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THE DIFFERENTIAL EFFECTS OF SEASONAL STRESS AND PREDATION ON THE STABILITY OF  
REEF-FLAT ECHINOID POPULATIONS

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ABSTRACT

Patterns of mortality of nine species of echinoids were monitored for fifty-eight weeks on a fringing reef-flat at Galeta, Panama. The chief cause of mortality of sea urchins was the physical stress generated by extended, twice yearly, subaerial exposures of the reef platform. Coinciding with emersions there were peaks of mortality inflicted by shorebirds during their migrations. In contrast, the effects of a predatory gastropod, Cypraecassis testiculus, were sporadic and low-level. Fluctuations in the predation of octopus on Cypraecassis were not reflected by changes in the mortality of echinoids.

Under these conditions of periodic stress, urchins show divergent life-history adaptations. Species that occupy exposed habitats die almost exclusively from physical stress and reach sexual maturity in less than one year. They constitute fugitive populations in the intertidal zone. Cryptic species are more resistant to stress and more buffered from it. They reproduce during their second year of growth. They suffer a greater attrition to predation than the fugitive forms, but their losses to predation are trivial compared to mortality from physical stress.

The success of a species-rich community at Galeta which is physically controlled and little affected by predation contradicts the expectations of both the predation and the time-stability hypotheses of diversity. The discrepancies between the hypotheses and the reef-flat system can be resolved if there is a functional trade-off between the effects of stress and the intensity of predation.

KEY WORDS: Mortality, Predation, Disturbance, Echinoids, Intertidal, Seasonality, Shorebirds, Cypraecassis, Octopus, Diversity.

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Introduction

Grazing sea urchins are responsible for denuding extensive areas of the benthos, thus the nature of the factors controlling echinoid populations has long been a problem of practical interest (1). The regulation of urchin numbers and the conservation of algal cover has been attributed to predators, as in the case of the sea otter-urchin-kelp troika of the Aleutian Islands (2) or the lobster-urchin-kelp triangle in Nova Scotia (3).

These predator-oriented studies do not consider the effect of environmental stress on urchin populations. In order to quantify the relative importance of physical stress I have compared the magnitudes of mortality due to predation and physical stress of 9 species of echinoids on a Panamanian reef-flat. This comparison permits an evaluation of the relative importance of these two forms of disturbance in the "stable" tropics:

The investigation site is Galeta Reef, about 6 km northwest of Colon, Panama, on a reef platform typical of the Caribbean coast of Panama (4). Nearly all of the platform is several cm below MLW. The co-occurrence of low tides, calm seas and offshore winds lead to subaerial exposure of the reef-flat during much of the year (Fig. 1). The reef emersions are most serious during March-April from the coincidence of lowest low tides with midday hours, and during September-October from the low-pressure calms generated by tropical storms and from southerly winds (5).

Water temperature on the reef-flat is generally 26-29°C and the salinity is usually 32-35 ppt, but extreme values of 39°C and 38 ppt (25 ppt during heavy rain) occurring only during subaerial exposures, exceed the tolerance of many intertidal organisms (5). Despite this unpredictable, catastrophic phenomenon, the reef-flat supports a prolific, species-rich community. An algal carpet and patches of zoanthid, sponge, and corals cover the reef-flat and a preliminary survey yielded at least 80 species of macro-algae and a conservative listing of 520 identified species of invertebrates (6).

Methods

The incidence and duration of reef-flat exposures during low tides is determined with a tide gauge on the reef platform. Critical values of water level for differentiating between mild exposures (exposure of elevated reef-edge) and

severe exposures (almost total emersion of reef-flat) were determined empirically (5).

Mortalities of 9 echinoid species is monitored by making daily collections of dead urchins and tests from several permanent quadrats on the reef-flat. Samples of the number dead per unit area are quantitatively accurate as transport of dead tests is minimal in this environment. The tests are categorized as new (having spines and flesh or pigmentation), intermediate (clean but lacking pigmentation) and old (stained or overgrown). Their size, the greatest length at the ambitus, is measured with calipers.

