Pacific Science (1995), vol. 49, no. 3: 247–265
© 1995 by University of Hawai'i Press. All rights reserved

Comparison of Water Quality and Reef Coral Mortality and Growth in Southeastern Kāne'ohe Bay, O'ahu, Hawai'i, 1990 to 1992, with Conditions before Sewage Diversion[1]

STEPHEN L. COLES AND LARA RUDDY[2]

ABSTRACT: Growth and mortality of the three dominant coral species occurring in Kāne'ohe Bay were determined for four periods from November 1991 to January 1993 at four stations in the bay's southeast basin. Twelve water quality parameters were monitored biweekly to monthly at these stations from November 1991 to August 1992. Both water quality measurements and coral survival and growth indicated considerable improvement to conditions that prevailed when treated sewage was discharged into this area of Kāne'ohe Bay. Mean concentrations for orthophosphate, nitrite + nitrate, ammonia, and chlorophyll *a*, and mean values for light extinction and sedimentation were significantly less than those measured during time of sewage discharge in 1976–1977. Means of all of these except orthophosphate were not significantly different from means measured in 1978–1979 during the first year after sewage diversion. Mean orthophosphate concentration was approximately double the mean of the first year after diversion, and this increase may relate to increased abundances of the green macroalgae *Dictyosphaeria cavernosa* (Forskål) Boergesen that have been observed in this section of the bay in recent years. *Montipora verrucosa* (Lamarck) survived and grew well throughout the study period at all four stations, including stations in areas where rapid mortality and minimal growth occurred for this species in 1969–1971. The other two species, *Porites compressa* Dana and *Pocillopora damicornis* (Linnaeus), showed different survival and growth patterns according to station location. Most rapid mortality and lowest growth generally occurred for *P. compressa* at the station most affected by land runoff in the southernmost section of the bay. However, the major cause of early mortality and poor growth of *Porites compressa* at that location was the nudibranch *Phestilla sibogae* (Bergh), which rapidly consumed tissues of corals transplanted to that station, suggesting that predators that control *P. sibogae* parasitism elsewhere in the bay are absent from that area. *Pocillopora damicornis* survival and growth declined at all stations throughout the study, and this species may have been affected by fish predation. Growth of *M. verrucosa* and *P. damicornis* showed significant positive relationships with water turbidity values within a range of up to ca. 1.0 NTU.

KĀNE'OHE BAY IS the largest embayment in the state of Hawai'i and is the site of one of the major coral reef systems in the state. Formerly described as one of the most pristine marine environments, which supported a thriving and diverse coral community (MacKay 1915, Edmondson 1928, 1946), the southeastern section of the bay came under increasing pollution pressure after World War II, when population in the Kāne'ohe area rose from ca. 5000 in 1940 (Laws 1993) to 60,000 in 1980 (Smith et al. 1981). The two principal sources of water pollution to the

[1] Manuscript accepted 18 July 1994.
[2] AECOS Inc., 970 N. Kalāheo Ave., Kailua, Hawai'i 96734.

southeastern bay were increased runoff from hillsides and paved surfaces that resulted from urbanization and road building in the general watershed and two sewage outfalls. The smaller of these outfalls disposed ca. 4000 m^3/day from the Kāne'ohe Marine Corps Air Station (KMCAS) from 1951 through 1977 at the most southeast section of the bay. After 1977, this effluent was routed to the Kāne'ohe Municipal sewage treatment facility, which began operation in 1963 and by 1977 was discharging ca. 20,000 m^3 of secondary treated sewage effluent through a submarine outfall at ca. 8 m depth (Smith et al. 1981).

The deterioration in water quality and coral reef communities during this time of sewage discharge was apparent to anyone familiar with the earlier conditions in the southeast bay (Banner and Bailey 1970, Maragos 1972, Banner 1974), and these declines were directly related to proximity to the outfall (Bathen 1968, Maragos 1972). Increased public awareness of the deteriorating environmental conditions in the bay prompted changes in state water quality regulations that required removal of sewage discharge from the bay. Diversion was completed by June 1978 to an offshore deep outfall discharging at ca. 35 m depth off Mōkapu Peninsula, and only intermittent discharge of small volumes of sewage has occurred in the bay since that time.

The short-term effects of sewage diversion from the bay were the subject of a comprehensive study of changes in water quality, plankton, reef benthos, and fishes (Smith et al. 1981), which has become a classic account of the effects of both eutrophication and recovery of a coral reef ecosystem (Laws 1993). That study showed rapid change from eutrophic conditions of high phytoplankton and zooplankton abundance and a benthos dominated by suspension and filter feeders when the bay was receiving sewage effluent to lower abundances of plankton and benthic filter feeders after sewage diversion. However, because of the longer time required for reef corals and coralline algae to establish themselves and grow after more optimal conditions occur, the Smith et al. (1981) study did not evaluate effects of sewage diversion on the reef corals or other components of the reef community that form the basis of reef growth.

A comprehensive study of the distribution, mortality, and growth of reef corals in Kāne'ohe Bay during the time of sewage discharge was conducted by Maragos (1972). That study evaluated the conditions in the bay for corals under stress and provided a baseline for comparing coral survival and growth after sewage discharge ceased. A major portion of the Maragos (1972) study concerned growth and survival measurements on corals transplanted to various sections of the bay. Surveys in 1983 (Maragos et al. 1985, Alino 1986, Evans et al. 1986, Holthus et al. 1986) and 1990 (Evans 1992, Hunter and Evans 1992) compared general abundances of corals on Kāne'ohe Bay reefs with values before diversion. However, no recent studies have been made that utilize the controlled experimental techniques afforded by measuring the mortality and growth of transplanted corals.

In this study we present the results of water quality determinations at four stations in southeastern Kāne'ohe Bay measured over a 9-month period in 1991–1992, and mortality and growth determinations on three species of corals transplanted to these stations and measured for four growth periods (Table 5) from November 1991 to January 1993. We compare these results with values obtained by similar methods during the era before sewage diversion and draw conclusions concerning the current state of southern Kāne'ohe Bay as a suitable and healthy environment for reef coral growth and survival.

MATERIALS AND METHODS

Station Locations

Four stations were established in Kāne'ohe Bay in November 1991 at strategic locations on reefs around the southeast basin (Figure 1). The characteristics of the stations were as follows:

