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Coral Reefs

Ecological impact of a fresh-water "reef kill" in Kaneohe Bay, Oahu, Hawaii

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Abstract. Storm floods on the night of December 31, 1987 reduced salinity to 15 ‰ in the surface waters of Kaneohe Bay, resulting in massive mortality of coral reef organisms in shallow water. A spectacular phytoplankton bloom occurred in the following weeks. Phytoplankton growth was stimulated by high concentrations of plant nutrients derived partially from dissolved material transported into the bay by flood runoff and partially by decomposition of marine organisms killed by the flood. Within two weeks of the storm, chlorophyll *a* concentrations reached $40\ \mathrm{mg\ m^{-3}}$, one of the highest values ever reported. The extremely rapid growth rate of phytoplankton depleted dissolved plant nutrients, leading to a dramatic decline or "crash" of the phytoplankton population. Water quality parameters returned to values approaching the long-term average within 2 to 3 months. Corals, echinoderms, crustaceans and other creatures suffered extremely high rates of mortality in shallow water. Virtually all coral was killed to depths of 1–2 m in the western and southern portions of the bay. Elimination of coral species intolerant to lowered salinity during these rare flood events leads to dominance by the coral *Porites compressa*. After a reef kill, this species can eventually regenerate new colonies from undifferentiated tissues within the "dead" perforate skeleton. Catastrophic flood disturbances in Kaneohe Bay are infrequent, probably occurring once every 20 to 50 years, but play an important role in determination of coral community structure. The last major fresh water reef kill occurred in 1965 when sewage was being discharged into Kaneohe Bay. Coral communities did not recover until after sewage abatement in 1979. Comparison between recovery rate after the two flood events suggests that coral reefs can recover quickly from natural disturbances, but not under polluted conditions.

Introduction

Reef corals and coral reefs were once thought to be highly stenohaline ecosystems (e.g., Wells 1957), however salinity tolerance is now known to be greater than previously suspected. Coral reefs occur under natural conditions at salinities ranging from 25‰ to 42‰ (Coles and Jokiel 1992). "Reef kills" caused by low salinity associated with flooding have been reported throughout the world (Coles and Jokiel 1992). Shallow-water reef communities are vulnerable to fresh water damage because low-salinity water is less dense than sea water and forms a persistent surface layer. Few measurements of salinity were made during studies of previous fresh-water reef kills due to the sudden and unexpected occurrence of such disturbances. Often the damage was not noticed until after the flood event. Experimental data on salinity tolerance of corals are limited, with existing data coming largely from the classic literature of 60 to 75 years ago. A survey of the literature and new experimental data suggest that most species of reef corals are killed if salinity is reduced to 15‰ to 20‰ for 24 h or more (Coles and Jokiel 1992).

Kaneohe Bay, Oahu is one of the richest coral reef areas in the Hawaiian Archipelago. The coral reef communities in the bay are extremely vulnerable to fresh-water floods because of restricted water exchange between the bay and the open ocean. Also, most of the coral coverage in Kaneohe Bay is found at relatively shallow depths. Coral is most abundant on shallow patch reefs and fringing reefs within the bay, with 50% of the total area of the bay being less than 3.3 m in depth (Bathen 1968). A fresh-water "reef kill" occurred in Kaneohe Bay following a major flood in May 1965 (Banner 1968). The volume of fresh water that enters the bay during such storms is considerable. During the 1965 flood, the amount of fresh water discharged into the bay in a 24 h period was calculated to be equivalent to a surface layer of 27 cm over the entire bay (Bathen 1968).

Oahu's greatest rain storm in 23 years struck the southeast side of the island on New Year's Eve, 1987. Reduction of salinity in the surface waters of Kaneohe Bay again caused a massive "kill" on shallow reefs. This storm

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provided a rare opportunity to study disturbance and subsequent recovery of the extensive shallow water reefs of Kaneohe Bay. These reefs were severely impacted by sewage discharge between 1964 and 1979 (e.g., Banner 1974; Smith et al. 1981). Thus, we could compare the recovery of reefs under non-polluted conditions to recovery following the similar flood of 1965 that occurred during the time of sewage discharge. The purpose of this paper is to summarize our findings.

Methods

The sudden and unexpected nature of the flood event required an immediate response to obtain salinity data and record the onset and patterns of mortality in Kaneohe Bay. Field methods used in the first phase of this study were dictated by the need to rapidly assess conditions over a large area of the bay. Later, we resurveyed specific areas where detailed baseline data had been taken prior to the storm. We used the methods and sites of previous investigations to facilitate before and after comparisons. Standard meteorological, hydrological and water quality measurement methods were already in use as part of long-range monitoring programs operated by various agencies.

Meteorological – hydrological measurements

Meteorological conditions on Oahu are continually monitored by the National Weather Service using ground-based instruments and satellites. The Kaneohe Bay watershed is monitored directly at 7 rain gauges and 9 stream gauging stations over an area of approximately 97 km^2. Stations cited in the present study are shown in Fig. 1. These data are compiled and published at regular intervals (e.g., US Dept of Commerce 1965, 1988; US Geologic Survey 1966, 1989).

