

A modelling study of environmental influences on bivalve settlement in The Wash, England

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ABSTRACT: A previous statistical study (Young et al. 1996; Mar Ecol Prog Ser 143:121–129) has suggested that interannual variability in wind-driven transport of planktonic larvae may be responsible for fluctuations in fishery yields in The Wash, England. Predicted currents and depths from a validated, depth-integrated hydrodynamic model were used to drive an advection-diffusion model for the prediction of larval transport. Tides and the location of the larval release site had some effect on larval retention and settlement in The Wash, but the influence of winds was predicted to be considerably more important, causing up to a 3-fold greater variability in the predicted number of settled larvae. Differences in larval transport between years could produce as much as a 40-fold difference in the number of successfully settling larvae. Predictions of settlement for 7 yr strongly suggest that wind-induced larval transport contributes to interannual recruitment variation, although predicted settlement success was dependent upon spawning date. It is concluded that numerical modelling techniques have useful applications to the study of influences on larval settlement. However, predictions of settlement cannot be directly related to recruitment and future fishery yields without further consideration of post-settlement processes.

KEY WORDS: *Mytilus edulis* · *Cerastoderma edule* · Recruitment variability · Commercial shellfish · Supply side ecology

INTRODUCTION

The majority of marine invertebrates have free swimming, feeding larvae, but the fate of larvae during their planktonic life still remains largely unknown (Young & Chia 1987, Rumrill 1990). Thorson (1950) suggested that the hazardous nature of a planktonic life stage implies greater variations in survival and settlement of planktotrophic larvae (which spend time feeding in the plankton) than of lecithotrophic species (non-feeding larvae) or direct developers, and recently, 'supply side ecology' (Young 1987) has focused on the influence on adult population dynamics of temporal and spatial variability of larval settlement. Although there is considerable evidence from rocky shores that

variations in settlement success affect the adult population (Kendall et al. 1982, Roughgarden et al. 1994), in soft sediments the relative importance of pre- and early post-settlement processes is less clear. Olafsson et al. (1994) concluded that post-settlement processes were often more important in soft sediments, and Beukema (1991, 1992) has shown that interannual variability of early post-settlement predation is the dominant influence on the variability of adult bivalve population size in the Wadden Sea.

Historical records of *Cerastoderma edule* (common cockle) and *Mytilus edulis* (common mussel) fishery yields in The Wash, UK (Fig. 1), show considerable interannual variability (HMSO 1991, 1994). Following a study of variability in the abundance of early benthic juveniles, Dare & Walker (1992) hypothesized that this may be caused by variability in the recruitment of larvae to the adult beds. The Wash is a semi-enclosed system with no other large populations of cockles and

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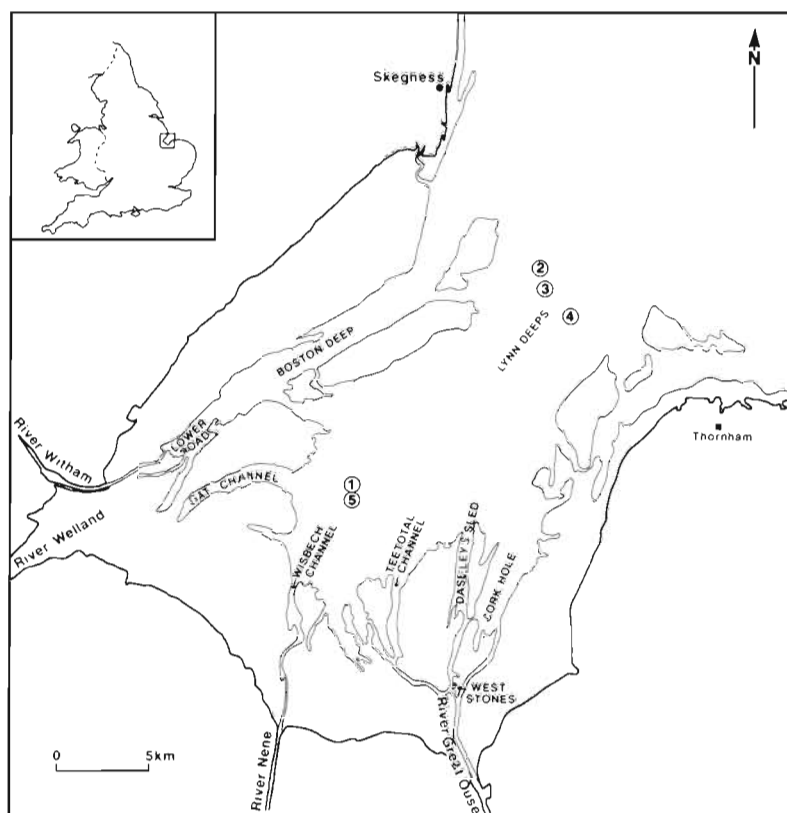


Fig. 1. Location and main physical characteristics of The Wash, England, where the lighter line indicates the level of lowest astronomical tide (LAT). The encircled numbers indicate current meter locations

mussels nearby to enable larval exchange, suggesting that the system is necessarily discrete and self-sustaining. It is therefore an ideal study site for furthering our understanding of pre-settlement influences. A statistical study of influences on the recruitment variability of *Mytilus edulis* and *Cerastoderma edule* in The Wash (Young et al. 1996) found that enhanced recruitment was associated with an increased frequency of easterly winds during the planktonic life stage. It was hypothesized that currents induced by easterly winds may act as a mechanism to retain larvae close to suitable settlement sites. Further investigation of this mechanism, using numerical modelling techniques, is the primary aim of this study.

In this paper, a hydrodynamic model for the prediction of tidally and wind-induced currents and elevations in The Wash is described and the validation of this model considered. Predicted currents and elevations from this model have been used to drive an advection-diffusion larval transport model. The methodology and results of model experiments to investigate environmental influences on recruitment are discussed. Influences considered were winds,

tides, the location of the spawning site, and larval mortality on the tidal flats. The application of the numerical models to the prediction of observed recruitment levels is also considered.

Description of study area

The Wash (Fig. 1) is the remnant of a large depression cut into the Jurassic clays of Eastern England by fluvial and glacial action during the Quaternary (Evans & Collins 1987). Although it receives the drainage of about 12 500 km² of Eastern England through the Great Ouse, Nene, Welland and Witham river systems, freshwater runoff is low and it is in essence a large bay rather than an estuary (Young 1996). It covers an area of about 620 km² of which approximately 290 km² is permanently covered by water, the remainder consists of a broad belt of marshes, mudflats and sandflats.

The most extensive survey of the hydrodynamics of The Wash was undertaken by the Hydraulic Research Station (HRS 1974), with data collected during June and July 1971 and April to October 1972. These data suggested that in general The Wash is horizontally and vertically well mixed, although at low water,

surface tongues of low salinity were observed to extend out into The Wash with recorded salinity variations of up to 0.7 psu over the depth of the water column (HRS 1972). However, during the late spring and early summer when the cockle and mussel larvae are in the water column, outflow from the rivers is usually very low (Young 1996) and the effects of fluvial input are small compared to tidal processes. An analysis of residual current directions in The Wash (Ke et al. 1996) found vertical homogeneity at all the sampling stations, again suggesting a dominance of tidal, rather than fluvial, processes.

Water flows within The Wash are dominated by strong semi-diurnal tides with a mean tidal range of approximately 5 m and peak flood current speeds in the centre of the embayment in excess of 1.5 m s⁻¹ (HRS 1972). Water circulation in the North Sea offshore of The Wash has a general anticlockwise pattern with residual water flow towards the southeast (Salomons et al. 1988). In The Wash, the central deep water area is dominated by a residual southwestwards water movement, whilst on the margins, the residual movement is northeastwards (Ke et al. 1996).

METHODS

The hydrodynamic model. A depth-integrated finite difference model, originally developed for tidal predictions in Spencer Gulf, South Australia (Noye 1984), was adapted for The Wash region by incorporating a flooding and drying scheme based on that of Flather & Heaps (1975). In this scheme, tests were performed before each velocity calculation to determine whether the associated grid point was 'wet' or 'dry'. If the point was dry then the current was set to zero. If the point was wet, the new velocity value was calculated by solving the appropriate equation of motion.

