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ABNORMAL GROWTH PATTERNS IN THE SEA URCHIN *TRIPNEUSTES* CF. *GRATILLA* (L.) UNDER POLLUTION (ECHINODERMATA, ECHINOIDEA)

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Abstract: Two populations of deformed sea-urchins were found in the vicinity of a combined power and desalination plant in the Gulf of Eilat (Aqaba), Red Sea. This area is highly polluted by thermohaline and heavy metal ion effluents. More than 60% of the urchins showed irregular bulging of the aboral half of the test. The height (H) to diameter (D) ratio for the most affected population was 0.70 (±0.15), compared with 0.53 (±0.04) for a normal population, away from the power plant. In extremely deformed individuals the H/D ratio reached 1.4. The deformed sea-urchins had a wider peristome aperture and larger Aristotle's lantern, and fewer interambulacral plates than a normal urchin of the same diameter.

Growth rate of highly deformed urchins in aquaria, under non-polluted conditions, was very low. In 2 months their average diameter increased by only 0.2 mm, compared with 7–8 mm in normal or slightly deformed urchins, under the same conditions.

Growth lines in the deformed urchins' plates indicate excessive growth in the meridional direction which is normally much less. It is suggested that controlled growth was disrupted. Some possible controlling mechanisms are discussed.

INTRODUCTION

The sea-urchin skeleton consists of close-fitting calcium carbonate plates that are added in the apical region. Differential plate growth accounts for the definite form that is characteristic to each species. The morphology of the echinoid test and its variation has been studied by Lovén (1871, 1875), Deutler (1926), Jensen (1969), Pearse & Pearse (1975), and Märkel (1975, 1976). Raup (1968) discussed the test shape and plate patterns and formed a computer simulated model that explains the echinoid growth and plate configuration as a result of two main factors, plate supply rate and the gradient that affects the rate of meridional growth. A wide variety of plate configurations can be achieved by changing these factors.

The biometrical relations in regular sea-urchins have been documented (Mortensen, 1943; Regis, 1969, 1973; Märkel, 1975) and abnormalities in the shape of the echinoid test have been discussed by Koehler (1924) and Jackson (1927) and reviewed by Swan (1966). Additional data on aberrant growth are given by Moore (1974), according to whom many abnormalities result from previous injury and ensuing imperfect regeneration, but others result from metabolic disturbances.

Other abnormal phenomena involve deviant skeletal proportions, especially the relations between test height (H) and ambital diameter (D). Mortensen (1943) observed and illustrated abnormal individuals of *Salmacis bicolor* and *Holopneustes inflatus* with exaggerated H/D ratio resulting from parasitic infection by a snail. Ernst (1973) calculated H/D ratio (L/H in his terminology, which is the reciprocal of H/D) for *Arbacia lixula* and *Paracentrotus lividus* and found that different populations of the same species may have different H/D due to possible environmental factors. Allain (1978) reported a large concentration of deformed *Lytechinus variegatus* from Cartagena Bay, Colombia. About 5% of a total of more than 2000 urchins had skeletal deformations. He believed that oil and wastewater pollution caused the deformations.

Tripneustes cf. *gratilla* (L.) is a large and common sea-urchin in the northern Red Sea. It lives subtidally on protected rocky beaches and reef flats (James & Pearse, 1969). Contrary to other Indo-Pacific localities, in the Red Sea this species prefers the algal covering of boulders and rarely occurs in sea-grass beds, as reported for Indo-Pacific *T. gratilla* (Lawrence, 1975). According to T.A. Ebert (pers. comm.) and data collected by the author, the Red Sea *Tripneustes* differs from the Indo-Pacific *T. gratilla* in some aspects and its taxonomy needs revision. It will hereafter be referred to as *T.* cf. *gratilla*.

In this paper two highly deformed populations of *T.* cf. *gratilla*, probably due to acute pollution, are described. The biometry and the possible deformation mechanisms are discussed.

MATERIAL AND METHODS

AREA STUDIED

The most severely polluted area in the Gulf of Eilat (Aqaba) is near the Eilat harbour, in the vicinity of a combined power station and desalination plant (Fig. 1). The discharged water effluent is thermohaline (39 °C and $S = 46‰$) and shows high concentrations of dissolved copper and iron (Dafni, 1974a,b). Occasionally, during cleaning of the pipe system, acidic water is discharged, which may contain up to 70 mg/l dissolved iron and 30 mg/l copper as well as residual organic compounds, applied to reduce calcite precipitation in the system. Hydroxides of iron and copper precipitate in the sea around the outlet (Lev-er *et al.*, 1976). As the effluent is denser than sea water, it spreads along the bottom and is carried southwards by the prevailing southerly surface current. This effluent affects the sublittoral fauna for a distance of 200 m to the south, and to a depth of 12 m (Dafni, 1974a). It creates an almost sterile area, 70 m wide, opposite the discharge point, only invaded by fish schools. The conditions improved 2 yr ago when measures were applied to reduce the pollution. The sea-urchin populations now being studied were probably established following this improvement.

From the outlet for a distance of 200 m southwards there are suitable substrata for sea-urchins. From 200 m to 1000 m southwards the beach consists of non-consolidated gravel, which does not offer a suitable substratum for sea-urchins. Northwards and further than 1000 m southwards the beach consists of boulders and beachrock and is populated by sea-urchins.

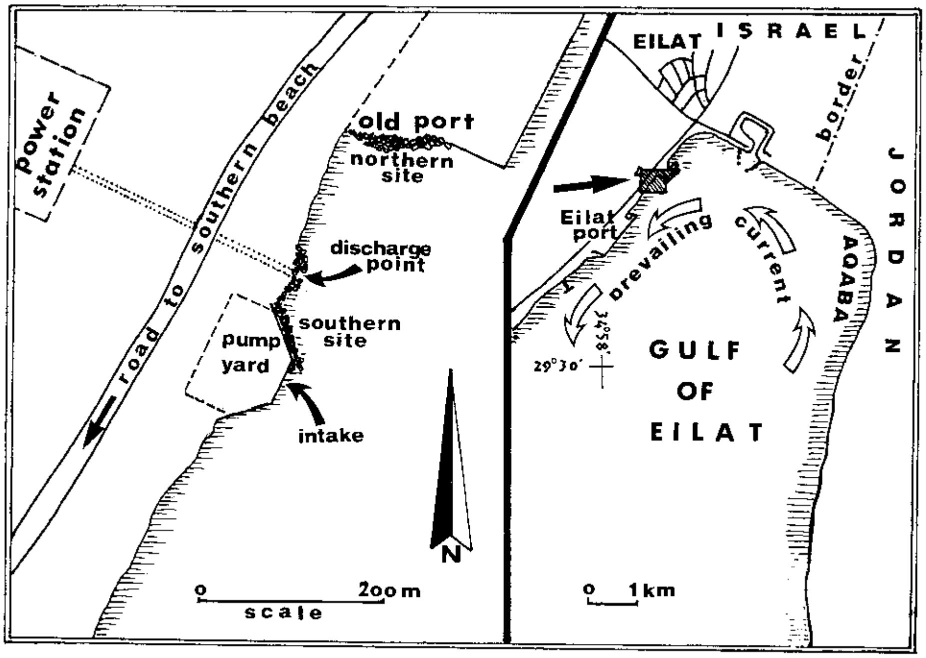


Fig. 1. Map of the northern Gulf of Eilat (Aqaba), showing the polluted area and the location of the affected populations, the northern and southern sites: the non-affected sea-urchins were collected from the southern beach, not included in the map.

