

EFFECTS OF MATERNAL AND LARVAL NUTRITION ON GROWTH AND FORM OF PLANKTOTROPHIC LARVAE

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Abstract. Maternal nutritional stress lowers the organic content of eggs and slows the initial growth of larvae of sea urchins and bivalves. Also, larval nutritional stress changes the form and developmental sequence of larvae as an adjustment to scarce food. If effects of nutrient supplies in eggs were like those of nutrient supplies in planktonic food, then maternal nutrition would affect larval form and developmental plasticity in the same way as larval nutrition. We used natural variation in maternal habitat to test this hypothesis, using laboratory growth experiments. In the sea urchin *Strongylocentrotus droebachiensis*, mothers from greater depth (100 m) had smaller ovaries and smaller eggs than mothers from shallower depth (<6 m), which indicated poorer maternal nutrition at depth. Effects of maternal habitat, gonad size, and egg size on larval growth rate were significant but small compared to the effect of abundance of larval food. The growth of larvae was little affected by differences in maternal habitat that had a large effect on fecundity and some effect on egg size. There were no effects on larval body or juvenile rudiment that resembled the developmental plasticity in response to larval food. Food-limited mothers did not produce larvae with larger larval feeding apparatus or retarded development of juvenile rudiments. Uncoupled morphogenetic effects of endogenous and exogenous nutrients should be advantageous where benthic and planktonic food supplies vary independently. Finely tuned responses to stimuli may restrict the evolutionary consequences of developmental plasticity. Because maternal nutrition did not affect form of the larvae, larval form can be used as an index of planktonic conditions affecting feeding larvae.

Key words: developmental plasticity; echinoid; larva; maternal nutrition; maternal effect; north-east Pacific coast; pluteus; *Strongylocentrotus droebachiensis*.

INTRODUCTION

Developmental plasticity can increase survival or reproduction when there are adequate environmental cues and an appropriate developmental response (Stearns 1989). In addition to increasing fitness here and now, developmental plasticity may contribute to divergence between species and the origin of new structures (West-Eberhard 1989, Strathmann et al. 1992, Harvell 1994).

Our study focuses on developmental plasticity of larval sea urchins, with maternal and larval nutrition as environmental stimuli and with changes in larval growth and form as the response. The development of feeding larvae is influenced by both the nutrient reserves in eggs and by food that is captured during development. Maternal nutrition affects the material supplied to each egg and hence to each offspring. This leads to the question, do differences in the nutrients provided to eggs affect larval development in the same

way as differences in nutrients obtained by the feeding larva? There are at least two possible explanations for a similar developmental response to maternal and larval nutrition. One is the adaptive explanation that both sources of nutrition to offspring provide cues for the appropriate developmental response; however, we shall argue that maternal nutrition is a poor cue to the larval environment. Another is the mechanistic explanation that the two sources of nutrition, from the egg and from exogenous food, provide indistinguishable stimuli and thus have similar effects on larval development. It is the mechanistic explanation that we shall test. The answer has implications for the effect of maternal nutrition on rates of growth and development of larvae and also for the evolutionary transition from a feeding to a non-feeding larva.

Maternal nutrition can affect nutrient reserves in eggs and subsequent larval growth, even in animals with no postzygotic parental care. The effectiveness of maternal nutrition as a cue to nutritional environment of offspring differs among life histories. For many terrestrial plants, the seeds fall close to the parent tree (Okubo and Levin 1989), and for many benthic marine invertebrates, the nonfeeding larvae settle close to the

Manuscript received and accepted 13 March 1997 (originally submitted 27 February 1996).

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mother (Knowlton and Jackson 1993). In such cases, nutritional stress for the mother could indicate nutritional stress for the offspring, and that may account for cases in which inferior maternal nutrition results in greater parental investment per offspring (Qian 1994). In contrast, for many other benthic invertebrates the larvae feed during a planktonic life of long duration (Strathmann 1990) and are subject to wider dispersal (Palumbi 1995). The larval food is often entirely different from that of adults. The larvae commonly disperse more than the adults and can settle at sites distant from and dissimilar to the maternal site. Also, intraspecific competition for food appears to be rare or absent for planktonic larvae of marine benthic invertebrates (Strathmann 1996), and high fecundity associated with a good maternal diet should not result in density-dependent competition for larval food. Thus the effectiveness of maternal nutrition as a cue to nutrition of offspring is expected to differ among life histories, and positive or negative correlations between food available for mother and offspring should be especially weak for benthic marine invertebrates with feeding larvae.

The sea urchins employed in our study exemplify the dissociation of adult and larval nutritional environments. The adults graze macrophytes and animals on the sea bed whereas the larvae feed on phytoplankton and other small suspended particles. Factors influencing the abundance of these adult and larval foods are quite different. Temporal separation further dissociates adult and larval food supplies. In these sea urchins of mid to high latitudes, the gonads grow during several months in fall and winter (Pearse and Cameron 1991), whereas the larvae grow during several weeks in the spring (Strathmann 1987a). Larvae are commonly carried far from the parental site by ocean currents so that the juveniles also encounter different conditions. Hence maternal nutrition is a poor cue to the nutritional environment of offspring.

Differences in exogenous food available to larvae affect both growth rates (Strathmann 1987b) and body form (Hart and Scheibling 1988, Strathmann et al. 1992, Strathmann et al. 1993, Fenaux et al. 1994, Shilling 1995). For some types of larvae, larger feeding structures develop when food is scarce, and development of juvenile structures is accelerated when food is abundant. The most studied example is the larval sea urchin (the pluteus). Plutei use ciliary bands on feeding arms to capture particulate food. Plutei with longer arms can clear water of food at greater rates than larvae with shorter arms (Hart and Strathmann 1994). When food is abundant, larvae reduce allocation to growth of feeding arms and accelerate the development of juvenile structures that develop within the larval body (the echinus rudiment). Conversely, when food is scarce, allocation to feeding arms is increased and development of the echinus rudiment is retarded. The change in body form that results from this develop-

mental plasticity has been demonstrated in both the laboratory and field (Strathmann et al. 1992, Fenaux et al. 1994). Similar developmental plasticity may occur in larvae of molluscs (Strathmann et al. 1993). Such developmental responses of suspension feeders are not limited to marine larvae. For example, larger filter screens develop in species of *Daphnia* reared with less food (Lampert 1994). Larval developmental plasticity is considered to be advantageous because it should reduce the duration of the larval period (Strathmann et al. 1992, Hart and Strathmann 1994). Shortened larval duration could increase survival by reducing exposure to planktonic predators and by reducing the probability of advective loss from adult habitat.

