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Stress and Deviant Reproduction in Echinoderms

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ABSTRACT

John M. Lawrence and Joan Herrera (2000) Stress and deviant reprodction in echinoderms. *Zoological Studies* **39**(3): 151-171. Normal reproductive characteristics in echinoderms include non-maternal nutrition with a planktonic feeding developmental stage, sexual reproduction with gonochorism, seasonal reproduction, and no protection of young by secondary metabolites. Deviant reproductive characteristics include maternal nutrition of the developmental stage that may be planktonic, demersal, or brooded; hermaphroditic sexual reproduction; intermittent or continuous low-level reproduction; protection of young by secondary metabolites; and asexual reproduction. We tested the hypothesis that stress, which causes a decrease in capacity for production, was a factor responsible for deviant reproductive characteristics by comparing taxa from the subphylum to species levels. In the examples used, deviant reproduction occurred in the taxa for which stress could be predicted. Although other factors undoubtably affect reproductive characteristics, the analysis indicates that stress must be considered an important one.

Key words: Echinoderms, Stress, Reproduction, Life-history.

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INTRODUCTION

The repetition of reproduction followed by differentiation and growth comprises the life cycle. The processes an individual undergoes from its production to its death involve a series of stages that constitute its life history. In asexual reproduction, the only stages are the individual and the asexual products. With sexual reproduction, more stages exist. Some stages are ubiquitous, such as the gamete, zygote, embryo, juvenile, and adult (reproductive stage) that occur in a simple life cycle. An additional stage, the larva, occurs between the embryo and juvenile stages in a complex life cycle. The stages between the zygote and the adult vary in morphology, location, and nutrient source (Chia 1974, McEdward and Janies 1993 1997, Hickman 1999). A continuum exists in marine invertebrates between extreme obligate planktotrophy and functional lecithotrophy (i.e., facultative planktotrophy) to complete lecithotrophy or dependence upon the parent for development (Herrera et al. 1996). Planktotrophy is considered the pleisiomorphic condition in the life cycle pattern in marine invertebrate phyla (Jägersten 1972, Strathmann 1978 1993), although it has been suggested that a holopelagic planktotroph similar to contemporary planktotrophic larvae was the original adult from which a revolutionary 2nd developmental program emerged, resulting in the contemporary adult (Davidson et al. 1995, Ransick et al. 1996, Cameron et al. 1998, Nielsen 1998). Raff (1999, p. 256) stated that he favored the hypothesis that the first metazoans were small and produced a small number of large eggs that underwent direct development, and that the evolution of large body size made possible the production of large numbers of small eggs and feeding larvae of complex life cycles.

Whichever the case, it is thought that feeding larval stages have been lost in the extant phyla but rarely gained in the world's oceans since Paleozoic times (Strathmann 1993, Levin and Bridges 1995, Wray 1995). The question is obvious: What selective pressure could be sufficient to counter the apparent adaptiveness or stability of a feeding larval stage as indicated by its wide occurrence and persistence? Pechenik (1999) listed the advantages and disadvantages associated with a larval (i.e., planktonic) stage. McMillan et al. (1992) stated that loss of the feeding stage in marine invertebrates often is not associated with major changes in adult morphology or ecology. However, it is likely that the loss of the feeding stage is associated with such changes and that it is adaptive, if not for the adult then for the developmental stage itself. Although each stage should be subject to evolution independently (Jägersten 1972, Strathmann 1978, Calow 1984, Wray 1995, Smith et al. 1996), the characteristics of each stage undoubtedly have consequences for the other stages. The degree to which the characteristics of the developmental stages are coupled with those of the adult is an important question.

Variation in reproduction is not restricted to the type of development. Most marine invertebrate groups have separate sexes (gonochoric), do not protect their young, and have reproductive cycles; but many species do not conform to these characteristics. Why not? Recognizing the complexity of living systems, one should not expect that a single control exists, but we suggest that 1 factor, energy, affecting reproductive success may be involved in all characteristics. This results from the fact that reproduction necessarily involves transfer of part of the parents' bodies to the offspring.

The provision of nutrients (energy) has been used as a criterion to define the development stages of marine invertebrates (Chia 1974, Giese and Pearse 1974, Strathmann 1993, Herrera et al. 1996, McEdward 1997, McEdward and Janies 1997). Kooijman (1993) used energy acquisition and allocation to separate the life history of animals into 3 stages: embryo, juvenile, and adult (Figs. 1, 2). The

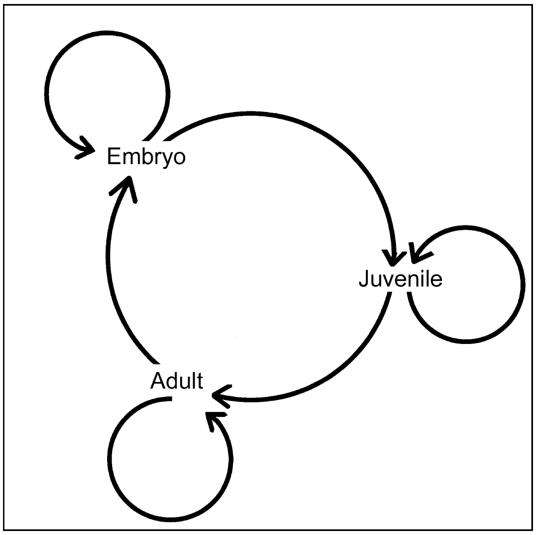

Fig. 1. Stages in a life cycle based on source of nutrients, growth, and reproductive condition (modified from Kooijman 1993). The embryo receives its nutrients from the mother; the juvenile and adult do not. The juvenile grows; the adult typically does not. The adult is reproductive; the juvenile is not. Asexual reproduction in echinoderms occurs in the field in the adults of some species and in the juveniles of several species. Asexual reproduction is known from echinoderm embryos in the laboratory but has not been reported from the field.

embryo is dependent on energy supplied by the mother; the juvenile and adult are not. By Kooijman's criteria, the embryo does not feed; the juvenile and adult do. The juvenile grows, the adult does not. The adult is reproductive; the juvenile is not. By this definition, the traditional larva would be a juvenile if it feeds externally, an embryo if it does not. To Kooijman, the embryo relies on energy obtained from the mother. The amount of energy provided by the mother varies in marine invertebrates, so a continuum exists from that required for a completely feeding developmental stage to a completely non-feeding developmental stage (Herrera et al. 1996). The important point is the difference in the source of energy used for growth by the developmental stage. The juvenile allocates resources to maintenance and growth. The adult allocates resources to maintenance and reproduction as well as to growth in some species.

Although Kooijman's terms are jarring because of their differences from traditional usage, the value of his criteria for the embryo, juvenile, and adult is that they explicitly recognize the basis for the tradeoffs of resources: parent and offspring; reproductive and somatic production. It is important to note that this does not consider other criteria which have been used to define the developmental stage including post-embryonic morphogenesis, stage-specific structures, metamorphosis, and location (Thorson 1950, Mileikovsky 1971, Chia 1974, McEdward and Janies 1993, Levin and Bridges 1995). These other characteristics of developmental stages obviously are subject to selection themselves. Thus Pechenik (1999) considered the advantages and disadvantages of the larva defined by whether or not it is located in the plankton, with no consideration of the source of nutrients. To avoid the contentious issue of what constitutes an embryo or larva (Hickman 1999) which is not pertinent to our purpose, we shall refer to both as the developmental stage and only distinguish between non-feeding and feeding (Fig. 1). This allows us to focus on the role of stress in reproduction and development. Whether the developmental stage is planktonic or not is another issue that clearly affects reproduction and development (Pechenik 1999).

Grime (1979) emphasized the role of stress in determining the life-history strategies of organisms. He defined stress as environmental factors that cause a decrease in the capacity for production resulting from environmental conditions. Thus stress has consequences for the functioning of an individual and the life-history characteristics of a species. Stress is often considered only in terms of physical environmental factors such as temperature and salinity (Hoffman and Parsons 1991), but in more general terms, it is the result of any environmental change that decreases production (Levitt 1972). Just as the low availability of nutrients (such as nitrates and phosphates) required for production is a stress for plants, low availability of food or a low capacity to obtain food resulting from environmental or structural constraints is a stress for animals (Roff 1992, Rollo 1994). Constraints of body structure that limit the potential to store production seem a reasonable extension of the concept. Stearns (1992, p. 154) observed that morphology and physiology affect feeding as well as the storage and use of reserves, and that these physiological constraints limit the number of young that can be produced. We propose that a decrease in energy available for production is a cause of deviant reproduction in echinoderms and may be responsible for their diverse strategies. Although most echinoderms have a number of reproductive characteristics in common, a number show deviant characteristics (Table 1). The deviant characteristics can be proposed to be adaptations to stress that increase the probability of completion of the developmental stage.