The general equations of motion for depth-integrated fluid flow may be expressed in their Cartesian form as (Kowalik & Murty 1993),

$$\frac{\partial \xi}{\partial t} + \frac{\partial U}{\partial x} + \frac{\partial V}{\partial y} = 0 \quad (1)$$

$$\frac{\partial U}{\partial t} + \frac{\partial}{\partial x} \left(\frac{U^2}{h} \right) + \frac{\partial}{\partial y} \left(\frac{UV}{h} \right) - fV = \quad (2)$$

$$-\frac{h}{\rho} \frac{\partial p_a}{\partial x} - gh \frac{\partial \xi}{\partial x} - \frac{C_b U (U^2 + V^2)^{1/2}}{h^2} + \frac{C_s \rho_a}{\rho} u_{10} (u_{10}^2 + v_{10}^2)^{1/2}$$

$$\frac{\partial V}{\partial t} + \frac{\partial}{\partial x} \left(\frac{UV}{h} \right) + \frac{\partial}{\partial y} \left(\frac{V^2}{h} \right) + fU = \quad (3)$$

$$-\frac{h}{\rho} \frac{\partial p_a}{\partial y} - gh \frac{\partial \xi}{\partial y} - \frac{C_b V (U^2 + V^2)^{1/2}}{h^2} + \frac{C_s \rho_a}{\rho} v_{10} (u_{10}^2 + v_{10}^2)^{1/2}$$

where U and V are depth-integrated velocities, ξ is the time-varying surface mean elevation, h is the total water depth, ρ is the fluid density (assumed constant), $f = 1.16 \times 10^{-4} \text{ s}^{-1}$ is the Coriolis parameter (assumed constant), p_a is the time-averaged atmospheric pressure (assumed constant), $C_b = 0.0025$ is a non-dimensional drag coefficient, C_s is the surface drag coefficient which may be related to wind speed by (Wu 1982) $C_s \times 10^3 = 0.8 + 0.065 \bar{w}$, where $\bar{w} = (u_{10}^2 + v_{10}^2)^{1/2}$, ρ_a is the density of air, and u_{10} , v_{10} are the horizontal wind velocity components measured 10 m above mean sea level (MSL) in the x and y directions respectively. The horizontal shear stress terms are generally considered to be negligible in shallow regions (Schwiderski 1980) and numerical experiments with this model indicated that they have a negligible effect on the water motion (John Noye pers. comm.), thus these terms have been neglected.

Variations of elevation and velocity were obtained by solving Eqs. (1) to (3) on the Arakawa C-grid (Mesinger & Arakawa 1976), using a semi-implicit Forward Time Centred Space (FTCS) finite difference approximation (Noye 1984). Tidal elevations were prescribed at each open boundary point by interpolation of elevations and

phases predicted by the Proudman Oceanographic Laboratory (POL) North Sea model (Flather et al. 1991). A grid spacing of 0.005° was chosen, which at a latitude of 53°N implies spacings of 334 and 555 m in the x and y directions respectively. The model domain extended from $52^\circ 46' \text{N}$, 0°E to $53^\circ 10' \text{N}$, $0^\circ 38' \text{E}$. Model bathymetry was obtained from a Kingfisher chart and Admiralty chart numbers 1200 and 108, and depths were converted from chart datum to MSL. The level of mean high water at spring tide (MHWS) was assumed to delineate the permanent coastline.

Hourly mean winds at Marham, approximately 20 km southeast of the mouth of the river Great Ouse (south of the region shown in Fig. 1), were provided by the Ministry of Agriculture, Fisheries and Food (MAFF) for the months April to July in the years 1978, 1980, 1984, 1985, 1986, 1988 and 1993; these were used to provide the wind forcing in the model (Young 1996).

The moving coastal boundary scheme was optimised by choosing limiting values of local water depth and sea surface slope such that oscillations induced by the drying of tidal flat elements were minimised. The irregularities in the elevation and velocity fields induced by these oscillations dissipated rapidly and thus it was not considered necessary to refine the moving boundary scheme further. Comparison of the model predicted tidal flat extent with that shown by a satellite image [LANDSAT 5 Thematic Mapper (TM)] of The Wash region on 15 July 1989 suggested that the tidal flat scheme accurately predicted the drying of intertidal regions at low tide (Young 1996).

Verification of the hydrodynamic model: The tidally forced model was validated by comparing predicted currents with observations from Aanderaa RCM-4 current meters, deployed for between 16 and 40 d at 5 sites (Fig. 1) in 1990 and 1993. The east and north components of the records were analysed for tidal constituents (see Gmitrowicz & Brown 1993 for a fuller description of the technique) and the amplitudes and phases of the 2 main tidal constituents, M_2 and S_2 (lunar and solar semi-diurnal respectively), compared with the predicted velocities (Table 1).

Predicted amplitudes of the M_2 and S_2 tidal constituents were generally accurate to within 0.04 m s^{-1} and phases to within 10° . A comparison with model results from other studies (Banks 1974, Flather & Heaps 1975, Flather & Hubbert 1990, Bills & Noye 1992) suggests that the accuracy of this model is not atypical. The observed phases of S_2 at Site 2 differed considerably from the other 4 sites, suggesting that the observed values at Site 2 may have been in error, but there was no record of a current meter failure in the data documentation so this cannot be confirmed. Site 2 was also located in an area of rapidly changing bathymetry, thus poorly resolved bathymetry in the

Table 1. Observed (O) and predicted (P) values of x - and y -velocity for 5 locations in The Wash, where amplitudes (Amp.) are in m s^{-1} and phases are in degrees relative to the equilibrium phase angle for the tidal constituent at the Greenwich meridian, midnight 0/1 January 1900

	Site 1		Site 2		Site 3		Site 4		Site 5	
	Amp.	Phase	Amp.	Phase	Amp.	Phase	Amp.	Phase	Amp.	Phase
M₂: x-component										
O	0.31	266.2	0.29	282.2	0.40	260.1	0.40	255.9	0.22	262.0
P	0.33	275.7	0.40	273.0	0.42	264.0	0.41	253.0	0.33	265.8
M₂: y-component										
O	0.34	264.4	0.63	294.0	0.54	266.3	0.54	261.7	0.24	261.1
P	0.37	277.4	0.69	276.2	0.65	266.2	0.58	258.0	0.36	267.0
S₂: x-component										
O	0.11	307.7	0.07	150.4	0.14	306.6	0.15	301.7	0.08	304.0
P	0.11	322.1	0.14	321.6	0.15	315.0	0.14	299.7	0.10	311.8
S₂: y-component										
O	0.11	304.6	0.16	161.1	0.19	311.8	0.20	309.0	0.09	299.5
P	0.13	325.2	0.23	321.4	0.23	313.5	0.20	302.4	0.11	314.4

model may have been responsible for the overprediction of currents at this site. The location of the current meter at Site 5, at only 1 m above the sea bed, implies an influence of bottom friction on recorded currents and thus observed values were considerably lower than the predicted depth-mean velocity.

The larval transport model. Predicted currents and elevations from the hydrodynamic model were used to drive an advection-diffusion larval transport model for the investigation of environmental influences on shellfish recruitment variability. The advection-diffusion model solved the flux conservative form of the continuity equation describing the transport of a scalar quantity in 2 dimensions, given by

$$\frac{\partial C}{\partial t} + \frac{\partial}{\partial x}[(u + w_x)C] + \frac{\partial}{\partial y}[(v + w_y)C] = 0 \quad (4)$$

where u and v are the depth-mean velocity components in the x - and y -directions respectively, C is the scalar quantity, given by $C = \bar{c}H$, where \bar{c} is the depth-mean concentration and H is the total water depth, and w_x , w_y are diffusive fluxes defined by

$$w_x = -\frac{K_x}{C} \frac{\partial C}{\partial x} \quad w_y = -\frac{K_y}{C} \frac{\partial C}{\partial y}$$

for $C > 0$ ($w_x = w_y = 0$ if $C = 0$), where K_x and K_y are the horizontal diffusion coefficients (Smolarkiewicz & Clark 1986). Although larval mortality is an important consideration for the prediction of absolute values of larval settlement and recruitment, this study was concerned solely with relative differences in the numbers of settled larvae so the mortality term in the transport model could be neglected. This assumes that there is no spatial or temporal variation in mortality rates. The numerical scheme used to solve this equation was based on that of Smolarkiewicz (1983) and Smo-

larkiewicz & Clark (1986), which reduces the level of numerical diffusion through a number of anti-diffusion corrective steps. It was found that 3 corrective steps were optimum.

