

Fecundity-time models of reproductive strategies in marine benthic invertebrates: fitness differences under fluctuating environmental conditions

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ABSTRACT: Fecundity-time models have been widely used to analyze the evolution of larval strategies in marine benthic invertebrates. To further explore the behavior of this influential class of models, we examined the effect of fluctuating food availability on the expected duration of the planktonic larval period and the number of offspring that survive to metamorphosis in marine invertebrates with planktotrophic larvae. Food concentrations were allowed to fluctuate randomly on a daily basis between specified upper and lower bounds. Variation in food levels generally had a much stronger effect on development time and reproductive success when the level of egg provisioning was low (small-egg strategies). When food was abundant, smaller eggs were favored. Fluctuations in planktonic food concentrations affected small-egg strategies more strongly than large-egg strategies, but the variation in fitness was small relative to fitness differences across egg sizes. There should be consistently strong directional selection to minimize egg size whenever food is abundant, even if the concentrations fluctuate widely. However, when larvae were strongly food-limited, larger eggs were favored and fluctuations in planktonic food supply led to variation in fitness that was large relative to fitness differences among strategies. There was no clear peak on the fitness curve, due to overlap of fitness distributions across reproductive strategies. This leads to the prediction that there should be a range of intermediate- to large-egg strategies, rather than a single optimal egg size. With facultative feeding by planktotrophic larvae, there were intermediate egg sizes above which variation in food level had only negligible effects on development and survival. When the magnitude of environmentally caused variation in reproductive success exceeds the fitness differences among reproductive strategies, this should flatten out the adaptive landscape, reduce the intensity of disruptive or directional selection, and facilitate evolutionary transitions between planktotrophy and lecithotrophy or vice versa.

KEY WORDS: Fecundity-time model · Life history · Facultative feeding · Egg size · Reproductive strategy · Larva

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INTRODUCTION

Several mathematical models have been developed to analyze the evolution of reproductive strategies in marine benthic invertebrates (e.g. Vance 1973a,b, Christiansen & Fenchel 1979, Perron & Carrier 1981, Roughgarden 1989, Havenhand 1993, 1995, Levitan 1996, 2000, McEdward 1997). The most influential models emphasize the trade-off between fecundity and development time (which determines offspring

survival). They are deterministic optimality models that predict the relationship between reproductive strategies and fitness. A reproductive strategy is characterized by the level of resources allocated by the parent to individual offspring via the egg. Although often referred to as 'egg size', this is an issue of egg provisioning, and the important quantity is energy content, not egg dimensions. In these models, fitness is defined as reproductive success, and is measured as the number of offspring that develop to metamorphosis

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per unit of energy allocated to reproduction by the parent (see Vance 1973a).

The fitness relationship is used to predict the evolution of reproductive strategies. Natural selection is expected to drive the level of egg provisioning towards reproductive strategies with high fitness. If the fitness curve has a single maximum, then selection will be directional towards that best strategy. However, if the fitness curve is concave (i.e. curved upward), then there may be an adaptive valley between 2 local optima, and selection will be disruptive across that region. Selection will drive investment levels away from the low-fitness reproductive strategies on the valley floor and towards the strategies that maximize reproductive success.

Concave regions on the fitness curves characterize nearly all models of marine invertebrate reproductive strategies. This is important because the 2 major modes of planktonic larval development, planktotrophy (obligate feeding on exogenous particulate food) and lecithotrophy ('yolk-feeding' without a requirement for exogenous food) always lie on opposite sides of the adaptive valley. From this result, evolution between these modes via natural selection is predicted to be difficult or impossible; yet, phylogenetic analyses indicate that evolutionary transitions between these modes have occurred repeatedly (Wray 1995, Rouse 2000, McEdward & Miner 2001).

How are adaptive valleys crossed during transitions between modes of larval development? This paper examines one possible explanation, which is based on variation in fitness associated with environmental variation in larval food supply. We approach this by asking a simple question: Is the variation in fitness within a reproductive strategy substantial compared to fitness differences among strategies? If so, then selection (whether directional or disruptive) would probably be weak or inconsistent. This would have the effect of flattening out the adaptive landscape and would present less of an obstacle to transitions between strategies that lie on opposite sides of an adaptive valley.

METHODS

Approach. The question was explored largely using the original fecundity-time model published by Vance (1973a), modified to allow input of specific food levels (see McEdward 1997). For comparison, we will also present some results from a model that incorporates facultative larval feeding (McEdward 1997).

The analysis concentrated on fitness variation due to food supply, because food availability is an important environmental variable that influences rates of development, and hence fitness, *differently* across repro-

ductive strategies. Although we focus on food, similar arguments could be developed for other factors that influence fitness, such as mortality rate. Food levels are not reported as absolute particle concentrations or energy content, but rather as relative values. Food level was specified as a proportion of the minimum nonlimiting food concentration that would support maximum development rate.

We evaluated 2 aspects of variation in food supply: different food levels that were held constant throughout larval life, and food levels that fluctuated randomly between specified upper and lower bounds. In order to calculate the variation in fitness for a set of environmental conditions, replicate simulations were run for each reproductive strategy. Each simulation involved calculating the duration of the larval period based on daily acquisition of food until sufficient fuel was obtained to complete development to metamorphosis. The amount of food needed depends on egg provisioning and differs among reproductive strategies. From the replicated simulations, a distribution of fitnesses was obtained for each reproductive strategy under a given set of environmental conditions. The question of interest is whether the fitness differences across reproductive strategies are large relative to the variation in fitness within a strategy when larvae encounter fluctuations in the supply of particulate planktonic food.

