

Mass mortalities of echinoids and other reef flat organisms coincident with midday, low water exposures in Puerto Rico

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Abstract

Echinoids, notably *Lytechinus variegatus* and *Tripneustes ventricosus*, and other reef flat animals (brachyuran crabs, chitons and ophiuroids) were observed to suffer heavy mortality in Puerto Rico during extreme, midday low water stands which occur in the spring and summer seasons. Death often resulted from prolonged exposure to intense heating (up to 40 °C) in pools and slowly circulating bodies of water over periods of clear and calm weather; desiccation caused death in echinoids which subsequently floated away from the reef with the rising tide. The tolerance limits to exsiccation and high thermal stress were determined and found to lie within the lethal range realized on the reef. Unprotected *Tripneustes* may also be killed from exposure to the shorter radiations of sunlight. Severe mortalities were observed in populations of *Lytechinus* (64%) and *Tripneustes* (86%) located at a shallow depth toward the lee side of the reef. Less affected were the echinoids *Echinometra lucunter*, *Diadema antillarum* and *Brissus unicolor*. Similar, tide-related echinoid kills are expected to occur at other localities in the Caribbean region.

Introduction

The catastrophic destruction of marine organisms exposed to extreme temperatures has been well documented for coastal environments, ranging from high polar latitudes to tropical seas (BRONGERSMA-SANDERS, 1957). In temperate regions when low atmospheric and sea-water temperatures become critical in winter the death of littoral forms often results (TOKIOKA, 1963; CRISP, 1964; FISCHER-PIETTE, 1964). At this time shore life is especially susceptible to severe atmospheric chilling during periods of low tide when the comparatively warm sea-water is no longer present as a protective medium.

Extensive destruction of shallow water subtropical and tropical organisms from exposure to high temperatures has also been observed (VAUGHAN, 1918; HODGKIN, 1959). TOKIOKA (1966) has reported on certain intertidal populations which were subject to conditions of extreme thermal stress twice a year, to the winter minima and the summer maxima. Particularly critical with respect to mortalities resulting from temperature maxima is the occurrence of a low water phase during the daylight hours. At such times in the summer on cloudless and windless days, shallow and isolated bodies of water can heat up rapidly and excessively, desiccation can then become pronounced and solar radiation will impinge directly on the organisms exposed by the tide. Frequent seasonal

observations of mass echinoid kills on reefs in Puerto Rico, coupled with measurements of high temperature and exsiccation tolerance limits, demonstrate that periods of high temperature and desiccation, which may prevail during midday, low water, tidal exposures in the spring and summer, contribute significantly to the mortality rates of three shallow water urchin species. The kills are more severe in some years than in others but generally of such intensity as to have been regarded as a common phenomenon by the local fisherman.

Analysis of the tidal regime on a seasonal basis, and as it is related to local weather conditions, indicates that this particular kind of mass mortality has probably occurred frequently in the past and can be expected to continue in the future, usually at least once annually. Systematic enumeration of dead echinoids, and incidental enumeration of other organisms, coupled with observations on the extent of repopulation in affected areas, reveal in quantitative terms the magnitude of the kills relative to the population densities of the species present on the reef flats.

Description of reefs

Physiography

Only brief attention has thus far been devoted to the topography and zonation of the numerous coral reefs present in the vicinity of La Parguera, Puerto Rico. Because this information is critical in understanding the circumstances which can lead to mass mortalities, the relevant facts available on the local coral reef environment are summarized and a schematic profile is presented of the zonation typical of the "inner reefs".

The abundance of reefs along the south coast of Puerto Rico, in contrast to their virtual absence on the north shore, has been attributed by ALMY and CARRIÓN (1963) to low rainfall, minor influx of rivers, strong currents and the presence of suitable surfaces raised off the insular shelf for their growth. Most conspicuous at La Parguera are the so-called "outer reefs" (Turrumote, Media Luna, Laurel) and "inner reefs" (Enrique and La Gata), located roughly 3 km and 1 km from the shore, respectively. These principal, linearly arranged, reef formations, often with individual lengths of 1 km, have been most commonly termed bank (SMITH, 1948) or platform reefs (WELLS,

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1957), but are also known as weakly formed barrier reefs or ribbon reefs (KAYE, 1959). Many smaller patch reefs are interspersed shoreward off the "inner reefs". The local pattern of reef distribution can be readily visualized with reference to ALMY and CARRIÓN's (1963, Plate I) submarine topographic chart of the inner shelf and the mosaic aerial photograph of the same area in ODUM et al. (1959, p. 160).

The majority of the larger reefs typically have a broad, shallow reef flat, which in some instances may attain a breadth of 50 m. The development of this near-surface feature apparently follows the successional scheme outlined by MARGALEF (1962, p. 428) for protected portions of a reef subject to heavy sedimentation. Turrumote Reef, a member of the "outer reefs" series, is unique in possessing a relatively narrow flat and a nearly completely enclosed lagoon (GOREAU et al., 1960). As MARGALEF (1962) and WELCH (1962) indicated, the seral stage represented by the "inner reefs" (particularly Caracoles and Májimo which make up the NE segment of the Gata complex) is characterized by varying proportions, depending on the successional stage, of the following key species: the green alga *Halimeda opuntia*, turtle grass (*Thalassia testudinum*) and the coral *Porites porites* var. *furcata*.

In the study area (Caracoles and Májimo Reefs, Fig. 1) the reef flat can be subdivided into seven more or less distinct zones, which are oriented parallel to the long axis of the reef from the windward to the lee side as follows: 1. lattice network of *Millepora complanata* and encrusting, calcareous red algae; 2. pool with dead, coral debris bottom; 3. emergent reef flat (A, coral rubble surface; B, isolated pool); 4. mixed *Thalassia* coral rubble bottom; 5. sandy bottom; 6. massive clumps of the alga *Acanthophora spicifera*;

7. sandy, leeward lagoon. Dense algal mats are not always present in zone 6 and often living mounds of *Porites* are present in zone 7. These zones are illustrated in Fig. 2 in relation to MSL (mean sea level) and MLW (mean low water). An overall view of the reef flat at high and low water tides can be seen in Fig. 3 (a, b) and Fig. 4. Zones 1, 3 and 4 are visibly exposed at a low water stand of 3.0 cm below MLW. It is on such occasions that all members of the sessile and most of the benthic biota are subject to drying and high temperature stress.

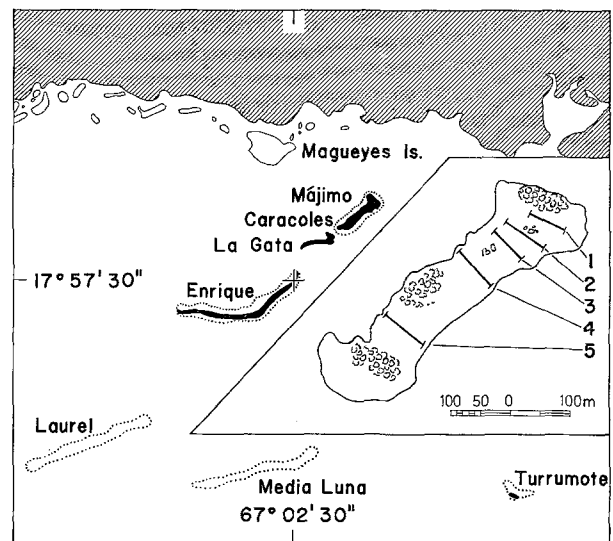


Fig. 1. Location of the principal study area at La Parguera, Puerto Rico. Details of inset of the Májimo-Caracoles reef were obtained from an aerial photograph taken on February 16, 1963; courtesy of the Cartographic Division, Soil Conservation Service, Beltsville, Md. The names of the coral reefs are those used by the local populace.

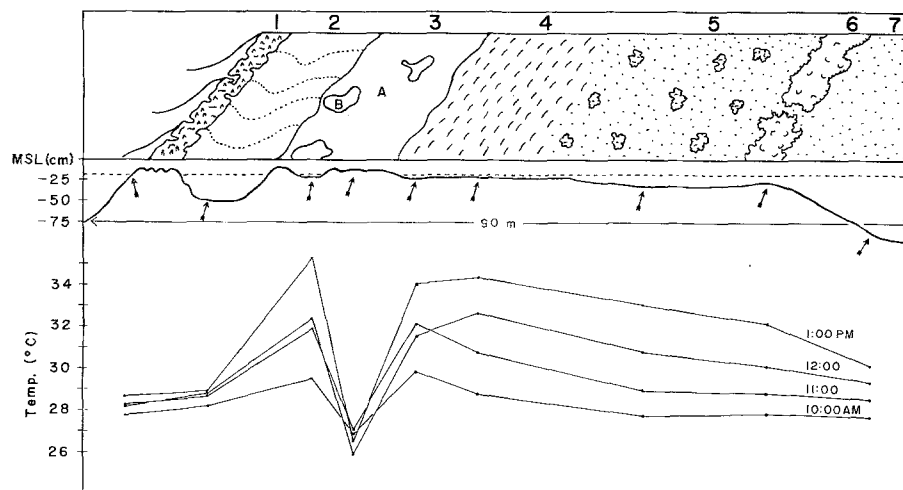


Fig. 2. Profile of the Caracoles reef flat at transect 4 in relation to the low water exposure of April 23, 1966. The various zones across a 90 m stretch are illustrated pictorially and their depths are shown in profile relative to MSL and when the tide stood at 9.2 cm below MLW (MLW is 8.8 cm below MSL) over the 2 h period 12:00 to 2:00 PM. Arrows indicate where temperature measurements were made; all of these were water temperatures except 3 A which was measured in the sediment 5 cm below *Porites* shingle. The vertical scale of the reef profile is exaggerated about 13 ×.