1. Non-feeding development eliminates the exposure of the developmental stage to inadequate food. All provision for development comes from the mother by direct supply of nutrients to the egg or developing individual. The resulting effect on fecundity is the basis for the well-known trade-off models (Vance 1973, Roff 1992, McEdward 1997). Trade-off models involving egg size/egg number typically consider the absolute amount of energy allocated to reproduction (reproductive output) or the proportional amount of the gonads to the whole body (reproductive index) rather than the relative amount of energy consumed that is allocated to reproduction (reproductive effort). It is the latter, reproductive effort, that is essential for constructing energy budgets and for interpreting life history characteristics (Roff 1992, Kooijman 1993). We agree with Havenhand (1994) that the measures purported to calculate reproductive effort have varied and should not be expected to show any meaningful pattern of

Embryo	Juvenile	Adult
maternal resources	non-maternal resources	non-maternal resources
non-reproductive	non-reproductive	reproductive

Fig. 2. Matrix of life-history stages based on source of energy and reproductive state.

association with larval type. It is important to recognize that non-feeding development may or may not be planktonic. Pechenik (1999) referred to all free-living developmental stages as larval, whether feeding or not, and considered the advantages and disadvantages of the free-living developmental stage.

2. Hermaphroditism should be adaptive by increasing the probability of successful fertilization (Ghiselin 1987).

3. Intermittant reproduction is predicted in habitats with low and variable food availability as resources are too low for a high reproductive effort and too erratic for synchrony (Grime 1979). Tyler (1986 1988) noted aperiodic reproduction to be the dominant pattern in the deep sea. Hendler (1991) suggested unpredictable food resources might result in asynchronous reproduction.

4. Protection increases the probability of survival of the developmental stages. Physical protection is provided by the mother holding the developmental stages on or within its body. In most cases, it is usually associated with non-feeding development (Philip and Foster 1971, Strathmann and Strathmann 1982, Giese and Kanatani 1987). However, nutrient provision during development can be direct by maternal feeding or indirect by adelphophagy. Brooding requires provisioning by the mother as the developmental stage cannot feed on external resources except perhaps dissolved organic material (Manahan 1990). Eggs can be provisioned with secondary metabolites to provide chemical protection from predation (McClintock and Pearse 1987, McClintock and Vernon 1990). Brooded larvae are less palatable and have aposematic coloration, being more brightly colored that planktonic larvae (Lindquist and Hay 1996).

5. Asexual reproduction by fission or arm autotomy is the ultimate lower limit of the offspring-parent ratio, 2:1, and is the extreme response to stressful conditions that limit production. It is also the rarest. The existence of closely related and often sympatric pairs of fissiparous and non-fissiparous species suggests adaptiveness. Sibly and Calow (1986, p. 141) predicted that when sexual and asexual reproduction are possible within a particular taxonomic group, the latter will be favored if the potential for production is low. We know of no echinoderm with obligatory asexual reproduction, although it may be the primary or sole mode of reproduction in populations (e.g., Emson 1978, Ottesen and Lucas 1982, Mladenov et al. 1983, Emson and Wilkie 1984, Mladenov et al. 1986, Emson and Mladenov 1987, Mladenov and Emson 1988, Chao et al. 1994).

It is noteworthy that the occurrence of these deviant characteristics is often rare except within a taxon, ranging from class to genus. This indicates that, although conditions may be appropriate for these traits to evolve, the change does not come about readily and is not obligatory. The deviant characteristics seem to occur individually except for the well-known association of hermaphroditism and brooding with small size (Strathmann et al. 1984, Ghiselin 1987). Brooding may be constrained to small-sized individuals by allometric effects (Strathmann et al. 1984), but both brooding and hermaphroditism may be adaptations to a limited capacity for reproduction in small-sized individuals.

What is the ultimate explanation for these deviant reproductive characteristics? Although any of them may be associated with environmental or biological conditions that can be considered stressful, this does not prove that they are adaptations to stress. The interpretation would be supported, however, if deviant reproduction occurs in unrelated taxa that are subject to stress (convergent evolution) or occurs in a taxon subject to stress but not in related taxa not subject to stress (divergent evolution). It would be disproven if deviant reproduction occurs contrarily to the direction predicted by convergent or divergent evolution unless a phylogenetic link can be

Table 1. Normal and deviant reproductive characteristics in echinoderms

Normal	Deviant
1. Non-maternal nutrition: planktonic, feeding developmental stage	1. Maternal nutrition: 1.1. Feeding developmental stage (viviparity). 1.2. Non-feeding developmental stage. 1.2.1. Planktonic 1.2.2. Demersal 1.2.3. Brooded
2. Gonochoric	2. Hermaphroditic
3. Seasonal reproduction	3. Intermittent or continuous low-level reproduction
4. No chemical protection of young	4. Chemical protection of young
5. Sexual reproduction	5. Asexual reproduction

shown. Here we present examples of divergent evolution within taxa as an approach to understanding the basis for deviant reproduction in echinoderms.

DIVERGENT EVOLUTION AT THE SUBPHYLUM LEVEL

Crinoidea and extant Eleutherozoa

The Crinoidea (Pelmatozoa) (Fig. 3) appeared 530-500 million years ago (Smith 1988) and are a primitive sister group of the extant Eleutherozoa (Asteroidea, Ophiuroidea, Echinoidea, Holothuroidea) (Smith 1984, Littlewood et al. 1997). Yet the developmental stage of extant crinoids has no mouth and does not feed (Holland 1991). This contrasts with the extant eleuthrozoans, in which a feeding developmental stage is common. Strathmann (1978), followed by McEdward et al. (1988) and Holland (1991), proposed the extinction of all crinoids with a feeding developmental stage and the continuation of those with non-feeding development. Although the irreversibility of the change would be the historical explanation for the uniformity of the condition in all extant crinoids, neither Strathmann, McEdward et al., nor Holland considered why the change occurred. A lack of food for the larvae is a plausible scenario, but so is high predation on the larva. Stress on the adult through a direct effect of a lack of food, an indirect effect through the inability to feed efficiently, or anatomical limitations on gonad production are others. Certainly crinoids can feed very effectively when food availability is high, which suggests a high capacity for production. Life-history characteristics of some crinoids reflect this high capacity for production, e.g., *Antedon bifida* is an annual species living in dense populations in the shallow, food-rich waters of the northeast Atlantic Ocean, reproducing in the spring following their year of birth (Lahaye et al. 1990). But non-feeding development in crinoids does not entail the usual increase in egg size, which ranges from 100 to 300 µm (Messing 1984). The fecundity of crinoids is low even with their small egg size (Mladenov 1986, McClintock and Pearse 1987). Does this mean a potential trade-off between egg size and fecundity is not possible because of physical or anatomical constraints resulting from the location of the ovaries on the arms that reduce the amount of eggs that can be produced? McEdward et al. (1988) suggested the restriction of the gonads to the pinnules might limit fecundity and egg size.

Other adaptations which increase survival of the developmental stage are not widespread. Protection of the developmental stage on or in the mother's body occurs in a few stalkless crinoids, primarily in Antarctic species (Holland 1991). Does the higher occurrence of protection in the Antarctic indicate a greater selective pressure there? The eggs are white or pale yellow in the Bahamian *Endoxocrinus* and *Cenocrinus* (C. Young, pers. comm.), white-beige to yellow in *Antedon bifida* (N. Holland, M. Jangoux, pers. comm.), and pink in *Comanthus japonicus* (N. Holland, pers. comm.) and *Florometra serratissima* (P. Mladenov, pers. comm.). Whether the pink color is both a protective secondary metabolite and aposematic coloration is not known.