Models. The models we used to examine the effects of variation in food level on the number of offspring that survive to metamorphosis (through effects on development time) are based on previous modifications of the fecundity-time model of Vance (1973a). In particular, McEdward (1997) presented 2 models: (1) a 'reformulated Vance model' that explicitly incorporated the effects of exogenous particulate food on larval development but did not allow for facultative feeding by planktotrophic larvae, and (2) a 'facultative feeding model'. Both these models, nonfacultative and facultative versions, were modified to incorporate fluctuating planktonic food levels.

The reproductive strategies (s) evaluated in this study ranged from 0.2, the minimum viable level of egg provisioning, to 1, the threshold for lecithotrophy. We chose the minimum value of 0.2 to illustrate how food variation can affect the fitness curve. However, s values in nature have been estimated below this minimum (Hoegh-Guldberg & Emler 1997).

Total development time (T) is the sum of the durations of the lecithotrophic (λ) and the planktotrophic (ρ) phases of larval life, and the constant D specifies the minimum duration of larval life (T_{\min}) under given physical conditions (e.g. temperature) (Table 1). Thus, the maximum rate of development results in $T = D$. For both the nonfacultative and facultative models, larvae always develop at the maximum rate of development

Table 1. List of variables and constants used in the models

Symbol	Quantity	Units	Permissible values
R	Reproductive success	# individuals (energy units) ⁻¹	$0 \leq 1/s$
N_T	Metamorphs	# individuals	$0 \leq N_T$
N_0	Fecundity	# individuals	$0 \leq N_0$
m	Mortality rate constant	Fraction of individuals d ⁻¹	$0 \leq m \leq 1$
T	Time to metamorphosis	d	$0 < T$
C	Total investment	Energy units	$0 \leq 1/s$
s	Reproductive strategy	Proportion (of energy units)	$0.2 < s \leq 1$
f	Prefeeding constant	Proportion (of D)	$0 \leq f \leq 1$
λ	Lecithotrophic duration	d	$f \leq \lambda \leq D$
ϕ	Facultative duration	d	$0 \leq \phi \leq D(1 - f)$
ρ	Planktotrophic duration	d	$0 \leq \rho$
D	Development time constant	d	$0 \leq D$
F	Food level	Proportion (of maximum ration)	$0 \leq F \leq 1$
\bar{F}_{plank}	Food level during obligate planktotrophic period	Proportion (of maximum ration)	$0 \leq F \leq 1$
\bar{F}_{fac}	Food level during facultative feeding period	Proportion (of maximum ration)	$0 \leq F \leq 1$

during the lecithotrophic phase. The duration for the lecithotrophic phase (λ) is calculated as $s \times D$. In the nonfacultative model, the duration of the planktotrophic period depends on reproduction strategies and the food levels encountered by the planktotrophic larval stages (F). In the facultative feeding model, the planktotrophic duration also depends on the amount of food acquired by the facultative feeding larval stage (see McEdward 1997).

Fluctuating food levels: Food level (F) was specified as a proportion of the food concentration necessary for the maximum development rate. Planktonic food levels were allowed to fluctuate randomly on a daily basis, between specified upper (F_{max}) and lower (F_{min}) bounds. For example, on the first day of larval feeding, the food level (F_1) might be 0.6, equivalent to 60% of the food concentration that supports the intrinsic maximum rate of development. The food level was held constant throughout the entire first day and then abruptly changed to a new randomly selected level (F_2), say 0.83, that would be held constant for the entire second day. There was no temporal correlation among daily food levels. The special case where $F_{\text{max}} = F_{\text{min}}$ represented a constant food supply and was equivalent to the original, deterministic versions of these models.

Given that we have modeled neither costs nor advantages for offspring that experience fluctuating food, the frequency of fluctuation has no effect on predictions of the models. However, this assumption is probably false, and experiments have shown assimilation is reduced (Jørgensen 1990) and development time is increased (B. G. Miner unpubl. data) when food fluctuates. Because currently only limited data are available and it is unclear how to model these costs, we have chosen not to add them, and to keep the model simple. If future models are to incorporate these costs, then the frequency of fluctuations will need to be considered.

The effect of food level on development time to metamorphosis is most clearly seen by considering the amount of energy that is required to fuel development. The amount of energy that must be acquired by feeding is $(1 - s)$. This can be expressed in terms of the number of days of full-speed development (i.e. development at the maximum intrinsic rate = not food-limited) by taking the product of $1 - s$ and D . To fuel 1 d of full-speed development requires 1 'unit' of food, and this involves feeding until that amount of food is obtained. The time required to acquire a unit of food is given by the reciprocal of the food level, since food level is specified as a proportion of the food that supports full-speed development. The total duration of the planktotrophic period (ρ) is therefore given by Eq. (1):

$$\rho = \frac{D(1-s)}{\bar{F}_{\text{plank}}} \quad (1)$$

where \bar{F}_{plank} is the mean food level during the planktotrophic period, calculated by averaging the randomly fluctuating daily food levels from the onset of feeding through metamorphosis. This cannot be calculated directly because the duration of the planktotrophic period, and hence the number of food levels that need to be included in the calculation of the average, depends on the randomly varying daily food levels. Instead, the duration of the planktotrophic period is obtained by modeling the cumulative acquisition of food. The daily food levels are chosen randomly, and the food acquired is subtracted from the amount of food needed to complete larval development. The model allows for partial days of feeding so that the acquired food exactly balances the required food, and this yields an exact numerical solution for the duration of the planktotrophic period (i.e. it is not limited to a resolution of 1 d by the time steps of the model).

