Reprinted from
BULLETIN OF MARINE SCIENCE
OF THE GULF AND CARIBBEAN
Vol. 13, No. 2, pp. 267-281
JUNE, 1963

A CONTRIBUTION TO THE BIOLOGY OF *TRIPNEUSTES ESCULENTUS*[1]

H. B. MOORE, THELMA JUTARE, J. A. JONES, B. F. McPHERSON AND C. F. E. ROPER
Institute of Marine Science, University of Miami

ABSTRACT

The biology of *Tripneustes* has been studied for several years in Miami and Bermuda. It spawns in the spring and summer but with a very different spawning pattern in different years. First spawning seems to be triggered by temperature, and successive spawnings by attainment of a gonad size which increases during the season. Winter growth of the gonad and its rate of build up between spawnings is negatively correlated with temperature, as is test growth. Hermaphroditism was common in a year group which was in the immature stage during an unusually cold winter. A tentative estimate has been made of food intake and of the efficiency of its conversion into urchin tissue.

INTRODUCTION

Commencing in 1937, a few observations on *Tripneustes esculentus* (Leske) were made by one of us (H.B.M.) in Bermuda. In 1959, McPherson and, in 1960, Roper made the species the subject of a special study in a course in marine ecology at the University of Miami. In 1961, Jones carried out, in the same course, a series of field experiments. In 1960-61, a grant from the National Science Foundation (G-14967) allowed the senior author and Thelma Jutare to bring together the existing data and amplify them, particularly by extending the series of observations on gonad changes and growth. This study was carried out along with one on the urchin, *Lytechinus variegatus* (Moore, *et al.,* 1963), and affords a comparison of the biology of the two species. Of the two, *Tripneustes* is the more tropical in its distribution. It does not extend as far north as *Lytechinus* on either the Atlantic or Gulf of Mexico coasts and is probably not abundant north of south Florida.

Lewis (1958) has made a valuable study of *Tripneustes* in Barbados, in which he describes their growth, gonad changes, and planktonic history, together with notes on their general biology.

We wish to thank the National Science Foundation for their support of these studies, as well as many members of the University of Miami Marine Laboratory who have helped from time to time.

DISTRIBUTION

Tripneustes does not extend quite so high into the intertidal region as does *Lytechinus,* rarely being exposed at low water. It may, however, occur in intertidal pools in Bermuda, and in Bimini young individuals

[1]Contribution No. 472 from The Marine Laboratory, Institute of Marine Science, University of Miami.

have been seen in pools in a heavily splashed area above high water mark but no adults were seen there. At Sewage Beach, on Virginia Key, Miami, where most of the recent collecting was done, "grass" flats extend out from the lower intertidal zone for about a kilometer, and the heavy grass cover gives place to open sand at a depth of about a meter at extreme low water. *Lytechinus* is abundant over the entire extent of the grass flats, but *Tripneustes* is much less abundant and mainly confined to the outer edge. *Tripneustes* also showed some seasonal movement. *Lytechinus* tends to mask itself with pieces of shell at all times. *Tripneustes,* during the winter, was frequently found in open patches among the grass and without masking. During the spring, as the light became stronger, they were seen to mask themselves, but usually with pieces of alga rather than shell and, as summer advanced, they tended to move from the open areas into the cover of dense grass. When kept in indoor tanks, both species showed only small tendency to mask if conditions were rather dark, but they masked with anything available and moved into shaded areas when sunlight was admitted. Lewis states that, in Barbados, *Tripneustes* tends to aggregate on and under rocks in March and April and has dispersed into the open again by August. He associates this aggregation with spawning, which occurs in that period. He also states that the older individuals tend to move offshore for part of the year.

Breeding

Tripneustes was not common in Bermuda, so only small samples could be examined. At Miami, fifty urchins were examined each time. Test diameter was taken as a standard measure of size, but a calibration curve was established relating diameter to test volume by displacement, this value including spines. A smear of the gonad was examined to determine sex and condition, and the gonads then removed and their volume determined by displacement. Relative gonad size is expressed as $\frac{10.\ \text{Gonad Volume}}{\text{Test Volume}}$. This value is comparable with that previously used by the senior author (Moore, *et al.,* 1963), but not with that of Lewis (1958).

The Bermudian series was not sufficient to show more than an indication of autumn or winter spawning (Fig. 1). The three years of studies at Miami showed a strikingly different pattern of gonad changes. The fact that even minor fluctuations were closely parallel in males and females point to such fluctuations being significant and not due to inadequate sampling. In 1959, gonad volumes $\frac{10.\ \text{G.V.}}{\text{T.V.}}$ were small, not attaining a value of 0.7 until June, and with a maximum for the year of about 0.8. There were apparently four successive spawnings, and there must have been at least one more in the autumn-winter period when observations were

