

REPRODUCTIVE PERIODICITY OF THE ECHINOIDS *DIADEMA* AND *ECHINOMETRA* ON THE TWO COASTS OF PANAMA

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Abstract: Patterns of reproductive periodicity in the regular echinoid species *Diadema mexicanum* A. Agassiz and *Echinometra vanbrunti* A. Agassiz from the Bay of Panama, and *Diadema antillarum* Phillipi, *Echinometra lucunter* (Linnaeus) and *E. viridis* A. Agassiz from the Caribbean coast of the Isthmus of Panama exhibit dissimilarities that reflect the differences of the environments they inhabit. Populations of the two species from the seasonal Bay of Panama display synchronous, well-defined, reproductive cycles. Spawning appears to be timed so that newly metamorphosed sea urchins, rather than larvae, can benefit from the increased food production concomitant with dry season upwelling. On the less seasonal Caribbean shore reproductive periodicity is less defined. Populations of *Diadema antillarum* and *Echinometra lucunter* from the vicinity of the Panama Canal show indications of periodicity, while those from a locality 20 km to the east display little tendency for synchrony between individuals. The much rarer *E. viridis*, on the other hand, maintains well-defined, population-wide cycles in both localities. It is suggested that in a constant environment the intensity of selection for synchrony between individual gametogenic cycles may be inversely proportional to population density.

INTRODUCTION

The degree to which environmental seasonality influences the reproductive patterns of marine invertebrates has been the subject of speculation ever since Orton (1920) proposed that in the thermally constant tropics marine animals should breed throughout the year. Despite the accumulation of considerable quantities of data regarding the reproductive cycles of both temperate and tropical invertebrates (reviewed by Giese, 1959; Giese & Pearse, 1974; Pearse, 1974), however, the relationship between fluctuations of the environment and breeding seasons remains obscure. The expected positive correlation between environmental seasonality and reproductive periodicity is contradicted by examples of tropical and deep-water species that have distinct breeding seasons or temperate ones that breed throughout the year (Giese & Pearse, 1974).

One way to explore the relationship between the two variables is to study the reproductive cycles of closely related populations that are found in separate environments, differing in degree of seasonality. The echinoid species pairs formed by the emergence of the Isthmus of Panama in the Pliocene provide such an opportunity for comparisons between populations that still bear a good deal of genetic similarity (Lessios, 1979).

Each pair of so-called "geminate species" (Jordan, 1908) has one representative

in the eastern Pacific and at least one closely related counterpart in the Caribbean (Chesher, 1972). *Diadema* and *Echinometra* are two of the genera of regular echinoids that include species pairs with one member on each side of the Isthmus. The eastern Pacific *Diadema mexicanum* A. Agassiz is matched on the Atlantic coast by *D. antillarum* Philippi. *Echinometra* has one species, *E. vanbrunti* A. Agassiz on the west coast of America, while in the Caribbean it is represented by the presumed geminate *E. lucunter* (Linnaeus), and an additional species, *E. viridis* A. Agassiz, which, although morphologically distinct, bears a high electrophoretic resemblance to its sympatric congener (Lessios, 1979). Dissimilarities in the reproductive patterns of Atlantic and Pacific species can be presumed to arise either from genetic differentiation accumulated during the $2 - 5 \times 10^6$ yr of independent evolution or from phenotypically divergent responses of basically similar genotypes to different environments.

Despite the small distance that separates the Atlantic from the Pacific coasts of the Isthmus of Panama, the physical profiles of their shallow-water environments are decidedly different (Glynn, 1972). The strong trade winds that traverse the Isthmus from the north during the dry season (mid-December to April) displace the surface water of the Bay of Panama towards the open sea and cold, nutrient-rich water upwells to replace it. The result is marked seasonality with respect to temperature and primary productivity on the southern coast of the Isthmus (Glynn, 1972; Smayda, 1966), whereas these two variables remain relatively constant throughout the year on the Atlantic side (Glynn, 1972; Hendler, 1977). The same winds, however, buffet the Caribbean reef flats with strong waves during the dry season, and create a pattern of seasonal fluctuations in turbulence along this coast.

In the wet season the Atlantic coast receives more rain than its Pacific counterpart, and salinity drops to a lower value at Cristobal than it does at Balboa (Glynn, 1972). More significantly for the intertidal biota, the small amplitude of the tides (≈ 0.5 m) may be slower in flushing the diluted sea water from the shallows (Rubinoff, 1968). The result is seasonality with respect to salinity in the Caribbean intertidal zone.