Total development time is calculated using Eq. (2):

$$T = Ds + \frac{D(1-s)}{\bar{F}_{\text{plank}}} \quad (2)$$

Fitness: The number of offspring that develop to metamorphosis can be used to calculate a measure of fitness by which different reproductive strategies can be compared. It is assumed, for the sake of comparison, that there is a fixed total amount of energy (C) devoted to reproduction. Reproductive strategies differ in the level of resources actually allocated to individual eggs ($=s$). Fecundity (N_0) is the quotient C/s and gives the initial number of offspring at the start of development. The number of offspring is reduced by mortality throughout the total developmental duration from fertilization to metamorphosis. The daily mortality rate (m) is expressed as the proportion of offspring lost per day, and it is assumed to be constant (at 0.135 d^{-1}) across egg sizes, larval stages, and food levels. This daily mortality rate is within the range measured for planktonic echinoderm larvae (Rumrill 1987, 1990, Lamare & Barker 1999). The number of offspring at metamorphosis is calculated as the product of fecundity and survivorship based on an exponential decay curve with a decay constant m and duration T :

$$N_T = \frac{C}{s} e^{-m \left[Ds + \frac{D(1-s)}{\bar{F}_{\text{plank}}} \right]} \quad (3)$$

Fitness is reported here as 'reproductive efficiency' R (sensu Vance 1973a), which is defined as the number of metamorphs per unit energy devoted to reproduction:

$$R = \frac{N_T}{C} = \frac{1}{s} e^{-mT} \quad (4)$$

One 'unit' of reproductive energy (C) is sufficient to produce $1/s$ eggs of any given egg size (e.g. a single fully lecithotrophic egg: $s = 1.0$). R is the product of the reciprocal of egg size (hence proportional to fecundity) and e^{-mT} that gives the proportion of offspring surviving throughout the developmental period (T) from spawning to metamorphosis. Reproductive efficiency is a measure of fitness that is independent of the total investment of energy in reproduction. R values range from 0 to $1/s$.

Facultative feeding: In the facultative feeding model, the lecithotrophic phase is broken up into a prefeeding period and a facultative feeding period. The proportion of development spent in the prefeeding period is f , and $f \times D$ gives the duration of the prefeeding period. The proportion of development spent in the facultative period is calculated as $s - f$, and the duration of the facultative period (Φ) is calculated as follows:

$$\Phi = D(s - f) \quad (5)$$

Both the prefeeding and facultative feeding periods are fueled by egg energy and develop at the maximum intrinsic rate of development. However, the prefeeding period is nonfeeding, and the facultative period is feeding. Thus, the end of the prefeeding period marks the onset of the ability to feed, and the end of the facultative period marks the end of egg energy reserves. The average food level during the facultative period is calculated by summing the random food levels sampled during the facultative period divided by the exact duration of the facultative period (Φ). The amount of food acquired during the facultative feeding period depends on both \bar{F}_{fac} and Φ , and reduces the amount needed during the planktotrophic stage to complete larval development. Consequently this also decreases the duration of the obligate planktotrophic period:

$$\rho = \frac{D(1-s) - \Phi \bar{F}_{\text{fac}}}{\bar{F}_{\text{plank}}} \quad (6)$$

If egg size is large, then the duration of the lecithotrophic period is long and the amount of energy needed from larval feeding (i.e. not provided in the egg) is small. In addition, if the food levels are high, then all of the food needed to fuel development to metamorphosis could be obtained by the facultative stage before the obligate feeding period begins. This would result in development at the maximum intrinsic rate throughout larval life and make development time independent of the food level encountered by the planktotrophic stages (no food limitation). Under these conditions, given Eq. (6), it is numerically possible for the calculated duration of the planktotrophic period to be less than the minimum possible duration of the planktotrophic period. For example, say the food level ($\bar{F}_{\text{plank}}, \bar{F}_{\text{fac}} = 1$ throughout development, the minimum time to develop (D) is 10 d, the proportion of time spent in the facultative period (f) is 0.5, the duration of the facultative period (Φ) is $0.5 \times 10 \text{ d} = 5 \text{ d}$, and the proportion spent in the planktotrophic period is 0.3. The shortest duration possible for the planktotrophic period is therefore 3 d ($0.3 \times 10 \text{ d}$). However, using Eq. (6), we calculate that feeding during the facultative period has reduced the planktotrophic period to -2 d . This scenario is of course biologically impossible. Thus, a lower limit is set on the value of ρ with a conditional statement (Eq. 7) that sets the minimum value of ρ to that corresponding to the maximum intrinsic rate of development (ρ_{min}). The value of ρ_{min} can be calculated using Eq. (1) with the average food level, \bar{F}_{plank} set to 1 ($= D[1 - s]$):

$$\rho = \max \left[\rho_{\text{min}}, \frac{D(1-s) - \Phi \bar{F}_{\text{fac}}}{\bar{F}_{\text{plank}}} \right] \quad (7)$$

Eq. (7) is analogous to Eq. (15) in the original facultative feeding model (McEdward 1997). The differences are that in the current model the food levels are not constant; rather, they fluctuate daily, and the food levels can be different during different phases (i.e. facultative feeding and planktrophic periods) of larval life. In the case where the planktrophic period has the minimum duration (ρ_{\min}), the duration of larval development simplifies to D , the development time corresponding to the maximum intrinsic development rate.

