Vol. 279: 215–224, 2004 | MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser | Published September 28

Random walk models for the movement and recruitment of reef fish larvae

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ABSTRACT: The factors influencing the movement and recruitment of settlement stage larvae are investigated using random walk models. Individual-based sensing and orientating abilities are included explicitly in the model. We consider 2 simple reef environment models consisting of a simple circular reef with and without a constant cross-current. The sensing ability of the larvae is modelled as either fixed or spatially dependent, together with a fixed orientating ability. The survival probability is found to be highly sensitive to both the sensing and orientating abilities of the larvae, as well as to the properties of the reef environment itself.

KEY WORDS: Reef fish settlement · Larval swimming ability · Biased random walks

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INTRODUCTION

Most reef fishes have a dispersing larval stage that ends when the larvae leave the pelagic environment and recruit into adult reef populations. The supply rate of larvae to reefs for recruitment is believed to be a critical determinant of the structure of reef fish populations (Doherty & Williams 1988), and the importance of considering supply rates is acknowledged by those managing reef fisheries and other industries exploiting these populations (Done et al. 1997). The dispersal paths of pelagic larvae are determined in part by local advection in the hydrodynamic regime around reefs and it is thought that recirculatory features in the lee of reefs could entrap dispersing larvae. This idea has led to considerable investment in fine-scale numerical simulations of the hydrodynamic features of flows around individual reefs (Wolanski & Sarenski 1997). Larger scale studies of the dispersal of reef fish larvae populations in the pre-settlement pelagic phase assume movement through either diffusion (e.g. Cowen 2000) or passive drift on currents (e.g. Porch 1998, James 2002). However, recent evidence shows that during the settlement stage, reef fish larvae can exhibit directed motion and are not simply passive (e.g. Leis et al. 1996). If swimming of the larvae is included in dispersal models, then the probability of recruitment is increased (Wolanski et al. 1997). The most recent theoretical models in the literature that include swimming effects are mainly deterministic using the assumption that the introduced component of velocity due to swimming of the settlement stage larvae aims directly at the target destination (Wolanski et al. 1997, Porch 1998, Armsworth 2000, 2001, James 2002). We shall show that such deterministic models may be too simple and that the random variability in the movement of the settlement stage larvae can have a significant effect on the probability of recruitment.

There is a large amount of experimental data in the literature on the behaviour of various coral reef fish species, mainly from observations made around the Great Barrier Reef (GBR). Average current speeds measured on the GBR are of the order 0.1 to 0.17 $\mathrm{ms^{-1}}$ (Frith et al. 1986, Leis & Carson-Ewart 2003), while *in situ* observations suggest an average swimming speed for settlement stage reef fish larvae of between

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0.116–0.339 ms^{-1} (Leis & Carson-Ewart 1997, 2003). Further experiments on settlement stage reef fish larvae suggest that they are capable of sustained swimming speeds of 0.135 ms^{-1} (Stobutzki & Bellwood 1997), and between 0.04 and 0.16 ms^{-1} (Fisher & Bellwood 2002), although it must be stressed that there is great inter- and intra-species variation in these empirical results. Fisher et al. (2000) observed threshold behaviour in the development of swimming ability in pelagic stage reef fish larvae; larvae would not swim for prolonged periods until reaching a certain age at which point they would swim all day. *In situ* observations also suggest that settlement stage fish larvae can swim directionally and or change depth (Leis & Carson-Ewart 1999, 2000). Leis et al. (1996) and Leis & Carson-Ewart (2003) observed directed motion relative to the reef from up to 1 km away, while Stobutzki & Bellwood (1998) measured movement towards the reef during the night and suggested that this was in response to reef sounds. McCauley & Cato (1998, 2000) collected statistics of reef noise and found nocturnal peaks in noise attributed to adult reef fish calling, while Tolimieri et al. (2000) and Simpson et al. (2004) observed that some settlement stage reef fish larvae are attracted to reef noise during the settlement process. Other possible orientation cues such as chemosensory or visual cues are discussed by Montgomery et al. (2001). Reef fish larvae are subject to high predation rates and mortality rates of 3 to 46% d^{-1} have been observed (Houde 1989, Morse 1989).

In this paper, we present the results of a simple model for the movement and subsequent recruitment of a population of settlement stage reef fish larvae (henceforth referred to as 'settlement stage larvae'). We look at 2 different reef environments: a simple circular reef and a circular reef with a cross-current, and consider 2 models for orientation: a fixed sensing ability and a spatially dependent sensing ability, together with a directed (but random) movement model and a simple mortality model. We use typical values for swimming speed, current speed and reef distance, and look at a range of reorientation parameter values to show that the survival probability is highly sensitive to the orientating and sensing ability of the settlement stage larvae. The qualitative results are general and are applicable to a number of different reef environments or fish species.

METHODS

The movement of settlement stage larvae as a biased random walk. We know that settlement stage larvae can swim and there is strong evidence that they can sense and orientate themselves to directional cues. However, individual variations, and environmental stochasticity due to local fluid velocity and turbulence, mean that they will not be able to do this perfectly. In the absence of explicit data concerning settlement stage larvae reorientation, we employ a biased random walk model to describe their movement as they attempt to reach the reef and recruit into the adult population. The following biased random walk algorithm (Codling 2003) is used to simulate the directed movement of swimming microorganisms.

