

Consequences of larval feeding environment for settlement and metamorphosis of a temperate echinoderm

Planktotrophy
Juvenile
Larvae
Metamorphosis
Settlement

Planktotrophie
Juvénile
Larve
Métamorphose
Fixation

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ABSTRACT

Relationships between phytoplankton biomass and recruitment strength of benthic invertebrates with feeding larvae have been considered only in the numerical sense, not in terms of the condition of individuals at settlement. Since material and energy in some larval structures is transformed at metamorphosis into post-larval structures, and since their development is food-dependent, we hypothesized that plankton food availability links the ecology of the transition between invertebrate larvae and juveniles. We tested this hypothesis in laboratory and field experiments with the sea star *Asterina miniata*. Sibling larvae were reared in sea water containing natural phytoplankton at three concentrations simulating either (1) oligotrophic offshore, (2) temperate nearshore, or (3) eutrophic bloom water masses. Other siblings were reared in mesh-covered field chambers with naturally varying nearshore plankton assemblages. Competent larvae were produced in all food conditions, but exhibited differences related to feeding history. Those in oligotrophic water had small, transparent bodies and juvenile rudiments, few or no body ossicles, and small brachiolarian arms and papillae. In contrast, larvae reared at higher food levels were progressively larger, more opaque, pigmented and ossified, and had developed further. Competent larvae differed in swimming and substrate searching behaviors and the times to complete settlement and metamorphosis were inversely related to larval food abundance. The preferred type and orientation of substrates settled on by larvae also appeared to be related to larval feeding history, as did initial juvenile size and appearance. Differences in larval food availability appear to have a strong influence on the ecological and life history transitions occurring before, at, and after settlement and metamorphosis.

RÉSUMÉ

Effets des facteurs de l'environnement sur la nutrition larvaire, la fixation et la métamorphose d'un échinoderme de région tempérée.

Les relations entre la biomasse du phytoplancton et l'importance du recrutement des invertébrés benthiques à larves nourries ont fait l'objet d'études consacrées uniquement à l'importance numérique des recrues et non à leur état au moment de la fixation. L'énergie des structures larvaires qui, à la métamorphose, se transforment en structures post-larvaires, dépend de la nourriture que les larves ont

eue. Nous avons suggéré que l'écologie du passage au stade juvénile est liée à la disponibilité de la nourriture au cours de la vie larvaire. Cette hypothèse a été contrôlée sur l'étoile *Asterina miniata* au cours d'expériences en laboratoire et sur le terrain. Des larves jumelles ont été cultivées dans des eaux de mer dont la concentration en phytoplancton naturel simulait (1) le milieu oligotrophe de haute mer, (2) les régions côtières tempérées, (3) les explosions eutrophes des masses océaniques. D'autres larves jumelles ont été élevées en mer dans des chambres en tissu à mailles fines installées dans différents milieux planctoniques côtiers. Dans tous les cas, des larves viables ont été produites, mais les résultats varient avec les conditions d'élevage. En eau oligotrophe, le corps des larves est transparent et de petite taille; les rudiments ont peu ou pas d'osselets, ils ont des papilles et des bras brachiolaires réduits. Les larves cultivées dans les eaux eutrophes sont de plus grandes tailles, plus opaques, plus pigmentées et mieux ossifiées; elles ont un développement plus rapide. La nage des larves et leur façon de rechercher le substrat sont différentes. Le temps nécessaire pour que la fixation soit effective et pour que la métamorphose s'achève est inversement proportionnel à l'abondance de nourriture. Le choix du type de substrat sur lequel la larve se fixe et son orientation semblent aussi dépendre de l'alimentation larvaire, de la taille et de l'aspect initial des juvéniles. Les différences dans la nourriture des larves semblent avoir un effet marqué sur l'écologie et l'histoire naturelle des transitions avant, pendant et après la fixation et la métamorphose.

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INTRODUCTION

Many marine benthic invertebrates have complex life histories which include a catastrophic metamorphosis, usually accompanied by a habitat shift from a terminal planktonic larval stage to a settled microscopic benthic juvenile that grows into a macroscopic, reproductive adult (Thorson, 1950; Pearse *et al.*, 1987; Werner, 1988). Understanding of the stage-specific processes affecting larvae in suspension, at settlement and at metamorphosis has advanced recently (Reviews: Keough and Downes, 1982; R. Strathmann, 1987; Young and Chia, 1987; Olson and Olson, 1989; Pechenik, 1990; Rumrill, 1990; Rodriguez *et al.*, 1993). Less is known about how these processes combine to foster the successful transition of life stages from plankton to benthos in many taxa. In particular, little or nothing is known about how processes during larval life affect later transitional and early post-settlement juvenile phases, or how these, in turn, affect the dynamics of benthic recruitment cohorts and adult populations. The chronology and interplay of environmental factors acting on successive early life stages of marine invertebrates is modulated by intrinsic and extrinsic processes acting before, at, or after settlement and metamorphosis. Transitional processes primarily intrinsic to the settling or metamorphosing stages of an organism often occur simultaneously at several levels of organization. For example, in response to environmental factors prior to and during settlement and metamorphosis, intrinsic processes may include integration of neural and biochemical cues, ontogenetic changes in behavior, various means of attachment to the bottom, and the often remarkable structural transformations of metamorphosis (Chia and Rice, 1978; Burke, 1981, 1983, 1984; Wald, 1981; Hadfield, 1986; Morse, 1990; Rodriguez *et al.*, 1993).

Other transitional processes exert mainly extrinsic influences on the settling or metamorphosing animal, yet occur close in time and space to settlement itself. The probability that a larva next to the bottom will settle in a given time interval and place depends on several spatially and temporally proximate environmental conditions. Such biotic and abiotic environmental conditions include hydrodynamics at or near the benthic boundary layer (Crisp, 1955; Eckman, 1983; Sebens, 1983; Nowell and Jumars, 1984; Jackson, 1986; Butman, 1987; Butman *et al.*, 1988), the concentration of a chemical cue(s) in the near-bottom water or on the benthic surface (Crisp and Barnes, 1954; Crisp, 1974, 1984; Morse *et al.*, 1980; Raimondi, 1988; Roberts *et al.*, 1991), the composition, microtopography or rugosity, exposure, and other physical properties of the substrate (Wilson, 1951; Young and Chia, 1984; Wetthey, 1986), variation in the type or percent cover of biota, settlement habitat patch size, and the abundance of con- and hetero-specifics, whose activities as potential facilitators, disturbance agents, competitors or predators may increase or lower post-settlement survival (Dayton, 1971; Day, 1975; Grosberg, 1981; Yoshioka, 1982; Connell, 1985; Menge and Sutherland, 1987; Keough, 1989; Osman *et al.*, 1989; Hurlbut, 1991; Rodriguez *et al.*, 1993).