Thus, populations of one geminate in each pair are found in an environment that is strongly seasonal in temperature and primary productivity, while those of the other are subjected to more haphazard fluctuations in either wave action or salinity. A comparison of the gametogenic cycles of Atlantic and Pacific species can shed some light on the importance of these environmental variables for the existence and the timing of echinoid reproductive cycles.

MATERIALS AND METHODS

SAMPLING

Two collecting stations, as different in their habitat profiles as possible, were established for each species (Fig. 1) and were sampled at monthly intervals.

Diadema mexicanum was collected subtidally in a *Pocillopora* patch reef on the windward (north) side of the Island of Urabá and under alga-encrusted rocks off Boy Scout Beach at Culebra Island. *Echinometra vanbrunti* was obtained intertidally from crevices on Rocky Point next to Boy Scout Beach at Culebra Island, and from rock depressions at Punta Paitilla. *Diadema antillarum* was sampled in the lagoon behind the fringing reef at Fort Randolph in the vicinity of the Panama

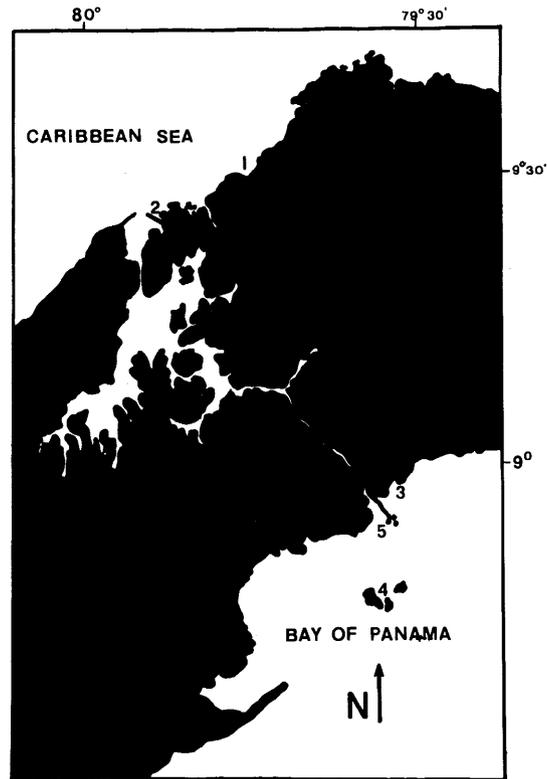


Fig. 1. Localities where the sea urchins were collected: 1, Maria Chiquita; 2, Fort Randolph; 3, Punta Paitilla; 4, Isla Urabá; 5, Culebra Island.

Canal and on the reef flat at Maria Chiquita in the Republic of Panama. *Echinometra lucunter* was collected on the reef flat at Fort Randolph and at Maria Chiquita. *E. viridis* was acquired from a dead *Porites* patch reef in the lagoon behind the fringing reef of Fort Randolph and from the reef flat at Maria Chiquita.

Approximately 20 individuals per month were collected from each locality for each species except *Echinometra viridis*, the population density of which at Maria Chiquita was so low as to make sample sizes of < 10 individuals unavoidable in certain months. Monthly collections of each species were made at approximately

the same phase of the moon to minimize artifacts introduced by a possible lunar subcycle in spawning (Pearse, 1975).

ASSAY PROCEDURES

Animals from the Pacific side were transported to the laboratory at Naos Island in insulated containers, but Atlantic urchins had to be dissected in situ because of the danger that ripe individuals might spawn during the long trip.

The sea urchin test was opened by cutting the oral side, and fecal pellets were removed by puncturing the gut membrane and washing in a gentle stream of sea water. Then the cavity was drained, the gonads removed, and their volume was determined to the nearest 0.1 ml by displacement in sea water.

The tests, with the spines attached, along with the removed oral piece and the lantern, were labeled and allowed to dry for at least 3 days in an air-conditioned room. Then they were weighed to the nearest 0.01 g. Subsequent weighing of some samples showed that weight loss due to further desiccation after the first 3 days did not amount to more than a few hundredths of a gram.

Gonadal indices were calculated as the ratio of gonadal volume to dry body weight, multiplied by 100. Only urchins above the size of first sexual maturity (Lessios, 1979) were used in the calculation of the mean gonadal index of each month. When regressions of the logarithm of gonadal index on body weight were calculated for each month, their slopes were often significantly different from zero, indicating that there is an allometric relationship between gonadal volume and body weight. To remove the possible bias introduced by the different size composition of each sample (Gonor, 1972), adjusted means were calculated by analysis of covariance (Snedecor & Cochran, 1967) with weight as the covariate (independent variable). A logarithmic transformation of the gonadal indices was necessary to normalize their distributions. The reported adjusted means and 95% confidence intervals are the antilogarithms of their respective values on a logarithmic scale (Sokal & Rohlf, 1969).

