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AN ABSTRACT OF THE THESIS OF Alexander M. Kerr for the
Master of Science in Biology presented June 24, 1994.

Title: Effects of Disturbance on Holothuroid
(Echinodermata) Community Structure

Approved:

Charles E. Birkeland, Chairman, Thesis Committee

Disturbance is an important factor structuring assemblages of sessile marine organisms, but the responses of mobile animals to disturbance is less known. I studied the long-term effects of typhoons on assemblages of mobile marine animals, holothuroids, that inhabit the fringing coral reefs of Guam, Mariana Islands. Specifically, I sought to corroborate the hypothesis that typhoon-generated waves, which generally propagate westward, create predictable local- and island-scale patterns in the community composition of mobile invertebrates based on reef exposure and microhabitat selection.

Line-transect surveys of the abundances of holothuroids were conducted at an east-facing (windward) reef flat (Pago) and a west-facing (leeward) reef flat (Tumon) through seven typhoons from 1989 to 1993. Previously reported surveys from 1975 to 1977 on the effects of an eighth typhoon at Pago were also analyzed. Twenty-two other reef-flat sites along Guam's ca. 200 km of coastline were surveyed in 1994 after the typhoons to assess possible typhoon-related islandwide trends in species richness, Simpson's diversity and density. The forereef slope to 30 m in depth was examined at ten

sites around Guam from 1992 to 1993 to find possible depth-related patterns in species richness due to typhoons.

Typhoons caused massive mortalities of holothuroids on windward reef flats at least three times in 20 yr. The three most severe typhoons, each with waves over 8 m, drastically reduced abundances of holothuroids at Pago. The remaining typhoons had smaller waves and caused no significant mortality. The density, Simpson's diversity and species richness of holothuroids was similar on all windward reef flats when reef-flat width was held constant, suggesting that the typhoons affected the entire windward coast. Though windward reef flats were devastated, abundances of holothuroids to leeward at Tumon appeared stable throughout the survey period of 1989 to 1993. Total density, species richness and Simpson's diversity was higher on leeward than on windward reef flats. Holothuroids on the windward forereef slope appeared to be severely affected, also, as species richness was less on shallow than on deep windward reef slopes. Conversely, species richness was higher on leeward forereef slopes and evenly distributed with depth.

Microhabitat use did not predict the degree of relative mortality between exposed and cryptic holothuroids. The dominant cryptic species Holothuria leucospilota was reduced as much as the combined remaining cryptic species (26.2% and 35.0%, respectively) during Typhoon Pamela, but was reduced relatively much less (40.6% versus 95.7%) during typhoons

Russ and Yuri. Mortality to the exposed Actinopyga echinites (81.4%) was intermediate between mortality of H. leucospilota and combined cryptic species during Russ and Yuri. Most of the cryptic habitat on reef flats consists of unconsolidated rubble that is easily shifted by storm waves and may have contributed to the high mortality of some cryptic species.

Several populations repeatedly went locally extinct or were severely reduced on the windward coast. Despite this turnover, the windward community appeared resilient, having returned in 1990 to its pretyphoon composition in 1975 as measured by Simpson's diversity and species richness.

EFFECTS OF DISTURBANCE ON HOLOTHUROID (ECHINODERMATA)
COMMUNITY STRUCTURE

BY
ALEXANDER M. KERR

A thesis submitted in partial fulfillment of the
requirements for the degree of

MASTER OF SCIENCE
IN
BIOLOGY

UNIVERSITY OF GUAM
JUNE 1994

ACKNOWLEDGEMENTS

Finane'na, especiamenti hu ágradesi i guinaiyá-ñiha i asaguá-hu, si Jo Nita, yan i famagu'on-hu, si Alexandra, si Alana yan si Roy. Lokkue', donkulu na si Yu'us ma'áse pot i sagro-ku, si Siñot yan si Siñora Sergio S. Quenga. Meggai na puengi, ma pulan i famagu'on-mámi annai umestudiu yu'; hu ágradesi i inayudá-ñiha yan i fabot-ñiha. (I thank first my wife and children for their support and understanding. I also thank my in-laws, Mr. and Mrs. Sergio S. Quenga. Many nights, they watched the kids while I studied; I greatly appreciate their help and kindness.) I thank C. Birkeland, E. Matson, S. Nelson and V. Paul, and particularly, G. Paulay and S. Pennings (University of Georgia), for valuable comments on ecology, statistics and presentation. I thank R. Richmond for generous financial support and for introducing me to the wonderful world of sea cucumbers. I also thank M. Landers (Joint Typhoon Warning Center) for meteorological data and advice, as well as C. Massin (Royal Belgian Institute of Natural Sciences) and D. Pawson (Smithsonian Institution) for taxonomic advice. I thank D. Hopper, E. Stoffell and R. Yoon for assistance in the field. Parts of this manuscript were written by candlelight during typhoon Omar.

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INTRODUCTION

Wave disturbance from occasional intense storms is an important factor structuring shallow-water marine communities and has been extensively studied in sessile organisms. The composition of sessile communities is influenced by the amount of space cleared for recolonization, whether the space consists of a few large or many small patches, and how often patches are formed relative to the frequency of the organisms' interspecific interactions and rates of growth and recruitment (Paine and Levin 1981, Abugov 1982). Patch characteristics in turn are primarily influenced by the frequency and intensity of storms and the ability of organisms to resist, or persist in spite of, dislodgement (Sousa 1984). For example, sessile, clonal taxa on hard substrata may escape significant mortality, despite their often large size, through encrusting or mounding growth forms (e.g., faviid corals: Stoddart 1962, Woodley et al. 1981). Upright, arborescent species often rely on flexibility (e.g., kelp: Denny et al. 1985) or, if rigid, may persist via vegetatively propagating fragments (e.g., arborescent Acropora corals: Highsmith et al. 1980, Dollar 1982, Rogers et al. 1982).

The responses of mobile organisms to wave disturbance have been studied much less often, but are probably similar in some ways to those of sessile forms. Like sessile organisms, very slow-moving marine taxa depend upon hydrodynamically stable morphologies, small size, structural

rigidity, strength of attachment, as well as gregariousness for survival in exposed locations (Denny et al. 1985).

Short generation times and rapid recruitment after a storm also contribute to the quick recovery of some mobile and sessile species (Sousa 1979, Moran and Reaka-Kudla 1991).

Among mobile species, persistence in an area with occasional episodes of high wave energy is also enhanced by the ability to move to shelter. For example, fishes may survive storms by migrating to deep, calm water (Woodley et al. 1981, Walsh 1983). Small epibenthic invertebrates survive strong surge by hiding in crevices and depressions (Kohn 1980), while infauna burrow deeper into the sediment (Dobbs and Vozarik 1983). Following the storm, these animals return to their former habitats or quickly spread to other depopulated areas. Thus, as a consequence of their rapid movement, mobile organisms are affected by and can recover from disturbance in different ways than sessile organisms.

Models of community response to disturbance would, therefore, benefit from tests of their generality using mobile marine animals. However, long-term field studies of the effects of extreme storms on mobile organisms are lacking. Studies of severe wave disturbance to mobile marine animals to date document effects at relatively small spatial or temporal scales (Glynn et al. 1964, Beecher 1973, Saloman and Naughton 1977, Kohn 1980, Woodley et al. 1981,

Tribble et al. 1982, Kaufman 1983, Walsh 1983, Dobbs and Vozarik 1983, Williams 1984, Pfeffer and Tribble 1985, Burch and Thorsson 1985, Kirby-Smith and Ustach 1986, Bokkin et al. 1987, Fenner 1991, Moran and Reaka-Kudla 1991, Aronson 1992, Kobluk and Lysenko 1993, Aronson 1993). In this study, I report the local-reef and islandwide impacts over 20 yr of three major and five minor typhoons on holothuroids, a diverse group of mobile organisms common on tropical reefs. Specifically, I tested the following hypotheses:

(1) Holothuroids on windward reef flats suffer greater mortality from storm-generated waves than holothuroids on leeward reef flats. Cyclonic storms travel in a westerly direction in the tropics, and as a result, windward (east-facing) reefs on islands are more strongly affected by waves than those on leeward (western) reefs (Goreau 1959, Emery 1962, Roberts 1974, Hubbard et al. 1991). Thus, holothuroids are predicted to also be most disturbed on windward coasts.

(2) Wave disturbance restricts reef-slope species to deep water at storm-frequented windward locations. Energy from breaking waves is greatest along the seaward reef margin and in adjacent shallow areas of the forereef slope (Young 1989, Young and Hardy 1993). Therefore, holothuroids are predicted to be least abundant on shallow windward reef

slopes, abundant on deep windward reef slopes, and abundant and uniformly distributed with depth on leeward reef slopes.

(3) Exposed species will suffer greater mortality than forms living in crevices. Gastropods (Kohn 1980) and fishes (Tribble et al. 1982) that seek shelter in rock crevices suffer less mortality during severe storms than corresponding taxa that do not. Habitat choice is expected to be related in a similar way to holothuroid mortality. Cryptic holothuroids inhabiting sheltered microhabitats such as crevices are predicted to be more protected from storm-generated waves than exposed species.

Natural history of study organisms

Tropical holothuroids are primarily epibenthic, deposit feeders from the order Aspidochirotida (in contrast to the dominance of dendrochirotid, suspension-feeding holothuroids in temperate waters) and are a predominant element of coral reefs and adjacent soft bottoms. Twenty species cooccurring at a site are not uncommon (Rowe and Doty 1977, Hammond et al. 1985, Kerr et al. 1992, Kerr et al. 1993, Kerr 1994). Some species occur at densities of over 1 kg/m² (Conand and Chardy 1985, Lawrence 1980), consume up to 40% of the daily primary production in the sediment (Moriarty et al. 1985) and considerably reduce abundances of certain infaunal organisms (Renaud-Mornant and Helléouet 1977, Moriarty et al. 1985).

Several aspects of a holothuroid's natural history probably influence its response to disturbance. Tropical holothuroids can live to five or more than 15 yr (Ebert 1978, Shelley 1985, Conand 1988, 1989, 1993) and, like other tropical echinoderms, generally recruit slowly or sporadically (Doty 1977). These traits suggest that their population structure is affected by even quite rare disturbances. Several species reproduce asexually by transverse binary fission (Harriot 1982, Conand 1990), and thus may recover more quickly from disturbance than holothuroids that rely solely on annual broadcast spawning and recruitment from distant sources.

Many holothuroids are infaunal or cryptic, coming out of crevices at night or extending only their anterior ends to feed and can rapidly hide when disturbed. Other species, however, live permanently on open, exposed substrata. Exposed aspidochirotid holothuroids can weigh 5 kg (e.g., Thelenota spp.: Conand 1988, 1989). Exposed apodid species weigh considerably less, but reach lengths over 2 m (i.e., Synaptidae: Bakus 1968, Cutress and Rowe 1986). Slow-moving, unsheltered, and often large holothuroids seem especially vulnerable to being dislodged by large waves, particularly when inhabiting shallow reef platforms.

Study sites

Surveys were performed on Guam (540 km²; 13°00"N, 145°45"E), a small, volcanic and uplifted-limestone island in the tropical western Pacific Ocean (Fig. 1). Guam is surrounded by narrow fringing reefs and has a mean tidal range of ca. 0.7 m.

