Echinoderm egg and larval quality as a function of adult nutritional state

Echinoderm
Diet
Egg
Larvae
Development

Echinoderme
Diète
Œuf
Larve
Développement

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ABSTRACT

Differences in egg and larval quality for some sea urchins and seastars were investigated in the field and in the laboratory. In the field, sea urchins and seastars found at sites with an abundant supply of food were larger, and they produced large numbers of large, high quality eggs. For some female seastars, nutritional history determined the response to variation in food supply in the laboratory. While an increase in food ration did not affect the size of eggs produced by females from the favorable site, an increase in food ration led to an increase in egg size for those from the less favorable site. For all the echinoderms examined, egg numbers decreased when conditions became unfavorable. Larvae from females living in favorable environments grew and developed faster, and larval survival was high. A large percentage of sea urchin larvae from females living in favorable environments metamorphosed compared to those living in less favorable environments. Juvenile size did not vary as a function of past nutritional state in sea urchins but it did in seastars. Large numbers of high quality juveniles were produced by seastars from the favorable site. The differences in egg and larval quality observed in field studies might be due to differences in the abundance of preferred algae (food for some sea urchins) and molluscan species (food for some seastars) at the different sites. In laboratory studies, the responses to food availability were also influenced by the nutritional and gametogenic states of the females at the time of collection and by the duration of the experiments.

RÉSUMÉ

Influence des conditions nutritionnelles des adultes sur la qualité des œufs et des larves d'échinodermes.

Les différences dans la qualité des œufs et des larves de quelques oursins et étoiles de mer ont été recherchées en milieu naturel et au laboratoire. Dans le milieu naturel, les oursins et les étoiles présents dans des zones où la nourriture est abondante, produisent un grand nombre d'œufs de grande taille et de haute qualité. Mais chez les trois espèces d'oursins côtiers et une espèce profonde élevées en laboratoire, la quantité et la qualité de la nourriture n'affecte pas la taille des œufs. La réponse à la variation du taux de nourriture au laboratoire, chez certaines étoiles de mer femelles, est conditionnée par les conditions de nutrition antérieures. Si un accroissement de la ration alimentaire n'affecte pas la taille des œufs produits par les femelles dans des conditions naturelles favorables, il

conduit par contre à une augmentation de leur taille dans les sites les plus trophiquement défavorisés. Chez tous les échinodermes examinés, le nombre d'œufs décroît quand les conditions deviennent défavorables. Les larves des femelles vivant dans un environnement qui leur est propice grandissent et se développent plus vite et ont une meilleure survie. Les larves d'oursins se métamorphosent en plus grand nombre lorsqu'elles sont issues de femelles vivant dans de bonnes conditions, au contraire de celles provenant de femelles présentes dans un environnement moins favorable. Quant à la taille des juvéniles, elle varie en fonction des conditions de nutrition antérieures chez les étoiles de mer mais pas chez les oursins. Un grand nombre de juvéniles de bonne qualité sont produits par les étoiles de mer de sites favorables. Les différences dans la qualité des œufs et des larves observées en milieu naturel pourrraient être dues à des différences, selon les sites, dans l'abondance des algues (pour certains oursins) ou des mollusques (pour certaines étoiles de mer) préférentiellement consommés. Au laboratoire, les réponses à la nourriture disponible sont également influencées par l'état nutritionnel et le stade de reproduction des femelles au moment de leur récolte et par la durée de l'expérimentation.

INTRODUCTION

Most life history models (McGinley *et al.*, 1987; Roff, 1992) assume a trade-off between egg size and number, *i.e.* females produce more, but smaller eggs in favorable environments and few, but larger eggs in unfavorable environments. Other models predict that females with different amount of resources should make different numbers of eggs, not different sizes of eggs, as there is only one optimal egg size that maximizes the survival of the parent (Kaplan and Cooper, 1984). Recent models (Sibly and Calow, 1986; Morris, 1987; Venable, 1992) have addressed not only how environmental variation but how adult size affects egg size and numbers. Parker and Begon (1986), McGinley (1989), Sargent *et al.* (1987) and Venable (1992) predicted that bigger females with more resources for reproduction should produce bigger eggs and large numbers of eggs. With the exception of McGinley and Charnov (1988) these models have not considered egg and larval quality. McGinley and Charnov (1988) looked at how changing the size of two resource pools (carbon and nitrogen) available for investment in offspring would affect the optimal pattern of investment. They predicted that offspring survival would increase by the addition of either carbon or nitrogen to the egg. The purpose of this review is to test the assumptions and predictions of these models using the two most studied groups of echinoderms, sea urchins and seastars, and to examine the consequencies of variation in adult nutritional state on subsequent larval growth, survival and development to metamorphosis.

While all the sea urchins studied produce small eggs with planktotrophic larval development (egg diameter ranging from 70 to 160 μm) two of the seastars exhibit this type of development (egg diameter approximately 150 μm); the others produce large eggs (> 800 μm diameter) with lecithotrophic pelagic or benthic larval development. If the production of lecithotrophic eggs is energetically more expensive than planktotrophic eggs, a slight drop in the nutritional state of the adult might have serious consequencies on the larvae which do not feed in the plankton. The specific questions addressed were: Would these two groups of echinoderms produce many small eggs in favorable environments and a few large eggs in unfavorable environments? Would bigger individuals produce bigger eggs and more eggs? Would variation in adult nutritional state affect larval growth, development, metamorphosis and juvenile size at metamorphosis? Would the response to variation in food supply differ between species with planktotrophic and lecithotrophic larval development?

Effect of food availability on adult nutritional state, egg size, and number

Egg size and number varies within and among females at a site and between sites (Emlet *et al.*, 1987). Gugliemi (1969), Menge (1972, 1974, 1975), Lawrence (1975), Ridder and Lawrence (1982) and Jangoux (1982) observed variation in food supply with site, season, and year. Echinoderms found in areas with a rich supply of preferred food items respond by increasing body weight, gonad weight and content (Vadas, 1977; Keat *et al.*, 1984; Andrew, 1986; Berthon, 1987, Menge, 1972, 1974, 1975; George, 1990 *a*). Laboratory studies also confirmed that poor diets lead to smaller body sizes, lower gonad and pyloric indices (Lawrence 1973; Dehn 1980, 1982; Keat *et al.*, 1984; Thompson, 1984; Chiu, 1988; Xu and Barker, 1990 *a*, 1990 *b*; Tab. 1). Variation in the biochemical composition (Lowe and Lawrence, 1976 and Montgomery and Gerking, 1980) and in the digestibility of the sea weed *Sargassum* spp. and the sea grass *Thalassia testudinum* might explain the differences in body and gonad weight observed for the deep sea urchin *Stylocidaris lineata*. Those fed *Sargassum* spp. were larger with larger gonads than those fed *Thalassia testudinum* (George and Young, unpublished). Thus food quantity and quality affect gonad

weight and content (see Xu and Barker, 1990) and might account for part of the variation in egg size and number.