Still other extrinsic processes that can affect the planktonic-benthic transition occur well before settlement, perhaps reflecting an integration of environmental conditions experienced by larvae over a considerable portion of the planktonic period. In such instances settlement success will depend on the history of the larval cohort, in so far as this affects the abundance and intrinsic condition or performance of larvae, whereas only the latter can affect metamorphic success. Of the principal forces influencing larval phases in the life cycle-predation, advection and nutrition, predation on larvae and their advection from settlement habitats place solely numerical constraints on the availability or size of

settlement cohorts. In contrast, of these water column processes, only planktonic feeding environments or larval nutrition can determine the ensuing success of planktotrophic forms both quantitatively and qualitatively, by determining both the numbers of invertebrate individuals and their condition at settlement or metamorphosis. Such linkages are well known for fishes (e.g. Cushing, 1990), but less so for marine invertebrates (e.g. Qian *et al.*, 1990).

Phytoplankton abundance varies seasonally and spatially in near-shore temperate systems (e.g. Raymont, 1980; Valiela, 1984). This variation is typical in Monterey Bay, central California, where this study was done (Bolin and Abbott, 1963; Silver and Davoll, 1975, 1976, 1977; Garrison, 1976, 1979). Temporal and spatial variation in availability of planktonic food may exert differential effects on planktotrophic larvae produced in different seasons and locations. Reproductive adults of the asteroid *Asterina miniata*, the study animal, are found throughout the year (although there is often a mid-summer spawning peak) over a broad geographic and habitat range (Farmanfarmaian *et al.*, 1958; Feder, 1980; Davis, 1985; M. Strathmann, 1987; Rumrill, 1989). Hence larvae of *A. miniata*, relative to those of sympatric species, experience potentially enormous variation in food availability over several space and time scales. It follows that larvae of *A. miniata* are appropriate for tests of the effects of extreme variation in planktonic resource availability.

In this paper we postulate an oceanographically influenced linkage mediated by spatial and temporal variation in planktonic primary production, which not only influences larval development, but which is manifested beyond the larval period to affect settlement, metamorphosis and succeeding events early in benthic life. We report here an experimental test of the hypothesis that conditions reflecting planktonic food abundance for invertebrate feeding larvae exert a strong influence on success at settlement and metamorphosis. This, in turn, can affect the initial condition and subsequent long-term growth and survival of newly settled microscopic early juveniles, and ultimately, numbers recruiting to adult populations, topics discussed elsewhere (Basch, 1993).

MATERIALS AND METHODS

Obtaining larvae

Adults of *Asterina miniata* that had been recently collected from Monterey Bay were induced to spawn on 16 March 1992 by injection with approximately 3 ml of 100 M 1-methyl adenine (Sigma Chemical Co.) in distilled water. Ova from one female were fertilized with sperm from one male, and the resulting embryos and planktotrophic larvae cultured *in vitro* using standard techniques (M. Strathmann, 1987).

Substrates inducing settlement and metamorphosis

An initial experiment, using larvae fed a uniform laboratory-cultured algal diet, was done to determine the types of natural substrates that induce larval settlement and meta-

morphosis. Metamorphically competent late brachiolarians were placed in unstirred jars with unfiltered sea water and one to several small field-collected rocks covered with a primary microbial film and a variety of algae and sessile invertebrates. We used a dissecting microscope to observe the cover type and orientation (top, side or bottom; 0°, 90°, or 180°, respectively [per Barker and Nichols, 1983]) of the substrates on which newly settled larvae and metamorphosed juveniles were found (Basch, 1993).

Settlement experiments with larvae in simulated field feeding conditions

Full siblings from the March 1992 larval cohort were compared in tests of the effects of different planktonic food conditions on larval development, settlement and metamorphosis. Larvae were reared in the laboratory as above until they started feeding, and were then raised in one of three simulated water column feeding conditions, or in the field, rather than on a single uniform diet.

Larval feeding conditions — simulations of water column primary production regimes

Laboratory rearing

Early bipinnaria larvae were transferred to 2.5 l clear, tightly sealed polycarbonate bottles filled with sea water. Initial larval density was 0.2 /ml. The three feeding conditions had chlorophyll *a* and particle concentrations (measured using methods of Parsons *et al.*, 1984) which were (1) equivalent to ambient coastal phytoplankton standing stocks, (2) one-half that of coastal standing stocks, and (3) more than double that of coastal phytoplankton concentrations. Measured phytoplankton abundances spanned the range of spatial and temporal variation in planktonic primary production characteristic of central California shelf waters where larvae of *Asterina miniata* are dispersed (see Silver and Davoll, 1975, 1976, 1977; Garrison, 1976, 1979; picoplankton and DOM in suspension were not considered, since other experiments demonstrated that *A. miniata* larvae do not develop or survive on these rations [Basch, 1993]). Phytoplankton concentrations for each treatment were established as follows. (1) Temperate spring coastal surface sea water (= "Near-Natural Sea Water" [NSW] treatment; based on mean chlorophyll *a* values from a nearby coastal hydrographic station over three years [Silver and Davoll, 1975, 1976, 1977]) was obtained by collecting fresh sea water directly from the shore and immediately filtering it through a 64 µm Nitex mesh. This removed (a) particles larger than the size range that larvae feed on (ca. 5-70 µm [Chia and Walker, 1991]), and (b) competing herbivorous and predatory metazoan zooplankton. (2) Oligotrophic water (= "oligotrophic" or «reduced» food ration treatment), based on chlorophyll *a* values from an oceanic mid-Bay station, was produced by taking water as in (1), and diluting it by one-half with sea water freshly filtered through 5.0 µm, 1.0 µm, and 0.2 µm Nucleopore cartridge filters in series, to a particle concentration 50 % that of NSW. (3) Eutrophic (= "eutrophic" or "enhanced" treatment) bloom or strong upwelling water

(Garrison, 1976, 1979) was simulated by taking water as in (1) and adding a total of 5×10^3 cells/ml of a 1:1 mixture of two cultured algal species, *Dunaliella tertiolecta* and *Rhodomonas* sp. (Cultured algae were added because it was impractical to create large volumes of highly concentrated natural phytoplankton by reverse filtration.). Each treatment had ten bottle replicates that were placed on a revolving (ca. 4 rpm) plankton wheel and bathed in a tank with running sea water to ensure uniform temperatures and agitation. All bottles were observed every 24 to 48 hours, and more frequently (at < 24 hour intervals) after brachiolaria appeared.

