BULLETIN OF MARINE SCIENCE, 67(3): 989–996, 2000

ANNUAL REPRODUCTIVE PERIODICITY OF THE SEA URCHIN *DIADEMA ANTILLARUM* PHILIPPI IN THE CANARY ISLANDS

M. J. Garrido, R. J. Haroun and H. A. Lessios

ABSTRACT

The tropical sea urchin *Diadema antillarum* is found on both coasts of the Atlantic Ocean. Several studies exist of the reproductive cycles of western Atlantic populations, but despite the extreme abundance of the species in the Canary Islands, nothing is known about its reproduction in this region. We present data on annual reproductive periodicity of eastern Atlantic populations. We determined gonadal indices at two locations in the island of Gran Canaria, Canary Islands. Though water in the southern location is warmer, reproductive cycles are similar. Gonadal content increases between October and April (or May), then declines (presumably due to spawning) until September (or October). The spawning season coincides with the period of most rapid temperature rise, but the new reproductive cycle is initiated as temperature continues to increase. In addition to temperature, reproductive cycles may be related to seasonal increases of benthic algal productivity.

Intraspecific comparisons of reproductive cycles of marine invertebrates can aid in isolating environmental factors that promote synchrony between individuals and influence the timing of spawning of each population. Studies of conspecific populations of tropical echinoids have revealed wide variation in annual reproductive periodicity (Pearse and Cameron, 1991). In the Indo-West Pacific, *Diadema setosum* spawns from June to September in both Japan (Yoshida, 1952) and the Red Sea (Pearse, 1970), and also spawns in the austral summer months in the Great Barrier Reef (Stephenson, 1934), but it reproduces continuously throughout the year in the Philippines (Tuason and Gomez, 1979) and Singapore (Hori et al., 1987). *Tripneustes gratilla* reproduces from November to April in the Red Sea (Pearse, 1974, 1983), from September to November in Taiwan (Chen and Chang, 1981), from June to November in the Philippines (Tuason and Gomez, 1979) and from April to June in New South Wales, Australia (O'Connor et al., 1978). In the Caribbean, *Lytechinus variegatus* breeds between April and June in Bermuda (Moore et al., 1963), continuously with no discernible peaks in Panama (Lessios, 1985) throughout the year but with peaks between May and August in Florida (Moore et al., 1963; Moore and Lopez, 1972), between October and December in Puerto Rico (Cameron, 1986), and between June and September in Jamaica (Greenway, 1976). *Tripneustes ventricosus* breeds continuously in Florida (McPherson, 1965) and in Panama (Lessios, 1985), but it concentrates its reproduction to mid-winter and mid-summer in Puerto Rico (Cameron, 1986), or just the summer in Barbados (Lewis, 1958). *Echinometra lucunter* in Barbados spawns once a year in wave-swept areas, but twice a year in protected habitats (Lewis and Storey, 1984). The same species has well-defined reproductive periods in Florida (McPherson, 1969) and Puerto Rico (Cameron, 1986), but no discernible peaks in Panama (Lessios, 1981, 1985). *Diadema antillarum* is no exception to this variation in annual reproductive pattern among different populations. It spawns throughout the year in the Virgin Islands (Randall et al., 1964) and in Panama (Lessios, 1981), from January to April at Barbados (Lewis, 1966), from October to December in the Florida Keys (Bauer, 1976), and from April to October at Bermuda (Iliffe and Pearse, 1982). We were interested in determining whether populations on the other side of the Atlantic reproduce periodically, and if so, the nature of the cycles.

