Factors That Influence the Reproduction of Sea Cucumbers

by

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(Biol 515 at SDSU, Fall 2001)

INTRODUCTION

The echinoderm class Holothuroidea consists of sea cucumbers, which can be described as worm-like organisms with elongated, soft bodies. Like most echinoderms, holothuroids have 5 rows of tube feet along their bodies. These tube feet aid the animal in attachment, locomotion and respiration (Pearse et al. 1987). Within the class Holothuroidea, there are about 1250 species, and these are distributed among 200 genera (Smiley et al. 1991).

There is much variety among the habitats in which sea cucumbers reside. Some species, like *Cucumaria fallax*, inhabit quiet, still waters, while others, such as *C. miniata*, are found in areas that are constantly swept by tidal currents (McEuen 1988). Some holothuroids are tropical reef dwellers (Uthicke 1997); others live in temperate or polar waters (Hamel and Mercier 1995). Even the depth at which these animals can be found varies greatly. Many species live within the intertidal zone, but a few sea cucumbers live deep in the ocean, some among hydrothermal vents (Smirnov et al. 2000). Regardless of the environment in which they are found, sea cucumbers have become highly adapted to life in that environment, especially in their reproductive cycles.

Sea cucumbers can reproduce through sexual reproduction as well as asexual reproduction. Each mode of reproduction has several environmental factors that have been proposed to control its timing. This paper will first introduce the two types of reproduction found in sea cucumbers. I will then discuss some of the factors that have been shown to regulate sexual reproduction, specifically the processes of gametogenesis and spawning, and the factors assumed to control asexual reproduction. Finally, I will make a few suggestions as to directions that should be taken during future studies on external cues for reproduction in holothuroids.

TYPES OF REPRODUCTION IN HOLOTHUROIDS

Sexual Reproduction

For most sea cucumbers, the primary means of reproduction is sexual reproduction. Male and female sexes are usually separate, but there have been a few reports of hermaphroditism in some species (Smiley et al. 1991). Sexual reproduction consists of two main phases: gametogenesis and spawning. Gametogenesis is the formation of sperm and ova, and this process takes place in the sea cucumber's single gonad (Pearse et al. 1987). The term spawning refers to the act of releasing mature gametes into the water. Smiley et al. (1991) report two ways by which the process of spawning can occur. One method is called broadcasting in which sea cucumbers scatter their gametes in the water. Although a majority of holothuroids broadcast their gametes, it is estimated that 41 species (about 3%) of holothuroids are brooders (Smiley et al 1991). Brooders collect fertilized eggs and hold them either internally or externally, rather than releasing their gametes and leaving them. By doing this, brooders offer protection to the developing embryos.

McEuen (1988) found that regardless of the method of spawning, a particular stance is taken by the mature sea cucumbers prior to spawning. Each individual releases its grip on the substrate and lifts its anterior end. Shortly after taking this stance, males will release their gametes into the sea. Females then follow male spawning, typically within a timeframe of minutes to hours. McEuen (1988) also noted that males rarely shed all of their gametes at once, where as females do not spawn repeatedly.

Asexual reproduction

Asexual reproduction is another method by which sea cucumbers propagate. Dalyell (1851, in Crozier 1917) first presented the idea of asexual reproduction, through the process of transverse fission, among holothuroids. This was based largely on observations of individuals kept in aquariums. The idea was approached with uncertainty by Crozier (1917) who felt that self-division was not a method of propagation among holothuroids in their natural environment. However, through his own research on transverse fission in *Holothuria surinamensis*, he found evidence that it is indeed a process that occurs under natural conditions.

Smiley et al. (1991) describe three patterns of fission among holothuroids. One process involves the individual attaching its anterior and posterior tube feet to the substrate and walking in opposite directions. This thins the middle of the body, which eventually ruptures. The animal is then left connected only by the gut, which eventually breaks and two separate sections are formed. In the second pattern of fission, the animal divides into three parts by constricting its body at both ends and inflating the middle region. After twisting forcefully, the body wall ruptures at the site of constriction. The third pattern of fission is similar to the second in that it involves the constriction of the body, but instead of dividing into three parts, the sea cucumber divides into halves. This is the process of fission that was observed by Crozier (1917) and is illustrated in Figure 1. After each pattern of fission is completed, each section formed must then regenerate either the anterior or posterior end, depending on which end was lost.

