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Water-level Fluctuations, Emersion Regimes, and Variations of Echinoid Populations on a Caribbean Reef Flat

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This paper examines fluctuations in water level over a Caribbean reef flat at Punta Galeta, Panamá. In an analysis of approximately ten years of records, the mean diurnal range of the tides was 24·5 cm and varied <2 cm from year to year. Daily mean water levels varied erratically over a range of approximately 30 cm. Monthly mean water levels fluctuated seasonally over a range of about 10 cm and were consistently higher than those at the regional tidal reference station at Cristóbal. On days with more wave action, water levels at Galeta increased relative to those at Cristóbal, suggesting that waves were ' pumping ' water onto the reef flat. The monthly mean water levels at the two sites were not correlated, indicating that tidal data from conventional stations in deeper water cannot be extrapolated to reef flats, except as estimates of minimum potential water levels.

Most of the reef flat was within 6 cm vertical span just below mean lower low water. The highest elevations within this range were exposed above water level for an average of 918 hours per year, as compared with 144 hours per year at the lowest elevation. Most exposures lasted less than 10 hours, with a modal duration of 3–5 hours; however, exposures longer than 12 hours occurred at nearly all elevations in all years. Exposures of the reef flat were most frequent between February and June and between August and November, a pattern apparently caused by a combination of seasonal oscillations of regional sea levels, the annual pattern of the solstitial tides, and waves generated by seasonal trade winds.

The fluctuations in water levels apparently affected the abundances of some species of sea urchins on the reef flat. Populations of *Lytechinus variegatus* and *Diadema antillarum* declined or disappeared from the reef flat during seasons of repeated subaerial exposures, but recolonized the habitat in periods of higher water levels. Although they are reported to suffer heavy mortality during emersion, *Echinometra lucunter* and *E. viridis* did not exhibit reductions in abundance that were synchronous with the seasonal exposures of the reef flat.

Introduction

Although the amplitudes of Caribbean tides are generally between 10 and 50 cm, with most less than 20 cm (Kjerfve, 1981, U.S. National Ocean Survey, 1983), fluctuating

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water level is an important variable affecting physical and biological processes on Caribbean reefs. In combination with other factors, the height and rate of change of the tides determine the speed, volume, and direction of currents over Caribbean reef structures (Glynn, 1973; Roberts *et al.*, 1975; Roberts & Suhayda, 1983), thereby determining rates of solar heating of the water (Glynn, 1973; Jaap, 1979). In addition, water depth over these reefs is one of the factors controlling the distribution of wave energy over the reef surfaces (Roberts *et al.*, 1975; Roberts & Suhayda, 1983).

Caribbean reef flat communities on surfaces within the lower range of the tides are particularly affected by fluctuations of water level. Though periodically exposed above water level, these communities tend to be dominated by organisms with little tolerance for the effects of emersion. During low tides desiccation, direct insolation, temperature extremes, rainfall, and predation by shore birds cause extensive mortality or diebacks of algae, sea grasses, corals, sea urchins and other invertebrates (Mayer, 1914; Randall *et al.*, 1964; Glynn, 1968; 1972; 1973; Jackson, 1973; Birkeland *et al.*, 1976; Hendler, 1977*b*; Jaap, 1979; Hay, 1981*a*; Sebens, 1982). Holocene reef flats themselves are results of changes in species composition and accretion rates that occur when the upwardly growing reefs reach the range of the tides and suffer the effects of subaerial exposures (Macintyre & Glynn, 1976).

Emersion of reef flats during extreme low tides is probably the most severe perturbation of physical origin experienced by the organisms in reef flat communities, other than damage from hurricanes and tropical storms. Information regarding the temporal patterns, frequencies, amplitudes, and causes of fluctuations in water level over reef flats is therefore fundamental to understanding ecological processes in these habitats. Studies in other locations have generally relied on extrapolating tidal information from deeper locations to reef flats, and some relationships have been noted among the predicted tides, deeper water tidal data, and the water level regimes over reef flats (Glynn, 1968; 1973). However, it has been suggested that water levels over shallow reef flats cannot be reliably predicted from tables of the estimated tides or entirely derived from measurements of deeper water tides (Glynn, 1972; Pugh, 1978; Pugh & Raner, 1981). Tank models indicate this is partly because waves 'pump' water onto shallow reef structures, raising water levels above those of the open ocean (Sibul, 1955). Accurate measures of water levels over reef flats therefore must be obtained in these habitats themselves. In this paper we describe tidal and longer term variations in water levels over a Holocene reef flat on the Caribbean coast of Panamá for 1973–1983. Possible causes of variation are examined, and some of the biological effects are illustrated using long-term censuses of sea urchin populations on the reef flat.

Site description

Water-level measurements were made on a fringing reef flat at Punta Galeta, on the Caribbean coast of Panamá (9°24′18″N, 79°51′48·5″W), the site of the Galeta Marine Laboratory of the Smithsonian Tropical Research Institute. The reef flat is one of a series occurring along this coast. The coring and radiocarbon studies of Macintyre and Glynn (1976) have established the Holocene origin of this reef, which began growing about 7000 years ago. The present reef flat was formed when the upward growing reef reached the lower range of the tides. The *Acropora palmata* framework was then capped on the seaward side by a matrix of crustose coralline algae and vermetid gastropods and filled on the landward side by coral rubble and sediment (Macintyre & Glynn, 1976).

TABLE 1. Monthly variation of winds from the northern 3 octants (northwest, north, and northeast) for 1982

Month	Mean of wind speeds from the northern 3 octants ($km\ h^{-1}$)	Percent time that winds were from the northern 3 octants
Jan	20·9	71
Feb	22·8	88
Mar	24·7	97
Apr	21·1	77
May	13·3	42
Jun	11·9	48
Jul	16·7	72
Aug	16·7	80
Sep	12·1	48
Oct	9·2	43
Nov	17·4	78
Dec	23·7	91

Consequently the surface of the reef flat is at about mean low water level; it is similar in appearance to the Puerto Rican reef flats in the photographs of Glynn (1968). Further description of Galeta reef can be found in Cubit and Williams (1983).

This coast has mixed semidiurnal tides. At the regional tidal reference station at Cristóbal, about 8 km southwest of Galeta, the mean diurnal range of the tides is 33·5 cm, and the mean range is 21·3 cm (U.S. National Ocean Survey, 1983). The Cristóbal tide gauge is located behind the breakwaters of Bahia Limón, where it is protected from waves arriving from the open sea. In addition to the normal cycle of the astronomical tides, there is an annual variation of approximately 8 cm in mean sea level at Cristóbal with a peak around November and a low around March–April (Pattullo *et al.*, 1955; Glynn, 1972).