Model boundaries: In the development of the larval transport model, there were 3 types of boundary to consider: open, closed and moving. At the open boundaries, no transport of larvae into the models was permitted and larvae that left the model domain could not return. The validity of this assumption was assessed by investigating transport patterns at the entrance to The Wash using an adapted version of the large area oil spill model, EUROSPILL (Elliott 1991). The results of this study (Young 1996) suggested that neither tides nor any but very specific wind conditions would transport particles at or beyond the open boundary of the model back into The Wash.

Closed, or permanent land, and moving boundaries were treated as perfectly reflecting. However, it was possible for larvae to become stranded on tidal flats if a grid element dried between one timestep and the next. The implications of this are discussed later.

Estimation of residual numerical diffusion: Values for the horizontal diffusion coefficients to be used in an advection-diffusion model are not easily quantified. Observed levels of diffusion vary considerably with site location (Bowles et al. 1958, Groen et al. 1971, Elliott et al. 1997) and local environmental conditions (Bowden et al. 1974, Morales et al. 1997), and there is therefore a problem in defining the amount of diffusion to be predicted by a model. In addition, implicit numerical diffusion will contribute to the overall levels of diffusion in a model. Hence, before a value for the physical horizontal diffusion coefficients K_x , K_y could be chosen, it was necessary to evaluate the level of residual implicit numerical diffusion in the model. This was

achieved by using the model with the explicit diffusion terms omitted to simulate a discrete dye release experiment, estimating the degree of diffusion from the predicted concentrations at successive time steps using formulae given by Elliott et al. (1997). Dye releases were simulated for 4 stages of the M_2 tide (high, low, flood and ebb tides) resulting in estimates of latitudinal diffusivity ranging from $0.002 \text{ m}^2 \text{ s}^{-1}$ at high tide to $5.39 \text{ m}^2 \text{ s}^{-1}$ at flood tide. These values are comparable with observed values quoted in the literature of between 0.01 and $2 \text{ m}^2 \text{ s}^{-1}$ (Bowles et al. 1958, Veth & Zimmerman 1981, Zimmerman 1986, Elliott et al. 1997). It was therefore concluded that the residual numerical diffusion in the advection-diffusion model was comparable with observed levels of physical, horizontal diffusion and the explicit diffusive fluxes in Eq. (4) were neglected.

Incorporation of settlement processes: There are 2 hypotheses for the mechanism controlling larval settlement: active habitat selection and passive deposition. The former proposes that larvae are able to select favourable sites for their future survival as adults. The latter stipulates that larvae behave like passive particles and initially reach the sea floor at sites where sinking particulates, with fall velocities similar to larvae, settle. Evidence in the form of laboratory and field experiments to support both these hypotheses may be found in the literature (for example, Muus 1973, Eckman 1979, Mullineaux & Garland 1993). However, Butman (1987) argued that both processes may operate, but over different scales of space and time. It was suggested that the relative importance of the 2 processes may vary for different species (depending, for example, on the fall velocity and swimming capabilities of the organisms), for different flow environments, or depending on how long the organisms have been in the plankton. However, it was hypothesized that, in general, larvae may be passively deposited and accumulate at the large spatial scales (tens of metres to tens of kilometres) which apply to sediment transport and deposition, and that active habitat selection occurs over much smaller scales (centimetres to metres) within these broad depositional areas.

For the purposes of the numerical advection-diffusion model, it was necessary to choose settlement conditions which could easily be incorporated into the numerical scheme. Two possibilities were considered; a depth restriction and a flow condition. The species under consideration in this paper are intertidal and would therefore preferentially choose intertidal sites. The depth restriction chosen for the model to satisfy this criterion only allowed larvae to settle at sites shallower than 1.0 m below mean low water at springs [MLWS, equivalent to 0.1 m above lowest astronomical tide (LAT)].

For the development of a flow condition, the larvae of the common cockle and the common mussel were assumed to sink to the bed like particulate matter once competent to settle. As they are poor swimmers, with maximum recorded swim speeds of only 0.004 m s^{-1} (Bayne 1976), this is not an unreasonable assumption. The main characteristic of boundary-layer flows relevant to larval settlement is the presence of a region in the immediate vicinity of the bottom known as the viscous sublayer, where flow speeds are very low and larvae can undergo periodic sampling of the surface (Butman 1987). It was assumed that the viscous sublayer provides a suitable flow regime for the larvae both to settle without undergoing immediate resuspension, and to manoeuvre sufficiently to allow active habitat selection. As this study was only concerned with the prediction of the initial larval settlement, post-settlement resuspension was not considered. Based on formulae described by McCave (1988), and assuming that a larva requires a viscous sublayer of at least 5 body widths in depth to enable active habitat selection, with the size of competent mussel and cockle larvae assumed to be about $300 \mu\text{m}$ (Baggerman 1953, Bayne 1976), the maximum velocity at 1 m above the bottom for suitable near-bed flow conditions was estimated at 0.15 m s^{-1} . Although the number of assumptions required to achieve this result suggested a high degree of uncertainty in the suggested velocity, sensitivity tests suggested that the model was relatively insensitive to the choice of threshold velocity (Young 1996).

The velocity restriction alone permitted larvae to settle in areas which were unsuitable, such as the Lynn Deeps (Fig. 1). However, when both the depth and velocity restrictions were combined to limit settlement, larvae were only permitted to settle in suitable intertidal areas, but with enhanced settlement in regions with generally lower depth-mean velocities, as observed for *Mytilus edulis* settlement (Bayne 1976).

The parameter used to represent the propensity of larvae to settle onto the bottom was a composite measure of the relative competence of the larvae and their tendency to select the substratum encountered (active habitat selection) (Eckman 1990). As there was no information available on the settlement rates of mussel and cockle larvae in The Wash, 3 arbitrary rates were tested: 0.1 , 0.5 and 1.0% , where these are the percentages of larvae in a grid element satisfying the settlement criteria, which settle in 1 model timestep. The results suggested that a settlement rate of 1.0% per model timestep was the most suitable, allowing nearly 50% of the total retained larvae to settle over a settlement period of 2 d . This decision was not founded on observational evidence, but was purely to allow sufficient larvae to settle during a 2 d period for any changes in settlement due to influences such as winds

or tides to be clearly visible. Although the choice of settlement rate influenced the predicted number of settled larvae, the main areas of settlement remained the same for all 3 settlement rates.

The sensitivity of the model to variations in the length of settlement period, which is a measure of the ability of the larvae to delay metamorphosis until a suitable substratum is reached, was investigated by extending the settlement period from 2 to 4 d. It was found that while the number of settled larvae increased with increasing settlement period, the differences between the settlement patterns achieved with settlement periods of 2 and 4 d were small. Larvae can delay metamorphosis for considerably longer than this and with longer planktonic lives, wind-induced flow may transport some of these longer-lived larvae to suitable settlement sites. However, limitations on computer time restricted the length of model simulations and thus the length of settlement period.

Model experiments. Influences on larval settlement:

The numerical models were used to investigate the influences of winds, tides, location of spawning site, and tidal flat mortality on larval settlement. The mortality rate of larvae stranded in retained water on tidal flats during the planktonic phase is unknown and is likely to depend on a number of environmental factors. These include the length of time before the next tidal inundation, the intensity of predation by shore predators, and the degree of solar heating, which may increase mortality rates through heat stress and desiccation. It will therefore vary both temporally and spatially. An additional factor to consider is the contribution of the model-induced larval stranding mentioned earlier, which probably results in a greater number of predicted stranded larvae than would occur in reality. The sensitivity of the model to variations in the degree of tidal flat mortality on settlement was investigated by considering mortality rates of 0, 50 and 100%. The higher mortality rates caused a significant reduction in the numbers of retained and settled larvae, with a greater proportion of larvae settling in the central region of The Wash and a smaller proportion in the southeast and western margins (Young 1996). However, with no observational data available to guide otherwise, a 0% tidal flat mortality rate was chosen because the

higher levels of larval retention and settlement would produce a clearer distinction between good and poor larval settlement. Thus in the model simulations described below, all larvae survived until the next tidal inundation when they could re-enter the water column.