MATERIAL

Two populations of *T.* cf. *gratilla*, showing a high degree of skeletal deformation, were found in the subtidal zone at a depth of 1–3 m on either side of the discharge point (Figs. 2, 3). The first population was found 60–120 m south of the discharge point. Until 11 May, 1979, when an acid spill killed all the sea-urchins in this locality, dense populations of the three common species were found here: *Echinometra mathaeii* (Blainville), *Diadema setosum* (Leske), and *Tripneustes* cf. *gratilla*. Only the third species showed such deformations. The second *Tripneustes* population was living on boulders bordering the old port, only 150 m north of the discharge point. The two populations were separated by a sterile zone.

For the purpose of comparison, urchins were also examined at other localities, 1–12 km south of the power station.

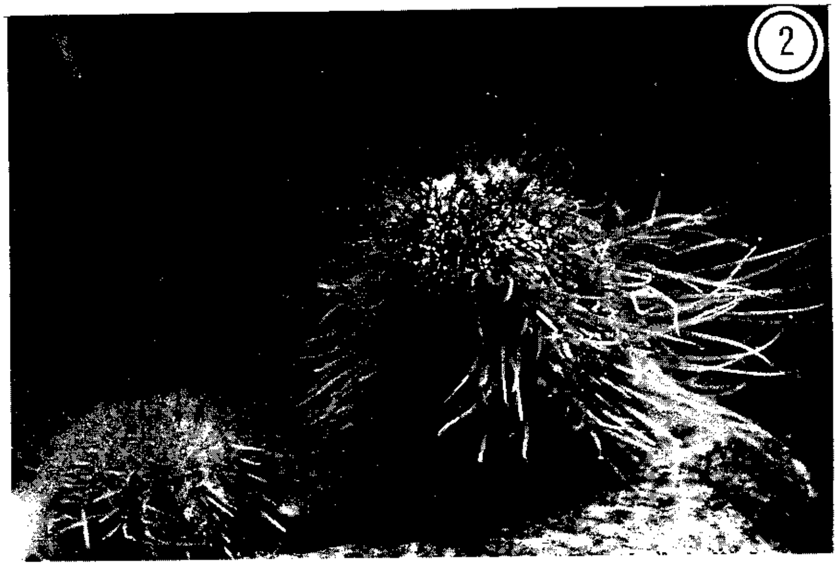


Fig. 2. Two living *Tripneustes* cf. *gratilla* with the same ambital diameter (27 mm): right, a highly deformed sea-urchin from the southern site, with H/D ratio of ≈1.3; left, a normal urchin from a non-polluted environment, with H/D of 0.53.

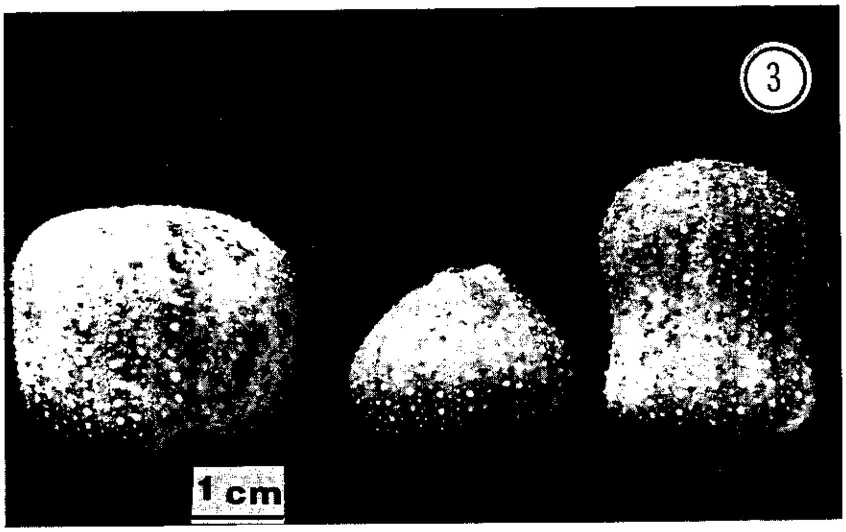


Fig. 3. Three skeletons from the southern population, demonstrating the bizarre shapes of the deformed urchins.

FIELD OBSERVATIONS AND MEASUREMENTS

Test ambital diameter (D) and test height (H) of 117 randomly collected living individuals of *T.* cf. *gratilla* from the southern population, 95 from the northern population, and 139 from other localities were measured using venier calipers with a precision of 0.1 mm. For an estimate of the diameter, the average of five measurements for each individual was used. The single largest value was used in height. The H/D ratio was calculated in order to demonstrate abnormalities in the test shape.

LABORATORY GROWTH EXPERIMENTS

Living sea-urchins were transferred to tanks with running water in the H. Steinitz Marine Laboratory under non-polluted conditions. The water temperature in the tanks varied between 24–26 °C, the ambient sea-water temperature in summer. The sea-urchins fed by scraping encrusting algae off stones that were frequently supplied.

The following groups of sea-urchins were kept in different tanks during a period of 2 months, from 27 May to 27 July, 1979.

(1) Group 1, 10 highly deformed sea-urchins from the southern population, with a mean H/D ratio of 1.02 at the beginning of the experiment.

(2) Group 2, 29 sea-urchins from the northern population, only slightly deformed, with an initial mean H/D ratio of 0.60.

(3) Group 3, 9 urchins from a non-polluted area (near the Marine Laboratory), with an initial H/D ratio of 0.53.

After the final measurements most of the animals were maintained in the tank and further data were recorded.

BIOMETRICAL DATA

Two days after the lethal spill on 11 May, 1979, ≈300 skeletons of *Tripneustes* from the southern population were collected at random. Measurements of test diameter, height, peristome and Aristotle's lantern were made together with counts of plates and other observations for a biometrical analysis.

PLATE MICRO-STRUCTURE

Growth lines of single plates, whole ambulacral (A) and inter-ambulacral (IA) plate rows of normal and deformed sea-urchins were examined following the technique described by Pearse & Pearse (1975). Cleaned plates were charred for 10–20 min at 300–350 °C in a furnace and then immersed in xylene and embedded in Canada Balsam. Since Red Sea *Tripneustes* has only a few small spine tubercles no grinding of the plates was necessary for skeletons up to a diameter of 50–60 mm.