DIVERGENT EVOLUTION AT THE SUBCLASS LEVEL

The Cidaroidea and the regular Euechinoidea (Echinoidea)

The regular (radially symmetrical) sea urchins are distributed between 2 distinct subclasses: the Cidaroidea, which contains the cidaroids, and the Euechinoidea, which contains all other echinoids.

Fig. 3. The stalked crinoid, *Neocrinus decorus*. (Photograph by Charles Messing)

Among the major differences separating the 2 groups are those associated with the feeding structures, the lantern, and the perignathic girdle. The cidaroids are considered to have less efficient feeding structures (Kier 1974, De Ridder and Lawrence 1982, Smith 1984, Lawrence 1987) and to eat lower-quality food (De Ridder and Lawrence 1982). Consequently they should show less capacity for production. Non-feeding developmental stages and brooding of the developmental stages are more prevalent in cidaroids than in regular euechinoids (Emlet et al. 1987). Entire orders of euchinoids lack species with non-feeding development. All cidaroid species with non-feeding development are in a single family (Cidaridae) that also contains species with feeding development.

Brooding is found in only 2 extant species of regular euechinoids in 2 distinct families (Emlet et al. 1987) and in only 4 genera of extinct regular euechinoids (Philip and Foster 1971). One of the brooding extant euechinoid species is a temnopleurid, *Hypsiechinus coronatus* (Fig. 4), which is found in the deep sea in the far northern North Atlantic and feeds on bottom material and decayed wood (hardly a productive situation). They are "real pygmies" (down to 6-7 mm diameter) according to Mortensen (1943). Mortensen suggested that egg size indicated feeding development in several species and non-feeding development in 1 species of this deep-sea subfamily (Trigonocidarinae). The retention of feeding development in most species of the subfamily, despite their tiny size and low-quality food, is notable. It is possible they have retained the ancestral condition, but brooding in 1 species and apparent non-feeding development in another within the group indicate that the historical condition was overcome. Non-feeding development is relatively recent in all echinoids, including cidaroids, as the fossil record indicates it first appeared and was independently adopted in 9 clades immediately prior to the Cretaceous-Tertiary boundary (Jeffery 1997).

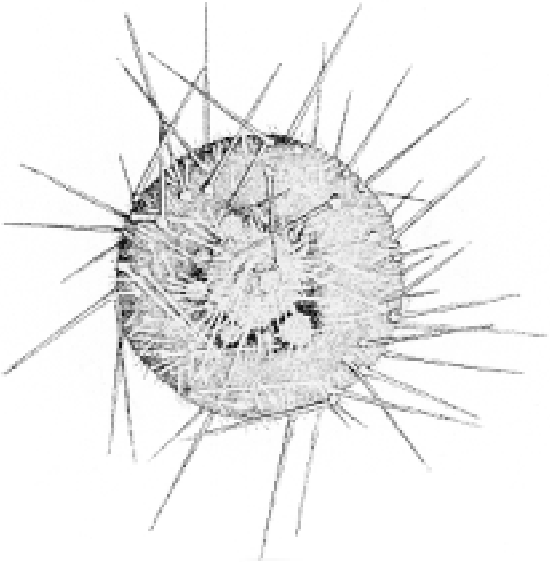

Fig. 4. *Hypsiechinus coronatus*: female with young in the marsupium on the aboral surface. (from Mortensen 1943).

DIVERGENT EVOLUTION AT THE SUPER-ORDER LEVEL

Arbacia, Tetrapygus (Superorder Stirodonta, Order Arbacioda), *Echinus, Loxechinus, Strongylocentrotus, Paracentrotus, Lytechinus,* and *Tripneustes* (Superorder Camerodonta, Order Echinoida) produce small eggs with a feeding developmental stage. The eggs of different orders of sea urchins differ in color. Those of *Arbacia* and *Tetrapygus* (Superorder Stirodonta, Order Arbacioda) are purple while those of *Echinus, Loxechinus, Strongylocentrotus, Paracentrotus, Lytechinus,* and *Tripneustes* (Superorder Camerodonta, Order Echinoida) are yellow. Smith (1984) pointed out that the camarodont lantern is mechanically stronger than the earlier stirodont lantern (Fig. 5) and that the camerodonts became the dominant regular echinoids over the stirodonts during the Tertiary. In addition to the improvement in the lantern, the tube feet of the camerodonts are well developed while those of arbaciids have tiny suckers. *Loxechinus albus* has a greater capacity than *Tetrapygus niger* to capture drifting food (Contreras and Castilla 1987). The purple color of the egg results from the presence of high concentrations of echinochrome which may function simultaneously as aposematic coloration and chemical protection. The presence of secondary metabolites in the eggs of stirodonts and not camerodonts is in the direction predicted from differ-

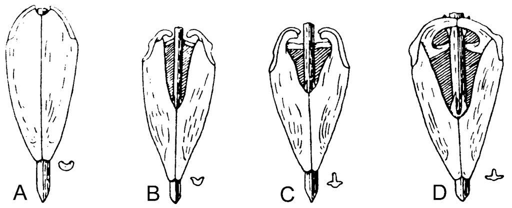

Fig. 5. Jackson's morphological-evolutionary series of the development of the Aristotle's lantern in regular echinoids. A: cidaroid, B: aulodont; C: stirodont; D: camarodont. (From Kier 1974, after Hawkins and Jackson).

ences in capacity for production.

DIVERGENT EVOLUTION AT THE COHORT LEVEL

Irregularia and Echinacea (Echinoidea)

In the Euechinoidea, the Cohort Irregularia includes the orders Spatangoida (heart urchins) and Clypeasteroida (sand dollars and sea biscuits), while the Cohort Echinacea includes all orders of regular sea urchins except the cidaroids (Smith 1984). The groups separated ca. 200 mya (Smith et al. 1992). The food of irregular sea urchins includes sediment, infauna, and particulate matter, while that of the echinaceans consists usually of macroscopic organisms (De Ridder and Lawrence 1982). The latter generally should have a greater capacity for production. In contrast to the extant echinaceans in which only 2 of the species that have non-feeding development are also brooders, many irregular sea urchins are brooders (Emlet et al. 1987). This is in the predicted direction if non-feeding development is an adaptation to low abundance of quality food. As stated above, brooding in extant echinaceans is extremely rare. In the Irregularia, brooding is common in the spatangoids but occurs in only 1 species of extant (Emlet et al. 1987) and 3 species of extinct clypeasteroids (Philip and Foster 1971). Brooding may be constrained in the clypeasteroids by space as the coelom is restricted to the central portion of the body (Emlet et al. 1987).

However, non-feeding development is uncommon in clypeasteroids even if the capacity for reproductive output is low. Facultative feeding development through metamorphosis occurs in only one clypeasteroid species, *Clypeaster rosaceus* (Emlet 1986). A less-developed capacity occurs in *Encope michelini*, which will not develop to the juvenile rudiment stage without feeding (Eckert 1995, Herrera 1998) and which has a higher energy investment than usual for feeding planktonic eggs (George et al. 1997). Facultative planktotrophy occurs in several species of echinoids (Herrera et al. 1996). These authors have emphasized this capacity as an adaptation of the larvae to food limitation.

Chemical protection may be another adaptive response for some clypeastseroid eggs. The eggs are purple in *Echinodiscus bisperforatus* (A. Bentley, pers. comm.) in contrast to those of *Dendraster excentricus* (R. Mooi, pers. comm.) and *Clypeaster* (Herrera unpub.), which are yellow to yellow-orange as is typical of eggs of species with feeding developmental stages.