Maternal nutrition affects both number of eggs and egg size. Intraspecific variation in the size of ripe gonads is much greater than intraspecific variation in the size of eggs, which indicates that the number of offspring varies much more than maternal investment per offspring and that maternal investment per offspring is maintained over a wide range of maternal nutrition (Lessios 1987). Nevertheless, less food or poorer food for mothers does decrease investment per offspring in such diverse animals as bivalves, sea urchins, and copepods (Bayne et al. 1978, Thompson 1982, George 1990, George et al. 1990, de Jong-Westman et al. 1995, Guisande and Harris 1995). This decreased investment per offspring is usually interpreted as a direct result of maternal nutritional stress rather than as an adaptive adjustment of maternal investment per offspring. We accept this interpretation because a negative correlation (or any reliable correlation) between adult and larval nutrition is unlikely for sea urchins. Although a decrease in material per egg does not appear to be an adaptive response to maternal nutritional stress, it could affect growth or form of the larvae. De Jong-Westman et al. (1995) found evidence that maternal nutrition affects larval form, but their measures of larval form did not admit a comparison with effects of larval nutrition. Here we asked whether effects of maternal nutrition resembled effects of larval nutrition. We were concerned with three implications for the ecology of larvae.

The first implication concerns the proximate or ecological effects. Maternal nutrition could affect larval planktonic duration by affecting larval growth rates, but effects of exogenous food (phytoplankton) could overwhelm the effects of maternal nutrition on planktonic duration. Maternal nutrition could also influence the duration of the planktonic period by effects on larval form. Reduced maternal investment per offspring could mimic the effects of low concentrations of food for larvae, or it could affect the developmental plasticity of larvae in response to high or low concentrations of larval food. The endogenous nutrients supplied in the egg may or may not affect larval development in the same way as exogenous nutrients supplied by larval feeding. Maternal nutrition might therefore af-

fect larval growth through either one or a range of developmental trajectories.

The second implication concerns methods for assessing planktonic conditions that limit feeding and growth of larvae. The degree to which planktonic food limits growth rates and development times for larvae has been a subject of controversy (Olson and Olson 1989, Fenaux et al. 1994). Absolute and relative sizes of larval structures are potentially valuable biological indicators of food-limited growth in the field. For larval sea urchins, for example, scarcer food for larvae results in larger larval feeding structures, and abundant food accelerates development of the echinus rudiment, which forms structures that will be retained in the juvenile and adult. Larval form could therefore be a gauge of planktonic conditions affecting larval growth or survival. However, if maternal nutrition has similar effects, then either benthic food for adults or planktonic food for larvae could cause "food-limited" larval forms, and consequently larval form could not be used as a gauge of conditions in the plankton that affect larvae.

The importance of this methodological implication stems from difficulties in studying planktonic larvae. Estimates of growth are difficult to obtain because mixing and advection prevent reliable tracking of individual larvae or cohorts (Levin 1990). In addition, the nutritional value of their heterogeneous food is unknown (Boidron-Métairon 1995). Estimating larval growth and food limitation from growth in containers of sampled sea water is unreliable because their planktonic food rapidly changes in abundance. Therefore, chemical or morphological indicators of condition are the most practical and perhaps best indicators of food-limited growth of larvae (Fenaux et al. 1994). Morphological indicators offer a rapid method of assessing nutritional state of individuals. Confirming that a larva's morphology reflects its own nutritional history and not its mother's would open another window to the obscure but important planktonic stage in these complex life histories.

The third implication concerns possible effects of developmental plasticity of larvae on the evolutionary transition from a feeding larva to a more direct development to the adult form. Development with a feeding larva represents the ancestral condition for many clades of animals and remains a common mode of development among extant species (Thorson 1950, Milneikovsky 1971), but nonfeeding development has evolved many times (Emlet 1990). Evolution is predominantly from feeding to nonfeeding larval development (Strathmann 1993). The transition to nonfeeding can have profound ecological and evolutionary consequences because of its effect on duration of planktonic development and hence dispersal and gene flow (Thorson 1946, Shuto 1974, Scheltema 1977, Hansen 1978, Jablonski and Lutz 1983, Strathmann 1986, Kohn and Perron 1994, Palumbi 1995).

Studies of sea urchins suggested that preexisting adaptive developmental plasticity in feeding larvae might contribute to the evolutionary transition to non-feeding larval development (Strathmann et al. 1992). Among closely related species, those with larger eggs are more independent of exogenous planktonic food (Emlet 1986, Eckert 1995, Jaekle 1995, Herrera et al. 1996). With sufficient material in the egg for development to metamorphosis, the larvae do not need to feed. In most species, the capacity for feeding is then lost. Nevertheless, there are similarities between non-feeding larvae and food-satiated larvae. Both nonfeeding larvae and food-satiated larvae have an abundant supply of organic material, though from different sources. In both nonfeeding larvae and food-satiated larvae, less material is allocated to growth of larval arms, and material is allocated earlier to the development of structures that will be functional in the juvenile and adult. In both cases, accelerated development of the echinus rudiment should reduce the time to competence for metamorphosis and thereby increase survival. Reduction of ephemeral larval structures that are not needed should save material or time. A difference is that the advantages that are conferred on food-satiated larvae by phenotypic plasticity are conferred on nonfeeding larvae by evolutionary changes in development. The developmental plasticity of a feeding larva helps it cope with varying abundance of planktonic food, and presumably selection maintains that plasticity for that reason. Does this evolved morphogenetic response to nutritional state also contribute to evolution of nonfeeding larval forms? One hypothetical scenario is that an evolutionary increase in material provided to the ovum in oogenesis has the same morphogenetic effect as an increase in planktonic food. This would be a case of endogenous and exogenous nutrition producing the same developmental response simply because both deliver the same stimulus to the developing larva. An evolutionary increase in investment per ovum that eliminated dependence on exogenous food could thereby gain an immediate extra advantage. An increase in material in the egg can reduce time to metamorphic competence by eliminating the need for feeding and growth, but if that were the only change in development, there would still be a delay in the development of juvenile structures, and unneeded larval structures would still develop only to be resorbed. Accelerated development of the echinus rudiment provides an additional reduction in time to metamorphic competence, and loss of unneeded and ephemeral larval structures provides an additional saving in time or materials. If an increase in material in the egg provides the same stimulus as increased food from the plankton, then a gene that increases material invested per ovum has a fortuitous pleiotropic effect on larval development that can increase its selective advantage.

