AN ABSTRACT OF THE THESIS OF Ann Hillmann-Kitalong for the Master of Science in Biology presented May 10, 1983.

Title: Two-Year Study of Temporal Variation in Zooplankton Communities in an Inner Region of Apra Harbor, Guam.

Approved: ______________________________

A two-year survey of zooplankton was conducted in a partially enclosed region of Apra Harbor, Guam. Significant ($p<.001$) temporal (annual, seasonal, lunar, diurnal) variations and cross-areal variations in the abundances of selected zooplankters (Cresius acicula, Orbulina universa, Armandia intermedia, Perinereis cultrifera, Sagitta enflata, Lucifer chacei, Acartia clausi, an Acetes sp., a Leptocarpus sp., fish larvae, fish eggs, a crab zoea, and a shrimp mysis) were found. Significant ($p<.001$) biological and physical correlations between these zooplankters were also found.

The composition of the holoplanktonic species represents a typical coastal community, consisting of relatively few genera. The predominant holoplanktonic species in this study are well represented throughout the Indo-Pacific. However, the mean annual dry weight of zooplankton in this study was less than that of other tropical Indo-Pacific areas.

Significant seasonal variation was found for ash-free dry weight, which was strongly correlated with Cresius acicula. Crab zoeae, Sagitta enflata, and shrimp mysis also showed significant seasonal

variation. Total zooplankton abundance and biomass were highest in February and March as has been found in other Indo-Pacific studies. Most individual species or groups of zooplankton showed no consistent seasonal peaks in abundances.

Perinereis cultrifera was significantly more abundant at new moon, Armandia intermedia at full moon, crab zoeae at the third and last quarters of the moon, and Lucifer chacei at new moon. In four 24-hour studies, Acartia clausi was significantly more abundant at 0700-0900, Sagitta enflata at 0200-0400, fish larvae at 0200-0400, and shrimp mysis at 1800-2000.

Rainfall showed significant correlations with more zooplankters than did any of the other physical variables examined. Acartia clausi and Sagitta enflata were significantly correlated with each other. However, no exogenous factor was correlated with peaks in total biomass or abundances of the total zooplankton.

TO THE GRADUATE SCHOOL AND RESEARCH

The members of the Committee approve the thesis of Ann Hillmann-Kitalong presented May 10, 1983.

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INTRODUCTION

Zooplankton communities contain virtually all the major groups of marine animals as adults or as early life forms. Many fishery resource species depend upon zooplankton for food and many have planktonic larval stages (Cushing and Walsh, 1976). In addition, quantitative studies permit world-wide comparisons of productivity that are especially important in predicting fishery abundance (Cushing, 1976). Knowledge of the factors controlling the fluctuations in density, composition, and distribution of planktonic fauna has important ecologic and economic ramifications.

Although several qualitative and quantitative studies of the tropical Indo-Pacific zooplankton have been reported, surprisingly few seasonal studies have been conducted. Lagoonal studies have been mostly short-term quantitative studies (reviewed by Gerber, 1981). The few longer term studies have suggested seasonality (Russell and Colman, 1934; Sale et al., 1978; Gerber, 1981). Open ocean and inshore tropical plankton communities have been most extensively studied in India and Hawaii. A five-year study in India (Subrahmanyan, 1959) has shown that zooplankton biomass peaks during the southwest monsoon season immediately after a phytoplankton peak. Other Indian studies have confirmed the seasonal peaks found in the latter study (Wickstead, 1961; literature reviewed by Subrahmanyan, 1959). The larval abundance and gonadal ripening of the oil sardine (*Sardinella longiceps*) have been significantly correlated with monsoonal rains (Raja, 1972). Definite spawning peaks were found in two studies of Indian meroplankton, and for some species these seasons were related to rainfall (Panikkar and Aiyar, 1939). The Hawaiian zooplankton fauna, especially that in Kaneohe Bay, has been studied by several investigators (reviewed by Kimmerer, 1980; Smith et al., 1982). In addition to work at Kaneohe Bay, a few other studies on specific groups of zooplankton (reef fish larvae, Watson and Leis, 1974; Miller, 1973; anchovy larvae, Tester, 1951) have shown high abundances to be associated with calm winds and currents (Watson and Leis, 1974; Miller, 1973). In Australia, a two-year study of the Great Barrier Reef lagoon showed significant seasonality for copepods and chaetognaths (Crenshaw, pers. comm.). In southeast Africa, mysids have shown possible seasonal trends and several copepod species were most abundant during periods of heavy rainfall (Woolridge, 1977). In several Indo-Pacific islands, outbreaks of Acanthaster planci, the coral-eating starfish, have shown a strong correlation with heavy rainfall (Birkeland, 1982). It is hypothesized that spawning during periods of extra heavy rainfall preceded by a very dry period can result in a situation in which successful larval recruitment can occur.

Seasonal patterns for tropical Indo-Pacific zooplankton are variable and many are inconclusive. Most studies were conducted over only a one-year period (Kimmerer, 1980; Sale et al., 1978; Watson and Leis, 1974; Woolridge, 1977; Miller, 1973; Wickstead, 1961; Subrahmanyan, 1959; Russell and Colman, 1934), therefore seasonal patterns were not demonstrated repeatedly. More conclusive seasonal studies were performed in India (Raja, 1972; Subrahmanyan, 1959; Panikkar and Aiyar, 1939). A five-year study in Hawaii (Smith et al., 1982) showed conclusive patterns of seasonality. However, the seasonal patterns in India and Hawaii were not similar. Geographically, India and Hawaii represent two extremes of the tropical Indo-Pacific. India is a subcontinent that is subject to marked seasonal monsoons. The Hawaiian Islands are subject to tradewinds and are considered subtropical. Guam may provide a much different picture of temporal trends for Indo-Pacific zooplankton.

Fluctuations in zooplankton density have been attributed to several climatic variables which influence reproduction. Although temperature has been considered the major factor that affects breeding in the tropics (Thorson, 1946), breeding has also been shown to be affected by salinity, available food, tides, and lunar periodicity (Prasad, 1954). The present study examined most of these factors to determine whether or not they were correlated with high zooplankton densities. In many of the cited studies, rainfall has been shown to have an influence on zooplankton density (Crenshaw, pers. comm.; Woolridge, 1977; Raja, 1972; Subrahamanyan, 1959; Panikkar and Aiyar, 1939). It has been hypothesized that monsoons initiate an increase in the abundance of zooplankton. The heavy rains wash nutrient-rich soils into surface waters and the strong winds allow the mixture of deeper, nutrient-rich waters which cause phytoplankton blooms which are subsequently followed by an increased abundance of zooplankton (Bardach and Santerre, 1972). It has been suggested that successful larval recruitment of both Sardinella longiceps (Raja, 1972) and Acanthaster planci (Birkeland, 1982) are caused by timely spawning during or immediately following monsoons. Abundances of fish larvae are associated with periods between monsoons, when the prevailing winds or currents are weakest

(Johannes, 1978; Watson and Leis, 1974; Miller, 1973; Wickstead, 1961; Prasad, 1954). In contrast, Wolanski et al. (1981) showed that peak abundances of plankton were found during periods of strong winds. Lunar periodicity in spawning has also been demonstrated for many reef fishes (Johannes, 1978), polychaetes (Hauenschild, 1955) and two gastropods (Heslinga and Hillmann, 1980). It has been suggested that spawning on evening flood tides during periods of calm winds or currents can minimize predation upon larval fishes (Johannes, 1978).

The compositional patterns of zooplankton in shallow-water communities may be more universal than previously thought (Hirota, 1978). Certain predominant holoplanktonic species have been found in several geographic locations. The general composition of several zooplankton communities in the studies reviewed above has been represented by certain predominant species. Perhaps these species are more adaptable than other species, which enables them to invade established communities (Hirota, 1978). The hypothesis of "universal" zooplankters was tested by comparing six predominant holoplankters in a shallow-water community in Guam with other parts of the world.

In summary, the zooplankton community in Apra Harbor, Guam, was analyzed with respect to species composition, total biomass, and total abundance for all the zooplankton. Comparisons of world-wide distribution were based upon five predominant species (*Cresius acicula*, *Lucifer chacei*, *Sagitta enflata*, *Euconchoecia elongata*, and *Orbulina universa*) and two less predominant species (*Armandia intermedia* and *Perinereis cultrifera*). Based on variations in the abundances of thirteen macroplanktonic zooplankters (C. acicula, an Acartia sp., S. enflata, L. chacei, O. universa, A. intermedia, P. cultrifera, an Acetes sp. and a Leptocarpus sp., a shrimp mysis, a crab zoea, fish larvae, and fish eggs), the following questions are addressed:

1) Are there significant similarities between the zooplankton communities sampled in Apra Harbor and other areas?

2) Do significant temporal variations (annual, seasonal, lunar, and diurnal), especially seasonal variations, exist for predominant zooplankters in Apra Harbor and other areas?

3) Are changes in the abundance of representatives of selected taxa correlated with variations in a) rainfall, b) water temperature, c) wind velocity, d) wind direction, and e) tides?

This study provides information on the composition and temporal patterns of a typical tropical Indo-Pacific zooplankton community and establishes a basis for future in-depth studies of zooplankton communities in Guam.

METHODS

Net sampling was done at four stations on a weekly or biweekly basis over a 24-month period. Preliminary work based on non-replicated samples was done during the first 6 months (Marsh et al., 1980). Replicate samples were taken after this initial six-month study. Diurnal cycles were studied on four occasions during 24-hour periods; samples were taken on each ebb and flood tide.

No significant difference was found between the first and second tow at each site (Table 1). Therefore, the preliminary data (May-November 1980), in which no replicates were collected, were included in all the statistical tests. Replicate tows were averaged, and the averages were used as data. The variability between tows was not included in the following tables, since it was not significant. (Throughout the text, a significant variation refers to a probability of a difference being a result of chance being less than .001).

One sampling station ran perpendicular to the eastern end of the Commercial Port dock and parallel to several patch reefs adjacent to a dredged area (Fig. 1). Three other sampling stations were in the Lower Piti Channel, in the peripheral Secondary Channel, and in the Outfall Lagoon. These sites were chosen because a substantial amount of data was already available. Two 8-minute tows were taken within a 30-minute time interval at each site. The sites were sampled in the following order each time: Secondary Channel, Commercial Port, Lower Piti Channel, and Outfall Lagoon. This sampling scheme reduced the total sampling time to two hours (sampling by random ordering of sites would have increased this time interval). Thus, it had to be assumed that changes in the zooplankton community within this 2-hour period

Table 1. Total means and standard deviations (in parentheses) for the abundances of the zooplankters (per m^3) for first and second tows, respectively. At the far right are the probabilities (p) that the ratios of variance between tows differ from the expected as a matter of chance as determined by a one-way analysis of variance (anova).

