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Annual reproductive periodicity in eight echinoid species on the Caribbean coast of Panama

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ABSTRACT: Monthly samples of eight species of echinoids from the San Blas Islands, Panama were injected with isotonic Potassium Chloride solution to test their readiness to spawn. The percentage of animals that responded to these injections each month was used as an index of the reproductive activity of the populations. The samples revealed annual cycles in the reproduction of Echinometra viridis, Lytechinus williamsi, Clypeaster rosaceus, and Leodia sexiesperforata. These species are reproductively active during Panama's wet season from April to December, and reproductively quiescent during the dry season. Lytechinus variegatus, Tripneustes ventricosus, and Clypeaster subdepressus are ripe throughout the year, while Echinometra lucunter shows non-periodic fluctuations in readiness to spawn. The data do not support the hypothesis (Lessios 1981) that in constant environments rare species should exhibit greater reproductive synchrony than common species.

1. INTRODUCTION

The comparative approach has been employed extensively to investigate possible links between reproductive periodicity of echinoderms and fluctuations in their environment. Comparisons between populations of the same species from different localities have been used to explore the relationship between reproduction and environmental seasonality (Pearse 1968, 1969, 1970, 1974), food availability (Crump 1971; Dix 1970; Gonor 1973), water depth (Moore 1934), and degree of exposure to wave action (Lewis and Storey 1984). Reproductive cycles of different species in the same area have also been compared (Bennett and Giese 1955; Pearse 1968; McPherson 1969; O'Connor et al. 1978; Hendler 1979; Lessios 1981; Tyler et al. 1982). Similarities between reproductive cycles of unrelated species in the same environment often suggest the existence of a strong environmental factor defining a particular time period as optimal for reproduction. For example, the synchronous reproduction of many arctic invertebrate species suggests that they are taking advantage of the spring plankton bloom in this area to release their larvae (Giese 1959; Giese and Pearse 1974). Differences in breeding seasons of various species inhabiting the same area are also instructive; one can ask what aspect of the biology of these species accounts for their different response to the same environment. For instance, dissimilarities in the degree of reproductive periodicity of various species in the environmentally constant deep sea led Rokop (1974) to suggest that population density and mobility are important in determining the presence of reproductive periodicity; rare and sessile species have to maintain reproductive synchrony to increase the probability of fertilization of the gametes they shed into the water. Lessios (1981) also invoked population density to explain why in two abundant species of tropical echinoids reproductive periodicity was lax, while in a third, rare one, breeding cycles were well-defined.

Such correlations seldom constitute elegant demonstrations of the importance of a single environmental factor in the reproduction of the species concerned; they do, however, provide working hypotheses about the relative significance of various parameters, hypotheses which can then be tested either by experiments or by additional comparisons between appropriately chosen localities or species. Thus, Lessios's (1981) post hoc hypothesis that, in a relatively aseasonal tropical environment, population density has a role in determining the presence or absence of reproductive periodicity can be tested in a locality where many echinoid species coexist in different population densities. This paper describes the reproductive cycles of eight species of shallow water echinoids with different population densities at the San Blas Archipelago off the north coast of Panama.

The Caribbean coast of Panama exemplifies the kind of tropical environment envisioned by Orton (1920), when he suggested that in the thermally constant tropics marine animals should breed throughout the year. It is characterized by constant temperatures, small tidal fluctuations, and low but constant primary productivity (Glynn 1972; Meyer & Birkeland 1974; Meyer et. al. 1975; Hendler 1976, 1977). Wind velocity is a variable that does exhibit seasonal changes. During the Panamanian dry season, from mid-December to April, the trade winds blow steadily from the north, creating a seasonal increase in seawater turbulence, reducing cloud cover, and eliminating practically all rainfall. The San Blas Archipelago shares these physical characteristics with the Caribbean coast of Panama. It is also a site of lush coral reefs that support a diverse echinoid fauna. The annual reproductive cycles of eight echinoid species from three different habitats were studied in 1982 and 1983. Tripneustes ventricosus and Lytechinus variegatus inhabit Thalassia beds, L. williamsi and Echinometra viridis are found on live coral reef, E. lucunter and Clypeaster rosaceus live on the shallow reef flat, while C. subdepressus and Leodia sexiesperforata are encountered infaunally in sand bottoms. I collected data on the annual reproductive cycles of these species in an attempt to answer the following questions: 1) Which of these species reproduce cyclically, and which breed throughout the year? 2) If reproductive cycles exist in the various species, do they coincide? 3) If there are differences between the cycles of these species, living in the same environment, what are their possible causes? 4) Is there a negative correlation between population density of the various species and degree of reproductive synchrony?