Weather

In the following sections we refer to certain aspects of weather as affecting water levels or stressing the reef biota during subaerial exposures. The annual weather pattern in this part of Panamá is generally described as being divided into a ' dry season ', a ' little dry season ', and a ' rainy season '. The dry season at Galeta usually begins in late December, ends in April, and is characterized by reduced cloud cover, little rainfall, and northerly trade winds averaging approximately 20–25 $km\ h^{-1}$ (Meyer & Birkeland, 1974; Meyer *et al.*, 1975; Hendler, 1976; 1977*a*; Cubit, Windsor, and Thompson, unpubl. data). As an example, seasonality of the trade winds for 1982 is shown in Table 1. The seaward side of Galeta reef faces north, into the trade winds and the wind-generated waves. The rainy season makes up most of the remainder of the year, with winds of reduced speed and more variable direction, increased cloud cover, and approximately 300 cm of rainfall per year at Punta Galeta. The ' little dry season ' or ' veranillo ' is weather similar to that of the dry season which sporadically interrupts the rainy season, usually between July and October (Meyer & Birkeland, 1974; Meyer *et al.*, 1975; Hendler, 1976; 1977*a*, *b*). Panamá is south of the Caribbean ' hurricane belt ' (Neumann *et al.*, 1981), but long period swells reach this coast from cyclonic storms passing through the Caribbean to the north. Like other sites within the Caribbean Sea (Roberts *et al.*, 1975), this site is protected from the high latitude swell of the Atlantic Ocean.

Methods

Measurements of water levels

Water levels above the reef flat were measured with a Stevens Type A water level recorder (Leupold and Stevens Inc., Beaverton, Oregon, U.S.A.). The pen of this mechanical chart recorder is directly driven through a 5:1 gear reduction by a 21 cm diameter float and counter weight. Water levels were recorded from a 25 cm diameter still well; the entrance to the still well was a tube 2·54 cm in diameter and approximately 58 cm long. A filter of bronze wire (coarse scouring pad material) in the entrance tube inhibited the growth of fouling organisms, excluded sediment, and damped short-period wave oscillations. The recorder and still well were mounted in a depression on the reef flat approximately 36 m from its seaward edge. Water flowed in a seaward–landward direction past the recorder, exiting through a channel on the landward side of the reef. Rates of chart movement and accuracy of water level measurement were manually checked approximately 5 times per week. Water level data for the years 1973 to 1977 were recorded by the same apparatus and have been reported in Meyer and Birkeland (1974), Meyer *et al.* (1975), and Hendler (1976; 1977*a*). For analysis, elevations of water level at hourly intervals were either measured directly from the charts by hand, or were read into a computer using a Hewlett Packard 9864 electronic digitizer. Water-level data are expressed in reference to an arbitrary datum level at the base of the tide gauge.

Censuses of sea urchins

Populations of sea urchins were censused in permanent transects in three habitats on the reef flat: (1) in a zone formed primarily by crustose coralline algae and the fleshy red alga *Laurencia papillosa* (Forsskal) Greville at the seaward edge of the reef flat, (2) in a bed of the sea grass *Thalassia testudinum* Konig and Sims about 45 m from the seaward edge, and (3) in an area of coral rubble and beds of the red algae *Laurencia papillosa* and *Acanthophora spicifera* (Vahl) Borgesen in the central area of the reef flat, approximately 70 m from the seaward edge. Each transect was 1 m wide and 20 m long. The latter two transects were established in 1971 and 1972 by D. Meyer and subsequently censused by G. Hendler (Meyer & Birkeland, 1974; Meyer *et al.*, 1975; Hendler, 1976; Hendler, 1977*a*, *b*). In late 1977 the transect at the seaward edge of the reef flat was added and transects were censused monthly, except when waves, turbidity, strong currents, or high water levels prevented an accurate count. We attempted to count urchins of all sizes, but individuals with test diameters less than 5 mm were rarely seen and may have been hidden in small cavities of the reef.

Results

Fluctuations of water level over the reef flat

In the ten-year period from 1973 to 1982 water level ranges were relatively consistent from year to year. The diurnal range of the tides (i.e. the difference between the highest and lowest tides of each day) averaged approximately 24·5 cm; year-to-year variation was within 2 cm of the 10 year mean (Table 2). The mean levels of the lower low tides and higher high tides of each day (' MLLW ' and ' MHHW ') were approximately 32 cm and 56·5 cm, respectively, above the Galeta datum level, again with variation among years being within 2 cm of the ten-year mean (Table 2). The range between extreme low and high water levels of each year averaged 59 cm, more than double the diurnal range:

TABLE 2. Basic tidal statistics for the reef flat at Galeta Point. Measurements are in cm above Galeta datum

	Ranges		Levels			
			Daily		Yearly	
Year	Mean diurnal[a]	Yearly[b]	Mean min.	Mean max.	Minimum	Maximum
1973	26·4	62·0	30·3	56·7	21·0	83·0
1974	25·8	64·0	32·0	57·7	21·0	85·0
1975	23·7	56·0	31·3	55·0	21·0	77·0
1976	24·0	64·0	33·1	57·2	21·0	85·0
1977	23·2	52·0	30·5	53·6	20·5	72·5
1978	24·3	58·4	32·0	56·4	20·0	78·5
1979	23·9	56·9	32·7	56·7	21·2	78·1
1980	23·5	60·0	34·0	57·5	22·4	82·3
1981	24·8	59·2	31·7	56·6	22·9	82·0
1982	24·9	59·9	32·6	57·5	23·5	83·4
Means	24·5	59·2	32·0	56·5	21·5	80·7

[a] The average difference between the highest and lowest water levels of each day.
[b] The difference between the highest and lowest water levels of the year.

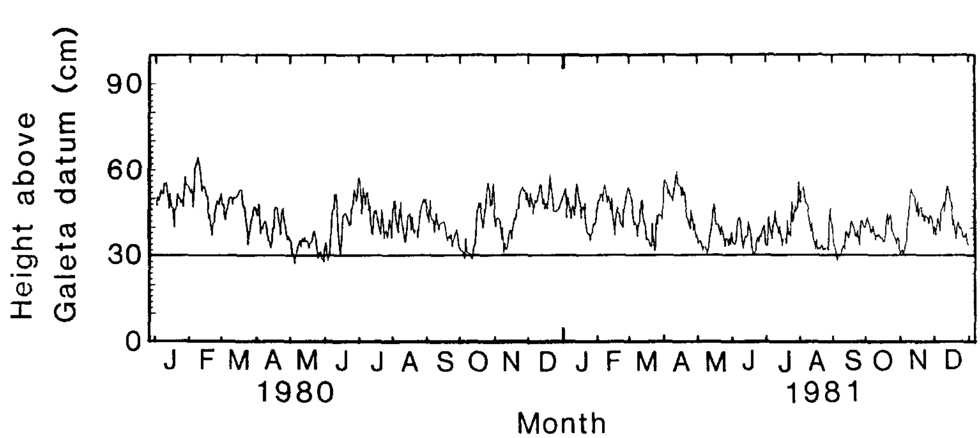

Figure 1. Variations of daily mean water levels over the Galeta reef flat for the years 1980 and 1981. Heights are above the Galeta datum level. The line at 30 cm indicates the upper elevation of the reef flat.

the lowest and highest water levels recorded each year averaged 21·5 cm (range 20·1 to 23·5 cm) and 80·7 cm (range 72·5 to 85 cm), respectively, above the datum level (Table 2).