The cause of death is deduced from characteristic damage to the test. Urchins are assumed to have succumbed to environmental physical stress when there is no indication of damage to the test made by predators. The "stress" category therefore includes urchins that die from disease and senility. The 4 major predators on echinoids on the reef-flat each attack urchins in a characteristic manner which allows one to determine the predator from damage to the dead test as follows: 1) Ruddy turnstones (Arenaria interpres) eviscerate Echinometra species by pecking out the peristomial tissue, but they attack Lytechinus and other fragile urchins by removing a circular portion of the dorsal surface of the test (7, pers. obs.). 2) Reticulated helmet-cowries (Cypraea testiculus) bore a 1-2 mm diameter, irregular hole at right-angles to the test wall. The spines are removed from the test in a halo around the borehole (8, pers. obs.). 3) Porcupinefish (Diodon hystrix) usually consume entire urchins, but they may leave portions of the test with attached spines. Such fragments are attributed to predation by fish, but they are rarely collected and predation by fish and other test-fragmenting forms probably exceeds the estimates presented below. 4) Urchins are reported to feed on other urchins (9). In several cases the thick-walled tests of Echinometra and Echinoneus show wide holes framed with etchmarks similar to the scrapes of urchins' teeth. These dead tests are attributed to predation by urchins.

Results

The 9 echinoid species treated here fall into three groups (three species each), each group having a characteristic body-form and habitat. Brissus unicolor Agassiz, Paraster floriidensis (Kier and Grant), and Echinoneus cyclostomus Leske, burrow beneath the sediment and have elongate tests with extremely abbreviated spines. Lytechinus variegatus (Lamarck),

Tripneustes ventricosus (Lamarck), and Diadema antillarum Philippi, are strictly epifaunal forms with globose, thin-walled tests. Lytechinus and Tripneustes, both common in seagrass beds, have short spines, but Diadema, concentrated in deep pools on the reef-flat has long, needle-like spines. The remaining species are cryptic. Echinometra viridis Agassiz and Eucidaris tribuloides (Lamarck), live under slabs of coral rubble or in fissures in the reef pavement. Echinometra lucunter (Linnaeus) excavates shallow burrows in a densely populated (60/m<sup>2</sup>) band 10 m to either side of MLW. The Echinometra species have acute spines of moderate length and Eucidaris is protected by widely-spaced peglike spines.

### Fluctuations in the Intensity of Mortality

Periods of extensive mortality are distinct from the persistent, low-level flux in "test-counts". It is evident from Figure 1 that the surges in mortality are roughly synchronous with 3 periods of prolonged reef-flat exposure.

Dominant peaks of mortality marking reef emersion catastrophes coincide for all species during one or more of 3 periods (Table 1, Fig. 1). In all, 69% of the total number of dead tests were collected during the 15 wk subsample from periods of exposure (only 25% of the total study) (Table 1). For Echinometra species the 3 periods were nearly equipotent, but for all other species (except Brissus and Paraster) the second period was overwhelmingly important. Clearly the number of urchins killed by stress is greater during exposures than at any other time of the year, and the timing and intensity of mass mortalities change from year to year.

Table 1. Ratio of the numbers of urchins killed by physical stress for 5-wk intervals at the height of the 3 major periods of mortality. The ratio is the number dead per interval/N, where N is the total number of dead collected during all 58 wks of sampling (excluding the initial wk). Period 1 is 27 October-30 November 1975 (wks 3-7), period 2 is 22 March-25 April 1976 (wks 24-29), and period 3 is 11 October-14 November 1976 (wks 53-58).

Species	Period 1	Period 2	Period 3	N
<u>E. lucunter</u>	.22	.26	.16	1507
<u>E. viridis</u>	.12	.22	.32	81
<u>Eucidaris</u>	.27	.64	.09	22
<u>Echinoneus</u>	.04	.61	.14	509
<u>Brissus</u>	.01	.05	.93	119
<u>Paraster</u>	0.00	0.00	.67	3
<u>Lytechinus</u>	.01	.48	.07	202
<u>Diadema</u>	.04	.43	.13	46
<u>Tripneustes</u>	0.00	.77	.08	13

Some major trends of mortality are recurrent. Echinometra species, which inhabit a relatively benign environment, show frequent, damped fluctuations in population density that mirror the periodicity of lethal environmental stress (Fig. 2). In contrast, the Lytechinus and Diadema populations were reduced by 90% by precipitous kill-offs during April-May of 1973, 1974, and 1976. Late-year reef emersion following these catastrophes incur little mortality because of the attenuation of the numbers of these species. Both Diadema (5.0 to 1.7 cm) and Lytechinus (2.6 to 1.7 cm) showed a decrease in mean size  $p < 0.05$ , t-test assuming unequal variances (10) of dead tests from periods 2 to 3, indicating that the post-catastrophe populations are dominated by surviving young or new recruits. However, the mean size of dead E. lucunter tests increased slightly ( $p < 0.05$ ), and the size of tests did not change for Brissus or Echinoneus ( $p > 0.05$ ).

