

Environmental factors influencing asexual reproductive processes in echinoderms

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Philip V. MLADENOV

Department of Marine Science, University of Otago, PO Box 56, Dunedin, New Zealand.

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ABSTRACT

This review provides a brief update of the occurrence and adaptive significance of asexual reproduction in echinoderms. It then focuses on the state of knowledge of biotic and abiotic factors that influence asexual processes in this group, particularly factors that may play a role in regulating the expression and relative proportion of asexual *versus* sexual phenotypes within populations of species, as well as factors modulating and triggering asexual processes. The information presented in the review is synthesized into the form of a basic model depicting how environmental factors may interact with physiological factors to regulate asexual reproduction in echinoderms, and to show how such regulatory processes may parallel in some ways those known to regulate sexual reproduction. Since the model is based mainly on correlational evidence derived from comparative field observations, a number of experimental approaches for testing the predictions of the model are discussed briefly.

RÉSUMÉ

Facteurs influençant les processus de reproduction asexuée chez les échinodermes.

Dans cette revue une brève mise à jour est faite sur l'existence et la signification adaptative de la reproduction asexuée chez les échinodermes. Cette mise au point porte sur l'état des connaissances concernant les facteurs biotiques et abiotiques qui influencent les processus asexués de ce groupe, particulièrement ceux qui jouent un rôle dans la régulation de l'expression et les proportions relatives des phénotypes asexués *versus* sexués à l'intérieur des populations d'espèces et ceux qui modulent et déclenchent les processus asexués. L'information présentée est synthétisée sous la forme d'un modèle décrivant comment les facteurs de l'environnement peuvent avoir avec les facteurs physiologiques une action réciproque régulant la reproduction asexuée chez les échinodermes. Ce modèle montre aussi comment de tels processus régulateurs peuvent, dans quelques cas, être parallèles à ceux qui régulent la reproduction sexuée. Comme le modèle est fondé principalement sur des relations dérivées d'observations faites dans le milieu, un certain nombre d'approches expérimentales testant les prédictions du modèle sont brièvement discutées.

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INTRODUCTION

Asexual proliferation, leading to the production of genetically identical modules, or clonemates, is a component of larval or benthic phases of the life history of some echinoderms (Emson and Wilkie, 1980; Bosch *et al.*, 1989; Chia and Walker, 1991; Hendler, 1991; Pearse and Cameron, 1991, Smiley *et al.*, 1991; McAlary, 1993; Mladenov and Burke, 1994; Jaekle, 1994). Echinoderms exploit a number of different methods of asexual reproduction including (1) fragmentation into multicellular components capable of regenerating into complete organisms, (2) budding, (3) amictic (= apomictic = ameiotic) parthenogenesis, (4) and polyembryony. Asexual echinoderm species can be very successful, possessing extensive geographic ranges, and occurring in very high densities in certain habitats (Emson and Wilkie, 1980; Mladenov and Burke, 1994).

Although the biology of asexual echinoderms has received increasing attention in recent years (see reviews by Emson and Wilkie, 1980; Mladenov and Burke, 1994), there have been few, if any, definitive studies aimed at elucidating the environmental factors that regulate asexual reproduction in this phylum. This review provides a brief overview and update of the occurrence and adaptive significance of asexual reproduction in echinoderms. It then focuses on the state of knowledge of biotic and abiotic influences regulating asexual processes in this group, particularly factors that may play a role in regulating the expression and relative proportion of asexual versus sexual phenotypes within populations of species, as well as factors modulating and triggering asexual processes. The results are used to produce a basic model of regulation of asexual propagation in echinoderms to try to identify productive avenues for future research.

OCCURRENCE AND ADAPTIVE SIGNIFICANCE OF ASEQUAL REPRODUCTION IN ECHINODERMS: AN OVERVIEW

Fragmentation

The benthic phase of about 21 species of asteroid, 45 species of ophiuroid, and 8 species of holothuroid is currently known to be capable of reproducing asexually by fission (Tab. 1-3). In these "fissiparous" species, the body generally divides into two parts, each of which is capable of regenerating into a whole animal. In addition, six species of asteroid are known to possess a benthic phase that propagates asexually by arm autotomy (Tab. 4) In these forms, an autotomized arm can regenerate a new disc and arms to form a complete new animal.