Sex was determined by microscopic examination of gonadal smears for eggs or sperm; animals with completely unripe gonads could not be sexed. Although the sex ratios were often skewed (excess of males in *Echinometra* and of females in *Diadema*), this skewness was consistent from month to month in every population except *D. antillarum* at Maria Chiquita (Lessios, 1979). This population, however, did not exhibit any significant differences between the sexes in mean gonadal index. It was, therefore, deemed legitimate to lump gonadal indices of males, females and unsexed individuals of each species in every locality in order to determine population-wide trends in gametogenesis.

RESULTS

GAMETOGENIC CYCLES OF THE PACIFIC SPECIES

In the Bay of Panama, populations of *Echinometra vanbrunti* (Fig. 2) and *Diadema mexicanum* (Fig. 3) show well-defined gametogenic cycles. The majority of individuals of both species reach a peak of gonadal size in September, probably spawn during September and October and enter the dry season with a minimum development of the gonads. The gonads remain small through the early dry season, and start their cycle in March. *Echinometra vanbrunti* in Punta Paitilla seems to reach its peak gonadal size 2 months earlier, but otherwise conforms to the general pattern. The ophiuroids *Ophiocoma aethiops* and *O. alexandri*, sampled a year

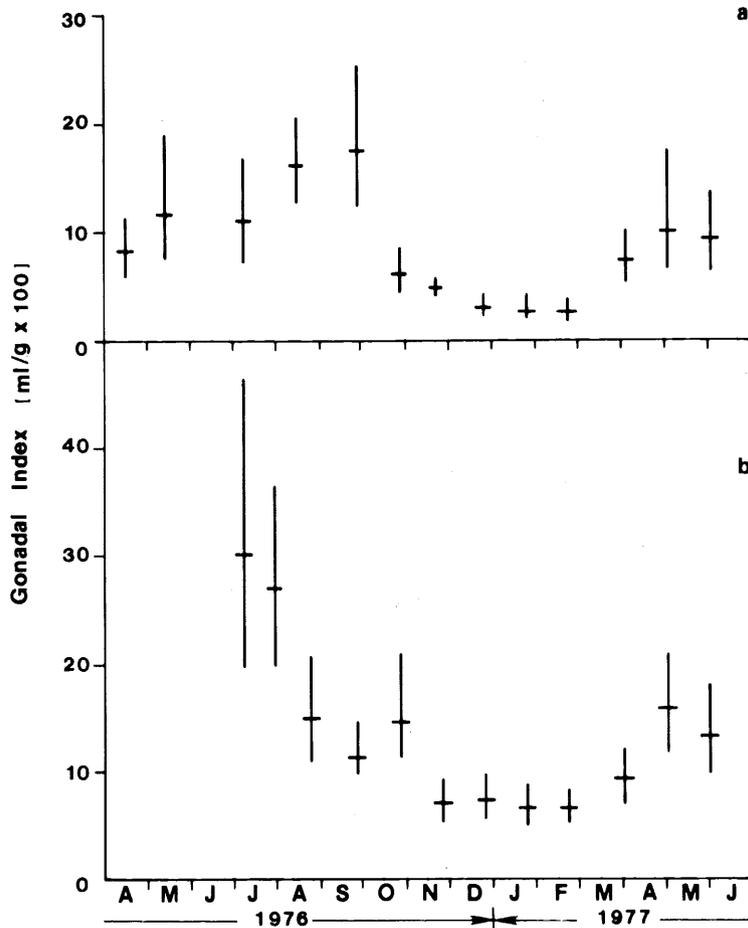


Fig. 2. *Echinometra vanbrunti*: monthly mean gonadal indices, adjusted by analysis of covariance, and 95% confidence intervals at Culebra Island (a) and Punta Paitilla (b); sample sizes of successive months: Culebra, 16, 10, 13, 33, 15, 18, 19, 16, 14, 12, 18, 11, 13; Paitilla, 10, 19, 16, 23, 19, 18, 21, 19, 20, 20, 19, 17.

earlier than these echinoids, exhibited the same pattern (Hendler, 1979). Mortensen (1921) found that in November 1915 *Echinometra vanbrunti* at Taboga Island was at the end of its breeding season. He also noted that *Eucidaris thouarsi* at the same island had "ripe specimens... at considerable numbers" in October 1915, but very few individuals with mature gonads in November and December of the same year,