Total development time and the number of metamorphs in the facultative feeding model are given by Eqs. (8) & (9), respectively. Fitness is calculated using Eq. (4):

$$T = \max\left[D, \frac{D(1-s) - \Phi \bar{F}_{\text{fac}}}{\bar{F}_{\text{plank}}} + Ds\right] \quad (8)$$

$$N_T = \max\left\{\frac{C}{s} e^{-mD}, \frac{C}{s} e^{-m\left[\frac{D(1-s) - \Phi \bar{F}_{\text{fac}}}{\bar{F}_{\text{plank}}} + Ds\right]}\right\} \quad (9)$$

Simulations: The calculations of the development times, the numbers of metamorphs, and the fitnesses described above represent the outcome of a single bout of reproduction (the spawning and development of a clutch of eggs) for a given reproductive strategy. These results are dependent on the particular set of daily food levels that were randomly generated to simulate the planktonic environment during development of that particular spawn. For each reproductive strategy, 10 000 replicate simulations were run to generate different sets of food levels within specified upper (F_{\max}) and lower (F_{\min}) bounds, and a distribution of fitness values (R s). Fitness distributions were generated in this way for each egg size within a range of reproductive strategies, from the minimum viable egg size to eggs at the threshold for lecithotrophy ($s = 0.2, 0.25, 0.30, \dots, 1.0$).

RESULTS

Effect of different constant mean food levels

Fitness (R), as a function of egg size (s), was evaluated at 3 different food levels: 10, 40, and 70% of the nonlimiting concentration. When food is very scarce ($F = 0.1$), fitness is very low for small-egg strategies and increases with increasing egg size to a well-defined maximum at $s = 1$ (Fig. 1A). At $s = 1$, the eggs contain all the energy needed for larval development to metamorphosis and to develop at the maximum intrinsic rate regardless of food level. With more abundant food ($F = 0.4$), the low investment strategies have higher fitness than at 10% food levels, but there are no

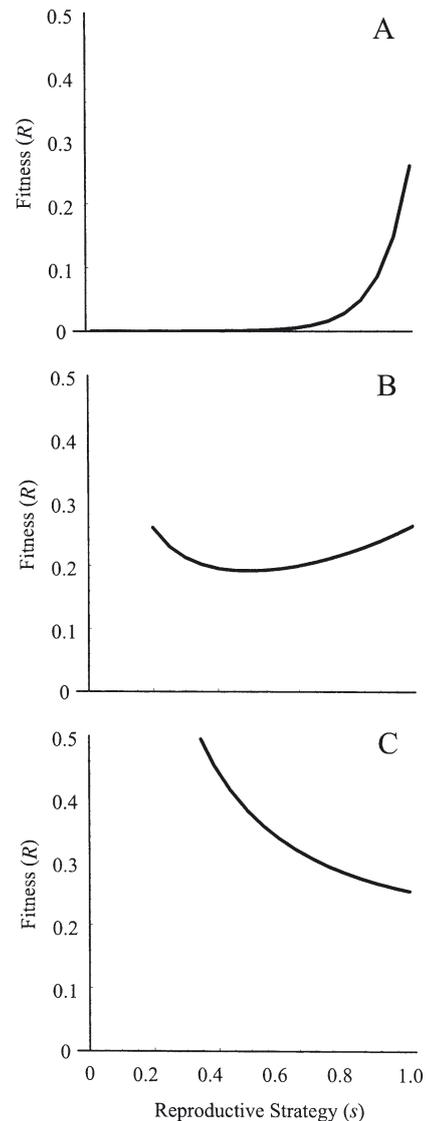


Fig. 1. Fitness (reproductive success, R) versus reproductive strategy (s) with (A) a constant low level of food ($F = 0.1$), (B) a constant intermediate level of food ($F = 0.4$), and (C) a constant high level of food ($F = 0.7$). Planktrophic strategy corresponds to $s < 1$, lecithotrophy to $s = 1$. For (A) relatively high levels of parental investment per offspring are favored; for (B) fitness maxima occur at minimum viable egg size of $s = 0.2$ and at the threshold between planktrotrophy and lecithotrophy at $s = 1$; for (C) low levels of egg provisioning are favored

differences at large egg sizes. This intermediate food level results in a concave fitness curve and 2 local optima, at $s = 0.2$ and $s = 1$ (Fig. 1B). At higher food levels ($F = 0.7$), there is very high reproductive success for small-egg strategies (Fig. 1C).

Planktonic food levels have a strong effect on larvae that develop from eggs provisioned with low levels of energy (e.g. $s < 0.4$). The number of metamorphs is very low when food is scarce and very high when food