2. MATERIALS AND METHODS

2.1. Collection sites

The study was conducted near San Blas Point in the San Blas Archipelago, (9° 34' N, 78° 79' W). The infaunal sea urchins Leodia sexiesperforata and Clypeaster subdepressus were collected at an approximate depth of 1 m in a sand patch surrounded by Thalassia beds on Tiantupu reef [see Lessios et al. (in press) for a map of the reefs in the area]. The other species were sampled on or around House Reef, approximately 500 m away. Lytechinus williamsi and Echinometra viridis were collected in areas of live Agaricia and Porites on the reef slope at a depth of 2 to 5 m; E. lucunter and C. rosaceus were gathered at less than a meter of water from the subtidal reef flat; L. variegatus and Tripneustes ventricosus were collected in Thalassia beds (1 to 5 m depth) between House Reef and Nalunega Island.

2.2. Sampling method

Twenty individuals of each species were collected four to two days before new moon each month, for thirteen or fourteen consecutive months. This sampling regime was adopted to avoid possible complications arising from a possible lunar spawning subcycle (Pearse 1975). Each echinoid was placed in a separate container and injected with a 0.5 M solution of Potassium Chloride. KCl induces spawning in ripe echinoids (Tyler 1949; Hinegardner 1975). Echinometra viridis, E. lucunter, Leodia sexiesperforata and Lytechinus williamsi received 5 ml of this solution per animal, while Tripneustes ventricosus, L. variegatus, Clypeaster subdepressus and C. rosaceus received 10 ml because of their larger body cavity. The quantities injected are in excess of what is usually required to induce spawning in ripe individuals. The data consist of the percentage of animals in each sample that spawned in response to the KCl injection. No attempt was made to determine whether shed gametes were fertile. As a means of determining annual reproductive periodicity, this method has some disadvantages when compared with the more widely used gonadal indices (Grant and Tyler 1983a) or oocyte measurements (Grant and Tyler 1983b). It does not distinguish between animals that are at a quiescent stage of their cycle and animals that have recently spawned. It also classifies individuals in one of two stages, and thus makes no allowances for variability in the degree of ripeness. It, therefore, tends to be rather insensitive to subtle changes in reproductive condition. However, the method was chosen because it is a direct measure of readiness to spawn at the time the sample was taken and thus provides information necessary to determine spawning synchrony in each species; it is also rapid, and does not necessarily result in the death of the assayed animals, salient considerations given the total number of animals sampled. The method has proven to be useful in the determination of annual cycles in Lytechinus variegatus and of lunar cycles in two species of Diadema (Lessios 1984).

Population density of each species was determined between July and September 1982 in 1.8 m wide transects, stretching from the shallowest point of each habitat to the habitat end, or (in Thalassia beds) to a distance of 30 m. Numbers of epifaunal echinoids were determined visually; infaunal echinoids were located by searching by feel under the sand to a depth of approximately 5 cm.

A "reproductive synchrony index" had to be devised in order to correlate relative synchrony and population density in each species. For the kind of data used in this study, the best measure of relative reproductive synchrony of a species is the maximum positive deviation from the annual mean percent spawning. This measure attains its highest value if the entire population is reproductively quiescent during some months and spawning in synchrony during others; its lowest value would be attained if each individual spawned at random, so that at any given month the percentage of animals responding to KCl hovered around a mean value. Its chief disadvantage is that it also yields a low value for species in which the majority of individuals is ready to spawn at any given month. However, such year-round breeding may constiute an alternate strategy for avoiding gamete watage. If individuals in a species have the capacity to remain reproductive most of the time, they are under no additional selection pressure to time their reproduction so that it coincides with that of conspecifics. Species that spawn continuously through the year, therefore, are not especially useful in testing the hypothesis that reproductive synchronization in a constant environment helps rare species increase the probability of gamete fertilization. Since each species was sampled for thirteen or fourteen months, the last one or two months of each sample were disregarded in the calculation of annual means.