RESULTS

FIELD OBSERVATIONS AND MEASUREMENTS

Measurements of H/D ratio of living *T.* cf. *gratilla* are shown in Table I. The population from the most polluted southern site showed an abnormally high H/D, up to 1.40 in individual cases. In this work only urchins with H/D >0.6 are considered abnormal or deformed. The mean H/D ratio for sea-urchins of the southern population was 0.70 with a high SD (0.15). The northern population showed a lower mean H/D (0.59) and contained a smaller number of deformed urchins. Since the H/D ratio varied differently in the populations, a non-parametric analysis (Kruskal & Wallis, 1952) was applied to test the difference between the H/D ratios of the populations. It was found to be significant at $P < 0.01$. Fig. 4 shows the

TABLE I

Test height to diameter ratio (H/D) for sea-urchins from various populations, mentioned in the text: N = number measured.

Population	N	Mean H/D and SD
Southern population	117	0.70 (± 0.15)
Northern population	95	0.59 (± 0.06)
Other localities	139	0.53 (± 0.04)

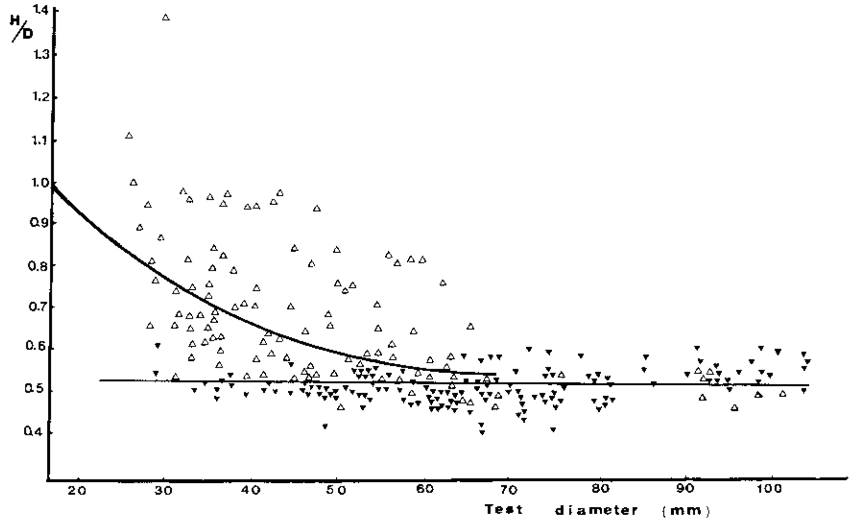


Fig. 4. The relation between H/D ratio and test diameter for 117 sea-urchins from the southern population (▼) and 139 from other, non-polluted localities (△).

relation between test diameter and H/D of the southern population and sea-urchins from non-polluted localities and a wide range of individual H/D values.

The correlation between H/D as a function of diameter for the southern population was $r = 0.57$, which is significant at $P < 0.05$. Urchins from non-polluted localities showed a constant H/D ratio at all sizes, although a small increase is noted for urchins >70 mm. The regression slopes merged at ≈70 mm. From Table II it may be seen that in the southern population up to 94% of the urchins at the size of 25–35 mm showed abnormal H/D, while at >65 mm all the urchins had normal H/D ratio. Irregularities not expressed in H/D ratio were, however, not uncommon in larger urchins' tests.

TABLE II

Relative frequency (%) of the H/D ratio for various size groups in urchins from the southern population: N = number measured.

Test diameter (mm)	N	Non-deformed (H/D = 0.4–0.6)	Slightly deformed (H/D = 0.6–0.8)	Highly deformed (H/D > 0.8)
25–35	33	6.1	54.5	39.4
35–45	27	18.5	48.1	33.3
45–55	21	33.3	47.6	19.0
55–65	22	50.0	36.4	13.6
>65	14	100.0	0	0
Entire population	117	33.3	41.9	24.8

Similar results were observed also for the northern population, although not presented here.

GROWTH EXPERIMENTS

Results from the growth experiments are summarized in Table III. Group 1 (highly deformed sea-urchins from the southern population) showed no significant

TABLE III

Diameter size (mm) and H/D change in urchins from various populations during 60 days in non-polluted conditions: for key to groups see text; N = number measured.

Group	Population	Initial measurements (27 May)			Final measurements (27 July)		
		N	Diameter ± SD	H/D ± SD	N	Diameter ± SD	H/D ± SD
1	Southern	10	36.84 (9.08)	1.02 (0.17)	10	37.06 (9.36)	1.05 (0.18)
2	Northern	29	37.53 (7.04)	0.60 (0.07)	29	44.64 (5.26)	0.59 (0.05)
3	Marine laboratory	9	39.67 (6.30)	0.53 (0.01)	7	47.25 (3.65)	0.54 (0.03)