Many of the fluctuations in water level over the reef flat were non-tidal. Even though astronomical tides have little effect on mean water levels, daily mean water levels shifted erratically over a range of approximately 30 cm (Figure 1). Water levels averaged by month fluctuated semiannually with an amplitude of approximately 10 cm [Figure 2(a)]. Water levels at Galeta were highest in the dry season months of December–February and lowest in the beginning of the rainy season (April–June), followed by a second high in July–August and second low in September–October [Figure 2(a)].

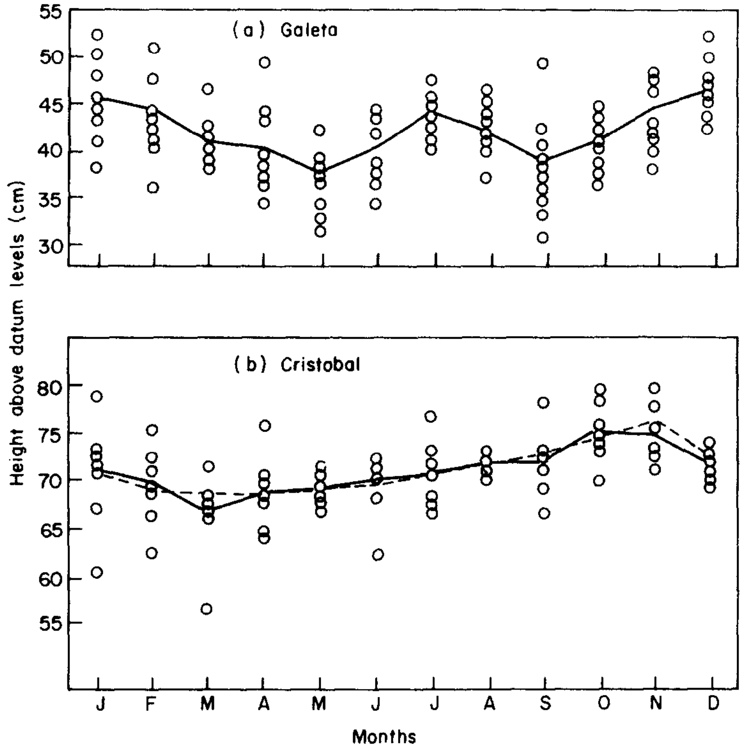

Figure 2. Mean monthly sea levels at Galeta and Cristóbal. Vertical scales are the same; water levels are above the datum level for each site. The Galeta data are for the years 1973 to 1983, the Cristóbal data are for 1973 to 1979. The solid lines represent the means for these periods; the mean for Galeta for the years 1973 to 1979 does not deviate more than 1 cm in any month from the 1973–1983 mean. The dashed line in the Cristóbal plot represents the long term means determined by Pattullo *et al.* (1955). The data for Cristóbal are courtesy of J. Brady of the Panamá Canal Commission.

Causes of variations of water level over the reef flat

Visual examinations of the original pen tracings showed that changes in mean water level were not a result of a cancelling or damping of high or low waters, nor of other gross distortions of the tidal curves. The traces were of tides oscillating around the varying mean water level. The only observed exceptions were during extreme low tides (less than 30 cm above Galeta datum) when the reef flat depression where the tide gauge was mounted drained more slowly than the tide fell, attenuating and skewing the lowest part of the tidal curve.

Correlations between monthly mean water levels at Galeta and Cristóbal were weak, indicating that the seasonal variations of water level over the Galeta reef flat were not part of a coast-wide phenomenon: for the years 1973–1979 the correlations were significant only in the years 1976 and 1978 (Table 3, Figure 2). (Cristóbal data for later years were not used because of problems with the Cristóbal tide gauge that affected its accuracy.) The patterns of monthly mean water levels over the year did not coincide: the major peak at Cristóbal was in October–November as compared with the peak at Galeta in December–February (Figure 2).

Wave action could have contributed to the differences in water levels between Cristóbal and Galeta. This hypothesis was tested by comparing water levels between

TABLE 3. Correlations between monthly mean sea levels at Galeta and Cristóbal[a]

Year	N (months)	r
1973[b]	9	0·09
1974[c]	12	0·04
1975[d]	12	0·15
1976[e]	12	0·57*
1977	11	0·02
1978	12	0·57*
1979	12	0·16

[a] Cristóbal data courtesy of J. Brady, Panamá Canal Commission.
[b] Galeta data from Meyer and Birkeland (1974).
[c] Galeta data from Meyer *et al.* (1975).
[d] Galeta data from Hendler (1976).
[e] Galeta data from Hendler (1977).
* Correlation significant at $P<0{\cdot}005$.

TABLE 4. Differences and correlations of higher high water levels (HHW) between Cristóbal and Galeta on calm and rough days. Differences are the Cristóbal level minus the Galeta level at the same high tide

Wave conditions	N	Difference of HHW levels in cm ($\bar{x}\pm1$ s.d.)	Correlation between HHW levels (r)
Calm	12	38·5±2·7*	0·90**
Rough	13	26·6±3·9*	0·90**

* Difference between the means is significant at $P<0{\cdot}001$ (by t-test).
** Correlations are significant at $P<0{\cdot}001$.

sites on calm and rough days. Such days were selected by visual inspection of the original pen traces on the charts from the Galeta tide gauge. The criteria for acceptably low wave action were determined from fluctuations in the pen traces on days when field observations showed that waves had little effect on water levels over the reef flat, an effect that was least at high tide. In the year of comparison, 1978, only 12 days fit these criteria, and occurred between January and April. To avoid the possible confounding effects of seasonal variations, rough days (those with the maximum amplitude and frequency of wave activity in the chart trace) were selected from the same months. For both sets of conditions we compared only the level of higher high water (HHW). Within the categories of calm and rough days, the levels of HHW were strongly correlated between sites; however, on rough days water levels at Galeta were approximately 12 cm higher relative to those at Cristóbal (Table 4).

Because filtering of short period waves by the inlet to the still well was variable, wave information in the chart recording could not be quantified in units that were comparable over time; therefore, to further examine the possible effects of waves on water levels we used wind runs out of the northerly 3 octants (the seaward side of the reef flat) as an indirect measure of wave action. In this analysis total daily wind runs from the northeast, north, and northwest were compared by correlation with daily mean water levels, on a

TABLE 5. Correlations of mean daily water levels with total daily wind runs out of the northern 3 octants (NE, N, NW)

Year	*r*
1974	0·3226*
1975	0·3461*
1976	−0·026
1977	0·1027
1978	0·0265
1979	0·5647*
1980	0·5742*
1981	0·5908*
1982	0·3806*

* Correlations are significant at $P < 0{\cdot}01$.

