

Planktotrophy  
Lecithotrophy  
Life history

Planctotrophie  
Lécithotrophie  
Cycle de vie

# Diversity of energetic strategies among echinoid larvae and the transition from feeding to nonfeeding development

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## ABSTRACT

Our current work investigates a major ecological transition in echinoderm life cycles: the evolution from planktotrophic to lecithotrophic larval development. We have discovered a wide range of feeding requirements among subtropical echinoid larvae. Differences in maternal investment determine how much external food is required to build the larval body and subsequently the juvenile rudiment. There appears to be a continuum of nutritional strategies between extreme obligate planktotrophy and functional lecithotrophy (*i.e.* facultative planktotrophy). We suggest that the ecological boundary between planktotrophy and lecithotrophy is easily crossed and that unlike morphological changes, ecological transitions are readily reversible.

## RÉSUMÉ

La diversité des stratégies énergétiques chez les larves d'échinides et la transition entre le développement exotrophe et endotrophe.

Nos travaux actuels portent sur une transition écologique majeure dans les cycles de vie des échinodermes : l'évolution de la larve planctotrophe vers la larve lécithotrophe. Nous avons observé des régimes alimentaires fort variés parmi les échinides des mers subtropicales. La quantité de nourriture exogène, requise pour constituer la larve ainsi que le rudiment, varie en fonction de l'apport maternel initial (réserves endogènes). Il semble exister une certaine continuité de stratégies alimentaires entre la planctotrophie absolue et la planctotrophie facultative. Nous pensons que la frontière écologique entre la planctotrophie et la lécithotrophie est facilement franchie ; à l'encontre des changements morphologiques, les transitions écologiques sont aisément réversibles.

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## NUTRITIONAL MODE AND LIFE CYCLE PATTERNS

There are two common contrasting types of pelagic larval development (feeding and nonfeeding) in marine benthic invertebrates (Thorson, 1950; Mileikovsky, 1971; Chia, 1974; Grahame and Branch, 1985; Jablonski and Lutz, 1983; Levin and Bridges, 1995). Pelagic feeding larval development is the pleisiomorphic life cycle pattern in

many marine invertebrate phyla, including echinoderms (Jägersten, 1972; Strathmann, 1978a, 1993). Nonfeeding larvae have evolved in many taxa (Strathmann, 1978a, 1993; Ghiselin, 1987; Bridges, 1993; Wray, 1995; Levin and Bridges, 1995).

Feeding and nonfeeding modes of development are correlated with egg size. Eggs that develop into feeding larvae are smaller and contain  $\approx$  1000 times less energy

than eggs that develop into nonfeeding larvae (Strathmann and Vedder, 1977; Turner and Lawrence, 1979; McClintock and Pearse, 1986; McEdward, 1991; McEdward and Chia, 1991; Eckelbarger, 1994). In species which free spawn, and do not provide parental care, the contents of the egg are the entire maternal investment. It is assumed that the level of maternal investment per offspring determines the fitness of the offspring by influencing larval traits that affect survival during the pelagic larval period (*e.g.*, Vance, 1973*a, b*; Christiansen and Fenchel, 1979; Strathmann, 1985; reviewed by Havenhand, 1995).

Closely related species with feeding larvae often have very different egg sizes. Thus, egg size is a life history characteristic that can easily change. Selective pressures which may lead to the increase of egg size in species with feeding larvae probably include selection for increased juvenile size, decreased pelagic period (Strathmann, 1985), shorter generation time (Havenhand, 1993, 1995), and higher fertilization success (Levitan, 1993). Selective pressures which might cause an increase in egg size in species with nonfeeding larvae include selection for an increase in juvenile size (Lawrence *et al.*, 1984; Wray, 1995) or an increase in post metamorphic energy stores. Because the material necessary to build the juvenile is already present within the egg, pelagic period and generation time are less likely to be affected by an increase in egg size in species with nonfeeding larvae. Thus, some of the selective pressures which act to increase egg size in species with feeding larval development, and possibly lead to a transition from feeding to nonfeeding development, may not be the same pressures which lead to increases in egg size after the transition to nonfeeding larval development.

