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Influences of habitat distribution and maternal investment on settlement of lecithotrophic larvae: modelling an ecological transition

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ABSTRACT

Life-history models to investigate the larva–juvenile transition in benthic invertebrates have primarily been static models that focus on the larval portion of the process. Here we develop a dynamic optimization model to quantify the roles of (1) habitat quality, (2) habitat distribution and (3) maternal investment in the successful settlement of hypothetical lecithotrophic marine invertebrate larvae. In particular, we focused on the roles of these variables in the proportion of larvae settling successfully, their post-settlement state, and their post-settlement fitness (state plus habitat settled in). We evaluated the fitness consequences of larvae making one of two decisions: (1) searching for 'better habitats' and thus staying pelagic in order to settle at a later time, or (2) settling to the benthos and acquiring some measure of future fitness, pending successful settlement. Our results suggest that habitat distributions have a substantial impact on the proportion and state of larvae that settle to specific habitat qualities (and thus fitness) but little impact on the total number of larvae that settle. Maternal investment had the strongest positive effect on post-settlement state where more maternal investment generally resulted in more energy-rich settlers. Increases in maternal investment above the initial minimum resulted in diminishing returns in terms of successful larval settlement or the distribution of settlers in better habitat qualities. We discuss our results in light of the current debate on marine reserve designs.

Keywords: dynamic optimization, habitat distribution, habitat quality, lecithotrophic larva, maternal investment, settlement.

INTRODUCTION

Most marine invertebrate life histories are characterized by a larval stage that, upon reaching metamorphic competence, undergoes a transition to a juvenile stage. Typically the larva–juvenile transition in the organism's life history entails a shift from a pelagic, mobile stage to a benthic, relatively sessile stage. The evolution of life-history strategies for successfully bridging this transition has been diverse, spanning a range of pelagic periods,

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settlement delay capabilities, and settlement specificities to habitats (e.g. Strathmann, 1985; Emlet *et al.*, 1987; McEdward and Janies, 1997; Pechenik, 1999).

One can imagine a number of selection pressures potentially mediating the timing of an individual's decision to metamorphose to the benthic habitat. On the one hand, the timing may be dictated by inherently 'larval' selection pressures. Pelagic predation on larvae may be sufficiently high such that a reduction in development time reduces the probability of pelagic mortality, which is likely to be extreme for larvae (15% per day reported by Rumrill, 1990; 16.4% per day reported by Lamare and Barker, 1999). Other potential selection pressures for larvae to reduce pelagic time may include starvation after depletion of maternal reserves and the probability of offshore transport to inhospitable habitats. Therefore, larvae may be under significant selection to settle to the benthos as quickly as possible regardless of the quality or relative danger of the benthos.

On the other hand, 'metamorph' selection pressures may select for the timing of settlement. The metamorph selection pressures may include a number of factors, both immediate and long term. Immediate selection pressures would include factors influencing how a larva 'decides' to settle and immediate post-settlement consequences. The ability of planktonic larvae of benthic invertebrates to delay their settlement has been examined for several species (e.g. Peckenik, 1985; Qian *et al.*, 1990). Delay would potentially allow for more extensive sampling of the benthic environment that may result in settling in a better quality habitat where the likelihood of juvenile growth and survival are higher (Rowley, 1990; Gibson, 1995). Trade-offs for delaying metamorphosis could include both an additional likelihood for exposure to the 'larval' selection pressures, but also a decrease in intrinsic energy content that may reduce successful survival in the benthic stage (Pechenik, 1985; Gebauer *et al.*, 1999; Maldonado and Young, 1999). Larger juvenile size can result in quicker juvenile development rates (Miller and Emlet, 1999; Roberts and Lapworth, 2001; Phillips, 2002), increased longevity (Emlet, 1986; Emlet and Hoegh-Guldberg, 1997), increased intra- and inter-specific competitive ability (Connell, 1985), and a size refuge from predation (Stoner, 1990; Gosselin, 1997).

Life-history models for investigating the larva–juvenile transition in benthic invertebrates have primarily been static models. These models isolate strategies that optimize maternal fitness based on evaluations of larval and metamorph selection pressures, typically with a greater emphasis on the larvae. Obrebski (1979) characterized settlement behaviour with a quantitative model to address colonizing strategies for marine invertebrate larvae. This model's results suggested that larvae should delay metamorphosis more frequently when colonizing rare patches and, in conditions of strong selection against larvae, energy should be allocated to increase energy reserves for early metamorphs due to decreased habitat searching times. Previous and subsequent models derived for other biological systems have also characterized habitat selection decisions in terms of frequency of optimal habitat and relative fitness in suboptimal habitats (e.g. Levins and MacArthur, 1969; Ward, 1987). Havenhand (1993) characterized this transition not in terms of habitat selection but in terms of time spent from egg to juvenile periods. In his analysis, reducing the time from egg to juvenile directly decreases time to first reproduction, thereby increasing fitness.

Models of marine invertebrate life histories have not simultaneously investigated two factors that likely influence the transition to the benthos: (1) habitat quality and the distribution of these habitats, and (2) quantity of maternal investment. In this paper, we address both variables and their effects on settlement behaviour in a hypothetical larva.

Habitat quality and distribution influence larval settlement as well as juvenile survival and growth. Larvae will differentially settle in response to cues from their environment and

delay this transition in the absence of these cues. Ample evidence has accumulated from marine invertebrates that chemical cues elicit settlement behaviour to specific habitat types (see Hadfield and Koehl, 2004, and references therein). Empirical studies of larval settlement on benthic habitats have shown that certain habitats correlate with increased survival and growth (Rowley, 1989, 1990; Osman and Whitlatch, 1996). What is less clear is how a spatially complex habitat with a range of habitat qualities would influence the settlement of a particular larva. Larvae may encounter an area that is predominately high-quality habitat, thereby potentially making the timing of settlement more dependent on how dangerous the pelagic environment is than the payoffs of the future adult habitat. It is probably more common that the potential settling area has a mix of poor, intermediate and high quality habitat, making an individual larva's decision important for future fitness. A larva encountering an environment dominated by poor habitat but with a few high-quality sites could either delay as long as possible, potentially encountering a better quality site, or could settle earlier in a poor quality site with a larger proportion of energy.

