

Pelagic dispersal of Norway lobster *Nephrops norvegicus* larvae examined using an advection-diffusion-mortality model

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ABSTRACT: Norway lobster *Nephrops norvegicus* (L.) larvae are hatched into the water column from areas of fine mud and spend about 50 d in the plankton before resettling onto mud as juveniles. Whilst in the pelagic environment, however, advection and horizontal turbulent diffusion spread larvae away from the mud region and thus potentially could limit recruitment. A simple advection-diffusion-mortality model has been used to examine the likely losses of larvae from an *N. norvegicus* system due to pelagic dispersal. Turbulent diffusion alone causes insufficient loss to affect recruitment on mud patches larger than 20×20 km for reasonable estimates of eddy diffusivity. Low levels of mean advection (0.04 to 0.05 m s⁻¹), however, severely limit settlement even on very large mud areas (100×100 km). Distributions of larvae released from a mud region in the western Irish Sea consistently show them to be spread southward away from the mud patch although it remains unclear whether advection in the region is sufficiently large for these losses to influence recruitment.

INTRODUCTION

A planktonic larval phase is a common feature of the life-cycle of many marine organisms. During such time, the larvae are subject to controls that operate in the pelagic environment and, in particular, to the processes of horizontal advection and turbulent diffusion. For some species, advection of larvae by current systems is crucial in order to transport them to specific locations. North Sea herring *Clupea harengus*, for example, are spawned to the north and east of Britain and their larvae are transported by the mean anticlockwise circulation of the North Sea to nursery areas off the Danish and German coasts of continental Europe (Fig. 1). Bartsch et al. (1989) have argued that disruption of the general anticlockwise circulation for significant periods under anomalous wind forcing conditions can severely limit the number of larvae that successfully reach the nursery areas. The circulation pattern during the larval phase thus constitutes an important environmental control on the level of recruitment in any given year class.

Another example concerns the larvae of blue crab *Callinectes sapidus*. These larvae are flushed out of estuaries onto the inner continental shelf of the eastern

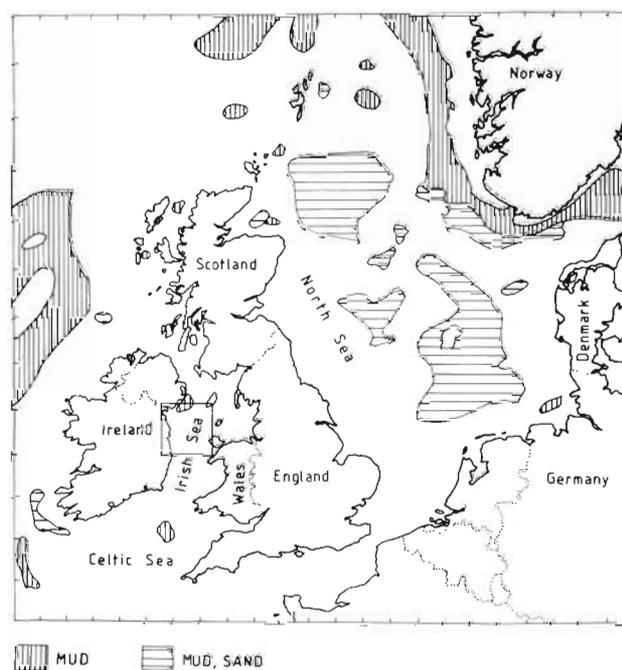


Fig. 1. Distribution of fine mud on the European continental shelf showing the western Irish Sea mud region (adapted from Lee & Ramster 1981)

United States where they are subject to dispersal processes. Blue crab postlarvae return to an estuarine environment in order to settle into nursery areas. Epifanio et al. (1989) have argued that although blue crab larvae are transported southward away from the mouth of the Delaware estuary by a narrow buoyancy-driven coastal current, larvae that are dispersed offshore may be carried northward again by the mean wind-driven flow on the inner continental shelf thus enabling them to be retained in the vicinity of the estuary. Likewise Goodrich et al. (1989) have argued that wind-driven surface flows, particularly those related to storm events, are important for transporting blue crab megalopae from the open continental shelf into Chesapeake Bay prior to settlement.

The present case concerns the Norway lobster *Nephrops norvegicus*, which is a substrate-specific benthic organism that lives on patches of fine mud on the European continental shelf. It releases larvae into the water column which, after a pelagic phase of about 50 d, must settle back onto mud. For isolated mud patches, therefore, advection and turbulent diffusion transport larvae away from the settling area and hence represent a general loss to the system. In this paper observations relating to the larval ecology of an *N. norvegicus* population in the western Irish Sea (Fig. 1) are briefly reviewed before applying a simple model that includes advection, turbulent diffusion and larval mortality to quantify the likely effects of pelagic losses on the recruitment of *N. norvegicus*.

NEPHROPS NORVEGICUS IN THE WESTERN IRISH SEA

Nephrops norvegicus is a benthic, marine decapod which is prevalent on the continental shelf of western Europe. It has a variety of common names including Norway lobster, langoustine, scampi and, in the western Irish Sea, is known as Dublin Bay prawn. Adult *N. norvegicus* are substrate-specific requiring a habitat of fine mud in which to burrow (Farmer 1975). The distribution of such mud areas on the European shelf is shown in Fig. 1 and shows the location of the Irish Sea patch in particular. In the Irish Sea females hatch their larvae into the water column from March to June where they develop through 3 stages over a period of 50 to 60 d. At the end of the pelagic phase larvae metamorphose into postlarvae (Stage IV) and settle onto the sea bed. Chapman (1980) discussed the ecology of juvenile *Nephrops*. He argued that juveniles inhabit burrows in the same areas as adults and rarely emerge from the burrows in their first year. Crnkovic (1968) showed in aquarium studies that juvenile *N. norvegicus* burrow in mud and concluded that they did so to feed. *N. nor-*

vegicus are thus hatched from mud areas and must ultimately settle onto mud as juveniles in order to survive. Whilst in the water column the larvae are planktonic, having little independent capacity for horizontal movement although, like many zooplankton, their later stages are capable of limited vertical migration.