A fringing reef consists of a shallow platform, the reef flat, extending from shore and adjoining a moderately to steeply inclined forereef slope. The reef-flat study sites are shallow (<2 m), 0.1 to 0.8 km wide, predominately subtidal reef benches. The inner reef flats (the inner two-thirds) at most sites are sandy with scattered coral and, occasional seagrass beds. Reef flats narrower than 200 m, however, lack an inner reef zone. The entire areas of these narrow reefs and the outer reef flats of wide reefs are covered with rubble, small coral colonies and algal-turf-covered pavement, and extends to the seaward reef-flat margin. The outer reef flat is subaerially exposed during extreme low tides. The seaward edges of the outer reef flats are largely covered by brown foliose and encrusting red coralline algae.

The studied forereef slopes are gently to moderately inclined at least to 30 m depth, the deepest area surveyed in this study. From 0 to 4 m depth, reef slopes have a dense covering of low-growing branching species. From 4 to 15 m depth, windward slopes have a sparse covering of

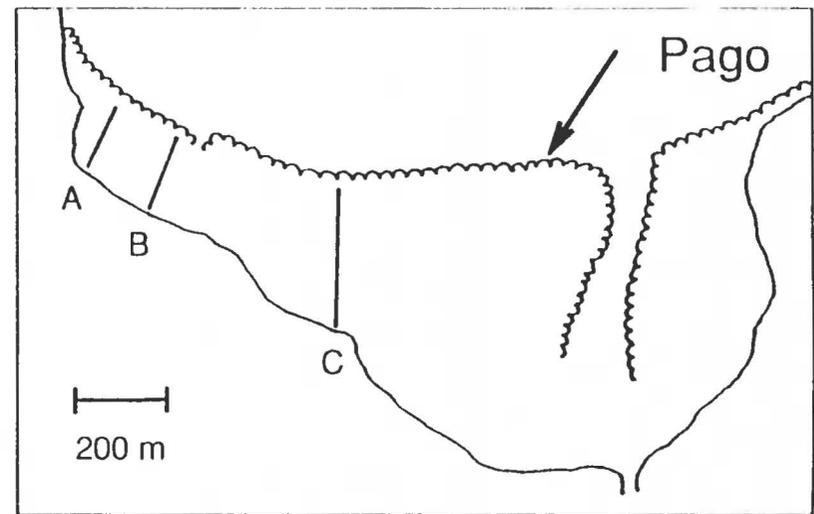
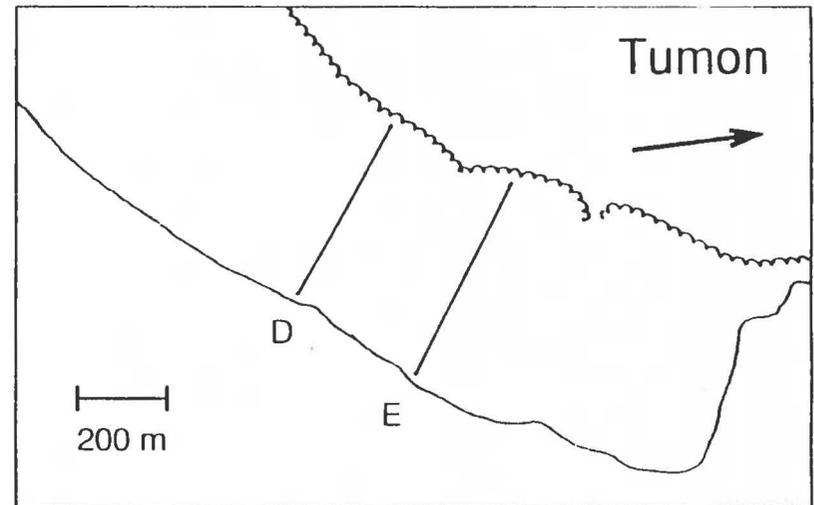
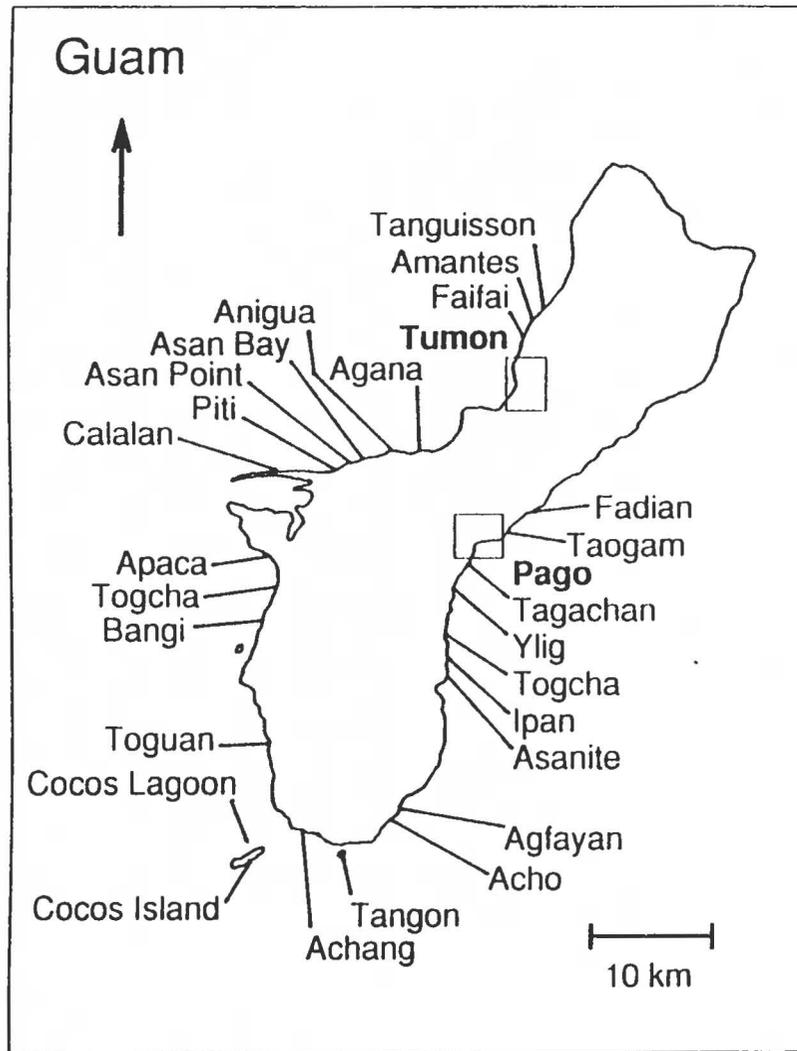


Figure 1. Study sites and transect locations. Scalloped line indicates the seaward reef-flat margin; arrow denotes north.

encrusting and low-growing, corymbose corals in shallow water and scattered large colonies of massive species as well below about 15 m depth. Coral cover and diversity are generally greater on leeward slopes than on windward slopes at all depths. Descriptions of the reef-flat and reef-slope study sites are given by Emery (1962), Randall and Eldredge (1976), Marsh et al. (1981), and Kerr et al. (1993).

Typhoons

Guam lies along a major cyclonic storm track in the north Pacific. Twice a year, from August to November and again in April to May, a trough of low pressure extends eastward past Guam providing a favorable environment for the formation of tropical cyclones. Since 1945 Guam has received an average of one typhoon (sustained wind velocity >34 m/s or 75 mi/h) per year passing within 300 km of the island (the distance at which gale force winds usually affect Guam) (USNOCC/JTWC 1991a). Eight typhoons occurred during the survey periods of 1975 to 1977 and 1989 to 1994 (Table 1, Fig. 2). Of these, Typhoons Pamela, Yuri and Russ had estimated maximum wave heights over 8 m on windward shores. Based on maximum sustained wind speeds, these typhoons are rated as the third, fourth and fifth most intense cyclones, respectively, to affect Guam this century (USNOCC/JTWC 1991a). The other typhoons in the study period produced less intense surf, despite sometimes high sustained

Table 1. Typhoons affecting Guam during the survey periods. Data from FWC/JTWC (1976) and USNOCC/JTWC (1990, 1991a-b, 1992).

Name	Date (d.mo.yr)	Closest approach (km)	Maximum sustained	Mean sea-level	Closest height on Guam	Maximum surge height (m)		Maximum wave height (m)	
			winds at closest approach (m/s)	pressure at closest approach (mb)		Fore	Tanen	Fore	Tanen
Pamela	21.05.76	0	62	930	49	ND	ND	10 ^b	ND
Russ	20.12.90	93	62	922	42	2	0	10	3
Yuri	28.11.91	102	77	885	31	3	0	12	3
Omar	28.08.92	0	54	940	23	1	1	3'	2'
Brian	21.10.92	0	33	989	6	0	0	3'	2'
Elsie	02.11.92	102	46	954	11	0	0	3'	2'
Hunt	18.11.92	37	33	976	7	0	0	3'	2'
Gay	23.11.92	0	44	971	24	2	2	3'	2'

^aWinds greater than 16 m/s.

^bOgg and Koslow (1978).

^cA. M. Kerr (personal observation).

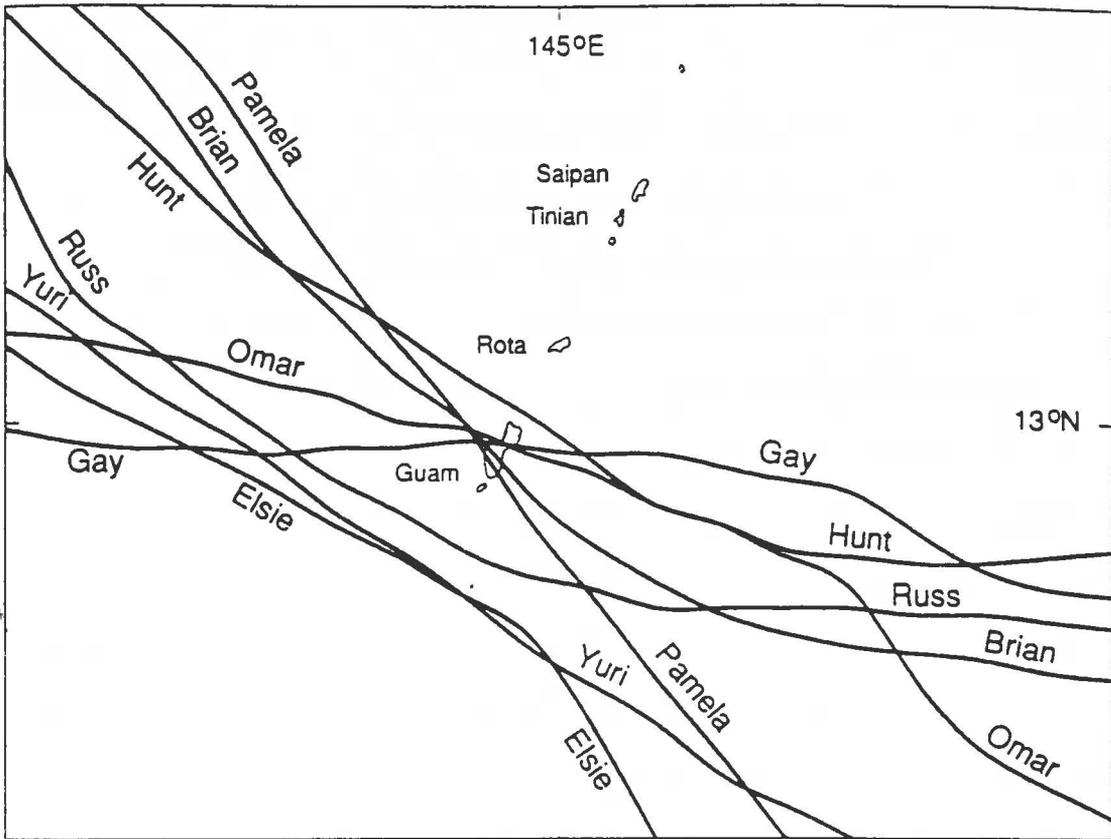


Figure 2. Typhoons affecting Guam during the study periods. Typhoons track from east to west. Data from FWC/JTWC (1976) and USNOCC/JTWC (1990, 1991a, 1992).

winds (Omar) and closeness of approach to the island (the centers of Omar, Brian and Gay passed directly over Guam) (Table 1, Fig. 2).