Maternal investment (i.e. variation in energy content) may play three roles in the evolution of reproductive strategies. It may (1) influence development time, (2) allow for delayed metamorphosis of larvae, or (3) affect juvenile size at metamorphosis. Despite many life-history models describing optimal maternal investment strategies for maximizing fitness (e.g. Vance, 1973; McEdward, 1997), these models focus on the larval development time, in particular food environments, with little or no attention being given to settlement or benthic processes. Larvae developing from better provisioned eggs may have two distinct advantages in the transition to the benthos over those from more poorly provisioned eggs. First, more energy-rich larvae metamorphose into larger juveniles that are more successful in poorer quality habitat. Therefore, richly endowed larvae may be more likely to settle in these habitats and avoid the risks of pelagic predation. We would then expect to observe an increasing proportion of larvae settling in poorer quality habitat as the quantity of maternal investment increases. We may expect this strategy when the habitat quality has a weaker effect on overall individual fitness. Second, larvae developing with more energy may have the advantage of prolonged habitat sampling due to their energy reserves. If this strategy is employed, we would expect larvae developing with more energy to settle more frequently in higher quality habitat than larvae developing with less energy. This strategy would be expected when habitat has a larger influence on fitness than an individual's state upon settlement.

Both variation in the timing of settlement and size of metamorphosed juveniles from different maternal investments have received empirical support. A review by Emlet *et al.* (1987) revealed that asteroids with lecithotrophic larvae show high variability of size at settlement, but relatively low variability in time to settlement and show a strong positive correlation between egg size and juvenile size (for comparison with species with planktotrophic larvae, see Emlet *et al.*, 1987; Levitan, 2000). Emlet *et al.* (1987) and Emlet and Hoegh-Guldberg (1997) proposed that egg size might play a role in lecithotrophic development, where increased energy from the egg is used to build a larger juvenile. Juvenile energy has not been quantitatively modelled to assess potential influences on life-history evolution for marine invertebrates but has been qualitatively considered multiple times (e.g. Strathmann, 1977; Eckert, 1995; Hentschel, 1999; Hentschel and Emlet, 2000; Phillips, 2002).

Here we develop a dynamic optimization model to quantify the roles of (1) habitat quality, (2) habitat distribution and (3) maternal investment in the successful settlement of lecithotrophic marine invertebrate larvae. We reason that this model has two unique

features compared with previous life-history models. One, our model considers multiple factors (three listed above) in deriving life-history strategies for a theoretical marine invertebrate with pelagic, non-feeding larvae and benthic adults. Second, by using a dynamic optimization model, we track individual, state-dependent decisions that are more likely to reflect an individual's behaviour than a static model.

METHODS

We used a dynamic optimization approach to model the decisions that a larva makes to maximize expected fitness in the transition from the water column to the benthos. The power of dynamic modelling is that with each time step and subsequent decision, the state in which a larva finds itself changes, thus affecting decisions it makes in the future. Dynamic optimization determines time-specific optimal decisions for individuals at each level of a state variable, X, at a given time, t. Through the use of backwards iteration through time, the model is solved for the optimal decision by evaluating the expected fitness outcomes for all possible decisions, given a current state and time, $X(t)$. Thus, the model will select for the decision that maximizes fitness at each time and state. The resulting matrix is a complete list of optimal solutions for each $X(t)$. With this matrix, we can describe the trajectory through time (from $t = 0$ to T) for an individual of any initial level of maternal investment (X_0) (Clark and Mangel, 2000; McCauley *et al.*, 2000).

The dynamic optimization model

For this model we assume a hypothetical sessile invertebrate species with lecithotrophic (i.e. non-feeding) pelagic larvae. We chose this type of species to avoid modelling complications such as larval feeding and post-settlement movement that are not central to our question. Our hypothetical species has the ability to invest various amounts of energy into its offspring. In addition, this species exhibits selective settlement for habitats that yield higher post-settlement fitness, and thus has the ability to delay metamorphosis from the point of competency (defined as $t = 1$) until energy reserves are exhausted.

For each time step through the model, each individual samples the benthic habitat it finds, in that time step, and makes one of two decisions: (1) search (i.e. stay pelagic) or (2) settle to the benthos. Of these two decisions, only successful settlement to the benthos was terminal, thus ending future 'decisions' through the model. When an individual decided to search, that individual would remain in the model, until either successful settlement or death in future time steps. If an individual decided to settle, but was unsuccessful (discussed below), that individual too remained in the model, until either successful settlement or death in future time steps. For simplicity, each time step corresponds to a day, where total time (T) is positively related to the quantity of maternal investment (X_0). We assumed an individual died if $X(t) < 1$. As an individual larva went through each time step, it had the opportunity to encounter habitats of five different qualities (h). These qualities were arbitrarily given the values of 0, 1, 2, 3 and 4. Upon successful settlement, each individual received a measure of post-settlement fitness (Φ), which was a function of an individual's post-settlement state (X_{ps}) (energetic state immediately after settlement) and the habitat quality (h) in which the individual settled:

$$\Phi = X_{ps} \times 2^h \quad (1)$$

where X_{ps} is a function of the energetic state immediately before settling, $X(t)$, and specific costs (discussed below):

$$X_{ps} = X(t) - C_p - C_s - C_m \tag{2}$$

Each decision had associated costs, both energetic and predatory. Energetic (i.e. metabolic) costs included (1) the cost of being pelagic (C_p):

$$C_p = 0.133X(t)^{0.9489} \tag{3}$$

(2) the cost of sampling the benthos (C_s):

$$C_s = 0.0665X(t)^{0.9489} \tag{4}$$

and (3) the cost of metamorphosis ($C_m = 3$), where again $X(t)$ is an individual's state (X) at time t. The equation for the cost of being pelagic (C_p) was derived from estimates of metabolic rates for *Dendraster excentricus* and *Crassostrea gigas* larvae, as described in Hoegh-Guldberg and Manahan (1995). By using an image analysis program (Image Pro Plus), data from figures 9A and 9C of Hoegh-Guldberg and Manahan (1995) were extracted and digitized. Only 68 of 100 data points were used in this analysis because several data points overlapped (particularly in their figure 9C), therefore making it difficult to digitize every data point. A single best-fit power function (equation 3) was then applied to the combined data sets ($n = 68$, $r^2 = 0.8641$). Since the cost of sampling (C_s) has not been quantitatively measured, we assumed it to be half of that for being pelagic. We chose this value because we assumed that the larvae are undergoing some active transport while pelagic (e.g. vertical transport) and therefore use less energy during sampling, due to a temporary suspension of active transport. Furthermore, since the cost of metamorphosis (C_m) is not well established, we assume that this cost should be constant among larvae of different X_0, in order to better investigate the role of maternal investment in larval settlement.