### THEORETICAL BACKGROUND

The life history trade-off between a large number of small, inexpensive eggs *versus* a few large, yolky eggs has been repeatedly analyzed in an attempt to understand the adaptive significance of these reproductive strategies (*e.g.*, Vance, 1973*a, b*; Strathmann, 1977; Christiansen and Fenchel, 1979; Roughgarden, 1989; Havenhand, 1995). The underlying theme behind these models is well illustrated in Vance's model (1973*a, b*) which examined

the correlation between egg size, planktonic mortality, and development time. The goal of the model was to mathematically determine the conditions favoring the evolution of different reproductive strategies, which would indicate the expected distribution of these strategies in marine benthic invertebrates. For simplicity, the model only examined pre-metamorphosis selection pressures.

Vance's model viewed pre-metamorphosis development as two successive stages: prefeeding (*i.e.*, fueled by reserves in the egg) and feeding (*i.e.*, dependent on exogenous food) (Fig. 1). The feeding period for planktotrophic larvae begins as soon as the feeding structures develop. Lecithotrophic larvae can't feed until after the end of larval development (post-metamorphosis). In terms of this framework, planktotrophy and lecithotrophy can be viewed as extremes in the timing of the developmental transition between the prefeeding and feeding stages.

The energy content of the egg [*s*] is expressed as the proportion (*i.e.*,  $0 \leq s \leq 1$ ) of the amount of energy required for development to metamorphosis. An egg size with a value of 1.0 provides sufficient energy to reach metamorphosis without needing to acquire exogenous food (*i.e.*, lecithotrophic development). All egg sizes with  $s < 1.0$  have insufficient energy to complete development to metamorphosis, and require some degree of feeding.

In the model, as egg size increases, the duration of the feeding stage decreases and the duration of the nonfeeding stage increases. Based on relationships among mortality, fecundity, and development time, Vance's model predicted a relationship between reproductive efficiency and egg size. This produced a concave curve, in which maximum reproductive efficiencies were for the extremes of the range  $0 \leq s \leq 1$ . This indicates that maximum reproductive efficiency would be achieved by completely feeding or completely nonfeeding development. It appears that an egg size of intermediate energetic content would not be favored and should be selected against.

Modifications of the original model (Vance, 1973*b*; Strathmann, 1977; Christiansen and Fenchel, 1979; Roughgarden, 1989; Havenhand, 1995) all yield the same qualitative result: there can be two egg sizes (energetic) which are evolutionarily stable. These models take into account the selective pressures of energy allocation, larval growth, and mortality rates. If an intermediate strategy exists and is successful, it may be the result of different selective pressures not yet accounted for by these models. The predictions from Vance's model have been supported

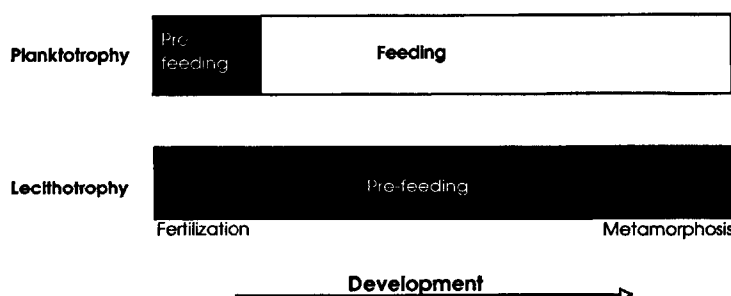


Figure 1

Diagram based on Vance's model (1973*a*) comparing the duration of the prefeeding and feeding stages in both lecithotrophic and planktotrophic species during larval development.

by the bimodal distribution of egg sizes among species in many taxa (*e.g.*, echinoids and asteroids, Emler *et al.*, 1987; but not molluscs, Kohn and Perron, 1994).

#### "INTERMEDIATE" NUTRITIONAL MODES

A few species, mostly of gastropod molluscs and echinoid echinoderms, have larvae that do not fit cleanly into the two nutritional strategies that characterize most larvae, feeding development and nonfeeding development. Some examples include: *Adalaria proxima*, (Thompson, 1958; Kempf and Todd, 1989), *Phestilla sibogae* (Kempf and Hadfield, 1985), and *Conus pennaceus* (Perron, 1981; Kohn and Perron, 1994) among the molluscs, a clypeasteroid *Clypeaster rosaceus* (Emler, 1986), and *Brisaster latifrons* (Strathmann, 1978b; Hart, in press), and other spatangoids. The common feature of these species is that their larvae can capture and utilize exogenous particulate food but do not need to feed to complete development to metamorphosis. They have been described as "facultative planktotrophs" (Chia, 1974; Kempf and Hadfield, 1985).

