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Strategies and trajectories of coral reef fish larvae optimizing self-recruitment

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Abstract

Like many marine organisms, most coral reef fishes have a dispersive larval phase. The fate of this phase is of great concern for their ecology as it may determine population demography and connectivity. As direct study of the larval phase is difficult, we tackle the question of dispersion from an opposite point of view and study self-recruitment. In this paper, we propose a mathematical model of the pelagic phase, parameterized by a limited number of factors (currents, predator and prey distributions, energy budgets) and which focuses on the behavioral response of the larvae to these factors. We evaluate optimal behavioral strategies of the larvae (i.e. strategies that maximize the probability of return to the natal reef) and examine the trajectories of dispersal that they induce.

Mathematically, larval behavior is described by a controlled Markov process. A strategy induces a sequence, indexed by time steps, of "decisions" (e.g. looking for food, swimming in a given direction). Biological, physical and topographic constraints are captured through the transition probabilities and the sets of possible decisions. Optimal strategies are found by means of the so-called stochastic dynamic programming equation. A computer program is developed and optimal decisions and trajectories are numerically derived.

We conclude that this technique can be considered as a good tool to represent plausible larval behaviors and that it has great potential in terms of theoretical investigations and also for field applications.

Keywords: Dispersal; Coral reef fish; Larva; Optimality; Stochastic dynamic programming

1. Introduction

Like most marine organisms, the life cycle of coral reef fishes is divided into two phases, exemplified by a quite sedentary, littoral-associated phase recruited from a dispersive, mobile, pelagic phase (Leis, 1991; Leis and Carson-Ewart, 2000). Two direct consequences of such a complex life cycle can be underlined. First of all, individuals have to negotiate the hazards of two totally different environments within their lifetime, which increases the number of factors which potentially limit the population size. Second of all, marine populations are mostly organized in metapopulations with sedentary adult populations connected by larval flux.

The success of the planktonic stage is highly variable (Sissenwine, 1984; Steele, 1984), therefore dispersal often disconnects adult population size and the size of the cohort of larvae it produces. This has been the basis for an active debate about whether the size of an adult population is limited primarily by recruitment or resources (see reviews by Ehrlich, 1975; Sale, 1980; Doherty and Williams, 1988; Caley et al., 1996). Nevertheless, within the field of fish ecology, the term "recruitment" is hard to define. Indeed, it is a human defined period of the life cycle and does not refer to a precise biological phenomenon (Fraschetti et al., 2003). Recruitment is more or less related to the entry of newly produced individuals into the adult population and therefore is a critical parameter for population demography. This explains the intense focus around this concept and also the difficulties that arise when looking

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for a consensus between studies that define recruitment in different ways. Nevertheless, recruitment is preceded by "settlement" which, in contrast, is a precisely defined biological period. Settlement is the time at which fish larvae become associated with the substrate (Fraschetti et al., 2003). This precise time period marks the end of the pelagic larval phase. Some studies pointed out some important events occurring between settlement and recruitment (Jones, 1991). Be that as it may, from the point of view of a pelagic study, we are primarily interested in whether larvae reach (i.e. settle on) a reef or not and are not concerned whether settlement is directly followed by recruitment. In order to be able to relate this study to the abundant literature dealing with recruitment we will use this term (recruitment) to define the end of the pelagic phase even if "settlement" would be more precise.

The geographic origin of the recruits determines the scale at which a population can be considered as demographically closed (i.e. self-replenishing). Connectivity between geographical areas is of great concern for fisheries management as well as for conservation programs (Dight et al., 1988; Doherty et al., 1995; Cappo and Kelley, 2001), and therefore, population dispersal is a central issue in coral reef ecology. Dispersal of coral reef fish is known to be bounded, as species composition is not identical everywhere and often species-specific or assemblage-wide geographic boundaries can be observed (Springer, 1982). Nevertheless, reefs not separated by vast expanses of open water were thought to be connected via larvae at a high frequency. This paradigm culminated in the paper by Roberts (1997), which suggested that general current flow and larval duration alone would dictate the exchange rate of larvae from a specific "upstream" reef to a specific "downstream" reef.

The direct study of dispersed larvae is difficult because dilution of larvae in oceanic waters prevents efficient plankton analysis far from the reefs and high mortality rates make capture–mark–recapture studies difficult. Considering these limitations, it seems worthwhile to reduce the scale of the study from an entire closed metapopulation to an open subpopulation of this metapopulation. Therefore we tackle the question of dispersal from an opposite perspective by determining larval retention and rates of self-recruitment (recruitment of a larva back to its natal reef). Technically, rates of self-recruitment can be inferred by incidences of inbreeding, considering that the only other source of individuals represents dispersal from other populations independent of their origin. Furthermore, a direct study of local retention rather than dispersion seems much more feasible as field-work, through tagging. For example, using artificial tagging Jones et al. (1999) were able to demonstrate that 15–60% of the damselfish *Pomacentrus amboniensi* were recruiting to their natal reef. However, such an approach is still limited by technical restrictions in the tagging methodology and by the small proportion of the total population that can be tagged. More importantly, this approach does not provide any information on the factors favoring self-recruitment since the activity during the larval stage and the potential decisions of the larvae in open water remain unknown.

Mathematical modelling may help to understand the events occurring during the pelagic stage and their influence on the outcome of this phase. Initial modelling studies considered larvae as passive particles and focused on hydrodynamic features to explain their distribution (Black et al., 1990, 1991). These models predict that larvae are flushed away from their natal reef in a direction determined by predominant currents. Therefore, self-recruitment was predicted to be rare or even impossible. This idea persisted for years as it is the basis for Roberts' (1997) paper. Nevertheless, field studies pointed out significant rates of self-recruitment (Jones et al., 1999). Moreover, larvae of many coral reef fishes were found capable of strong, sustained swimming thus being able to regulate their distribution and dispersion (Stobutzki and Bellwood, 1997; Leis et al., 1996; Leis and McCormick, 2002). At least late-stage larvae were suggested to have cues to orientate them toward the island, including sound (Leis et al., 1996; Leis and Carson-Ewart, 2002; Tolimieri et al., 2000), chemical signals (Sweatman, 1988; Kingsford et al., 2002) or temperature gradients (Doherty et al., 1996). Therefore current thinking is that reef fish larvae may use their swimming and sensory abilities to reduce dispersal and, hence, favor self-recruitment (Cowen, 2002).

The model of the pelagic phase presented in this paper takes the behavior of larvae into consideration (other examples in Wolanski et al., 1997; Porch, 1998; Armsworth, 2000, 2001; Armsworth et al., 2001). Furthermore, we model the theoretical situation of an isolated island where self-recruitment is the only recruitment possibility (no dispersal to other reefs). Indeed, as mentioned above, studying self-recruitment rather than dispersal ensures more feasible field validation of the results of the model. The design of the model is focused on the larvae to emphasize the importance of their behavior, even if the attention is on their trajectories. Therefore, we regard recruitment as the probability of a larva returning to its natal reef. In addition, we represent a larva's dynamic behavior by considering that, at different time steps, this larva faces alternative behavioral decisions from which to choose. Thus, we need to determine a choice criterion: our theoretical larva takes the "best" strategy (i.e. the one maximizing recruitment probability), knowing its state (a strategy is a function of state and time). This allows us to compute "optimal" trajectories which are state trajectories for which the sequence of decisions is generated by an optimal strategy. Here, we have to cope with a dynamic optimization problem that will be solved by stochastic dynamic programming. The present paper describes this modelling method and assesses whether this approach and its results are reasonable, for a given description of the environment. Furthermore, we discuss the consequences of the modelling method chosen and underline the potential of such models.

