Environmental Fluid Mechanics **4:** 305–331, 2004.

Stratification and Tidal Current Effects on Larval Transport in the Eastern English Channel: Observations and 3D Modeling

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Received 30 January 2003; accepted in revised form 27 January 2004

Abstract. We study how the combination of tides and freshwater buoyancy affects the marine organisms accumulation and horizontal transport in the ROFI system of the eastern English Channel. The Princeton Ocean Model coupled with a particle-tracking module is used to study the migration of fish eggs and larvae under different forcing conditions. Results of modeling are validated against observed concentrations of Flounder (*Pleuronectes flesus*) larvae. Numerical Lagrangian tracking experiments are performed with passive and active particles, representing sea-water organisms. Passive particles are neutrally buoyant whereas active particles are able to exercise light dependent vertical migrations equating to the swimming behavior of larvae. The experiments reveal that the strongest accumulation of particles occurs along the French coast on the margin of the ROFI. This happens because the interaction between the turbulence, the freshwater buoyancy input, and tidal dynamics, produces particle trapping and vertical spreading within the frontal convergence zone. Tides and freshwater input induce net alongshore horizontal transport toward the North. Tidal currents modulate the magnitude of horizontal transport whereas the fresh water input controls more the location of accumulation zones. Tracking experiments with active particles indicate that the vertical migration leads to a significant departure from the passive particle transport pattern. Differences lie in the shape of the particle transport pattern and the rate of the northward migration. In particular, vertically migrating particles travel slower. To find possible Flounder migration pathways, particles are released within the assumed spawning area of Flounder. The model predicts larvae drift routes and demonstrates that throughout the entire particle-tracking period the horizontal structure of the particle distribution is consistent with the larvae concentrations observed during the field experiments.

Key words: English Channel, freshwater buoyancy, larval transport, particle tracking, tides

1. Introduction

In recent years increased attention has been focused on the role of circulation in larval recruitment processes. Larvae of many species depend on currents for transport to their appropriate nursery areas. In the North Sea and English Channel, advection of larvae seems to be the crucial factor determining recruitment. The movement of

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water through the English Channel is a combined result of the interaction of astronomical tides, freshwater discharge, meteorological forcing and non-tidal sea-level changes. Due to the temporal and spatial variations of physical processes and larval abundance, sampling limitations make it difficult to interpret larval abundance data and, therefore, to discern the dominant processes influencing recruitment. As an alternative, dynamically based numerical models can be used for examining the role that various physical and biological processes have in influencing recruitment. Such models may aid in the sampling design for larval studies.

A particle-tracking model coupled with a hydrodynamic model should be particularly efficient for examining the role played by various physical processes in water and aquatic biota movement. Particle methods, with or without a random component, have already been used in coastal oceanography to display residual circulation [1], to study mechanisms influencing the transport of fish larvae [2–5], or to examine the effects of physics and physiology on the larval dynamics [6].

Particle tracking is better suited to modeling the transport of organisms where the attribution of some behavioral properties to organisms is required. This 'active' behavior can be used to match the ability of organisms to float, sink or swim in addition to the water movement.

There have been relatively few models developed that simulate 'active' organism displacements. In the framework of a 2D-model of steady cross-frontal flow, Franks [7] has investigated the mechanisms, by which horizontal and vertical patchiness of organisms may arise at fronts through retention and accumulation zones according to swimming behavior of organisms. Hill [8] has considered a transport-inducing interaction between diurnal vertical migration of marine organisms and the S_2 – period tidal currents and elucidated a strict dependence of the migration-induced transport direction upon the S_2 current phase. This allowed him to identify convergences, divergences and regions of maximum transport of diurnal migrating organisms on the northwest European continental shelf. Jenkins *et al.* [3] performed simulations using a random-walk Lagrangian particle-tracking model including several vertical migratory behaviors of the particles. They concluded that in Port Philip Bay (south Australia) the vertical migration does not influence the transport of particles.

Bartsch [9] obtained different results in numerical simulations of the drift routes of herring larvae across the North Sea. His model, although three-dimensional, included only residual advective fields and was thus unable to account for migration-tide interaction. However vertical migration of larvae was found to be significantly affected by interaction with the mean current shear.

The combination of tides and freshwater buoyancy input has not previously been considered to be implicated in the generation of marine organisms assemblages and net transport within the English Channel. In the present study, we apply a random-walk particle-tracking model to investigate the transport and to determine the dominant physical processes that influence the recruitment of Flounder (*Pleuronectes flesus*) to coastal nursery areas. Two methods are employed. First, simula-

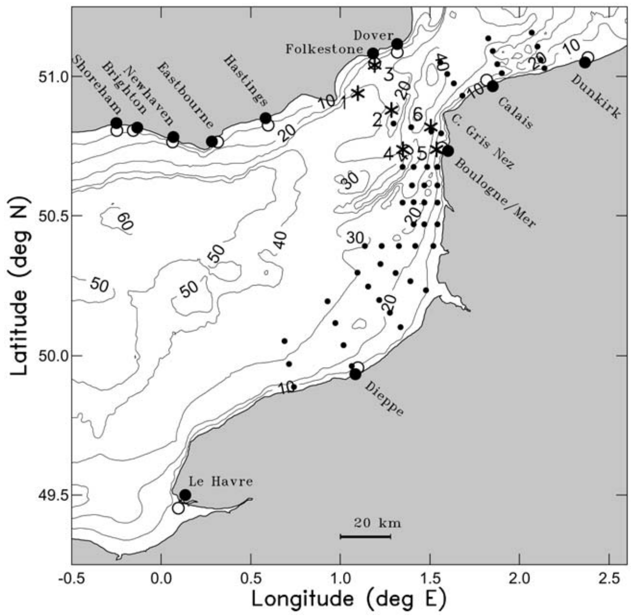


Figure 1. Domain of the numerical model with depth contours given every 10 meters. Symbols indicate locations of tide pressure gauges in ports (large solid circles), the nearest to them model grid nodes (open circles), sampling stations (small solid circles), and locations of the selected HF Radar measurements numbered from 1 to 6 (asterisks).

tions of larvae migration use only passive particles which represent non-swimming organisms. Then, we consider organisms that can swim vertically. Another relatively novel feature of the present study is the investigation of the transport pattern by means of the particle-tracking model within the region of fresh-water influence (ROFI), in the presence of a front.

The paper is organized as follows. In the next section we briefly describe the biological situation observed during two consecutive surveys in the eastern English Channel in the spring 1995. We also describe a sampling technique and analysis methods used for mapping the larvae abundance. In Section 3, we describe the model, its validation and the methodology of the Lagrangian particle tracking. In Section 4, we present and analyze particle-tracking experiments. Discussion and conclusions complete the paper.

2. Data

In the English Channel and North Sea fish eggs are found most often in spring within the central part while larvae reside in the coastal nursery grounds. The mechanisms of larvae migration and larval transport pathway from source to nursery grounds for some species have not been completely recognized until recently.