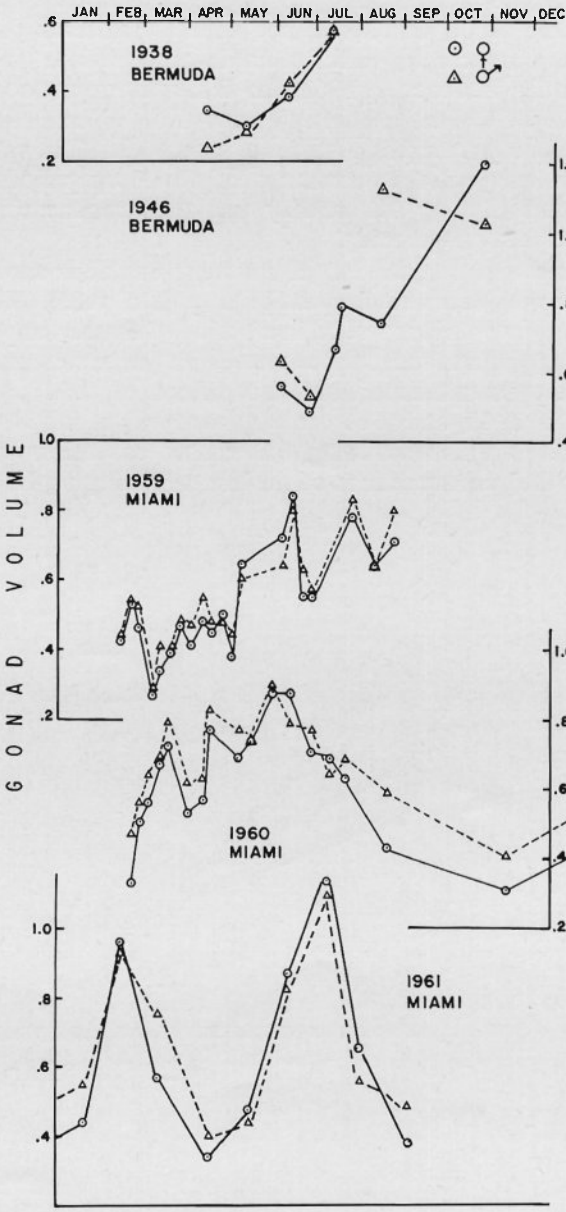

FIGURE 1. Seasonal changes in gonad volume expressed as $\frac{10.\ \text{Gonad Volume}}{\text{Test Volume}}$ in *Tripneustes.*

discontinued. In 1960, the build up of the gonads took place earlier, reaching a value of 0.7 in March, and with a maximum of about 0.9. However, spawning ceased earlier than in the previous year, the last cycle commencing in June. In 1961, the first spawning was in February, compared with March the previous year, and at its commencement the gonads had already reached a value of over 0.9. This spawning was prolonged and heavy. There was then a long build up period, the gonads reaching a value of over 1.1 in July and then commencing a second prolonged and heavy spawning.

In many animals, the initiation of spawning has been shown to occur when rising spring temperatures attain a certain value. With samples taken only every two to four weeks, in a period when the temperature may rise several degrees a month, we cannot define the exact temperature at which spawning commenced; but the values of 23.5°, 21.4°, and 21.9°C in 1959, 1960, and 1961 are consistent with a critical temperature of about 22°C at which spawning commences but below which it will not occur. At the commencement of the first spawning of the year, gonad

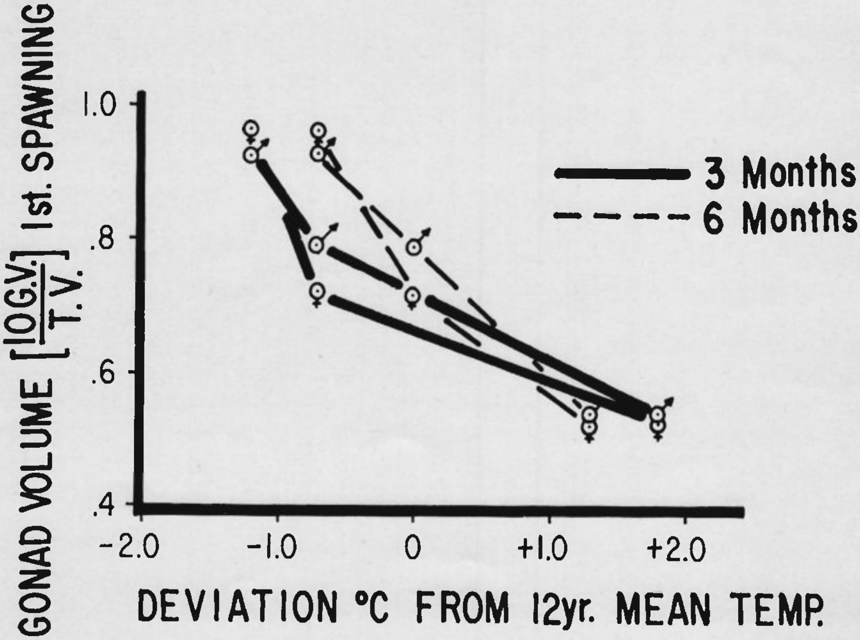

FIGURE 2. The relation of the gonad volume of *Tripneustes* at the start of the first spawning of the season $\left(\frac{10.\ G.V.}{T.V.}\right)$ to deviation of the sea temperature in the previous three and six months from twelve-year mean values.