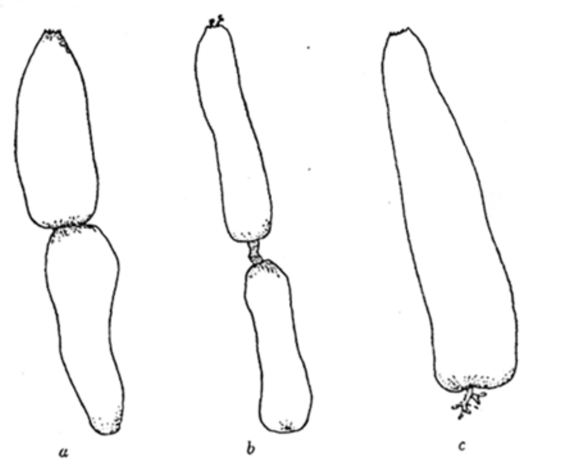

Figure 1. Outlines of individuals dividing or recently divided. In a and b the division is shown in progress; in b the exposed portion of the undivided intestine is visible; in c is given the outline of a recently separated oral half. From Crozier (1917).

FACTORS THAT INFLUENCE SEXUAL REPRODUCTION

It is often mentioned in the literature that holothuroids have synchronous reproductive cycles. Many environmental factors have been proposed as causes of this synchronization. These include temperature (Tanaka 1958), phytoplankton blooms (Cameron and Fankboner 1986), lunar periodicity (Kubota and Tomari 1998), and chemical communication (Hamel and Mercier 1996, 1999). What is the possible advantage in having a cue that coordinates the production gametes and/or the release of them? The answer: maximization in the rate of fertilization and minimization of wasted gametes (Hamel and Mercier 1999). Both of these aspects are important in sexual reproduction.

Sexual reproduction has metabolic costs. It takes energy to generate and ripen gametes, as well as to release them. In most invertebrates, at least half of the total energy taken in is diverted into gamete production (Randall et al. 1997). It is best not to waste this energy when nothing may come of it. For instance, it would be disadvantageous for a sea cucumber to release its gametes at a time when few or no others are releasing theirs. The gametes released by that individual would then become nothing more than food for other organisms. Likewise, if the environmental conditions were not favorable for embryonic development, the same result would occur. It is also important for different species of sea cucumbers to spawn at separate times in order to reduce the amount of gametes that are lost to hybridization (Babcock et al. 1992).

Water temperature is often cited as a primary factor that influences spawning in holothuroids. This is largely based upon the results of Tanaka's (1958) studies on spawning in *Stichopus japonicus*. Studies have also found that suddenly raising water temperature, even a few degrees, will induce spawning among some species of holothuroids (Costelloe 1985, Morgan 2000).

On the other hand, Cameron and Fankboner (1986) suggest that temperature has a greater influence on the *season* of the reproductive cycle. Conand (1993) and Hamel et al. (1993) found that many species of holothuroids undergo an increase in gametogenesis after the winter months, when the water temperature begins to increase. This, in turn, leads to spawning that takes place in the warmer summer months, something that has been shown in both temperate and tropical species of sea cucumbers (Chao et al. 1994).

Photoperiod also has been suggested to be a factor controlling reproductive cycles of echinoderms. While it has not been studied widely in sea cucumbers, photoperiod has been studied in depth in another echinoderm, the sea urchin *Strongylocentrotus purpuratus.* Bay-Schmith and Pearse (1987) found that photoperiod has a large influence on the initiation of gametogenesis in this species. When *S. purpurpratus* was exposed to a fixed photoperiod of short days (8-12 hours of daylight), the growth and maturation of gametes was activated, but when the length of daylight was increased, gametogenesis was inhibited. Furthermore, Bay-Schmith and Pearse (1987) were able to shift the reproductive period of *S. purpuratus* by six months, causing gametogenesis to take place out of season. A study by Conand (1993) found that, like in *S. purpuratus*, photoperiod is an initiating factor for gametogenesis in sea cucumbers. Yet, when it comes to spawning, Cameron and Fankboner (1986) propose that photoperiod takes on a more passive role, mainly by enhancing phytoplankton productivity.