As might be expected, fissiparous reproduction provides a mechanism for potentially rapid amplification of individual genotypes. There is good evidence, for example, that populations of fissiparous ophiuroids and asteroids are often highly clonal in structure, each clone, or genet, consisting of many discrete, genetically identical bodies, or ramets (Johnson and Threlfall, 1987; Mladenov and Emson, 1990). The effective body size of a genet may potentially be very large, both in terms of the total number and total

biomass of the contributing ramets. Furthermore, although the fecundity of a single ramet may be very low, because fissiparous forms are often very small in body size (Mladenov and Emson, 1984), the aggregate fecundity of all the ramets comprising the genet may be very high (Hendler and Littman, 1986; Mladenov and Emson, 1990). The genet may thus possess high fitness in terms of size, survival, and fecundity compared to genotypes confined to a single body.

Some fissiparous species, particularly ophiuroids, seem well adapted for saturating patchy, widely separated habitats through rapid clonal proliferation, particularly within habitats that favour small body size (Hendler and Littman, 1986; Mladenov and Emson, 1988). For example, fissiparous ophiuroids are often common among the thalli of algal turfs and within the exhalant channels of sponges (Mladenov and Burke, 1994).

As has been recently discovered, asexual propagation by fragmentation also occurs in some larval echinoderms. This is discussed below in a separate section on asexual propagation in larvae.

Amictic Parthenogenesis

Parthenogenesis in echinoderms is usually viewed as a laboratory phenomenon and considered to occur infrequently in natural populations (Mladenov and Burke, 1994). There is recent evidence, however, that intra-bursally brooded juveniles are produced asexually by amictic parthenogenesis in the ophiuroid, *Ophiomyxa brevirima*, a dioecious brooder endemic to New Zealand (Garrett and

Table 1

Fissiparous sea stars (from Mladenov and Burke, 1994)

Family	Species
Asterinidae	<i>Asterina anomala</i> H. L. Clark
	<i>A. burtoni</i> Gray ¹
	<i>A. corallicola</i> Marsh
	<i>A. heteractis</i> H. L. Clark
	<i>Nepanthia belcheri</i> (Perrier)
	<i>N. brevis</i> (Perrier) ²
	<i>N. briareus</i> (Bell)
	<i>N. fisheri</i> (Rowe and Marsh) ³
	<i>N. variabilis</i> H. L. Clark ²
Asteriidae	<i>Coscinasterias acutispina</i> (Stimpson)
	<i>C. calamaria</i> (Gray)
	<i>C. tenuispina</i> (Lamarck)
	<i>Sclerasterias alexandri</i> (Ludwig)
	<i>S. euplecta</i> (Fisher)
	<i>S. heteropes</i> (Fisher)
	<i>S. richardi</i> (Perrier)
	<i>Stephanasterias albula</i> (Stimpson)
	<i>Allostichaster inaequalis</i> (Perrier)
	<i>A. insignis</i> (Farquhar)
<i>A. polyplax</i> (Müller and Troschel)	
Solasteridae	<i>Seriaster regularis</i> Jangoux

¹ The fissiparous form of this species has also been referred to as *Asterina wega* (Achituv, 1969, 1973).

² Rowe and Marsh (1982) consider *N. brevis* and *N. variabilis* to be junior synonyms of the variable *N. belcheri*.

³ Potentially fissiparous (Rowe and Marsh, 1982).

Table 2

Fissiparous brittle stars (from Mladenov and Burke, 1994)

