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## CHAPTER NINE

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# The Biology of External Fertilization in Deep-Sea Echinoderms

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### ABSTRACT

External fertilization by free spawning is much more common than internal fertilization among bathyal and abyssal echinoderms. A few species of echinoids may pseudocopulate by exchanging gametes in masses of mucus, which are retained on the adult spines. In deep-sea species of *Aspidodiadema*, elongate sperm nuclei may be an adaptation for swimming through the thick mucus that holds the eggs. Denny's (1988) model of fertilization success predicts that, all else being equal, external fertilization should be a more viable strategy on smooth sedimentary bottoms in the deep sea than in the more turbulent flow conditions found in shallow water. This is contrary to Thorson's Rule, which predicts greater incidence of brooding (and, by inference, internal fertilization) with depth. Reproduction at low population density is sometimes achieved by echinoids, holothuroids, and ophiuroids by aggregation behaviors. Some species aggregate year round and others remain with spawning partners only during the reproductive season. Gametes of echinothuriids contain lipid reserves that apparently allow sperm to remain motile more than three times as long as typical shallow-water echinoid sperm. Functional significance of some gamete modifications, including biflagellate, dimorphic, and pigmented sperm, remains unknown.

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Despite early opinions to the contrary (Thorson 1966), many marine organisms waste a substantial portion of their reproductive effort at the time of fertilization (Pennington 1985; Brazeau and Lasker 1990; Levitan et al. 1992). This loss is minimized most effectively by copulation and internal fertilization. External fertilization, in which eggs and sperm are spawned freely into the water, is a gamble of gametes under even the best of conditions. Shallow-water animals that succeed at this lottery often do so by precise synchrony of gametogenesis and spawning (reviewed by Giese and Kanatani 1987), and by producing so many gametes that substantial losses can be tolerated (Thorson 1950). Most of the cues used by shallow-water organisms for synchronizing gametogenesis and spawning are not available to organisms living in the continuously dark habitats of the deep sea (table 9.1). One might expect, therefore, that copulation, internal fertilization, and postcopulatory sperm storage mechanisms as well as brooding should be common in deep-sea animals. However, seasonal reproduction is surprisingly common in the deep sea (reviewed by Tyler 1988) indicating that cues must exist for synchronizing reproductive processes in the absence of light. Moreover, the generalization that deep-sea animals should brood their young (Thompson 1878; Thorson 1950), is rapidly losing acceptance with the discovery that many deep-sea species produce planktotrophic or pelagic lecithotrophic larvae (see chapters by Pearse, Gustafson and Lutz, and Bouchet, this volume). These recent changes in our thinking about reproductive frequency and modes in the deep sea raise the possibility that external fertilization may be much more common than previously thought.

In this review, I present the existing evidence for free spawning in deep-sea echinoderms and discuss some advantages and disadvantages of external fertilization in the deep sea. I also review behavioral, morphological, and physiological mechanisms that may increase the probability of fertilization. Echino-

TABLE 9.1 *Environmental Cues Used by Shallow Water Animals to Synchronize Reproductive Processes, and Their Availability in the Deep Sea*

Reproductive Process	Cue	Shallow-Water Example	Available in Deep Sea
Gametogenesis	lunar cycles	echinoids	no
	day length	asteroids	no
	temperature	echinoids	maybe
	salinity	mussels	maybe
	food availability	echinoids	yes
Spawning	phytoplankton	mussels	yes (with lag)
	temperature	clams	lag)
	bright sunlight	echinoderms	maybe
	lunar period	corals	no
	sunrise	ascidians	no
	sunset	cnidarians	no
	rain storms	mussels	no
	wave actions	mussels	no

bodied echinothuriids, but spontaneous spawning has been observed in two species (table 9.2). Although the species coverage is smaller, bathyal and abyssal animals in the northeast Atlantic Ocean show a similar pattern. Seven species have been induced to spawn in the laboratory, and there is no evidence for brooding or internal fertilization in any of the other echinoid or asteroid species in this region. Most of the deep-sea species in the North Atlantic are now known to produce pelagic lecithotrophic larvae (reviewed by Pearse, this volume), so free spawning is likely to be the predominant mechanism of fertilization.

