REPRODUCTIVE PERIODICITIES OF INDO-PACIFIC INVERTEBRATES IN THE GULF OF SUEZ. II. THE ECHINOID *ECHINOMETRA MATHAEI* (DE BLAINVILLE)

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ABSTRACT

Seasonal reproductive changes in several populations of the echinoid *Echinometra mathaei* near both the head and mouth of the Gulf of Suez were followed for more than a year. Well-defined reproductive periodicities occurred near the head of the Gulf; gametogenesis began in different individuals in the spring and early summer, and spawning occurred in the summer and fall. At other times of the year the gonads were completely quiescent reproductively. Nutritive phagocytic tissue in the gonads accumulated mainly in the fall and early winter, and decreased mainly in the late spring and summer. Much less well-defined reproductive periodicities occurred near the mouth of the Gulf, and in the adjacent Red Sea and farther south there was no synchronized periodicity within the populations. It is suggested that both a critical minimal temperature and a critical minimal level of nutrient reserves are important for the regulation of the reproductive periodicities.

INTRODUCTION

The unusual conditions in the Gulf of Suez, including a relatively temperate environment with a tropical fauna and flora, have been described in the first part of this series (Pearse, 1969). Among the most typical and widespread members of the Indo-Pacific fauna found in the Gulf of Suez is the echinoid *Echinometra mathaei* (de Blainville). This species occurs commonly in and about reefs; it is found from central Japan in the north, to southwest Australia in the south, and from Clarion Island off Mexico in the east, to the Gulf of Suez in the west (Mortensen, 1943). Reproduction of *E. mathaei* apparently occurs throughout the year in most areas of its distribution, including in the northern Red Sea, within the tropics, and at its southernmost occurrence off southwest Australia (Pearse, 1968). It is a restricted summer spawner, however, off central Japan (Onoda, 1936) and within the Gulf of Suez (Pearse, 1968). More detailed analyses of the reproductive activity of *E. mathaei* in the Gulf of Suez and in the adjacent northern Red Sea are presented in this paper.

METHODS AND MATERIALS

Samples of *E. mathaei* were collected from seven localities in the Gulf of Suez and the northwestern Red Sea (Fig. 1). Most of the samples were

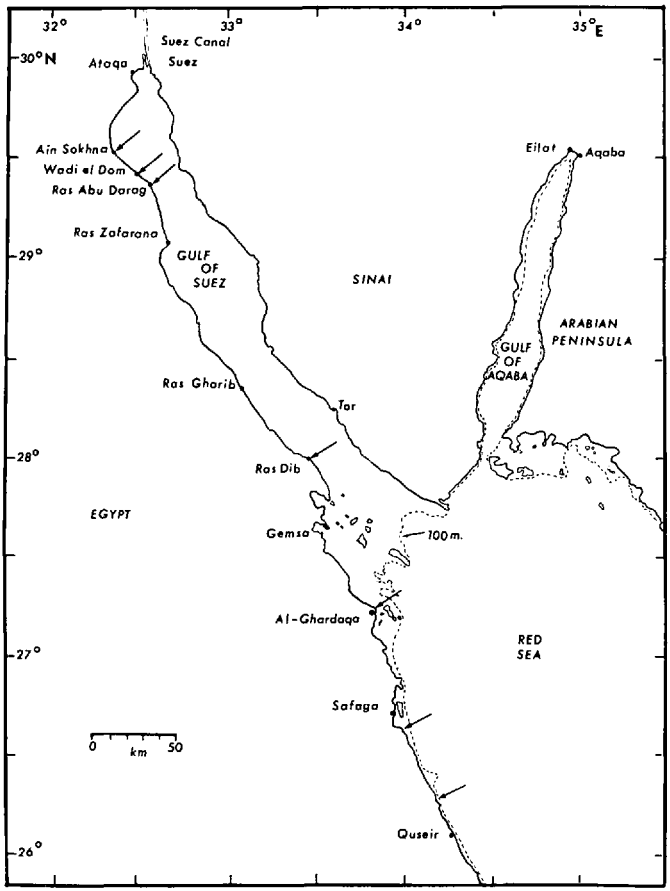

FIGURE 1. Map showing the collecting sites (arrows) and other localities in the Gulf of Suez and adjacent areas.

taken from Wadi el Dom (29°26′N, 32°30′E), a previously described site (Pearse, 1969) on the North Qalala Plateau on the coastline of the Gulf of Suez. Samples were collected at Wadi el Dom in 1965 on August 22, September 12, November 21, and December 24; in 1966 on January 16, February 12, March 6, April 2 and 24, May 29, June 26, July 19, August 2 and 15, September 13, October 16, and December 4; and in 1967 on January 11, February 8, March 11, and April 16. One sample was taken on May 21, 1965, at Ain Sokhna (29°34′N, 32°21′E) on the coastline of the western edge of the North Qalala Plateau, and another was taken on October 9, 1965, at Ras Abu Darag (29°23′N, 32°34′E) on the coastline

of the eastern edge of the North Qalala Plateau (see Pearse, 1969, Fig. 1, for more details of this coastline). A sample was taken on February 5, 1967, at Ras Dib (28°02′N, 32°25′E) near the southern end of the Gulf of Suez. At the Gulf of Suez–Red Sea junction, at Al-Ghardaqa (27°15′N, 33°49′E), samples were taken on February 10, July 17, September 27, and November 26, 1966, and on February 7 and April 9, 1967. The samples from Al-Ghardaqa were all collected from a narrow reef off the point between the fishing port and administrative center of the town. In the Red Sea proper, samples were taken off a point supporting a small mangrove colony (26°37′N, 34°00′E) 15 km south of Safaga on July 15, 1965, and February 7, 1967, and at a small natural harbor (26°17′N, 34°11′E) 21 km north of Quseir on July 16, 1966, and February 6, 1967.

Between 20 and 30 animals were collected for each sample. All were of a sexually mature size. Those collected from Wadi el Dom ranged in length of test from 40 to 69 mm, and averaged 53 mm. Sexual maturity can be attained at much smaller sizes; one animal collected from the Safaga site on July 15, 1966, measured 23 × 20 mm (length × width) and had large testes full of spermatozoa. On the other hand, an animal collected on December 24, 1965, from Wadi el Dom measured 21 × 17 mm (weight, 4.4 gms) and its gonads could not be found during dissection.

After collection, the length and width of the test of each animal were measured with calipers, and the general condition of the gonads was noted. Periodically, all the animals in a collection and their gonads and guts (from esophagus to rectum, washed free of contents) were weighed, and organ indices were calculated by the following formula: weight of organ × 100, divided by weight of animal.

The oral tip of one gonad from each animal was fixed for over one day in Bouin's fixative. Paraffin sections of these were cut at 5 μ or 7 μ and stained with hematoxylin and eosin Y. Usually all the gonadal pieces in each sample were fixed together, and 5 to 10 gonadal pieces were embedded and sectioned together. This procedure resulted in the loss of some information on single animals, but allowed a large number of animals to be processed. Occasionally, both the oral tips and aboral portions of all five gonads in one animal were embedded and sectioned together; all portions of the gonads were very similar.

Histological analyses of the gonadal sections were done as previously described (Pearse, 1969). Usually sections from 10 different males and 10 different females were chosen at random and analyzed for each sample. The thickness in transverse section of the nutritive phagocyte layer was measured in both the ovaries and testes. The thicknesses of the spermatogenic cell layer (spermatogonia, spermatocytes, spermatids) and the spermatozoa to the center of the lumen of testicular lobes approximately 210 μ in radius were also measured. Fifty oocytes showing a nucleolus in

section, or ova showing a nucleus, were selected at random from each ovary. These were grouped into 17-μ size-classes ranging from 0 μ upwards, and size-frequency polygons were plotted. The abundance of the basophilic, eosinophilic and golden-brown globules in each gonad was estimated on a 7-point scale, in which 1 indicated none or very few present, and 7 indicated many present.

The percentage of sectioned gonads with numerous mature gametes (ova or spermatozoa) filling over half of the gonadal lobes was estimated for each sample as done previously with samples of *E. mathaei* (Pearse, 1968; Pearse & Phillips, 1968). Estimating the percentage of ripe animals from sections differs from counting the number of animals oozing gametes upon dissection as used in some other studies (e.g., Moore, 1934, 1937; Buchanan, 1966; Pearse, 1969). It is preferable for *E. mathaei*, because often many nutritive phagocytes ooze upon dissection, making field examination difficult. In some other species (e.g., *Prionocidaris baculosa*, see Pearse, 1969) the gonads usually do not contain numerous mature gametes in section and the number of oozing mature gametes upon dissection is a more accurate method for estimating the percentage of ripe animals in a sample.

Methods used for estimating maximum and minimum sea temperatures at the collection sites, either by hourly measurements at the surface or by use of a maximum-minimum thermometer, have been described (Pearse, 1969).

Results

Coastline of the North Qalala Plateau.—On May 21, 1965, the sample from Ain Sokhna was taken during a preliminary survey of the area, and on October 9, 1965, the sample from Ras Abu Darag was taken when the water around Wadi el Dom was extremely muddy because of unusually heavy local rains (described by Pearse, 1969). Neither sample seemed out of place in the patterns established by the samples from Wadi el Dom, so they are all considered as representatives of the coastline of the North Qalala Plateau. This coastline, extending in a NNE-SSW direction for about 50 km from Ain Sokhna to Ras Abu Darag (Fig. 1), is relatively uniform; in most places the plateau rises steeply from the shore. The intertidal zone is mainly a pebble-cobble beach broken intermittently with sandy coves and rocky points. A narrow, mostly dead, coral reef fringes much of the coastline, Ain Sokhna being the northern limit of major reef systems on the western side of the Gulf of Suez. The Wadi el Dom area, however, may be somewhat atypical because some species, such as the echinoids *Prionocidaris baculosa*, *Lovenia elongata*, and *Diadema setosum*, seem to occur more abundantly there than elsewhere.

