J. Mar. Biol. Ass. U.K. (2000), **80**, 921–928
Printed in the United Kingdom

Hydrographic circulation and the dispersal of yolk-sac herring (*Clupea harengus*) larvae in the Blackwater Estuary

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Each spring, a localized stock of herring (*Clupea harengus*, Teleostei, Clupeidae) spawn in the Blackwater Estuary (Essex, UK). The eggs are laid on a gravel bank (Eagle Bank) at the mouth of the estuary. Incubation takes three to four weeks and, after hatching, the larvae can be caught in the area for several months. In this paper, results are presented from a finite-element circulation model used to simulate tidal and wind driven flow fields for the region. A particle tracking model was then used to simulate the dispersal of young herring larvae, up to first feeding, hatching from the Eagle Bank. The simulations predicted that, over a period of 12 d, around 63% of particles would be retained in the area of the Eagle Bank at high water whilst 22% of particles would be further south towards the Buxey Sands. Over the same time, ~7% of the particles released would be found in the River Blackwater itself. Imposing a steady state wind of 10 m s^{-1} from the south-west (the dominant wind direction during spring in this area) or north-east had the effect of moving the majority of particles into the river or offshore to the south respectively.

INTRODUCTION

The Blackwater Estuary is a small, tidally energetic estuary, generally less than 10 m in depth on the south-east coast of England (Figure 1). Between February and May, a localized stock of herring (*Clupea harengus* Linnaeus, 1758) spawn on the Eagle Bank, at the estuary mouth. The eggs take three to four weeks to develop and, following hatching, the larvae can be found in the area throughout the spring and early summer (Fox et al., 1999; Henderson et al., 1984; Wood, 1981). During the spring of 1996 and 1997, a series of surveys were undertaken in this region with the aim of measuring herring larval production and mortality. For this, an estimate of the potential loss rates of larvae due to advection from the sampling area was required. Transport of herring larvae in this region has previously been modelled by Henderson & Cartwright (1980) using a simple, one-dimensional, box-channel model. They were principally concerned with modelling the transport of larvae from the Eagle Bank into the River Blackwater. Their model was unable to resolve dispersal offshore due to the complex bathymetry in this region. In the present paper, we report results from a two-dimensional, depth-integrated, finite element model of this region. The hydrodynamic model was tuned against historical current meter records from this area. Larval dispersal was then simulated by tracking particles within the hydrodynamic flow fields under varying tide and wind conditions. Results were compared with patterns of herring larval distribution derived from field surveys.

MATERIALS AND METHODS

Hydrodynamic modelling

Flow field simulations were generated using TELEMAC-2D (Hervouet & Janin, 1994). A variable-mesh bathymetric grid was constructed covering the rivers Blackwater, Colne and Crouch. Coverage extended 25 km north and 20 km south of the estuaries and out to 20 km offshore. Within the Blackwater Estuary internode spacing was 200 m increasing to 1300 m near the model boundaries. Bathymetric data were taken from the most recent Admiralty Charts for the region (3741, 3750 and 1183). Digitized depths were reduced relative to ordnance datum (Newlyn), which is approximately mean sea level, and interpolated onto the model grid (Figure 2). Boundary conditions were generated by running a coarse regional model of the southern North Sea based upon 12 tidal

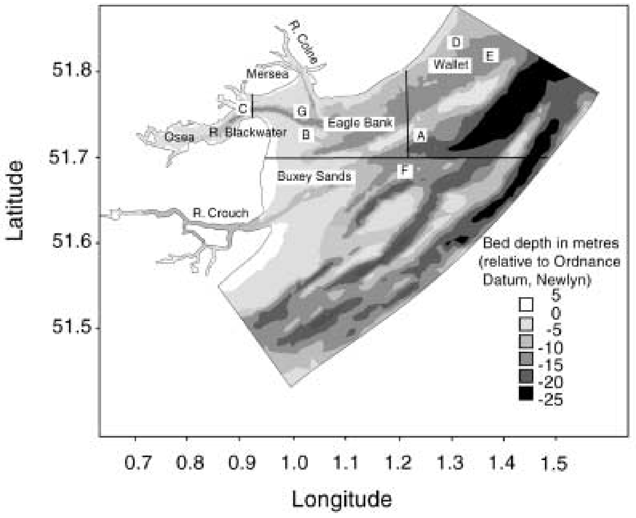

Figure 1. Bathymetry of the modelled area; letters refer to positions of historical current meter records; solid black lines delimit the areas (River Blackwater, Eagle Bank, Wallet and Buxey Sands) over which the distribution of simulated particle dispersal was assessed.

Table 1. *Details of current meter records used to calibrate the flow model.*

Position	Longitude (°N)	Latitude (°E)	Height above bed (m)	Sounded depth (m)	Date started	Duration (days)	Simulation	
							From	To
A	51.713	1.215	4	14	12/02/72	38	17/02/72	20/02/72
B	51.723	1.040	3	10	29/04/75	9	29/04/75	02/05/75
C	51.755	0.895	3	9	28/04/75	9	29/04/75	02/05/75
D	51.810	1.297	4	16	19/01/73	18	20/01/73	23/01/73
E	51.792	1.347	4	17	19/01/73	29	20/01/73	23/01/73
F	51.662	1.202	4	17	18/01/73	54	20/01/73	23/01/73
G	51.748	1.027	3	7	29/04/75	9	29/04/75	01/05/75

harmonics. Tidal elevation curves were extracted at ten points around the model boundary and tidal height at each node in the local model boundary estimated by linear interpolation.