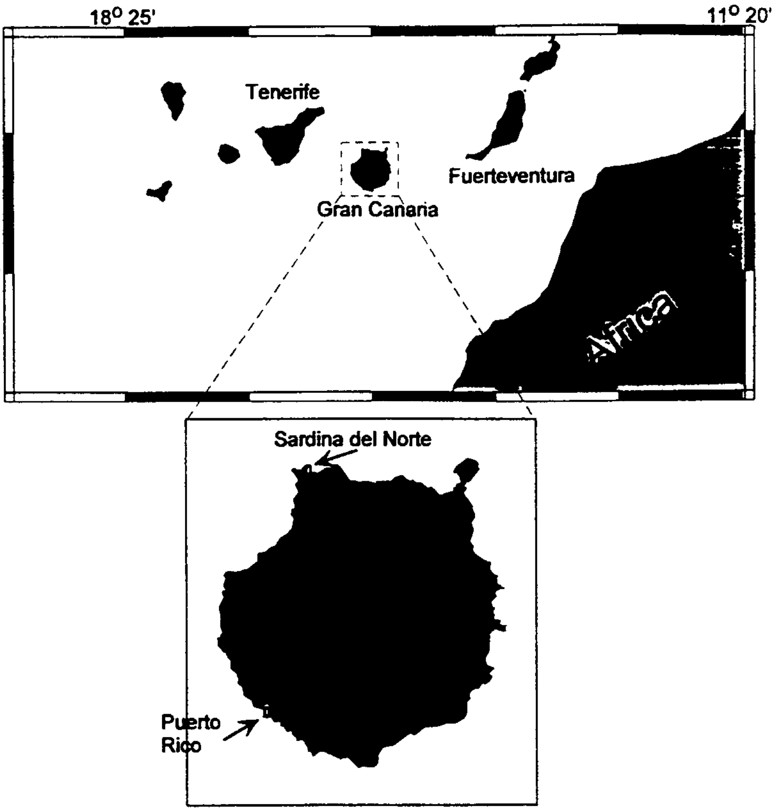

Figure 1. Localities in Gran Canaria Island (eastern Atlantic Ocean) where sea urchins were collected.

MATERIALS AND METHODS

The island of Gran Canaria is located in the Canarian Archipelago, between Tenerife and Fuerteventura (Fig. 1). The prevailing trade winds blow from the northeast; they drive the sea surface waters southwards, forming the Canary Current. Coastal water temperatures in Gran Canaria from 1981 to 1985 fluctuated between 18° and 25°C (Llinas, 1988). The northern coast is subjected to higher turbulence and more mixing of the thermocline; during the winter months it becomes colder than the southern coast. Average temperatures in February are 1°C colder in the North than in the South. These environmental differences between North and South coasts of each island are a common feature of the entire Canary Archipelago (Arístegui et al., 1989).

We established two collecting stations, Sardina del Norte on the north coast of Gran Canaria, and Puerto Rico on the south coast (Fig. 1). 22 to 25 individuals of *D. antillarum* larger than 3 cm in horizontal diameter were sampled at depths of 4–6 m in monthly intervals from January 1997 to March 1998 . Collections were made each month at the same phase of the moon, to avoid complications arising from the lunar spawning cycle, which in *D. antillarum* is superimposed on the annual cycle (Iliffe and Pearse,1982; Lessios, 1984, 1988a, 1991). During each collection, sea surface temperature was measured with a hand thermometer.

Two dimensions were measured in each sea urchin to the nearest 0.1 mm: (1) the horizontal diameter of the test at the ambitus, and (2) the oral-aboral axis, as the distance between the apex of the periproct and the plane defined by the three lowest points of the test at the oral side. Then the sea urchins were dissected, and the total volume of the gonads was measured 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 dried for 24 h at 110°C. Then they were weighed to the nearest 0.01 g.

Gonad content was normalized through the calculation of gonadal indices. We defined gonadal index in two ways: (1) as the ratio of gonad volume to dry body weight, multiplied by 100 and (2)