Seastars (Echinaster spp.) on seawalls heavily encrusted with oysters, sponges, ascidians and bryozoans were larger and produced large numbers of eggs than those in seagrass beds (Scheibling and Lawrence, 1982; Tab. 1). These authors suggested that the high quantity and quality of food sources on the seawall might account for the larger seastars and greater reproductive output. Similarly, the seastar Leptasterias epichlora were larger and produced more large eggs at sites with a wide variety of large molluscs, and were smaller and produced few small eggs at sites with a variety of small molluscs (George, 1994 a; Tab. 1). Thus under favorable environmental conditions, these seastars are bigger and produce more and bigger eggs. This agrees with the predictions of Parker and Begon (1986), McGinley (1989), Sargent et al. (1987) and Venable (1992) which indicated that bigger females with more resources for reproduction should have bigger eggs and large numbers of eggs. However, these models used very different biological assumptions. While that of Parker and Begon (1986) is based on the assumption that competition and egg size are important components of larval success, that of McGinley (1989) is based on the assumption that the number of larvae settling increases with the number of eggs produced, and that of Sargent et al. (1987) is based on the assumption that larger juveniles which hatch from larger eggs have lower mortality, experience faster growth, and take less time to become adults. Under certain environmental conditions the assumptions by Parker and Begon (1986) and Sargent et al. (1987) might apply for these seastars.

In the laboratory, a decrease in food ration led to a significant drop in egg numbers while egg size remained constant for the seastar Leptasterias epichlora from the favorable site (Tab. 1). Producing bigger eggs might be favored if competition for food among juveniles of the same species or other species is high at this site. Egg numbers might have thus decreased to maintain size and quality. As assumed in models by McGinley et al. (1987), Sargent et al. (1987), Sibly et al. (1988) and observed in experiments by McEdward (1986 a; 1986 b), Sinervo and McEdward (1988) bigger offspring have higher growth and survival rates. A decrease in food ration had no effect on egg numbers though a slight but significant decrease in egg size was observed for seastars at the less favorable site (Tab. 1). Small eggs might have equivalent fitness to that of big eggs if food for juveniles is abundant and competition among juveniles is low at the less favorable site. Similar conclusions were drawn by Berven and Chadra (1988) and Sinervo (1990) who suggested that offspring from big or small eggs might have equivalent fitness depending on the environmental conditions in which the offspring develop. To test the above assumptions, experiments controlling for growth and survival rates of juveniles from a single female (low density of juveniles) and from several females (high density of juveniles) are required for each site. For each site, the number of juveniles and the amount of food must be kept constant.

These studies show that adult and offspring survival might not be independent of environmental conditions as predicted

Table 1

Effect of variation in food supply on echinoderm body weight, pyloric caeca weight, egg size and number (field and laboratory studies).

SPECIES		Source	
FIELD STUDIES			
Echinaster sp.	Favorable site	Less favorable site	
Body weight (g)	5.759	1.975	Scheibling and Lawrence 1982
Numbers of eggs	7609	954	
Leptasterias epichlora			
Body weight (g)	11.5 ± 1.9 (6)	4.5 ± 0.9 (12)	George 1994a
Egg diameter (μm)	953.1 ± 20 (288)*	802.1 ± 15.6 (288)	
Numbers of eggs	541 ± 57 (9)	307 ± 31 (10)	
Arbacia lixula			
Body weight (g)	47.1 ± 16.1 (19)	34.6 ± 8.8 (29)	George 1990a
Egg diameter (μm)	76.6 ± 3.3 (100)*	72.9 ± 3.9 (100)	
Paracentrotus lividus			
Body weight (g)	71.6 ± 18.7 (27)	46.0 ± 20.7 (34)	George 1990a
Egg diameter (μm)	92.0 ± 7.8 (100)*	89.6 ± 8.8 (54)	
LABORATORY STUDIES			
	High food	Low food	
Leptasterias epichlora			
Body weight (g)			George 1994a; George, unpublished
Favorable site	7.8 ± 1.1 (9)	7.2 ± 0.5 (6)	
Less favorable site	4.4 ± 0.6 (10)	3.0 ± 0.5 (8)	
Egg diameter (μm)			
Favorable site	949.9 ± 71.8 (243)*	956.6 ± 65.9 (242)	
Less favorable site	830 ± 60.8 (239)*	805.1 ± 54.3 (180)	
Numbers of eggs			
Favorable site	583	183	
Less favorable site	331	285	
	High	Low/Starved**	Source
Scerasterias mollis**			
Pyloric caeca index	>30%	<10%	Xu and Barker 1990a
Egg size range (μm)	83-94	79-87	
Numbers of eggs	-	-	
Luidia clathrata			
Body weight (g)	32.1 ± 1.3 (10)	24.5 ± 1.5 (10)	George et al., ; 1991
Egg diameter (μm)	165.5 ± 12.0 (100)*	178.4 ± 17.1 (100)	
Percentage fertilization	100 (100)	20 (100)	
Arbacia lixula			
Body weight (g)	43.7 ± 13.2 (10)	43.4 ± 9.5 (10)	George 1990a
Egg diameter (μm)	76.5 ± 3.0 (100)*	76.4 ± 2.9 (100)	
Numbers of eggs	0.75×10^6 (10)	0.30×10^6 (10)	
Paracentrotus lividus **			
Body weight (g)	57.4 ± 16.5 (21)	56.2 ± 15.4 (22)	George 1990a
Egg diameter (μm)	80.5 ± 6.8 (100)*	80.8 ± 5.9 (100)	
Numbers of eggs	0.8×10^6 (21)	0.4×10^6 (20)	
Strongylocentrotus droebachiensis			
Test diameter (mm)	49.8 ± 2.4 (24)	45.4 ± 0.8 (24)	Thompson 1982
Egg diameter (μm)	90.8 ± 14.5 (4)	93.3 ± 9.7 (3)	
Dry weight of gametes released (g)	1.0	0.5	
Stylocidaris lineata #	Sargassum	Thalassia	George and Young (unpublished)
Body weight (g)	6.4 ±1.6 (6)	8.2±2.0 (3)	
Egg diameter (μm)	90.8 ±14.5 (4)	93.3±9.7 (3)	
Numbers of eggs	23604 (6)	7714 (3)	