Only one risk of predation was included into the model, that of pelagic predation. For this, we assumed a daily predation rate of 15%, a rate that approximates field estimates (Rumrill, 1990; Lamare and Barker, 1999). Due to its mostly ignored status, lack of agreement among empirical measurements (Gosselin and Qian, 1997) and lack of estimates from habitats of different quality, we did not include benthic predation specifically, although one could consider a value for habitat quality to include some aspect of benthic predation risk. Finally, we included a probability for settling successfully (Pr_{ss}), which was dependent on an individual's post-settlement state (X_{ps}):

$$Pr_{ss} = 1 - e^{(-0.1 \times X_{ps})} \tag{5}$$

The generalized form of the dynamic programming equation, which maximizes future fitness from time t forward, given that $X(t) = x$ is:

$$F(x,\ t, T) = \max\ s_i F(x_i',\ t+1,\ T) \tag{6}$$

where the subscript i refers to the decision for this time step, s_i is survivorship and $F(x_i',\ t+1,\ T)$ is the future fitness, given x', the tactic-specific state in time $t+1$. The expected fitness associated with each of the two behaviours differed. For an individual that searches, the expected fitness is:

$$F_{search}(x,\ t,\ T) = (Pr_{pel})^t \times F(x - C_p - C_s,\ t+1,\ T) \tag{7}$$

where Pr_{pel} is the daily probability of survivorship through pelagic predation and is constant ($Pr_{pel} = 0.85$), and $F(\bullet)$ is the future expected fitness at $t + 1$, given the current state $x - C_p - C_s$, where C_p is the metabolic cost of being pelagic (equation 3) and C_s is the metabolic cost of sampling (equation 4). Individuals that settle have additional costs for that decision and some probability of fitness if settlement is successful. Therefore, their expected fitness is described by the equation:

$$F_{settle}(x,\ t,\ T) = (Pr_{pel})^t((Pr_{ss} \times \Phi) + (1 - Pr_{ss})(F(X_{ps},\ t + 1,\ T))) \quad (8)$$

where Pr_{pel} is the daily survivorship through pelagic predation (as above), Pr_{ss} is the probability of successful settlement (equation 5), and Φ is the post-settlement fitness (equation 1). The second part of this equation corresponds to the case of unsuccessful settlement, where $F(\bullet)$ is the future expected fitness at $t + 1$, given the post-settlement state X_{ps}. This portion of the equation would mean that a larva that unsuccessfully settles during an initial settling attempt but is successful at a future time point will pay the cost of settlement at least twice. We then iterated forward in the model using the state- and time-dependent optimal decisions. Maternal investment (X_0) took one of four levels: 10, 25, 50 and 100. In the basic model, our starting population consisted of 1000 individuals, all of which started with the same level of maternal investment (10, 25, 50 or 100).

Parameter analysis

Manipulations of parameters were performed to investigate the roles of: (1) habitat quality (h), (2) habitat distribution and (3) maternal investment (X_0) on the successful settlement of lecithotrophic marine invertebrate larvae. In addition, we examined the role of these parameters on the state and fitness with which larvae settle. Habitat quality (h) consisted of five levels, which, as mentioned earlier, were given values of 0–4. Habitat distribution consisted of five types of distribution patterns, which were given the following descriptive names: (1) 'bimodal', (2) 'equal', (3) 'normal', (4) 'weight-high' and (5) 'weight-low' (see Fig. 1, solid circles, for distribution values). As mentioned earlier, the values used for the investigation of maternal investment (X_0) were 10, 25, 50 and 100.

Sensitivity analysis

In determining the fitness equation for our model, we realized that the relationship of state to post-settlement fitness may have a dramatic effect on an individual's decision. To test the sensitivity of the model to post-settlement fitness (Φ), we changed the fitness function from an exponential function (equation 1) to a linear relationship between state and post-settlement fitness:

$$\Phi = X_{ps} \times 2h \quad (9)$$

where X_{ps} is an individual's post-settlement state and h is the quality value given to the habitat in which that individual settles successfully. Due to its structure, this new fitness function creates a 0% probability of settlement to habitats of quality 0. Therefore, this result will not be covered in the subsequent section. However, any other changes in the behaviour of the model will be discussed. This test was conducted for all habitat distribution types at only the $X_0 = 50$ level.

RESULTS

Proportion settling successfully

For all possible habitat distribution types, habitat quality had a strong effect on the proportion of larvae settling successfully (Fig. 1, open symbols), which was relatively consistent among the higher levels of maternal investment ($X_0 = 25$, 50 or 100). Overall, there was strong selection for habitats of greater quality ($h = 2$, 3 or 4). In fact, only when poor-quality habitats ($h = 0$ or 1) were most abundant (i.e. 'weight-low' distribution