A number of surveys of the distribution of *Nephrops norvegicus* larvae have been conducted in the western Irish Sea by the United Kingdom Ministry of Agriculture Fisheries and Food with a view to assessing the female spawning stock (Nichols et al. 1987). These surveys suggest that a total of about 3.9 to 5.2×10^{11} larvae are released into the water column over a 3 mo hatching season from late March to June. With estimates of mean effective female fecundity, γ , in the range 580 to 890, Nichols et al. (1987) estimated a female spawning stock in the range 4.4×10^8 to 8.9×10^8 . The area of the western Irish Sea mud patch is about 5×10^3 km² and this implies a mean adult (benthic) population density of 0.1 to 0.4 m⁻². Repeated larval surveys in the course of a single year enabled Nichols et al. (1987) to estimate an instantaneous larval mortality rate of 0.03 to 0.04 d⁻¹.

The spatial distribution of *Nephrops norvegicus* larvae in the Irish Sea is of considerable interest. Distribution patterns consistently show a preferential displacement of larvae to the south of the mud area from which they are released (Nichols et al. 1987, White et al. 1988). Fig. 2, taken from White et al. (1988), shows the distribution of larvae in May 1984 and clearly shows a

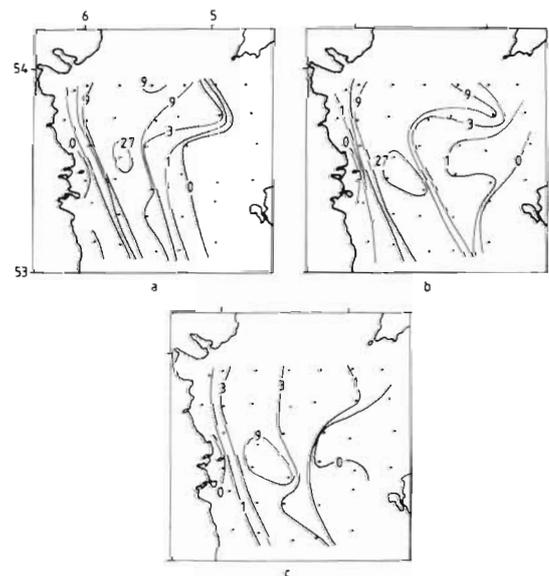


Fig. 2. *Nephrops norvegicus*. Distribution of larval stages in the western Irish Sea in May 1984. (a) Stage I; (b) Stage II; (c) Stage III. Distribution of each stage shows a pronounced tongue of high numbers extending southward away from the mud patch region (White et al. 1988)

tongue of high numbers spread to the south of the southern limit of the mud patch. White et al. (1988) suggested that this distribution was consistent with the presence of a southward flowing current close to the Irish coast inferred from the density field at the time of the survey. The western Irish Sea mud patch is isolated and there are no suitable settling areas within 300 km to the south of it. Larvae dispersed to the south of the patch are thus likely to be completely lost to the Irish sea population. Does such pelagic loss constitute an important control on recruitment to the population?

NEPHROPS NORVEGICUS PRODUCTION AND RECRUITMENT

The total number, N_0 , of *Nephrops norvegicus* larvae that are released into the water column over the hatching season is determined by the number of spawning females on the mud patch, thus

$$N_0 = \gamma N_f \approx \gamma \frac{N_a}{2} \quad (1)$$

where N_f = number of spawning females (assumed to be approximately half of the number of adults, N_a); γ = mean effective female fecundity.

In order for a population to be self-sustaining it is necessary for sufficient larvae to survive to the settling stage in order to replace benthic organisms (juveniles and adults) that have been lost through mortality. Let M_j and M_a be the juvenile and adult mortalities respectively. Let τ_j and τ_a be respectively the durations of the juvenile and adult parts of the life-cycle.

Loss of juveniles and adults by mortality is illustrated schematically in Fig. 3. N_1 juveniles are recruited per

year from settling post-larvae and N_2 adults are recruited per year from juveniles. It is assumed that τ_a is such that most adults have died after this duration. The level of juvenile recruitment that is required to sustain the population is readily shown to be

$$N_1 = N_a M_a \exp(M_j \tau_j) \quad (2)$$

Using Eq. (1) the number of larvae that must be retained at settling time to ensure the population is sustained is N_{ret} where

$$N_{ret} \geq N_1 = \frac{2 N_0 M_a \exp(M_j \tau_j)}{\gamma} \quad (3)$$

In the western Irish Sea, mortality (including fishing mortality) of adult *Nephrops norvegicus* lies between 0.2 and 0.7 yr^{-1} (Brander & Bennet 1986). There is little evidence relating to mortality during the juvenile period and, in the absence of a better estimate, it is supposed that this lies in the same range as adult mortality. The juvenile duration is taken as 3 yr and γ is assumed to be in the range 500 to 1000. Putting these values into Eq. (3) gives N_{ret} in the range 0.07% $\times N_0$ to 2.2% $\times N_0$. With $M_a = M_j = 0.4 \text{ yr}^{-1}$ and $\gamma = 500$, $N_{ret} = 0.5\% \times N_0$.