The sperm of some deep-sea echinoderms are spawned in thick mucus which remains attached for a time to the spines or to the aboral surface of the male adult. For example, the tiny bathyal echinoid *Salenia goesiana* releases strands of sperm which quickly become entangled on the spines (figure 9.1A, B). The sperm of this species, which have small, circular heads (Eckelbarger et al. 1989a) not unlike the sperm of some sea cucumbers, are retained in the mucus strands for at least several hours. The sticky sperm strands are not easily removed by pipette. Spines of *S. goesiana* are covered with small spinelets which accumulate debris (figure 9.1C) and to which the sperm masses attach readily.

We have also observed the spawning of mucus-bound gametes in two species of the genus *Aspidodiadema*, *A. jacobyi* in the Bahamas and *A. arcitum* off Hawaii. Both released their sperm and eggs in a cloud of viscous mucus that was held in a tight mass on the aboral surface of the body between the spines. The surface microstructure of the spines of *Aspidodiadema* spp. is shown in figure 9.1E, F. Spinelets roughen the spine surface and seem to assist in the retention of the viscous gamete masses. Elsewhere, we have described development of *Aspidodiadema jacobyi*, noting that the mouth does not develop in the larva until 21 days after settlement (Young et al. 1989). We assumed at that time that development of these small eggs took place in the plankton and speculated that the extended pre-feeding period could provide nutritional flexibility needed during planktonic development in a food-poor environment. However, our repeated observations of mucus-bound gametes now raise the possibility that eggs are actually brooded on the spines during the early developmental stages. If this is the case, then fertilization may occur by a form of pseudocopulation when the mucus masses of adjacent individuals come into contact.

The few echinoids known to brood their young are mostly from relatively shallow Antarctic waters (Thompson 1878; David and Mooi 1990), and the mode of fertilization is not known for any of these species. It seems likely that males release sperm into the water, and that fertilization of eggs retained on or in the female takes place without any form of copulation. Copulation is suspected, however, in the tiny Concentricycloidea, which inhabit deep-sea wood. These animals are sexually dimorphic; males have pairs of marginal spines thought to function in sperm transfer. Ultrastructural studies of the sperm support the hypothesis that fertilization takes place internally (Healy et al. 1988).

Numerous asteroids are known to brood their young either externally or internally (reviewed by Hyman 1955), though most of these are from shallow temperate and polar waters. Deep-sea members of the family Pterasteridae probably brood their young in an internal nidamental chamber as do some (but not all: cf. Chia 1966; McEdward 1992) shallow-water species (Fisher 1940). Freely spawned sperm are probably passed into the chamber with respiratory currents similar to those described in a nonbrooding species by Nance and Braithwaite (1979). The deep-sea Antarctic brisingid *Odinella nutrix* (Fisher 1940) forms a brood chamber by interlocking spines at the bases of the arms. External fertilization probably occurs even in those asteroid species that retain their embryos. Internal brooding has been documented in at least two deep-sea holothurians, *Oneirophanta mutabilis* (Hansen 1968) and *Ocnus sacculus* (Pawson 1983). Details of fertilization remain completely unknown for all brooding asteroids and holothuroids from the deep sea.

Taking into account all of the species for which reproductive mode has now been described or inferred, it is apparent that external fertilization by free spawning is the rule rather than the exception among deep-sea echinoderms.

### Population Densities Required for External Fertilization in the Deep Sea

Nutrients have commonly been assumed to limit population size in the deep sea (reviewed by Rowe 1983; Gage and Tyler 1991). This assumption is supported by data showing an inverse relationship between biomass and depth (Rowe 1971; Lampitt et al. 1986) and between population density and depth (Smith and Hamilton 1983). Many species of macrofauna and meiofauna are represented by single individuals in box core samples, and rarefaction curves often fail to reach asymptotes, indicating that the majority of deep-sea species are rare (Gage and Tyler 1991). On the basis of these observations, one might assume that external fertilization would be problematic for many deep-sea species. However, there have been no attempts to estimate the population size that would be required for successful fertilization in a deep-sea animal. One approach to this problem is to consider natural population densities in light of hydrodynamic models that allow us to predict the likelihood that sperm will encounter eggs under flow regimes characteristic of deep-sea habitats.

