Daily, Seasonal, and Annual Fluctuations Among Zooplankton Populations in an Unpolluted Tropical Embayment

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During 1973–74 biweekly collections of zooplankton in Jobos Bay, Puerto Rico revealed that major differences in the abundance and variety of several populations were related to water circulation, seasonal rainfall, and diel behavior. Total densities of zooplankton ranged from 225 to 9050/m^3 for night and 30 to 4700/m^3 for day samples. Abundance levels increased about twofold from coastal to isolated regions of the bay but at least twice as many species occurred in the coastal areas. Rapid, short-term changes in abundance, pulses of about one order of magnitude, occurred shortly before and during the wet season. Diel differences in density, most notable among the copepod, *Acartia tonsa*, coincided with a seasonal increase in abundance.

The size and composition of the zooplankton communities in Jobos Bay were similar to those found in one polluted, tropical embayment (Guayanilla Bay, Puerto Rico) but differed greatly from those described in another (Kingston Harbour, Jamaica).

Introduction

Studies of the size and composition of zooplankton communities from shallow, tropical marine bays are uncommon (Moore, 1967; Youngbluth, 1976; Grahame, 1976). Information about zooplankton around tropical islands is based primarily on research in open coastal and offshore oceanic environments. Reports on zooplankton from the Caribbean and adjacent subtropical regimes have been reviewed by Bjornberg (1971), Reeve (1964, 1970, 1975) and Moore & Sander (1976, 1977). Previous investigations around Puerto Rico have been restricted to the small bays and shelf regions along the southwestern coast of the island (Duran, 1957; Coker, & Gonzalez, 1960; Bowman & Gonzalez, 1961; Gonzalez & Bowman, 1965). In most of these studies major differences in standing stocks have been related to changes in water mass structure but seasonal shifts in density and diversity were not well documented principally because collections have been made at irregular or infrequent intervals and little attention has been given to replicating data or studying diel behavior. This paper describes daily, seasonal, and annual variations in the biomass, density, and variety of zooplankton in relation to meterological and hydrological conditions within 3 regions of Jobos Bay, Puerto Rico during a 2-year period.

Description of the environment studied

Jobos Bay is a small, shallow embayment, about 10 km long and 2 km wide, surrounded by mangrove swamps and sugar cane fields (Figure 1). A variety of benthic communities exist in the bay—turtlegrass, mangrove root, mud, and coral reef. Water depths range from 1–3 m throughout most of the bay and up to 8 m in a dredged ship channel. The movement of water in the bay is influenced primarily by wind and secondarily by tidal and geostrophic factors (Anonymous, 1972). During the day surface currents, propelled in a southwesterly direction by prevailing easterly trade winds, force coastal surface water through the fringing cayos and the Boca del Infierno (= area 4) and across the southern region of the bay.

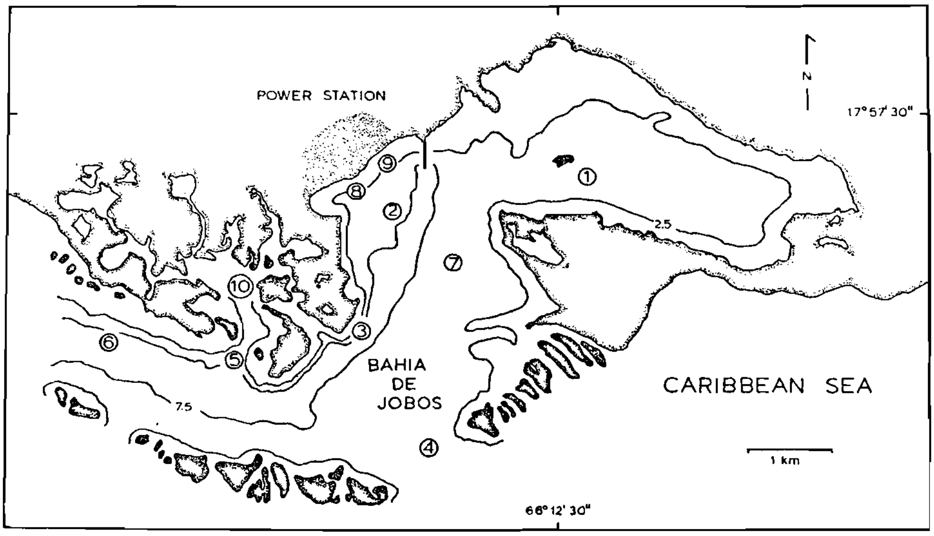

Figure 1. The regions where zooplankton were collected are designated by numbers. Depth contours are in m.