2. Models development

2.1. A general modelling framework

In the classical framework of stochastic optimal control (Bertsekas, 2000; Puterman, 1994), a stochastic dynamic model describes the evolution of the state, with decisions (or "controls") influencing the dynamics, and an optimization quantity ("gain") is given. A strategy (which generates as sequence of controls) is optimal if it maximizes the mean value of the gain. Here, we outline the main features of our dynamic optimization problem.

Time. Time is measured in discrete units until a fixed finite horizon. The duration of dispersal in the field was proved to be more or less variable around a fixed mean for each species (Victor, 1986; Wellington and Victor, 1989), with for example some species capable of delaying their metamorphosis and hence retarding their contact with the reef (McCormick, 1999). Nevertheless, in this study we only consider the mean for mathematical simplicity. The time unit is 6 h in order to account for daily variations in environmental conditions and larval behavior.

State. The state of the system is entirely characterized by the state of the larva, made of its energetic resources and position. Energetic resources evolution is incorporated to obtain biologically realistic strategies. For example, if their energetic resources were not limited, larvae would be able to swim at their maximum speed eternally without having to rest or eat. Energetic resources are represented as a scalar. The position can be a vector of dimension 1 (distance to the reef) or 3 (three-dimensional space), depending on the model.

Environment. Environmental variables such as predation pressure, food availability and current velocity are involved in the dynamical evolution of the state. They are described by functions of position and period of the day (day or night). Predation pressure and food availability are represented as probabilities, to survive or to eat at each time step.

Controlled dynamics. At each time step, the larva may choose between two types of behavior: foraging or directional swimming. We consider that there is a trade-off between these decisions. In both cases, the larva swims. Indeed, fish larvae have been observed to eat "on the run" (Leis and Carson-Ewart, 1998). Nevertheless when foraging, their movement is assumed random as it probably follows the erratic movements of their planktonic prey. Depending on the model, each behavior may be divided into sub-decisions such as swimming to the left, swimming downwards, etc. Each behavior has consequences on the state of the larva, as follows.

- Directional swimming changes the position of the larva, but reduces its energetic resources.
- Foraging may increase energetic resources but the larva cannot choose its future position.

Present state, environmental factors, time and decision of the larva affect its future state, possibly in a stochastic way.

Optimization criteria. As underlined before, we focus here on recruiting trajectories. Therefore we are mainly interested in strategies inducing sequences of decisions which maximize the probability that the larva returns to the natal reef precisely at the last time step, which is the only possibility, in this model, for a larva to recruit. There is potentially an infinite number of self-recruiting trajectories. By maximizing self-recruitment probability we select the trajectories that maximize survival. In other words, as self-recruitment is a pre-requisite, survival is in fact the quantity optimized along a recruiting trajectory. From this point of view, our criterion is probably more intuitive, nevertheless this choice will be further discussed later. Other criteria can be specified, for example: probability of return with maximum energy, with given energy, etc. In addition, focus is always only on the final state: there are no constraints on the rest of the trajectories as long as they achieve the given criterion at the last time step.

2.2. A first simple stochastic model

This model is presented *only* to aid in understanding. It provides a highly simplified portrayal of the state and environment of the larva (i.e. one-dimensional ocean, binary decisions for larvae) in order to be able to detail Markov chain modelling and its control.

2.2.1. Model description

Time. Time horizon is 2 months (240 time steps).

State.

$$\text{Energetic resources:}\quad \theta \in [0, \theta_{max}]. \tag{1}$$

When the energetic resources equal zero, the larva is dead.

$$\text{Position (distance from natal reef):}\quad x \in [0, x_{max}]. \tag{2}$$

Environment. Predation pressure, food availability and currents are uniform on the whole space. Survival probability equals a constant: p. Probability to eat equals 1 (the food is sufficient). Current intensity equals $\Delta x^0 > 0$ (current is taking the larva away from the reef of Δx^0 units in one time step).

Controlled dynamics. Here, only two choices are offered to the larva at each time step: foraging ($u = 0$) or swimming toward the reef ($u = 1$). Let us suppose that the larva is, at time t, in state (θ_t, x_t); its decisions are illustrated in Fig. 1.

1. *Foraging decision.* Either the larva dies, or it survives with probability p and then increases its energy by a fixed quantity $\Delta\theta^0$ and is taken away by the current on a distance Δx^0. Thus

$$(\theta_{t+1}, x_{t+1}) = \begin{cases} (0, x_t) & \text{w.p. } 1-p, \\ (sat_{[\theta_{min},\theta_{max}]}(\theta_t + \Delta\theta^0), sat_{[x_{min},x_{max}]}(x_t + \Delta x^0)) & \text{w.p. } p, \end{cases}$$

where w.p. stands for "with probability" and the *sat* function is defined by

$$sat_{[\xi_{min},\xi_{max}]}(\xi) = \begin{cases} \xi_{max} & \text{if } \xi > \xi_{max}, \\ \xi & \text{if } \xi \in [\xi_{min}, \xi_{max}], \\ \xi_{min} & \text{if } \xi < \xi_{min}. \end{cases}$$

This function is necessary because of the boundaries on energy and position (see Eqs. (1) and (2)).

2. *Swimming decision.* Either the larva dies, or it survives with probability p and then swims toward the reef on a distance Δx^1, consuming $\Delta\theta^1$ units of energy. Thus

$$(\theta_{t+1}, x_{t+1}) = \begin{cases} (0, x_t) & \text{w.p. } 1-p, \\ (sat_{[\theta_{min},\theta_{max}]}(\theta_t - \Delta\theta^1), sat_{[x_{min},x_{max}]}(x_t - \Delta x^1)) & \text{w.p. } p \end{cases}$$

and the same remarks as above apply.

This can be summarized in four conditional transition probabilities as follows:

$$\begin{cases} \mathbb{P}[(\theta_{t+1}, x_{t+1}) = (0, x) | \theta_t = \theta, x_t = x, u_t = 0] = 1 - p, \\ \mathbb{P}[(\theta_{t+1}, x_{t+1}) = (sat(\theta_t + \Delta\theta^0), sat(x_t + \Delta x^0)) | \\ \quad \theta_t = \theta, x_t = x, u_t = 0] = p, \\ \mathbb{P}[(\theta_{t+1}, x_{t+1}) = (0, x) | \theta_t = \theta, x_t = x, u_t = 1] = 1 - p, \\ \mathbb{P}[(\theta_{t+1}, x_{t+1}) = (sat(\theta_t - \Delta\theta^1), sat(x_t - \Delta x^1)) | \\ \quad \theta_t = \theta, x_t = x, u_t = 1] = p. \end{cases}$$

These probabilities are used to build the transition matrices that characterize a Markov chain. The element (i,j) of a transition matrix $\mathscr{M}$ is the probability of the transition between the initial state indexed by i and the final state indexed by j. Therefore, to simulate a step from the initial state indexed by i, focus is on line i and a final state is drawn according to the probabilities on this line. In this model, the Markov chain is controlled. This means that a different transition matrix is associated with each decision of the larva.