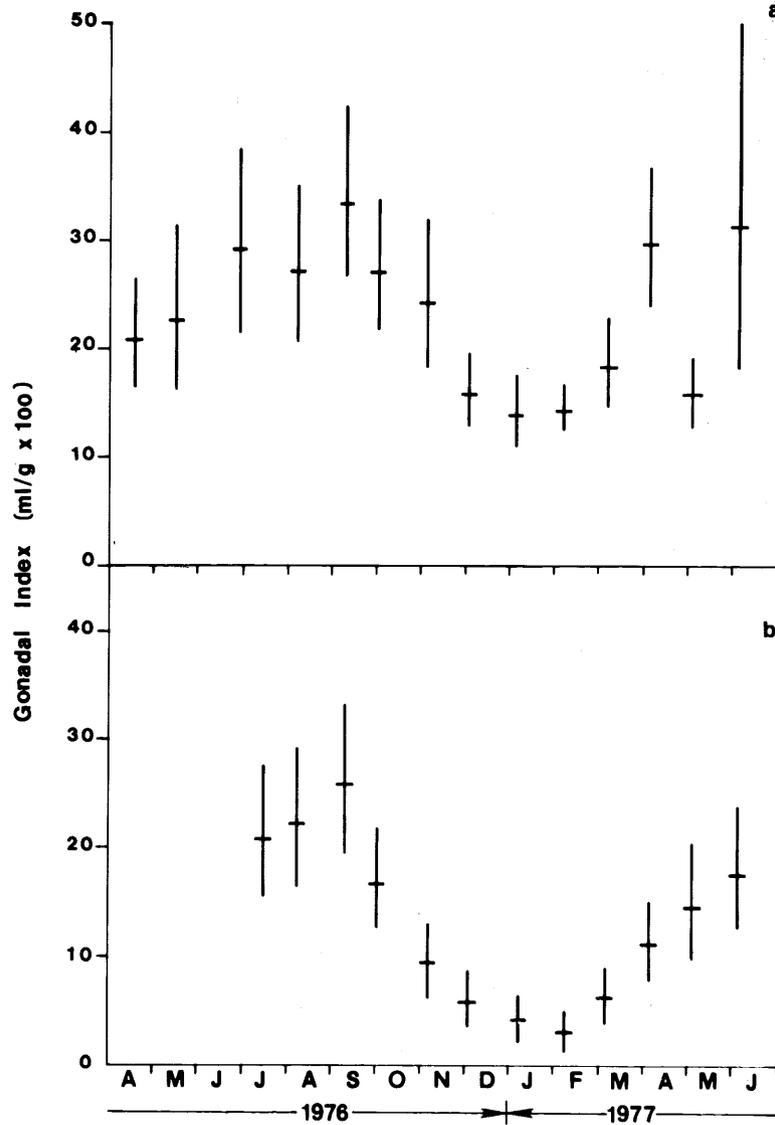


Fig. 3. *Diadema mexicanum*: monthly mean gonadal indices, adjusted by analysis of covariance, and 95% confidence intervals at Culebra Island (a) and Urabá Island (b); sample sizes of successive months: Culebra, 15, 9, 11, 13, 21, 17, 12, 20, 16, 19, 18, 18, 20, 5; Urabá, 20, 20, 21, 23, 19, 18, 19, 17, 18, 20, 16, 20.

while *Toxopneustes roseus* "was evidently at the end of its breeding season most of the specimens being empty" on 11 November 1915. It appears, therefore, that the cycles displayed by the species I studied in 1976-1977 conform to a general pattern for echinoderms living in the Gulf of Panama, and that this pattern is repeatable from one year to the next.

GAMETOGENIC CYCLES OF THE ATLANTIC SPECIES

In contrast to their geminates in the Bay of Panama, the Caribbean echinoid species exhibit mixed patterns of reproductive periodicity. *Echinometra lucunter*