Water column measurements

Water quality parameters have been monitored at a single station in the Kaneohe Bay at weekly intervals for many years (Taguchi and Laws 1989). Concentrations of inorganic plant nutrients, chlorophyll *a* (chl *a*), particulate organic carbon (POC) and other parameters are measured every Wednesday at a station which is located in the south basin as shown in Fig. 2 (solid triangle). Methods have been described previously (Taguchi and Laws 1989).

Immediately after the flood we measured temperature, salinity and oxygen profiles throughout the south basin. Measurements continued on nearly a daily basis for a month following the storm. Salinity and temperature were measured with a Yellow Springs Instrument Co. Model 33 salinity – conductivity – temperature meter with a 10 m sensor cable. Dissolved oxygen was determined in situ using a Yellow Springs Instrument Co. Model 51 oxygen meter also with a 10 m sensor cable. Light attenuation was measured with a Li-Cor Model LI-188B quantameter with LI-192SB underwater sensor. Secchi disc readings were also taken.

Benthic communities – measurements and observations

Observations on the condition of the reef flat were made starting on the afternoon of 1 January 1988. Initially, reef communities in the vicinity of the Hawaii Institute of Marine Biology were visually surveyed. Photographs were taken of the reef communities at various stages of destruction and subsequent recovery. Study sites throughout the bay that had been investigated by Banner (1968) after the 1965 storm were resurveyed in late January 1988, March 1990 and January 1992 at the same 46 stations and using the same methods as in Banner's initial study (Fig. 2, stations shown as solid circles on 1966 map). At each station, the distance from the surface to the shallowest surviving coral was measured with a plumb line marked in centimeter intervals, and adjusted to depth below MLLW. These values were contoured by computer graphical technique into "isonecros" (term coined by Banner 1968) or "depth of total coral death" throughout the bay.

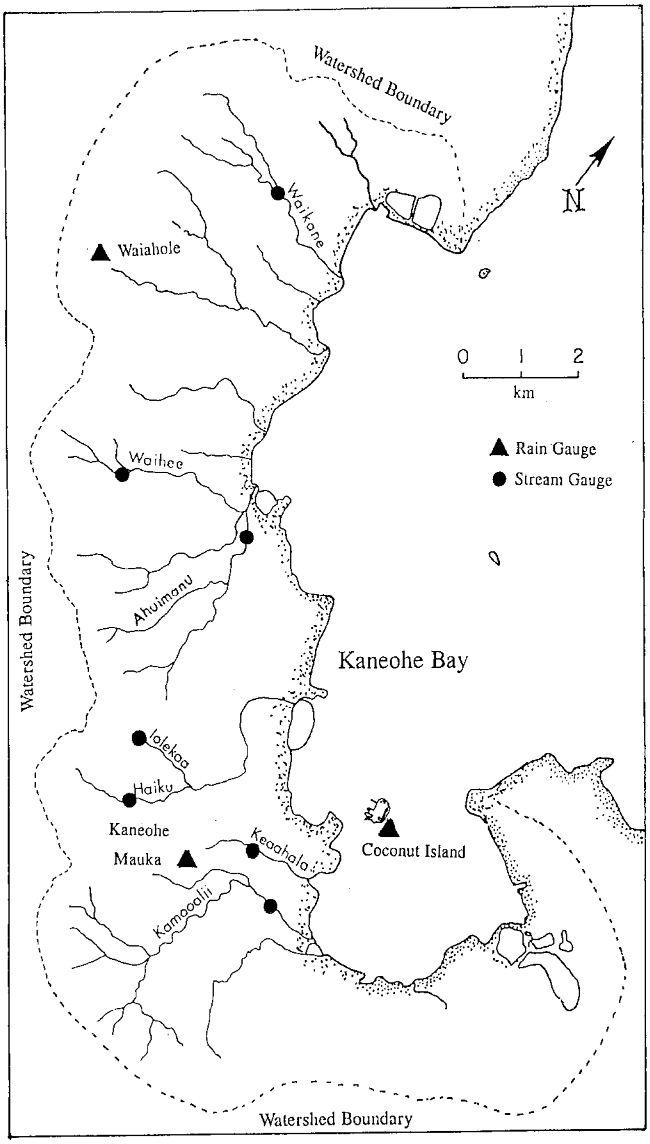

Fig. 1. The Kaneohe Bay watershed showing streams, stream gauging stations and rain gauges referred to in the text

Coral coverage data for reef flat coral communities in Kaneohe Bay (Fitzhardinge 1985, 1993; Fitzhardinge and Jokiel unpublished data) were taken at 3 stations located on reef flats along the actively growing reef margins (Fig. 2, solid squares on 1988 map). These stations were all within the reef kill area. Data were taken by the point-intercept method using a 1 m^2 quadrat strung with line. Twenty-five random points were measured per 1 m^2 plot. Ten random 1 m^2 plots were measured per station.