Phytoplankton is considered to be an important component that influences spawning among sea cucumbers. This is because many species have planktotrophic larvae, which feed on phytoplankton (Smiley et al. 1991). Hamel and Mercier (1995) found that *Cucumaria frondosa* spawned abruptly when chlorophyll concentrations were high, indicating a phytoplankton bloom. Himmelman (1975) speculated that a chemical released by phytoplankton initiates nervous and physiological events that ultimately cause spawning in marine invertebrates, such as the sea urchin *Strongylocentrotus droebachiensis*. This may be the same mechanism by which phytoplankton induces spawning in sea cucumbers.

Another external factor that has been implicated in affecting spawning in holothuroids is the lunar cycle. Babcock et al. (1992) found that they were able to predict the day and hour of spawning in three species of sea cucumber: *Bohadschia argus*, *Euapta godeffroyi* and *Stichopus chloronotus*, which were observed to spawn around sunset on the first, second and third nights after a full moon during the breeding season. *Polycheira rufescens* (Kubota and Tomari 1998) and *Holothuria scabra* (Morgan 2000) also show a lunar spawning rhythm in their breeding seasons by spawning at dusk, close to a new or full moon, when the tides are at their highest level. Kubota and Tomari (1998) believe that lunar periodicity may control spawning by stimulating endogenous cues in sea cucumbers.

Chemical communication is the most recent area of study among factors that influence reproduction in holothuroids. Hamel and Mercier (1996) report a use of chemical cues during the reproductive cycle in sea cucumbers, specifically *Cucumaria frondosa*. They found that when exposed to the same constant environmental conditions, *C. frondosa* kept in groups exhibited synchronous gamete synthesis, where as those that were kept in isolation did not. It was also found that a mature individual had a significant influence on the maturation process of an individual at an earlier stage of gametogenic development. This influence, however, was only observed in individuals of the same sex. A later study by Hamel and Mercier (1999) concluded that mucus is the chemical mediator of gametogenic synchrony among *C. frondosa*. The study also showed that individuals living at different photic levels are affected by mucus in the same ways. Therefore, mucus may be the agent by which sea cucumbers located at depth, where other exogenous factors (i.e. photoperiod or temperature changes) are negligible, attain reproductive synchrony.

FACTORS THAT INFLUENCE ASEXUAL REPRODUCTION

Uthicke (2001) suggested that the body size of a sea cucumber could have an effect on the likelihood that asexual reproduction will take place. He hypothesized that certain habitats will favor large individuals. If this is the case, the sea cucumbers may put their energy toward growth (and eventually sexual reproduction) rather than fission. If the habitat favors individuals of a smaller size, asexual reproduction will be enhanced. The specific factors that determine suitable size are not known, but it is suggested that water current, sediment grain size and available shelter are a few (Uthicke 2001).

Food availability may influence the occurrence of asexual reproduction. During the cold winter months, bacteria, detritus and diatoms, which some holothuroids feed on, are generally less abundant (Uthicke 1997). Uthicke (1997) found that there is a significant increase in asexual reproduction during this time. Since sea cucumbers cease to feed during the period of regeneration that follows fission (Uthicke 1997), reduced food availability may be a signal that fission should take place.

Food availability may also contribute to the stability of the habitat in which sea cucumbers reside, consequently influencing reproduction. Uthicke (2001) suggests that a stable habitat may inhibit asexual reproduction. This is due to the stress that an unstable habitat, including large fluctuations in water temperature, salinity and food sources, can impose on sea cucumbers (Uthicke 2001). This added stress, in turn, may lead to an increase in mortality rates. Thus, in order to maintain the population density, asexual reproduction will be enhanced (Chao et al. 1994).