An individual settlement stage larva moves in a straight line in a direction, θ', with a fixed speed, s, for a certain time-period, τ, which is randomly drawn from a Poisson process with turning rate, λ, so that the mean time period is $\bar{\tau} = 1/\lambda$. At the end of this time period, the larva reorientates to face a new direction, θ. This new direction is randomly drawn from a von Mises distribution, $T(\theta, \theta')$, which is the simplest unimodal circular distribution (Batschelet 1981, Mardia & Jupp 1999) and is dependent on 2 parameters, κ and μ_δ (which we define in the next section). The process then continues until an appropriate boundary is reached, i.e. either death or settlement on the reef occurs.

This random walk is biased because, if $\mu_\delta > 0$, there will be a tendency to move in the preferred direction towards the reef. In a population of settlement stage larvae using this process, each individual larva will map out a different trajectory even if the whole population uses the same parameters. For random walkers moving with this simple model, Codling (2003) has derived asymptotic equations for the average position, absolute velocity and average spread of the population.

The random walk process described above is known as a velocity jump process (Othmer et al. 1988, Codling 2003). A velocity jump process includes correlation between successive directions of movement and is therefore, a more realistic model for animal movement than the traditional uncorrelated purely random walk (position jump process) that results in diffusive movement (see discussion in Okubo & Levin 2001). The velocity jump process allows one to readily distinguish between the specific processes that individuals may use to direct their movement (in this paper we distinguish between sensing and orientating abilities) and therefore, extends the classic model of Patlak (1953) as discussed for example in Turchin (1998).

Reorientation model. The von Mises distribution is defined for $-\pi \le \theta < \pi$ and is dependent on 2 parameters, the concentration parameter, κ, and the mean turning angle μ_δ (where $\delta = \theta - \theta'$). It is given by:

$$T(\theta, \theta') = \frac{1}{2\pi I_0(\kappa)} \exp[\kappa \cos(\theta - \theta' - \mu_\delta)] \quad (1)$$

where $I_0(\kappa)$ is a Bessel function defined so that

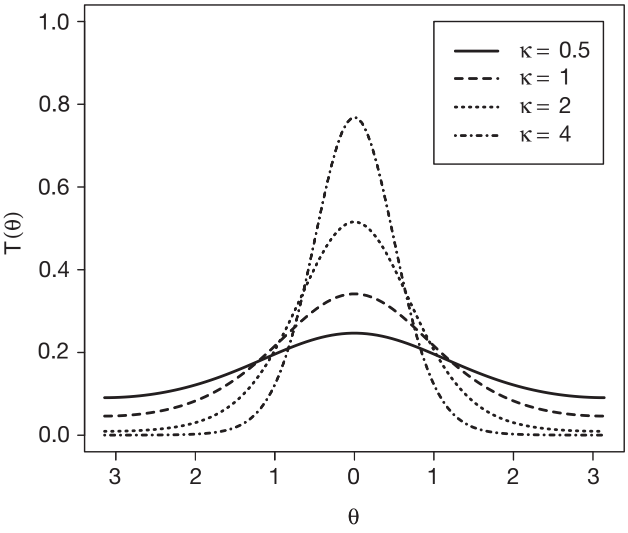

Fig. 1. The von Mises distribution for $-\pi \leq \theta \leq \pi$, centred on $\theta = 0$, with various values for the concentration parameter, κ. We use the von Mises distribution to draw random directions of movement in our simulation algorithm. As the concentration parameter, κ, controls the amount of randomness in the choice of each new direction, we can think of κ as the orientating ability of each individual larva

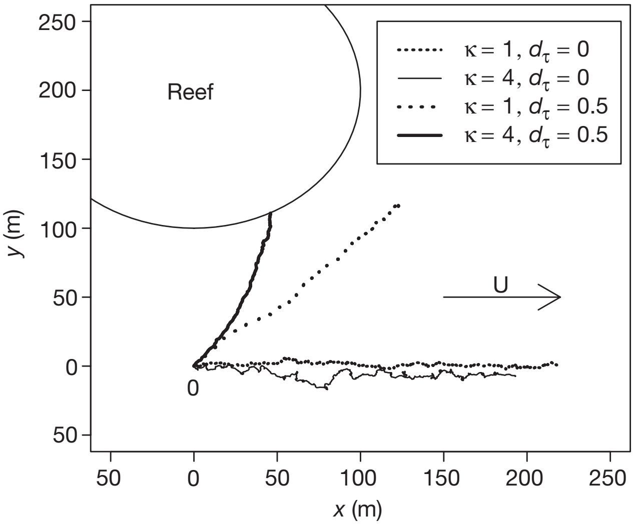

Fig. 2. Typical examples of random walk trajectories generated by our simulation algorithm after 4000 s for different values of the reorientation parameters, d_τ and κ (where d_t represents the sensing ability and κ represents the orientating ability). In these simulations, the reef is centred at (*x*, *y*) = (0, 200)—in most of the subsequent simulations we use (*x*, *y*) = (0, 500) as the centre of the reef—and has a radius of 100 m, and there is a fixed cross-current, $U = 0.05$ ms^{-1}. All trajectories start at (*x*, *y*) = (0, 0) and have a fixed swimming speed of $s = 0.1$ ms^{-1}. Only those trajectories where d_τ is not equal to 0 show a bias in movement towards the reef, although even if d_τ is not equal to 0, it is clear that it is still possible to miss the reef if κ is too small