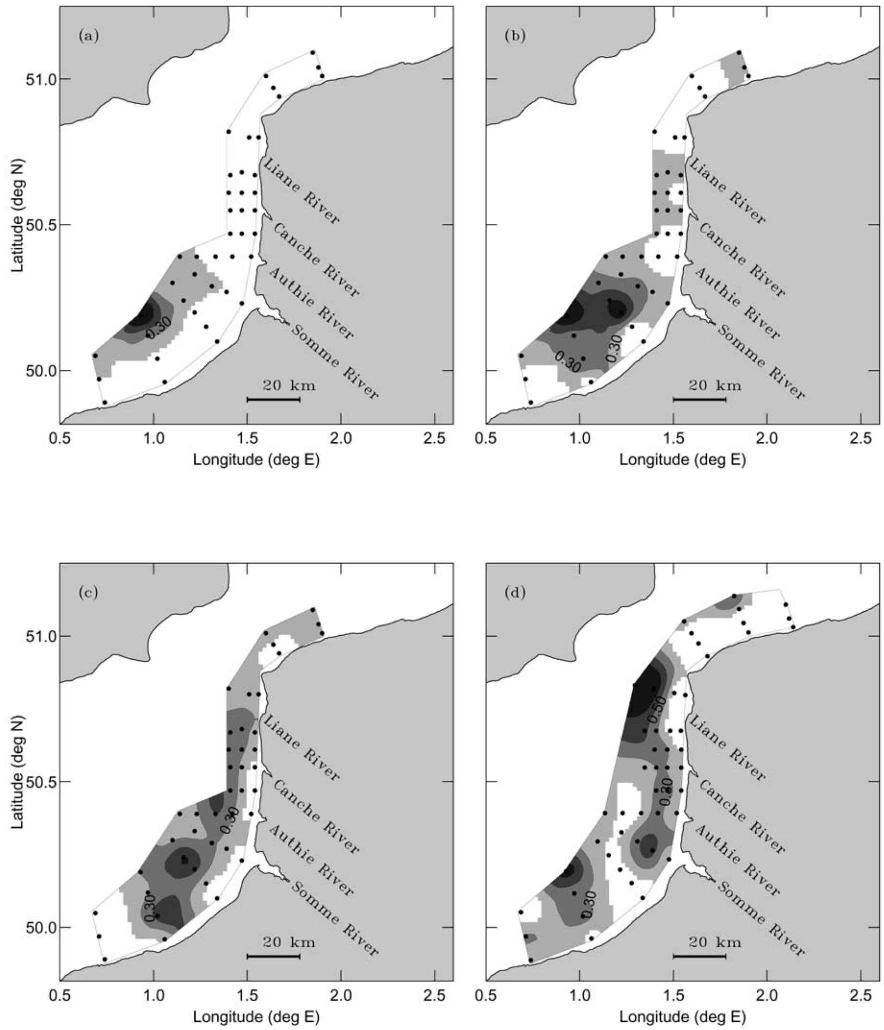


Figure 2. Contour plots of the abundance of Flounder (*P. flesus*) for different developmental stages and surveys: Eggs (a), larvae stage 2 (b), and larvae stage 3 (c) during the first survey (April 1995), and larvae stage 2 (d) during the second survey (May 1995). Values of the abundance were normalized by the maximum value for each plot. Solid circles indicate locations of sampling stations.

In April–May 1995, an extensive larval transport field experiment was conducted in the eastern English Channel. Two shipboard surveys were conducted in April 11–13 and May 2–5, 1995. Cross-shore sections were repeatedly occupied by a survey vessel in the vicinity of the French coast extending from the Picard to the Belgium coast (Figure 1). The surveys provided conductivity-temperature-depth (CTD), chlorophyll-*a* fluorescence measurements, and zooplankton and ichthyoplankton samples at each section. The measurements were interpolated spatially for the synoptic representation of the water properties and used for model validation. The temperature and salinity measurements from the far-field sampling stations were used as initial conditions for the model. No current measurements were performed during the surveys.

Ichthyoplankton was sampled using a bongo net from surface to near the bottom, with a filtered volume of 50 to 100 m^3. Flounder eggs and larvae were sorted for each bongo net, and all larvae were staged. The resultant larvae abundance was expressed in numbers per 100 m^3. In this study, the spatial structure of the abundance was obtained by data interpolation without introducing any hypothesis of patchiness. Contour plots of Flounder abundance normalized by the maximum value are presented in Figure 2.

Figure 2a shows that, in April 1995, Flounder eggs formed one patch located 40 km westward from the Somme estuary (spawning area) with the maximum abundance of the order of 10 eggs per 100 m^3. Eggs were absent everywhere else in the French coastal waters. Larvae of stage 2 (one-week old) were found also in a single patch extended in the north-east direction (Figure 2b). The maximum abundance of larvae, up to 30 larvae per 100 m^3, and the fish eggs were detected at the same location. Important variations in the spatial distribution of the larvae abundance were seen for larvae stage 3 (two-weeks old). The highest concentrations, more than 10 individuals per 100 m^3, were found within two patches located 20–25 km off-shore the French coast (Figure 2c). They showed a northward displacement along the coast. The dominant wind was N-W during the field experiments, and could not explain larvae displacement toward the north. The spatial distribution of stage 2 larvae, sampled in May 1995 (Figure 2d), suggested northward larvae migration along the French coast in the three weeks between field experiments.

In addition, fresh water inflows and meteorological data for the corresponding period were collected. The fresh water inflow varies seasonally with the highest flow during the winter/spring months (December–April) and lowest flow during the summer/fall months, showing also strong interannual variations. In this study, values of the fresh water inflow representing six rivers on the Picard and Opale coasts were extracted from National Water Resource Society data bank available at the website. The value of inflow of the Seine River was extracted from the website of the ‘Seine-aval’ national scientific project. These data correspond to the period of the field experiments conducted in April and in May.

The meteorological data comprised 3-hourly observations in Boulogne and Le Hourdel (the Somme river estuary), both situated on the French coast.

Tidal elevations required for model validation were reconstructed using tidal prediction software [10] for 12 tidal gauge locations along the French and the English coasts. The tidal constants for the principal tidal constituents were extracted from the International Hydrological data Bank (IHB).

Finally, the observed surface tidal current ellipse parameters were used for comparison with the values predicted by the model. The Ocean Surface Current Radar

(OSCR) measurements were made between May 1990 and September 1991 in the Strait of Dover [11]. A standard harmonic tidal analysis was carried out for the radar current time series yielding up to 39 tidal constituents. Tidal current ellipse parameters of M_2 constituent will be analyzed in the present study.

3. Numerical Models

3.1. HYDRODYNAMIC MODEL

The numerical model used in this study is the sigma-coordinate Princeton Ocean Model (POM) described by Blumberg and Mellor [12]. POM solves finite-difference analogues of the primitive equations in the three spatial dimensions with fully prognostic temperature and salinity fields, thus allowing time-dependent, baroclinic motion. A free surface, essential for modeling tides, is also included. The model domain used in this study is shown in Figure 1. The entire region of the eastern English Channel, including the Strait of Dover and the southern part of the North Sea, is represented by a horizontal grid spacing of 2 km. This is a region of relatively shallow depth (inside the 60-m isobath), influenced by strong tidal currents, tidal mixing, wind-driven currents, and buoyant discharges giving rise to a haline front. Small-scale features, such as eddies, filament often dominate the flow near capes.

Model depths were obtained by digitizing the existing bathymetric maps and by averaging these depth values within a circle of 2-km radius at each grid point. No smoothing was done to the ensuing topographic fields. In the vertical direction, there are 21 sigma levels, distributed such as to provide enhanced resolution in proximity of the surface and seabed. The time step, limitted by the Courant number, was set to 20 s for the external mode, and 120 s for the internal mode. A quadratic bottom-friction approximation was used with a uniform drag coefficient of 0.0025, usually adopted for the English Channel [13].

Tidal forcing with the three primary astronomical constituents, M_2, S_2, N_2, and one overtide constituent, M_4, was introduced at the open boundaries. A radiation condition, based on the long gravity-wave speed, was used to determine the boundary elevation and a forced, gravity-wave radiation condition was used to specify the normal component of the depth-averaged current at the model open boundaries, according to the method of Flather [14]. Elevations and normal velocities at the open boundaries were determined from a two-dimensional finite-element spectral tidal model, and the forcing terms for this model were extracted from the FES95.2 global tidal database [15]. To specify the depth-varying part of the normal component of velocity at the open boundaries, an Orlanski-type radiation condition was employed [16].

The model was initialized with horizontally and vertically uniform distributions of temperature and salinity. Tidal mixing within the center of the English Channel leads to vertical homogeneity of water properties. This was confirmed during the field experiments.

3.2. MODEL-DATA COMPARISON

The model was run for a 35-day period, simulating April 1 to May 5, 1995. To assess the performance of the model, tidal amplitude and phase lag, surface water elevation, surface current velocities, and salinity distribution predicted by the model were compared with observations for the corresponding period of time. We discuss below the results of two numerical experiments. For each experiment a spin-up period was allowed, 5 days for the case of tidal forcing and 10 days for the case of tidal forcing in conjunction with fresh water inflow. Therefore, results of 25-day simulations will be shown in the following model-data comparison.

Time series of simulated surface elevation were analyzed and tidal constants were extracted through least-squares harmonic analysis [10]. In Figures 3a,b, the model amplitude and phase of the M_2 tide have been plotted against the values obtained by analyzing tidal records at tidal stations along the French and English coasts. The latter values were extracted from IHB. The points are scattered about the ideal line with a standard deviation of about 9 cm for the tidal amplitude. The model appears to represent the M_2 tidal amplitude with an accuracy better than 4%. The only large discrepancy (18 cm) between observed and calculated values occurs at Dunkirk and is probably associated with the error in prescribing the boundary conditions. The scatter for the phase values is about 2.5° ($\cong$ 5 min) for the French ports and about 1.5° for the English ports. Overall, the model may be considered to represent the M_2 tidal phase with an accuracy of about 2%.