In each simulation, 100 000 larvae were released at a specified location, this being either East Gat Sand (G), Inner Westmark Knock (I) or Site 1 (Fig. 2, Table 2) for the investigation of winds, East Gat Sand or Site 1 for the investigation of tides, and one of the 15 sites of historically high cockle or mussel population densities (Fig. 2, Table 2) for the investigation of spawning site. The timing of larval release within the M_2 tidal cycle was found to have a small influence on the retention and settlement of larvae, with minimum retention and settlement predicted for a release at high tide (Young 1996). However, as the common cockle and common mussel are intertidal species, the peak in larval release is likely to be at high tide when the adult beds are submerged, and thus for this study all larvae were released at high tide. The stage of the M_2 tide at the



Fig. 2. Map of The Wash, England, indicating the 15 sites of frequently high density cockle and mussel populations (labelled A to O, see Table 2 for key), simulation-release Site 1, and the 6 possible bed groups (circled numbers), as determined by their characteristic settlement patterns. The lighter line indicates the level of lowest astronomical tide (LAT)

Table 2. Key to release sites shown in Fig. 2

Site label (Fig. 2)	Name of location
A	Wainfleet Sand
B	Wrangle Flats
C	Long Sand
D	Roger Sand
E	Toft Sand
F	Black Buoy Sand
G	Gat Sand
H	Holbeach
I	Inner Westmark Knock
J	Thief Sand
K	Breast Sand
L	Daseley's Sand/Nun Sand
M	Styleman's Middle/Blackguard Sand
N	Pandora Sand
O	Stubborn Sand

onset of settlement had no significant influence on larval settlement but to remove any additional influences from the results of the simulations settlement was commenced and concluded on a high tide.

For the investigations of the influences of winds and the location of the spawning site, larval lives of 21 d were assumed (approximately the larval life of the common cockle; Creek 1960) with a settlement period of 4 M_2 tidal cycles (about 2 d). Two series of experiments were conducted to investigate the influence of tides, firstly by releasing larvae at springs and varying the length of larval life from 17 to 32 d which thus varied the stage of the spring-neap cycle at the onset of settlement, and secondly by releasing larvae at 4 stages of the spring-neap cycle (springs, neaps, and 2 intermediate stages) and assuming larval lives of either 21 d for a release at Site 1 or 28 d for a release at East Gat Sand (approximately the larval life of the common mussel; Bayne 1976). By varying the length of the larval life it was possible to distinguish between the influences of tidal variations at release and the onset of settlement. Again, the settlement period was 4 M_2 tidal cycles.

For the investigation of the influence of winds, 5 types of wind forcing were applied to the model. These were constant winds of 5 m s^{-1} from the 4 compass directions (north, south, east, west) and the observed winds for the period of the simulation, which was arbitrarily chosen to commence on 6 June 1993 (springs). For the investigation of spawning site, the simulations were conducted both with and without the addition of the observed winds.

Predictive capability of the numerical models: Following these simulations, the ability of the models to predict cockle and mussel recruitment in The Wash was considered. For this, the models were used to hind-

cast settlement for 3 yr of observed good cockle and mussel spatfall (1978, 1980, 1986), 3 yr of poor cockle and mussel spatfall (1984, 1985, 1988), and 1 yr when cockle spatfall was good but mussel spatfall was poor (1993). The records of spatfall quality were available in the form of an ordinal, non-parametric 5-point scale, ranging from 'nil' to 'very heavy' (Dare & Walker 1992). These data were based on a combination of limited MAFF and Eastern Sea Fisheries Joint Committee (ES-FJC) surveys, and reports by fishermen. They also incorporate some post-settlement mortality and thus are not directly comparable with predictions of settlement. However, it was hoped that they would provide a basic comparison for the model predictions in the absence of more rigorous data. For the mussel simulations, information on the location of mussel beds was available and these were used as the larval release sites. However, observations of cockle beds were limited, so for the cockle release sites the 15 most frequent high density beds (Fig. 2) were used. For each simulation, 100 000 larvae were released into the model divided equally between the sites. Larvae were released on a high tide and commenced settlement on a high tide after planktonic periods of 21 d for the common cockle and 28 d for the common mussel. Larvae were allowed 8 complete M_2 cycles in which to settle (about 4 d). For these predictive simulations, information was required on the time of larval release. However, the lack of observations necessitated an estimate of spawning time based on a consideration of possible cues for larval release described in the existing published literature.

Estimation of spawning time: The timing of larval release in response to exogenous and endogenous cues is not well understood. Possible environmental cues for spawning include oscillations in illumination from the sun and moon, tidal rhythms, fluctuations in hydrostatic pressure, temperature, salinity changes in estuaries with tidal sweep, or salinity changes along the coast after seasonal rains. Other important factors include immersion time, exposure to rise in temperature, desiccation or low oxygen at low tide, wave action between low and high tide, food supply, and local changes in chemical constitution as a result of pollution, both natural and man-made (Korringa 1947, Palmer 1974, Forward 1987, Giese & Kanatani 1987, Morgan 1995). Exogenous cues may stimulate larval release directly, but many species time larval release more reliably by tracking environmental cycles endogenously (Morgan 1995). When full moons and high tides are obscured by clouds and winds, endogenous rhythms enable animals to anticipate these events and release larvae at the appropriate time.

Spawning may therefore be stimulated by a variety of environmental or endogenous cues and undoubtedly varies between marine species. Unfortunately,

field observations of spawning in the common mussel and the common cockle are limited and can lead to contradictory conclusions. There is some evidence to suggest that spawning in *Mytilus edulis* is synchronised by lunar cycles (Korringa 1947, 1957, Chipperfield 1953), although temperature is also thought by many people to influence, if not control, the sequence and timing of reproduction (e.g. Bayne 1976). Chipperfield (1953) suggested a threshold temperature of between 11 and 13°C for spawning in British waters. Savage (1956) observed mussels in The Wash to spawn late April to May, although it was also noted that severe frost induced earlier spawning.

Other studies of spawning initiation in the common mussel found no evidence for daylight-induced spawning (Korringa 1957), and no influence of exposure time to air (Lubet 1957). However, laboratory studies of spawning initiation by food availability (Starr et al. 1990) found that *Mytilus edulis* spawning could be triggered by a metabolite of phytoplankton in the surrounding water.

There are very few studies of spawning initiation in the common cockle. A study of the reproductive cycle of *Cerastoderma edule* in the Crouch estuary (UK) concluded that while the coordination of spawning was dictated by a variety of environmental factors, water temperature was a major influence (Boyden 1971). In the 2 years of the study, the water temperatures at spawning were 12.9 and 13.2°C, based on the mean maximum weekly temperatures 13.1 km downstream. However, a study of the population dynamics of the common cockle in northwestern Europe suggested that spawning was more likely to be stimulated by a sudden rise in temperature than by the suggested threshold temperature of 13°C (Ducrotoy et al. 1991).

After considering the above evidence for environmental initiation of spawning in the common cockle and common mussel, larval release times were chosen based on threshold temperatures of 13°C for *Cerastoderma edule* and 12°C for *Mytilus edulis*. As there was no evidence for the influence of tidal cycles on the spawning of the common cockle, the larval release time was chosen purely on the consideration of this threshold temperature. However, as several studies suggested that the common mussel spawns on a spring tide, a relationship which has been collaborated by recent observations of mussel spawning in The Wash by the ESFJC (Chris Beach pers. comm.), this was also considered in the choice of mussel larval release time. For ease of incorporation into the model, larvae were assumed to be released as a discrete pulse. The implications of this assumption are discussed later.

Sea temperature data: For the estimation of spawning time, sea temperature data from Brancaster,

approximately 9 km east of the mouth of The Wash, were available for 1978 to 1993 (Jones & Jeffs 1991). These were observations of near-surface temperatures, taken between 8 and 12 times per month, close to the time of high water. Data were obtained by lowering a thermistor accurate to $\pm 0.1^\circ\text{C}$ from the Brancaster harbour wall. Although Brancaster harbour is joined to the open sea by a series of narrow channels which are almost completely dry at low tide, and thus temperature data will include the influences of both direct solar heating and of air temperature above the periodically exposed channel bed, the common cockle and common mussel are intertidal species with established populations in tidal flat regions interspersed by narrow channels. Thus the situation for temperature recorded at Brancaster is similar to the tidal flats and recorded temperatures from Brancaster harbour are likely to be reasonable indicators of sea temperatures near the intertidal populations.

