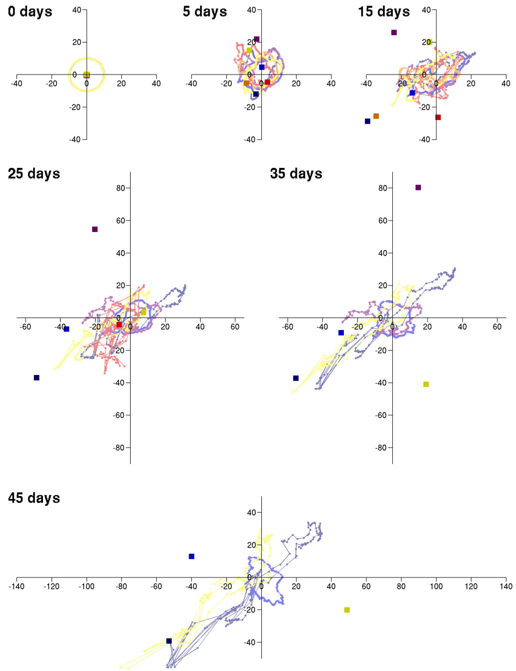

Fig. 3. At different moments during the dirfter-buoy track, the difference between the drifter path and the corresponding modelled trajectory are shown (as squares, with the different tracks shown in different colours) with on top of that the current position of particles released in a circle around the the drifter position. The x and y axis represent kilometers of spread. With time, the distance between the actual drifter position, and that of the modelled particles increases (as can also be seen in Fig. 2). The spread of particles originally released in a circle around the the central particle deforms and expands over time.

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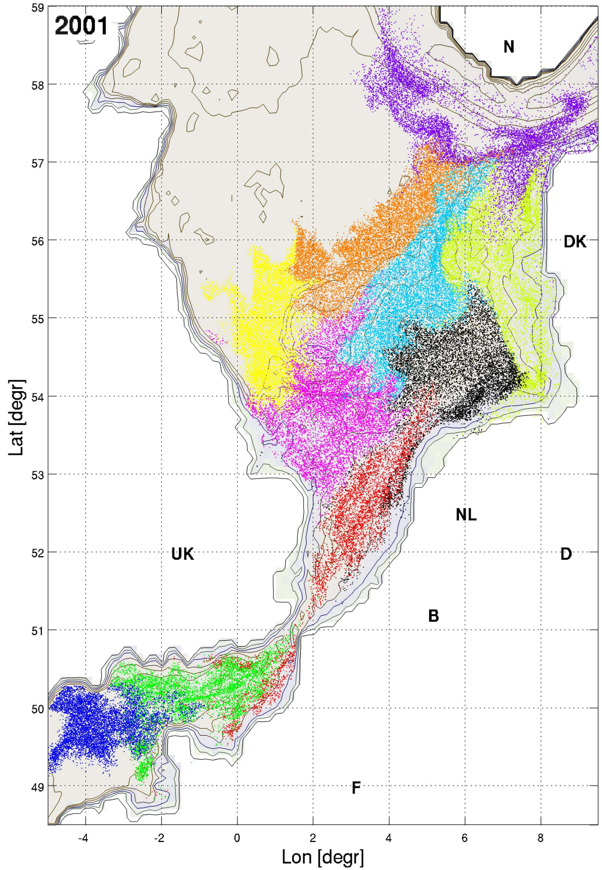

Fig. 4. Distribution of particles at the end of their pelagic life span (up to 120 days). Only shown are particles that do not settle. Only 100 000 particles are included that were released around 1 January. The colour of the dots corresponds to the release location of the particles, and is the same as in Fig. 1.