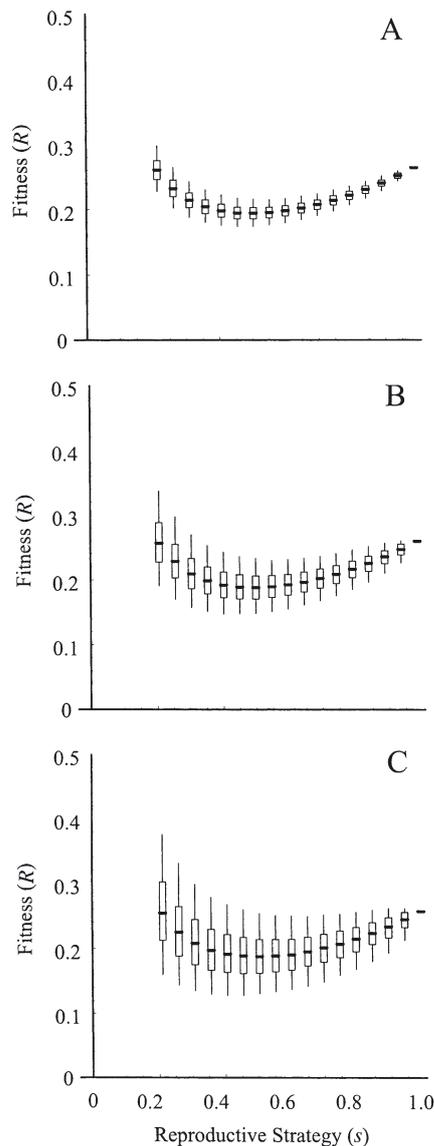


Fig. 2. Fitness (reproductive success, R) versus reproductive strategy (s) with (A) minor fluctuations ($F_{\min} = 0.3$ to $F_{\max} = 0.5$) around an intermediate level of food ($F_{\text{mean}} = 0.4$), (B) moderate fluctuations ($F_{\min} = 0.2$ to $F_{\max} = 0.6$) around an intermediate level of food ($F_{\text{mean}} = 0.4$), and (C) wide fluctuations ($F_{\min} = 0.1$ to $F_{\max} = 0.7$) around an intermediate level of food ($F_{\text{mean}} = 0.4$). Fitness values are plotted as median (horizontal line) for each strategy, based on 10^4 simulation runs; boxes indicate 25 and 75% quantiles, and whiskers 5 and 95% quantiles of the distributions. Fitness maxima occur at $s = 0.2$ and 1

is abundant. At larger egg sizes (e.g. $s = 0.5$ to 0.9), food level has only a limited effect on fitness. In lecithotrophs ($s > 1$), food supply has no effect on the development time and therefore the number of metamorphs. This is because lecithotrophs do not depend on exogenous food for development to metamorphosis and therefore cannot be food-limited.

Effect of different degrees of fluctuation around constant mean food level

With a constant food level of 0.4, the fitness curve is concave with maxima at the minimum viable egg size ($s = 0.2$) and at the threshold for lecithotrophy ($s = 1.0$; Fig. 1B). The fitness values at the 2 peaks are approximately the same. Holding the mean food level at 0.4, different degrees of random fluctuation between F_{\min} and F_{\max} were modeled. When food level varies on a daily basis, fitness varies substantially around the median fitness (10^4 replicate simulations) (Fig. 2). Minor fluctuations, within the range of 0.3 (F_{\min}) to 0.5 (F_{\max}), result in fitness variation in all planktotrophic strategies ($s < 1$; Fig. 2A). The variation is greater for small-egg strategies than for large-egg strategies. Fluctuating food has no effect on lecithotrophs ($s = 1$); they have constant fitness despite environmental variation in food supply.

Greater fluctuations in food supply, from 0.2 (F_{\min}) to 0.6 (F_{\max}) (Fig. 2B), result in increased fitness variance for any given strategy, but the greatest effect is at small egg sizes, where larvae are most strongly dependent on exogenous food. With large-scale fluctuations in food supply, from 0.1 (F_{\min}) to 0.7 (F_{\max}) (Fig. 2C), the fitness variation is very great, and the 25 to 75% quantiles overlap across all strategies in the adaptive valley between the 2 peaks. The overlap of the fitness distributions across egg sizes is very different for different levels of food fluctuation (Fig. 2). When the fluctuations in food supply are minor, only the reproductive strategies at the floor of the adaptive valley have distributions that overlap (Fig. 2A). However, when food supply varies widely, then there is at least 25% overlap in the fitness distributions across nearly all planktotrophic strategies (Fig. 2C).

Effect of same degree of fluctuation around 3 different mean food levels

The effect of fluctuating food supply varies with the mean food level. When food is relatively scarce ($F_{\text{mean}} = 0.4$), small-egg strategies have relatively low fitness, and even moderate fluctuations in food supply ($F_{\min} = 0.2$, $F_{\max} = 0.6$) result in fitness variation that greatly exceeds fitness differences across a wide range of egg sizes (Fig. 3A). Moderate food levels ($F_{\text{mean}} = 0.6$) result in greater reproductive success for small-egg strategies (Fig. 3B) compared to lower food concentrations. Fitness differences between the smallest and largest egg strategies exceed the greatest fitness variation (e.g. 5 to 95% quantiles, small-egg strategies). Substantial overlap (>25%) is restricted to short ranges of neighboring reproductive strategies, especially $0.75 \leq s \leq 1.0$ (Fig. 3B).

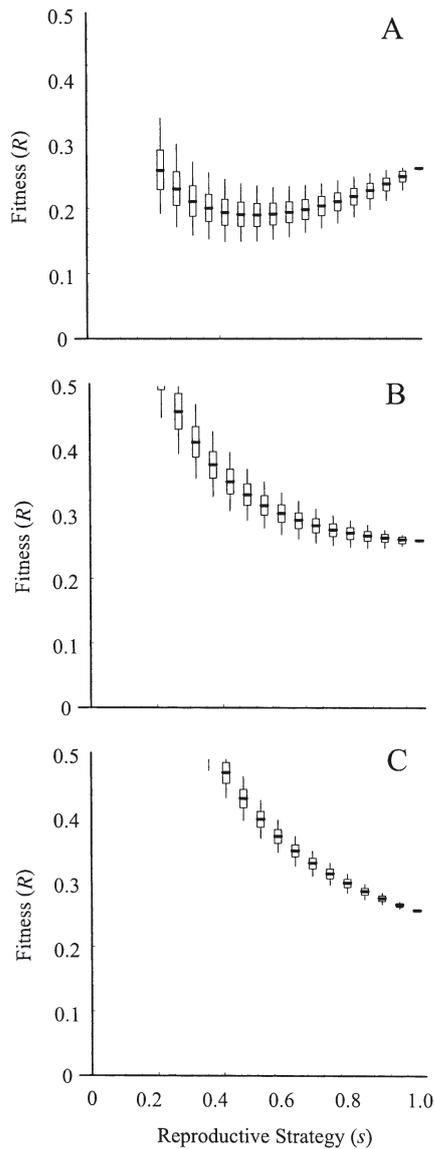


Fig. 3. Fitness (reproductive success, R) versus reproductive strategy (s) with (A) moderate fluctuations ($F_{\min} = 0.2$ to $F_{\max} = 0.6$) around a low level of food ($F_{\text{mean}} = 0.4$), (B) moderate fluctuations ($F_{\min} = 0.4$ to $F_{\max} = 0.8$) around an intermediate level of food ($F_{\text{mean}} = 0.6$), and (C) moderate fluctuations ($F_{\min} = 0.6$ to $F_{\max} = 1.0$) around a high level of food ($F_{\text{mean}} = 0.8$). Fitness values are plotted as median (horizontal line) for each strategy, based on 10^4 simulation runs; boxes indicate 25 and 75% quantiles, and whiskers 5 and 95% quantiles of the distributions