The surface water elevation as a function of time is another important parameter for model validation. The model results for 25-day period were compared with surface elevation time series at 12 tidal stations used in the previous analysis. The tidal prediction software [10] was used to simulate these surface elevation time series as the sum of four major tidal constituents (M_2, S_2, N_2 and M_4) available in the database for different ports. The comparison showed that tidal phases are in excellent agreement for all tidal stations but tidal amplitudes are not so good. The model overestimates tidal elevations for almost all tidal gauge locations with the exception of Folkestone, Boulogne and Calais. The largest rms, on the order of 0.32 m, occur at tidal stations located in the Strait of Dover and can be attributed to the non-linear interactions among various forcing functions and uncertainties in the boundary conditions. Overall, the model results may be considered to represent the synthesized tidal amplitudes to within 15% of observed values. The model properly reconstructs the major aspects of the tidal wave propagation from the North Sea and the North Atlantic into the English Channel.

To further assess the model performance, the computed tidal current velocities in the surface layer were compared with the Ocean Surface Current Radar (OSCR) measurements available in the Strait of Dover. These measurements were made by Martex Technology LTD in 1990–1991. The operating principles and performance of the OSCR system have been described in some detail by [11]. The surface current time series represent measurements made every 20 min at a number of

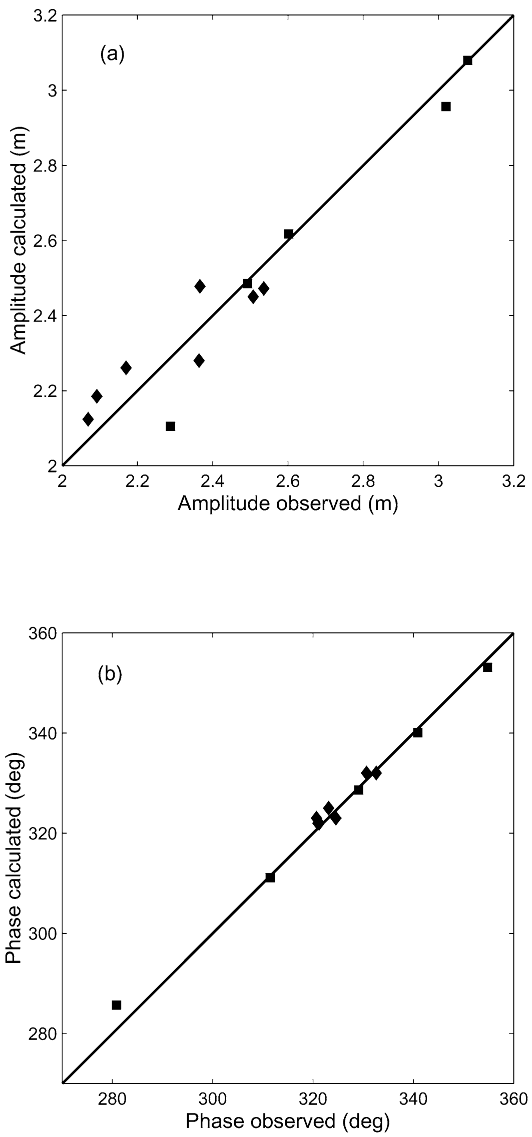


Figure 3. Scatter plot of the predicted M_2 tidal amplitude (a) and phase (b) against values observed at tidal stations in the eastern English Channel. Squares correspond to French ports and diamonds to English ports, respectively.

locations (cells) which consist of 1 km diameter circles. The number of locations was slightly more than 1000. For each of these locations a standard harmonic tidal analysis of the current time series was carried out giving 39 tidal constituents.

Figure 4 presents comparisons between modeled and observed tidal current ellipses for the M_2 tide for six selected locations. To select them, we were looking for areas with different topographic structure (e.g., sand banks, nearshore shallow

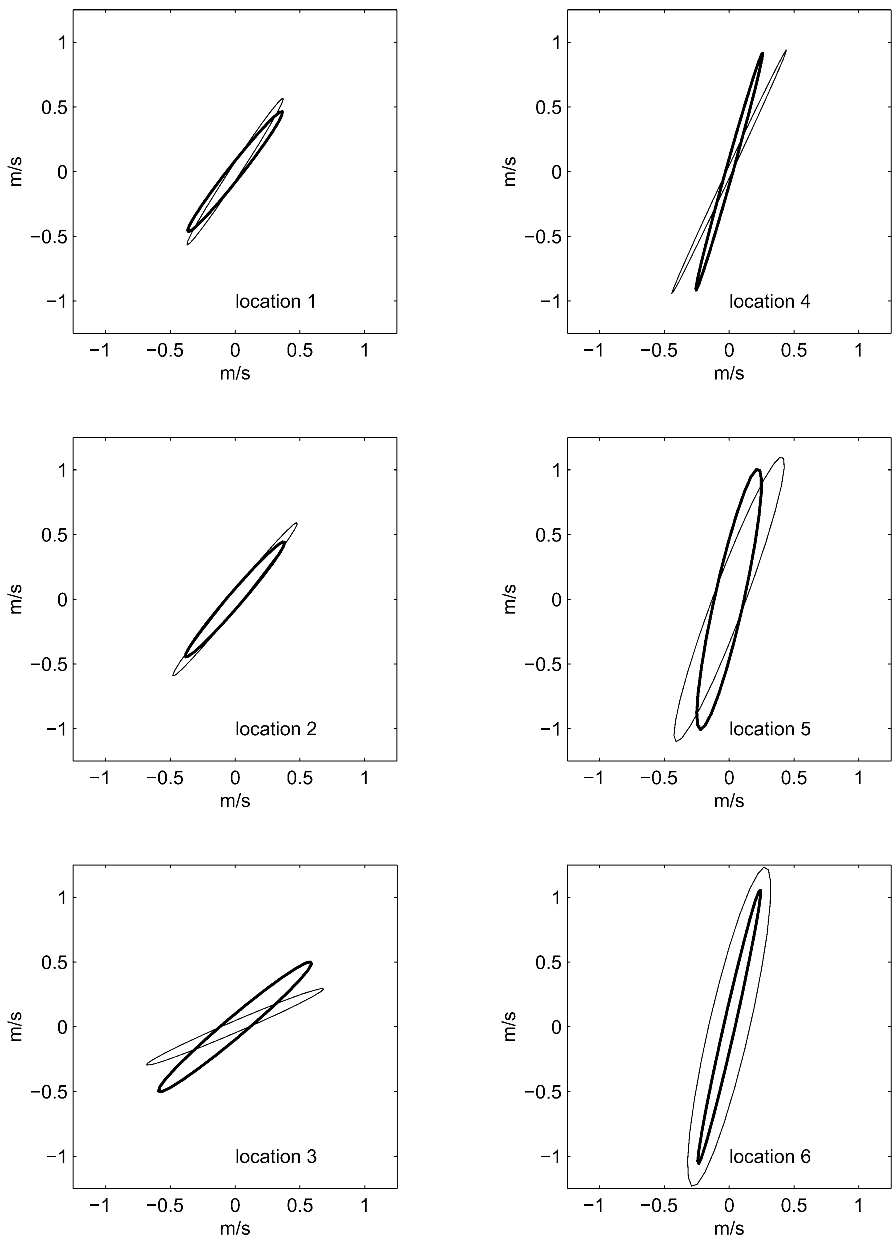
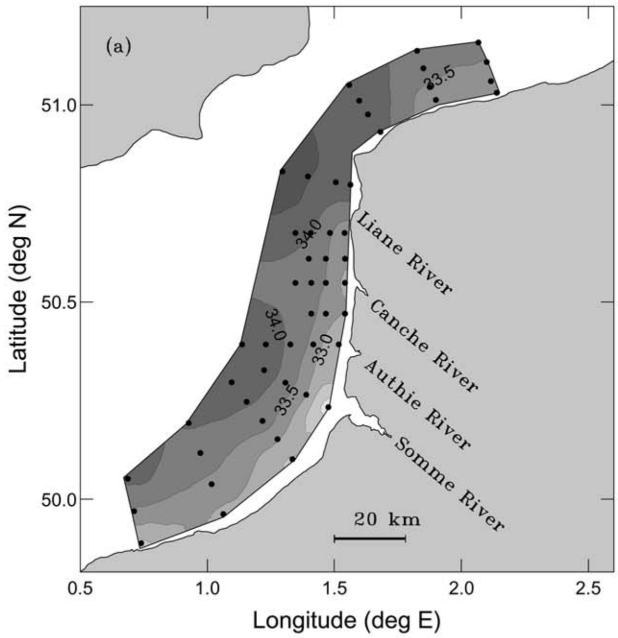


Figure 4. Comparison of model M_2 current ellipses (thin lines) and current ellipses from the HF Radar measurements (thick lines) in the surface layer at a number of selected locations. The locations are indicated in Figure 1.