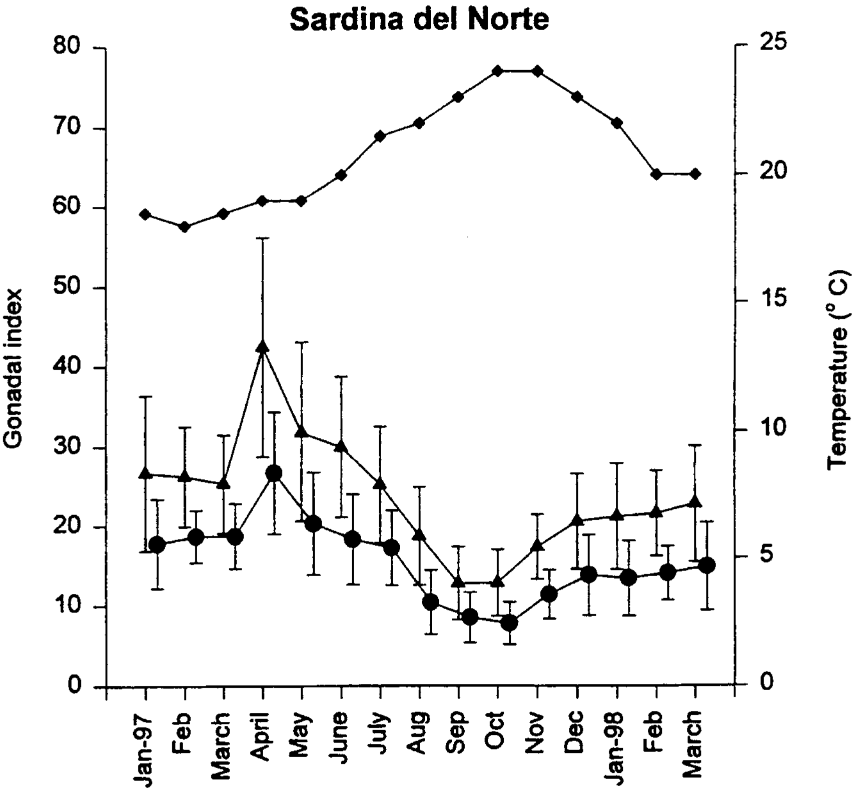

Figure 2. Mean and 1 SD of gonadal index of *Diadema antillarum* over time at Sardina del Norte . Gonadal index is calculated as ml of gonad per gram somatic dry weight, multiplied by 100 (triangles), or as ml of gonad per ml of test volume, multiplied by 100 (circles). Temperature (squares) is plotted on the right y axis.

as the ratio of gonad volume to test volume, multiplied by 100. Test volume was calculated as that of a solid created by an ellipse rotated around its shortest axis, i.e., $V= (4/3)\ \pi\ a^2\ b$, where a is the radius of the ambitus and b is 0.5 of the oral-aboral axis.

RESULTS

As might be expected, there was a tight relationship between test volume and test weight [Volume (in ml) = $-5.65 + 2.32$ weight (in g), $r^2 = 0.76$, $P < 0.00001$]. Thus, fluctuations in gonadal content through time can be represented without altering conclusions as either volume of gonad per volume of test, or as volume of gonad per weight of somatic tissue. Both in Sardina del Norte (Fig. 2) and at Puerto Rico (Fig. 3) the trends deduced by either method are equivalent. Gonadal content increases between October and February as sea water temperatures decline. It continues to increase between February and April (in Sardina del Norte) or May (in Puerto Rico) as the temperature rises, then declines until September or October as the temperature continues to rise. The lowest gonadal content of the year does not coincide with the warmest month, because after October the sea urchins appear to start a new cycle of building up their gonads, even though the temperature continues to increase until November. The three months (January to March) sampled in both 1997 and 1998 have similar values of gonadal index between years, suggesting that the fluctuations are, indeed, periodic.