While the term "facultative planktotrophy" emphasizes the ability of these larvae to feed during their development, it is important to recognize that these larvae are functionally lecithotrophic. They are capable of developing through metamorphosis using only the nutritional reserves stored in the egg. The question of dissolved organic matter (DOM) uptake and utilization has not been specifically addressed in these species, but there doesn't seem to be any reason to expect that these larvae have different capacities to acquire, or requirements for, DOM than do obligately feeding larvae or obligately nonfeeding larvae. What is clear is that facultative planktotrophs do not require exogenous particulate food in order to develop to metamorphosis: *i.e.*, they can not be starved. The level of parental investment in relative energetic terms [*s*], as defined and used in evolutionary models (*e.g.*, Vance, 1973a, see above), is equal to or greater than 1.0; hence they are lecithotrophic. However, they are not strictly nonfeeding larvae. They possess a set of characteristics that don't match the traditional patterns of feeding and nonfeeding development. This necessitates distinguishing between the capacity to feed and the requirement for exogenous food. We follow Kempf and Todd (1989) in advocating the following definitions: feeding larvae = larvae that can capture and utilize exogenous food; nonfeeding larvae = larvae that cannot capture or utilize exogenous food; planktotrophic larvae = larvae that require exogenous food for development to metamorphosis; lecithotrophic larvae = larvae that do not require exogenous food for development to metamorphosis.

Facultative planktotrophy can be characterized as a mixture of traits from the more typical patterns of larval nutrition. The main differences between facultative planktotrophs and obligate planktotrophs are egg size and the need for exogenous food. The differences between facultative planktotrophs and obligate nonfeeding lecithotrophs are egg size and larval morphology. In facultative planktotrophs, larval morphology is very

similar to that of obligate feeding larvae and nutritional requirements are very similar to those of obligate nonfeeding larvae (Emler, 1986; Strathmann, 1987; Kempf and Hadfield, 1985; Kempf and Todd, 1989; Hart, in press). Facultative planktotrophs have been seen as intermediate between strict feeding and nonfeeding larval types because of the unusual association of these two traits. Complex feeding larval structures are not associated with the ability to develop without the need to capture food (Williams and Anderson, 1975; Amemiya and Emler, 1989), except in the few cases of facultative planktotrophy. Obligate nonfeeding larvae can not take particulate food because they lack the feeding structures necessary to create water currents, capture suspended particles, and ingest them. They have very simple larval morphology compared to feeding larvae. In facultative planktotrophs, egg size and energy content are intermediate between those typical of strictly feeding and nonfeeding larvae (*see* Emler *et al.*, 1987; McEdward and Carson, 1987; McEdward and Coulter, 1987; McEdward and Chia, 1991). This higher level of maternal investment per offspring provides sufficient nutritional reserves to fuel all of larval development and accounts for the capacity to metamorphose without feeding.

While facultative planktotrophy can be described as an intermediate pattern between planktotrophy and lecithotrophy (*i.e.*, a mixture of traits from each) it has not been clear whether it should be considered a transitional stage in the evolution from feeding to nonfeeding types of larval development. The loss of a feeding larva is thought to be an irreversible evolutionary change (Strathmann, 1978a), so that if facultative planktotrophs are to be considered transitional then they must be in the process of evolving a nonfeeding type of larval development (Kempf and Todd, 1989; Hart, in press; Wray, 1995).

To date, facultative planktotrophs have received little attention, other than to document the occurrence of this type of larval development. There are so few species known to have this type of larva that it seems to be a minor component of the ecological diversity of larvae. This interpretation is supported by the predictions from theoretical models which indicate that species with intermediate levels of maternal investment always produce fewer metamorphs for a given reproductive input (Vance, 1973a) than species with very high or very low levels of investment; intermediate species should be rare. However, even if they are rare and ecologically unimportant, facultative planktotrophs might be evolutionarily important as the transitional stages between feeding and nonfeeding types of larvae. Facultative planktotrophs might be evolutionarily short-lived, hence rare at any given time, but generated frequently and thus account for all of the transitions between larval nutritional modes (McEdward and Janies, submitted).