Specimens of *E. mathaei* were extremely abundant along most of the coastline of the North Qalala Plateau, occurring mainly on coral rubble and

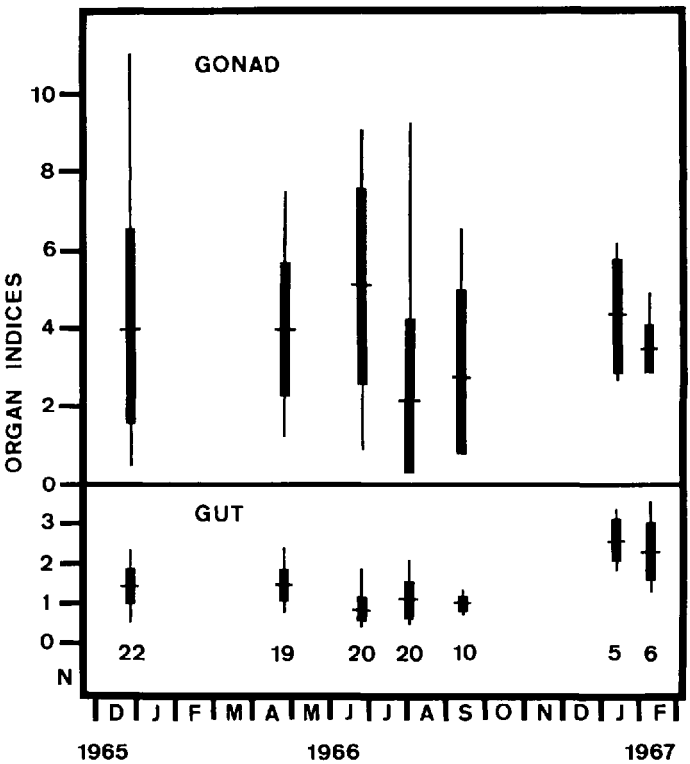

FIGURE 2. Means, standard deviations, and ranges of the gonadal and gut indices in samples of *E. mathaei* taken from Wadi el Dom, Gulf of Suez. (Number of animals in each sample is given at the bottom.)

cobble on the inner side of the reef. During the sampling period, a total of 695 animals was collected from an area of about 10 × 100 m at Wadi el Dom, yet the density of the population did not seem to decrease. At Wadi el Dom and along most other areas of the coastline of the North Qalala Plateau, specimens of *E. mathaei* were completely in the open and not hidden under ledges or in burrows. At Ain Sokhna, however, the animals were scarce, and all were in deep crevices and burrows within the reef. Ain Sokhna is a major resort area, and perhaps specimens of *E. mathaei* were depleted there by swimmers. (Specimens of *E. mathaei* are not eaten by people of the area, but often large numbers are collected and piled on the shore.)

A total of 260 males and 216 females of *E. mathaei* were collected and analyzed from the coastline of the North Qalala Plateau. The deviation

from a 1 : 1 sex ratio is significant at the 0.5 level by the chi-square test. A similar predominance of males also has been noted in some tropical populations of *E. mathaei* (Pearse, 1968), but not at Rottnest Island, Western Australia (Pearse & Phillips, 1968).

The general condition of the gonads of *E. mathaei* varied greatly within each sample, as occurs in populations elsewhere in the Indo-Pacific (Pearse, 1968). Gonadal color varied through most of the shades of grey, tan, brown, ochre, yellow, and orange, with no relation to sex. Gonadal size also varied within each sample, as indicated by the gonadal indices (Fig. 2). Often the same sample included animals with extremely large, lobulated gonads (usually ochre or orange in color) while others had thin, weblike gonads (usually dark brown in color) spread along the wall of the test. The size of the gonads was not indicative of their maturity; very large gonads in the winter contained only numerous nutritive phagocytes, while very small gonads in the summer often contained numerous gametes.

The average for the gonadal index varied little over the year (Figs. 2; 3, A). A significant drop by about one-half occurred in the average between late June and early August, however. Most of the gonads contained numerous mature gametes during this period (Fig. 3) and most of the spawning occurred during this period. The increase in the mean of the gonadal index between early August and mid-January was due entirely to an increase in the nutritive phagocytic tissue. Although there was no difference in the gonadal indices of the samples taken on December 24, 1965, and April 23, 1966, there may have been a slight dip during the intervening period. A drop occurred between January and February of the following year (Figs. 2; 3, A). Moreover, the average thickness of the nutritive phagocytic tissue decreased in February-March 1966 (Fig. 3, B, C), and this decrease might have been reflected in the gonadal indices if they had been taken.

The gut indices varied little during the sampling period, although they were generally lower in the summer and fall than in the winter and spring (Fig. 2). During the second winter, in January and February 1967, they were especially high. The guts themselves were usually full of small food pellets containing mostly fine sand, silt, and amorphous material, but diatoms and bits of algae and phanerogams could be identified occasionally.

The percentage of animals with numerous mature gametes increased sharply between April and June (Fig. 3, A), reaching a peak of over 90 per cent in June and July. The decrease in the percentage of animals with numerous mature gametes, indicating spawning, was erratic and gradual, occurring between July and November-December. After September, however, numerous mature gametes were found only in a few males, and spawning probably occurred mainly in July, August, and September.

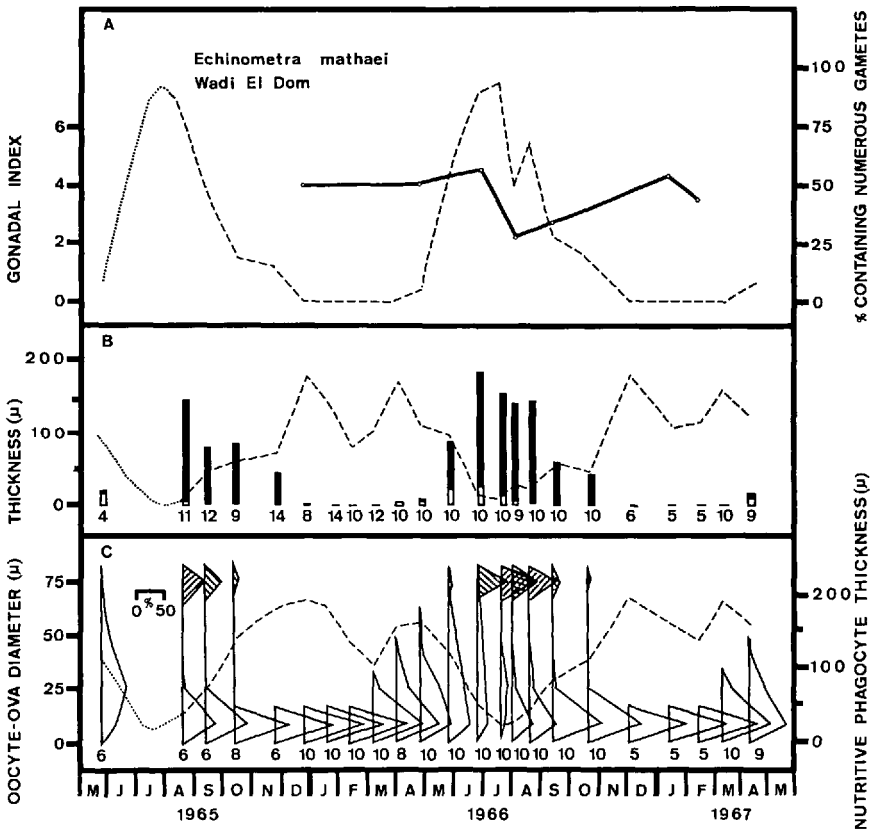

FIGURE 3. Reproductive changes in samples of *E. mathaei* taken from Wadi el Dom, Gulf of Suez: A, mean of gonadal indices (solid line) and percentage of animals containing numerous mature gametes (broken line); B, averaged thicknesses of the layers of spermatogenic cells (open bars), spermatozoa (solid bars), and nutritive phagocytes (broken line) in typical transverse sections of testes 210 μ in radius; C, polygons for averaged size-frequencies of oocytes (open) and ova (hatched); and the average thickness of the nutritive phagocytic layers (broken line) in transverse sections of the ovaries. (Number of animals in each sample is also given.)

Definitive seasonal changes occurred in the testes of the animals sampled from the coastline of the North Qalala Plateau (Figs. 3, B; 4; 5). These changes, however, were not well synchronized among the different males of each sample (Fig. 4). In early April a few males had begun spermatogenesis, as evidenced by small nests of spermatocytes, and by late April a few had accumulated some spermatozoa in their testicular lumens. Fifty

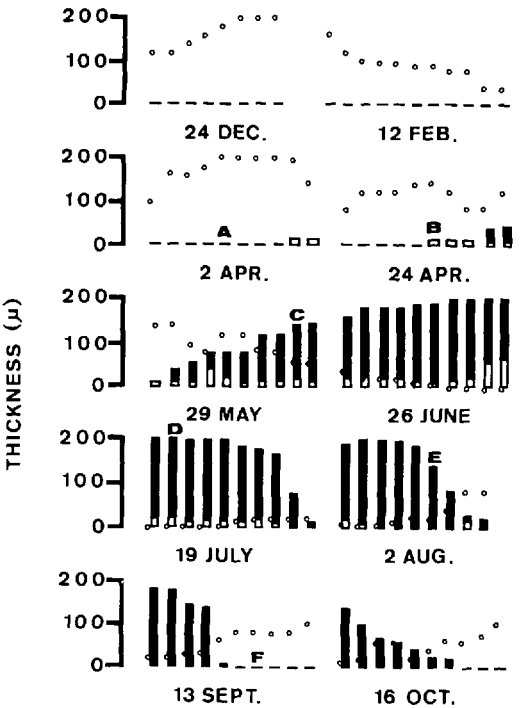

FIGURE 4. Histograms for each of the individual males of *E. mathaei* in several samples collected from Wadi el Dom, Gulf of Suez, during 1966, showing thicknesses of the layers of spermatogenic cells (open bars), spermatozoa (solid bars) and nutritive phagocytes (dots). Note the lack of synchrony among the individuals of each sample; this has allowed the arrangement of the histograms from left to right, to show the probable changes occurring during spermatogenesis and spawn-out. (The letters correspond to individuals whose gonads are shown in the photomicrographs in Figure 5.)

per cent of the animals in the sample in late April, however, had not begun any spermatogenic activity. In late May and mid-June, all the animals were undergoing spermatogenesis, as indicated by the layer of spermatogenic cells, and the testes of all those in the sample in June were full of spermatozoa. The disappearance of the layer of spermatogenic cells from the testes of a few animals in July indicated the end of spermatogenic activity. No spermatogenesis was occurring in any of the animals in the samples taken in mid-August (Fig. 3, B), September, or October. More and more animals spawned, as indicated by the decrease in the amount of spermatozoa present, from mid-July through mid-October. Very few spermatozoa were present after early December.