DIVERGENT EVOLUTION AT THE FAMILY AND GENUS LEVELS

Leptasterias hexactis, L. polaris, Pisaster ochraceus, and *Asterias vulgaris* (Asteroidea)

All these asteroids are in the family Asteriidae and vary in characteristics (Table 2). Except for *L. polaris* (Fig. 6), all *Leptasterias* species have a maximum radius of about 35 mm, rarely to 50 mm (Clark and Downey 1992) and are brooders (Hendler and Franz 1982, Himmelman et al. 1982, Emlet et al. 1987), and all but *L. polaris* are small. Menge (1975) suggested brooding evolved in *Leptasterias hexactis* as a coadaptation with small body size resulting from interspecific competition for food with the co-occurring larger *Pisaster ochraceus*. This would appear to be an inadequate explanation as the co-occuring *Leptasterias polaris* and *Asterias vulgaris* reach similar large sizes and have the same prey (Himmelman and Dutil 1991). It is probable that brooding and small size co-evolved as Menge (1975) suggested but not as a response to competition for food with *P. ochraceus* (Himmelman et al. 1982). We suggest that non-feeding development and brooding are in the direction predicted from the small size of *Leptasterias*, whatever its origin, and the consequent restriction in size of its prey and the amount eaten (Mauzey et al. 1968, Menge 1972). It seems that *L.*

Table 2. Characteristics of *Pisaster ochraceus, Asterias vulgaris, Leptasterias hexactis,* and *L. polaris*

Species	Development	Maximum radius (mm)	Distribution
Pisaster ochraceus	Feeding, planktonic	170	Coast of Alaska to California
Asterias vulgaris	Feeding, planktonic	160	East coast of N. America
Leptasterias hexactis	Non-feeding, brooding	50	Coast of Alaska to California
Leptasterias polaris	Non-feeding, brooding	200	Circumpolar Arctic Ocean, northeast N. American coast, north Pacific Ocean

Compiled from Fisher 1930, Lambert 1981, Himmelman et al. 1982, Emlet et al. 1987, Clark and Downey 1992.

polaris has escaped the phylogenetic history of small size but not of non-feeding development and brooding found in its congeners, as Himmelman et al. (1982) suggested. Strathmann (1980) and Strathmann and Strathmann (1982) stated the question is not only why brooding may be adaptive in small animals, but why it is not adaptive in large animals. They gave alternative hypotheses for this that include fewer advantages or greater costs for brooding by large adults. Brooding in *L. polaris* may be adaptive or an example of a phylogenetic constraint and the inability to re-evolve the planktonic feeding stage.

The *Ophiocoma-Ophiocomella* complex (Ophiuroidea)

Ophiocoma (*O.*) contains large, 5-armed, non-fissiparous species, while *Ophiocomella* (*Oph.*) consists of small, epizoic, 6-armed, fissiparous species. Small *Ophiocoma* species are so similar morphologically to those of *Ophiocomella* that they were once considered the same species (Clark 1976). Allozymic data indicate a close sibling species relationship between *O. pumila* and *Oph. ophiactoides* (Mladenov and Emson 1990). Their ophioplutei are said to be almost indistinguishable (Mladenov and Emson 1988). Despite the obvious taxonomic closeness, the species have different reproductive characteristics (Table 3). *Ophiocoma pumilla, O. wendtii, O. echinata*, and *Oph. ophiactoides* occur sympatrically in the Caribbean Sea (Hendler et al. 1995). These species all have small eggs (70-80 μm diameter) and a feeding developmental stage. The first 3 have only sexual reproduction while *Oph. ophiactoides* is also fissiparous. *Ophiocoma wendtii* has synchronous reproduction, *O. echinata* has facultative asynchronous reproduction, and *O. pumila* has asynchronous reproduction only. *Ophiocomella ophiactoides* reproduces sexually almost continuously in Jamaica.

Mladenov and Burke (1994) noted that all fissiparous ophiuroids are small (disc diameter < 5-6 mm). They suggested that the lack of fissiparity in

Fig. 6. *Leptasterias polaris*: the female in brooding posture. The body size in this species can be large, with the length of the arm exceeding 200 mm. (Photograph by John Himmelman)

Table 3. Characteristics of *Ophiocoma wendtii, O. echiniata, O. pumila,* and *Ophiocomella ophiactoides* (Caribbean Sea)[a]

Species	*O. wendtii*	*O. echinata*	*O. pumila*	*Oph. ophiactoides*
Disc diameter (mm)	35	32	17	5
Habitat	all reef zones	reef rubble	primarily from shallow-water of reef	rubble, coral, algae
Fissiparous	no	no	no	yes: throughout the year.
Egg size (mm)	–	70	70	80
Development type	feeding	feeding	feeding	feeding
Sexual reproduction	synchronous	synchronous at temperate latitudes, asynchronos at tropical latitudes	asynchronous	asynchronous: throughout the year.
Food	mostly fine sand/silt, only small calcareous particles (< 0.1 mm), plant material	fine to medium-sized particles (0.1-0.3 mm), plant material	calcareous particles up to several millimeters, plant material	–

[a]Compiled from Hendler 1979, Mladenov 1983, Mladenov and Emson 1984, 1988, Mladenov et al. 1983, Sides and Woodley 1985, Hendler and Littman 1986, Mladenov and Emson 1990, Hendler et al. 1995.

larger ophiuroids might be related to functional disadvantages, energetic constraints in growing to a reproductive (fissiparous) size, or structural and physiological constraints. They also noted that these small ophiuroids are often epiphytic or epizoic. Selection for small size associated with these microhabitats might cause deviant reproduction. It is remarkable that fissiparity is the deviant reproduction in this case and not the less extreme production of a non-feeding developmental stage. Fission may better maintain a population in habitats where recruitment is restricted (Mladenov et al. 1983, Mladenov and Emson 1984).

DIVERGENT EVOLUTION AT THE SPECIES LEVEL

Heliocidaris **and** ***Pachycentrotus*** **(Echinoidea)**

The genera *Heliocidaris* and *Pachycentrotus* are both in the family Strongylocentrotidae, have only 2 species each, and are found on the southern coast of Australia and adjacent waters (Clark 1946). In each genus, one of the 2 species has deviant reproductive characteristics.

The 2 species of *Heliocidaris, H. erythrogramma* and *H. tuberculata*, diverged only 8-12 mya (McMillan et al. 1992). *Heliocidaris erythrogramma* has a large egg and a non-feeding developmental stage, while *H. tuberculata* has a small egg and a feeding developmental stage (Mortensen 1915, Williams and Anderson 1975) (Fig. 7). Although McMillan et al. (1992) stated that the adult morphology and ecology of the 2 species are similar, this seems not to be the case. One would expect differences from the geographical distribution (Clark 1946, Dakin 1952). They are sympatric only on the New South Wales coast (Dakin 1952) as at Botany Bay (Laegdsgaard et al. 1991, Lawrence and Byrne 1994). Clark (1946) reported *H. erythrogramma* as a rock-boring species at low-tide level on the southern Australian coast, while Endean et al. (1956) reported it in crevices from neap to spring low water. Clark (1946) reported *H. tuberculata* on the reef flat at Lord Howe Island, while Dakin (1952) reported it in shorepools there. Dakin (1952) stated that *H. tuberculata* seemed to occur lower in the sub-littoral zone than *H. erythrogramma* where they co-occurred in New South Wales. The difference in size is striking. Although *H. erythrogramma* is relatively large (to 86 mm), *H. tuberculata* is much larger (to 106 mm).

The 2 species of *Pachycentrotus, P. australiae* and *P. bajulus*, similarly differ in development and size (Dartnall 1972). *Pachycentrotus australiae* apparently has a feeding developmental stage, while *P. bajulus* broods its young. *Pachycentrotus australiae* is minimally larger (to 38 mm) than *P. bajulus* (to 33 mm).

Do *H. erythrogramma* and *P. bajulus* have a decreased capacity for production due to ecological conditions and reduced body size? The latter is particularly important as many echinoids much smaller than these species have a feeding developmental stage. But Kooijman (1993) pointed out that the allometric relation must be sought in closely related taxa, not broadly related ones, and the occurrence of deviant reproduction here is in the direction predicted. Non-feeding development in *H. erythrogramma* and *P. bajulus* may be correlated with a decreased capacity for production associated with ecological conditions reducing the amount of food, perhaps exaggerated by a relatively smaller adult size and not simply a non-adaptive modification of development. A comparison of their habitats would be of great interest.