Denny (1988) and Denny and Shibata (1989) have advanced a useful time-averaged hydrodynamic model which predicts the downstream distribution and density of gametes on the basis of gamete release rate and various flow parameters. The concentration of sperm at any set of  $x$ ,  $y$ , and  $z$  coordinates with respect to a spawning male at coordinates  $0, 0, 0$  can be predicted with the equation:

hydrothermal vents entrain surrounding water and cause local currents to flow toward vents (Mullineaux, this volume).

Wimbush (1976) and Wimbush and Munk (1970) have suggested as a generalization that values of both current velocity and friction velocity are about one order of magnitude lower on abyssal plains ( $\bar{u} = 3$  cm/sec,  $u_* = 0.1$  cm/sec) than on continental shelves ( $\bar{u} = 30$  cm/sec;  $u_* = 1.0$  cm/sec). The same flow parameters are about 1 order of magnitude higher on some wave-swept rocky shores and shallow subtidal reefs (e.g.,  $\bar{u} = 110$  cm/sec and  $\bar{u} = 10$  cm/sec; Denny 1988) than at greater depths on continental shelves. For the purpose of illustration, I will use these generalized values in Denny's equation. However, it should be kept in mind that current velocities vary both spatially and temporally, so the generalizations will have many exceptions. For the other flow parameters in the equation (e.g., directional diffusivity values, sperm release rates), I use values suggested by Denny (1988). One potential source of

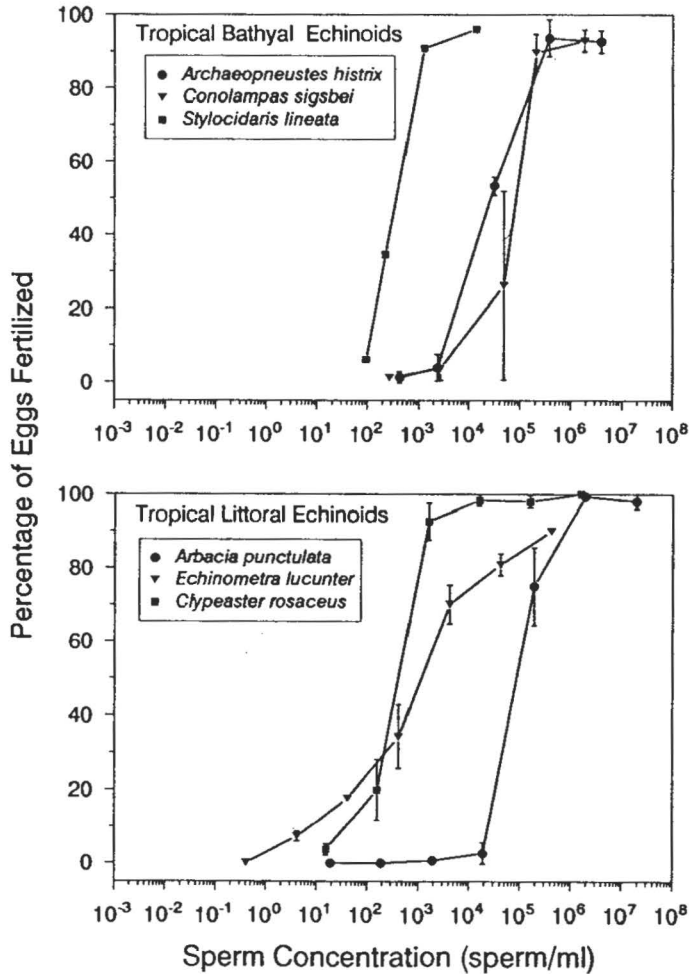


FIGURE 9.2. Percentage of eggs fertilized as a function of sperm concentration for representative tropical bathyal echinoids (upper panel) and tropical echinoids from shallow water (lower panel). With the exception of unreplicated data on *Stylocidaris lineata* (after Young et al. 1992), each point represents mean of 3 samples with standard deviation.