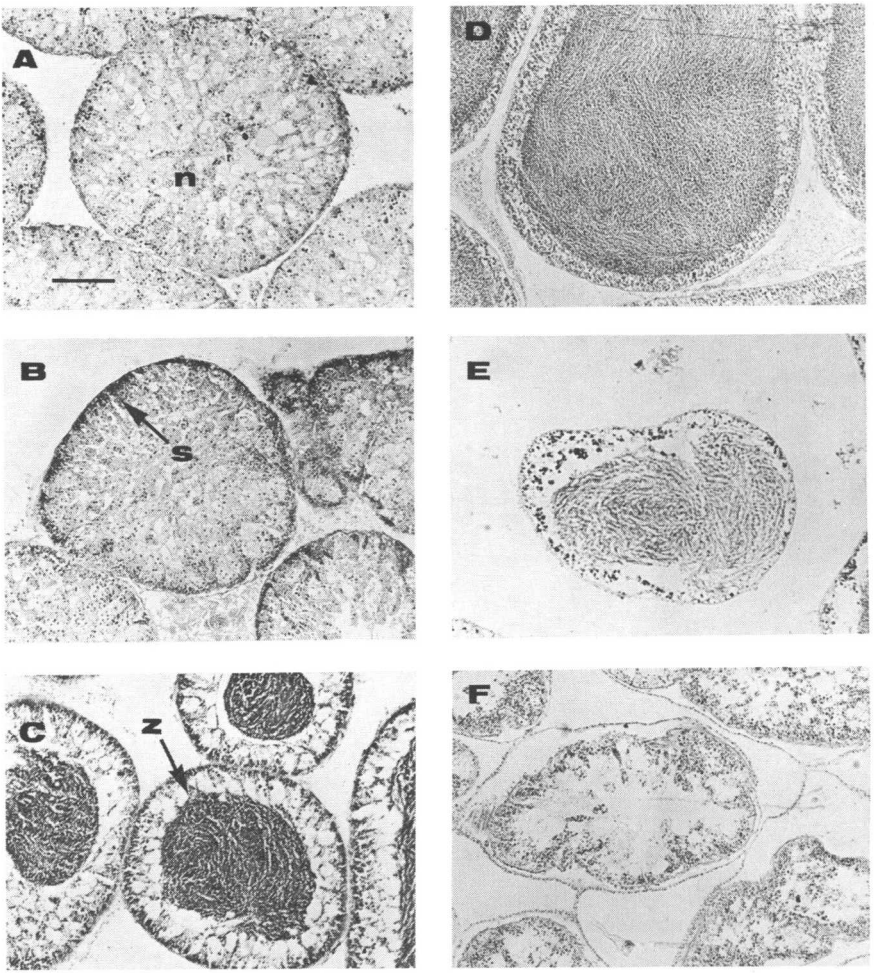

FIGURE 5. Histological sections of testes of specimens of *E. mathaei* collected from Wadi el Dom, Gulf of Suez, during 1966: A, April 2, solid mass of nutritive phagocytes (n); B, April 24, a thin layer of spermatogenic cells (s); C, May 29, spermatogenic and nutritive phagocytic layers, and the lumen partly filled with spermatozoa (z); D, July 19, ripe, with spermatogenic cell layer, no nutritive phagocytic layer, and the lumen full of spermatozoa; E, August 2, partly spawned, with thin nutritive phagocytic layer, spermatozoa in the lumen, and no spermatogenic cell layer; F, September 13, completely spawned, with ingrowing nutritive phagocytic tissue. (All of these individuals are depicted as histograms in Figure 4. Scale-line in A is 100 μ; all are at the same magnification.)

The average thickness of the nutritive phagocytic tissue in the testes fluctuated seasonally (Figs. 3, B; 4; 5), decreasing in the spring and summer as spermatogenesis proceeded, and increasing in the fall after spawn-out. The spring-summer decrease probably was associated with transfer of nutrients to the developing gametes, while phagocytosis of the spermatozoa and spermatogenic cells occurred during the fall increase. A second, less marked decrease in the thickness of the nutrient phagocytes occurred during the midwinter when no effective spermatogenesis occurred. The midwinter decrease in the thickness of the nutritive phagocytic tissue suggests that nutrient assimilation was low during midwinter, and reserves in the nutritive phagocytes were being utilized by somatic cells.

The nutritive phagocytes in most of the testes examined in most of the samples were full of phagocytized spermatogenic cells (Fig. 5); the samples in June, July, and early August were the only ones in which little phagocytosis occurred. Most of the phagocytized cells appeared to be spermatids or spermatozoa. Apparently, initiation of spermatogenesis occurred throughout the year, but most of the time the nutrient phagocytes destroyed the spermatozoa as rapidly as they formed.

The nutritive phagocytic tissue usually contained various amounts of basophilic, eosinophilic, and golden-brown globules, and these amounts fluctuated during the year. Basophilic globules, being mainly phagocytized spermatogenic cells and spermatozoa, were abundant in most of the testes except those examined during June, July, and early August. The eosinophilic globules probably were products of advanced degradation of both the gametogenic cells and nutrient stores. The amount of these globules generally followed the fluctuations in the thickness of the nutrient phagocytic tissue, being most abundant in November, December, and April, and least abundant in July and early August. The golden-brown globules, of unknown origin and composition, were always fairly abundant in some testes, but seemed to be most abundant in the fall, after spawn-out.

Seasonal changes in the ovaries are shown in Figures 3, C; 6; and 7. As in the males, synchrony among the females of each sample was very imperfect (Fig. 6), but when the size-frequency polygons for the oocytes and ova of the individuals in each sample were averaged together, definitive seasonal changes were evident (Fig. 3, C). The ovaries of the animals in November, December, January, and February contained very few oocytes, and these were all below 20 μ in diameter. Oocytes had increased in size and had become increasingly numerous in the individuals sampled in March and April; by late May, a few animals contained ova. A good series of stages of oocytic growth is shown by the different individuals sampled in May (Fig. 6), from one animal with a few oocytes mainly under 20 μ in diameter (left of figure) to one with numerous ova (right of figure). Most of the females of the sample taken in late June and all the females of the

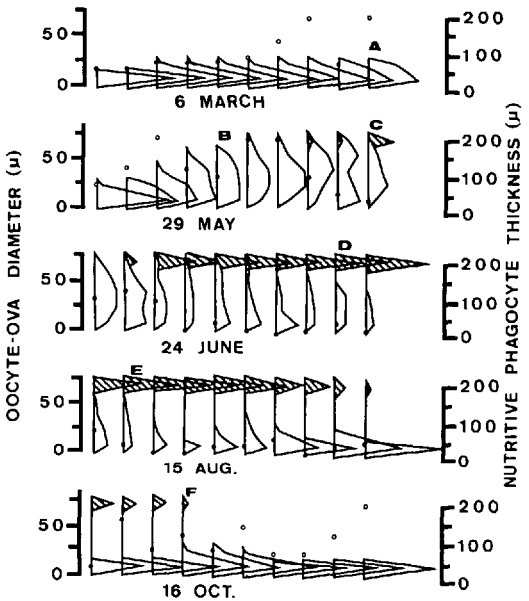

FIGURE 6. The thicknesses of the nutritive phagocytic layers (dots) and size-frequency polygons for the oocytes (open) and ova (hatched) of each of the individual females of *E. mathaei* in several samples collected from Wadi el Dom, Gulf of Suez, during 1966. Note the lack of synchrony among the individuals of each sample; this has allowed the arrangement of the polygons from left to right, to show the probable changes occurring during oogenic growth and spawn-out. (The letters correspond to individuals whose gonads are shown in the photomicrographs in Figure 7.)

sample in mid-July contained numerous ova. Moreover, by mid-July, initiation of oogenic growth had ceased, as judged by the scarcity of large- and medium-sized primary oocytes. After July, small oocytes less than 20 μ in diameter predominated among the oocytes. Many oocytes in July, August, September, and October were disintegrating and being phagocytized by the nutritive phagocytic tissue.

Spawned females were found first on August 2, and by mid-September all the females had completed spawning. The few ova found in some females in August, September, and October were probably relicts, and some were disintegrating.

Fluctuations in the average thickness of the ovarian nutritive phagocytic tissue were similar to those in the nutritive phagocytic tissue of the males. The average thickness increased sharply in the fall after spawn-out, reached a peak in December of both 1965 and 1966, then decreased until March, increased again in April, and finally decreased to a low in July and early

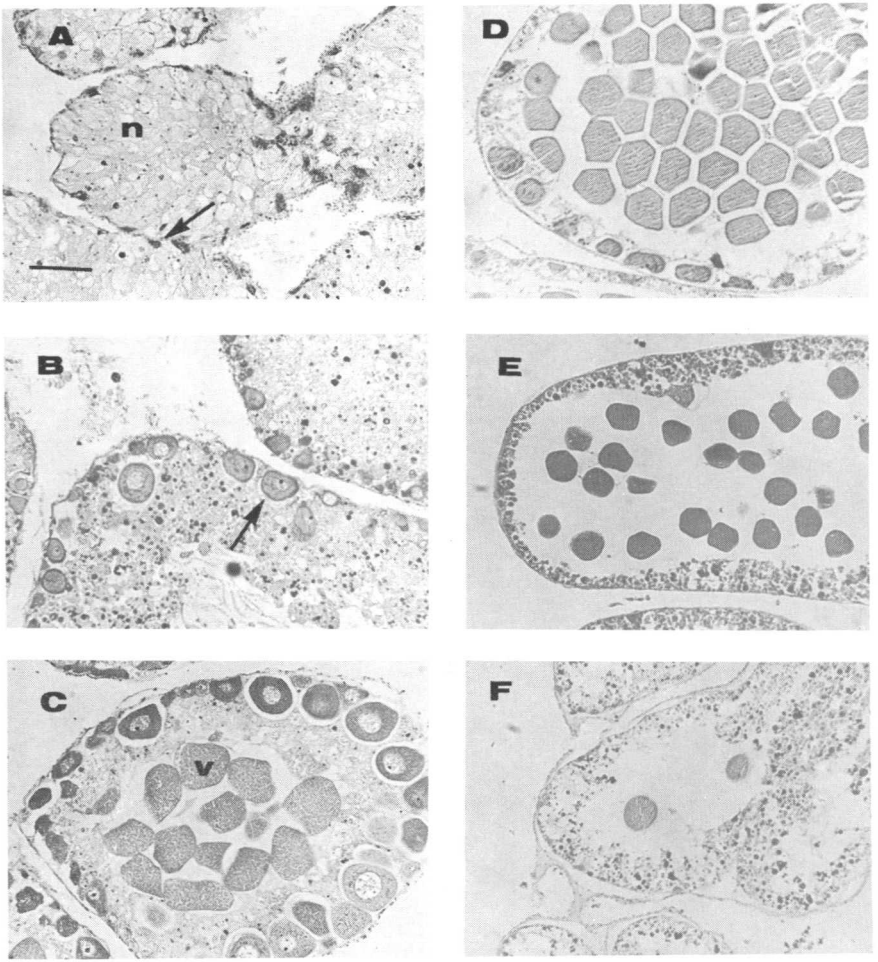

FIGURE 7. Histological sections of ovaries of specimens of *E. mathaei* collected from Wadi el Dom, Gulf of Suez, during 1966: A, March 6, scattered small oocytes (arrow), and extensive nutritive phagocytic tissue (n) containing numerous globules; B, May 29, continuous layer of growing oocytes (arrow); C, May 29, oocytes of many sizes, a few ova (v), and nutritive phagocytic tissue; D, June 24, ripe, with numerous ova, few oocytes, and sparse nutritive phagocytic tissue; E, August 15, partly spawned, with empty spaces in the lumen, a thin layer of nutritive phagocytes, and very few oocytes; F, October 16, completely spawned, with a few relict ova, very few oocytes, and ingrowing globulated nutritive phagocytic tissue. (All of these individuals are depicted as size-frequency polygons in Figure 6. Scale in A is 100 μ; all are at the same magnification.)