Results and discussion

Meteorological – hydrological observations

The New Year's Eve flood and reef kill resulted from unusual meteorological conditions during December 1987. A strong and sharp upper tropospheric trough had developed and persisted over the Hawaiian Islands from December 10 to December 20, 1987 with consequent heavy precipitation. The unusually heavy and prolonged rainfall had saturated the soil throughout the watershed of Kaneohe Bay (State of Hawaii 1988). On December 31 a second upper tropospheric trough moved through the islands from the southwest. At the same time, a weak surface cold front moved toward Oahu from the north, setting the stage for the record-breaking storm. The superposition of rain clouds from opposite directions over the Koolau mountains greatly increased the intensity and duration of the rains. Rainfall was greatest in the mountains of east Oahu, exceeding 64 cm (24 inches) in 24 h. Rainfall diminished at lower elevations, with approximately 41 cm (16 inches) falling in 24 h along the coastline to the east of the mountains.

The storm center of 1 January 1988 appears to be the largest ever recorded on Oahu as defined by the area within the 64 cm (25 inch) rainfall line. Amount of rainfall recorded in the 24 h period vastly exceeded the predicted value for "hundred year floods" in the area (State of Hawaii 1988). The center of the storm was located to the south of the Kaneohe Bay watershed (State of Hawaii 1988). In contrast, the storm center during the 1965 flood occurred directly to the west of central Kaneohe Bay (Banner 1968). Patterns of rainfall for the two storms are shown in Fig. 3.

The intensity of the 1987–1988 storm did not appear to be severe in the Kaneohe Bay area. Several storms that occurred between 1965 and 1987 produced extensive flood damage to urban areas on the watershed without producing extensive mortality on the reefs of the bay. Discoloration of the Kaneohe Bay surface waters by suspended soil was not as conspicuous as noted in storms of previous years (J. Naughton, personal communication; P. Jokiel personal observation). In general, the storm at first appeared to be a relatively "normal" winter flood event of the type frequently observed on the Kaneohe Bay watershed. Analysis of rain gauge data supports this initial impression. The 1987–88 storm rainfall on the Kaneohe Bay watershed was well below that which occurred in the 1965 flood. Daily rainfall and cumulative storm rainfall for the 1987–88 flood was typically considerably less than 50% of values measured in the 1965 flood. Data for rain gauge stations are shown in Table 1. Comparison of maximum stream flow data (Table 2) for major streams on the Kaneohe Bay watershed further supports the initial observations that the 1987–88 flood was not severe, especially when compared to the 1965 flood. At five of the seven stream stations, the maximum flow in the 1987–88 flood was only 20% to 50% of maximum flow in the 1965 flood, while the remaining