Using historical current meter records at seven locations within the region (Table 1), a comparison was made between observed currents and simulated depth mean currents under conditions of zero wind stress. Bed roughness and bathymetric smoothing were altered to obtain the best fit to the observations. Following calibration, a full springneap cycle with no imposed wind was simulated. Flow simulations were also made with constant winds of 10 m s^{-1} blowing from the south-west or north-east.

Particle modelling

The dispersal of herring larvae within the flow fields generated above was simulated using a particle tracking model based upon PLUME-RW version 2.0 (HR Wallingford, Oxford, UK). This model simulates the movement of particles within a depth-averaged current field. Tidal current vectors are interpolated from the nodes of the flow field to the positions of individual particles. A logarithmic profile is assumed in the vertical to obtain velocity vectors appropriate to the depth of each particle. The effects of turbulent motion not resolved in the tidal flow fields are modelled as random displacements in the horizontal and vertical. Horizontal displacements are calculated from the specified horizontal eddy diffusivity constant. Vertical displacements are based on a vertical eddy diffusivity dependent upon the local tidal velocity. Random displacements applied to each particle during a time-step are added to the advective vectors so that particle motions are the sum of ordered and random components. The particles are assumed to be neutrally buoyant. Full control is available over particle release rates, location and time of release during the tidal cycle.

The main spawning site for Blackwater herring is the Eagle Bank, (Figure 1; Dempsey & Bamber, 1983). Herring spawn on the Eagle Bank typically covers an area of 10,000 m^2 (Dempsey & Bamber, 1983), equivalent to a circular patch with a radius of 56 m. To simulate the dispersal of larvae, particles were released from a 50 m radius circle centred on this location. In each simulation, 1000 neutrally buoyant particles were released and tracked. Total simulation time was 24 tidal cycles and particle positions were output every four tidal cycles. Runs were undertaken to examine the sensitivity of the particle dispersal to the following conditions: effect of the random diffusion in repeated runs; number of particles released; changes in the horizontal diffusion constant; changes in the timing of particle release within the tidal cycle; the effect of steady state winds on particle dispersal.

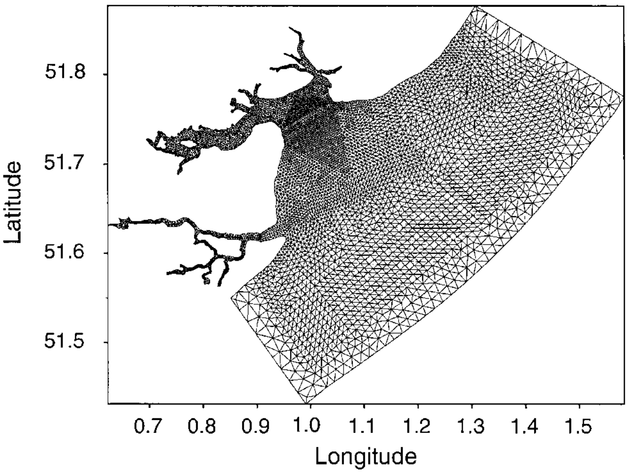

Figure 2. Model grid.

Meteorological data

Hourly wind data were obtained from the UK Meteorological Office for Walton-on-the-Naze (51.85°N 01.28°E). Data were available from 1993 to 1998 and were analysed for the period February to May inclusive. This covers the time when herring larvae are present in the Blackwater Estuary (Fox et al., 1999).

Field sampling

During the spring of 1996 and 1997, plankton surveys were undertaken each week in the Blackwater Estuary. Station locations are shown in Figure 12 and were worked using a Lowestoft Gulf VII high-speed plankton sampler fitted with a 270-μm net (Nash et al., 1998). At each station, the sampler was deployed in a multiple oblique tow to within 2 m of the bottom for 10 min at a towing speed of 3 kn against the flooding tide. Upon recovery, the net was washed down and the catch fixed in 4% formaldehyde in distilled water buffered with 2.5% sodium acetate trihydrate (Tucker & Chester, 1984). Sampling commenced in the River Blackwater adjacent to Osea Island at low-water and proceeded towards the estuary mouth along the deep-water channel. The final stations around the Eagle Bank were worked about six hours later, around high-tide. Because of the shallow water depth, even at high tide, it was not possible to sample over the Buxey Sands. Samples were returned to the laboratory and herring larvae sorted. Larvae were classified as yolk-sac or post yolk-sac and standard larval lengths (measured from tip of the lower jaw to the end of the notochord) recorded using an inter-active image analysis system (ColourMorph, Perceptive Instruments, Haverhill, Suffolk, UK). Live lengths were estimated from fixed material using the formula for formaldehyde fixed larvae subjected to an average 5 min tow given in Fox (1996).