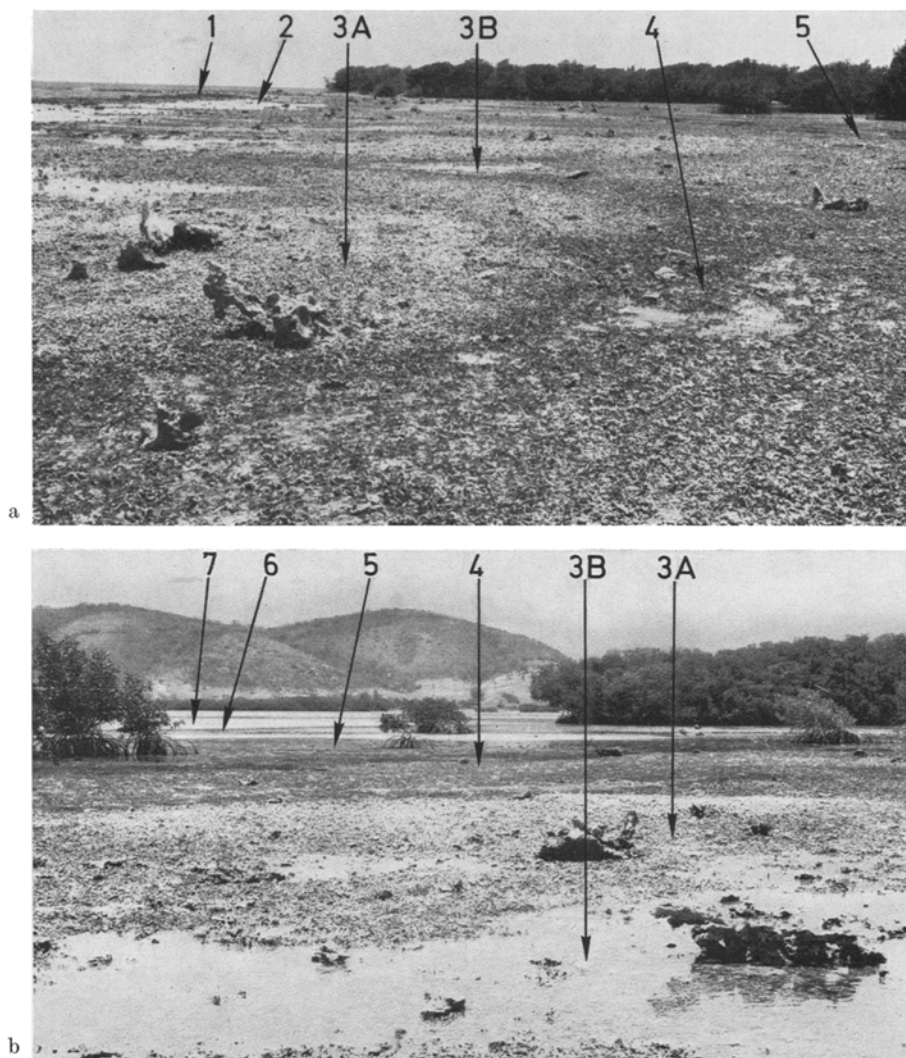


Fig. 3. Májimo Reef at a -0.3 cm tide, May 16, 1965. Views of the windward side looking toward Caracoles Reef to the SW (a) and of the leeward side toward the NE (b)



Fig. 4. View of reef flat comparable to Fig. 3a at a water height of $+5.8$ cm, only 3 cm below MSL (May 17, 1967)

Climate and weather

In general the atmospheric weather conditions considered most likely to have a harmful influence, either directly or indirectly, on tidally exposed organisms in the low latitudes are cloud cover, wind,

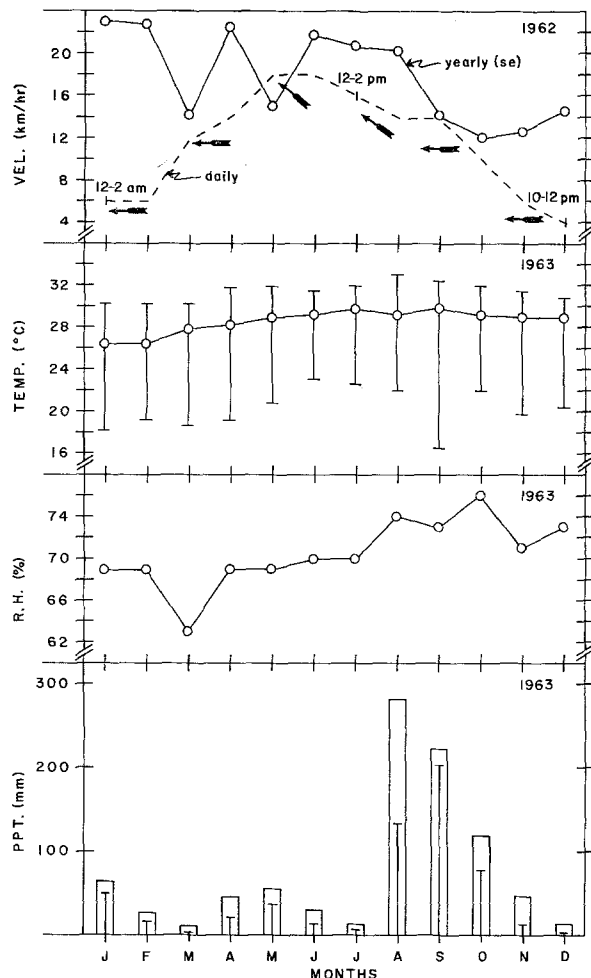


Fig. 5. Composite seasonal climatic regime recorded at Magueyes Island Climatological Station, La Parguera. The particular years plotted are noted in the upper right-hand corner of each graph and were selected as the most severe or highly variable with respect to the conditions examined over the period 1961 to 1966. In the wind diagram the unbroken line connects monthly mean values of the SE component for 1962, and the broken line connects daily point observations recorded on June 16, 1962. Arrows indicate the characteristic late morning shift in wind direction from the E to the SE quarter. The temperature plot is of monthly mean and extreme values. The monthly mean relative humidity values were observed between 8 and 9 AM. Bars in the rain plot denote monthly totals and the lines maximum daily records

temperature, relative humidity and rainfall. A brief account of these parameters, as they have been assessed in Puerto Rico and the U.S. Virgin Islands, (mainly after SMEDLEY, 1961) follows and is collated with observations available for the south coast of

Puerto Rico (Santa Isabel) and Magueyes Island, La Parguera.

Cloud observations taken at four different localities in Puerto Rico and the Virgin Islands show a similar record. Maximum diurnal cloudiness occurs from the late morning hours until around 3:00 to 6:00 PM. Maximal seasonal variations occur in May or June and in September or October, and the yearly minimal cover occurs in March. Peak, daylight cloud cover values ranged from 6.4 to 8.6, compared with a minimum night value of 1.9. Only infrequently does cloud cover obscure the sky for any prolonged period of time at La Parguera (see Table 1, April 23, 1966).

Along the south coast of Puerto Rico the easterly trade winds are influenced by the land-sea breeze effect to the extent that in the afternoon hours the wind characteristically shifts to the SE quadrant. Significant daily and seasonal variations in wind velocity are evident (Fig. 5). Wind speeds were variable over the period January through April. High mean velocities exceeding 22 km/h were recorded in January, February and April. Quite high wind speeds were again observed from June through August, followed by significantly reduced values in the autumn, which is typical for this region of the Caribbean.

While the mean temperatures show a range of only about 4 °C in the different seasons, the monthly maximum and minimum temperatures do demonstrate a wide range. For example, in September the range of extreme temperatures amounted to 17.1 °C. An extreme minimum temperature of 16 °C was recorded on September 27, 1963, at which time Hurricane Edith was located approximately 91 km from La Parguera (GLYNN et al., 1964).

Relative humidity is normally high throughout the year. Variations of this factor over a 24 h period are usually rhythmic, with the highest values prevailing during the night and the lowest in the day when atmospheric temperatures are at a maximum.

Much of the southern coastal belt has a low annual rainfall due to its location in the rain shadow of the central mountain range. A total annual precipitation of 884 mm at Magueyes Island in 1963 was unusually high. In recent years the annual figure has usually been around 760 mm or somewhat less.

Hydrography

COKER and GONZÁLEZ (1960) reported maximum surface water temperatures of 32 °C in shallow, partially enclosed canals and a normal range in salinities for the reef area of 34.2 to 36.7 ‰. One exceptionally low salinity value of 9.8 ‰ was observed near shore following a heavy rain. Two years of weekly temperature observations at Laurel Reef showed that the maximum seasonal range in freely circulating waters did not exceed 4 °C. March was the coldest month at about 26 °C and September or October the warmest at about 30 °C. Following a light rain squall at Caracoles Reef on May 16, 1965,

dilution of shallow, isolated pools resulted in a slight reduction of salinity to only 33.30‰.

The direction of the prevailing currents around the reefs usually trends from east to west, thus producing a substantial stream flow over the reefs at high water. ODUM et al. (1959) reported current rates over several different La Parguera reef flats which commonly fell in the range of 4 to 8 m/min. At Laurel Reef current velocities on the reef flat have been measured over a range of 0.5 to 2 m³/min by the author.

The tides are essentially diurnal in character with low and high water stands occurring at about the same time of day over extended periods. The maximum daily amplitude amounts to only about 34 cm. An additional feature of the local tides seems crucial

conditions thus far considered may interact in the following manner to cause a mass destruction of the reef biota: clear sky, low wind velocity, high atmospheric temperature, low relative humidity, ascending seasonal sea-water temperature, cessation of current flow across reef flat at ebb tide.