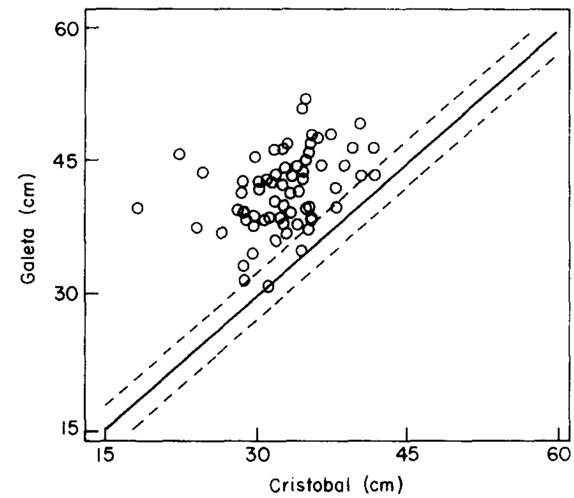

Figure 3. Mean monthly sea levels at Galeta plotted against Cristóbal's for the years 1973–1979. For comparison, the datum level at Cristóbal has been adjusted to approximate Galeta's. The solid line represents estimated equal water levels at the two sites; the broken lines indicate this estimate ±1 s.d. (see text for further explanation). In this period as a whole there was no significant correlation between sea levels at the two sites ($r = 0{\cdot}13$, $P > 0{\cdot}5$), although there were significant correlations in some individual years (see Table 3).

year-by-year basis. In six of the nine years examined, daily mean water levels were significantly correlated with the daily wind run out of the northern 3 octants ($0{\cdot}3 < r < 0{\cdot}6$; Table 5).

The HHW levels on calm days were used to estimate the difference between Cristóbal and Galeta datum levels; that is, to arrive at an approximate datum level in common for the two sites. Most of the monthly mean water levels at Galeta were above the levels expected from this equality (Figure 3), again suggesting that factors, such as breaking waves (Sibul, 1955), were raising water levels over the reef flat at Galeta and were responsible for the general lack of correlation between water levels at Galeta and Cristóbal.

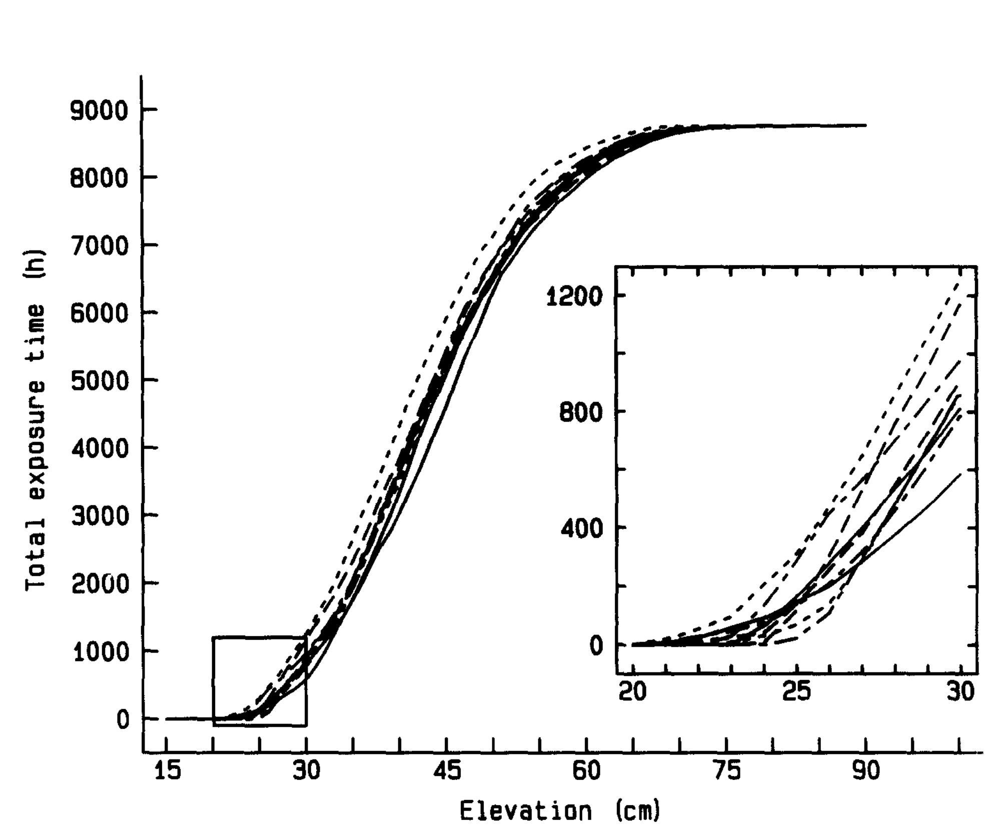

Figure 4. Total hours of exposure per year versus elevation. Inset shows detail of exposure time for elevations of the reef flat. The different lines represent different years; as shown at the 30 cm elevation in the inset, the lines from top to bottom are for the years 1981, 1975, 1974, 1983, 1982 (line of short dashes), 1979 (line of short and long dashes), 1980, 1978, and 1976. For this comparison the data have been standardized to a 365 day year. The years 1973 and 1977 have been omitted because of missing data.

Exposures of the reef flat above water level

At the time of this study, most of the surface of the reef flat was between 25 and 30 cm above the Galeta datum level. (The reef flat is probably growing upwards at about 1 mm year^{-1} [Macintyre & Glynn, 1976; Cubit, in press].) The highest parts of the reef flat (the seaward edge and loose coral rubble lying on the reef flat) were above water level when the water level registered 30 cm above Galeta datum. Most of the emersible substrate of the reef flat was above water level when the water level was at 25 cm (Meyer & Birkeland, 1974); areas not emersed at this water level were primarily in shallow depressions that drained slowly or held water throughout the period of the low tides.

The total time of exposure for the 30 cm elevation ranged from 785 h to 1168 h year^{-1}, averaging 918 h (s.d. = 140), as compared with total exposure times at the 25 cm elevation ranging from 22·5 to 287 h year^{-1}, averaging 144 h (s.d. = 85) (Figure 4). These comparisons do not include the years 1973, 1975, 1976, 1977, and 1979, which had more than a week of missing data in months of probable exposures.

For elevations of the reef flat between 25 and 30 cm, the durations of most exposures were less than 9 h, with a peak of frequencies between 3 and 5 h (Figure 5). The frequency distribution of exposures was slightly bimodal, with exposures of $\leqslant 9$ h forming one group, and exposures of > 12 h forming a second, much smaller, group.