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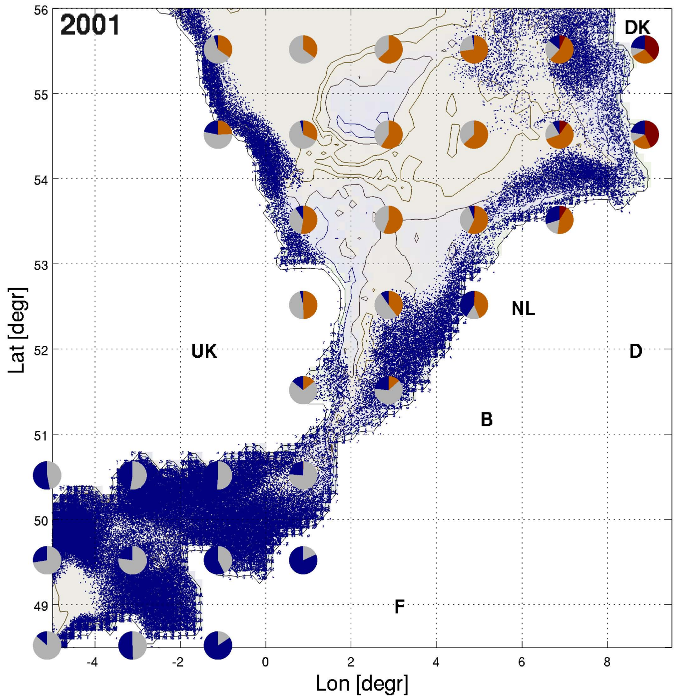

Fig. 5. Distribution of the origin of particles that eventually settle (shown in blue dots). On top of that, different pie charts show the geographic variation of the different outcomes of particle development and drift: (blue) particles settle; (grey) particles do not settle; (red) particles do not settle, as these do not reach the settling stage; (orange) particles do not settle, and do not reach the end of the settling stage before the end of their pelagic lifespan.

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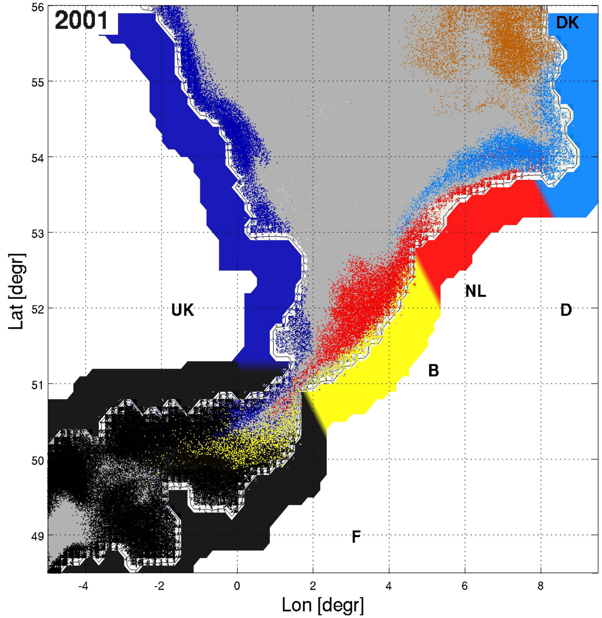

Fig. 6. Release location of particles, with the settle location shown in the colour of the dots. Additionally, the different settlement areas are indicated with a colour-corresponding band along the coastline. (grey) no settlement; (dark blue) settlement in the North Sea coastal zone of the UK; (black) settlement along the coast of the English Channel (both France and UK); (yellow) settlement in the French, Belgian and Dutch North Sea coast; (red) settlement in the Western Wadden Sea; (light blue) settlement in the Northern part of the Wadden Sea; (orange) settlement outside of the shown domain (generally along the Northern Danish and Norwegian coast). Please note that the coarse model grid does not include any Wadden Sea islands, and therefore there is no distinction between settlement on the North Sea side of these islands, and in the Wadden Sea itself.