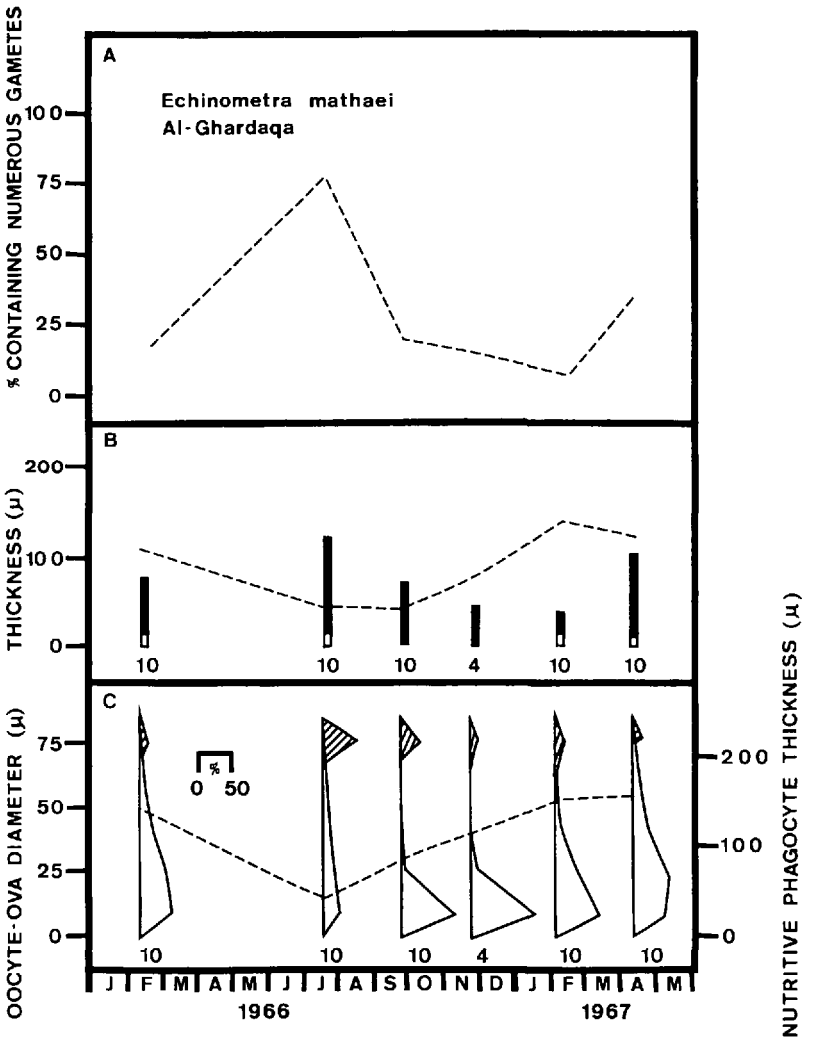

FIGURE 8. Reproductive changes in samples of *E. mathaei* taken from Al-Ghardaqa, at the Gulf of Suez–Red Sea junction (presented as in Fig. 3): A, percentage of animals containing numerous mature gametes; B, averaged thicknesses of the layers of spermatogenic cells (open bars), spermatozoa (solid bars), and nutritive phagocytes (dashed line) in typical transverse sections of testes 210 μ in radius; C, polygons for averaged size-frequencies of oocytes (open) and ova (hatched); and the average thickness of the nutritive phagocytic layers (dashed line) in transverse sections of the ovaries. (Numbers give sizes of samples.)

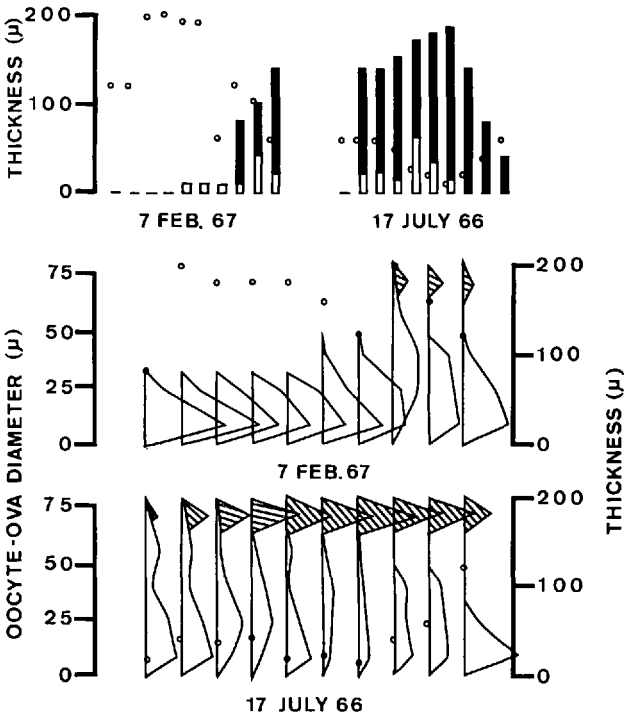

FIGURE 9. Data for individuals of *E. mathaei* sampled on July 17, 1966, and February 7, 1967, at Al-Ghardaqa (presented as in Figs. 4 and 6): Top, histograms of the testes; middle and bottom, size-frequency polygons for oocytes and ova. Note the occurrence of gametogenesis in some individuals in February, and the variability among the individuals in July.

August. The April-July decrease in the thickness of the nutrient phagocytic tissue probably was associated with oocytic nourishment, while the December-March decrease may have been due to midwinter utilization of the nutrient reserves by the urchins' somatic tissues.

The ovarian nutrient phagocytic tissue also contained basophilic, eosinophilic, and golden-brown globules, all of which varied considerably in abundance among the individuals of most samples. The basophilic globules tended to be most abundant in the fall, however, when phagocytosis of disintegrating oocytes and relict ova was most intense. Eosinophilic globules were most abundant in the early winter and midwinter. No seasonal fluctuation could be detected in the abundance of the golden-brown globules.

Al-Ghardaqa.—Seasonal reproductive periodicities of *E. mathaei* at Al-Ghardaqa were not nearly as well delineated as they were along the coastline

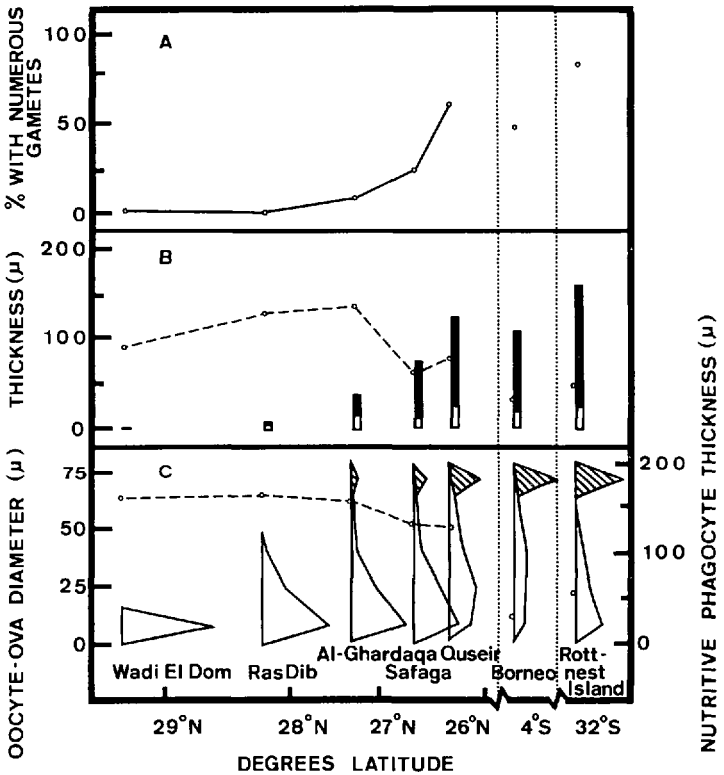

FIGURE 10. A, B, C, comparison of samples taken during early February from Wadi el Dom and Ras Dib in the Gulf of Suez; from Al-Ghardaqa, Safaga, and Quseir in the northern Red Sea; from Borneo near the equator; and from Rottnest Island, western Australia (presented as in Figures 3 and 8, except that latitudinal position, rather than time, is plotted on the abscissa). Data for the samples from Borneo and Rottnest Island are from Pearse (1968) and Pearse & Phillips (1968), respectively.

of the North Qalala Plateau (Figs. 8, 9). While over 90 per cent of the animals at Wadi el Dom contained numerous mature gametes in mid-July, only 80 per cent of the animals at Al-Ghardaqa were ripe in mid-July. In mid-July, most stages of gametogenesis and spawning were found at Al-Ghardaqa (Fig. 9) and there was much less synchrony among the individuals than at Wadi el Dom.

In September and November, the samples from Al-Ghardaqa were similar to comparable samples from Wadi el Dom; little gametogenic activity occurred at either site. The oocytes in the ovaries were scarce and small, and most of the males contained many spermatozoa but few spermato-

genic cells. The females at Al-Ghardaqa, however, contained more ova in September than at Wadi el Dom, and a few contained ova in November, while none did at Wadi el Dom.

No reproductive activity occurred in the animals at Wadi el Dom during February, yet gametogenesis was active in many of the animals at Al-Ghardaqa. Moreover, 16 per cent of the animals in 1966, and 7 per cent in 1967, contained numerous mature gametes. About 21 per cent of the specimens of *E. mathaei* taken from Al-Ghardaqa on April 9, 1967, contained numerous mature gametes, and gametogenesis was much in advance of the comparable sample from Wadi el Dom. Mortensen (1937) also found ripe individuals of *E. mathaei* at Al-Ghardaqa in April and May of 1936. The gametogenic period at Al-Ghardaqa therefore probably extends from before February to after July, and some mature animals can be found at any time of the year.