Other events occurring before and between the survey periods affected or may have affected holothuroid abundance. During October 1972, an extremely low tide (monthly mean sea level 44.2 cm below the previous 26-yr mean) lasting more than 14 d decimated reef-flat organisms, including holothuroids, on Guam's eastern and northern coasts (Yamaguchi 1975). Animals were less affected on western reef flats with deeper moats. Between 1977 and 1989, three typhoons passed within 100 km of Guam. One of these, Typhoon Roy in January 1988 with maximum sustained winds of 52 m/s passed 45 km north of Guam, bringing 19 h of gale force winds (USNOCC/JTWC 1991a). Maximum estimated wave heights during Typhoon Roy were about 4 m on the eastern and western coasts (United States Naval Oceanographic Command Center/ Joint Typhoon Warning Center, unpublished data).

MATERIALS AND METHODS

Surveys

Reef-flat holothuroids were censused periodically and during the day at Pago and Tumon from December 1989 to December 1993 (Table 2). I counted the number of each species in contiguous 30-m \times 2-m quadrats placed lengthwise along belt transects extending perpendicularly from shore to the seaward edge of the reef flat (Fig. 1). To find cryptic species, I overturned rocks and examined crevices and stands of macroalgae. Because of its abundance, Holothuria (Halodeima) atra was sampled in 10-m \times 2-m quadrats placed lengthwise at 30-m intervals on the transect, then its abundance was estimated for the entire 60 m² quadrat. This method was used in central Pago for H. atra (transect C, Fig. 1) only from 1992 to 1993 (surveys 7 to 11; Table 2). From 1990 to 1993 (surveys 5 to 8, 11; Table 2), however, H. atra was also enumerated in three adjacent 5-m \times 2-m quadrats placed lengthwise on the shoreward portion of transect C.

Abundance data for Pago from 1975 to 1977 were taken from Doty (1977); data for Tumon in July 1977 were taken from Birkeland (1978) (Table 2). Briefly, Doty recorded abundances of each species within 25 m² (November 1975 and February 1976) and 100 m² (July 1976 and February 1977) circular plots surveyed with a graduated tape extending from a central permanent stake and placed at 15-m intervals on

Table 2. Survey dates for Pago and Tumon reef flats. ND= day not recorded by Doty (1977) and Birkeland (1978).

Surveys and typhoons	Eastern Pago	Central Pago	Tumon
1	-	10.11.75	-
2	-	ND.02.76	-
Pamela	21.05.76	21.05.76	21.05.76
3	-	ND.07.76	-
4	-	ND.02.77	ND.07.77
5	19.12.89, 21.12.89	06.07.90	27.12.89
Russ	20.12.90	20.12.90	20.12.90
6	30.04.91, 14.05.91	01.05.91	29.05.91
Yuri	27.11.91	27.11.91	27.11.91
7	23.04.92	16.04.92	02.04.92
Omar	28.08.92	28.08.92	28.08.92
8	07.09.92	04.09.92	09.09.92
Brian	21.10.92	21.10.92	21.10.92
Elsie	02.11.92	02.11.92	02.11.92
Hunt	18.11.92	18.11.92	18.11.92
9	-	21.11.92	22.11.92
Gay	23.11.92	23.11.92	23.11.92
10	07.12.92, 29.12.92	-	-
11	-	26.10.93	30.11.93

one of the same transects (transect C, Fig. 1) at Pago that I used in the 1989 to 1993 surveys. Birkeland (1978) recorded abundances of each species in contiguous 5-m x 2-m quadrats laid lengthwise along a belt transect (transect E, Fig. 1) extending perpendicularly from shore to the seaward reef-flat margin and placed ca. 400 m north of transect D used in the 1989 to 1993 surveys. He presented the data as sample sizes, means and standard deviations for five sections of the transect. Using these data, I computed the weighted means and standard deviations (Sokal and Rohlf, 1981) of abundances for the entire transect.

Several features, in addition to its windward location, may contribute to greater holothuroid mortality at Pago than at Tumon. The reef flat at Pago is shallower than at Tumon and, therefore, a larger area of Pago is subaerially exposed for longer time periods during low tides. Subaerial exposure during low tides is an important source of seasonal mortality for reef-flat echinoderms (Hendler 1977). In addition, water is transported on and off the reef flat quickly at Pago because of a large, deep river channel bisecting the reef. In contrast, the rate of water exchange at Tumon is lower, occurring primarily through two small breaches in the reef-flat margin (Marsh et al. 1981). Typhoon-generated waves and surge set up strong currents as storm-driven water flows off a reef flat. Hydrodynamic transport of holothuroids to inhospitable habitat in deep

water, therefore, could be a more important cause of mortality at Pago than at Tumon.

Thus, to determine whether the difference in post-typhoon holothuroid abundance and species composition between Pago and Tumon was typical for windward and leeward reef flats islandwide, I counted the number of each species seen during the day on 2-m wide belt transects at 11 windward (Achang, Acho Point, Agfayan, Asanite, Fadian Point, Taogam Point, Ipan, Tagachan, Tangon Rock, Togcha, Ylig) and 11 leeward (Amantes Point, Anigua, Apaca Point, Asan Bay, Asan Point, Bangi, Elvis lives, Faijai, Piti, Tanguisson, Togcha Beach, Toguan Bay) reef flats in February to May 1994. Names of sites mentioned in this study were taken from United States Geological Survey topographic maps. I also searched outside the transects for less abundant species so that a total of 0.5 to 1 h was spent at each reef flat.

To examine how the distribution of reef-slope species varied with depth islandwide, I recorded the presence or absence of each of the eight most common, permanently exposed holothuroids occurring on the forereef slope [Actinopyga mauritiana, A. obesa, Bohadschia argus, Holothuria (Halodeima) atra, H. (Halodeima) edulis, H. (Microthele) nobilis, Stichopus chloronotus, and Thelenota ananas] during ca. 0.5-h diurnal and nocturnal surveys from May 1992 to August 1993, in shallow (0 to 15 m depth) and

deep (15 to 30 m) water at five windward (Iates Point, Pago, Tagachan, Ipan and the eastern forereef slope of Cocos Island ["Cocos Dropoff"]) and five leeward [Faifai ("Gun Beach"), Agana Channel, Calalan Bank, Toguan Bay, and the western forereef slope of Cocos Lagoon] locations.

Statistical analyses

Holothuroid mortality was defined as a positive difference in the abundance of a population between surveys done before and after a typhoon. While small juveniles were occasionally observed, recruitment between pre- and post-typhoon surveys was probably minimal compared to the magnitude of typhoon-induced mortality. Recruitment in tropical holothuroids is usually slow (Doty 1977). Seasonal large-scale migrations of holothuroids are only reported for temperate species (Muscat 1983). Moreover, immigration and emigration of most holothuroids to and from the reef-flats at Pago and Tumon probably does not occur as the study areas are bounded by rocky headlands and deep water not inhabited by reef-flat species. Some holothuroids (e.g., Holothuria nobilis) inhabiting both the reef flat and reef slope may migrate from shallow to deep water as they mature (sensu Da Silva et al. 1986, Bulteel et al. 1992, Conand 1993), but large-scale increases of such species on the reef slope after a typhoon were not observed. Most tropical holothuroids appear restricted as adults to activity within

small-scale foraging patches or preferred microhabitats (Hammond 1982, Conand 1991). Hence, I assumed there was no net movement in or out of the transects.

Hypothesis 1.-Changes in a species' abundance through time on the reef flats of windward (Pago) and leeward (Tumon) sites were analyzed separately for central Pago, eastern Pago and Tumon via two-way anovas without replication or Friedman's method of randomized blocks (Sokal and Rohlf 1981) with quadrats and dates as factors. Most cryptic holothuroids [Afrocucumis africana, Bohadschia marmorata, Euapta godoffrovi, Holothuria (Thymiosycia) arenicola, H. (Semperothuria) cinerascens, H. (Cystipus) rigida, H. (Platyperona) difficilis, H. (T.) hilla, H. (T.) impatiens, Labidodemas semperianum, Opheodesoma grisea and Stichopus horrens] in these analyses were pooled because they were rare.

I separately compared species richness, Simpson's diversity, as well as the total density of holothuroids, between windward and leeward reef flats via one-way anovas, using these measures and coasts as factors and sites as replicates. I also regressed species richness, Simpson's diversity and total density against reef-flat width for each coast with simple linear regressions.

Hypothesis 2.-Islandwide differences in depth distributions of reef-slope species between windward and leeward coasts were examined with a two-way anova with

replication, using coastlines and depth as fixed factors and sites as replicates.

Hypothesis 3.-To check how microhabitat use affects susceptibility to disturbance, I compared the mortality of the exposed species Holothuria atra and Actinopyga echinites, the cryptic H. leucospilota, and combined remaining cryptic species from the reef flat in central Pago separately for 1975 to 1977 and 1989 to 1993 via two-way anovas without replication using microhabitat and quadrats as factors. To permit comparisons independent of population means, the abundance of each species or species group in each quadrat was converted to a coefficient of variation corrected for small sample size (Sokal and Rohlf 1981):

$$V^* = \left(\frac{s}{\bar{x}} \right) \left(1 + \frac{1}{4n} \right)$$

where s and \bar{x} are the standard deviation and mean, respectively, of the surveys for a species within a quadrat, and n is the number of surveys.

Before using parametric tests, counts and densities of holothuroids were transformed when necessary. Then the data sets were checked with Bartlett's tests to ensure homoscedasticity, Rankit plots to confirm normality and, when appropriate, Tukey's tests for nonadditivity (Sokal and Rohlf 1981); otherwise, analogous nonparametric procedures were used. A posteriori comparisons of means in parametric analyses were made with Tukey's honestly significant

difference tests (Sokal and Rohlf 1981). Statistical procedures were performed on STATISTIX 4.0 package (Analytical Software, St. Paul, Minnesota, USA).

RESULTS

Hypothesis 1. Typhoon effects on reef flats

Density.-The density of all holothuroids combined was severely reduced in central and eastern Pago during typhoons Pamela, Russ and Yuri (Fig. 3). No species was significantly reduced during typhoons Omar, Brian, Hunt, Elsie and Gay (Table 3). Holothuria leucospilota, however, was not significantly reduced in central Pago following typhoon Russ, nor during any typhoon in eastern Pago (Fig. 4, Table 4). Similarly, Synapta maculata was not reduced in central Pago following typhoon Russ (Fig. 5, Table 4). Bohadschia argus and Opheodesoma grisea occurred in central Pago from 1975 to 1977, but were not recorded from 1990 to 1993.