Simulated larval dispersal and comparison with field data

A final model run was performed by steadily releasing 1000 particles from the spawning site over a complete tidal cycle commencing at high water over the Eagle Bank. The dispersal of particles over the subsequent 24 tidal cycles (approximately 12 d) was simulated and the data plotted every four tidal cycles. The distribution of particles within the areas shown in Figure 1 (River Blackwater, Eagle Bank, Buxey Sands and Wallet) were then evaluated. The potential losses of larvae from the area covered by the field sampling were estimated by considering the numbers of particles retained in the River Blackwater and Eagle Bank areas.

RESULTS

Hydrodynamic modelling

During the calibration of the hydrodynamic model an initial bed roughness value of 0.01 m was used. This led to under-estimated current speeds, so the bed roughness value was reduced to 0.001 m, corresponding to a smooth sandy or muddy-sand substrate. Increasing bathymetric smoothing in the model generally had little effect upon simulated current speeds and so was not included in the final model runs.

Comparisons of the simulated flow field with historical current meter data at seven sites suggested that the hydrodynamic model was capable of simulating current flows in the Blackwater region. Results from three representative current meter positions are presented in detail (Figures 3, 4 & 5). Peak current speeds at position A were slightly under-estimated but current directions were well simulated. At location B, current speed and direction appeared to be well simulated. Observed current speeds at position C up to 20:30 on 30 April 1975 appear lower than simulated, but later on, the simulation and observations match well. Reduced current speeds early on could have been caused by fouling of the current rotor.

The simulated residual flows with no imposed wind are shown in Figure 6. The pattern of circulation is complicated, reflecting the complex bathymetry of the region. Circulation offshore shows a broadly north-easterly directed flow in accordance with reported transport patterns in the region (ICONA, 1992). Boundary effects are evident on the south-west edge, where excessive residual current speeds occur but these appear not to affect simulated flows closer inshore where the majority of larvae are found. Here the residual circulation is dominated by the interaction of the tidal flow with the complex bathymetry generating residual speeds between 0.1 and 0.2 m s^{-1} around inshore sandbanks. The model predicts the existence of several gyres in residual flow, which might retain larvae in the Eagle Bank region (Figure 7).

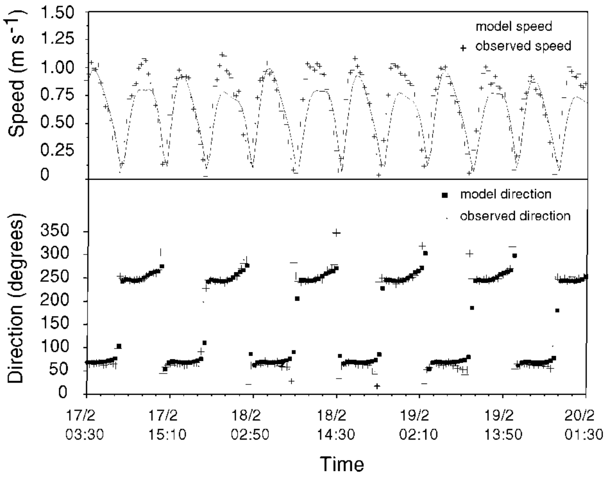

Figure 3. Comparison of simulated currents and historical data from position A.

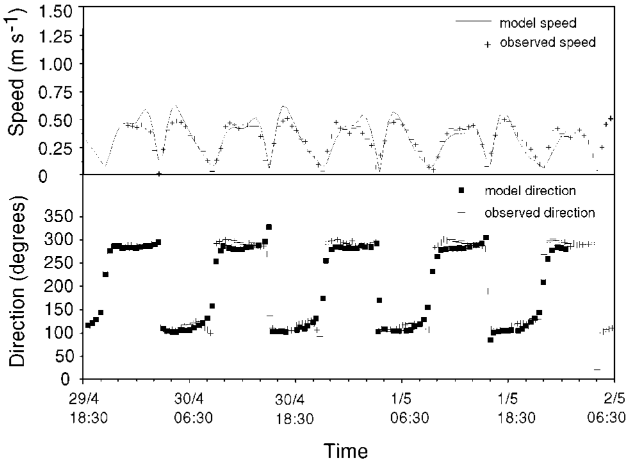

Figure 4. Comparison of simulated currents and historical data from position B.

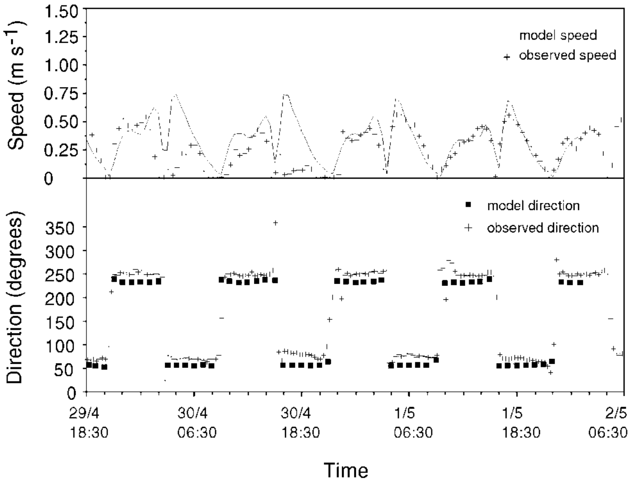

Figure 5. Comparison of simulated currents and historical data from position C.