Family	Species
Astroschematidae	<i>Astrogymnotes catasticta</i> H. L. Clark <i>Astrocharis ijimai</i> Matsumoto <i>A. virgo</i> Koehler
Euryalidae	<i>Astroceras annulatum</i> ¹ Mortensen <i>A. nodosum</i> Koehler <i>Asteromorpha perplexum</i> Koehler
Gorgonocephalidae	<i>Schizostella</i> ² <i>bifurcata</i> A. H. Clark <i>S. bayeri</i> A. H. Clark
Hemieuryalidae	<i>Ophiocolus sexradiata</i> Koehler
Ophiomyxidae	<i>Ophiostiba hidekii</i> Matsumoto <i>Ophiovesta granulata</i> Koehler
Amphiuridae	<i>Amphiacantha dividua</i> Matsumoto <i>Amphiodia dividua</i> Mortensen <i>Amphipholis torelli</i> Ljungmann <i>Amphiura sexradiata</i> Koehler <i>Ophiostigma isocanthum</i> (Say)
Ophiactidae	<i>Ophiactis acosmeta</i> (H. L. Clark) <i>O. arenosa</i> Lütken <i>O. cyanosticta</i> H. L. Clark <i>O. hirta</i> Lyman <i>O. lymani</i> Ljungmann <i>O. maculosa</i> (von Martens) <i>O. modesta</i> Brock <i>O. mülleri</i> Lütken <i>O. nidarosiensis</i> Mortensen <i>O. parva</i> Mortensen <i>O. plana</i> Lyman <i>O. profunda</i> Lütken and Mortensen <i>O. rubropoda</i> Singletary <i>O. savignyi</i> (Müller and Troschel) <i>O. seminuda</i> Mortensen <i>O. simplex</i> (Le Conte) <i>O. versicolor</i> H. L. Clark <i>O. virens</i> (M. Sars) <i>O. sp.</i>
Ophiocanthidae	<i>Ophiologimus hexactis</i> Clark
Ophiocomidae	<i>Ophiocomella ophiactoides</i> (H. L. Clark) <i>O. schmitti</i> A. H. Clark <i>O. sexradia</i> ⁴ (Duncan)
Ophionereididae	<i>Ophionereis dictydisca</i> ⁵ (H. L. Clark) <i>O. dubia</i> ⁵ Müller and Troschel <i>O. sexradia</i> Mortensen
Ophiotrichidae	<i>Ophiotela danae</i> ⁶ Verrill <i>O. hadra</i> H. L. Clark <i>O. mirabilis</i> Verrill

¹ Matsumoto (1917) referred to this as the young, fissiparous form of *Astroceras pergamenum*. However, Mortensen (1933) indicates that *A. annulatum* and *A. pergamenum* are distinct species, the former fissiparous, the latter non-fissiparous.

² Diagnostic features of this genus include 7 arms and fissiparity (A. M. Clark, 1952, p. 451).

³ Both 6-armed and 5-armed forms have been reported. Hotchkiss (1982) suggests that the fissiparous forms may be specifically distinct and refers to such specimens as *Ophiostigma* sp.

⁴ Synonyms include *Ophiocomella parva*, *O. schultzi*, *Ophiocnida sexradia*, *Amphiacantha sexradia*.

⁵ *Ophionereis dictydisca* may be synonymous with *O. dubia* (A. M. Clark, 1967).

⁶ Probable synonyms include *O. isidicola* and *O. verrilli* (Matsumoto, 1917, H. L. Clark, 1921, A. M. Clark, 1980).

Table 3

Fissiparous sea cucumbers and their geographic distribution (from Mladenov and Burke, 1994, unless otherwise indicated)

Family	Species
Holothuridae	<i>Holothuria difficilis</i> Semper <i>H. parvula</i> (Selenka) <i>H. surinamensis</i> (Ludwig) <i>H. atra</i> (Jaeger)
Cucumaridae	<i>Ocnus planci</i> Brandt <i>O. lactea</i> (Forbes and Goodsir) <i>O. brunneus</i> (Forbes) ¹ <i>Squamocnus aureoruber</i> O'Loughlin and O'Hara ²

¹ McKenzie, 1984.

² O'Loughlin, 1991, 1994; O'Loughlin and O'Hara, 1992.

Mladenov, 1994; Garrett, 1995). Isozyme electrophoresis was used to study the genetic relationship between parent and brooded offspring in this brittle star and it was observed that, in many of the family lines studied, the genotypes of all of the juveniles were identical to the maternal genotype. It was also found that the sex ratio was significantly skewed towards females in some populations. Together, these observations suggest that unfertilised eggs of this species can develop by amictic parthenogenesis. However, in other family lines examined, the genotypes of the juveniles were not all identical to that of the parent, indicating that at least some of these offspring had been produced by sexual reproduction. It thus appears that *O. brevissima* is capable of both sexual reproduction by outcrossing and asexual reproduction by amictic parthenogenesis.

There is evidence that other species of ophiuroid, asteroid and echinoid may also be naturally parthenogenetic, but it is not known if the mechanism is amictic (and thus asexual) or automictic (a process akin to self-fertilization) (Mortensen, 1936; Yamaguchi and Lucas, 1984; Bak *et al.*, 1984; Medeiros-Bergen, pers. comm.) (Tab. 5).