$$\int_{-\pi}^{\pi} \mathrm{T}(\theta, \theta')\mathrm{d}\theta = 1 \qquad (2)$$

The concentration parameter, κ, determines the amount of randomness in the choice of new direction; if $\kappa \approx 0$, then the choice of direction is almost entirely random, but if κ is large, then the new direction chosen will be very close to the mean turning angle, μ_δ. Fig. 1 shows the von Mises distribution for typical values of κ.

The mean turning angle μ_δ, is dependent on the current direction of movement, θ. In this model, we use linear reorientation (Hill & Häder 1997, Codling 2003), where the mean turning angle is largest if the settlement stage larva is facing away from the preferred direction and smallest if the larva is already facing the preferred direction (where the preferred direction is always towards the centre of the reef). If $\mu_\delta = 0$, then there is no directed motion and the settlement stage larvae will tend to continue in the same direction. The mean turning angle takes the form (Hill & Häder 1997):

$$\mu_\delta = -d_\tau(\theta' - \theta_0) \qquad (-\pi < \theta', \theta_0, \mu_\delta \leq \pi) \qquad (3)$$

where θ′ is the current direction of movement, θ_0 is the preferred direction of movement (towards the centre of the reef) and $0 < d_\tau$ is the amplitude of the mean turning angle, which we later consider as the sensing ability. Thus, if $d_\tau \approx 0$, then $\mu_\delta \approx 0$ and on average the settlement stage larvae will not reorientate back towards the reef, but if $d_\tau \approx 1$, then the average reorientation will be back towards the centre of the reef. If $d_\tau > 1$, we can expect over-correction, see Codling (2003). Note that even if $d_\tau \approx 1$, it is only the mean turning angle that produces a reorientation back towards the centre of the reef; the amount of randomness in the choice of direction (determined by κ) will still influence the actual new direction chosen. Examples of the type of trajectories generated by this algorithm are given in Fig. 2.

Hill & Häder (1997) analysed the trajectories of swimming microorganisms such as the alga *Chlamydomonas nivalis* undergoing phototaxis and their observed values for the angular variance and the inverse of the mean reorientation time can be used as estimates for the 2 reorientation parameters, κ and d_τ, in their model. In our simple biased random walk, the parameter, d_τ, controls how quickly the swimming direction returns to the preferred direction during the reorientation process, so for the purposes of this model we think of d_τ as the sensing ability of the larvae. The parameter, κ, determines the randomness in the choice of direction at each step, so we consider κ as the orientating ability or the ability of the larvae to overcome the inherent turbulence in the environment and orientate correctly to the preferred direction that has been sensed. Thus, the parameter, κ, is a measure of the swimming (orientating) ability of the larvae relative to the underlying turbulence that is present in the environment.

There is a lack of experimental data in the literature that we can use to estimate the values of the reorientation parameters, κ, d_τ and λ (the turning rate) for settlement stage larvae, so in the subsequent simulations we look at a range of values for κ and d_τ. Over large times, the turning rate, λ, does not affect the results (Codling 2003) and we use a fixed value of $\lambda = 0.5$ s^{-1} in the following simulations.

Reef Model 1: simple circular reef. We initially assume a simple model for the reef environment where the settlement stage larvae move around the (x,y) plane with no current and no interactions between individuals. We assume that all settlement stage larvae move in random walks as described above, with fixed reorientation parameters, d_τ and κ, turning rate, λ, and speed, s, that are the same for the whole population. There is a small circular reef of radius r, centred at the point $(0, C_0)$, and the settlement stage larvae attempt to direct their motion towards the centre of this reef.

Reef Model 2: simple circular reef with cross-current. We assume exactly the same environment as in Reef Model 1, except that a perpendicular cross-current of fixed magnitude and direction, U, is introduced (see Fig. 2). Currents that run parallel to the reef (where the reef is either directly upstream or downstream of the origin point of the settlement stage larvae) simply act to increase or decrease the absolute velocity of the settlement stage larvae and the consequent survival probability. A current that takes the settlement stage larvae towards the reef can give a non-zero survival probability for a completely passive larva, although the survival probability is increased greatly if the settlement stage larvae are able to direct their motion to avoid being carried past the reef (Armsworth 2000).