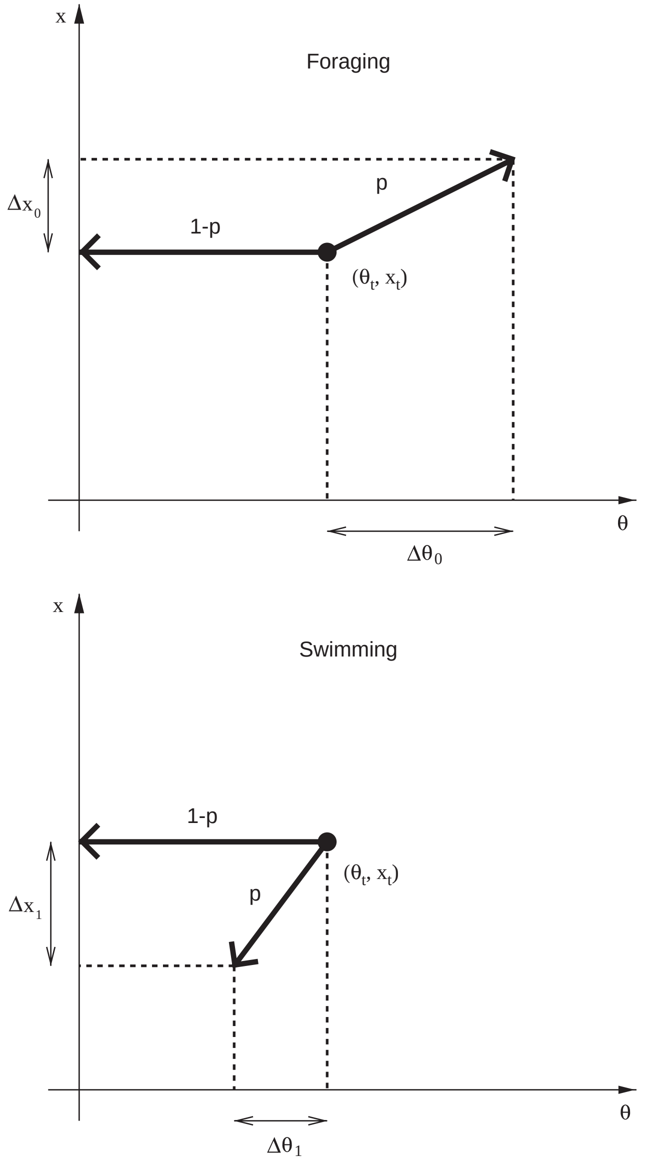

Fig. 1. State space representation of the transitions in the simple model. The arrows represent the transitions from the state (θ_t, x_t) and the associated probability is specified above. Two sketches are presented, one for each decision. θ is the amount of energetic reserves, x is the distance to the reef.

The simplest meaningful transition matrices for this simple model are presented in Fig. 2. State is defined by three energy levels and four distances from the reef. When the larva swims, it gains one distance unit but expends one energy unit; when it forages, it loses one distance unit because of the current but gains one energy unit. Matrices are indexed by the decision (0 for foraging, 1 for swimming).

Let us detail what these matrices mean in a few relevant cases. First of all, a dead larva (initial energy equals 0) remains dead (final energy is 0), at the same

$$\begin{array}{ccc|cccc|cccc|cccc}
 & E\rightarrow & & & 0 & & & & 1 & & & & 2 & & \\
 & \downarrow & P\rightarrow & 0 & 1 & 2 & 3 & 0 & 1 & 2 & 3 & 0 & 1 & 2 & 3 \\
\hline
 & & 0 & \mathbf{1} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 & & 1 & 0 & \mathbf{1} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 & 0 & 2 & 0 & 0 & \mathbf{1} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 & & 3 & 0 & 0 & 0 & \mathbf{1} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\hline
 & & 0 & \mathbf{1-p} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \mathbf{p} & 0 & 0 \\
\mathrm{A} & & 1 & 0 & \mathbf{1-p} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \mathbf{p} & 0 \\
 & 1 & 2 & 0 & 0 & \mathbf{1-p} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \mathbf{p} \\
 & & 3 & 0 & 0 & 0 & \mathbf{1-p} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \mathbf{p} \\
\hline
 & & 0 & \mathbf{1-p} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \mathbf{p} & 0 & 0 \\
 & 2 & 1 & 0 & \mathbf{1-p} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \mathbf{p} & 0 \\
 & & 2 & 0 & 0 & \mathbf{1-p} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \mathbf{p} \\
 & & 3 & 0 & 0 & 0 & \mathbf{1-p} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \mathbf{p}
\end{array} = \mathcal{M}^0$$

$$\begin{array}{c|cccc|cccc|cccc}
 & \mathbf{1} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 & 0 & \mathbf{1} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 & 0 & 0 & \mathbf{1} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 & 0 & 0 & 0 & \mathbf{1} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\hline
 & \mathbf{1-p+p} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\mathrm{B} & \mathbf{p} & \mathbf{1-p} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 & 0 & \mathbf{p} & \mathbf{1-p} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 & 0 & 0 & \mathbf{p} & \mathbf{1-p} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\hline
 & \mathbf{1-p} & 0 & 0 & 0 & \mathbf{p} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 & 0 & \mathbf{1-p} & 0 & 0 & \mathbf{p} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\mathrm{C} & 0 & 0 & \mathbf{1-p} & 0 & 0 & \mathbf{p} & 0 & 0 & 0 & 0 & 0 & 0 \\
 & 0 & 0 & 0 & \mathbf{1-p} & 0 & 0 & \mathbf{p} & 0 & 0 & 0 & 0 & 0
\end{array} = \mathcal{M}^1$$

Fig. 2. Transition matrices for the simplest meaningful parameterization of the first simple model. Lines are the initials states, columns are the final states. Elements of the matrices are transition probabilities between the initial and final states. States are defined by energy and position values. The legend for energy (E) and position (P) specified for $\mathcal{M}^0$ is also true for $\mathcal{M}^1$.

position, whatever the decision. Thus the identity matrix is placed at the upper left corner of each matrix. Then consider case A in Fig. 2. The larva's initial state is (energy = 1, position = 1) and the larva's decision is to forage ($u = 0$). Either it dies with probability $1 - p$ or it survives with probability p. Only these two non-zero probabilities have to be placed on the line corresponding to the initial state. When it dies (energy becomes 0), it remains at the same position (position is 1); thus we put $1 - p$. When it survives, it forages (energy becomes 2) but is taken away from the reef (position becomes 2); thus we put p.

Let us now consider the same initial state but the alternative decision ($u = 1$), that is case B. When the larva dies, nothing changes. When it swims, it loses one energy unit (energy becomes 0) and comes closer to the reef (position becomes 1).

Finally, let us consider a two-step scenario. Larva starts from case A. It survives with probability p. It is now at state (energy = 2, position = 2), i.e. in case C. Either it dies and its state becomes (energy = 0, position = 2) with probability $1 - p$; or it survives and swims toward the reef: its state becomes (energy = 1, position = 1) with probability p.