The following deals firstly with the results of the study of influences on larval settlement and secondly describes the applicability of the models to the prediction of observed levels of cockle and mussel spatfall in The Wash, including the sensitivity of the model predictions to small variations in spawning time.

RESULTS

Influences on larval settlement

Tides

The stages of the spring-neap cycle at larval release and at the onset of settlement had different influences, with the former influencing larval retention within The Wash and the latter influencing the transport of larvae to suitable settlement sites. The level of retention depended primarily on the number of spring tides occurring during the larval life which thus depended on the time of larval release in the spring-neap cycle and the length of larval life (Table 3). The greater the number of spring tides, the lower the level of retention. The percentage of retained larvae succeeding in settling was highest for an onset of settlement at springs when the higher tides resulted in the submergence of more of the suitable settlement sites as defined by the depth restriction on settlement incorporated in the larval transport model, and in the resuspension of more stranded larvae which were then available for settlement. Depending on the length of the larval life, these 2 influences interfered either constructively or destructively. With a larval life of 21 d, the influences of the spring-neap cycle at larval release and settlement were predicted to inter-

Table 3. Influence of spawning at different stages of the spring-neap cycle on larval retention and settlement for releases at Site 1 (21 d planktonic life, approximately that of the common cockle) and East Gat Sand (28 d planktonic life, approximately that of the common mussel). Here, %Settled is the percentage of retained larvae that succeeded in settling

Stage of spring-neap	Release at Site 1			Release at East Gat Sand		
	Retained	Settled	%Settled	Retained	Settled	%Settled
Springs	21163	9266	43.8	36887	20957	56.8
Springs-neaps	23156	10592	45.7	48846	26894	55.1
Neaps	24092	14130	58.7	46652	25270	54.2
Neaps-springs	20299	10437	51.4	40647	20549	50.6

fered constructively to produce a pronounced peak in the number of settled larvae for a release at neaps (and thus settlement at springs). However, with a larval life of 28 d, they were found to interfere destructively. Thus a release at springs with low retention but high percentage settlement resulted in a greater number of settled larvae than a release midway between neaps and springs which had a higher level of larval retention (Table 3).

Location of spawning site

The location of the larval release site was found to influence both the retention and settlement of larvae, with least retention predicted for release sites close to the northern open boundary and adjacent to the Boston Deep. The predicted settlement patterns for releases at the 15 sites showed similar distributions of peak larval settlement. However, the relative distribution of larvae showed considerable variation, although the addition of forcing from the observed winds for the period of the model simulation considerably reduced the magnitude and modified the distribution of the predicted differences. The tidally induced variation in larval settlement is most clearly illustrated by considering the differences between the normalised settlement pattern for a release at Gat Sand (G) and those for releases at the other 14 sites (Young 1996). These difference patterns suggested that the release sites could be classified into the 6 distinct groups shown in Fig. 2, each group having common characteristics of settlement distribution, although Pandora Sand (N) was found to exhibit some of the characteristics of both group 3 and group 2. The differences in settlement patterns between groups were attributable to localised settlement about the release site, which was due to the stranding and resuspension of larvae on tidal flats close to the release site. These results showed that accurately defining the location of a release site for the recruitment prediction simulations was unimportant.

Winds

The effect of wind forcing on larval retention and settlement showed some variation with release site as a result of variations in the local bathymetry, however the broad characteristics of the results were the same. The greatest influence was predicted for the intertidal sites (East Gat Sand and Inner Westmark Knock), and results are presented for East Gat Sand in Table 4.

The maximum increase in retention (compared to tidal forcing only) at each site was achieved with a constant northerly wind. However, the maximum increase in the percentage settlement of retained larvae was achieved with a constant easterly wind. The maximum decrease in retention was achieved with a constant southerly wind, except at Inner Westmark Knock where the complex local bathymetry reduced the deleterious influence of a southerly wind. Of the 4 wind directions, a constant westerly wind resulted in the lowest percentage settlement of retained larvae. However, the maximum decrease in the percentage settlement of larvae was achieved with the observed winds. This may be a result of a period of strong southerly and westerly winds between 15 and 19 June 1993 (Young 1996), although the variable magnitude and direction of the observed winds were likely to induce greater mixing which may also have influenced the results. These results suggest that periods of combined northerly and easterly winds are likely to enhance larval settlement, while periods of combined westerly and southerly winds are likely to reduce larval settlement.

The variability in the patterns of larval distribution and settlement due to the influence of wind forcing was studied by considering the differences between the normalised distribution and settlement patterns due to tidal forcing only, and those after the addition of the 5 types of wind forcing described earlier. The pre-

Table 4. Influence of wind forcing on larval retention and settlement for a release at East Gat Sand during 1993. %Settled is as defined in Table 3

Type of forcing	Retained	Settled	%Settled
Tides only	36823	19022	51.7
Constant E wind	42679	30187	70.7
Constant S wind	24472	15766	64.4
Constant W wind	41430	19039	46.0
Constant N wind	57344	30935	53.9
Observed winds	26528	10703	40.3