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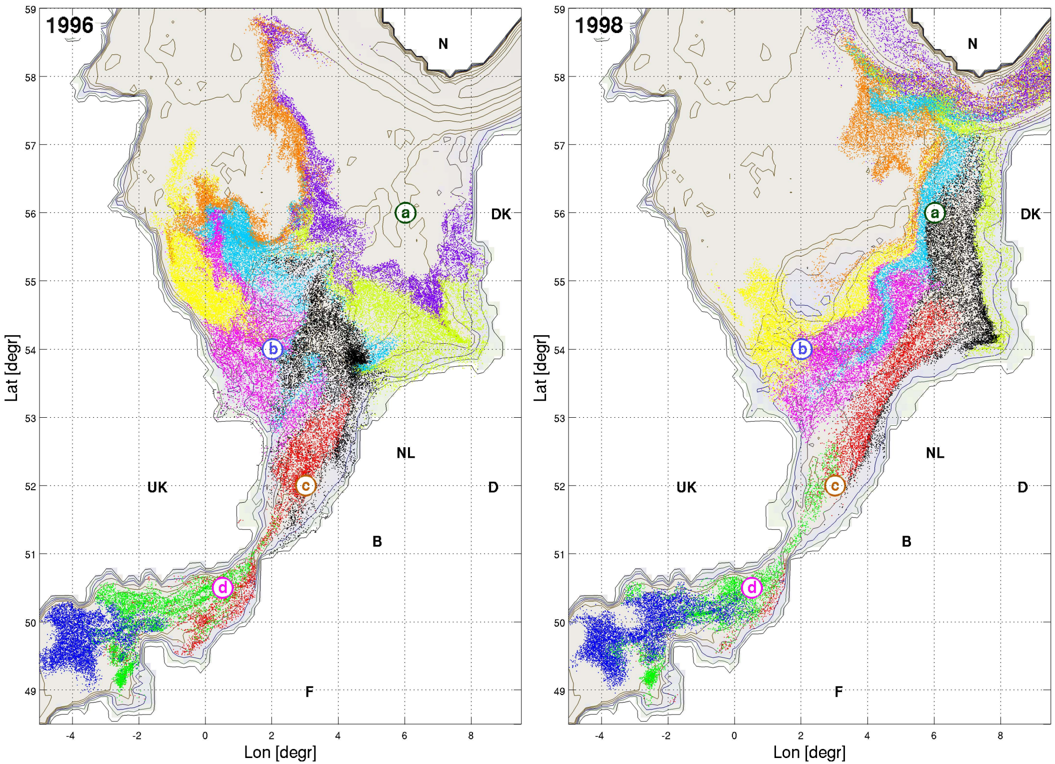

Fig. 7. Distribution of particles at the end of their pelagic life span (up to 120 days) (left: 1996; right: 1998). Only shown are particles that do not settle. Only 100 000 particles are included that were released around January 1st. The colour of the dots corresponds to the release location of the particles, and is the same as in Fig. 1. Locations "a" to "d" correspond to data shown in Figs. 8 and 13.

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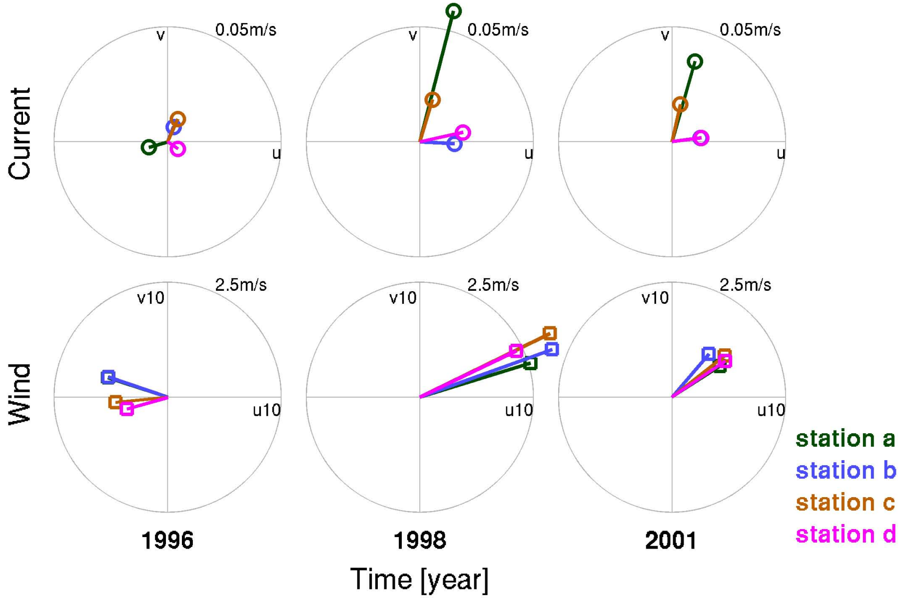

Fig. 8. Averaged current and wind speed and direction at the different stations (see Fig. 7) for 1996 (left), 1998 (middle) and 2001 (right). The currents were averaged over the 8 months over which the particle drift was computed, starting with December of the previous year, while finishing with July.