Although much more research in this area must be done, it seems likely that the incidence of natural parthenogenesis among échinoderms is much higher than presently believed. Facultative parthenogenesis in echinoderms, including amictic parthenogenesis, may be adaptive at low popula-

Table 4

Sea stars capable of propagation through arm autotomy (from Mladenov and Burke, 1994)

Family	Species
Ophidiasteridae	<i>Linckia columbiae</i> Gray ¹ <i>L. guildingi</i> Gray ² <i>L. multiflora</i> (Lamarck) <i>Ophidiaster cribrareus</i> de Loriol ³ <i>Ophidiaster robillardii</i> de Loriol
Echinasteridae	<i>Echinaster luzonicus</i> (Gray)

¹ Called *Phataria unifascialis* by Monks (1904), although H. L. Clark (1940) lists *P. unifascialis* as distinct from *L. columbiae*.

² Probably synonymous with both *Linckia diplax* and *L. pacifica* (Fisher, 1919; Yamaguchi, 1975, p. 21).

³ A morphologically similar congener, *Ophidiaster lorioli*, does not propagate asexually by arm autotomy (Marsh, 1977).

tion densities (e.g. after a mass mortality, Bak *et al.*, 1984), providing a mechanism for individuals to produce offspring when mates are not present, and facilitating rapid colonisation of new habitats by one or a few individuals.

Asexual propagation of larvae

Asexual propagation of larvae of echinoderms was, until recently, considered to be very rare or non-existent. It is now known that asexual reproduction occurs naturally in some sea star larvae from the tropical Northwest Atlantic Ocean (Bosch *et al.*, 1989; Jaeckle, 1994). Bipinnaria larvae of an unknown species of *Luidia*, as well as brachiolaria larvae of an unknown species from a different asteroid order, can reproduce asexually through paratomous cloning of the posterolateral arms. Bipinnaria larvae of yet other unknown species reproduce asexually through autotomy of the anterior portion of the preoral lobe, or through budding of the larval arms. There is also some evidence that sexual reproduction in larval ophiuroids is possible through regeneration of abandoned posterolateral arms following metamorphosis in some *Ophiothrix*-type ophiopluteus larvae (Mortensen, 1921).

These exciting observations on mechanisms of larval asexuality in echinoderms will undoubtedly stimulate more work on the occurrence and distribution of this phenomenon within the phylum. As pointed out by Jaeckle (1994), there are significant adaptive advantages associated with larval cloning. Species with an asexual larval phase have a mechanism for increasing the length of the larval life span, leading to the possibility of teleplanic transport of larvae across ocean basins. It also provides a potential means of clonal amplification of genotypes and of increasing the total number of dispersive propagules, without an associated increase in the reproductive effort of the parent generation.

Polyembryony

Mortensen (1938) reported that a significant proportion of embryos derived from laboratory fertilisation of the cida-roid echinoid, *Prionocidaris baculosa*, often consisted of twins or triplets within the same fertilisation envelope. The resulting larvae appeared normal, although they were comparatively small in size. Presumably, these twins and triplets had been derived from blastomere separation. Such observations suggest that polyembryony may occur naturally in some echinoids and, perhaps, other classes of echinoderms.

Overall occurrence of asexual reproduction in echinoderms

In summary, about 80 (1.3 %) of the roughly 6000 extant species of echinoderms are capable of asexual reproduction by fission or arm autotomy during the benthic phase (Tab. 6). Although the number of species known to be capable of asexual propagation by fragmentation during the benthic phase will continue to grow slowly, it is clear that this ability is restricted to a small portion of extant

Table 5

Occurrence of natural parthenogenesis in echinoderms

Class	Species	Source
Asteroidea	<i>Ophidiaster granifer</i>	Yamaguchi and Lucas, 1984
Ophiuroidea	<i>Ophiomyxa brevirima</i>	Garrett, 1995, Garrett and Mladenov, 1994
	<i>Ophiacantha vivipara</i>	Mortensen, 1936
	<i>Amphiura microplax</i>	Mortensen, 1936
	<i>Amphiura eugeniae</i>	Mortensen, 1936
	<i>Amphipholis squamata</i>	Medeiros-Bergen, unpublished
Echinoidea	<i>Diadema antillarum</i>	Bak <i>et al.</i> , 1984

species. There is, however, recent evidence that more cryptic forms of asexuality, such as naturally occurring amictic parthenogenesis and asexual reproduction in larvae may be more widespread within the Echinodermata than hitherto appreciated, and that the true extent of asexual reproduction within the phylum may be underestimated.