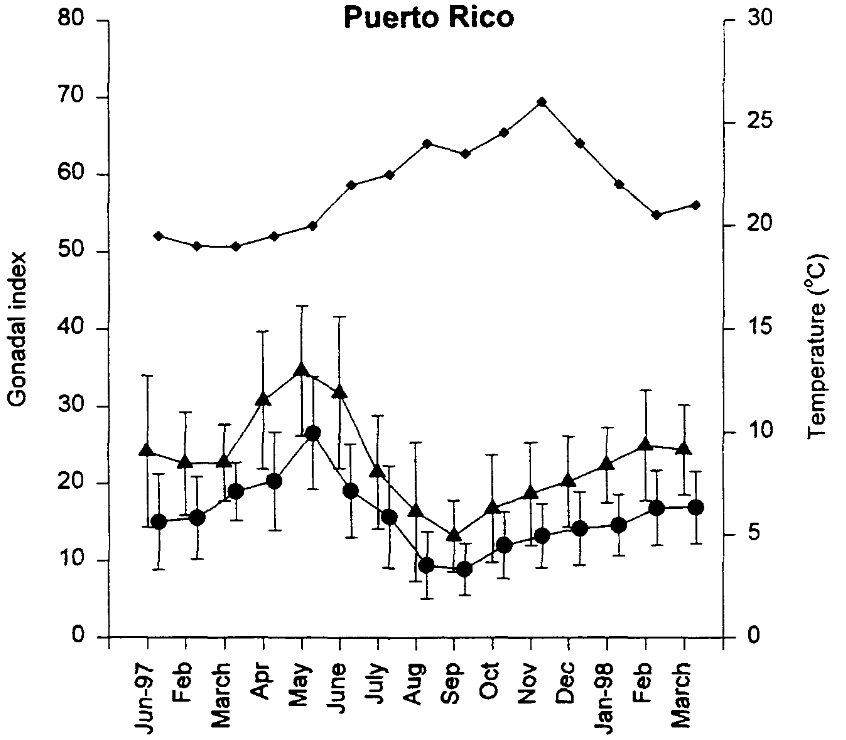

Figure 3. Mean and 1 SD of gonadal index of *Diadema antillarum* over time at Puerto Rico. Gonadal index is calculated as in Fig. 2. Note change of scale (relative to Figure 2) of the temperature axis on the right.

DISCUSSION

Though the Canary Archipelago is south of Bermuda, it (along with Madeira) is the least tropical environment in which *D. antillarum* is found, because of water temperature regimes imposed by currents. The differences in water temperature between these areas are reflected in faunal composition. Unlike Bermuda, the Canaries lack hermatypic corals. *Diadema* is the only genus of tropical sea urchin extant in the Archipelago (Sanchez and Batet, 1991). The environment is seasonal not just in temperature, but also in primary productivity and zooplankton concentration (Braun et al., 1985; Aristegui et al., 1989; Fernández de Puelles and García-Braun, 1989). Thus, it is not surprising that populations in both localities we sampled showed well-defined, synchronized reproductive cycles. The question is which environmental variable (or combination of variables) controls reproductive cycles as a proximate or ultimate factor.

Evidence regarding the effects of temperature on gametogenic cycles of echinoids is often uncertain and sometimes conflicting (review in Pearse and Cameron, 1991). However, correlations between the reproductive cycles of natural populations and seasonal temperature fluctuations tend to support the possible existence of a link between the two. This tentative relation between temperature fluctuations and annual reproductive cycles is seen in previous studies of *D. antillarum*. On the Atlantic coast of Panama, where temperature fluctuations are minimal, this species shows little synchronization of the reproductive cycles of individuals comprising each population (Lessios, 1981). Limited data support a similar lack of a population-wide cycle in the Virgin Islands (Randall et al., 1964). In Florida, where temperature fluctuates seasonally, there is clear accumulation of gonadal material between July and November, with a sharp decrease between November and December, correlated with decreasing sea water temperatures (Bauer, 1976). In Barbados, despite annual temperature fluctuations <1.5° C, *Diadema* has pronounced reproductive cycles, repeated from one year to the next, with spawning concentrated during the coldest months of April and May (Lewis, 1966). In Bermuda, another seasonal environment, gonads are being built up as temperature increases, but there are two apparent spawning periods, one in early summer, the other in late fall, thus complicating any direct correlation between temperature and reproduction (Iliffe and Pearse, 1982).

Our data indicate that in the Canaries there is a relation between water temperature and *D. antillarum* reproduction, but do not clarify whether the reproductive cycles respond to temperature per se. The animals appear to begin spawning in April at Sardina del Norte when the temperature reaches 19°C and in May at Puerto Rico, when the temperature has reached 20°C. In both locations the period of gonadal decline, which presumably signifies active spawning, coincides with the period of rapid temperature rise. Gonadal content reaches its minimum in September, when it is 23°C in Sardina del Norte and 23.5°C in Puerto Rico. In both localities, the spawning period coincides with the times of most rapid temperature increase, up to the point that the gonads reach their minimum relative size. However they stop declining in September–October, even though the temperature continues to rise. Iliffe and Pearse (1982) have attributed a similar quiescence of gonadal growth in *D. antillarum* at Bermuda to direct inhibition by high temperatures. This may well be true, but it also possible that this is an indirect result of repeated spawning. If the decline in gonadal index is the result of the inability of each animal to build up nutrients faster than they are depleted by the release of gametes, and if reproduction is triggered by increasing temperatures, a point will be reached at which gonads are at their minimum size, even as temperature continues to increase. Only when spawning stops, possibly as the result of a drop in temperature, will gonadal size begin to increase once again.