We may notice that these matrices are very sparse. Indeed, only two final states are possible (transition probability $\neq 0$) from each initial state. This is still true for greater state dimensions. Hence, matrices become relatively sparser as the state dimension increases.

Optimization criterion. The "gain", previously defined, is itself divided into "instantaneous" gains (gains at each time step) and "final" gain (gain at last time step). In this model we have decided to maximize the energetic resources of the larva when it reaches the reef at final time and this gives zero instantaneous gains

$$\forall t = 0, \ldots, T-1, \quad L(\theta, x, u, t) = 0 \tag{3}$$

and a final gain

$$\Phi(\theta, x, T) = \theta \times \mathbf{1}_{\{x=0\}}. \tag{4}$$

When $x_t = x$ and $\theta_t = \theta$, the optimization problem can be written as the value function

$$\begin{aligned} V(\theta, x, t) &= \max_{u_t, \ldots, u_{T-1}} \mathbb{E}\left(\sum_{s=t}^{T-1} L(\theta_s, x_s, u_s, s) + \Phi(\theta_T, x_T, T) \right) \\ &= \max_{u_0, \ldots, u_{T-1}} \mathbb{E}(\theta_T \times \mathbf{1}_{\{x_T=0\}}) \end{aligned} \tag{5}$$

meaning that the energy, θ_T, is maximized at time T but only if the larva reaches the island at time T (i.e. only if $x_T = 0$).

2.2.2. Stochastic dynamic programming equation

Now that the evolution of the state is described and that an optimization criterion is specified, optimal strategies $(u_0^{\#}, \ldots, u_{T-1}^{\#})$, functions of state and time, have to be found. This is done by means of the stochastic dynamic programming equation (or Bellman's equation) which is the backward induction (Bertsekas, 2000; Puterman, 1994)

$$\left\{ \begin{aligned} & V(\theta, x, T) = \theta \times \mathbf{1}_{\{x=0\}}, \\ & V(\theta, x, t) \\ & \quad = \max((1-p)V(0, x, t+1) + pV(\theta + \Delta\theta_0, x + \Delta x_0, t+1), \\ & \qquad (1-p)V(0, x, t+1) + pV(\theta - \Delta\theta_1, x - \Delta x_1, t+1)) \\ & u^{\#}(\theta, x, t) \\ & \quad \in \arg\max(\overbrace{(1-p)V(0, x, t+1) + pV(\theta + \Delta\theta_0, x + \Delta x_0, t+1)}^{\textit{Foraging},\ u=0}, \\ & \qquad \underbrace{(1-p)V(0, x, t+1) + pV(\theta - \Delta\theta_1, x - \Delta x_1, t+1)}_{\textit{Swimming},\ u=1}). \end{aligned} \right.$$

These equations give Bellman's value function V backwards, from the final gain $V(\theta, x, T)$ which is known. They also give subsequent optimal decisions $u^{\#}(\theta, x, t)$ in feedback form (i.e. as functions of state and time). Furthermore, when initial state conditions are $\theta_0 = \theta$ and $x_0 = x$, we can remark from Eq. (5) that

$$V(\theta, x, 0) = \max_{u_0, \ldots, u_{T-1}} \mathbb{E}(\theta_T \times \mathbf{1}_{\{x_T=0\}}), \tag{6}$$

hence providing a direct access to the optimal self-recruitment rate once V is known.

Here, these equations can be simplified. Indeed, when the larva is dead (zero energetic resources), it remains in the same state (energy = 0, position = x) with probability one. Hence, for any t, $V(0, x, t) = V(0, x, t+1) = \cdots = V(0, x, T)$. From the definition of final gain in Eq. (4), we have $V(0, x, T) = 0$ for any x. Thus, $V(0, x, t) = 0$ for any t and any x, and the expression of the induction simplifies itself:

$$\begin{cases} V(\theta, x, T) &= \theta \times \mathbf{1}_{\{x=0\}}, \\ V(\theta, x, t) &= \max(pV(\theta + \Delta\theta_0, x + \Delta x_0, t+1), \\ & \qquad pV(\theta - \Delta\theta_1, x - \Delta x_1, t+1)), \\ u^{\#}(\theta, x, t) &\in \arg\max(\underbrace{pV(\theta + \Delta\theta_0, x + \Delta x_0, t+1)}_{Foraging,\ u=0}, \\ & \qquad \underbrace{pV(\theta - \Delta\theta_1, x - \Delta x_1, t+1)}_{Swimming,\ u=1}). \end{cases}$$

This backward equation is solved using Scilab scientific software. However, the last two optimal decisions can easily be inferred as they are quite intuitive. The last optimal decision, at time $T-1$, should be to swim if the island is reachable. Otherwise, there is no difference between swimming and foraging: the island will never be reached anyway. At time step $T-2$, if the island is very far (beyond two times the larva's swimming capacity in one time step) there is no optimal choice for the same reason: the island cannot be reached at $t = T$. If the island is at twice the distance that a larva can swim in one time step, the optimal choice should be to swim so that the island becomes reachable at time $T-1$. If the island is very close, the decision of the larva should be to eat, increasing its energetic resources, and then swim at time $T-1$ to reach the island; in this way, energetic resources are maximized. The reader can find mathematical justifications of these conclusions in the appendix .

2.2.3. Trajectories

Given the previous environment description and characteristics of the larva, optimal strategies (sequences of optimal decisions) and optimal trajectories (state trajectories for which the sequence of decisions is optimal) are computed. There is no finite number of optimal trajectories. Indeed, in this version of the model, stochasticity is introduced by predation. Here, two characteristic examples of optimal trajectories are presented.

Simulations of this first simple model are presented in Fig. 3. As noted for the last two decisions, larvae behavior seems very intuitive. When it survives (subplot 1), the larva lets itself be taken away by currents until it reaches its maximum energetic resources. Then, it alternates swimming and foraging in order to maximize its energy. In subplot 2, larval behavior begins the same way but it is eaten, at time step 25 approximately, and dies. We can conclude from this model that the algorithm used to simulate the behavior of the larvae and to solve the optimization problem is correct.

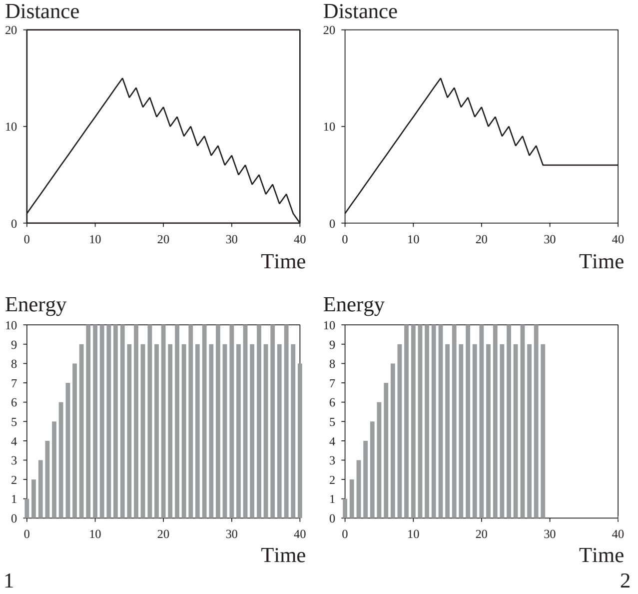

Fig. 3. Examples of some optimal trajectories for the simple model. Subplot 1 is a larva surviving and recruiting successfully to the island. Subplot 2 is a larva dying before reaching the island. The upper plot of each subplot is a trajectory; lower shows energetic resources. Notice that, even for the plot of trajectory, abscissa represents time and not a component of position given that position is one dimensional.