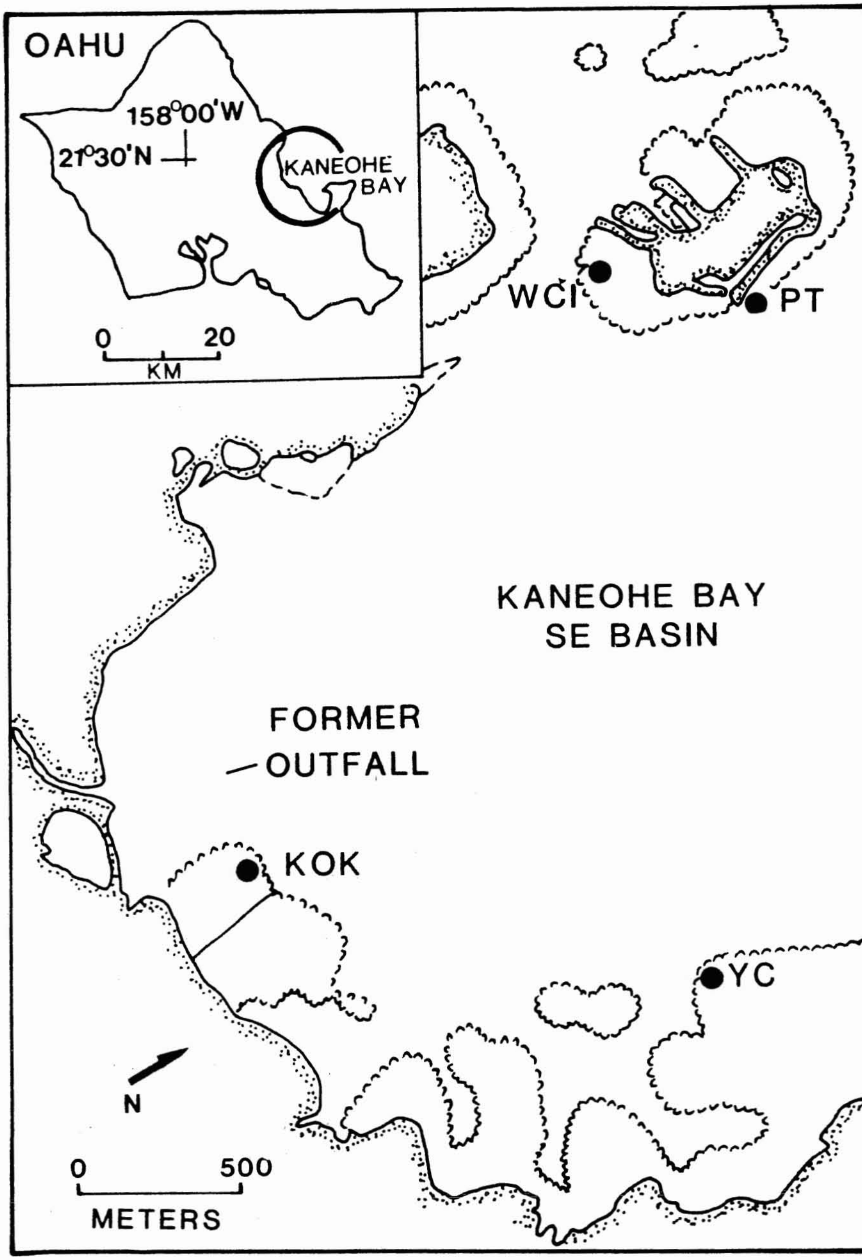

FIGURE 1. Locations of water quality and coral growth stations in Kāne'ohe Bay southeastern basin.

STATION KOKOKAHI (KOK): On edge of fringing reef near Kokokahi YWCA pier, within 0.5 km of the Kāne'ohe sewage point of discharge, within 0.25 km of the mouth of Kawā Stream, and 0.5 km from the mouth of Kāne'ohe Stream. This is in the area most stressed by sewage discharge in the past and by land runoff through the current time and is at the farthest point south and west in the bay where live corals currently occur. The station corresponds to coral transplant Station 6 of the Maragos (1972) study, which was located ca. 0.75 km to the west of this station.

STATION YACHT CLUB (YC): On edge of fringing reef north and east of channel entrance to Kāne'ohe Yacht Club. The station is immediately downwind of a large, shallow fringing reef on which water can be heated or cooled considerably. No substantial stream runoff affects this station. Corresponds to location of Maragos (1972) Station 5.

STATION WEST COCONUT ISLAND (WCI): On the west side of the fringing reef south of Coconut Island, ca. 0.25 km east of Coconut Island pier. Moderately affected in past by sewage discharge and to the current time by land runoff because this area is on the principal route by which runoff water from the southeast basin circulates to the north. Corresponds to Maragos (1972) Station 2, which was ca. 0.2 km to the northwest.

STATION POINT (PT): Outside the fringing reef east of the Coconut Island channel entrance to Hawai'i Institute of Marine Biology. This is the area least likely to be affected by land runoff and having the most pristine water conditions. Nearest station in Maragos (1972) study was Station 7, on a patch reef ca. 0.3 km to the southeast.

Water Quality Measurements

The stations were measured for water quality parameters on 10 occasions every 2–3 weeks in the annual wet season, from 24 November 1991 through 18 April 1992. Four monthly measurements were made during the dry season from 15 May to 9 August 1992. Analyses were made for the following parameters:

TEMPERATURE AND SALINITY: Measured in situ at surface and 3 m depth to 0.1°C and 0.1‰ using an induction salinometer (Beckman).

LIGHT EXTINCTION: Measured in situ using a digital integrating quantum meter (Licor LI-188) with underwater probe. Measurements of photosynthetically active radiation (PAR) were made at each station for 10-sec periods in quick succession at 1 and 3 m, and the integrated values for each depth were used in determining the light extinction coefficient k by the formula:

$$k = -\ln (I_3/I_1)/z$$

where I_3 and I_1 = the light intensities at 3 m and 1 m, respectively, and $z = 2$ m.

TURBIDITY AND TOTAL SUSPENDED SOLIDS (TSS): Turbidity was measured in the laboratory within 4 hr of sampling using a nephelometer (Turner) and commercially prepared sealed standards that were calibrated quarterly with freshly prepared formazin standards. Results are reported in nephelometric turbidity standards (NTU). TSS was determined on 1-liter water samples taken at the surface and at 3 m at each station that were taken to the laboratory and analyzed within 24 hr. Water was drawn through washed, dried, and tared glass filters (GFC), and the filters were dried at 100°C for 24–48 hr and reweighed. When suspended solids were too concentrated to pass the entire sample through a filter, subsamples were filtered and the residue obtained extrapolated to concentrations per liter.

SEDIMENTATION: Sedimentation was measured on the reef using the method described by Maragos (1972). A 1-liter polypropylene bottle with a mouth diameter of 2.7 cm was anchored in an upright position to a stake driven into the reef at each station and left for periods of 2 weeks to a month. At time of sampling visits, the bottles were replaced and capped and taken to the laboratory for analysis. Each bottle was shaken thoroughly and its contents emptied into a sediment cone (Imhoff), allowed to stand for at least 24 hr, and the volume of sediment settling to the bottom of the cone was determined to the nearest 0.1 ml. Values were expressed in ml cm^{-2} day^{-1} basis using the area of the bottle mouth and the number of days the bottles were in place on the reef. This technique measures sediment that is resuspended into the water by wave action as well as sediment from land runoff and is a measure of the sediment that comes into contact with a coral's surface in a given time period.

NUTRIENTS, TOTAL NITROGEN, AND PHOSPHORUS: Surface water samples were taken in acid-washed 100-ml polypropylene sample bottles and held in a cooler while being transported to the laboratory within 4 hr. The samples were held frozen until analyses within 1 month. A Technicon Autoanalyzer II was used for analyses of nitrate + nitrite, ammonia nitrogen, total nitrogen, orthophosphate, and total phosphorus. All samples were done in triplicate and a quality control check was analyzed with each set of 10 samples. Nitrate + nitrite was analyzed using EPA Method 353.2 (USEPA 1979) at a detection limit of 1 μg/liter. Ammonia nitrogen was analyzed at a detection limit of 1 μg/liter by the Solorzano (1969) alkaline phenol method as modified for the autoanalyzer by C. J. Patton and T. E. Whitledge (unpublished). Total nitrogen samples were digested using a modification of the alkaline persulfate digestion technique described by D'Elia et al. (1977), and the digested samples analyzed for nitrate + nitrite to a detection limit of 10 μg/liter. EPA Method 365.1 was used for determination of orthophosphate to a detection limit of 1 μg/liter. Samples for total phosphorus were digested by a modification of F. Korroleff's (unpubl. data) acidic digestion method and analyzed for resulting orthophosphate to a detection limit of 2 μg/liter.

CHLOROPHYLL: Surface water samples were obtained and treated as described above for nutrients and filtered through 0.45-μm pore size methyl cellulose filters after being held in the dark under refrigeration for no more than 24 hr. Filters were frozen until acetone extraction and analysis by Standard Method 1002 G (APHA 1985) using a fluorometer (Turner) calibrated with Environmental Protection Agency (EPA) calibration standards and an EPA quality control sample analyzed at the same time to verify the calibration. The detection limit is 30 $\mu g/m^3$ for 1 liter of sample filtered.

Coral Measurements

Forty colonies each of *Montipora verrucosa* (Lamarck), *Porites compressa* Dana, and *Pocillopora damicornis* (Linnaeus) were collected from the fringing reef adjacent to the "Point" laboratory at the Hawai'i Institute of Marine Biology in October 1991. These were held on the reef at 2 m depth until 1 November, when healthy appearing specimens were transferred to fiberglass tanks that received flowing aerated seawater. Each colony was labeled with a colored and numbered plastic tag and weighed underwater to the nearest 0.1 g using a top-loading electronic scale held in a housing above the tank (see Jokiel et al. 1978, fig. 3). All 120 corals were weighed within 2 days and returned to the reef holding site on 3 November.