3. RESULTS

Despite the fact that each species was sampled at the same day of the lunar month, conclusions reached regarding annual reproductive cycles have to be modified with one caveat. The sampling regime assumes that a monthly spawning sub-cycle either does not exist, or, if it does, it follows a lunar period. If the day-to-day variation in readiness to spawn is either haphazard or follows a cycle that is not lunar, it could confound the determination of annual periodicity. That the monthly changes in spawning of seven out of the eight species follow rather regular patterns (see below) suggests that daily variation has not induced spurious results. Specifically, the species can be classified into three functional groups according to their reproductive cycles: a) Species in which the majority of individuals are ripe at any month of the year (year-round breeders); b) species that reproduce during the wet season, but stop reproducing during the dry season (seasonal breeders); c) species in which some individuals are ripe at any given month, but the percentage of ripe individuals fluctuates in a haphazard manner (acyclical breeders).

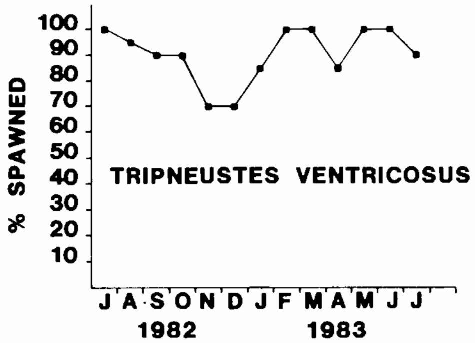

Figure 1. Tripneustes ventricosus: Percent of individuals that spawned when injected with 10 ml of 0.5 M KCl solution. Monthly samples of twenty individuals each were taken 4-2 days before new moon.

3.1. Year-round breeders

Tripneustes ventricosus (Figure 1), Lytechinus variegatus (Figure 2), and Clypeaster subdepressus (Figure 3) spawn throughout the year. In these three species the percentage of individuals responding to KCl injections never fell below 60 %. If a more sensitive technique for the assessment of reproductive condition had been employed, an annual peak might have been detected in these three species. The possibility of such a peak does not change the fact that the majority of individuals in these species contain gametes, ready to be released at any month of the year.

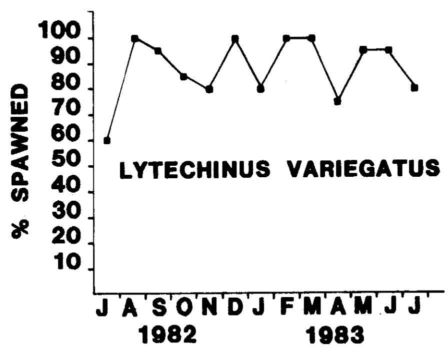

Figure 2. Lytechinus variegatus: Percent of individuals that spawned when injected with 10 ml of 0.5 M KCl solution. Monthly samples of twenty individuals each were taken 4-2 days before new moon.

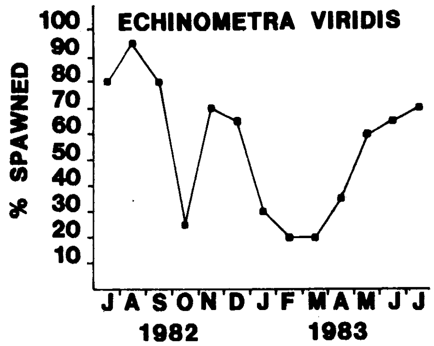

Figure 4. Echinometra viridis: Percent of individuals that spawned when injected with 5 ml of 0.5 M KCl solution. Monthly samples of twenty individuals each were taken 4-2 days before new moon.

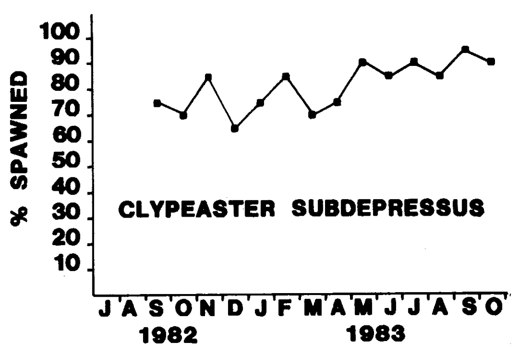

Figure 3. Clypeaster subdepressus: Percent of individuals that spawned when injected with 10 ml of 0.5 M KCl solution. Monthly samples of twenty individuals each were taken 4-2 days before new moon.