In terms of mechanism, the hypothesis is plausible because exogenous and endogenous nutrients could de-

liver the same stimulus to the developing larva. Changes in a gene or genes that affect nutrient supplies in eggs would be sufficient to produce an appropriate developmental response by a mechanism that was already in place for other reasons. To test this mechanistic hypothesis, we used eggs differing in quality because of differences in maternal nutrition and asked whether maternal and larval nutrition had similar effects on the development of larval and juvenile structures.

METHODS

We employed natural variation in maternal nutrition by using ripe adult green sea urchins (*Strongylocentrotus droebachiensis* (O. F. Müller)) from field sites that varied in availability of food. Gonads are larger in sea urchins from shallower depths, where preferred macroalgal food is more abundant (Keats et al. 1984, Rogers-Bennett et al. 1995). The amount of algal food affects gonad size and lipid content of eggs in green urchins maintained in the laboratory (Thompson 1982). Egg quality also varies with season and with location of adults of the sea urchin *Arbacia lixula* (George 1990).

On 8 and 9 February 1994 we collected green sea urchins from two sites in the northeast Pacific Ocean, ~30 km apart and both close to San Juan Island. The first site was at 100–120 m depth in San Juan Channel near Point Caution (48°34' N, 123°1' W). The “deep mothers” were from this site. Benthic algae that are of high quality as food do not grow at 100 m, although algae may be supplied to the deep mothers as pieces drifting from shallower sites (Irvine 1973). The second site was at 1–6 m depth in Haro Strait near Dead Man Bay off the more exposed side of San Juan Island (48°31' N, 123°9' W), where kelp and other macroalgae were abundant. The “shallow mothers” were from this site.

The urchins were sampled at a time when gonads were near maximal size and ova mature. Completion of oogenesis in February is indicated by fertilization and development of eggs obtained in January (Strathmann 1987a) and by the beginning of natural spawning in March (R. Strathmann, unpublished observations of appearance of embryos and larvae in the plankton). Similar spawning seasons of shallow and deep urchins is indicated by simultaneous decrease in sizes of gonads of shallow and deep green urchins in San Juan Channel during April and May (B. F. McPherson, personal communication).

It was not essential for this study that the cause of differences in maternal nutritional stress were the result of differences in food, but differences in food were obvious and no other cause was apparent. Because tidal currents mix the water column, temperatures were similar at the two sites. Given the velocity of currents, rates of mixing, and durations of planktonic periods, genetic divergence between populations this close was

not expected, nor has it been found (Palumbi and Wilson 1990).

The sea urchins were held at the Friday Harbor Laboratories at ambient sea temperature (8–10°C) for 13 d prior to use. The animals from the deep site were not fed in the laboratory. The urchins from the shallow site were given fronds of bull kelp (*Nereocystis luetkeana*) every 2–3 d.

On 21 February 1994, we selected four females on the criterion of similar test diameter (70–80 mm) from each population, measured the volume of all five gonads of each female in a graduated cylinder, and transferred a single gonad from each female to filtered (0.45 µm pore) sea water where it leaked the eggs used for experimental rearing of larvae. For an unbiased measure of size of eggs from each female, a sample from an egg suspension was placed on a glass slide and scanned; the diameters of the first 10 eggs to cross an ocular micrometer line were measured to the nearest 2 µm with an ocular micrometer in a constant orientation.

Eggs from each female were fertilized with sperm from one male from the deep site to create eight half-sibling families. A single father minimized the paternal genetic variation and the possibility of interactions between the male and female genomes. Semlitsch and Schmiedehausen (1994) found evidence for such effects for anurans. Eggs, embryos, and larvae were incubated at the temperature of ambient seawater. Water was filtered through a 0.45-µm mesh membrane filter and continuously stirred with motor driven paddles at 10 strokes per minute (Strathmann 1987a). Immersion of jars in a bath supplied by the laboratory's sea water system kept temperatures between 8.5° and 12°C (mean ± SD = 10.1 ± 0.08°C), near the temperatures in the field at that season.

For experimental feeding of larvae, the offspring of each mother were exposed to three food regimes: no additional food, addition of 200 cells of *Rhodomonas* sp./mL, and addition of 5000 cells of *Rhodomonas* sp./mL. Cultures were also inoculated with other microorganisms because the gametes were not obtained under sterile conditions and the stirred jars were open. The jars with no addition were therefore not devoid of food >0.45 µm in diameter, although growth was enhanced with greater additions of *Rhodomonas*. Experiments were initiated with 200 advanced gastrulae placed in 1.5 L of water in each culture jar, with a total of 24 jars (2 sites × 4 mothers per site × 3 larval food treatments per mother). At 2-d intervals, ~90% of the old water was removed from jars of all treatments through reverse filtration through a 50-µm mesh and replaced with new filtered water and new food.

Under these conditions, grazing by larvae could reduce the concentration of food but could not change the rank order of food concentrations. The maximum volume of water that could be cleared of particles by the 200 larvae in 2 d was well below the volume of the containers. Removal of sampled larvae kept total

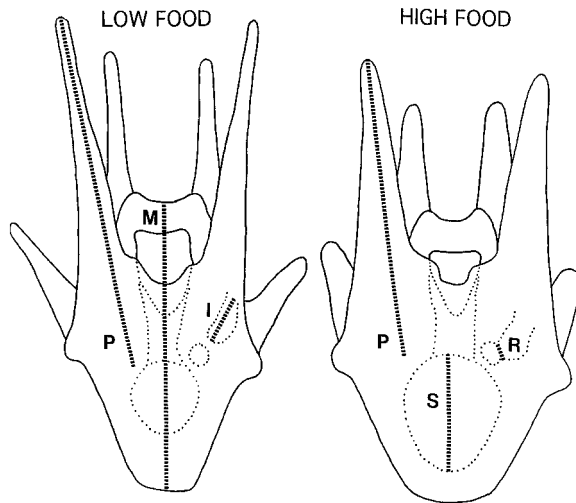


FIG. 1. Developmental plasticity of pluteus larvae of the sea urchin *Strongylocentrotus droebachiensis* in response to low and high concentrations of food. Measured body parts: *I* = length of the ectodermal invagination, *M* = body length at the midline, *P* = postrodorsal arm rod, *R* = diameter of the echinus rudiment, *S* = length of the stomach.

clearance rates low as individuals developed greater clearance rates.