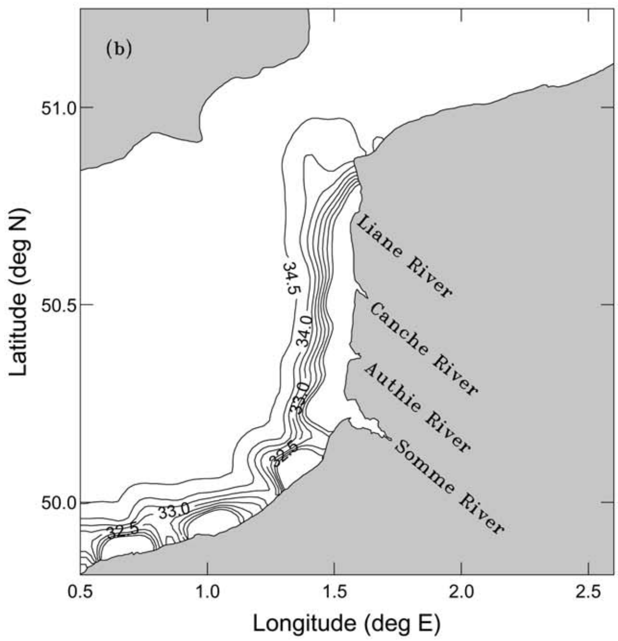


Figure 5. Surface salinity distribution from the fields experiments (a) and the model results (b) for the spring tide conditions during May 2–5, 1995.

water region, or deep water). As can be seen in this Figure, the model reasonably reproduces the velocity observations and the major features of the horizontal flow shear. It tends to overpredict the observed velocity magnitude by up to 20%, depending upon location.

In the Strait of Dover, the character of the flow changes from highly rectilinear to rotating according to water depth and geographic position. Current ellipses in Figure 4 reflect these typical situations. The first three points are located in the area between the English coast and a series of sandbanks situated in the middle of the Strait. Current ellipses are oriented along the coast and show that the flow is rather rectilinear in the major part of the area with a moderate velocity magnitude (less than 0.75 m/s). The largest discrepancy in current amplitude (0.15 m/s) was found at location 2, situated in the middle of the Strait above the Ridge sandbank.

For three other points, located between the sandbanks and the French coast, the structure of the flow varies from highly rectilinear in the area with larger depth (location 4) to mainly rotating at small depth (location 5). Peak velocities of up to 1.25 m/s indicate flow intensification near the French coast. The largest discrepancy in amplitude (0.15 m/s) and in ellipse eccentricity is found at location 6, near the Cape Gris Nez. For each location, a phase difference between the computed and the observed tidal current lies within 30°. Overall, the agreement between model results and observed surface tidal currents appears quite satisfactory.

Additional model verification was performed by comparing salinity distribution obtained from the model with observed salinity fields. For the second field experiment (May 2–5, 1995) carried out at the end of the neap tidal period, salinity in the model domain near the French coast showed spatial variations similar to the observed salinity field, with salinity differences less than 1 psu inside the domain where the data were available (Figure 5). A haline front is one of the most significant features of the eastern English Channel. It separates offshore waters of Atlantic origin from the region of fresh water influence (ROFI). The model reproduces reasonably well the position of the front and its spatial extension in the field of salinity distribution. Vertical profiles of salinity observed in April 1995 at four hydrographic stations are plotted in Figure 6a. Computed salinity profiles at the model grid points closest to the station locations (Figure 6b) show the similar vertical distribution of salinity within the ROFI. For this comparison we used stations of the third cross shore transect located South of the Somme estuary. The results of comparison of salinity profiles for other locations were also satisfactory. Generally, the computed salinity was in good agreement with data as they exhibit similar spatial variations and low-frequency variability owing to neap-spring tidal cycle.

3.3. PARTICLE TRANSPORT MODEL

The transport model used in the present study was developed on the base of the random-walk approach that is significantly more effective than the finite-difference

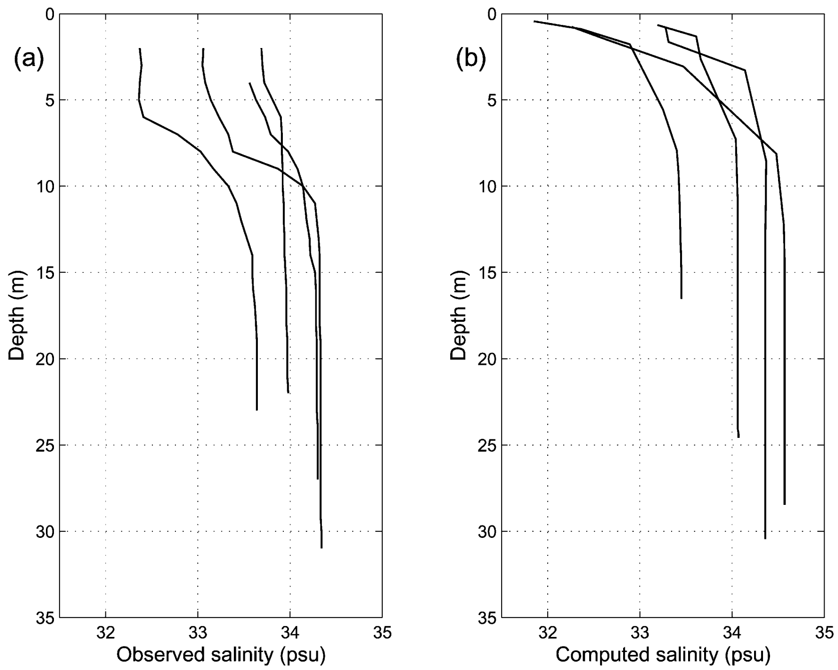


Figure 6. Vertical profiles of salinity observed in April 1995 at the stations of cross shore transect located south of the Somme estuary (a), and computed salinity profiles (b) at the model grid nodes closest to the hydrographic station locations.

method mainly in describing advection, which is the most important transport process for marine organisms. It also provides the turbulent transport of matter with the advantage being, that there is no artificial diffusion. According to Korotenko [22], displacements of each particle, moving in 3-D space, is given by the following expression:

$$(\Delta x_i)_{j,k} = V_{i,j}\Delta t_j + (\eta_i)_{j,k}(i = 1,\ 2,\ 3;\ j = 1,\ 2,\ ...,\ N_t; \quad k = 1,\ 2,\ ...,\ N). \tag{1}$$

The displacements $(\Delta x_i)_{j,k}$ are defined as the deterministic part of the motion due to the mean velocity field, $V_{i,j}$ and the random displacement, $(\eta_i)_{j,k}$ due to fluctuations of velocity and denotes the displacement of the *k-th* particle moving along the x_i – axis at the *j-th* instant of time; N_t is the number of time steps, Δt is the time step, N is the number of particles.

Particles can be launched in the model as passive or active tracers. In the latter case, a randomly distributed size or buoyancy is assigned to particles depending on the type of the simulated additive. To simulate fish larvae behavior, particles are assigned a predetermined vertical velocity matching diurnal migration.

In addition to regular movements due to the mean current velocity and their own motion, particles are supposed to be influenced by velocity fluctuations. The

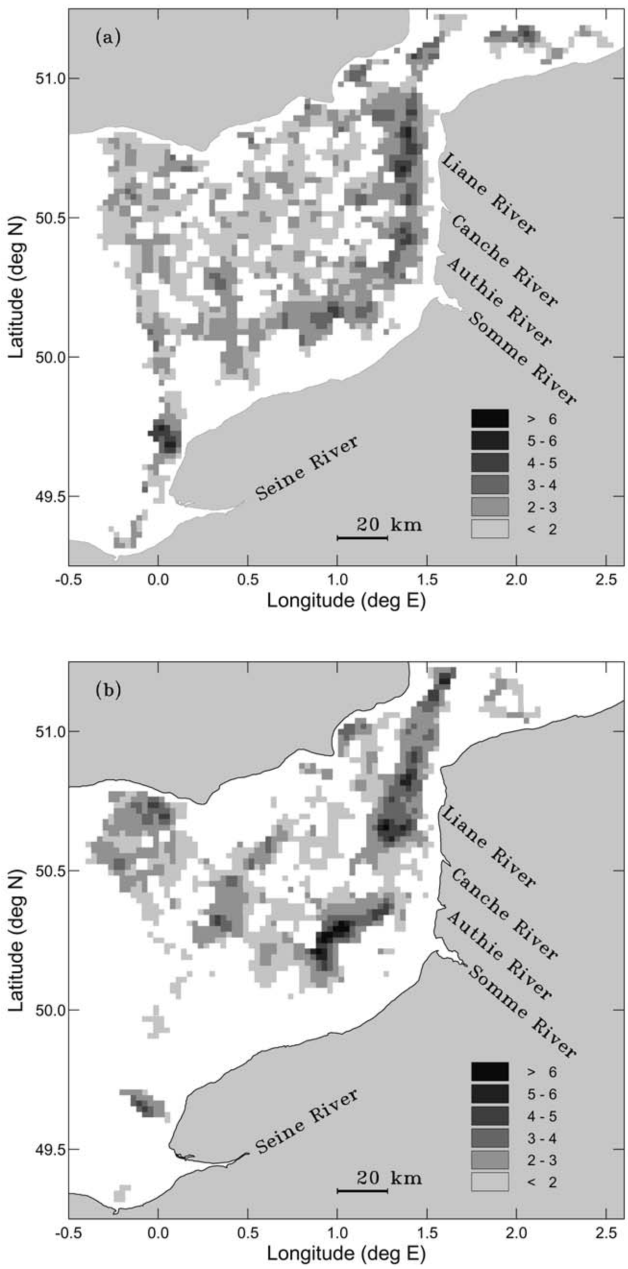


Figure 7. Number of particles in model grid boxes after 4-day tracking (a), 13-day tracking (b), and 24 days (c). Forcing terms included tides and freshwater buoyancy input. Distribution of particles after 13-day tracking under tidal forcing and no buoyancy input (d). At release, particles were homogeneously distributed over the model domain. Grid boxes with only one particle per box are not represented.