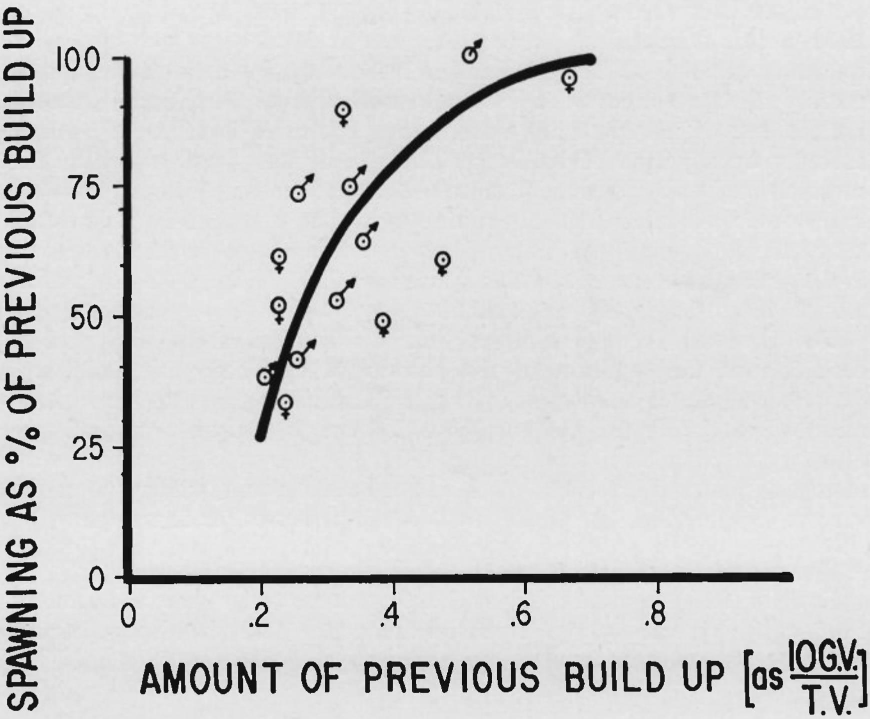

FIGURE 3. The relation in *Tripneustes* of the extent of spawning (expressed as per cent of the previous build up) to the extent of this build up, as $\frac{10.\ G.V.}{T.V.}$.

sizes were very different in the three years—0.54, 0.79, and 0.93 in the males, and 0.53, 0.72, and 0.96 in the females. It has been shown in *Lytechinus* (Moore *et al.,* 1963), and will be shown later for *Tripneustes,* that there is a close correlation between test growth and temperature, but that, surprisingly, the growth is greatest at low temperatures. The average sea temperature deviations from a twelve-year mean in the three months preceding were $+1.8°$, $-0.7°$, and $-1.4°$C respectively in 1959, 1960, and 1961; and for the six months preceding spawning the values were $+1.3°$, $0.0°$, and $-0.7°$C. This suggests that, while spawning is triggered at a temperature of about 22°C and does not occur below this temperature, the size of the gonad at first spawning depends on the degree of cold during the preceding winter (Fig. 2). We do not have comparable observations of the relation between gonad growth and temperature in *Lytechinus.*

The completeness of emptying of the gonad at spawning is a function of the previous build up of the gonad (Fig. 3). The massive build up in 1961 before the critical temperature was reached was followed by a spawning equal to 95-100 per cent of the build up. Smaller build ups in other years were followed by as little as 33 per cent spawning. Except for the end of the spawning season, each spawning is succeeded rather abruptly by a period of build up. The size of the gonad at which the successive spawnings commence increases as the season advances, possibly in relation to the increasing temperature. It may be suggested that spawning, after the first of the season, is initiated by attainment of a certain tension in the gonad, as in some asteroids (Greenfield, 1959), but that this critical tension increases during the season.

The intervals between samples were too long to allow very precise definition of the duration of the periods of spawning and build up. However, if rate of build up is expressed as percentage per 30 days of the mean value during the build up period, there is a significant (<1 per cent) correlation with temperature (Fig. 4), the rate decreasing with increasing temperature. Thus, both winter build up and build up after the successive spawnings are greatest at low temperatures, as is test growth.

Test Growth

Lewis (1958) has afforded excellent coverage of growth in Barbados from cage experiments and from size frequency analysis of populations. He found that *Tripneustes* reached a diameter of about 80-90 mm in the

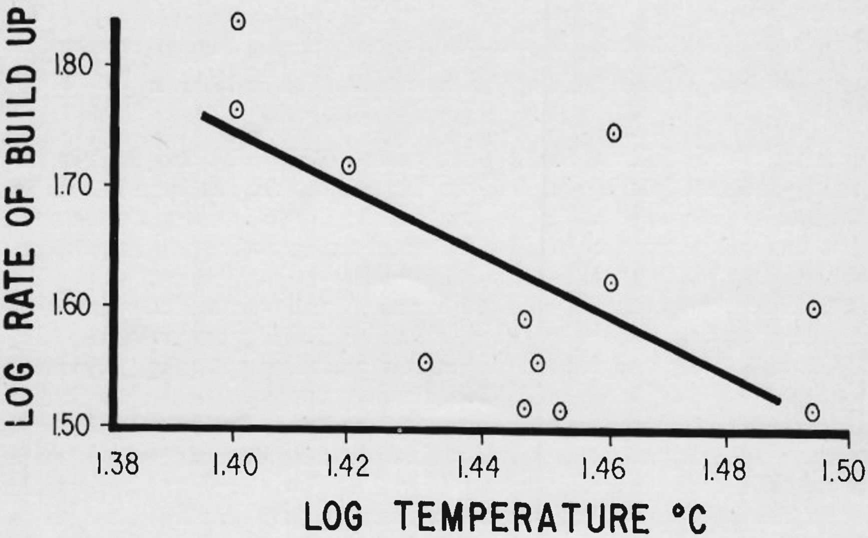

FIGURE 4. The relation in *Tripneustes* between the rate of gonad build up and temperature, both on logarithmic scales.