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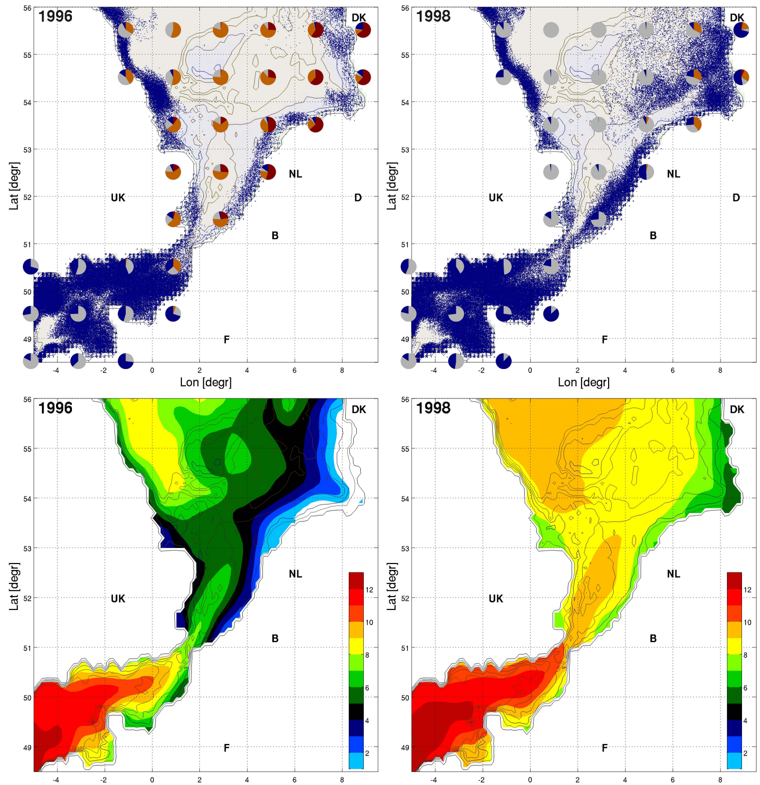

Fig. 9. Inter-annual differences (1996, 1998) in development rates give rise to variations in settlement success. **(a, b)** Particle development characteristics (see Fig. 5 for an explanation of the colours coding); **(c, d)** Sea surface temperature in February for different years.

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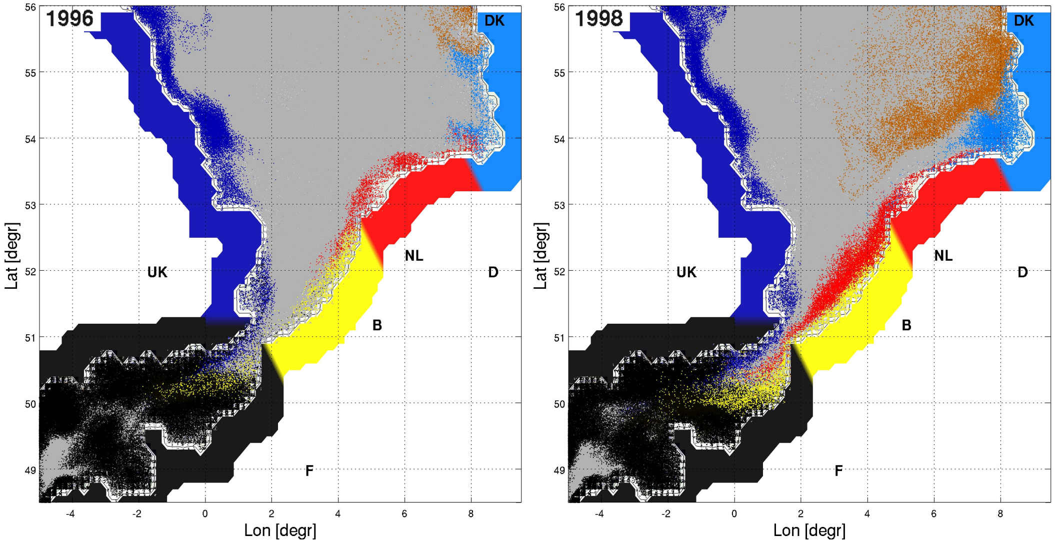

Fig. 10. Settle locations of all particles for different years (left: 1996; right: 1998) shown in the colour of the dots. For explanation of colour coding see Fig. 6.