Whilst in the water column larvae are lost from above the mud patch by the processes of advection, turbulent diffusion and mortality. These processes thus control the number of larvae that can potentially settle onto the patch and ultimately be recruited to the population. In the following section a simple advection-diffusion-mortality model is presented that can be used to investigate the likely effects of these controls upon retention and recruitment.

THE MODEL

Consider a rectangular mud patch of dimensions L_x and L_y in the x and y directions respectively and centred at $x = y = 0$ (Fig. 4). Suppose that at some initial time, $t = 0$, $N_0(x_p, y_p)$ larvae are released into the water column at an arbitrary point P with coordinates (x_p, y_p) . The concentration $C(x, y, t)$ of larvae at position (x, y) at subsequent time, t , is governed by the following advection-diffusion-mortality equation:

$$\frac{\partial C}{\partial t} + u \frac{\partial C}{\partial x} = K \left(\frac{\partial^2 C}{\partial x^2} + \frac{\partial^2 C}{\partial y^2} \right) - m C \quad (4)$$

(a) (b) (c) (d)

Term (a) represents the rate of change with time, t , of larval concentration at a given point. This change is brought about by terms (b), (c) and (d). It is supposed, for simplicity, that horizontal advection (term b) takes place only in the x direction with constant speed u . Larvae are dispersed in 2 dimensions by horizontal

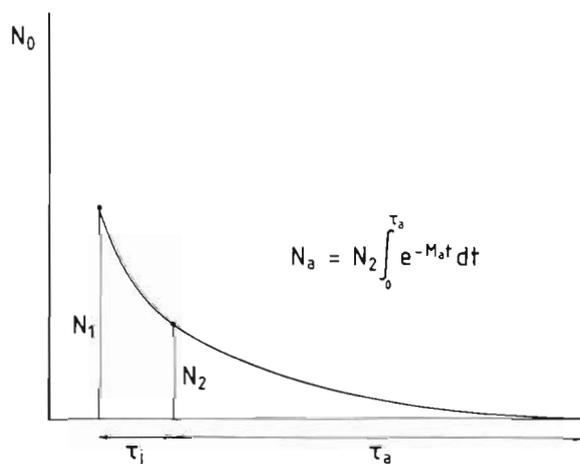


Fig. 3. *Nephrops norvegicus*. Schematic representation of the mortality of juveniles and adults. N_0 larvae are released from a total adult population N_a . N_1 organisms are recruited as juveniles of which N_2 are recruited τ_j years later as adults

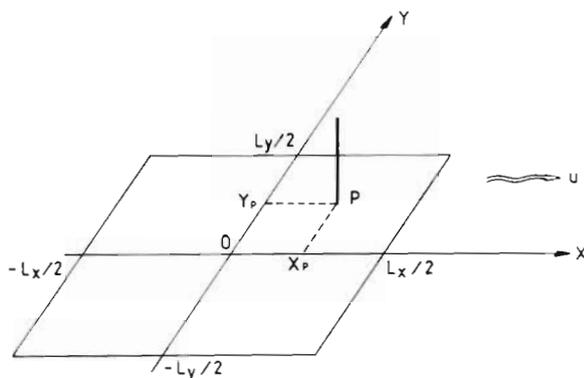


Fig. 4. Definition figure for the *Nephrops norvegicus* advection-diffusion-mortality model. The basic building block of the complete solution is a release of larvae as a spike of infinite concentration at an arbitrary point P on the mud patch. The mean flow is in the x direction only and horizontal turbulent diffusion is equal in the x and y directions

turbulent diffusion (term c) with constant eddy diffusivity, K , which is assumed to be equal in both x and y directions (isotropic turbulence). The final term (d) represents reduction of larval concentration due to mortality of the organisms at an instantaneous mortality rate, m . McGurk (1989) used a similar model to investigate the advection, diffusion and mortality of Pacific herring larvae *Clupea harengus pallasii* in the Bamfield Inlet, British Columbia.

The model is 2-dimensional in space and thus contains no information about vertical variations, hence the concentration in Eq. (4) should be regarded as depth-averaged. Neither does the model include vertical structure of the current and turbulence fields which should also be regarded as depth-mean values. Horizontal dispersal of larvae can, however, be influenced by vertical current structure and, in particular, organisms that have a capacity for vertical migration may potentially control their horizontal movement by making use of vertical current shear (Bartsch et al. [1989] have included this effect in their model of herring larvae dispersal). It is assumed in the model that larvae have no capacity for sustained independent horizontal movement (and are thus truly planktonic). This simplifying assumption was also employed by Bartsch et al. (1989). Many zooplankton larvae, including decapods, do have the ability to swim horizontally at speeds in the range 0.04 to 0.18 m s^{-1} (Shanks 1985). Such speeds are sustained only for short periods, however. If swimming events are directionally random (in response to food particles, say) this motion will effectively contribute to the horizontal diffusion term. If, on the other hand, large swimming speeds were both sustained in time and consistent in direction, treatment of larvae as passive tracers would not be valid. There is, however,

no evidence that *Nephrops norvegicus* larvae behave in this way.