Species or Group	Tow 1	Tow 2	p
O. universa	40(66)	43(79)	.61
A. intermedia	1.7(3.4)	1.8(3.6)	.72
P. cultrifera	.48(1.28)	.49(1.38)	.97
Acartia sp.	119(498)	123(322)	.93
Shrimp mysis	26(30)	24(21)	.88
L. chacei	18(49)	22(59)	.32
Acetes sp.	.51(1.66)	.43(1.38)	.62
Leptocarpus sp.	.52(1.35)	.64(1.55)	.36
Crab zoeae	142(198)	140(174)	.32
C. acicula	80(284)	84(386)	.94
S. enflata	8.2(16.7)	8.1(17.2)	.88
Fish larvae	4.7(6.0)	5.2(7.0)	.42
Fish eggs	4.3(8.5)	4.1(8.6)	.83
Observations (n)	243	243	486

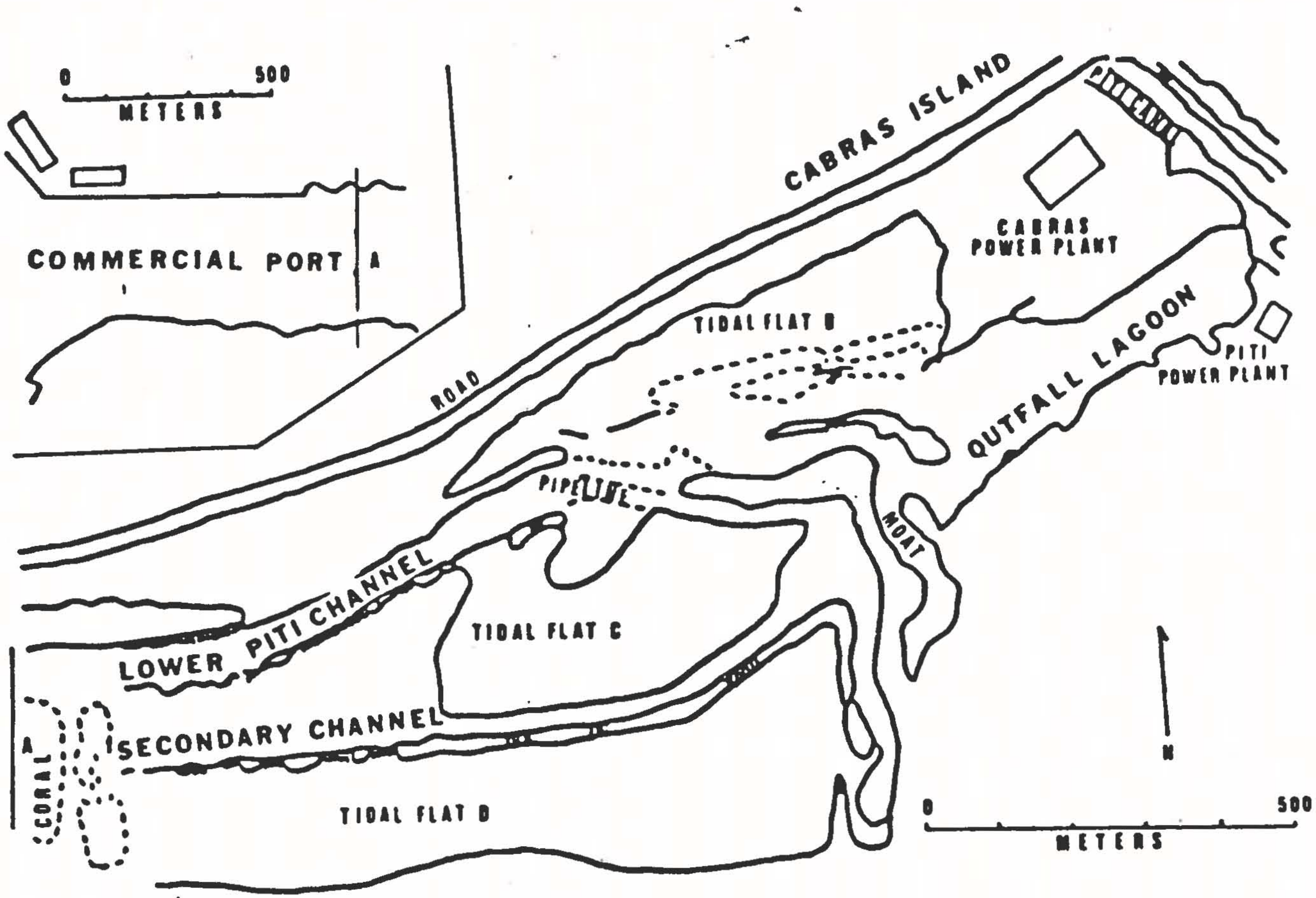

Figure 1. Sampling sites for the zooplankton tows. The figure was modified from figure 2 in Marsh et al. (1977).

were negligible. Replicate tows began at the same starting point for each station. Volume of water filtered was calculated by using a digital flowmeter (General Oceanic, Inc.) and by timing triplicate fluorescein dye patches over a known distance (assuming a cylindrical volume of water passed through the net without friction). Samples were collected with a standard 0.35-mm mesh plankton net with a 0.5-m diameter mouth and a #6 or #2 cod end. The top of the net was about 0.1 m above the water surface, and the flowmeter was mounted across the mouth of the net. A 10-m tow rope was attached to the bridle of the net. A specified towing time (8 min), distance (600 m), and speed (1.6 m/sec) were maintained as closely as possible.

Plankton samples were placed in glass jars and preserved in 5% seawater formalin (neutralized with calcium carbonate in excess) immediately upon collection. Subsamples were taken by adjusting the sample volume with an addition of seawater while simultaneously mixing the sample. Graduated beakers were used to remove specified portions of the total sample while it was being vigorously stirred. All organisms in the subsample were counted on a plastic petri dish with a grid.

Dry weight and ash-free dry weight of zooplankton were obtained as follows. The total zooplankton sample was poured into a plastic beaker and brought to a constant volume of 250 mℓ with additional seawater. This sample was mixed with a magnetic stirrer for at least thirty seconds or until all the settled plankton was off the bottom of the beaker and within the water column. A 10-mℓ sample was scooped from the center of the water column while the stirrer was running and was filtered onto a preweighed, precombusted, 4.7-mm Whatman glass fiber filter by means of suction filtration with a Buchner funnel (diameter, 5.0 mm). The sample was dried at 60 °C for 48 hours, stored in a desiccator for at least 12 hours and weighed. Finally, the sample was combusted at 450° C for 4 to 6 hours and weighed to determine the ash-free dry weight. It was assumed that the dry weight and ash of preserved samples were not significantly different from freshly collected samples. However, differences have been reported in other studies (Ahlstrom and Thrailkill, 1962; Fudge, 1968; LeBourgne, 1975).

Chlorophyll a samples were collected in two 4-liter polyethylene containers which had been acid washed and rinsed with distilled water. These samples were analyzed within two hours, following the procedure of Strickland and Parsons (1968).

The zooplankton chosen for the temporal and physical analyses were representatives of eleven macroplanktonic species (C. acicula, O. universa, A. intermedia, P. cultrifera, S. enflata, L. chacei, Acartia sp., Acetes sp., and Leptocarpus sp., and unknown species of crab zoea and shrimp mysis) and two taxonomic groups (fish larvae and fish eggs). These eleven species and two zooplankton groups were chosen because they were predominant species or because previous temporal studies on these categories were available. All known and unidentified species of zooplankton were grouped into major taxonomic orders and suborders to determine the total number of organisms per cubic meter.

A Hach turbidity meter (Model 2100A) was used to analyze turbidity of water samples. Surface water temperature was measured in the field with a maximum-minimum thermometer. Climatological data on monthly precipitation, wind direction, and velocity were obtained from the Naval Oceanography Command Detachment, Naval Air Station, in Agana, Guam (1980–1982).

To calculate correlations between physical variables and each of the zooplankton species and groups examined, the mean for each physical variable 30 days prior to the date of collection was used. The assumption was made that the zooplankters would react to a change in the environment within this period. Grahame (1976) found more significant correlations between zooplankters and physical variables with this "lag" than with zooplankters and physical variables at the time of collection.

STUDY SITE

Apra Harbor, Guam, lies at 13°29'29"N, 144°44'55"E and is about 5 km long and between 2 and 4.5 km wide (Fig. 2). The Commercial Port and Piti Channel areas are inshore regions at the northeastern corner of the harbor. The Commercial Port is about 1 km long and 0.2 to 0.55 km wide. Piti Channel is about 1.75 km long and 0.25 to 0.65 km wide and leads into the Commercial Port. The physical and biological features of these regions have been described (Marsh and Doty, 1975, 1976; Marsh and Gordon, 1972, 1973, 1974; Marsh et al., 1977; UGML, 1977; Grovhoug, 1978; Eldredge and Kropp, 1982) and will be only briefly reviewed here.

The Commercial Port area has extensive shoreline development. Turbidity and turbulence are caused primarily by ship activity that stirs up the bottom. The Piti Channel area is shallow (1-3 m), with three extensive tidal flats, five channels, and one lagoon. Scattered mangrove trees (predominantly *Rhizophora mucronata*) border all these areas. The algae *Padina tenius*, *Gracilaria arcuata*, and *Halimeda opuntia* and the sponge *Spirastrella vagabunda* are predominant benthic organisms here. At the eastern end, two power plants discharge heated effluent. Construction of the Piti and Cabras power plants was completed in the early 1950s and in 1974, respectively. Temperature gradients, depth profiles, and limited current data have been reported for the study area (Marsh et al., 1977; UGML, 1977).

The environmental conditions prior to the constructon and initial operation of the Piti Power Plant and the Commercial Port have not been reported. However, the conditions prior to and during the operation of the Cabras Power Plant are well documented in the studies

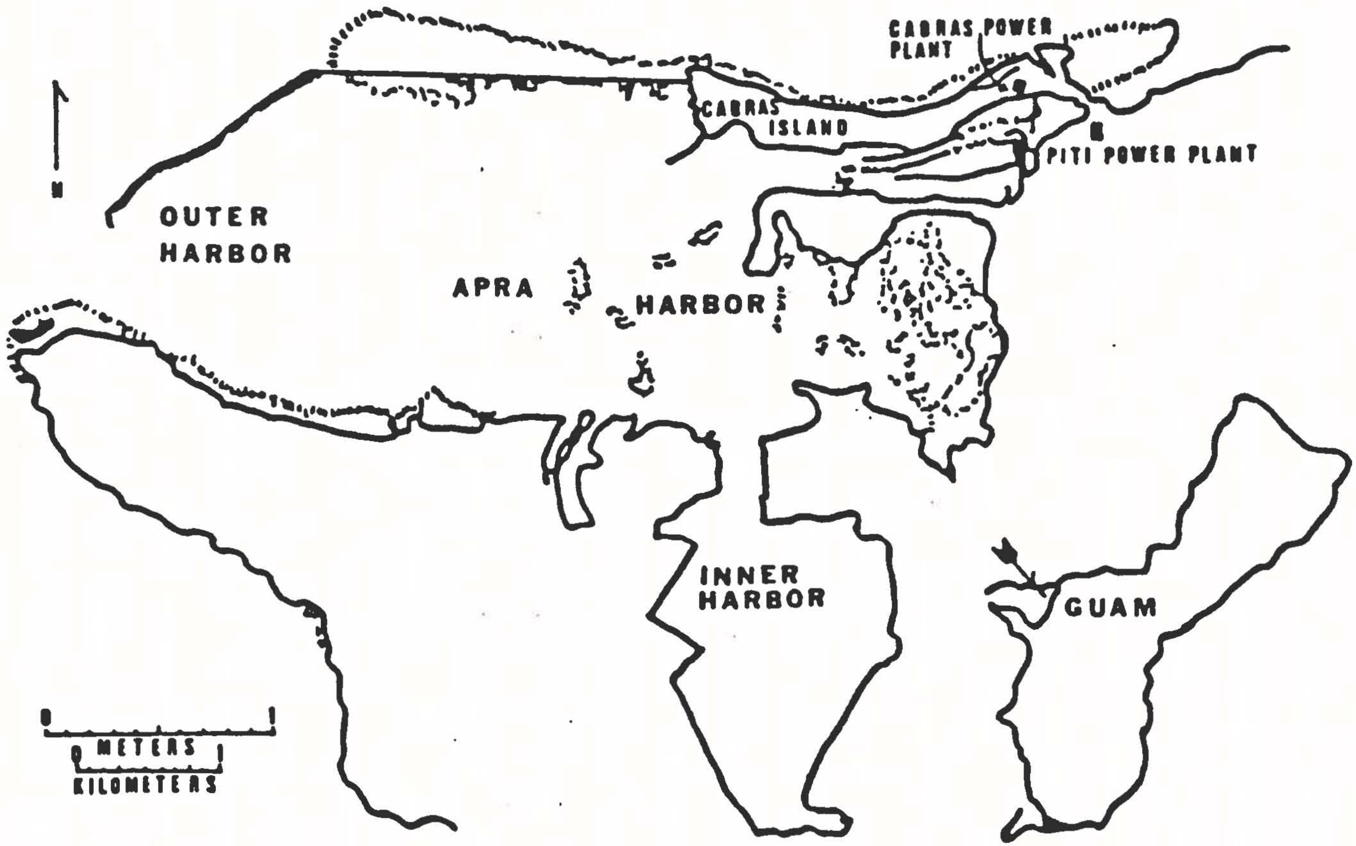

Figure 2. Map of Apra Harbor, Guam. Figure modified from figure 125 in Randall and Holloman (1974).

cited above. Turbidity was very high during the construction of the Cabras Plant and the water circulation increased when its operation began (Marsh et al., 1977; Marsh and Gordon, 1974). Presently the study site has high turbidity, a strong westward current, and a silty substrate. The thermal effect has been considered minimal for the Piti Plant (Grovhoug, 1978), and no major temperature change was reported after the Cabras Plant began operation (Marsh et al., 1977). Surveys of the marine biota indicated that only minimal adverse effects are attributable to the power plants (Marsh et al., 1977). Occasional spills of chemicals (e. g., chlorine and oil) may have a much greater effect on the marine community (Marsh et al., 1977).