Records of kills

The severe echinoid kill of April 14, 1965, was the first assessed quantitatively (Table 2). All dead urchins were counted and then removed from a sampling plot at Caracoles Reef over a two day period. Population size of the living animals was determined from sample, square meter counts in the study area. Both the dead and living counts probably estimate only minimum

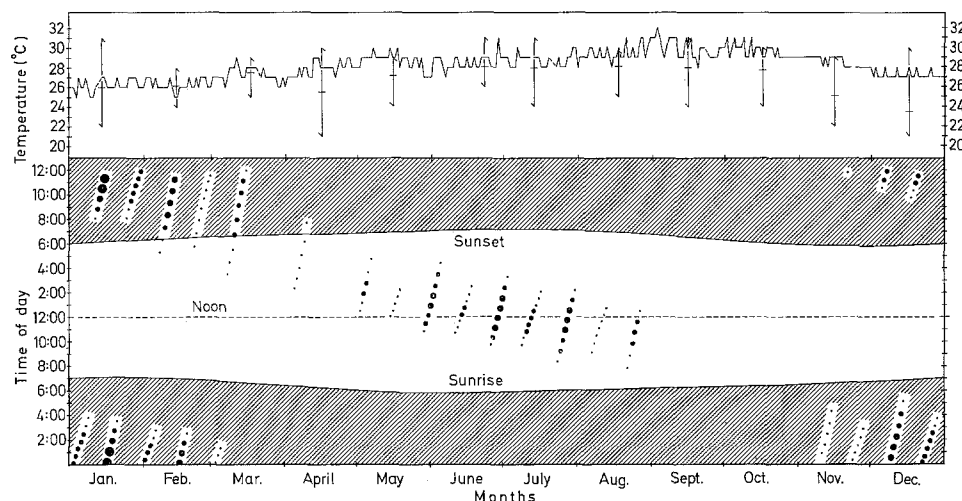


Fig. 6. Seasonal distribution of minus tides at La Parguera, Puerto Rico, in relation to the time of day and the atmospheric and sea-water temperatures in 1965. Dots indicate the time of month and day of the minus tides; their size the magnitude of low water in cm below MLW as follows: • (3.0 to 6.1), • (9.2 to 12.2), • (15.2 to 18.3), • (21.4 to 24.4). Mean, maximum and minimum atmospheric temperatures for each month are indicated by vertical lines and daily sea-water temperatures by the curve. Breaks in the temperature curve indicate a lack of data. The temperature measurements were taken at 7:00 AM at the U.S. Coast and Geodetic Survey tidal station operated on Magueyes Island by the Institute of Marine Biology. Tidal data and the time of sunrise and sunset were obtained from the C. and G.S. Tide Tables (1965) and corrected for La Parguera

regarding the present findings, namely the reversal in timing of the diurnal cycle which takes place suddenly during the spring season (Fig. 6). By May, and through the summer months of June, July and August, several series of minus tides occur during midday when heating and desiccation may approach extreme levels (Table 1). Temperatures exceeding 32 °C were observed frequently, and on two occasions, in May and June, 1965, extreme values in excess of 39.0 °C were recorded. The rapid rise in sea-water temperature which took place on a receding tide at Caracoles Reef is shown in several zones in Fig. 2. The highest temperatures were recorded at zones 3, 4 and 5. An abrupt dip in temperature is evident in zone 3 A, where calcareous mud underlying *Porites* shingle was sensibly cool at a depth of 3 cm.

With respect to the seasonal timing of midday, low water exposures, the various atmospheric and marine

abundances, since some of the urchins were undoubtedly transported away from the reef flat and possibly some of the living forms escaped notice. In any case, the high losses suffered by three species must certainly approach a correct order of magnitude. *Tripneustes* experienced a mortality of 86.4% (166 dead), *Lytechinus* 64.0% (374 dead), *Brissus* 25.9% (7 dead), and *Echinometra lucunter* 1.2% (33 dead).

Two subsequent mass kills, which devastated several other reef populations, occurred on May 16 and June 28, 1965. Particularly hard hit on these two occasions were the brachyuran crabs *Pitho aculeata* and *Mithrax sculptus*, the chitons *Acanthochitona pygmaea* and *Ischnochiton papillosus*, and the brittle stars *Ophioderma appressum* and *Ophiocoma echinata*. Even though these species live secretively among the anastomosing branches of living *Porites* and dead *Porites* encrusted with red calcareous algae, they can

Table 1. *Extreme high sea-water temperatures recorded during periods of low water at Caracoles Reef, La Parguera. The observations for August 8, 1962, were obtained at Turrumote Reef. All thermometers used in this study were calibrated against a standard thermometer certified by the National Bureau of Standards*

Date	Maximum sea-water temperatures (°C)	Time	Station	Tide (cm below MLW)	Range in air temperature (°C)	Supplementary weather notes
August 8, 1962	30.5 33.8 35.8 36.2 35.0 33.0 30.0	10:00 AM 12:00 Noon 2:00 PM 4:00 6:00 8:00 10:00	Lee side of reef; average depth 20 cm	0.0 6:37 AM	—	Cloud cover < 10%; wind light
May 16, 1965	30.4 33.8 38.7 39.0 39.7 36.6 32.3	2:19 PM 2:17 2:15 2:13 2:11 2:09 2:06	1 2 3 B 3 B 5, depth 10 cm 5, depth 15 cm 7	— 11.0 1:30 to 4:00 PM	—	Cloud cover < 10% early PM; overcast 100% between 3:00 and 4:00 PM with 13.0 mm ppt. ^a
June 2, 1965	31.9 33.2 33.7 33.8 34.7 34.7 34.5 34.5	11:32 AM 12:02 PM 12:32 1:02 1:32 2:02 2:32 3:02	5	— 13.4 11:30 AM to 3:00 PM	28.8—30.3	—
June 28, 1965	40.2 40.0 39.2 35.6 29.1	1:10 PM 1:15 1:20 1:25 1:28	3 B 5, depth 25cm 6 7, depth 1 m	— 18 11:52 AM	—	—
April 23, 1966	33.8 32.4 34.9 35.3 34.2	11:36 AM 12:06 PM 12:36 1:06 1:36	3 B	— 8.5 11:30 AM to 2:30 PM	25.6—29.2	Cloud cover ca. 80%; wind 5 to 8 km/h NW
May 21, 1966	32.8 34.4 33.8 34.5 34.2	12:05 PM 12:35 1:05 1:35 2:05	4	— 5.5 10:30 AM to 2:00 PM	28.0—29.4	—
June 3, 1966	33.0 33.2 34.6 35.1 34.0	11:35 AM 12:05 PM 12:35 1:05 1:35	4	— 7.9 9:30 AM to 1:15 PM	27.1—28.2	—
June 4, 1966	33.2 34.0 34.2 34.2	12:07 PM 12:37 1:07 1:37	3 B	— 4.9 10:45 AM to 1:45 PM	27.9—29.0	—

^a Precipitation observed at U.S. Weather Bureau weather station on Magueyes Island, approximately 1.3 km to the NW of Caracoles Reef.

not escape the sudden and intense heating of the shallow pools in which they are found. The majority of the *Thalassia* plants in zone 4 exhibited burned blades and after a few days underwent fragmentation. Parched blades observed on May 17, 1967, were entirely covered with a nearly pure, epiphytic growth of *Enteromorpha flexuosa*, which imparted a grass green

appearance to zone 4. Numerous echinoids were again observed killed, including several individuals of *Dia-*

Certain inhabitants of the reef flat consistently survived even the most severe of the low water exposures. The exposed blades of *Thalassia* were often visibly affected, but since the shallowest patches

Table 2. (continued)

Date	Organism	Number dead	Comments
	Echinoidea do. May 16, 1965		
	Pisces <i>Pomacentrus fuscus</i> (CUVIER and VALENCIENNES, 1830)	+	
April 23, 1966	Pelecypoda <i>Codakia orbicularis</i> LINNAEUS, 1758 <i>Arcopagia fausta</i> PULTENEY, 1799	++ ++	100 m ² area sampled
March 20 and 21, 1967	Echinoidea <i>D. antillarum</i> and other unidentified spp.	+++	Observed floating at surface by L. R. ALMODÓVAR
April 26 to 28, 1967	Echinoidea do. May 16, 1965 except <i>D. antillarum</i>	+++	1000 m ² area sampled
May 23 to 27, 1967	<i>Tripneustes esculentus</i>	+++	Observed floating at surface by M. & A. C. JOHNSON and R. TURNER
June 21, 1967	<i>Lytechinus variegatus</i> <i>Tripneustes esculentus</i> <i>Brissus unicolor</i>	+++ +++ +	Observed exposed on reef flat by F. FERNÁNDEZ and G. PADILLA

usually recovered later in the summer and fall it is assumed that the subsurface rhizomes were not irreparably damaged. In general, most of the larger algae composed of massive thalli survived well. The heat tolerance of a variety of intertidal algae at La Parguera was determined by BIEBL (1962) to lie in the range 35° to 40°C in the summer season. The following animal species, subject to heating up to 40°C in isolated pools, experienced no apparent mortalities: Anthozoa — *Zoanthus sociatus*, *Porites porites* var. *furcata*; Gastropoda — *Bulla striata*, *Batillaria minima*, *Petalonchus* (*Macrophragma*) *varians*; Anomura — *Clibanarius tricolor*, *C. antillensis*, *Phyllactis flosculifera*, a large actinian embedded in the sediment in the shade of the red mangrove (*Rhizophora mangle*), was not visibly affected. Several species of bivalves which attach to solid surfaces in the intertidal zone have been shown by READ (1964) to have relatively high thermal tolerances, usually above 40°C.