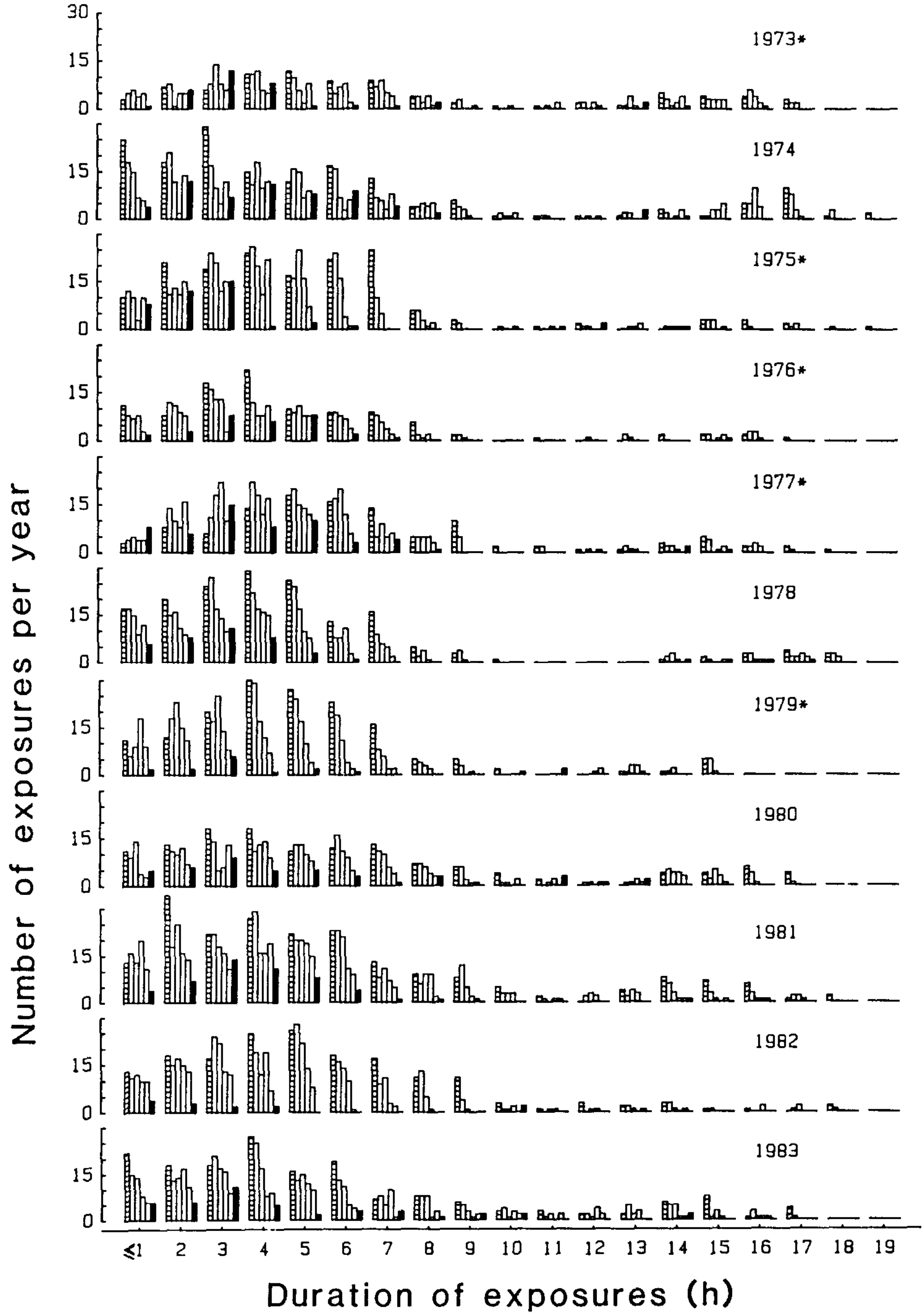

Figure 5. Frequencies of exposure durations for the Galeta reef flat, by tidal elevation. From left to right the sets of bars within each cluster represent elevations above the Galeta datum level as follows: 30·00–29·01 cm (with horizontal shading), 29·00–28·01 cm, 28·00–27·01 cm, 27·00–26·01 cm, 26·00–25·01 cm, and <25 cm (with solid shading). Graphs for years marked with (*) lack more than one week of data at times of year when exposures were probable (as shown in Figure 6) and may, therefore, underrepresent the total exposure time.

The 30 cm elevation experienced more than 100 exposures per year in the ⩽9 h range; the 25 cm elevation experienced about a third of this amount, except in 1982, when there were only 11 exposures in the ⩽9 h range. In nearly all years, all elevations were subjected to at least several exposures of greater than 12 h duration (Figure 5).

Exposures of the reef flat tended to be seasonal. Emersions of the reef flat were generally of shorter duration or lower frequency between November and February and between June and September, as indicated by the flatter sections of the cumulative exposure curves at these times of year (Figure 6). The total hours of exposure tended to accumulate rapidly in the period between February and June (the steep portions of the curves in Figure 6). Less consistent among years was a second concentration of reef flat exposures between August and November (Figure 6).

Daytime exposures of the reef flat followed a similar, but more restricted, pattern. In the years studied, a period of three to eight months extended from the end of one year into the beginning of the next year when water levels did not fall to the 25 cm level during the daylight hours. Daytime emersions of the reef tended to be concentrated immediately after this period, as shown by the relatively steep portions of the cumulative exposure curves in the second quarter of the year (Figure 6).

Effects of water level on waves

Waves tended to stop moving across the reef flat at water levels near MLLW. As measured from the original chart recordings for the years 1978–1982, the mean height of wave disappearance during a falling tide was 30·2 cm above Galeta datum (Table 6), corresponding to the emergence of the reef crest above water level. During the rising tide, waves washed over the crest into the depression around the tide gauge before the tide was able to seep or overflow into the depression; consequently, wave patterns reappeared in the traces at lower levels than they disappeared (Table 6).

Seasonal and year-to-year fluctuations in the abundances of sea urchins

Seasonal variations in the abundances of the sea urchins *Diadema antillarum* and *Lytechinus variegatus* on the reef flat were associated with the occurrence of subaerial exposures. These species essentially disappeared each year during the concentration of exposures that occurred between March and June; recolonization, if any, took place during the period of less frequent exposures in the last and first quarters of the year (cf. Figures 6 and 7). In contrast, the abundances of the two *Echinometra* species did not exhibit patterns of seasonal declines corresponding to exposures above water level (Figure 7).

In the longer term, *L. variegatus* and *D. antillarum* exhibited peaks of abundance in late 1972 to early 1973. *L. variegatus* was unusually abundant again in late 1983 and early 1984, as was *E. lucunter* on the reef edge and to a lesser extent in the mid-reef area (Figure 7). In 1983 *D. antillarum* had almost completely disappeared from all parts of the reef during an epidemic that was Caribbean-wide (Lessios *et al.*, 1984*a*, *b*); thus, it was not available to colonize the reef flat. The two *Echinometra* species in the reef-edge transects showed an additional peak of abundance in 1981. As will be discussed later, some of these peaks in abundance may have resulted from sea levels that were higher than usual.