A one-week survey (Grovhoug, 1978) and a one-day survey (Tseng, 1973) were the most intensive compositional studies of zooplankton reported from this inner region of Apra Harbor. A six-month study (Marsh et al., 1977) is the only long-term account of zooplankton in this area. Seven stations (including the four stations of my study) were sampled for six consecutive months. Zooplankton, especially copepods, were most abundant in the Commercial Port compared to other areas in the harbor. Crab zoeae and fish eggs were abundant in the Outfall Lagoon (Fig. 2). Pteropods (*C. acicula*) were characteristically more abundant in the Commercial Port. My eight-month preliminary studies (reported in Marsh et al., 1980), comparing only similar months, has also shown the same results for the Commercial Port site as did the six-month study. A significant increase in abundance of zooplankton in nighttime counts as compared with daytime counts was found in both the six- and eight-month studies. No significant difference was observed between areas in total zooplankton volume.

RESULTS

Composition of the Zooplankton Community

The composition of the plankton consisted primarily of crab and shrimp larvae, gastropods, and copepods. The predominant holoplanktonic species were 1) Gastropoda - *Cresius acicula*, 2) Chaetognatha - *Sagitta enflata*, 3) Mysidacea - *Lucifer chacei*, and 4) Copepoda - *Acartia* sp. (Table 2).

Physical Variables

Temperature ($F_{s[3,16]}$=.53 ns) and turbidity ($F_{s[3,10]}$=.27 ns) showed no significant differences between sites. There was a significant difference between days and turbidity ($F_{s[3,14]}$=2.44).

Significant annual variations and annual/seasonal interactions were found for wind velocity, wind gusts, and air temperature. Rainfall and wind gusts showed no significant annual variations (Table 3 and Fig. 3). However, the mean values and standard deviations of all the physical variables indicate that the first year (1980-1981) tended to have stronger winds and wind gusts, lower temperatures, less rainfall, and more variable wind directions, although the differences between years were not significant for these variables.

Significant seasonal variations and annual/seasonal interactions were found for all the physical variables (rainfall, wind directions, wind velocity, wind gusts, and air temperature) (Table 3 and Fig. 3). However, the monthly means and standard deviations of these variables indicate that the heaviest rainfall occurred from July to November with a consistent peak in August. March and April had the least rainfall. July and August had strong southeasterly winds and the

Table 2. Total means and standard deviations (in parentheses) for the abundances (number of individuals per m^3) of each group or species of zooplankter identified at each site during this two-year study. In the columns on the right are the site, year, the month for each year, and the lunar phase that had the greatest mean abundance of each zooplankter. The probabilities that the ratios of variance between sites, years, months, and lunar phases to the variance within sites, years, months, and lunar phases, respectively, differ from the expected as a matter of chance are given. These probabilities were determined by a two-way analysis of variance between years and months and between years and lunar phase, and one-way analysis of variance between sites. Significant probabilities are indicated by one asterisk (p<.01), two asterisks (p<.005), or three asterisks (p<.001). The following symbols are used: SC=Secondary Channel, CP=Commercial Port, LP=Lower Piti Channel, OF=Outfall Lagoon, LQ=last quarter, NM=new moon, FQ=first quarter, and FM=full moon.

Taxa	Location				Site	Year	Month	Moon
	SC	CP	LP	OF			Y1/Y2	
Protozoa								
Foraminifera								
Orbulina universa d'Orbigny	9.90(21.26)	9.90(21.26)	15.70(27.84)	19.34(8.46)	OF***	2	AP/AP	NM
Cnidaria								
medusae (several species)	.01(.06)	.49(1.98)	.05(.17)	.02(.07)	CP	2	DE/DE	NM
Annelida								
unidentified polychaetes	.14(.28)	.44(1.74)	.60(3.54)	.18(.41)	LP	2	JA/AP	NM
Armandia intermedia Fauvel	.55(.84)	.34(.71)	2.07(4.53)	.67(1.16)	LP***		SP/NO	FM
Polynereis cultrifera Grube	.15(.39)	.13(.25)	.20(.52)	.08(.29)	LP***	2	MY/JA	NM
Arthropoda/Crustacea								
Ostracoda								
species A	1.06(2.61)	.35(.71)	.35(.88)	.16(.32)	SC*	1	OC/JA	FM
cyprindid sp.	.20(.62)	1.10(2.18)	.28(.55)	.32(1.11)	CP***	1	AU/AP	FQ
Euconchoecia elongata Müller	.07(.26)	4.40(15.69)	.09(.33)	.02(.11)	CP*	1	MR/JA	NM
Copepoda								
Calanoida								
unidentified calanoids	.67(1.99)	3.39(6.63)	3.40(15.32)	.57(2.14)	CP	2	AP/AU	FM
Acartia sp.	27.04(54.85)	58.37(213.00)	45.63(90.16)	2.72(7.80)	CP***	1*	AP/AU	LQ
Pontellina sp.	.08(.45)	.02(.11)	.01(.08)	.44(1.11)	OF***	2	OC/JU	FQ
Cyclopoida								
Corycaeus sp.	.01(.04)	.29(1.00)	.02(.09)		CP**	2	MR/JL	NM
cyclopoid sp. A	.10(.42)	.16(.66)	.06(.24)	.06(.20)	SC	2	MY/AU	LQ
cyclopoid sp. B	.06(.16)	.06(.38)	.03(.10)	.06(.20)	SC	2	MY/AU	LQ

Table 2 Continued.

Taxa	SC	CP	LP	OF	Site	Year	Month Y1/Y2	Moon
Oncaea sp.	.05(.17)	.24(.97)	.02(.08)	.02(.10)	SC	2	DE/AP	LQ
Sapphirina spp.	.17(.29)	.24(.97)	.21(.39)	.53(.94)	OF	2	JA/FB***	LQ
Harpacticoida								
Microsetella sp.	.64(1.92)	.21(.93)	.21(.26)	.42(.84)	OF	1	NO/OC	FQ
Malacostraca								
Mysidacea	.11(.15)	.21(.53)	.19(.66)	.06(.20)	SC	1	DE/OC	LQ
Cumacea spp.	.14(.34)	.18(.45)	.16(.44)	.11(.19)	LP	1	AP/DE	LQ
Tanaidacea sp.	.02(.07)	.01(.04)	.52(2.78)	.21(1.46)	LP	1	AP/MY	NM
Isopoda	.12(.18)	.18(.53)	.08(.16)	.06(.13)	CP	2	MR/AP	FQ
Amphipoda								
Gammaridea sp. A	.21(.45)	.30(1.48)	.26(.76)	.29(.32)	OF	2	MR/OC	LQ
Gammaridea sp. B	.03(.11)	.48(2.99)	.09(.25)	.08(.17)	OF	1	MR/JU	FM
Hyperidea sp. A	.02(.107)	.01(.05)	.05(.13)	.11(.32)	CP	1	AP/AP	NM
Decapoda								
shrimp mysis sp. A	5.98(6.55)	5.09(5.40)	10.31(9.38)	8.35(10.68)	LP***	1	AU/AP	NM
shrimp mysis sp. B	.47(.99)	.19(.92)	.93(3.45)	.34(1.09)	LP	1	AP/JL	FM
shrimp mysis sp. C	7.28(13.86)	4.92(8.48)	26.54(34.41)	4.43(9.87)	LP	1	AP/NO	FM
shrimp mysis sp. D	3.28(5.82)	4.26(12.29)	5.24(13.42)	5.96(16.34)	LP	1	AP/NO	FM***
shrimp mysis sp. E	1.06(7.31)	.67(1.81)	2.83(5.72)	.38(.83)	LP	1	FB/MY	FQ
shrimp mysis sp. F	0	5.29(24.44)	1.23(1.64)	1.82(5.18)	CP	1	ME/AP***	FM
shrimp mysis sp. G	.09(.31)	8.22(32.60)	75.96(83.51)	.85(2.40)	CP	2	MR/MR	FQ
	.98(4.22)	.12(.50)	.46(1.96)	.28(.69)	SC	1	AP/MR	NM
	0	.38(1.71)	.25(1.00)	.16(.38)	LP	2	JA/AP	FM
Lucifer chacei Bowman	4.08(10.67)	9.84(21.92)	8.39(17.60	.68(2.02)	CP***	2***	OC/FB	NM
Acetes sp.	.17(.47)	.09(.37)	.03(.10)	.26(.62)	OF	2	MY/MY	LQ
Acetes larvae	3.42(9.62)	3.57(12.30)	2.34(7.08)	2.95(22.27)	CP	2	FB/JA	NM
Leptocarpus sp.	.22(.44)	.15(.40)	.13(.25)	.25(.89)	LP	2	FB/AP	LQ
crab zoeae sp. A	47.23(64.05)	15.88(26.55)	58.33(69.02)	38.33(30.27)	LP***	2***	JL/NO*	FQ
crab zoeae sp. B	.64(2.16)	.34(1.48)	3.59(12.26)	1.53(4.33)	LP	1	JA/NO	NM
crab zoeae sp. C	3.97(21.99)	2.40(18.64)	5.78(15.22)	6.90(22.24)	LP	1	JA/MR	FM
crab zoeae sp. D	1.18(4.56)	3.73(22.87)	3.49(19.08)	2.97(9.31)	LP	2	MA/JL	FM
crab megalops sp. A	.20(.59)	.97(2.48)	.40(.81)	.18(.72)	LP*	1	OC/JN	FM
crab megalops sp. B	.09(.27)	.74(3.71)	.27(.48)	.08(.38)	LP	1	AP/OC	NM
Porcellanidae sp.	.09(.27)	.02(.12)	.22(.83)	.03(.09)	SC	2	FB/JN	NM

Table 2 Continued.