Experiments with Stylocidaris was to determine the effect of diet using Sargassum spp and Thalassia testudinum as food. Numbers of eggs in parentheses with asterisks, number of females in parentheses without asterisks.

by Morris (1992) but increase as environmental conditions improve and decrease as environmental conditions deteriorate (McGinley et al., 1987). Body weight and pyloric caeca weight of seastars from the less favorable site increased in the laboratory (Tab. 1). This indicates that food conditions in the laboratory were better than in the field leading to bigger seastars with more large eggs per gram body weight (George, 1994 a). Laboratory studies carried out during two or more reproductive seasons that determined the number of adults surviving and the number of offspring produced from one breeding season to another might give some insight as to whether survival of adults producing many large eggs or a few small eggs is equivalent.

The nutritional state and eggs of the seastar Sclerasterias mollis decreased as laboratory conditions deteriorated (Xu and Barker, 1990 b; Tab. 1). These seastars were collected in the field when active gametogenesis had started. In the laboratory, half of these seastars were fed and half starved. At the end of 55 days one lot of seastars was used to determine differences in egg sizes between treatments and at the end of 110 days another lot was used. Egg size did not differ between treatments after 55 days in the laboratory. Between the 55th and 110th day, egg size increased for both starved and fed seastars but the increase in size was less for those from starved seastars (Xu and Barker, 1990 b). This study shows that the response to variation in food supply might be influenced by the duration of laboratory experiments. Due to the sampling techniques used variation among females might account for the major part of the differences in egg sizes observed. Nonetheless, when food is scarce this seastar produces smaller eggs. Whether survival of offspring from large and small eggs differed is not known. Similar experiments were carried out for the seastar Luidia clathrata (George et al., 1991). Two replicate tanks for the high food and two replicate tanks for the low food were used and the experiments ended after 107 days in the laboratory. At low food ration, smaller seastars produced larger eggs and at high food ration larger seastars produced smaller eggs (George et al., 1991; Tab. 1). However, percentage fertilization of large eggs was lower (20 %) than that of small eggs (100 %) indicating that though the size of the egg increased its quality did not. Further investigation on the effect of food availability on egg numbers and content are needed to ascertain whether egg size and number are negatively correlated for seastars with planktotrophic larval development as predicted by some life history models.

Significant differences in egg size between field populations were observed for the sea urchins Psammechinus miliaris (Lonning and Wennerberg, 1963) and Arbacia lixula (George, 1990 b; George et al., 1990) but not for Paracentrotus lividus (George, 1990 a) (Tab. 1). The sea grass Posidonia oceanica, preferred food for P. lividus (Kempf, 1962; Traer, 1980; Maggiore et al., 1987), was found in abundant supply at the two sites studied. This might explain why no differences in egg size was detected for this species at these sites. However, P. lividus was significantly smaller at the less favorable site (Tab. 1). P. lividus might decrease growth rates to maintain egg size and quality or the population at the less favorable site might be a younger population than at the favorable site. A. lixula are generally found on rocks

covered with a dense algal cover rich in encrusting algae and exposed to considerable wave action (Kempf, 1962). George (1990 b), George et al. (1990) noted that A. lixula collected from a site with the above characteristics (i.e. exposed with a rich algal cover) were larger and produced significantly larger eggs than those from a sheltered site with a poor algal cover (Tab. 1). Thus under favorable environmental conditions, A. lixula are bigger and produce bigger eggs. This response is similar to that of the seastar Leptasterias epichlora with lecithotrophic eggs. The response to low food rations in the laboratory by these sea urchins was also similar to that of the seastar Leptasterias epichlora from the favorable site. A decrease in food ration for the shallow water sea urchins, A. lixula, P. lividus and S. droebachiensis (George, 1990 a, 1990 b; George et al., 1990; Thompson, 1982), and a difference in food quality for the deep sea urchin Stylocidaris lineata (George and Young, unpublished) led to a significant drop in egg numbers while egg size remained constant (Tab. 1). However, unlike the experimental design for the seastar Leptasterias epichlora, laboratory experiments were not run concurrently for sea urchins from favorable and less favorable sites. Thus definite conclusions as to why sea urchins maintained egg size while the numbers of eggs decreased cannot be made.

The prediction that females produce more, but smaller eggs in favorable environments and few, but larger eggs in unfavorable environments does not apply for the echinoderms examined in this review. For these echinoderms, [and many other marine invertebrates (Bayne et al., 1975, 1978; Lucas and Crisp, 1987; Hirche, 1993) and vertebrates (Horwood, 1989)], field and laboratory studies indicate that the number of eggs produced tend to decrease when food conditions deteriorate. The present studies revealed no definite pattern for the effect on egg size. In most of the echinoderms examined, egg size remained constant and in a few cases decreased when food conditions deteriorated.

Effect of adult nutritional state on the biochemical composition of the eggs

Egg size is not a reliable predictor of the content of the egg within a species (McEdward and Carson, 1987; McEdward and Coulter, 1987, and McEdward and Chia, 1991). Measuring the protein and lipid content of the eggs, important energy reserves in eggs of most marine invertebrates (Lucas and Crisp, 1987; Crisp, 1984; Holland, 1978), might give a better indication of egg quality. Under favorable environmental conditions, the sea urchin Arbacia lixula with planktotrophic eggs and the seastar Leptasterias epichlora with lecithotrophic eggs, produced large eggs rich in protein and lipid (George et al., 1990; George 1994 a; Tab. 2). Thus for these species, when environmental conditions improve, egg size and content increases irrespective of mode of development.