2.3. A more elaborate stochastic model

2.3.1. Model description

Now that we have checked the quality of the algorithm, the aim of this new version of the model is to set the basis for a biologically relevant description of the dispersal phenomenon for coral reef fishes. We focus here on introducing potential key biological features into the model, with special care regarding the capacity of the model to be further developed. Numerical values of the parameters of the model used in simulations are given in the sequel. They are chosen as a basis for this work (for testing the model), and are not necessarily intended to provide generality or to represent a precise field situation. Nevertheless, literature data enable us to choose correct size order parameters. Further studies should follow with more carefully chosen parameter values.

In this more elaborate model we represent an isolated island (no other island in a 100 km range) in an archipelago. The island is modelled in three dimensions as a cylinder, on a horizontal sea bottom. All quantities are discrete, including space. The horizontal mesh of the model is approximately 700 m. As we will explain later, the value of the mesh of this model is determined by other parameters and is not a direct choice of the user. As space is three dimensional, larva's possibilities increase. Seven decisions are now available: swimming northward, southward, eastward, westward, towards the bottom, towards the surface or foraging (and then swimming in a random direction).

Water around isolated tropical islands is often driven by a quite uniform, stable in time, high scale current regime, possibly disturbed by winds and tides (Rougerie and Rancher, 1994). Furthermore, islands induce perturbation in this current field, thus creating eddies (Pingree and Maddock, 1980) or other complex features (Cowen and Castro, 1994) in their lee. In our model, currents are roughly approximated by a uniform and unidirectional vector field of intensity 10 cm s^{-1} (Rougerie and Rancher, 1994). Armsworth (2000) used such a description, which may seem oversimplified. However, he underlined that, depending on what is asked of the model, this can be sufficient. Furthermore, currents are coded here as a 3D matrix that can be filled with the results of a hydrodynamic model if available. Finally, we decide arbitrarily that this velocity (10 cm s^{-1}) corresponds to a three space units movement. As the time unit is 6 h, the space unit is $6 \times 3600 \times 10/3 = 72\,000$ cm or 720 m.

Tropical islands can be compared to oases in a desert of oligotrophic oceanic waters. Nearshore waters are sites of high primary production due to terrigenous input and/or upwelling of deep, nutrient-rich waters (Rougerie and Wauthy, 1986). Hence, phyto- and zooplanktonic densities are higher near the island than away from it. This is called the “reef effect” (Ricard and Delesalle, 1982; Renon, 1989). Consequently, fish densities are often higher in the vicinity of an island than in distant oceanic water (Wolanski and Hamner, 1988). Moreover, the current regime described above tends to create a plume of nutrient-rich water in the lee of the island. This phenomenon is known as the “island mass effect” (Doty and Oguri, 1956). Therefore, environmental conditions are described in three concentric areas, centered on the island and elongated in a direction determined by the current field. The values of food availability and predation rate are assumed to be different in each area, higher in the area closest to the island, and then decreasing. To sketch this, values of 1.0, 0.85 and 0.75 are arbitrarily chosen for feeding probability in close, mid- and farfield areas. Similarly, values of 0.85, 0.95 and 0.99 are chosen for survival probability. Finally, zooplankton completes a daily vertical migration (Valiela, 1995) and is abundant in the top water layer during the day and in the bottom layer during the night. Therefore, the availability of prey also depends on the depth and time of the day and we decided that a larva in the vicinity of abundant plankton is one and a half times more likely to eat than a larva in the vicinity of low plankton densities.

Reef fish larvae can present very different behavioral characteristics, mainly depending on their dispersal strategy (Thresher, 1984).

1. Eggs can be directly dispersed in the water, thus advected as passive particles; then larvae hatch in the ocean.
2. Eggs can be demersal: laid on the substrate, inside the reef. Parents care for the eggs until larvae hatch. Then larvae disperse into the ocean but with greater swimming and sensory abilities than in case 1.
3. The larval phase is completed entirely inside a lagoon (rare).

In order to test this elaborate version of the model and to evaluate the importance of a few parameters, we represent the dispersal of two theoretical larvae following different dispersal strategies, namely an Acanthurid following dispersal strategy number 1 (i.e. planktonic eggs) and a Pomacentrid following strategy number 2 (i.e. demersal eggs).

They first differ by the length of their larval stage: around 50 days for Acanthurids (Lo-Yat, 2002) and from 14 to 35 days among Pomacentrids (Wellington and Victor, 1989). We choose pelagic stage durations of 50 and 20 days as examples.

Their dispersal strategy has consequences on the development of their swimming abilities. Acanthurids disperse eggs that are completely passive. After approximately 24 h, the larvae hatch and develop 4 days before the first food intake. Afterwards, their swimming abilities improve substantially, as late-stage Acanthurid larvae have been shown to be very good swimmers (Stobutzki and Bellwood, 1997). On the contrary, Pomacentrids that produce demersal eggs disperse larvae that are active as early as the beginning of dispersal. Their swimming abilities improve brutally around the middle of the pelagic phase (Fisher et al., 2000) but stay below those of Acanthurids (Stobutzki and Bellwood, 1997). Therefore we divide the larval phase of our two theoretical larvae into three time periods (Thresher, 1984) in order to account for their changes in swimming abilities. Swimming speed values are evaluated from Leis and Carson-Ewart (1997), Stobutzki and Bellwood (1997) and Fisher et al. (2000). Most studies measured the critical swimming speed (maximal speed of a current against which a larva can maintain its position). These speeds are probably greater than actual swimming speeds in the field. Therefore, we choose lower swimming speeds for both species while retaining the difference factor observed between them (Table 1).

During the first period, the energy of the larvae comes from their yolk sac and they do not need to forage. Therefore we consider that their energetic resources are constant and maximal. Afterwards, they lose one energy unit per unit time. As they have a maximum resource of five units they can only swim four time steps (24 h) until food is needed. Stobutzki and Bellwood (1997) pointed out much longer swimming durations before starvation (up to 194 h for Acanthurids for example). Nevertheless, it has to be considered that, in the field, larvae are likely to avoid starvation and keep their energetic resources

Table 1
Pelagic intervals and swimming speeds for the two families represented in the model

	Acanthuridae	Pomacentridae
Pelagic larval duration (days)	50	20
Three periods durations (days)	5, 25, 20	3, 10, 7
Swimming speeds (cm s^{-1})	0, 13, 36	3, 10, 20

For the two types of larvae used in the elaborate version of the model (Acanthuridae and Pomacentridae) the duration of the pelagic interval is given. It is divided into three periods, the durations of which are given on the second line. The last line specifies the swimming speed in cm s^{-1} during these three periods.

level as high as they can. Furthermore, Stobutzki and Bellwood (1997), as many other studies of this kind, focused on the time that a larva can swim against a given current before starving or being exhausted without any consideration of maintaining the growth rate or the integrity of the metabolic pathways. Houde and Zastrow (1993) underlined the fact that the daily food intake of fish larvae needed to maintain their growth rate is high (50% of body weight is a general mean), especially for fast-growing, warmwater fish larvae. Therefore, fish larvae should eat often, probably on a daily basis, during dispersal.