Of course, it is also quite possible that there is no direct link between temperature and reproduction, and that correlation between the two is the unavoidable coincidence of two independent variables each cycling with an annual period. Other seasonally fluctuating variables that may regulate reproduction in *D. antillarum* are photoperiod, phytoplankton blooms, and food availability. Pearse et al. (1986) have shown experimentally that gametogenesis in *Strongylocentrotus purpuratus* is under photoperiodic control. McClintock and Watts (1990) found a similar effect of photoperiod on the annual reproduction of the tropical species *Eucidaris tribuloides*. However, if photoperiod affects the reproductive cycles of *D. antillarum*, it must do so in different ways on the two sides of the Atlantic. Even though the latitude of Florida Keys and the Canaries only differs by 3°C, the cycles of *Diadema* populations from the two locations are 2 mo out of phase. Phytoplankton blooms have been shown to trigger spawning in *S. droebachiensis* (Starr et al., 1990, 1993). However, the seasonal peak in phytoplankton in the Canaries is reached in February, 2–3 mo before *D. antillarum* initiates its spawning (Braun et al., 1985; Arístegui et al., 1989; Fernández de Puelles and García-Braun, 1989). Thus, *Diadema* does not appear to time its reproduction in a manner that would maximize food for its larvae.

Though photoperiod and plankton blooms seem unlikely proximate or ultimate factors of *D. antillarum* annual reproductive cycles, food availability for the adults may not be entirely unrelated to reproduction. Though the species suffered severe mass mortality in the entire western Atlantic during 1983–4 (Lessios et al., 1984; Lessios, 1988b), its populations in the Canaries continue to be extremely dense. Subtidal hard substrata where *Diadema* is found are bare of macroalgae, even though shallower areas are thickly covered by *Cystoseira* and other erect algae (Johnston, 1969; Carillo Pérez and Cruz Simó, 1992). It is, therefore, possible that *Diadema* in the Canaries is food limited. No data exist on seasonal changes in benthic primary productivity. It is, however, known that where *Diadema* is absent, biomass of *C. albies-marina* increases rapidly between March and June (Medina and Haroun, 1993). This is likely to be due to the Spring disruption of the thermocline by turbulence that also causes an increase of nutrients and phytoplankton blooms. In areas where *Diadema* is present, these algae may be quickly consumed, so that there is no visible increase in standing crop; yet, they would represent a seasonal pulse of nutrition for *Diadema* . Such a pulse may be a contributing factor to the gonadal buildup we have seen between March and April. Increased benthic primary productivity due to turbulence may also account for the earlier initiation of reproduction (despite lower temperatures) in the northern locality, which is more exposed to the trade winds. Of course, fluctuations in food availability would be a factor in reproduction only to the extent that reproduction is negatively affected by inadequate food supply during part of the year. It remains to be determined whether such a limitation exists. Experimental studies are needed to determine the relative contributions of temperature and food in the control of gemetogenesis of *Diadema*.

ACKNOWLEDGMENTS

We thank Á. Santana for statistical advice, and J. Suárez and the students of Marine Science Faculty, L. Alou, A. Torres, J. García, J. M. Alsina and J. C. Suárez for their help in the field and in the laboratory.

LITERATURE CITED

Arístegui, J., S. Hernández-León, M. Gómez, L. Medina, A. Ojeda and S Torres. 1989. Influence of the north trade winds on the biomass and production of neritic plankton around Gran Canaria island. Topics Mar. Biol. 53: 223–229.

Bauer, J. C. 1976. Growth, aggregation and maturation in the echinoid, *Diadema antillarum* Philippi. Bull. Mar. Sci. 26: 273–277.

Braun, J. G., I. Orzaiz, J. D. Armas and F. Real 1985. Productividad y biomasa del ultraplancton, nanoplacton y fitoplancton de red en aguas de las Islas Canarias. Bol. Inst. Esp. Oceanogr. 2: 192–204.

Cameron, R. A. 1986. Reproduction, larval occurrence and recruitment in Caribbean sea-urchins. Bull. Mar. Sci. 39: 332–346.