### Differential Effects of Stress and Predation

Mortality due to physical stress is the paramount cause of death for the reef-flat echinoids (Table 2). Predatory birds are active on the reef only during exposures because they cannot hunt when the water is deeper than a few cm. Therefore, the importance of predation by birds varies, depending on the co-occurrence of unpredictable periods of reef emersion with the movements of large flights of migratory birds. In contrast to the unpredictable but seasonal deaths from bird predation, mortality caused by Cypraecassis is sporadic but year-round.

Table 2. Per cent of new and intermediate state tests attributed to various sources of mortality. S is the percentage of mortality attributed to lethal stress. P is the total percentage of mortality caused by predation. Numbers at the head of each column denote mortality from: 1, turnstones; 2, Cypraecassis; 3, fish; and 4, echinoids. N is the total number of tests collected from the study quadrats during the 58 wk survey.

Species	S	P	1	2	3	4	N
<u>E. lucunter</u>	58	41	24	16	1	1	1270
<u>E. viridis</u>	85	15	10	5			83
<u>Eucidaris</u>	95	5		5			40
<u>Echinoneus</u>	88	11		11			582
<u>Brissus</u>	92	8		8			465
<u>Paraster</u>	100	0					20
<u>Diadema</u>	98	2	2				433
<u>Lytechinus</u>	82	18	17	1			438
<u>Tripneustes</u>	100	0					29

Cypraecassis, which preys on echinoids, is in turn eaten by Octopus species (11). In a sample of 243 Cypraecassis shells from Galeta, 28% were bored and eaten by octopus, 20% were cracked or fragmented (presumably by predators), and 32%