In Tumon overall holothuroid density was relatively unchanged from 1989 to 1993 and was comparable to overall density in 1977 (Fig. 3). Bohadschia argus, however, was much less abundant in 1989 to 1993 than in 1977 (Fig. 5). Conversely, H. atra, Stichopus chloronotus, H. leucospilota and Actinopyga echinites were much more abundant from 1989 to 1993 than in 1977 (Figs. 4, 5). The abundances of the remaining species appeared stable between the survey periods. Islandwide, the log density of holothuroids was positively associated with log reef-flat width on windward ($F=17.26$, $P=.0020$, $r^2=0.6331$), but not on leeward coasts

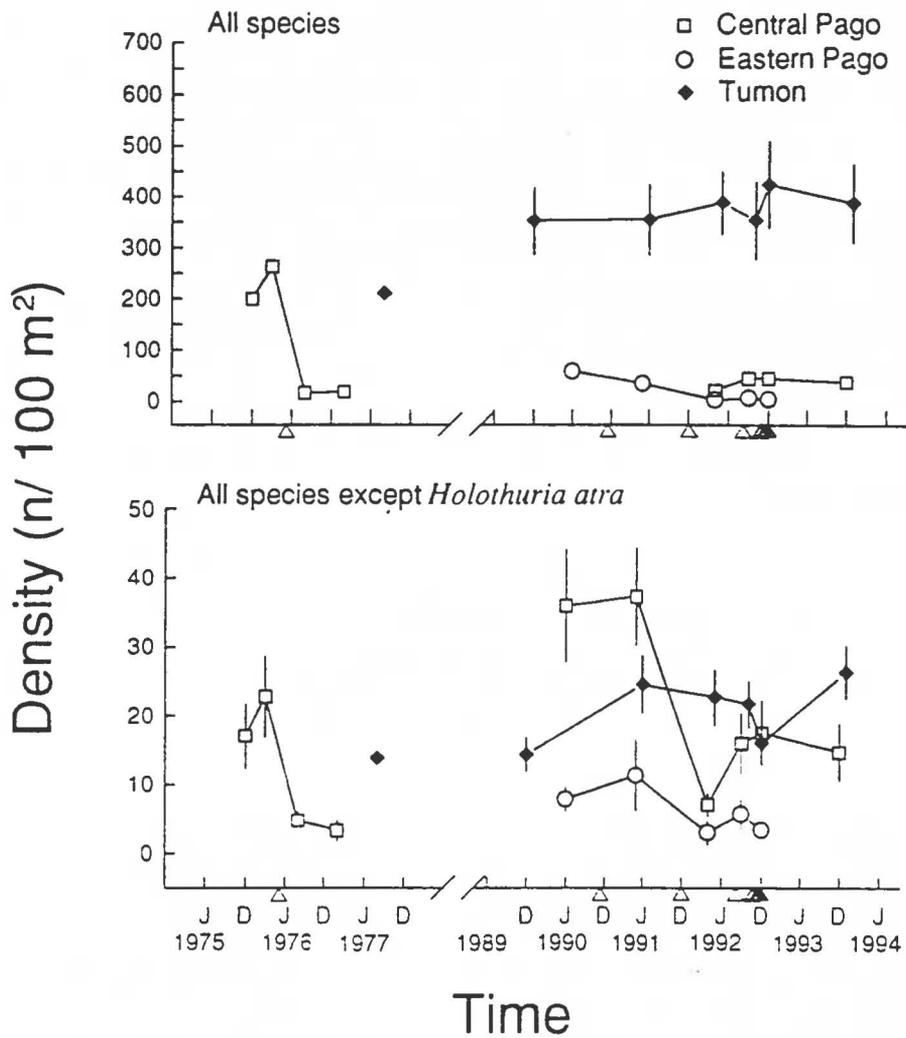


Figure 3. Density of reef-flat holothuroids at Pago and Tumon. Triangles along abscissae denote typhoons. Data are presented as means±one standard error.

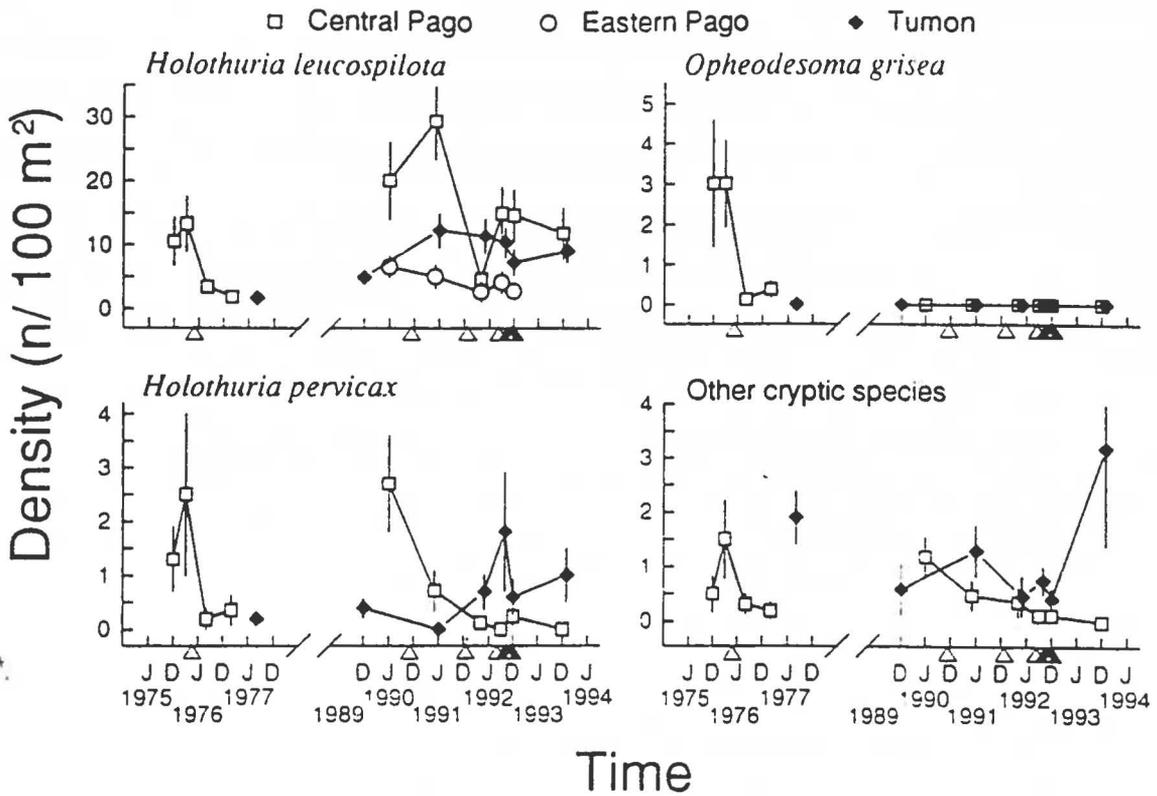


Figure 4. Density of cryptic reef-flat holothuroids at Pago and Tumon. Triangles along abscissae denote typhoons. Data are presented as means±one standard error. Holothuria leucospilota was the only cryptic holothuroid recorded in eastern Pago.

Table 3. Tukey's a posteriori comparison of means of the abundance of holothuroids surveyed from 1989 to 1993. For each species at each site, letters differing among surveys denote significantly different abundances. Survey numbering follows Table 1.

Site	Species	Survey							
		5	6	7	8	9	10	11	
Eastern Pago									
	<u>Holothuria atra</u>	a	a	b	b	-	b	-	
	<u>H. leucospilota</u>	a	a	a	a	-	a	-	
	<u>H. cinerascens</u>	a	a	a	a	-	a	-	
Central Pago									
	<u>H. atra</u>	a	a	b	b	-	b	-	
	<u>H. leucospilota</u>	ab	a	c	abc	abc	-	bc	
	<u>H. pervicax</u>	a	b	b	b	b	-	b	
	<u>Actinopyga echinites</u>	a	ab	bc	c	bc	-	bc	
	<u>Synapta maculata</u>	a	a	b	b	b	-	b	
	Other cryptic spp.	a	ab	c	c	bc	-	c	
Tumon									
	<u>H. atra</u>	abc	ab	bc	a	c	-	abc	
	<u>H. leucospilota</u>	a	c	bc	bc	ab	-	bc	
	<u>A. echinites</u>	ab	a	ab	ab	bc	-	c	
	<u>Bohadschia argus</u>	a	a	a	a	a	-	a	
	<u>H. pervicax</u>	ab	a	ab	b	ab	-	b	
	<u>Stichopus chloronotus</u>	ab	b	b	b	b	-	a	
	<u>Synapta maculata</u>	a	b	a	a	a	-	ab	
	Other cryptic spp.	a	a	a	a	a	-	a	

Table 4. Summary table of two-way anovas without replication and Friedman's tests on the abundance of holothuroids surveyed from 1989 to 1993. Factors are surveys (East Pago=5, Central Pago [H. atra]=4, Central Pago [other species]=6, Tumon=6) and quadrats (Eastern Pago=13, Central Pago [H. atra]=3, Central Pago [other species]=14, Tumon=17).

Site	Species	% Change ^a	Statistic	<u>P</u>
Eastern Pago	<u>Holothuria atra</u>	- 96.5	<u>F</u> = 52.63	.0000
	<u>H. leucospilota</u>	- 57.7	<u>F</u> = 2.26	.0765
Central Pago	<u>H. atra</u>	- 92.1	<u>F</u> = 8.38	.0145
	<u>H. leucospilota</u>	- 40.6	<u>F</u> = 5.62	.0002
	<u>H. pervicax</u>	-100.0	<u>Y</u> ² = 27.78	.0000
	<u>Actinopvga echinites</u>	- 81.4	<u>X</u> ² = 19.14	.0018
	<u>Synapta maculata</u>	- 92.3	<u>Y</u> ² = 30.02	.0000
	Other cryptic spp.	-100.0	<u>Y</u> ² = 37.92	.0000
Tumon	<u>H. atra</u>	+ 7.0	<u>F</u> = 1.99	.0683
	<u>H. leucospilota</u>	+ 84.3	<u>F</u> = 2.49	.0377
	<u>A. echinites</u>	+123.9	<u>F</u> = 3.70	.0047
	<u>Bohadschia argus</u>	+ 80.0	<u>Y</u> ² = 6.12	.2944
	<u>H. pervicax</u>	+150.0	<u>Y</u> ² = 3.07	.1535
	<u>Stichopus chloronotus</u>	+ 37.5	<u>X</u> ² = 11.84	.0370
	<u>Synapta maculata</u>	+100.0	<u>Y</u> ² = 9.05	.1535
	Other cryptic spp.	+120.0	<u>Y</u> ² = 5.05	.4096

^aFrom 1989 (Tumon) or 1990 (eastern and central Pago) to 1993.