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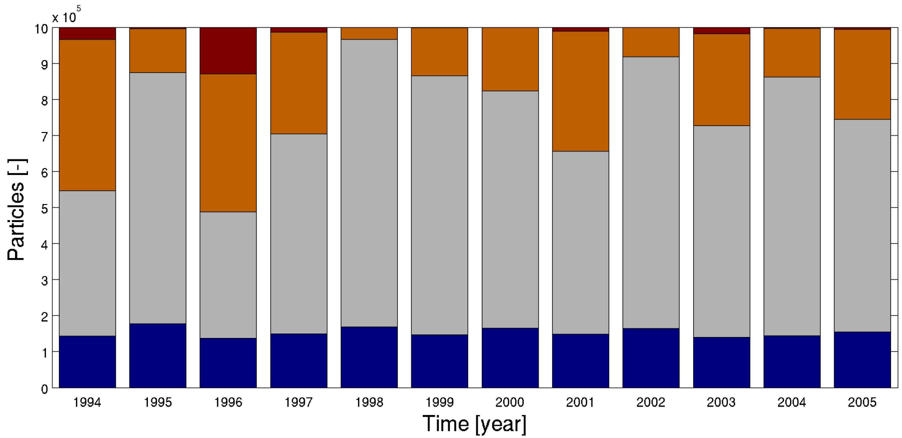

Fig. 11. Final status of all particles for each year: (blue) settle; (gray) do not settle; (orange) do not settle and do not reach end of settlement stage; (red) do not settle as these do not reach the beginning of the settlement stage.

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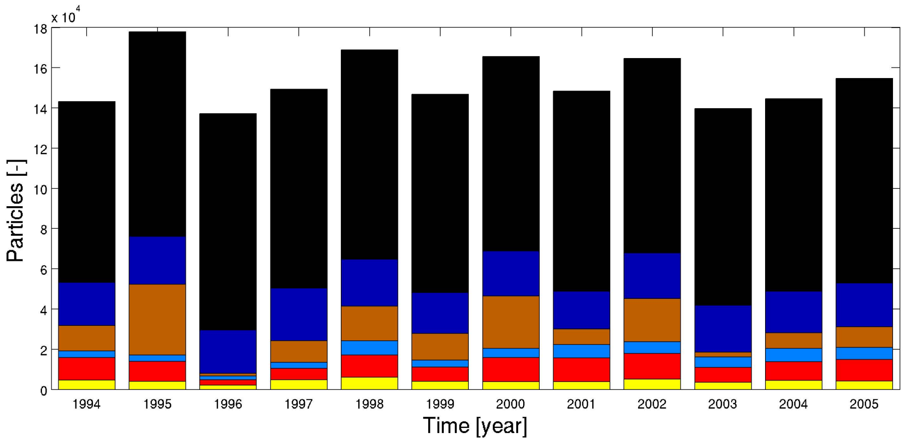

Fig. 12. Numbers of particles settling in the different coastal zones for the different years: (dark blue) settlement in the North Sea coastal zone of the UK; (black) settlement in the English Channel; (yellow) settlement along the French, Belgian and Dutch North Sea coast; (red) settlement in the Western Wadden Sea; (light blue) settlement in the Northern part of the Wadden Sea; (orange) settlement outside of the shown domain (generally along the Northern Danish and Norwegian coast).

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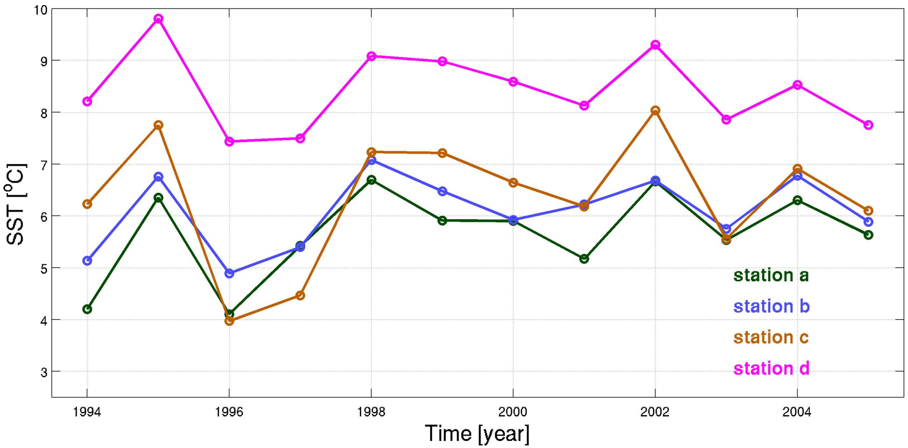

Fig. 13. Sea surface temperature for the different years of particle distribution runs, averaged over February of each month. The colour of the lines represent the different stations as presented in Fig. 7.