For Strongylocentrotus droebachiensis a decrease in food ration led to a decrease in the lipid content of the egg though egg size remained constant (Thompson, 1982; Tab. 2). For this species when food supply decreases egg quality decreases. Similarly, for the seastar Luidia clathrata a decrease in food ration led to a decrease in egg quality

Table 2

Protein and lipid content of eggs of Leptasterias epichlora, Strongylocentrotus droebachiensis *and* Arbacia lixula *(values are means ± standard deviation, number of females in parentheses; * number of filters used).*

SPECIES		Favorable	Less favorable	Source
Leptasterias epichlora	Protein content (µg/egg)	41 ± 2 (9)	31 ± 3 (9)	George 1994a
Strongylocentrotus droebachiensis	Lipid content (mg/g)	137 ± 5 (4)	125 ± 15 (4)	Thompson 1982
*Arbacia lixula**	Protein content (ng/egg)	61 ± 7 (3)	35 ± 13 (3)	George et al. 1990
	Lipid content (ng/egg)	12 ± 2 (3)	10 ± 1 (3)	George et al. 1990

(George *et al.*, 1991). The proportions of protein, lipid and water in the eggs produced by echinoderms held at high and low food rations might differ without affecting egg size. In addition, an increase in egg size might not necessarily indicate an increase in organic content (McEdward and Carson, 1987) but an increase in water content. Turner and Lawrence (1979), Craik and Harvey (1987), Kjesbu *et al.* (1992) and Nissling *et al.* (1994) indicated that the nutritional state of the female affects not only the protein and lipid content of the eggs but also its water content and thus egg buoyancy. Nissling *et al.* (1994) noted that egg buoyancy increased with successive spawnings from the same female but egg quality and larval viability decreased. They noted that this might affect egg and larval survival. Thus in experimental studies on the effect of food availability on egg quality, the protein, the lipid and the water content of echinoderm eggs need to be analysed and these parameters need to be considered by life history models. Variation in food supply might also account for the seasonal and annual differences in egg size and content observed for some echinoderms (Turner and Lawrence, 1979; Emlet *et al.*, 1987; George, 1990 *b*).

Effect of adult nutritional state on larval growth, development and metamorphosis

Studies on the effect of the nutritional state of the adult on larval growth and development are scanty. Kawamura (1973) noted that larvae of the sea urchin *Strongylocentrotus intermedius* collected from 0.5 meters depth developed faster and had higher survival rates than those from 5 meters depth. Only a few females were used in this study and laboratory experiments were not carried out to determine the effect of food on adult nutritional state, egg and larval quality from different depths. Nonetheless, the differences observed in larval growth and development might be due to variation in adult nutritional state with depth. The present review examined in more detail the consequences of variation in adult nutritional state on subsequent larval growth, development and metamorphosis. Echinoderm larvae from females that had been exposed to different environmental conditions (in the field and in the laboratory) were cultured using a system of swinging paddles (Strathmann, 1987) or a rotating drum to which twelve to twenty four culture jars were attached. For larvae with planktotrophic larval development, a mixture of algal
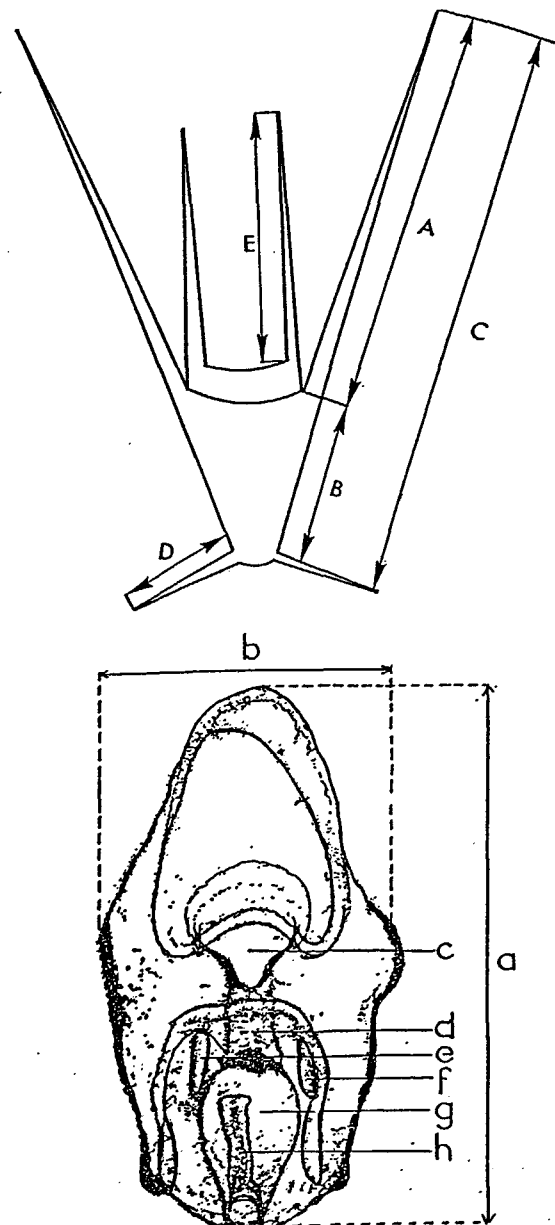

Figure 1

A) Body outline of a six-armed larva of A. lixula *(not drawn to scale). A. postoral arm; B, somatic arm; C, total larval length; D, posterolateral arm; E, anterolateral arm. B) Bipinnaria of* L. clathrata. *a) larval length, b) larval width, c) mouth; d) œsophagus; e) and f) left and right coelomic pouches, g) stomach; h) intestine.*
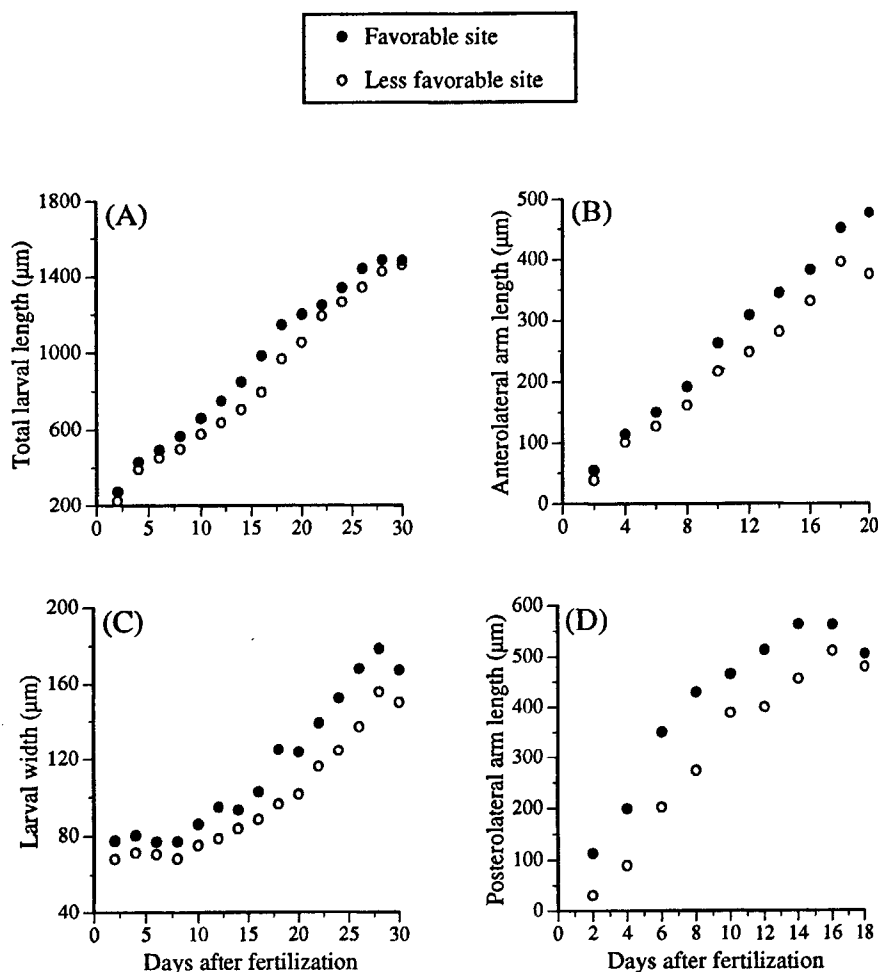
Figure 2