Reef Model 3: simple spatial sensing ability. We assume exactly the same environment as in Reef Model 1 (zero current), except that we now include a spatially dependent sensing ability. If we model the sensing ability as spatially dependent, it is necessary to consider the orientation cues to the reef that the settlement stage larvae use (Montgomery et al. 2001). If the cue is sound (McCauley & Cato 1998, 2000, Stobutzki & Bellwood 1998, Tolimieri et al. 2000, Simpson et al. 2004), then although the currents and turbulence of the water could affect the dispersal of the sound wave, it is not unreasonable to model the signal as spreading out in all directions from the centre of the reef. If the cues are chemical, then currents and turbulence will have a much more obvious effect on the dispersal of the signal; the orientation cue will be different depending on whether the settlement stage larvae are upstream or downstream of the reef (Armsworth 2000). It is likely that settlement stage larvae use a number of different orientation cues at different scales, e.g. sound at large distances and then chemical or even visual cues at smaller distances (Montgomery et al. 2001). We introduce a simple spatial dependence into the sensing ability of the settlement stage larvae with the following linear relation:

$$d_\tau(\mathbf{x}) = 1 - \frac{C}{1000} \qquad (4)$$

where C is the distance to the centre of the reef from the current position, $\mathbf{x} = (x, y)$ and $d_\tau(\mathbf{x}) = 0$ if $C \geq 1000$ m. Thus, the settlement stage larvae get better at sensing as they move closer to the reef, while any larvae further than 1 km from the centre of the reef are assumed to not be able to sense it. Leis et al. (1996) and Leis & Carson-Ewart (2003) observed a response to the reef by settlement stage larvae from up to 1 km away and we assume that this is the upper limit of their sensing ability (the results given later are not qualitatively different if this upper limit assumption is changed to be larger or smaller than 1 km). This simple spatial dependence model is reasonable if the orientation cue is sound but is less applicable if the orientation cue is chemical and there is a significant current, as any settlement stage larvae upstream of the reef would not be able to sense it (Armsworth 2000).

Mortality effects. To model the effects of predation and other mortality effects as the settlement stage larvae attempt to reach the reef, we include a simple Poisson process death rate, γ, so that at each time step there is a small but finite chance of each larva dying. Thus, the longer an individual settlement stage larva swims around without settling on the reef, the more likely the larva is to die. This is the simplest plausible choice of mortality model and is appropriate to any scenario where the predation pressure remains spatially and temporally constant during the modelled dispersal phase. The mortality model could readily be modified for specific applications, e.g. to account for higher predation rates on smaller size classes (Pitchford & Brindley 2001), but the general individual-based conclusions of this study would not be qualitatively affected.

The simple model we present here only considers the movement of the settlement stage larvae up to the point when they either settle on the reef or die in the open water outside the reef. Any larva reaching a position (x, y), such that $C < r$, is assumed to have settled on the reef and is no longer considered in the model. Each larva has an unlimited time available to reach the reef but is subject to the same constant mortality rate γ until it reaches the reef or dies.

In the following simulations, we use a constant death rate of $\gamma = -\ln(0.5)/36\,000\ \text{s}^{-1}$, so that half the population are expected to survive a 10 h period. This is equivalent to a daily mortality rate of 80%, which is high when compared to published estimates of larval mortality rates of 3 to 46% d^{-1} (Houde 1989, Morse 1989), but comparable to the mortality rate of 0.9 close to the reef used by Porch (1998). However, it should be stressed that the results of the following simulations are not qualitatively changed by altering the mortality rate. In our model, any settlement stage larvae that do not have strong enough sensing and orientating abilities to find the reef will die irrespective of the mortality rate. This is especially true when a current is present and can be seen clearly in Fig. 2.

Table 1. Parameters used in the simulation algorithm with ranges of values (min, max) and typical values used. na: not applicable

Parameter	Description	Range of values	Typical value	Units
κ	Orientating ability	(0, 5)	1	na
d_τ	Sensing ability	(0, 2)	0.5	na
λ	Turning rate	na	0.5	s^{-1}
γ	Death rate	na	$-\ln(0.5)/36\,000$	s^{-1}
s	Swimming speed	na	0.1	ms^{-1}
U	Cross-current speed	(0, 0.1)	0.05	ms^{-1}
C_0	Initial distance to centre of reef	(100, 2100)	500	m
r	Radius of reef	na	100	m
D_0	Initial distance to edge of reef	(0, 2000)	400	m

Parameter values used. Simulations of 1000 settlement stage larvae moving in the different reef environments have been completed for various values of the parameters, κ, d_τ, C_0 and U (see Table 1). As we assume no prior knowledge of the earlier pelagic stage of the settlement stage larvae in our simulations, we need to make an assumption about their initial distribution. For simplicity, and in order to compare results between different simulation runs, we assume that in all the simulations the larvae start at the origin, (0, 0), and the population is initially orientated uniformly. For the same reason, we assume that the swimming speed of the settlement stage larvae is fixed over the population and given by $s = 0.1\ \text{ms}^{-1}$, which is realistic when compared with empirical data from the references given in the 'Introduction'. In those simulations where we introduce a cross-current, this is assumed to be $U = 0.05\ \text{ms}^{-1}$, except when we run simulations over a range of values: $0 \leq U \leq 0.1\ \text{ms}^{-1}$. These values for the current speeds are comparable to empirical data from the references given in the 'Introduction', although we do not consider the case when $U > s$, as this results in a zero survival probability in our model. We assume the turning frequency is given by $\lambda = 0.5\ \text{s}^{-1}$ and the death rate is $\gamma = -\ln(0.5)/36\,000\ \text{s}^{-1}$ (or 80% d^{-1}). In all simulations, we assume the reef radius to be $r = 100$ m and unless otherwise stated, we use a fixed initial distance to the centre of the reef, $C_0 = 500$ m. We also consider a range of values for the initial distance to the centre of the reef: $100 \leq C_0 \leq 2100$ m, when comparing spatially varying and fixed sensing abilities. Thus, the range of the initial distance to the edge of the reef, $D_0 = C_0 - r$, is given by $0 \leq D_0 \leq 2000$ m. A summary of these parameter values used is given in Table 1. It should be noted that the results of the following simulations are not qualitatively different if the parameter values are changed slightly. We are interested in the effect of the parameters that determine sensing and orientating ability (d_τ and κ respectively) on the probability of surviving to settle on the reef.