Recent research conducted in our laboratory has identified a number of species that have larvae with intermediate nutritional patterns. Our discoveries come from studies on echinoids, primarily clypeasteroids (*e.g.*, sand dollars) from the subtropical Atlantic and Gulf of Mexico. There had been few studies of larval feeding and nutrition on this fauna. Most echinoid larval studies have been conducted using

cold temperate species of sea urchins located in close proximity to major marine laboratories. This raises the question of whether the rarity of "intermediate" nutritional strategies is real or is an artifact of geography and taxonomy. We are finding that there is greater diversity of nutritional strategies than has been previously appreciated and we believe that these intermediate strategies might be fairly common in some taxa and/or geographic regions. If so, then, in contrast to current interpretations and predictions from life history theory, facultative planktotrophy and other intermediate nutritional patterns in larvae could potentially be important ecological strategies. In this paper, we discuss the diversity of energetic strategies in echinoid larvae, in light of their potential ecological importance and the nature of the evolutionary transition between feeding and nonfeeding larval development.

#### DIVERSITY OF ENERGETIC STRATEGIES

Our studies on subtropical echinoids (mostly clypeasteroids) have revealed a diversity of energetic strategies, and a range of egg sizes (Tab. 1). The egg sizes for these species range from 75 to 280  $\mu\text{m}$  in diameter. The eggs of *Clypeaster rosaceus* (280  $\mu\text{m}$  diam.) contain  $\approx$  10 times more energy than the eggs of *Arbacia punctulata* (75  $\mu\text{m}$  diam.) and *Lytechinus variegatus* (110  $\mu\text{m}$  diam.).

Time to the initial feeding stage is very short, only 1 to 2 days, for all of the species that we studied (Tab. 2). But for most of the clypeasteroids (*Mellita*, *Encope*, *Clypeaster*, and *Leodia*), with egg sizes from 110  $\mu\text{m}$  to 280  $\mu\text{m}$ , time to the fully developed 8-arm pluteus was much shorter (2-3 days) than for regular urchins (*Arbacia* and *Lytechinus*) with egg sizes of 75 and 110  $\mu\text{m}$  (6-8 days).

For subtropical echinoids with feeding larval development, as egg size increases, time to metamorphosis and juvenile

size decrease. Times for development to metamorphosis range from three weeks for *Arbacia punctulata* to five days for *C. rosaceus* and are inversely related to egg size. Juvenile sizes range from 680  $\mu\text{m}$  in diameter for *A. punctulata* to 260  $\mu\text{m}$  diameter for *C. rosaceus* and again, are inversely related to egg size (Tab. 1). It is important to note that the time to metamorphosis and juvenile size data from previous studies differed substantially from ours (*Arbacia* [Harvey, 1956], *Lytechinus* [Mazur and Miller, 1971], *Clypeaster subdepressus* [Emler, 1986]). These studies were carried out under various temperature and culturing regimes, used different species and combinations of food organisms, and probably lacked a common determinant for timing of the induction of metamorphosis. A common set of temperature, feeding, and culturing conditions (Tab. 1), in combination with consistent criteria and methods for the induction of metamorphosis allow us to more reliably compare growth and development in these eight species of echinoids.

Larvae of species with larger eggs (*Clypeaster subdepressus*, *C. rosaceus*, *Encope michelini*, *E. aberrans*, and *Leodia sexiesperforata*) are less dependent on exogenous particulate food. In species with larger eggs, later stages of larval development can be reached without feeding (Tab. 1). The developmental stage which can be reached without exogenous feeding ranges from the 4-arm pluteus for *Arbacia punctulata* and *Lytechinus variegatus*, to the 6-arm stage for *Mellita quinquesperforata*, to the 8-arm stage for subtropical clypeasteroid larvae with egg sizes at or exceeding 150  $\mu\text{m}$  (e.g., *L. sexiesperforata*, *C. subdepressus*), and finally to the formation of a competent juvenile rudiment in *C. rosaceus*. However, all of these species except *C. rosaceus* (280  $\mu\text{m}$ ), require particulate food to build the juvenile rudiment and metamorphose.

The development of species with feeding larvae has been divided into two sequential stages: prefeeding and feeding (Vance, 1973a; Strathmann, 1985; Havenhand, 1995). The division between the prefeeding and feeding stages is

Table 1

Degree of dependence on exogenous food among echinoid larvae. Egg size, energy contents: (a) Turner and Lawrence, 1979; (b) Emler, 1986. Juvenile size: test diameter (without spines). Culture conditions: temperature = 27 °C; food = *Dunaliella tertiolecta*; 8 cells  $\mu\text{m}^{-1}$ ; \* = not fed.