Growth of A) total larval length, B) anterolateral arm length, C) larval width, D) posterolateral arm length from Arbacia lixula *collected from a favorable and less favorable site (means plotted).*

Table 3

Protein and lipid content (ng/larva or juvenile) for Arbacia lixula *and* Paracentrotus lividus *from a favorable and a less favorable site. Values are means ± standard deviation. n in parentheses corresponds to number of filters used for protein and lipid analyses.*

SPECIES	Favorable site	Less favorable site
Arbacia lixula		
Total protein content		
26 days after fertilization	3244.3 ± 103.6 (3)	2707.0 ± 80.0 (3)
30 days after fertilization	4250.0 ± 29.7 (3)	3781.0 ± 227.9 (3)
Total lipid content		
26 days after fertilization	1689.0 ± 85.9 (3)	1044.3 ± 9.3 (3)
30 days after fertilization	2293.0 ± 50.9 (3)	1828.7 ± 126.5 (3)
Total lipid content of juveniles		
34 days after fertilization	2029.0 (1)	2085.5 (2)
Paracentrotus lividus		
Total protein content		
6 days after fertilization	129.0 ± 9.3 (5)	112.1 ± 1.8 (5)
8 days after fertilization	169.0 ± 4.2 (5)	162.1 ± 10.1 (5)
10 days after fertilization	180.8 ± 11.5 (5)	211.3 ± 13.4 (5)
14 days after fertilization	501.8 ± 38.0 (5)	462.3 ± 17.0 (5)
Total lipid content		
6 days after fertilization	48.3 ± 1.9 (5)	41.8 ± 7.0 (5)
8 days after fertilization	64.8 ± 13.0 (5)	48.8 ± 6.6 (5)
10 days after fertilization	58.0 ± 5.9 (5)	59.1 ± 40.2 (5)
12 days after fertilization	109.2 ± 20.2 (5)	96.0 ± 15.0 (5)

cells *Isochrysis galbana* (Parke), *Hymenomonas elongata* Droop (Parke and Green), and *Dunaliella tertiolata* were provided. Cultures were changed every two days and food added. To ascertain differences among larvae from adults with different past nutritional states morphometric measurements and biochemical analyses were made. For the sea urchin *Paracentrotus lividus* total larval length (the length of the post-oral and somatic rods) was measured, for *Arbacia lixula* the antero-lateral, postero-lateral rods and total larval length were measured (Fig. 1a). For the seastar Luidia clathrata the length and width of the larvae and the length of the left and right coelomic pouches were measured (Fig. 1b). The seastar *Leptasterias epichlora* was observed to abandon its brood when disturbed. To avoid loosing broods larval measurements were not made during the brooding period. At the end of the brooding period (2.5 months approximately) the size, number and protein content of newly metamorphosed juveniles were made.

Larvae produced by sea urchins (*Arbacia lixula* and *Paracentrotus lividus*) in favorable environments were larger with a higher protein and lipid content than those produced by sea urchins in less favorable environments (George, 1990 a; George, 1990 b; George et al., 1990; Tab. 3, Fig. 2 a to 2 d, and Fig. 3 a). For these sea urchins, larval survival was higher, the duration of a larval stage was shorter and the percentage of larvae that passed to a new stage was always higher for those produced by females from favo-

rable sites than for those from less favorable sites (George, 1990 a; Figs. 4 and 5 a). Thus favorable conditions for the adults is translated into the production of high quality eggs. Larvae from these high quality eggs, grow bigger, and develop faster. Planktonic predation during the early larval stages might be low for rapidly growing larvae (Thorson, 1950; Sinervo and McEward, 1988). Starvation might also have less of an effect on larvae from high quality eggs than on larvae from low quality eggs. When sea urchin larvae from parents in favorable and less favorable environments are raised under optimal food conditions in the laboratory initial differences in total larval length and developmental rates disappeared by the end of the developmental period (Figs. 4 and 5 a). When sea urchin larvae were raised under sub-optimal food conditions differences persisted till the end of the developmental period (Figs. 5b and 6a to 6c). When *Arbacia lixula* larvae from parents in favorable and less favorable environmental conditions were starved continuously for 14 days larvae produced by parents from favorable sites had longer larval arms than those from less favorable sites (George, 1990 b). Similarly, when the density of *P. lividus* larvae was increased from 1 larva / ml to 5 larvae / ml keeping the amount of food constant (*i.e.* decreasing the amount of food available per larva), larvae produced by parents from favorable sites grew bigger and developmental rates were faster throughout the larval developmental period, than those from less favorable sites (Figs. 4, 5 b). Larvae from parents in less favorable sites did not develop rudiments and mortality rates were high 16 days after fertilization. These studies indicate that the presence of initially greater vitellogenic reserves leads to larvae with longer arms. This is advantageous as with longer larval arms and thus longer ciliated bands and higher clearance rates (Strathmann *et al.*, 1992; Fenaux *et al.*, 1994; Hart and Strathmann 1994; George, 1994 c) larvae have the possibility of developing faster and surviving longer.