first year and probably had a life span of about two years. Unfortunately, we have not been able to find a population of small *Tripneustes* during the present work, despite extensive search. We did, however, find a population at Bimini in pools above high water. These pools were kept supplied by

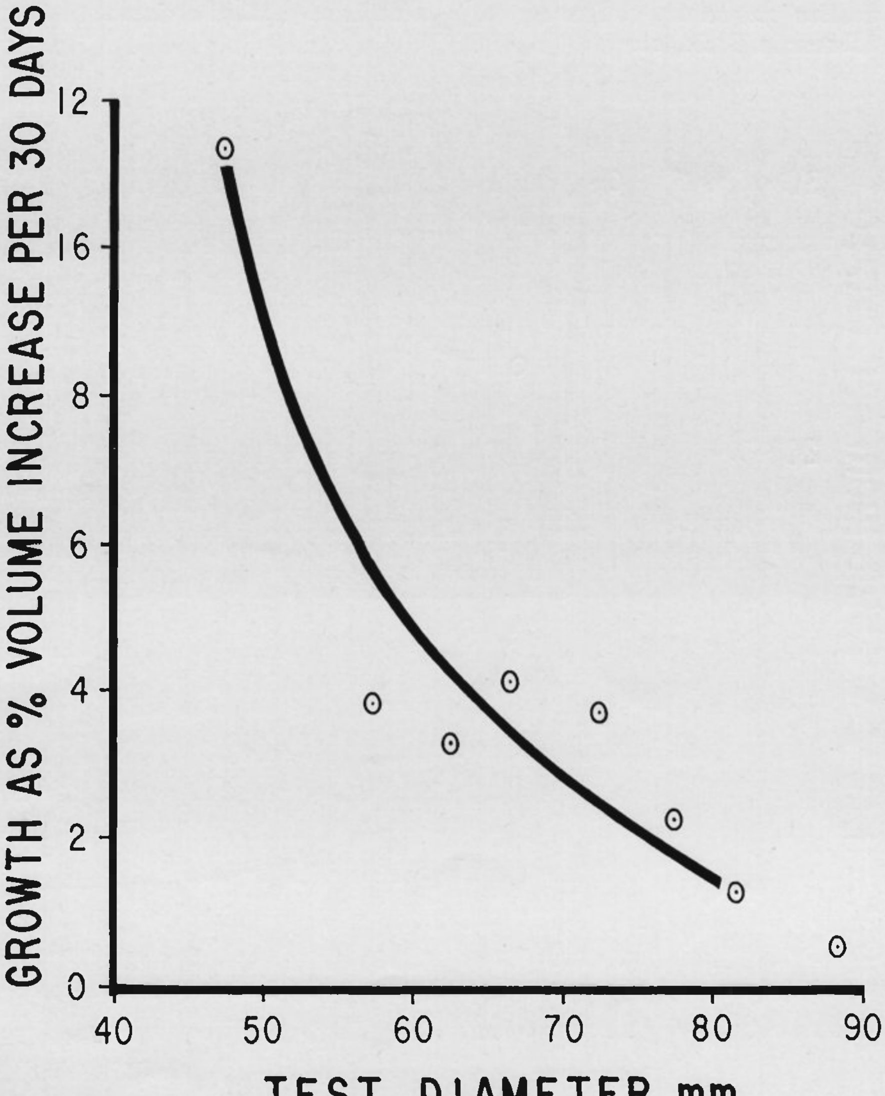

FIGURE 5. The relation of the growth rate of *Tripneustes* in tanks (expressed as percentage volume increase per 30 days) to size of urchin.

rather continuous wave action. The urchins had a mean diameter of 24.8 mm on June 20, 1961. This size was reached in Barbados in October-November, and, if the breeding periods are at all similar, it would appear that the Bimini population must have grown very much more slowly, since urchins presumably of the same age would have reached a size of about 75 mm in Barbados.