Shanks (1985) and Shanks & Wright (1987) have discussed how internal waves may facilitate the horizontal movement of larvae. Again the model is unable to specifically resolve these processes which are instead subsumed into the gross value given to u . Likewise the assumption that $K_x = K_y$ is probably not realistic in many shelf sea situations, particularly where there is strong current shear in one direction such as the major axis of the tidal ellipse. In these circumstances the shear diffusion process (Fischer et al. 1989) tends to enhance the effective eddy diffusivity in the direction of the shear. Furthermore, no attempt has been made to explicitly include tidal motions in the problem. The model is, however, concerned with dispersal on time scales much longer than a tidal cycle. The main long-term effect of the tide is through its contribution to horizontal diffusion which is thus subsumed into the value given to K . Long-term residual transport associated with tidally rectified flow may be considered to be incorporated into the value given to u . In the present model only the gross effect of horizontal dispersal is of interest and the precise mechanisms that bring this about, such as those discussed above, are not explicitly considered.

N_0 larvae are released as a 'spike' of infinite concentration at (x_p, y_p) at $t=0$ so that

$$C(x, y, 0) = N_0 \delta(x - x_p) \delta(y - y_p) \quad (5)$$

where δ = the Dirac-delta function that mathematically represents a spike (Fischer et al. 1979). Assuming that u , K , and m are constant, the solution of Eq. (4) subject to the initial condition (Eq. 5) is

$$C(x, y, t) = \frac{N_0}{4\pi Kt} e^{-mt} \exp\left[-\frac{(x - x_p - ut)^2 - (y - y_p)^2}{4Kt}\right] \quad (6)$$

The physical and biological interpretation of this expression is straightforward. Setting aside the term e^{-mt} and putting $u=0$ leaves an expression which is simply a gaussian curve centred at x_p, y_p . The gaussian curve represents diffusion and spreads outward in the x and y directions with time, and the peak of the curve decreases proportional to t^{-1} . Inclusion of the term ut simply translates the whole curve in the x direction with speed u and thus represents advection. Finally the e^{-mt} term makes the concentration at all points decay exponentially with time as larvae die.

Integration of Eq. (4) over the area of the mud patch gives the total number $N(x_p, y_p, t)$ of larvae (initially released at P) that remain above the mud patch after time t , hence

$$N(x_p, y_p, t) = \int_{-L_x/2}^{L_x/2} \int_{-L_y/2}^{L_y/2} C(x, y, t) dx dy \quad (7)$$

Performing the integration using Eq. (6) gives

$$N(x_p, y_p, t) = \frac{N_0 e^{-mt}}{4} \left[\operatorname{erf}(\alpha_1) + \operatorname{erf}(\alpha_2) \right] \left[\operatorname{erf}(\beta_1) + \operatorname{erf}(\beta_2) \right] \quad (8)$$

where

$$\alpha_1 = \frac{L_y - 2 y_p}{4 \sqrt{K t}} \quad \alpha_2 = \frac{L_y + 2 y_p}{4 \sqrt{K t}} \quad (9)$$

$$\beta_1 = \frac{L_x - 2 x_p - 2 u t}{4 \sqrt{K t}} \quad \beta_2 = \frac{L_x + 2 x_p + 2 u t}{4 \sqrt{K t}}$$

and $\operatorname{erf}(x)$ is the error function (Fischer et al. 1979) defined as

$$\operatorname{erf}(x) = \frac{2}{\sqrt{\pi}} \int_0^x \exp(-\eta^2) d\eta$$

and η is an arbitrary variable. Note that $\operatorname{erf}(x) \rightarrow 1$ as $x \rightarrow \infty$. As $t \rightarrow 0$, $\alpha_1, \alpha_2, \beta_1, \beta_2 \rightarrow \infty$ so the solution (Eq. 8) behaves correctly in that $N(x_p, y_p, t) \rightarrow N_0$ as $t \rightarrow 0$. The derivation of Eq. (8) is explained in detail in Appendix 1.

The solution (Eq. 8) applies to the release of larvae at a single point, P. In general, however, the release is distributed over a wide area on the patch. A simple way to deal with this is to suppose that larvae are released in a series of spikes on a regular grid of points (x_i, y_j) covering the mud patch (Fig. 5). The total number of larvae released is the sum of releases over all the spikes

$$N_0 = \sum_i \sum_j N_0(x_i, y_j) \quad (10)$$

and the total number that remain above the patch after time t is obtained by summing the solutions (Eq. 8) for all spike releases over the grid

$$N(t) = \sum_i \sum_j N(x_i, y_j, t) \quad (11)$$

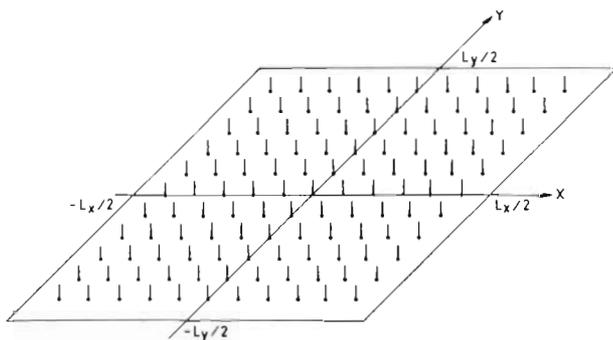


Fig. 5. Simplified distribution of *Nephrops norvegicus* larvae release over the area of a mud patch. It is supposed that the same number of larvae are released in each spike and that the spikes are distributed on a regular grid of points (x_i, y_j)

A further point to note is that Eq. (8) applies to the case where all larvae are released at the same instant ($t = 0$). In reality, of course, larvae are released over a hatching season of about 3 mo duration and consequently settling is also staggered over a 3 mo period. Because K, u and m have been assumed constant, however, the form of the time-dependence of release is unimportant. The total number of larvae, $N(\tau)$, retained above the patch after each larva has completed its pelagic duration, τ , is the same whether all larvae are released together at the same instant or whether the release is spread over a longer hatching season. The solution [Eq. (8)] summed over all releases on the mud patch [given by Eq. (11)] can therefore be applied directly to calculate the number of larvae retained over a mud patch after the completion of the pelagic phase.