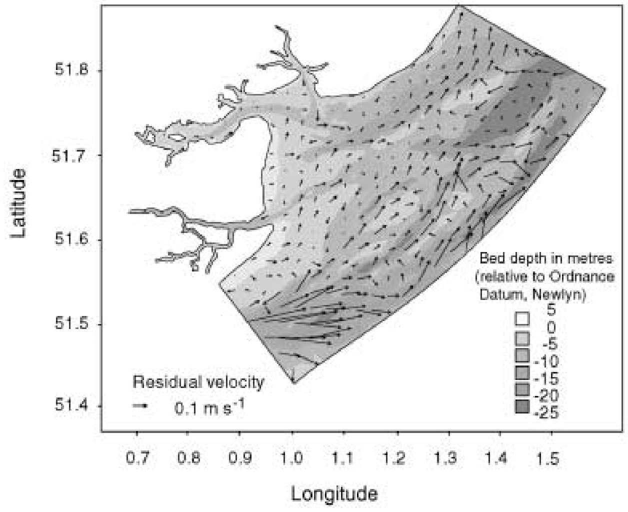

Figure 6. Simulated residual current velocities averaged over four tidal cycles with no winds imposed upon the flow model.

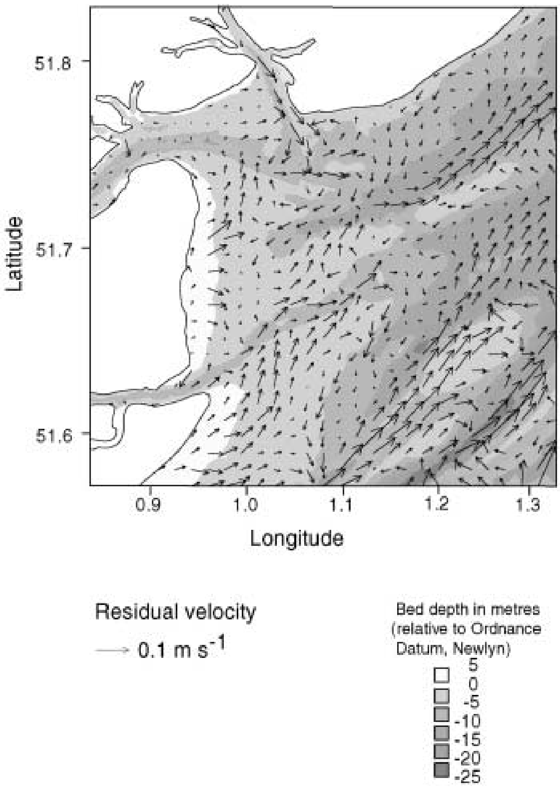

Figure 7. Simulated residual current velocities at the mouth of the Blackwater Estuary averaged over four tidal cycles with no winds imposed upon the flow model.

Particle modelling

The dispersal of particles released instantaneously into the simulated flow field at low (just prior to the flood) or high water (just prior to the ebb) was examined separately. For this test the flow field generated under zero wind was used. The flow fields commenced at a state corresponding to high water springs over the Eagle Bank. Following 24 tidal cycles (approximately 12 d) of dispersal, particles released at low water were either carried into the Blackwater or spread out over the area known as the Buxey Sands (Figure 8A). On the following ebb tide, these particles tended to be carried back towards the deeper water between the Eagle Bank and Buxey Sands. When particles were released at high water they spread in a compact plume to the north-east (Figure 8B). Repeating model runs with identical start conditions resulted in small variability in final particle distributions as a result of the random walk process (<2% difference in the distribution of particles into the four regions: Blackwater, Eagle Bank, Wallet and Buxey Sands, after 24 tidal cycles simulated dispersal). Increasing the number of particles released up to 100,000 also had little effect upon the final distribution of particles (<1% difference in the proportion of particles by area after 24 tidal cycles). Subsequent simulations therefore used 1000 particles. Increasing levels of horizontal eddy diffusivity in the range 0.05 to 1 m^2 s^{-1} had a slight effect on the final distribution of particles by area and particle plumes were more widely spread. High levels of diffusivity caused around 4% more particles to be removed from the Eagle Bank area after 24 tidal cycles. Horizontal eddy diffusion was fixed at 0.15 m^2 s^{-1} for subsequent model runs.