Field rearing

To simultaneously compare development rates to competence and metamorphosis in the laboratory and field, sibling larvae to those used in the laboratory treatments were reared in screened field cages (one liter volume, 64 μ m mesh size; $n = 4$) in naturally varying sea water conditions like those in the laboratory NSW treatment (above). Cages were deployed nearshore at 2-3 m depth at one field site, checked daily and changed every 1-2 d (with few exceptions). Chlorophyll *a* concentrations and particle densities within cages did not change significantly over 2 d periods; these values were indistinguishable from ones taken just outside of cages and in the NSW laboratory treatment, based on duplicate samples taken during three days that spanned the larval development period (see Basch, 1993, for detailed methods).

Development rates to first competence and metamorphosis

The first instance when brachiolaria larvae became competent to metamorphose (indicated by temporary adhesion of non-metamorphosing larvae to container surfaces), and the first complete metamorphosis (indicated by firm adhesion of fully metamorphosed juveniles), were noted in each of the four treatments. Treatments ended when three or more of their replicates each contained several (about 10-25) recently metamorphosed juveniles. At these times, the number of larvae and newly settled juveniles remaining in each replicate were counted to estimate survival (presettlement, and to metamorphosis, respectively. Stage of morphological differentiation of larvae was also noted for randomly sampled individuals; most were metamorphically competent late brachiolaria).

Substrate preference and settlement time

When competent brachiolaria larvae from the March 1992 cohort were present in all three laboratory treatments, we haphazardly subsampled three larvae from each replicate, pooled animals within treatments, then randomly assigned larvae to three small clear plastic bowls ($n = 10$ /bowl) per treatment (9 bowls total). All bowls were incubated in a sea table with running sea water. Each bowl contained a set of substrates similar to those that induced larval settlement and metamorphosis in the substrate induction experi-

ment (above). These were: (1) a small rock covered with microbial film, (2) another small rock encrusted with red coralline algae, (3) sprigs of erect coralline (*Bossiella* sp.) and (4) foliose (*Pterocladia* sp.) red algae, (5) an empty mussel shell with small epizoic barnacles, and (6) the surface of the bowl itself. Each bowl was checked daily over eight days. The numbers of swimming, non-settled late brachiolaria and recently metamorphosed juveniles were counted daily in each treatment. Larval swimming behaviors or settlement substrates and orientations were noted in each bowl as in the substrate induction experiment (above). Mean time to settlement was calculated for larvae from each feeding history, on each substrate type and orientation. Several bowls were upset and some of their contents were disturbed or lost when the sea table flooded due to a mechanical disruption during the evening of the seventh day. Some non-settled larvae were lost. These were presumably either still in suspension or not firmly attached to substrates, and were included as non-settled larvae in calculations. Other non-settled larvae were recovered at the end of the experiment and their appearance and swimming behavior noted.

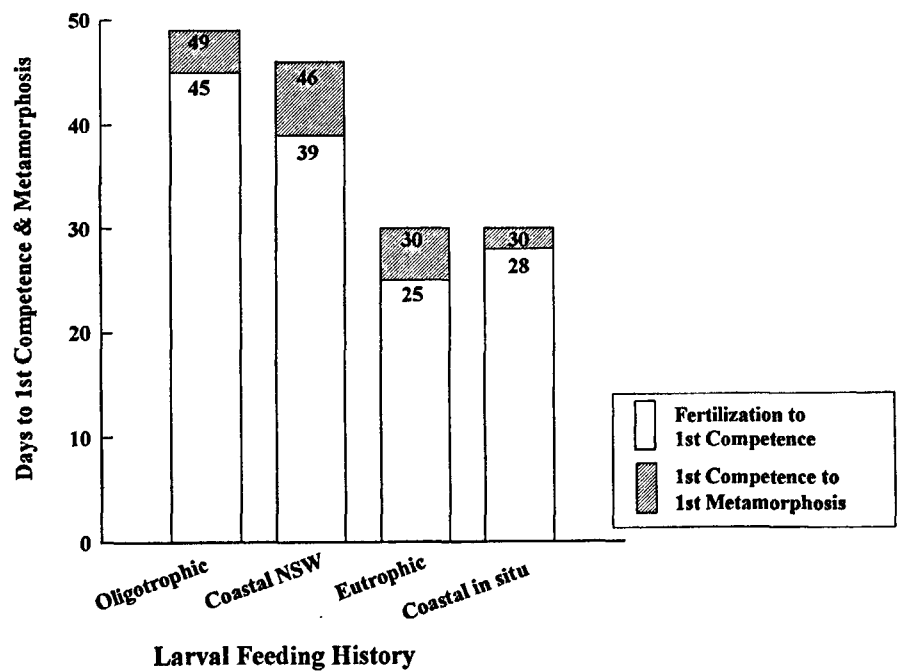
RESULTS

Larval development rates to competence and metamorphosis

The more abundant the phytoplankton, the earlier sibling larvae were first able to undergo metamorphosis (Fig. 1). The first larvae to become competent were those in the eutrophic condition, followed three days later by their siblings in the field. The first competent larvae were observed in the next two or three weeks in the NSW and oligotrophic conditions, respectively (Fig. 1). The first fully metamorphosed juveniles were observed 30 days after fertilization in both the eutrophic and field conditions, followed 16 and 19 days later in the coastal NSW and oligotrophic treatments, respectively (Fig. 1). Our observations suggest that the interval between settlement and metamorphosis was inversely related to larval feeding history: time from initiation (first non-reversible contraction of the larval body) to completion (functional juvenile) of metamorphosis was protracted for larvae that had fed in oligotrophic water. Larvae that had fed in coastal NSW metamorphosed at an intermediate rate, while those given eutrophic food levels metamorphosed most rapidly. During the experiment there was a distinct, rapid increase in planktonic primary production at the field site, as the prevailing typical coastal condition developed into a eutrophic bloom. Water column clarity decreased markedly during this event. Meanwhile average chlorophyll *a* levels increased by an order of magnitude over the period from 10 April through 15, 17 and 24 April 1992, while phaeophytin levels stayed fairly constant. Shortly thereafter, large schools of phytoplanktivorous anchovies and piscivorous sea birds moved into the area (Basch, 1993). The first competent brachiolaria appeared in field chambers a few days after the bloom began and metamorphosed within two days (Fig. 1).

Figure 1

Days to first competence and first metamorphosis of larvae with contrasting feeding histories.