On 9 November 1991, 10 specimens of each species were distributed randomly to each of the four station sites. The 30 corals at each station were placed on a 1-m^2 tray made of rubber-coated heavy wire mesh. The trays were anchored at the reef edge at a depth of 3 m at the PT, WCI, and YC stations and at 2.5 m at the KOK station. These trays were indicated to be nontoxic by the fact that live coral was growing as part of the mesh pattern when the trays were retrieved in August 1993.

The condition of the corals at each station was noted when sediment bottles were retrieved at the time of water quality samplings, and corals were retrieved for thorough inspection and reweighing in the laboratory tanks on 24 January, 9 May, 8 August 1992, and 24 January 1993. Total time that corals were removed from their respective stations did not exceed 3 days for each of the four reweighings.

The buoyant weighing technique (Jokiel et al. 1978) is the most precise method for determining coral growth as increased calcium carbonate mass, and the technique imparts no stress to the living coral tissue, because all measurements are made underwater. Buoyant weighing has been used to determine coral growth for intervals as short as 3–7 days (Spencer Davies 1990). A size-independent method of expressing the buoyant weight growth data was developed by Maragos (1972, 1978) that relates the buoyant weight of a coral to its theoretical mean radius by the formula:

$$r = (3w/2\pi D)^{1/3}$$

where r = the mean radius of the coral, w = its buoyant weight, and D = its skeletal density.

Therefore, the theoretical radius increases in growing coral can be calculated by:

$$\Delta r = (3w_2/2\pi D)^{1/3} - (3w_1/2\pi D)^{1/3}$$

where w_1 and w_2 are the buoyant weights at the beginning and end of the weighing period, respectively.

Bulk skeletal densities of 1.41 for *Porites compressa*, 1.37 for *Montipora verrucosa*, and 1.99 for *Pocillopora damicornis* (Maragos 1972) were used in the calculations for estimating coral radius increases.

RESULTS

Physical and Chemical Factors

The average values ±95% confidence intervals (CI) for the water quality variables measured at each station are shown in Table 1 and compared with values determined before and after sewage diversion in 1978 (Maragos 1972, Laws and Redalje 1979, Smith et al. 1981). Mean values for our study agree well with those obtained after diversion, with no significant changes indicated for extinction coefficient, $NO_3 + NO_2$, NH_4, total N, and mean chlorophyll *a* (Chl *a*). Mean PO_4 increased significantly from the mean after diversion by 60%. However, our study's mean for PO_4 was still less than half and significantly less than the PO_4 mean determined before sewage diversion.

Our study was conducted over a 9-month period during which 10 water quality samples were taken at each station during the wet season (November to April) and four samples during the dry season (May to August). Previous studies of Kāne'ohe Bay water

TABLE 1

COMPARISON BEFORE AND AFTER SEWAGE DIVERSION OF MEANS ± 95% CI VALUES FOR WATER QUALITY PARAMETERS IN KĀNE'OHE BAY (MARAGOS 1972, LAWS AND REDALJE 1979, SMITH ET AL. 1981) AND MEANS ±95% CI OF THIS STUDY

PARAMETER	BEFORE DIVERSION (1976–1978)[a]	AFTER DIVERSION (1978–1979)	THIS STUDY (1991–1992)
Surface temperature (°C)	25.1 ± 0.41	25.2 ± 0.65	25.2 ± 0.53
3-m temperature (°C)	—	—	24.8 ± 0.52
Surface salinity (‰)	34.9 ± 0.09	34.6 ± 0.20	34.2 ± 0.23
3-m salinity (‰)	—	—	34.4 ± 0.13
Light extinction coefficient (K)	0.37 ± 0.08	0.29 ± 0.02	0.27 ± 0.04
Surface turbidity (NTU)	—	—	0.91 ± 0.13
3-m turbidity (NTU)	—	—	0.96 ± 0.18
Surface TSS (mg liter^{-1})	—	—	3.69 ± 0.80
3-m TSS (mg liter^{-1})	—	—	3.06 ± 0.73
Sediment (ml cm^2 day)	4.19[b]	—	3.74 ± 0.74
$NO_3 + NO_2$ N (mM m^{-3})	0.38 ± 0.08	0.27 ± 0.16	0.23 ± 0.05
NH_4 N (mM m^{-3})	0.77 ± 0.15	0.51 ± 0.15	0.50 ± 0.22
Total N (mM m^{-3})	10.6	9.8	9.47 ± 0.67
PO_4 P (mM m^{-3})	0.48 ± 0.05	0.15 ± 0.02	0.24 ± 0.02
Total P (mM m^{-3})	1.01	0.52	0.67 ± 0.17
Chl. *a* (mg m^{-3})	1.78 ± 0.17	1.23 ± 0.24	0.90 ± 0.18

[a]Prediversion values sampled 1976–1978 except for sediment, which was sampled 1971–1972.

[b]Mean of annual values for Stations 2, 5, 6, and 7 (Maragos 1972) converted to daily volumes in milliliters using bulk density for pure aragonite of 2.95 g/cm^2.

quality were conducted during 1.5 yr before sewage diversion and 2 yr after diversion. It is therefore possible that our water quality values were biased by wet-season conditions. This was tested using one-way analysis of variance (ANOVA). The only nutrient-related parameter in Table 1 that was found to be significantly affected ($F = 7.44$, df = 1, 54, $P < 0.01$) by season was $NO_3 + NO_2$, which averaged 0.26 mM m^{-3} in the wet season compared with 0. 13 mM m^{-3} during the dry season. Therefore, additional sampling during the dry season might have decreased the overall average lower than the 0.23 mean value. This suggests that current overall concentrations of $NO_3 + NO_2$ in southern Kāne'ohe Bay may be even more reduced from values after diversion than are shown by the data reported here.

The data making up these mean values were tested for significant differences among stations using one-way ANOVA. Only surface turbidity ($F = 2.87$, df = 3, 44, $P < 0.05$) and turbidity at 3 m ($F = 14.53$, df = 3, 48, $P < 0.01$) showed a significant difference among stations. Three other parameters, light extinction coefficient ($F = 2.56$, df = 3, 36, $P = 0.07$), PO_4 ($F = 2.19$, df = 3, 48, $P = 0.10$), and Chl *a* ($F = 2.68$, df = 3, 49, $P = 0.057$) showed station effects that approached significance. The pattern of all five parameters showed consistent increases in means going from the Coconut Island stations PT and WCI to the shoreline stations YC and KOK (Table 2). This pattern suggests an influence from land runoff into the southeastern basin that is related to these parameters. This influence was most apparent in the significantly greater 3-m turbidity mean for the KOK station. The PT station was the most remote from land-based influences, and the means for all five parameters there were significantly less than the respective means for KOK.

Coral Mortality and Growth

The coral survival that had occurred at each station by the end of the 15-month study is shown in Table 3 and compared with results available for the same species reported by Maragos (1972). Our results are reported as visual estimates of the total number of corals that survived, including partial survival, of the 10 colonies of each species held at each station. These results are not strictly comparable with the coral survival data of Maragos (1972), who reported the mean number of months survived by two specimens of each species for up to 24 months. However, relative comparisons can be made.

TABLE 2

COMPARISONS OF DIFFERENCES AMONG STATION MEANS OF WATER QUALITY PARAMETERS WITH LSD

	STATION			
PARAMETER	KOK	YC	WCI	PT
Light extinction coefficient	0.35	0.26	0.26	0.21
Surface turbidity	1.10	1.08	0.78	0.69
3-m turbidity	1.70	0.93	0.60	0.59
PO_4	0.27	0.25	0.21	0.21
Chl *a*	1.26	0.93	0.70	0.66

NOTE: Stations not connected with same underline are significantly different ($P < 0.05$).