For measurements of growth and form, 6 to 13 larvae were sampled without replacement from each jar and preserved in 2–4% formaldehyde in sea water buffered with CaCO_3 . Larvae were sampled daily until the ectodermal invagination contacted the mesoderm in the echinus rudiment. Larvae were subsequently sampled every 2 d from the high food treatment and every 4 d from the low food and filtered water treatments until they reached the late eight-armed stage. Age was recorded as number of days since fertilization. Of the sampled larvae, five larvae were measured from each female and treatment. Measurements were for postoral rod length (from the tip of the rod to its connection with the transverse and body rods), midline body length, stomach length, length of ectodermal invagination (at early stages), and diameter of the echinus rudiment (at later stages) (Strathmann et al. 1992) (Fig. 1). Rudiment diameter was measured as the contact between ectodermal invagination and hydrocoel during the early stages of contact; at later stages rudiment diameter included the enveloping ectoderm. Measurements were made with an ocular micrometer to the nearest 4 μm .

We refer to size-at-age plots as growth curves although they represent composites for the larvae from four females from each population. We used ANCOVA to test for differences in growth rates and size-at-age of structures in larvae from the deep and shallow mothers and also for differences between larval food levels within maternal sites. For those analyses we compared the longest linear portion of growth curves for which larvae from both populations were represented. We

used the same ranges of data to test for the effects of maternal gonad volume and maternal mean egg size on the size of larval and juvenile structures with multiple regression. We report the tests for homogeneity of slopes in the ANCOVA. If the interaction term was nonsignificant (slopes homogeneous), the interaction was dropped from the model. For multiple regression we report tests for the significance of variable coefficients.

In most ecological studies, practical constraints affect the degree of replication. We were constrained by the number of rearing jars that could be maintained during the study. We replicated the number of mothers from each site. We used single shallow and deep sites. We used a single experimental unit (one jar of larvae) for each mother and larval food level. Because maternal effects and jar effects were combined, differences between mothers within a site would be difficult to detect, but this was not our aim. Similarly, there was only one shallow and one deep site, but our aim was to use maternal depth as a means of examining effects of differing maternal investment per offspring, not to demonstrate effects of depth, which had already been done for red urchins (Rogers-Bennett et al. 1995) and also green urchins near San Juan Island (B. F. McPherson, *personal communication*; L. McEdward and R. Strathmann, *unpublished observations*). We raised many larvae within each jar and (to avoid pseudoreplication) used the means from each jar and day as the sample unit. All statistical analyses were performed on means for each jar and day. Each point in Figs. 3–6 is a mean for a jar and day.

RESULTS

Maternal eggs and ovaries

Shallow mothers had significantly larger gonad volumes and egg diameters than deep mothers (Table 1). Overall, there was a positive relationship between egg diameter and gonad volume (Fig. 2, $r = 0.78$, $n = 8$ mothers, $P = 0.023$). That relationship also held for the shallow population ($r = 0.99$, $n = 4$ mothers, $P = 0.012$) but not for the deep population ($r = -0.69$, $n = 4$ mothers, $P = 0.3$). The smaller gonads from the deep mothers indicates food limitation. The smaller eggs from deeper mothers suggest that food limitation affected quality as well as numbers of offspring.

Larval nutrition and larval growth

As expected, the concentrations of food supplied to larvae affected larval growth rate, as exemplified by midline body length (Fig. 3A,B). Food treatment level had a significant effect on mean larval size at 20 d for larvae of females from both the deep and shallow sites: for the deep site $F = 335$, $df = 2, 7$, $P < 0.00001$; for the shallow site $F = 416$, $df = 2, 7$, $P < 0.00001$. Pairwise comparisons between treatments based on a Tukey hsd post hoc test were all significant for both

TABLE 1. Physical measurements of green sea urchins (*Strongylocentrotus droebachiensis*) from deep water ($n = 4$ females) and shallow water ($n = 4$ females).

Measure	Shallow		Deep		Ratio (shallow/deep)	<i>t</i> test	
	Mean	SD	Mean	SD		<i>P</i>	df
Gonad volume (mL)	41.4	12.1	16.7	7.0	2.48	0.012	6
Egg diameter (μm)	159	1.2	153	2.0	1.04	0.002	6
Egg volume (mm^3)	2.10×10^{-3}		1.88×10^{-3}		1.12		
Test diameter (mm)	74.4	2.7	74.2	2.8	1.00		

sites, indicating that larvae from the high food treatment were indeed largest at 20 d, followed by larvae from the low food and filtered water treatments.

Larval nutrition and larval form

Larvae exhibited developmental plasticity in body form in response to amount of food. The length of postoral rods in relation to midline body length was significantly different between food treatments for larvae from both the shallow mothers (ANCOVA for homogeneity of slopes, $n = 103$ means for larvae from each jar and day [as described in last paragraph of *Methods*], $F = 33.3$, $P < 0.0001$) and deep mothers ($n = 102$ day-jar means, $F = 26.9$, $P < 0.0001$). The concentration of food available to larvae affected the timing of development of the echinus rudiment from the earliest stages of rudiment formation. It affected the timing of the invagination of ectoderm before its contact with the coelomic mesoderm (Fig. 4A), and it affected the timing of subsequent development of the echinus rudiment (Fig. 4B) and the size of the stomach. Food level affected the timing of the ectodermal invagination similarly for larvae from the deep and shal-

low mothers. For postoral rod lengths between 400 and 730 μm the ANCOVAs for homogeneity of slopes were $F = 74.04$, $n = 50$ day-jar means, $P < 0.00001$ for the shallow site and $F = 75.3$, $n = 55$ day-jar means, $P < 0.00001$ for the deep site. Rudiment formation was

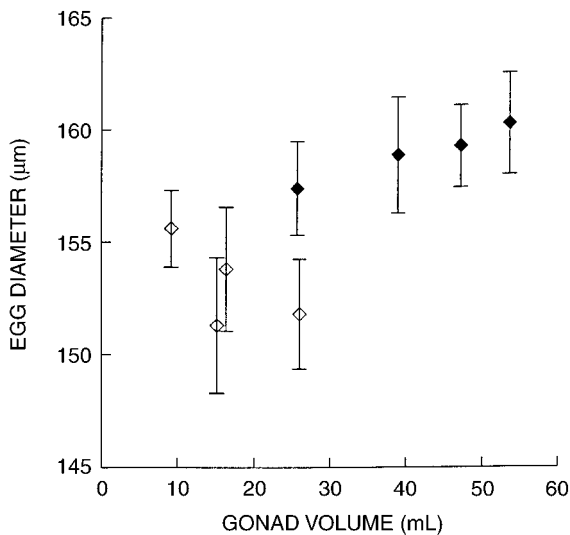


FIG. 2. The effect of maternal nutrition on gonad volume and egg diameter. Solid symbols (\blacklozenge) represent mothers from the food-rich, shallow water site; open symbols (\diamond) represent mothers from the food-poor deep water site. Data for egg diameters are means ± 1 SD.