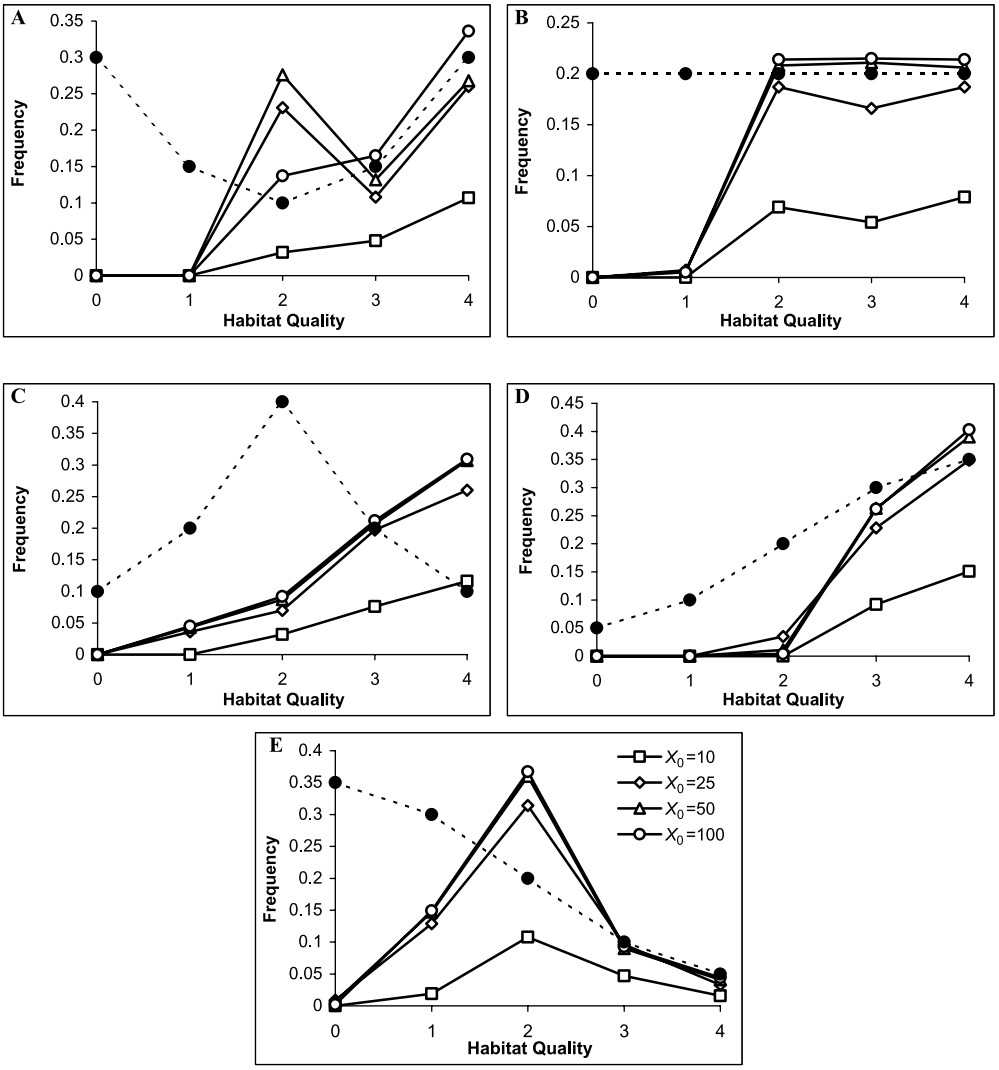

Fig. 1. Frequency of habitat qualities (solid circles) and larvae settling (open symbols) to habitat qualities for each level of maternal investment (X_0) for (A) 'bimodal', (B) 'equal', (C) 'normal', (D) 'weight-high' and (E) 'weight-low' habitat distribution types.

type), did we see more than 5% of larvae settling to those habitats. In addition, the frequency of particular habitat qualities within each distribution type typically did not reflect the observed frequency of settlers to that particular habitat quality (Fig. 1). There was a bimodal distribution of settlers in the 'bimodal' habitat distribution case. However, this bimodal distribution was skewed towards habitats of intermediate ($h = 2$) and best quality ($h = 4$) (Fig. 1A). In the case of an 'equal' distribution of habitat qualities, there was a fairly equal distribution of settlers among the habitats of intermediate and higher quality ($h = 2$, 3 and 4), whereas very few, if any, settled to the habitats of lowest quality ($h = 0$ or 1) (Fig. 1B). The 'normal' habitat distribution resulted in a distribution of settlers that was highly skewed towards the highest quality habitats (Fig. 1C). A similar result was encountered in the 'weight-high' habitat distribution case, where virtually no settlers were encountered in the lowest ($h = 0$ or 1) or intermediate ($h = 2$) quality habitats (Fig. 1D). Finally, the 'weight-low' habitat distribution resulted in a normal-like distribution of settlers, with most settlers settling to the habitat of intermediate quality ($h = 2$) (Fig. 1E).

For a given level of maternal investment (X_0), there was very little difference in the total proportion of successful settlers among the different habitat distribution types (Fig. 2). Overall, as maternal investment (X_0) increased, the total proportion of larvae that settled successfully also increased, although at a decelerating rate (Fig. 2). One exception was the 'bimodal' habitat distribution type where the highest proportion of larval settlement was with an intermediate investment ($X_0 = 50$). The overall mean total proportion of larvae settling successfully (± standard deviation) for each level of maternal investment was 0.20 ± 0.03 for $X_0 = 10$, 0.58 ± 0.03 for $X_0 = 25$, 0.65 ± 0.02 for $X_0 = 50$, and 0.65 ± 0.01 for $X_0 = 100$.

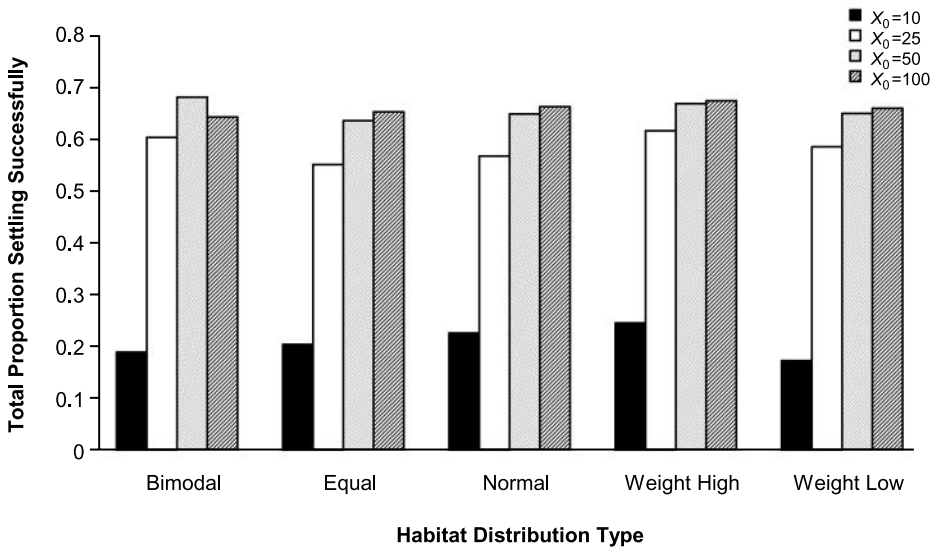

Fig. 2. Total proportion of larvae settling successfully for each habitat distribution type among the different levels of maternal investment (X_0).

State at settlement

When larvae settled to habitats of lesser quality ($h = 0$ or 1), those larvae generally had post-settlement states that were at most 45% of that of larvae that settled to habitats of intermediate or higher quality ($h = 2$, 3 or 4) (Fig. 3). However, there was one exception to this. In the 'weight-low' habitat distribution, those larvae that settled to $h = 1$ had roughly the same post-settlement state as those settling to $h = 2$, 3 or 4, while those in $h = 0$ were dramatically lower (Fig. 3E).

Habitat distribution type does not appear to have an effect on the mean overall state at which a larva settles to the benthos (Fig. 4), within a single level of maternal investment (X_0). Within a given habitat distribution type, maternal investment (X_0), however, seems to have a strong positive effect on the state at which a larva settles (Fig. 4). In fact, a doubling in maternal investment (X_0) resulted in approximately a doubling in the state at settlement. The overall mean post-settlement state for each level of maternal investment (X_0) was 4.72 ± 0.14 for $X_0 = 10$, 14.29 ± 0.24 for $X_0 = 25$, 30.53 ± 0.72 for $X_0 = 50$, and 61.14 ± 2.11 for $X_0 = 100$.

Fitness

As expected, due to the form of the fitness function (equation 1), habitat quality had a strong effect on an individual's mean post-settlement fitness (Φ) (see Fig. 5 for an example). Furthermore, there was also a strong positive effect of maternal investment (X_0) on mean post-settlement fitness (Φ), which was consistent among all the habitat distribution types.