Food levels experienced by larvae had a marked effect beyond that on age at first metamorphosis. Brachiolarians from each of the three lab treatments had initially somewhat staggered development rates; larvae also differed in appearance. The larvae from the enhanced treatment were all at a more advanced developmental stage and were more opaque and yellow (perhaps indicating greater lipid content, see Discussion) than siblings in NSW, which were virtually indistinguishable from their field-reared siblings. These, in turn, were more advanced in development and more pigmented than the translucent and colorless larvae in the oligotrophic treatment. Within 24 hours after exposure to coralline algae, many larvae in the eutrophic condition had metamorphosed, several in coastal NSW had begun to metamorphose, and all oligotrophic larvae were still unattached and swimming. Four days later all larvae in the eutrophic and nearly all in the NSW treatment had completed metamorphosis, while only one oligotrophic larva had begun to metamorphose. After eight days all juveniles from larvae with eutrophic and NSW food levels were similar in size, but those reared with eutrophic food retained their yellow coloration, while the juveniles from larvae with NSW as food were translucent white. The juvenile produced in the oligotrophic food condition was considerably smaller, translucent and colorless. The other animals remaining in this condition were swimming, transparent late brachiolarians, with no visible indication of possible lipid stores.

Effect of larval feeding history on settlement and metamorphosis

Overall proportion of metamorphosed animals as a function of feeding history

More newly metamorphosed settlers were recovered from the coastal NSW (53 %) than the oligotrophic (23.3 %) or eutrophic (40 %) conditions (Fig. 2).

However, the actual percentage of settlers produced in the eutrophic condition was probably considerably greater (estimated 70 %), since approximately one-half of the wet weight of erect coralline algae, on which settlement was highest in this treatment (Fig. 5), was lost due to disturbance (see Methods). If the settlement estimate for the eutrophic condition is accurate, this

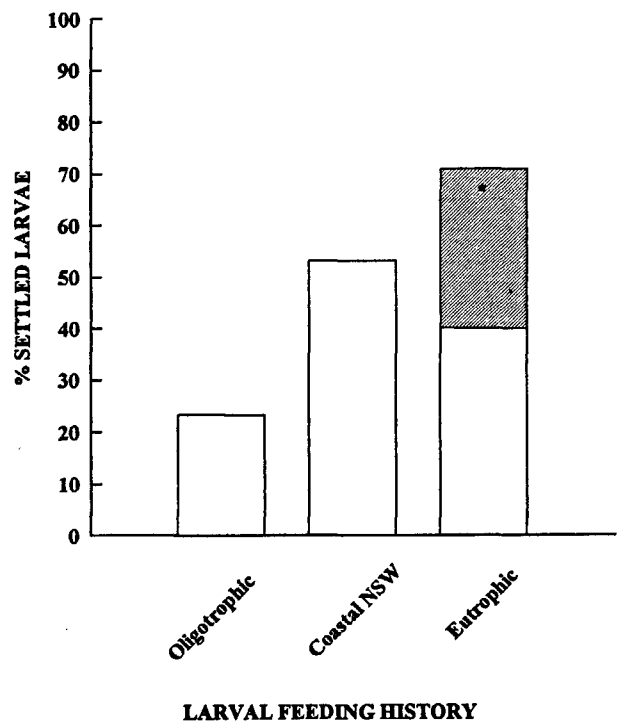


Figure 2

Percent of larvae with contrasting feeding histories that settled after eight days. All substrate types and orientations pooled. $N = 30$ larvae per treatment at beginning of experiment. White bars represent actual values. Actual percent for eutrophic condition is underestimated due to loss of samples (see text). * Expected percent for eutrophic is represented by hatched bar.

suggests that overall settlement and metamorphosis success is directly proportional to available food and time to first competence for preceding larval stages.

Settlement time as a function of feeding history

Planktonic food availability had an overall strong inverse relationship with time to settlement of competent brachiolarians exposed to settlement inducing substrates (Fig. 3). Fewer settlers from the oligotrophic condition were found on substrates after eight days, indicating that a considerably smaller proportion of these larvae had settled and undergone metamorphosis up to that time, relative to siblings given more food as larvae (Figs. 2, 5). Daily checks for recently settled juveniles from all feeding conditions indicated that most animals in coastal natural sea water and eutrophic conditions had settled within < 1-2.5 d after exposure to the substrates, while only one larva in oligotrophic water had just started to settle after four days (Figs. 3, 4).

For larvae in a given food condition, there was no apparent pattern in time to settlement on different substrate orientations, regardless of type (Fig. 4).

Settlement and metamorphosis on different substrate types

Larvae from the initial experiment settled on substrates covered with microbial films (bacteria, diatoms, and other benthic microalgae) as well as crustose (*Lithothamnium* sp. and *Lithophyllum* sp.) and articulated (*Bossiella* sp.) coralline algae and bivalve shells (*Mytilus* sp.). No larvae settled on other algal or invertebrate covered substrates (Basch, 1993).

Most (71.4 %) brachiolaria larvae from all laboratory feeding conditions that settled and metamorphosed did so more on the undersurfaces of erect coralline algal turf or on rocks with encrusting corallines than other substrates (Figs. 5, 6). These algal types, including

Bossiella sp., are known to provide a cue for settlement and metamorphosis for many invertebrate larvae (Morse *et al.*, 1979; Rodriguez *et al.*, 1993). Larvae that had fed on plankton levels characteristic of oligotrophic conditions settled fairly uniformly on the five available settlement substrates. Of those from the oligotrophic condition that settled and metamorphosed (23.3 %), many (28.5 %) settled on both erect and crustose coralline algae (Fig. 5). A similar percentage were on the plastic bowl itself, while half as many settled on a microbial film-covered rock, suggesting that these poorly nourished larvae had little ability to discriminate among substrate types. Larvae fed the coastal NSW ration showed substrate affinities intermediate to those of siblings in the oligotrophic and eutrophic conditions. More animals from NSW settled and metamorphosed on erect than crustose corallines, and these substrates were preferred over all others (Fig. 5). Larvae from the eutrophic condition had the most pronounced settlement pattern. Like siblings in the other food conditions, animals that fed in eutrophic water settled more on coralline algae, preferring erect over crustose forms. Few settled on non-coralline surfaces and none were seen on the plastic bowl (Fig. 5). This overall pattern suggests that larvae developing in planktonic conditions with more available food have a greater ability to discriminate among substrate types.

Settlement and metamorphosis on different substrate orientations

Most brachiolarians settled and metamorphosed on the undersurfaces of substrates; larvae from the eutrophic and coastal NSW conditions did so predominantly (Fig. 6). Eutrophic animals also settled somewhat (42 %) on sides of substrates; none were found on top surfaces. Most (75 %) coastal NSW animals were on the undersides of substrates; some (19 %) occurred on sides and only one was found on the top of the erect coralline alga. In contrast, most (57 %) oligotrophic animals were found on exposed tops or sides of substrates (Fig. 6).