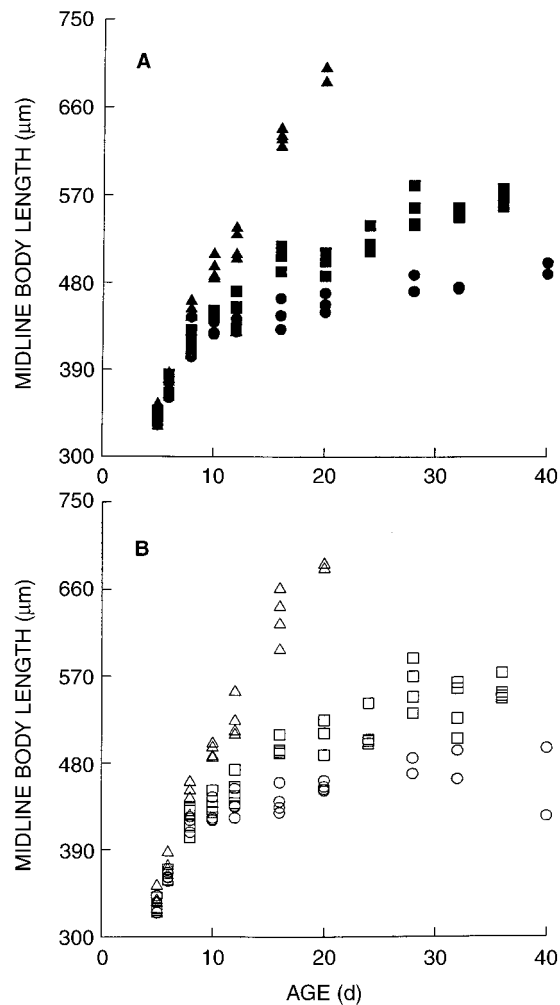


FIG. 3. The effect of larval nutrition on the growth rate of midline body length in pluteus larvae. The food treatments were filtered sea water (circles), low addition of food (squares), and high addition of food (triangles). Each point represents the mean for one mother's larvae on one day. Larvae were from (A) shallow-site mothers or (B) deep-site mothers.

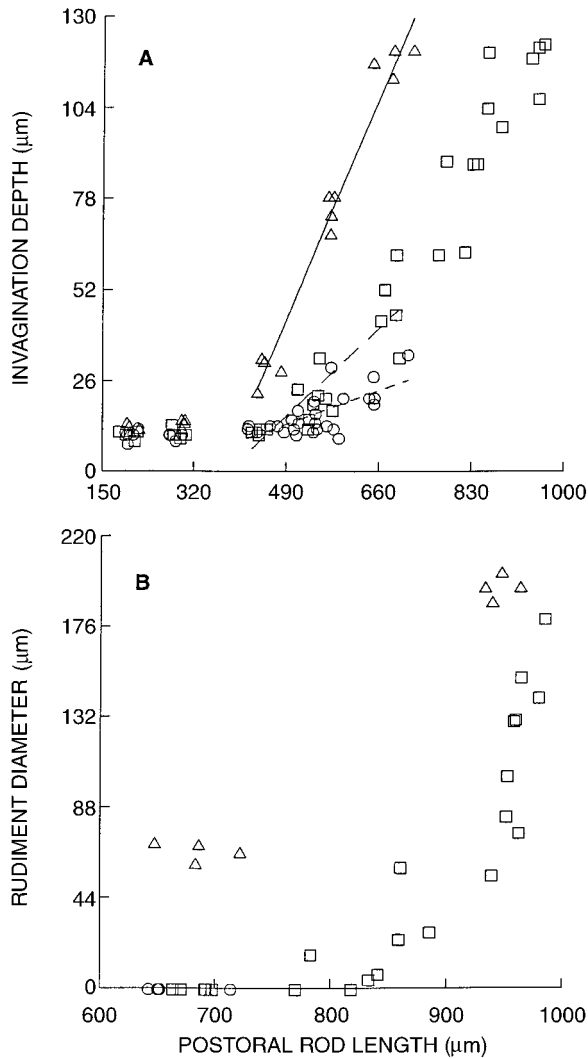


FIG. 4. Phenotypic plasticity in response to different levels of larval nutrition. The invagination of the ectoderm (A) and the diameter of the echinus rudiment (B) measure development of juvenile structures. The postoral rod length indicates size of the larval body and feeding apparatus. The food treatments were filtered sea water (circles), low addition of food (squares), and high addition of food (triangles). Data are means for larvae from one mother on one day. Mothers were from the deep site (open symbols). Regression lines in part A are for postoral rod lengths from 400 to 750 μm .

most rapid at high food levels for larvae from both shallow and deep water mothers, as judged by rudiment size when postoral rod lengths were close to 700 μm . For larvae from shallow mothers the rudiment diameters averaged $1.3 \pm 2.65 \mu\text{m}$ (mean \pm 1 SD) with low addition of food and $63.8 \pm 9.5 \mu\text{m}$ with high addition of food. For larvae from deep mothers, it was 0 μm with low food and $65 \pm 4.5 \mu\text{m}$ with high food ($n = 4$ means of rudiment diameter for larvae, one larval mean from each mother).

Larval survival rates within each treatment were high: 82%, 83%, and 74% for the filtered, low, and

high food treatments, respectively. Consequently, the differences in larval form in response to food ration were the result of different development in response to amounts of food rather than selective deaths.

Maternal nutrition and larval growth

In general, larvae from mothers at the shallow, food-rich site grew and developed more rapidly than larvae from mothers at the deep water, food-poor site. Moreover, there was a tendency for those effects to be more noticeable at lower food rations. The growth rate of the ectodermal invagination was greater for larvae from shallow mothers than for larvae from deep mothers at low food levels (Fig. 5A), but not at high food levels (Table 2). Size-at-age of the ectodermal invagination was larger for larvae from shallow water mothers on the filtered ration. Similarly, for larvae from shallow mothers at the low food ration, rudiments formed earlier, as indicated by differences in size at 20 d (Mann-Whitney $U = 16$, $P = 0.018$), and remained larger-at-age (Fig. 5, Table 2). Postoral rods were longer-at-age for larvae from the shallow mothers at all food rations (Table 2). We could detect no effect of maternal nutrition on larval stomach length. In summary, differences in maternal habitat and hence maternal nutrition did affect the growth rate, as indicated by the size-at-age of the ectodermal invagination, the echinus rudiment, and larval arms.