There was an effect of habitat distribution type on overall mean post-settlement fitness (Φ), with highest overall fitness in the 'weight-high' distribution and lowest in the 'weight-low' distribution (Fig. 6). This pattern was consistent among all levels of maternal investment (X_0). However, among the different levels of maternal investment (X_0), the magnitude of this effect was variable. For example, when $X_0 = 10$ the difference in overall mean post-settlement fitness (Φ) between the 'weight-low' and 'weight-high' distributions was 2.34-fold, where as for $X_0 = 100$ the difference was 2.73. Within a given habitat distribution type, there was a strong positive effect of maternal investment (X_0) on overall mean post-settlement fitness (Φ) (Fig. 6). On average, for each level of increase in maternal investment (X_0), there was a 2.32-fold increase in overall mean post-settlement fitness (range 2.02–2.85). Finally, when all habitat distribution types are pooled, the mean overall post-settlement fitness (Φ) for each level of maternal investment (X_0) was 50.58 ± 25.9 for $X_0 = 10$, 137.49 ± 85.27 for $X_0 = 25$, 293.71 ± 177.17 for $X_0 = 50$, and 613.55 ± 359.2 for $X_0 = 100$.

Sensitivity analysis

A change in the post-settlement fitness function (Φ) (from equation 1 to equation 9) resulted in very little change in the proportion of individuals that settled to the habitats of intermediate ($h = 2$) and highest quality ($h = 3$ or 4), for all habitat distribution types. This linear fitness function (equation 9) resulted in a 9.5- and 1.81-fold increase in the number of individuals settling to the lower quality habitat ($h = 1$) for the 'equal' and 'normal' habitat distribution types, respectively (compare with Fig. 1B and 1C, respectively). In addition, we encountered seven individuals settling to this lower quality habitat in the 'weight-high'

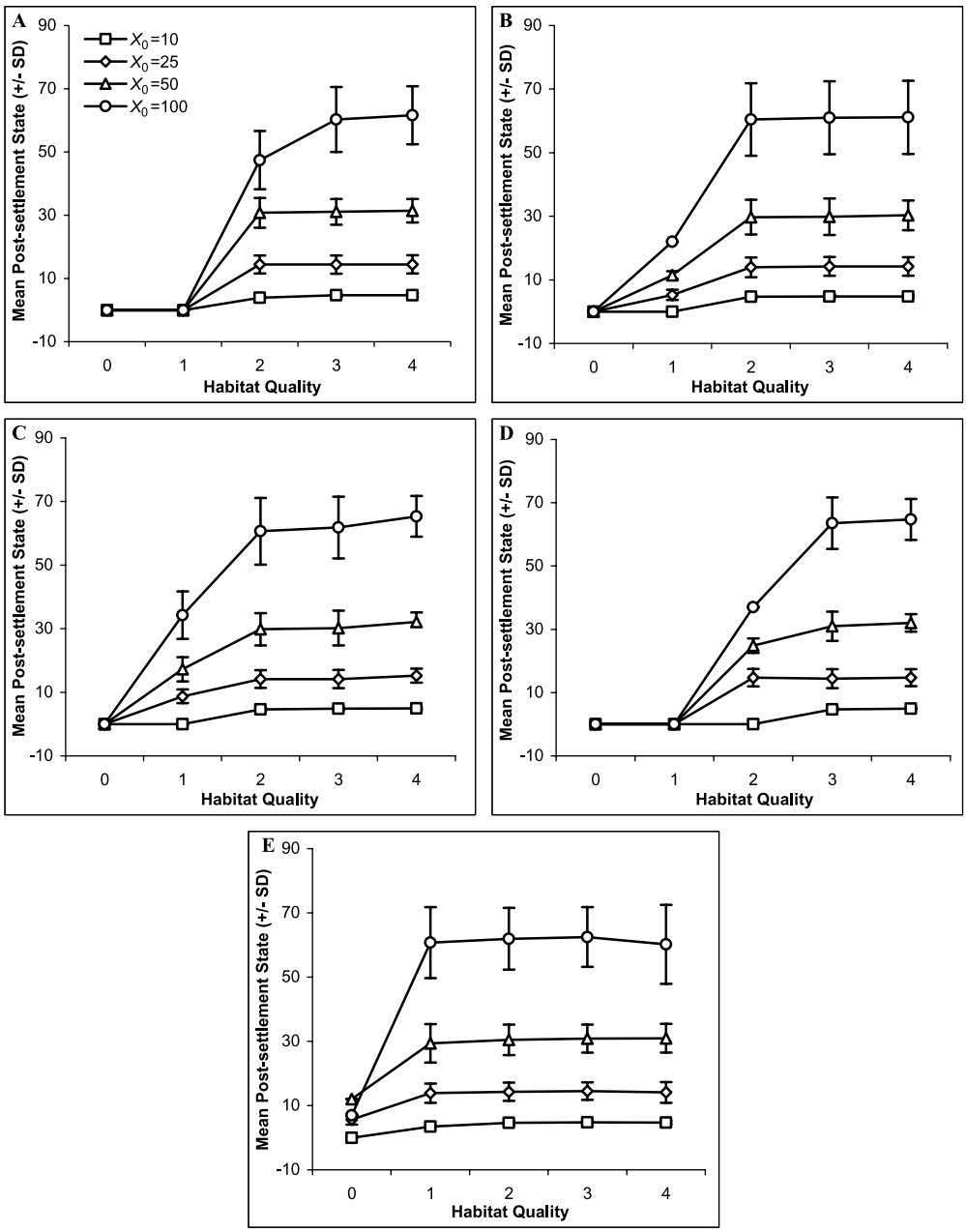

Fig. 3. Mean (± standard deviation) post-settlement state at each level of habitat quality and maternal investment (X_0) for each habitat distribution type: (A) 'bimodal', (B) 'equal', (C) 'normal', (D) 'weight-high' and (E) 'weight-low'. Note that a post-settlement state of 0 indicates that no successful settlers were encountered in that particular habitat. Furthermore, when $X_0 = 10$, the estimates of standard deviation are minimal and, therefore, difficult to detect in the figure.

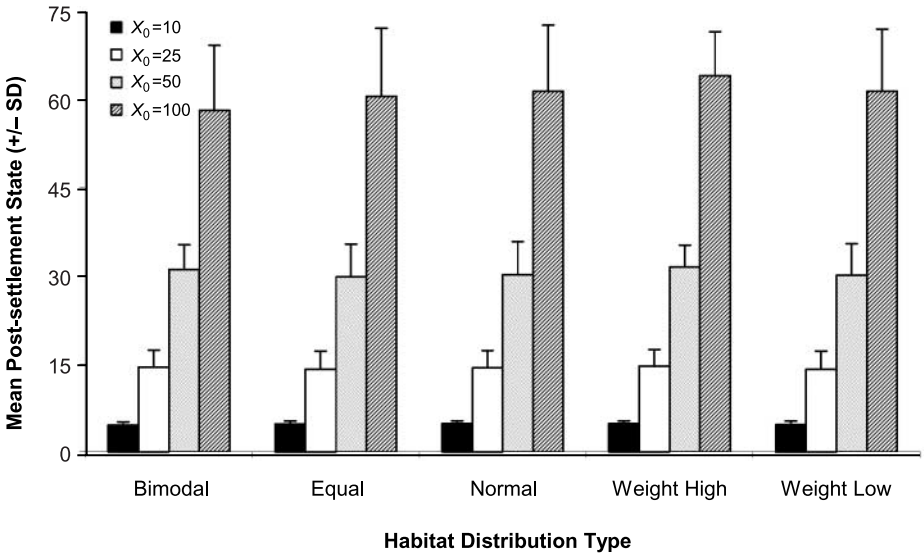

Fig. 4. Mean (± standard deviation) post-settlement state for each habitat distribution type among the different levels of maternal investment (X_0).