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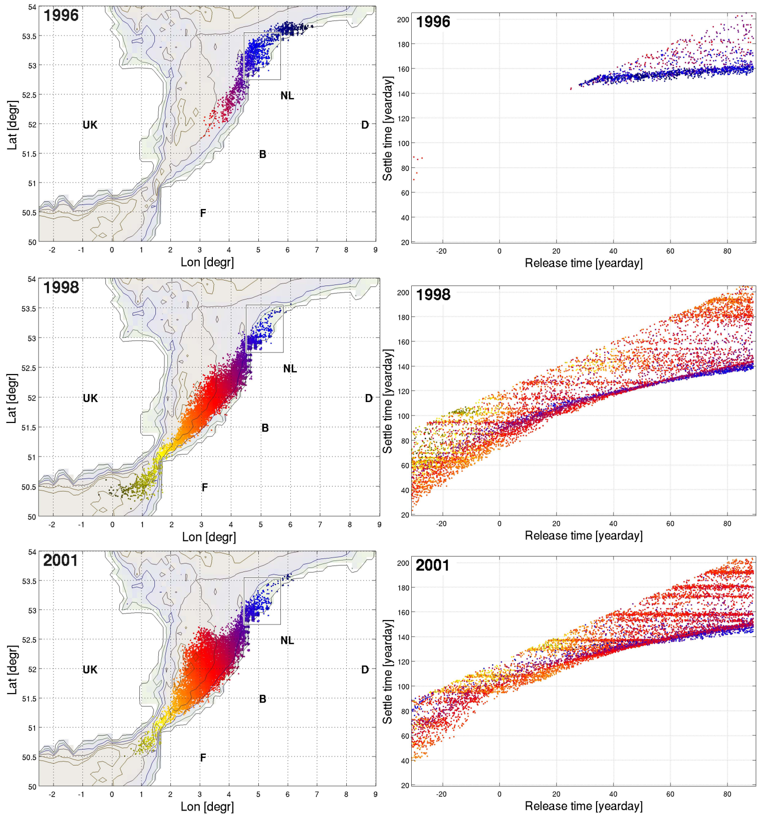

Fig. 14. Particle settlement in the Western Wadden Sea. **(a, c, e)** Release position of particles settling in the Western Wadden Sea (shown as a black box). The colour of the dots represent the release position of the particles. **(b, d, f)** The drift duration, presented as the link between the release time and settle time of the particles. Colour coding is the same as in **(a, c, e)**. **(a, b)** 1996; **(c, d)** 1998; **(e, f)** 2001.

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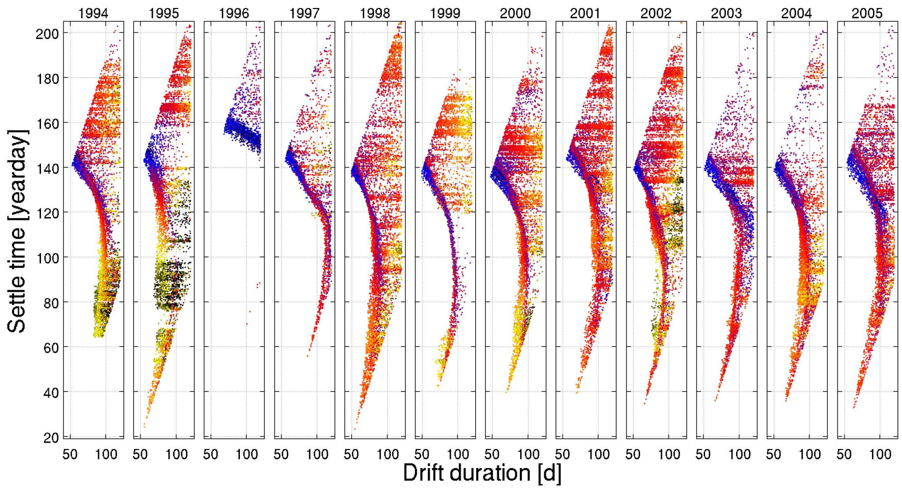

Fig. 15. Drift duration and settle time of particle settling in the Western Wadden Sea for the modelled years. Colour of the dots represents again the distance from the settle location, and is the same as in Fig. 14.