Few other species of sea urchins were present in the transects. *Tripneustes ventricosus* was occasionally present in the transects in the *Thalassia* bed and mid-reef flat, and

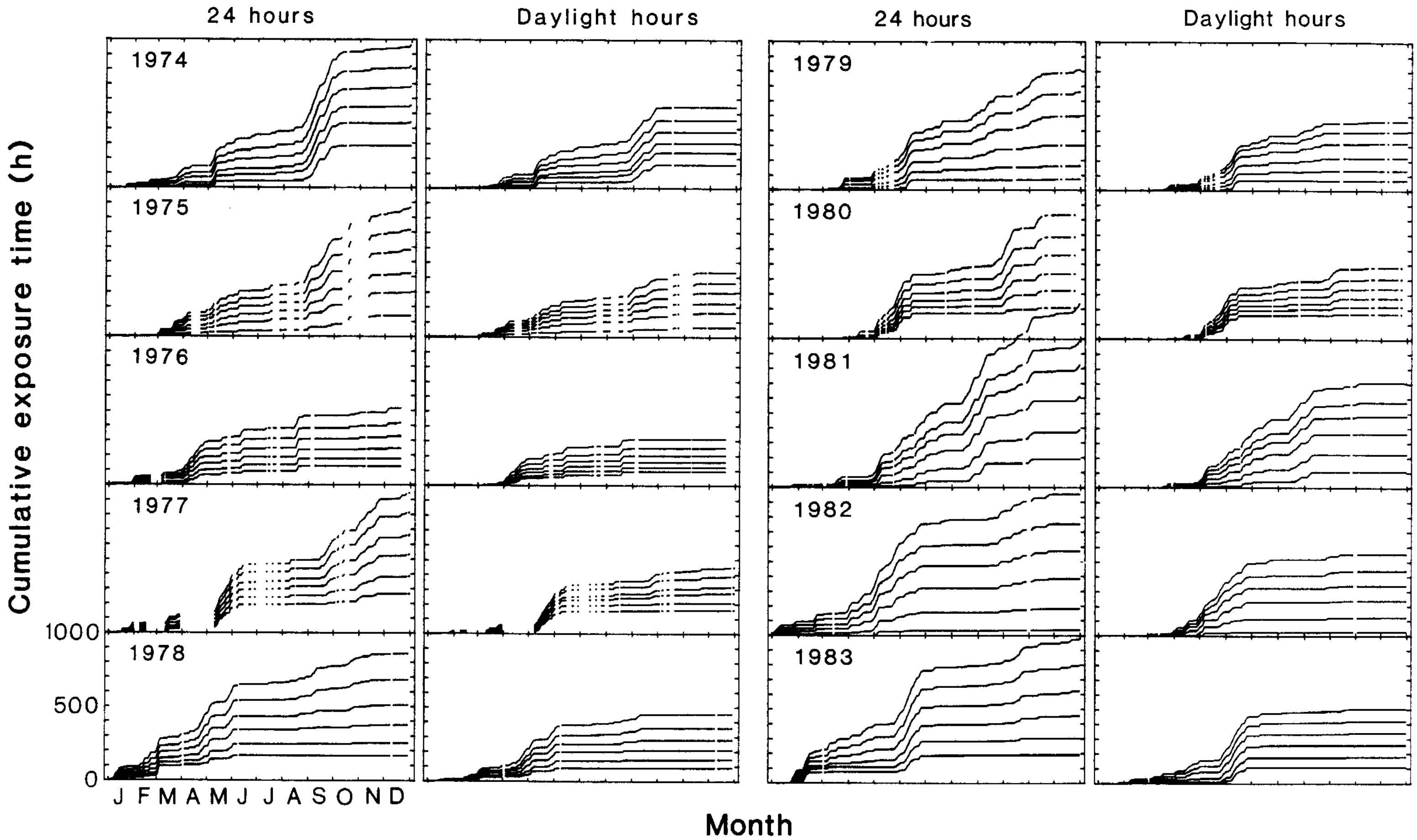

Figure 6. Seasonal and year-to-year variation in subaerial exposures of the Galeta reef flat. In the pair of figures shown for each year, the left figure shows the total exposure time for all hours of the day, and the right figure gives the total exposure time during the daylight hours (0700–1800). From top to bottom the six curves in each plot represent 1 cm decrements in elevation from ⩽30 cm to ⩽25 cm. The blank areas indicate missing data. The scales for all plots are the same as shown for the year 1978.

TABLE 6. Tidal heights above Galeta datum at which waves disappeared from the chart traces during falling tides and reappeared during rising tides

		Tidal heights (cm)		
	N	Mean	s.d.	Range
Disappearance	50	30·2	2·1	26·5–38·0
Reappearance	50	27·2	2·0	23·0–34·0

Eucidarus tribuloides was present in the transects on the reef-edge, but the abundances of both these urchins were less than 1 m^{-2} and are not reported here.

Discussion

Because the amplitudes of the astronomical tides at Galeta were small, non-tidal factors made a substantial contribution to the actual water levels over the reef flat. For example, mean monthly water levels fluctuated approximately 10 cm seasonally [Figure 2(a)], which was more than 40% of the mean diurnal range of the tides over the reef flat (Table 2) and about 30% of the mean diurnal range in the adjacent deeper water (U.S. National Ocean Survey, 1983). Most of the reef flat is within a 6 cm vertical span at the bottom range of the tides where a 10 cm rise in sea level can potentially eliminate the occurrence of exposures (Figure 4), the biological significance of which will be discussed later.

Such variation in mean water level is not unusual compared with other types of sites and other regions in the Caribbean. In an analysis of 38 years of records from the deeper water location at Cristóbal, monthly mean sea levels varied seasonally over an amplitude of approximately 8 cm [Pattullo *et al.*, 1955, see also Figure 2(b)]. In other parts of the Caribbean seasonal variations in monthly mean sea levels are closer to 20 cm (Marmer, 1954; Pattullo *et al.*, 1955; Haan & Zaneveld, 1959), approximately equal to the narrower diurnal ranges of the tides in these places (Kjerfve, 1981). In the western Indian Ocean, such fluctuations also have been reported for the shallow atoll of Aldabra (Farrow & Brander, 1971), but not for the deeper atolls of the region where only the astronomical tides appear to be important in causing variations of water level (Pugh & Rayner, 1981).

The possible causes of non-tidal variations in the water levels over the reef flat at Galeta can be divided into two categories: (1) factors which affect overall sea levels along the coast [e.g. wind forcing and barometric pressure (Lisitzin, 1974)], and (2) factors which affect water levels primarily over the reef flat and other shallow structures [e.g. wave action (Sibul, 1955)]. Water levels at Cristóbal would respond primarily to factors in the first category. Although water levels are generally 'coherent' among tidal stations in the same region (Pattullo, 1963), those at Cristóbal and Galeta were not strongly correlated in 5 out of 7 years (Table 3), suggesting that factors causing variations in water levels at Galeta to a large degree included processes restricted to the reef flat itself. In this context, the consistently higher water levels (Figure 3), the moderate, positive correlations between onshore winds and mean water levels (Table 5), and the higher relative water levels at Galeta on rough days (Table 4) all suggest that the non-tidal variations were caused by waves 'pumping' water onto the reef flat (Sibul, 1955), rather than by wind-forcing or barometric effects. Consistent with this explanation is the fact that the two years of significant correlations between mean monthly water levels at Cristóbal and

Galeta were 1976 and 1978 (Table 3), when onshore winds and water levels at Galeta were not correlated (Table 5).'The correlations between onshore winds and water levels at Galeta might have been stronger if we had been able to take into account factors such as fetch of the wind, which also contribute to the generation of waves (Bascom, 1980), but the correlations might have been weaker if our analysis had taken into account possible autocorrelations in the data. A better analysis would use direct measurements of the waves themselves, which arrive from distant sources in addition to generation by the local winds.