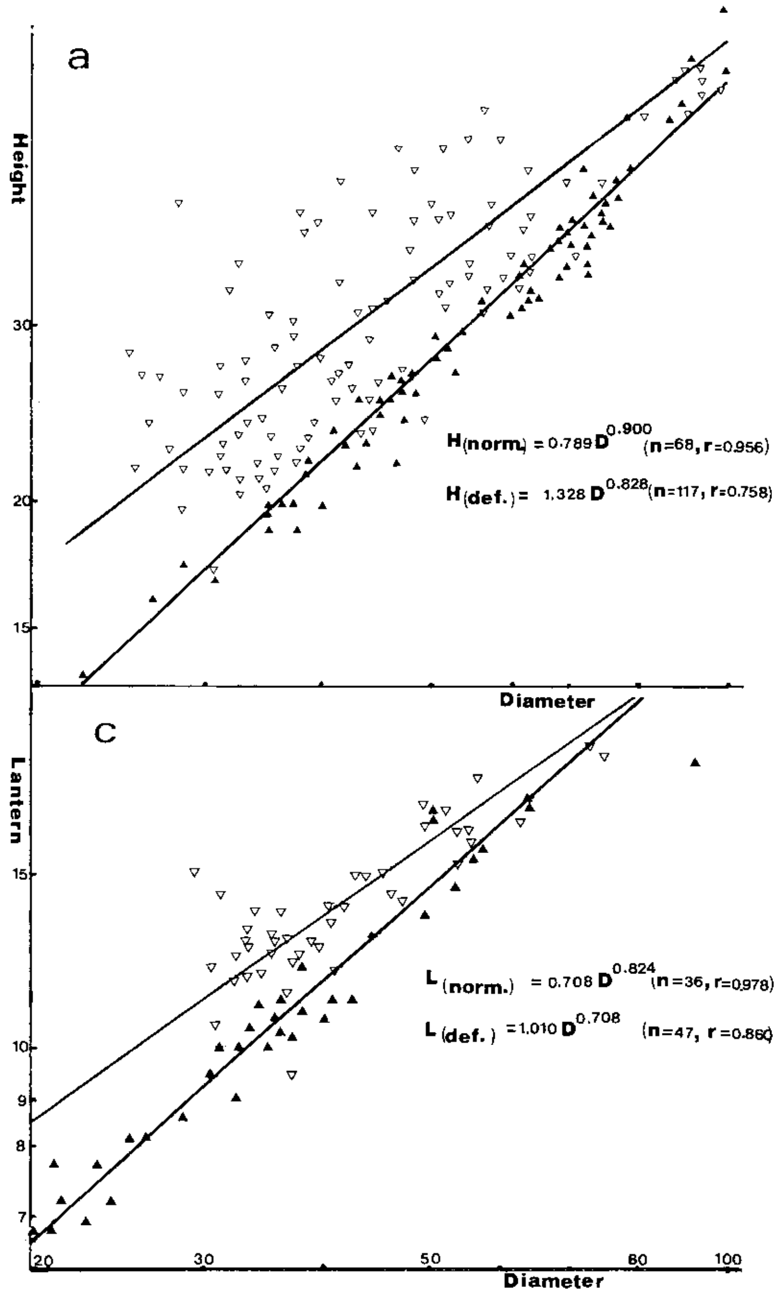
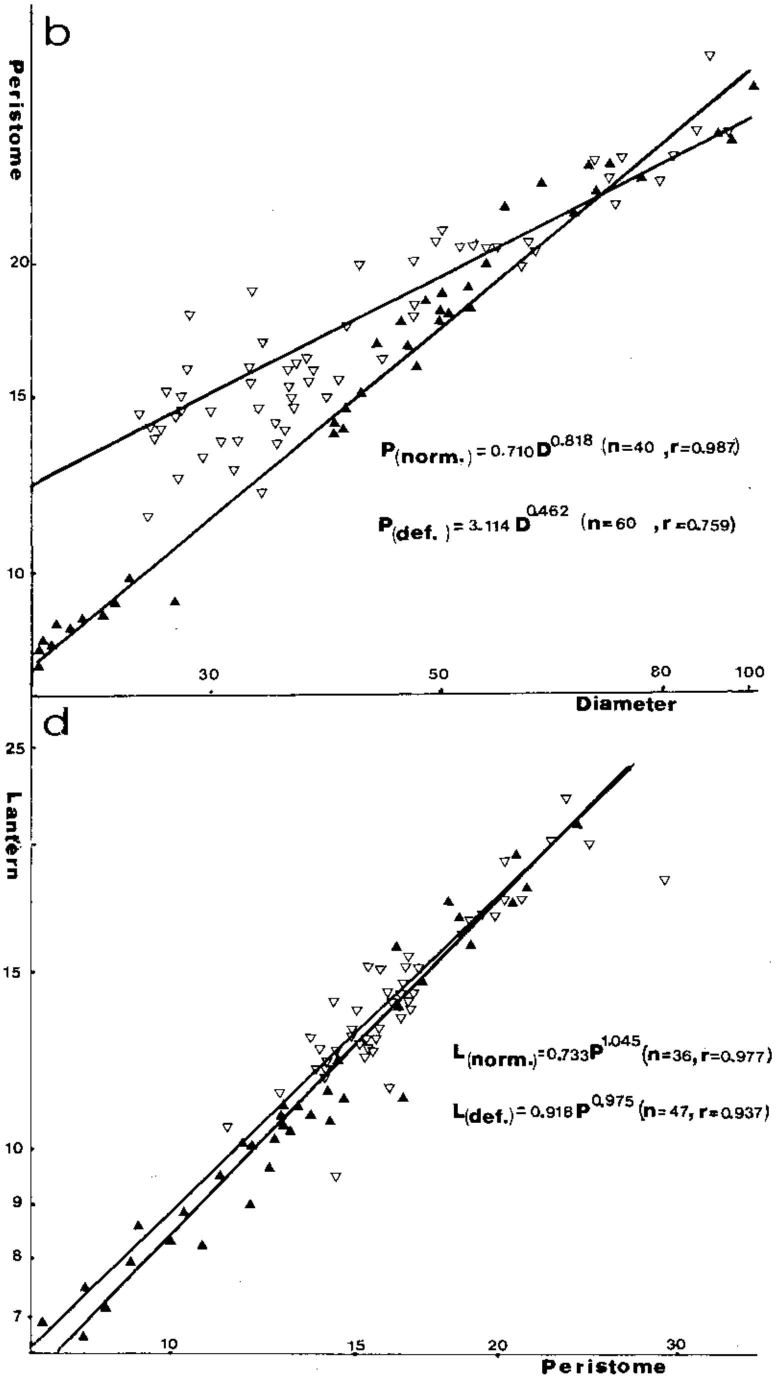


Fig. 5. Regression lines for the allometrical relations (log scale) between diameter (D), height (H), peristome (P), and lantern (L) for sea-urchins from the southern population (▽) and from other, non-polluted localities (▲): all sizes are in mm.


b
Peristome
20
15
10
30
50
80
100
Diameter
P(norm.) = 0.710 D^0.818 (n=40 ,r=0.987)
P(def.) = 3.114 D^0.462 (n=60 ,r=0.759)
d
Lantern
25
15
10
9
8
7
10
15
20
30
Peristome
L(norm.)=0.733P^1.045 (n=36, r=0.977)
L(def.)= 0.918 P^0.975 (n=47, r=0.937)

growth in test diameter (t-test, $P > 0.5$) even after removal from the polluted environment. (This result was also confirmed by further measurements. On 4 October, 4.5 months after the experiment had started, Group 1 urchins had a mean diameter of 37.7 mm, an average increase of only 1 mm.) The mean H/D ratio of the test of these animals increased, non-significantly, from 1.02 to 1.05. Group 2 (less deformed urchins from the northern population), showed a significant increase in diameter, similar to the growth rate observed in the non-deformed population (Group 3) ($P < 0.05$). The H/D did not change in either of the groups.

BIOMETRICAL DATA

The biometrical relations between various parts of an animal's body are often described by the allometry equation (Teissier, 1960):

$$Y = AX^{B} \tag{1}$$

or by its logarithmic transformation

$$\ln Y = B \ln X + \ln A \tag{2}$$

B, the exponent, or slope of equation (2) was used by Regis (1969, 1973) as the allometry constant (α), while $\ln A$ ($\ln Y$ when $\ln X = 0$) is the initial growth index.

The allometrical constants for the relations between ambital diameter and height, peristome and Aristotle's lantern diameters were calculated for sea-urchins from the southern population, deformed and non-deformed, and for urchins from non-polluted localities (Fig. 5). It was suggested by Ricker (1973) that in regressions, in which both categories are measurements subjected to errors, the use of the functional regression slope, B/r, is more suitable for the description of the relationship between them (r is the correlation coefficient). A covariance analysis (Snedecor & Cochran, 1967) was used to test the homogeneity, the differences between the allometrical constants (slopes) and the elevations for each pair.

From Fig. 5 it can be seen that the allometrical proportions for a normal population are similar. Nevertheless, some noticeable differences should be mentioned. Regression slope of peristome-diameter (Fig. 5b) for normal urchins is flatter than the slope of height-diameter (Fig. 5a). This is mainly due to the lesser expansion of the peristome compared with the diameter growth. It was found that for a young normal urchin (D = 10 mm) the peristome/diameter ratio is 0.45, and for an old urchin (D = 70 mm) it is only 0.3.