FACTORS CORRELATED WITH INTRASPECIFIC VARIATION IN EXPRESSION OF ASEXUAL AND SEXUAL PHENOTYPES

Geographic variation in the relative importance of asexual and sexual reproduction has been documented in a number of echinoderm species. In the sea star, *Asterina burtoni*, for instance, there is a gradation from 5-armed, non-fissiparous forms in the tropical Red Sea to multi-armed, fissiparous forms in the more temperate Gulf of Suez and Mediterranean (Achituv, 1969; James and Pearse, 1969). It has been suggested that the harsher, more seasonal temperate environment of the Gulf and Mediterranean promotes fissiparity in this species. Similarly, in the sea star, *Nepanthia belcheri*, there is a preponderance of small, multi-armed fissiparous forms along the more temperate east coast of Australia, but a greater proportion of larger, 5-armed, non-fissiparous forms along the tropical north coast (Kenny, 1969; Rowe and Marsh, 1982).

Mladenov and Emson (1988) observed within-habitat variation in levels of sexual reproduction and fission in the West Indian brittle star, *Ophiocomella ophiactoides*. A population of *O. ophiactoides* occupying algal turf in protected coves at Jamaica was present at moderate to high densities and contained both sexual and fissiparous indivi-

Table 6

Known incidence of asexual proliferation in echinoderms by fission or arm autotomy

Class	# of species	% of species	# of families	% of families
Crinoidea	0 of ~ 615	0	0 of 15	0
Asteroidea	27 of ~ 1600	1.7	5 of 31	16
Ophiuroidea	45 of ~ 2000	2.2	11 of 16	69
Holothuroidea	8 of ~ 1000	0.8	2 of 25	8
Echinoidea	0 of ~ 800	0	0 of 48	0
Total	80 of ~ 6015	1.3	16 of 135	13

duals. Here, clonal propagation predominated among the many small individuals in the population, whereas gonads were present mainly in the small number of large individuals present. However, a population of the same species living in algal turf in more exposed back reef and reef crest areas at Belize was present at much lower densities, showed a higher incidence of fission at all body sizes, and did not possess individuals with gonads. Between habitat variation in levels of asexual and sexual reproduction has been observed in the West Indian brittle star, *Ophiactis savignyi* (Mladenov and Emson, 1988). This species was collected from both algal turf and sponge habitats at Jamaica, Belize and Bermuda. At each location, the mean body size of *O. savignyi* in sponges was significantly larger than that of *O. savignyi* in algae. Furthermore, at each location, *O. savignyi* in algae occurred at lower densities and were almost exclusively fissiparous, whereas *O. savignyi* in sponges occurred at much higher densities and sexual as well as fissiparous individuals were present. In these brittle star examples, strictly asexual phenotypes were associated with small body size, unstable algal habitats and low population densities, whereas the occurrence of sexual phenotypes was correlated with larger body size, more stable algal and sponge habitats and high population densities.

Between habitat variation in levels of asexual and sexual reproduction has also been documented in sea stars. Well-fed subtidal populations of the sea stars, *Allostichaster polyplax* and *Coscinasterias calamaria*, generally have a larger body size, a lower incidence of fission and larger gonads than intertidal populations subjected to more stress and poorer food conditions (Emson, 1978; Crump and Barker, 1985).

These various observations lead to the generality that in heterogonic species of echinoderms (*i.e.* species capable of both sexual and asexual reproduction) the asexual phenotype is associated with harsher, less stable, resource poor environments and with populations present at low densities, whereas the sexual phenotype is associated with more favourable, stable, resource rich environments, and with populations present at high densities.

ENVIRONMENTAL AND INTERNAL MODULATORS OF ASEXUAL REPRODUCTION

Some populations of echinoderms exhibit distinctly seasonal patterns of asexual reproduction by fission (Mladenov and Burke, 1994). For example, Emson and Mladenov (1987) found that the proportion of individuals of the sea cucumber, *Holothuria parvula*, at Bermuda showing evidence of regeneration varied from 43-83 % over the year, with fission taking place principally in the summer, and subsequent regeneration occurring during the late summer, autumn and winter. Conand and De Ridder (1990) found that the mean incidence of dividing individuals was about 10 % in a population of *H. atra* at New Caledonia, although the incidence of fission varied seasonally, peaking during the cool season. The sea star, *Stephanasterias albula*, at Maine splits most frequently in the spring and summer (Mladenov *et al.*, 1986). It may be advantageous for individuals within this population to split in the sum-

mer, since there is a large seasonal range in sea temperature. The higher summer sea temperatures may maximize rates of regeneration, thereby decreasing recovery time, and thus the interval, between fissions. Other examples of seasonal variation in fission in sea stars are provided in Mladenov and Burke (1994, Tab. 2).