TABLE 3

COMPARISON OF CORAL SURVIVAL REPORTED BY MARAGOS (1972) IN MEAN NUMBER OF MONTHS SURVIVED WITH PERCENTAGE OF CORALS SURVIVING AFTER 15 MONTHS IN THIS STUDY

SPECIES	STATION	MEAN MONTHS SURVIVED (MARAGOS 1972)	% SURVIVAL (THIS STUDY)
P. compressa	KOK	2	0
	YC	2	95
	WCI	8	100
	PT	6	100
M. verrucosa	KOK	4	90
	YC	11	90
	WCI	24	90
	PT	11	99
P. damicornis	KOK	3	20
	YC	10	35
	WCI	7	5
	PT	7	20

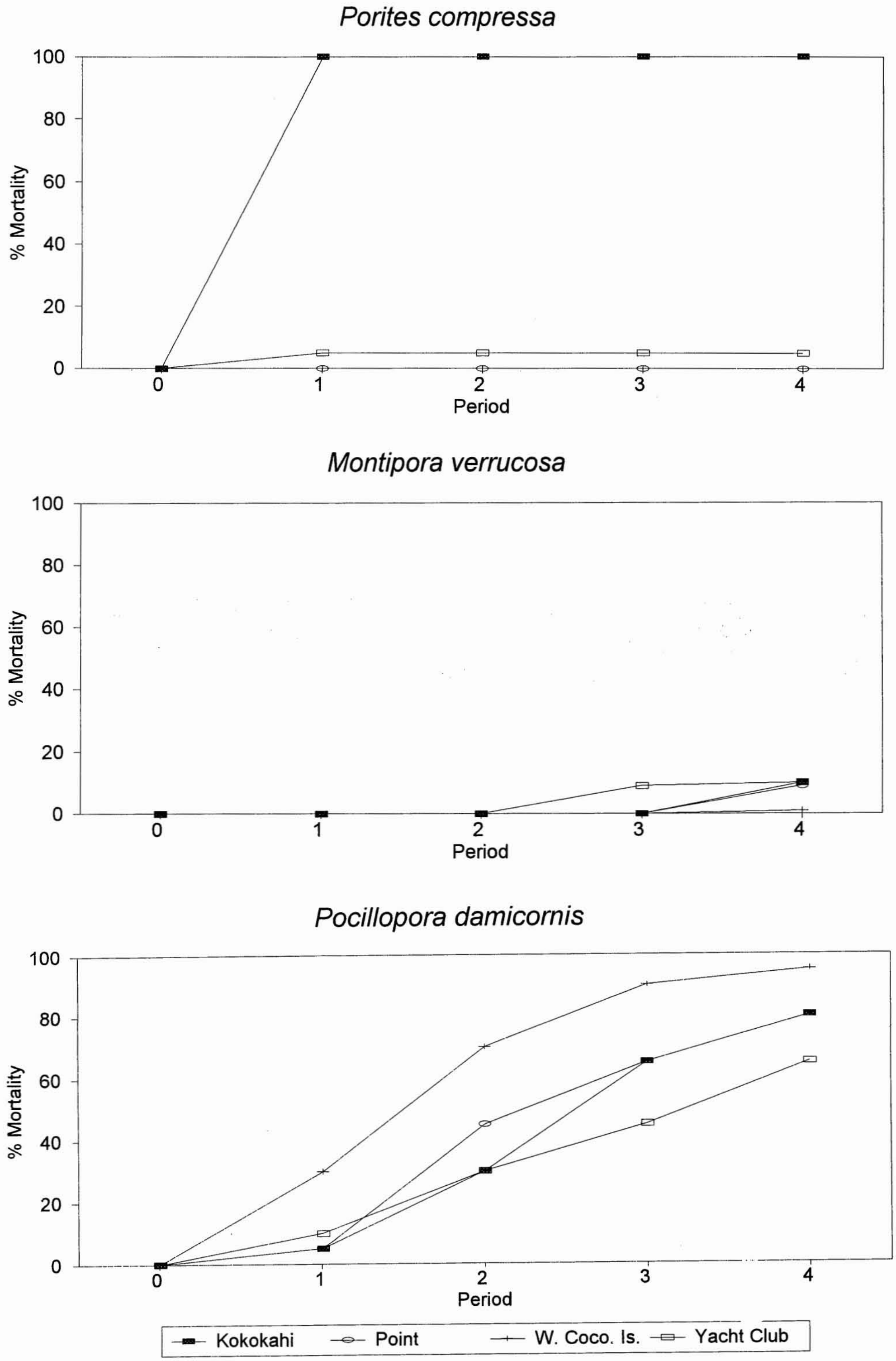

FIGURE 2. Mortality of three coral species at times of growth measurements, November 1991 to January 1993.

Substantially greater survival occurred for all three species in our study at virtually all the stations compared with survival before sewage diversion. All *Porites compressa* and 90% or more of the *Montipora verrucosa* colonies survived in a normal condition to the end of our study at all but the KOK station. By comparison, only *M. verrucosa* in the vicinity of the WCI station showed complete survival to the end of the Maragos (1972) study. The species showing lowest survival rate in both studies was *Pocillopora damicornis*. It survived only 3 to 10 months in 1970–1971, and showed survival of only 5 to 35% after 15 months in our study, with lowest survival occurring at the WCI station. The lowest survival before sewage diversion by all three species occurred near the KOK station, but only *Porites compressa* had highest mortality at that station during our study. Mortalities occurring at each station through the course of our study are shown in Figure 2. Complete mortality of *Porites compressa* at station KOK had already occurred by the time of the first coral weighing in January 1992. On 5 January, *P. compressa* at that station was infested by the nudibranch *Phestella sibogae,* and eight corals were dead and covered with *P. sibogae* eggs. Only two *P. compressa* at station YC and none at the other two stations had *P. sibogae* infestations on that date. Clearly, parasitism by *P. sibogae* within 3 months from transplant of the corals was responsible for early mortality and poor growth of *P. compressa* at the KOK station.

By contrast, the modest mortality that occurred for *Montipora verrucosa* was not expressed until the third weighing period, in August 1992, and never rose above 10% at any station. Although mortality at the PT station was only 1% compared with 10% at the other locations, this difference is insubstantial and does not indicate a spatial pattern of mortality for this species.

Pocillopora damicornis showed a gradual decline in survival at all stations throughout the study. The highest mortality occurred at the WCI station, where mortality was higher from the time of the first coral weighing and reached 95% by the study's end. Rates of increase in mortality of *P. damicornis* were approximately the same for all stations after the first weighing period. This resulted in mortalities of 65 to 80% at the other three stations by the final weighing.

Coral growth calculated from weight changes for each species and station are shown in Figure 3 and compared in Table 4 with values recalculated from Maragos (1972) using a bulk density corresponding to each species. Mean radius increases of around 1 cm/yr occurred for *Porites compressa* at stations YC, WCI, and PT, and for *Montipora verrucosa* at KOK, WCI, and PT. Under conditions before sewage diversion this rate of growth occurred only for *M. verrucosa* at station YC. *Pocillopora damicornis* showed substantially less growth than the other two species in both studies, but growth was greater in our study at all stations except WCI compared with the same locations before sewage diversion.

Coral growth based on annualized solid radius increases during each period throughout the study is shown in Table 5 and Figure 4. *Porites compressa* showed an annualized growth of ca. 1 cm/yr from the beginning to the end of the study at all stations except KOK. At that station *P. compressa* growth was only ca. 0.7 cm/yr for period 1 and subsequently declined to ca. zero or less for the remainder of the study, because of the high mortality and bioerosion of corals that occurred at that station (Figure 2). *Montipora verrucosa* growth was also ca. 1 cm/yr throughout the study at stations KOK, YC, and PT, but growth was less at station WCI, where it varied around 0.75 cm/yr during all periods. In this case lower growth cannot be attributed to higher mortality, because mortality by the end of the study was no more at WCI than at KOK or PT.