Characteristics of the larvae are described here for one larva and intraspecific interactions are not taken into consideration. Nonetheless, even if larvae are known to disperse in patches (Doherty, 1987; Thorrold et al., 1994), representing the dispersion of one larva is technically equivalent to representing the dispersion of a patch of these larvae.

The optimization framework used here implies that our theoretical larvae are aware of their state, energy and position. As underlined by Armsworth (2000) and Kingsford et al. (2002), sensory capacities of larvae have been poorly investigated even if thought to be important. Nevertheless, as mentioned in the introduction, at least late-stage larvae are capable of orientation and exhibit sensory capabilities to some extent. Fisher et al. (2000) underlined that swimming abilities of fish larvae developed much earlier than what was expected. It might be the same for sensory abilities and early-stage larvae may also be able to locate the island. This model focuses on the behavioral response of larvae and this is the reason for the emphasis on their sensory abilities. Furthermore, it must be kept in mind that the aim of this model is to identify optimal dispersal trajectories and not to describe precisely the behavior of each dispersing larva.

In this model, final gain equals one for every non-dead larva arriving to the island at the given time horizon. Otherwise final gain equals zero. Instantaneous gains still equal zero and therefore the criterion maximized is the probability of recruitment ($\mathbb{P}(x_T = 0)$). Thus the optimization problem can be written as

$$\max_{u_0,\ldots,u_{T-1}} \mathbb{E}(\mathbf{1}_{\{x_T=0\}}) = \max_{u_0,\ldots,u_{T-1}} \mathbb{P}(x_T = 0). \tag{7}$$

As previously mentioned in Section 2.1, when the focus is on successful (i.e. recruiting) trajectories, this criterion means optimizing survival along the trajectories. Furthermore, as noticed in Eq. (6), for a larva starting from position (x, y, z) and energy resources θ, this optimal (i.e. maximal) probability to reach the island is given by $V(\theta, x, y, z, 0)$, where V is the value function. This gives direct access to the maximum self-recruitment rate.

2.3.2. *Stochastic dynamic programming: memory and speed remarks*

Dynamic programming requires lots of physical memory when the state dimension grows. This phenomenon is called the "curse of dimensionality" (Puterman, 1994; Bertsekas, 2000). As descriptions of the environment and of the state become more detailed, technical problems appear associated with computational capacity.

The building of transition matrices is the critical step. Such matrices are very large because each matrix defines the probabilities to reach all (θ, x, y, z) final states from an initial state, for a given control. For instance, let us consider a typical frame of 100 x and y space steps, 3 depth steps and 6 different levels of energetic resources. There are $100 \times 100 \times 3 \times 6 = 180\,000$ possible states. So, each transition matrix is $180\,000 \times 180\,000$. As Scilab uses long float numbers in this computation, it means that each transition matrix needs $180\,000^2 \times 32/8 = 130$ MB of RAM to be stored, and there are fourteen of them in the elaborate model, which greatly exceeds RAM capacities of most computers.

This appears as a major obstacle in the use of dynamic programming for two reasons: speed and RAM requirement. First of all, these large matrices are filled by loops. Scilab has a way of managing loops that is very time-consuming. The solution to this problem is to use C code to manage these loops and to link this code to Scilab. The resulting progress is significantly high: from one whole day to two seconds for a $20 \times 20 \times 2 \times 6$ state space. However, the high RAM requirement still poses problems. Nevertheless, transition matrices are very sparse. As underlined before, few final states can be reached from each initial state: a maximum of two in the simple model and of fifteen in the elaborate model. This means that on one line, there are at most fifteen non-zero probabilities. The solution in Scilab is therefore to store transition matrices as "sparse matrices": only non-zero probabilities are physically stored in RAM.

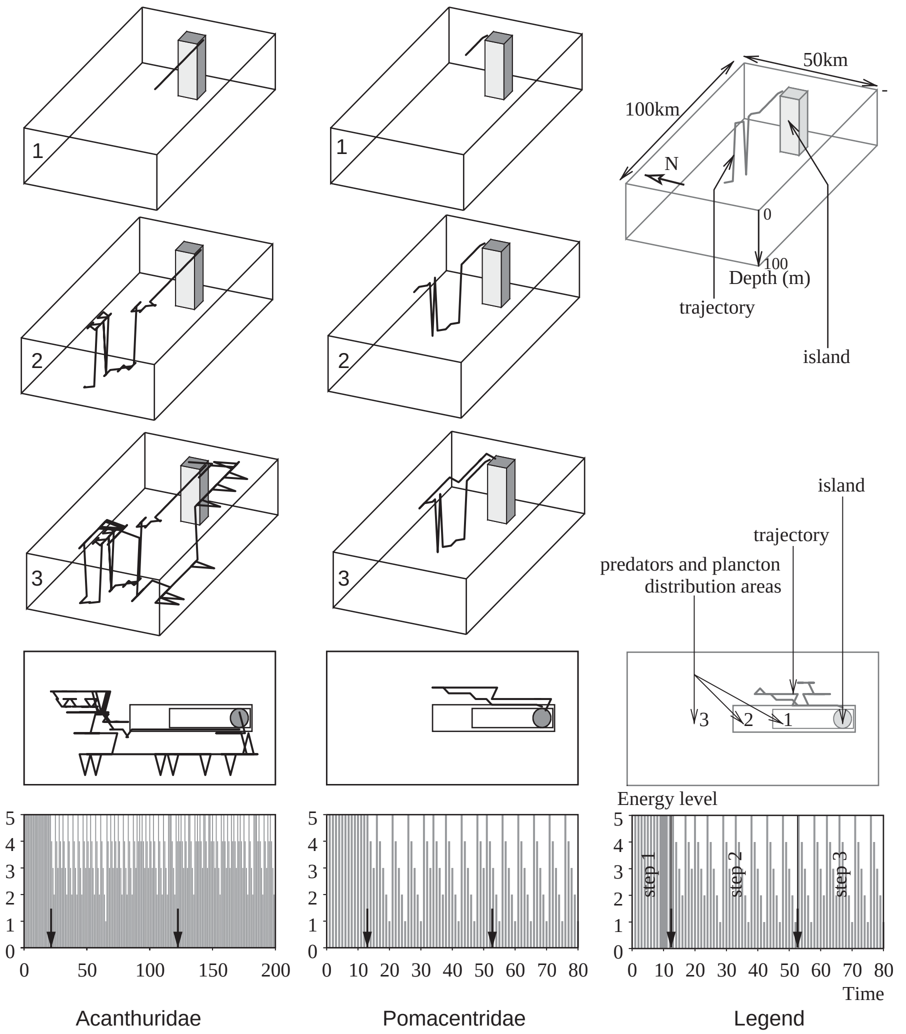

Fig. 4. Comparison of a characteristic example of optimal trajectory for a larva of type Acanthuridae and a larva of type Pomacentridae, in the elaborate model. The first column gives an example of a trajectory for a larva of type Acanthuridae, the second for a larva of type Pomacentridae. In each column, the first three plots are a three-dimensional representation of the trajectory for time step one (1), time steps one and two (2) and time steps one, two and three i.e. complete trajectory (3); the fourth plot is a two-dimensional representation of the complete trajectory; the last plot depicts the evolution of the energetic resources through time. The last column specifies legends for the different plots.