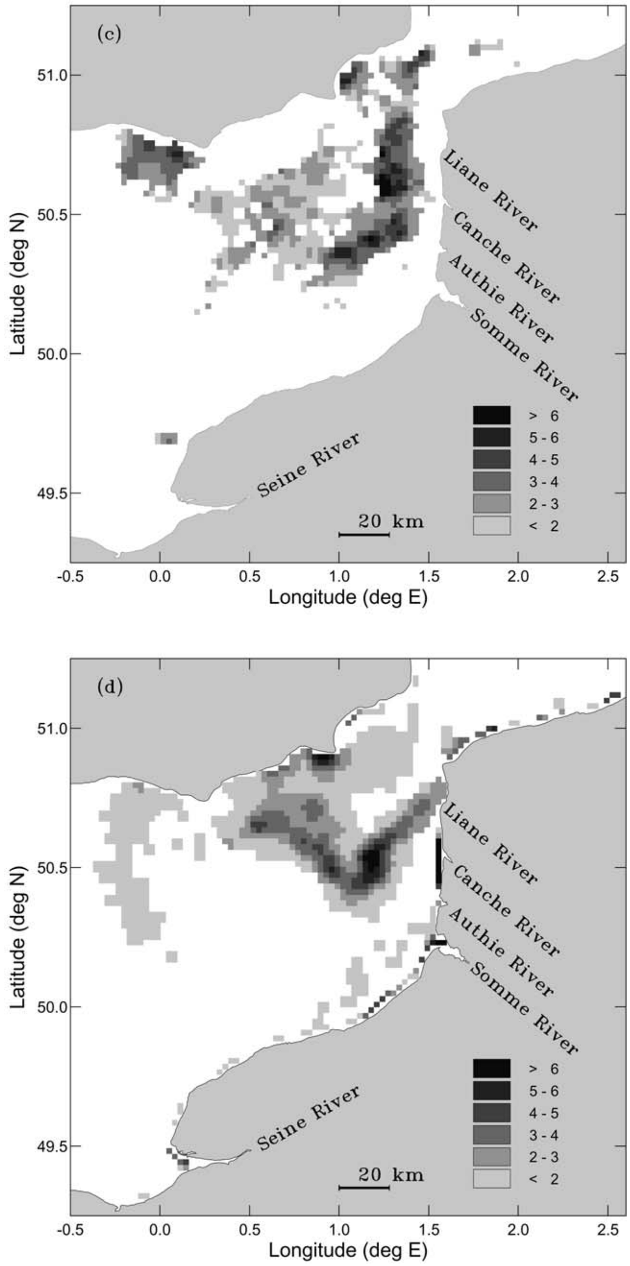


Figure 7. (Continued.)

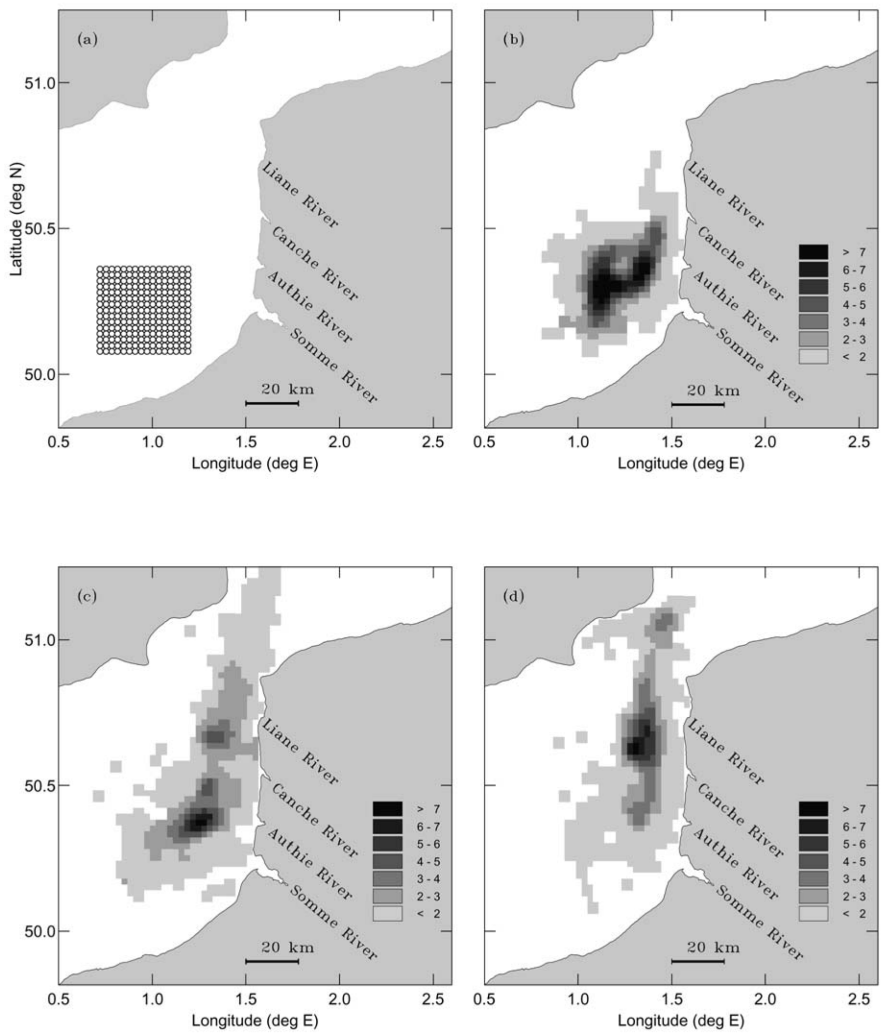


Figure 8. Initial positions for the 960 particles used in particle-tracking model (a). Number of particles in model grid boxes after one-week tracking (b), two-week tracking (c), and three weeks (d). Grid boxes with only one particle per box are not represented.

distribution law of these fluctuations is represented by the term, $(\eta_i)_{j,k}$, the latter being in general a function of time and space. The type of law for $(\eta_i)_{j,k}$ is determined by the statistical structure of deviations (fluctuations) of velocity about its mean value at each time step Δt. Since these fluctuations can be considered independent, the law for $(\eta_i)_{j,k}$ is expected to be normal [17]. In this case, the $(\eta_i)_{j,k}$ can be represented as $(\eta_i)_{j,k} = \gamma_{j,k}\left(2K_{i,j}\Delta t\right)^{1/2}$, where $\gamma_{j,k}$ is a random vector normally distributed with an averaged value of zero and unit standard deviation; $K_{i,j}$ represents coefficients of diffusion along the - axis at the time $t_j = t_0 + j\Delta t$. The random vector, γ_{ik}, is obtained by the use of the random-number generator.

The horizontal and vertical diffusion coefficients, $K_{x,j}$, $K_{y,j}$ and $K_{z,j}$, as well as the mean current velocity $U_{i,j}$ are provided by the flow model. In the present version of the hydrodynamic model, the horizontal diffusion coefficients,$K_{x,j}$ and $K_{y,j}$, were calculated from Smagorinsky formula, while the vertical diffusivity, $K_{z,j}$, was obtained from the level 2.5 turbulence model [18].

At every time step, computations give coordinates $S_j = \{(X_1; X_2; X_3)_j\}$, which are stored and then used to identify a grid box where particles are found at time t_j.