Growth of *Pocillopora damicornis* showed similar declines in growth rate for all four stations (Figure 4) as more corals died with time (Figure 2). At maximum, growth for this species was only ca. 0.5 cm/yr, half of that which occurred for *P. compressa* or *M. verrucosa.* Although lower growth occurred at station WCI during period 1 than at any of the other stations, no differences were appar-

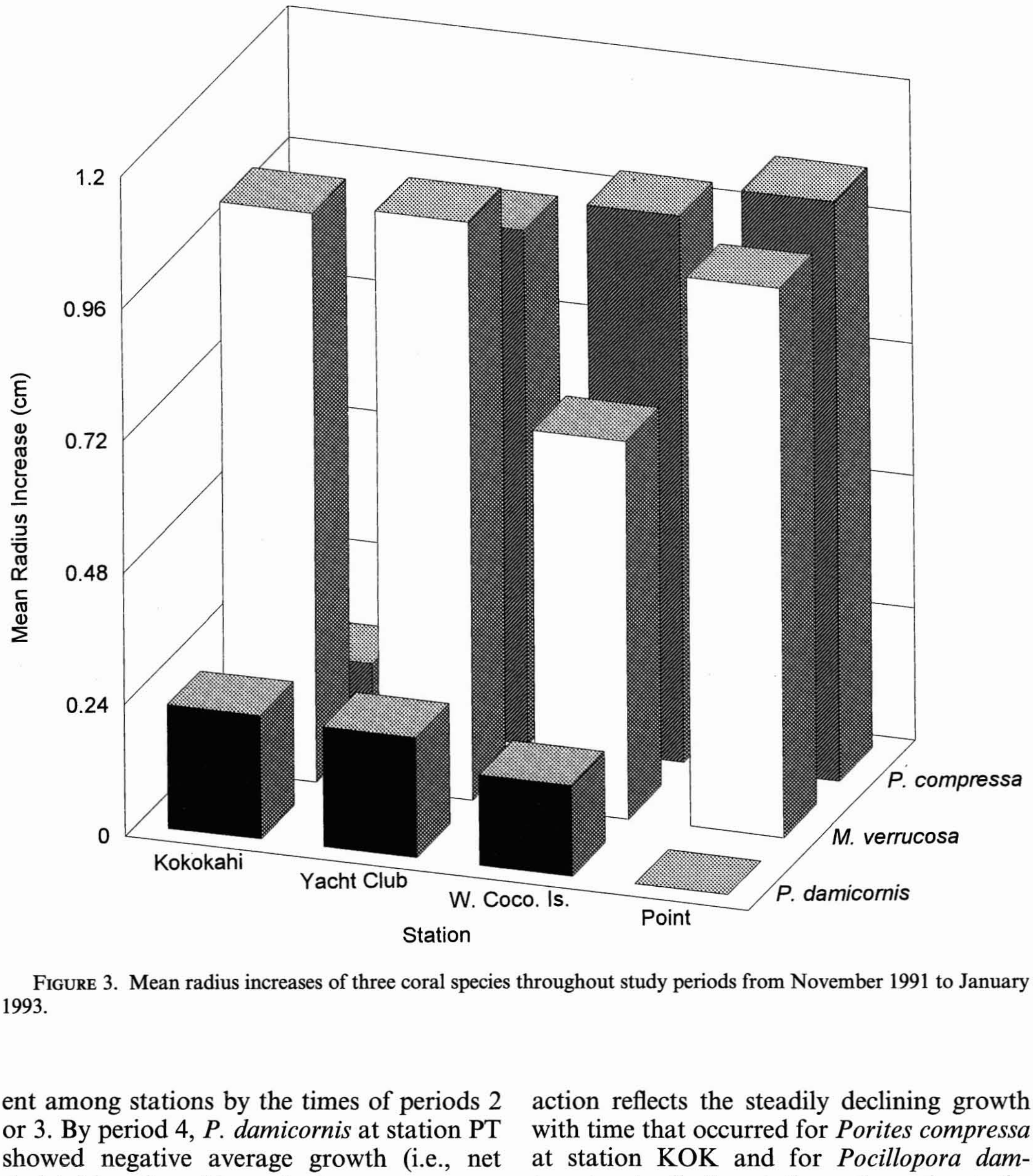

FIGURE 3. Mean radius increases of three coral species throughout study periods from November 1991 to January 1993.

ent among stations by the times of periods 2 or 3. By period 4, *P. damicornis* at station PT showed negative average growth (i.e., net skeletal loss from bioerosion).

The growth data results summarized in Table 5 were tested using two-way factorial ANOVA for significant effects from species and growth period for the entire data set and for significant effects from stations and growth period for each species (Table 6). The ANOVA for the total data array indicates significant effects due to species, growth period, and interaction. The significant interaction reflects the steadily declining growth with time that occurred for *Porites compressa* at station KOK and for *Pocillopora damicornis* at all the stations throughout the study (Figure 4). ANOVA for individual species (Table 6) indicated significant effects for station and period for both *Porites compressa* and *Pocillopora damicornis*, and a significant effect for station alone for *Montipora verrucosa*. Significant interaction between station and period occurred only for *Porites compressa*, where mean growth declined throughout the study only at station KOK.

TABLE 4

COMPARISON OF CORAL GROWTH (MEAN ± SD) IN THIS STUDY WITH MEAN VALUES REPORTED FOR THESE SPECIES AT NEAREST LOCATIONS BY MARAGOS (1972)

SPECIES	STATION	RADIUS INCREMENT (cm) (MARAGOS 1972)	RADIUS INCREMENT (cm) (THIS STUDY)
P. compressa	KOK	0	0.11 ± 0.11
	YC	0.67	0.94 ± 0.43
	WCI	0.86	1.00 ± 0.21
	PT	0	1.05 ± 0.22
M. verrucosa	KOK	0.08	1.04 ± 0.20
	YC	1.14	1.05 ± 0.26
	WCI	0.52	0.69 ± 0.20
	PT	0.21	0.94 ± 0.29
P. damicornis	KOK	0	0.25 ± 0.15
	YC	0.09	0.25 ± 0.30
	WCI	0	0.18 ± 0.08
	PT	0.17	0.03 ± 0.18

Analyses of Fisher's least significant difference (LSD) were made to determine significant differences among species within periods for the lumped data and for significant differences among stations within periods for each species (Table 7). Mean growth of *Pocillopora damicornis* was significantly less than for the other two species during all periods, and *Porites compressa* mean growth was significantly less than that of *Montipora verrucosa* after period 1.

Looking at station effects within periods for individual species, LSD analysis (Table 7) indicated growth of *P. compressa* to be significantly less at station KOK than at all other stations for all measurement periods. Growth of *Montipora verrucosa* at station WCI was significantly lower than at all other stations during the first growth period and significantly less than at two of the stations during periods 2 through 4. No consistent pattern of mean growth with station occurred for *Pocillopora damicornis.* Although lowest values all occurred at the PT station after period 1, no significant differences among means occurred for periods 2 through 4.

Relationships of Coral Growth with Water Quality Parameters

Average values for water quality parameters at each station averaged for the first

TABLE 5

CORAL GROWTH (MEAN ± SD) AT KĀNE'OHE BAY STATIONS EXPRESSED AS ANNUALIZED RADIUS INCREASES FOR FOUR GROWTH PERIODS[a] AND TOTAL STUDY DURATION

SPECIES	STATION	PERIOD 1	2	3	4	ALL
P. compressa	KOK	0.68 ± 0.29	0.10 ± 0.07	−0.08 ± 0.18	−0.04 ± 0.17	0.11 ± 0.11
	YC	1.05 ± 0.32	0.95 ± 0.40	0.81 ± 0.49	0.94 ± 0.56	0.94 ± 0.43
	WCI	0.98 ± 0.21	0.85 ± 0.22	1.06 ± 0.26	1.06 ± 0.24	1.00 ± 0.21
	PT	1.01 ± 0.28	0.84 ± 0.25	1.01 ± 0.19	1.18 ± 0.36	1.05 ± 0.22
	All Sta.	0.93 ± 0.31	0.68 ± 0.43	0.70 ± 0.55	0.79 ± 0.60	0.76 ± 0.47
M. verrucosa	KOK	0.98 ± 0.19	1.02 ± 0.22	1.24 ± 0.33	0.95 ± 0.45	1.04 ± 0.20
	YC	1.13 ± 0.21	1.06 ± 0.27	0.92 ± 0.47	1.10 ± 0.49	1.05 ± 0.26
	WCI	0.66 ± 0.25	0.76 ± 0.14	0.75 ± 0.25	0.63 ± 0.28	0.69 ± 0.20
	PT	0.92 ± 0.29	0.87 ± 0.30	1.08 ± 0.31	1.08 ± 0.30	1.00 ± 0.26
	All Sta.	0.88 ± 0.33	0.92 ± 0.26	0.99 ± 0.39	0.93 ± 0.42	0.93 ± 0.36
P. damicornis	KOK	0.53 ± 0.14	0.32 ± 0.16	0.25 ± 0.19	0.07 ± 0.20	0.25 ± 0.15
	YC	0.65 ± 0.26	0.38 ± 0.49	0.18 ± 0.40	0.01 ± 0.43	0.25 ± 0.30
	WCI	0.36 ± 0.14	0.27 ± 0.13	0.23 ± 0.27	0.02 ± 0.15	0.18 ± 0.08
	PT	0.56 ± 0.14	0.19 ± 0.08	0.09 ± 0.16	−0.34 ± 0.52	−0.03 ± 0.19
	All Sta.	0.52 ± 0.20	0.25 ± 0.24	0.16 ± 0.25	−0.05 ± 0.35	0.24 ± 0.36

[a]Period 1: 3 Nov. 1991–24 Jan. 1992; Period 2: 24 Jan. 1992–9 May 1992; Period 3: 9 May 1992–8 Aug. 1992; Period 4: 8 Aug. 1992–24 Jan. 1993.