Asterina gibbosa, A. phylactica**, and** ***A. burtoni*** **(Asteroidea)**

Differences in behavior of individuals led to the discovery that the small asterinid starfish found on the rocky intertidal shores of Great Britain and the northern coast of the Mediterranean Sea consist of 2 species, both with non-feeding development but with only one brooding its young (Emson and Crump 1979). Although found together, *A. gibbosa* is larger (maximum diameter 40 mm), has a long life span (7 or more yrs), is protandrous, and shows no parental care, while *A. phylactica* is smaller (maximum diameter 14 mm), has a short life span (4 yrs), is a simultaneous hermaphrodite, and broods its young. *A. gibbosa* occurs in more sheltered habitats than *A.*

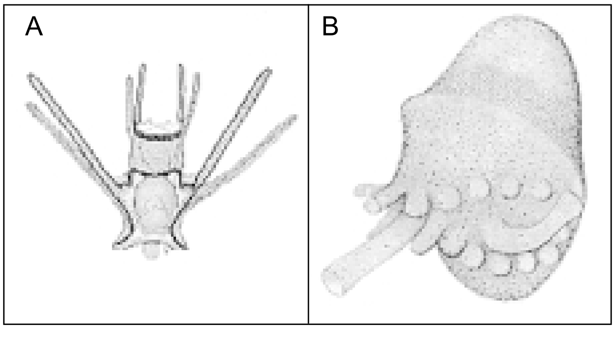

Fig. 7. A: Echinopluteus larva of *Heliocidaris tuberculata* and **B:** embryo of *Heliocidaris erythrogramma*. (From Mortensen 1921)

phylactica and has a greater availability of food (Crump and Emson 1983, Emson and Crump 1984). Emson and Crump (1976, p. 107) stated that the brooding species were found only with low availability of food. The occurrence of the brooding species in habitats with increased exposure and decreased food availability is in the predicted direction.

Strathmann et al. (1984) found that the number of embryos brooded to hatching in *A. phylactica* decreased with increased body size, and suggested an allometric hypothesis that large individuals are less capable of brooding than are small ones. By extension, this might explain the absence of brooding in *A. gibbosa* which does not differ morphologically from *A. phylactica*. However, as noted above, the large *Leptasterias polaris*, which broods, is not constrained by size. The simultaneous hermaphroditism of *A. phylactica* and the protandric hermaphroditism of the larger *A. gibbosa* are interesting. It also can be related to the size difference between the 2 species. In sea urchins in general, males becoming mature at a smaller size than females has been related to the minimal body size necessary to produce a functional number of gametes. Crump and Emson (1983) concluded that *A. phylactica* matures at an earlier age and has a shorter life-span than *A. gibbosa*, opposite to that predicted from the suggested difference in stress for the 2 species.

Neither *Asterina gibbosa* nor *A. phylactica* show the extreme deviant reproductive condition of fission as does *A. burtoni*. Fission seems facultative in *A. burtoni* as only fission and no sexual reproduction occurs in populations of the Gulf of Suez (Pearse 1968 1983), but both fission and sexual reproduction occur in those of the Gulf of Aqaba and the Egyptian coast of the Red Sea (Achituv 1969, James and Pearse 1969, Pearse 1983). The fissiparous form that predominates in the Gulf of Suez and the Mediterranean Sea is small and asexual, while the non-fissiparous form predominant in the Red Sea is larger and sexual (Mladenov and Achituv 1999). The occurrence of fission is in the direction predicted.

The *Patiriella complex* (Asteroidea)

This extraordinary complex of closely related species (Fig. 8) is found on the shores of Australia and New Zealand. They are reminiscent of *Asterina gibbosa* and *A. phylactica* in being very small, occurring at different levels in shallow water or the intertidal, and showing a difference in size that is correlated with reproductive characteristics (Byrne 1996). The complex has variously adopted deviant reproductive characteristics (Table 4) in the direction predicted with a decreased capacity for production: decrease in depth, increase in exposure, and decrease in size. *Patiriella regularis* is subtidal (Crump 1971); *P. gunnii*, shallow sub-tidal; *P. calcar*, lower shore; *P. exigua*, midshore (Byrne 1992); and *P. vivipara* and *P. parvivipara*, upper intertidal, a distribution gradient with reproductive correlates like that seen for *Asterina gibbosa* and *A. phylactica*. Other than their characteristic small body size, Hart et al. (1997) did not consider adults in their analysis of the evolution of life history traits in asterinid starfish.

Kooijman's use of the source of energy for development and growth being maternal to identify the developmental stage is clear here. In traditional usage, juveniles develop internally in viviparous species. Byrne (1996) and Byrne and Cerra (1996) suggested the evolution of viviparity involved a secondary reduction in egg size from an ancestor with a large egg and non-feeding development. Similarly,

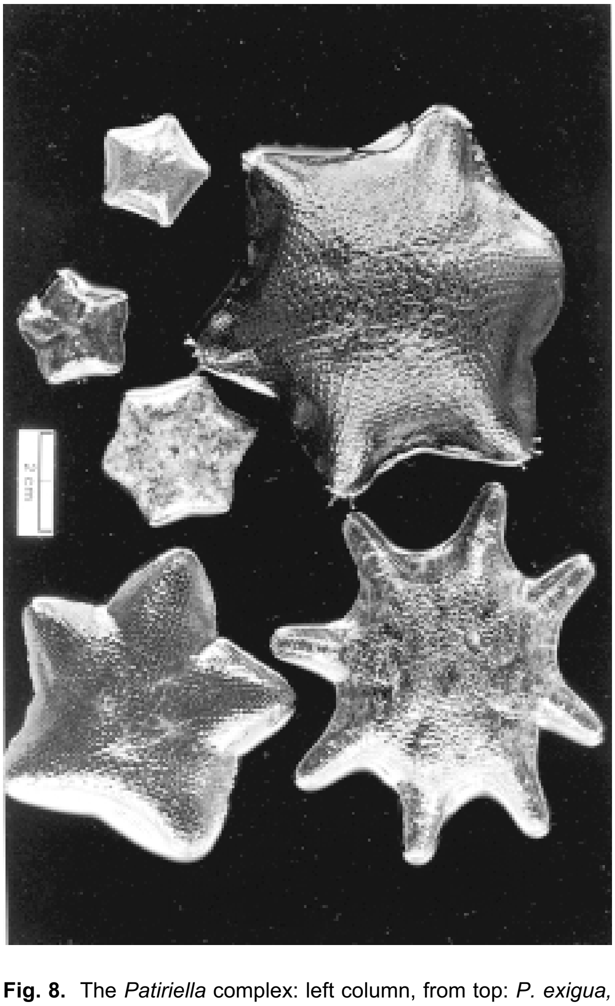

Fig. 8. The *Patiriella* complex: left column, from top: *P. exigua, P. pseudoexigua, P. gunnii, P. regularis*; right column, from top: *P. brevispina, P. calcar*. (Photograph by Maria Byrne)

Sewell (1996) suggested the mortality of pentactula larvae in the ovary of the viviparous holothuroid *Leptosynapta clarki* may provide nutrients for siblings. Although a switch from a non-feeding to feeding has occurred, both types of developmental stage have a maternal source of energy. The obvious difference between the two is that no growth occurs in species with non-feeding development while it does in the feeding species.

Holothuria atra and *H. leucospilota* (Holothuroidea)

Holothuria atra and *H. leucospilota* are common on coral reef-flats in the Indo-Pacific Ocean. Although they are of similar size and co-occur, they are distinct in microhabitats and in characteristics (Bonham and Held 1963, Massin and Doumen 1986). Although *H. atra* can be found at several meters depth, it is most common on the open reef-flat and may be exposed at low tide. It is exposed to high insolation and temperature. *Holothuria leucospilota* is usually not found on the open flat, but under boulders or in holes and crevices of the reef flat from where it extends its anterior body to feed at high tide (Bonham and Held 1963, Massin and Doumen 1986). Both species feed on low-quality sand, rubble, and debris. Fission is common in *H. atra* (Bonham and Held 1963, Lawrence 1981) but has been reported only once for *H. leucospilota* (Conand et al. 1997).

Populations of *H. atra* differ in the incidence of fission. Individuals on exposed inner reef-flats and on back reefs are smaller and have a higher incidence of fission than those on outer reef-flats and in lagoons (Harriott 1982, Conand 1989 1996, Chao et al. 1993 1994). This indicates that asexual reproduction in *H. atra* is facultative and not obligatory. Individuals in exposed, stressed environments undergo asexual reproduction in lieu of growth and sexual reproduction. Asexual reproduction seems facultative in *H. leucospilota* also, being restricted to exposed populations and with high yearly variation. (Conand, pers. comm.) The adaptiveness of this form of asexual reproduction in such stressful situations is apparent. Ebert (1978), Emson and Mladenov (1987), and Chao et al. (1994) suggested the fission of *Holothuria* species to be an adaptation for maintaining populations in habitats where recruitment is improbable.