The isometric lantern-peristome growth in normal urchins can be seen from their similar slopes (Figs. 5b, c) ($B/r = 0.824$ and 0.818, respectively) and from Fig. 5d. As for the deformed urchins, except for the afore-mentioned excessive height to diameter ratio (Fig. 5a) a large peristome (54% of the test diameter) is shown (Fig. 6). Peristome-diameter slope (Fig. 5b) is lowest ($B/r = 0.462$). The lantern of a deformed urchin is also significantly larger than shown for the normal (Fig. 5c), although not as large as the peristome (Fig. 5b). Lantern to peristome growth was, however, found to relate isometrically for both populations (Fig. 5d).

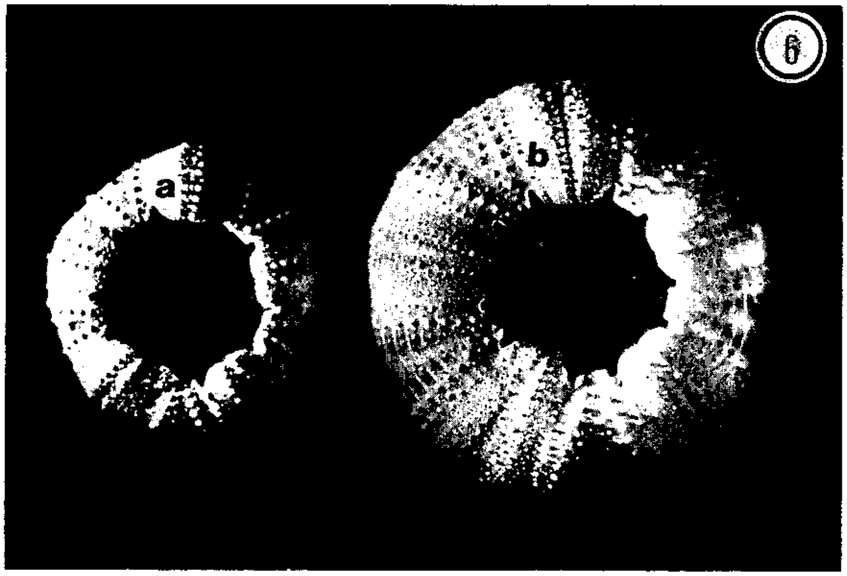


Fig. 6. Oral view of a deformed (a) and a normal (b) sea-urchin with the same peristome size (15 mm): peristome/test diameter ratio for the normal urchin is 0.38 and for the deformed urchin it is 0.54.

Since covariance analysis between groups assumes equal homogeneity within each pair, the high variance of the deformed population's data rendered this analysis non-significant for Figs. 5a, b, c. In the light of the observation that highly deformed urchins stop growing in the horizontal axis (Table III), for a considerable time, the last mentioned facts may imply that peristome and lantern growth continued unaffected.

NUMBER OF INTERAMBULACRAL PLATES

In all regular sea-urchins the number of interambulacral and ambulacral plates increases with age and is proportionally related to size. Fig. 7a shows counts of the IA plates of normal *T.* cf. *gratilla* from non-polluted localities and from the southern population, plotted against their test diameter. Normal urchins showed a straight line for animals up to 70 mm, >70 mm the slope was steeper. This last-mentioned observation will be discussed below. Southern population urchins, both with abnormal and normal H/D ratio formed a significantly different slope ($P < 0.01$). Thus, small deformed urchins had 1–2 fewer IA plates than normal animals of the same diameter size.

For deformed sea-urchins diameter is a poor indicator of age, because of its much reduced growth rate. In this case the peristome may show a better correlation with age, in the light of its presumed unaffected increase. Therefore, IA plate number was plotted against peristome size (Fig. 7b). It appears that small deformed urchins show 3–4 fewer plates than normal urchins with the same peristome size ($P < 0.01$).

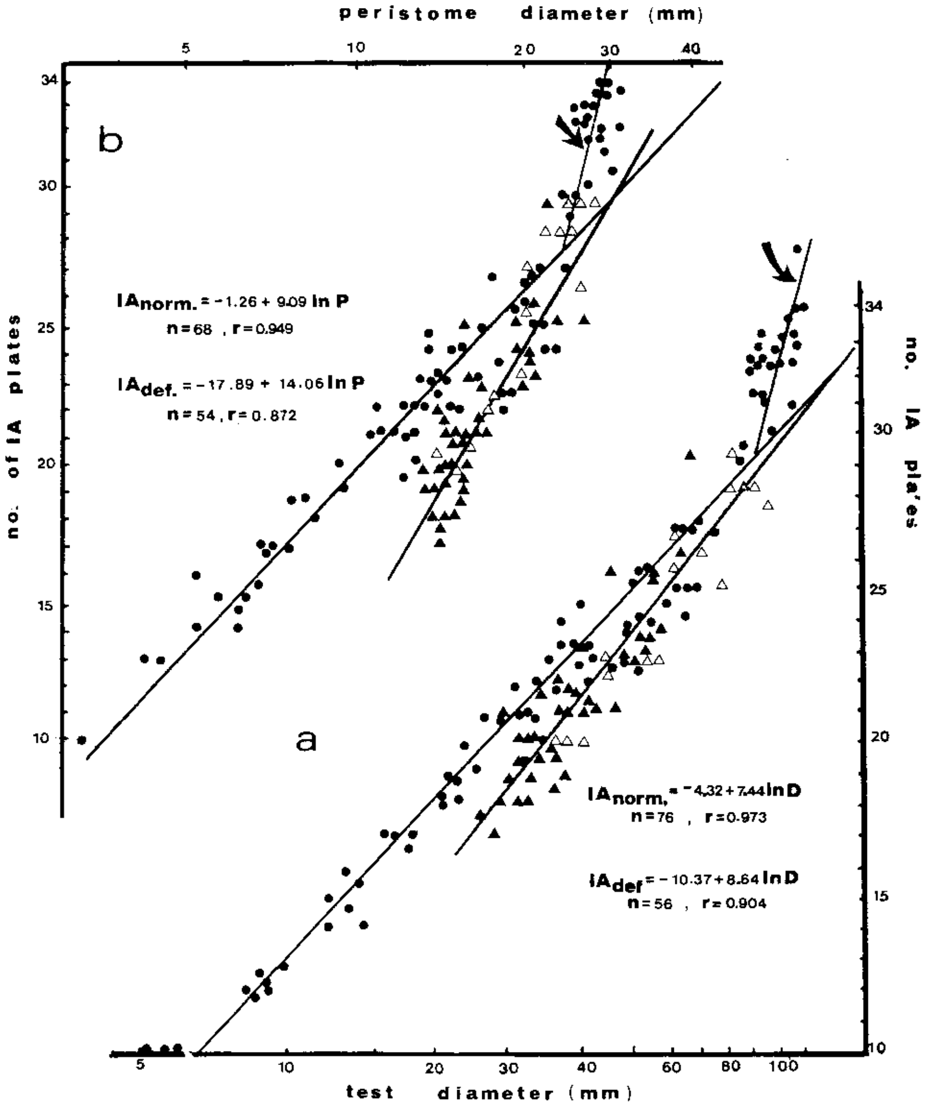


Fig. 7. Relation between number of interambulacral plates and (a) test diameter or (b) peristome diameter, for urchins with normal (△) and abnormal (▲) H/D ratio from the southern population, and for urchins from non-polluted populations (●): arrows point to a tendency shown by normal larger urchins to add IA plates with only a slight increase of the diameter.