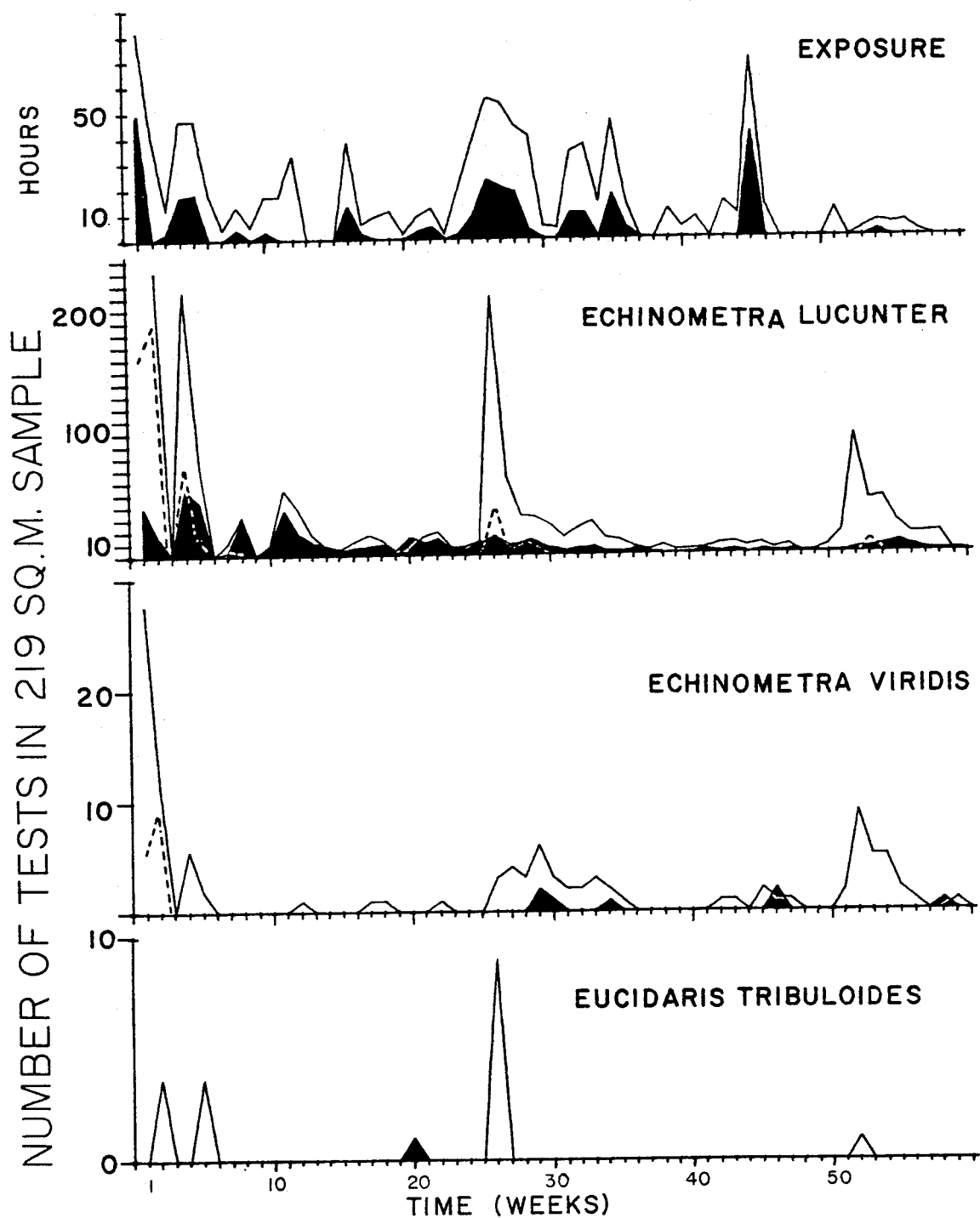
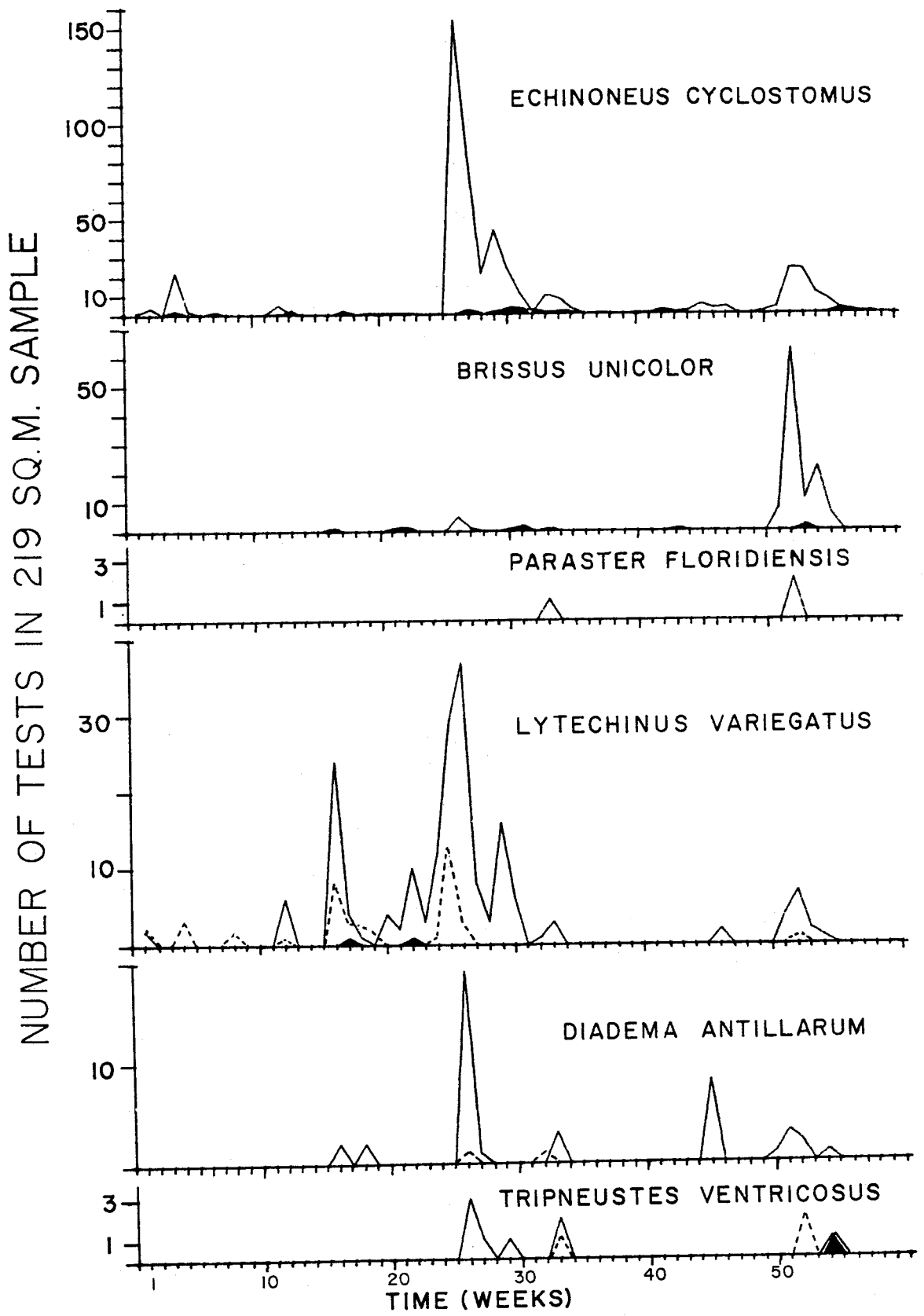