RESULTS

Horizontal turbulent diffusion, no advection

The retention of larvae under varying levels of turbulent diffusion (K) but in the absence of mean advection ($u = 0$) is first considered. Larvae are released from a mud patch of dimensions $L_x = L_y = 100$ km and are subject to a natural mortality $m = 0.04 \text{ d}^{-1}$. Turbulent diffusion on the European continental shelf is relatively large because of the highly energetic tidal regime there and a reasonable estimate for K in the Irish Sea is $500 \text{ m}^2 \text{ s}^{-1}$ (Bowden 1950, Prandle 1984). In the model, K has been varied from $50 \text{ m}^2 \text{ s}^{-1}$ to an extremely large value of $2000 \text{ m}^2 \text{ s}^{-1}$. Fig. 6 shows the number of larvae that survive above the mud patch (as a percentage of the total number released, N_0) with increasing time after release. Even for the very highest levels of diffu-

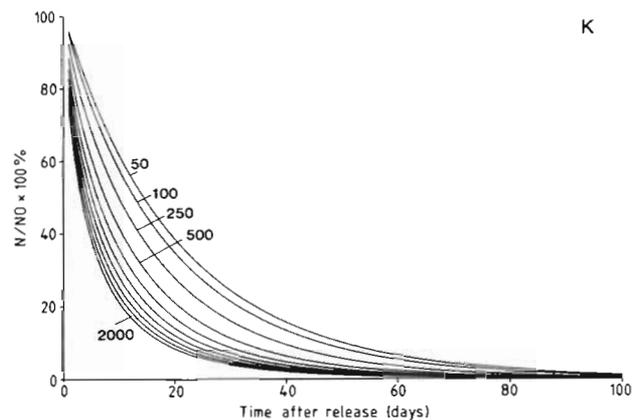


Fig. 6. *Nephrops norvegicus*. Number of larvae (as a percentage of the number released) that remain over a square (100×100 km) mud patch at various times after release for different values of eddy diffusivity, K . Advection is zero and $m = 0.04 \text{ d}^{-1}$

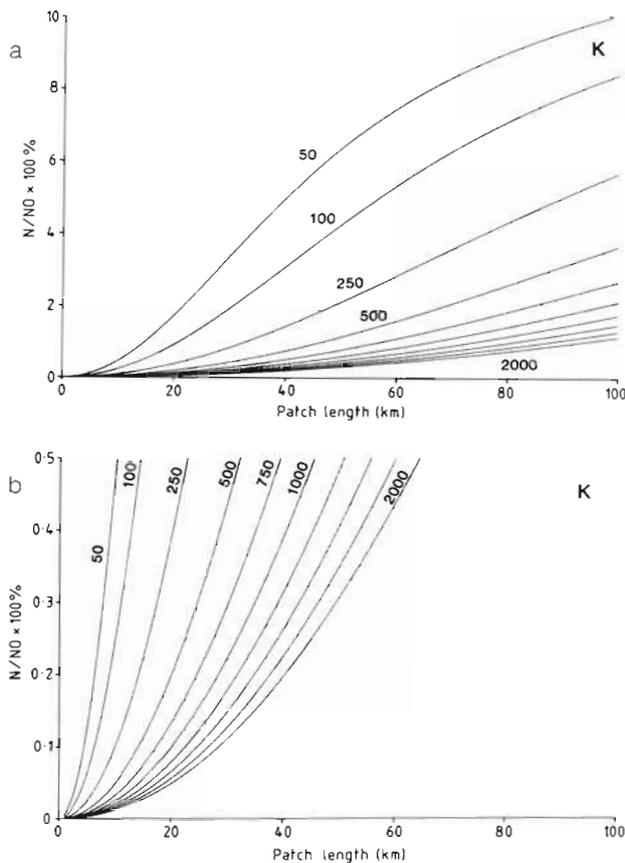


Fig. 7 *Nephrops norvegicus*. (a) Percentage of larvae that remain above square mud patches of different sizes at $t = 50$ d after release for varying levels of eddy diffusivity, K . Advection is zero and $m = 0.04$ d^{-1} . (b) As (a) but with an expanded vertical scale. For mud patches greater than 20×20 km, 0.05% of larvae remain above the patch for even the highest values of K

sion, the number of larvae remaining above the patch at settling ($t = 50$ d) exceeds 2% of the number released. This value is thus generally greater than the range of 0.07 to 2% required to sustain sufficient recruitment. Retention of 2% means that the number of larvae settling on the patch greatly exceeds the number of adults already present which, using Eq. (1), is in the range 0.2 to 0.4% of the larvae released (for γ in the range 500 to 1000).