Postsettlement

In all treatments, once settled, most animals moved very little, and very few moved from their initial settlement substrate cover or orientation within the first week of benthic life. At times 2-5 juveniles were found aggregated. Qualitative observations made on brachiolarians and early juveniles from this experiment and others support these results.

Regardless of the conditions experienced by larvae, juveniles were found most frequently on coralline algae. Progressively fewer were on microbial or diatom films, within rock crevices, on mussel shells, plastic or foliose red algae. There was no indication of juvenile feeding during the first 7-10 days postsettlement. Thereafter, putative feeding scars were seen adjacent to some juveniles from the NSW and eutrophic conditions, but none in the oligotrophic condition. Scars were found on several cover types. Scars on corallines usually appeared as small,

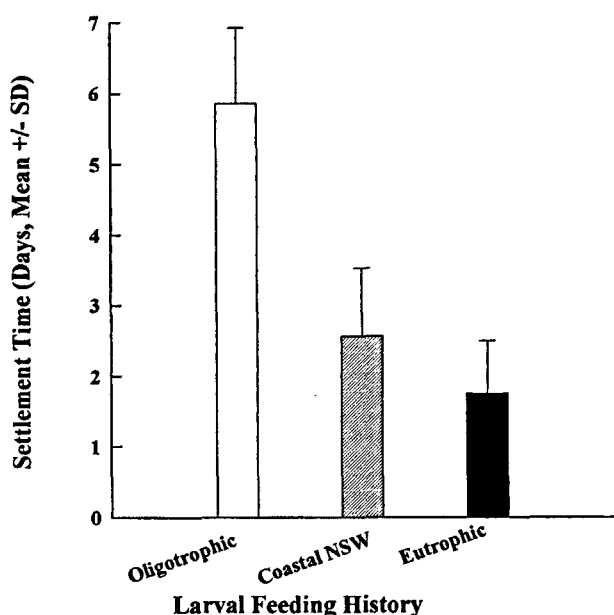
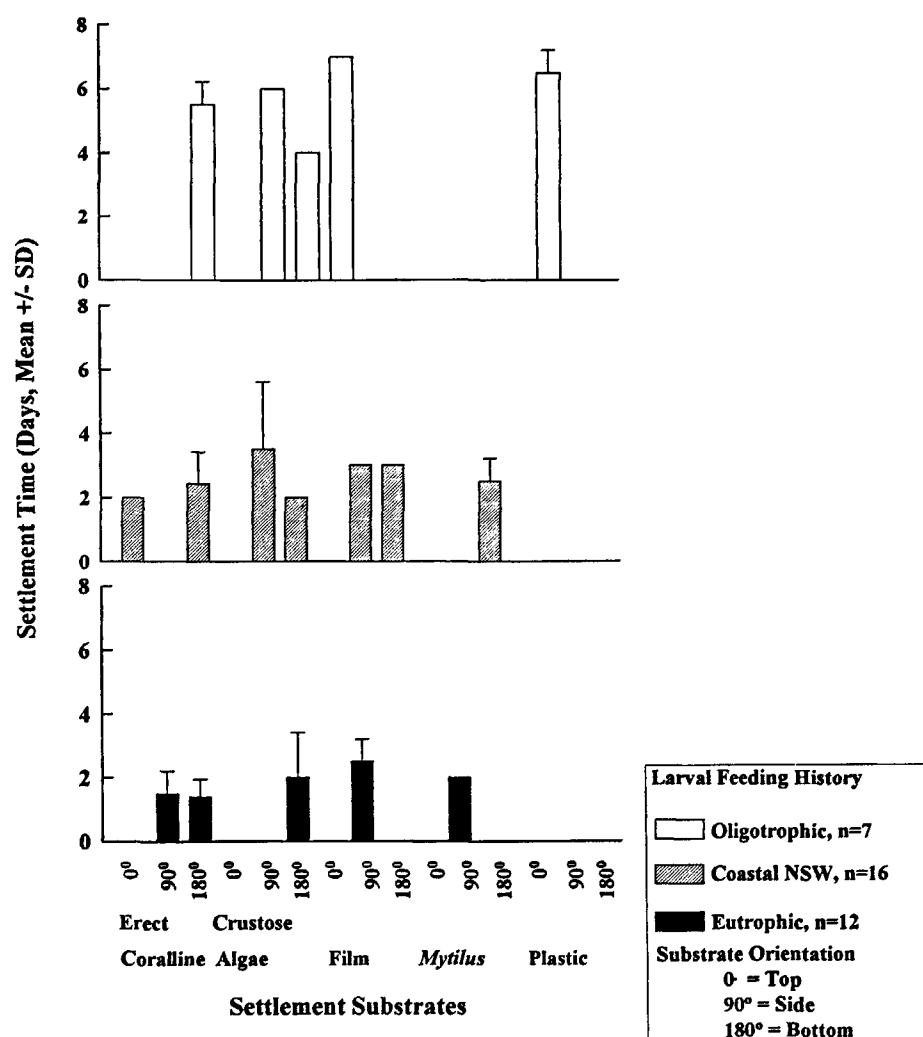


Figure 3

Settlement time (after exposure to substrates) of larvae with contrasting feeding histories.

Figure 4

Time to settlement of larvae with contrasting feeding histories on different substrate types and orientations.



slightly bleached or necrotic patches, but were sometimes completely bleached or slightly pitted. Scars on microbial/diatom films looked like randomly oriented grazing tracks that sometimes crossed over other, similar tracks. No scars were seen on several substrates without juveniles. These observations suggest that for larvae experiencing lower food levels in the plankton, resulting early juveniles have a reduced initial feeding ability on the benthos. Moreover, they suggest that early juveniles of *Asterina miniata* do not feed much on "solid" food, especially animal prey, during early benthic life. Other, longer term postsettlement consequences of larval feeding history are considered elsewhere (Basch, 1993, in prep.).