Wind effects

An analysis of wind records (Table 2) from 1993 to 1998 covering the period of the year when herring larvae

Table 2. *Cross-tabulation of frequency distribution of wind speeds and directions during the period 1 February to 31 May, 1993 to 1996 recorded at Walton-on-the-Naze. (Total number of records =17304).*

	Quadrant wind blowing from					
Wind speed (m s^{-1})	North-east	South-East	South-west	North-west	Un-assigned	All quadrants
0					4.1	4.1
0>x=>2	1.4	1.6	2.1	3.1		8.2
2>x=>4	3.4	3.1	5.4	6.7		18.6
4>x=>6	5.2	4.2	8.6	6.9		24.9
6>x=>8	3.9	2.8	8.7	4.9		20.3
8>x=>10	1.8	1.8	4.6	2.2		10.4
10>x=>12	1.0	1.1	1.8	1.1		5.0
12>x=>14	0.4	0.4	0.7	0.5		2.0
>14	0.1	0.2	0.3	0.1		0.7
Missing data					5.8	5.8
All speeds	17.2	15.2	32.2	25.5	9.9	

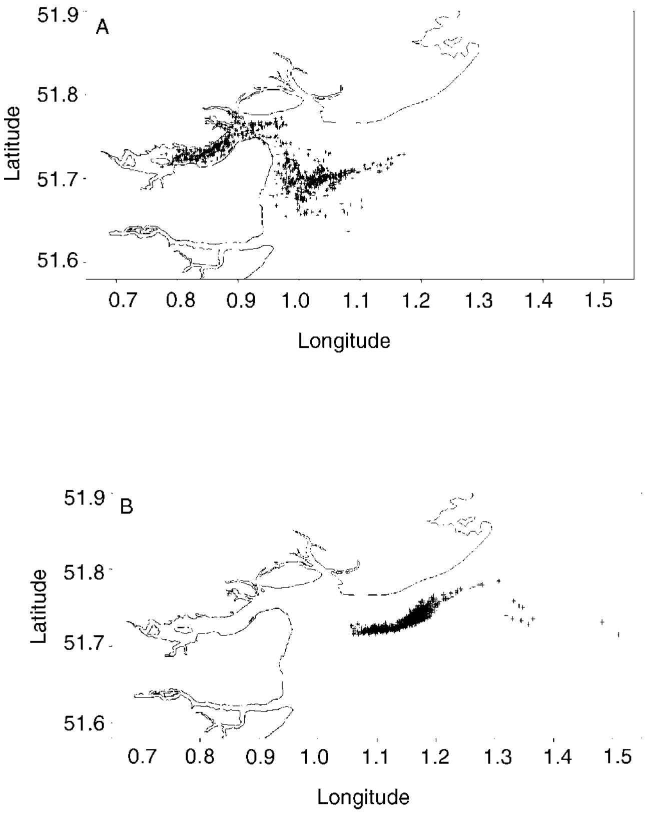

Figure 8. Particle positions plotted at high water at Eagle Bank after 24 tidal cycles (approximately 12 d) of dispersal, no winds were imposed on the flow-field: (A) particles released at first low water at the Eagle Bank; (B) particles released at first high water at the Eagle Bank.

are typically present in the area (February to May inclusive) shows that the majority of winds blew from the south-west quadrant (32.2% of the time) or north-west quadrant (25.5% of the time) during these periods. North-easterly winds comprised 17.2% of the records. The median wind speed was 5.1 m s^{-1} with wind speeds in excess of 10 m s^{-1} only occurring for 7.7% of the time (number of observations = 17,304). An analysis of the distribution of the length of time winds blew from a consistent quadrant during February to May (1993 to 1998) revealed that wind direction was highly variable. This was also apparent during the specific years when field sampling of larvae was undertaken (Figure 9). Steady winds of 10 m s^{-1} therefore represent fairly extreme conditions and simulations under these conditions represent worst-case scenarios. The effect of steady, 10 m s^{-1} winds blowing from the south-west and north-east were assessed in the model. Winds blowing from the north-west were considered to be likely to have less effect due to the sheltering influence of the land. The effect of a steady 10 m s^{-1} wind imposed from the south-west was to drive the majority of particles released at low water into the Blackwater (Figure 10A). There was less effect upon the plume formed by particles released at high water; in this case the plume was pushed slightly to the north-east (Figure 10B). In contrast, the simulation suggests that an extended period of strong north-easterly winds would drive particles released at low water to the south (Figure 11A) and the plume resulting from particles