Upper bounds for the survival probability. Using these parameter values, the minimum time to reach the reef is $t_{\min} = 4000$ s for Reef Models 1 and 3 (corresponding to moving directly from the origin to the edge of the reef in a straight line). The expected probability of reaching the reef and surviving in this extreme case is $E\ (\text{p}_\text{S}) = 0.926$, which gives an expected upper bound for the survival probabilities in the subsequent simulations (p_S being the probability of surviving to reach the reef and settling). More generally, the minimum time taken to reach the reef if a perpendicular cross-current is present is given by:

$$t = \frac{C_0 - r}{\sqrt{s^2 - U^2}} \qquad (U < s) \qquad (5)$$

which is derived by applying Pythagoras' theorem to a triangle with hypotenuse $s\ t$ and vertical and horizontal lengths $U\ t$ and $C_0 - r$, respectively. This corresponds to movement slightly into the current so that the drift takes the settlement stage larvae to the reef. As the speed of the cross-current increases, the time to reach the reef will increase with a subsequent reduction in the survival probability until $U > s$, when the survival probability is zero. Models that include upstream and downstream current effects (but do not include random fluctuations in the individual movement) have been considered by Armsworth (2000, 2001), who shows that if $U > s$ the settlement stage larvae can only reach the reef if they start upstream of it.

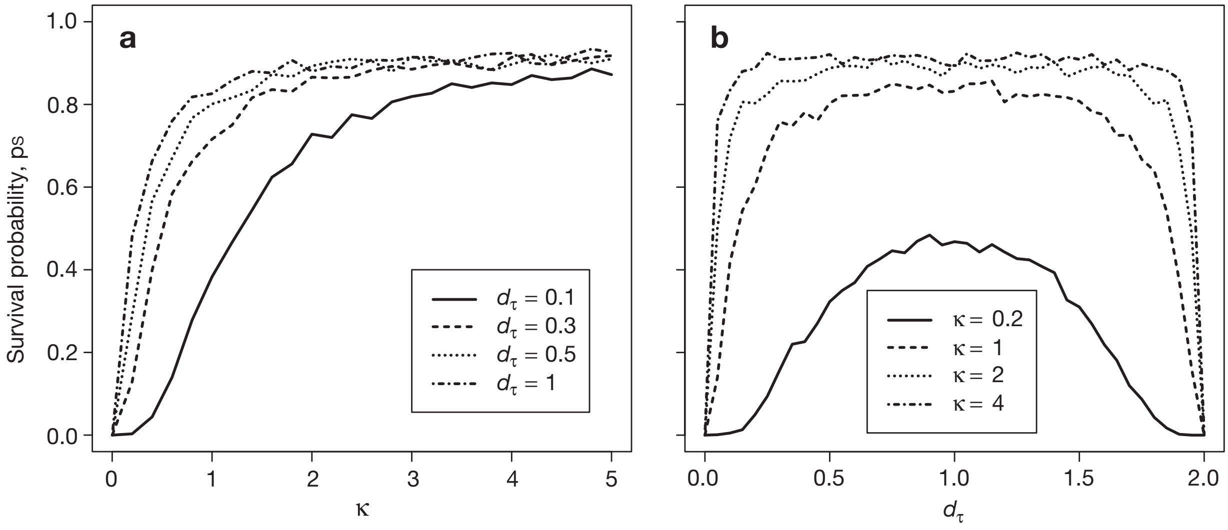

Fig. 3. Plots showing survival probability (p_S) for 1000 runs of Reef Model 1 with fixed initial distance to centre of reef C_0 = 500 m, reef radius r = 100 m, fixed speed s = 0.1 ms^{-1}, cross-current U = 0 ms^{-1}, and showing (a) p_S versus κ for various values of d_τ and (b) p_S versus d_τ for various values of κ. d_τ and κ are the reorientation parameters that correspond to sensing and orientating ability, respectively. In (b) overcorrecting occurs when $d_\tau > 1$

RESULTS

Reorientation parameters (Reef Model 1)

The plots in Fig. 3a show how the survival probability for Reef Model 1 changes as κ increases for 4 values of d_τ. It is clear that the survival probability $p_S > 0$ if $d_\tau > 0$ and κ is larger than some critical value κ_{crit}. As κ increases past κ_{crit}, there is a sudden jump from a survival probability close to zero to a survival probability that is close to the theoretical maximum ($E(p_S) = 0.926$), and then as κ increases further, the survival probability tends asymptotically to the theoretical maximum. Recall that a low value of κ corresponds to a poor orientating ability or a highly turbulent environment, so that there is a lot of randomness in the choice of direction. If this is the case, then the settlement stage larvae can significantly improve their survival probability with only a small increase in the orientating ability. However, if the settlement stage larvae are already good at orientating or the environment is not turbulent (high κ value), then a similar increase in orientating ability will not give much improvement in the survival probability.