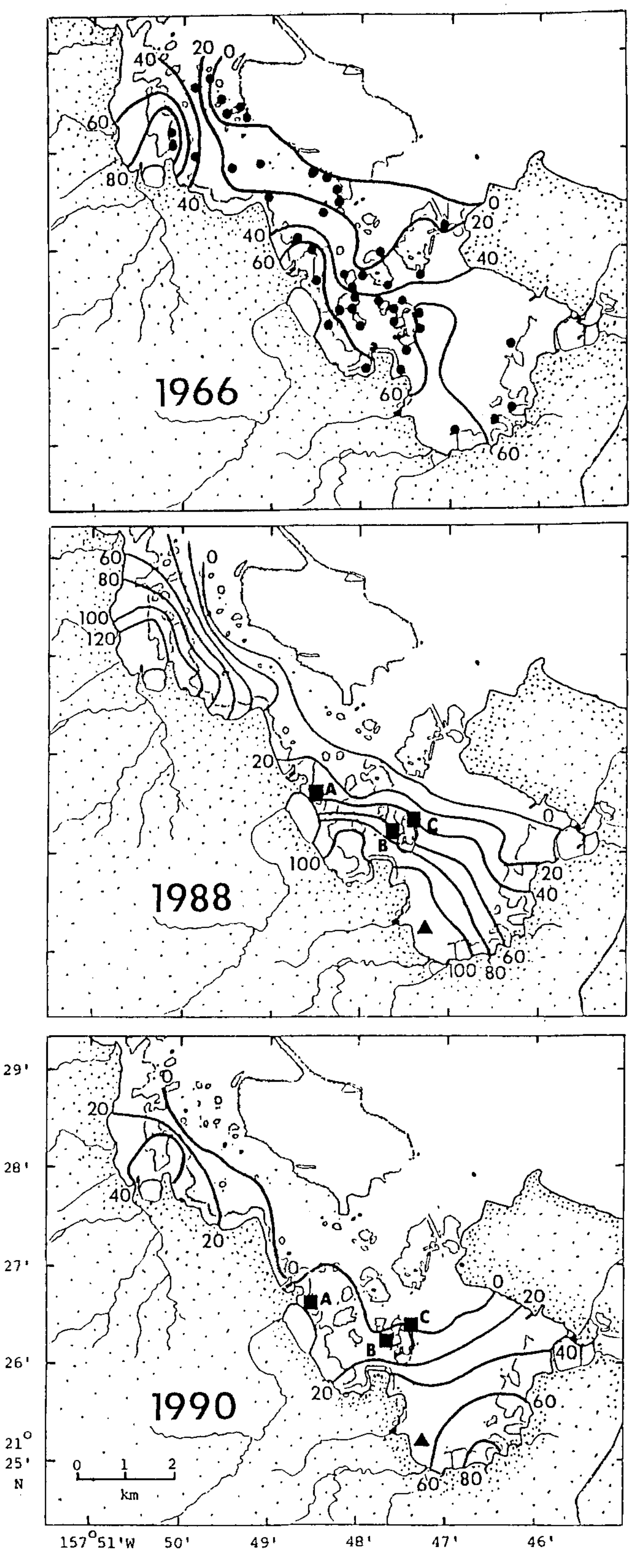

Fig. 2. Depth of total coral destruction (expressed in cm below MLLW) one year after the 1965 flood (1966 map) compared to the destruction immediately following the 1988 New Year's Eve flood (1988 map) and partial recovery of corals by mid-1990 (1990 map). The 1992 map is not shown because living coral was found to a depth of 0 m at all stations. Survey stations (Banner 1968) which were revisited in 1988 and 1990 are shown as solid circles on the 1966 map. Lines are "isonecros" (Banner 1968) that represent the depth to which all coral was killed. Contour lines on all three maps were fitted with a computer graphics program. The 1988 map shows locations of coral quadrat stations as solid squares with the following letter symbols: *A* Heeia patch reef flat (windward), *B* Coconut Island reef flat (leeward), *C* Coconut Island reef flat (windward). The location of the water sampling station in the south basin is shown as a solid triangle on the 1988 and 1990 maps

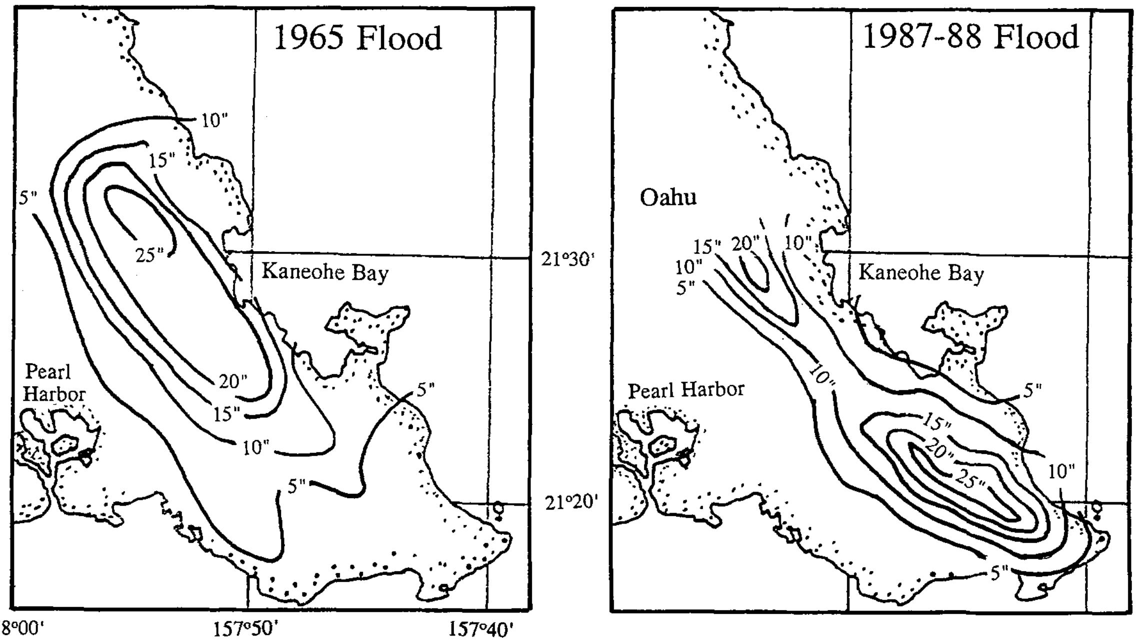

Fig. 3. Rainfall distribution during the 1965 storm versus the New Year's Eve Storm of 1987–88. Isohyetal lines are approximate for total rainfall during the 24 h period of maximum precipitation (Banner 1965; US Geol Survey 1966; State of Hawaii 1988; US Geol Survey 1989; unpublished data). Metric conversions for the isohyets are: 25″ = 63.5 cm, 20″ = 50.8 cm, 15″ = 38.1 cm, 10″ = 25.4 cm and 5″ = 12.7 cm

Table 1. Comparison of maximum daily and cumulative 5 day rainfall for the 1965 flood event versus the 1987–88 flood event for several stations on the Kaneohe Bay watershed (see Fig. 1). Data from US Dept of Commerce (1965, 1988)

	1965 Flood (rainfall in mm)					
	2 May	3 May	4 May	5 May	6 May	Total
Moku O Loe (Coconut Island)	266	16	93	16	10	401
Kaneohe Mauka	17	549	48	55	1	670
Waiahole	*	597	102	65	13	777
	1987–88 Flood (rainfall in mm)					
	31 Dec	1 Jan	1 Jan	2 Jan	4 Jan	Total
Moku O Loe (Coconut Island)	17	*	*	*	125	142
Kaneohe Mauka	3	109	53	19	1	185
Waiahole	*	*	*	*	399	399