Fission thus seems habitat related and environmentally induced (Pearse 1968, Ebert 1978, Emson and Wilkie 1980, Mladenov and Burke 1994, Mladenov 1996). Environmental stress is not only the stimulus but also the selective pressure for it. Although it would seem that many holothuroids would not be constrained by their body form from undergoing fission, it occurs in only 8 species in 2 families (Mladenov 1996). This suggests that the extremely low offspring/parent ratio and long generation time (time required for growth between fission events) exerts a powerful counter-pressure.

The *Ophiura* complex (Ophiuroidea)

The genus *Ophiura* has such a variety of combinations of reproductive characteristics (Table 5) that patterns are not clear. The 3 species (*O. loveni, O. meridionalis,* and *O. rouchi*) that have non-feeding development also brood their young. One is her-

Table 4. Reproductive characteristics of the *Patiriella* complex[a]

Species	Maximum arm radius (mm)	Egg size (µm)	Gonochoric/ hermaphroditic	Seasonal/ continuous reproduction	Planktonic/benthic/ viviparous development	Feeding/ non-feeding development
P. regularis	80	150	gonochoric	seasonal	planktonic	feeding
P. calcar	60	415	gonochoric	seasonal	planktonic	non-feeding
P. brevispina	52	400	gonochoric	-	planktonic	non-feeding
P. gunnii	40	400	gonochoric	seasonal	planktonic	non-feeding
P. pseudoexigua Taiwan	15	320	gonochloric	seasonal	planktonic	non-feeding
P. pseudoexigua Queensland	15	440	gonochoric	seasonal	viviparous	non-feeding
P. pseudoexigua pacifica Japan	–	450	hermaphroditic	seasonal	viviparous	non-feeding
P. exigua	15	390	hermaphroditic	continuous	benthic	non-feeding
P. vivipara	15	150	hermaphroditic	continuous	viviparous	feeding
P. parvivipara	5	135	hermaphroditic	continuous	viviparous	feeding

[a] Compiled from Komatsu et al. 1990, Chen and Chen 1992 and Byrne 1996, Byrne and Cerra 1996, and Byrne et al. 1999.

maphroditic as well. Their occurrence in the non-productive deep-sea and the Arctic and sub-Antarctic regions is in the direction predicted. The 2 largest species (*O. sarsi* and *O. testurata*) have a feeding developmental stage as would be predicted, although *O. sarsi* does have a circumpolar distribution. However, two small species have a feeding developmental stage. One species (*O. albida*) is found in the northeast Atlantic Ocean and Mediterranean Sea, and another (*O. ljungmani*) is found in the deep sea. Madsen (1961) suggested that abyssal fauna such as *O. lectocnia* of the North Pacific Ocean (123-3239 m depth) descend from the sublittoral, bathyal depths into the abyss or are dependent upon exogenous nutrients. Perhaps *O. ljungmani* is in the latter category as its biology is clearly affected by the seasonal input of phytoplankton. Thus Tyler (1980) and Gage and Tyler (1991) concluded that the dominant pattern in deep-sea echinoderms is continuous reproduction of non-feeding developmental stages, while seasonal sinking of organic matter from above provides for seasonal reproduction and larval food in *O. ljungmani*. Gage and Tyler also singled out *O. ljungmani* as a trophic specialist in contrast to other deep-sea ophiuroids that are generalists. *Ophiura albida* has a distinct annual reproductive cycle related to the seasonal production of micro-algae (Tyler 1977).

The Synaptidae complex (Holothuroidea)

The synaptid holothuroids are surface feeders on small particles including diatoms, microalgae, detritus, and sediment (Massin 1982). They have the least-developed body-wall of any echinoderm, being transparent and thin. This may indicate that their capacity for production is limited. A high incidence of hermaphroditism is correlated with small size and brooding in synaptids (Smiley et al. 1991) as for marine invertebrates in general (Strathmann et al. 1984). These reproductive characteristics (Table 6) are in the direction predicted if synaptid production is indeed low.

The shallow-water species of 2 subfamilies of the Synaptidae show a quite interesting difference. The known sexual condition of sufficient species in the subfamilies led Clark (1907) to conclude that the Synaptinae are all hermaphroditic and the Chirotinae are all gonochoric. Hermaphroditism in the Synaptinae occurs in species that range from 3 to 3000 mm in length. Although the giant species probably have a low capacity for production, their hermaphroditism may have a historical basis. In the Synaptinae, the overall trend of size and nutritional mode of the developmental stage is in the direction predicted: the giant *Opheodesoma grisea* and *Synapta maculata* have a feeding developmental stage while the smaller species have non-feeding developmental stages. Three of the smaller species are also viviparous.

The gonochoric Chirotinae have no obvious differences in capacity for production and are of similar small size to the Synaptinae, but they are viviparous (Fig. 9). That viviparity occurs in *Taeniogyrus contortus* and not in *T. australianus* of the same size suggests small size alone is not always a sufficient explanation of its occurrence. Again, perhaps the added stress of sub-Antarctic conditions for *T. contortus* is the explanation. *Chiridota rotifera* reaches twice the size of *T. australianus* but is viviparous. This is opposite to the direction predicted were stress alone the explanation, but the comparison here is between genera. The Synaptidae would appear not to fit the hierarchy of responses predicted

Table 5. Characteristics of *Ophiura* species^a

Species	Gonochoric/ hermaphroditic	Egg color	Disc diameter (mm)	Distribution	Depth (m)
Feeding, planktonic development					
O. albida	gonochoric	green	6	northeast Atlantic Ocean, Mediterranean Sea	100-250
O. ljungmani	gonochoric	reddish-orange	9	North and South Atlantic Ocean	630-2,400
O. robusta	gonochoric	green	10	North Sea, northeast Atlantic Ocean	6-450
O. sarsi	gonochoric	–	35	circumpolar (Arctic)	10-3,000
O. texturata	gonochoric	–	37	N. Atlantic Ocean, North Sea, Mediterranean Sea	< 200
Non-feeding, brooded development					
O. loveni	–	–	15	global	deep-sea
O. meridionalis	hermaphroditic	–	6	sub-Antarctic	60-250
O. rouchi	gonochoric	–	7	sub-Antarctic	400

^{a}Compiled from Mortensen 1927, 1936, Thorson 1946, Madsen 1956, Tyler 1977, 1980, Tyler and Gage 1980, and Hendler 1991.

as all have small eggs and feeding development.

DISCUSSION

If ancestral echinoderms had a feeding planktonic developmental stage, the evolution of deviant reproductive characteristics must be explained. Pechenik (1999) considered disadvantages of a feeding planktonic developmental stage as the force responsible for the evolution and present distribution of modes of development in benthic marine invertebrates. He emphasized the location of development (planktonic and nonplanktonic), but did not consider the great differences that occur in the planktonic mode (feeding and non-feeding) or their implications. In contrast, deviant reproduction has been considered here primarily from the viewpoint of the adult, while recognizing that the developmental stage has its own evolutionary response to its environment, and that multiple factors are probably involved. Our thesis is that stresses resulting from environmental conditions or internal constraints are important factors causing a decrease in the potential for production.

A number of deviant conditions that seem to form a continuum with a hierarchy of responses to a decreased capacity for production can be recognized. They are a non-feeding planktonic developmental stage, a non-feeding benthic or brooded stage, continuous or intermittent spawning, hermaphroditism, and asexual reproduction by fission. Strathmann et al. (1984) proposed an evolutionary order of reduced adult size, benthic development, and self-fertilizing hermaphroditism. But Hart et al. (1997) found no ordered transformation series from a feeding planktonic developmental stage to viviparous brooding in asterinid asteroids. Ebert (1996) ranked reproductive modes according to probability of survival of offspring in the order of planktonic feeding development, planktonic non-feeding development, benthic non-feeding development, brooding non-feeding development, and asexual reproduction.