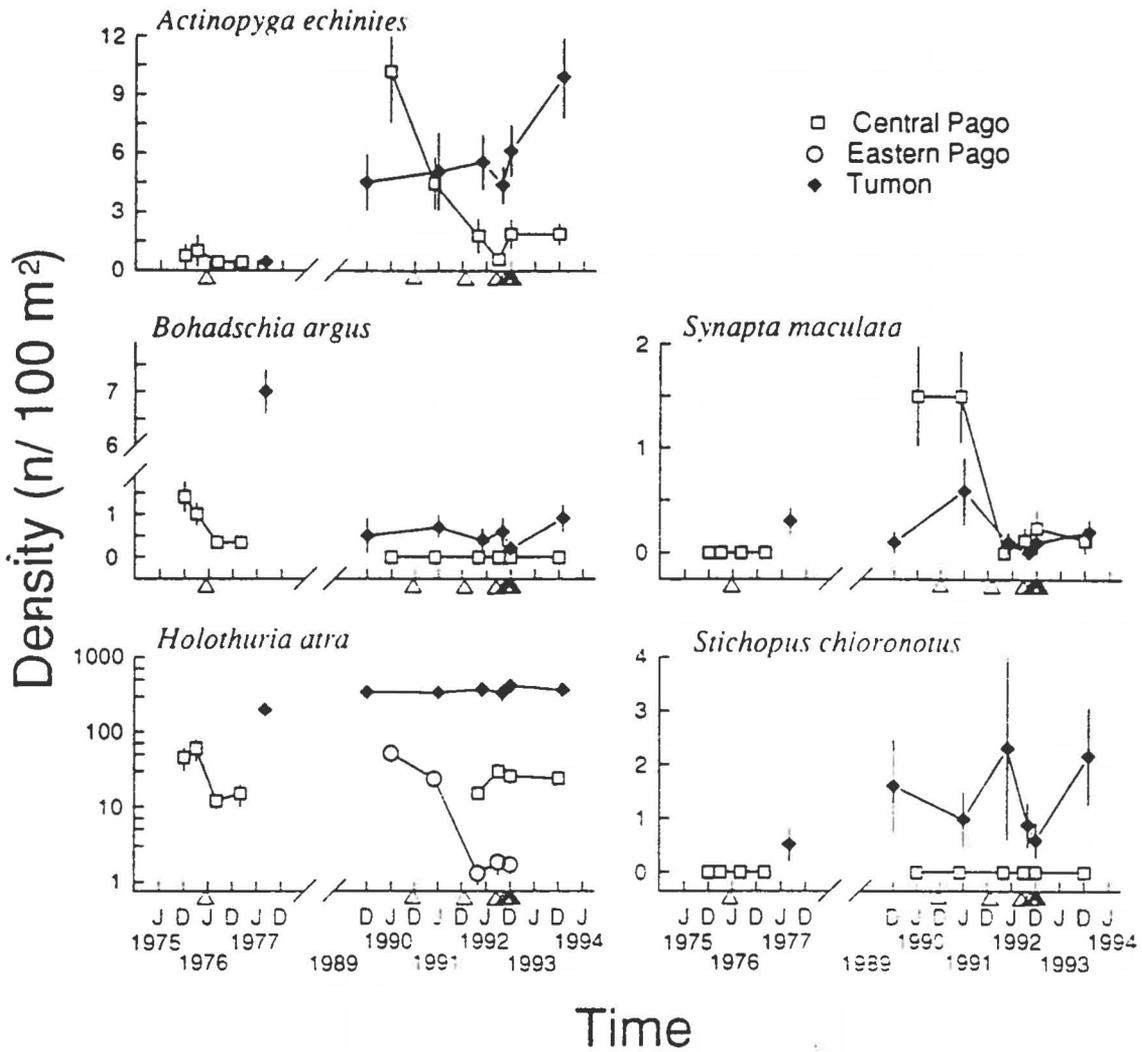


Figure 5. Density of exposed reef-flat holothuroids at Pago and Tumon. Triangles along abscissae denote typhoons. Data are presented as mean \pm one standard error. Holothuria atra was the only exposed holothuroid recorded in eastern Pago.

($F=0.48$, $P=.5028$, $r^2=0.0461$) (Fig. 6). Log density was significantly higher on leeward reef flats ($F=6.46$, $P=.0186$).

Species richness.-Differences in species richness also occurred between windward and leeward reef flats islandwide. Twenty-two species of holothuroids were recorded from the reef-flat surveys in 1994. Seventeen species were found on the windward reef flats, 7 (41%) of which were sightings of single individuals and 9 (53%) of which were only found on the widest reef flat at Achang. Conversely, 22 species were recorded on leeward reef flats, only 3 (14%) of which were single sightings. Log species richness was correlated with log reef-flat width on both coasts (windward: $F=10.46$, $P=.0090$, $r^2=0.5112$; leeward: $F=15.05$, $P=.0031$, $r^2=0.6008$), and was lower on windward than on leeward reef flats ($F=9.44$, $P=.0056$) (Fig. 6).

Simpson's diversity.-Diversity was higher in eastern and central Pago than in Tumon (Fig. 7). Diversity increased in eastern Pago, but not in Tumon, after both typhoons Russ and Yuri. Because Holothuria atra was surveyed differently in 1990 and 1991, community diversity in central Pago was not measured during those years. Simpson's diversity was correlated with log reef-flat width on the windward ($F=9.51$, $P=.0116$, $r^2=0.4872$), but not the leeward ($F=0.85$, $P=.3792$, $r^2=-0.0781$) coast, and was significantly higher on the leeward coast ($F=9.46$, $P=.0055$) (Fig. 6).

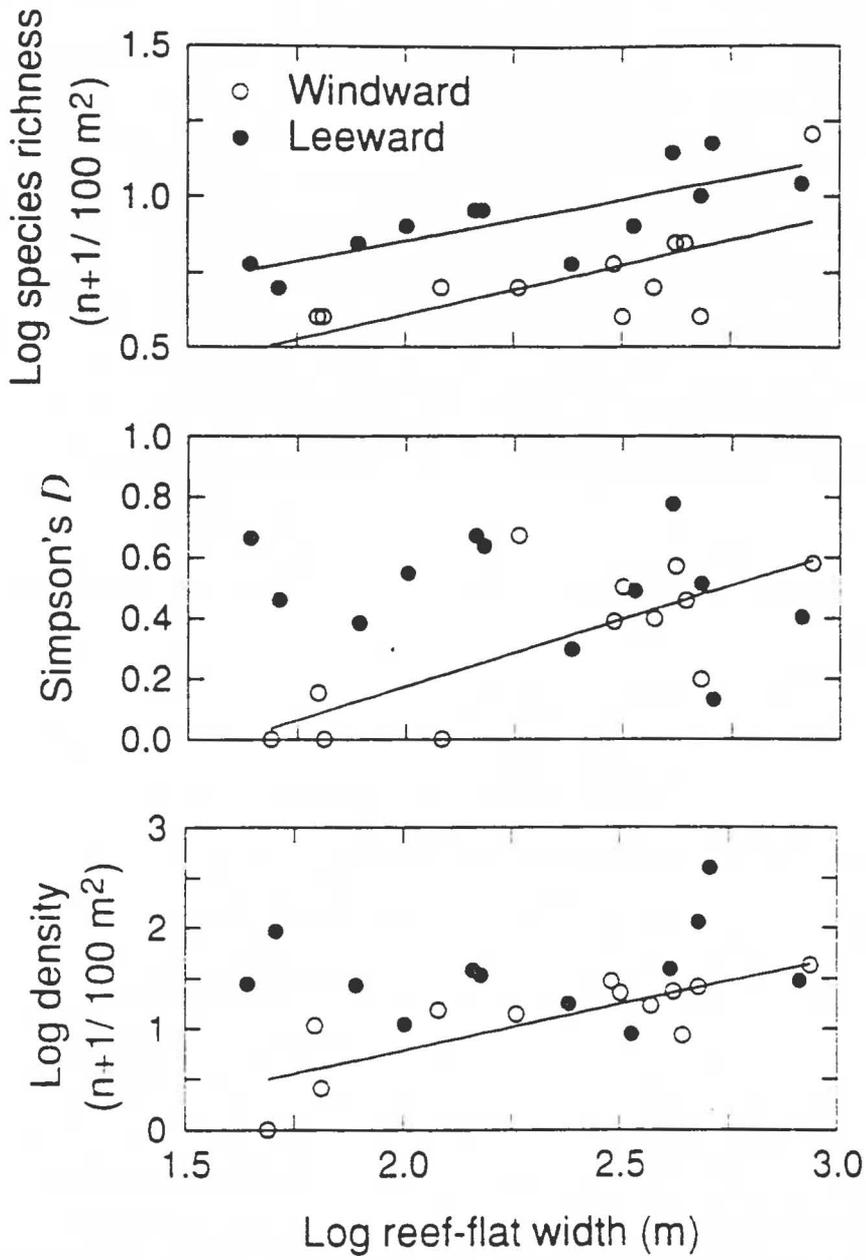


Figure 6. Density, diversity and species richness of holothurcoids on windward and leeward reef flats. Lines are best-fit regression lines.

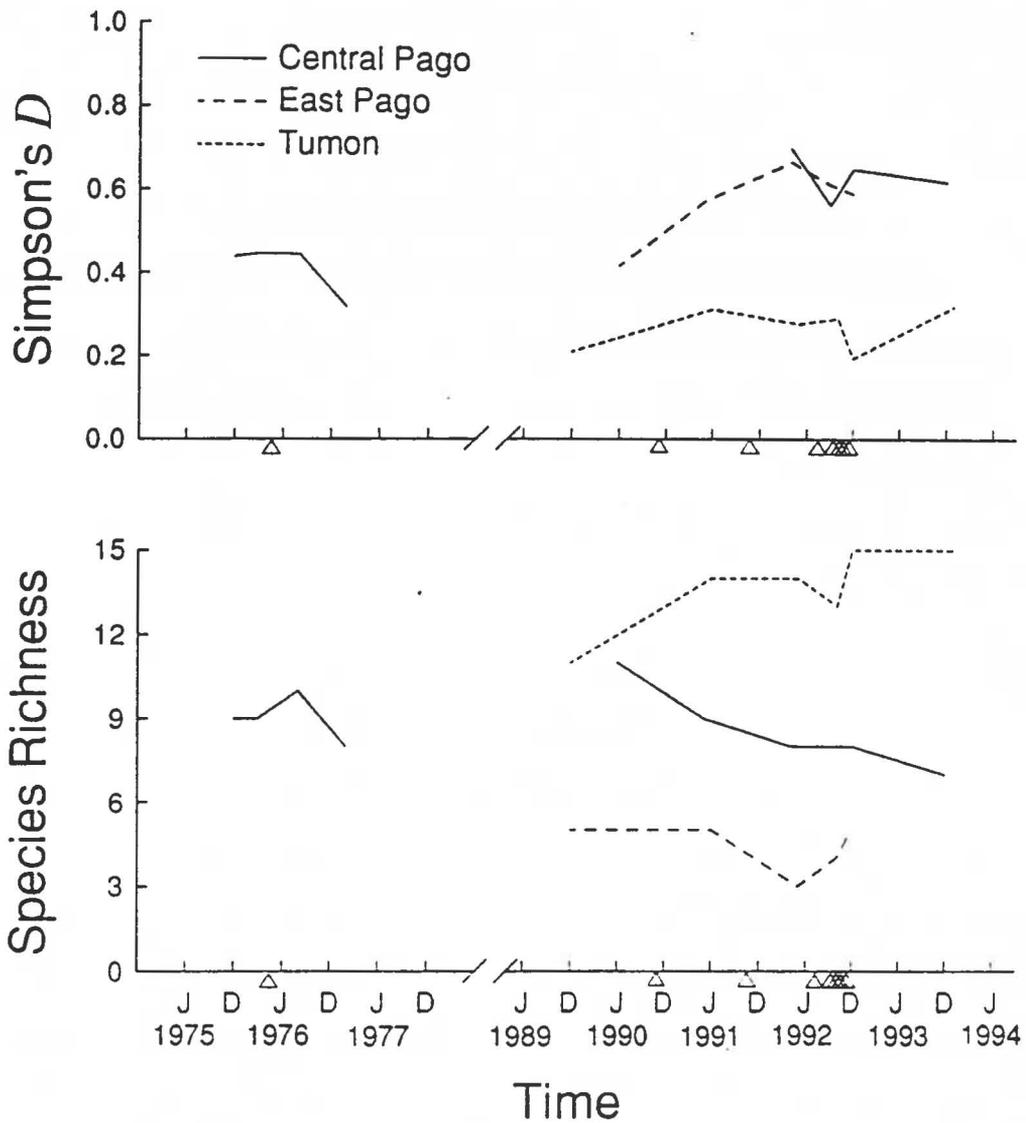


Figure 7. Simpson's diversity and species richness of Pago and Tumon reef flats. Triangles along abscissae denote typhoons.