Taxa	Location SC	CP	LP	OF	Site	Year	Month Y1/Y2	Moon
Mollusca								
Gastropoda								
Cresius acicula Rang	5.85(21.52)	67.83(17.55)	14.98(42.83)	.65(2.34)	CP***	2***	FB/AP	NM
gastropod veliger sp. A	.66(1.48)	8.75(38.12)	.96(2.58)	.38(1.43)	CP	2	MR/AP	NM
Bivalvia								
bivalve sp. A	1.12(3.98)	5.12(22.53)	4.28(13.29)	.25(1.48)	CP	1	MR/FB**	NM
bivalve sp. B	.13(.38)	7.27(34.91)	.82(2.66)	.09(.39)	CP	1	MR/JA	NM
Cephalopoda								
Octopus larvae	.10(.73)	.08(.18)	.08(.29)	.01(.06)	LP	1	SP/JL	FM
Chaetognatha								
Sagitta enflata Grassi	1.59(3.92)	11.15(15.71)	1.90(3.55)	.03(.22)	CP***	1	DC/DC	LQ
Chordata								
Urochordata								
Larvacea								
Oikopleura sp.	.07(.27)	2.94(5.86)	.45(1.92)	.01(.05)	CP***	1	NO/FB	FM
Vertebrata								
Osteichthyes								
fish larvae	1.15(1.49)	1.26(1.95)	1.01(1.71)	2.25(1.99)	OF***	1	OC/OC	LQ
fish eggs	.64(1.48)	.84(2.63)	.79(1.86)	2.49(3.03)	OF***	2**	JL/MR	NM
No. of observations	116	118	117	112				
Biomass dry weight (g/m^3)	.016(.017)	.049(.096)	.021(.017)	.012(.007)	CP*	2	FB/FB	NM
Biomass ash-free dry weight (g/m^3)	.008(.010)	.018(.027)	.012(.010)	.006(.004)	CP*	2	FB/FB	FQ
Total number/m^3	4245.75(3614)	11698.60(33448)	6607.55(4706)	4023.2(3955.88)	CP	2	FB/FB	NM

Table 3. Total means and standard deviations (in parentheses) of the values for the physical variables for each year. Below are the probabilities that the ratios of variance between years and months to the variance within years and months differ from the expected as a matter of chance as determined by a two-way anova.

	1980-1981	1981-1982
Rainfall (cm per month)	6.66(5.14)	8.45(6.77)
Wind velocity (km per hour)	9.8(1.6)	8.6(1.4)
Wind gust (km per hour)	15.0(1.3)	13.5(3.5)
Wind direction (° True per month)	1(1)	2(1)
Temperature (°C)	30.8(.3)	31.2(0.4)

	Rainfall	Wind speed	Wind gust	Wind direction	Temperature
Year (Y)	.489	.000	.454	.000	.010
Month (M)	.000	.000	.000	.000	.000
Y x M interaction	.000	.006	.000	.001	.001

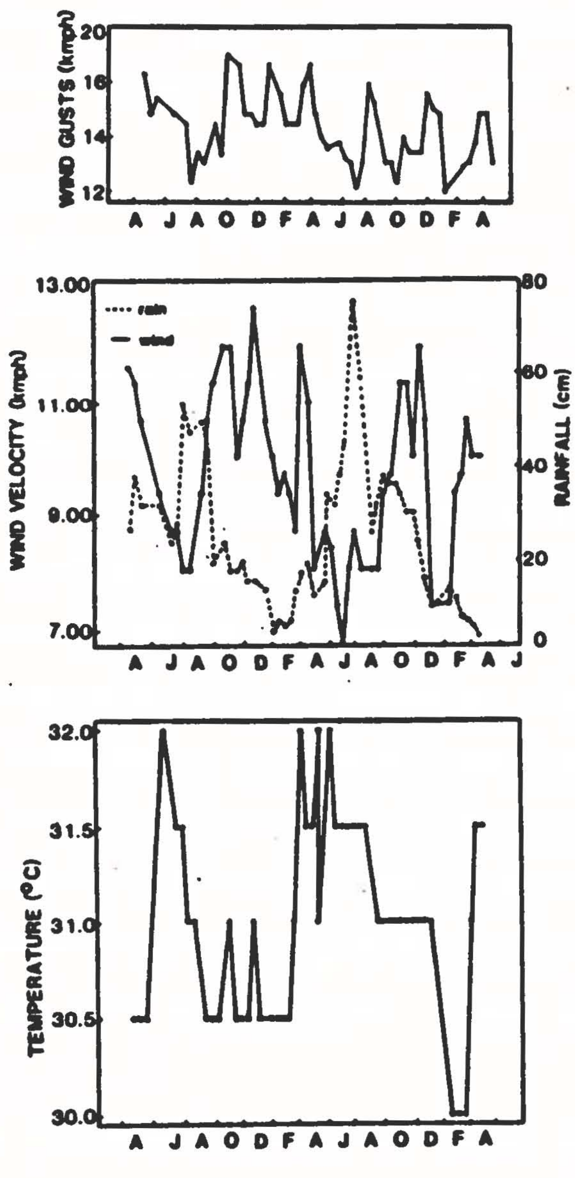

Figure 3. The mean temperature, wind velocity, and wind gusts for each month during the two-year survey.

remaining months had predominantly northeasterly winds. July and August had the highest air temperatures, and February and March had the lowest air temperatures. The highest wind velocities and gusts were in November and December.

Biological Variables

Cross-Areal Variations

All of the selected zooplankters, except P. cultrifera and Leptocarpus sp., showed significant cross-areal variations in abundance (Table 2). The Commercial Port had the highest and most variable abundances of holoplanktonic animals (C. acicula, the Acartia sp., S. enflata, and L. chacei) and ash-free dry weight.

The Lower Piti Channel had the highest abundances of crab zoeae, shrimp mysis, A. intermedia, and P. cultrifera. The Outfall Lagoon had the highest abundances of O. universa, fish eggs, Leptocarpus sp., Acetes sp., and fish larvae. The Secondary Channel had no significantly greater abundances of the zooplankters when compared with the other sites. However, the Secondary Channel had relatively high abundances of crab zoeae, Leptocarpus sp., Acetes sp., and P. cultrifera.

Because the abundances of zooplankton varied significantly between sites, the analyses of temporal variability were examined separately at each site to control for this source of variation.

Annual Variations

Significant annual variations were found for ash-free dry weight and dry weight in the Secondary Channel and Commercial Port, respectively (Table 4). At specific sites, significant annual

Table 4. Total means and standard deviations (in parentheses) for the abundances (number of individuals per m^3) of zooplankters and total biomass values for each year. To the right are the probabilities that the ratios of variance between years to the variance within years differ from the expected as a matter of chance. Probabilities were determined by two-way anova. The sites where significant variances occur are indicated in the far right column. The sites are abbreviated as follows: SC=Secondary Channel, CP=Commercial Port, LP=Lower Piti Channel, and OF=Outfall Lagoon. The significant probabilities are indicated by one asterisk ($p<.01$), two asterisks ($p<.005$), or three asterisks ($p<.001$).

	1980-1981	1981-1982	Anova Probability	Site
Acartia sp.	17.55(50.31)	41.35(142.23)	**	SC
O. universa	9.29(21.55)	14.65(25.49)	NS	
crab zoeae	25.71(27.02	47.04(61.22)	***	LP,OF
shrimp mysis	10.55(12.41)	5.91(5.06)	NS	
C. acicula	14.98(36.30)	26.03(112.63)	NS	
A. intermedia	1.34(3.89)	.71(1.32)	NS	
P. cultrifera	.122(.234)	.15(.43)	NS	
Leptocarpus sp.	.16(.43)	.20(.60)	NS	
Acetes sp.	.11(.37)	.15(.43)	NS	
L. chacei	.17(.67)	8.54(18.30)	***	CP
fish eggs	1.45(3.16)	1.05(1.97)	NS	
fish larvae	1.03(1.56)	1.60(1.86)	NS	
dry weight (g/m^3)	.024(.033)	.024(.058)	*	CP
ash-free dry weight (g/m^3)	.011(.012)	.011(.017)	*	SC

variations in the abundances of the following zooplankters were found: L. chacei in the Commercial Port, the Acartia sp. in the Secondary Channel, and crab zoeae in the Outfall Lagoon and Lower Piti Channel. Significant annual variations with annual/seasonal interactions were found for shrimp mysis and fish eggs in the Outfall Lagoon and for C. acicula in the Commercial Port. No significant annual variations were found in the abundances of O. universa, S. enflata, A. intermedia, and Acetes sp. (Table 5).

Seasonal Variations

Significant seasonal variations were found for ash-free dry weight and dry weight in the Commercial Port and Lower Piti Channel, respectively (Table 5). Ash-free dry weight was strongly correlated with C. acicula and the total abundance of zooplankton in the Commercial Port (Figs. 4b and 5b and Table 6). At specific sites, significant seasonal variations in the abundances of the following zooplankters were found: crab zoeae in the Lower Piti Channel and Outfall Lagoon, S. enflata in the Lower Piti and Secondary Channels, and shrimp mysis in the Secondary Channel (Table 5, Fig. 6a-c).

In the Commercial Port, ash-free dry weight biomass showed a more significant seasonal variability than have the abundances of any of the zooplankters examined. C. acicula showed a stronger correlation both with ash-free dry weight and the total number of zooplankton than did any of the other zooplankters (Table 6, Figs. 4b and 5b). This correlation occurred in the Commercial Port and suggests that the winter-spring (February-April) increase in abundance of C. acicula was the major cause of the seasonal variation in biomass. The abundances

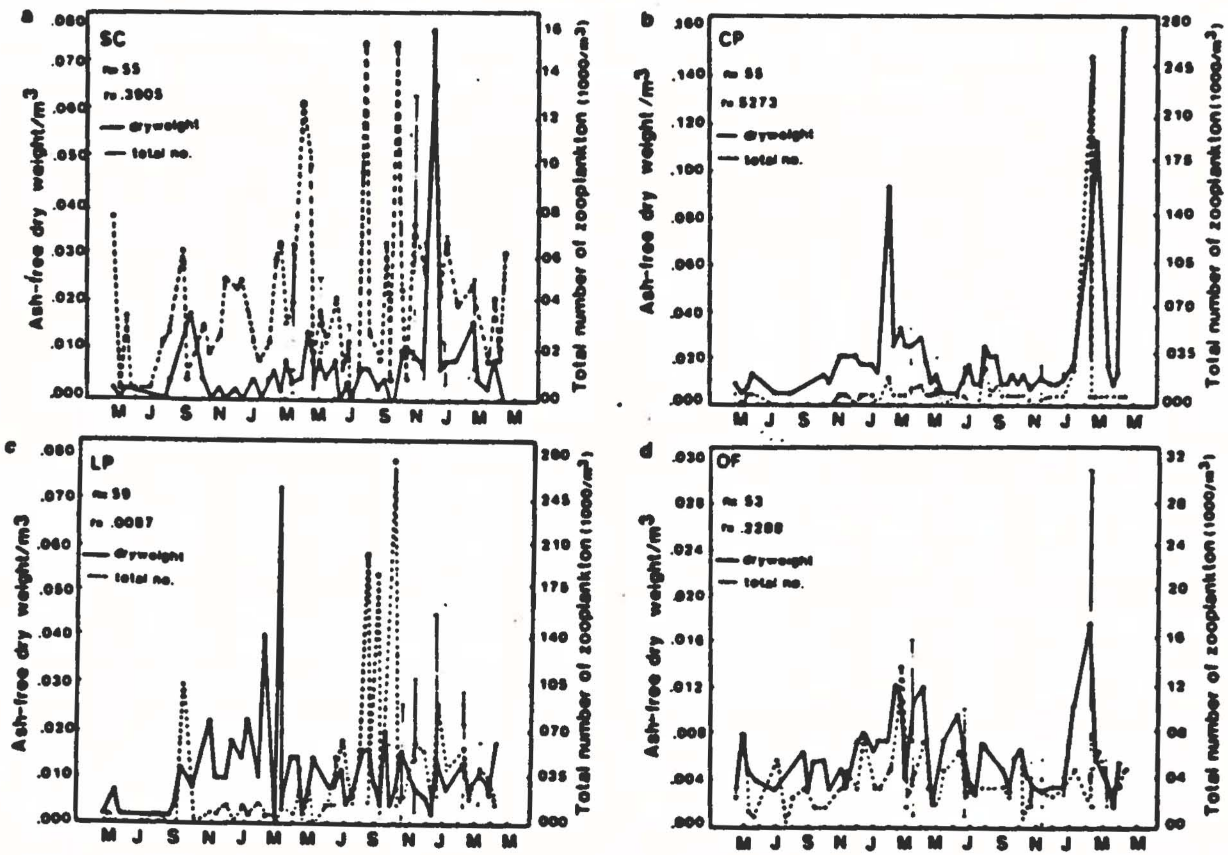

Figure 4. The means and standard deviations of ash-free dry weights and the total numbers of zooplankters. The number of observations (n) and the correlation coefficient (r) are given ($r_{.01[50]} = .354$, $r_{.001[50]} = .443$). The four stations are indicated by the following symbols: SC=Secondary Channel, CP=Commercial Port, LP=Lower Piti Channel, and OF=Outfall Lagoon.