The plots in Fig. 3b that show how the survival probability for Reef Model 1 changes as d_τ increases for 4 values of κ, exhibit similar 'threshold' behaviour to Fig. 3a. There is a sudden jump in the survival probability for a critical value of d_τ. It should be pointed out that, even if the sensing ability is optimal (d_τ = 1), a small value of κ (corresponding to large turbulence in the environment or weak orientating ability of the larvae) will always result in a low survival probability. The plot is roughly symmetric about d_τ = 1, illustrating that in the linear reorientation model, over-correcting (where the mean turning angle reorientates the larvae too far past the direction of the reef at each step) by a certain amount has the same effect as under-correcting.

Simulations have been completed with different values for the speed, turning rate, reef radius and death rate, but the results are not qualitatively different and there is the same sudden jump or threshold behaviour in the survival probability for critical values of the reorientation parameters. For the same reorientation parameter values, the survival probability is found to be lower if there is a higher death rate, the reef is smaller or the speed of movement is slower, although the same qualitative behaviour is observed.

Cross-current (Reef Model 2)

The plot in Fig. 4a shows how the simulation survival probability for Reef Model 2 changes as κ increases for 4 values of d_τ. The behaviour is similar to the results for Reef Model 1 as there is the threshold behaviour in the survival probability for critical values of the reorientation parameters. Comparing the results for Reef Models 1 and 2, it is clear that the addition of the perpendicular cross-current in Reef Model 2 results in a much lower survival probability for the same parameter values.

Fig. 4b shows how the simulated survival probability for Reef Model 2 changes as U increases, where there is a fixed sensing ability d_τ = 0.5. As expected from Eq. (5), $p_S \to 0$ as $U \to s$, but the behaviour is not

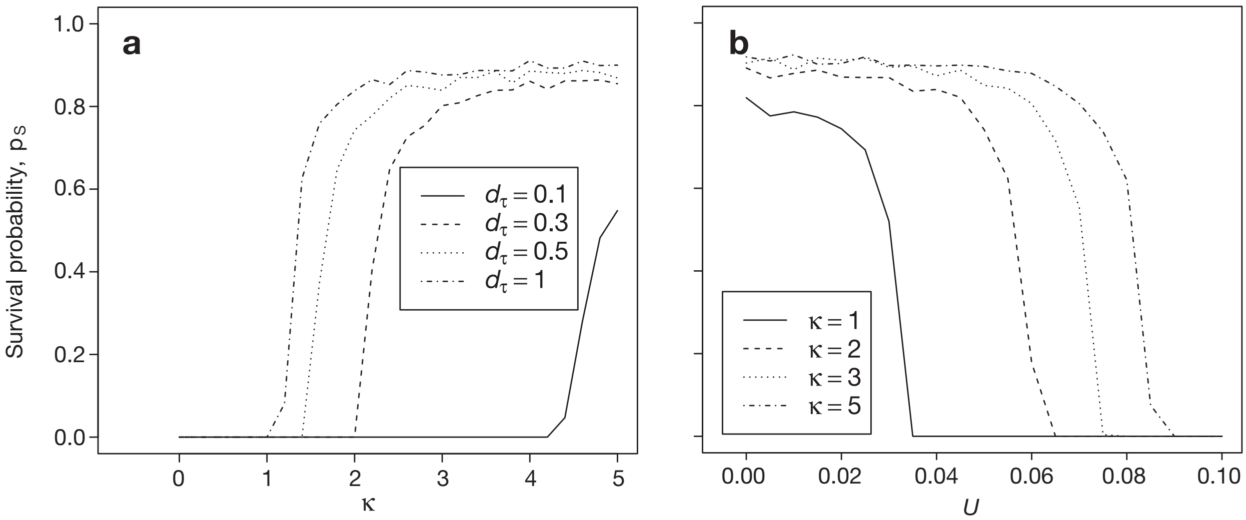

Fig. 4. Plots showing survival probability (p_S) for 1000 runs of Reef Model 2 with fixed initial distance to centre of reef C_0 = 500 m, reef radius r = 100 m, fixed speed s = 0.1 ms^{-1}, and showing (a) p_S versus κ for various values of d_τ with fixed current speed U = 0.05 ms^{-1} and (b) p_S versus U for various values of κ with d_τ = 0.5. d_τ and κ are the reorientation parameters that correspond to sensing and orientating ability, respectively

smooth and features the same threshold behaviour as discussed previously. For fixed reorientation parameters, the survival probability is critically dependent on the current magnitude, U. For small U, the survival probability is close to the upper bound predicted, with a slow decrease in survival probability as U increases. However, once $U > U_{\text{crit}}$, there is a substantial drop in the survival probability, which becomes close to zero. If the current is faster than the speed of movement, $U > s$, then the settlement stage larvae have zero survival probability in this reef environment (see Fig. 2).