Two environments with low primary productivity are the deep sea and the polar regions. The most famous hypotheses about the reproductive responses of animals in these conditions are known as Orton’s and Thorson’s rules (Young 1994). The soundness of Orton’s rule (animals living in the deep sea should reproduce continuously) and Thorson’s rule (animals living in the deep sea or in polar regions should have a brooded, non-feeding developmental stage) has been challenged by those who point out that exceptions occur (Pearse et al. 1991, Pearse 1994, Young 1994). Although exceptions clearly occur, does this alter the basic idea that changes from the ancestral condition are in the direction predicted? Much of the controversy seems to be related to the requirement that non-feeding development and brooding co-occur. They probably should not be coupled. Thus Pearse et al. (1991) and Pearse (1994) emphasized the existence of planktonic and non-feeding development in Antarctic and deep-sea echinoderms. Pearse (1994, p. 32) stated, “It now seems likely that most deep-sea echinoderms with large yolky eggs produce pelagic lecithotrophic larvae that live for months in the plankton,

Table 6. Characteristics of 2 subfamilies of the Synaptidae[a]

Species	Gonochoric/ hermaphroditic	Feeding/ non-feeding development	Planktonic/ viviparous	Egg size (μm)	Length (mm)	Distribution
Synaptinae						
Opheodesoma grisea	hermaphroditic	feeding	planktonic	100	3,000	eastern tropical Pacific Ocean
Synapta maculata	hermaphroditic	feeding	planktonic	75	900	tropical Indo-Pacific Ocean
Synaptula hydriformis	hermaphroditic	non-feeding	viviparous	200	150	Caribbean Sea to Brazil, Gulf of Mexico
Leptosynapta inhaerens	hermaphroditic	non-feeding	planktonic	200	18	N. Atlantic Ocean
Leptosynapta clarki	hermaphroditic	non-feeding	viviparous	240	113	northwest Pacific Ocean
Leptosynapta minuta	–	non-feeding	viviparous	–	3	North Sea
Labidoplax digitata	hermaphroditic	feeding	planktonic	–	30	N. Atlantic Ocean
Chirotinae						
Chiridota rotifera	gonochoric	non-feeding	viviparous	200	100	Caribbean Sea, Gulf of Mexico
Taeniogyrus australianus	–	–	planktonic	–	50	New South Wales
Taeniogyrus contortus	–	–	viviparous	–	45	sub-Antarctic

[a]Compiled from Clark 1898 1907, Mortensen 1927 1938, Thorson 1946, Smiley et al. 1991, Sewell 1994, Sewell and Chia 1994, Chao et al. 1995, and Hendler et al. 1995.

and nonpelagic development, including brooding, is as unusual in the deep-sea as it is elsewhere." Young et al. (1998) also concluded that planktonic, non-feeding development is the most common developmental mode of deep-sea echinoderms. If a hierarchy exists in changes in reproduction with stress, the most important point is that non-feeding development is more usual than feeding development in polar and deep-sea environments. The next step would be the evolution of brooding rather than planktonic develop-ment. The persistence of planktonic development suggests advantages associated with it or disadvantages or difficulty with brooding.

The evolution of non-feeding development has been related to the low-energy environment of the deep sea (Tyler 1980, Gage and Tyler 1991). It would seem reasonable to extend this to the polar regions. The studies summarized by Pearse (1994) for different environments show that non-feeding development is dominant in polar and deep-sea environments. The obvious caveat is that this creates no expectation or requirement that every deep-sea or high-latitude species has evolved a non-feeding developmental stage. Arntz et al. (1994) suggested food limitation to be the primary factor affecting life-history strategies in the Antarctic. They gave 2 scenarios that are like those suggested for the deep sea: reproduction coupled or uncoupled to the seasonal cycle of food availability, with gametogenesis being slow over a long period of time in the latter.

Orton (1920) based his hypothesis that reproduction is continuous in the deep-sea on the belief that temperature is the primary factor controlling seasonal reproduction in marine animals. He did not consider the potential for production. Continuous or intermittent reproduction is a predicted response to stress. Gage and Tyler (1991) suggested that food availability is possibly the most important limiting factor in the deep sea and stated this would restrict reproductive potential. Young (1994, p. 3) cited several studies showing non-continuous reproduction in several invertebrate phyla, including Tyler (1988) and Scheltema (1994), to conclude that "...Orton's generalization...has been put to rest by modern (deep-sea biologists)." Yet Gage and Tyler (1991, p. 313) concluded that continuous reproduction with a non-feeding developmental stage is the dominant reproductive pattern in deep-sea echinoderms. Similarly, Tyler et al. (1994) suggested that unpredictable inputs of large food falls ("windfalls") may enhance reproductive activity that would result in aperiodic, intermittent reproduction. Certainly gonadal production of echinoderms responds quickly to increased food supply (Lawrence and Lane 1982, Lawrence 1987).

Many years ago Madsen (1961) distinguished an endemic abyssal fauna from a considerable number of co-occurring, secondary deep-sea species ("guests"). He concluded that most of them are in sublittoral-bathyal depths in higher latitudes. One might suggest that the strong seasonal pulse of phytoplankton detritus in these regions (Tyler 1988, Gage and Tyler 1991) would result in seasonal reproduction by these secondary deep-sea species. Seasonal reproduction, found in a number of deep-sea echinoderms, involves initiation of gametogenesis in the spring (Tyler 1988, Gage and Tyler 1991). Some of these species studied in the Rockall Trough, such as 3 *Echinus* species and *Ophiura ljungmani*, have shallow-water congeners in the British Isles (Mortensen 1927). There seems to be no question that phylogenetic constraints determine reproductive patterns in some deep-sea invertebrates (Eckelbarger 1994, Eckelbarger and Watling 1995). Notably, despite the frequency of occurrence of non-

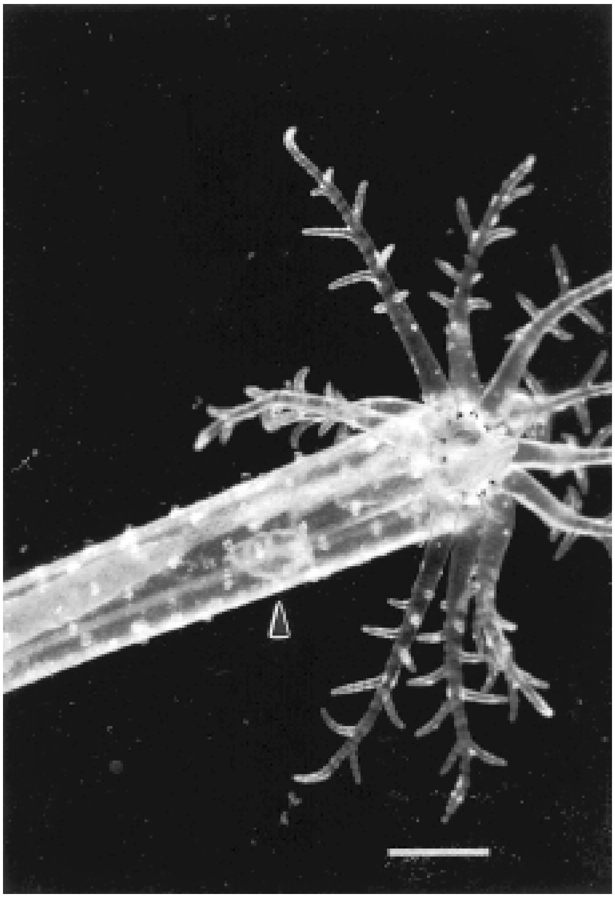

Fig. 9. *Leptosynapta clarki*: female with feeding developmental stage (arrow) in the coelom. (Photograph by Jennifer Fricke)

feeding development in deep-sea echinoderms, Gage and Tyler (1991) found few reports of brooding or hermaphroditism. This again indicates that there is a hierarchy of reproductive responses to stress and the importance of a planktonic developmental stage, whether feeding or non-feeding.