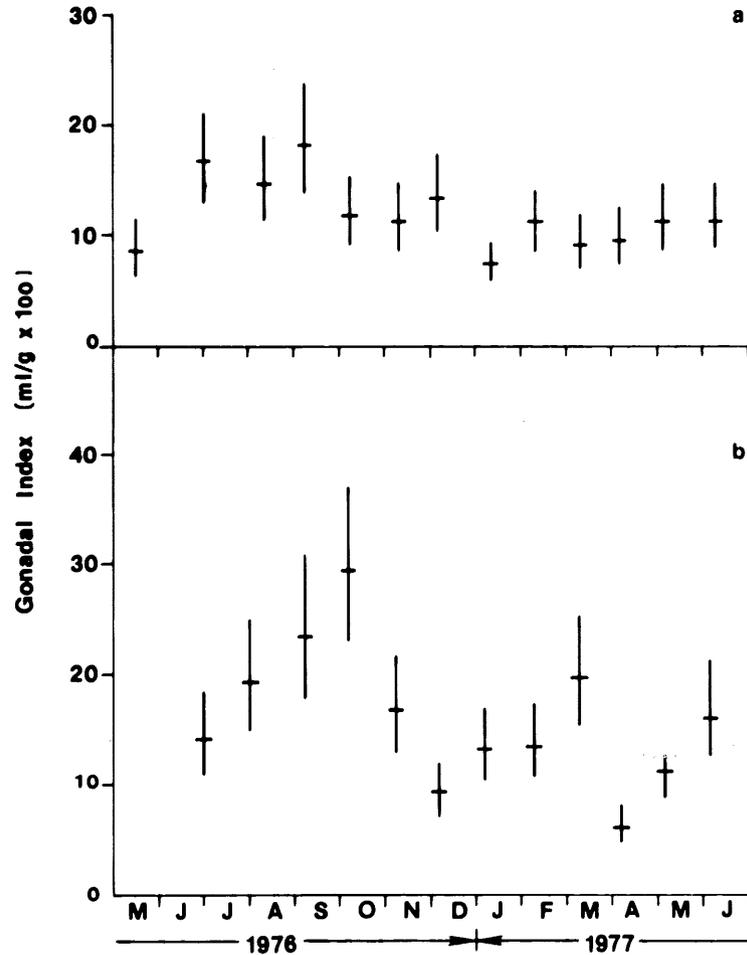


Fig. 4. *Echinometra lucunter*: monthly mean gonadal indices, adjusted by analysis of covariance, and 95% confidence intervals at Maria Chiquita (a) and Fort Randolph (b); sample sizes of successive months: Maria Chiquita, 19, 20, 21, 20, 19, 20, 20, 23, 20, 20, 20, 19; Fort Randolph, 18, 19, 17, 20, 19, 20, 19, 21, 20, 19, 20, 20.

(Fig. 4) in Fort Randolph reaches a peak of gonadal content in October, probably spawns until December, and starts building up its gonads subsequent to that. There may be a secondary spawning right after March. In Maria Chiquita, on the other

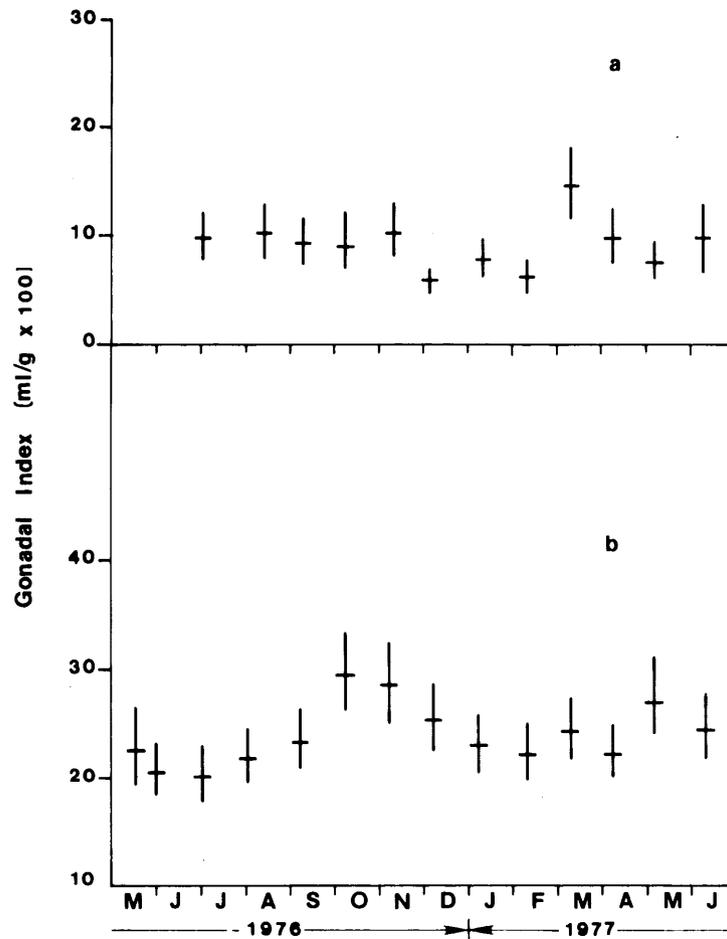


Fig. 5. *Diadema antillarum*: monthly mean gonadal indices, adjusted by analysis of covariance, and 95% confidence intervals at Maria Chiquita (a) and Fort Randolph (b); sample sizes of successive months: Maria Chiquita, 20, 20, 20, 20, 20, 20, 20, 20, 19, 20, 18, 20, 20; Fort Randolph, 11, 20, 13, 19, 19, 20, 20, 20, 20, 20, 21, 20, 20, 19.