Table 5. Significance of variances and interactions between years and months in the abundances of zooplankters. Log-transformed data were used. The values given are probabilities that ratios of variance between categories to variance within categories differ from the expected as a matter of chance as determined by a two-way anova.

Site		*Acartia* sp.	*O. universa*	crab zoeae	shrimp mysis	*C. acicula*	*S. enflata*	*A. intermedia*	*P. cultrifera*	*Leptocarpus* sp.	*Acetes* sp.	*L. chacei*	fish eggs	fish larvae	dry weight	ash-free dry weight
Secondary Channel	Year (YR)	.008	.330	.212	.017	.720	.587	.404	.098	.031	.350	.000	.002	.029	.014	.009
	Month (MO)	.432	.691	.432	.000	.970	.001	.000	.019	.000	.052	.008	.001	.501	.193	.312
	YR x MO	.423	.836	.220	.102	.972	.169	.000	.030	.000	.002	.007	.000	.600	.216	.051
Commercial Port	Year (YR)	.479	.068	.218	.667	.000	.830	.886	.519	.443	.301	.002	.422	.036	.009	.035
	Month (MO)	.811	.566	.189	.100	.000	.423	.040	.165	.062	.118	.595	.253	.202	.000	.000
	YR x MO	.785	.550	.151	.496	.000	.338	.076	.740	.198	.113	.597	.058	.232	.017	.037
Lower Piti Channel	Year (YR)	.012	.981	.002	.000	.408	.037	.081	.691	.443	.404	.000	.180	.073	.132	.400
	Month (MO)	.018	.029	.000	.073	.550	.002	.000	.005	.062	.031	.000	.755	.587	.006	.000
	YR x MO	.026	.933	.067	.009	.391	.012	.000	.008	.198	.989	.000	.305	.958	.185	.003
Outfall Lagoon	Year (YR)	.017	.139	.001	.000	.286	.350	.469	.273	.374	.504	.143	.004	.524	.741	.209
	Month (MO)	.000	.340	.011	.000	.673	.995	.044	.262	.848	.347	.329	.001	.003	.000	.000
	YR x MO	.000	.298	.625	.000	.496	.995	.001	.222	.766	.581	.280	.004	.009	.000	.000

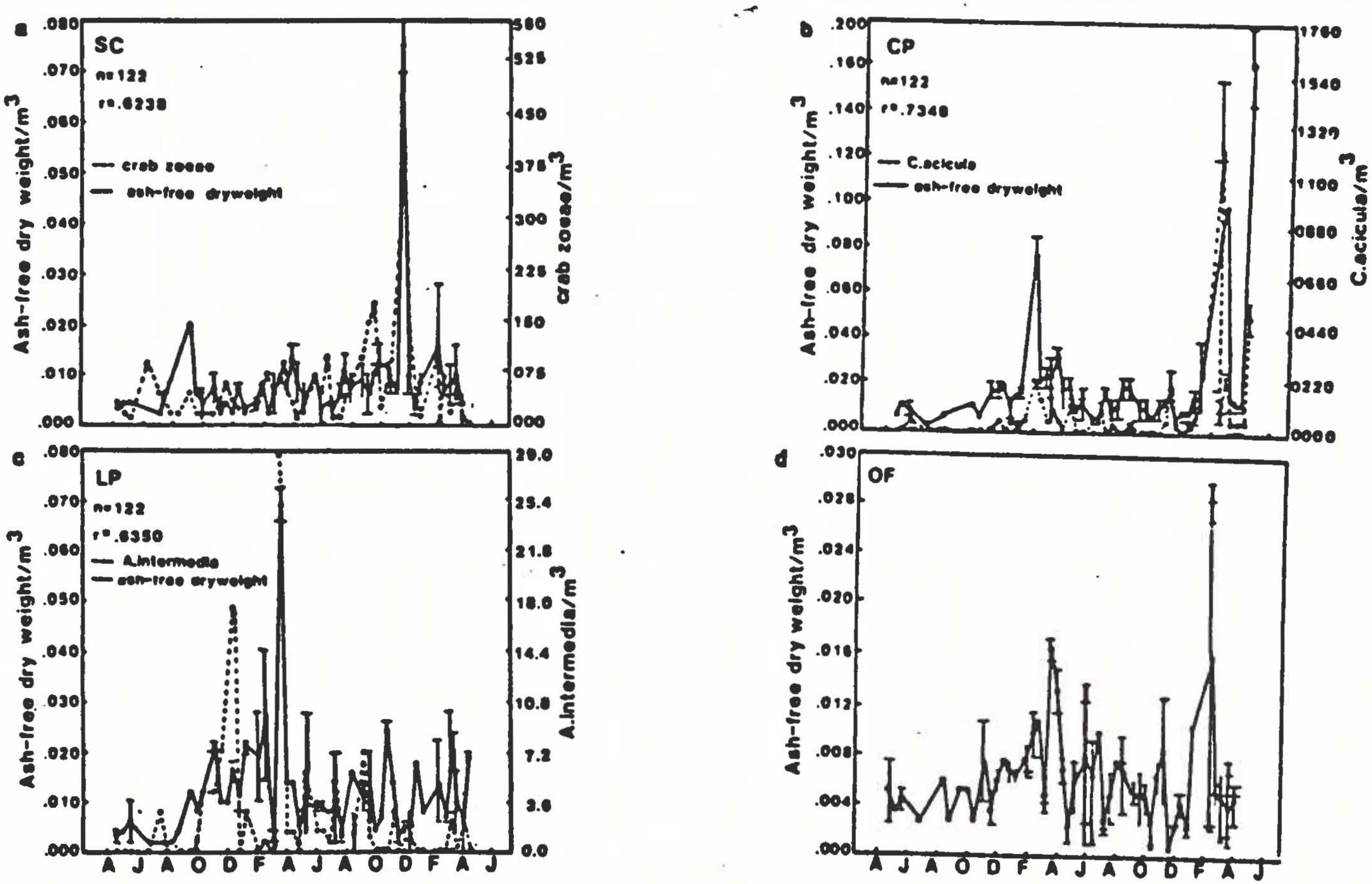

Figure 5. The means and standard deviations of ash-free dry weights and the abundances of zooplankters that showed a strong correlation with ash-free dry weights. The two-year data were averaged over each 12-day interval. The number of observations (n) and the correlation coefficient (r) are given. The four stations are indicated by the following symbols: SC=Secondary Channel, CP=Commercial Port, LP=Lower Piti Channel, and OF=Outfall Lagoon.

Table 6. A product-moment correlation coefficient matrix between physical and biological variables during the two-year survey. Each site (60 physical observations/site and 120 biological observations/site) was analyzed separately and the significant correlations ($r_{.01[58]}$ = .331, $r_{.001[58]}$ = .4178, and $r_{.001[118]}$ = .297) were summarized into one table. Symbols for each site are: S=Secondary Channel, C=Commercial Port, L=Lower Piti Channel, F=Outfall Lagoon and A=Agana Weather Station.

	YR	MO	RN	WV	WG	WD	T	ACR	FOR	CRB	SHR	PTR	SAG	A.i	P.c	LP	AC	LU	FE	FL	DW	AS
Year (YR)	**																					
Month (MO)		**																				
Rainfall (RN)		.600A	**																			
Wind velocity (WV)	-.400A		-.301	**																		
Wind gust (WG)	-.570A			.575A	**																	
Wind direction (WD)	-.511A	.415A	.700A	-.380A		**																
Temperature (T)	.334A		.312A	.306A		.464A	**															
Acartia sp.(ACR)			.411C				.353F	**														
O. universa (FOR)									**													
crab zoeae (CRB)	.362F	.339L	.438F .362L			.307L		.327F		**												
shrimp zoeae (SHR)	-.384F -.403L									.397C	**											
C. acicula (PTR)								.357L				**										
S. enflata (SAG)		.325S	.346C					.372F .765C .526S		.312F			**									
A. intermedia (A.i)														**								
P. cultrifera (P.c.)	-.304									.430F		.383L	.597F		**							
Leptocarpus sp. (LP)														.329S		**						
Acetes sp. (AC)				.335S												.577C	**					
Lucifer chacei (LU)	.318F .330C		.303F		-.348C		.305S	.379L	.331L .585C .471S			.478S .340F .314C			.373L			**				
fish eggs (FE)		.304F																	**			
fish larvae (FL)			.321L				.358F			.312F .477L .422S										**		
dry weight (DW)									.390L	.544S		.745C		.627L				.328C		.378S	**	
Ash-free dry weight (AS)									.364L	.624S		.735C		.635L				.330C		.465S	.870F .929L .991C .922S	**