At first glance the mass mortality of echinoids reported for March 20 and 21, 1967, would seem discordant compared with the other records because the predicted times of low water (—4.0 cm) occurred at 8:14 PM and 9:20 PM, respectively. Actually, minus tides occurred during the midday hours, presumably the result of meteorological disturbances, thus implicating again the deleterious effects of desiccation and extreme high temperatures.

Tolerance limits of the shallow-water echinoid fauna

Desiccation

Since field observations showed that both exposed and submerged urchins succumbed during midday, low water periods, the tolerance of animals under these conditions was investigated. Particular emphasis was

placed on survival under exsiccation and high temperature stress as a function of time, since the time factor is such an integral part of any tidal cycle. The importance of the time variable in delimiting the boundaries of heat death has been clearly demonstrated by ORR (1955).

The ability of the following five species to withstand drying conditions was examined in unprotected and protected situations: *Lytechinus variegatus*, *Tripneustes ventricosus*, *Echinometra lucunter*, *Diadema antillarum* and *Brissus unicolor*. Twenty-one individuals of each species were exposed on coral rubble in the open sunlight (unprotected) over a period of six hours. At one-half and then hourly intervals, the wet weights of three individuals were recorded, then the animals returned to sea-water where they were allowed a recovery period of 15 to 20 h. The same experimental procedure was carried out on a similar complement of urchins, except that they were provided with some degree of protection. *Diadema*, *Echinometra* and *Tripneustes* were shaded under large, dead coral rocks; *Lytechinus* was allowed to cover itself with algae, coral shingle, etc. prior to exposure; *Brissus* was buried just below the surface of wet, calcareous sediment held in liter capacity bowls. Further details on procedure are given in the captions to Figs. 7 and 8.

Loss in weight as a function of exsiccation is seen to be an essentially linear relationship in both unprotected and protected animals. Among unprotected individuals, however, the weight loss-time course is considerably steeper, even though weather conditions were slightly less conducive to drying than for the protected animals. Weight loss in *Brissus* was least, amounting to about 70% of the initial wet weight after 6 h. *Echinometra* experienced the most pronounced loss in weight, which amounted to 50% after

6 h. Exposure of unprotected urchins for 3 h duration caused death in all species except *Echinometra*. Even after drying for only 2 h all *Lytechinus* and *Diadema* had succumbed.

Among the protected urchins, *Tripneustes* showed the highest resistance to desiccation, with a mean weight of about 80% of the initial wet weight after 6 h. *Lytechinus*, despite its habit of heaping debris on the aboral surface during the daylight hours, was affected most by atmospheric drying. After 4 h of

experienced only a slight increased rate of survival, up to about 2 h exposure instead of one. The survival rate of *Lytechinus* was essentially the same, indicating that the heaping of even large amounts of moist substances like the thalli of algae, does not significantly prolong its ability to withstand exposure. Survival of protected *Brissus* was shown to be less than that of unprotected individuals. The explanation for this apparent discrepancy seems to lie in the intense heating of the moist sediment, which approached the

upper lethal temperature of the spatangoid. By 2:17 PM the temperature of the sediment had climbed to 37.7 °C (Fig. 8). As is shown in the next section, no *Brissus* survived a water temperature of 38 °C for 2 h exposure.

Maximum thermal tolerance

Urchins and other organisms confined to shallow pools are perforce directly subject to the intense heating which can occur on this portion of the reef. A great number of the echinoid species involved in mass kills, particularly *Tripneustes* and *Lytechinus*, were found dead in shallow water at zones 5 and 6, indicating that they were not exposed to drying. The tolerance of echinoids to seawater of high temperature was investigated to more precisely evaluate the possible effects of extreme thermal conditions which may occur naturally.

Healthy adult urchins, collected from the Caracoles reef flat on the same day they were tested and in the months of May and June, were exposed to six distinct temperature regimes, each of which varied in time intervals of 1/2, 1, 2, 3 and 4 h. Three individuals of each of the six species were introduced into a 100 l fiber glass tank, provided with aeration and vigorous stirring. The actual thermostatically controlled tem-

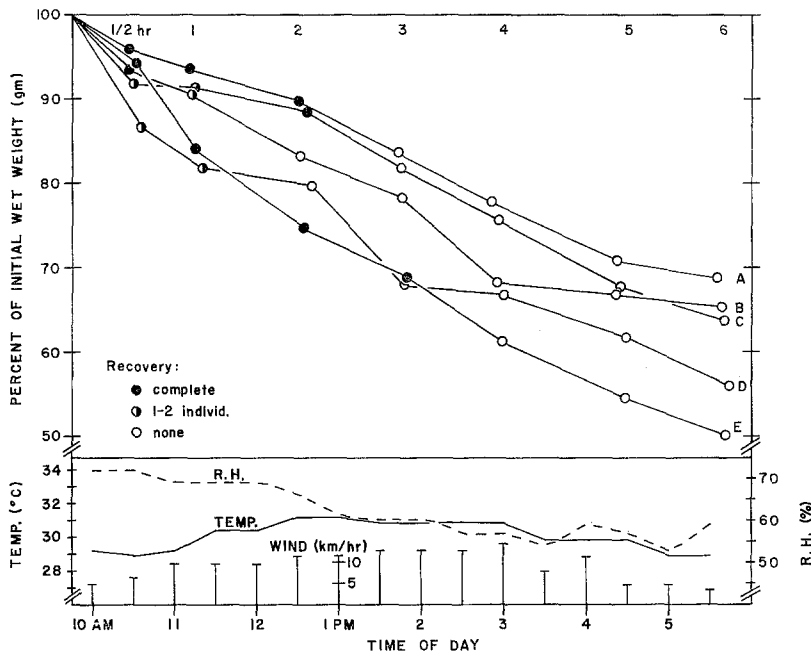


Fig. 7. Exsiccation and recovery of five echinoid species subject to direct atmospheric exposure (A: *Brissus*, B: *Lytechinus*, C: *Tripneustes*, D: *Diadema*, E: *E. lucunter*). Each symbol denotes the mean weight of three individuals as well as their ability to recover (see inset legend). Initial weights were obtained from animals after shaking in order to rid them of any excess water; later weighings were carried out directly without shaking or blotting. Because loss in weight due to defecation amounted to less than 1% (in one instance 0.8% over a period of 5 h) of the wet body weight, this factor was omitted from the calculations. The ranges in wet weight of the adult animals employed were: *Lytechinus* 18.4 to 59.1 g, *Tripneustes* 25.6 to 101.6 g, *E. lucunter* 8.2 to 12.4 g, *Diadema* 80.3 to 212.1 g, *Brissus* 30.0 to 48.7 g. Death was based on the absence of spine movement in all forms and from cessation of movement of the jaw apparatus for all animals except *Brissus*. Dead individuals frequently shed numerous spines, and animals exposed for more than 3 h often floated. A summary of the weather conditions in the experimental area over the period of observation on April 23, 1965 (atmospheric temperature, relative humidity and wind velocity) is given along the bottom of the figure. The sky was clear until 3:30 PM

exposure it had declined in weight to about 65% of its initial wet weight. *Echinometra* and *Diadema*, which were shaded under coral rocks, were able to maintain something better than 70% of their initial weights. While the final loss in weight of unprotected and protected *Brissus* was similar (< 70% of the initial wet weight), the comparatively high rate of exsiccation of animals buried in sediment over the first hour is not readily understood.

Survival of *Tripneustes* and *Echinometra* was significantly prolonged and nearly complete. *Diadema*

peratures were 33.9°, 34.9°, 36.2°, 37.2°, 38.2° and 39.0° ± 0.05 °C. At the end of each time interval the animals were transferred to cages suspended in the sea where they were allowed to recover over a period of 15 to 20 h. The criterion of death was cessation of movement of spines and the jaw apparatus (except in *Brissus*). Test animals were spared at the higher temperatures when at lower temperatures death of all three individuals over the same length of time or less made it obvious that they would succumb under further thermal stress. For example, it was not

necessary to subject *Tripneustes*, *Lytechinus*, *Diadema* and *Brissus* to a temperature of 39°C for 2 or more h since all individual echinoids died over these same periods of time at 38°C.

In physiological literature the tolerance of a species to a given critical factor is usually determined on the basis of 50% mortality (LT_{50}), where large numbers of experimental animals are employed, especially when individual variability is great. Departure from standard procedure in the present study was felt necessary because a second variable, time, was given equal importance to desiccation and high temperature stress. Many more animals would have had to be sacrificed in order to determine the LT_{50} for each temperature-time regime. This was considered undesirable, particularly when certain species (*Brissus*, *E. viridis* and *Tripneustes*) were not overly abundant.

Nearly complete recovery of all six species was observed at 34°C up to 4 h exposure and at 35°C for 3 h (Fig. 9). Mortality in *Tripneustes* was fully realized for an exposure of 4 h at 35°C. All of the urchins survived temperatures of 36° and 37°C when subjected to these higher levels for no longer than 1/2 h. *Tripneustes*, *Lytechinus* and *Diadema* were especially sensitive to temperatures of 36° and 37°C over an exposure period of 1 h and 1/2 h, respectively. Partial survival of *Brissus* was observed at 37°C for up to 2 h, whereas only one individual recovered from exposure to 38°C for a period of 1 h. Most tolerant to extreme high temperatures were *Echinometra viridis* and *E. lucunter*. In *E. lucunter*, recovery was complete at 38°C for an exposure period of 4 h, but only partial at 39°C for 1/2, 1 and 2 h.