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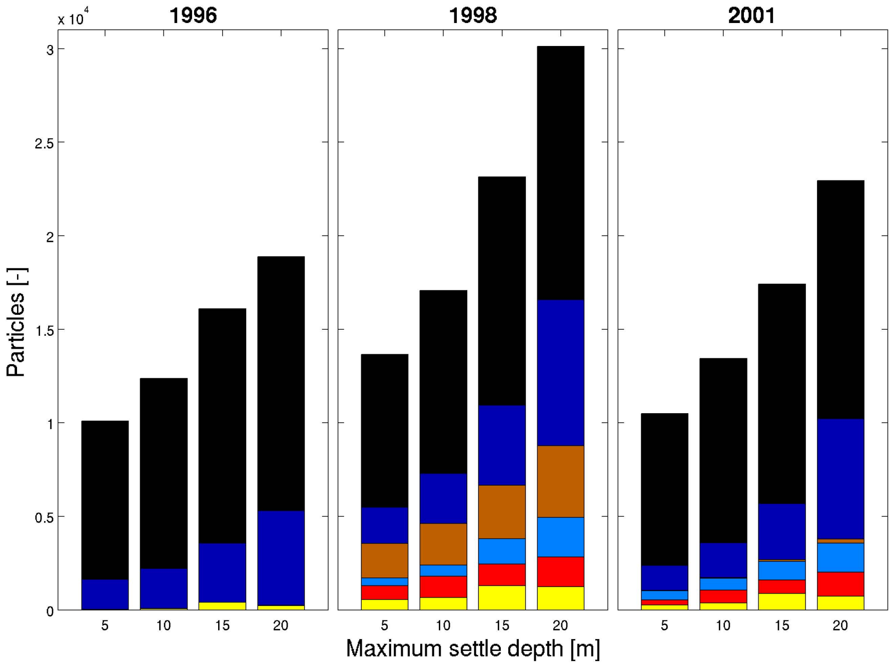

Fig. 16. Settlement into the different areas as shown in Fig. 6, for different maximum settle depths. Only 100 000 particles released around 1 January, are taken into consideration (similar to Fig. 4).

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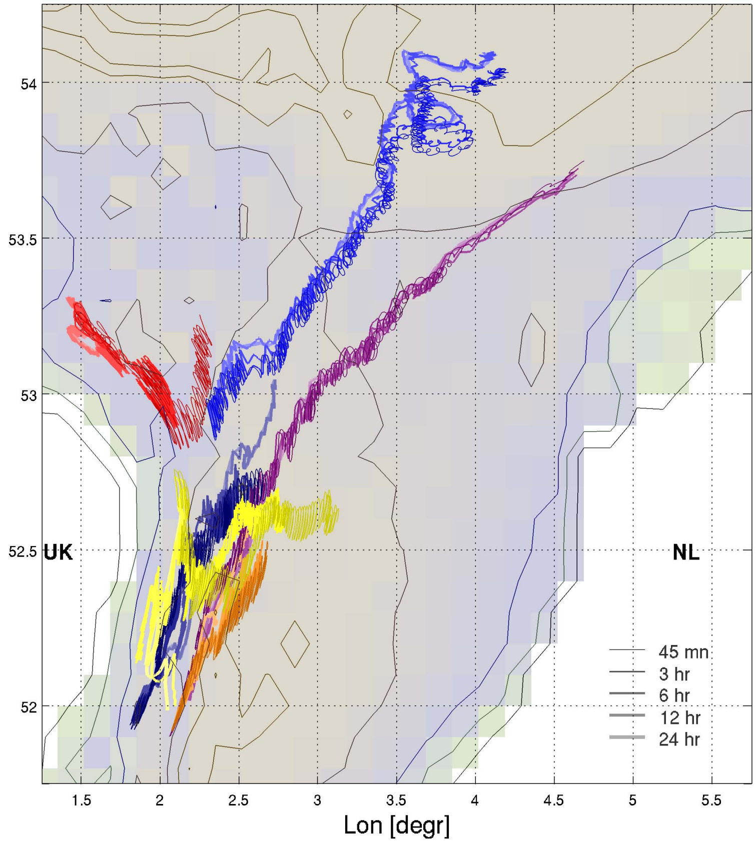

Fig. 17. The effect of altering the hydrodynamic forcing time-step on the particle drift paths, reproducing the drifting buoys (discussed in Sect. 3.1). In the particle tracking routine, the hydrodynamics were updated every 45 min, every 3 h, 6 h, 12 h and every 24 h. These update intervals are shown in the thickness and darkness of the lines, while the colour of the lines correspond to the different drifter-buoys (as presented in Fig. 2).

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