* Rain gauge not read. Precipitation is included in reading following the asterisks

Table 2. Maximum storm discharge comparisons at major streams on the Kaneohe Bay watershed for which crest stage data exist for both flood versus New Year's Eve Storm (1987–1988)

Stream	Maximum flow in $m^3 s^{-1}$		
	Largest recorded pre-1965 Flood	1965 Flood	1987–1988 Flood
Kamooalii	187.2	152.9	46.7
Keaahala	50.7	77.9	17.0
Haiku	89.5	162.5	21.3
Iolekaa	4.9	22.6	26.9
Ahuimanu	169.9	187.2	31.1
Waihee	48.1	29.7	15.5
Waikane	249.2	93.5	112.4

two stations showed comparable maximum flow. Nevertheless, a severe reef kill occurred on the reefs of Kaneohe Bay.

How can we account for the reef kill? Two unique features of the 1987–88 storm were described previously. First, the storm was immediately preceded by prolonged rainfall during mid-December. Soil on the Kaneohe Bay watershed was already saturated or nearly saturated. Second, the duration of the storm was prolonged by unusual meteorological conditions. A comparison of total stream discharge over the 72 h period of maximum rainfall for the 1965 flood versus the equivalent 72 h period for the 1987–1988 storm provides the explanation for the kill (Table 3). Both storms were similar in terms of 72 hours stream discharge into Kaneohe Bay, although the 1987–1988 storm was less severe if defined in terms of total

Table 3. Daily total flow and combined 72 h total flow at major streams on the Kaneohe Bay watershed for which comparable data exist for both 1965 and 1987–1988. Data from US Geol Survey 1966, 1989

Stream	Flow in $m^3\,day^{-1} \times 10^4$							
	1965				1987–1988			
	2 May	3 May	4 May	Total	31 Dec	1 Jan	2 Jan	Total
Haiku	150	11	11	172	31	24	3	58
Kahaluu	15	2	1	18	20	16	3	39
Waihee	94	7	5	106	29	19	4	52
Waikane	49	21	17	86	132	110	25	268
Combined four stream total				382				417

rainfall or peak flow. Residence time of water in Kaneohe Bay is approximately two weeks (Smith et al. 1981), so a slightly longer duration (72 h vs. 24 h) of fresh water storm discharge is not as important as total volume of fresh water discharge over several days. Salinity was lowered to lethal levels within the bay during both storms.

Changes in the water column

The most important factor was reduced surface salinity, which led to mortality of organisms in shallow water. A summary of our salinity measurements is as follows.

Surface salinity during the first day of the storm fell to 15‰ in the surface layer (to depths of 1–2 m) in the southern most portion of the bay and along the western shore. Salinity remained below 20‰ in this area until after 4 January 1988. At Coconut Island, which is farther from river influence and closer to the ocean, the salinity was 20‰ on January 2 and remained below 22‰ until January 4. The low-salinity surface layer began to attenuate as a result of tidal flushing and down-mixing, but values as low as 21‰ were still encountered to depths of 1 m near the southwest shore of Kaneohe Bay on January 5. Salinity in the south basin took a day or two to rebound. By January 7 surface salinities throughout the bay generally exceeded 30‰.

The New Year's eve storm influenced other physical factors, often in a complex manner. Temperature of the surface water was lowered by 1–3 °C below the winter ambient temperature of 24 °C. Surface incident irradiance was reduced dramatically by the heavy cloud cover. Incident light levels dropped to 10–20% of normal for several days. Light penetration of the water column was reduced for several weeks, initially by sediment load and subsequently by a phytoplankton bloom. Reduced light and decomposition of organisms killed by the storm led to lowered levels of dissolved oxygen and high levels of particulate and inorganic nitrogen, phosphorus and carbon. The effect on the plankton and nekton was of short duration; these communities recovered within weeks.

Results of the weekly water sampling of the south basin station are shown in Fig. 4. Nitrate is an inorganic plant nutrient that is associated with fresh water inputs into reef systems. Levels of nitrate increased gradually from less than 1 μM to 10 μM in the month preceding the flood due to increased runoff during December. Following the major storm, levels of 30 μM were recorded.

A dramatic bloom of phytoplankton occurred during the two weeks following the flood as evidenced by changes in chl *a* concentration and POC concentration (Fig. 4). Water in the bay became the color of coffee due to a bloom consisting mostly of diatoms of the genus *Chaetocerous*. Secchi disc readings in the south basin prior to the flood normally range between 5 and 7 m. In the month following the flood, readings generally fell into the 1.5–2.0 m range with readings of less than 1.0 m during the peak of the bloom.