Hypothesis 2. Typhoon effects on the forereef slope

Log species richness was significantly less on the windward reef slope ($\underline{n}=9$, $\bar{x}\pm 1\text{ SD}=2.11\pm 1.05$) than on the leeward slope ($\underline{n}=9$, 3.89 ± 1.05) (Figure 8, Table 5). Though depth was not a significant factor overall (shallow: $\underline{n}=10$, 2.90 ± 1.79 ; deep: $\underline{n}=8$, 3.13 ± 0.64), the interaction term Coast \times Depth in Table 4 indicates that species numbers were significantly lower on windward reef slopes in shallow water (windward: $\underline{n}=5$, 1.40 ± 0.55 ; leeward: $\underline{n}=5$, 4.40 ± 1.14), but not in deep water (windward: $\underline{n}=4$, 3.15 ± 2.45 ; leeward: $\underline{n}=4$, 3.15 ± 0.95) (Figure 8).

Species composition also varied between depths and coasts. Actinopyga mauritiana occurred only in shallow water and was the only holothuroid commonly found on the windward reef slope. Holothuria atra occurred nearly always in shallow water, Thelenota ananas nearly always in deep water, while H. edulis was found only on leeward slopes. I was able to conduct nocturnal surveys at only five reef-slope sites (Bile, Calalan, Faifai, Pago and Tagachang), but nocturnal holothuroids appeared to be distributed similarly to exposed species. I saw the nocturnal Stichopus horrens and H. (Theelothuria) turriscelsa at shallow and deep leeward sites (Faifai, Calalan), but only on a deep windward slope (Pago).

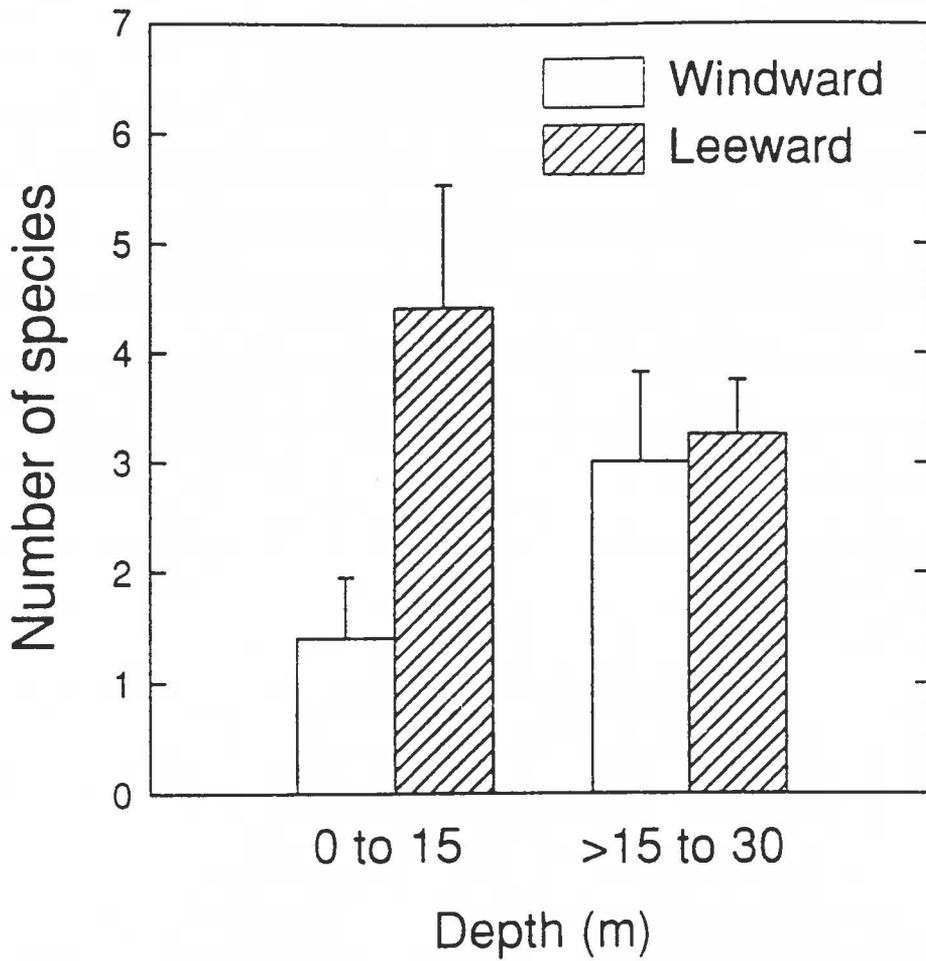


Figure 8. Species richness of windward and leeward forereef slopes. Bars and vertical lines represent means and single standard deviations, respectively; Shallow: $\underline{n}=5$ on each coast, deep: $\underline{n}=4$ on each coast.

Table 5. Summary table of two-way anova of depth distributions of forereef-slope holothuroids on windward and leeward coastlines.

Source of Variation	Degrees of freedom	Sum of squares	<u>F</u>	<u>P</u>
Coast	1	11.250	12.770	.007
Depth	1	0.313	0.680	.441
Coast×Depth	1	11.250	24.550	.003
Coast×Site	8	7.050		
Coast×Depth×Site	6	2.750		

Hypothesis 3. Effects of microhabitat

During typhoon Pamela, the exposed Holothuria atra in central Pago did not suffer significantly greater mortality (67.0%) than the cryptic H. leucospilota (26.2%) or combined cryptic holothuroids (35.0%) (Table 6). The low number of other exposed species during 1975 to 1977 precluded using this group in the above analysis. From 1990 to 1993, mortality to the exposed species Actinopyga echinites (81.4%) in central Pago was intermediate between H. leucospilota (40.6%) and combined cryptic species (95.7%) (Table 6).

Table 6. Effect of microhabitat use on holothuroid mortality in central Pago. Coefficient of variation was adjusted for small sample size. Tukey's honestly significant difference test was used to compare means. F values represent the between-species term from two-way anovas without replication; within-species comparisons of quadrats are not significant and not shown.

Survey period	Percent mortality	Mean coefficient of variation	Comparison of means	<u>F</u>	<u>P</u>	Degrees of freedom
1975 to 1977						
<u>Holothuria atra</u>	67.0	0.7413	a	1.18	.3280	3, 10
<u>H. leucospilota</u>	26.2	0.9276	a			
Other cryptic spp.	35.0	0.9490	a			
1990 to 1993						
<u>Actinopyga echinites</u>	81.4	1.4390	ab	4.06	.0315	7, 11
<u>H. leucospilota</u>	40.6	0.9989	a			
Other cryptic spp.	95.7	1.5281	b			

DISCUSSION

Hypothesis 1. Typhoon effects on reef flats

Typhoons are an important source of mortality for holothuroids inhabiting windward reef flats on Guam. Typhoons caused massive reductions of holothuroid densities at least three times at Pago in 20 yr. The generality of this observation is supported by post-typhoon surveys of other windward reef flats. Windward sites, including Pago, had similar densities of holothuroids, when the effect of reef-flat width is considered (Fig. 7), suggesting that holothuroids on the entire windward coast were also reduced. Species richness was similarly depressed by the typhoons on windward reef flats. Excluding the widest reef flat (864 m) at Achang, only nine species, three as single sightings, were found during the post-typhoon surveys (Fig. 7). In contrast, Rowe and Doty (1977) found 17 species on the windward coast, excluding Achang, in 1975, prior to Typhoon Pamela.

In contrast to the great losses of holothuroids on windward reef flats, populations on the leeward reef flats of Guam appeared relatively stable over 20 yr despite three severe typhoons. On the reef flat at Tumon, overall abundance from 1989 to 1993 was comparable to that in 1977 (Birkeland 1978, Fig. 3 this study). Other reports of high densities further support the long-term stability of holothuroid abundance at Tumon: Emery (1962) estimated the

density of Holothuria atra to be 120/100 m² in 1952. R. Randall (unpublished data) recorded this species at xxx/100 m² in 1969. Birkeland (1978) recorded H. atra at nearly 200/100 m² in 1977. By comparison, this holothuroid occurred at about 300/100 m² from 1989 to 1993 (Fig. 5).

Much of the leeward coast also probably provides protection to shallow-water holothuroids from typhoons. The post-typhoon species richness, Simpson's diversity and density of holothuroids on leeward reef flats, including Tumon, were significantly higher on the leeward coast and, for Simpson's diversity and density, not correlated with reef-flat width (Fig. 7). That is, narrow, more exposed reef flats were as likely to be as diverse and have high densities of holothuroids as wide reef flats.

Hypothesis 2. Typhoon effects on forereef slopes

Holothuroids inhabiting shallow portions of the windward forereef slope appear to be even more affected by wave disturbance than those on windward reef flats. Most of the energy from breaking waves is expended on the shallow reef slope and seaward reef-flat margin (Young 1989, Young and Hardy 1993). Only three species, two of which are records of single specimens, were seen on the windward slope at less than 15 m deep. The remaining species, Actinopyga mauritiana, is a specialist of turbulent habitats (Birkeland 1989). In contrast, post-typhoon species richness on

leeward forereef slopes was uniform with depth and similar to that on deep windward slopes (Fig. 8).

While the island probably shelters leeward reefs from the waves of most westward-tracking typhoons, holothuroid populations may occasionally experience significant storm-associated mortality. Depending on a typhoon's speed and track, sufficient fetch and winds may exist to generate large waves along Guam's normally leeward western coast (FWC/JTWC 1976, USNOCC/JTWC 1991a). For example, Typhoon Lynn in 1987 tracked to the north of Guam and brought waves of 4 m to Guam's western reefs (USNOCC/JTWC unpublished data), possibly affecting shallow-water holothuroids.