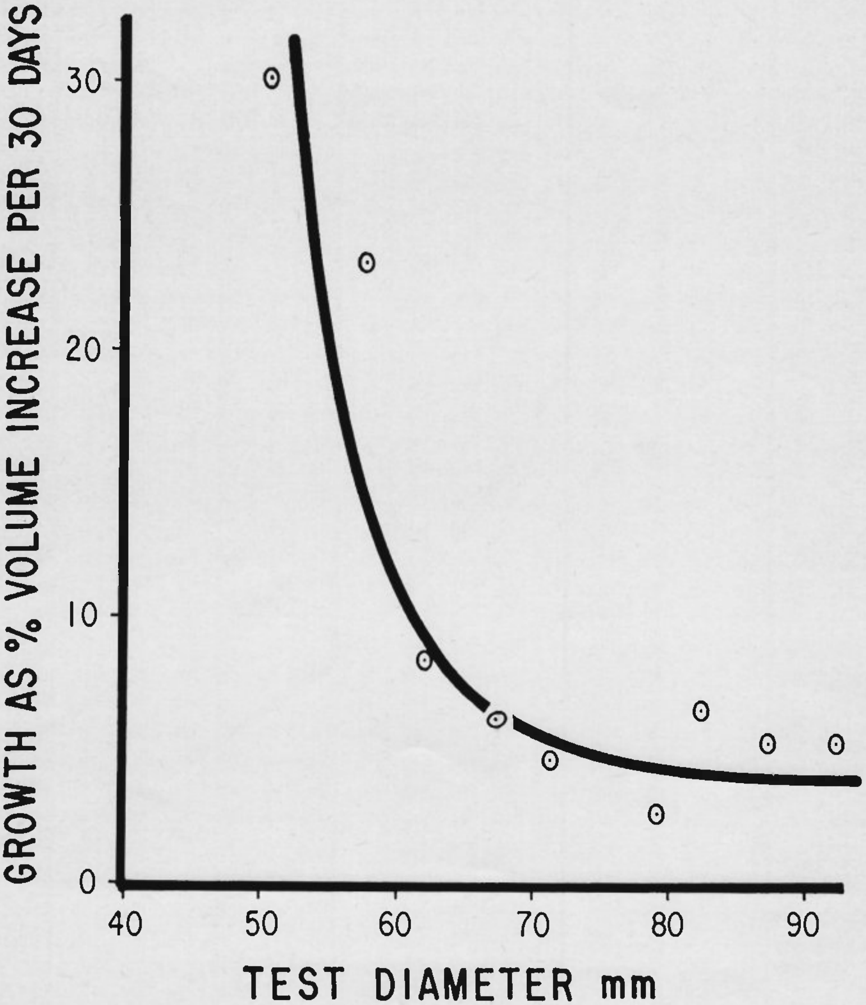

FIGURE 6. The relation of the growth rate of *Tripneustes* in field pens (expressed as percentage volume increase per 30 days) to size of urchin.

For larger urchins we have a year of observations under tank conditions and several months under natural conditions in a cage on the grass flats. In *Lytechinus* (Moore *et al.,* 1963), it was found that tank growth was much less than that in cages. In *Tripneustes,* tank growth, on a linear basis, was about half that in the sea. As shown below, there is a marked effect of temperature on growth rate, and allowance can be made for this so as to compare growth rate with size at a constant temperature (Figs. 5, 6).

Growth, expressed as percentage increase in volume per 30 days, shows a rapid decrease with increasing size. At a test diameter above 60 mm, the

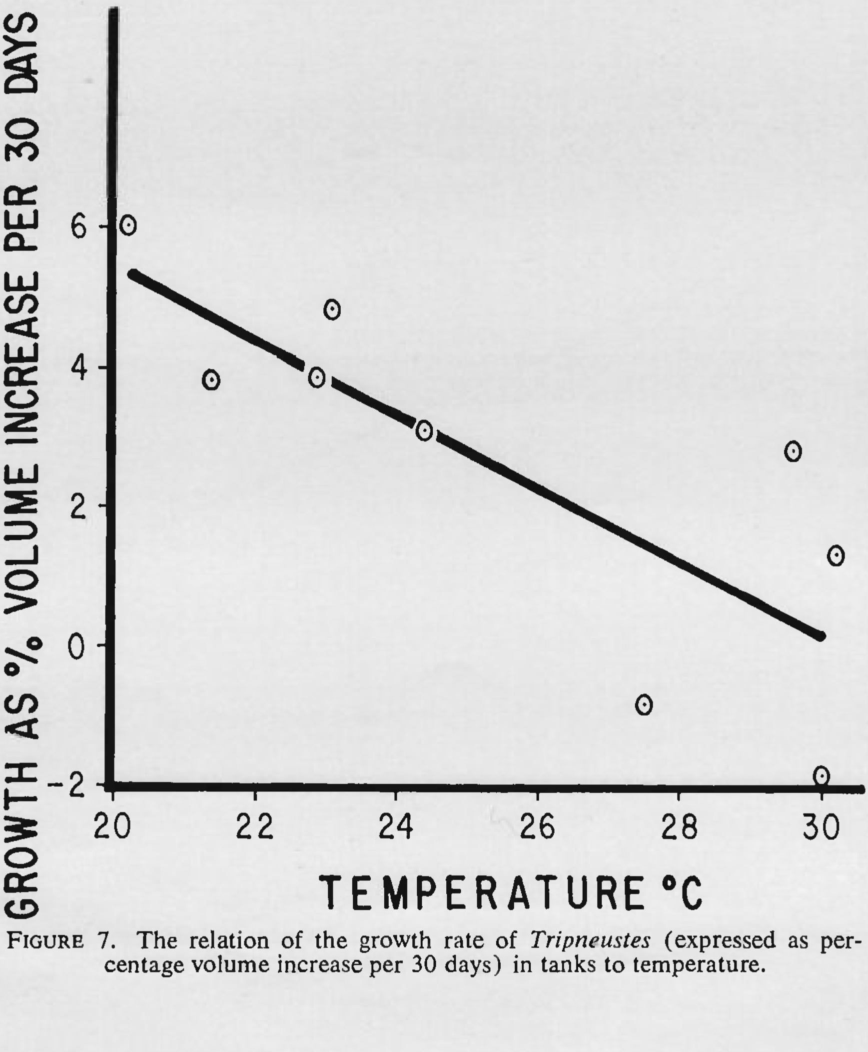

FIGURE 7. The relation of the growth rate of *Tripneustes* (expressed as percentage volume increase per 30 days) in tanks to temperature.