Other Sites.—The above comparison of samples from the coastline of the North Qalala Plateau and from Al-Ghardaqa suggests that a gradient in the reproductive activity of *E. mathaei* occurs along the western shore of the Gulf of Suez. This gradient is further shown by samples taken in early February 1967, from Wadi el Dom, Ras Dib, Al-Ghardaqa, Safaga, and Quseir (Fig. 10, and see Fig. 1 for localities). South of Ras Dib the percentage of animals containing numerous mature gametes increased to reach 60 per cent at the Quseir site. A gradation in the level of gametogenesis in both males and females also occurred from Wadi el Dom to the Quseir site. The thickness of the nutrient phagocytic tissue, however, varied little among the samples, although it was least in the animals from Quseir and Safaga.

Samples collected on February 1, 1965, from northeast Borneo near the equator, and on February 2, 1966, from the southern limits of the distribution of *E. mathaei* off southwestern Australia are also included in Figure 10. They are both similar to the sample taken from near Quseir; probably most populations of *E. mathaei* south of the Gulf of Suez are reproductively active in February. The highest percentage of animals containing numerous mature gametes in February occurred in the sample from Rottnest Island, February being in the middle of the austral summer.

Figure 11 compares all the females in the samples taken in early February 1967, from the Gulf of Suez and northern Red Sea. The increase in the number of females undergoing oogenic growth is clear; the females from Quseir in February are most similar to those collected in the summer from Wadi el Dom (Fig. 7) and Al-Ghardaqa (Fig. 9).

Samples taken from Wadi el Dom, Al-Ghardaqa, Safaga, and Quseir in mid-July are compared in Figure 12. In contrast with the samples in February, the percentage of animals containing numerous mature gametes

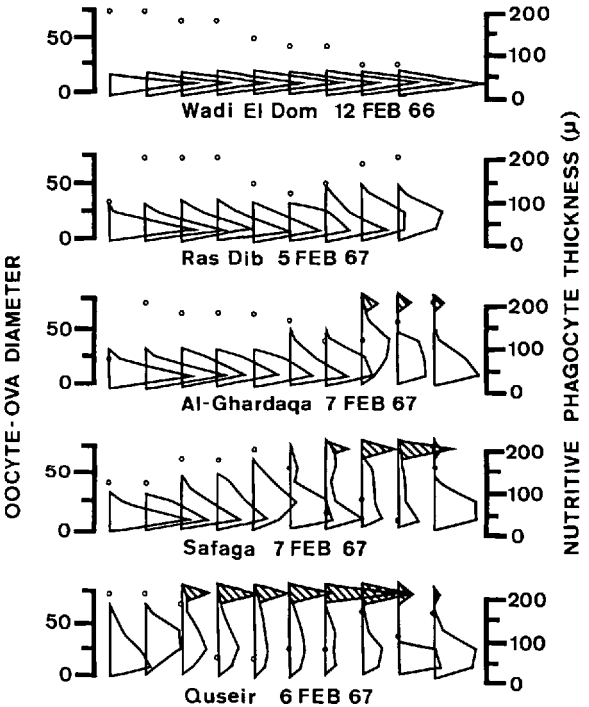

FIGURE 11. Size-frequency polygons for the oocytes (open) and ova (hatched) of each of the individual females in the samples taken in early February from the Gulf of Suez and adjacent northern Red Sea. Note the increasing number of mature females present from Wadi el Dom to Quseir, as well as the increasing amount of variability among the individuals in the samples.

decreased from Wadi el Dom to Quseir, and the Quseir population had nearly the same percentage ripe in both July (55 per cent) and February (60 per cent). The amount of ova relative to oocytes in the ovaries also decreased from Wadi el Dom to Quseir. The thickness of the nutritive phagocytic tissue was less in all of the samples taken in July than in those taken in February, but, except for the male nutritive phagocytes in the sample from Quseir, the thickness increased from Wadi el Dom to Quseir.

Samples taken in July 1964, from Samoa near the equator, and on July 13, 1966, from Rottnest Island, southwestern Australia, most resemble the sample from Quseir in the percentage containing numerous mature gametes (Fig. 12). As proposed elsewhere (Pearse, 1968), populations of *E. mathaei* south of the Gulf of Suez probably reproduce throughout the year. The ovaries of the animals from Samoa and Rottnest Island, however, most

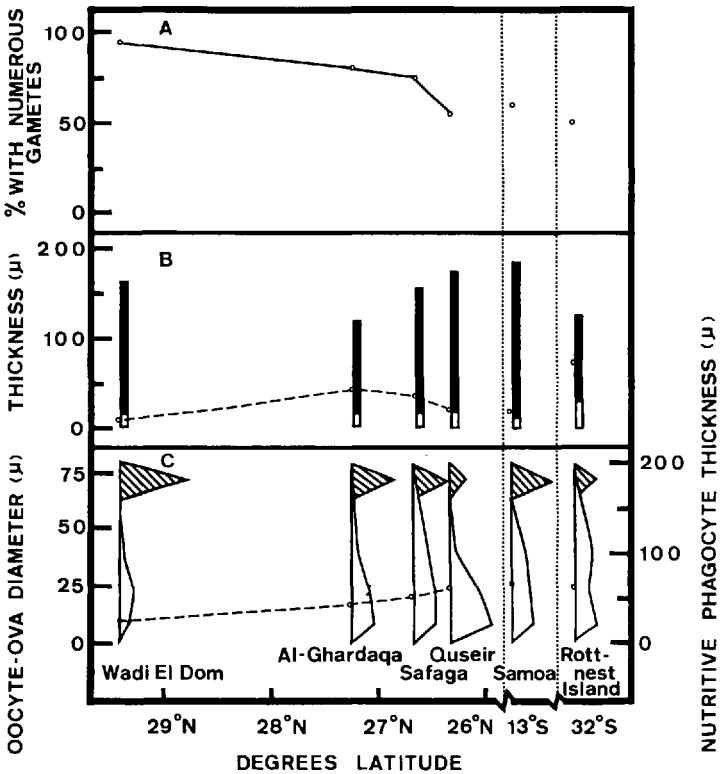

FIGURE 12. Comparison of samples taken during mid-July from Wadi el Dom in the Gulf of Suez; from Al-Ghardaqa, Safaga, and Quseir in the northern Red Sea; from Samoa near the equator; and from Rottnest Island, western Australia (presented as in Fig. 10). Data for the samples from Samoa and Rottnest Island are from Pearse (1968) and Pearse & Phillips (1968), respectively.

resemble the Safaga sample in having numerous, medium-sized, growing oocytes.

Other differences also occur among the different populations of *E. mathaei* along the western shore of the Gulf of Suez and adjacent Red Sea. Along the coastline of the North Qalala Plateau (except at Ain Sokhna) and at Ras Dib, specimens of *E. mathaei* occurred mostly in the open on coral blocks and rubble, and few were hidden. At Al-Ghardaqa and the Safaga site, most animals were partially hidden, nestled under coral ledges on the reef. These ledges were probably made, at least in part, by the animals themselves. The animals at the Quseir site were nearly always completely hidden under rocks or in deep crevices in the coral blocks.

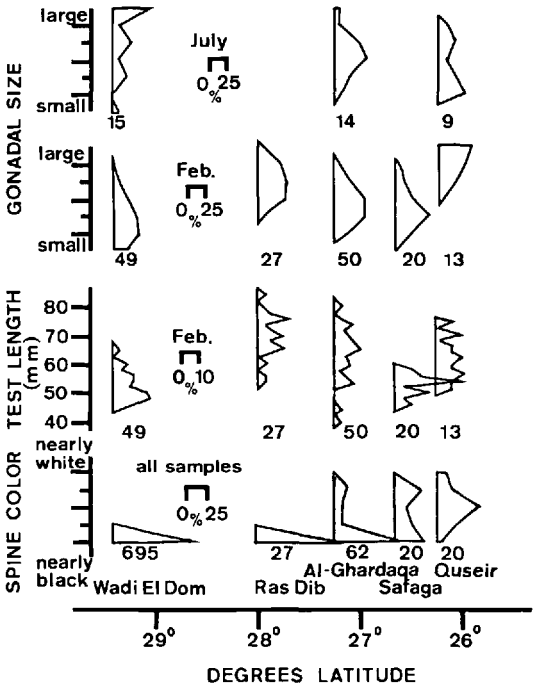

FIGURE 13. Data for the Gulf of Suez and adjacent northern Red Sea: from top to bottom, frequency polygons of gonadal sizes in July and February, animal sizes in February, and coloration of spines in all the individuals sampled. (Number of individuals in a sample is given below each polygon.)

The cryptic habit at the Quseir site is typical of what I've seen of *E. mathaei* in many other parts of the Indo-Pacific, including off northeast Borneo, northeast New Guinea, the Solomon Islands, and Eniwetok Atoll. At Rottnest Island, however, the animals occur in shallow burrows in the reef (Pearse & Phillips, 1968) and are perhaps most similar in habit to those at Al-Ghardaqa and Safaga.