hand, if there is a seasonal trend, it is much less pronounced. This species is also reported to spawn in the summer and early fall in Bermuda (Harvey, 1947) and in Barbados (Doran, in Pearse, 1974), and to attain a peak in gonadal index during June and July in Florida (McPherson, 1969).

In *Diadema antillarum* (Fig. 5) the same trend is apparent, namely a cycle for the

entire population with a major peak in October at Fort Randolph, and no seasonality at Maria Chiquita. *Diadema antillarum* is also reported to spawn in the

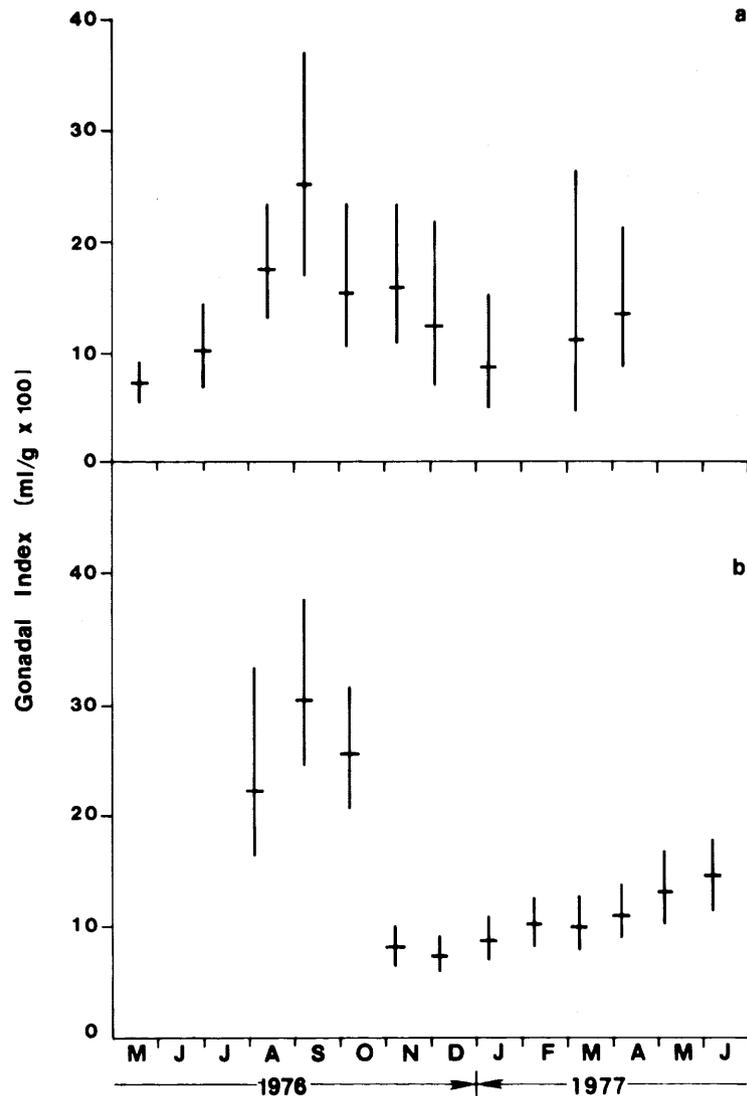


Fig. 6. *Echinometra viridis*: monthly mean gonadal indices, adjusted by analysis of covariance, and 95% confidence intervals at Maria Chiquita (a) and Fort Randolph (b); sample sizes of successive months: Maria Chiquita, 18, 10, 16, 10, 11, 10, 6, 6, 4, 8; Fort Randolph, 9, 20, 20, 17, 21, 20, 20, 16, 20, 16, 20.

summer and early winter at Bermuda (Harvey, 1947), year round in the Virgin Islands (Randall *et al.*, 1964), and throughout the year but with a pronounced peak in January and February in Curaçao (Kristensen, in Randall *et al.*, 1964). More

thorough studies have discovered gonadal peaks during March and April in Barbados (Lewis, 1966) and during November in Florida (Bauer, 1976). Geographic variation in reproductive periodicity, therefore, seems to be the rule in *Echinometra lucunter* and *Diadema antillarum*.