temperature-corrected rate of increase was 1-4 per cent in the tanks and about 5 per cent in the sea. An attempt to obtain a comparable figure from the Barbados data, but without a temperature correction, gives about 16 per cent, which is much higher than at Miami and is consistent with the suggested difference in growth rates of small individuals between Bimini and Barbados.

Growth and Temperature

It was shown that there is a correlation between gonad growth and temperature, growth being most rapid at low temperatures. The same is true of the test, as it was shown to be in *Lytechinus*. Figures 7 and 8 show the growth expressed as percentage in volume per 30 days in relation to

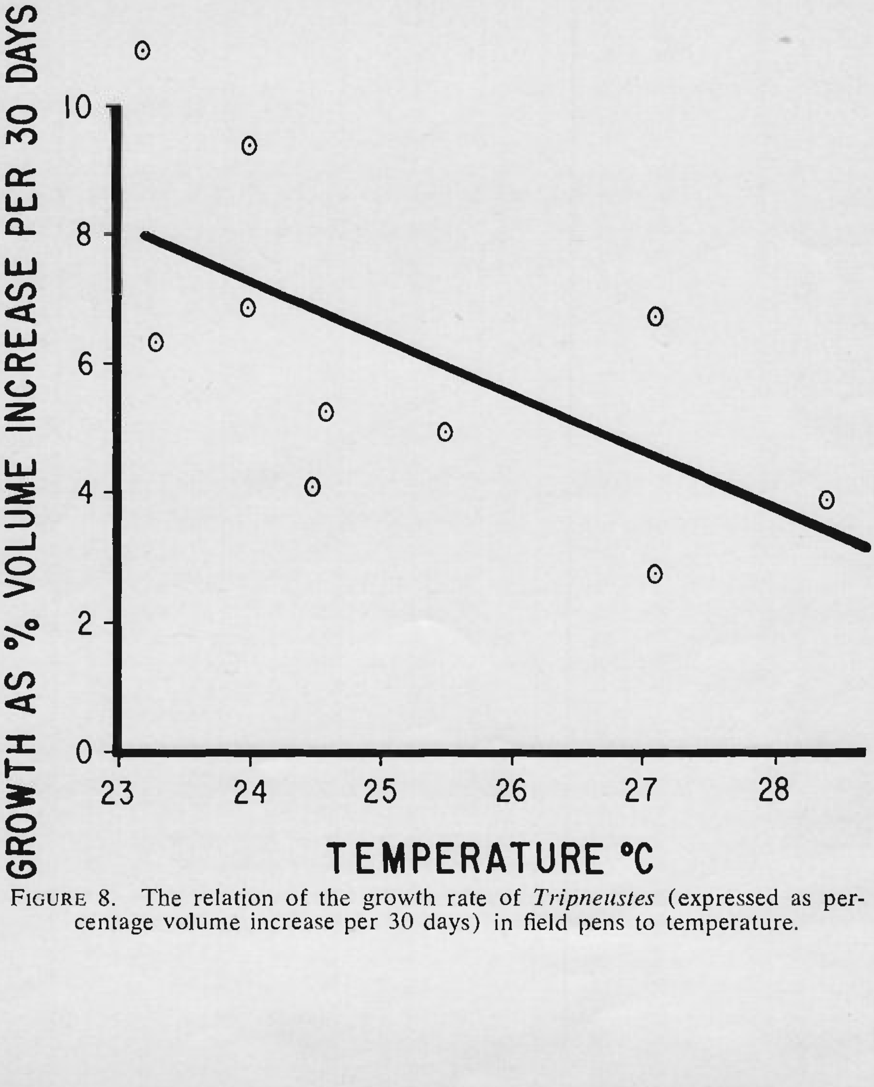

FIGURE 8. The relation of the growth rate of *Tripneustes* (expressed as percentage volume increase per 30 days) in field pens to temperature.