DISCUSSION AND CONCLUSION

Recruitment has been described as having three principal components: (1) larval supply, (2) settlement, and (3) survival and growth of newly settled juveniles to visible recruits (Cameron and Schroeter, 1980). Larval supply (1) is simply the number of competent larvae that come in contact with suitable settlement habitat. Larval mortality

may reduce supply by over 99 % during the preceding planktonic period (Thorson, 1946; Mileikovsky, 1971; Vance, 1973; Rumrill, 1990). Planktonic predation, offshore advection, and poor nutrition all can substantially reduce numbers of larvae available for settlement (Thorson, 1946; Cameron and Rumrill, 1982; Young and Chia, 1982, 1987; Ebert and Russell, 1988; Olson and Olson, 1989; Rumrill, 1990; Farrell *et al.*, 1991; Basch, 1993; Sewell and Watson, 1993). Settlement (2) is the transition from the pelagic larval to the benthic juvenile stage, and involves attachment to suitable substrate and metamorphosis. The microscopic newly settled juveniles must (3) survive the habitat transition and the risks associated with early benthic life (*e.g.* Highsmith, 1982; Oliver *et al.*, 1982) and grow large enough to be seen and included in naked-eye counts of recruitment cohorts (Ebert, 1983).

A fourth, seldom assessed factor with potential direct effects on both settlement and recruitment of marine invertebrates with benthic adults is not simply the available number or supply of invertebrate larvae at settlement, but the condition of these larvae. Is the survival and growth of juveniles resulting from the one percent or so of larvae that might survive to settle and metamorphose partly determined by the intrinsic condition of surviving larvae and tran-

sitional stages? This study asked: Could particular environmental conditions that larvae are exposed to in the plankton qualitatively affect events at settlement and metamorphosis? We found that availability of food for planktotrophic larvae may affect pelagic development rates and processes (as seen by others, e.g. Qian and Chia, 1993), as well as many events around settlement and metamorphosis (this study), and later, the survival and growth of benthic juveniles (Basch, 1993).

Effects of planktonic primary production regime:

Larval growth & differentiation

In other experiments with *Asterina miniata* (Basch, 1993) larval development (change in total body length, biomass, juvenile rudiment diameter, and morphological differentiation) was strongly correlated with planktonic food conditions very similar to the simulations in this study. Overall, poorly fed larvae were less well developed and were smaller at metamorphosis than siblings that had fed in waters with progressively higher phytoplankton standing stocks. These findings corroborated earlier data on the importance of nutrition to planktotrophic larval development (review: Olson and Olson, 1989).

Larval development rates to competence and metamorphosis

In the present study larval food availability had a considerable effect on development time to competence for metamorphosis (see Fig. 1). Planktotrophic larvae in relatively oligotrophic water had considerably slower development rates to metamorphosis. Consequently, as proposed by Thorson (1950) and others, it is likely that their nutritionally prolonged planktonic period increases larval susceptibility to various sources of mortality in

the water column directly or indirectly related to feeding. Therefore, both the numbers and condition of larvae in low food situations that live to settlement should be reduced, relative to larvae in more phytoplankton-rich waters. Moreover, larvae that develop in low-food conditions, once competent and provided with attractive settlement substrates, take longer to settle and to complete metamorphosis than well-fed siblings. Further, once metamorphosed, juveniles from larvae that develop in low food concentrations are smaller than juveniles resulting from better fed larvae (Basch, 1993). These results are supported by other experiments in which increased phytoplankton abundance led to faster rates of larval development and settlement (Fenaux *et al.*, 1988; Strathmann *et al.*, 1992; Basch, 1993; Allison, 1994). In summary, effects of lower food availability include an increase in the precompetent period, time to settle once larvae are near suitable substrate(s), and in the interval between attachment and metamorphosis, and less success in metamorphosis.

The slow development rate of larvae in the coastal NSW simulation, relative to simultaneously field-reared siblings, suggests that some factor important for larval development in the laboratory differs in quality or magnitude—perhaps temperature, food availability, or small-scale hydrodynamic or light regimes. There were no discernible differences in temperature and food availability between the field and laboratory. Contrasting small-scale hydrodynamic or light conditions may underlie observed differences in development rates. For example, shear forces potentially affecting particle capture (Shimeta and Jumars, 1994) by larvae in closed bottles rotating on a plankton wheel may differ from forces experienced by larvae in passive flow-through chambers in the field. Differences between field and laboratory in levels of photosynthetically active radiation may also affect both the nutritional quality and growth rates of phytoplankton food.

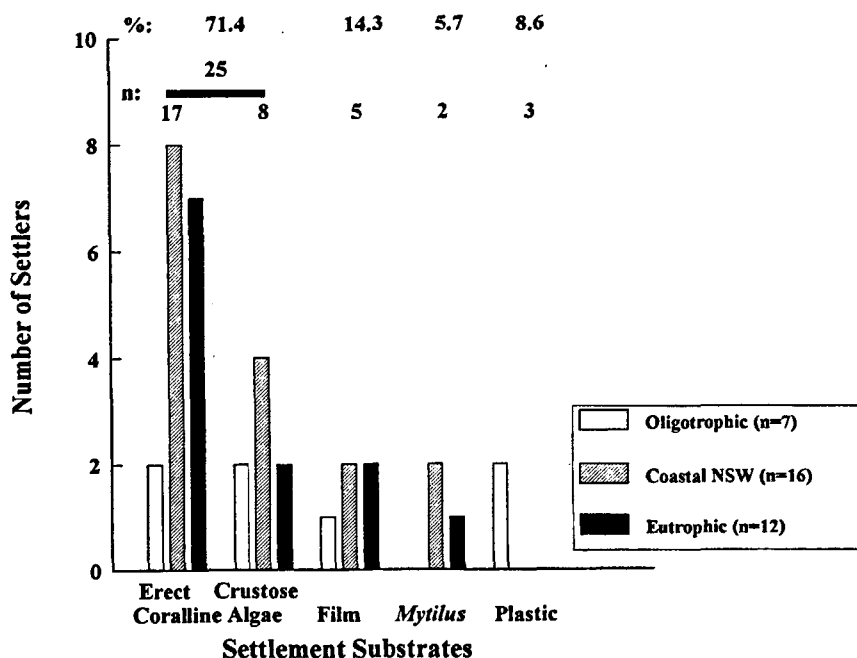


Figure 5

Cumulative settlement and metamorphosis over eight days by larvae with contrasting feeding histories. Numbers (n) (and % of total number) of larvae settled on different substrate types appear above corresponding bars.