Apparently the occurrence of reef flat exposures is dependent on three factors: the range of the astronomical tides, regional sea levels, and processes that take place on the reef flat itself. Together these factors produce the seasonal patterns of exposures shown in Figure 6. If the non-tidal effects were absent, exposures of the reef flat would probably occur during the lowest spring tides of each month, and be more frequent around the solstices, when the amplitudes of the astronomical tides increase (Wood, 1978). Non-tidal factors modify this pattern. As a basal water level to which other variations are added, the 8 cm seasonal fluctuation in off-reef sea levels [Pattullo *et al.*, 1955; Figure 2(b)] probably has the following effects: the peak sea levels in October–November probably diminish the potential for reef flat exposures at that time, and the low sea levels around March–April probably contribute to the higher frequency of exposures following Panamá's dry season. Waves maintaining higher water levels over the reef flat probably reduce the frequency of reef flat exposures during the dry season and during the similar weather later in the year when the northerly tradewinds (e.g. Table 1) drive waves onto the reef. Thus the period of frequent exposures that would otherwise result from the solstitial tides around December is diminished by the higher off-reef sea levels entering into the solstitial period and attenuated by the dry season waves in the latter part of this period. In contrast, the solstitial period around June coincides with lower off-reef sea levels and calmer weather, resulting in a period of maximal exposures (Figure 6).

It should be noted that the still water levels recorded by tide gauges are not necessarily good measures of physical stresses, such as desiccation, during periods of low water levels: waves may continue to wash over organisms that are above the mean measured water level. Thus, ' exposure ' times may not adequately measure how much the habitat at the reef edge is subjected to the stress that would result from being continuously above water level. However, this is not the case in the central area of the Galeta reef flat, where wave phenomena essentially disappeared during low water levels (Table 6), and still water levels existed both inside and outside the tide gauge.

Although water levels are determined by non-tidal factors combined with the astronomical tides, we found no evidence to support the suggestion of Kjerfve (1981) that ' local and synoptic meteorological/oceanographic conditions may at times entirely mask the tidal response '. Visual examination of the original charts of the water level recordings showed a sinusoidal tidal curve to be present at all times, oscillating around the longer term water level variations caused by other factors; however, some compression or expansion of tidal amplitude or period could have escaped detection. Non-tidal fluctuations in mean water levels did at times exceed those of the tides (Figure 1), and Kjerfve's (1981) remark applies in the sense that weather and sea conditions can cause the heights of the actual tides to be much different from those that are predicted.

The reduction of reef flat exposures in Panamá's dry season (roughly December through March) affords the biota some protection from the potentially severe effects of emersion during the part of the year that is sunnier, less humid, and more populated by overwintering shore birds. As a result, the plants and animals in this type of reef flat community probably exhibit different seasonal patterns of abundance and species composition from those on a leeward, more wave-protected, shore. Each years the standing crop (dry weight) and percent coverage of algae, sea grasses, and sessile invertebrates on the reef flat at Galeta reach their maxima during the period of less frequent exposures in the dry season and then decline drastically during the onslaught of subaerial exposures that follow (Connor, Cubit, Hay, Kilar, and Norris, unpubl. data).

Diadema antillarum and *Lytechinus variegatus* exhibited similar seasonal patterns of abundance (Meyer & Birkeland, 1974; Meyer *et al.*, 1975; Hendler, 1977*b*; Figure 7). Subaerial exposures relegated both of these echinoids to being ' annual species ' on the reef flat (Hendler, 1977*b*, Figure 7), even though they are perennial species in deeper water (e.g. Lessios *et al.*, 1984*b*). Without the respite from exposures in the dry season, when these urchins recolonize the reef flat, they would probably be eliminated from the reef flat community altogether. Even though physical stresses and predation by birds have been reported to be principal causes of mortality for *Echinometra lucunter* and *E. viridis* at Galeta (Hendler, 1977*b*), periodic reductions in the abundances of these two urchins were not synchronous with the seasons of subaerial exposures; if anything, they were out of phase (cf. Figures 6 and 7). The contrast between the seasonal abundance of the *Echinometra* species on one hand, and *D. antillarum* and *L. variegatus* on the other, may be due to physiological and behavioral differences. The *Echinometra* species are more tolerant of elevated temperatures (Glynn, 1968) and unlike *D. antillarum* and *L. variegatus* dwell in holes in the reef or under rocks. On the reef flat, *D. antillarum* with test diameters less than 2 cm were occasionally found under or between pieces of coral rubble, but these refuges were not large enough to shelter larger *Diadema*. *L. variegatus* covers itself with pieces of shell and other materials (Sharp & Gray, 1962; Lawrence, 1976), but this is not sufficient protection against physical stresses and predatory shorebirds to prevent mortality during subaerial exposures (Hendler, 1977*b*). Mass mortalities of echinoids during exposures also have been described on other reef flats in the Caribbean (Mayer, 1914; Glynn, 1968).

Some of the year-to-year variations in the abundances of sea urchins on the reef flat may have resulted from annual differences in the severity of exposures, in addition to other factors, such as variations in settlement or abundances of predators. The higher abundances of *D. antillarum*, and *L. variegatus* in late 1972 and early 1973 may have been a result of fewer hours of subaerial exposure. Although the tide gauge records from Galeta for 1972 are sparse, data from Cristóbal show mean sea levels in 1972 were the highest in 72 years of records, which probably reduced the frequency of exposures (Cubit, in press). Meyer and Birkeland (1974) estimate the total hours of daytime exposure at the 25 cm elevation of the Galeta reef flat as being approximately 91 h from March to December 1972 followed by 306 h in 1973, with only 3 h of cumulative daytime exposure in the 8 month period between July 1972 and February 1973. For the same periods, night-time exposures totalled 93 h in 1972 and 133 h in 1973, with 66 h total exposure between July 1972 and February 1973. Through increased settlement or survival, the relatively few hours of daytime exposure in 1972 and early 1973 may have contributed to the larger populations of these two species on the reef flat. In subsequent years *D. antillarum* gradually disappeared from the reef flat (Figure 7). Indicating that exposure times alone cannot explain variations in the abundance of urchins is the contrast between the high water periods at the ends of 1982 and 1983. In both years few daytime exposures occurred in the last six months of the year (Figure 6). In 1982 the