Reproductive periodicity in *D. antillarum* and *Echinometra lucunter* is rather asynchronous even in Fort Randolph; *E. viridis*, on the other hand, displays well-defined synchronous cycles in both localities, with gonadal peaks in September and probable spawning periods until December or January (Fig. 6). In Florida the gonads of this species attain their maximum development in the summer (McPherson, 1969).

DISCUSSION

POSSIBLE REASONS FOR THE PATTERNS OF THE PACIFIC SPECIES

Reproductive periodicity in marine invertebrates serves two, mutually compatible, functions. It allows individuals of a population to take advantage of the best time of the year for reproduction (if there is one), and it ensures reproductive synchrony between conspecifics. When the environment is seasonal, certain times of the year are bound to be more favorable for the production of offspring; individuals that are able to take advantage of these periods will have a higher probability of propagating their genes. It is, therefore, not surprising that reproductive cycles in the seasonal Bay of Panama are synchronized so that the entire population reaches a distinct peak in gonadal development. The reasons for the particular timing of these cycles, however, are less obvious.

Diadema mexicanum and *Echinometra vanbrunti* spawn during roughly the same period in the wet season; unless they possess an abnormally long larval period, their populations undergo recruitment of metamorphosed juveniles before the onset of upwelling. The two instances that I observed an influx of young (≈ 5 mm) *E. vanbrunti* in Culebra Island were in December 1976 and in January 1980, at the beginning of the dry season.

It appears, therefore, that these echinoids do not release their eggs at a time that would allow their planktotrophic larvae to be in the water column during the peak of phytoplankton production. Unlike many temperate (Thorson, 1950; Barnes, 1957; Giese, 1959) and polar (Giese, 1959; Pearse, 1965; Giese & Pearse, 1974) invertebrates, they do not seem to take advantage of the seasonal increase of food for their larvae.

There are many reasons why breeding during the dry season upwelling may not be advantageous despite the increased primary production. Even during the wet season, phytoplankton production in the Bay of Panama is high (Forsbergh, 1963, 1969; Smayda, 1966) and the population densities of echinoids are low (Lessios, 1979). Food for the larvae may, therefore, not be a limiting resource at any time of

the year. Menge (1975) has argued that animals with planktotrophic larvae may time their reproduction to coincide with the time of peak phytoplankton production because surplus food can increase survival rates of their offspring through the shortening of the hazardous larval period. However, the lower temperature of the Bay of Panama waters during the dry season (Glynn, 1972) is known to retard metamorphosis (Thorson, 1950; Hinegardner, 1975); any benefit brought about by increased growth rate due to abundance of food during upwelling may be counter-balanced by the correlated shift of the thermal regime.

An added problem that individuals spawning during the dry season would face is mortality of their larvae due to transport to open sea. During the upwelling, the upper 40 (Schaefer *et al.*, 1958) to 78 m (Forsbergh, 1963) of water are driven offshore. Since larvae tend to be positively phototactic during their early stages (Thorson, 1964), they would run the risk of being transported to water so deep that they could not find appropriate settling sites.

Thus, breeding during upwelling is not as advantageous as it might appear at first glance, and it seems that the echinoids avoid it for good reason; the question why they reproduce during the late wet season, however, remains unanswered. The most likely explanation for the observed timing of gametogenic cycles is that the seasonality of resource production affects the life stage which has the highest probability of suffering from food limitation. In contrast to the abundance of phytoplankton, there is a scarcity of attached algae in the Bay of Panama (Earle, 1972). Benthic diatoms, bryozoa and other potential food items for juvenile sea urchins may also be in short supply. Newly metamorphosed urchins, therefore, could be expected to face the problem of getting an adequate food supply. If food is a limiting resource for the juvenile urchins, but not for the larvae, we would expect these species to time their reproduction so that recruitment would coincide with the period of upwelling. The exhibited cycles would fit this hypothesis.

My assumption in this argument is that populations in the Bay of Panama are able to track the local optimum in spite of possible genetic influx from larvae originating from other areas of the eastern Pacific where upwelling is absent. I believe that in species with high rates of migration between patches of a spatially heterogeneous environment selection does not favor genotypes that conform to a specific optimum but those that allow phenotypic plasticity and ability to predict and respond to local conditions. Thus different populations may track their respective environments through developmental responses and produce locally optimal life history traits even though they are genetically similar.