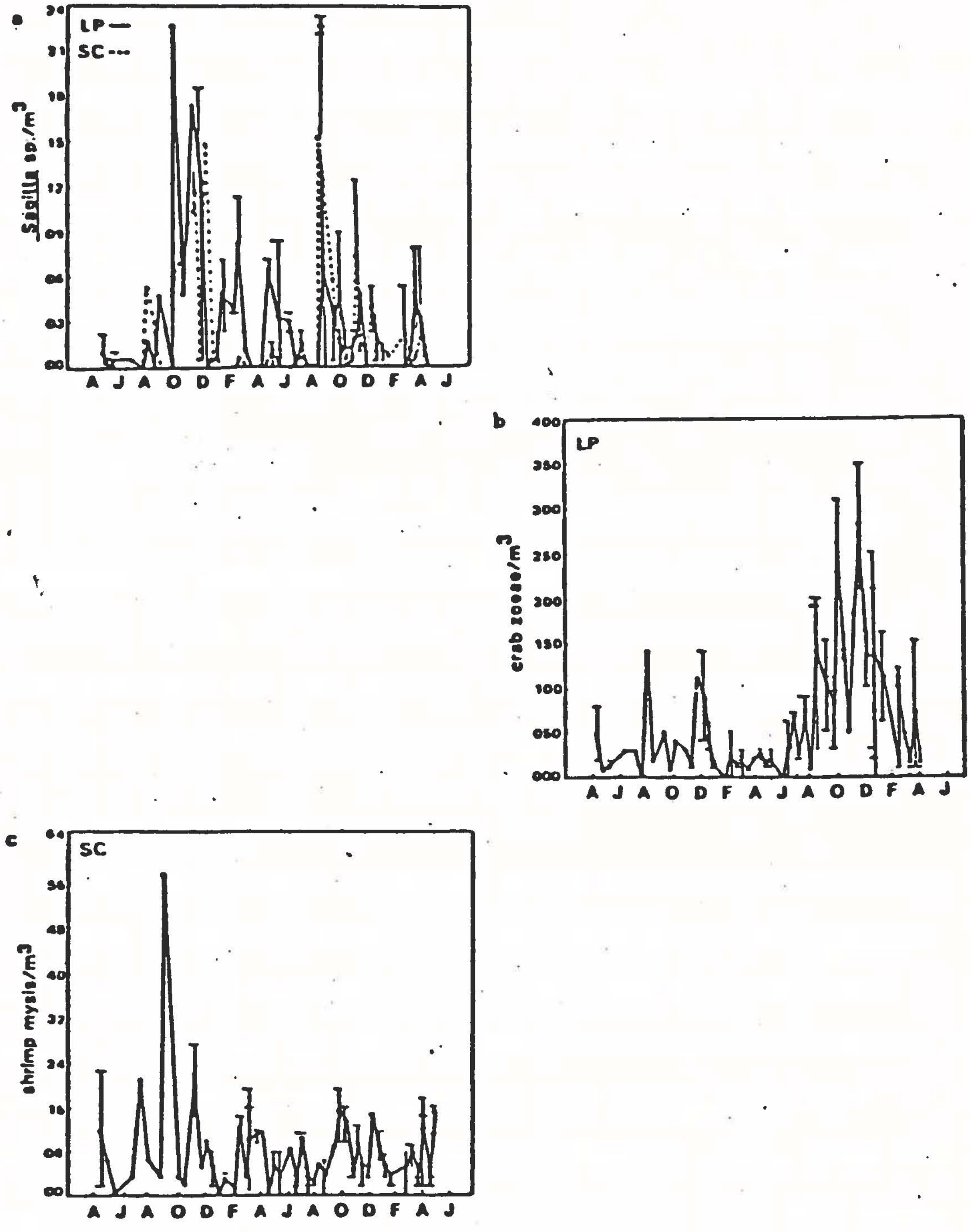

Figure 6. The means and standard deviations of ash-free dry weights of the zooplankters that showed significant seasonal variation for each site. The stations are indicated by the following symbols: SC=Secondary Channel, LP=Lower Piti Channel.

of *O. universa* and shrimp mysis correlated strongly with biomass in the Lower Piti Channel; fish eggs were also characteristic of this winter-spring increase (Tables 2 and 6).

A fall peak (September-November) in the abundance of zooplankton was characterized by the abundance of crab zoeae which was strongly correlated with dry weight and with the total number of zooplankton in the Secondary Channel (Table 6, Figs. 4a and 5a). A winter peak (December) in the abundance of zooplankton was characterized by a large number of *S. enflata* (Table 2 and Fig. 6a).

Lunar Variations

In the Lower Piti Channel, the abundances of crab zoeae, *A. intermedia*, *P. cultrifera*, and *L. chacei* had significant lunar variations (Table 7). Crab zoeae were significantly more abundant during the first and last quarters of the moon, *A. intermedia* during the full moon, and *P. cultrifera* during the new moon.

Diurnal Variations

Significant diurnal variations in the abundance of zooplankters were found at specific sites (Table 8). *Acartia* sp. and *S. enflata* were significantly more abundant from 0700-0900 in the Secondary Channel. *S. enflata* was significantly more abundant from 0200-0300 in the Commercial Port. The shrimp mysis were significantly more abundant from 1800-2000 in the Lower Piti Channel. Fish larvae were significantly more abundant from 0300-0400 in the Lower Piti Channel. *O. universa* was significantly more abundant from 1800-2000 in the Lower Piti Channel. The day/night correlations substantiate these

Table 7. Total means and standard deviations (in parentheses) of the abundances (number of individuals per m^3) of each zooplankter, zooplankton group, and biomass value for each moon phase. In the column on the right are the probabilities that the ratios of variance between moon phases to the variance within moon phases differ from the expected as a matter of chance as determined by a two-way anova. The site where these significant ($p<.001$) between moon-phase variances occur is also listed as LP which indicates the Lower Piti Channel. One asterisk indicates $p<.01$, two asterisks indicate $p<.005$, and three asterisks indicate $p<.001$.

Taxa	Last Quarter	New Moon	First Quarter	Full Moon	One-way anova probability (p)	
Acartia sp.	55.48(247.69)	36.55(91.21)	23.33(66.81)	26.29(49.83)	NS	
O. universa	12.70(20.53)	17.61(32.93)	10.38(21.36)	10.45(17.70)	NS	
crab zoeae	49.87(80.99)	30.08(41.02)	53.88(58.08)	34.60(37.33)	***	LP
shrimp mysis	6.30(5.10)	8.33(12.45)	6.85(6.23)	7.60(6.52)	NS	
S. enflata	5.43(17.25)	3.48(6.58)	2.80(6.52)	3.51(6.99)	NS	
C. acicula	5.86(13.40)	43.32(161.29)	7.595(17.26)	22.17(58.76)	**	
Lucifer chacei	2.17(6.12)	10.65(21.68)	2.21(5.40)	5.65(15.67)	***	LP
fish larvae	2.18(2.58)	1.39(1.75)	1.21(1.53)	1.23(1.60)	**	
fish eggs	.87(1.53)	1.68(3.50)	1.20(1.78)	.94(1.91)	**	
A. intermedia	.84(1.46)	.74(1.32)	.38(.60)	1.49(3.98)	***	LP
Leptocarpus sp.	.23(.52)	.16(.70)	.15(.40)	.21(.49)	*	
Acetes sp.	.24(.62	.07(.26)	.14(.41)	.13(.48)	*	
P. cultrifera	.04(.1)	.22(.53)	.05(.13)	.18(.39)	***	LP
dry weight (g/m^3)	.016(.019)	.037(.085)	.014(.010)	.025(.040)	**	
ash-free dry weight (g/m^3)	.006(.004)	.009(.012)	.014(.024)	.007(.005)	**	
No. of observations	65	134	95	137	Total	431

Table 8. Significance of variances between days, between times, and interactions between days and times in the abundances of zooplankters. Log-transformed data from zooplankton samples during the twenty-four hour periods were used. The values given are probabilities that ratios of variance between categories to variance within categories differ from the expected as a matter of chance as determined by a two-way anova (n=40).

		fish eggs	fish larvae	*A. clausi*	*O. universa*	crab zoeae	shrimp mysis	*C. acicula*	*S. enflata*	dry weight	ash-free dry weight	chlorophyll *a* (all sites*)
Secondary Channel	Day (D)	.0478	.0053	.0921	.0004	.0007	.0004	.0000	.0060	.0146	.0233	.0000
	Time (T)	.1200	.6004	.0049	.0002	.0002	.0000	.0000	.0016	.0205	.0338	.0005
	D x T	.0194	.0148	.1748	.0024	.0004	.0001	.0001	.0126	.0230	.0847	.0260
Commercial Port	Day (D)	.2214	.0430	.0000	.0738	.0006	.0027	.0000	.0392	.0000	.0000	
	Time (T)	.7040	.0002	.0375	.0388	.0172	.0002	.0002	.0140	.0007	.0001	
	D x T	.3773	.0227	.0002	.4391	.0007	.0040	.0001	.1022	.0001	.0001	
Lower Piti Channel	Day (D)	.3258	.6669	.0405	.0122	.0095	.4947	.0000	.0004	.0209	.0612	
	Time (T)	.0076	.0252	.0026	.0002	.0243	.0007	.0062	.0091	.0103	.0018	
	D x T	.0095	.6587	.0017	.0173	.0128	.0750	.0000	.0008	.0029	.0023	
Outfall Lagoon	Day (D)	.0000	.0381	.0031	.0163	.0057	.0431			.0031	.0001	
	Time (T)	.0000	.0052	.0017	.0773	.0053	.0054			.004	.0000	
	D x T	.0000	.0064	.0581	.0726	.0084	.0474			.0040	.0024	

*There were not enough data to examine chlorophyll a for each site.

Table 9. A product-moment correlation coefficient matrix between physical and biological variables during the diurnal study. The significant correlations ($r_{.01[38]} = .403$, $r_{.001[38]} = .501$) for each site (40 observations/site) are summarized. The following symbols were used for each site: S=Secondary Channel, C=Commercial Port, L=Lower Piti Channel, and F=Outfall Lagoon.

	Tide	Day/ Night	CHL	FE	FL	ACR	FOR	CRB	SHR	PTR	SAG	DW	AS
Tide	**												
Day/Night		**											
Chlorophyll *a* (CHL)			**										
fish egg (FE)				**									
fish larvae (FL)				.593F	**								
	.510F												
	.420L												
Acartia (ACR)	.402S					**							
O. universa (FOR)							**						
crab zoeae (CRB)	.634C							**					
		-.599F											
		-.512L											
		-.461C					.406L						
shrimp mysis (SHR)	.429C	-.610S					.513C	.565C	**				
C. acicula (PTR)	-.505L					.787C				**			
						.435C							
S. enflata (SAG)	-.486L		.554S			.469S				.576C	**		
	-.630L								.408L		.828F		
dry weight (DW)	-.427C	-.476F				.659C	.541S	.461F	.551S	.677C	.745L	**	
												.890*	
									.471F			.924L	
ash-free	-.577L								.563L			.918C	
dry weight (AS)	-.435C	-.545F				.609C	.424L	.422F	.526S	.568C	.694L	.950S	**

results (Table 9). All of the preceding zooplankters at the different sites and the remaining zooplankters showed significant diurnal variations and day/diurnal interactions.

At specific sites, strong correlations between tide and the abundance of zooplankters were found. Crab zoeae and shrimp mysis were more abundant on ebb tides in the Commercial Port. The abundances of C. acicula and S. enflata were greater during flood tides in the Commercial Port. Biomass values were greater during flood tides in the Commercial Port and the Lower Piti Channel (Table 9).

Physical-Biological Correlations

Rainfall showed more significant correlations with zooplankton than did any of the other environmental variables considered (Table 6). Only a few significant correlations were found for all the sites. Significant positive correlations were found between rainfall and the abundances of the Acartia sp. and S. enflata in the Commercial Port and crab zoeae and fish larvae in the Lower Piti Channel. Significant negative correlations were found between rainfall and the abundances of L. chacei in the Secondary Channel and Outfall Lagoon and between rainfall and fish eggs in the Lower Piti Channel.

Wind velocity was positively correlated with the abundances of Acetes sp. in the Secondary Channel. Wind gusts were negatively correlated with the abundance of L. chacei in the Commercial Port. Temperature was positively correlated with the abundance of Acartia sp. in the Outfall Lagoon (Table 6).

Biological Correlations

During this two-year survey, ash-free dry weight of the total zooplankton and the abundance of *C. acicula* had a stronger positive correlation with each other than did any other pair of biological variables. This correlation was found in the Commercial Port. For at least three sites, significant positive correlations were found between the following pairs of zooplankton: the *Acartia* sp. and *S. enflata*, crab zoeae and fish larvae, and *O. universa* and *L. chacei*. Other strong correlations between pairs of zooplankters were primarily the result of similar seasonal peaks at specific sites (Tables 2 and 6).

During the diurnal study, chlorophyll *a* and *S. enflata* were strongly correlated with each other (Table 9).

DISCUSSION

Composition and Distribution of the Zooplankton

The predominant holoplankton consisted of the calanoid copepod *Acartia* sp., the pteropod *C. acicula*, the chaetognath *S. enflata*, the shrimp *L. chacei*, the foraminiferan *O. universa*, the ostracod *E. elongata*, the larvacean *Oikopleura* sp., and a bivalve. The predominant meroplankton consisted of several unidentified species of crab and shrimp larvae, two less predominant species of shrimp, an *Acetes* sp. and a *Leptocarpus* sp., and the polychaetes *Armandia intermedia* and *Perinereis cultrifera* (Table 2).

The composition of predominant zooplankters did not change during the two-year survey. Therefore, although the abundances of individual species varied during this study, the community remained persistent over time.