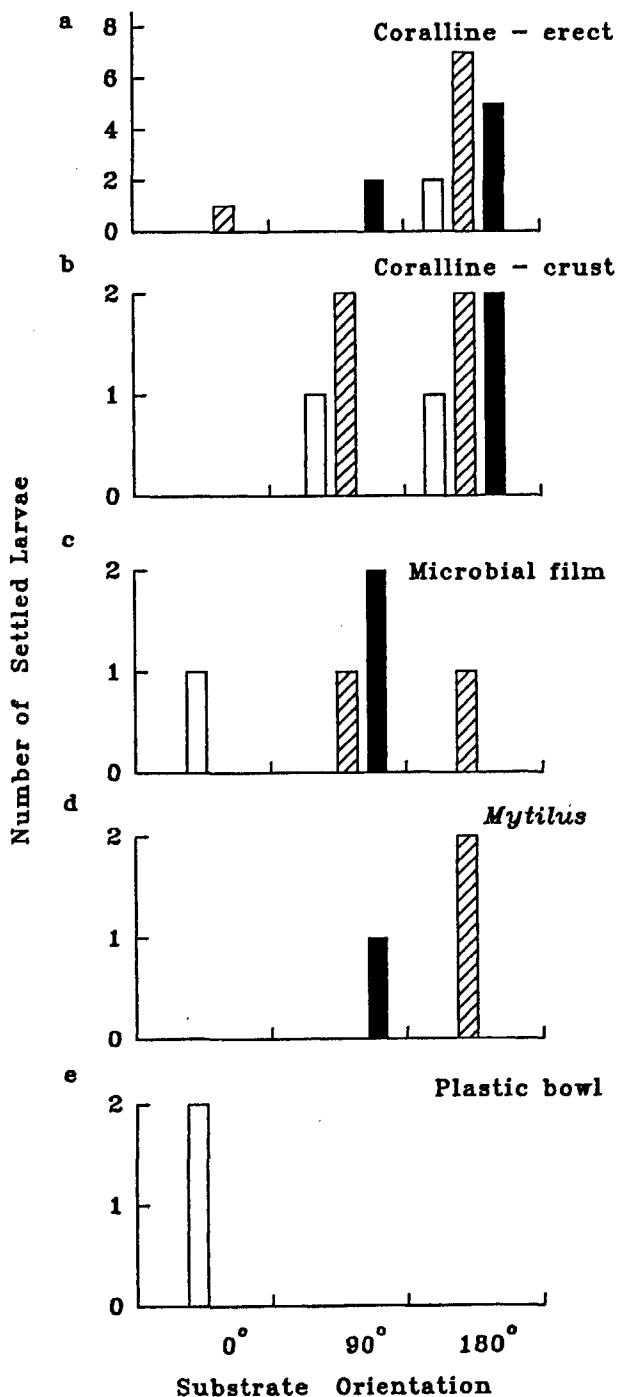


Figure 6
Larval settlement on different substrate orientations, denoted as in Figure 4.

Potential food-related mechanisms underlying patterns of settlement and metamorphosis on different substrates

Many asteroids and other echinoderms that have been studied do not appear to exhibit much settlement site specificity (Cameron and Hinegardner, 1974; Strathmann, 1978; Cameron and Schroeter, 1980; Chia *et al.*, 1984; Rowley, 1989; exception: Highsmith, 1982, for *Dendraster excentricus*). However, like early juveniles of *Acanthaster planci*, *Asterias rubens*, *Culcita novaeguineae*, *Linkia laevigata*, *Stichaster australis* and other asteroids (Henderson and

Lucas, 1971; Yamaguchi, 1973 *a, b*, Barker, 1977, 1978; Barker and Nichols, 1983, and others), *A. miniata* settle predominantly on coralline algae (both articulated and crustose forms). Like larvae of *A. rubens* (Barker and Nichols, 1983) most of those of *A. miniata* settled on the down-facing, often shaded surfaces of corallines and other substrates, but had no apparent photoresponse to different light intensities. Cameron (1981) found that brachiolaria of *Asterina miniata* (as *Patiria miniata*) settled on any bacterially filmed surface, and that they preferred shaded undersurfaces to lighted areas, though undersurfaces were not required to induce metamorphosis. He did not specify whether larvae use phototaxis to locate shaded surfaces (Cameron, 1981), but they probably do not, since other asteroid larvae examined were indifferent to light (Yamaguchi, 1973 *a*; Barker, 1977).

The settlement substrate distribution patterns observed in this study may result, in part, from observed differences in swimming and "searching" behaviors among late competent brachiolaria of *A. miniata*. Behavioral differences may be the result of contrasting larval feeding histories. In still or slowly moving water, many larvae passively settled or swam vertically down to the bottom of containers. Some individuals moving along the bottom appeared to test the suitability of the substrate(s) with sweeps of their anterior process and brachiolar arms as noted by Strathmann (1978) and others. This suggests that the anterior epithelium of the larva may be sensitive to substrate-borne chemical or tactile settlement cues. However, most larvae were oriented vertically, with their brachiolar attachment complex up. These larvae contacted the bottom with the posterior, downward-facing juvenile rudiment. Larvae moved slowly up and down above and along the bottom in this vertical orientation, sometimes searching as above, until the rudiment contacted an apparently favorable substrate. Larvae then often continued saltatory movements on and around these substrates. Many larvae contacted the undersides of settlement substrates (rocks, coralline algae, etc.) with their anterior brachiolar attachment structures on upward saltations, and attached in the characteristic manner described by Barker (1978) and Gemmill (1914, as reinterpreted by Strathmann (1978).

We did not observe attraction of settling larvae to recently settled juvenile conspecifics. But we did see recently settled juvenile cohorts on several occasions during experiments in small (2-3) and large (> 40) aggregations in the laboratory and field, respectively. It remains to be determined whether this gregariousness results from larval settlement behaviors or post-settlement juvenile migration, though the former seems more likely given the time period of our observations, the fact that there was little or no movement during the first week postsettlement (Basch, 1993), and Rumrill's (1989) calculations of movement rates for *A. miniata* juveniles.

How do the above observations relate to effects of larval feeding on transitional and postlarval life stages? Interestingly, Strathmann (1978) stated that planktotrophic forms continue feeding until the larval body is resorbed, so that lack of feeding should not limit