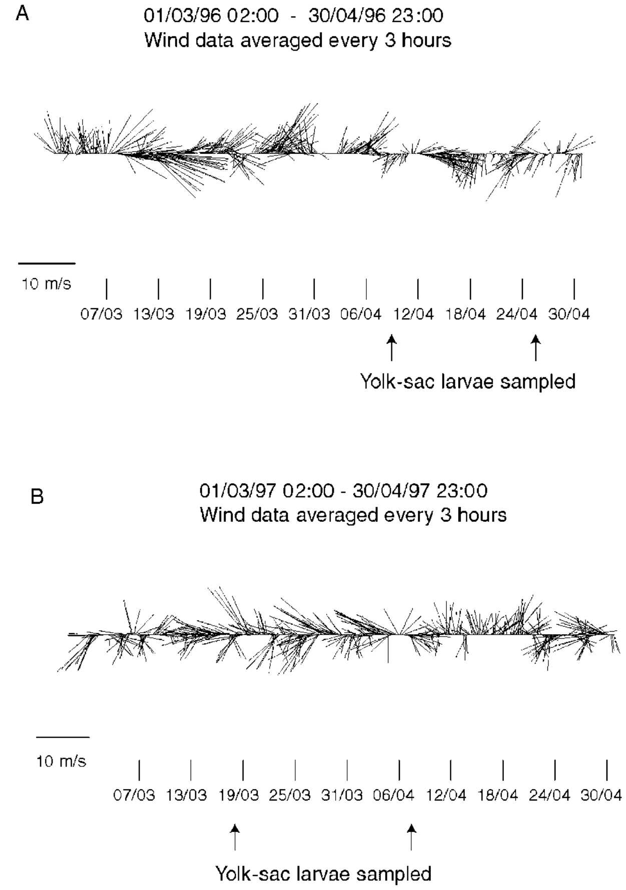

Figure 9. Wind records from Walton-on-the-Naze: (A) March–April, 1996; (B) March–April, 1997.

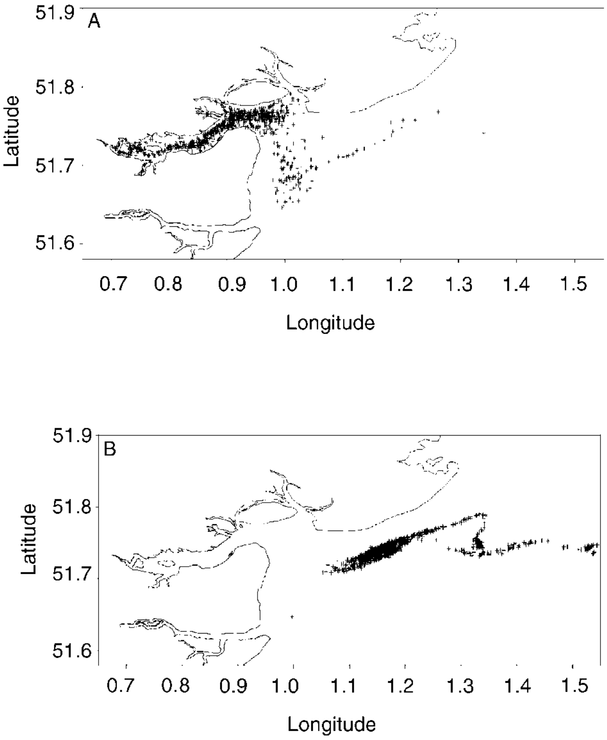

Figure 10. Particle positions plotted at high water at Eagle Bank after 24 tidal cycles (approximately 12 d) of dispersal, a constant south-westerly wind of 10 m s^{-1} was imposed on the flow-field: (A) particles released at first low water at the Eagle Bank; (B) particles released at first high water at the Eagle Bank.

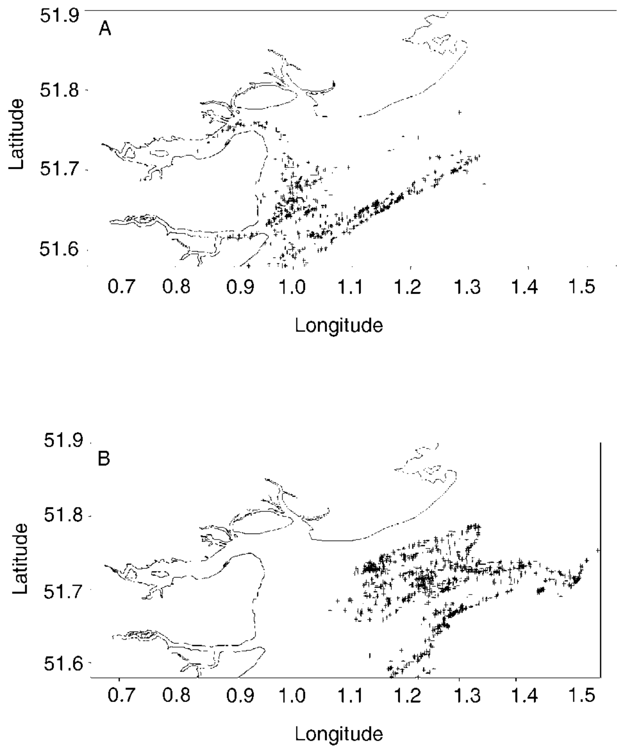

Figure 11. Particle positions plotted at high water at Eagle Bank after 24 tidal cycles (approximately 12 d) of dispersal, a constant north-easterly wind of 10 m s^{-1} was imposed on the flow-field: (A) particles released at first low water at the Eagle Bank; (B) particles released at first high water at the Eagle Bank.