The gonad and the egg sizes also had significant effects on the size-at-age of several structures (Table 2). Instead of using maternal site as a factor, gonad or egg size was used as a continuous variable in a multiple regression. The effects of gonad and egg size were more pronounced for structures that developed early such as length of postoral arms and depth of the ectodermal invagination as opposed to the diameter of the echinus rudiment. In general, mothers with larger gonads and egg sizes produced larvae with post oral arms and ectodermal invaginations that were larger-at-age. Mothers with larger gonad volume also had offspring with larger echinus rudiments at age, but maternal egg size had no significant effect on echinus rudiment.

Natural variation in maternal nutrition did affect larval growth rates, but not to the same degree as the experimental variation in larval nutrition. For example, for larvae from shallow mothers, the ectodermal invagination grew at a rate of 22.3 $\mu\text{m}/\text{d}$ with a high concentration of algae as food and at only 3.6 $\mu\text{m}/\text{d}$ with a low concentration of algae. The results were similar for larvae from deep mothers: 22.2 $\mu\text{m}/\text{d}$ and 2.95 $\mu\text{m}/\text{d}$ for the high and low concentrations of algal food, respectively. The ratio of those growth rates from high to low food treatments was 6.2 (high/low) for the shallow site and 7.5 for the deep site. In contrast, larvae from shallow mothers grew at only 1.0 and 1.2 times the rate of those from deep mothers. Over a more extended period at low food, the ectodermal invagination for larvae from shallow mothers (food-rich maternal

site) grew at 7.8 $\mu\text{m}/\text{d}$ vs. 5.8 $\mu\text{m}/\text{d}$ for larvae from deep mothers (food-poor maternal site), the ratio of growth rates still was only 1.3. (Comparisons were based on the longest linear portion of the growth curves for which data from both treatments were available: 7 to 14 d for effects of larval food and 9 to 27 d for effects of maternal nutrition). If the experimental variation in larval food was representative of variation in nature, then larval nutrition has a much greater effect on larval growth than maternal nutrition. Natural variation in larval nutrition is addressed in the *Discussion*.

Maternal nutrition and developmental trajectories of larvae

Differences in maternal habitat and hence maternal nutrition did not affect the relative timing of development of different larval structures to a degree that was detectable and similar to the effects of larval nutrition. This was true for larvae at all food levels, as exemplified by the relationship between invagination depth and postoral rod length (Fig. 6A, B, C). ANCOVA indicated that regression lines for females from shallow and deep sites did not differ significantly in either slopes (part A, $F = 2.0$, $n = 52$ day:jar means, $P = 0.16$; part B, $F = 1.2$, $n = 47$ day:jar means, $P = 0.27$; part C, $F = 0.5$, $n = 24$ day:jar means, $P = 0.47$) or elevations (part A, $F = 3.8$, $n = 52$ day:jar means, $P = 0.55$; part B, $F = 0.836$, $n = 47$ means, $P = 0.36$; part C, $F = 4.2$, $n = 24$ day:jar means, $P = 0.053$). Thus maternal nutrition affected larval growth rates without a detectable change in the developmental sequence of larval sizes or shapes. If maternal nutrition had effects similar to the larval developmental plasticity in response to exogenous food, the effects were too small to detect in this comparison.

DISCUSSION

Effects of larval nutrition

The concentration of particulate food had large effects on growth rates and body proportions of larvae. The plasticity in form exhibited by larvae of *Strongylocentrotus droebachiensis* agreed with observations on developmental plasticity for other echinoid larvae and larvae fed other foods (Boidron-Metairon 1988, Fenaux et al. 1988, Hart and Scheibling 1988, Strathmann et al. 1992, Fenaux et al. 1994, Hart and Strathmann 1994) but demonstrated effects at even earlier stages. Concentration of larval food affected the timing of development of the echinus rudiment from the earliest stages of rudiment formation: the invagination of ectoderm overlying the hydrocoel. Developmental plasticity in response to larval nutrition was easily detected.

Maternal nutrition and larval performance

The differences in gonad size indicated that the habitat differences affected maternal nutrition. The differ-

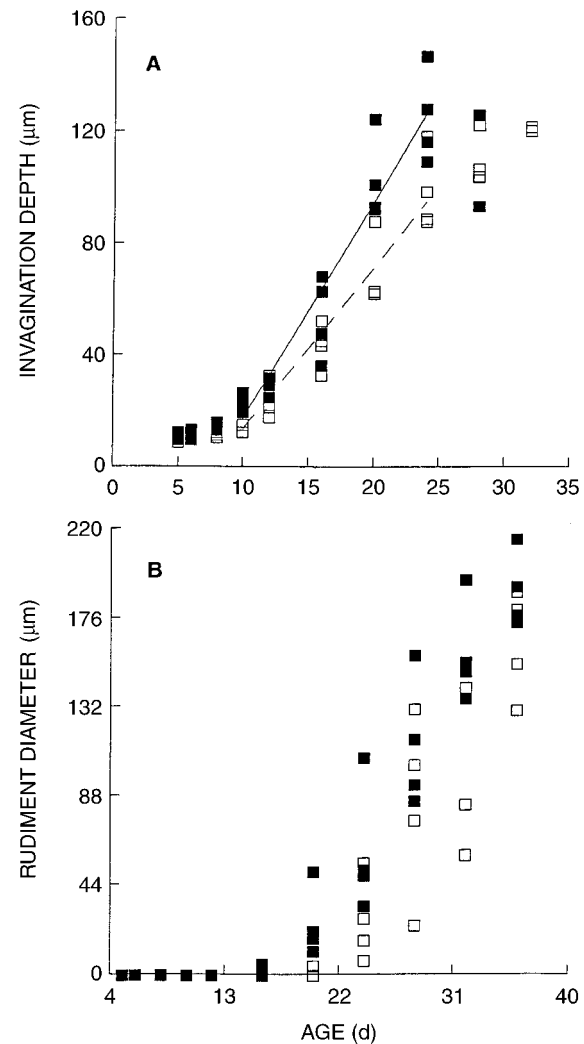


FIG. 5. The effect of maternal nutrition on (A) the growth in depth of the ectodermal invagination and (B) the diameter of the echinus rudiment of pluteus larval offspring. Solid squares represent larvae from mothers at the food-rich, shallow site; open squares represent larvae from mothers at the food-poor, deep site. All of the larvae received a low addition of food. Data are means for larvae from one mother on one day. The regression lines in part A were confined to the range of the data in the ANCOVA in Table 2.

ences in egg size suggested that maternal nutrition affected maternal investment per offspring in addition to total reproductive output. Maternal nutrition of echinoids can affect organic content of eggs without affecting their size (de Jong-Westman et al. 1995), but an effect on size was an additional indication of an effect of maternal habitat on egg organic content. Egg nutrient content is positively correlated with egg volume within species of varied invertebrates: shrimps (Clarke 1993), a copepod (Guisande and Harris 1995), and polychaetes (Bridges 1993, Qian 1994). For starfish with nutrient rich eggs and nonfeeding larvae, egg size and organic content usually have a low but positive

TABLE 2. The effect of maternal site (based on ANCOVA) and of gonad size and egg size (based on multiple regression) on the growth rates and size-at-age of *Strongylocentrotus droebachiensis* larval structures (length of postoral rod) and rudiments of juvenile structures (depth of ectodermal invagination, diameter of echinus rudiment) at each food level.