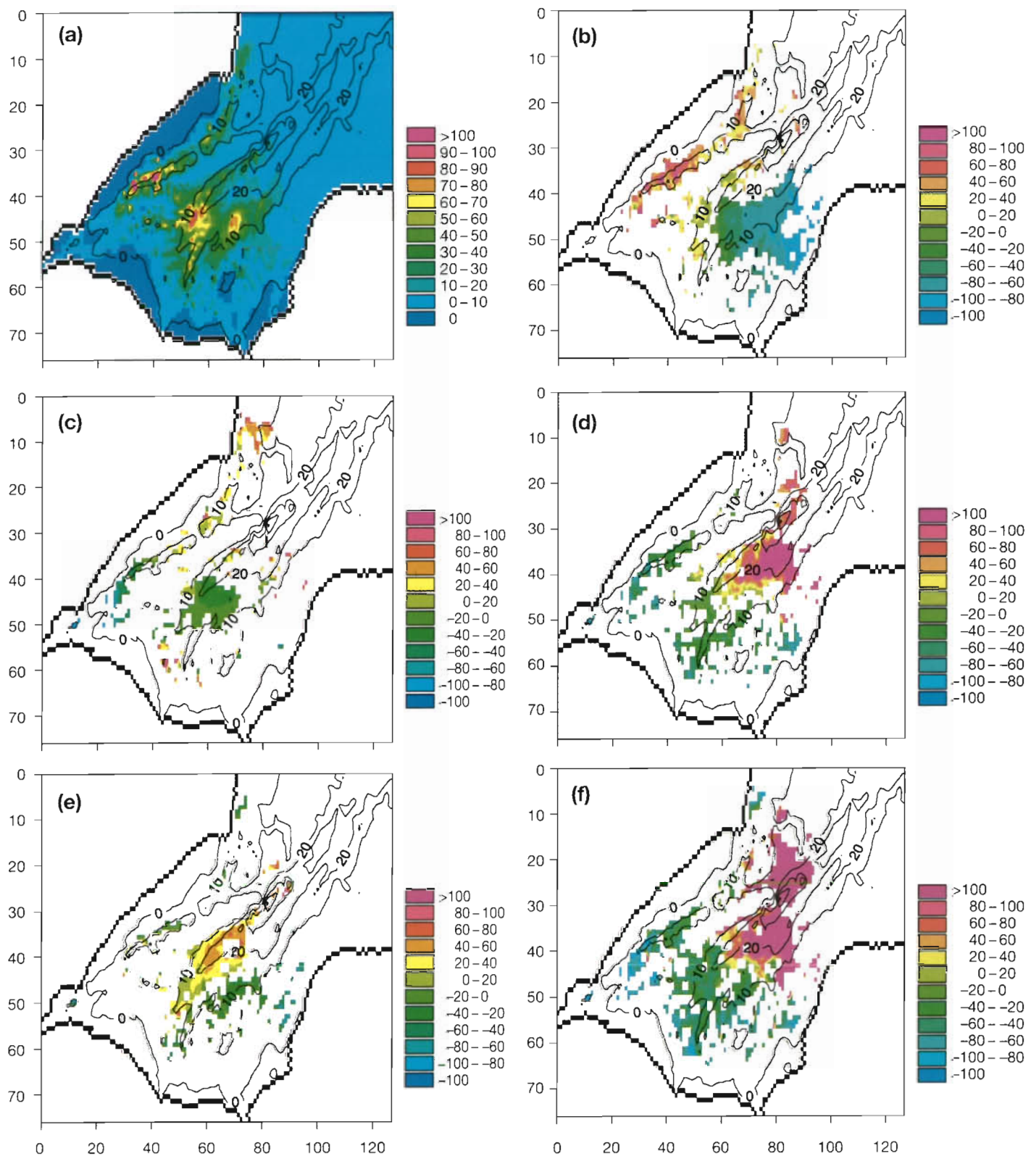


Fig. 3. (a) Predicted larval distributions 21 d after a release at East Gat Sand (G), and differences between this distribution pattern (normalised) and those predicted after additional forcing from a constant (b) easterly wind, (c) southerly wind, (d) westerly wind, (e) northerly wind, and (f) from the observed winds for this period. Units for (a) are number of larvae per 1/200° square and for (b) to (f) are differences in numbers of larvae per 1/200° square. The white fields in (b) to (f) are regions with differences of fewer than 5 larvae, hence only significant differences are shown

dicted larval distribution immediately prior to settlement due to tides only, following a release at East Gat Sand, is shown in Fig. 3a, and Fig. 3b to f illustrate the differences between this normalised distribution pattern and those after additional wind forcing. Here, the distribution patterns are shown for clarity, but the predicted settlement patterns revealed similar characteristics.

The development of these predicted larval distributions may be considered by comparing them with the predicted flow fields due to wind forcing only (Young 1996). The main characteristics of the larval distribution patterns are attributable to the deficit of larvae in the flows originating at the open boundaries of the model, and the initial concentration of larvae in the south of The Wash. Thus flows originating at the northern open boundary such as southwestwards flows along the Lynn Deeps induced by westerly and southerly winds, and southwestwards flows along Boston Deep induced by westerly and northerly winds, resulted in relative deficits of larvae in the central southwesterly regions and the Boston Deep respectively. Conversely, flows originating at the head of The Wash such as northeastwards flows along the Lynn Deeps induced by easterly and northerly winds, and northeastwards flows along Boston Deep induced by easterly and southerly winds, resulted in relatively more larvae in the central and northwest regions respectively. A relative deficit of larvae in the south-east of The Wash was predicted with the addition of easterly wind forcing due to southwestwards flows in the southeastern channels of The Wash which had originated at the eastern open boundary. Conversely, relatively more larvae were predicted in the central southeast region of The Wash with the addition of westerly wind forcing due to northeastwards flows in these channels which had originated at the head of The Wash.

The differences between the predicted larval distribution pattern for tidal forcing only and the predicted distribution after the addition of forcing from the observed winds (Fig. 3f) were similar to those due to a constant westerly wind (Fig. 3d). This suggests that the westerly component of the observed winds during the model simulation had a strong influence on the predicted larval distribution.

Predictive capability of the numerical models

Effect of small variations in spawning time

The predicted numbers of retained and settled cockle larvae, and the percentage settlement of retained larvae, both with and without wind forcing

with the observed winds, are shown in Table 5 for releases at different stages of the spring-neap cycle. The results of the simulations with tidal forcing only are readily explained by a consideration of the predicted influences of the spring-neap cycle discussed earlier (cf. Table 3). However, the addition of wind forcing was sufficient to completely disrupt these trends, inducing considerable decreases in the numbers of retained and settled larvae and in the percentage settlement of retained larvae, and considerable increase in the variation in these quantities over the 4 tidal stages. The low retention and settlement predicted following the 3 earlier spawning dates were a result of 5 d of strong south to southwesterly winds between 28 May and 1 June which occurred before the transition from neaps to springs. The predicted settlement distributions for the 4 simulations also showed some variability, with peak settlement regions showing a shift from the westernmost tidal flats for spawning at springs to the southeasterly flats for spawning between neaps and springs.

The results of this section suggest that while variation in the stage of the spring-neap cycle at larval release has some influence on larval retention and settlement, the variation in the wind field resulting from the different release times has a considerably greater influence. The large difference in retention and settlement predicted for release times separated by less than a week clearly demonstrates the sensitivity of the model to wind forcing, and indicates a necessity to more accurately define the time and duration of larval release if the model is to be used to produce accurate recruitment predictions. This sensitivity to winds also suggests that prolonged delay in metamorphosis, for example due to adverse environmental conditions, could have a significant influence on larval settlement distribution.

Table 5. Predicted numbers of retained and settled larvae, and the percentage settlement of retained larvae, for releases of larvae divided equally between the 6 known cockle beds at 4 stages of the spring-neap cycle, both with and without wind forcing from observed winds, for model simulations of 1993

Tidal stage	Retained	Settled	%Settled
Tidal and wind forcing			
Springs	21927	9709	44.3
Springs-neaps	15147	7684	50.7
Neaps	5749	2824	49.1
Neaps-springs	33777	18497	54.8
Tidal forcing only			
Springs	54650	35723	65.4
Springs-neaps	59521	40438	67.9
Neaps	61476	43806	71.3
Neaps-springs	55872	40504	72.5

The observed cockle spatfall in 1993 was good, with the highest recruitment levels on the southeastern tidal flats. A comparison of these observations with the model-predicted settlement for the 4 hypothesized release times suggested that a release of larvae between neaps and springs was the more likely release date as it resulted in both the highest levels of retention and settlement and relatively more settlement in the southeast. This release date was approximately 5 d after the release date suggested by a consideration of a threshold temperature of 13°C, suggesting either that using a threshold temperature as the sole indicator of cockle spawning in The Wash may not accurately define the time of larval release, or that if the period of spawning was spread over some days (centred on 18 May), those larvae spawned towards the end of the period made the largest contribution to the recruited population.

Prediction of recruitment success and distribution for specific years

Considerations of threshold temperatures and spring tides (mussels) in the estimation of cockle and mussel spawning times resulted in multiple possible larval release dates in some of the years modelled (1978, 1980, 1986, 1993) due to a combination of temperature fluctuations and coincidence of threshold temperatures with spring tides. For the simulation of cockle settlement in 1993, the most likely release date identified in the sensitivity study was used, based on a comparison with tidal forcing only simulations. Following these initial model simulations, further possible release dates were identified in an attempt to more closely match observed levels of recruitment. The choice of these dates included considerations of the threshold temperatures at a second site (Blakeney, about 25 km east of Brancaster), a sudden rise in temperature at Brancaster, and the observed winds for the simulation periods. The observed levels of spatfall, the predicted numbers of retained and settled larvae, and the percentage settlement of retained larvae for all these simulations are shown in Tables 6 & 7 for cockle and mussel settlement respectively. The larval release date most likely to have produced the observed recruitment in each of the years studied, based on a comparison with model simulations using purely tidal forcing, is highlighted in the tables.

Using the initial choices of release date, model simulations of cockle and mussel spatfall in 1980, 1988 and 1993 matched observed spatfall levels. Similarly accurate predictions were obtained for cockle spatfall in 1986. However, choosing a release date based on a consideration of a sudden rise in temperature produced more accurate predictions of cockle and mussel spatfall in 1978. Accurate predictions of cockle and mussel spatfall in 1985, and mussel spatfall in 1986, could be obtained by a consideration of the observed winds during the model simulations. The models failed to reproduce observed spatfall levels in 1984.