As with Reef Model 1, simulations have been completed with different parameter values but the results are not qualitatively different. A current that is parallel rather than perpendicular to the reef (so that the reef is up or downstream of the origin point) simply acts to increase or decrease the absolute velocity of the settlement stage larvae. Simulations completed with a parallel current produce qualitatively similar results to Reef Model 1, with either an increase or decrease in survival probability for the same parameter values, depending on whether the larvae start upstream or downstream of the reef and plots are omitted (see also Armsworth 2000).

Initial distance to the reef (Reef Models 1 and 3)

Fig. 5a shows how the survival probability for Reef Model 1 (with fixed sensing ability, $d_\tau = 0.5$) changes as the initial distance from the edge of the reef, $D_0 = C_0 - r$, increases. The decrease in survival probability appears to be approximately linear as D_0 increases, although for the most random movement (κ = 0.1) there appears to be an asymptotic decrease towards zero, as the survival probability gets small.

Fig. 5b shows how the survival probability for Reef Model 3 (spatially dependent sensing ability, $d_\tau(\mathbf{x})$) changes as the initial distance from the edge of the reef, $D_0 = C_0 - r$, increases. The initial decrease in survival probability is again approximately linear, followed by a sudden drop as D_0 increases past some critical value which is close to 900 m (at which point C_0 = 1000 m and $d_\tau(\mathbf{x}) \approx 0$ and the settlement stage larvae can no longer sense the reef). It is interesting to note that if κ is large and the motion is less random, the survival probability is still non-zero for $D_0 > 900$ m ($C_0 > 1000$ m), even though the larvae are unable to sense the reef. This is explained by the fact that if κ is large, the average dispersion is greater (Codling 2003) and it is more likely that some settlement stage larvae will move within 1000 m of the centre of the reef and become able to sense the reef even if their initial movement is not directed.

Simulations have also been completed where the limit of the larval sensing of the reef is less than or greater than 1000 m from the centre of the reef, but the results are not qualitatively different (the cut off point is close to the maximum limit of the sensing ability) and plots are omitted.

DISCUSSION

Using a simple individual based biased random walk model that includes mortality effects, we have been

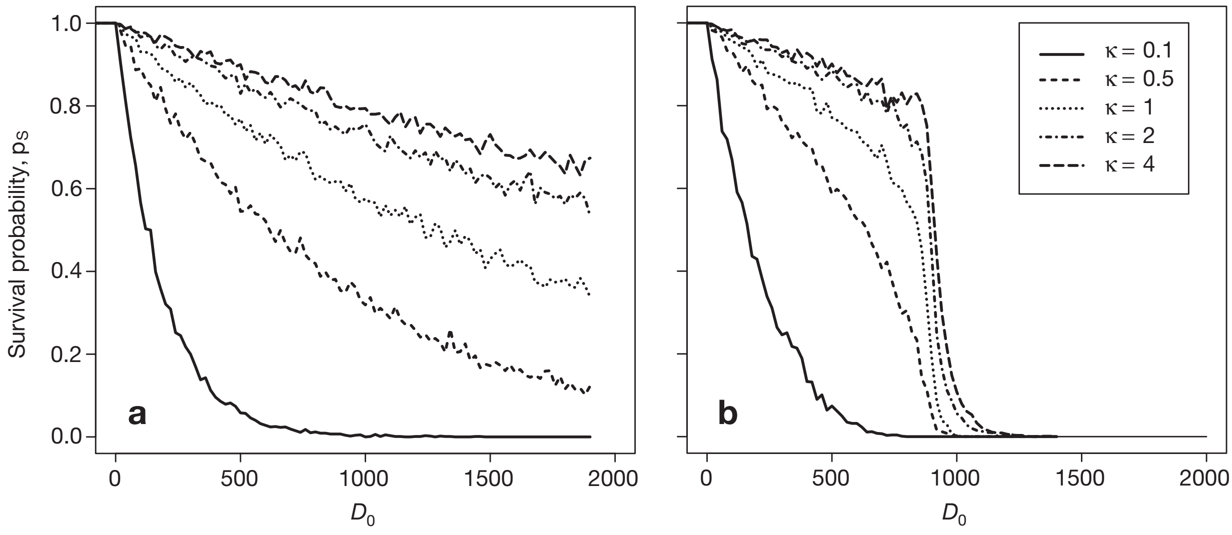

Fig. 5. Plots showing survival probability (p_S) versus the initial distance to the edge of the reef (D_0), for 1000 runs of (a) Reef Model 1 with fixed sensing ability $d_\tau = 0.5$ and (b) Reef Model 3 with spatially dependent sensing ability, $d_\tau(\mathbf{x})$. In both cases, $s = 0.1$ ms^{-1}, there is no current $U = 0$) and various values for the orientating ability (κ) have been used (κ values are the same in both plots)

able to model the movement and subsequent recruitment of a population of settlement stage reef fish larvae. There is strong evidence that settlement stage larvae can sense reefs and direct their motion towards them (e.g. Leis & Carson-Ewart 2003), but due to variance between individuals and inherent environmental stochasticity due to turbulence and local fluid velocity, they are unlikely to be able to do this perfectly. This makes a biased random walk model particularly appropriate to model the movement of settlement stage larvae as it captures these essential features (sensing and swimming abilities, together with environmental variability). The model does not consider post-settlement behaviour, as we are interested in the interplay between sensing and swimming (orientating) abilities in the migratory settlement phase.