4. Particle-Tracking Simulations

For the eastern English Channel, tides and fresh water discharge play a critical role in influencing larval transport. 3D flow and turbulence fields computed by the hydrodynamic model are used as input to a particle-tracking model to examine the mechanisms of passive particle and potential larval transport pathways in the Channel. As described in detail below, several particle model runs are conducted under mean tidal conditions, the spring-neap tidal cycle, and with or without freshwater inflow. Each model run simulates 25 days (about 48 M_2 tidal cycles after the model spin-up), which is the period covered by the field experiments, and also a typical time period, over which larvae of different age may remain passive in the water column. Results are presented quantitatively in terms of the number of particles within each model cell extending from bottom to surface. A reflection condition for particles is implemented at the model rigid boundary in all simulations. In the present study, we do not examine particle displacements in the vertical, although the tracking technique is applied to determine particle positions in three dimensions

4.1. PASSIVE PARTICLE TRANSPORT

For these simulations the particle-tracking model is initialized with the homogeneous distribution of particles within the surface layer, over the entire model domain, at every model grid point. Tidal forcing (4 major tidal constituents) and the freshwater inflow, are simulated by the hydrodynamic model, representing typical conditions for April 1995. At every time step during the simulations, the number of particles within each grid box is counted. Particles that are transported outside through the model open boundary are assumed to be lost.

Patchiness (i.e., accumulation or loss) in spatial distribution of particles develops over multiple tidal cycles (Figure 7). It should be noted that Figure 7 represents a vertically integrated distribution of particles, i.e., a horizontal distribution of the total number of particles throughout the entire water column. It is evident, that particle ‘accumulation’ means the local maximum of the horizontal distribution of particles occurred within the box of volume $\Delta X \times \Delta Y \times H$, where ΔX and ΔY form the horizontal resolution, and H is the water depth.

Particle-tracking simulations indicate the following features in particle behavior. After 4-day tracking, particles that were initially homogeneously distributed appear to be concentrated in a number of areas (Figure 7a). The first area of relatively high concentration (up to 5 per grid box) is spread along the French coast, from Dieppe to Cap Gris-Nez, 10–15 km offshore. The second area is neighboring the French coast North of the Seine estuary, and some others are found in the vicinity of the English coast, between Brighton and Newhaven, and around Dungeness (see Figure 1 for port locations). There is also a patch in the center of the domain, with concentration of particles up to 4 per grid box. At the end of the 13th day, the number of particles per grid box in all areas except one has increased, and their size has slightly decreased (Figure 7b). The exception is the area North of the Seine estuary, where particles move northward and join the patch of particles in the center of the Channel. At the end of the 25-day particle-tracking period, the highest concentrations, grid cells with more than six particles, are found within the patch along the French coast (Figure 7c). At the end of simulations, the total number of particles inside the domain decreases due to particle migration outside the domain through the northern boundary. As discussed, particle-tracking modeling indicates that the accumulation of particles and patch formation occurs mostly along the French coast. Particle accumulation also occurs in the vicinity of the English coast, between Dover and Folkestone. Whereas the patches along the French coast are always found 10–15 km offshore, on the margin of the region of fresh water influence (ROFI), accumulation along the English coast may be due to the existence of an eddy-like structure of flow field in the western Dover Strait. At the end of the particle-tracking period, some of the northward moving particles are entrained into this eddy (see Figure 9c).

The principal tidal forcing in the eastern English Channel is the semidiurnal M_2 constituent. Simulations of particle displacements associated with only this constituent show that the structure of the distribution of particles was similar to that when forcing included 4 major tidal constituents. In general more complete tidal forcing produces faster northward transport of particles with the transport rate modulation within the neap-spring tidal cycle.

To further assess the role that different forcing terms play in particle dynamics, simulations are performed with no freshwater buoyancy input and only with tidal forcing, which is prescribed at the open boundaries of the model domain, containing spatially homogeneous, non-stratified fluid. Particle-tracking experiments do not reveal any substantial accumulation of particles along the French coast at a distance of few kilometers offshore. The essential features of particle distribution are summarized in Figure 7d which shows the location of areas with higher concentrations of neutrally buoyant particles at the end of the 13-day period. The first area is the narrow band adjacent to the French coast, the second is confined to the middle of the Channel, and the third is adjacent to the English coast. Inspection shows that over multiple tidal cycles the resultant particle displacement is toward the North and that a net transport of particles is induced by the residual tidal velocities. The most significant particle accumulation occurs in the center of the domain and is related to the narrowing of the Channel to 30 km in the Strait of Dover.

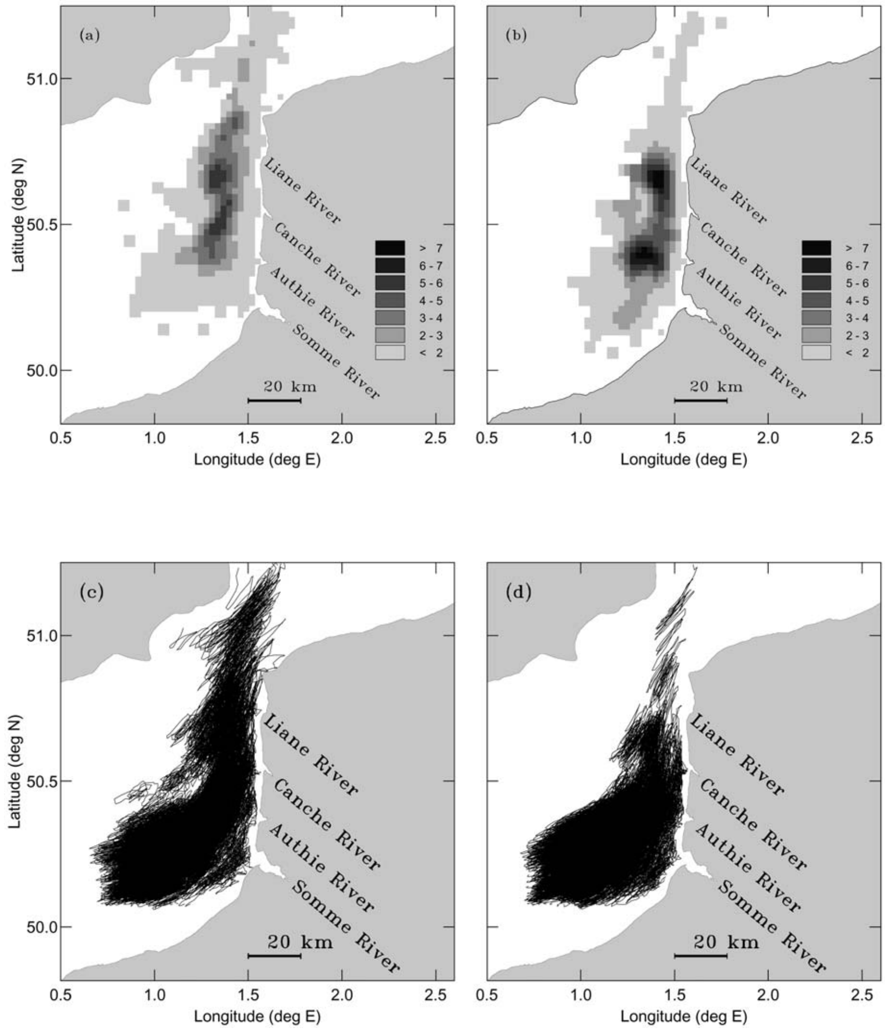


Figure 9. Distribution of passive (neutrally buoyant) particles (a) and vertically migrating particles (b) after 18-day tracking. 18-day trajectories for passive particles (c), and for active (with assigned vertical velocity) particles (d), released in front of the Somme estuary (see Figure 8 for the release location).

Comparison of particle distribution shown in Figures 7b and d suggests that strengthening of accumulation of particles along the French coast is mostly associated with the ROFI which affects the dynamics of neutrally buoyant particles. This leads to particle accumulation on the margin of the ROFI, and to net northward transport of particles induced by the combination of tidal residual and density driven flow. The ROFI associated with the English coast is not represented in our simulations. The input of buoyancy from river run-off along that coast and the role that the ROFI could play along this coast is found to be less significant.

4.2. SIMULATED LARVAL TRANSPORT

The Flounder spawning area, identified during the field experiments of 1995, is located in the southern part of the eastern English Channel in front of the Somme estuary. The field experiments provided the spatial distribution of fish eggs and larvae for different developmental stages. The route and the mechanisms of larvae migrations from the spawning area to nursery grounds have not been entirely determined. Larvae might employ the along-shore residual current to reach the nurseries located northward or may be transported in the middle of the Channel.