Chao et al. (1994) recognize that fission may be a mechanism for maintaining a population, but also point out that it can cause a reduction in the sexual reproduction potential. This is especially likely to occur if fission takes place during gamete growth; it will interfere with spawning. Conversely, Emson and Mladenov (1987) propose that asexual reproduction may be an effect of lowered sexual reproduction potential instead of its cause. They noticed in their study of fission in *Holothuria parvula* (Selenka) that there was an absence of small individuals other than those that had recently split. This was presumed to show that sexual reproduction had failed to produce enough larvae to later recruit, as juveniles, for sexual reproduction. Thus, there would be a need to replenish the population through asexual reproduction.

By combining the factors previously mentioned (body size, food availability, habitat stability, mortality and amount of larvae from sexual reproduction), Uthicke (2001) devised a model that predicts the reproductive response to these factors. This model is shown in Figure 2. Many of the factors interact with each other and are not independent influencers of the reproductive mode.

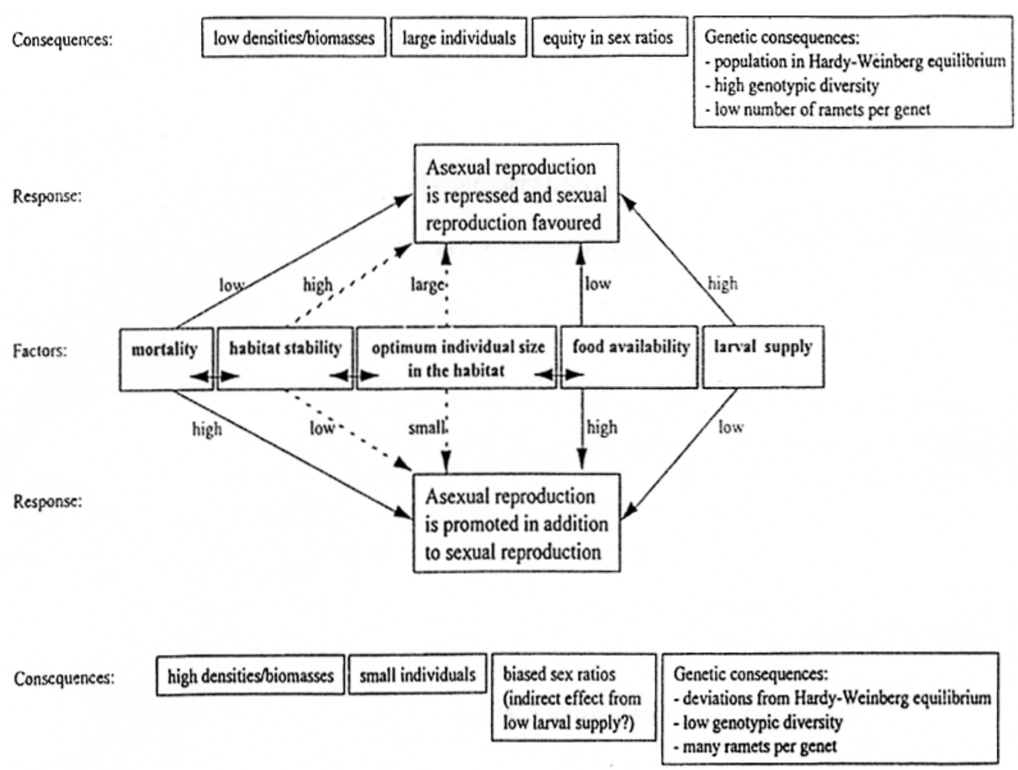

Figure 2. Uthicke's (2001) model for the factors influencing asexual reproduction in holothuroids.

One idea that Uthicke's (2001) model does not take into account is the interaction between food availability and larval supply. Food supply, in the model, is referring to the food available to sediment-feeding adults. However, if the food sources (i.e. phytoplankton) available to planktotrophic larvae are not sufficient, it could lead to a decrease in the amount of larvae. As a result, there would likely be an amplification of asexual reproduction.

FUTURE DIRECTIONS

Many studies have found that temperature-shock treatment (rapid increase in water temperature) is a way of inducing spawning among sea cucumbers (Costelloe 1985, Morgan 2000). Even though temperature-shock may stimulate spawning in some species, it is not correct to assume that temperature alone is a cue for spawning since erratic temperature variations can be found in many environments (Himmelman 1975). To discover the effects temperature has on spawning, in future experiments all other environmental conditions should be kept constant; only temperature should be varied. This way, it may be possible to find out whether a *change* in temperature is required for spawning to take place, or if certain temperature conditions are needed.