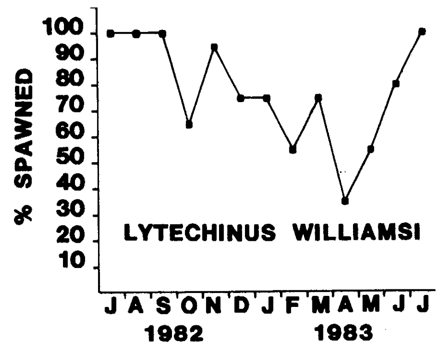

Figure 5. Lytechinus williamsi: Percent of individuals that spawned when injected with 5 ml of 0.5 M KCl solution. Monthly samples of twenty individuals each were taken 4-2 days before new moon.

3.2. Seasonal breeders

Four of the eight species in this study show seasonal variation in their spawning. Echinometra viridis displays a marked reduction in the percentage of animals ready to spawn during the dry season from December to April (Figure 4). Lytechinus williamsi, the other species encountered among live coral, also exhibits lower reproduction during the dry season, but the reduction in ripeness is less pronounced (Figure 5). This species is classified here among the seasonal breeders only because the percent of animals spawning drops below 50 % in April. Reproductive activity in Clypeaster rosaceus peaks in September, and then gradually diminishes, plunging to almost zero during the dry season (Figure 6). Most individuals of Leodia sexiesperforata remain ready to spawn throughout the wet season, but few of them are reproductive in January. There is a gradual increase during the rest of the dry season, until a plateau is reached once again in April (Figure 7). Two of the seasonal breeders, E. viridis and L. williamsi, also show a decline during October in the number of individuals responding to KCl injections. Unlike the dry season reduction, however, which shows a gradual decrease, then a gradual increase from month to month, the

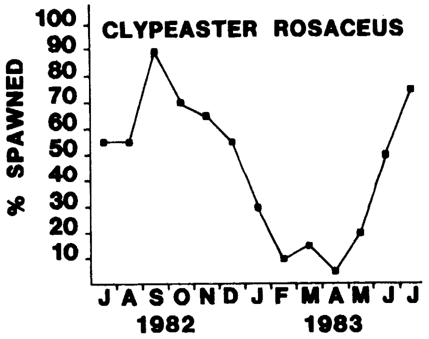

Figure 6. Clypeaster rosaceus: Percent of individuals that spawned when injected with 10 ml of 0.5 M KCl solution. Monthly samples of twenty individuals each were taken 4-2 days before new moon.

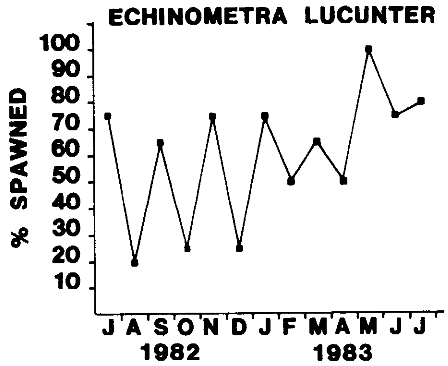

Figure 8. Echinometra lucunter: Percent of individuals that spawned when injected with 5 ml of 0.5 M KCl solution. Monthly samples of twenty individuals each were taken 4-2 days before new moon.

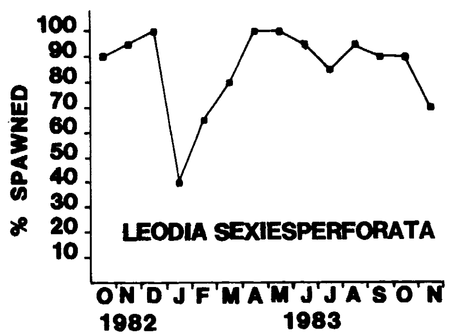

Figure 7. Leodia sexiesperforata: Percent of individuals that spawned when injected with 5 ml of 0.5 M KCl solution. Monthly samples of twenty individuals each were taken 4-2 days before new moon. Note that the origin of the abscissa is different from that of other Figures.

October reduction is limited to this month; the percent of spawning individuals is restored to its high level by November. It is, therefore, likely that this sharp decrease is the result of some environmental anomaly, such as a local increase in temperature, which may have caused spawning in these species (sampled within a few meters of each other) shortly before the time of collection.