To investigate the relationship between the hydrodynamics and the larvae transport pattern we performed simulations using the particle-tracking model. A set of 960 particles were released over a small region in front of the Somme River (assumed to be the spawning area of Flounder). The shape of the region is rectangular, with its center located 35 km offshore the Somme estuary (Figure 8a). The particles were released 1 m below the surface and their depth allowed to vary throughout the simulation period. The particles were tracked for 25 days, from April 11 to May 5, 1995.

The model results indicate that under the appropriate tidal forcing, including neap-spring cycle, particles initially released offshore of the Somme estuary are transported northward. The transport pattern suggests that particles would preferentially move, first, toward the French coast, then North along the coast, rather than being transported to the middle of the Channel. That means that in the central part of the eastern English Channel the transport pattern comprises a significant component toward the French coast. This structure remains stable over the whole period of simulations. Figures 8b-d show particle concentrations one, two and three weeks after the release. The concentrations are expressed in terms of the number of particles within the model grid box. As in the previous particle-tracking experiments, the highest concentrations of particles are found 10–15 km offshore, on the margin of the ROFI, and they move northward. Some particles are found within the ROFI but their amount is not significant. Particles begin to leave the domain through the northern model open boundary after 14 days.

To examine the effect of varying particle release location, a second set of 960 particles were released North of the previous particle release zone, at the beginning of the spring tidal period. The transport pattern looked similar. Most of particles were transported toward the French coast, then northward along the coast, and the highest concentrations of particles were detected again on the margin of the ROFI.

To further assess the effect of tidal forcing on particle displacement, additional simulations consisting in releasing neutrally buoyant particles at different moments of spring-neap tidal cycle were performed. The simulations indicate that the northward migration of particles, released at the beginning of neap period, appears to be faster than the migration under spring tide conditions.

4.3. ACTIVE LARVAE TRANSPORT

Flounder larvae migrate vertically, and a preliminary study [19] has already indicated a light-dependent diurnal cycle in vertical displacement with motions toward the bottom at daybreak and back up the following nightfall. Such migration perhaps for the purpose of avoiding visual predation might affect the transport. As no comprehensive theoretical model of vertical migration pattern exists, we have adopted a simple hypothesis-based on observations of Flounder larvae distribution in the vertical direction. According to these observations, a vertical velocity of diurnal migration of particles, locked on the day-night cycle, was introduced into the particle-tracking model. It is assumed that the deepest part of the migration cycle is centered upon local noon (12 h UT) and that particles are rising towards the surface after noon and falling toward the bottom after mid-night. As the day is just slightly longer than the night in April, the period of downward vertical velocity is a little shorter than the period of upward velocity. The magnitude of these velocities does not change during the numerical simulations. The length of diurnal vertical migration, strictly controlled by the velocity magnitude, was limited to 12 m.

To investigate the influence of the vertical migration on the spatial distribution of larvae along the French coast during the period of larvae transport field experiments (April–May 1995), additional model simulations were performed. Figures 9a and 9b show the behavioral response of modeled larvae to vertical migration. The major difference concerns the rate of the northward migration of particles along the French coast which appears to be smaller over multiple tidal cycles in the case of vertically migrating particles. Patches of these particles seem to be slightly shifted towards the South. In both situations the transport is confined to the area centered on the margin of the ROFI. Vertically migrating particles remain more concentrated within two patches at the end of the 18-day period, whereas neutrally buoyant particles are spread more widely over the domain with lower concentrations of particles in the patches.

Figures 9c and 9d show the transport pathways for 160 among 960 particles released. When the diurnal vertical migration is introduced to the model, particles released offshore the Somme estuary spend four days more to attain the northern boundary of the domain. The two particle transport patterns have slightly different shapes. An asymmetry develops in Dover Strait. Vertically migrating particles are transported toward the North when they exit Dover Strait. Some particles without vertical migration are entrained westward toward the English coast as can be seen in Figures 9a and 9c.

5. Discussion

This study considers the coupled effect of barotropic (tidal) and baroclinic (due to freshwater buoyancy input) circulation on the transport pattern in the eastern English Channel. It benefits from the increased spatial coverage of hydrographic and ichthyoplankton data available from the larval drift experiments. Observations indicate water stratification along the French coast produced by the freshwater inflow from a number of rivers: the Seine, the Somme and others. The river run-off, variable in time, gives rise to a specific water structure – a region of freshwater influence (ROFI). Within the ROFI, the buoyancy input is responsible for producing a physical regime which is radically different from that of the offshore waters. A variety of ROFI systems and the distinctive features of water dynamics were described in some detail by Simpson [20]. Buoyant spreading of low salinity water from the coastal sources under the influence of the Earth's rotation tends to generate a classical coastal current. The freshwater buoyancy input makes the baroclinic case an important part of a complete understanding of the circulation and the transport in the Channel. A haline front, separating offshore waters of Atlantic origin from the region of fresh water influence, is one of the most significant features of the eastern English Channel.

We developed an accurate model representation of the geometry, hydrology, and circulation in the study area by considering realistic tidal forcing and freshwater buoyancy input corresponding to the period of larvae transport field experiments (April–May, 1995). These experiments indicate Flounder larvae transport from the spawning area (offshore the Somme estuary) to nursery grounds located along the French coast and extending from the Picard region to the southern part of the North Sea.

According to Grioche *et al.* [20], the larval transport pattern in the eastern English Channel is characterized by a major pathway toward the North Sea in the middle of the Channel, and the larvae transfer from the central part toward the shore across the front with further northward migration along the shore. The rate of the northward migration is assumed to be higher in the middle of the Channel than in nearshore waters. To verify this hypothesis and to establish comprehensive transport patterns in the study area, we performed a number of particle-tracking model simulations. We investigated the influence of the complex forcing on the transport of completely passive particles within the eastern English Cannel. Forcing terms included 4 major tidal constituents and major river freshwater inflows. Patchiness in spatial distribution of particles, initially homogeneously spread, was observed over multiple tidal cycles. Processes of particle dispersion in a flow field driven by a combination of tides and freshwater buoyancy are essentially three-dimensional. Interaction between the turbulence, the buoyancy input, and the tidal forcing leads to a formation of patches of particles in a number of areas: along the French coast (strongest accumulation), in the vicinity of the English coast – in the western and in the eastern part and in the center of the Channel.

The results from numerical model indicate that the strengthening in accumulation of particles along the French coast is mostly associated with the ROFI, the haline front on the margin of the ROFI, and the friction turbulence generated by tidal currents. Contour maps of the vertical diffusivity, K_{H}, in the surface layer, and the subsurface vertical velocity produced by the hydrodynamic model are presented in Figure 10. The figure indicates that, along the French coast, the vertical turbu-

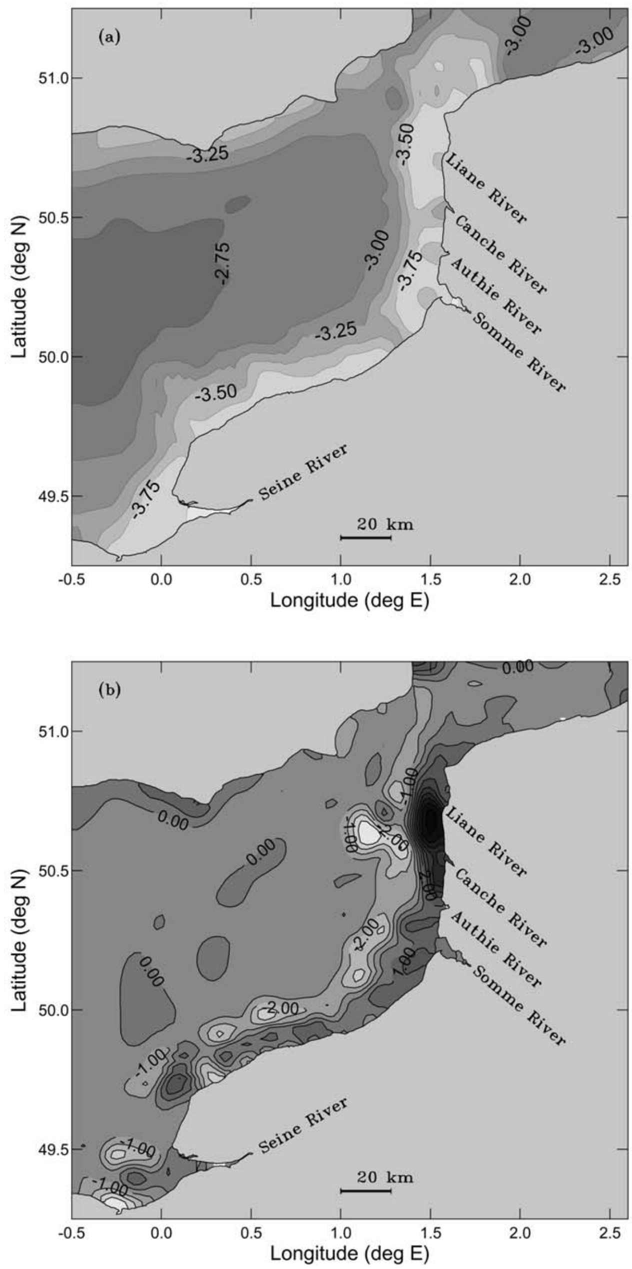


Figure 10. Contour plot of near-surface vertical diffusivity ($\log_{10}\left[\frac{K_H}{m^2 s^{-1}}\right]$) (a), and near-surface vertical velocity ($\times\ 10^5$ m s^{-1}) (b) produced by the numerical model under the neap tide conditions.

lence is suppressed by the freshwater input from river run-off and that a clearly defined frontal convergence zone is formed by the interaction between freshwater buoyancy input and tidal motions. This convergence zone is characterized by upward vertical velocities within the ROFI and downward motion in the frontal area. In this area, particles are trapped and spread in the vertical direction within the water column by downward motions. Therefore the distribution of the ensemble of particles is similar to the particle accumulation, after integration over the vertical.