the time during which settling can be delayed. In field and laboratory observations of late brachiolarians of *A. miniata*, non-reversed partial contraction (and presumably resorption) of the larval body often occurred prior to attachment, and the digestive tract wall in several of these swimming individuals had begun to break down, so that ingested particles were seen moving within the body cavity outside of the digestive tract. These pre-settlement changes were seen more often in larvae from well fed conditions (which metamorphosed into normal juveniles), suggesting a limited capability for delay of settlement and metamorphosis, even in well-fed larvae. On the other hand, larvae from oligotrophic water delayed settlement and metamorphosis; indeed their feeding history may make this response obligate. Unlike well-fed competent brachiolarians, ones in oligotrophic water did not saltate. Instead they remained suspended in the water column longer and contacted the bottom less frequently, suggesting that their poor nutritional history may have prolonged their time to settlement and metamorphosis. Earlier larval stages of other asteroids were negatively geotactic and became thigmotactic as late brachiolarians (Birkeland and Lucas, 1990; Basch, pers. obs.). This suggests an ontogenetic change in behavior. Alternatively, such changes may be due simply to variation in body composition. Examples include diet-related differences in amounts of buoyant energy storage compounds or formation of negatively buoyant skeletal ossicles in the juvenile rudiment (see below). Feeding history evidently affected settlement behavior, rate and success of metamorphosis. Feeding may also have influenced aspects of larval composition and morphology related to settlement and metamorphosis. The oligotrophic larvae were very transparent. Although they apparently contained little or no positively buoyant lipid that might tend to help them float, they also had almost no negatively buoyant rudiment ossicles that could cause them to sink. Hence their specific gravity was probably closer to that of sea water. This may, in part, explain why they stayed afloat (up to at least eight days) longer than their siblings from more productive conditions. Further, their poor nutritional history may have deleteriously slowed metabolic and developmental processes. This, in turn could have delayed their ability to settle and metamorphose. When they eventually did settle, these malnourished larvae were somewhat less discriminating in their choice of settlement substrate, choosing less preferable or more exposed substrata. Similarly, Knight-Jones (1953) found decreased settlement substrate discrimination after prolonged planktonic life in a serpulid polychaete. Decreased selectivity in *A. miniata* could result if these larvae had less well developed brachiolar sensory or attachment structures and hence were less able to sense and attach to a more suitable substrate(s). Moreover, once settled, oligotrophic larvae could lack sufficient energetic reserves to fuel morphogenesis, possibly reducing metamorphic and post-metamorphic success. Birkeland *et al.* (1971) and Pechenik *et al.* (1993) observed that increased time to

metamorphosis resulted in reduced postmetamorphic success in asteroids and barnacles, respectively.

Conversely, well-fed larvae of *A. miniata* with shorter times to metamorphosis settled much earlier on coralline algae. The latter behavior may be adaptive since: (1) it suggests that better fed siblings are more capable of discriminating and firmly attaching to good settlement substrates, (2) after metamorphosis these earlier settlers developed juvenile feeding structures sooner and, (3) based on observed feeding scars, they were also able to start to feed shortly (approximately 7-10 days) after settlement on this edible substrate (Basch, 1993, this study). Barker (1977) found that all but three of the larvae of *Stichaster australis* selected the juvenile food (a crustose coralline alga) to settle on; two of the three that settled on other substrata died shortly after metamorphosis, presumably of starvation.

Animals test and select their habitats according to a complex set of rules (Meadows and Campbell, 1972). Changes in habitat selection related to an organism's physiological state have occasionally been reported and may not be unusual (*e.g.* see Allee 1913 *a, b* for isopods). Food-related changes in habitat selection shown by invertebrates may be less expected. There are several examples of the effects of adult feeding history on habitat selection by marine, aquatic and terrestrial invertebrates (review: Meadows and Campbell, 1972). However, to our knowledge, there are no previous studies relating effects of larval feeding history to selection by subsequent early life stages of transitional habitats necessary for successful settlement and metamorphosis. The present study indicates that feeding history earlier in the pelagic development period influences subsequent larval condition-development, behavior, and presumably, composition and physiology. Further, food-related condition alters larval responses to a complex set of rules as larvae sample and select settlement habitats, settle, and metamorphose into juveniles.

The specific physiological and developmental mechanism(s) that are mediated by variation in larval nutrition and that can affect subsequent settlement and metamorphosis are not entirely known. Several possible mechanisms deserve further research. For example, we need to determine if marginally-nourished larvae are deficient, either in (1) energetic reserves, or (2) essential, food-derived precursor substrate(s) or catalyst(s) for enzymatic pathways requisite for development, settlement or metamorphosis. Diet-related energy or chemical sources may include those required for digestion and assimilation of planktonic food (*e.g.* Harms *et al.*, 1991), sensory pathways to perceive environmental cues related to settlement habitat(s) (*e.g.* Burke 1983 *a, b*, 1984), catabolism of larval tissues during metamorphosis, and morphogenesis of postlarval ones. As an example of the latter, Chino *et al.* (1994) found that development and growth of the rudiment in larval echinoids depends directly on the level of thyroid hormone. This, in turn, varies with phytoplankton diet. Thyroid hormone cannot be synthesized *de novo* by larvae. These facts suggest a strong potential influence of larval nutritional history on transitional and early post-metamorphic life stages.

Postsettlement

Newly metamorphosed juveniles

Juveniles metamorphosed from larvae that had fed in relatively oligotrophic conditions were smaller, morphologically less well differentiated, and less pigmented just after settlement. It appears that larvae must feed for much of their pelagic period on plankton standing stocks that at least equal those typical of temperate coastal waters, in order to produce juveniles which are normal in size and appearance (relative to entirely field-reared sibling and heterospecific juveniles; Barker, 1979; Basch, 1993). The appearance of newly metamorphosed juveniles is also related to larval feeding. Juveniles produced from larvae in oligotrophic water had only 1-2 podial pairs per arm, were not firmly attached to substrates, and had translucent, non-pigmented and lightly calcified bodies. In contrast, juveniles from larvae that fed in phytoplankton concentrations at or above those typical of coastal waters were firmly attached to substrates by at least two pairs of podia per arm (three pairs in at least one juvenile from the eutrophic condition), and had well-calcified, opaque, pigmented bodies. The ossicles in these more robust juveniles were larger, and pigmented areas of juveniles were larger and darker in the eutrophic condition than in coastal NSW. The degree of pigmentation in juveniles was nearly identical to that seen in the stomachs of larvae that juveniles were produced from. Pigments likely indicate lipids stored in the cells of the larval stomach wall, as occurs in larval echinoids. In echinoplutei, the cells of the larval stomach dissociate during metamorphosis and subsequently redifferentiate to form the juvenile digestive tract (Chia and Burke, 1978). These larval stomach cells apparently

constitute a lipid storage organ that is not catabolized during metamorphosis, and which may supply post-metamorphic energy resources for developing juveniles (Chia and Burke, 1978; Burke, 1981).

Some ill-fed larvae may deplete energy reserves below levels necessary to initiate or complete critical physiological, biochemical and developmental events (e.g. Harms *et al.*, 1991) before or during metamorphosis. There may be other indirect maladaptive consequences of feeding on reduced phytoplankton resources, for both presettlement and transitional life stages (see above). After settlement and metamorphosis even small differences in initial juvenile energy content, morphology or other attributes could have subtle, negative effects on juvenile behavior, physiology, or growth.

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