Fig. 7 shows the effect of varying levels of horizontal diffusion ($K = 50$ to 2000 $m^2 s^{-1}$) for increasing mud patch size. In this case the patch is taken as a square ($L_x = L_y = L$) with L varying from 1 to 100 km. Larval mortality has been set at $m = 0.04$ d^{-1} and the percentage larvae retained above the mud patch at $t = 50$ d is calculated. For $K = 500$ $m^2 s^{-1}$ the percentage retention falls below 0.5% for patches smaller than about 30 km in length. Patches of dimension 40 km or more lead to retention greater than 2% for even the highest levels of

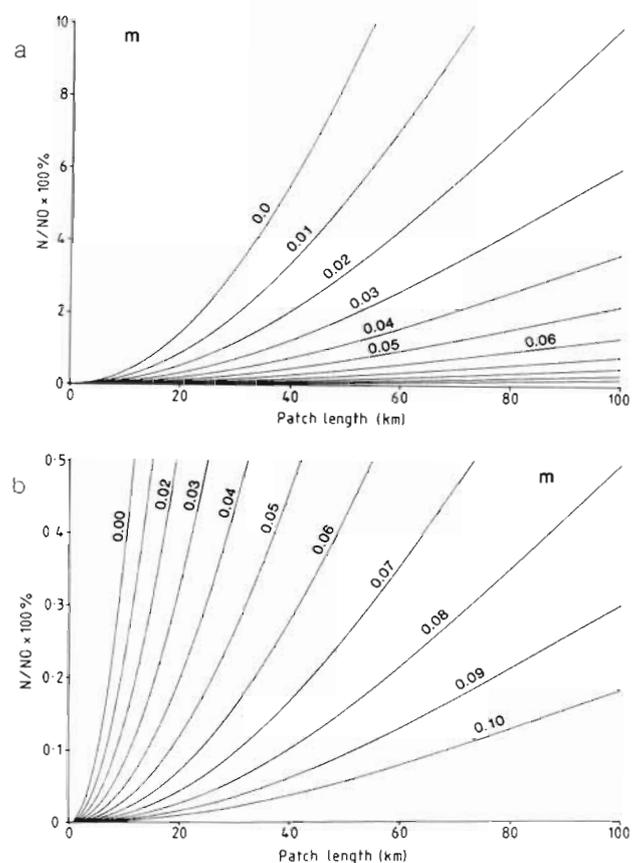


Fig. 8 *Nephrops norvegicus*. (a) Percentage of larvae remaining above square mud patches of varying sizes at $t = 50$ d after release for varying levels of larval mortality, m . $K = 500$ $m^2 s^{-1}$ and $u = 0$. (b) As for (a) but with an expanded vertical scale

diffusion. The effect of changing larval mortality, m , is depicted in Fig. 8. Advection is set to zero, $K = 500$ $m^2 s^{-1}$ and m is varied from 0 to 0.1 d^{-1} . With pelagic mortality up to 0.08 d^{-1} , retention above the patch at $t = 50$ d is greater than 0.5% for patches of dimension 100 km.

Horizontal turbulent diffusion with advection

In the absence of diffusion, a constant mean flow with speed u over a mud patch of length L_x in the x direction (Fig. 4) would completely remove all material released anywhere on the patch after a time

$$T = L_x/U$$

With $L_x = 100$ km, therefore, no larvae could be retained on a patch after 50 d for $u > 0.023$ $m s^{-1}$ (2 km d^{-1}). The above criterion is a severe one, however, and horizontal diffusion tends to increase retention by allowing some material to spread back towards the patch against the prevailing current.

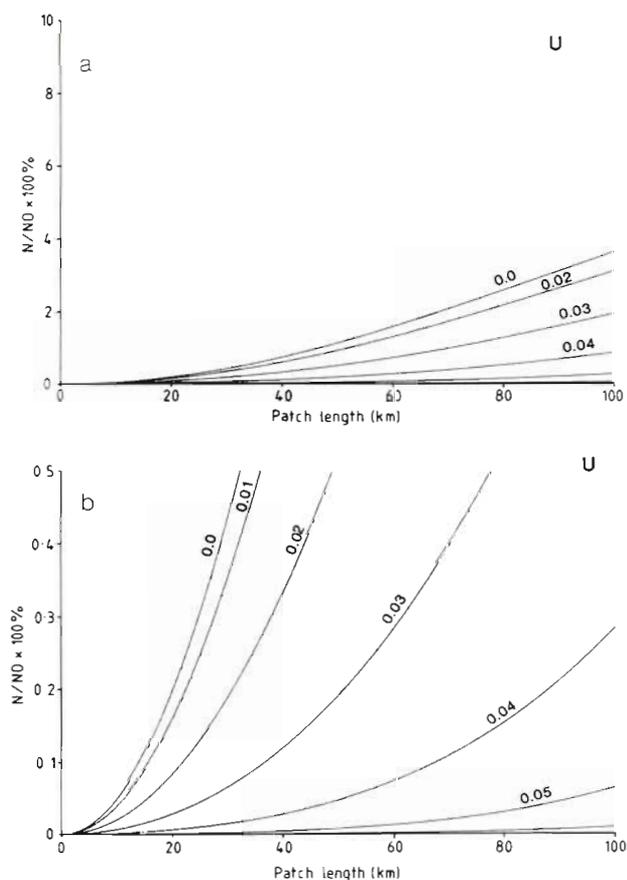


Fig. 9. *Nephrops norvegicus*. (a) Percentage of larvae that remain above square mud patches of different sizes at $t = 50$ d after release for varying levels of mean advection, u . $K = 500 \text{ m}^2 \text{ s}^{-1}$ and $m = 0.04 \text{ d}^{-1}$ (b) As (a) but with an expanded vertical scale. With $u = 0.05 \text{ m s}^{-1}$, 0.5% or fewer larvae are retained on mud patches of all sizes up to $100 \times 100 \text{ km}$

Fig. 9 shows the percentage of larvae retained above square mud patches ($L_x = L_y = L$) with L varying from 1 to 100 km, $K = 500 \text{ m}^2 \text{ s}^{-1}$, $m = 0.04 \text{ d}^{-1}$ and u ranging from 0 to 0.1 m s^{-1} . At $t = 50$ d, patches of dimension up to 100 km retain less than 0.1% of the larvae released in the presence of mean flows of 0.05 m s^{-1} or more. The western Irish Sea mud region is 60 km long in the north-south direction and can therefore retain sufficient larvae only for mean flows less than 0.03 to 0.04 m s^{-1} .