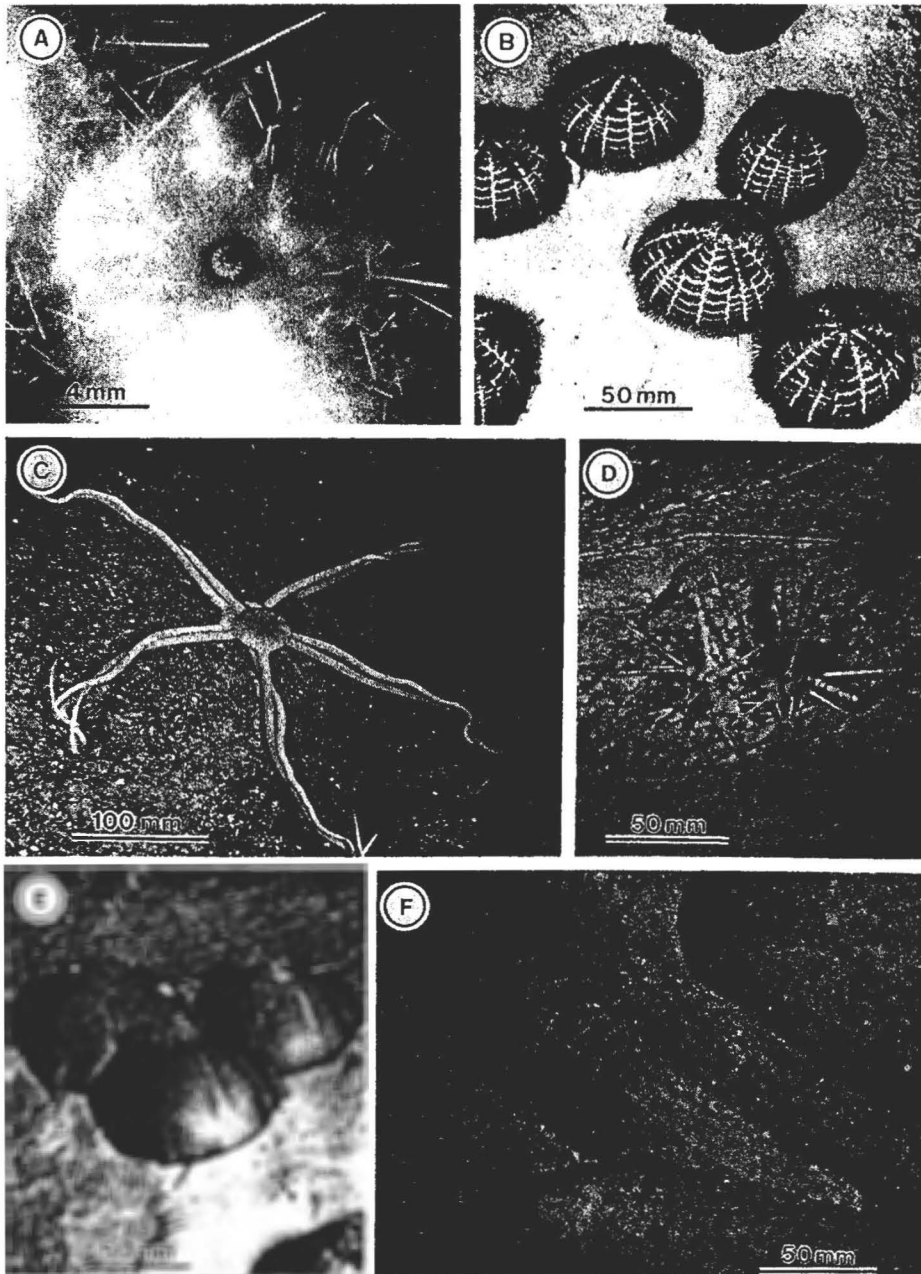


FIGURE 9.3. A: Masses of sperm resting on the aboral surface of a spawning echinothuriid sea urchin, *Araeosoma fenestratum*. B: A herd of the bathyal echinoid *Palaeopneustes cristatus* on soft substratum in the Bahamas. C: Reproductive pair of unidentified ophiuroids in the Bahamas. D: Pair of *Stylocidaris lineata* during the reproductive season at about 600 m depth in the Bahamas. E: Part of a herd of *Conolampas sigsbei* on the Bahamian slope. F: Four individuals of the hermaphroditic holothurian *Paroriza pallens* moving together across the bottom at 918 m depth in the Bahamas.

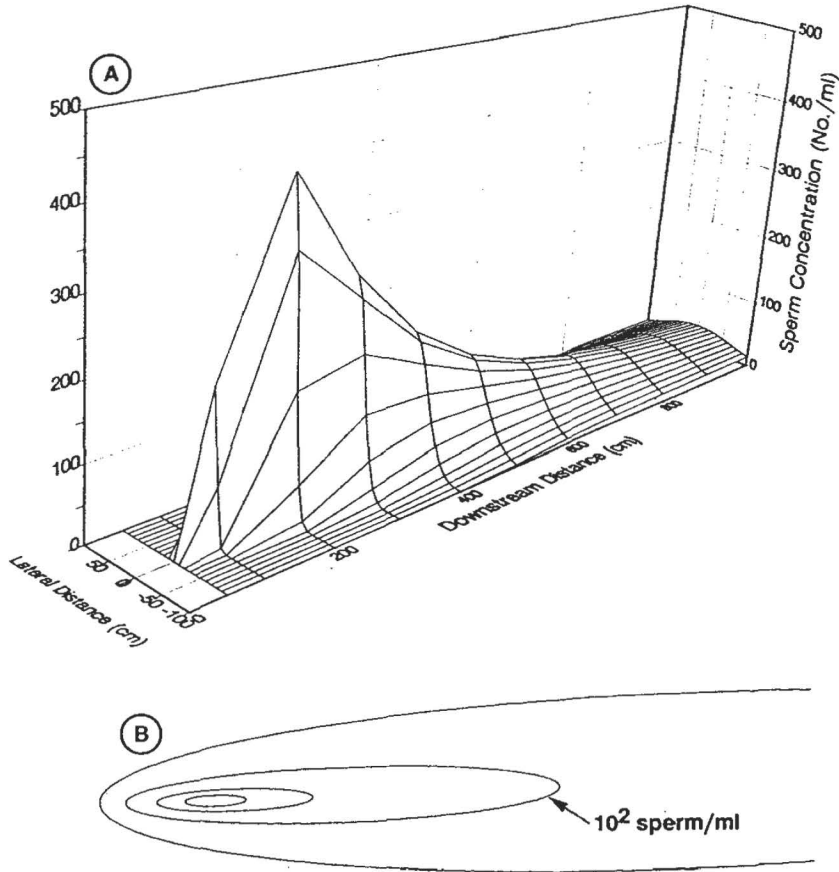


FIGURE 9.5. A: Two-dimensional plot of the sperm concentrations at a height 10 cm off the bottom downstream from a spawning sea urchin at abyssal depths. B: Isopleths of sperm concentration obtained by viewing "A" from below.

dispersed, intermediate density population of *Echinus affinus* from Alvin Dive 436 (1796–1831 m) by assigning the appropriate number of individuals to random Cartesian coordinates. Half of the individuals are randomly assigned to each sex. The positions of all individuals are shown in figure 9.6A. The elliptical portion of the sperm plume wherein more than 50 percent of eggs are likely to be fertilized (i.e., the threshold at which sperm concentration falls below  $10^2$  sperm per ml) is plotted as a 2-dimensional "cloud" extending downstream from each male, and an egg plume of similar dimensions, representing a high (but unknown) concentration of eggs, is plotted downstream from each female. If we assume synchronous spawning by the entire population the high concentration regions of the majority of individuals overlap one or more of those of other individuals in the population (figure 9.7). Wherever egg and sperm clouds overlap, fertilization is likely to be successful. Where sperm clouds overlap each other, the total sperm concentration increases, thereby increasing the effective sperm release rate and extending downstream the distance where concentration remains high enough for fertilization.