Chl *a* concentration increased from approximately 2 mg m^{-3} to more than 40 mg m^{-3}. This concentration is among the highest ever recorded for marine phytoplankton. POC showed a similar increase (Fig. 4). The phytoplankton response was probably due to increased growth rate stimulated by high levels of available plant nutrients. Elimination of zooplankton grazers by low salinity stress could have been a factor contributing to the bloom. In mid-January, almost no zooplankton could be found in the < 183 μ net fraction at the south basin water sampling station. Available inorganic nutrients were quickly depleted

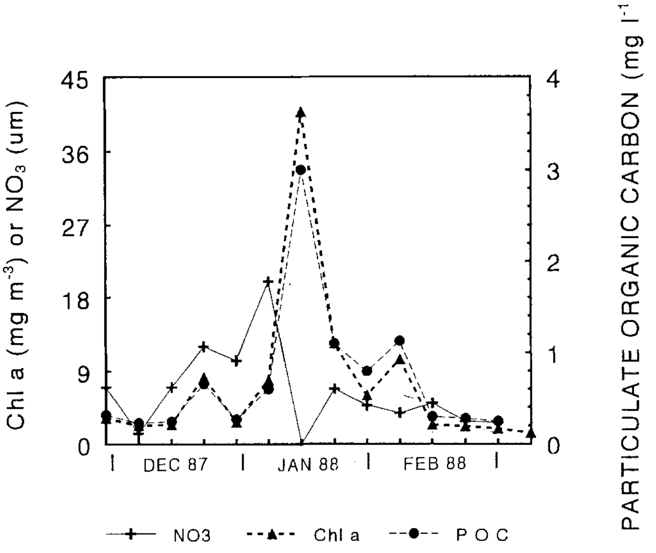

Fig. 4. Water chemistry measured at weekly intervals (every Wednesday) at the south basin station throughout late 1987 and early 1988. Water sampling location is shown as solid triangle in Fig. 2

by the high standing crop of phytoplankton. Nitrate concentration was drawn down to undetectable levels by mid-January and the phytoplankton population subsequently "crashed". Diatoms visually showed extreme degeneration of chloroplasts when examined under the microscope. Dinoflagellates were nonmotile.

Tidal flushing, deposition of organic material into the sediments and recovery of planktonic and benthic marine communities restored water column parameters to pre-flood conditions within a month of the storm. Nitrate, chl *a* and POC concentrations returned to near normal range by mid-February 1988. Zooplankton were again found in normal concentrations in the $<183\,\mu$ net fraction and phytoplankton populations returned to normal in terms of abundance and appearance.

Impact on reef communities

Intertidal organisms were the least affected of the reef flat organisms. Littorinid snails, periwinkle snails, hermit crabs, limpets, barnacles and other intertidal organisms generally remained in good condition. These animals are adapted to prolonged osmotic stress from rain or drying.

In contrast, subtidal reef-flat organisms suffered high rates of mortality. By 5 January 1988, dead and dying macroinvertebrates littered the fringing reef flats of the south basin. Corals, holothuroids, tunicates, annelids, mollusks, hydrozoans, sponges and crustaceans were killed on the reef flats along the entire fringing reef and extending onto those patch reefs close to shore. The smaller organisms rotted quickly, so evidence of the kill was most apparent among corals and larger invertebrates such as the swimming crabs *Thalamita* spp. and *Portunus* spp., the large burrowing crab *Macrophthalmus telescopicus*, and large sea cucumbers such as *Holothuria atra* and *Holothuria monocharia*. Damage diminished with increasing depth and with increasing distance from stream mouths (Fig. 2).

Response of fish communities

Direct mortality of fish did not occur. Reef fish simply moved off the reef flats and into deeper water to escape the low salinity layer. For several weeks following the flood, fish were rarely observed on the reef flats, but were abundant along the reef face. Within one month of the flood, schools of small herbivorous surgeon fishes and parrot fishes had returned to their normal feeding grounds on the reef flats. There were minor behavioral disruptions of fish populations and possible mortality of planktonic eggs and larvae, but the long-term impact of the storm on fish populations appeared to be minimal.

Response of reef corals and soft corals

Observations made during the present survey support previous estimates of 15‰ to 20‰ as the lower lethal salinity in reef corals (Coles and Jokiel 1992). The pattern of coral mortality in relation to low salinity observed in the field is consistent with the laboratory experiments of Edmondson (1928). Edmondson's results indicate that the common species of Hawaiian corals will succumb to an exposure of two days at a salinity of 15‰.

Pocillopora damicornis is common on reef flats in the bay and is clearly the most sensitive to lowered salinity. No colonies survived in the shallows along the fringing reef or on reef flats in the shoreward half of the bay. The coral *Montipora verrucosa* also proved to be highly sensitive and was completely eliminated to a depth of 1–2 m along the inshore margins of the bay. This coral is common in deeper water. The small encrusting coral *Cyphastrea ocellina* persisted on some reef flats where *P. damicornis* and *M. verrucosa* were eliminated. The dominant coral in Kaneohe Bay is *Porites compressa*, which accounts for over 90% of the coral coverage. This species is clearly the most flood-resistant of the scleractinians and survived in areas where all other coral species had been eliminated. Two species of soft corals (Zoanthidae) are common on the reef flats of the bay. *Zoanthus pacificus* forms extensive beds on sand flats while *Palythoa vestitus* is quite abundant on hard substratum (Cooke 1976, 1983). Initially the zoanthids on Coconut Island reef showed stress responses to the flood. Polyps were contracted and discolored with streaming mesenteries. Within one to two weeks the zoanthids began to show signs of recovery. They were again of normal appearance within one to two months of the flood. Thus, the zoanthids showed very high tolerance to reduced salinity compared to the reef corals.