Carillo Pérez, M., and T. Cruz Simó. 1992. Estudio de las comunidades vegetales marinas y poblaciones faunisticas del litoral de Timanfaya, Sevicio de Publicaciones de la Caja General de Ahorros de Canarias, Santa Cruz de Tenerife. 223 p.

Chen, C. P. and K.-H. Chang. 1981. Reproductive periodicity of the sea urchin *Tripneustes gratilla* (L.) in Taiwan compared with other regions. Int'l. J. Inv. Reprod. 3: 309–319.

Fernández de Puelles, M. and J. A. García-Braun. 1989. Dinámica de las comunidades planctónicas en una zona del Atlántico Subtropical (Isla de Tenerife). Bol. Inst. Esp. Oceanogr. 5: 87–100.

Greenway, M. 1976. The grazing of *Thalassia testudinum* in Kingston Harbour, Jamaica. Aquat. Bot. 2: 117–126.

Hori, R., V. P. E. Phang and T. J. Lam 1987. Preliminary study on the pattern of gonadal development of the sea urchin, *Diadema setosum*, off the coast of Singapore. Zool. Sci. 4: 665–673.

Iliffe, T. M. and J. S. Pearse 1982. Annual and lunar reproductive rhythms of the sea urchin, *Diadema antillarum* (Philippi) [sic] in Bermuda. Int'l. J. Inv. Reprod. 5: 139–148.

Johnston, C.S. 1969. Studies on the ecology and primary production of Canary Islands marine algae. Pages 213–222 *in* R. Margalef, ed. Proc. 6th Int'l. Seaweed Symp, vol. 6, Subsecretaria de la Marina Mercante, Madrid.

Lessios, H. A. 1981. Reproductive periodicity of the echinoids *Diadema* and *Echinometra* on the two coasts of Panama. J. Exp. Mar. Biol. Ecol. 50: 47-61.

__________. 1984. Possible prezygotic reproductive isolation in sea urchins separated by the Isthmus of Panama. Evolution 38: 1144–1148.

__________. 1985. Annual reproductive periodicity in eight echinoid species on the Caribbean coast of Panama. Pages 303–311 *in* B. F. Keegan and B. D. O'Connor, eds. Echinodermata. Proc. 5th Int'l. Echinoderm Conf., Galway, A.A. Balkema, Rotterdam.

__________. 1988a. Population dynamics of *Diadema antillarum* (Echinodermata: Echinoidea) following mass mortality in Panamá. Mar. Biol. 99: 515–526.

__________. 1988b. Mass mortality of *Diadema antillarum* in the Caribbean: what have we learned? A. Rev. Ecol. Syst. 19: 371–393.

__________. 1991. Presence and absence of monthly reproductive rhythms among eight Caribbean echinoids off the coast of Panama. J. Exp. Mar. Biol. Ecol. 153: 27–47.

__________, D. R. Robertson and J. D. Cubit. 1984. Spread of *Diadema* mass mortality through the Caribbean. Science 226: 335–337.

Lewis, J. B. 1958. The biology of the tropical sea urchin *Tripneustes esculentus* Leske in Barbados, British West Indies. Can. J. Zool: 36: 607–621.

__________. 1966. Growth and breeding in the tropical echinoid *Diadema antillarum* Philippi. Bull. Mar. Sci. 16: 151–158.

__________ and G. S. Storey. 1984. Differences in morphology and life history traits of the echinoid *Echinometra lucunter* from different habitats. Mar. Ecol. Prog. Ser. 15: 207–211.

Llinas, O. 1988. Análisis de la distribución de nutrientes en la masa de agua Noratlántica en las Islas Canarias. Ph.D. Thesis . Univ. La Laguna, Tenerife.

McClintock, J. B. and S. A. Watts. 1990. The effects of photoperiod on gametogenesis in the tropical sea urchin *Eucidaris tribuloides* (Lamarck) (Echinodermata, Echinoidea). J. Exp. Mar. Biol. Ecol. 139: 175–184.

McPherson, B. F., 1965. Contributions to the biology of the sea urchin *Tripneustes ventricosus*. Bull. Mar. Sci. 15: 228–244.