OTHER TEST DEFORMATIONS

In addition to the abnormalities mentioned above the skeletons of deformed urchins collected in the polluted area showed many other irregularities.

(1) There were irregularities in the shape and symmetry of IA plates, mostly in the aboral region. Some plates had secondary sutures that divided them, while other IA plates had their latitudinal sutures twisted and joining a parallel suture (Fig. 8). Some plates were completely fused with the neighbouring plates by omission of one or several sutures.

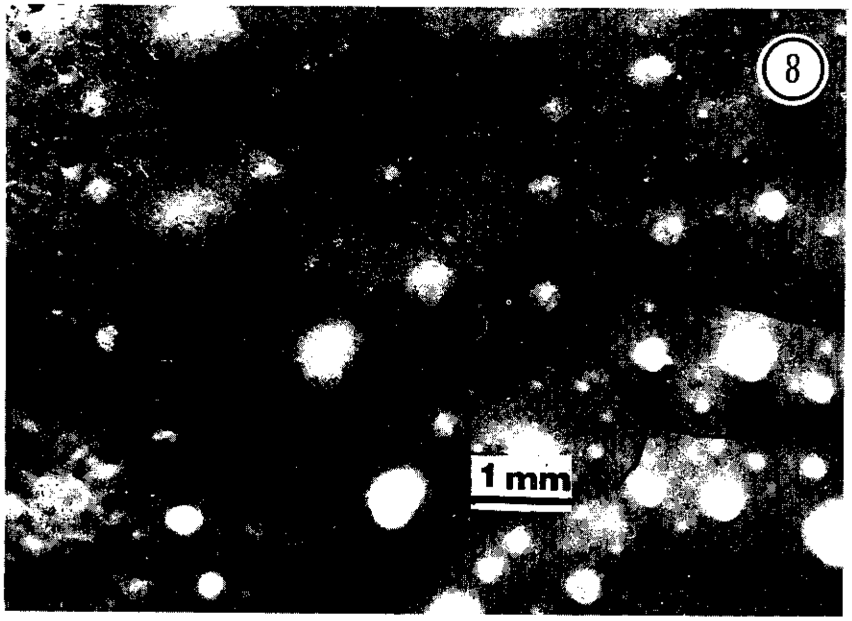
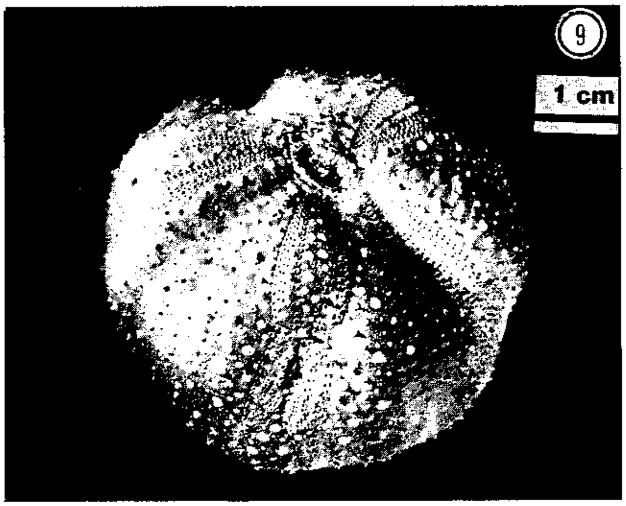
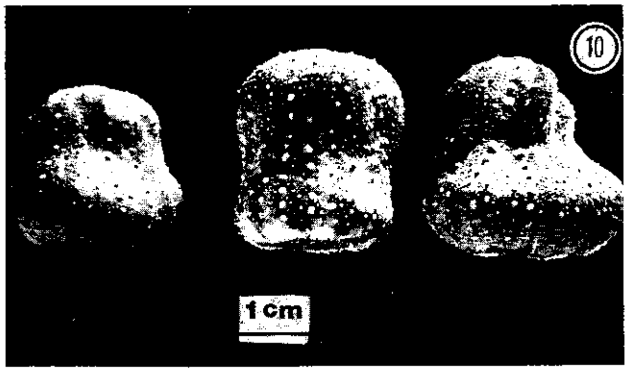


Fig. 8. Interambulacral plates of a highly deformed sea-urchin, showing a latitudinal suture bending and joining a parallel suture, while the adjacent plate meets in the interradial suture 3 plates: to the left, the irregular shape of the ambulacral plates can be seen (suture lines were drawn over with Indian ink).

(2) Ambulacral plates were often deformed and the pore rows were shifted in their position towards each other (Fig. 9), described by Moore (1974) as "pinching". This phenomenon was common and was also observed in older sea-urchin tests that did not show an abnormal H/D ratio. Pinching usually occurred in more than one A plate row and often in the same horizontal level. In some old urchins pinched A plates were found near the peristome margin.

(3) Most deformed tests showed a clear differentiation into an almost non-deformed oral half and a highly deformed aboral half, usually inflated or otherwise displaying the aforementioned irregularities. The oral half was more symmetrical and often retained what appears to be an early ambitus (Fig. 10). Some deformed





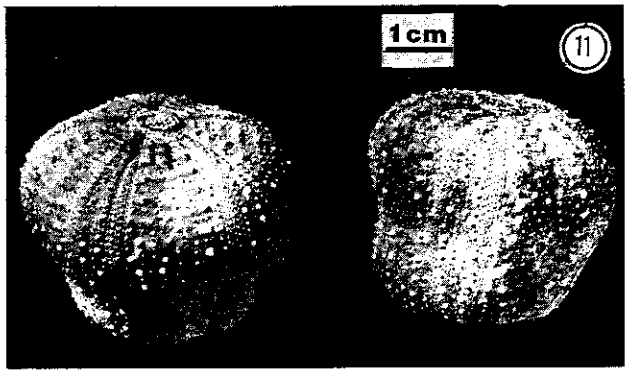


Fig. 9. A highly deformed test ($H/D > 0.8$), with irregularities of the ambulacral plate rows: pinching of the ambulacral system can be noted in the centre of the picture.

Fig. 10. Deformed urchins displaying an early ambitus: note that the irregular growth appears as superimposed aborally above an oral half of the test that retains the normal shape.

Fig. 11. Two deformed tests: they are aborally wider and had developed a secondary ambitus; note that the aboral half is almost perfectly regular, probably due to recovery from the preceding deformed growth; this can also be deduced from the irregularities in the transition zone (right).

sea-urchins had developed a new ambitus with a narrow transition zone, as shown by the middle urchin in Fig. 10. In the transition zone pinching of the A system was rather common.