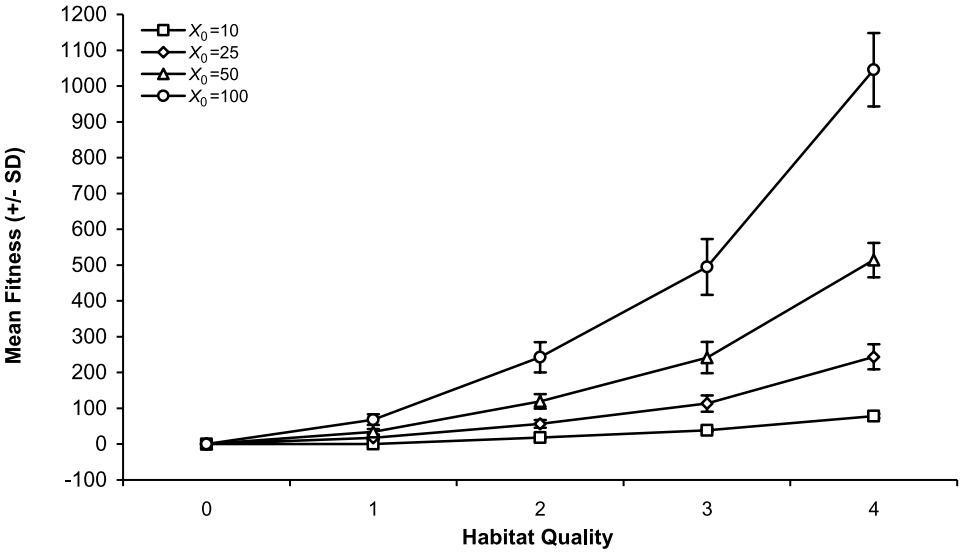

Fig. 5. Mean (± standard deviation) post-settlement fitness (Φ) for each level of maternal investment (X_0) in the 'normal' habitat distribution type. Note that a post-settlement fitness of 0 indicates that no successful settlers were encountered in that particular condition. Furthermore, when $X_0 = 10$, the estimates of standard deviation are minimal and, therefore, difficult to detect in the figure.

distribution type, as opposed to zero under the exponential fitness function (equation 1) (compare with Fig. 1D). Overall, the pattern between the habitat frequencies and the observed settler frequencies was consistent with that generated by the exponential fitness function (equation 1) (Fig. 1). Although the linear fitness function had some effect on the

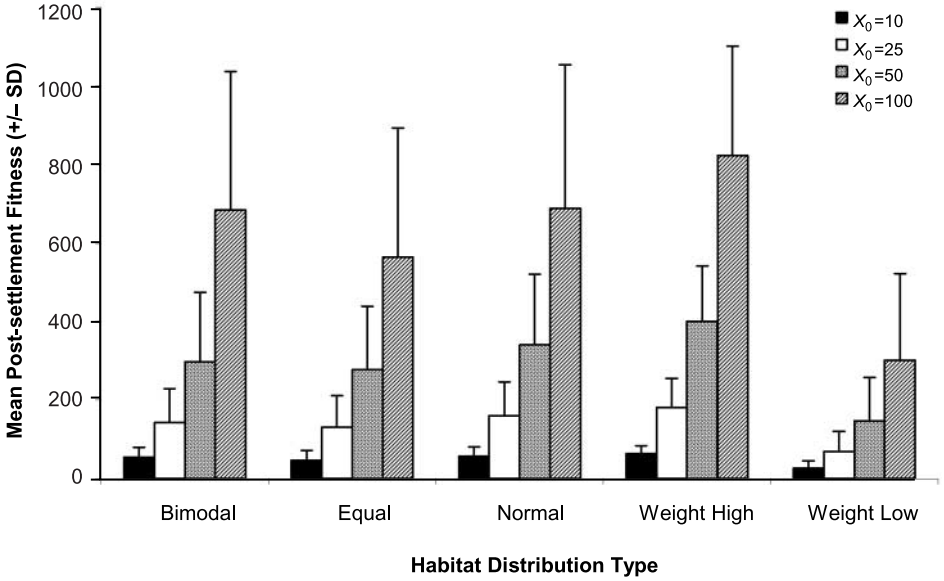

Fig. 6. Mean (± standard deviation) post-settlement fitness of each habitat distribution type among the various levels of maternal investment (X_0).

proportion of individuals settling to habitats of a certain quality, it had no effect on the total proportion of individuals settling successfully to a particular habitat distribution type.

For the 'equal', 'normal' and 'weight-high' habitat distribution types, the linear fitness function had a strong positive effect on the mean state at which a larva settles to the lower quality habitat ($h = 1$) ('equal' = 23.88, 'normal' = 24.72, 'weight-high' = 19.0; compare with Figs. 3B–D, $X_0 = 50$). Furthermore, under the 'bimodal' and 'weight-low' habitat distribution types, the mean post-settlement state of individuals settling to the lower quality habitat ($h = 1$) remained virtually the same ('bimodal' = 0, 'weight-low' = 29.41; compare with Figs. 3A and 3E, $X_0 = 50$). However, there was little change in the relationship between mean post-settlement state and habitat quality among the intermediate and higher quality habitats ($h = 2$, 3 or 4) (as in Fig. 3, $X_0 = 50$), as well as no change in the overall mean post-settlement state among the different habitat distribution types (as in Fig. 4, $X_0 = 50$).

DISCUSSION

In this study, we have used dynamic modelling to predict how larval settlement decisions would be influenced by distribution of habitats of various quality and maternal investment. In addressing these two variables, our analyses suggests two general results. First, habitat distributions have a substantial impact on the proportion and state of larvae that settle to specific habitat qualities (and thus fitness) but little impact on the total number that settle. Second, increases in maternal investment above a minimum investment pay diminishing returns in larval settlement but do substantially increase post-settlement state. Our model generates qualitative and quantitative predictions for how combinations of these factors would influence the decision for settlement or for additional searching by a larva.