Table 10 presents the geographical distribution of five predominant holoplanktonic species and two less abundant polychaetes. It is clear that all these species are well represented in the Indo-Pacific as well as in other areas of the world. This is not inconsistent with Hirota's hypothesis that there are holoplanktonic species of relatively few genera in shallow water communities that are "universal" species.

Cross-Areal Variations

Significant cross-areal variations result primarily from physical differences between sites; however, several biological explanations also may be considered, and it may be that habitat is an important factor in determining variability of plankton.

Table 10. The geographical distribution of seven species of zooplankton examined in this study.

Species Name and References	Distribution
Armandia intermedia Day (1976)	Senegal, Ghana, Angola; Indo-Pacific from Red Sea, Persian Gulf, and Ceylon to N. W. Australia, Japan, and New Calendonia
Cresius acicula Wormelle (1962) Wickstead (1961)	Arabian Sea, Singapore Strait, Java Sea
Russell and Colman (1934) Ikeda et al. (1980) Wormelle (1962) Van der Spoels (1972)	Australia, Bermuda, Florida Current, Cape Hatteras-Newfoundland, Open Atlantic 35°-50°N, Coast of Portugal, Gulf of Biscay
Euconchoecia elongata Tseng (1972)	Indian Ocean, Malayan Archipelago, Taiwan Strait
Lucifer chacei Bowman (1961)	East India, Hawaii, Line Islands, Fanning Islands, Tuamotu Islands, Tikahau Atoll, Society Islands, Tahiti, Moorea
Orbulina universa Boltovskoy and Wright (1976)	Subtropical 20°-40° latitude Equatorial and North Pacific
Perinereis cultrifera Day (1976)	N. E. Atlantic from the North Sea to Senegal, Mediterranean and tropical Indo-Pacific
Sagitta enflata Wickstead (1961)	Singapore Strait, Java Sea, South China Sea, Sundra Shelf, Hawaii, Florida

All the holoplanktonic species examined, except O. universa, were more abundant in the Commercial Port, the deepest and most oceanic site. Chlorophyll a values (a measure of phytoplankton, a food source for herbivorous zooplankton) were highest in the Commerical Port during the diurnal study, indicating that a greater food source may have been available at this site. Gerber (1981) also found more holoplanktonic zooplankters (copepods, chaetognaths, and larvaceans) in deeper lagoonal waters. He proposed that the greater water column provided more food and space (thus less predation) and so a large holoplanktonic community was supported.

Fish larvae, fish eggs, and O. universa were significantly more abundant in the Outfall Lagoon. Several explanations for the greater abundances of fish larvae and eggs are as follows: 1) the Outfall Lagoon is the innermost and most protected area from the influences of storms, 2) ecological surveys conducted over an eight-month period showed that the largest aggregations of fishes were found in the Outfall Lagoon (Marsh et al., 1980), and 3) Sagitta species, known to feed preferentially on fish larvae (Kuhlmann, 1977), were not common in the Outfall Lagoon. Therefore, more shelter, possibly more spawning by the fish aggregations, and less predation may explain the greater abundance of fish larvae and fish eggs in the Outfall Lagoon.

Polychaetes, crab zoeae, and shrimp mysis were more abundant in the Lower Piti Channel. The Lower Piti Channel is bordered on either side by mangroves and is relatively deep and may provide a better habitat for these animals. The Secondary Channel had no significantly greater mean abundances of zooplankters when compared with the other sites (Table 2). Since this site was the shallowest site, it may be subject to more extreme temperature and salinity ranges during ebb tides and greater turbulence during storms.

At specific sites, strong correlations ($p<.001$) were found between the abundances of certain zooplankters and biomass values. These correlations were not necessarily between biomass values and the most abundant zooplankters of a site (Table 6). This suggests that less abundant but larger zooplankters (A. intermedia, P. cultrifera, and fish larvae) were important contributors to the biomass for specific stations. The abundance of crab zoeae was strongly correlated with biomass in the Secondary Channel but not in the Lower Piti Channel, where crab zoeae were significantly more abundant. Perhaps the greater abundance of the large-sized A. intermedia in the Lower Piti Channel masked the significance of the smaller sized crab zoeae in the Lower Piti Channel (Figs. 4c and 5c).

The zooplankters in the Outfall Lagoon showed no significant correlation with biomass or total numbers of zooplankters (Figs. 4d and 5d), suggesting that no one of the species examined is consistently affecting the biomass at this site.

Annual and Seasonal Variations

The most significant finding in annual variations was that the mean biomass of all sites was the same each year. This suggests that although the numbers of specific zooplankters varied between years for the different sites, the overall standing crop remained constant.

The significant annual variations in biomass for different sites were the result of significant variations in the abundances of L. chacei in the Commercial Port and the Acartia sp. in the Secondary

Channel. In the Lower Piti Channel and the Outfall Lagoon, crab zoeae were significantly variable in abundance between years but were not strongly correlated with biomass at these sites (Tables 4 and 6).

Two other studies of zooplankton have also shown annual variations in dry weight biomass (Smith et al., 1982; Subrahmanyan, 1959). However, no annual variation in wet weight biomass was found in a two-year study in Australia (Crenshaw, pers. comm).

The mean annual dry weight values for other tropical Indo-Pacific areas showed that Hawaii (Smith et al., 1982) and East Africa (Woolridge, 1977) had similar values (.035 g/m^3) for inshore areas and India (Subrahmanyan, 1959) had a mean value (.145 g/m^3) that was four times greater than Hawaii and East Africa. Guam had the smallest mean value (.024 g/m^3), suggesting that the waters of this inner region of Apra Harbor had a smaller standing stock of zooplankton. However, Guam has the smallest land mass of those areas with which it was compared and may have less nutrient runoff to support the zooplankton community.

The winter-spring peak (February-April) of biomass and total zooplankton abundance in the Commercial Port was the most notable seasonal event in this study. This peak was characterized by the abundance of C. acicula. A less well marked fall peak (September-November) in dry weight was characterized by the abundance of crab zoeae and shrimp mysis in the Lower Piti and Secondary Channels, respectively. S. enflata showed a significant winter (December) peak in abundance in the Lower Piti and Secondary Channel (Figs. 4a, 5a-b, and 6a-c).

Other tropical Indo-Pacific studies have shown no consistent seasonal patterns for individual zooplankters (Table 11). However,

Table 11. Comparative studies of the months of peak abundances (number of individuals per m^3) and values derived from the total zooplankton in the tropical Indo-Pacific. A summary of the seasonal peaks from each group is presented. Total zooplankton values were derived from the total numbers, ash-free dry weight (g/m^3), dry weight (g/m^3), and N/g of zooplankton.

Region	Reference	Total zooplankton	Copepoda	S. enflata	crab zoeae	shrimp mysis	Foraminifera	Gastropoda	L. chacei	fish larvae	fish eggs	polycheates
HAWAII	Piyankarnchana (1965)	NO/FB/JL	MR						NO/JU			
	Watson & Leis (1974).	SP/MR								SP/MR	SP/MR	
	Hirota (1978)	MR										
	Leis (1978)	JN-JU*/FB/MR								JL/MR	JU/MR	
ENIWETOK	Smith et al. (1982)	JL*/SP										
	Gerber (1981)	JU-AU	JU-AU	JU-AU	JU-AU	JU-AU	JU-AU	JU-AU	JU-AU	JU-AU	JU-AU	
	JU-AU											
GUAM	Marsh et al. (1977)	NO	OC	JA	SP	DC	JA	NO	NO/FB	SP	SP	SP
	This study (1983)	FB-MR	AU	DC	JU/NO/DC	AU/OC	AU/AP	FB/AP	NO/JA/AP	SP/OC	FB/AP	JU/SP/JA
AUSTRALIA	Russell & Colman (1934)	NO-DC*/MR-AP	JL	MR	JA/MR	JU/JL				OC/DC	SP/NO	DC
	Ikeda et al. (1980)	MR-AP	ME-AP	FB/MR	JL/MR	JL-AU	SP/NO	NO-DC/MR-AP	DC/FB/AP	SP/OC		SP-OC/FB-AP
INDIA	Prasad (1954)	MR				MR		MR				OC/MY
	Subrahmanyan (1959)	JU-AU/JA-FB										
	Wickstead (1961)	JU/NO/DC/AP	DC/JN	NO/DC	JU/NO/AP			NO-DC	NO-DC	OC-NO/MR-AP	NO/AP	NO/AP
	Raja (1972)	SP										
EAST AFRICA	Wickstead (1963)	FB-MR	MR									
	Woolridge (1977)	FB										
	Summary	FB-MR	MR	DC/MR		AU	AU	NO/MR	NO/AP	SP/MR	SP	SP

several seasonal trends emerged from this comparison. First, when comparing dry weight, wet weight, total numbers, and nitrogen/g of zooplankton, I found that February and March had higher values than other months of the year. Second, significant annual/seasonal variations were found in several studies (Subrahmanyan, 1959; Piyankarnchana, 1965; Clutter, 1969; Smith et al., 1982). It should be pointed out that seasonal comparisons were difficult for several reasons: 1) only four out of the fifteen studies examined more than three taxonomic groups, i.e., two studies in Australia (Russell and Colman, 1934; Ikeda et al., 1980) and two studies in India (Prasad, 1954; Wickstead, 1961); 2) several studies were not continuous (Gerber, 1981; UGML, 1977); and 3) different methods were used to quantify the plankton communities (dry weight, wet weight, nitrogen/g, total numbers of zooplankton).

The greater seasonal peaks and overall abundances of zooplankton in the second year of this study may be attributed to the greater and more concentrated rainfall and less variable wind directions in that year (Fig. 3 and Table 3). Several long-term studies have indicated that rainfall and the strength of the winds are correlated with zooplankton peaks. Data from Subrahmanyan's (1959) five-year study show a trend in which strong winds (March-May) followed by heavy rains (June-August) were subsequently followed (one-month lag) by a bloom of phytoplankton and a subsequent increase in the abundance of zooplankton. The more pronounced and less variable the rain and winds, the greater the bloom of phytoplankton and increase in zooplankton abundance. In India, Raja (1972) found that when monsoons were erratic and the rainfall was feeble, the percentage of undeveloped ovaries of S. longiceps was so great that their spawning potential and, thus, their recruitment was affected. Rainfall has been correlated with many of the increased abundances of zooplankters. For several Indo-Pacific regions, Birkeland (1982:175) hypothesized that "on rare occasions, terrestrial runoff from heavy rains (following the dry season or a record drought) may provide enough nutrients to stimulate a phytoplankton bloom of sufficient size to produce enough food for the larvae of A. planci." Simultaneous to my study, Birkeland and Kitalong (1983) found that chlorophyll a values showed a significant increase during the rainy season at four bays in Guam, which supports this hypothesis.

In several studies, zooplankters were not correlated with rainfall [e. g., the abundance of C. acicula in this 2-year study and the abundance of gastropods in the 3-year Indian study (Prasad, 1954)]. Wind may have a significant effect on some zooplankters. In Hawaii, Smith et al. (1982) found a slight effect of a long-term wind factor on microplankton ash-free weight. In Australia (Crenshaw, pers. comm.) zooplankton abundances were correlated with rainfall, and zooplankton were also abundant during the peak windy season. In Australia, it was found that "...nearshore (ten meter deep) bottom sediments were strongly entrained in the water column, only for nearshore water is the wind important in affecting the concentration of suspended particles by stirring up bottom sediments which may also be an important source of nutrients...since suspended particles are partly of organic origin (detritus, phytoplankton, and microplankton...)" (Wolanski et al., 1981:329).