Figure 1. Weekly average of hrs of reef-flat exposure (upper graph), and average weekly mortality of 9 species of reef-flat echinoids. The period covered is from 13 October 1975 to 28 November 1976. In the exposure graph the solid line indicates hrs of mild exposure and the shaded area indicates hrs of severe exposure. In the mortality graphs the solid lines indicate mortality due to physical stress, dashed lines indicate mortality due to birds, and shaded areas indicate mortality due to *Cypraeacassis*. Samples for wks 1-12 are from a 119 m<sup>2</sup> quadrat (but data are extrapolated to 219 m<sup>2</sup>); an additional 100 m<sup>2</sup> was sampled subsequently.



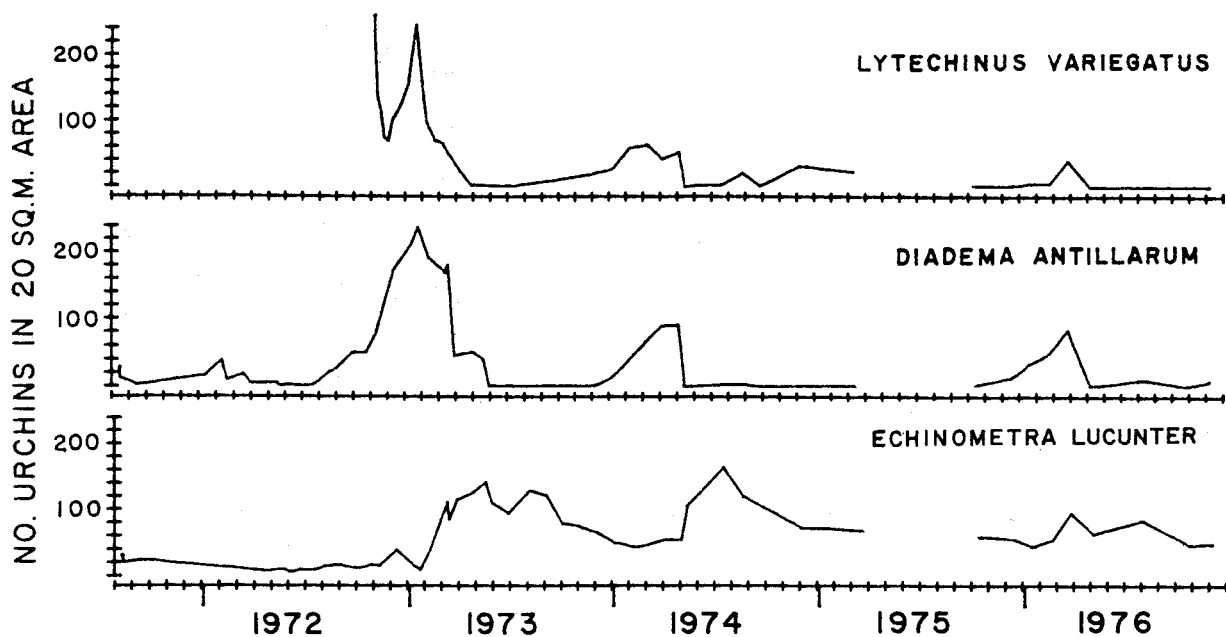


Figure 2. Size of 3 echinoid populations in a permanent quadrat monitored for 6 years (survey temporarily discontinued during 1975). Data for 1971 to 1975 were collected by David L. Meyer.

were unmarred; presumably dead from physical stress. Fluctuations of the numbers of collected shells indicate that a disproportionate number of *Cypraeacassis* are killed between December and May ( $p < 0.005$ ,  $\chi^2$  test) (Fig. 3).