Habitat quality and distribution

Our model suggests a mixed effect of habitat distribution on larval settlement, with little impact on the total proportion of larvae settling but a significant impact on the proportion in each habitat quality and their energetic state. In no habitat distributions were the observed patterns of larval settlement directly reflective of the habitat distribution. For example, when habitat qualities were distributed 'bimodally', the highest level of observed settlement was found in the habitat of intermediate quality ($h = 2$), even though this habitat quality was the least abundant (Fig. 1A). Only when habitats are of intermediate ($h = 2$) or higher ($h = 3$ or 4) quality do we see this pattern of higher observed settlement than expected (Fig. 1). This pattern was consistent even with the linear fitness function (equation 9), suggesting a robust response to habitat distribution.

Second, our model suggests a strong effect of habitat quality on post-settlement state for the higher maternal investments ($X_0 = 25$, 50 or 100; $X_0 = 10$ discussed below). Habitats of lesser quality ($h = 0$ or 1) received larvae of lower post-settlement state, with the exception of the 'weight-low' distribution type (Fig. 3). Lower post-settlement state indicates that larvae had undergone prolonged search periods in an attempt to encounter higher quality habitats. In cases where poor habitats were chosen, larvae eventually settled due to low energy reserves. Alternatively, in the 'weight-low' distribution, larvae settled with similar energy in poor and high-quality habitats, indicating that in environments dominated by poor habitats, settling with a large proportion of energy is favoured (Fig. 3E). Thus, the distribution of habitats directly influences larval settlement decisions with the largest qualitative differences between 'weight-low' and the other four distributions.

Our results suggest that the distribution of habitats of different qualities has little effect on the total number of larvae that settle. From the hypothetical clutch, approximately the same number of larvae successfully settled in each habitat distribution, but when considering the proportion of larvae in each habitat and their state, habitat distribution type did have an effect on overall post-settlement fitness (Φ) (Fig. 6). Among the habitat distribution types where intermediate ($h = 2$) and/or higher ($h = 3$ and 4) quality habitats were most abundant (i.e. 'weight-high', 'bimodal' and 'normal'), settlers had a higher post-settlement fitness. This pattern in fitness is due to the fitness function (equation 1).

Empirical evidence has accumulated to support the roles of specific habitat cues for successful larval settlement (e.g. Qian *et al.*, 1990; Gibson, 1995; Marshall and Keough, 2003). Larvae can delay settlement for extended periods of time while searching for the appropriate habitat(s) but usually at the cost of increased energy expenditure, lower proportion of successful settlement, or lower probability of a successful transition (Gebauer *et al.*, 1999; Maldonado and Young, 1999; Roberts and Lapworth, 2001). The quality of benthic habitat for a successful transition to a juvenile/adult stage in a life history is relatively unknown. Recent studies have suggested that quality of the settlement site may have dramatic effects on benthic recruitment (Chockley, 2002; Shima and Osenberg, 2003). For many species, the roles of habitat variation for successful recruitment are unknown but may be quite influential on settlement decisions, as suggested by our model.

Maternal investment and settlement decisions

In our model, we tested settlement behaviour for larvae developing from four different maternal investments ($X_0 = 10$, 25, 50, 100). Our results suggest two benefits for increased

maternal investment (X_0): (1) increased successful settlement (Fig. 2) and (2) an increased post-settlement state (X_{ps}) (Fig. 4). However, the effects of maternal investment (X_0) on settlement success and post-settlement state (X_{ps}) depend on the relative quantities of maternal investment being compared. For example, increases in maternal investment (X_0) had diminishing returns in settlement success (Fig. 2) but exponential returns in mean post-settlement state (X_{ps}) (Fig. 4). Finally, a third benefit, increased mean post-settlement fitness (Φ), was also suggested by our results (Fig. 6). However, this is simply a reflection of the effect of maternal investment (X_0) on post-settlement state (X_{ps}), as post-settlement fitness (Φ) is directly related to post-settlement state (equation 1).

The proportion of larvae settling successfully typically increased with a larger amount of maternal investment regardless of the habitat distribution. The largest increases in larval settlement occurred between the first ($X_0 = 10$) and second ($X_0 = 25$) lowest maternal investments. With a 2.5-fold increase in energy, larval settlement success increased approximately threefold, whereas further increases in maternal investment resulted in small (if any) increase in successful settlement (Fig. 2). Therefore, additional increases in energy would not facilitate more successful settlement of larvae regardless of the habitat distribution. Increases in maternal investment above $X_0 = 25$ also did not substantially increase the proportion of larvae settling in better quality habitat (Fig. 1). The greatest benefit from such an increase in investment could be seen in the 'bimodal' habitat distribution type. In this environment, the highest provisioning strategy ($X_0 = 100$) resulted in fewer larvae settling in habitats of intermediate quality ($h = 2$) and more settling to habitats of highest quality ($h = 4$) when compared with either intermediate investment ($X_0 = 25$ and 50) (Fig. 1A).

Maternal investment had a large effect on the mean post-settlement state of individuals (Figs. 3 and 4). Our model supports the general empirical result for non-feeding larvae that larger initial investment begets more energy-rich metamorphs. In no cases, except in the poorest quality habitat ($h = 0$), did we observe larvae initially starting with more energy settle with less than larvae that began with less energy (Fig. 3E). With $X_0 = 25$ or 50, larvae in 'bimodal' and 'weight-high' habitat distributions settled with more energy than those in 'equal', 'normal' or 'weight-low' distributions (Fig. 4). For the investment $X_0 = 100$, this result was true only for the 'weight-high' distribution, whereas the 'bimodal' distribution had the lowest post-settlement state among the habitat distributions. Higher post-settlement states can only be due to fewer sampling events when compared with other habitat distributions.

The proportion of energy expended during the pelagic stage was not conserved between the investments we investigated (Fig. 4). Variable energy expenditures for different maternal investments have been empirically supported for many invertebrates with lecithotrophic larvae (e.g. Emlet *et al.*, 1987; Emlet and Hoegh-Guldberg, 1997). Lecithotrophic larvae that are provisioned poorly typically use most of the provided energy in the transition to the benthic habitat, whereas well-provisioned larvae settle with a larger amount of energy (e.g. Emlet *et al.*, 1987). However, the actual energy expended was comparatively much higher in the more richly invested offspring, which has also received empirical support (Hoegh-Guldberg and Manahan, 1995; Hoegh-Guldberg and Emlet, 1997). Although this increased expenditure in our model was in part due to a larger cost per time step (equations 3 and 4), it is also due to more habitat sampling efforts.