A step in the procedure described above required further consideration, namely a possible effect on the animals of introducing them suddenly from the ambient to the experimental temperature and then suddenly back to ambient again. This factor was tested for all of the echinoids except *E. viridis*, by exposing the animals gradually, over a period of 1 h, to the particular

high temperature under consideration. The rate of increase in temperature was higher than occurs naturally, 11.6°C/h up to 39.0°C, but more closely approached the maximum field values of 3°C/h from

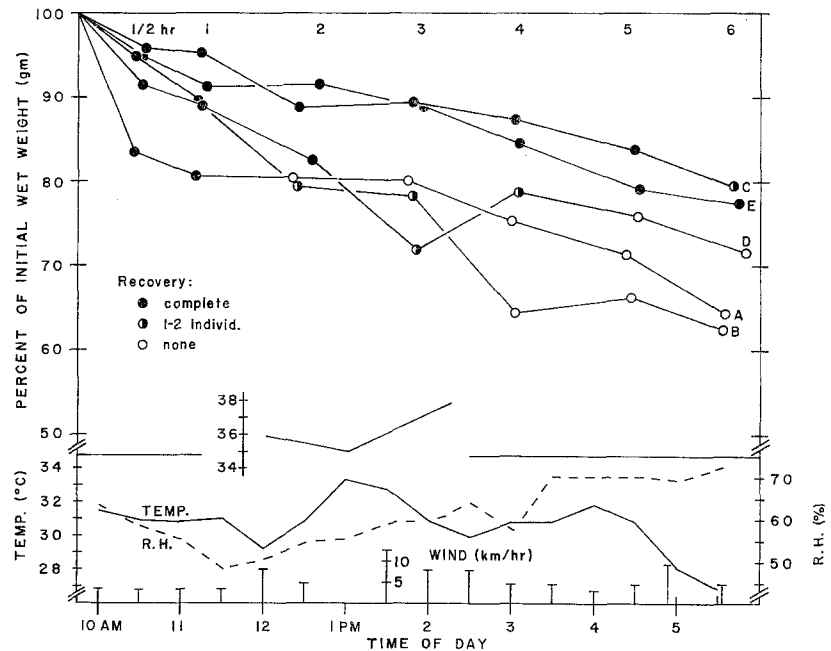


Fig. 8. Exsiccation and recovery of five echinoid species subject to atmospheric exposure with some degree of protection (species can be identified from same letters used in Fig. 7). Procedure as outlined in Fig. 7. The more important heaping materials employed by *Lytechinus* were: *Hypnea spinella*, *Acanthophora spicifera* (Rhodophyta); *Dictyota divaricata* (Phaeophyta); *Rhizoclonium riparium* (Chlorophyta); *Thalassia testudinum* (both living and dead blades); *Synaptula hydriformis*; *Cerithium litteratum*; fragments of echinoid tests, shells and *Porites*. The ranges in wet weight of the adult animals employed were: *Lytechinus* 9.9 to 47.4 g, *Tripneustes* 15.2 to 82.6 g, *E. lucunter* 5.2 to 24.5 g, *Diadema* 106.2 to 254.7 g, *Brissus* 29.2 to 70.6 g. Included with the weather observations (May 7, 1965) is a segment of the temperature curve for the sediment which contained *Brissus*. The sky was clear until 5:00 PM

TIME TEMP. (°C)	1/2	1	2	3	4
39	■	■	■		
38	●, ■, ▲, +	●, ■, ▲, +	●, ■, ▲, +	●, ■, ▲, +	●, ■, ▲, +
37	×, ▲, +, ●, ■	×, ▲, +, ●, ■	×, ▲, +, ●, ■	×, ▲, +, ●, ■	×, ▲, +, ●, ■
36	×, ▲, +, ●, ■	×, ▲, +, ●, ■	×, ▲, +, ●, ■	×, ▲, +, ●, ■	×, ▲, +, ●, ■
35	×, ▲, +, ●, ■	×, ▲, +, ●, ■	×, ▲, +, ●, ■	×, ▲, +, ●, ■	×, ▲, +, ●, ■
34	×, ▲, +, ●, ■	×, ▲, +, ●, ■	×, ▲, +, ●, ■	×, ▲, +, ●, ■	×, ▲, +, ●, ■

KEY: × TRIPNEUSTES ● BRISSUS
▲ LYTECHINUS * E. VIRIDIS
+ DIADEMA ■ E. LUNCUNTER

Fig. 9. Composite summary of echinoid survival under different temperature-time regimes

29.8° to 36.2 °C, a gradient of 6.4 °C/h. Inspection of Table 3 shows that animals exposed to higher temperatures either suddenly or gradually demonstrated nearly the same rate of survival. *Echinometra lucunter* and *Brissus* again proved to be among the hardiest species.

Table 3. Comparison of the number of echinoids surviving at different high temperatures after a sudden (sud.) or gradual (grad.) change from ambient sea-water temperature to the higher temperatures being tested. Animals subjected to a sudden change were transferred immediately from sea-water of normal temperature to a higher temperature of 2 h duration and then back again to sea-water. Animals subjected to a gradual change were brought up to the experimental temperature slowly over a period of 1 h, allowed to remain at the higher temperature for 2 h, and then brought down slowly to the sea-water temperature over a period of 1 h. Exposure to the maximum temperatures was for 2 h only. The number surviving was determined after a recovery period of 15 h

Temper- ature ^b (°C)	Species											
	<i>Diadema</i>	<i>E. lucunter</i>	<i>Lytechinus</i>	<i>Tripneustes</i>	<i>Brissus</i>							
	sud.	grad.	sud.	grad.	sud.	grad.	sud.	grad.	sud.	grad.	sud.	grad.
39.0	27.4	0 ^a	0	1	2	0 ^a	0	0 ^a	0	0 ^a	0	
	29.5											
38.2	28.3	0 ^a	0	3	3	0 ^a	0	0 ^a	0	0	0	0
	28.4											
37.2	28.3	0	0	3	3	0	0	0	0	2	1	
	28.5											
36.2	29.8	0	0	3	3	0	0	0	0	3	3	
	29.5											
34.9	29.6	2	3	3	3	3	3	3	2	3	3	
	28.3											
33.9	27.1	3 ^a	3	3 ^a	3	3 ^a	3	3 ^a	3	3 ^a	3	
	27.1											

^a Data inferred from Fig. 9.

^b The maximum, 2 h temperatures are indicated on the left in italics, and the initial and final temperatures adjusted gradually on the right at the top and bottom, respectively.

Solar radiation

In addition to the detrimental effects of desiccation and extreme high temperatures, it is also necessary to consider possible damage caused by natural, ultra-violet radiations. The effects of this factor on *Lytechinus* and *Tripneustes* were investigated on only one occasion (June 8, 1967), during the midday hours.

Table 4. Survival of urchins exposed to sunlight under a thin layer of water. All animals were collected from Caracoles Reef during the same morning. Their ranges in wet weight were 24.08 to 122.42 g (*Tripneustes*) and 14.61 to 49.69 g (*Lytechinus*). The extent of heaping amounted to 80 to 100% of the test being completely covered. A clear sky prevailed until 12:45 to 1:30 PM at which time a thin cover of cirro-stratus clouds partially obscured the sun for 3 to 4 h. The atmospheric temperature was 31° to 33 °C

Exposure conditions	Species	Exposure time (h)				
		1	2	3	4	5
Unprotected	<i>Lytechinus</i>	3	3	3	3	3
	<i>Tripneustes</i>	3	3	2	2	2
Protected (heaping of natural debris)	<i>Lytechinus</i>	3	3	3	3	3
	<i>Tripneustes</i>	2	3	3	3	3
Protected (plate glass)	<i>Lytechinus</i>	3	3	3	3	3
	<i>Tripneustes</i>	3	3	3	3	2

Three different groups of urchins, each including 15 individuals of the two species, were exposed to sunlight in water baths of sufficient depth to just cover the animals. Two groups received the sun's rays directly through the thin film of water; the animals in one group, however, were allowed to heap debris (*Thalassia* blades and *Porites* shingle) on their tests over a 1½ h period before exposure. The third group of echinoids was shielded from direct exposure by 3 mm thick plate glass. Temperatures were not allowed to exceed 32 °C through frequent sprinkling. The animals were set out at 10:00 AM, and one sample (three individuals of each species) was removed from the three groups at hourly intervals until 3:00 PM. After exposure, the urchins were allowed a recovery period of 48 h indoors in running sea-water. A total radiation intensity of 261 gm cal/cm², or 63% of the daily total, was recorded in the immediate vicinity over the 5 h period with a Kahlsico Model SO 28 bimetallic actinograph.

A total of five urchins died after 48 h, three in the unprotected group and one each in the two different protected groups, indicating that shorter wave radiations do not cause an immediate or very pronounced mortality (Table 4). After a further extension of recovery to one day (72 h), however, two more *Tripneustes* succumbed, unprotected urchins exposed for 4 and 5 h. No further deaths were noted by the end of one week. These results suggest that *Tripneustes* is vulnerable to the shorter, natural radiations received at shallow depths. Few deaths are actually attributed to this factor, though, because the urchin usually seeks concealment beneath the cover of coral debris and often assumes a heaping response. *Lytechinus* proved to be a more hardy species, where complete survival was realized under all the conditions tested. It appears that the availability of heaping materials may not be critical for survival on a short term basis.