Character	Food	Ages (d)	Probability levels				n
			Site × Age	Site	Gonad	Egg	
Invagination	Filtered	5–40	NS	0.01	0.001	0.01	68
Invagination	Low	10–26	0.01		0.01	0.01	40
Invagination	High	8–12	NS	NS	0.05	0.05	24
Rudiment	Low	24–36	NS	0.01	0.05	NS	32
Rudiment	High	10–16	NS	NS	NS	NS	24
Postoral rod	Filtered	10–40	NS	0.05	0.01	NS	44
Postoral rod	Low	8–24	NS	0.001	0.01	0.05	48
Postoral rod	High	5–16	NS	0.05	0.01	0.05	48

Notes: Food was *Rhodomonas* sp.; food treatments were filtered sea water, low addition (200 cells/mL), and high addition (5000 cells/mL). Ages = the range of ages at which increases were linear, which was the range used for each test. Each datum is a mean from one day and jar; n = number of means for the listed larval measure. NS = nonsignificant. If the Site × Age interaction was significant no test was performed for the effect of site.

correlation but sometimes no correlation within a spawn (McEdward and Carson 1987, McEdward and Coulter 1987).

Effects of maternal nutrition on eggs and offspring are common even for animals that lack parental care. The effects include egg size, size-at-age, growth rate, performance, and survival. Examples include insects (Rossiter et al. 1992), amphibians (Kaplan 1987), fishes (Hislop et al. 1978), and marine invertebrates (George 1990, George et al. 1990, Guisande and Harris 1995, Bayne et al. 1978). In our study greater maternal nutrition had either a positive effect or no effect on growth rate and size-at-age for larval and juvenile structures. The enhanced larval growth from enhanced maternal nutrition is expected to decrease the duration of the planktonic period or increase size at metamorphosis (Hart 1995) and thereby enhance larval survival.

Effects of maternal nutrition on quality of offspring are common and contrast with an assumption frequently made in life history theory. For organisms with high fecundity, parental investment per offspring is often assumed to be independent of total investment in reproduction (Winkler and Wallin 1987). The assumption seems plausible for organisms with thousands or millions of eggs, no postzygotic parental care, and no correlation between amount of food available for mothers and offspring. Observations on eggs of mothers with greatly differing fecundity usually indicate only small differences in size of eggs, but maternal nutrition nevertheless did affect growth of offspring in our study and others (George 1990, George et al. 1990, de Jong-Westman et al. 1995, Bayne et al. 1978). In these cases, nutritionally stressed mothers may have been unable to maintain the quality of ova. As discussed in the *Introduction*, a reliable correlation between maternal nutritional stress and food for larval offspring is unlikely for these animals. However, a decrease in food to mothers does not inevitably result in less organic

material per offspring. In a capitellid polychaete with nonfeeding larvae and in a copepod, mothers with a poorer diet produced eggs that were larger or contained more organic material (Qian 1994, Guisande et al. 1996), perhaps because a poor food supply for mothers is correlated with a poor food supply for offspring in these populations.

Maternal vs. larval nutrition

Maternal nutrition had significant and detectable effects on larval growth, but the effects on growth were small compared to the effects of larval nutrition. Moreover, effects of maternal nutrition did not resemble the developmental plasticity of larvae in response to larval food. Effects on larval proportions and acceleration or retardation of the echinus rudiment were undetectable. For the larvae with the least food, there appeared to be an effect of maternal nutrition that resembled developmental plasticity in response to larval food (Fig. 6A), but the difference was not significant. Before this negative result can be extended to larvae in the plankton, our experimental treatments for larval food must be compared to natural food supplies and their effects on larvae, because the variation in maternal nutrition was natural and the variation in larval nutrition was experimental.

There was a 25-fold difference in the algal cells added to the high food and low food treatments. A 25-fold variation in concentration of phytoplankton is near the extreme expected temporally and spatially near the sampled populations of *Strongylocentrotus droebachiensis* during the March to May season of spawning, when concentrations of chlorophyll *a* vary from <1 to >20 µg/L in waters along the coast of the Olympic Peninsula (Anderson 1964), the fjord Saanich Inlet (Takahashi et al. 1977), and Guemes Channel near the San Juan Islands (B. Bingham, unpublished data). A similar range was reported for concentration of phy-