3.3. Aseasonal breeders

Spawning in Echinometra lucunter fluctuates between 20 and 75 % throughout the wet season and between 50 and 90 % in the dry season (Figure 8). No clear annual pattern can be ascribed to these fluctuations; they may be an artifact of daily variation, perhaps induced by unpredictable temperature fluctuations in the shallow habitat the species inhabits.

3.4. Relationship between reproductive synchrony and population density

Population density of every species in the habitat where it was collected is shown in Table 1. Numbers of individuals per square meter vary by three orders of magnitude, presenting an opportunity to test the hypothesis that rare species should be reproductively better synchronized then abundant ones (Rokop 1974; Lessios, 1981). A correlation of the density of each species with the maximum positive deviation from the annual mean of the percent of animals responding to KCl injections yields a Spearman rank coefficient that is not statistically significant ($r = 0.03$, $p > 0.5$). If the three year-round breeders are excluded from the analysis, on the grounds that they may be employing a different strategy to avoid gamete wastage, the correlation coefficient changes towards the expected direction (becomes negative) but remains non-significant ($r = -0.6$, $0.5 > p > 0.02$). Naturally, with a sample size of five species, only a perfect correlation ($r = 1$) would have been significant. It could be argued that comparisons are meaningful only within each habitat, since the mode of gamete dispersal and, therefore, the probability of fertilization

Table 1. Population densities of echinoids on House and Tiantupu reefs, and maximum deviation from the annual mean percentage of animals responding to KCl injections, calculated from data presented in Figures 1 to 8.

Species	Number of Transects	Area Covered (sq. meters)	Mean Density (N/sq. meter)	Maximum Deviation from annual mean %
HOUSE REEF Thalassia bed:				
L. variegatus	9	482.66	0.12	11.25
T. ventricosus	9	482.66	0.12	9.58
Reef flat:				
C. rosaceus	9	293.20	0.08	46.67
E. lucunter	9	293.20	0.39	41.67
Reef slope:				
E. viridis	9	93.64	48.77	41.25
L. williamsi	9	93.64	5.66	24.17
TIANTUPU REEF				
Leodia sexiesperforata	10	126.21	1.84	13.75
Clypeaster subdepressus	10	126.21	1.26	14.17

may vary with the living habits of the species and with the degree of clumping of individuals. A habitat by habitat analysis, however, yields mixed results. On the reef flat the expected negative correlation is present; Echinometra lucunter is more abundant and less synchronized then Clypeaster rosaceus. The two infaunal species at Tiantupu, Clypeaster subdepressus and Leodia sexiesperforata, are roughly equal in abundance, and roughly equal in synchrony. The same holds true for the two species from the Thalassia bed, Lytechinus variegatus and Tripneustes ventricosus. However, the results from the reef slope are emphatically different from those expected from the hypothesis. Lytechinus williamsi is an order of magnitude less abundant than Echinometra viridis, yet it is less well synchronized. Thus, none of the ways that one can look at these data provides overwhelming support for the hypothesis that annual reproductive cycles of rare species are more synchronized than abundant ones.

4. DISCUSSION

The simultaneous assessment of reproductive cycles in eight species makes it clear that no single environmental variable can be invoked as an ultimate or proximate factor controlling the mode and timing of reproduction of all echinoids in an area. The hypothesis that in a fairly constant tropical environment rare species maintain better synchronized reproductive cycles to increase the probability of fertilization of their gametes is also not well supported by the data. Though some indications are present that population density may be one of the factors determining degree of synchrony, it seems more prudent to reject the hypothesis until more data are available. Data on monthly spawning cycles of these species are particularly desirable in this context, since reproductive synchrony need not be achieved by annual cycles alone.

In strongly seasonal environments the fluctuation of physical parameters may impose rigid selective regimes, which define the optimal timing of reproduction of most species present. The relatively constant tropical environment of the San Blas may allow enough room for factors other than physical seasonality to become important, so that even species belonging to the same group will follow disparate reproductive cycles. A glimpse of what these factors might be can be gained by trying to determine what characteristics are shared by species that follow a common reproductive pattern.

Three species, Tripneustes ventricosus, Lytechinus variegatus, and Clypeaster subdepressus are ripe for the entire year.