In an environment as seasonal as the Bay of Panama, any number of proximate factors can aid this synchronization. Between February and March, when the echinoids start building up their gonads, the temperature is beginning to rise and the salinity is beginning to fall (Glynn, 1972). Either variable may serve as a trigger for the initiation of gametogenesis. *Echinometra* and *Diadema*, however, continue to increase the size of their gonads after March when upwelling has ended and

when temperature and salinity regimes have stabilized. The spawning period does not coincide with a warming trend nor with a time of abrupt salinity decreases.

POSSIBLE REASONS FOR THE PATTERNS OF THE ATLANTIC SPECIES

Local variation that in all probability does not have a genetic basis can be seen in the Caribbean species. Unlike the Bay of Panama populations, which display a high degree of concordance between localities and between species, their Caribbean counterparts do not conform to a single pattern. In Fort Randolph all three exhibit roughly synchronous gametogenic cycles; in Maria Chiquita, 20 km away, *Echinometra lucunter* and *Diadema antillarum* do not show a seasonal trend, while *Echinometra viridis* does.

Some seasonal factor must be operating at Fort Randolph that is absent in Maria Chiquita. Temperature is not likely to be involved since fluctuations in this variable on the Caribbean coast are minimal and irregular (Glynn, 1972; Hendler, 1977). There is, however, a correlation between salinity changes and reproductive cycles. The general increase of salinity at the entrance to the canal, adjacent to Fort Randolph, during September and October (Glynn, 1972) coincides with the spawning of all three species in this locality. Whether a biological relationship underlies this correlation and, if so, whether salinity fluctuations act as a proximate or an ultimate factor cannot be determined with the present data. That populations of *E. lucunter* and *Diadema antillarum* at Maria Chiquita do not exhibit any population-wide cycles does not invalidate the possibility that salinity may somehow be involved. Although supporting data are lacking, it is probable that the gently sloping Maria Chiquita reef flat allows oceanic waves to wash over the platform and maintain a more constant salinity regime, even after heavy rains; at Fort Randolph, on the other hand, a sharp reef front protects the lagoon and the reef flat from heavy wave action, but it also prevents the quick flushing of rainwater away from these areas.

Whatever the actual reasons, synchrony between individuals of the *Echinometra lucunter* and *Diadema antillarum* populations even at Fort Randolph seems to be much less pronounced than it is in their Pacific geminates, a pattern not altogether surprising given the relative lack of seasonality in the Caribbean. Somewhat unexpected is the distinct periodicity exhibited by *Echinometra viridis* at Maria Chiquita, where the other two species show little tendency for reproductive synchrony. Population density may be the variable in which this species differs from the other two echinoids sampled.

As the environment becomes less seasonal, one of the selective advantages of maintaining population-wide reproductive cycles becomes less important. Individuals are no longer doomed to inferior reproductive success if they fail to reproduce during a discrete part of the year since the constancy of the environment ensures roughly similar conditions at any given moment. However, the second advantage

of reproductive periodicity, that of achieving synchrony with conspecifics, remains. Even in a completely constant environment there are selection pressures on the individual for maintaining a gametogenic cycle synchronized with that of other members of the population, since the probability of having one's gametes achieve fertilization increases with the number of conspecifics of the opposite sex that breed at the same time. These selection pressures are more intense when population densities are low (Rokop, 1974). While *Diadema antillarum* and *Echinometra lucunter* at Maria Chiquita are quite abundant, *E. viridis* is extremely rare (Lessios, 1979). The well-defined reproductive cycle of its population and the asynchrony of the other two species in the same locality could, therefore, be attributed to this biotic factor.

CONCLUSIONS

Studies which have compared reproductive periodicity in conspecific populations of echinoids from different latitudes (Pearse, 1968, 1969, 1970, 1974) have found that reproductive cycles of the individuals in each tend to become better synchronized with increased distance from the equator and – presumably – with more pronounced environmental seasonality. This relation seems to hold in the present comparisons between Atlantic and Pacific echinoids as well, but only partially. In the Bay of Panama, where the environment is seasonal, reproductive cycles are synchronized; in the Caribbean where the environment is more constant, synchronization seems to be (for dense populations) less pronounced. The distinct population-wide cycles of *E. viridis*, however, indicate that fluctuations of physical variables may not be the only factors which determine whether reproductive periodicity will be present. Biotic parameters, such as population density, may also play a role, and the importance of this role may be enhanced as the physical environment becomes more constant.

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