As generally mentioned above, there is little difference in the state or total proportion of larvae that settle among the different habitat distribution types for each investment strategy (Figs. 2 and 4). Conversely, habitat distribution type does have an effect on the proportion

of larvae settling in each habitat type, which is, to some extent, variable among the different levels of maternal investment (Fig. 1). Taken together, the resulting fitness for one investment strategy across the habitat distribution types resulted in divergent fitness expectations. We illustrate this general result with a specific comparison of two investment strategies between two habitat distributions: 'weight-low' and 'weight-high'. When comparing the state and fitness of settlers with large initial investments (e.g. $X_0 = 50$) in the 'weight-high' and 'weight-low' habitat distribution types, individuals in the 'weight-low' habitat distribution settle with roughly equal amounts of energy as in the 'weight-high' distribution (Fig. 4). However, individuals from the 'weight-low' distribution have an overall mean fitness that is approximately 60% less than the 'weight-high' distribution (Fig. 6). The relationship is due to a higher proportion of larvae in the 'weight-high' habitat distribution settling in higher quality habitats than larvae in the 'weight-low' habitat distribution (Figs. 1D and 1E). As the settlers in the 'weight-low' distribution still have an equal amount of energy, the decision for settlement was the best decision for maximizing fitness in that habitat structure, despite the lower comparative fitness.

However, for the lowest level of maternal investment ($X_0 = 10$), we do not observe patterns similar to those for the larger investments, with the exception of a markedly lower fitness in the 'weight-low' habitat distribution type. Larvae from this lowest provisioning strategy had far fewer successful settlement events in any habitat distribution (Fig. 1). This suggests one potentially important effect of low maternal investment in lecithotrophic larvae: offspring with low provisioning have fewer sampling attempts and can sample one to two times before settlement. A settler's fitness is thus more representative of the frequency of high- versus low-quality habitat than due to larval settlement decisions. For a benthic marine invertebrate, this may translate to larvae settling in habitats based on relative abundance, not relative fitness benefit.

The relative quantity of maternal investment for a marine invertebrate species is probably the direct result of a variety of selection pressures potentially including fertilization success (Levitan, 1993), larval survival (McEdward, 1997; George, 1999), dispersal distance (Shanks *et al.*, 2003; Siegel *et al.*, 2003), metamorphic delay in habitat selection (Pechenik *et al.*, 1998) and post-metamorphic survival (Hoegh-Guldberg and Emlet, 1997; Moran, 1999). The relative impact of each variable and the interaction between them is difficult to ascertain, as each appears to have some effect in both theoretical models and empirical studies. In our model, we have addressed the effect of varying degrees of maternal investment on settlement decisions in the pelagic-to-benthic transition. Our results suggest that increasing maternal investment would increase successful larval settlement in better habitats, but that further increases above some investment (in our model $X_0 = 25$) no longer benefit the settlement portion of this ecological transition. Above this investment, individuals benefit from increased energy at settlement that results in higher fitness.

Insights for marine reserves

The design and implementation of marine reserves as tools in the conservation and management of marine ecosystems and organisms is a growing field of research, which has benefited from many reviews and papers on their use, effectiveness and potential (e.g. Allison *et al.*, 1998; Roberts *et al.*, 2001, 2003; Gerber *et al.*, 2003). Marine reserves are defined as areas that are completely protected from all extractive and destructive activities (Lubchenco *et al.*, 2003). Although many advances have been made in this field of research, there are still areas that

require further investigation, including (1) the influence of habitat quality and habitat-specific demography in the design of marine reserves (Gerber *et al.*, 2003), and (2) their optimal size, number and distribution (Allison *et al.*, 1998). We feel our results may provide some insights into this growing field.

When attempting to develop a single marine reserve, particularly for the conservation of a single exploited species, results from our model stress the importance of determining habitat qualities within the area of interest before preserving any particular habitat. For different types of organisms, the assessment of habitat quality may be radically different. For example, one potential measure of habitat quality might be potential growth rates of juveniles. Several studies have determined that growth rates can differ among habitats, even when found in close proximity (e.g. Kube *et al.*, 1996; Hartnoll, 2001; Chockley, 2002), possibly due to resource availability, depth, temperature, salinity, or any interaction. Growth rate may influence not only short-term processes such as escape from size-selective predation, but also longer-term fitness correlates such as larger fecundity with increased adult body size.

Perhaps, to ensure the highest level of settlement and recruitment to an area, the most straightforward way of determining which habitat to protect would be to set aside the habitat with the highest growth rate (i.e. highest quality). However, according to our model, this would only be the most beneficial practice if the available habitats have particular distributions ('equal', 'normal' or 'weight high') with respect to growth rates (Figs. 1B–D). On the other hand, if the available habitats have a 'bimodal' or 'weight-low' distribution with respect to growth rates, it might be more beneficial to preserve a habitat with intermediate levels of growth (i.e. intermediate quality), to ensure the highest settlement (Figs. 1A and 1E). Thus, more individuals may result in potentially larger future reproductive output, so long as the benefits of fewer, more fecund individuals do not out-weigh those of more, less fecund individuals.

Second, our model begins to address the importance of habitat distribution when trying to establish a network of marine reserves, something that previous marine reserve models have failed to investigate (Allison *et al.*, 1998; reviewed in Gerber *et al.*, 2003). It has been argued that the protection of a diverse array of habitats is critical in the creation of marine reserve networks, for both biodiversity conservation (Roberts *et al.*, 2003) and fisheries management (St. Mary *et al.*, 2000). In our model, each of the five habitat distribution types received similar levels of total settlement for a given maternal investment (Fig. 2). This result indicates that it may not be any more beneficial to protect mostly habitats of high quality (i.e. 'weight-high' distribution) than it is to protect habitats of mostly intermediate quality together with limited protection of high-quality habitats (i.e. 'normal' distribution). This is an important point from a socioeconomic prospective, in that it may be easier to convince interested parties to protect more intermediate-quality habitats and fewer high-quality habitats. Protecting more intermediate-quality habitats and less higher quality habitats (i.e. 'normal' distribution) may lead to the protection of a greater total area of marine habitat, as well as the protection of different types of habitat.

The results of this model have identified issues that must be considered in the design and implementation of marine reserves and marine reserve networks. However, additional questions need to be addressed in future investigations of marine reserves. First, the model does not address the species composition of particular habitats and, therefore, how habitat preference may change as a result of species composition. This consideration may be particularly sensitive to reproductive strategies of resident species. Second, our model defines fitness as a function of post-settlement state and habitat quality (equation 1), while

assuming no benthic predation. Benthic predation is considered to have a broad range of potential impacts on marine invertebrate population dynamics and potentially life-history evolution (Gosselin and Qian, 1997). Several studies suggest that benthic selection pressure on early juveniles may be equally as high as pelagic predation resulting in extensive juvenile mortality for a cohort (Rowley, 1989; Gosselin and Qian, 1997). Although our definitions of habitat quality could be viewed as including benthic predation, future modelling exercises may benefit from the quantification of benthic predation among habitats of varying quality, in order to better determine its influence on settlement and future fitness.

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