(4) Some test shapes suggest that there may have been recovery from the deformation. The upper half of some tests showed normally arranged plates and a distinct transition zone that showed pinching and other irregularities, indicating earlier deformation (Fig. 11). The pinching, shown by older, non-deformed urchins in the peristome margin, may thus result from earlier slight deformation and recovery. In sea-urchins that show such signs of recovery the IA plate count is usually higher than in deformed urchins of equal diameter size.

(5) Deformed sea-urchins show fewer spines in the aboral region, and the spines are usually smaller.

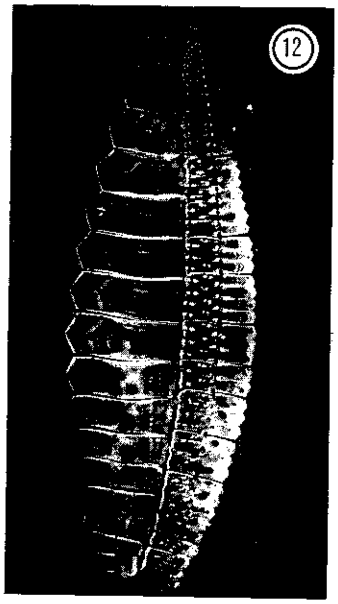
PLATE MICRO-STRUCTURES

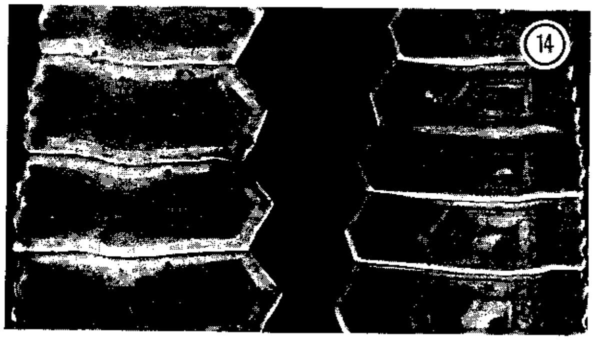
The technique of charring and immersing in xylene revealed, in transmitted light, a distinct pattern of natural concentric growth zones (Fig. 12). Jensen (1969) and Pearse & Pearse (1975) correlated such growth zones with seasons and periods of different food conditions, and found them to consist of different trabecular mesh size.

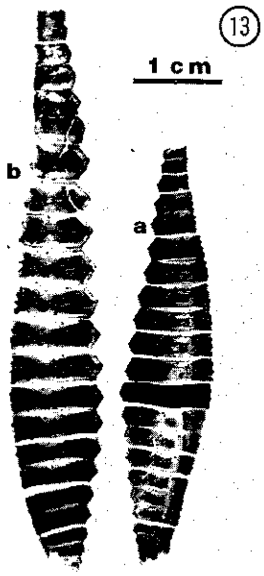
In normal *T.* cf. *gratilla* IA plate rows the growth lines form complete polygonals only in the upper plates. Below a certain level this pattern is interrupted by translucent triangles that develop in the meridional edges of each plate. The distance from a given growth line to the nearest plate edge, well represents the growth increment in that direction, since that line was formed. For each IA plate it can be seen that the maximal growth was directed towards the interradius (the middle suture of the IA row). A somewhat smaller growth rate was shown in the adradial direction (towards the ambulacral plates). A noteworthy growth gradient was seen in the meridional axis. Below the 5–8 upper IA plate level there was only a much reduced growth.

Fig. 13 shows IA plate rows of normal (Fig. 13a) and deformed (Fig. 13b) sea-urchins of almost equal diameter size. In the latter, the growth zones are less conspicuous and IA plates from below the 5–8 upper plate level were observed that show a continuous translucent growth ring surrounding the plates (Fig. 14, left). This ring pattern, that indicates equal accretion in both the meridional and the latitudinal directions, was preceded by a normal growth pattern comparable with the growth pattern of a normal urchin (Fig. 14, right). The abnormal growth pattern is seen mainly in the superambital region.

Abnormal growth in the meridional axis was also observed in the ambulacral system of deformed urchins, causing considerable distortion of the plates (Fig. 15). Growth was not limited to the border with the adjacent plates but also occurred in the demiplate sutures, which under normal conditions are not active. Such abnormal







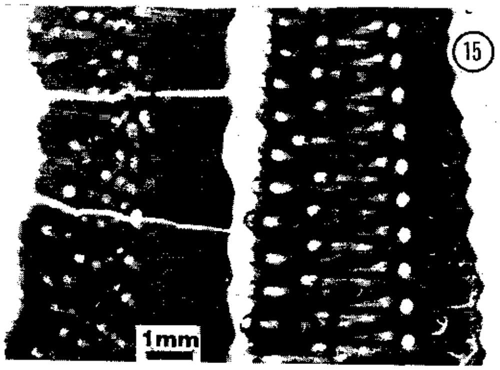


Fig. 12. Interambulacral and ambulacral plate rows of a normal *T.* cf. *gratilla* after charring and xylene immersion: the picture was taken in transmitted light and the translucent triangles and growth lines can be seen.

Fig. 13. Interambulacral plate rows of (a) normal and (b) deformed urchins with a diameter of 51 and 50 mm, respectively (upper 1–2 plates are missing): in the normal urchin meridional growth is mainly concentrated in the 5–8 upper plates while in the deformed one meridional growth zones can be detected 12–13 plates below the apex. The oral plates in both urchins are similar.

Fig. 14. Plates Nos. 11–14 of the deformed urchins and Nos. 8–12 of the normal urchins illustrated in Fig. 13 (counted downwards from the apex), are shown to illustrate the excessive growth in the meridional axis in the deformed urchin (left).

Fig. 15. Ambulacral plates of (a) normal and (b) deformed urchins: normal plates are narrow and densely packed, while deformed plates indicate uncontrolled growth along the meridional sutures; such growth can be also seen along the demiplate sutures (arrows).

growth was observed all along the A row. The oral side of the test was, however, less affected.

DISCUSSION AND CONCLUSIONS

Skeletal abnormalities in sea-urchins were often reported and described as sporadic phenomena, resulting either from genetic failures or from damage by predators and parasites. None of these factors is shown in this particular case to cause the deformations described here. The following evidence seems to point to pollution. The two deformed populations of *T.* cf. *gratilla* were inhabiting the sublittoral boulder zone on either side of the power plant, and were exposed to the same environmental disturbances created by it.

Although situated only 200 m apart, recolonization of the southern site from the northern population, after the spill, was not observed for more than 6 months. The sterile zone probably prevented the migration along the shallow beach and the movement along the sandy bottom at greater depth was also unlikely. Larval recruitment that had been observed elsewhere, evaded this site and introduction of newly settled young urchins from non-polluted localities, resulted in their total disappearance. One individual sea-urchin, however, was found to have lived in the southern site from November 1979 to January 1980, when it was collected. This single observation can prove that once adult urchins entered this area their survival was feasible.