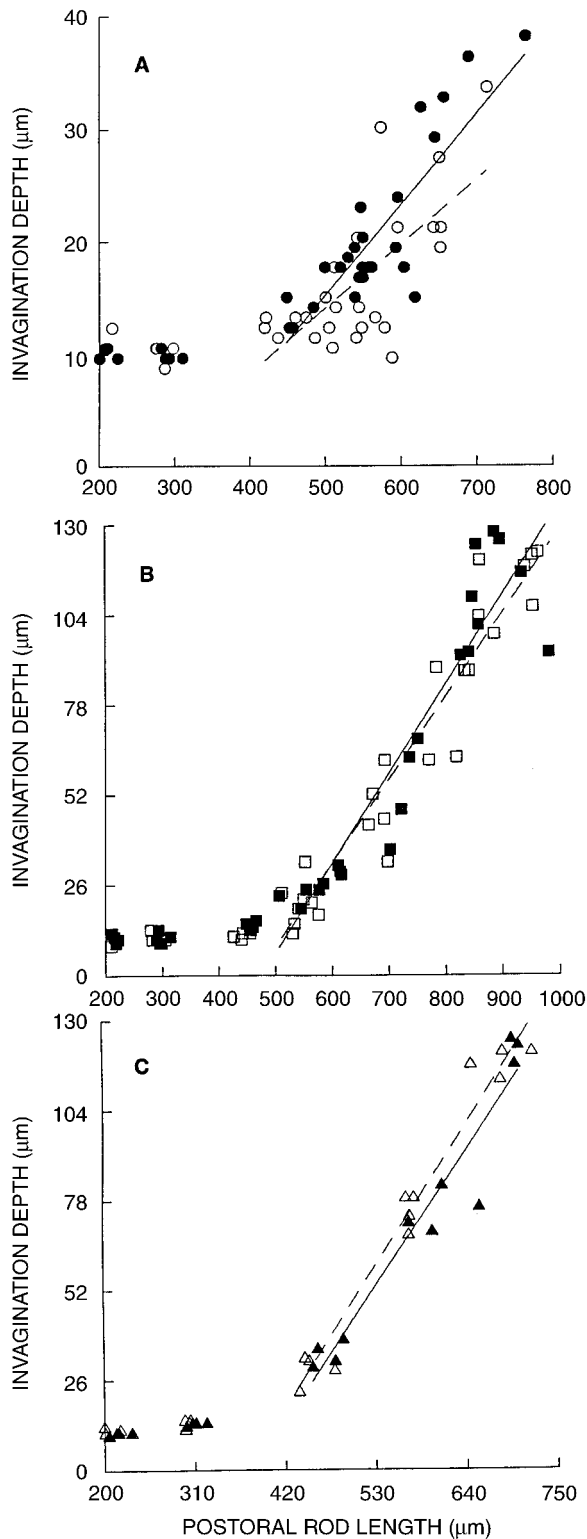


FIG. 6. Developmental trajectories in pluteus larvae of the sea urchin *Strongylocentrotus droebachiensis*, for depth of the ectodermal invagination (a rudiment of juvenile structures) vs. length of the postoral arm rod (part of the ephemeral larval feeding apparatus) for larvae from mothers at the shallow, food-rich site (solid symbols) and deep, food-poor site

toplankton by volume in the tidally mixed Haro Strait to the northwest of San Juan Island (Stockner et al. 1979). The addition of 5000 cells of *Rhodomonas*/mL does not exceed the peak concentrations of phytoplankton observed in these waters.

A much smaller difference in food for larvae can produce different larval forms. In laboratory experiments, two- to five-fold differences in concentration of algae are sufficient (Hart and Scheibling 1988). In a field comparison, larvae of a sea urchin exhibited predicted differences in form in spring and autumn plankton samples from the northwest Mediterranean when mean concentrations of chlorophyll *a* differed by a factor of only 1.7 and concentrations of 3–20 μm particles by a factor of 2.9 (Fenaux et al. 1994).

Thus the differences in larval nutrition in our experiments were large but near the extremes that occur in nature, and much smaller differences in natural food have been associated with differences in development of the larval arms relative to development of the echinus rudiment.

Implications for the evolutionary transition to nonfeeding larvae

The mechanistic hypothesis was that materials in the egg and exogenous food provide the same stimulus to the developing larva. Comparison of larvae from well-fed and food-deprived mothers did not support this hypothesis.

The hypothesis could fail because of selection for the appropriate response to a change in egg quality due to maternal nutritional stress. The food for benthic adults varies on spatial and temporal scales that are quite different from those for planktonic food of larvae. If variation in maternal nutrition is independent of variation in larval nutrition, it would not be advantageous for maternal nutritional stress to produce a larval form suited to scarce planktonic food or for maternal repletion to produce a larval form suited to abundant planktonic food. Because maternal nutrition affects organic content of eggs, selection may favor developmental processes that distinguish between nutrients packaged in the ovum and food from the plankton. In that case, selection for larger but fewer eggs (Vance 1973, Smith and Fretwell 1974, Strathmann 1985) would not immediately result in an adaptive adjustment of larval form. With an evolutionary increase in material per egg and independence from planktonic food, the functionally advantageous reduction of larval arms and acceleration of the juvenile rudiment would require other changes.

←

(open symbols). The treatments for larval food were (A) filtered sea water, (B) low addition of food, and (C) high addition of food. Data are means for larvae from one mother on one day. Regression lines were confined to the postoral rod lengths >400 μm (A), >480 μm (B), and >420 μm (C).

The other changes could be genetic changes that provide the same developmental response as food satiation. This alternative does not preclude a contribution of preexisting developmental plasticity to the evolutionary transition to nonfeeding development, but the morphogenetic changes would not occur as a direct consequence of increased materials in the egg.

Failure to support the hypothesis could also have occurred because environmentally induced changes in material per egg were insufficient to produce the developmental response. Reduction of larval arms and acceleration of juvenile structures might require that a novel and high threshold of internal nutrient supply be crossed. In that case, a small evolutionary increase in organic material per egg would not immediately result in reduction of arms and acceleration of rudiment, but these changes might directly and fortuitously occur when some threshold of dependence on internal materials was exceeded. For the shallow and deep urchins, the maternal effect on egg diameter was a factor of 1.04 and on egg volume was a factor of 1.12. The differences produced by maternal nutrition may have been insufficient to produce a morphogenetic effect.

CONCLUSIONS

Natural variation in maternal nutrition did affect larval growth rates but the effect on duration of the larval period was small in comparison to the effects of larval nutrition on larval growth rate. The differences in maternal nutrition were sufficient to have a great effect on the total reproductive output as indicated by gonad volume. This result confirmed the generalization that maternal nutrition has large effects on fecundity and small effects on quality of individual offspring.

Differences in maternal habitat and hence maternal nutrition did not affect the relative timing of development of different larval structures to a degree that was detectable or similar to the effects of larval nutrition. This result indicates that larval developmental plasticity can be used as a reliable indicator of conditions in the plankton that affect larvae. Predators might also influence development of arms as a defense, but preliminary experiments produced no effect (L. Rogers-Bennett, *personal communication*). If predators can induce morphological changes similar to those caused by larval nutrition, then developmental plasticity may also directly indicate risk from predators. If not, larval developmental plasticity may specifically indicate larval growth, and hence duration of larval development. In either case, larval developmental plasticity represents a biological assay for conditions in the plankton that affect larval survival.

The effects of maternal nutrition on oogenesis did not mimic the effects of variation in exogenous food with respect to larval developmental plasticity. The hypothesis that internal and external supplies of materials provide similar stimuli to developing larvae was not supported. A small change in investment per egg was

insufficient for reduction of larval arms and acceleration of juvenile structures. Preexisting developmental plasticity of larvae in response to food may contribute to the evolutionary transition to nonfeeding development, but not so directly as in our hypothesis. Some genetic change in addition to increased investment per ovum may be required, or a greater change in investment per ovum may be necessary.

ACKNOWLEDGMENTS

National Science Foundation grant OCE-9301665 to R. Strathmann and a Natural Sciences and Engineering Research Council of Canada Post Doctoral Fellowship to D. Bertram supported the research. We thank K. Banse, A. Beckman, B. Bingham, D. Duggins, R. Grosberg, P. J. Harrison, W. Jaekle, K. Krogslund, J. Newton, J. Pearse, C. Staude, S. Schwinge, M. F. Strathmann, and an anonymous reviewer for their help.

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