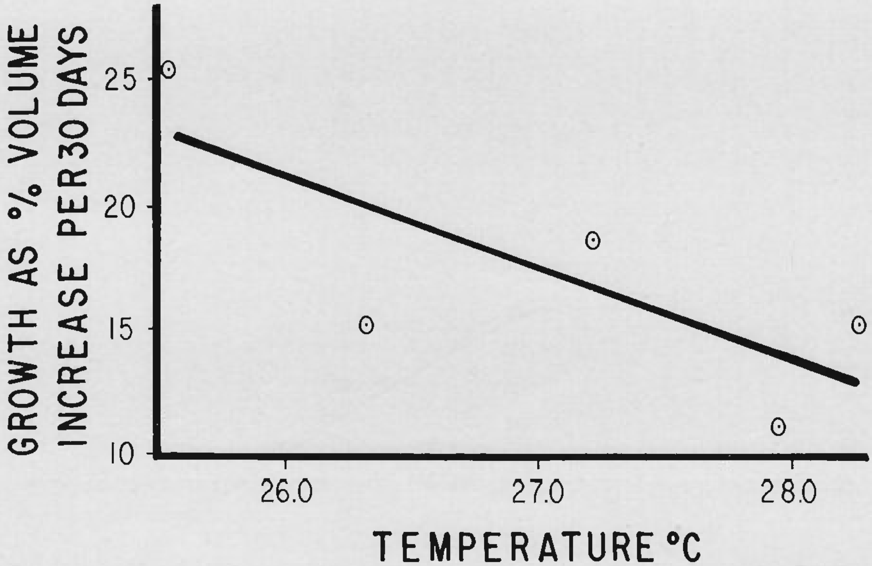

FIGURE 9. An approximation of the relation of growth rate of *Tripneustes* (expressed as percentage volume increase per 30 days) to temperature in Barbados, from Lewis's data.

temperature in tank and pen experiments. The regressions of growth on temperature are −0.53° and −0.88° respectively. Lewis, although he does not give actual temperatures, comments upon the slowing of growth in Barbados in the summer. A tentative analysis of his data, applying temperatures from Lewis, 1960, yields a regression of growth on temperature of −3.71° (Fig. 9), which is greater than the Miami values. However, this is in part due to a correlation in his data between size and temperature, and between growth rate and size.

In *Lytechinus,* it was possible to show the decrease in growth rate of the test at the size at which the gonads commenced to grow. Lewis states that individuals with a test diameter of 20-30 mm had full gonads containing ripe eggs and sperm. No urchins of this size were available at Miami, but the ones taken at Bimini showed only small gonads beginning to develop at test diameters of 38 and 40 mm, and only a trace of gonad below 30 mm. It is probable, then, that growth of the gonads occurs later in the northern populations. Judging from the smallest Miami individuals measured (Fig. 10), gonad development probably commences at a test diameter of about 50 mm. This graph was obtained by taking all the gonad volume $\left(\frac{10.\ G.V.}{T.V.}\right)$ data throughout the year and expressing them as

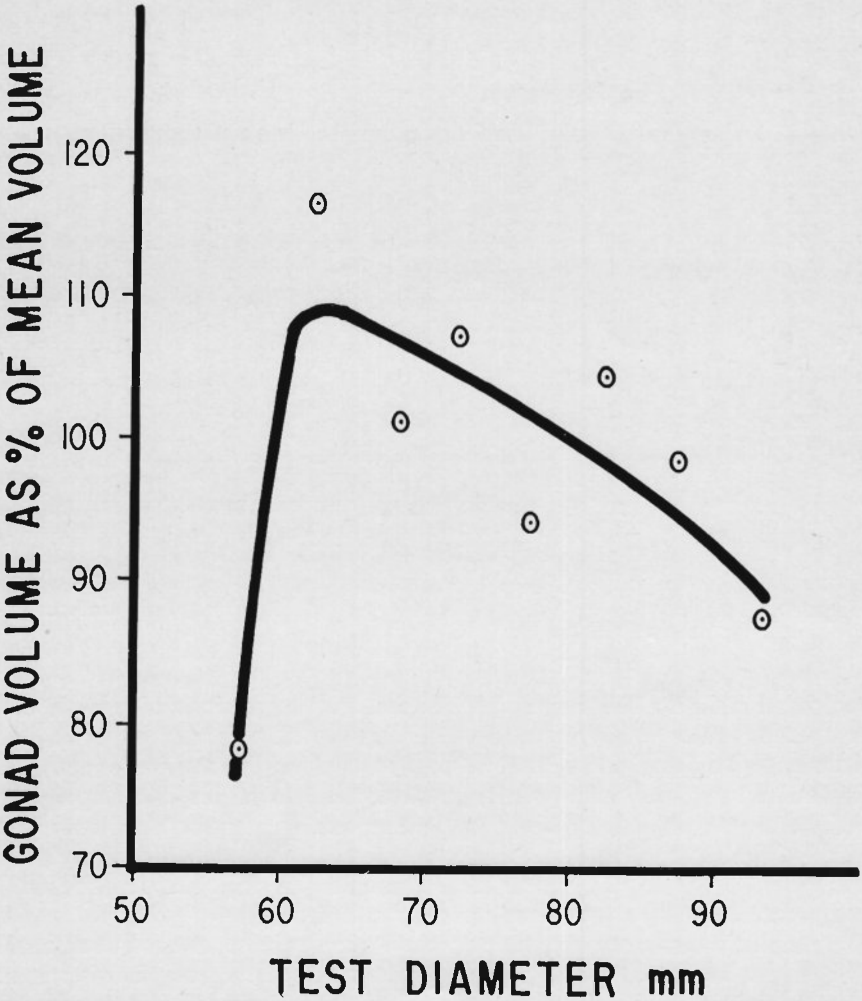

FIGURE 10. The relation of the gonad volume of *Tripneustes*, expressed as $\frac{10.\ G.V.}{T.V.}$, to test diameter. For explanation, see text.

percentages of the mean value for the sample. They were then combined and grouped by test diameter.