The effect of different egg quality on larval growth and development differed between these sea urchins and the seastar *Luidia clathrata*. Luidia larvae from low quality eggs were bigger although larval survival was lower (50 %) than for those from high quality eggs (80 % survivorship) (George, 1990 a; George *et al.*, 1991). This indicates that larval size like egg size might not be a good indicator of quality.

During the competent period *Arbacia lixula* larvae from females in favorable environments had a higher protein and lipid content than larvae from females in less favorable environments (George *et al.*, 1990). This might have led to the high percentage metamorphosis observed for larvae from females in favorable environments (Tab. 4). However, juvenile size and content did not vary (George, 1990; George *et al.*, 1990; Tab. 3). For these sea urchins, the past nutritional state of the female affects larval growth, development and percentage metamorphosis but not juvenile size and content. For the seastar *Leptasterias epichlora*, the past nutritional state of the female affects juvenile size and content. This seastar produced large numbers of large juveniles, with a high protein content when conditions were favorable and a few small juveniles with a low protein content when conditions were less favorable (George, 1994 a; Tab. 5). The diffe-
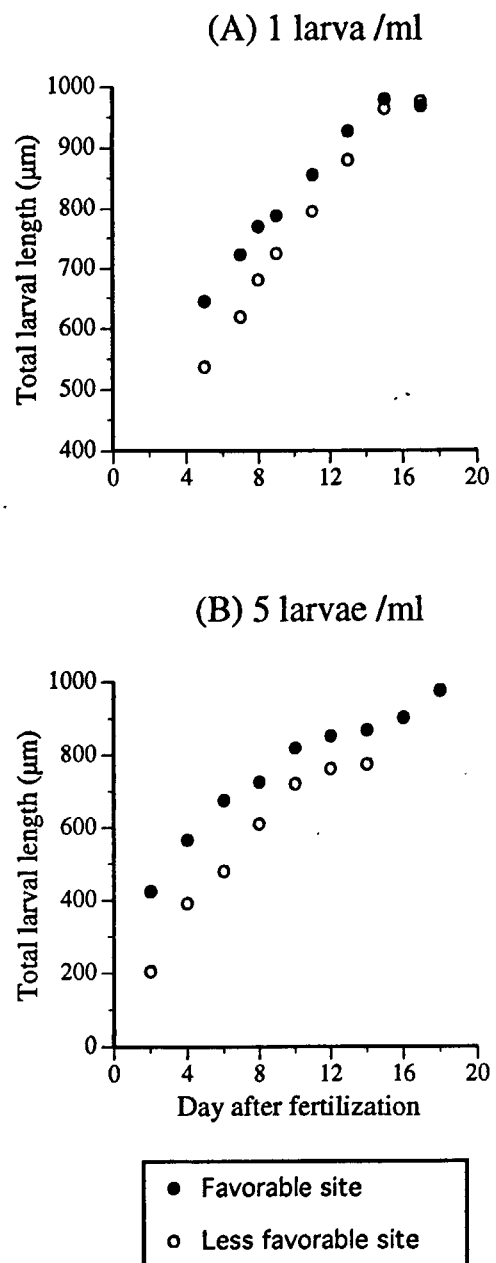

Figure 3

Mean total larval length of Paracentrotus lividus *at A) low density, 1 larva / ml B) high density, 5 larvae / ml. Adults collected from a favorable and less favorable site.*

rences observed between the sea urchin Arbacia lixula and the seastar *Leptasterias epichlora*, might be due to the type of larval development. There is little change in total organic content from egg to metamorphosis for echinoderms that brood their young (Turner and Rutherford, 1976; Lawrence *et al.*, 1984; McClintock and Pearse, 1986, and George, 1994 a; Tab. 5). Thus while sea urchin larvae with planktotrophic development can compensate for initial differences in egg quality, by feeding in the plankton seastar larvae with lecithotrophic brooding development cannot. This is a disadvantage for species with this type of development because under unfavorable conditions if females produce low quality eggs it might result in low quality juveniles.
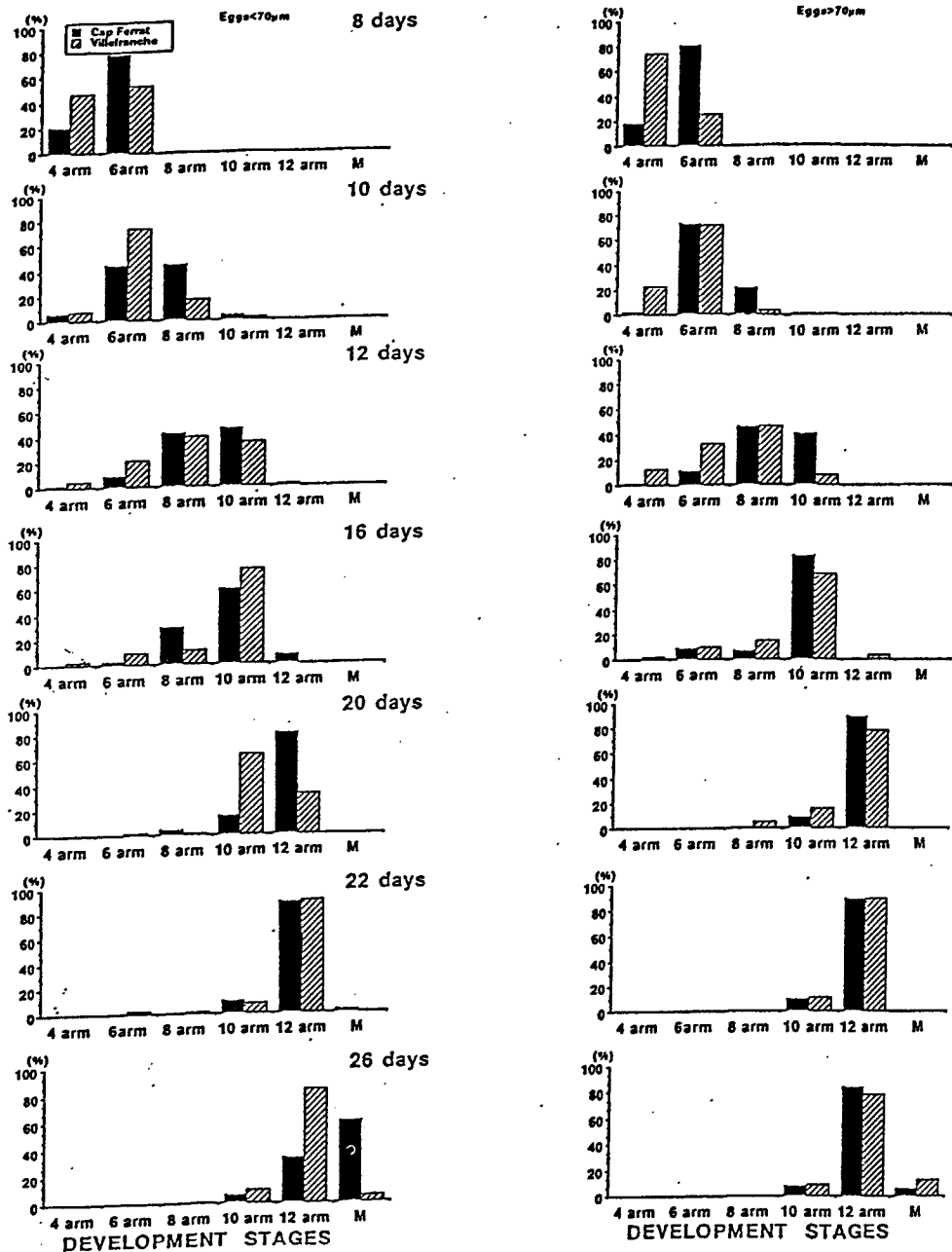
Figure 4