Echinoid distributions on the reef flat

As emphasized earlier, at low water some reef zones, by virtue of their elevation and location toward the leeward of the reef, are exposed and more readily subject to extreme conditions than others. This is especially true of zones 3, 4 and 5. Since the various echinoid species show a marked zonation across the reef, it is essential that their distributions be established relative to the critical areas mentioned. A scheduled assessment of population densities (discussed in the

next section) made possible such a quantitative description of the various zones (Table 5).

Table 5. Zonation of echinoids on the Caracoles reef flat expressed quantitatively in mean numbers per m²; the range is given in parentheses. These data are based on 7 transect analyses enumerated over the periods April 6 and 9, and August 30 to September 2, 1966

Species	Zones 3	4	5
<i>Lytechinus</i>	16.8 (9.3—23.8)	7.8 (3.8—17.5)	2.2 (0.3—4.5)
<i>Tripneustes</i>	1.3 (0.4—2.9)	0.4 (<0.1—0.9)	0.2 (0—1.3)
<i>E. lucunter</i>	27.7 (6.4—60.0)	3.6 (0—13.7)	0.2 (0—0.7)
<i>Diadema</i>	0	<0.1 (0—<0.1)	<0.1 (0—<0.1)
<i>Brissus</i>	0.1 (0—0.6)	0	0

It is apparent that all species, excluding *Diadema*, were most abundant on the emergent reef flat (zone 3) and decreased steadily toward the lee side. *Echinometra lucunter* was the most abundant species in zone 3, with a mean density of 27.7 individuals per m²; *Lytechinus* had a density here of 16.8 individuals per m². Zone 4 was dominated by *Lytechinus*, but at half the density recorded in zone 3. *Diadema* was scarce in zones 4 and 5. *Brissus* was found in zone 3 only, where it lives embedded in the fine sediment underlying the *Porites* rubble. Although urchins were not sampled quantitatively in zones 1, 2, 6 and 7, it should be noted that *Diadema* was most abundant in zone 1 and *Tripneustes* probably in zone 2. These regions, however, are usually under water or at least frequently wetted and thus not subject to extreme thermal disturbances. The possibility that certain urchin species may migrate away from the shallow, reef flat areas during a part of the year (LEWIS, 1958) is considered unlikely because the distribution-density data collected in April was essentially the same as that obtained in August-September. In summary, these data make it clear that *Lytechinus*, *Tripneustes*, *E. lucunter* and *Brissus* occur abundantly in a habitat which may experience harsh conditions at least once annually. Essentially similar intertidal echinoid distributions have been reported by KIER and GRANT (1965) at Key Largo, Florida, except that *Eucidaris tribuloides* was relatively common and *Brissus unicolor* was found only rarely under rock slabs in deeper water.

Effects of 1965 kill on populations

The series of mass echinoid mortalities which occurred in the spring of 1965 were of such severity that an impoverishment of some of the reef flat populations was clearly noticeable as the season progressed. In order to assess the intensity of the kill, five transect

stations were established on Caracoles, which included the critical zones 3, 4 and 5 (their location is shown in Fig. 1).

Following the spring and summer midday, low water stands, *Lytechinus* had an aggregate, mean density of 57.6 individuals, and *Tripneustes* 13.6 (Table 6). *Echinometra lucunter* was very abundant, numbering well over 1,000 individuals in all transects except 5. *Echinometra viridis*, *Diadema* and *Brissus* were relatively scarce. In the spring of 1966, before the onset of the midday, low tides, *Lytechinus* and *Tripneustes* demonstrated significantly higher densities, with mean values of 382.6 individuals and 37.2, respectively. Mean densities of 539.6 and 35.6 individuals of *Lytechinus* and *Tripneustes*, respectively, in the following autumn would suggest a marked numerical recovery and a tendency toward stabilization in *Tripneustes*. *Echinometra lucunter* was less abundant than in 1965, with a mean density of 903.4, which reached an even lower value of 347.0 by the succeeding autumn. Of the remaining three species, only *Brissus* seemed to show a significant increase in the spring of 1966, with a mean density of 5.0 individuals, compared with 1.8 recorded in 1965.

A comparison of selected size class-frequency distributions (Fig. 10) shows that the build up of *Lytechinus* and *Tripneustes* populations was apparently due to recruitment of young urchins following the 1965 census. Both the major and minor modes present in the size distributions of *Lytechinus* and *Tripneustes* in the spring of 1966 are probably of young which developed from the previous spring or summer breeding period. Ripe *Lytechinus* was observed by CARLOS CARRIÓN (personal communication) at La Parguera in 1962 from January through May and ripe *Tripneustes* from February through May (excluding in both cases the month of March). The modal test diameters of *Lytechinus* (2.9 cm) and *Tripneustes* (4.7 cm) presumably attained over the 7 month period, are commensurate with the growth rates reported for these forms (LEWIS, 1958; MOORE et al., 1963 a).

Unpublished studies on the breeding and growth of *E. lucunter* on Puerto Rican reefs indicate that the spring modal class of 1.4 cm is comprised of 5 to 6-month old metamorphosed urchins which resulted from a peak breeding activity in August and September. While sampling of *Echinometra* in September, 1966 just failed to encompass the time of year of major recruitment, it is still not understood why these populations tended to decline for over a year after the spring and summer mortalities observed in 1965. The high tolerance of *Echinometra* to desiccation and high temperature stress suggests that the observed decline in abundance was unrelated to mortality resulting from low water exposure. Furthermore, the increased living space resulting from the decline of *Echinometra* does not seem related to the marked increase in *Lytechinus* because the two species occupy different habitat niches.

Table 6. Number of urchins present in five permanently marked, transect stations sampled on three different occasions at Caracoles Reef. Each transect was a meter wide with the following lengths: 61 m (1), 72 m (2), 59 m (3), 77 m (4) and 76 m (5). The three different transects obtained at each station were adjacent and parallel to one another, thus providing essentially undisturbed areas at each sampling

Date	Species	Transect 1	2	3	4	5
August 23 to 27, 1965	<i>Lytechinus</i>	40	47	38	82	81
	<i>Tripneustes</i>	15	19	4	13	17
	<i>E. lucunter</i>	1,099	2,912	2,664	1,499	642
	<i>E. viridis</i>	1	0	1	1	0
	<i>Diadema</i>	0	1	1	1	0
	<i>Brissus</i>	2	0	3	4	0
April 5 to 9, 1966	<i>Lytechinus</i>	353	141	398	530	491
	<i>Tripneustes</i>	44	48	17	45	32
	<i>E. lucunter</i>	716	656	1,133	738	1,374
	<i>E. viridis</i>	0	0	0	0	0
	<i>Diadema</i>	1	0	0	0	1
	<i>Brissus</i>	0	1	12	10	2
August 30 to September 2, 1966	<i>Lytechinus</i>	620	357	472	739	510
	<i>Tripneustes</i>	50	33	22	14	59
	<i>E. lucunter</i>	633	287	166	192	457
	<i>E. viridis</i>	0	0	0	0	0
	<i>Diadema</i>	1	0	0	0	1
	<i>Brissus</i>	0	0	0	3	0

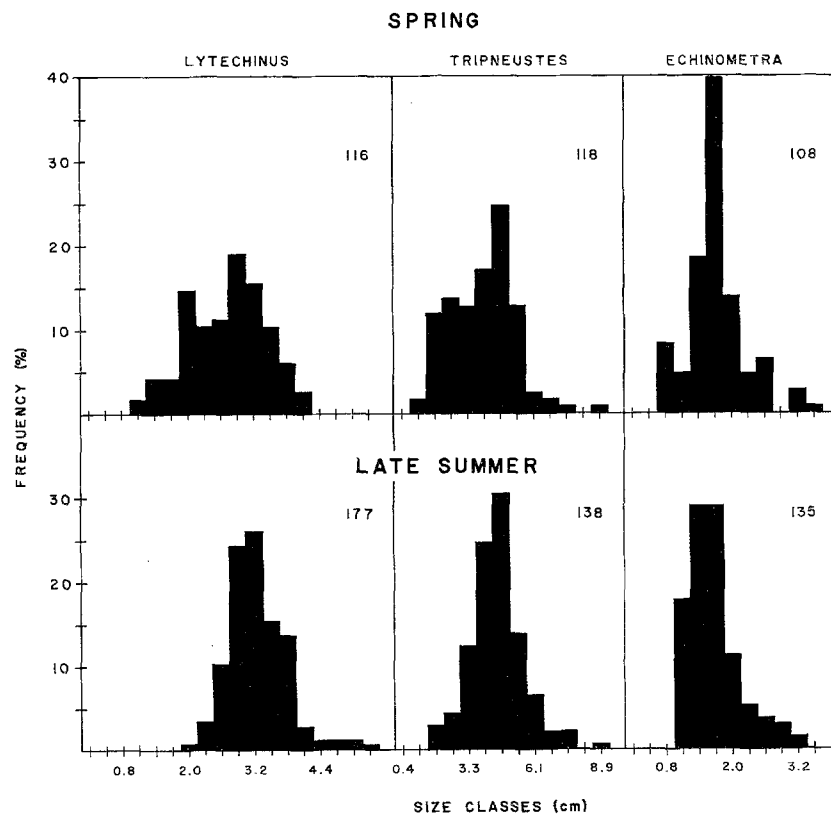


Fig. 10. Size class-frequency distributions of *Lytechinus*, *Tripneustes* and *Echinometra lucunter* obtained in spring (April 5 to 9) and late summer (August 30 to September 2) 1966, at Caracoles Reef. Test diameters are indicated by mid-point values. The sample size is noted in the upper right-hand corner of each distribution

The apparent increase in density of *Brissus* in the spring did not seem to result from a recruitment of young forms, since the mean test diameter (length of the antero-posterior axis) was 5.0 cm with the range 2.8 to 7.1 cm.