The availability of information on the spatial distribution of cockle and mussel spatfall in 1993 enabled a comparison of the predicted settlement with observed recruitment patterns. The predicted patterns of larval settlement for the mussel simulation of 23 April and the cockle simulation are shown in Fig. 4a and b respectively. Although the 2 mussel simulations of 1993 predicted peak settlement in the same areas, a plot of the percentage differences between the normalised settlement patterns revealed some differences, with the release of larvae in May resulting in relatively more larvae settling on the southeastern tidal flats and relatively fewer larvae settling in the west. This is attributable to differences in the wind forcing during the 2 periods with a stronger easterly component to the winds during the period of the first simulation. The currents induced by these winds transported larvae towards the western tidal flats and thus relatively more

Table 6. Results of model simulations of cockle larval settlement for 7 yr of observed good or bad spatfall. Results in bold indicate the most likely release time. The observed spatfall scale ranges from nil (0) to very heavy (4), with brackets indicating a localised spatfall. The qualifiers used in determining the choice of spawning date are as follows: A, original consideration of a threshold temperature at Brancaster; B, consideration of a sudden rise in temperature at Brancaster; C, consideration of observed winds; D, consideration of a threshold temperature at Blakeney

Year	Observed spatfall	Simulation start date	Qualifier	Retained	Settled	%Settled
1978	3	15 May	B	38371	23698	62.3
		25 May	D	27825	12919	46.4
		29 May	A	26058	10920	41.9
1980	3	21 May	A	28292	16222	57.3
1984	0	23 April	B	32348	17067	52.8
		6 June	A	33575	14286	42.5
1985	0	25 May	A	29427	12570	42.7
		8 June	C	13688	6577	48.0
1986	3	18 May	A	2277	1150	50.5
		27 May	A	16994	8180	48.1
		11 June	A	34273	18979	55.4
1988	(1)	21 May	A	16313	7051	43.2
1993	3	2 June	A	28855	15697	54.4

Table 7. Results of model simulations of mussel larval settlement for 7 yr of observed good or bad spatfall. Results in bold indicate the most likely release time. The observed spatfall scale ranges from nil (0) to very heavy (4), with brackets indicating a localised spatfall. The qualifiers used in determining the choice of spawning date are as follows: A, original consideration of a threshold temperature at Brancaster; B, consideration of a sudden rise in temperature at Brancaster; C, consideration of observed winds

Year	Observed spatfall	Simulation start date	Qualifier	Retained	Settled	%Settled
1978	2	8 May	B	35243	21757	61.7
		23 May	A	16093	7162	44.5
		7 June	A	13467	5164	38.3
1980	2	15 May	A	16491	10065	61.0
		1 June	A	5614	2524	45.0
1984	0	1 May	B	23356	10989	47.0
		31 May	A	23383	11104	47.5
1985	0	20 May	A	17555	8658	49.3
		4 June	C	14328	7315	51.1
1986	2	9 May	A	1036	485	46.8
		25 May	A	7236	3451	47.7
		8 June	A	9668	5112	52.9
		11 June	C	28213	14182	50.3
1988	0	16 May	A	11412	5006	43.9
1993	(1)	23 April	A	11175	5671	50.7
		23 May	A	12553	6443	51.3

larvae settled in this region following the release of larvae in April.

In 1993, mussel spat was observed in small quantities [level (1) on the spatfall index] on Inner Westmark Knock (I), West Gat Sand (G), Mare Tail, East Gat Sand (G) and Nun Sand (L) (ESFJC 1994). However, there was no information available on the relative magnitude of spatfall between the observed beds. Thus although there were differences in the model-predicted settlement patterns, both the mussel simulations predicted settlement on all the observed sites at the observed low magnitude and therefore it was not possible to identify the more likely time for mussel larval release in 1993.

The choice of the more likely time of cockle larval release from the sensitivity study included a consideration of the spatial distribution of predicted settlement, with the latest release date producing more settlement on the southeastern flats. Again this was attributable to wind forcing, with the first part of the simulation experiencing winds with a mean easterly component which thus aided retention, and winds with a mean westerly component during the latter half of the simulation to produce relatively more settlement in the southeast. There was a good cockle spatfall (level 3 on the spatfall index) in 1993 with the majority of settlement observed on the southeastern tidal flats, and no significant settlement in the western region of The Wash, in good agreement with the model predictions.

Although the model simulations successfully predicted cockle and mussel spatfall on the observed beds, they also predicted larvae to settle in regions where they were not observed. For example, mussel settlement was also predicted on Wainfleet Sand (A), Long Sand (C), Roger Sand (D) and Styleman's Middle (M), while cockle settlement was predicted on Styleman's Middle (M), Gat Sand (G) and Roger Sand (D).

DISCUSSION

Both the study of influences on larval settlement and the investigation into the predictive capability of the numerical models suggested a strong influence of wind forcing and consequently of the timing of larval release in relation to the applied winds. The former study suggested that periods of predominantly northerly and easterly winds would be conducive to good settlement while

periods of predominantly southerly and westerly winds would result in poor settlement. This simple hypothesis explains the majority of the results obtained in the predictive studies. Successful predictions of good cockle spatfall in 1978 (15 May simulation), 1980, 1986 (11 June simulation) and 1993, and of good mussel spatfall in 1978 (8 May simulation), 1980 (15 May simulation) and 1986 (11 June simulation) were due to a predominance of winds with northerly and easterly components during these simulations (Young 1996). The dominant north-easterly winds in May 1980 would also suggest that choosing larval release dates earlier in May could have further increased the predicted settlement. Successful predictions of poor cockle spatfall in 1985 (8 June simulation) and 1988, and poor mussel spatfall in 1985 (4 June simulation), 1988 and 1993, were due to periods of strong southerly and westerly winds during these simulations (Young 1996). However, other proposed spawning dates in all these years failed to produce good predictions of observed recruitment, suggesting either unsuitable choices of model spawning date, or the influence of factors not taken into account in the model such as post-settlement mortality. The simulations of mussel settlement in 1986 are of particular interest because delaying the spawning date by just 3 d, from 8 June to 11 June, changed a predicted poor settlement to a good settlement. The winds for the intervening 3 d were strong southwesterlies which induced a large loss of larvae immediately after spawning.

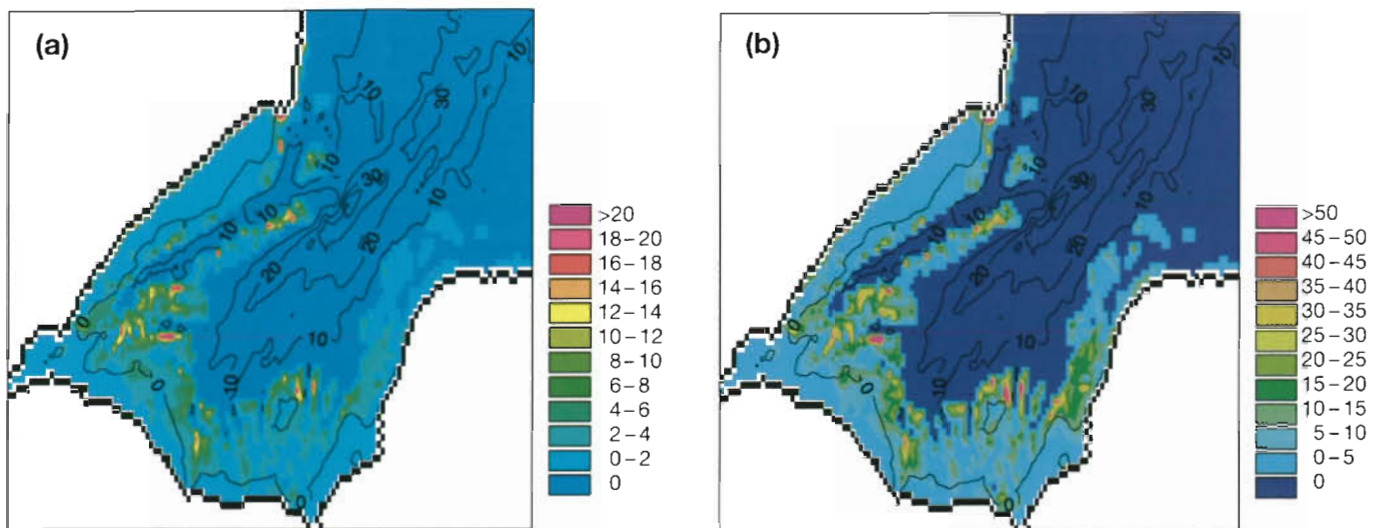


Fig. 4. (a) Predicted mussel larval settlement for a release of larvae on 23 April 1993. (b) Predicted cockle larval settlement for releases of larvae on 2 June 1993. Units are number of larvae per $1/200^\circ$ square

Wind-induced currents therefore play a significant role in the settlement of mussel and cockle larvae in The Wash and could have been responsible for the observed levels of spatfall in the majority of years studied. A number of other factors may, nevertheless, have limited the accuracy of the model predictions, including behavioural characteristics of cockles and mussels, environmental influences such as preceding winter temperatures, and substrate requirements for settlement, and the problem of comparing model predictions of settlement with observations of spatfall which include some post-settlement mortality. Mussels have been observed to undergo a process of primary and secondary settlement (Bayne 1964, 1976). Primary settlement of newly metamorphosed post-larvae takes place onto filamentous substrata such as hydroids and various algae. Subsequently, individuals re-enter the plankton by byssus drifting, and then undergo secondary settlement onto the adult habitat. However, a study of intertidal mussels in the west of Ireland found evidence for the direct settlement of mussel larvae onto adult beds (McGrath et al. 1988), suggesting that settlement processes may be site-dependent. The introduction of a second planktonic phase would expose young mussels to a second period of wind-induced currents which are not included in the model and may limit the accuracy of the predictions.