In sexually reproducing echinoids and asteroids, proximate factors such as sea temperature and light have been shown experimentally to control the reproductive cycle (see the reviews of Pearse and Cameron, 1991; Chia and Walker, 1991). In an analogous fashion, factors may be present that regulate the asexual reproductive cycle in echinoderms. In this regard, there is some evidence that seasonally fluctuating factors may regulate fission cycles. Mladenov *et al.* (1986) demonstrated a temporal correlation between seasonal changes in the incidence of fission and changes in day length in the fissiparous sea star, *Stephanasterias albula*. They hypothesized that increasing day length may stimulate the synthesis of an endogenous chemical substance that, upon reaching some threshold level, either initiates fission directly, or makes a sea star more responsive to external, fission-inducing triggers.

The level of endogenous factors leading to asexual reproduction may also be regulated by internal processes. For example, Mladenov *et al.* (1983) and Wilkie *et al.* (1984) hypothesized that fission in the brittle star, *Ophiocomella ophiactoides*, may be controlled by an endogenous chemical factor that accumulates in the brittle star during regeneration. They further speculated that when this factor reaches a threshold concentration, collagenous tissues in one interradius soften, and fission is invoked. In this way, fission would be regulated to occur only when the animal had regenerated sufficiently following the previous fission event.

It is known that chemical and nervous factors play an important role in the control of arm autotomy in sea stars (Chaet, 1962; Mladenov *et al.*, 1989) and evisceration in sea cucumbers (Smith and Greenberg, 1973), phenomena that are closely related to fission. Similar chemical factors are, therefore, likely involved in the regulation of fission. One of the ultimate effects of these chemicals may be to promote a reduction in the tensile strength of the collagenous component of the body wall in the plane of fission, thereby facilitating splitting (Mladenov *et al.*, 1983; Wilkie *et al.*, 1984). In this context, Motokawa (1982) has shown that the coelomic fluid of the brittle star, *Ophiarchna incrassata*, contains factors that affect the mechanical properties of echinoderm mutable connective tissues.

EXTERNAL FACTORS TRIGGERING ASEXUAL REPRODUCTION

In sexually reproducing echinoderms, certain factors have been discovered that trigger spawning in ripe individuals. For example, temperature and salinity stress, as well as chemicals associated with phytoplankton, can trigger spawning in sea urchins in the laboratory (Pearse and Cameron, 1991). In an analogous fashion, factors have been implicated in initiating asexual reproduction in echi-

noderns that are physiologically prepared for asexual propagation.

Fission can be triggered in some sea stars by shock associated with laboratory holding conditions, including temperature elevation, interruption of seawater circulation, and lack of aeration (Kowalevsky, 1872; Crump, 1969; Emson, 1978). Several authors have reported that the process of propagative arm autotomy in sea stars is sometimes inducible by exogenous stimuli, such as mechanical disturbance, temperature elevation, or ligation of an arm, although not all individuals respond to such treatment (Monks, 1904; Edmondson, 1935; Davis, 1967).

On the basis of such laboratory observations, it is often assumed that harsh physical conditions trigger fission in natural populations. Emson and Wilkie (1980) noted that many fissiparous brittle stars occupy intertidal or shallow water habitats where they would be subject to environmental fluctuations, and thought it possible that stressful exogenous stimuli might trigger fission in such populations. Bonham and Held (1963) noted the Indo-Pacific holothuroid, *Holothuria atra*, splitting in the field when the water temperature was 37 °C, and Conand and De Ridder (1990) hypothesised that fission in this species is triggered by desiccation and thermal stress during spring low tides. Similarly, Emson and Mladenov (1987) hypothesized that fission in *Holothuria parvula* at Bermuda is triggered by high summer sea temperature and physical disturbance at low tide. Other external stimuli, such as storms, and even damage resulting from feeding on sharp-edged items of food, have also been cited as initiating fission (Yamazi, 1950; Tartarin, 1953).