Another direction for future research concerns chemical communication between individual sea cucumbers. Hamel and Mercier (1999) discovered that mucus was the chemical mediator of gametogenesis in *Cucumaria frondosa*. Yet, it is currently not known if a component of the mucus itself or a chemical released with the mucus is the messenger. I would suggest that researchers look to see if mucus controls gametogenesis in other species, especially those in the deep sea, such as *Bathyplotes natans* (Roberts and Moore 1997) and *Paracucumaria capense* (Thandar 1998). This suggestion is made because in the deep sea environment factors such as changes in light or water temperature are not significant. In addition, researchers may want to focus on mucus, or another chemical released with it, as a chemical cue for spawning.

Another type of chemical cue that I believe could play a role in the synchronization of spawning is the presence of gametes in the water. Perhaps gametes of one species of sea cucumber may induce spawning of individuals in the *same* species. I base this suggestion on the research by Young (1945) who found that the mussel *Mytilus californianus* spawned when exposed to a spawning individual or to recently collected gametes. If this mechanism is present in sea cucumbers, synchronous spawning could be achieved in two ways. First, the release of sperm from one male could cause nearby males to spawn. Secondly, since females follow males in spawning (McEuen 1988), the sperm suspension in the water may be the cue used to initiate spawning in females.

Likewise, the presence of gametes of another marine invertebrate that shares the same habitat can act as a cue for spawning in sea cucumbers. This is known as heterospecific spawning and has been reported in coral reef invertebrates, such as the giant clam *Tridacna gigas* (Babcock et al. 1992).

SUMMARY

The factors that have been found to have an effect on reproduction in holothuroids do so on many levels. Some factors, like temperature, photoperiod and chemical communication are known to initiate the sexual reproduction process of gametogenesis. Others, such as phytoplankton blooms and lunar cycle have been shown to directly stimulate spawning among mature sea cucumbers. Asexual reproduction has its own set of controlling factors; body size, food availability, habitat structure and number of recruits are among these.

It is becoming increasingly important to know the factors that affect reproduction in sea cucumbers. The over-fishing of some species (e.g. *H. scabra*) for human consumption has left some populations severely depleted. Purcell et al. (2002) suggest that it may take decades for such populations to recover. By understanding the factors that influence reproduction among sea cucumbers, fisheries can be set up to expedite the recovery process, ensuring the presence of sea cucumbers for future generations.

LITERATURE CITED

Babcock, R., C. Mundy, J. Keesing and J. Oliver. 1992. Predictable and unpredictable spawning events: *in situ* behavioural data from free-spawning coral reef invertebrates. Invertebrate Reproduction and Development **22**:213-228.

Bay-Schmith, E. and J.S. Pearse. 1987. Effect of fixed daylengths on the photoperiodic regulation of gametogenesis in the sea urchin Strongylocentrotus purpuratus. International Journal of Invertebrate Reproduction and Development **11**:287-294.

Cameron, J. L. and P. V. Fankboner. 1986. Reproductive biology of the commercial sea cucumber *Parastichopus califonicus* (Stimpson) (Echinodermata: Holothuroidea) I. Reproductive periodicity and spawning behavior. Canadian Journal of Zoology **64**:168-175.

Chao, S.-M., C.-P. Chen and P. S. Alexander. 1994. Reproduction and growth of *Holothuria atra* (Echinodermata: Holothuroidea) at two contrasting sites in southern Taiwan. Marine Biology **119**:565-570.

Conand, C. 1993. Reproductive biology of the holothurians from the major communities of the New Caledonian Lagoon. Marine Biology 116:439-450.

Costelloe, J. 1985. The annual reproductive cycle of the holothurian *Aslia lefevrei* (Dendrochirota: Echinodermata). Marine Biology **88**:155-165.

Crozier, W. J. 1917. Multiplication by fission in Holothurians. American Naturalist **51**:560-566.