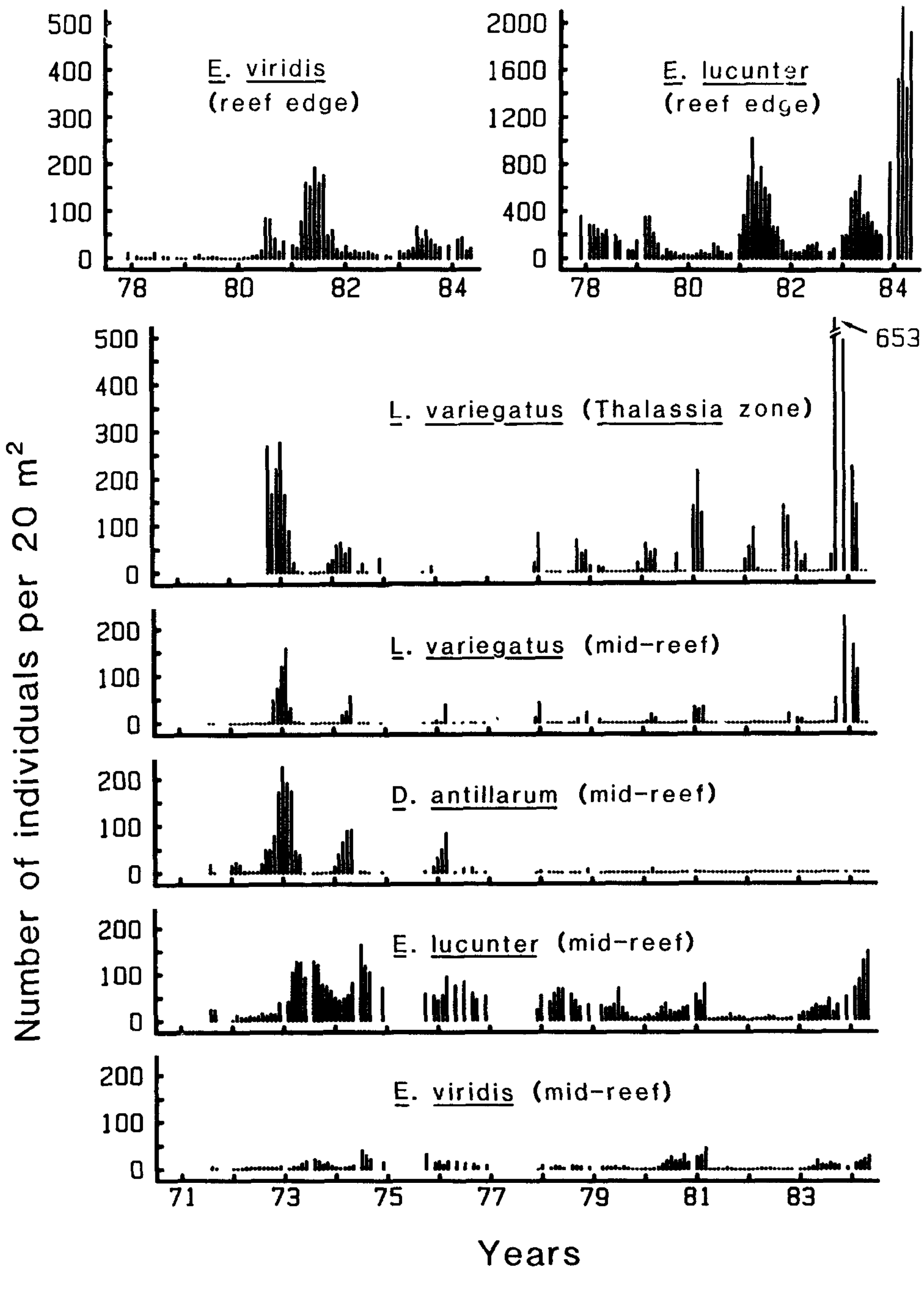

Figure 7. Populations of sea urchins in permanent 20 m^2 transects on the reef flat. Data for 1971–1977 are from Meyer and Birkeland (1974), Meyer *et al.* (1975) and Hendler (1977*a*, *b*). The smallest marks at the baseline indicate no individuals of the species were present in those censuses, and the blank areas indicate no censuses were made in those months. Note that the vertical scales in all graphs are the same except for *E. lucunter* in the reef-edge transect.

abundance of urchins exhibited no remarkable increase even though exposures of the lowest reef flat elevations were unusually rare (Figures 5 and 6); however, in late 1983 and extending into early 1984 *L. variegatus* and *E. lucunter* were much more abundant than average (Figure 7). Any recovery that *D. antillarum* might have shown at this time was precluded by an epidemic which killed off most of this species throughout the Caribbean in 1983 (Lessios *et al.*, 1984*a*, *b*). Contrary to the above patterns, reduction of exposure times cannot explain the higher than usual abundances of *E. lucunter* and *E. viridis* at the reef edge in 1981 (Figure 7), a year of maximum exposure time (Figures 5 and 6).

Although this analysis has emphasized the effects of water levels on the mortality of reef biota, water levels probably affect plants and animals of the reef through other processes as well. For example, the productivity of marine plants is increased by water movement [see Schwenke (1971) for review], and the distribution of wave energy and rate of current flow across reef platforms is dependent on water levels (Glynn, 1973; Roberts *et al.*, 1975; Roberts & Suhayda, 1983; Table 6). In the cases examined, algal productivity has been shown to increase when algae are partially desiccated (Stocker & Holdheide, 1938; Johnson *et al.*, 1974; Quadir *et al.*, 1979). Thus rates of algal productivity may be higher when water levels allow maximum wave and current action across the reef flat, or when low water levels result in short exposures of the reef flat. Production of calcium carbonate, and thereby reef growth, is also higher in areas of higher water motion (Smith & Kinsey, 1976). Water motion and water level probably have many more effects on the reef flat community, such as influencing the movements and feeding of reef animals, transporting sediments, and affecting the amount of light reaching the substratum (cf. Hay, 1981*b*, for subtidal areas); however, information regarding the role of these processes in reef flat communities is lacking, and further study should precede further speculation.

The extent of elevation of the reef flat relative to water level is not coincidental, but is a natural result of the upward growth of the reef being retarded by the effects of subaerial exposures (Macintyre & Glynn, 1976). This represents a terminal stage in reef development (Macintyre & Glynn, 1976), and if sea levels remain relatively stable, the number and areal extent of reef flats of this type probably will increase over time. At present, an estimated 15% of Caribbean reefs are at this stage of development (W. Adey in Hay, 1981*b*). However, sea levels are forecast to begin rising at an accelerated rate within the next few decades (Hoffman *et al.*, 1983; Revelle, 1983; Hoffman, 1984; Titus & Barth, 1984), and could exceed the rates of upward accretion of these reef flat habitats within 50 to 100 years (Cubit, in press). If the amplitudes of water-level fluctuations do not change, a 10 cm rise in mean sea level would reduce the total exposure time of the Galeta reef flat to near zero (see Figure 4), and would also affect other environmental conditions that are dependent on water depth. Such changes would probably cause large scale alterations in the distribution and abundance of the organisms on the reef flat (Cubit, in press).

To our knowledge these are the first long-term measurements of water level variations over a Caribbean reef flat. Other long-term water level data in the Caribbean have been recorded in harbors and other bodies of relatively deep water. The poor correlations in most years between water levels at Cristóbal and Galeta indicate, however, that tidal measurements made in deep water are restricted to certain uses for indicating water levels over shallow reef structures. Since the discrepancies between water levels in the two situations are probably caused by factors such as waves, which raise, but do not lower, water levels over the reef flat, deep water measurements are probably most useful as estimates of the minimum possible water levels over the reef. For example, water levels above a certain elevation at a deep station could be used confidently to predict the absence of exposures of a reef flat, but lower water levels could not be used to determine the actual occurrence or duration of exposures. From the information presented here regarding the importance of water levels to the ecology of the reef flat community at Galeta, and the lack of correspondence between water levels over the reef flat and those at a conventional tidal station, we concur with Pugh and Rayner (1981) that measurements of water level made *in situ* should be an integral part of reef ecological studies.

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