Degree of Dependence on Exogenous Food among Echinoid Larvae						
Species	Egg Size $\mu\text{m}$ (joules)	Development without Food	Time to Metamorphosis with Food (d)	Juvenile Size $\mu\text{m}$	References	
<i>Arbacia punctulata</i>	75(1.14x10 <sup>-3</sup> ) <sup>a</sup>	4-pl	20-21	680	Herrera & Williams (unpub.)	
<i>Lytechinus variegatus</i>	110(3.56x10 <sup>-3</sup> ) <sup>a</sup>	4-pl	10-12	485	Herrera & McEdward (unpub.)	
<i>Mellita quinquesperforata</i>	110	6-pl	5-7	350	McWeeney (unpub.) McEdward & George (unpub.) Herrera (unpub.)	
<i>Clypeaster subdepressus</i>	150	8-pl	11	295	Herrera (unpub.)	
<i>Encope michelini</i>	170	8-pl	9	305	Herrera (unpub.) Eckert (1994)	
<i>Encope aberrans</i>	190(4.01x10 <sup>-3</sup> )	8-pl	5-7	280	Herrera (unpub.) Herrera & Niciu (unpub.)	
<i>Leodia sexiesperforata</i>	208	8-pl	6-7	260	Herrera (unpub.)	
<i>Clypeaster rosaceus</i>	280(2.06x10 <sup>-2</sup> ) <sup>b</sup>	juvenile	5-7*	290*	Herrera (unpub.)	

Table 2

Time to various developmental stages in echinoid larvae. Culture conditions: temperature = 27 °C; food = *Dunaliella tertiolecta*; 8 cells  $\mu\text{l}^{-1}$ ; \* = not fed.

Time to Various Developmental Stages in Echinoid Larvae				
Species	Egg Size $\mu\text{m}$	Time to Feeding Stage 4-pl (d)	Time to 8-pl (d)	References
<i>Arbacia punctulata</i>	75	2	6-8	Herrera & Williams (unpub.)
<i>Lytechinus variegatus</i>	110	2	6	Herrera & McEdward (unpub.)
<i>Mellita quinquiesperforata</i>	110	<1	2.5	McWeeney (unpub.) McEdward & George (unpub.)
<i>Clypeaster subdepressus</i>	150	2	4	Herrera (unpub.)
<i>Encope michelini</i>	170	1	2	Herrera (unpub.)
<i>Encope aberrans</i>	190	1	2.5	Herrera (unpub.)
<i>Leodia sexiesperforata</i>	208	<1.5	2	Herrera (unpub.)
<i>Clypeaster rosaceus</i>	280	2	3	Herrera (unpub.)

marked by the onset of larval feeding activity (Fig. 1). Echinoids with planktotrophic development have a relatively short prefeeding period during which they are obligately lecithotrophic and utilize endogenous nutrient reserves from the egg to build the initial larval stage. The construction of larval feeding structures, such as ciliated bands and a digestive system, provides the offspring with the ability to process the surrounding seawater and eat suspended food particles. Lack of food results in lack of further development (addition of larval arms), lack of larval growth (increase in size or biomass), and eventually leads to deterioration and death.

Although we know of no cases in which the larva has to feed immediately upon acquiring the ability to feed, many species need to feed within a day or at most a few days of developing to the initial larval stage. Relative to the total

duration of the feeding period the onset of the ability to capture food is nearly coincident with the onset of the need to utilize exogenous food in most echinoids. In contrast, the diversity of energetic strategies that we find among subtropical echinoids involves a dissociation of the two aspects that comprise the "onset of feeding" (Fig. 2). Among all of the species with feeding larvae, the construction of the larval feeding apparatus occurs by the early 4-armed larval stage, at which time larvae can feed on exogenous food. But there is a wide range of stages at which larvae become dependent on exogenous food for further development (Fig. 2) and the degree of dependence is correlated with the amount of endogenous reserves in the egg (Tab. 1).