A gradation in spinal coloration of the animals also occurred in the different populations of *E. mathaei* (Fig. 13). All the animals along the coastline of the North Qalala Plateau and at Ras Dib had very dark, nearly black spines. Fourtau (1904) also noticed that the individuals of *E. mathaei* in the Gulf of Suez were unusual by their constant dark coloration. An increasing number of animals south of Ras Dib had paler brown, tan, or greenish spines, and near Quseir a few animals had nearly white spines. Like the population near Quseir, populations of *E. mathaei* within the tropics are characterized by having animals differing greatly in the colors

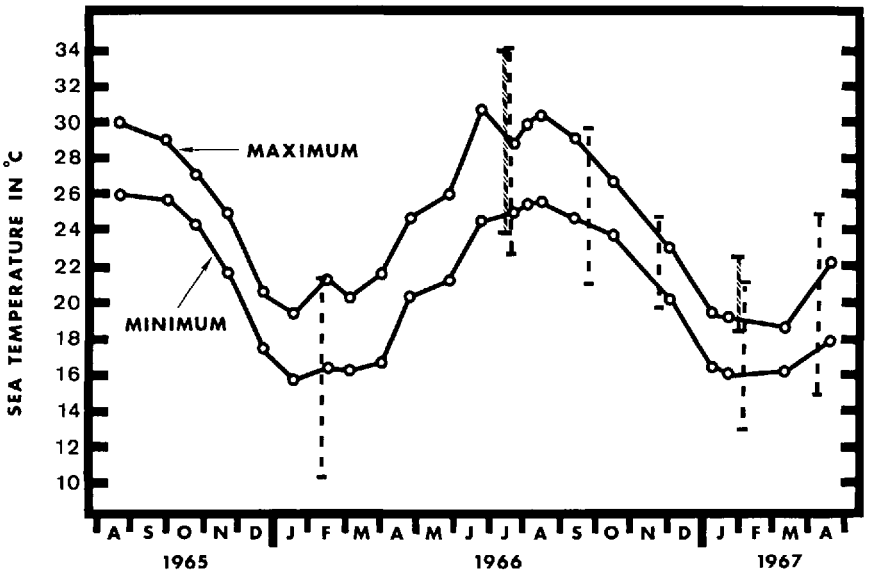

FIGURE 14. Maximum and minimum sea-surface temperatures recorded at the shore at Wadi el Dom (continuous lines), Al-Ghardaqa (dashed vertical lines), and near Quseir (diagonally hatched, vertical lines).

and shades of the spines (Mortensen, 1937, 1943; personal observation). A gradation in the spinal coloration of *E. mathaei* also occurs at the Tokara Islands off southern Japan, where "darkly coloured individuals are distributed nearer the reef edge than whitish individuals" (Tokioka, 1953). None of the animals seen in the Gulf of Suez or the northern Red Sea, however, had white-tipped spines, which are also often found within the tropics. At Rottnest Island, most of the animals have darkly colored spines (Pearse & Phillips, 1968), most similar to those at Al-Ghardaqa.

Animal and gonadal size also differed among the samples taken from the Gulf of Suez and northern Red Sea (Fig. 13). The animals at Ras Dib were the largest of any population, these being considerably larger than most animals in more equatorial areas (Pearse, 1968) or at Rottnest Island (Pearse & Phillips, 1968). Although the method of estimating gonadal size for Figure 13 was subjective, the subjective estimates correlated well with gonadal indices when these were taken at Wadi el Dom. Thus, there can be little question that the gonads in the animals at Wadi el Dom in February were generally small, while those from the animals at Quseir in February were generally very large. Of particular interest, the gonads of the animals from Ras Dib in February were generally large, even though gametogenic activity was low (Fig. 10).

Sea Temperature.—Seasonal fluctuations in sea temperature at Al-Ghardaqa and near Quseir appeared to be similar to those at Wadi el Dom (Fig. 14). Indeed, the lowest sea temperature ever recorded during this study (10.5°C) was taken over the reef at Al-Ghardaqa on February 10, 1966. Such a low temperature is not surprising; the shallow reefs around Al-Ghardaqa are extensive, and the prevailing northerly winds cool and drive surface waters out of the Gulf of Suez along the coast at Al-Ghardaqa. Mortensen (1938) and Crossland (1938) also reported quite low temperatures in the winter at Al-Ghardaqa, giving 10°C and 14°C, respectively. Because the reefs are so extensive and shallow, however, considerable warming occurs during the day, and the maximum daily sea temperatures at Al-Ghardaqa were always slightly above those at Wadi el Dom. Moreover, Mohamed (1940) found the surface temperatures in mid-December to range from about 20.75°C off the North Qalala Plateau to about 24.25°C near the mouth of the Gulf of Suez. The measurements for a single winter day at the Quseir site gave higher temperatures than at either Al-Ghardaqa or Wadi el Dom (Fig. 14). These few data indicate that the maximum surface temperatures are slightly higher during the winter near the mouth of the Gulf than near the head, although the overall differences are very slight.

Experimental.—Several groups of animals from Wadi el Dom were maintained in running sea water in aquaria at the Egyptian Institute of Oceanography and Fisheries at Ataqa (near Suez). Two groups of 20 animals were placed in different aquaria on June 26, 1966. One group was provided with a continuous supply of food consisting of local algae (*Enteromorpha*, *Padina*, and *Turbinaria*), sea grass, local vegetables (potatoes, zucchini, and cucumbers) and fish (*Tilapia* sp.). Potatoes, zucchini, and fish were most readily eaten. The other group was given no food. Fourteen fed and ten starved animals survived to August 3, 1966. The guts of the fed animals were full of food (mostly zucchini), while the guts of the starved animals were either empty or contained a few pellets of aquarium wax. No difference, however, could be detected among the fed, starved, and comparable field animals in gonadal and gut indices, or in the histological condition of the gonads. All were either ripe or recently spawned, and none showed evidence of either renewed gametogenesis or retardation.

Two groups of six animals were maintained in different aquaria from January 11 to February 8, 1967. Both groups were provided with food consisting mainly of potatoes, zucchini, and fish. The water temperature of one aquarium remained that of the adjacent sea, ranging from 11° to 20°C and averaging about 16°C. During the first week, the water temperature in the second aquarium was elevated gradually from 15° to 25°C, with aquarium heaters under thermostatic control. During the following

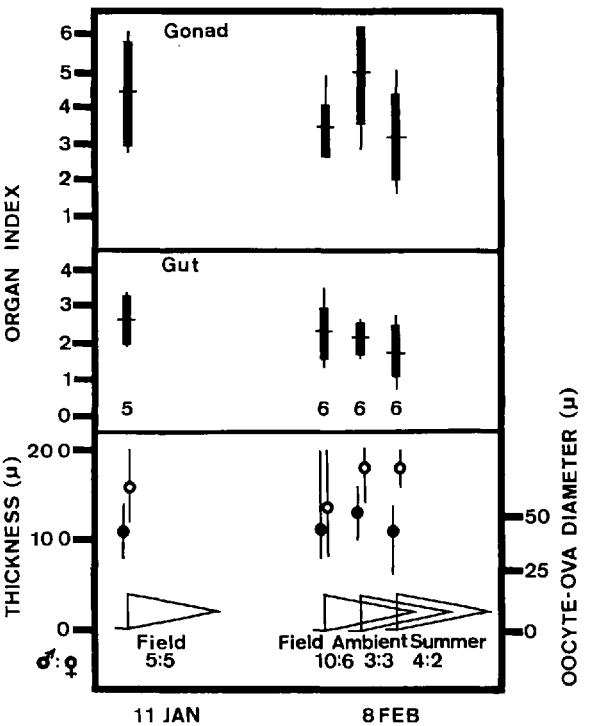

FIGURE 15. Comparison of animals in the field with those kept in aquaria from January 11 to February 8, 1967, at ambient (11° to 20°C) and simulated summer (25° to 34°C) temperatures. The means, standard deviations, and ranges of the gonadal and gut indices are given above. The size-frequency polygons for the oocytes and thicknesses of the layers of spermatogenic cells are given below, as well as the means (males, solid dots; females, open circles) and ranges for the thicknesses of the nutritive phagocytic layers. All the animals were from Wadi el Dom. (The numbers give the sizes of samples.)

weeks, the simulated summer temperature fluctuated between 23° and 34°C (due to fluctuating electrical power and water flow), averaging about 28°C.

The behavior of the animals at ambient winter temperatures and simulated summer temperatures differed markedly. The animals at ambient temperatures clustered in one corner of the aquarium and rarely moved or accepted food. Uneaten food was removed from the aquarium every five to seven days. In contrast, the animals at simulated summer temperatures constantly moved about the aquarium and accepted all food. Only large accumulations of fecal pellets were removed from the aquarium.

Despite the behavioral differences between the two groups of animals,

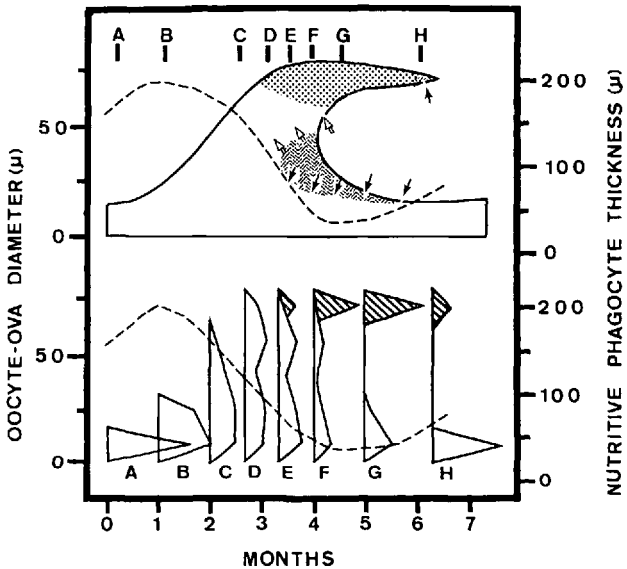

FIGURE 16. Diagram of an individual cycle of oogenic growth (top) in relation to size-frequency polygons for oocytes and ova (bottom). Derived mainly from the individual frequency polygons in Figure 6. Open areas represent oocytes; hatched or stippled areas, ova; wavy lines, disintegrating oocytes and ova; open arrows, nutrient transfer to growing oocytes; solid arrows, phagocytic activity of the nutrient phagocytes; and dashed lines, changes in the thickness of the nutrient phagocytic tissue. Letters A through H indicate different stages in the oogenic growth cycle from the stage immediately preceding oogenic growth (A), to fully ripe (G), to spawn-out (H). (See text for further details.)

upon dissection the guts of the animals at the ambient temperatures contained numerous food pellets while those of the animals at simulated summer temperatures were mostly empty. Apparently the animals at the higher temperatures rapidly passed food through their guts while those at ambient temperatures held their food. Moreover, as shown in Figure 15, there were no differences in gonadal or gut indices or reproductive activity among animals at ambient temperatures, animals at simulated summer temperatures, and comparable animals from the field. There was *no* evidence of any gametogenic activity in any animal. Perhaps at the relatively high simulated summer temperatures, all the food eaten was used immediately for metabolism by somatic cells rather than for gametogenesis.

DISCUSSION

Individual Gametogenic Cycles.—The populations of *E. mathaei* near the equator (Pearse, 1968) and off southwestern Australia (Pearse & Phillips,

1968) have little or no gametogenic synchrony among individuals; different individuals reach maturity and spawn at different times throughout the year. A similar lack of synchrony among individuals occurs at Quseir. Farther and farther north of Quseir, more and more animals are reproductively inactive in the late summer, fall, and winter, until at Wadi el Dom, near the head of the Gulf of Suez, gametogenesis leading to spawning begins only between March and May. Even at Wadi el Dom, gametogenic synchrony among individuals is very imperfect, and different individuals begin gametogenesis at different times during this 3-month period.