Percentage of Arbacia lixula *larvae at different developmental stages [four-armed larvae to metamorphosis (M)] from individuals from Cap Ferrat = favorable site and Villefranche = less favorable site (after George* et al., *1990).*

Table 4

Percentage metamorphosis and diameter of juveniles (μm) for Arbacia lixula *and* Paracentrotus lividus.

| SPECIES SITE		Days after fertilization				
		26 days	28 days	29 days	30 days	
A) Percentage metamorphosis						
Arbacia lixula						
Favorable		60.0	50.0	50.0	69.2	
Less favorable		5.0	30.0	30.0	41.3	
		Days after fertilization				
Paracentrotus lividus		21 days	22 days	23 days	24 days	25 days
Favorable		30.8	32.7	50	48.6	51.6
Less favorable		11.5	30.8	88.6	48.9	44.7
B) Juvenile sizes	Days after fertilization	Favorable site			Less favorable site	
Arbacia lixula	29	442.4 ± 42.9 (16)			473.9 ± 63.6 (20)	
	32	395.0 ± 36.1 (17)			386.0 ± 27.0 (13)	
Paracentrotus lividus	21	296.9 ± 19.4 (12)			300.1 ± 17.0 (8)	
	24	321.0 ± 27.6 (12)			325.8 ± 26.6 (18)	
	25	363.6 ± 22.1 (13)			337.5 ± 15.5 (13)	
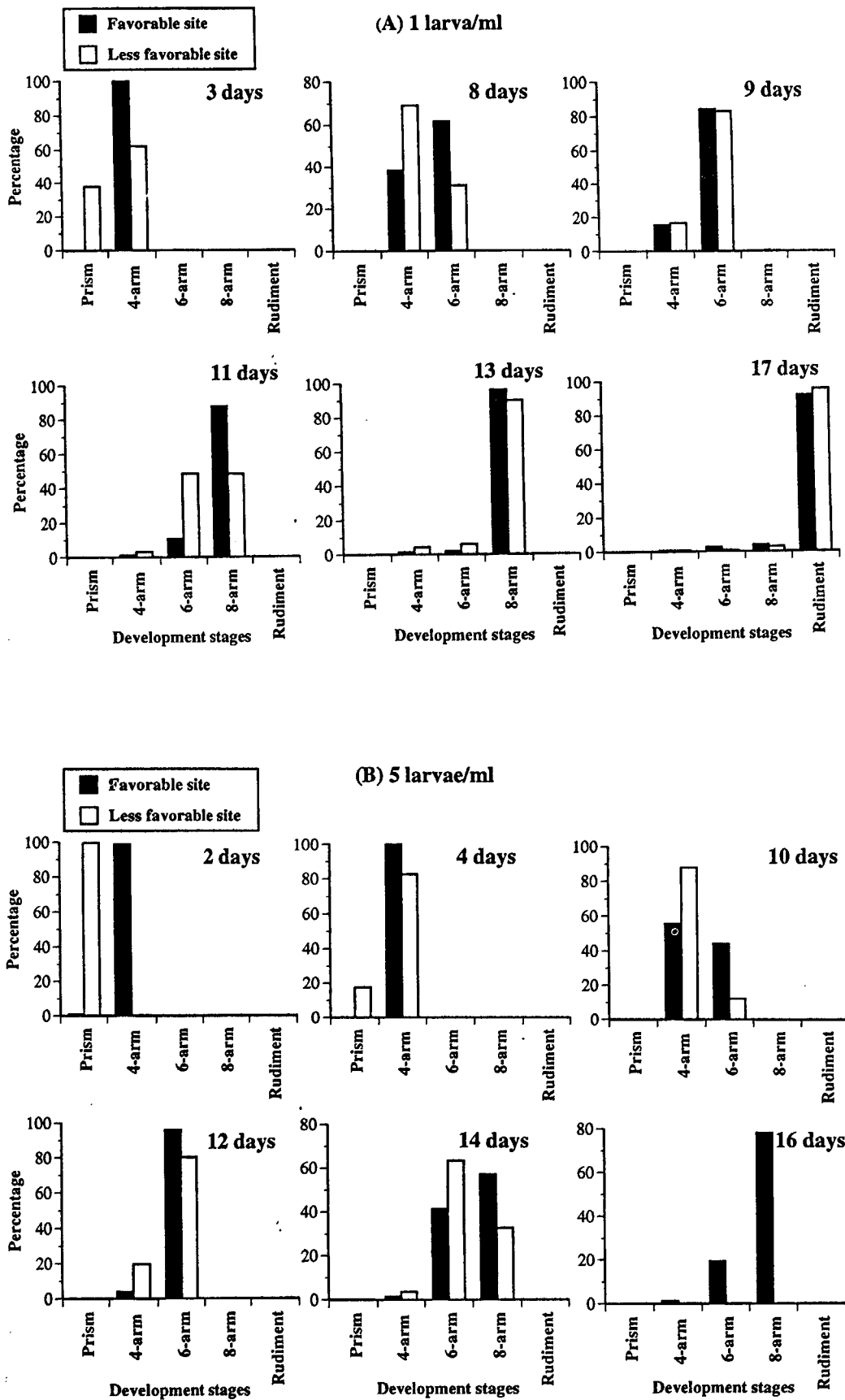
Figure 5