*Lytechinus* is an example of a species with the "typical" pattern of larval feeding that characterizes extreme obligate

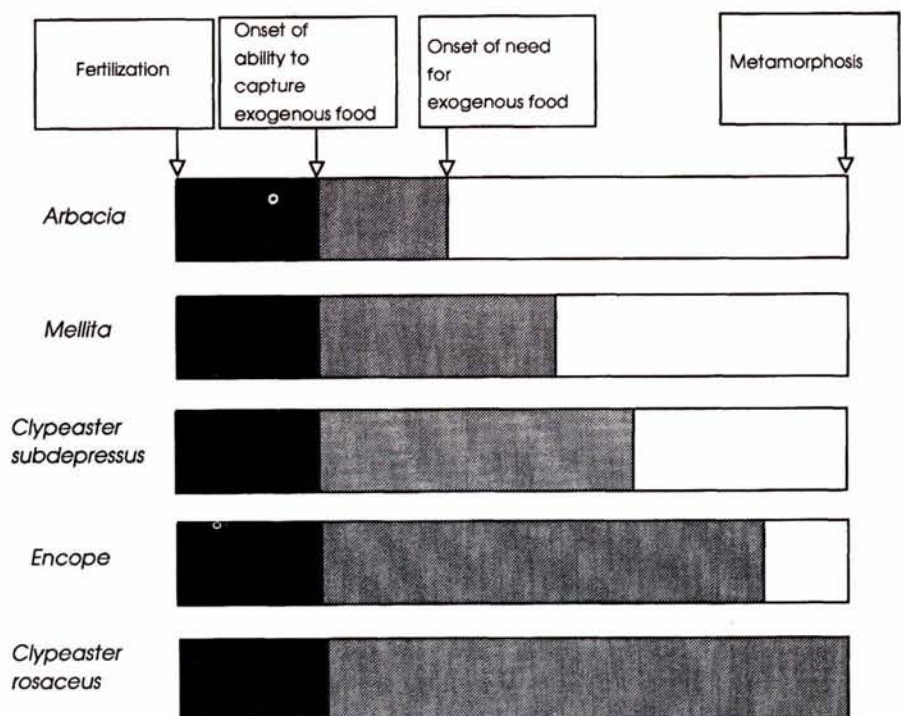


Figure 2

From the study of subtropical echinoderm species, it now appears that the feeding stage includes two critical points in time: the onset of the capacity to feed and the onset of the need to feed. The onset of the ability to feed occurs at the same stage of development but the onset of the need to feed varies dramatically from species to species.



planktotrophy, in which development does not proceed beyond the 4-armed stage unless food is available. *Mellita* can develop to the 6-armed larval stage before it needs to feed (McEdward and George, unpubl.). However, development cannot proceed beyond the 4-armed stage in this species, if the amount of endogenous reserves is reduced by half, by means of blastomere isolations (Herrera and McWeeney, in prep.). *Clypeaster subdepressus*, *Leodia sexiesperforata*, and *Encope* spp. can develop to the fully formed 8-armed larval stage in the absence of food, even though feeding structures are present and functional at the 4-armed stage (Fig. 2, Tab. 2). All of these species are obligate planktotrophs but they differ substantially in the degree of dependence on exogenous food. For example, *Encope michelini* has very limited dependence on exogenous food; approximately three days of feeding, at any time during the larval period, provides sufficient energy to complete development through metamorphosis (Eckert, 1994). *Clypeaster rosaceus* can take particulate food at the 4-armed larval stage, but can build the fully formed 8-armed larva and the juvenile rudiment as well as undergo metamorphosis without feeding on exogenous food. *C. rosaceus* acquires the capability to feed at the same stage as all other planktotrophic echinoid larvae, but never reaches a point at which it requires food (Fig. 2). It represents the extreme dissociation of the two components of the larval feeding strategy and results in a functionally lecithotrophic pattern of development. Hence, lecithotrophy and planktotrophy are ends of a continuum of energetic strategies and should not be considered as fundamentally different larval nutritional patterns.

In species with egg sizes at the lower end of the size scale, higher levels of exogenous food allow the larvae to reach metamorphosis sooner but do not appear to affect juvenile size (Herrera and McEdward, in prep.; Hart, 1995). With higher levels of exogenous food, species with larger eggs (including facultative planktotrophs) do not reach metamorphosis sooner but build a larger juvenile (Emlet, 1986; Hart, 1995). These differences in growth and development suggest that there are different responses and tradeoffs among species employing different energetic strategies, and these strategies depend on the level of maternal investment available within the egg.

We have conducted several studies manipulating (*via* blastomere separations) the level of endogenous food available to the developing larvae, and these studies reveal that reduced egg size can change the degree of larval development that can be reached with endogenous reserves alone (*Encope aberrans*, Herrera and McEdward, in prep.; *Mellita quinquesperforata*, Herrera and McWeeney, in prep.; *Dendraster excentricus*, McWeeney and McEdward, in prep.). This indicates a direct link between the level of parental investment and the degree of dependence on exogenous food.