DISCUSSION

The principal conclusion of the model is that observed levels of turbulent diffusion on the European shelf are insufficient to critically reduce larval retention over mud patches larger than $20 \times 20 \text{ km}$ after a pelagic duration of 50 d. On the other hand, rather low levels of mean advection (0.04 to 0.05 m s^{-1}), if sustained over the pelagic larval phase, would reduce

retention over most mud patches to levels where settlement (and recruitment to the population) would be severely reduced. Although mean advection of 0.05 m s^{-1} would affect *Nephrops norvegicus* recruitment, it is unclear whether such levels of sustained mean flow occur there. There are relatively few observations of mean currents in the western Irish Sea so much of the evidence is indirect. Salt and caesium-137 budgets for the Irish Sea suggest a basin-averaged northward mean flow of only 0.012 m s^{-1} (Bowden 1950, Wilson 1974). Furthermore, during late spring and summer (May onwards) a pronounced tidal mixing front is established in the western Irish Sea (Simpson & Hunter 1974) and water above the mud patch region become thermally stratified. The location of the western Irish Sea front is remarkably consistent with time which again points to low mean advection in the region as Simpson (1981) has argued that frontal locations would be significantly displaced from their predicted positions in the presence of mean flows greater than 0.01 m s^{-1} .

Against these observations, the *Nephrops norvegicus* larvae distribution patterns obtained by Nichols et al. (1987) and White et al. (1988) consistently show southward displacement of larvae from the mud patch region. White et al. (1988) suggested that a local southward flow close to the Irish coast (consistent with the density field) could be responsible for displacement of larvae. White et al. (1988) argued that the southward coastal current may be a feature of the winter and early spring seasons when coastal runoff is high but that it is switched off as thermal stratification develops in the western Irish Sea in late spring and summer. The *N. norvegicus* hatching season starts 1 to 2 mo before the onset of stratification in the Irish Sea so that larvae released early in the season may experience relatively high mean advection. Observations of currents in the western Irish Sea during the *N. norvegicus* pelagic phase are, however, inadequate at present to infer whether the mean advection over the period is at a critical level or that it may reach critical levels in certain years. If advection in the region is close to critical levels it is to be expected that the *N. norvegicus* population will exhibit considerable variability between year classes as a result of advective control upon recruitment. There is, however, presently insufficient data concerning *N. norvegicus* year class variability to test the role of advection in controlling recruitment. Although the role of advection in the western Irish sea remains uncertain, the continued existence of a *N. norvegicus* population clearly implies that it is able to withstand pelagic losses. Indeed the relatively long duration of the larval phase is consistent with pelagic losses having relatively little influence upon recruitment in the long term.

The model implies that larval retention (and consequent juvenile recruitment) is potentially very high for regimes which are primarily diffusive so that at the end of the larval phase significantly more organisms may settle on a mud patch than are necessary to sustain the population. If the population is at a level that is close to the carrying capacity of the patch then this implies some form of density-dependent mortality operates at the settling or juvenile stage. The possibility of such density-dependent control has been discussed by Hill & White (1990). To illustrate the point consider the following calculation of expected juvenile mortality. If adult mortality is known, rearranging Eq. (3) gives

$$M_j = \frac{1}{\tau_j} \ln \left[\left(\frac{N_{ret}}{N_0} \right) \frac{\gamma}{2 M_a} \right] \quad (12)$$

where all variables have been defined previously. In diffusive regimes (Fig. 7) percentage retention is great-

er than 2% for mud patches larger than 30×30 km. Setting $(N_{ret}/N_0) = 2\%$, $\tau_j = 3$ y, $M_a = 0.4$ yr⁻¹ and $\gamma = 1000$ gives a juvenile mortality of 1.6 yr⁻¹. Hill & White (1990) have argued that very high mortality may be brought about by space limitation on an overpopulated patch.

Pelagic dispersion leads to opportunities for colonisation of distant mud patches. To illustrate this consider Fig. 10 which shows the percentage larvae surviving above a mud patch of size 50×50 km due to a point release at varying distances away from the patch (along the x axis). $K = 500$ m² s⁻¹ and $m = 0.04$ d⁻¹. Fig. 10 shows that for a point release 150 km away from the centre of the patch, the peak numbers (0.3% of those released) over the patch arrive at about 50 d after release. Mud patches within this range are thus likely to be partially seeded by one another.