The observation that the most affected population was situated south of the discharge point, down current, while the northern population was less affected and survived the fatal spill, points towards the effluent as the probable cause of the deformations. Some constituents of this effluent are at present being tested for harmful effects on sea-urchins.

The highly deformed urchins showed little increase in their diameter for a considerable time (Table III). Horizontal growth on the aboral side was, however, observed to form a new ambitus. In some animals this even exceeded the diameter of the lower, original ambitus. The high H/D ratio and the horizontal growth of the upper ambitus proves that growth in the deformed urchins did not stop altogether, but it was resumed with an aberrant growth pattern. The H/D ratio of deformed sea-urchins was higher for small animals and lower for larger ones. As it is known for many regular urchins, including *Tripneustes*, that growth rate is inversely related to size (Ebert, 1975) it is suggested that the degree of deformation is a function of a growth potentiality which is maximal for small animals and minimal for animals in their ultimate size. Larger urchins did not develop abnormal H/D ratio because their growth, even under normal conditions is very slow.

Allometrical data used here (Fig. 5) to demonstrate the aberrant growth pattern typical of the deformed urchins, should be interpreted with care. For normal populations allometry is used to describe the growth pattern that is followed by the average individual. In the deformed population it displays, however, the amount of deviation from the normal proportions. Convergence of two such regression slopes, therefore, does not predict that at a certain size the deformed animal will return to the normal proportions, it only shows that animals at this size do not deviate from the normal growth pattern. The heterogeneity shown by the deformed urchins, as far as allometrical data are concerned, probably reflects individual differences in response to the pollution.

The peristome and the lantern probably continued normal growth during the deformed growth period, hence the higher peristome to diameter and lantern to diameter ratios in deformed urchins. From these observations a tentative estimate as to the time that had elapsed since the deformation started to the time of the urchins death (in the spill) can be attempted. Let us consider the two urchins illustrated in Fig. 6, with an equal peristome size (15 mm), assuming equal peristome increase for both and no horizontal growth in the deformed urchin. Thus, the deformed urchin (Fig. 6a), maintains the common diameter at the beginning of the deformation (27.5 mm), while the normal urchin (Fig. 6b) displays the final diameter, that the deformed urchin failed to reach (39 mm). Hence, the elapsed time corresponds roughly to a normal urchin's growth period between 27.5–39 mm. A diameter increase of that amount is reached by *T.* cf. *gratilla* in 2–3 months (Dafni, in prep.). Although merely speculative, this estimate was later confirmed by direct field observations. On 18 November, 1979, only one living individual, a non-deformed albinistic sea-urchin, was seen at the southern site. On 15 January, 1980, almost 2 months later, the same individual was recaptured, and was found to be deformed, with a H/D ratio of 0.88.

A problem, raised by the wider peristome of the deformed urchin, is whether peristome expansion is achieved through plate resorption or by relative displacement of the plates near its margin. In the literature this problem is unsolved and there are contradictory observations for different sea-urchin species. Lovén (1871, 1875) for *Strongylocentrotus droebachiensis* and Deutler (1926) for *Echinus esculentus*, showed that some plates are eliminated by resorption. The same was observed for cidarid urchins by Agassiz (1904) and Cutress (1965). On the other hand, in *Arbacia* there is no A plate resorption and negligible resorption of IA plates (Märkel, 1976). Moreover, Kobayashi & Taki (1969) demonstrated by tetracycline labelling of *Strongylocentrotus intermedius*, visible in UV light, that slow latitudinal growth continues even in plates on the oral side.

As the peristome growth of deformed *T.* cf. *gratilla* is not accompanied by diameter increase, it should be attained either by substantial resorption at the peristome margin or by downwards bulging of the peristome. Such bulging was observed in many individuals, but others still maintained their flat oral area, thus suggesting resorption. Their lower IA plate count (Fig. 7) may, therefore, result either from excessive resorption at the oral area or from reduced plate addition at the apex. As no conclusive answer to this problem can yet be offered, neither possibility should be rejected.

According to Raup's model (Raup, 1968) the echinoid test growth can be described as a result of two main factors, new plate addition rate and meridional growth gradient. Normal *Tripneustes* growth conforms well with this model, but observations show that minor changes in the H/D ratio may result from partial independence between growth factors. Normal urchins, >70 mm show a high number of IA plates, compared with size (Fig. 7). This may result from continuous plate addition, even after the ultimate size has been reached. It appears that growth at this stage is limited to the aboral region, and this probably accounts for the somewhat higher H/D ratio of larger urchins (see Fig. 4). Higher H/D ratios for larger sea-urchins were also reported by Ernst (1973) for *Arbacia*.

In addition, Raup showed that most echinoid skeletal plates are shaped in patterns typical of "close-packing" due to probable stress that exists between them and the neighbouring plates. He also suggested "that growth occurs around the periphery (of the plate) and is concentrated in those regions where pressure counter to this growth is lowest". He also concluded that the "growth gradient is a result of change of stress inhibiting growth".

It has been shown (Fig. 12), that IA plates shape in *T.* cf. *gratilla* varies from the almost square shape, of the uppermost plates, to the compressed appearance they assume near the ambitus. While a considerable increase occurs in the latitudinal direction, in the meridional direction their growth is very much reduced. The A plates also change their proportions and are strongly modified during their downwards shift. The plates that are complex and are composed of one primary plate and two smaller demiplates blend together. The demiplate's sutures, that are easily visible in the uppermost plates, disappear. Märkel (1975) showed by tetracycline labelling in *Paracentrotus lividus*, that once the demiplates are united to the primary plate, they grow as one unit. All these observations, of differential latitudinal meridional growth, and the compressed appearance of the plates at the lower part of the plates' row, agree with Raup's (1968) observations. Moreover, they suggest that if the growth inhibiting stress exists it should act mainly in the meridional direction.

There are some elastic or contractile elements, which may provide the mechanical force needed to cause such meridional directed stress. These elements are (a) the lantern retractor muscles, that pull the plate rows downwards and (b) the ambulacral system with the tube feet, that exert a constant pull towards the substratum. The collagenous fibres, that bind the plates together (Travis *et al.*, 1967; Kobayashi & Taki, 1969) may act as distributors of the stress, thus forming a stress gradient along the row. The inverse proportionality between calcification and concentration of these fibres (at a certain plate edge) has already been noted (Moss & Meehan, 1967).

The exaggerated growth of deformed urchins' plates in the meridional direction

(Figs. 13–15) indicates a departure from the controlled growth that is typical of normal *Tripneustes*. It is reasonable to assume that the pollutant, possibly one of the heavy metal ions or chemicals that are emitted in the effluent, affected the balanced growth by allowing growth in directions that are otherwise inhibited. It is tempting to conclude that the deformation results either from formation of an inner pressure that causes the expansion of the test against the alleged stress balance or from damage to the elasticity or mechanical properties of the above-mentioned elements. *T.* cf. *gratilla*, because of its rapid growth, easy manipulation and sensitivity to pollution is a suitable organism to test the growth regulation through stress hypothesis and the effects of environmental factors on it.

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