Species with intermediate energetic strategies may provide us with some insight into how evolutionary transitions between feeding and nonfeeding development may occur. As egg size increases, a functional threshold to lecithotrophy is crossed (Fig. 2). Larvae would be ecologically lecithotrophic, but would retain larval feeding structures and the ability, but not the necessity, to feed.

The morphological differences usually noted between feeding and nonfeeding larvae would require subsequent changes in developmental mechanisms of morphogenesis (McEdward and Janies, submitted), and once complex larval feeding structures are lost, they probably can not be re-evolved (Strathmann, 1978a; McEdward and Janies, submitted). We suggest that the ecological boundary between planktotrophy and lecithotrophy is easily crossed and that unlike morphological changes, ecological transitions are readily reversible.

## DISCOVERY OF PLASTICITY

Planktotrophic echinoid larvae are thought to be food limited under most circumstances in the marine environment, due to the low and fluctuating levels of phytoplankton (Paulay *et al.*, 1985; Strathmann, 1985; but also see Olson and Olson, 1989, for a different perspective). Given that planktotrophic larvae are dependent on exogenous food, the rate of their growth and development to metamorphosis could be seriously delayed or limited when food resources are scarce. In the presence of low food concentrations, larvae can alter their morphology by increasing the length of the ciliated arms, which increases the maximum clearance rate (Boidron-Metairon, 1988; Strathmann *et al.*, 1992; Fenaux *et al.*, 1994; Hart and Strathmann, 1994). This allows them to maximize their ability to capture particulate matter. This alteration of form is referred to as phenotypic plasticity.

Phenotypic plasticity is a mechanism which enables larvae to compensate for the different food conditions in the marine environment. It increases the likelihood that larvae reach metamorphosis when food concentrations are low. The discovery of plasticity indicates an additional source of diversity in the energetics of development. We predict that plasticity is more important, but more difficult to achieve, in larvae with a high dependence on exogenous food.

Vance's models (1973a, b) assumed that egg size was correlated with feeding period, and that as egg size increases, feeding period would decrease. This correlation between egg size and feeding period raises questions about a possible correlation between egg size and the capacity for phenotypic plasticity. This relationship between egg size and plasticity is currently being examined in our laboratory. It is predicted that the capacity for plasticity (as opposed to its importance) would increase with increasing levels of maternal investment.

## CONCLUSIONS

Using species comparisons, manipulations of egg size, and defined food concentrations, we have discovered a wide range of feeding requirements among echinoid larvae. Planktotrophic larvae have varying capabilities for development in the absence of food. There is a direct link between the level of parental investment and the degree of

dependence on exogenous food. The amount of nutritional reserves provided by the parent seems to determine the degree to which the larvae require exogenous food to construct the larval body and develop to metamorphosis.

These results suggest that echinoid larvae do not fit neatly into two discrete classes of energetic strategies: 1) very small eggs, with obligate feeding and strong dependence on exogenous food and 2) very large eggs, with nonfeeding development. Rather, there exists a continuum of energetic strategies between strict planktotrophy and strict lecithotrophy that has not been previously recognized. We predict that many other examples of "intermediate" strategies will be found in a wide range of taxa (Hadfield and Switzer-Dunlap, 1984; Kohn and Perron, 1994).

Are "intermediate" strategies really intermediate? It is clear that some species (e.g., facultative planktotrophs) have a mixture of characteristics that are intermediate between those found in most obligate planktotrophs and obligate lecithotrophs. However, with respect to the range of strategies that are the subject of quantitative models (see above) facultative planktotrophs are not intermediates but instead, represent one extreme. The highest level of parental investment treated in the models is represented by an egg size ( $s = 1.0$ ) that is sufficient to support complete development to metamorphosis. All smaller eggs ( $s < 1.0$ ) can not support complete development and require some larval feeding. In the case of eggs near the upper end of the range (e.g.,  $0.9 < s < 0.99$ ), only a minor amount of larval feeding might be required to supplement egg reserves. The important point here is that an egg size of  $s = 1.0$  is just barely sufficient for lecithotrophic development. This corresponds to facultative planktotrophy more than it does obligate lecithotrophy, which is generally characterized by high levels of parental investment ( $s \gg 1.0$ ). The minimum level of parental investment that supports facultative planktotrophy establishes the threshold for lecithotrophic development. All egg sizes above the minimum ( $s > 1.0$ ) fall outside of the range of investment levels that are considered by the evolutionary models, hence the models cannot predict the reproductive efficiency that results from investment levels  $s > 1.0$ . The appropriate interpretation of the U-shaped distribution of reproductive efficiency as a function of egg size ( $s$ ) is throughout the range of strategies that represent obligate planktotrophy (with varying degrees of dependence on exogenous food) ( $0 \leq s \leq 1.0$ ) and up to the threshold for lecithotrophy ( $s = 1.0$ ). The results of the models are not consistent with the bimodal distribution of egg sizes within many taxa nor the distribution of species into the traditional categories of feeding and nonfeeding development. The empirical patterns and the theoretical results pertain to different scales of investment. The models only address a small subset of the observed range of egg sizes found among free-spawning marine invertebrates.