The relation between body size and deviant reproductive behavior (particularly brooding, hermaphroditism, and fission) is intriguing. It has been noted in marine invertebrates in general and echinoderms in particular (Chia 1974, Emson and Wilkie 1980, Strathmann and Strathmann 1982, Jablonski and Lutz 1983, Strathmann 1990, Mladenov and Burke 1994). Strathmann and Strathmann (1982) made the important observation that it is just as important to ask why brooding does not occur in large species as it is to ask why it occurs in small ones. Most brooding and fissiparous ophiuroids are relatively small (Hendler and Littman 1986, Hendler and Peck 1988). These authors suggested that small body size was selected for patchy microhabitats, and that brooding and fissiparity would be adaptations that allow individuals of small apomictic species to reach large size and correspondingly high fecundities. They considered that microhabitats had low environmental stress but did not consider the availability of large amounts of high-quality food or the ability of the tiny brittlestars to feed and store nutrients.

Fission is such a spectacular phenomenon that we often forget how uncommon it is. Mladenov (1996) calculated that only 1.3% of the approximately 6000 extant species of echinoderms have this extremely deviant type of reproduction. It is constrained in many echinoderms by body forms that can not survive division (Mladenov and Burke 1994). It would seem impossible for an echinoid to undergo fission, but its absence in most holothuroids suggests that this is a strategy that is used only very rarely. It is most common in ophiuroids, perhaps as they are less constrained by body form. But even here it is limited, as fissiparity has been reported in only about 45 species (19 in a single genus!) of the approximately 2000 extant species (Mladenov and Burke 1994). However, as they represent 11 of the 17 extant families it is clear that it has evolved repeatedly. All examples we know seem to involve a decrease in productivity that, when coupled with the advantages/disadvantages of a planktonic stage, may be the selective basis.

Asexual reproduction by the developmental stages, the embryo and larva, is noted in figure 1. Asexual reproduction by the embryo is obviously possible, as blastomeres and parts of embryos separated in the laboratory can reorganize and develop (Hörstadius 1973). Marcus (1979) produced twins from single first-cleavage blastomeres obtained from embryos of the echinoid, *Arbacia punctulata*, by shaking and osmotic challenge. She actually raised these individuals through metamorphosis to reproductive adults. Twinning in echinoids can occur without such vigorous treatment. Mortensen (1938) reported twinning in the echinoid, *Prionocidaris baculosa*. Twins from embryos from the echinoids, *Encope aberrans* and *Mellita quinquiesperforata*, have been reared to metamorphosis (Herrera 1998) and those from *Lytechinus variegatus* and *Clypeaster rosaceus* to various larval stages (Herrera, unpubl. data). Mladenov (1996) raised the possibility that such embryonic asexual reproduction may occur naturally and could be important in the life history of echinoderms.

Asexual reproduction is known from the planktonic developmental stage (larvae) of several species of asteroids and ophiuroids in different areas of the world's oceans (Mortensen 1921, Bosch et al. 1989, Rao et al. 1993, Jaeckle 1994, Balser 1998). The rarity of this extraordinary phenomenon suggests that it may be subject to constraints. It may produce an individual too small to be viable in the natural state. If so, only large larvae such as those of *Luidia* would have the potential for asexual reproduction even though bisected larvae of asteroids rapidly and completely regenerate (Vickery and McClintock 1998). Sinervo and McEdward (1988) demonstrated that experimental reduction in egg size of echinoids yielded larvae that were smaller and developed more slowly than normal. This would constrain not only the lower limit of egg size, as they suggested, but also asexual reproduction of embryos and developmental stages.

In an energetic analysis, the same environmental factor could affect both the developmental and established stages. A change affecting either phytoplankton or benthic algal productivity should have implications for the reproductive characteristics of marine invertebrates. Lessios (1990) found a striking dissimilarity in egg size of pairs of geminate species of echinoids and asteroids presumed to have been divided by the rise of the Isthmus of Panama 3.1 to 3.5 mya. In 6 of 7 pairs, the Pacific species had eggs smaller than those of the Atlantic species, a pattern he attributed to adaptation to the higher levels of primary production in the eastern Pacific. An increase in egg size has been proposed to be adaptive for feeding larvae under certain environmental conditions (Eckert 1995, George et al. 1997, Herrera 1998). Whether food limitation is a controlling factor for feeding planktonic developmental stages is controversial.

Plankton concentration can affect feeding developmental stages of echinoderms (Fenaux et al. 1988, Basch 1996, Basch and Pearse 1996, George et al. 1997, Herrera 1998), but whether it is a factor in the field is not clear (Paulay et al., 1985, Olson and Olson 1989). Jeffery (1997) concluded that increasing seasonality was the forcing factor in the evolution of the non-feeding developmental stage in echinoids at the K/T boundary. However, Smith and Jeffery (1998) found that echinoid clades with a feeding developmental stage were not significantly more affected at the K/T boundary than those with a non-feeding developmental stage. They concluded that food supply was a crucial factor in driving K/T-boundary extinctions, but that selection was stronger on benthic adults than on feeding planktonic developmental stages. Jablonski (1986) likewise found similar levels of extinction at the K/T boundary in gastropods with different modes of development. One would expect conditions that decreased phytoplankton productivity to decrease that of benthic algae as well. This would affect both planktonic feeding stages as well as benthic adults. Another possibly important factor that we do not consider here is predation on planktonic developmental stages, which Pechenik (1999) noted as one of the disadvantages of planktonic development that could lead to deviant reproduction and development.

CONCLUSIONS

We have considered divergent evolution in echinoderm taxa. At various levels, from subphylum to species, deviant reproduction seems to be correlated with a decreased capacity for production. This decreased capacity can have its origin in the availability of food, the ability to feed, and in the allocation of energy to physical or chemical protection. Our analysis has been primarily from the point of view of impact of stress on the adult. It is important to note that increased stress in the larva, or predation on the larva, should also lead to deviant reproduction.

Just as with divergent evolution in related taxa under different conditions, convergent evolution in unrelated taxa under similar conditions indicates adaptation. We have seen convergent evolution in species of different classes of echinoderms under conditions that seem similar. Do deviant reproduction and development occur in other phyla under similar conditions? As with the deep-sea echinoderms, over 90% of both the bathyal (200-2000 m depth) and abyssal (2000-5000 m depth) deep-sea bivalves of the eastern Atlantic Ocean have non-feeding development, while a majority of both are planktonic (Scheltema 1994). Scheltema (p. 44) stated, "...there seems to be (no) evidence of a seasonal periodicity in reproduction (in the deep-sea molluscs studied)." He suggested that their mode of feeding led to their unresponsiveness to changes in the flux of organic matter, or that the unpredictability of food made either continuous, or at least intermittent, reproduction more adaptive. Anger (1995) noted that most marine decapod crustaceans in general, and brachyuran crabs in particular, produce a planktonic, feeding developmental stage. He compared marine with fresh water and terrestrial grapsid crabs and concluded that food limitation of the latter selected for deviant modes of reproduction and development, such as a decrease in fecundity, brood protection, non-feeding development, and abbreviated larval development. In his summary of parental care in invertebrates and its correlates, Roff (1992) concluded that Clutton-Brock's suggestion (1991) that parental care in ectotherms would be expected where the environment is harsh, predation is heavy, or competition for resources is intense, is supported by the data available for invertebrates. Two of these conditions, a harsh environment and competition for resources, should lead directly to a decrease in the capacity for production. Predation, if sublethal, should also decrease production. Lethal predation, which is the usual situation with animals in contrast to plants, is simply the extreme case. Stress seems to be a factor that must be considered as a selective force leading to deviant reproduction and development in echinoderms as well as in other taxa.

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壓力對棘皮動物特殊生殖行為的影響

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棘皮動物正常的生殖特徵包括了：卵不帶有卵黃營養物質、需要靠浮游攝食以維生的發育階段、雌雄異體的有性生殖、季節性的生殖行為和幼體並不受二次代謝產物的保護；而特殊的生殖行為特徵則包括了：依賴卵黃營養物質為生的發育階段，此階段可能是浮游性、沉底性、或孵育型的發育、雌雄同體生殖、間歇性或連續少量的生殖、幼體受二次代謝產物的保護以及無性生殖等等。我們檢驗了從亞門到種的層級當中，會降低生殖力的壓力因子是否會導致棘皮動物產生上述的特殊生殖行為。在被檢驗的生物當中，特殊生殖特徵出現在那些壓力可被預測的類群中。雖然其他的變因也同樣會影響生殖特徵，但是分析顯示，壓力是其中一項不可忽視的重要因子。

關鍵詞：棘皮動物，壓力，生殖，生活史。

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