This pulse of *Cypraeacassis* mortality provides an indirect check on the importance of the population size of this predator on its predation on echinoids. Despite the significant increase in the number of dead *Cypraeacassis* from December to May, there is no significant decrease in the number of drilled *Echinometra* species, *Brissus*, or *Echinoneus* during that period ( $p \gg 0.05$ ,  $\chi^2$  test). This suggests that the amount of predation by *Cypraeacassis* is not strongly related to their population density.

#### Discussion

Echinoids are adapted to the fluctuating stresses on the reef-flat by two divergent life-history strategies. Species that occupy exposed habitats and suffer the most serious mortality during exposures are fast-growing and quickly reach sexual maturity. The cryptic species are slow-growing and slow to mature. *Echinometra* species and *Eucidaris* have low-amplitude fluctuations in population density and they reach sexual maturity at about 2 cm diameter, but they attain that size after one year of growth (8, 12). If observations of other Caribbean spatangoid species can be applied to *Brissus* and *Paraster*, these urchins also do not mature until their second year of growth (13, 14). In contrast, *Diadema* and *Lytechinus*, which exhibit drastic

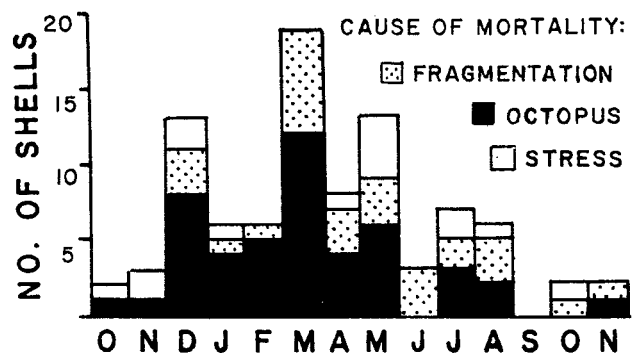


Figure 3. Variations in mortality of *Cypraeacassis* shown by the number of *Cypraeacassis* shells collected in a 410 m<sup>2</sup> area, monitored from 13 October 1975 to 28 November 1976.

fluctuations of population size, and *Tripneustes*, another epifaunal form that is commonly found in exposed areas, all mature at about 3 cm diameter and reach maturity well before the end of their first year (15, 16, pers. obs.).

Glynn (7) shows that *Tripneustes*, *Lytechinus* and *Diadema* are less tolerant to heat than *E. lucunter*, *E. viridis* and *Brissus*, and therefore are more likely to die during exposures. It appears that the sensitive species are better suited to subtidal habitats, but they survive as fugitive, short-lived populations in shallow water by virtue of their rapid rate of growth. *E. lucunter*, a stress-resistant species with a relatively stable population size, has the

heaviest loss to predators of all species considered. This suggests that, to some degree, the intensity of predation is a function of the stability and size of the prey population, but the data are not sufficient to substantiate a hypothesis of optimum foraging strategy. Intensity of predation is also a function of the accessibility of prey. This may be the reason that burrowing forms, Echinoneus and Brissus, suffer less attrition to Cypræacassis than does Echinometra. It is likely the reason that they are spared by birds.

Compared to the mortality from physical stress the proportion of echinoids killed by predators is trivial (Table 2). This is surprising considering the importance accorded to predators in other studies. Investigations of intertidal environments subject to physical stress have estimated loss to predators at 52% (balanoid barnacles), 70% (mac-trid bivalves), and 20-70% (lucinid bivalves) (17, 18, 19). Lethal physical stresses may take a lesser toll in these locations than at Galeta, and there may be an inverse relationship between physical stress and predation.