Although figure 9.6A is a reasonable representation of the regions where sperm will be effective, similar thresholds do not apply to eggs. A single,



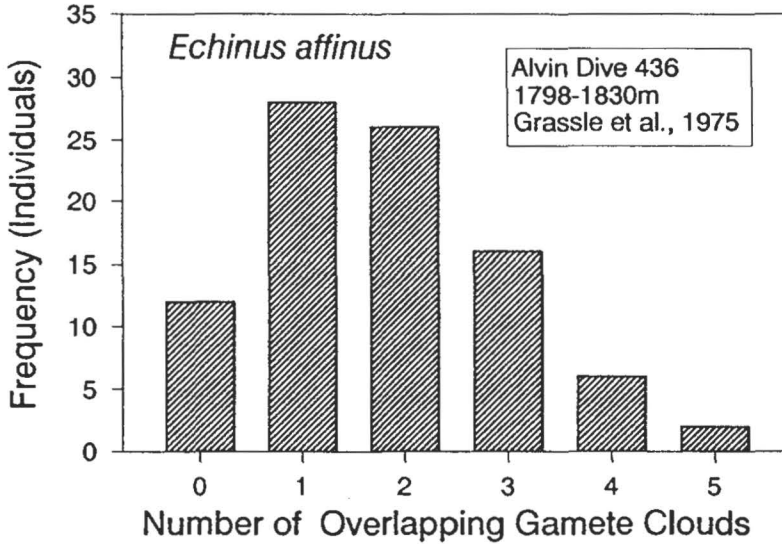


FIGURE 9.7. The frequency of individual gamete plumes in figure 9.6A that overlap various numbers of adjacent gamete clouds.

isolated egg can be fertilized as long as it occurs in a region of high enough sperm density; sperm concentration is the limiting factor, and the number of surrounding eggs is irrelevant. For this reason, the egg plume is more accurately represented as a series of concentric ellipses of increasing area, each representing a region of lower egg concentration. A single egg cloud is plotted in this manner in figure 9.6B. Even at only low current speeds, eggs should be able to drift for a considerable distance before losing viability. In the population illustrated here, most eggs are likely to encounter a high-density sperm plume before drifting very far downstream. Several field experiments on fertilization success (Pennington 1985; Yund 1990; Levitan 1991; Levitan et al. 1992) have examined the fertilization rate of eggs as a function of downstream distance from a spawning male. All show that fertilization is a very uncertain event for eggs held at any particular point in space. However, the few available estimates of population-wide fertilization rates following natural spawnings (Oliver and Willis 1987; Sewell and Levitan 1992) indicate that eggs allowed to drift freely have a much higher chance of becoming inseminated. In the recent study of natural fertilization rates in *Cucumaria miniata* by Sewell and Levitan (1992), more than 90 percent of naturally spawned eggs were found to be fertilized. The simple model with *Echinus affinus* presented here suggests that fertilization should be easily accomplished in a moderately dense deep-sea population as long as spawning is synchronous.

### Dealing with Isolation

Not all deep-sea populations occur at densities as high as those of *Echinus affinus*, nor are their spatial patterns always random. Indeed, as in animal

*Cidaris blakei*, demonstrates the same kind of seasonal aggregating behavior (Young and Tyler unpublished). A major advantage of these very tight aggregations is that gametes released by individuals in the clump will disperse along identical axes, thereby maximizing the chances of fertilization. Where two males spawn at the same time, the sperm release rate is effectively doubled, thereby increasing the downstream distance that concentrations remain high enough to successfully fertilize eggs (Young et al. 1992). Apparent reproductive pairing has also been observed in bathyal ophiuroids (figure 9.3C). It is not known if this species broods or broadcasts its eggs. However, in the pair illustrated, both individuals were very ripe and the male was resting on the female with arms intertwined.