By examining a range of reorientation parameter values (corresponding to a range of sensing and orientating abilities) together with realistic values for swimming speed, current speed and reef distance, we have shown that the survival probability is critically dependent on the reorientation parameters we use to describe the sensing and swimming abilities of settlement stage larvae. The parameter d_τ (sensing ability) can be estimated from the inverse of the average reorientation time observed relative to the rate of turning (Hill & Häder 1997), while κ (orientating ability) can be estimated from the variance of the distribution of turning angles observed. Further experimental work is necessary to find realistic values for these reorientation parameters with regard to settlement stage reef fish larvae. Methods for analysing trajectories of movement are available (Hill & Häder 1997, Codling 2003), although logistical restraints may limit experiments designed to establish orientation cues used at small scales of the order of metres (Sweatman 1988, Stobutzki & Bellwood 1998).

The critical dependence of the survival probability on the reorientation parameters (the threshold behaviour observed in our results) can be compared to similar threshold behaviour in the development stage of pelagic reef fish larvae. Fisher et al. (2000) observed that larvae would hardly swim at all until reaching a certain age at which point they would swim all day. It would make sense for settlement stage larvae to wait until their sensory abilities are reasonably well developed before attempting settlement in order to maximise their chances of reaching the reef. This is illustrated in the simple example in Fig. 2.

We have also applied our simple model to other reef scenarios. A feature of recent *in situ* experimental work is the use of a sound and light trap to trap settlement stage larvae (Tolimieri et al. 2000, Leis et al. 2003, Simpson et al. 2004). In the simplest possible case, this is equivalent to trying to reach a very small reef in our model. We have run simulations with a reef radius of 10 m but the results still exhibit threshold behaviour, where the survival probability is critically dependent on the reorientation parameters (sensing and orientating abilities). Field experiments have shown that reef fish larvae have a limited time period for settlement and metamorphosis (McCormick 1999) and there is also evidence of periodicity in settlement dates linked to the lunar cycle, with larvae waiting in the pelagic zone until the new moon period before attempting settlement (Doherty & Williams 1988, Robertson 1992, Kingsford & Finn 1997). To model this scenario, we have also run simulations that include a 'cut-off' time (for example 10 h) after which point any settlement stage larvae in our model that have failed to reach the reef are assumed to die. Once again, this produces results where the survival probability is critically dependent on the reorientation parameters used, although with the cut-off time present, the threshold behaviour is even more pronounced.

We have attempted to produce only a very simple general model to illustrate the importance that sensing and orientating abilities may play in the movement and successful recruitment of settlement stage reef fish larvae. Our model could readily be adapted to be used in specific reef environments where the shape of the reef is more complex and the underlying currents are allowed to vary in strength and direction.

It would be straightforward to fit our model into larger models of the pelagic dispersal phase where settlement has been modelled as a passive dispersal process relying on entrapment (Dight et al. 1990a, 1990b, Dight & Black 1991, Cowen et al. 2000), where movement during the settlement stage has been considered but not modelled explicitly (James et al. 2002), or where settlement stage movement has been modelled deterministically as a fixed vector towards the reef (Porch 1998, Armsworth 2000, 2001). Rather than making the unrealistic assumption in our model that all the settlement stage larvae start from the same origin point, it should be possible to incorporate data from these larger dispersal models to give a more realistic initial distribution.

A further extension to the model that may be worth considering is a variable death rate $\gamma(\mathbf{x})$ depending on the spatial position, so that there is more chance of predation closer to the reef (Porch 1998). There is evidence that settlement stage larvae can sense predators and will move away and or change their depth to avoid being eaten (Leis & Carson-Ewart 1999). There is also the possibility that settlement stage larvae use the fact that currents have different magnitudes (and possibly even different directions) at different depths, to maximise their chances of reaching the reef (Armsworth 2001). Simulations would need to be completed in 3 dimensions if depth were to be included in our simple model. To account for the large amount of inter- and intra-specific variation observed in empirical work on settlement stage reef fish larvae, further simulations could include variability in the individual larvae in the population (different sizes or speeds of movement). The effects of interactions between individual larvae could also be considered.

Our simple generalised model has shown that in different reef environments the survival probability is critically dependent on the reorientation parameters used, corresponding to the ability of the settlement stage larvae to both sense the reef and then reorientate and direct their motion towards it. Settlement stage larvae that rely on passive advection through pure diffusion or favourable currents are likely to have a very low survival probability. Our results demonstrate that by possessing even rudimentary sensing and reorientation abilities, settlement stage larvae can dramatically increase their chances of surviving to reach the reef and recruit into the adult population.

Acknowledgements. We would like to thank C. Dytham for help in the initial discussions of the model and 4 anonymous referees whose comments helped improve the present manuscript. E.A.C. was supported by a studentship from the E.P.S.R.C. in the UK.

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Editorial responsibility: Howard Browman (Contributing Editor), Storebø, Norway

Submitted: January 14, 2004; Accepted: June 9, 2004
Proofs received from author(s): September 8, 2004