Discussion

Mixed tides with a diurnal range of less than 61 cm are characteristic of the shores bordering the Caribbean Sea (U.S. Naval Oceanographic Office, Pub. No. 700, 1965). While the difference in height between

mean HHW and mean LLW is relatively slight, the possible deleterious effects of such midday, low tides on a shallow water biota may be considerable. In this connection it is of interest to examine the tidal cycles of the various coastal areas of the Caribbean Sea in relation to the occurrence of coral reefs with broad, reef flat developments.

Keeping in mind the minor differences in the tidal cycle which occur from year to year and the local variations in time and height, it is still possible to classify numerous localities on the basis of the following critical tidal regimes (Tide tables, 1961—67): (1) more or less abrupt shift in the timing of low tides so that they occur during the midday hours throughout at least part of the summer season; this change-over may occur during the late winter or early spring; (2) gradual shift of the low water periods to midday hours over the summer season; this takes place in the winter season; (3) occurrence of midday, low water tides throughout the year. Only infrequently have meteorological disturbances such as steady onshore winds or reduced barometric pressures been observed to markedly affect the tides at La Parguera. Midday, low water exposures of the first class usually commence in February or March and continue until July in Costa Rica (Puerto Limón), Panamá and the Canal Zone, the north shore of Colombia (from Turbo to Riohacha), Curaçao and Aruba, and certain regions in Venezuela, e.g. Amuay, Cumaná and Margarita Island.¹ Numerous localities demonstrate this same basic regime but it usually occurs somewhat later in the year, namely from March to August or September. These regions are: south coast of Cuba (from Guantánamo Bay to La Coloma), most of Jamaica, the south coasts of Haiti and the Dominican Republic (Port-au-Prince to Sánchez, Samaná Bay), most of Puerto Rico including Culebra and Vieques Islands, and some of the islands in the Lesser Antilles (e.g. St. Thomas, St. Croix, Antigua and Guadeloupe). Low tide predictions of the second class occur along the northwest coast of Cuba (Cabo San Antonio to Cárdenas), the eastern shores of Yucatán and on south through British Honduras and Guatemala to Honduras. Midday hour, low tides occur on the northeastern shore of Cuba and at Cabo Gracias a Dios, Nicaragua.

An essentially diurnal type tide will prolong the duration of the low water stand up to 4 to 6 h. The majority of the localities with tides of the first class do exhibit diurnal cycles at the times of maximum north or south declination of the moon. Cuba, Haiti, the Dominican Republic and Culebra, however, have tides of a semidiurnal character, which means that the lower water stands will be of shorter duration, of the order of 2 to 3 h. All localities with second class tides are of

this kind. It is expected that midday, low water stands of the diurnal type will prove to be more important in causing mass kills.

Even though it is generally understood that West Indian reefs are usually not exposed at low tide (NEWELL, 1962; WELLS, 1957), a slight drop in the water level on shallow reefs may well result in reduced circulation and subsequent heating of the overlying water. MAYER (1914) recorded one such incident observed at Dry Tortugas, Key West, Florida as follows: "... after several hot, calm days, the shallow water over Bird Key Reef rose to 33° to 38 °C and Dr. L. R. CARY observed that large numbers of *Diadema*, *Octopus*, *Fissurella*, and other mollusks and small fishes were killed in considerable numbers over extensive areas, and corals were injured even when not exposed to the air." Temperatures of up to 40 °C were observed by RANDALL et al. (1964) in the inshore waters of the Florida Keys.

Of equal significance, and apparently of common occurrence, is the flotation of numerous urchins of several species following very low tides (RANDALL, 1964). This would imply exposure of shallow areas, resulting in loss of moisture and increased buoyancy. In the tolerance experiments to atmospheric drying, *Diadema*, *Lytechinus* and *Triploneustes* which had died after 3 h exposure usually floated; submerged urchins killed at higher temperatures did not float. The presence of numerous, empty echinoid tests in shallow water on the reef flat indicates that subtidal animals killed by high temperatures probably do not become sufficiently buoyant during decomposition to float away. Clearly, though, mass transport of exposed, dead echinoids may occur thus leading to allochthonous deposition and an erroneous impression of echinoid distributions in paleoecologic studies.

STODDART (1962) has noted that certain atolls in British Honduras are frequently exposed, due to north winds which may depress the normal sea surface level. It is possible that the echinoid fauna of the reef flats is subject to seasonal kills in British Honduras, since the critical tides are of the class two type and the flats are broad and shallow. For example, the reef flats ranged in depth from 30 to 46 cm to 90 to 180 cm, and from 18 to 27 m to 180 m in width. Brief reference was given by SMITH (1941) to "very hot" water accompanied by low tides during June, 1939 in British Honduras. Although meteorological factors were not observed to seriously affect the predicted low water stands at La Parguera as they do in British Honduras, such atmospheric disturbances have been shown to be an important factor elsewhere, particularly on the French Mediterranean Coast where the amplitude of the mean spring tides does not exceed 30 cm (COLMAN and STEPHENSON, 1966). Since the tidal range is so slight, echinoids are probably little affected on exposed shorelines subject to splashing and spray even at low water. Also, echinoid populations living on shorelines with a relatively steep gradient, such as at

¹ A recent echinoid kill observed on the Atlantic side of Panamá deserves mention here. At Galeta Pt. approximately 100 individuals of *D. antillarum* were found dead on the reef flat on September 12, 1967, presumably a result of low water kills which accompanied a series of + 3.0 cm midday, low tides.

Barbados (LEWIS, 1960) and Dominica (KIER, 1966), would probably be little affected at low tide.

Shallow pools situated on the landward side of beachrock formations are subject to intense heating which can lead to mass kills during periods of midday, low water exposure. On the north coast of Puerto Rico near Cueva del Indio (east of Arecibo), hundreds of recently killed *Diadema* and *Tripneustes* were observed in such enclosed pools on June 27, 1967, following a series of low tides. The water temperatures measured in 3 pools of 30 cm depth were 38.0 °C, 39.3 °C and 40.0 °C around 2:00 PM.

That high lethal temperatures and desiccation were responsible for the sudden mortality of echinoids in the field was verified by establishing the time to death of the affected species under controlled conditions. *Lytechinus* and *Tripneustes* occur abundantly on the reef flat, with densities of 16.8 and 1.3 individuals per m², respectively, and both showed a comparatively low resistance to exsiccation and heating. *Lytechinus* and *Tripneustes* both succumbed after 2 h submersion at 36 °C or 2 to 3 h exposure to atmospheric drying conditions realized in the field. As mentioned previously, *Diadema* was killed on the Dry Tortugas reefs, where the water temperature rose as high as 38.0 °C. MAYER (1914) found the upper thermal limit of *Diadema* from Tortugas to be 37.4° to 37.6 °C after an exposure of about 4 h and *Lytechinus variegatus* from Montego Bay, Jamaica to be 37.7 °C after about 6 h. The test animals were brought up to these high temperatures gradually from ambient temperature at a rate of about 2 °C per h.

In order to ascertain whether death was due to a sudden change in temperature or to the high test temperature alone, a thermal gradient was employed (0.2 °C/min maximum), of the order of magnitude used by other workers (NEWELL, 1964). The apparent higher tolerances of *Diadema* and *Lytechinus* determined by MAYER (1914) over a lower gradient of 2 °C/h are not in disagreement with the present findings since exposure to the highest temperatures was of relatively short duration. In fact, a rough plot of MAYER's data shows a survival of both *Diadema* and *Lytechinus* for about 1 h at 36 °C. These results substantiate the belief that attainment of a high lethal temperature either over an abrupt or gradual thermal gradient is of little consequence.

Ideally, additional test animals should have been employed to more precisely show the time to death-temperature relations of the various species studied. Nonetheless, a rough plot depicting such data (obtained from Fig. 9) demonstrates a fundamental similarity to the family of curves reported on by ORR (1955) for a variety of marine animal groups. Graphically this relationship describes a hyperbolic trace, concave upwards. *Brissus*, *E. viridis* and *E. lucunter* were the hardiest species and accordingly their curves are located comparatively far out along the abscissa.

Severe low water kills due to desiccation and high temperature stress accompanying calm weather have been observed by HODGKIN (1959) in western Australia and by TOKIOKA (1966) in Seto, Japan. HODGKIN's observations showed that the kills affected most of the upper shore biota unselectively. Echinoids which succumbed were *Echinometra mathaei*, *Tripneustes gratilla* and *Heliocidaris erythrogramma*. It seems that the echinoid mortalities observed by TOKIOKA recur annually; species affected were *Mespilia globulus* and *Anthocidaris crassispina*. Windrows of floating urchins have been seen on one shore every year. The West Indian cidarid, *Eucidaris tribuloides*, has not been observed intertidally on coral reefs along the south coast of Puerto Rico.

Some extreme high temperatures recorded at low tide periods during calm weather indicate that lethal thermal extremes are also closely approached or realized in certain tropical areas of the Indo-Pacific. For example, on the reef flat at Low Isles Reef, ORR and MOORHOUSE (1933) observed maximum temperatures of 37.8 °C in a shallow sandy pool and 37.1 °C among growing coral, although no mortalities were reported. An incredibly high temperature of 56 °C, reported by GARDINER (cited in ORR and MOORHOUSE, 1933) for low tide pools with living coral at Minikoi, indicates a higher thermal tolerance of reef organisms than generally realized.

CARRIÓN (personal communication) observed many dead, floating *Diadema* and other echinoids at Laurel Reef on December 9, 1961. During this time the lowest tides of the fall and winter months were scheduled to occur at night. On the preceding day, a 17 cm tide was predicted for 12:24 AM. This record emphasizes the importance of exposure of echinoids to atmospheric drying, thus leading to mass mortalities unconnected with any temperature effect. It has also been observed that *Lytechinus* and *Tripneustes* are susceptible to desiccation and subsequent flotation when the test is only about half immersed.