APPENDIX

The integration of Eq. (6) using Eq. (7) may be performed as follows. The function $C(x, y, t)$ given by Eq. (6) is said to be separable in x and y because the part of the function that depends on x and y may be separated into a product of 2 functions, $X(x, t)$ and $Y(y, t)$, which depend only on x and t and y and t respectively. Thus

$$C(x, y, t) = \frac{N_0}{4 \pi K t} e^{-mt} X(x, t) Y(y, t) \quad (A1)$$

In this case

$$X(x, t) = \exp \left[\frac{-(x - x_p - ut)^2}{4 K t} \right]$$

and

$$Y(y, t) = \exp \left[\frac{-(y - y_p)^2}{4 K t} \right]$$

In general when a function is separable in this way a double integration with respect to x and y may be written as the product of single integrations with respect to x and y . Hence if x_1, x_2 and y_1, y_2 are the x and y limits of integration respectively

$$\int_{y_1}^{y_2} \int_{x_1}^{x_2} X(x, t) Y(y, t) dx dy = \int_{y_1}^{y_2} Y(y, t) dy \int_{x_1}^{x_2} X(x, t) dx \quad (A2)$$

This general result enables the integration to be performed easily. Consider the integration of the part of C that depends upon y

$$\int_{-L_y/2}^{L_y/2} Y(y, t) dy = \int_{-L_y/2}^{L_y/2} \exp \left[-\frac{(y - y_p)^2}{4 K t} \right] dy \quad (A3)$$

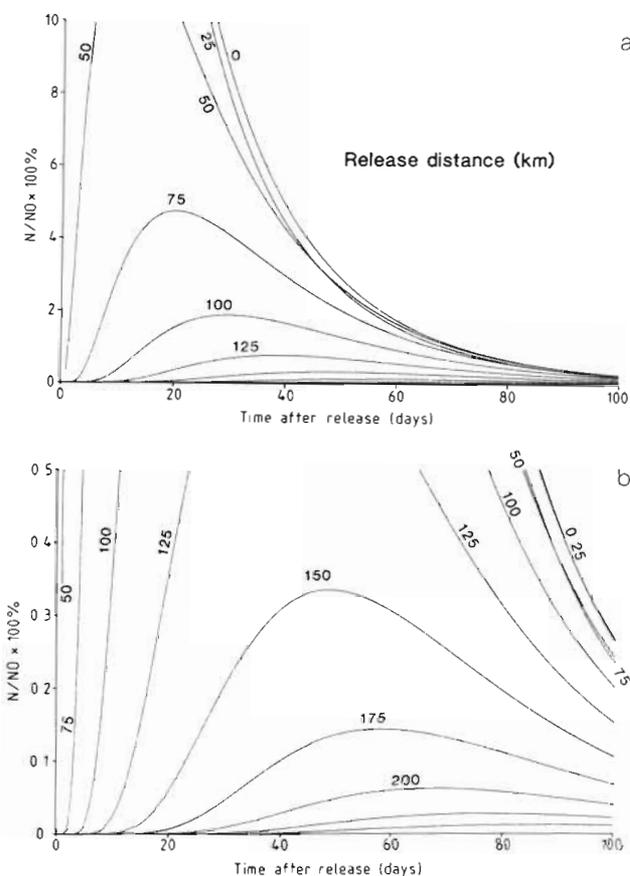


Fig. 10. *Nephrops norvegicus*. (a) Percentage of larvae that are found above a square mud patch of size 50×50 km at different times after release from a single point at varying distances from the centre of the mud patch. (b) As (a) but with an expanded vertical scale. At $t = 50$ d the peak number of larvae (0.3% of the number released) arrive from a release 150 km away from the centre of the patch

Introduce the variable ε where

$$\varepsilon = \frac{(y - y_p)}{2 \sqrt{Kt}} \quad (\text{A4})$$

also

$$dy = 2 \sqrt{Kt} d\varepsilon \quad (\text{A5})$$

Hence

$$\int_{-L_y/2}^{L_y/2} \exp \left[-\frac{(y - y_p)^2}{4Kt} \right] dy = \frac{2}{\sqrt{\pi}} \sqrt{\pi Kt} \int_{-\alpha_2}^{\alpha_1} \exp [-\varepsilon^2] d\varepsilon \quad (\text{A6})$$

where α_1 and α_2 are the limits of integration for ε obtained substituting the y limits of integration into the expression for ε . Thus when

$$y = L_y/2, \quad \varepsilon = \alpha_1$$

where

$$\alpha_1 = \frac{L_y - 2 y_p}{4 \sqrt{Kt}}$$

and when

$$y = -L_y/2, \quad \varepsilon = -\alpha_2$$

where

$$\alpha_2 = \frac{L_y + 2 y_p}{4 \sqrt{Kt}}$$

Now the integral between $-\alpha_2$ and α_1 can be rearranged into the sum of 2 integrals both with zero as their lower limit

$$\frac{2}{\sqrt{\pi}} \int_{-\alpha_2}^{\alpha_1} \exp [-\varepsilon^2] d\varepsilon = \frac{2}{\sqrt{\pi}} \left[\int_0^{\alpha_1} \exp [-\varepsilon^2] d\varepsilon + \int_0^{\alpha_2} \exp [-\varepsilon^2] d\varepsilon \right] \quad (\text{A7})$$

and by the definition of the error function given in the text the above integral is just

$$\left[\text{erf} (\alpha_1) + \text{erf} (\alpha_2) \right] \quad (\text{A8})$$

Thus the integral (Eq. A6) has value

$$\sqrt{\pi Kt} \left[\text{erf} (\alpha_1) + \text{erf} (\alpha_2) \right] \quad (\text{A9})$$

In precisely the same way the function $X(x, t)$ can be integrated with respect to x to give a value

$$\sqrt{\pi Kt} \left[\text{erf} (\beta_1) + \text{erf} (\beta_2) \right] \quad (\text{A10})$$

where β_1 and β_2 are given by Eq. (9) in the text. From the results Eqs. (A1), (A9) and (A10) the expression for the number of larvae retained above a rectangular mud patch, $N(x_p, Y_p, t)$, given by Eq. (8) in the text follows immediately.

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