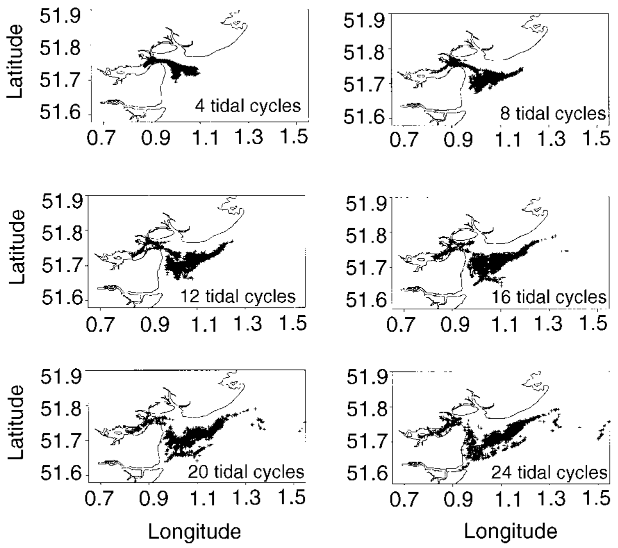

Figure 13. The simulated dispersal of particles over 24 tidal cycles (approximately 12 d) following release from the Eagle Bank, all the particles were released at a constant rate over the first tidal cycle, no winds were imposed upon the flow model, particle positions are plotted at high water at the Eagle Bank.

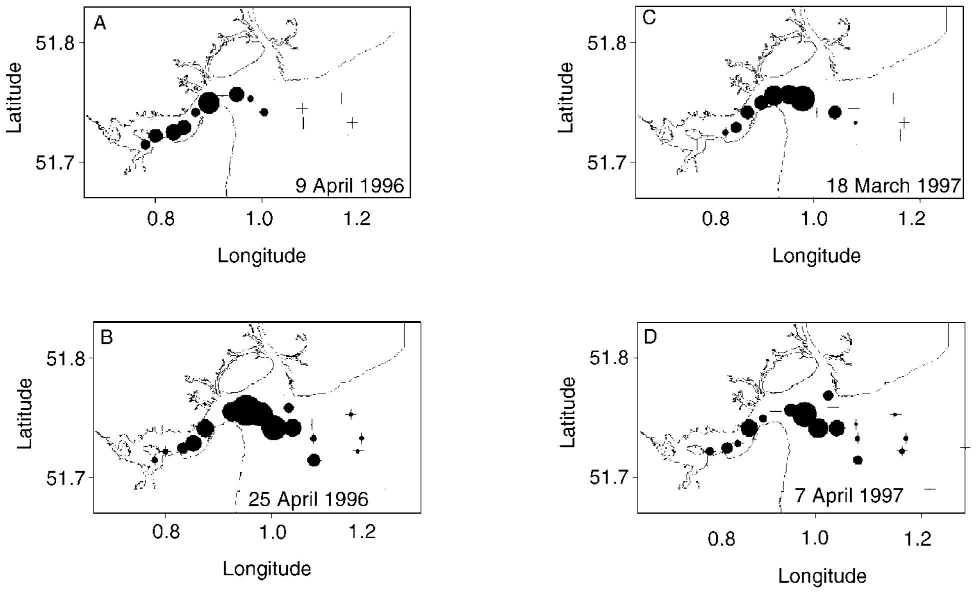

Figure 12. Distribution of sampled yolk-sac herring larvae in 1996 and 1997: (A) 9 April 1996; (B) 25 April 1996; (C) 18 March 1997; (D) 7 April 1997. Concentration (nos. m^{-3}): +, 0; •, 2.7; ●, 12.5; ⬤, 50.0.

released at high water would be dispersed over a wide area (Figure 11B).

Simulated larval dispersal and comparison with field data

Herring eggs are typically laid by several waves of incoming, spawning fish. The larvae therefore tend to hatch in discrete cohorts which are separated by up to several weeks (Dempsey & Bamber, 1983; Fox et al., 1999). First feeding commences between 8 and 12 d post-hatch as the yolk reserves become depleted (C.J.F., personal observation based on tank reared Blackwater herring larvae). During 1996, large numbers of yolk-sac larvae were recorded in samples collected on 9 and 25

Table 3. *Percentage distribution of particles by area at high-water (Eagle Bank). Results are based upon the dispersal of 1000 particles released from the Eagle Bank at a constant rate over one tidal cycle (high tide to the next high tide) with no imposed winds.*

Number of tidal cycles	Days after start of particle release	River Blackwater	Eagle Bank	Buxey Sands and Crouch	Wallet
0	0	0	100	0	0
4	2.1	11.7	88.2	0.1	0
8	4.1	4.4	78.7	16.9	0
12	6.2	5.1	71.7	21.4	1.8
16	8.3	6.1	71.2	19.1	3.6
20	10.4	5.4	67.3	22.7	4.6
24	12.4	7.1	63.0	22.1	7.8