In populations that have little or no gametogenic synchrony among different individuals, it is difficult to arrange the size-frequency polygons for the oocytes and ova of the females in one sample to show the course of one gametogenic cycle. This was attempted with samples of *E. mathaei* from Rottnest Island with little success (Pearse & Phillips, 1968). At Wadi el Dom, however, where oogenic growth begins in all the females during a 3-month period, and where only one oogenic growth cycle occurs each year, the changes occurring during one cycle can be reasonably followed (see the data for the sample on May 29 in Fig. 6). The probable changes occurring in one oogenic growth cycle in one individual are diagrammed in Figure 16. Oogenic growth begins when the layer of nutritive phagocytes is increasing in thickness (stages A-B); after the oocytic growth period starts, the layer diminishes in thickness. The layer is thinnest just before spawn-out (stages F-G). When the majority of the oocytes reach a diameter between 25 μ and 40 μ, a break occurs in the size-frequency polygons of the oocytes; the larger oocytes continue to grow to full size, but the smaller oocytes seem to stop growing and many disintegrate. Oocytic breakdown is facilitated by phagocytosis (solid arrows), and disintegrating, phagocytized oocytes are most abundant between stages D and G. Because the amount of the nutritive phagocytic tissue decreases during the period of oocytic disintegration, nutrients are probably transferred via the nutritive phagocytic tissue to the larger growing oocytes (open arrows). The system diagrammed in Figure 16 therefore shows that the growing oocytes are provided with enough nutrients to complete growth from both (1) the nutrient phagocytes at the beginning of the cycle, and (2) subsequent utilization of nutrients in oocytes formed in excess. Similar systems of storage and transfer of nutrients during oogenesis occur in other echinoids (Pearse, 1969), as well as in asteroids, where at least excessive oocytes are formed and destroyed (Pearse, 1965).

The minimal time required for small oocytes under 20 μ (stage A) to grow to full size and mature (stage D) at Wadi el Dom was about 3 months (from March 6 to May 28; see Fig. 3). Since oogenic growth had still not begun in some females on May 28, some females probably had just begun to fill with mature ova in late August. Ova were numerous in a few

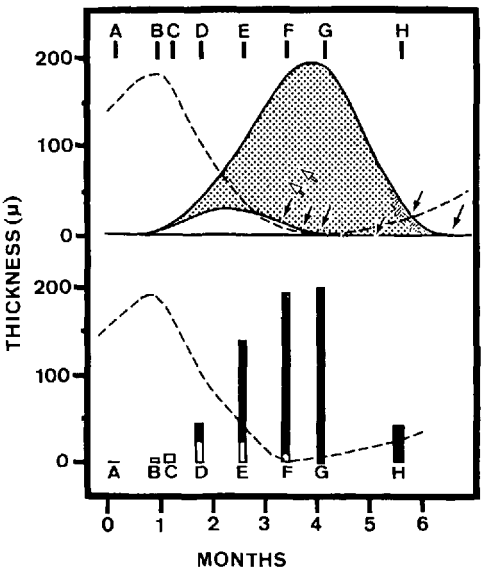

FIGURE 17. Diagram of an individual spermatogenic cycle (top) in relation to histograms of the testes (bottom). Derived mainly from the histograms in Figure 4. Open areas represent spermatocytes; stippled areas (or solid areas in histograms), spermatozoa; wavy lines, disintegration of spermatogenic cells and spermatozoa; open arrows, nutrient transfer to spermatogenic cells and spermatozoa; solid arrows, phagocytic activity by the nutrient phagocytes; and dashed lines, changes in the thickness of the nutrient phagocytic tissue. Letters A through H indicate different stages in the spermatogenic cycle from the stage immediately preceding spermatogenesis (A), to fully ripe (G), to spawn-out (H). (See text for further details.)

females until mid-September, indicating that storage of ova can last for about 2 months. Therefore at Wadi el Dom, one complete oogenic cycle from stage A to stage H took 5 to 6 months.

A definitive spermatogenic cycle within individuals, although not as discrete as the oogenic cycle, also can be diagrammed from the samples taken from Wadi el Dom (Fig. 4). The spermatogenic cycle in Figure 17 is diagrammed on the bases of the thicknesses of the various cell layers found in the testes. At the beginning of the cycle, at stage A, only spermatogonia and a few spermatocytes are scattered along the base of the germinal layer, and no discrete spermatogenic layer is formed. The nutritive phagocytic tissue increases at this time until it completely fills the testes. About 3 weeks after spermatocytic accumulation begins, spermatozoa begin to accumulate in large numbers in the lumina of the testes (from

April 1 to April 23 in 1966). Differentiation of individual spermatozoa from spermatocytes is probably much faster; Holland & Giese (1965) found labeled spermatozoa only 12 days after injection of tritiated thymidine in the echinoid *Strongylocentrotus purpuratus*. Accumulation of a large mass of spermatozoa in *S. purpuratus*, however, apparently took about a month, slightly longer than in *E. mathaei*. Spermatocytes form and differentiate, and spermatozoa accumulate, for the following 2 to 3 months in *E. mathaei* at Wadi el Dom. Nutrients utilized during spermatogenesis probably come mainly from the nutrient phagocytic tissue, because this tissue diminishes in thickness. Also, that the gonadal indices change little during this period is indicative that few nutrients are added to the gonads from outside. After about 3 months (stages F-G), the testes are full of spermatozoa, and the nutritive phagocytic tissue is at its minimal thickness; at this time the nutritive phagocytes begin to phagocytize the spermatogenic cells and spermatogenesis is terminated. In *E. mathaei* at Wadi el Dom, spawning apparently is gradual, and fewer and fewer spermatozoa are present in the testes for 2 to 3 months following the completion of spermatogenesis. In some individuals at Wadi el Dom, spawning apparently began before spermatogenesis was terminated (see the data for the samples in July and August in Fig. 4). When spawning is completed (stage H), the few relict spermatozoa are phagocytized by the nutritive phagocytes. As in oogenesis, therefore, one complete spermatogenic cycle, from the beginning of spermatocytic accumulation to phagocytosis of relict spermatozoa on completion of spawning, takes 5 to 6 months.

The oogenic and spermatogenic cycles diagrammed in Figures 16 and 17 are probably of general occurrence in all echinoids, because the process of gametogenesis is very similar in all the echinoids examined to date (Pearse, 1969). Similar gametogenic cycles also occur in at least the asteroids, but much or most of the nutrient reserves are held in the pyloric caeca rather than in the nutrient phagocytes of the gonads (Pearse, 1965). Differences occur among different species, however, mostly with respect to the time sequence of the cycles. In *Stylocidaris affinis*, for example, the spermatocytes accumulate for an unusually long period before maturing into spermatozoa, and the early part of the spermatogenic cycle is characterized by a thick layer of spermatocytes (Holland, 1967). Such a prolonged period of spermatocyte accumulation does not occur in *Prionocidaris baculosa*, the second cidaroid so examined (Pearse, 1969). In some other species, such as *Lovenia elongata* (Pearse, 1969) and *Tripneustes gratilla* (unpublished) spermatogenesis is never completely suppressed and a continuous layer of spermatogenic cells is always present.

The oogenic growth cycles in *Diadema setosum* (Yoshida, 1952; Pearse, 1968, and unpublished), *Strongylocentrotus purpuratus* (Holland & Giese,

1965), *Prionocidaris baculosa*, and probably *Lovenia elongata* (Pearse, 1969) are all similar to those of *E. mathaei*, and can be accommodated into the diagram of Figure 16. Oogenic growth from small oocytes (stage A) to maturation (stage D) takes between 2 and 3 months in all these species. Disintegrating, phagocytized oocytes, resulting in bimodal size-frequency polygons, occur in *D. setosum*, *P. baculosa*, and *L. elongata*, and were noted at least toward the end of the cycle in *S. purpuratus*. The time required for complete oogenic growth, from oogonial differentiation into oocytes to maturation, may be much longer. Tritiated thymidine, presumably taken up during synthesis of DNA by oogonia and pre-leptotene oocytes, was not found in growing oocytes of *S. purpuratus* up to 100 days after injection early in the oogenic cycle (Holland & Giese, 1965). Holland & Giese (1965) proposed that oocytes form a year or more before they actually enter the growth phase. Although Pikó *et al.* (1967) succeeded in labeling ova 1 to 2 months after injection of tritiated thymidine, this may well represent incorporation into cytoplasmic DNA rather late during oogenic growth.

The oogenic growth cycle in some other echinoids is considerably longer than in the four above-mentioned species. In both the antarctic echinoid *Sterechinus neumayeri* (Pearse & Giese, 1966) and *Stylocidaris affinis* off Naples (Holland, 1967), the oogenic growth period takes about a year, and the annual oogenic growth cycles overlap. Well over a year is also required for oogenic growth in the asteroid *Odontaster validus* of the Antarctic (Pearse, 1965) and the asteroid *Leptasterias hexactis* off western North America (Chia, 1968). Such differences in time are not clearly related to temperature; the sea temperatures in the Antarctic remain near −1.7°C; off Naples and western North America they are near 14°C, and in the Gulf of Suez they are between 20° and 30°C during the oogenic growth period.

Different species of echinoids also vary as to the size that the oocytes are kept during periods when oogenic growth does not occur (from stage G through A to B in Figure 16). As in *E. mathaei*, the oocytes remain smaller than 20 μ (by not growing or by disintegration and phagocytosis) when not in the growth period in *Strongylocentrotus purpuratus* (Holland & Giese, 1965), *Stylocidaris affinis* (Holland, 1967), *Lovenia elongata* (Pearse, 1969), and *Tripneustes gratilla* (unpublished). In *Prionocidaris baculosa* (Pearse, 1969) and *Diadema setosum* (unpublished), oocytes that are ½ to ¾ the full diameter are found all year, even though discrete periods of oogenic growth occur. This variation probably reflects only the size at which oocytes disintegrate and are phagocytized when growing out of season. As already pointed out (Pearse, 1969), the length of time that ova are held after maturation also varies considerably among different species of echinoids.

The individual cycles of oogenic growth and spermatogenesis depicted in Figures 16 and 17 are probably under endogenous control; that is, once started after stage A, the cycles probably run to completion in a species-specific, genetically determined manner little influenced by normal environmental changes. A "critical" level of nutrient reserves may be needed before the cycles begin, and this level may partly influence the length of the cycles. The variations, mentioned earlier, among different species probably reflect genetic differences. Exogenous regulation is probably superimposed on these essentially endogenous cycles in most populations. In particular, whenever the gametogenic cycles are synchronized among different individuals of a population so that all are reproductively active at the same time, exogenous regulation *must* be involved. Exogenous regulation may involve many diverse environmental factors, however, and these may perhaps combine mainly to enable the gonads to reach stage A in the gametogenic cycle. If the environmental factors are such that stage A can be reached during only one period, synchronized reproductive periodicities within a population should result. With *E. mathaei*, we have an example where exogenous regulation, although not clearly identified, affects and synchronizes reproduction in some populations, but not in other adjacent populations.