When food is abundant ($F_{\text{mean}} = 0.8$), small-egg strategies have very high fitnesses and there is negligible overlap of fitness distributions (Fig. 3C). Fitness differences exceed fitness variation for many strategies. Although the variation in fitness has not changed, there is much less overlap of fitness distributions because of greatly increased differences in the median fitnesses among strategies, especially for the smallest egg strategies (Fig. 3C).

Effect of different degrees of fluctuation around constant mean food level in a model incorporating the capability for facultative feeding

Facultative feeding is feeding that occurs before egg reserves are exhausted, i.e. before exogenous food is necessary for continued growth and development. Using the facultative feeding model, we examined the same food level and fluctuations used previously with the nonfacultative model (see Figs. 1B & 2). When food supply is constant at 40% of the nonlimiting concentration, the fitness curve (Fig. 4) is similar, but not identical, to that obtained with the model without facultative feeding (Fig. 1B). The curve is concave, with 2 fitness maxima: 1 at the minimum viable egg size ($s = 0.2$). The difference is that facultative feeding shifts the large-egg optimum away from lecithotrophy ($s = 1$) towards intermediate planktrophic strategies. Minor fluctuations in food supply ($F_{\min} = 0.3$, $F_{\max} = 0.5$) result in fitness variation for all egg sizes between the peaks ($0.2 \leq s \leq 0.7$), but minimal overlap of fitness distributions among strategies (Fig. 5A). Moderate fluctuations in food supply ($F_{\min} = 0.2$, $F_{\max} = 0.6$) result in fitness variation that exceeds the differences among strategies near the floor of the adaptive valley, but there are still distinct peaks on the fitness curve that overlap neighboring strategies by <10% (Fig. 5B). Large fluctuations in food supply ($F_{\min} = 0.1$, $F_{\max} = 0.7$) result in very large fitness variation that completely swamps the differences among strategies between the 2 adaptive peaks (Fig. 5C). The fitness distributions of nearly all planktrophic strategies overlap substantially (>25%), although strategies at the large-egg adaptive peak have less overlap (Fig. 5C). Due to facultative feeding capability, large-egg planktrophs

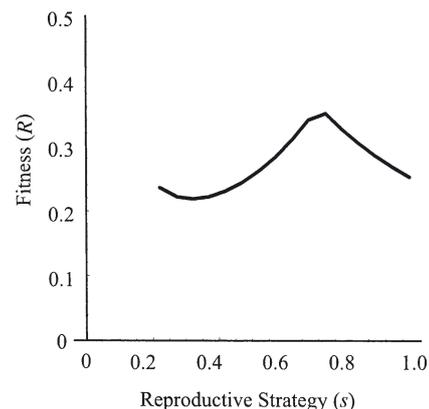


Fig. 4. Fitness (reproductive success, R) versus reproductive strategy (s) with a constant, intermediate level of food ($F = 0.4$) in a model with facultative larval feeding. Planktrophic strategies correspond to $s < 1$, lecithotrophy to $s = 1$. Distinct fitness maximum occurs at an intermediate strategy ($s = 0.7$)

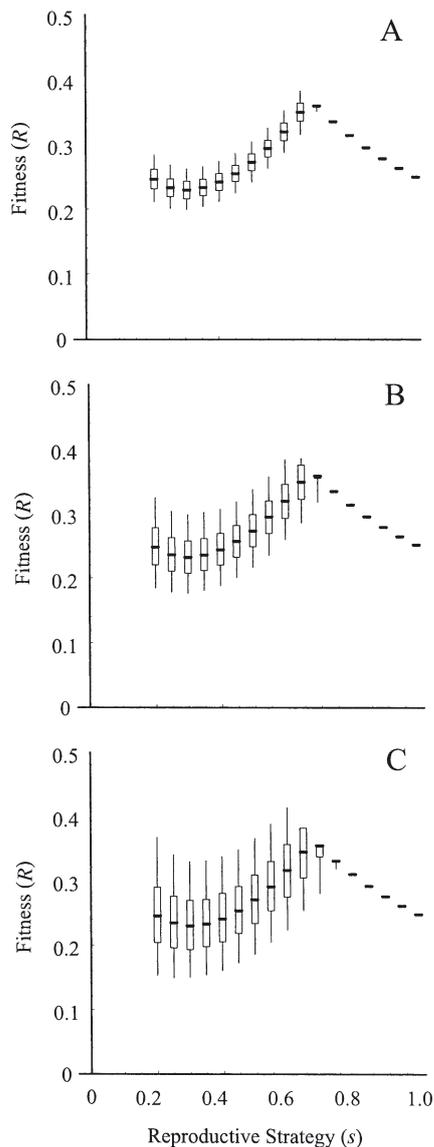


Fig. 5. Fitness (reproductive success, R) versus reproductive strategy (s) from facultative larval feeding model (cf. non-facultative feeding model in Fig. 2). (A)–(C) as in Fig. 2

($0.7 < s < 1$) have constant fitness despite the requirement for planktonic food and widely fluctuating food concentrations (Fig. 5C) (see also McEdward 1997).