There is thus correlative evidence that fission can be triggered by stressful environmental conditions. The physiological processes that might be initiated by stress, and that subsequently cause fission, have received little attention. It is intriguing in this context that cutting the nerve ring of fissiparous species of sea star in two places will often invoke fission (Hopkins, 1926; Emson, 1978; Carson, 1984), and that surgical incision in one interradius can trigger fission in fissiparous brittle stars, especially in those that have fully regenerated from their previous fission (Mladenov *et al.*, 1983). Surgical interference with the nervous system thus seems to play some role in triggering fission, and it is conceivable that environmental stress of various kinds may mediate fission through stimulation of the nervous system.

EFFECT OF PARASITES ON LEVELS OF ASEXUAL REPRODUCTION

Emson *et al.* (1985) observed that individuals of the brittle star, *Ophiocomella ophiactoides*, parasitized by the siphonostome copepod, *Ophiopsyllus reductus*, were significantly less likely to undergo fission. These authors suggested that the parasite somehow interferes with the chemical basis of fission. Davis (1967) showed that arms of the asexual sea star, *Linckia multifora*, that were parasitized by the gastropod, *Stylifer linckiae*, were significantly less likely to autotomize, either spontaneously, or in response to ligation, compared to unparasitized arms. Davis suggested that the parasite, which encysts in the body wall, somehow

suppresses autotomy of the host arm, perhaps by interfering with an unknown endocrinological controlling mechanism. No information on the propensity for autotomy of unparasitized arms on parasitized sea stars was provided in this study, so it is not known whether the effect of the parasite is a generalized one, or localized to the parasitized arm itself. In any case, it appears that parasites can play a role in modulating asexual processes in echinoderm populations.

SYNTHESIS AND FUTURE DIRECTIONS

This review summarises available information relating to proximate factors that may influence asexual reproduction in echinoderms, particularly factors regulating the expression of the asexual phenotype and modulating or triggering asexual reproductive processes. An attempt is made to organise and synthesize these various observations into the form of a basic model depicting how environmental factors may interact to regulate asexual reproduction in echinoderms, and to show how such regulatory processes may parallel in some ways those known to regulate sexual reproduction (Fig. 1). The model is presented in an effort to stimulate further thought and research in this field and will undoubtedly require considerable modification in future.

The model proposes that factors associated with environmental characteristics such as food availability, population density, predation levels, habitat stability and seasonal variation in sea temperature are perceived externally by individuals in a population and delivered to and interpreted by internal effectors which direct the expression of asexual or sexual characters. In the example of a fissiparous brittle star, the asexual phenotype would be represented by small body size, a lack of gonads and hexamerous symmetry; the sexual phenotype would be represented by larger body size, the presence of gonads and pentamerous symmetry. The model hypothesises that factors associated with low food availability, low population densities, and harsh or fluctuating environmental conditions (the latter would be encountered by populations living at the edge of their species' geographic range) regulate physiological processes causing the expression of the asexual phenotype. It is proposed that these physiological processes involve elevated levels of putative "asexual" hormones that prevent or switch off gonadogenesis and prepare the body for asexual reproduction. Individuals expressing the asexual phenotype then become more responsive to exogenous and endogenous factors that modulate and trigger asexual processes. Modulating factors may finely tune levels of asexual hormones, whereas triggering factors may stimulate nervous pathways which initiate behavioural (*e.g.* pulling of arms in opposite directions during fission) and other physiological processes (*e.g.* the softening of collagenous tissues in the plane of fission) that facilitate asexual reproduction. The model also incorporates the additional refinement of the possible dampening effects of parasites on levels of asexual reproduction.

For comparative purposes, the model depicts environmental factors, modulators and triggers that can regulate sexual