Emson, R. H. and P. V. Mladenov. 1987. Studies of the fissiparous holothurian *Holothuria parvula* (Selenka) (Echinodermata: Holothuroidea). Journal of Experimental Marine Biology and Ecology **111**:195-211.

Hamel, J.-F., J. H. Himmelman and L. Dufresne. 1993. Gametogenesis and spawning of the sea cucumber *Psolus fabricii* (Duben and Koren). Biological Bulletin **184**:125-143.

Hamel, J.-F. and A. Mercier. 1995. Spawning of the sea cucumber Cucumaria frondosa in the St. Lawrence Estuary, eastern Canada. SPC Beche-de-mer Information Bulletin **7**:12-18.

Hamel, J.-F. and A. Mercier. 1996. Evidence of chemical communication during the gametogenesis of holothuroids. Ecology **77**:1600-1616.

Hamel, J.-F. and A. Mercier. 1999. Mucus as a mediator of gametogenic synchrony in the sea cucumber Cucumaria frondosa (Holothuroidea: Echinodermata). Journal of the Marine Biological Association of the United Kingdom **79**:121-129.

Himmelman, J. H. 1975. Phytoplankton as a stimulus for spawning in three marine invertebrates. Journal of Experimental Marine Biology and Ecology **20**:199-214.

Kubota, T. and M. Tomari. 1998. Reproduction in the apodid sea cucumber *Polycheira rufescens*: semilunar spawning rhythm and sex change. Journal of the Marine Biological Association of the United Kingdom **78**:249-267.

McEuen, F. S. 1988. Spawning behaviors of northeast Pacific sea cucumbers (Holothuroidea: Echinodermata). Marine Biology **98**:565-585.

Morgan, A. D. 2000. Induction of spawning in the sea cucumber *Holothuria scabra* (Echinodermata: Holothuroidea). Journal of the World Aquaculture Society **31**: 186-194.

Pearse, V., J. Pearse, M. Buchsbaum and R. Buchsbaum. 1987. Living Invertebrates. Boxwood Press, Pacific Grove, California, USA.

Purcell, S., D. Gardner and J. Bell. 2002. Developing optimal strategies for restocking sandfish: a collaborative project in New Caledonia. SPC Beche-de-mer Information Bulletin **16**:1-4.

Randall, D., W. Burggren and D. French. 1997. Eckert Animal Physiology. W.H. Freeman and Company, New York, USA.

Roberts, D. and H.M. Moore. 1997. Tentacular diversity in deep-sea deposit-feeding holothurians: Implications for biodiversity in the deep sea. Biodiversity and Conservation **6**:1487-1505.

Smiley, S., F. S. McEuen, C. Chaffee and S. Krishan. 1991. Echinodermata: Holothuroidea. Pages 663-750 *in* A.C. Giese, J. S. Pearse, and V. B. Pearse, editors. Reproduction of marine invertebrates, echinodermata and lophophorates. Volume VI. Boxwood Press, Pacific Grove, California, USA.

Smirnov, A.V., A.V Gebruk. S.V. Galkin and T. Shank. 2000. New species of holothurian (Echinodermata: Holothuroidea) from hydrothermal vent habitats. Journal of the Marine Biological Association of the United Kingdom **80**:321-328.

Tanaka, Y. 1958. Seasonal changes occurring in the gonad of *Stichopus japonicus*. Bulletin of the Faculty of Fisheries, Hokkaido University **9**:29-36.

Thandar, A.S. 1998. A new genus and three new species of deep-sea holothuroids from the west coast of South Africa (Echinodermata). Journal of Zoology **244**:79-88.

Uthicke, S. 1997. Seasonality of asexual reproduction in *Holothuria* (*Halodeima*) *atra*, *H*. (*H*.) *edulis* and *Stichopus chloronotus* (Holothuroidea: Aspidochirotida) on the Great Barrier Reef. Marine Biology **129**:435-441.

Uthicke, S. 2001. Influence of asexual reproduction on the structure and dynamics of *Holothuria* (*Halodeima*) *atra* and *Stichopus chloronotus* populations of the Great Barrier Reef. Marine and Freshwater Research **52**:205-215.

Young, R.T. 1945. Stimulation of spawning in the mussel (Mytilys californianus). Ecology **26**:58-69.