In this study, a similar phenomenon may explain the winter-spring increase in zooplankton abundance immediately after strong winter winds. Nearshore mixing may be providing nutrients which initiate this increase in the abundance of C. acicula which had their guts packed with green phytoplankton. Data on nutrients from the Commerical Port (GEPA 1980-81), although incomplete, indicated that nitrates and phosphates were greatest in November and December. Thus, the period of greatest winds (November-December) also had the highest values for nutrients. These nutrients may initiate phytoplankton blooms in January and February, the months with peak abundances of C. acicula.

Although these results support Wolanski's findings, artificial mixing caused by ship activity in Apra Harbor may mask the effect of wind-induced mixing. Further investigation of the biological and physical variables affecting the abundances of C. acicula in the Commercial Port are needed to fully understand this phenomenon. For example, depth profiles of plankton, nutrients, temperature, salinity, oxygen, and suspended particles might show whether or not a thermocline or nutrient layers occur and how rains and winds affect these strata.

Lunar Variations

In the tropics, polychaetes and fish larvae (both meroplanktonic) are the only zooplankton for which lunar studies have been done. Polychaetes have shown the stronger lunar periodicity.

The Palolo worm (Eunice viridis) in the Fiji and Samoa Islands is an example of lunar periodicity. These polychaetes swarm in vast numbers during the last quarter of the moon at the lowest tide during October and November (reviewed by MacGinitie and MacGinitie, 1968). Although not tropical, Hauenschild's (1955, 1956) experiments with the nereid worm Platynereis dumerilli were the most thorough lunar studies available. P. cultrifera, also a nereid worm, is significantly more abundant during new moon, the moon phase with the least moonlight. P. cultrifera were all heteronereis forms, the free swimming form into which these two nereid worms metamorphose when sexually mature. This suggests that P. cultrifera were swarming near the surface for reproduction.

In California, Alldredge and King (1980) also found that polychaetes (including Armandia brevia Moore, Opheliidae) migrated to the surface less frequently on moonlit nights. This is consistent with the pattern for P. cultrifera, but not A. intermedia, in my study. They also found that a higher proportion of the total zooplankton, both by number and ash-free dry weight, avoided moonlight, migrating during moonless periods of the first and last quarters, and during the first two hours of full moon. This corroborates my results which also show greater biomass values during moonless nights, especially during the last quarter of the moon and new moon (Table 7).

The tropical coenobitid hermit crabs release zoeae into the ocean within a few days of new moon which may be a mechanism to get larvae off the reef during times of large tidal flow (Amesbury, 1980). This does not corroborate my results which show crab zoeae were significantly more abundant during the first and the last quarters of the moon.

Aggregated spawning may considerably increase the probability of successful fertilization and higher survival of the polychaetes and crab zoeae. The lunar variations of the animals examined indicated that a more diverse and greater number of organisms are collected during the new moon and during the last quarter of the moon.

Diurnal Variations

This and previous studies in Apra Harbor (UGML, 1977; Grovhoug, 1978) have shown an increased abundance of zooplankton at night. Nocturnal increases have been attributed to upward migration and an increased visual avoidance by plankton during the day. The usual explanation of vertical migration is avoidance of diurnal predation near the surface (Leis, 1978). An *Acartia* sp. and *S. enflata* were significantly more abundant during the late morning (0700-0900) and early morning (0200-0300), respectively, in the Commercial Port. These different temporal patterns may be a mechanism of predator avoidance by the *Acartia* sp. However, in the Secondary Channel, *Acartia* sp. and *S. enflata* were both significantly more abundant during the morning (0700-0900) and chlorophyll *a* was also high during the morning (0700-0900). So, food and predation may both affect the temporal abundances of these two species.

Fish eggs, *C. acicula* and *O. universa* tended to be more abundant during the day. Since *O. universa* and *C. acicula* possess protective shells and no evidence of predation was found, predation may not affect their diurnal patterns. Fish eggs, aside from bouyancy resulting from their oil droplets, have no means of active migration. The spawning strategy of the adult fish has more impact on their diurnal patterns. Observations of fish eggs inside the upper end of the shell of C. acicula suggest that C. acicula may be feeding upon fish eggs. However, the presence of fish eggs in C. acicula is more likely caused by either the effect of crowding within the net or crowding within the cod end during sampling, or both. Since Sagitta setosa and S. elegans have been experimentally shown to not feed upon fish eggs (Kuhlmann, 1977) chaetognath predation may not influence diurnal patterns of fish eggs.

Chlorophyll a, fish larvae, fish eggs, and O. universa showed similar diurnal patterns in other Indo-Pacific studies. Chlorophyll a peaked at 0800-0110 and again at 1600-2000 (Doty and Oguri, 1957). Fish eggs showed seasonal diurnal patterns, being more abundant at night in November and during the day in April (Watson and Leis, 1974). Leis (1978) also found that fish eggs began to become more abundant in samples taken at noon, with a maximum found in samples taken from 1800 to 2400. Fish larvae were most abundant at night (Watson and Leis, 1974; Leis, 1978). O. universa surfaced after 1600, went downward after midnight, rose at 1000, concentrated at the surface at noon, and then went down again (Tsi-Chung and Sauyee, 1964).

C. acicula, Sagitta sp., crab zoeae, Acartia sp., and total zooplankton biomass showed different diurnal patterns in other Indo-Pacific studies. C. acicula were more abundant at night at the surface (review by Wormelle, 1962). S. enflata and an Acartia sp. showed seasonal diurnal variations in Hawaii (Piyankarnchana, 1965). Anomura crab zoeae moved towards the surface and away from the bottom during the day, had some movement upward at sunset, went downward at post sunset, and were evenly dispersed at darkness (Wickstead, 1961). Crab zoeae considered here tended to be more abundant at 1800-2000. In India, Nair et al. (1977) found that biomass values (wet weight) were greater from 0000-0600, less from 0600-1200, and not significantly different from 1200-0000. Biomass values herein tended to be greater from 1800-2000.

Overall, greater abundances of organisms and higher biomass values were positively correlated with flood tides (Table 9). This may be attributed to less intense predation as a result of a greater volume of water at high tide, especially in the Secondary Channel. The greater abundance of crab zoeae in the Commercial Port at low tide, and of C. acicula and the Acartia sp. in the Secondary Channel and Lower Piti Channel at high tide, were probably the result of onshore movements of water at high tide and the opposite at low tide. However, Marsh et al. (1977) found no tidal reversal as a result of the strong westward current from the power plant discharge. The greater abundance of crab zoeae at low tide may also simply be the result of an increased concentration of the same number of crab zoeae at high tide in a smaller volume of water at low tide.

These diurnal patterns have shown that the Acartia sp., a strong daytime species, was underestimated during the 1900-2100 sampling regime of the two-year study. Shrimp mysis, significantly abundant at dusk, were overestimated.

Correlations Between Physical and Biological Variables

An Acartia sp., S. enflata, and heavy rainfall have shown strong positive correlations with each other. Grahame (1976) and Crenshaw (pers. comm.) found a similar phenomenon in Bermuda and the Great Barrier Reef, respectively. Piyankarnchana (1965) also found that an *Acartia* sp. peaked during the heaviest rainfall (March) and *S. enflata* (in their second stage of growth) peaked in March. *S. enflata* is known to be a predator of copepods (Piyankarnchana, 1965). In this study, *S. enflata* showed a stronger positive correlation (r=.7646) with the *Acartia* sp. than with rainfall (r=.3459). This suggests that predation upon the *Acartia* sp. has a more significant effect on the abundance of *S. enflata* than does rainfall alone.

Heavy rainfall has been hypothesized by several authors (Birkeland, 1982; Marsh, 1977; Subrahmanyan, 1959) to initiate phytoplankton blooms by enriching the water with nutrient salts from terrestrial runoff. Copepods have a very short life cycle (MacGinitie and MacGinitie, 1968) and thus may have shown a more pronounced response to phytoplankton blooms than the other organisms examined.

The crab zoeae, fish larvae, and rainfall were also all correlated with each other in the Lower Piti Channel. Similar significant seasonal patterns were also found for these two groups of species. Their correlation with rainfall may be the result of increased reproduction initiated also by an increased food supply caused by terrestrial runoff as discussed above.

L. chacei and *O. universa* also showed a consistent correlation with each other. Both animals had similar annual, seasonal, and lunar patterns, although these patterns were not significant for both animals. The *L. chacei* has been categorized as a carnivore (Hirota and Szyper, 1976) and *O. universa* is an omnivore (Boltovskoy and

Wright, 1976), yet no evidence of predation was found between these two species.

Correlations between the abundances of the zooplankters examined and the physical variables, temperature and wind direction were primarily the indirect result of rainfall, since most of the zooplankters showed stronger correlations with rainfall than with the other physical variables. However, wind velocity may have had a more direct physical effect upon the abundances of Acetes sp. in the Secondary Channel. The increased winds may have caused physical disturbance of the bottom which caused the Acetes sp. to come to the surface.

The correlations between the abundances of zooplankters were primarily the result of similar seasonal patterns in abundances between pairs of zooplankters. The following correlations between zooplankters exemplify this: 1) the Acartia sp., C. acicula, and L. chacei all had peak abundances in January in the Lower Piti Channel; 2) L. chacei and C. acicula had peak abundances in February in the Commercial Port; 3) crab zoeae and shrimp mysis had peak abundances in January and were also significantly more abundant on ebb tides during the diurnal study; 4) crab zoeae, S. enflata, and the Acartia sp. were all correlated with each other in the Outfall Lagoon and with rainfall; 5) crab zoeae and P. cultrifera had peak abundances in July in the Outfall Lagoon; 6) Acetes sp. and C. acicula had peak abundances from February to April in the Secondary Channel; 7) S. enflata and P. cultrifera had peak abundances in July in the Outfall Lagoon; 8) A. intermedia and Leptocarpus sp. had peak abundances in April and May; and 9) P. cultrifera and the L. chacei had peak abundances in November, January, and March in the Lower Piti Channel. Many of the above seasonal similarities between zooplankters were not necessarily significant seasonal variations.

SUMMARY

This two-year survey was conducted primarily to test whether or not significant seasonal variations in the abundances of zooplankton occurred in Apra Harbor. It was found that a significant increase in biomass and abundance of total zooplankton occurred in February and March. C. acicula, a gastropod, was most representative of this increase. S. enflata and crab zoeae were significantly more abundant in December and October. Zooplankton in other tropical Indo-Pacific areas also show a February-March increase in total standing stocks of zooplankton. The October-December increase in plankton was attributed to an increase in nutrients and consequent phytoplankton blooms caused by rainfall (terrestial runoff). No exogenous factor was correlated with the February-March increase in zooplankton; however, strong wind preceding the February-March peak may cause a mixing of organic sediments which may initiate this increase of zooplankton.

The mean abundances of zooplankton and biomass values were significantly greater during the second year in the Commercial Port and Lower Piti Channel. This annual increase was attributed to more concentrated and greater amounts of rainfall and more consistent wind direction the second year. The mean annual dry weight in other tropical Indo-Pacific areas has shown that the waters of this inner region of Apra Harbor had lower standing stocks of zooplankton than other tropical areas.

Endogenous factors may also affect seasonal patterns; reproduction may be initiated on a specific moon phase, relative to tides and the amount of moonlight. Several species have exhibited significant lunar variations in this study.

Diurnal variations in the abundances of _S. enflata_, the _Acartia_ sp., fish larvae, and shrimp mysis were attributed to predator avoidance and food availability.

Overall, the heterogeneity in temporal patterns of the abundance of zooplankters suggests that predictability of temporal variations depends upon the site as well as the individual zooplankters examined. No general pattern was found for all zooplankton at all sites. One must carefully define the areas examined. The general concepts of inshore or offshore do not adequately define areas because major differences in plankton communities are found on a much smaller scale.

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