The successive spawnings shown in Figure 1 allow a minimal estimate of total spawn output, but do not take into account such spawning as may have been taking place during the periods of build up. The annual output varies considerably in successive years. Expressed as $\frac{10.G.V.}{T.V.}$

it was 1.24, 0.81, and 1.34 in 1959, 1960, and 1961 respectively. Although the gonads were not consistently larger throughout the years in either sex, the annual output was consistently larger in each year in the females. The mean for the three years was 1.07 for the males, and 1.20 for the females, and expressed as a percentage of the maximum gonad volume, the mean output was 114 per cent in the males and 126 per cent in the females.

Food Intake

Some preliminary feeding experiments were carried out in the tanks. Newly collected urchins were kept in the tank for two to four days in running water and provided with an ample supply of clean *Thalassia* whose wet weight was obtained at the start and finish of the test. Further measurements will be needed throughout the year and under better controlled conditions, but the results so far available allow at least a tentative estimate of food requirements.

	Number of urchins	Mean temperature °C	Net weight of *Thalassia* per urchin per day gm
January-March	7	21.4	1.36
March-April	4	23.2	3.16
June-July	10	29.8	4.33

Since there was some variation in the size of urchins used, these data have been normalized to a standard test volume of 250 cc, assuming that food intake is proportional to test volume. Comparable results for *Lytechinus*, if scaled up to a 250-cc urchin, would give an annual mean feeding rate of 7.15 gm dry weight per urchin per day, which is considerably greater than in *Tripneustes*. Further, there was no evidence of a seasonal change in feeding rate in *Lytechinus*. An average of the *Tripneustes* values gives about 3.0 gm wet weight per day, which is equivalent to 0.6 gm dry weight.

A *Tripneustes* with a test diameter of 80 mm would increase in volume about 80 per cent in a year. From determinations, after decalcification, of the dry weights of gonads and of other tissues, this growth would be equivalent to non-gonad tissue production of 1.90 gm, compared with a gonad output of 4.37 gm, or a total of 6.27 gm. The dry weight of *Thalassia* eaten by an urchin this size would be 166 gm per year, so its efficiency would be about 3.8 per cent. This is close to the value of 3.0 per cent obtained for *Lytechinus*. The feeding rate measurements were made in tanks, and growth rates were only about half the field values in these tanks. On the other hand, in the feeding tests the animals were brought straight in from the shore and kept for only two or three days, so probably behaved more normally than those kept in the tanks for long periods. Normal feeding rates might perhaps be faster, in which case the efficiency might be less than 3.8 per cent but probably not as low as half this value.

Hermaphrodites

Studies of the gonads of *Tripneustes* and *Lytechinus* in 1959 showed that a considerable number of hermaphrodites were present. This had never been observed before by us in Bermuda or Miami, or, in the case of *Tripneustes,* by Lewis in Barbados. Hermaphroditism is a very rare occurrence in echinoids in general (Harvey, 1956). More complete studies were made on *Lytechinus,* where it was shown that there was a progression from predominantly male hermaphrodites early in the year to predominantly female ones later. The occurrence of the hermaphrodites was associated with the unusually low water temperatures early in 1958 when the urchins were small and their gonads were just beginning to form. In *Tripneustes* it was noted that, at the end of February, as many as 27 per cent were hermaphrodites and that the majority of these were predominantly male. Normal procedure was to examine a smear from only one of the five gonad sectors. It was found in *Lytechinus* that the hermaphroditism was not always found in all five gonad sectors and that examination of a single sector would locate only 43 per cent of the hermaphrodites. Even this figure is too high, since the condition might be localized in a portion of the section not taken in the smear sample. It is safe, then, to say that more than half the population, and possibly almost all of it, was hermaphroditic.

Sumario

Una Contribucion a la Biologia de *Tripneustes esculentus*

La biología de *Tripneustes* ha sido estudiada durante varios años en Miami y Bermuda. Desova en la primavera y el verano, pero con diferente tipo de desove en años distintos. El primer desove parece estar amenazado por la temperatura y los sucesivos por el aumento de tamaño de las gonadas, que crecen durante la estación. El crecimiento de las gonadas en invierno y su proporción de crecimiento entre puestas está en relación negativa con la temperatura, igual que el crecimiento de la concha. El hermafroditismo fué común en un grupo de un año que se presentó en estado no maduro durante un frío invierno poco corriente. Se ha intentado un estimado de alimento tomado y su eficiencia para convertirse en tejido del erizo.

REFERENCES

Lewis, J. L.
1960. The fauna of rocky shores of Barbados, West Indies. Can. J. Zool., *38*: 391-435

GREENFIELD, L. J.
1959. Biochemical and environmental factors in the reproductive cycle of the sea star *Pisaster ochraceus* (Brandt). Unpublished doctorate thesis, Stanford Univ., 1-143.

HARVEY, E. B.
1956. The American *Arbacia* and other sea urchins. Princeton, Princeton Univ. Press, 1-298.

MOORE, H. B., THELMA JUTARE, J. C. BAUER AND A. C. JONES
1963. The biology of *Lytechinus variegatus*. Bull. Mar. Sci. Gulf & Carib., *13* (1): 23-53.