The intertidal system at Galeta is a physi-cally controlled, species-rich reef-flat community with a low level of predation pressure. This combination of attributes contradicts the expecta-tions of the predation hypothesis of diversity (i.e., a complex system of predators operating in an environment of high productivity), and despite the specializations and partial habitat-divergence of the various echinoids, it contradicts the as-sumptions of the time-stability hypothesis which equates diversity with environmental stability (20, 21). This implies that the cause of coral reef diversity is more complex than presumed by either hypothesis. These discrepancies suggest the possibility that there is a trade-off between the intensity of stress and the intensity of pre-dation. If this is correct, it suggests that the quantification of predation pressure in communi-ties with different degrees of physical stress can be used to frame a model of ecological "dis-turbance" and contribute to an understanding of community diversity.

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#### References

1. Lawrence, J. M. 1975. On the relationships between marine plants and sea urchins.

- Oceanogr. Mar. Biol. Ann. Rev. 13: 213-286.
2. Estes, J. A. and J. F. Palmisano. 1974. Sea otters: Their role in structuring nearshore communities. *Science*, 185: 1058-1060.
3. Breen, P. A. and K. H. Mann. 1976. Changing lobster abundance and the destruction of kelp beds by sea urchins. *Mar. Biol.* 34: 137-142.
4. Glynn, P. W. 1973. Aspects of the ecology of coral reefs in the Western Atlantic Region. In: *Biology and Geology of Coral Reefs*, O. A. Jones and R. Endean (eds.), Academic Press, New York, 2: 271-324.
5. Meyer, D. L., C. Birkeland and G. Hendler. 1975. Environmental sciences program marine studies. In: *1974 Environmental Monitoring and Baseline Data*, D. M. Windsor (ed.), Smithsonian Inst., Washington, D.C., pp. 223-409.
6. Birkeland, C., A. A. Reimer and J. R. Young. 1976. Survey of marine communities in Panama and experiments with oil. U.S. Environmental Protection Agency Rpt. 600/3-76-028: 100-166.
7. Glynn, P. W. 1968. Mass mortalities of echi-noids and other reef flat organisms coincident with midday, low water exposures in Puerto Rico. *Mar. Biol.* 1: 226-243.
8. McPherson, B. F. 1968. Contributions to the biology of the sea urchin Eucidaris tribuloides (Lamarck). *Bull. Mar. Sci.* 18: 400-443.
9. Quinn, B. G. 1965. Predation in sea urchins. *Bull. Mar. Sci.* 15: 259-264.
10. Sokal, R. R. and F. J. Rohlf. 1969. *Biometry*. W. H. Freeman, San Francisco, Ca., pp. 374-376.
11. Wodinsky, J. 1969. Penetration of the shell and feeding on gastropods by octopus. *Am. Zoologist*, 9: 997-1010.
12. McPherson, F. B. 1969. Studies on the biology of the tropical sea urchins, Echinometra lucunter and E. viridis. *Bull. Mar. Sci.* 19: 194-213.
13. Moore, H. B. and N. N. Lopez. 1966. The ecology and productivity of Moira atropos (Lamarck). *Bull. Mar. Sci.* 16: 648-667.
14. Chesher, R. H. 1969. Contributions to the biology of Meoma ventricosa (Echinoidea: Spatangoida). *Bull. Mar. Sci.* 19: 72-110.
15. Lewis, J.B. 1958. The biology of the tropical sea urchin Tripneustes esculentus Leske in Barbados, Brit. West Indies. *Canad. J. Zool.* 36: 607-621.
16. Randall, J. W., R. E. Schroeder and W. A. Stark II. Notes on the biology of the echinoid Diadema antillarum. *Carib. J. Sci.* 4: 421-433.
17. Connell, J.H. 1961. Effects of competition, predation by Thais lapillus, and other factors on natural populations of the barnacle Balanus balanoides. *Ecol. Monogr.* 31: 61-104.
18. Green, R. H. 1968. Mortality and stability in a low diversity subtropical intertidal community. *Ecology*, 49: 848-854.
19. Jackson, J. B. 1972. The ecology of the molluscs of Thalassia communities, Jamaica, West Indies. II. Molluscan population variability along an environmental stress gradient. *Mar. Biol.* 14: 304-337.
20. Paine, R. T. 1966. Food web complexity and species diversity. *Am. Nat.* 100: 65-75.
21. Sanders, H. L. 1968. Marine benthic diversity: a comparative study. *Am. Nat.* 102: 243-282.