Recovery of reef-flat coral communities

The rapid formation of large numbers of new colonies of *Porites compressa* at the base of "dead" parent colonies of this species led us to conclude that isolated patches of coral tissue remained viable within the perforate skeleton. This phenomenon had been noted previously by other workers in Kaneohe Bay. Regeneration of polyps in *P. compressa* from atrophied non-differentiated tissues has been shown by Franzisket (1970) for colonies held in the dark and subsequently returned to light, while *P. compressa* colonies killed by burial under large accumulations of macroalgae during storms were classified as "dead", but subsequently regenerated tissues (W. Tyler and R. Fitzhardinge, personal communication).

Likewise, coralla of the solitary coral *Fungia scutaria* appeared to have been killed on most reef flats, but many "dead" skeletons began to develop small buds within a year of the storm. The buds apparently are derived from small bits of tissue that persist between the septal plates (Krupp et al. in press). The buds gave rise to many new coralla of this species.

The rate of coral recovery in the years following the 1988 flood was rapid at three reef-flat stations (Fig. 2) sampled for coral coverage in the zone of complete coral kill (Fig. 5). The documented increase in coral coverage from the time of sewage abatement to 1983 (e.g., Maragos et al. 1985; Aliño 1986) apparently continued between 1983 and 1986 at the three sites. This trend was eradicated suddenly by the flood of 1988. The immediate post-flood survey gave

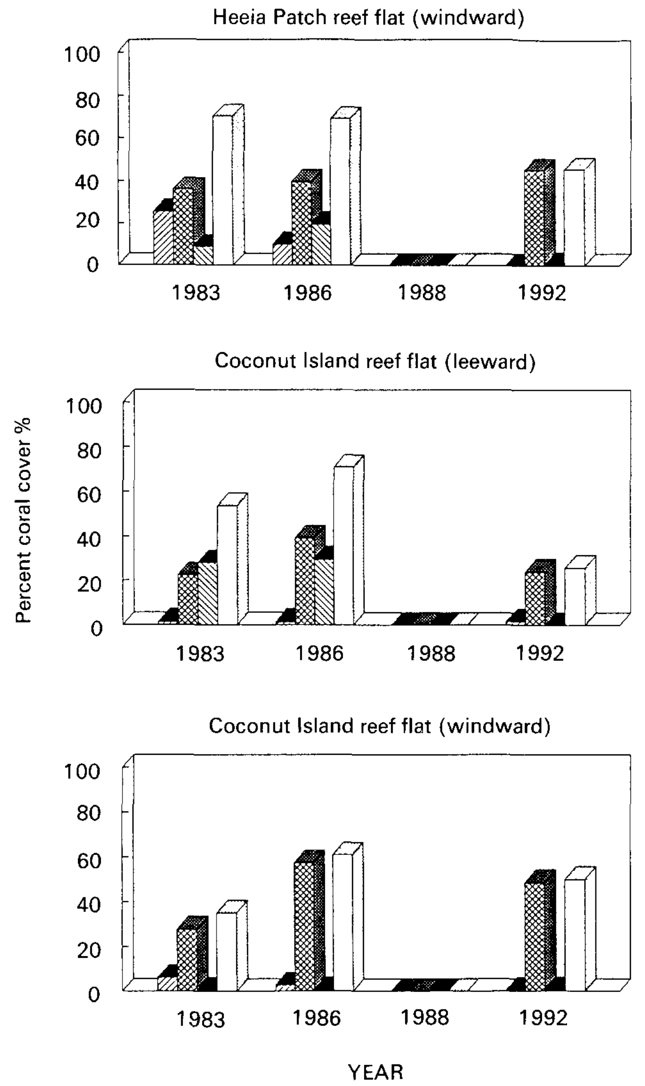

Fig. 5. Changes in reef-flat coral community structure between 1983 and 1992 for seaward reef-flat coral communities in Kaneohe Bay that were damaged by the 1987–88 flood. Data are from Fitzhardinge (1985, 1993) and from Fitzhardinge and Jokiel (unpublished data). Locations of sample sites are shown as solid squares in Fig. 2. ▨ *Pocillopora damicornis*, ▩ *Porites compressa*, ▧ *Montipora verrucosa*, ☐ Total coral cover

an estimate of total mortality of coral on the reef flats (i.e. 0% coverage), but the method did not account for the possibility of live tissues remaining within the "dead" skeletons. Within four years of the 1988 reef kill, total coral coverage had increased substantially. The rapid increase, however, can be attributed almost entirely to the regeneration of *Porites compressa*.

Regeneration of "killed" colonies was not observed in species other than *Porites compressa* and *Fungia scutaria*. Various other coral species recruited onto the reefs through settlement of planula larvae. During the 1992 survey we noted new recruits of *Montipora verrucosa* ($52 \pm 21\,\mathrm{m}^{-2}$) in quadrats on the leeward Coconut Island station. These ranged in size from barely visible to 4 cm diameter, and cover less than 1% of the available substrate (Fig. 5). Likewise, small settlements of *Pocillopora damicornis* (<1 cm diameter) were also abundant. If conditions remain favorable, these species will continue to grow in diameter at a rate of from 1 to 4 cm per year (e.g., Aliño 1986, Fitzhardinge 1993) and will again make up a significant part of the coral coverage.