In The Wash, suitable settlement areas for mussels are mostly confined to previously established beds where the shells of old mussels provide a suitably solid substratum. Settlement processes in the numerical model do not take into account the suitability of the substratum and thus mussel larvae may be predicted to settle in areas where they would physically

be unable to settle [such as Long Sand (C) and Wainfleet Sand (A)]. Mussels have also been observed to delay metamorphosis until they find a suitable substratum (Bayne 1965). Prolonged delay of metamorphosis is not incorporated into the numerical model and would result in a longer planktonic larval phase with subsequently longer exposure to the influences of wind-induced currents, again limiting the accuracy of the model predictions. Similarly, cockle larvae may be able to delay metamorphosis until a suitable substratum is reached (Pechenik 1990). However, as cockles settle on sand, which is abundant in the intertidal regions of The Wash, the substratum is unlikely to be a significant limitation to the accuracy of the model predictions.

In a statistical study of environmental influences on mussel and cockle recruitment in The Wash, Young et al. (1996) found that good mussel recruitment was associated with low preceding winter temperatures. Cold winters enhance recruitment either by a reduction or delay in crab predation (Beukema 1991) or possibly by a reduction in maintenance metabolism releasing more energy reserves for gametogenesis (Dare & Walker 1992). Thus, 1986 had below-average preceding winter temperatures which may have enhanced mussel spatfall.

The difference in the nature of the observations and predictions may have been a significant limitation to the accuracy of model predictions; whilst the predictions are of larval settlement, the observations are of spat in September and thus include some post-settlement mortality. It has been observed (Matthew Mander pers. comm.) that storm events and periods of strong northeasterly winds can annihilate recently

settled mussel spat in The Wash through increased wave action. Thus predictions of settlement are not necessarily an accurate predictor of recruitment. Post-settlement mortality may have contributed to discrepancies between model predictions of the spatial distribution of cockle and mussel settlement in 1993 and observed spatfall. Although the models correctly predicted recruitment at the observed locations, additional settlement was predicted to occur at sites where no spatfall was observed. However, these observations were compiled from limited surveys undertaken by MAFF and the ESFJC in which only the beds considered most likely to become commercially viable were sampled, thus producing a further potential discrepancy between observations and predictions.

The numerical models failed to reproduce the observed poor levels of cockle and mussel spatfall in 1984. The observed winds in 1984 were predominantly northeasterly in May and variable in June with a frequent northerly component. These winds would be conducive to good retention and settlement. Thus it is unlikely that wind-induced currents were responsible for the poor larval spatfall in 1984. In addition to the potential sources of inaccuracy discussed above, the level of mussel brood stocks was observed to be low in 1984 and although adult cockle stocks were good, the quality of cockle meat was observed to be poor, which may have influenced gametogenesis. The hot summer in the previous year may have decreased the size and quality of brood stocks through increased desiccation. Thus, although Dare & Walker (1992) found no relationship between the size of the adult stock and spatfall, there is evidence to suggest that there may have been fewer than average larvae released into the water column in 1984 which may have contributed to the poor spatfall.

Although wind-induced currents clearly have a strong influence on larval settlement, predictions of larval settlement for specific years were strongly dependent on the choice of spawning date. Choosing a spawning date based on a consideration of threshold temperatures and spring tides resulted in model predictions of settlement in good agreement with observed cockle spatfall in 4 of the 7 years studied, and with observed mussel spatfall in 3 of the years. Observed levels of spatfall in 1978 were more closely predicted using a consideration of a sudden rise in sea temperature in Brancaster as the cue for spawning. This environmental cue would also suggest a spawning date in early May in 1980 which would result in higher levels of settlement, more closely matching observations as discussed earlier. Simulations of cockle and mussel settlement in 1984 and 1985, and mussel settlement in 1986, failed to reproduce the observed levels of spatfall using hypothesized release dates based on considera-

tions of temperature. These results would suggest that assuming a threshold temperature to be the primary stimulus for spawning in cockle and mussel populations in The Wash may not be wholly applicable and that spawning is more likely to be initiated by the co-ordination of a number of environmental factors, as suggested by Boyden (1971). The large variability in predicted settlement for simulations separated by only 3 d in 1986 emphasises the necessity to more accurately define the time of larval release. This result also highlights the problem of assuming larvae to be released into the model as a discrete pulse, whereas in reality, both cockle and mussel larval release may be spread over several weeks, although it is generally agreed that the release curves have a distinct peak (Rasmussen 1973). If it is assumed that the time of larval release used in the model simulations is the peak of the release curve, it is necessary to consider the possible contribution of larvae released before or after the peak.

CONCLUSIONS

Interannual variability in the recruitment of cockle and mussel larvae to suitable settlement sites has been hypothesized as a major contributor to variability in fishery yields in The Wash, England (Dare & Walker 1992). This numerical modelling study has shown that wind-induced currents have a significant effect on the quantity and distribution of cockle and mussel larval recruitment in The Wash. From an initial release of 100 000 larvae, those predicted to settle for a range of wind conditions was found to differ by as much as 20 232, more than 3 times the variability of 6345 predicted for a range of tidal conditions. Model simulations for specific years suggested that interannual variability in wind direction and strength could produce greater than a 40-fold difference in the number of successfully settling larvae. For example, while the predicted number of settled mussel larvae for a spawning date of 9 May 1986 was only 485, that for a release date of 8 May 1978 was more than 40 times greater at 21 757. These results are in good agreement with a previous statistical study (Young et al. 1996) which found that wind-induced currents during the period of larval drift (spring and early summer) could be responsible for interannual recruitment variability. The concept of supply side ecology has been shown to be the key factor controlling some rocky shore communities (Kendall et al. 1982, Roughgarden et al. 1994). However, an extensive review of previous studies of marine soft sediment communities (Olafsson et al. 1994) concluded that pre-settlement processes were not important for the shaping of these communities. Whilst less dramatic

than the upwelling frontal systems dictating larval recruitment on the Californian coastline (Roughgarden et al. 1988), this study strongly suggests that wind-induced larval transport in The Wash is a major contributor to interannual cockle and mussel recruitment variation.

However, the application of numerical modelling to the prediction of future fishery yields would at present appear to be limited. The lack of biological information, in particular on the timing and duration of spawning, is a considerable restriction to the accurate prediction of cockle and mussel retention and settlement. In addition, there is evidence to suggest that other pre- and post-settlement processes exist which influence recruitment to a similarly high degree. These include the enhancement of mussel spatfall by cold temperatures during the period of gametogenesis (Young et al. 1996), and the temporally and spatially variable influences of predation, adult-juvenile interactions, and storms on post-settlement mortality. Previous studies have concentrated on either observational work or numerical modelling. The conclusions of this study would suggest that understanding of mussel and cockle populations in The Wash could be significantly enhanced by a combined observational and modelling study. Ideally, this would involve the monitoring of spawning, the behaviour of larvae in the plankton, and the preliminary survival of settled larvae, combined with numerical modelling of the wind-driven larval transport. This would not only provide further insight into the relative importance of pre- and post-settlement processes on cockle and mussel recruitment in The Wash but would provide sufficient data for a rigorous test of the use of the numerical model as a predictive tool.

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