April (Figure 12A,B). In 1997, yolk-sac larvae were caught in significant numbers on 18 March and 7 April (Figure 12C,D). The highest concentrations of larvae (as nos. m^{-3}) were at the river mouth with few being caught on stations to the east of the Eagle Bank. Larvae were caught all the way up the river as far as Osea Island. Since few yolk-sac larvae were caught in the week preceding these dates and nearly all the larvae sampled in the week following were post yolk-sac, these dates are indicative of the approximate time of hatching of the cohorts. Because of the moderate wind speeds and variability in direction at the times when yolk-sac larvae were abundant in the estuary, wind effects were not included in the final simulation run. There is no information reporting whether herring larval hatching is synchronized to the state of the tide so particles were released in the simulation at a constant rate over an entire tidal cycle (one high water to the next high water). Figure 13 shows how the simulated plume of particles released from the Eagle Bank would spread over the subsequent 24 tides. Particle locations are displayed at high water over the Eagle Bank in order to correspond with the state of tide when the stations towards the estuary mouth were sampled. As expected, the overall distribution of particles is an average of the patterns shown in Figure 8. In numerical terms, only ~7% of particles were carried into the River Blackwater (defined as being west of longitude 0.9°W) with the majority (63%) staying in the region of the Eagle Bank. The proportion of particles carried by the flood tide to the south was around 22% (Table 3). A comparison of the field observations and model predictions shows broad agreement, with few larvae being sampled to the east of the Eagle Bank.

DISCUSSION

The hydrodynamic model presented here represents an advance in terms of resolution for this area of the English coast. Unstructured grids are ideal for representing areas with complex coastlines and bathymetry. Models where the flow field is depth averaged generally perform well in regions where the flow is tidally dominated, as is the case in the Blackwater region. The accuracy of the model with respect to residual flows is difficult to assess, since current meter records can be complicated by the addition of wind and local bathymetric effects. Nevertheless, comparison with current meter observations suggests that the model is capable of reproducing the gross characteristics of the tidally generated flows in the area.

The dispersal of herring larvae from the Eagle Bank spawning site has previously been modelled by Henderson & Cartwright (1980). They utilized a simple diffusion based model and were concerned with estimating the concentrations of larvae carried up the River Blackwater into the region where cooling water is extracted for Bradwell nuclear power station. Their model was not capable of resolving the complex hydrodynamic flows offshore. They estimated that between 18 and 25% of the larval population would be carried past the cooling water intakes over a 70 d period. The present simulation found that there was a brief initial influx (12% of released particles) most of which were removed again after eight tides. Numbers of particles in the River Blackwater then increased linearly at around 0.3% per day of the total number released. If extrapolated over 70 d, the results are comparable to those obtained by Henderson & Cartwright (1980).

Modelling the dispersal of organisms within flow fields presents some unique challenges. The present particle tracking model, and that of Henderson & Cartwright (1980), treats herring larvae as inert, neutrally buoyant particles. In fact, yolk-sac herring larvae have slight negative buoyancy and it has been suggested that this may enhance their retention close to spawning sites (Henri et al., 1985). It is also known that the dispersal of many organisms within estuaries is affected by active behaviour (Boehlert & Mundy, 1988; Graham & Townsend, 1985). Henderson (1987) reported that densities of Blackwater herring larvae were higher near the sea bed on the ebb than during the flood tide and this was interpreted as a behavioural adaptation aimed at reducing losses from the river. However, active vertical migration does not become fully developed until herring larvae are larger than 10 mm so this behaviour is not relevant to the dispersal of yolk-sac and first feeding Blackwater herring larvae (Fortier & Leggett, 1982; Seliverstov, 1973).

The importance of estuaries to the early life stages of many marine organisms has been widely recognized (Churchill et al., 1999; Gunderson et al., 1990; Strathmann, 1982; Yamashita et al., 1996). The advantages of estuarine habitats to early life stages may include elevated temperatures leading to enhanced growth rates, higher levels of food availability and, protection from predators. This has led to considerable research on the mechanisms by which organisms are moved into, and retained within estuaries (Boehlert & Mundy, 1988; Bolcourt, 1982; Chen et al., 1997; Koutsikopoulos et al., 1991; Norcross & Shaw, 1984; Smith & Stoner, 1993). These views pre-suppose that entering the estuarine habitat is a pre-requisite for high survival. No studies have been made comparing growth or survival between herring larvae in the River Blackwater and those dispersed offshore although it has been reported that herring larvae advected away from larger estuarine systems may suffer reduced survival (Fortier & Leggett, 1982; Graham & Townsend, 1985).

CONCLUSIONS

The results of the dispersal simulation suggest that from hatching, till the time of first feeding, in excess of 63% of the herring larvae produced from the Eagle Bank will remain in this region. At high water, around 22% may be carried to the south and around 8% to the east. Under strong, steady north-easterly winds, in excess of $10\,\mathrm{m\,s^{-1}}$, the model predicts that the proportion moved south would increase considerably. In years with steady south-westerly winds, a higher proportion of larvae would be moved into the River Blackwater itself but meteorological records show that these wind conditions are rare for this region. With no imposed winds, particles tended to circulate into and out of the River Blackwater resulting in ~7% being present in the river during any one high tide. Conditions at the estuary mouth, rather than in the river itself, will therefore be most relevant to the growth and survival of the majority of first-feeding Blackwater herring larvae.

The present study was funded by MAFF under programme MF0420, Physical and Biological Controls on Fish Stocks. The Telemac 2D model was set up and run under sub-contract by A. Cooper and J. Baugh of HR Wallingford, Howberry Park, Oxon, UK. Meteorological data were supplied by the UK Meteorological Office, Bracknell, Berkshire.

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Submitted 7 October 1999. Accepted 19 May 2000.