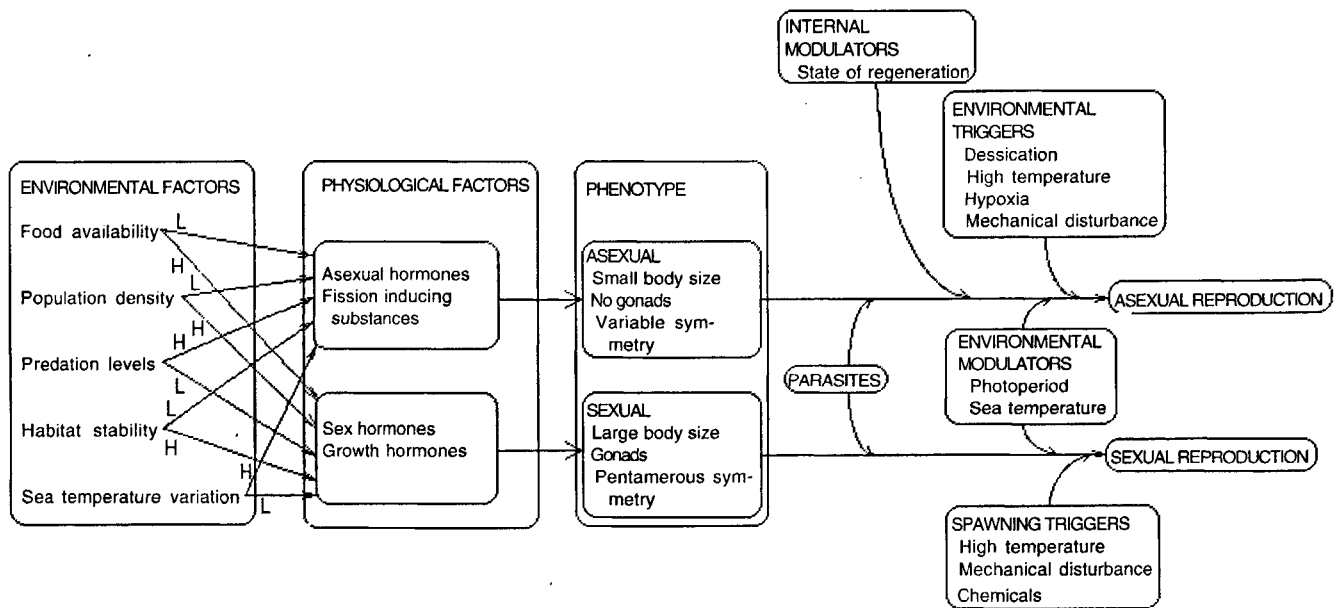


Figure 1

Basic model of factors regulating asexual and sexual reproduction in echinoderms ($H = \text{high}$, $L = \text{low}$).

processes in these echinoderms. In this case, the model predicts that factors associated with high food availability, high population density, low levels of predation, and more benign environmental conditions cause increased levels of sex and growth hormones resulting in expression of the sexual phenotype. Sexual processes are then modulated by environmental factors that cue reproductive cycles and trigger spawning.

It should be emphasised that the asexual components of the model are based largely on correlational evidence derived from comparative field observations. However, the correlational evidence obtained from echinoderms is often in agreement with observations and experimental work on asexual reproduction in other groups of animals. For instance, correlations between high population density, a decline in rate of asexual reproduction, and appearance of sexual individuals have been experimentally demonstrated for the polychaete *Pygospio elegans* (Wilson, 1983), several genera of rotifers (*e.g.* Carmona *et al.*, 1994) and, in freshwater habitats, for *Daphnia* spp. and *Hydra pseudoligactis* (Bell and Wolfe, 1985). Such results are compatible with the model presented here and also with the predictions of the 'tangled bank' hypothesis (Ghiselin, 1974; Bell, 1982) that proposes that heterogonic animals should reproduce asexually when population density is low, thereby saturating a localized habitat with genetically identical copies, but switch to sexual reproduction when population density increases, to produce genetically diverse progeny capable of dispersal and colonization. In this regard, stable, predator-free habitats should favour the creation of high density populations and the switch to sexual reproduction.

Unfortunately, the model suffers from a lack of experimental verification of the correlative observations made on asexual echinoderms. Possible experimental approaches include the manipulation of food supply, levels of stress (*e.g.* desiccation, temperature) and density in captive populations of fissiparous echinoderms while monitoring the relative levels of growth, fission and gonad production. Similarly, one might manipulate these factors within cultures of larvae capable of asexual reproduction and monitor relative levels of asexual proliferation. It might also be possible to manipulate exogenous factors, such as photoperiod, to identify factors that regulate asexual reproductive cycles. Further effort should also be expended on isolating and identifying internal fission inducing substances and putative asexual hormones. This work could build on the knowledge that heat-generated, autotomy promoting factors have already been described for a variety of sea stars (Chaet, 1962; Shirai and Walker, 1988; Mladenov *et al.*, 1989; Murphy and Mladenov, 1992), and that similar factors are known for sea cucumbers (Smith and Greenberg, 1973; Smith, 1989).

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