All three have large body sizes; the test diameter of an adult T. ventricosus is about 12 cm, that of L. variegatus about 9 cm, and the anterior-posterior axis of C. subdepressus is about 15 cm. A large body size may allow a species to perceive the environment as more "fine grained" (MacArthur & Wilson 1967), by making small changes in space or time inconsequential for the biological needs of the animal. For example, fluctuations in food availability may be less important for large echinoids, which can store more nutrients in their gonad than small ones. If the rate of utilization of these nutrients is not proportional to body size, the probability that some ripe gametes will be present at any given time in a large animal would be higher. However, a large body cavity alone is not sufficient for the maintenance of year-round breeding cycles. C. rosaceus is also large (ca 14 cm in anterior-posterior axis), yet it shows marked seasonality in its reproduction. The latter species, however, is also rare. By conserving its resources through part of the year, each individual C. rosaceus may be able to produce more gametes during a shorter time in synchrony with its conspecifics. Though the preceding explanation falls in the category of mental gymnastics, it underscores the point that no single factor can explain the variation between species. It may be that a two-factor explanation is necessary; species that are large and common reproduce throughout the year, species that lack one of these attributes have to limit their reproduction to a more discrete time interval.

A seasonal component in the tropical shallow water environment of the San Blas Archipelago is introduced by the changes in wave action, turbidity and salinity caused by the shift in wind pattern during the dry season. Four species seem to respond to these changes by reducing or stopping their reproduction during this period. There is no obvious common characteristic linking these four species. Echinometra viridis and Lytechinus williamsi, are both small and live among live coral. Leodia sexiesperforata has a small body cavity and lives infaunally. Clypeaster rosaceus is large and can live on reef flats, rubble, sand or Thalassia beds. The most interesting question with regard to this group is why all of these species avoid reproducing in the dry season. One can only speculate as to how increased wave action and turbidity in the dry season may affect each of the four species.

Reproductive cycles of some of the species in this study have also been determined in other areas of the Caribbean. Geographic variability in the existence and timing of reproduction seems to be the rule. T. ventricosus and L. variegatus remain ripe throughout the year in the San Blas. The presence of ripe gametes throughout the year in at least some individuals holds true for T. ventricosus and L. variegatus in other localities as well, though the constant ripeness of the majority of the population does not necessarily apply to the entire range of the species. Some ripe individuals of L. variegatus can be found at any time of the year in Florida, but there are clear reproductive peaks in spring and summer (Moore et al. 1963a; Brookbank 1968; Ernest and Blake 1981), with a good deal of variation in timing between local populations (Ernest and Blake 1981) and between years (Moore and Lopez 1972). In Bermuda a single spawning event occurs between mid-April and early June (Moore et. al. 1963a). Tripneustes ventricosus in Florida shows the same pattern as in the San Blas, i.e. constant ripeness of the majority of individuals throughout the year (McPherson 1965), but it also shows peaks in gonadal growth in late spring and early summer (Moore et. al 1963b), or in early winter and early summer (Moore et al. 1963b; McPherson, 1965). In Barbados ripe individuals can be found from January to September, but their percentage decreases drastically after the general spawning in August (Lewis 1958). Echinometra viridis is a seasonal spawner not only at the San Blas but also at two localities on the coast of the Panamanian mainland, where its gonadal content also remains low through the dry season (Lessios 1981). This species also reproduces seasonally in Florida, but there its gonads attain their maximum development during the summer (McPherson 1969). E. lucunter shows no particular annual pattern of reproduction in the San Blas. Development of gonads of this species also fluctuates haphazardly in two localities on the Caribbean coast of the Panamanian mainland (Lessios 1981). In Barbados E. lucunter populations from wave-swept areas spawn once a year, while those from low wave energy habitats spawn twice a year (Lewis and Storey 1984). In Florida this species shows seasonal reproduction, attaining its peak gonadal development during June and July (McPherson 1969). Such variability suggests that local populations have the necessary flexibility to track their respective environments, and that larval exchange does not homogenize the response of populations to the particular environmental challenges they face. Thus, one can hope that ultimate factors controlling echinoid reproduction can be identified in studies limited to a small portion of the species range. In seeking ultimate factors, correlation between reproductive patterns and environmental fluctuations is usually the only available tool. Correlations, however, can be misleading, and the chances that they will mislead increase with decreasing number of species studied. The value of comparing reproductive patterns of many species in the same locality may lie precisely in that, by revealing disparate patterns, they prevent facile explanations and misleading correlations.

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