The observation that there are echinoids with larvae that are obligately planktotrophic but have different requirements for food as a result of different levels of parental investment leads to the conclusion that, even within planktotrophy (and up to the threshold for lecithotrophy), the distribution of egg sizes and energetic strategies are not strikingly bimodal and therefore do not

match the U-shaped distribution predicted by the theoretical models. We hope that this will stimulate fresh efforts to model the relationships between egg size, larval development, and fitness among marine invertebrates.

We are starting new experiments to investigate the effects of egg size (endogenous nutritional material) and exogenous food concentration on the growth of larvae during the larval and rudiment building phases of development. Growth is defined here as the addition of biomass to the larval body. Growth can be described in two different ways: increase in the size of the larval body (geometric growth) and accumulation of material and biochemical energy in the larval body (energetic growth). Geometric measures of growth provide information on size *per se* (i.e., volume of larval tissue and number of cells) but also have a functional interpretation. Larval size influences feeding capability (ciliated band length), swimming speed, metabolic requirements, and defense (susceptibility to predation). Energetic measures of growth indicate the accumulation of resources by the larva, and therefore provide information on food requirements and larval reserves.

Only a few studies have been conducted on echinoid larval growth but they suggest that there are interesting and potentially important effects of egg size and food. Fenaux *et al.* (1992) reported that delayed initiation of larval feeding caused a reduction in the accumulation of protein, lipid, and carbohydrate in larvae of the sea urchin *Paracentrotus lividus*. McEdward (1984) measured protein content and estimated larval tissue volume in *Dendraster excentricus*, fed excess food. Larvae grew substantially (protein: 7.5-fold; metabolic activity: 29-fold) during development, but the majority of the growth occurred in the later larval stages with formation of the juvenile rudiment. In most life history studies, only larval length and juvenile diameter are reported. These measures are insufficient for functional interpretations of size or analysis of the energetics of growth. Better information is needed to elucidate the consequences of differing levels of parental investment and food concentration for larvae, thereby allowing empirical tests of life history theory.

We see three areas of particular importance in the study of larval growth for understanding the evolution of energetic strategies. First, it would be useful to distinguish between the factors that influence growth of the larval body and the juvenile body and to elucidate the extent to which these components of development can be uncoupled. The effect of changes in egg size on larvae vs. juveniles might be quite different in planktotrophs with relatively large eggs compared to planktotrophs with very small eggs. In species with a minimal dependence on exogenous food the rate of development is potentially limited by the processes of differentiation and morphogenesis, rather than by the rates of energy acquisition. For example: Species with large eggs might possess sufficient material and energy to construct a full-size feeding larva at the usual rate, even after a substantial reduction in egg size. The effect of reduced egg size would then be limited to the rate of juvenile development or the size of the juvenile at metamorphosis. In contrast, planktotrophs with very small eggs might be forced to construct smaller early stage

larvae requiring a substantial increase in the duration of larval development. In this case, the effect on juvenile size or rate of rudiment development might be negligible. Second, it is important to determine if larval (and juvenile rudiment) growth is affected in the same way by changes in endogenous nutritional reserves as by changes in the availability of exogenous food. Heterochronic shifts in development of the larval body versus the juvenile rudiment that have been observed under conditions of high exogenous food concentrations have led to the suggestion that the inherent compensatory growth responses of larvae (morphological plasticity), might underlie the evolutionary loss of feeding structures in lecithotrophs that are associated with the evolution of very large eggs (Strathmann *et al.*, 1992). Third, we believe that a clearer understanding of plasticity in larval morphology and development requires knowledge of the energetic causes, costs, and benefits of how larvae grow.

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