Hypothesis 3. Effects of microhabitat

I expected that holothuroids living in crevices would be more protected from typhoon-generated waves, and thus suffer less mortality, than unsheltered species. In this study, however, microhabitat use did not predict the degree of relative mortality between cryptic and exposed holothuroids. The dominant cryptic species, Holothuria leucospilota was reduced as much as the combined remaining cryptic species during typhoon Pamela, but much less during typhoons Russ and Yuri (Table 6). The mortality of the exposed species Actinocyrga echinites was intermediate between mortality to H. leucospilota and combined cryptic species (Table 5). Cryptic species in this study live

mainly under unconsolidated coralline rubble on the outer reef flat (Kerr et al. 1993). Rubble was moved about during Typhoons Pamela (Randall and Eldredge 1977), as well as during Russ and Yuri (A. Kerr, personal observation), and therefore, probably provided little protection to cryptic holothuroids.

One cryptic species, Holothuria leucospilota, however, increased slightly in central Pago after Typhoon Russ (Fig. 4). This increase may be related to changes in habitat. Kobluk and Lysenko (1993) observed an increase in the abundances of loose rubble and cryptic molluscs following a severe typhoon. These authors and others (Woodley 1981, Moran and Reaka-Kudla 1991, Aronson 1993) propose that some rapid increases in post-typhoon abundances of cryptic coral-reef invertebrates are attributable to areal increases in habitat area and subsequent increased recruitment of invertebrates. Rubble under which H. leucospilota hides may have increased in central Pago after Typhoon Russ. However, a concomitant increase in the abundance of other cryptic holothuroids was not observed (Fig. 4).

Other effects of typhoons

A major characteristic of holothuroid assemblages on Guam's shallow windward reefs is turnover, the recurrent extinction and immigration of a population. In 20 yr several holothuroids have repeatedly gone locally extinct or

become very rare. Bohadschia argus, Stichopus chloronotus and Synapta maculata were common in Pago prior to an extremely low tide in 1972 (Yamaguchi 1975). By 1975, only B. argus was again abundant, but it was decimated by Typhoon Pamela in 1976 (Fig. 5). This species was still very rare in 1989, but S. maculata was again common. Both were apparently eliminated from the reef flat after Typhoon Yuri in 1991, though S. maculata is recovering (Fig. 5).

Stichopus chloronotus is still only rarely found.

Opheodesoma grisea was common in Pago in 1976 (Fig. 4), but presently only occurs on leeward reefs (Kerr et al. 1993).

Holothuria nobilis was recorded on the windward coast at Ipan in 1975, but not at Pago (Rowe and Doty 1977). It occurred at Pago in 1990 (Kerr et al. 1993), but is presently (1994) not recorded from any windward reef flat.

The frequency of severe typhoons affecting Guam (USNOCC/JTWC 1991a) suggests that shallow-water populations of most holothuroids on windward reefs are significantly reduced or eradicated about once every 10 yr. This time period is close to or exceeded by the estimated lifespans of some shallow-water holothuroids. Holothuria atra can live from 10 to 15 yr (Ebert 1978). Actinopyga echinites and A. mauritiana may live over 20 yr (Conand 1989). Thelenota ananas and Stichopus chloronotus are estimated to live to 14 and 6 yr, respectively (Conand 1988). Consequently, the chance of an individual of these species experiencing a

severe typhoon is high. Typhoon-induced mortality, therefore, appears to be a dominant force structuring holothuroid assemblages on Guam's windward coast.

Populations of holothuroids are apparently affected by multiple disturbances differently than are populations of sessile organisms reported from the literature. A coral population that has been cleared of vulnerable members by a storm experiences less mortality during a second, more severe storm (Woodley 1989 in Rogers et al. 1991, Witman 1992). This suggests that the degree of mortality to a coral population is not only a function of the severity of a disturbance, but also depends on the time elapsed since the last severe perturbation (Witman 1992). In contrast, the intensity of holothuroid mortality at Pago appeared to be primarily associated with typhoon intensity. Populations of the three most abundant holothuroids Actinopyga echinites, Holothuria atra and H. leucospilota were devastated during Typhoon Yuri, despite high mortality from Typhoon Russ one year previous (Figs. 4 and 5).

Water turbulence has been implicated in the control of the depth distributions of other large mobile marine invertebrates. The temperate echinoids Strongylocentrotus spp. are reduced in shallow water by storm-associated waves (Himmelman 1984, Witman 1987). Wave action on exposed coasts prevents the coral-eating asteroid Acanthaster planci from feeding on forereef slopes at depths generally less

than 2 m (Moran et al. 1985, Birkeland 1990). Another asteroid, Linckia laevigata, occurs naturally on Guam only on leeward reef flats (Yamaguchi 1975). Yamaguchi (1975) postulated that the reduction of a population of L. laevigata transplanted to the windward coast of Guam was primarily due to wave action.

Storm-generated waves are important at a local to islandwide scale in structuring assemblages of shallow-water mobile invertebrates, and may also be influential over larger geographical areas. In the tropical northern Pacific Ocean, typhoons normally occur between 7° and 25° latitude and are considerably less frequent east of 130° longitude (Fig. 9). If typhoon frequency regulates holothuroid diversity at a geographic scale, islands lying outside the region of frequent storms should have assemblages of shallow-water holothuroids on windward reefs at least as dense and diverse as those on leeward reefs. Kerr (1994) found more species at higher densities inhabiting windward than leeward reef flats on Kosrae, eastern Caroline Islands (5°N, 163°E). Similarly, on Tarawa, Gilbert Islands (1°N, 173°E), the large exposed holothuroid Holothuria nobilis occurs on both the shallow and deep windward forereef slope (A. Kerr, unpublished data). Other factors, notably habitat availability, variable recruitment and the time elapsed since the last typhoon, would strongly influence the abundance of mobile invertebrates between adjacent reefs on

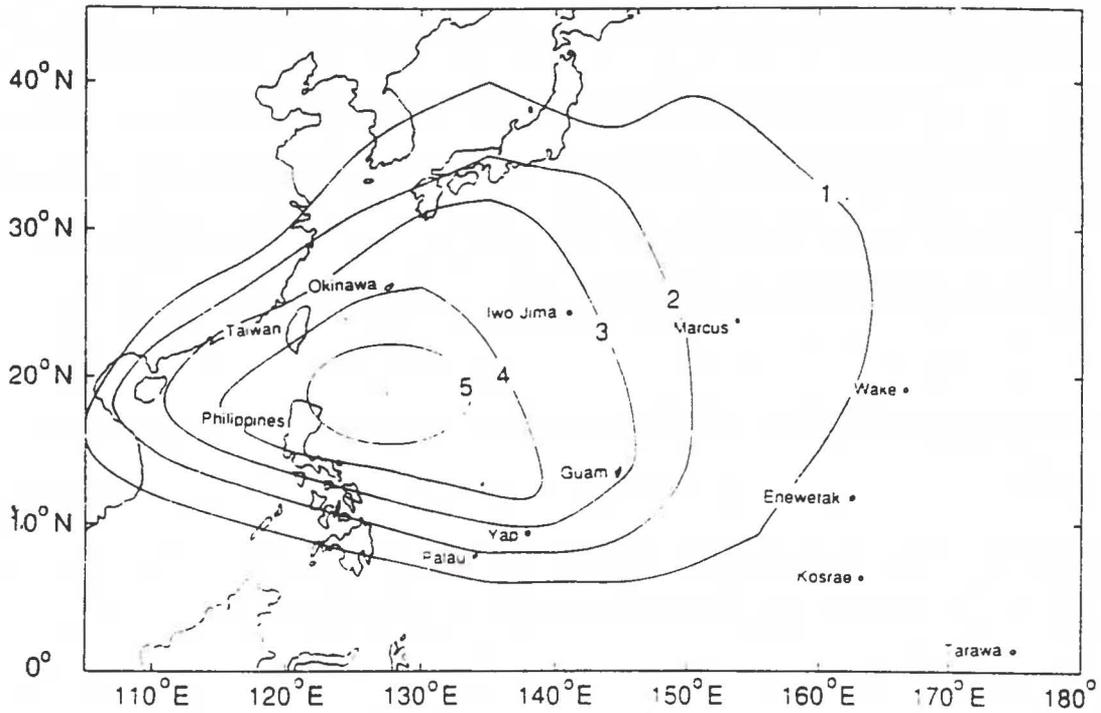


Figure 9. Mean annual number of tropical storms and typhoons traversing 5° squares in the western Pacific (after USNOCC/JTWC 1991a).

an island. Therefore, assessing possible typhoon-caused, basin-wide patterns of diversity will require surveys of many islands.

Summarizing, tropical cyclonic storms in the western Pacific are of sufficient intensity and frequency to prevent holothuroids from maintaining stable populations on shallow windward reefs and contribute to the turnover of some species. Microhabitat use was not a robust indicator of mortality intensity. Mortality to holothuroid populations appeared simply related to typhoon intensity and not to the recent history of disturbance as proposed for corals. These responses to wave disturbance may also characterize shallow-water populations of other large mobile invertebrates. Finally, I speculate that geographical patterns of typhoon frequency influence the relative abundances of mobile invertebrates on windward and leeward reefs of Pacific islands.

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APPENDICES

Appendix 1. Reef-flat holothuroids at Pago and Tumon. Data presented as mean density of individuals per 100 m² and one standard deviation. Data from surveys 1 to 4 in Pago from Doty (1977); data from survey 4 in Tumon from Birkeland (1978). Survey dates follow Table 2.

Species	Survey										
	Site	1	2	3	4	5	6	7	8	9	10-11
Aspidochirotida, Holothuriidae											
<u>Actinopyga echinites</u>											
Tumon					0.42, 1.64	4.51, 5.71	5.10, 8.27	5.59, 5.95	4.41, 1.86	4.18, 5.57	10.10, 9.47
Eastern Pago					0.38, 0.73	0.26, 0.47	0.00, 0.00	0.00, 0.00	0.00, 0.00		0.11, 0.46
Central Pago	0.75, 2.18	1.00, 3.10	0.44, 0.73	0.44, 0.89	10.24, 9.91	4.52, 5.00	1.79, 1.17	0.60, 1.05	1.67, 1.58	1.90, 2.05	
<u>Actinopyga mauritiana</u>											
Tumon					0.00, 0.00	1.27, 4.46	2.65, 10.49	1.18, 4.85	2.45, 9.69	0.20, 0.55	0.39, 1.62
Eastern Pago					0.51, 0.85	0.64, 2.31	0.26, 0.97	0.00, 0.00	0.00, 0.00		0.11, 0.46
Central Pago	0.25, 1.00	0.00, 0.00	0.06, 0.25	0.00, 0.00	0.00, 0.00	0.36, 0.71	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00
<u>Behadachia argus</u>											
Tumon					2.04, 1.94	0.49, 1.64	0.59, 1.19	0.39, 1.11	0.59, 1.31	0.20, 0.55	0.88, 1.33
Eastern Pago					0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00		0.00, 0.00
Central Pago	0.50, 1.37	0.25, 1.00	0.13, 0.34	0.13, 0.34	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00
<u>B. marmorata</u>											
Tumon					0.00, 0.00	0.10, 0.40	0.47, 1.27	0.00, 0.00	0.49, 0.78	0.00, 0.00	0.10, 0.40
Eastern Pago					0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00		0.00, 0.00
Central Pago	0.00, 0.00	0.75, 2.18	0.19, 0.54	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00
<u>Holothuria arenicola</u>											
Tumon					0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.10, 0.40	0.10, 0.40
Eastern Pago					0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00		0.00, 0.00
Central Pago	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00

Appendix 1 (continued). Central Pago1=Holothuria atra sampled along entire transect;
 Central Pago2= H. atra sampled in three adjacent 5-m x 2-m quadrats laid lengthwise
 from shore.