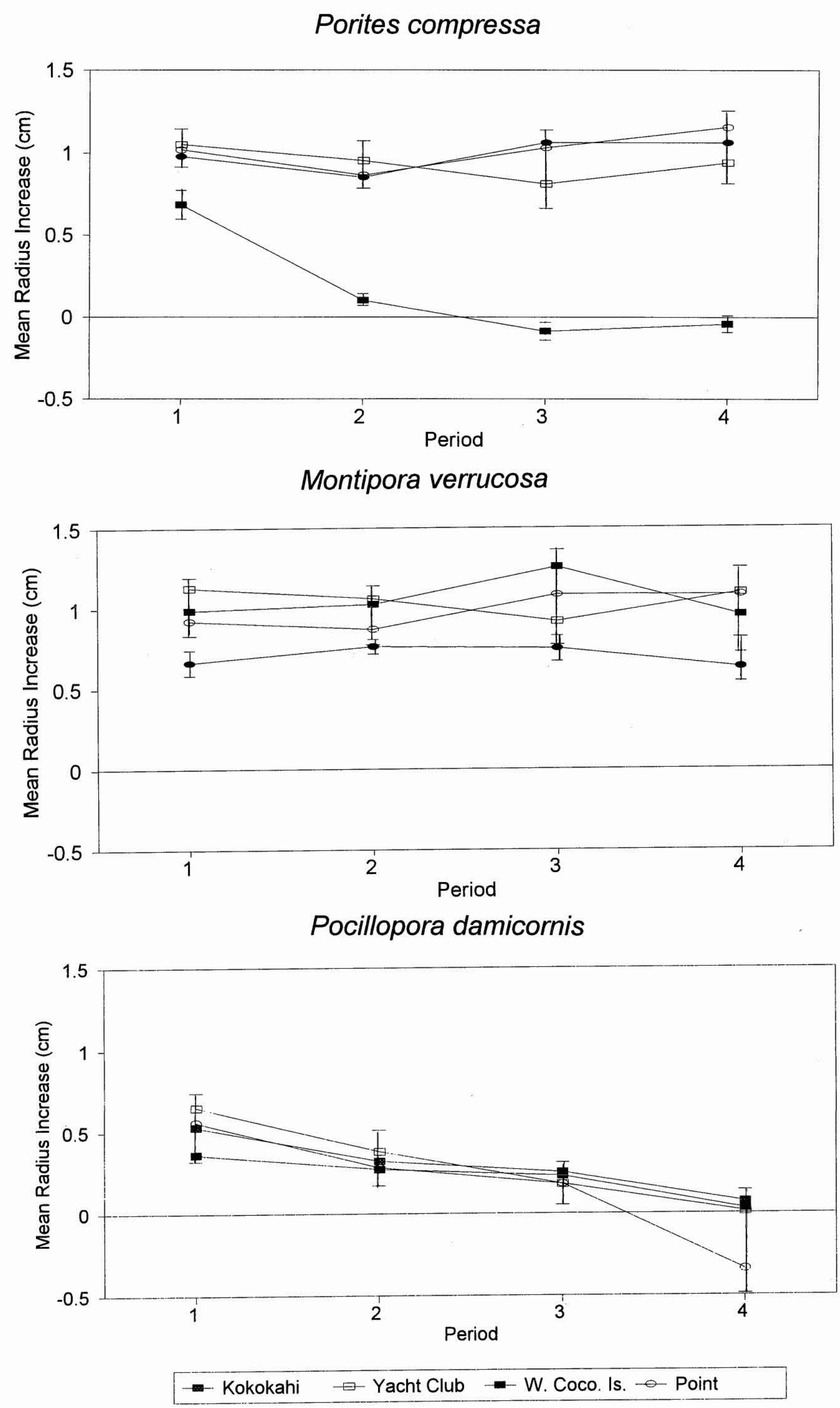

FIGURE 4. Radius increases (means ± SEM) of three coral species during four growth measurement periods from November 1991 to January 1993.

TABLE 6

TWO-WAY ANOVA OF SPECIES AND PERIOD EFFECTS FOR ALL CORAL GROWTH DATA AND STATION AND PERIOD EFFECTS FOR INDIVIDUAL SPECIES

ANOVA TEST	SOURCE OF VARIATION	F	df	P
All growth data	Species	149.1	2,468	<0.001
	Period	7.9	3,468	<0.001
	Interaction	5.3	6,468	<0.001
P. compressa	Station	73.6	3,144	<0.001
	Period	5.4	3,144	<0.001
	Interaction	4.1	9,144	<0.001
M. verrucosa	Station	10.8	3,144	<0.001
	Period	0.5	3,144	0.71
	Interaction	1.2	9,144	0.29
P. damicornis	Station	3.0	3,144	<0.05
	Period	27.7	3,144	<0.001
	Interaction	1.3	9,144	0.25

three growth periods were used as independent predictor variables in stepwise regression analysis to determine significant relationships with the average growth of the three coral species at each station during growth periods 1 to 3. The predictor variables showing F values for regression of >4.0 and significant regression coefficients ($P < 0.05$) for each coral species are given in Table 8.

Porites compressa showed significant negative relationships with turbidity at 3 m and with extinction of light (i.e., reduced growth with increasing values of these parameters). However, these relationships, which together explained 78% of the variability in growth, are misleading as a full explanation of the pattern of *P. compressa* that occurred. Both turbidity and light extinction increased significantly at the KOK station (Table 3) where high infestation of *P. compressa* by *Phestilla sibogae* occurred early in the first growth period, resulting in mortality of this species at that station by the time of the first coral weighing. The significant relationship with growth therefore reflects the inability of this species to resist parasitism at station KOK, probably because any predators that would normally have controlled *P. sibogae* may have been restricted by the generally lower water quality conditions in that section of the bay.

A significant relationship with turbidity at 3 m accounting for nearly 50% of variability in growth was found for *Montipora verrucosa*. However, this relationship was positive, indicating increased growth with higher turbidity at the depth of the coral transplant stations. The source of this relationship was apparently that five of the six highest quarterly growth means occurred at the KOK and YC stations, which also had the highest 3-m turbidities throughout the study (Tables 2 and 3). These levels of turbidity appeared to favor growth of this species, which commonly occurs in relatively turbid conditions near the Kāne'ohe Bay shoreline.

The independent variable most highly related to *Pocillopora damicornis* mean growth was growth period, which reflects the gradual decline in survival and condition of this species throughout the study. This variable alone explained nearly 75% of the mean growth. Surface temperature was also highly correlated with *P. damicornis* growth, but because of high autocorrelation of temperature with period, this variable was excluded by the analysis as a significant predictor variable. The two remaining independent variables that, along with period, explained a total of 92% of the variability in growth were sedimentation and turbidity at 3 m. Rather than being negative factors as might have been anticipated, these three parameters were positively correlated with *P. damicornis* growth. Therefore the results offer no clear explanation of the reason for the decline of this species at all the stations.