DISCUSSION

A current theory of larval evolution is based on a set of fecundity-time models that examine the effect of egg size on fitness, measured as reproductive success (Havenhand 1995, Levitan 2000, McEdward 2001). Reproductive strategies that are characterized by low levels of egg provisioning (small-egg strategies) have

high fecundity but can have prolonged development time to metamorphosis. Increased levels of parental investment per offspring (large-egg strategies) result in lower fecundity but rapid development through the larval period. Development time is important because daily rates of larval mortality in the plankton are very high (6 to 27% d^{-1} , Rumrill 1987, 1990, Lamare & Barker 1999). Most models predict that only 2 levels of provisioning can maximize fitness.

The relationship between reproductive strategy (egg size) and development time depends on 2 factors. The first factor concerns the intrinsic nutritional requirements of the larvae: the resources provisioned in the egg cover some fraction of the total energy needed to fuel development to metamorphosis; the remainder must be obtained by larval feeding, and this determines the degree of dependence on exogenous food and consequently the *potential* for food limitation of development rate. The second factor is the planktonic food supply: although the potential for food limitation varies with the level of egg provisioning, the *actual* larval development time depends on the availability of food and its acquisition by the larvae. Larvae that develop from small, poorly provisioned eggs require more larval feeding than do larvae that develop from large, well-provisioned eggs. If food is scarce, then the former larvae should take a very long time to develop compared to the latter larvae. However, if food is very abundant, then the difference in development time will depend on the efficiency of food capture and utilization by the larvae.

Despite the importance of food availability as a determinant of development time and hence reproductive success, most models do not explicitly evaluate the effects of food supply. In this study, we examined the effect of exogenous food supply on larval development. Two questions were addressed: How do different food levels (held constant throughout larval life) affect the relationship between fitness reproductive strategy and fitness? How does fitness vary within a reproductive strategy when food supply fluctuates during the larval period?

Constant food levels

Different food levels result in different shapes for the fitness curves. When food is abundant, development rates are not limited by food, and all larvae develop at the intrinsic maximum rate. Hence, in this model, all reproductive strategies suffer the same mortality, and the strategy that yields the highest fitness is the one that has the highest fecundity. High food favors small-egg strategies (Fig. 1C). Conversely, when food is very scarce, larvae that are strongly dependent on exo-

genous food develop very slowly and suffer greater mortality. Low food favors large-egg strategies (Fig. 1A). It is important to recognize that the difference in the fitness curves between high and low food conditions is entirely due to the effects of food supply on planktotrophic larvae ($s < 1$) and that the effect is inversely related to the value of s . In other words, the reproductive success of those strategies in which the larvae have the greatest need for exogenous food varies greatly with environmental conditions. Although this result is biologically reasonable, it depends on an implicit assumption of all fecundity-time models, namely that the size of the metamorphs does not differ among reproductive strategies and does not vary with food availability (McEdward 2001).

When food availability does not fluctuate during larval life, there are always distinct optima in the fitness curve. However, fitness maxima occur at only 2 egg sizes—in these models, either at the minimum viable egg size ($s = 0.2$) or at the threshold for lecithotrophy ($s = 1.0$), or both. For the hypothetical species considered here, reproductive strategies with $s < 0.2$ are inviable because the eggs contain insufficient energy to develop to the initial feeding larval stage. Intermediate strategies are never favored. If food levels are moderate, there are 2 distinct fitness optima and selection is disruptive toward the extremes (Fig. 1B). Although intermediates are never favored, long-term changes in planktonic food level can change the direction of selection acting on reproductive strategies and drive species between planktotrophy and lecithotrophy, or vice versa. For example, if food were very abundant, extremely small planktotrophs ($s = 0.2$) would be favored (Fig. 1C). However, if planktonic productivity started to decrease, the fitness of small-egg planktotrophic strategies would decrease but the fitness of the large-egg planktotrophs would change little and the lecithotrophic strategies would remain unchanged (Fig. 1A). Selection would now favor increased levels of egg provisioning and drive reproductive strategies towards the fitness maximum at lecithotrophy ($s = 1$). Likewise, increases in planktonic productivity would shift reproductive strategies from lecithotrophy to planktotrophy. The latter transition is likely only if lecithotrophic larvae retain their feeding capability (McEdward & Janies 1997).

Fluctuating food levels

Fluctuation in the food level during larval life resulted in considerable variation in fitness for all planktotrophic strategies ($s < 1$). For a given level of fluctuation in food supply, the greatest fitness variation occurred in the small-egg strategies ($s = 0.2$), less in

intermediate strategies, and none in lecithotrophs (e.g. Figs. 2 & 3). Likewise, the magnitude of fluctuations had a strong effect on fitness variation in small-egg strategies, but not in large-egg strategies (Fig. 2). This effect is not surprising given that small-egg strategies have strong dependence on exogenous food supply and therefore high potential for food limitation.

Recognition of environmentally induced variation in fitness within a given reproductive strategy and differences in fitness variation among strategies provide new insights into the interpretation of fitness curves obtained from fecundity-time models. When food supply is assumed to be constant, the models are completely deterministic, and each reproductive strategy is characterized by a single fitness value (Fig. 1). It is not clear how features of the resulting fitness curves should be interpreted. For instance, is there strong selection towards those strategies when there are 2 fitness optima (Fig. 1B), and does the adaptive valley between them effectively limit transitions between the optima? One answer is provided by examining the variation in fitness that occurs within a reproductive strategy under fluctuating environmental conditions compared to the fitness differences across a range of reproductive strategies. We used measures of overlap of fitness distributions across reproductive strategies to address this issue.