2.3.3. *Trajectories*

One characteristic example of trajectory is presented for each type of larva. Indeed, optimal trajectories are not unique because there are two sources of stochasticity: predation (as in the simple version of the model) and non-directional swimming when foraging.

Comparing the two trajectories presented in Fig. 4, we can identify features common to both species and conclude that, as in the first, simple case, this modelling framework gives reasonable trajectories, understandable from our point of view. Indeed, at the beginning of dispersal, the only requirement for the larva is to survive because its energetic resources come from its yolk sac and so it does not need to feed (notice that, in our representation, the energetic resources are therefore constant and maximal). Hence, when swimming is possible (i.e. for Pomacentrids) optimal trajectories go out from the high predation zone, ensuring the survival of the larva (plot 1). Then, as death by predation is negligible, the priority of the larve becomes food acquisition. Indeed, we can notice that the energetic resources begin to vary during time step 2. During this mid-time period, the trajectory is characterized by vertical movements which are linked to the vertical migration of the plankton: when the larva needs to feed, it moves to the high plankton density layer, hence maximizing its probability to find food (plot 2). Finally, when its swimming abilities are well developed, it comes back to the island. Approaching the island, predation risk increases, therefore optimal trajectories are those reaching the island by the sides (North or South in our geometry) in order to pass through the thinner portions of the high predation areas, hence maximizing survival of the larvae (plot 3).

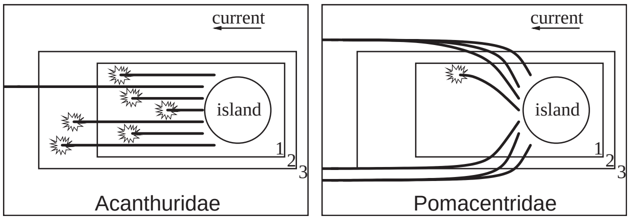

Fig. 5. Schematic comparison of the beginning of dispersal for Acanthurids and Pomacentrids. Trajectories, starting on the downwind side of the island, are plotted in bold. The three areas define the area of high predation and resources (1), mean predation and resources (2), low predation and resources (3). Notice that the Acanthurids cannot swim and are only driven by the uniform current field represented. They stay in the high predation areas and are mostly eaten (stars). On the contrary Pomacentrids can swim and flee from these areas, hence few are eaten.

We can identify a main difference between these trajectories, namely that Pomacentrids trajectories stay closer to the island than Acanthurids trajectories (this is easy to notice in the two-dimensional plots of Fig. 4). This is probably related to the greater duration of the pelagic phase of Acanthurids and also to their greater swimming abilities that allow them to travel further while still being able to come back to the island to recruit.

The absolute value of the maximum self-recruitment rate, which is also provided by the model, is of little interest here. Firstly, because self-recruitment is not usually the only possible conclusion of the larval phase (natural situations of completely isolated islands are rare). And also because the parameterization of the model does not represent precise field situations, nor are they intended to provide generality. Nevertheless we can notice that the recruitment rate is two orders of magnitude lower in Acanthurids than in Pomacentrids. Once again, this is probably related to the greater duration of their pelagic phase that implies a greater global mortality rate. However, this may also be related to their incapability of swimming during the first part of dispersal. Indeed, all Acanthurids trajectories beginning in the lee of the island will pass completely through the predator-rich zones and this will result in high mortality. As shown in Fig. 5, this is not true for Pomacentrids as they can use their rudimentary swimming abilities combined with predominant currents to avoid these high predation zones, hence diminishing their early mortality rate.

We noticed that the differences in the behavior of our two theoretical larvae, implied by their reproductive strategy, have important consequences on their optimal pelagic trajectories. The differences observed globally fit with the few observations of fish larvae densities around tropical islands (Leis, 1986; Leis and Goldman, 1987). Indeed, species with non-pelagic eggs are more abundant in the vicinity of the island, on the downwind side of the island, which is interpreted as retention. On the contrary, species with pelagic eggs are found mainly on the windward side of the island. In that case, they are supposed to come from an upstream reef because they were not retained there. In our case, recruitment on another reef is not possible; nevertheless, we remarked that Pomacentrid larvae (demersal eggs) are more retained in the vicinity of their natal island than Acanthurid larvae (pelagic eggs). This underlines the fact that the trajectories identified by this model seem correct and that some behavioral parameters are crucial in determining dispersal trajectories and recruitment rate.

3. Discussion

3.1. Model contributions

Firstly, the contributions of this modelling approach to present research can be highlighted. From a modelling point of view, the use of optimal control in larval dispersal is new. To our knowledge, the only other study that has used this framework is Armsworth (2001). He modelled the end of the pelagic phase of larval fishes, in the vicinity of a coral reef, finding trajectories that minimize energetic expenditure or transit time to reach the reef. In our study, optimal control is calculated from the whole environment on large temporal and spatial scales, hence widening the scope of this modelling framework. The interesting point of this method is that it enables us to focus on the reaction of the larvae to environmental conditions rather than on the environment itself. This study is the first to place such emphasis on larval behavior. As noted previously, the majority of models of larval dispersal focus first on current description and then add particles in this model with absent (Dight et al., 1990; Black et al., 1991) or simple (Wolanski et al., 1997; Porch, 1998; Armsworth, 2000) reactions to this current field. The originality of our model is the possibility to describe a more complete environment (currents but also predators and plankton), and above all to integrate this whole environment to choose a larva's reaction. Therefore, there are no fixed bounds to the complexity of larva's reactions and of the trajectories they induce. Indeed, they will be driven by the environmental level of detail. This ensures broad applications and very flexible use of this kind of models.

3.2. Why optimal strategies?

In this study, we consider that the larvae follow a behavioral strategy (i.e. decision rule) such that, on average, their decisions induce the greatest recruitment (here necessarily self-recruitment) probability. We consider that this is an *optimality* criterion and hence define the trajectories induced by these decisions as "optimal trajectories". Nevertheless, as remarked before, these trajectories still have a stochastic component (predation, swimming direction when foraging). Furthermore, this model aims at evaluating the importance of such behavioral strategies and should not be viewed as a description of the behavior of *each* larva during its pelagic stage. Therefore the real question is not whether larvae do react optimally but rather why trajectories that result in a maximization of the recruitment rate are interesting.

First of all, fish larvae could be selected toward the optimal strategy presented here. Indeed, the great mortality occurring during the pelagic stage (Doherty, 1983) is likely to act as a strong selective pressure. Selection is usually considered to occur on fitness, related in some way to the number of offspring per individual (Mylius and Metz, 2003, in prep.). Nevertheless, in order to reproduce, an individual has to be alive. Therefore, we could consider that selective pressure on reproduction would be transferred on survival during the larval, pre-reproductive, stage. This possible selective pressure could lead the mean phenotype (here a dispersal strategy) of fish populations toward a maximization of survival during the pelagic interval. Therefore, from an evolutionary point of view, it is interesting to study the ideal case of a population in which all fishes choose the optimal strategy as it could be an evolutionary end point.