DISCUSSION

The results indicate that conditions for coral survival and growth in the southeastern basin of Kāne'ohe Bay are considerably improved from the time of sewage discharge. Our growth rates of >1 cm/yr are less than, but compare favorably with, previous estimates of coral growth in sections of the bay that were not influenced by sewage discharge. Maragos (1972) measured maximum rates of 1.27 to 1.76 cm/yr for these species in the northern and central sections of the bay,

TABLE 7

LSD Tests of Differences in Growth among Species and Species Among Stations during Four Growth Measurement Periods and Total Study Duration

DIFFERENCES	SPECIES	PERIOD	SPECIES			STATION			
Among Species			*P. compressa*	*M. verrucosa*	*P. damicornis*				
		1	0.93	0.92	0.52				
			M. verrucosa	*P. compressa*	*P. damicornis*				
		2	0.93	0.69	0.28				
		3	1.00	0.72	0.18				
		4	0.94	0.79	−0.05				
Among Stations	*Porites compressa*								
						YC	PT	WCI	KOK
		1				1.05	1.01	0.98	0.68
						YC	WCI	PT	KOK
		2				0.95	0.85	0.84	0.10
						WCI	PT	YC	KOK
		3				1.06	1.01	0.81	−0.08
						PT	WCI	YC	KOK
		4				1.18	1.06	0.94	−0.04
	Montipora verrucosa								
						YC	KOK	PT	WCI
		1				1.13	0.98	0.92	0.66
						YC	KOK	PT	WCI
		2				1.06	1.02	0.87	0.76
						KOK	PT	YC	WCI
		3				1.24	1.08	0.92	0.75
						YC	PT	KOK	WCI
		4				1.10	1.08	0.94	0.63

Pocillopora damicornis					
	1	YC 0.65	PT 0.56	KOK 0.53	WCI 0.36
	2	YC 0.38	KOK 0.32	WCI 0.27	PT 0.19
	3	KOK 0.25	WCI 0.23	YC 0.18	PT 0.09
	4	KOK 0.07	WCI 0.02	YC 0.01	PT −0.34

NOTE: Species or stations not connected with same underline are significantly different ($P < 0.05$).

remote from sewage discharge and where greater circulation may be expected to stimulate coral growth. Jokiel (1986), using alizarin stain marking, found growth rates of *Porites compressa* over a 2.5-yr period to range from 1.5 cm/yr in a backwater lagoon to 3.5 cm/yr on a windward reef slope in Kāne'ohe Bay. Our values approximate the maximum rates determined for these species in 1970–1971 at stations north of Coconut Island and just west of the KMCAS (Maragos 1972), in areas of the southeastern basin most remote from the Kāne'ohe Municipal sewage outfall then in operation. This suggests that the growth and survival rates normal for the physical and chemical conditions of the southeastern basin have been restored to areas formerly affected by sewage discharge.

Significant decreases in light extinction, nutrient, and chlorophyll *a* concentrations followed termination of sewage discharge into southeastern Kāne'ohe Bay (Laws and Redalje 1979, Smith et al. 1981). The data in Table 1 indicate that, with the exception of orthophosphate, values for these parameters during our study had not changed from conditions after diversion. Only orthophosphate increased significantly above concentrations measured in the first year after sewage diversion, and this higher value was significantly less than levels before diversion. Orthophosphate is strongly influenced by land runoff, and the higher levels in our study may reflect higher rainfall than occurred during the relatively dry year that followed sewage diversion (Smith et al. 1981).

The pattern in orthophosphate, light extinction, turbidity, and chlorophyll *a* showing highest mean values of these parameters at the KOK station (Table 2) indicates a strong influence of land runoff from the streams and shoreline adjacent to that station. Despite this influence and in contrast to the finding that negligible coral survival and virtually no coral growth occurred in that vicinity in 1970–1971, *Pocillopora damicornis* and *Montipora verrucosa* growths at this station were the highest and second highest, respectively, that occurred among the four stations in the study (Figure 3, Table 4). Both

TABLE 8

STEPWISE LINEAR REGRESSION ANALYSIS OF CORAL GROWTH DURING THE FIRST THREE MEASUREMENT PERIODS WITH AVERAGES OF WATER QUALITY PARAMETERS DURING THE GROWTH PERIODS

DEPENDENT VARIABLE	PREDICTOR VARIABLE	REGRESSION COEFFICIENT ± SE	F VALUE	P	MODEL $R^2 \times 100$ PARTIAL	MODEL $R^2 \times 100$ TOTAL
P. compressa growth	Turbidity, 3 m	-0.36 ± 0.111	10.4	0.010	55.6	55.6
	Extinction coefficient	-2.08 ± 0.683	9.3	0.014	22.7	78.2
M. verrucosa growth	Turbidity, 3 m	0.21 ± 0.069	9.8	0.011	49.4	49.4
P. damicornis growth	Growth period	-0.09 ± 0.023	11.4	0.012	74.6	74.6
	Sedimentation	0.04 ± 0.013	27.2	0.001	11.4	86.0
	Turbidity, 3 m	0.01 ± 0.004	15.0	0.006	5.7	91.7

species also showed significant positive relationships with turbidity at 3 m (Table 8). This relationship is contrary to the usual view that elevated turbidity and influence from land runoff is detrimental to coral vitality and growth. However, previous work on *Montipora verrucosa* in Kāne'ohe Bay has suggested that growth of this species is favored by intermediate levels of water turbidity and light extinction. Maragos (1972) found highest abundance and growth for *M. verrucosa* to occur in shallow areas of Kāne'ohe Bay where salinity was moderately reduced by land runoff. However, Maragos (1972) also found a significant negative relationship between extinction coefficient and growth for this species, in contrast to the results of our study. These contrasting findings may be due to the generally higher light extinction and turbidity that occurred in the bay in 1970–1971.

In similar studies (Tomascik and Sander 1985, Tomascik 1990) of the effects of eutrophication and other water quality parameters on the growth of the coral *Montastrea annularis* off Barbados, nutrient concentrations ranged from about equal to those of this study to more than 20 times higher in the case of nitrate + nitrite. However, the best estimator of coral growth (Tomascik and Sander 1985) was a highly significant negative relationship with suspended particulate matter (SPM) within a range of 4.2 to 7.1 mg/liter of SPM. However, at lower concentrations down to 1.8 mg/liter SPM a curvilinear relationship was indicated with an optimum for coral growth of around 3.5 mg/liter, which those authors interpreted as suggesting that moderate concentrations of SPM may provide a heterotrophic energy source for *M. annularis*. Because turbidity in our study was correlated with concentrations of suspended particulate matter, the positive relationships between turbidity and growth may suggest a similar positive effect of moderate particulate matter concentrations on coral growth.

Phestilla sibogae is rarely observed in situ in Kāne'ohe Bay, although it rapidly attacks *Porites* specimens that are placed in running seawater tables for experimentation at Hawai'i Institute of Marine Biology (S.L.C., pers. obs.). Haramaty (1991) determined that *P. sibogae* from Kāne'ohe Bay laid eggs totaling up to 17% of body weight per day, indicating an usually high proportion of the energy consumption of this species being directed to reproduction. The rapid proliferation of *P. sibogae* on *Porites compressa* at the KOK station suggests that the predators that normally control *P. sibogae* were absent from that section of the bay. The resulting uncontrolled parasitism appears to be the primary factor that restricted *P. compressa* from an area where the other two species survived and grew as well as at any other station.

Pocillopora damicornis had higher mortality and significantly lower growth throughout the study than the other two species. Although we observed no indications of predation either in the field or on *P. damicornis* at times of weighings, colonies of this species transplanted to the reef slope may have been affected by fish predation. This species does not normally occur beyond the reef margin in Kāne'ohe Bay, and Neudecker (1977) found that uncaged colonies of *P. damicornis* that were transplanted to 15 and 30 m depth in Guam lost about one-fourth of their initial weight to fish predation compared with controls left at the reef margin that showed no fish predation. By contrast, alizarin staining (Neudecker 1977) showed the mean growth rate of caged *P. damicornis* colonies at 15 m to be nearly double that of reef margin controls, indicating that reduced light with depth was not a factor for reducing growth. In our study, the highest *P. damicornis* mortalities throughout the study and the lowest growth rates after period 1 occurred at the PT station, and this is the location where the greatest fish abundances and numbers of species occur (S.L.C., pers. obs.).