If there is no buoyancy input, the numerical results do not indicate any consistent accumulation of particles along the French coast, a few kilometers offshore. A large number of particles are concentrated in the middle of the Channel instead. The major reason for this accumulation is the northward narrowing of the Channel.

As Simpson [20] showed, the interaction between the density-driven flow and tidal stirring gives rise to a residual flow along the coast. This current can be considered as one of the major factors influencing particle transport over multiple tidal cycles along the French coast. Numerical Lagrangian tracking reveals that particles form patches on the margin of the ROFI, 10–15 km offshore of the French coast, and move preferentially northward along the coast. The tidal residual currents induce net transport of particles toward the North Sea but do not give rise to alongshore particle accumulation. This suggests that the freshwater input controls the location of accumulation zones whereas tidal currents modulate the magnitude of the horizontal transport. This modulation is related to the neap-spring tidal period.

Particle-tracking simulations provide important insights into the larval transport patterns in this part of the Channel. The larval transport field experiments conducted in 1995 revealed that eggs and larvae of Flounder follow similar pathways during the migration from spawning area to nursery grounds. In particular, larvae of stage 2 and 3 display a local maximum of concentrations northward the spawning area, 10–15 km offshore.

Abundance represents the mean concentration of larvae in the water column, matching the larvae sampled from the bottom to the surface. The method of sampling, described in some detail in Section 2, is commonly used by biologists in order to investigate the horizontal distribution of ichthyoplankton and the correlation with environmental variables. From this point of view, the vertically integrated distribution of particles within the model grid cell, adopted in this study to describe the spatial structure of particle distribution, appears to be consistent with the larvae abundance representation.

In order to reconstruct the Flounder larvae migration pathways in the Channel, the particle-tracking model was implemented. In the first step, particles were released in front of the Somme estuary, assumed to be the spawning region of Flounder (Figure 8a). Tracking of passive particles (without vertical migration ability) gave rise to a horizontal structure of particle distribution which was consistent with the observed larvae concentrations during the field experiments (see Figures 2 and 8).

Tracking of particles released northward of the initially chosen area showed that there are weak relationships between the particle transport pattern and the releasing location. Trajectories of particle migration indicated a shoreward flow in the central part of the Channel and a northward displacement along the coast, and confirmed the previous results.

We have also performed tracking of particles which have the ability to swim vertically. This represents the behavior of real organisms, for instance, fish larvae at advanced development stages. It was assumed that the swimming behavior of the organisms was restricted to diurnal vertical motions. Usually diurnal-migrating organisms stay higher in the water column during the night and descend to greater depth, where currents are weaker, during the day. This pattern of migration is thought to be an adaptation for avoidance of visual predators. Hill [8] has pointed out that the diurnal (24 h period) vertical migratory behavior of marine organisms which is synchronized specifically with the semi-diurnal S_2 constituent, can produce net horizontal transport. The rates of this migration-induced transport are comparable to characteristic residual flow speeds. Diurnal migration-S_2 tide interaction operates as a horizontal transport inducing mechanism and produces westward (south-westward) net transport of abyssal organisms in the eastern English Channel. In the southern part of the North Sea migration-induced transport is in the opposite direction (toward the North-East). This suggests the existence of a divergence zone in the Strait of Dover.

Our modeling results indicate that the vertical migration of organisms might cause relatively significant departure from the passive particle transport pattern. The essential differences are illustrated in Figures 9a–d which show the location of neutrally buoyant and vertically migrating particles at the end of the 18-day tracking period, and particle trajectories. The first difference concerns the rate of the northward migration along the French coast. The analysis of particle location after the instantaneous release west of the Somme estuary has revealed that active particles (with vertical migration ability) would move more slowly than passive particles. More precisely, it might take the active particles four more days to reach the northern boundary of the domain, within 24 days of tracking. Thus, significant vertical migration-induced transport inferred by Hill [8] in the eastern English Channel appears to be the major factor contributing to the decrease of the rate of particle displacement toward the North, obtained in our modeling experiments. The second revealed difference is the shape of the transport patterns (Figures 9c–d). In the vicinity of the northern boundary, the active particles appear to be transported mainly northward to the North Sea. Only a small number of particles might deviate northeast behind Cape Gris-Nez. On the contrary, a significant fraction of passive particles is entrained westward toward the English coast.

6. Conclusions

A calibrated and validated hydrodynamic model of the eastern English Channel in conjunction with a particle-tracking model was used to investigate transport patterns and dispersion processes within the model domain. The study benefits from the increased spatial coverage of hydrographic and ichthyoplankton observations available from the larval drift experiments conducted in April–May 1995.

Observations indicated a water stratification along the French coast arising from the freshwater inflow from a number of rivers and, also, a haline front, which separates the off-shore water of Atlantic origin from the region of freshwater influence (ROFI). The ROFI is one of the most significant features of the eastern English Channel. The hydrodynamic model properly reproduced it.

The random-walk particle-tracking model was used to help examine the mechanisms of passive particle displacement and the potential larval transport pathways in the Channel. The analysis of the model runs revealed patchiness in the spatial distribution of particles observed in a number of areas over multiple tidal cycles. Particle accumulation is essentially three-dimensional process emerging from the interaction between the turbulence, the buoyancy input, and the tidal forcing. This interaction could be realistically reproduced only by means of a 3D hydrodynamic model. In the vicinity of the French coast, the particle accumulation is mostly associated with the ROFI and is found to be particularly intense. A frontal convergence zone is formed on the margin of the ROFI as the result of the interaction between freshwater buoyancy input and tidal motions. In this area, particles are trapped and spread in the vertical direction within the water column by downward motions, and the distribution of the ensemble of particles is similar to the particle accumulation.

The particle-tracking model was then used to facilitate an understanding of the mechanisms of migration of Flounder (*Pleuronectes flesus*) larvae from the spawning area, west of the Somme estuary, to nurseries. The tidal forcing and the freshwater river discharge had a major effect on the larval transport. Different tidal conditions may affect the transport. Generally, under the neap tide conditions, the larvae migration toward the North Sea appeared to be faster than under the spring tide conditions.

Under realistic tidal forcing and freshwater input corresponding to the period of larvae transport field experiments, passive particles (without vertical migration ability), released West of the Somme estuary, traveled within 25 days of tracking. The model results revealed that a horizontal structure of particle distribution was consistent with the observed during the field experiments Flounder larvae concentrations. Also, our results indicate only one principal pathway of larvae migration from the English Channel to the North Sea – northward migration along the French coast on the margin of the ROFI.

In addition to the dependence on freshwater input and tidal conditions, the transport pattern of marine organisms is found to be related to their vertical migratory behavior. In the model, this behavior is restricted to simple dial vertical motions.

Active particles (with vertical migration ability) seem to move toward the North much more slowly. Diurnal migration-S_2 tide interaction operates as a horizontal transport mechanism and contributes to the decrease of the rate of particle displacement toward the North. With the exception of northward migration, both types of particles follow the same pathway, i.e., they are transported toward the North Sea along the French coast on the margin of the ROFI.

Finally, it is concluded that the hydrodynamic model in conjunction with the random-walk transport model properly reproduces circulation patterns and particle transport in the eastern English Channel, especially in the vicinity of the French coast, and can be used for the prediction of larval movement.

Acknowledgements

This study was conducted as a part of the project supported by CNRS grant 12217. We thank A. Grioche and P. Koubbi for providing the biological data, and L. Seuront for useful ideas and valuable comments. Constructive remarks and critical comments by anonymous referees and the editor on our modeling experiments were very helpful to improve the paper.

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