__________. 1969. Studies on the biology of the tropical sea urchins, *Echinometra lucunter* and *E. viridis*. Bull. Mar. Sci. 19: 194–213.

Medina, M. and R. Haroun. 1993. Preliminary study on the dynamics of *Cystoseira abies-marina* populations in Tenerife (Canary Islands). Courier Forsch.-Inst. Senckenberg. 159: 109–112.

Moore, H. B., T. Jutare, J. C. Bauer and J. A. Jones. 1963. The biology of *Lytechinus variegatus*. Bull. Mar. Sci. Gulf Carib. 13: 23–53.

__________ and N. N. Lopez. 1972. Factors controlling variation in the seasonal spawning pattern of *Lytechinus variegatus*. Mar. Biol. 14: 275–280.

O'Connor, C., G. Riley, S. Lefebre and D. Bloom. 1978. Environmental influences on histological changes in the reproductive cycle of four New South Wales sea urchins. Aquaculture 15: 1–17.

Pearse, J. S. 1970. Reproductive periodicities of Indo-Pacific invertebrates in the Gulf of Suez. III. The echinoid *Diadema setosum* (Leske). Bull. Mar. Sci. 20: 697–720.

__________. 1974. Reproductive patterns of tropical reef animals: three species of sea urchins. Proc. 2nd Int'l. Coral Reef Symp. 1: 235–240.

__________. 1983. The Gulf of Suez: signs of stress on a tropical biota. Pages 148–159 *in* M. F. Thompson, A. F. Latif and A. R. Bayoumi, eds. Proc. Int'l. Conf. Mar. Sci. Red Sea, Bull. Inst. Oceanogr. Fish (Egypt).

________ and R. A. Cameron. 1991. Echinodermata: Echinoidea. Pages 513–662 *in* A. C. Giese, J. S. Pearse and V. B. Pearse, eds. Reproduction of marine invertebrates, vol. 6. Echinoderms and Lophophorates, Boxwood Press, Pacific Grove, California.

________, V. B. Pearse and K. K. Davis. 1986. Photeperiodic regulation of gametogenesis and growth in the sea urchin *Strongylocentrotus purpuratus*. J. Exp. Zool. 237: 107–118.

Randall, J. E., R. E. Schroeder and W. A. Starck. 1964. Notes on the biology of the echinoid *Diadema antillarum*. Carib. J. Sci. 4: 421–433.

Sánchez, J. M. P. and E. M. Batet. 1991. Invertebrados marinos de Canarias, Ediciones del Cabildo Insular de Gran Canaria, Las Palmas de Gran Canaria. 335 p.

Starr, M., J. H. Himmelman and J. C. Therriault. 1990. Direct coupling of marine invertebrate spawning with phytoplankton blooms. Science 247: 1071–1074.

________, ____________, and ____________. 1993. Environmental control of green sea urchin, *Strongylocentrotus droebachiensis*, spawning in the St. Lawrence Estuary. Can. J. Fish.. Aquat. Sci. 50: 894–901.

Stephenson, A. 1934. The breeding of reef animals. II. Invertebrates other than corals. Great Barrier Reef Exped. 1928–1929. Sci. Rep. 3: 247–272.

Tuason, A. Y. and E. D. Gomez. 1979. The reproductive biology of *Tripneustes gratilla* (Echinoidea: Echinodermata) with some notes on *Diadema setosum* Leske. Proc. Int'l. Symp. Mar. Biogeogr. Evol. Southern Hemisphere, Auckland, New Zealand. 17–20 July 1978 2: 707–716.

Yoshida, M., 1952. Some observations on the maturation of the sea urchin, *Diadema setosum*. Annotnes Zool. Jap. 25: 265–271.

DATE SUBMITTED: November 1, 1999. DATE ACCEPTED: May 19, 2000.

ADDRESSES: (M.J.G., R.J.H.) *Departamento de Biología, Facultad de Ciencias del Mar, Universidad de Las Palmas de Gran Canaria, 35017 Las Palmas de Gran Canaria, Spain.* CORRESPONDING AUTHOR: (H.A.L.) *Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Panama. Tel. (507) 212-8708, Fax (507) 212-8790, E-mail: <lessiosh@naos.si.edu>.*