Percentage of larvae at different developmental stages (prism to rudiment stage) for Paracentrotus lividus *at A) low density, 1 larva / ml and B) high density 5 larvae / ml. Adults collected from Cap Ferrat = favorable site and Ville-franche = less favorable site.*

● Cap Ferrat   O Villefranche sur Mer

Days after fertilization
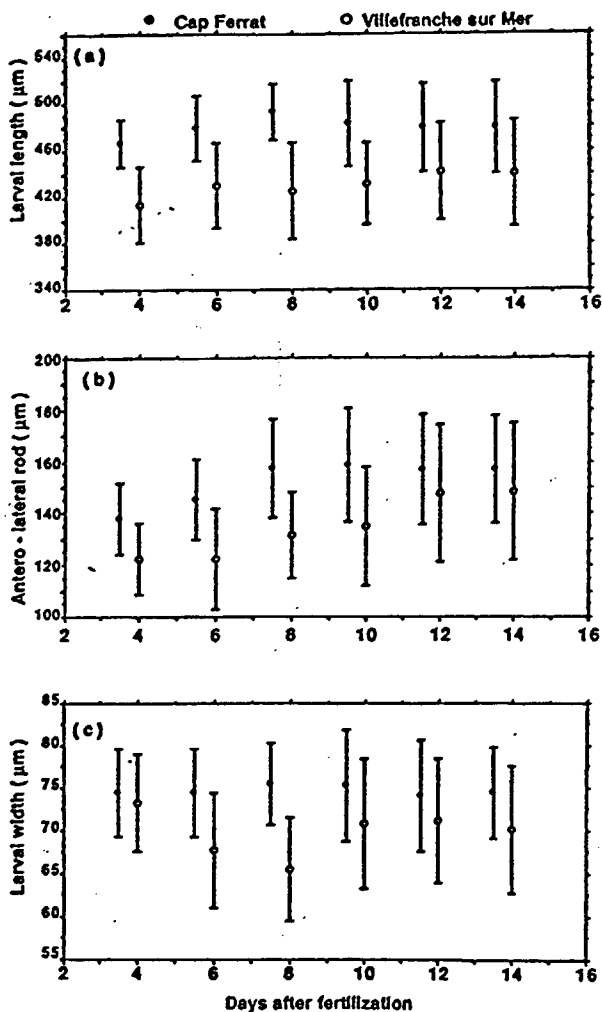
Figure 6

Growth of A) larval length, B) anterolateral arm length, and C) larval width, for starved Arbacia lixula larvae. Adults collected from a favorable and a less favorable site (means ± standard deviation, after George, 1990 b).

CONCLUSIONS

This review has highlighted the importance, and the paucity of data on the consequencies of variation in adult nutritional state on egg quality, subsequent larval growth, survival and development to metamorphosis. The failure of their use in life history models might explain discrepancies between theory and observation. The complexity of the different factors that could be correlated with both egg size and number in the field point to the value of laboratory experiments where these variables can be controlled. However, the response to food availibility in the laboratory is influenced by a combination of factors, the collection site, sample size, adult nutritional and gametogenic state at the time of collection, the food type, the duration of experiments, feeding strategies, and digestive constraints of echinoderms. To ease comparison between studies, some of these factors need to be carefully controlled in future experiments with other echinoderm groups.

This review has shown that conclusions from constant egg size or differences in egg size in response to variation in food supply could be misleading. The content of the egg might change without affecting egg size and large eggs might contain more water. Mareci *et al.* (1991) succeeded in measuring the relative amounts of water and lipids in the embryos (diameter = 4 mm) of the lizard *Sceloporus undulatus* using magnetic resonance imaging (MRI). Using this technique they were able to identify water and lipid stores in different parts of the embryo. Similar techniques could be developed to measure the lipid and water content of echinoderm eggs non destructively and embryos could be allowed to develop normally (McEdward, pers. comm.). This might aid in determining whether large energy-poor eggs are larger simply because they contain more water. An attempt could be made to correlate lipid/water ratios from NMR spectroscopy with lipid*/egg volume ratios (lipid* being obtained from biochemical analysis of a single egg). This might be a major breakthrough in the development and testing of life history models for marine invertebrates. Providing echinoderms with supplemental food of different compositions (*e.g.* high protein and low lipid) might allow determination of the potential nutrient constraints on egg production. In addition, experimental manipulation of egg size and composition (Sinervo and McEdward, 1988; Sinervo, 1990; Bernardo, 1991) might aid in understanding how these parameters affect offspring survival.

Acknowledgements

Table 5

a) The number and b) the diameter of juveniles (μm) produced by brooding females of Leptasterias epichlora from a favorable and less favorable site, maintained in the laboratory under high and low food rations. Wet body weight in parentheses. c) Protein content of eggs and juveniles (μg) of Leptasterias epichlora from field and laboratory studies. Number of samples in parentheses.

	FAVORABLE SITE		LESS FAVORABLE SITE	
a) Numbers of juveniles produced				
	HIGH FOOD	LOW FOOD	HIGH FOOD	LOW FOOD
Female 1	480 (9.5)	82 (8.7)	300 (3.5)	180 (1.5)
Female 2	321 (8.0)	75 (5.6)	125(3.1)	71 (1.9)
Female 3	337 (3.9)	–	–	219 (2.5)
Female 4	757 (10.9)	–	–	200 (2.3)
b) Diameter of juveniles (mm)				
Female 1	2.2 ± 0.4 (10)	1.4 ± 0.3 (10)	1.4 ± 0.2 (10)	1.4 ± 0.3 (10)
Female 2	1.8 ± 0.5 (10)	–	1.6 ± 0.3 (10)	1.3 ± 0.1 (10)
Female 3	1.7 ± 0.3 (10)	–		1.3 ± 0.2 (10)
Female 4	1.6 ± 0.4 (10)	–		1.4 ± 0.3 (10)

	FAVORABLE SITE	LESS FAVORABLE SITE
c) Protein content of eggs and juveniles		
Protein content of eggs	40.470 (42)	31.046 (46)
Protein content of juveniles	56.225 (40)	33.260 (36)

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