Comparison of recovery from the 1965 flood and from the 1981–88 flood

Between 1964 and 1979 the Bay received municipal sewage discharge. The resulting nutrient enrichment stimulated the growth of phytoplankton, which in turn led to an increase in zooplankton standing crop. The increased plankton concentration decreased water transparency and diminished light reaching the corals. Increase of plankton led to domination of the benthic communities by filter feeding barnacles, tunicates, sponges and other filter-feeding organisms, which competed with the corals for space. The green "bubble algae" *Dictyosphaeria cavernosa* increased greatly in biomass and out-competed the corals along the reefs below a depth of 1–2 m (Banner and Bailey 1970; Banner 1974). Reef flats became increasingly dominated by zoanthids (Cooke 1976, 1983). Recovery of reef corals after the 1965 reef kill was slow or non-existent (e.g., Maragos 1972; Banner 1974; Smith et al. 1981), apparently because of the eutrophic conditions. Sewage discharge was finally terminated in 1979. Fourteen years had elapsed since the reef kill of 1965, yet little coral recovery had occurred (Smith et al. 1981). Following removal of the sewer outfalls, there was an immediate change in water quality. Nutrient levels diminished, phytoplankton and zooplankton populations decreased, water transparency increased, and striking changes began to take place in the benthos (Smith et al. 1981). Reef flat communities rapidly increased in coral coverage and diversity (Aliño 1983; Maragos et al. 1985; Holthus et al. 1989).

One of the most striking faunal changes that had occurred in the south sector of Kaneohe Bay between 1960 and 1975 was the encroachment of zoanthids across reef flats formerly dominated by reef corals (Cooke 1976, 1983). Two hypotheses had been presented to explain this encroachment. The first was that eutrophication favored the zoanthids over the corals. The second hypotheses was that zoanthids are more resistant to lowered salinity than corals and the 1965 flood eliminated competition from corals. Both hypotheses were supported by observations made during the present study. Zoanthids have persisted since the removal of the outfall, but the polyps are much smaller and less vigorous. The extensive beds that choked out reef corals have diminished. Our observations in early 1988 indicated that zoanthids are much more tolerant to flood conditions than reef corals.

In hindsight, it is now apparent that Banner's (1968) map of damage caused by the 1965 flood is an underestimate of initial damage, because it was conducted a year after the 1965 reef kill. In view of our observations during the present study, we suspect that extensive coral regeneration by *Porites compressa* had already taken place within the first year. Hence, the 1966 data of Banner (1968) probably is more comparable to our 1990 data if we are to compare the relative damage caused by the two storms (Fig. 2). Overall, it appears that both storms had similar total impact, but with slightly different patterns. The 1988 damage extended deeper along the shoreline in the south basin. The difference can be explained partly in terms of differences in the location of the storm centers (Fig. 3). The 1965 storm center was located on the watershed directly north and west of the bay while the 1987–88 storm was located to the south.

A major difference between the two storms was the lack of a "fish kill" in the 1988 event. Banner (1968) noted lack of initial fish mortality, followed by extensive mass kills of labrids, holocentrids, pomacentrids and eels within one week of the flood. He noted that the fish kills occurred when the hydrogen sulfide odor became most conspicuous. It is likely that the 1965 fish kill was caused by influence of the two major sewage outfalls that discharged into the south basin of Kaneohe Bay at that time. Approximately $8000\,m^3$ per day of sewage was being injected into the deeper portion of the bay in 1965 (Smith et al. 1981). Conditions throughout the basin were highly eutrophic. Stratification of the bay during the 1965 flood could have trapped sewage under the low-salinity surface layer. Low incident light and high turbidity following the storm would have reduced photosynthetic production of oxygen in the deeper water. High respiratory demand of these eutrophic communities coupled with the high biochemical oxygen demand of the sewage itself might have reduced dissolved oxygen levels in the subsurface water to lethal levels. Severe oxygen depletion in the bay was noted following the 1965 storm (Banner 1968).

Conclusions

The 1987–1988 reef kill was an example of a natural disturbance that occurs only rarely on coral reefs in Kaneohe Bay. Planktonic communities were restored to near normal within months of the flood, while most components of the reef flat community recovered within one to two years. Reef coral communities appear to show nearly complete recovery within five to ten years provided that they are not under stress from pollution. Fresh water kills have a strong influence on the structure of reef coral communities in Kaneohe Bay. For example, it is likely that the corals *Pocillopora damicornis* and *Montipora verrucosa* would dominate reef flats if rare flood events did not occasionally eliminate them from this environment. Disturbance events control many aspects of coral reef community ecology and need to be studied as part of long-term research programs. Results of the present study support the idea that we must begin implementing detailed studies designed to last for 25 to 50 years or more, rather than more typical one to two year research efforts.

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