Species	Survey										
	Site	1	2	3	4	5	6	7	8	9	10,11
<u>Aspidochirotida, Holothuriidae</u>											
<u>Holothuria atra</u>											
Tumon					196.23, 115.82	112.94, 99.74	119.39, 101.25	122.95, 91.44	111.08, 112.85	116.47, 136.90	129.98, 114.89
Eastern Pago					51.28, 41.61	23.46, 15.54	1.28, 1.09	1.79, 2.09			1.57, 1.15
Central Pago1	45.50, 60.77	60.00, 76.04	11.88, 10.81	15.00, 16.18			5.00, 3.20	9.88, 7.38	9.28, 7.75		2.98, 5.62
Central Pago2					25.14, 17.16	66.00, 10.66	0.11, 0.58	0.67, 0.58			0.00, 2.00
<u>H. cinerascens</u>											
Tumon					0.00, 0.00	0.08, 1.24	0.78, 2.24	0.59, 2.41	0.00, 0.00	0.00, 0.00	0.00, 0.00
Eastern Pago					0.28, 0.61	5.28, 14.95	0.00, 0.00	1.15, 3.22			0.26, 0.61
Central Pago	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.12, 0.45	0.11, 0.15	0.00, 0.00	0.12, 0.45	0.05, 0.06		0.12, 0.45
<u>H. difficilis</u>											
Tumon					0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00
Eastern Pago					0.00, 0.00	0.00, 0.60	0.00, 0.00	0.00, 0.00	0.00, 0.00		0.00, 0.00
Central Pago	0.00, 0.00	0.00, 0.00	0.06, 0.25	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.15, 0.56	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00
<u>H. hilla</u>											
Tumon					3.42, 8.65	0.00, 0.00	0.19, 0.40	0.00, 0.00	0.10, 0.49	0.00, 0.00	0.29, 0.55
Eastern Pago					0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00		0.00, 0.00
Central Pago	0.50, 1.17	0.00, 0.00	0.06, 0.25	0.12, 0.54	0.24, 0.61	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.12, 0.45	0.00, 0.00
<u>Holothuria impatiens</u>											
Tumon					0.00, 0.00	0.00, 0.00	0.19, 0.40	0.00, 0.00	0.10, 0.49	0.00, 0.00	0.29, 0.55
Eastern Pago					0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00		0.00, 0.00
Central Pago	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.36, 0.71	0.24, 0.61	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.12, 0.45	0.00, 0.00

Appendix 1 (continued).

Species	Survey										
	Site	1	2	3	4	5	6	7	8	9	10,11
Aspilochneptidae: Holothuridae											
<u>H. leucospilota</u>											
Tumon				1.71, 6.35	5.00, 4.68	12.95, 11.02	11.47, 10.85	10.49, 9.66	7.35, 8.00	9.22, 7.69	
Eastern Pago					6.67, 6.01	5.14, 6.40	2.69, 5.95	4.23, 5.15		2.82, 4.05	
Central Pago	10.50, 15.03	13.25, 17.26	3.50, 4.02	1.94, 3.13	20.24, 22.93	29.64, 22.99	4.78, 3.13	15.12, 15.29	14.52, 20.81	12.02, 14.98	
<u>H. nobilis</u>											
Tumon				0.00, 0.00	0.00, 0.00	0.00, 0.00	0.20, 0.55	0.19, 0.40	0.20, 0.30	0.20, 0.40	
Eastern Pago					0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	
Central Pago	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	
<u>H. perricax</u>											
Tumon				0.19, 0.93	0.39, 0.73	0.03, 0.00	0.69, 1.33	1.76, 4.35	0.79, 1.33	0.99, 2.21	
Eastern Pago					0.00, 0.00	0.00, 0.00	0.09, 0.00	0.00, 0.00		0.00, 0.00	
Central Pago	1.25, 2.41	2.50, 6.18	0.19, 0.75	0.36, 0.92	2.74, 3.37	0.71, 1.42	0.12, 0.45	0.00, 0.00	0.81, 1.42	0.00, 0.00	
<u>Holothuria rigida</u>											
Tumon				0.00, 0.00	0.00, 0.00	0.00, 0.00	0.19, 0.40	0.00, 0.00	0.00, 0.00	0.00, 0.00	
Eastern Pago					0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	
Central Pago	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	
Stichopodidae											
<u>Stichopus chloronotus</u>											
Tumon				1.51, 3.06	1.57, 3.56	0.98, 2.05	2.25, 6.90	0.98, 1.68	0.59, 1.33	2.16, 4.03	
Eastern Pago					0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00		0.00, 0.00	
Central Pago	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.12, 0.45	0.00, 0.00	

Appendix 1 (continued).

Species	Survey										
	Site	1	2	3	4	5	6	7	8	9	10,11
<u>Aspidochirotida, Stichopodidae</u>											
<u><i>S. horrens</i></u>											
Tumon				0.19, 0.97	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00
Eastern Pago					0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00
Central Pago	0.00, 0.00	0.75, 2.18	0.00, 0.00	0.00, 0.00	0.48, 1.02	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00
<u>Dendrochirotida, Phyllophoridae</u>											
<u><i>Aficucumis africana</i></u>											
Tumon				0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00
Eastern Pago					0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00
Central Pago	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.12, 0.45	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00
<u>Apodida, Synaptidae</u>											
<u><i>Euapta godoffroyi</i></u>											
Tumon				0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00
Eastern Pago					0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00
Central Pago	0.25, 1.00	1.25, 5.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.10, 0.70	0.00, 0.00
<u><i>Ophodesoma grisea</i></u>											
Tumon				0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00
Eastern Pago					0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00
Central Pago	3.00, 6.28	3.00, 4.26	0.11, 0.50	0.38, 0.72	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00
<u><i>Synapta maculata</i></u>											
Tumon				0.30, 1.15	0.10, 0.40	0.50, 1.11	0.10, 0.40	0.00, 0.00	0.10, 0.40	0.10, 0.40	0.20, 0.55
Eastern Pago					0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00
Central Pago	0.00, 0.00	0.00, 0.00	0.00, 0.00	0.00, 0.00	1.55, 1.79	1.55, 1.66	0.00, 0.00	0.12, 0.45	0.12, 0.45	0.12, 0.45	0.12, 0.45

Appendix 2. Holothuroids on windward reef flats. P= present outside transect.

Species	Achang	Acho	Agfayan	Aaanite	Fadian	Taogam	Ipan	Fago	Tajashan	Tangan	Togcha	Ylig
<u>Actinopyga echinites</u>	10	1	P					16		1	2	P
<u>A. mauritiana</u>	P		P	P	P		P	P	P	1	4	P
<u>Afrocodium africana</u>	1											14
<u>Bonadschia argus</u>	2											
<u>B. marmorata</u>	3											
<u>Euapta godoffroyi</u>	1											
<u>Holothuria atra</u>	626	211	10	1	P	1	64	67	P	16	88	126
<u>H. cinerascens</u>	1							1				
<u>H. difficilis</u>	2											
<u>H. edulis</u>	1											
<u>H. hilla</u>	6											
<u>H. impatiens</u>	1											
<u>H. leucospilota</u>	54	25	17	11	P	P	72	101	14	18	23	43
<u>H. peruviana</u>												
<u>Leiododera semperianum</u>												
<u>Melanopus minoratus</u>	1											
<u>Synapta maculata</u>	2							1	P			1
Reef-flat width (m)	964	480	160	62	48	64	317	421	127	442	374	312
Date (day/month)	16.05.94	05.04.94			17.05.94		19.01.94	05.04.94		16.05.94		
		19.02.94		05.04.94		17.05.94	26.01.93			19.02.94		09.02.94

Appendix 3. Holothuroids on leeward reef flats. P= present outside transect; AsanB= Asan Bay, AsanP= Asan Point.

Species	Anantes	Anigua	Apaca	AsanB	AsanP	Bangi	Fafai	Piti	Tanguisson	Togcha	Toguan	Tumon
<u>Actinopyga echinites</u>	3	P	12	66	36	49	12	1	6	5	8	103
<u>A. mauritiana</u>	1	1	5	5	P				7	P	13	4
<u>A. obesa</u>						P						
<u>Afropocurus africana</u>												14
<u>Behadachia argus</u>				2	3	2		3				9
<u>B. marmorata</u>						P						1
<u>Holothuria arenicola</u>												1
<u>H. atra</u>	31	32	1	80	24	358	4	665	15	12	5	3699
<u>H. cinerascens</u>	4			13			2					
<u>H. difficilis</u>				1								
<u>H. edulis</u>								236				
<u>H. flavomaculata</u>				5				1				
<u>H. flavocipera</u>			P									
<u>H. hilla</u>						27		43				5
<u>H. impatiens</u>		P	P	1	P							2
<u>H. leucospilata</u>	P	19	2	171	42	17	3		14	40	45	34
<u>H. melius</u>		P							P			1
<u>H. parvula</u>										2		
<u>H. peruviana</u>				2	P	1			P			10
<u>Stichopus punctatus</u>				2				17				
<u>S. subcapitatus</u>	2	P		2		3	1	4	34			22
<u>Stenopus maculata</u>			P	3	P	3		1				1
Feet-flat width (m)	77	326	100	413	143	518	40	48	7	241	51	510
Date Sampled	19, 25, 94		23, 24, 94	19, 25, 94	19, 25, 94	17, 15, 94		14, 14, 94		19, 24, 94		19, 24, 94
		22, 24, 94		24, 4, 94		13, 2, 94		14, 5, 94		22, 74, 94		3, 11, 94

Appendix 4. Holothuroids on windward and leeward forereef slopes. X=present at site.

A. Windward sites

Species	Shallow					Deep			
	Tagachan	Cocos	Pago	Taogam	Ipan	Tagachan	Cocos	Pago	Taogam
<u>Actinopyga mauritiana</u>	X	X	X	X	X				
<u>A. obesa</u>							X	X	
<u>Bahaduschia argus</u>						X	X	X	X
<u>Holothuria atra</u>				X					
<u>H. edulis</u>									
<u>H. nobilis</u>								X	X
<u>Stichopus chloronotus</u>		X					X		
<u>Theilenota ananas</u>						X	X		X
Date (d.mo.yr)	11.08.93	13.03.92	05.08.92	19.05.93	14.08.93	10.09.91	09.03.93	13.08.93	13.07.92

B. Leeward sites

Species	Shallow					Deep			
	Ayana	Cocos	Fafai	Topuan	Calalan	Ayana	Cocos	Fafai	Calalan
<u>Actinopyga mauritiana</u>	X	X	X	X	X				
<u>A. obesa</u>					X	X	X		
<u>Bahaduschia argus</u>			X				X	X	
<u>Holothuria atra</u>	X		X	X	X			X	
<u>H. edulis</u>				X			X		
<u>H. nobilis</u>	X	X	X		X	X		X	X
<u>Stichopus chloronotus</u>	X	X	X	X	X		X	X	X
<u>Theilenota ananas</u>					X	X			X
Date (d.mo.yr)	22.02.93	01.09.93	19.15.92	14.17.92	1.08.92	22.02.93	01.09.93	19.05.92	01.07.93