Surveys of coral abundance in Kāne'ohe Bay in 1983, 6 yr after diversion of sewage effluent (Maragos et al. 1985, Alino 1986, Evans et al. 1986, Holthus et al. 1986) indicated substantial recovery of reef coral abundance, especially *Porites compressa* and *Montipora verrucosa* in the southeastern and central basin. The green macroalga *Dictyosphaeria cavernosa*, which had dominated large areas of reef in the central area of the bay by smothering and outcompeting reef corals, was found in 1983 to have decreased to one-fourth of its former coverage. However, resurveys in 1990 (Evans 1992, Hunter and Evans 1992) suggested that the rate of coral recovery had slowed and that *D. cavernosa* relative cover had doubled from 1983. *D. cavernosa* was abundant at the time of our study on a large reef 200 m south of the WCI and PT stations (S.L.C., pers. obs.). *D. cavernosa* was not reported to occur in abundance in the southeastern bay before 1990, but rather was restricted to the central and northwestern sectors north of Coconut Island (Banner and Bailey 1970, Smith et al. 1981).

Comparing orthophosphate concentrations in our study with those of the central and northwestern sectors during time of sewage discharge may provide at least a partial explanation of this resurgence of *D. cavernosa*. The 1976–1977 mean $\pm$ 95% CI values of orthophosphate in the central and northwestern sector of the bay were 0.26 ± 0.04 and 0.23 ± 0.03 mM m^{-3} (Smith et al. 1981), almost identical to the 0.24 ± 0.02 mM m^{-3} mean concentration found for the four southeastern bay stations of our study (Table 1). This represents a doubling of the orthophosphate mean value that occurred in the southeastern basin during the first year of sewage diversion (Smith et al. 1981), and this higher availability of dissolved phosphorus may be stimulating growth of *D. cavernosa*.

ACKNOWLEDGMENTS

This study was conducted using facilities and equipment generously provided by the Hawai'i Institute of Marine Biology (HIMB) and AECOS Inc. We are grateful to Philip Helfrich, Director of HIMB, and Paul Jokiel for allowing us access to HIMB facilities. The nutrient and water quality analyses were performed pro bono by AECOS, for which we thank Eric Guinther, Jacqueline Mello, and the AECOS staff, especially David Fry, who provided valuable assistance in the field. Helpful comments on the manuscript were provided by M. Siddeek, J. Stirn, and an anonymous reviewer.

LITERATURE CITED

ALINO, P. M. 1986. A comparison of coral community structure on reef flats in Kaneohe Bay, Hawaii. Pages 91–100 *in* P. L. Jokiel, R. H. Richmond, and R. A. Rogers, eds. Coral reef population biology. Hawaii Inst. Mar. Biol. Tech. Rep. 37, Honolulu.

APHA (AMERICAN PUBLIC HEALTH ASSOCIATION). 1985. Standard methods for the examination of water and wastewater. A. E.

Greenberg, J. J. Connors, and D. Jenkins, eds. APHA, Washington, D.C.

BANNER, A. H. 1974. Kaneohe Bay, Hawaii: Urban pollution and a coral reef ecosystem. Proc. 2nd Int. Coral Reef Symp. 2: 685–702.

BANNER, A. H., and J. H. BAILEY. 1970. The effects of urban pollution upon a coral reef system: A preliminary report. Hawaii Inst. Mar. Biol. Tech. Rep. 25, Honolulu.

BATHEN, K. H. 1968. A descriptive study of the physical oceanography of Kaneohe Bay, Oahu, Hawaii. Hawaii Inst. Mar. Biol. Tech. Rep. 14, Honolulu.

D'ELIA, C. F., P. A. STEUDLER, and N. CORWIN. 1977. Determination of total nitrogen in aqueous samples using persulfate digestion. Limnol. Oceanogr. 22:760–763.

EDMONDSON, C. H. 1928. Ecology of a Hawaiian coral reef. Bernice P. Bishop Mus. Bull. 45:1–64.

———. 1946. Reef and shore fauna of Hawaii. Bernice P. Bishop Mus. Spec. Publ. 22.

EVANS, C. W. 1992. Patterns of recovery and change of coral reef communities in Kaneohe Bay, Hawaii. Pac. Sci. 46:381.

EVANS, C. W., J. E. MARAGOS, and P. F. HOLTHUS. 1986. Reef corals in Kaneohe Bay. Six years before and after termination of sewage discharges (Oahu, Hawaiian Archipelago). Pages 76–90 *in* P. L. Jokiel, R. H. Richmond, and R. A. Rogers, eds. Coral reef population biology. Hawaii Inst. Mar. Biol. Tech. Rep. 37, Honolulu.

HARAMATY, L. 1991. Reproduction effort in the nudibranch *Phestilla sibogae*: Calorimetric analysis of food and eggs. Pac. Sci. 45:257–262.

HOLTHUS, P. F., C. W. EVANS, and J. E. MARAGOS. 1986. Coral reef recovery subsequent to the fresh water kill of 1965. Pages 66–75 *in* P. L. Jokiel, R. H. Richmond, and R. A. Rogers, eds. Coral reef population biology. Hawaii Inst. Mar. Biol. Tech. Rep. 37, Honolulu.

HUNTER, C. L., and C. W. EVANS. 1992. Kaneohe Bay: An update in recovery and recent trends to the contrary. Proc. 7th Int. Coral Reef Symp. 1:346 (abstract).

JOKIEL, P. L. 1986. Growth of the reef coral *Porites compressa* on the Coconut Island reef, Kaneohe Bay. Pages 101–110 *in* P. J. Jokiel, R. H. Richmond, and R. A. Rogers, eds. Coral reef population biology. Hawaii Inst. Mar. Biol. Tech. Rep. 37, Honolulu.

JOKIEL, P. L., J. E. MARAGOS, and L. FRANZISKET. 1978. Coral growth: Buoyant weight technique. Pages 529–541 *in* D. R. Stoddart and R. E. Johannes, eds. Coral reefs: Research methods. UNESCO, Paris.

LAWS, E. A. 1993. Aquatic pollution. John Wiley & Sons, New York.

LAWS, E. A., and D. G. REDALJE. 1979. Effect of sewage enrichment on the phytoplankton population of a subtropical estuary. Pac. Sci. 33:129–144.

MACKAY, A. I. 1915. Corals in Kaneohe Bay. Pages 136–139 *in* Hawaiian almanac and annual for 1916. B. P. Bishop Museum, Honolulu.

MARAGOS, J. E. 1972. A study of the ecology of Hawaiian reef corals. Ph.D. diss., University of Hawai'i, Honolulu.

———. 1978. Coral growth: Geometrical relationships. Pages 543–550 *in* D. R. Stoddart and R. E. Johannes, eds. Coral reefs: Research methods. UNESCO, Paris.

MARAGOS, J. E., C. EVANS, and P. HOLTHUS. 1985. Reef corals in Kaneohe Bay six years before and after termination of sewage discharges (Oahu, Hawaiian Archipelago). Proc. 5th Int. Coral Reef Congr. 4: 189–194.

NEUDECKER, S. 1977. Transplant experiments to test the effect of fish grazing on coral distribution. Proc. 3rd Int. Coral Reef Symp. 1:317–323.

SMITH, S. V., W. J. KIMMERER, E. A. LAWS, R. E. BROCK, and T. W. WALSH. 1981. Kaneohe Bay sewage diversion experiment: Perspectives on ecosystem responses to nutritional perturbation. Pac. Sci. 35: 279–402.

SOLORZANO, L. 1969. Determination of ammonia in natural waters by the phenylhypochlorite method. Limnol. Oceanogr. 14:799–801.

SPENCER DAVIES, P. 1990. A rapid method

for assessing growth rates of corals in relation to water pollution. Mar. Pollut. Bull. 21 : 346–348.

TOMASCIK, T. 1990. Growth rates of two morphotypes of *Montastrea annularis* along a eutrophication gradient, Barbados, W.I. Mar. Pollut. Bull. 21 : 376–381.

TOMASCIK, T., and F. SANDER. 1985. Effects of eutrophication on reef-building corals. Mar. Biol. (Berl.) 87 : 143–155.

USEPA. 1979. Methods of chemical analysis of water and wastes. EPA 600/4-79-020. USEPA, Environmental Monitoring and Support Laboratory, Cincinnati.