Be that as it may, optimal trajectories are of interest even if fish larvae are not brought to maximize their recruitment rate by natural selection. Indeed, let us consider a population in which the behavioral strategy during dispersal is not under selection. Many phenotypes (strategies) should be present. In such a population, it is likely that the very few larvae that survive and recruit on an island are those having followed trajectories along which survival is high. There is little probability that they followed these trajectories only by chance. Therefore these larvae are probably those having chosen a strategy that we define as optimal: a strategy which maximizes survival. From this point of view, the great mortality occurring during the pelagic interval can be considered as a ‘‘filter’’ that lets only the best strategies through. Studying the trajectories induced by these optimal strategies is therefore related to real successful trajectories of fish larvae.

Finally, it has to be highlighted that self-recruitment is a pre-requisite in this study. Therefore, the results produced above do not allow inference about the optimality of a self-recruiting strategy as opposed to a dispersing strategy. As mentioned before, the quantity optimized here is survival along self-recruiting trajectories. Hence, our results do not mean that dispersing to another reef cannot be optimal.

3.3. Perspectives

This study provides a theoretical basis for subsequent work on trajectories of self-recruiting larvae. Many important features of the environment and of the behavior or the larvae are described here and some of them at least (differences in swimming abilities, in the duration of the pelagic stage) have important consequences on the outcome of the dispersal phase. This has two implications for future research.

Firstly, a better parameterization of the present model is needed. For example, other studies pointed out the importance of the current field in explaining the spatial distribution of fish larvae (Leis, 1986, 1993; Cowen and Castro, 1994). Therefore it seems interesting to provide our model with a more realistic current field. Data used here are particularly simple for presenting and testing purposes but it does not prevent precise field data, concerning currents, predators, zooplankton or larval abilities from being incorporated in the model. Once these data are available, field validation of the model has to be considered. We remarked that our initial results roughly agreed with the few field studies available concerning fish larvae distribution around coral reefs. This has to be studied further and, as mentioned before, the restriction to self-recruitment alone should facilitate this validation of the model.

If the absolute value of self-recruitment rate is of little interest here, its dependence on various factors of the model is of great concern. For example, we noticed that differences in swimming abilities have important consequences on recruiting trajectories. This has to be quantified and compared to other factors. Self-recruitment rate is a numerable currency which allows such a comparison, using sensitivity analysis. This quantification permits re-interpretation of qualitative studies of the influence of various factors on self-recruitment rate such as the work of Sponaugle et al. (2002).

In this study, we considered that self-recruitment is the only outcome for the pelagic stage of coral reef fish larvae. Nevertheless, completely isolated reefs are rare and often, if not always, some larvae self-recruit and others disperse to surrounding reefs. Focus is at first on self-recruitment, for mathematical simplicity and ease of field validation, but the question of self-recruitment versus dispersal could also be tackled with this model, for example by adding a second region of positive final gain, which represents another island. In this perspective, not only would factors that influence self-recruitment rates be emphasized, but also crucial parameters that decide between dispersing or self-recruiting could be highlighted. Once these factors are known, predictions can be made using the model and verified in precise field situations.

We provide here what we think is an efficient modelling framework to represent the dispersal phase of marine organisms, with an emphasis on the active behavior of dispersing particles. This model allows both study of the self-recruiting trajectories and of the dependence of this phenomenon on various factors, including the development of the abilities of the larvae, the length of the larval phase, the distribution of predators and zooplankton or the intensity of the current field. Furthermore it has a broad range of applications from detecting general features of dispersal to directing future field studies.

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Appendix

This appendix describes the choice of the last two optimal decisions in the simple model, presented in Section 2.2.2.

Last optimal decision: $u^{\#}(\theta, x, T-1)$

$$\begin{aligned} V(\theta, x, T-1) & \\ &= p \times \max(\overbrace{V(\theta+\Delta\theta^0, x+\Delta x^0, T)}^{\textit{Foraging}}, \\ &\quad \overbrace{V(\theta-\Delta\theta^1, x-\Delta x^1, T)}^{\textit{Swimming}}) \\ &= p \times \max((\theta+\Delta\theta^0) \times \mathbf{1}_{\{x+\Delta x^0=0\}}, \\ &\quad (\theta-\Delta\theta^1) \times \mathbf{1}_{\{x-\Delta x^1=0\}}). \end{aligned}$$

Now, $\mathbf{1}_{\{x+\Delta x^0=0\}} \equiv 0$ since $x \geqslant 0$ and $\Delta x^0 > 0$. Thus

$$\begin{cases} V(\theta, x, T-1) = p \times (\theta - \Delta\theta^1) \times \mathbf{1}_{\{x-\Delta x^1=0\}} \\ u^{\#}(\theta, x, T-1) = 1. \end{cases}$$

Therefore, the optimal decision at the time $T-1$ is swimming if $x = \Delta x^1$. It means that the larva will swim if it can reach the reef by choosing swimming. However, if x is not equal to Δx^1 (it cannot reach the island), the value function (V) equals zero for any decision. It means that the larva cannot recruit whatever happens. Therefore it does not have any favored decision for its last choice.

Before the last optimal decision: $u^{\#}(\theta, x, T-2)$

$$\begin{aligned} V(\theta, x, T-2) & \\ &= p \times \max(\overbrace{V(\theta+\Delta\theta^0, x+\Delta x^0, T-1)}^{\textit{Foraging}}, \\ &\quad \overbrace{V(\theta-\Delta\theta^1, x-\Delta x^1, T-1)}^{\textit{Swimming}}) \\ &= p \times \max((\theta+\Delta\theta^0-\Delta\theta^1) \times \mathbf{1}_{\{x+\Delta x^0=\Delta x^1\}}, \\ &\quad (\theta-2\Delta\theta^1) \times \mathbf{1}_{\{x-\Delta x^1=\Delta x^1\}}). \end{aligned}$$

As we cannot have at the same time $x = \Delta x^1 - \Delta x^0$ and $x = 2\Delta x^1$, it comes that:

$$\begin{aligned} V(\theta, x, T-2) = p \times ((\theta+\Delta\theta^0-\Delta\theta^1) & \\ \times \mathbf{1}_{\{x=\Delta x^1-\Delta x^0\}} + (\theta-2\Delta\theta^1) \times \mathbf{1}_{\{x=2\Delta x^1\}}). \end{aligned}$$

- If $x = \Delta x^1 - \Delta x^0$, then $u^{\#}(\theta, x, T-2) = 0$, the larva chooses to forage. This result seems natural. When the larva chooses to eat at time $T-2$, it is taken away from the reef (Δx^0). So, it will be at the correct distance (Δx^1) at time $T-1$ in order to come back to the island. The larva optimizes its energetic resources value.
- If $x = 2\Delta x^1$, then $u^{\#}(\theta, x, T-2) = 1$, the larva decides to swim. Here again, this choice is natural since swimming brings the larva to a distance Δx^1 from the coral reef. It will only have to swim once more at the last time step to reach the island.

The explicit calculation of $V(\theta, x, t)$ is becoming more and more complex. Scilab programs will numerically find all optimal decisions, but we have noted that solving Bellman's equation gives very intuitive results at time $T-1$ and $T-2$.

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