Perhaps the most surprising reproductive aggregations have been observed in hermaphroditic holothurians of the genus *Paroriza* (Tyler et al. 1992). Pairs to quadruplets (figure 9.3F) of these animals have been observed in the North Atlantic (Mauviel and Sibuet 1985; Tyler et al. 1992), in the Bahamas (Tyler et al. 1992, figure 9.1F) and in the Philippine Trench (Fujitoti et al. 1987). Mauviel and Sibuet (1985) present a remarkable photograph showing tracks of two individuals that pass over a substantial area of the bottom. This and other observations suggest that individuals may remain together for extended periods, perhaps spawning together over an extended reproductive season (Tyler et al. 1992).

The physiological and behavioral mechanisms by which deep-sea echinoderms form aggregations remain uninvestigated. Some shallow-water starfish are known to release pheromones that synchronize spawning (Beach et al. 1975; Miller 1989). Such pheromones could also be used to attract individuals. However, since at least one species, *Stylocidaris lineata*, is apparently incapable of differentiating gender, it seems equally plausible that individuals encounter each other randomly, remaining together if spawning is imminent and going their separate ways if it is not.

## Ecological Importance of Gamete Modifications

An unexpectedly high proportion of deep-sea echinoderms display sperm modifications, including gigantism, pigmentation, elongate nuclei, lipid stores in the midpiece, and dimorphism (Eckelbarger et al. 1989a, b, c; Eckelbarger, this volume). These have sometimes been interpreted as adaptations for fertilization in the deep sea, but some may be attributed to ancestry and none are apparently associated with internal fertilization.

The sperm of soft-bodied echinothuriid sea urchins have elongate nuclei and are endowed with large globules of lipid attached to the posterior end of the midpiece (Eckelbarger et al. 1989b). Phospholipids are known to fuel swimming in the sperm of other echinoderms (Mita and Yasumasu 1983) and are metabo-

the spines of the adults. In seawater, the sperm swim in tight circles in the direction of the head curvature, presumably because the head acts as an anterior rudder. It seems likely that these very long and unusual sperm may be adapted for locomotion in the viscous mucus in which the eggs are initially embedded.

Males of the abyssal echinoid *Phrissocystis multispina* produce dimorphic spermatozoa including an euspermatozoon typical of echinoids and a paraspermatozoon which is bipolar-tailed. Superficially, the paraspermatozoon resemble the sperm of *Aspidodiadema*. However, in this case, the curved anterior process is not formed of nuclear material, but of the anteriorly directed portion of the sperm tail. This is the only species of echinoderm known to produce dimorphic sperm, and the function of two sperm types remains unknown. We have speculated elsewhere (Eckelbarger et al. 1989c) that the bipolar-tailed sperm may bind the functional sperm into packets, thereby increasing the distances which sperm can disperse without having their concentration reduced by turbulent diffusion. However, recent observations (Young, Tyler, and Emson, unpublished) of the living biflagellate sperm indicate that they do not form sperm aggregations and that the bipolar-tailed sperm swim by beating the posterior flagellum in much the same way as typical sperm. The anterior portion of the flagellum does not beat; it is held stationary, pointing forward, and causes the sperm to swim in circles, like the sperm of *Aspidodiadema*. Perhaps *Phrissocystis* also spawns gametes in mucus and retains them on the spines. The spines have spinelets similar to those of the three species known to have mucus-bound gametes (figure 9.1D). Unfortunately, gametes of *Phrissocystis* have only been obtained by dissection, so the nature of the spawning process is not known. The function of these unusual dimorphic sperm will remain a mystery until the fertilization process is observed in spawned, living gametes.

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