Geographical Gradations in Reproductive Activity.—Reproductive differences between adjacent populations of animals have been reported for many species, including echinoderms. Nearly adjacent populations of the echinoid *Echinus esculentus* (Moore, 1934, 1937) and the asteroid *Asterias rubens* (Vevers, 1949) off Great Britain; the asteroid *Asterias forbesi* off eastern North America (Galtsoff & Loosanoff, 1939); the echinoid *Strongylocentrotus purpuratus* off western North America (Boolootian, 1966; Leighton, 1967); and the echinoid *Sterechinus neumayeri* (Pearse & Giese, 1966) and the asteroid *Odontaster validus* (Pearse, 1965) in the Antarctic, for example, produce more gametes in some areas than in other areas. In a related example, populations of the echinoid *Echinocardium cordatum* in shallow waters off Great Britain reproduce in the summer, but adjacent populations in deeper waters do not reproduce at all (Buchanan, 1966). In these cases, differences in the production of gametes are related to differences in food supply. The timing of the reproduction does not seem to be affected, however. Indeed, the timing of the reproduction of *O. validus* (Pearse, 1966) and *S. purpuratus* (Boolootian, 1966) does not appear to vary over the whole of their ranges of distribution.

Other populations that are separated by larger distances are known to differ in the timing of their reproduction; e.g., *Arbacia punctulata* off eastern North America and *Paracentrotus lividus* off western Europe (Harvey, 1956), *Diadema setosum* in the Indo-Pacific (Pearse, 1968),

Echinocardium cordatum off western Europe, and others (Moore, 1966). Differences in temperature seem to be most clearly related to the differences observed in the timing of reproduction of these species. The populations of *E. mathaei*, in the relatively small area of the Gulf of Suez and the adjacent Red Sea, differ in *both* the timing and the amount of reproduction that occurs.

At Wadi el Dom, a quiescent period between the completion of one gametogenic cycle (stage H) and the beginning of the succeeding one (stage A) lasts for 6 to 7 months through the fall and winter. Animals taken during this period all had only scattered small oocytes or spermatocytes, many of which were being phagocytized. The amount of nutritive phagocytic tissue increased during this period, reached a maximum in midwinter, and then decreased.

The quiescent period was much shorter near the mouth of the Gulf of Suez; at Al-Ghardaqa, gametogenesis ended in July-August as at Wadi el Dom, but it began in at least some animals before the following February. South of the mouth of the Gulf of Suez, at Quseir, and also near the equator (Pearse, 1968) and even off southwestern Australia (Pearse & Phillips, 1968), a quiescent period usually does not occur, and stages like A are only rarely found. If the time required for one gametogenic cycle to be completed in these areas is the same as at Wadi el Dom, about two gametogenic cycles should occur each year in animals south of the Gulf of Suez. There is no synchrony at all among different animals in these populations south of the Gulf of Suez, and, throughout the year, between 50 and 60 per cent of the animals contain numerous mature gametes.

Other gradations also occur in the Gulf of Suez (Pearse, 1969). The coral reefs within the gulf are generally small and poorly developed, while they flourish near the mouth of the gulf at Al-Ghardaqa. Such typically Indo-Pacific species as the echinoid *Tripneustes gratilla* and the ophiuroid *Ophiocoma scolopendrina* (and many other ophiuroids) are very abundant at Al-Ghardaqa, but absent or at least very rare on the western shores of the Gulf of Suez.

Without more hydrologic data for the Gulf of Suez, definitive reasons cannot be given for these differences. The environmental factors responsible for the gradation in reproductive activity of *E. mathaei* are especially difficult to identify because, with critical examination, none of the usually accepted factors seem especially important by themselves. Because *E. mathaei* reproduces throughout the year off southwestern Australia (Pearse & Phillips, 1968), and this is farther south of the equator than the Gulf of Suez is north, no factor dependent on geographic position, such as photoperiod, should be responsible for restricting the reproduction in the Gulf of Suez.

As with the echinoids *Prionocidaris baculosa* and *Lovenia elongata* at

Wadi el Dom (Pearse, 1969), temperature differences do not relate well to the restricted reproduction of *E. mathaei* in the Gulf of Suez. Direct regulatory importance of seasonal fluctuations in temperature on the reproduction of *E. mathaei* seems especially unlikely because: (1) the sea temperatures are usually relatively low off southwestern Australia (about 18° to 22°C), being similar to the sea temperatures in the winter at Wadi el Dom, yet *E. mathaei* reproduces throughout the year there (Pearse & Phillips, 1968); (2) seasonal and daily fluctuations in sea temperature are more marked at Al-Ghardaqa, and it gets colder there than at Wadi el Dom in the winter, yet nearly continuous reproduction occurs at Al-Ghardaqa; and (3) gametogenesis could not be induced with elevated temperatures during midwinter in the animals from Wadi el Dom. The elevated temperatures in the experiments, however, were perhaps too high. Moreover, the maximum daily sea temperatures at Al-Ghardaqa were always slightly higher than at Wadi el Dom (Fig. 14). Perhaps a minimum daily amount of time above 18° to 20°C is needed for gametogenesis to begin in *E. mathaei*, and this requirement is not met at Wadi el Dom during the winter.

The possible importance of seasonal fluctuations in nutrient reserves for regulating reproduction in echinoids has already been considered (Pearse, 1969). It was suggested that the nutritive phagocytes in the gonads alternate during the year between phagocytic and nourishing functions, i.e., that they phagocytize disintegrating gametogenic cells and thereby possibly restrict gametogenesis during part of the year, and nourish gametogenic cells during the reproductive period. Nutrient reserves seem to accumulate to some "critical" level at which disintegration of the gametogenic cells and phagocytic activity cease. With adequate nutrient reserves, gametogenesis is assured completion, once started. As gametogenesis proceeds to maturity, the nutrient reserves are depleted until the younger gametogenic cells begin to disintegrate and the nutritive phagocytes revert to phagocytic activity. This hypothesis is implicit in the gametogenic cycles diagrammed in Figures 16 and 17.

Although seasonal fluctuations of the nutrient phagocytic tissue occur in the population of *E. mathaei* at Wadi el Dom, even these fluctuations do not relate well to those of the reproductive activity. During the fall and early winter, the thickness of the nutritive phagocytic tissue increased until a maximum was reached in December. No gametogenic activity began in December, however, and between December and March, the thickness of the nutritive phagocytes decreased. In the early spring, when sea temperatures began to increase, both the beginning of gametogenesis and an increase in the thickness of the nutrient phagocytic tissue occurred. It should be noted, however, that animals in early stages of gametogenesis in the spring tended to have the greatest thickness of the nutritive phagocytic tissue.

Fluctuations of the nutrients in the gonads of *E. mathaei* appear to be similar to those occurring in *Echinus esculentus* (Moore, 1934, 1937). In this echinoid, off Great Britain, reproductive activity terminates by midsummer, but the total size of the gonads increases during the late summer, fall, and early winter. Gametogenesis does not occur during this period; the increase in gonadal size is due entirely to accumulated nutrient stores. In midwinter, when feeding activity appears to be low, the gonadal size decreases, while in the spring, when warming of the sea begins, gametogenesis begins and the gonads increase in size.

Perhaps both a "critical" level of accumulated nutrients and a "critical" minimal temperature are required for gametogenesis to proceed. Thus, with *E. esculentus* off Great Britain, and *E. mathaei* in the Gulf of Suez (but not farther south) midwinter temperatures may be too low for gametogenesis to begin, even though there are adequate nutritional reserves, and only in the spring may both the temperatures and the nutritional reserves be favorable for reproduction.

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Sumario

Periodicidades Reproductivas de Invertebrados Indo-Pacíficos en el Golfo de Suez. II. El Equinoideo *Echinometra mathaei* (de Blainville)

La reproducción en poblaciones del equinoideo Indo-Pacífico *Echinometra mathaei* (de Blainville) fue seguida al nivel celular por cerca de dos años en el Golfo de Suez y el adyacente Mar Rojo. En la parte norte del Golfo de Suez, la gametogénesis empieza en los diferentes animales entre abril y junio y el desove ocurre entre julio y mediados de octubre. Durante el resto del año, las gónadas descansan reproductivamente. Se describen

cambios en los ciclos individuales de crecimiento espermatogénico y oogénico en estas muestras. Los ciclos son probablemente endógenos y posiblemente se aplican a equinoideos y asteroideos en general. Los cambios en los fagocitos nutritivos son importantes durante los ciclos gametogénicos individuales. Estas células acumulan nutrientes en el otoño y principios del invierno, aparentemente alimentan todo el animal a mediados del invierno cuando la actividad alimenticia es baja, acumulan más nutrientes en la primavera y entonces alimentan las células gametogénicas durante los finales de la primavera y principios del verano. También ayudan en la destrucción de células gametogénicas a la terminación de la gametogénesis y de gametos residuales cuando se ha completado el desove.

En contraste con las poblaciones cerca de la parte superior del Golfo de Suez, en la boca del Golfo la gametogénesis empieza en algunos animales antes de febrero y se encuentran animales maduros durante todo el año. Al sur del Golfo de Suez y a través de la mayor parte del promedio de distribución de *E. mathaei*, la gametogénesis y el desove ocurren contínuamente en diferentes animales y no hay sincronización entre ellos.

Se propone que tanto un nivel crítico de reservas de nutrientes en las gónadas como una temperatura mínima crítica son requeridos para la iniciación de un ciclo gametogénico. Dentro del Golfo de Suez, pero no más al sur, las temperaturas del mar en el invierno están aparentemente justo por debajo de la temperatura crítica requerida (18°C-20°C), resultando así la reproducción estacional sincronizada.

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NOTE: After this paper was accepted, B. F. McPherson (Studies on the biology of the tropical sea urchins, *Echinometra lucunter* and *Echinometra viridis*. Bull. Mar. Sci., *19*(1): 194-213) described some aspects of reproduction and gametogenesis in two species of *Echinometra* off southern Florida. Both species appear to be very similar to *E. mathaei* in the Gulf of Suez; gametogenesis occurred in the spring and early summer, and spawning occurred in the late summer and fall. It could be expected that both species would reproduce throughout the year in localities nearer the equator.