Although direct exposure of *Lytechinus* and *Tripneustes* to sunlight under a thin layer of water did not result in significant mortality after a recovery period of 48 h, it is not possible to say at this point what long term deleterious effects the shorter radiations may have had on the superficial tissues of the echinoids. This is especially true for *Tripneustes* with relatively little pigmentation, and which does not heap its test so thoroughly as does *Lytechinus*. The tolerance of the urchins to UV radiation was determined under nearly maximal, natural dosage at Puerto Rico's latitudinal position (18°00' to 18°30' N). Essentially all of the radiations between 300 and 400 mμ impinged directly on the animals, since virtually no attenuation occurs within this range to a depth of 0.5 m (DIETRICH, 1957). The observations were carried out on the clear, sunny day of June 8, some 3 weeks following the zenith sun, which again occurs in the first half of August (Nautical Almanac, 1967). The daily solar radiation recorded

approached the highest, monthly average value in April at 10° N latitude (SVERDRUP et al., 1942, p. 103).

At times tropical downpours exact a heavy toll on shallow, sedentary forms. Mortalities of this kind were observed by GOODBODY (1961) to follow heavy rains of over 100 mm in a 24 h period; surface salinities in Kingston Harbor fell from 35‰ to less than 20‰. Marked dilution does not occur at La Parguera, which has no permanent rivers and experiences free circulation. Following Hurricane Edith, which caused a precipitation of about 100 mm for 2 days, the salinity at Cayo Májimo was reduced by less than 3‰ from the normal. On May 16, 1965, around 13 mm of rain fell on Caracoles Reef at low tide; the salinity of isolated pools, however, fell to only 33.30‰, about 2‰ below normal. Even if a greater dilution were realized, however, to as low as 20 to 25‰, probably most echinoids would survive in the absence of prolonged exposure. *Strongylocentrotus purpuratus*, in the lower intertidal zone on the California coast, was shown to survive for 2 to 3 h in 50% and 72% seawater (GIESE and FARMANFARMAIAN, 1963).

A weakening of echinoids from exposure to the sun, assuming such a harmful response, may not be too important in rendering the animals more susceptible to predation. The two most prominent predators of sea urchins observed around La Parguera on shallow reefs are the ruddy turnstone *Arenaria interpres morinella* and the porcupine fish *Diodon hystrix*; their success in feeding on urchins, particularly *E. lucunter*, apparently depends more on first encountering the prey than anything else. At low tide *Arenaria* moves along the exposed reef flat in small flocks pecking through the peristomial membrane of all animals present in order to feed on the internal organs. On August 27, 1965, three of the turnstones left the following numbers of dead *E. lucunter* behind in separate piles after a feeding period of approximately 30 min: 8, 14, 15, 20, 22, 31, 36. This bird is a common fall and spring transient; a fairly common winter resident; appearance in the summer is due only to a few stragglers (F. ROLLE, personal communication). *Diodon* moves onto the reef flat at high tide at night where it feeds on small (test diameter 2 to 3 cm), whole urchins; as many as six *E. lucunter* have been found in the stomach of this fish.

Still, it is not enough to just keep record of the obvious mortalities due to environmental extremes or predation. Recent studies reveal that more subtle factors which may influence the size of successive generations will also have to be taken into account. Some pertinent examples are a depression in the feeding rate of *Tripneustes* and *Lytechinus* during the summer and a higher growth rate of the two species during the winter (MOORE and McPHERSON, 1965; LEWIS, 1958); an unusually high proportion (> 50%) of *Lytechinus* and *Tripneustes* were hermaphrodites and *Lytechinus* had an abnormally formed test following a particularly cold winter (MOORE et al., 1963 a, b).

SHARP and GRAY (1962) have shown that the heaping response in *Lytechinus* is a behavioral reaction which affords shelter from intense light, particularly of shorter wavelengths. It seems unlikely from evidence gathered in this study that the heaping response in *Lytechinus* could significantly abate the harmful effects of drying and heating at low tide, as was suggested by ORTON (1929) for *Psammechinus* on English shores. Naked *Lytechinus* exposed to natural, midday, atmospheric drying had completely succumbed after 2 h, and the group of individuals with a protective cover of debris had suffered partial mortality after 2 and 3 h exposure. In both groups after 2 to 3 h desiccation, the initial body weight had declined to about 80%. The algae and *Thalassia* blades used as heaping material had lost considerable moisture by the first 1 to 2 h of exposure.

It is doubtful that acclimatization to the extreme high temperatures which frequently accompany midday, low tidal exposures can be of much significance in an enhancement of survival, since the heating is erratically intermittent and of short duration. However, acclimatization to higher summer temperatures would be expected in shallow water species subject to a gradual, seasonal rise of this parameter. READ (1967) has shown that subtidal populations of *Lima scabra* at La Parguera undergo an increase of about 1.3 °C in their lethal temperature in summer as compared with winter.

Some investigators have defended the thesis that the zonation of adult organisms on the shore is in close adjustment with the prevailing thermal conditions and little affected by even exceptional extremes of temperature (e.g. SOUTHWARD, 1958). This certainly seems to apply to most intertidal mollusks; some boreal species have been observed to survive for several hours at -15 °C, where 60 to 70% of the body water was actually frozen (KANWISHER, 1955). Conversely, ORTON (1929) has shown that the distribution of *Echinus esculentus* in the intertidal zone is partly controlled by the occurrence of low water spring tides during the hottest part of the day and the coldest part of the night. HODGKIN's (1959) observations lend further weight to the potency of low tidal exposures and accompanying spells of hot weather in the control of zonation. This study has demonstrated in like manner how desiccation and high temperature stress kill off echinoids and other species which have populated reef flats following the previous year's exposure to these harsh conditions.

Summary

1. Mass kills of reef flat organisms, particularly the echinoids *Tripneustes ventricosus* and *Lytechinus variegatus*, observed at La Parguera, Puerto Rico, over several years have coincided with midday low water spring tides, which occur suddenly during spring and early summer.

2. The principle study area was located on the "inner reefs" Májimo and Caracoles; their shoal areas of about 25 m breadth are exposed at low water stands a few cm below MLW.

3. Atmospheric weather conditions prevailing over the low tide periods, which contribute most importantly toward intense heating and stagnation, are: clear skies, reduced wind velocities and increasing air temperatures with the onset of the summer season. At low tide the sea-water temperature in isolated pools and on shallow flats may rise to 35° to 40° C for as long as 1 to 2 h. A reduction in tonicity of the water from rains or river outflow does not seem to affect the local biota.

4. Mortalities involving a high proportion of the echinoid populations, as high as 86% of *Tripneustes* and 64% of *Lytechinus*, were observed on several occasions. Other organisms adversely affected were *Thalassia*, brachyuran crabs, chitons and ophiuroids.

5. Exposure of echinoids directly to atmospheric drying leads to a linear loss in weight with time. *Lytechinus* and *Diadema* were least tolerant; they were all dead at 2 h, after having declined 15 to 20% in body weight. *Brissus* and *Tripneustes* had died after 3 h with a nearly similar loss in weight. *E. lucunter* survived longest and died only after having lost 30% of its initial weight. Tolerance to desiccation was usually higher when the test animals were afforded some kind of protection against direct exposure. *Lytechinus* with heaped debris succumbed completely only after 4 h. Shaded *Diadema* were dead after 5 h, whereas *Tripneustes* and *Echinometra* were still alive after 6 h. *Brissus* buried in sand had died at 2 h exposure, from heating of the water contained in the sediment. These established tolerance limits to exsiccation show that a high proportion of individuals in a mass echinoid kill die from exposure to air.

6. The tolerance limits of echinoids to high sea-water temperatures showed that animals left behind in shallow water areas by a receding tide will also succumb after a certain critical time at the higher temperature. In an ascending order of resistance, *Tripneustes* did not survive a temperature of 35° C after 4 h exposure, *Lytechinus* and *Diadema* 36° C after 2 h, *Brissus* 36° C after 4 h, *Echinometra viridis* 38° C after 3 h, and *E. lucunter* 39° C after 3 h.

7. A single, simple experiment showed that *Tripneustes* exposed directly to the sun's rays (under a thin stratum of water of constant temperature) for up to 4 to 5 h die in 3 days. Both unprotected and protected *Lytechinus* were not so affected.

8. Quantitative assessment of the distribution of echinoids on the reef flat indicated high population densities in zones subject to exposure and heating. The most abundant forms (and their highest mean densities per m²) were *E. lucunter* (27.7), *Lytechinus* (16.8), *Tripneustes* (1.3).

9. Census records of *Lytechinus* and *Tripneustes*, following the severe mortality in the spring season of

1965, showed a steady increase in numbers over a year's time. *Lytechinus* demonstrated a ninefold increase and *Tripneustes* nearly a threefold increase. *E. lucunter* actually declined in abundance with no apparent explanation. Data from size class analyses and breeding activity indicate that the build up of *Lytechinus* and *Tripneustes* populations was probably due to recruitment of young urchins which developed from the spring or summer breeding period of 1965.

10. Examination of predicted tides for the Caribbean region reveal that tidal cycles with a relatively abrupt shift in the timing of low water stands to the midday hours of the day in the spring and summer seasons occur at several localities along the coasts of Central and South America, and in the West Indies. Although only brief reference has been made to tide-related echinoid kills, it is believed that such mass mortalities will eventually be found to be of common occurrence in this marine area.

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