When food supply fluctuates slightly around a moderate mean level of food (Fig. 2A), fitness distributions overlap substantially only among strategies located on the floor of the adaptive valley. There is less than 10% overlap around the peaks, indicating that there are distinct fitness optima towards which selection would be expected to drive egg-provisioning strategies. Note that there is less overlap among strategies adjacent to the large-egg peak compared to the small-egg peak (Fig. 2A). This reflects the reduced potential for food limitation of development rate in strategies that have only a minimal need for exogenous food. Increasing the magnitude of the fluctuations in food supply (without changing the mean food level) leads to greater variation in fitness (Fig. 2). When food supply fluctuates greatly (0.1 to 0.7), the fitness distributions overlap by more than 25% across nearly the entire range of planktotrophic strategies (Fig. 2C). In this case, selection would be expected to operate weakly or inconsistently on the level of egg provisioning. Intermediate strategies might be common, even though they are not explicitly favored, precisely because the extreme strategies are not strongly favored either.

The effect of fluctuating food supply depends on the mean food level. When food is scarce or moderately abundant, fluctuations result in fitness variation that is large relative to the fitness differences among reproductive strategies (Fig. 3A), but when food is abun-

dant, there are large differences in reproductive success between organisms with small eggs and large eggs (Fig. 3B,C). The fitness variation due to fluctuation in food supply is small relative to the fitness differences among strategies, and there is overlap only between adjacent strategies (Fig. 3B,C). Consequently, there should be consistently strong directional selection to minimize egg size whenever food is abundant, even if the concentrations fluctuate widely.

Facultative larval feeding

Models that include the capacity for facultative feeding by larvae produce similar results to nonfacultative models, but lead to different conclusions for larval evolution. Facultative feeding shifts the large-egg optimal strategy to intermediate sizes ($s_{\text{optimum}} < 1$) and restricts the adaptive valley to small-egg strategies (Fig. 4). This shift reduces the range of reproductive strategies that are affected by fluctuations in food concentration. There is no effect of fluctuations on any strategy characterized by $s > s_{\text{optimum}}$ (Fig. 5), even though those larvae require food in order to develop to metamorphosis. The surprising implication is that fluctuating food influences evolution only among a subset of planktonic strategies. It is not important at large egg sizes or for the transition to lecithotrophy.

Need for new empirical studies

Previous models of the evolution of reproductive strategies have all made the implicit assumption that environmental conditions remain constant throughout larval life. This assumption is unrealistic, especially for species with planktonic larval periods on the order of weeks to months (Pechenik 1987; p. 551–608). The assumption about food supply is not specifically about the constancy of food concentration, but rather about the constancy of the extent of food limitation. If food concentrations vary strongly but always exceed the concentrations required to sustain maximum development rates, then the duration of the larval period would be unaffected by those fluctuations. However, if larvae were never food-limited, then selection would drive species towards the minimum egg size and extreme obligate planktotrophy. This is not the case. Planktonic species vary widely in the level of egg provisioning (Jaeckle 1995, McEdward & Morgan 2001) and have very different degrees of dependence on exogenous food (Eckert 1995, Herrera et al. 1996). Furthermore, some larvae can achieve maximum development rates at moderate algal concentrations in the laboratory (e.g. the echinoid *Lytechinus variegatus* develops

at the maximum rate on 8 cells μl^{-1} of *Dunaliella tertiolecta*; Herrera 1998). The larval growth and development rates of at least some species of marine invertebrates can be strongly limited by natural concentrations of planktonic food, even in productive coastal waters (Paulay et al. 1985, Lamare & Barker 1999). Whether food limitation is common among marine invertebrate larvae is uncertain (Olson & Olson 1989). Indirect tests of larval growth in the field, using relationships between feeding history and morphology, indicate that food limitation does occur and affects numerous species within a geographic area (Fenaux et al. 1994).

The results presented here suggest that when food limitation occurs, and food availability fluctuates during larval life, reproductive success can vary widely within a reproductive strategy. Two questions arise: How much does food supply fluctuate, and how does this fluctuation affect larval development and fitness? These questions cannot be answered at the present time. New empirical studies are needed to determine the degree of food limitation that occurs in nature and how fluctuations in food particle concentrations change the degree of food limitation. Detailed nutritional studies will be necessary in order to quantify food limitation in the laboratory. A better understanding of the natural diet of larvae is needed to relate measurements of the concentration and composition of particulate food in the oceans to the effects on larval development rate and growth. The diet of most larvae is not known, but in the laboratory ciliated larvae eat unicellular algae ranging from 5 to 50 μm in diameter or length (Boidron-Metairon 1995). However, algal species differ substantially in nutritional quality. For example, the larval survival, development rate, growth, and metamorphic success of *Paracentrotus lividus* and *Arbacia lixula* all vary with diet, but juvenile size at metamorphosis does not (Pedrotti & Fenaux 1993).

The results from the facultative feeding model tell us that the way in which larvae capture food is not a trivial detail. Knowing whether facultative feeding capability is widespread among marine larvae is important to our understanding of reproductive success in different environments. Again, detailed empirical studies of larval feeding activity, nutritional requirements, metabolism, growth, and development rate are badly needed for a range of species with different reproductive strategies and under different environmental conditions.

Although such studies will be difficult and time-consuming, they are the only means by which to generate precisely the information that we need to understand how selection acts on life histories to produce the patterns of reproduction and larval development that occur among marine invertebrates.

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