Slow bottom currents transport some coastal water into the bay from the west end of the navigation channel (= area 6). A shallow sill prevents major intrusions of subsurface water through other coastal passageways. Tides are diurnal and the mean tidal range is about 20 cm. The tidal prism was estimated to be $5{\cdot}4 \times 10^6 m^3$ (Wood, 1974) and the flushing time (Ketchum, 1954) about 3 weeks. Water temperatures in the bay are warm throughout the year, averaging 27 °C (Anonymous, 1972). Rainfall is usually highest from May through October (Anonymous, 1973, 1974). About 75% of the annual average of 115 cm falls during this period. Precipitation from year to year is variable, e.g. totals of 60 and 120 cm have been recorded in successive years. Typically, 40% or more of the rainfall in a given month occurs on one or two days. Drainage along the shoreline accounts for much of the freshwater input since no rivers empty into the bay.

During this study two 460 MW fossil fuel power facilities were under construction. In the second year of this investigation one of these plants operated sporadically, never at more than 30% of its capacity, and water temperatures near the outfall (= area 9) were only 1–3 °C above ambient during operations.

Materials and methods

Field procedures

Samples were gathered nearly every 2 weeks from 5–10 stations distributed among four regions within the bay (Figure 1). Station 1 was located within the Inner Bay where shallow waters are most isolated from intrusions of nearshore waters. Stations 2, 7, 8 and 9 were situated in the Central Bay, an area where waters from the Inner and Outer sectors of the bay mix. In the Outer Bay waters around Stations 3, 4, 5 and 6 are mixtures from the Central Bay and coastal sources. The Mangrove region, Station 10, is a relatively isolated area like, but much smaller than, the Inner Bay.

Zooplankton populations were collected with a bridled, 0·5 m diameter, cylinder-cone shaped, nylon net of 202 μm mesh. The net was designed to have a filtration ratio of 7·8 to 1 in order to maximize filtration efficiency and thereby reduce clogging error (Smith *et al.*, 1968). All tows were undulated in a circular path throughout the uppermost *ca.* 2·5–3 m at speeds ranging from 2–3 kts. All but the lowermost *ca.* 0·5–1 m of the water column was sampled.

The duration of each tow was 10 min unless severe clogging was apparent. Clogging was judged in two ways, i.e. when the net was covered with a brown layer consisting of diatoms or, when the quotient formed by dividing flowmeter revolutions inside and outside the net was less than 0·85. At these times the net was hauled for only 5 min. Samples were taken day (0700–1500 h) and night (2030–0130 h). One sample was routinely collected at each station. During the first year 3 consecutive tows were made during the day at 2 of the sites (Stations 2 and 5) to determine the range of variability to be expected between replicate tows.

After each tow, before the cod end was removed, the net was thoroughly washed with seawater. Every catch was preserved in buffered 4% seawater-formalin. The volume of water filtered was estimated with flowmeters fixed inside and outside the net. The filtered volume ranged from 120–160 m^3. Flowmeters were calibrated every 2 months.

Surface temperature and salinity were measured at each station. A rough approximation of water transparency was determined with a Secchi disk.

Laboratory procedures

Within 24 h after samples were collected the pH of the formalin solution was checked and adjusted, if necessary, to 7·6. If a sample contained a noticeable conglomerate of phytoplankton or detritus, the zooplankton portion was separated from this material by gentle filtration through 202-μm mesh netting. Before estimates of biomass or density were made, all organisms larger than 1 cm, usually hydrozoan medusae, were removed.

Biomass was estimated as wet volume (Ahlstrom & Thraikill, 1963). This method was employed because it can be performed quickly and does not damage the organisms. Measurements were reproducible but undoubtedly overestimated the true volumes by a small percentage since variable proportions of interstitial water and detritus were always present.

Densities were estimated by volumetric subsampling with replacement. The method, modified from Brinton (1962), consisted of diluting the catch in a known amount of seawater, pouring this volume back and forth between two graduated beakers, and, when the sample was judged to be well mixed, quickly decanting a small portion, usually about 25 or 50 ml, into one beaker. The procedure was repeated until the final aliquot contained 400–600 organisms. Usually only two splits were required. Three subsamples were counted from each sample. Copepods, often the most numerous organisms, were identified to species from these subsamples which contained 250–500 specimens in most instances.

Adult and late copepodite phases were lumped together in the tallies. Other organisms were recorded in broader taxonomic categories. Species within some of these groups were identified, e.g., larvaceans, chaetognaths, and barnacle nauplii.

Results

A total of 571 net tows was taken during the 2-year period. Of this number 188 hauls were made in 1973, mostly during the daylight hours. Night as well as day samples were collected at Station 2 for over a year (September 1973 to December 1974) and during the dry and wet seasons of 1974 at all other stations (May to December 1974). In all, 162 samples were obtained at night.

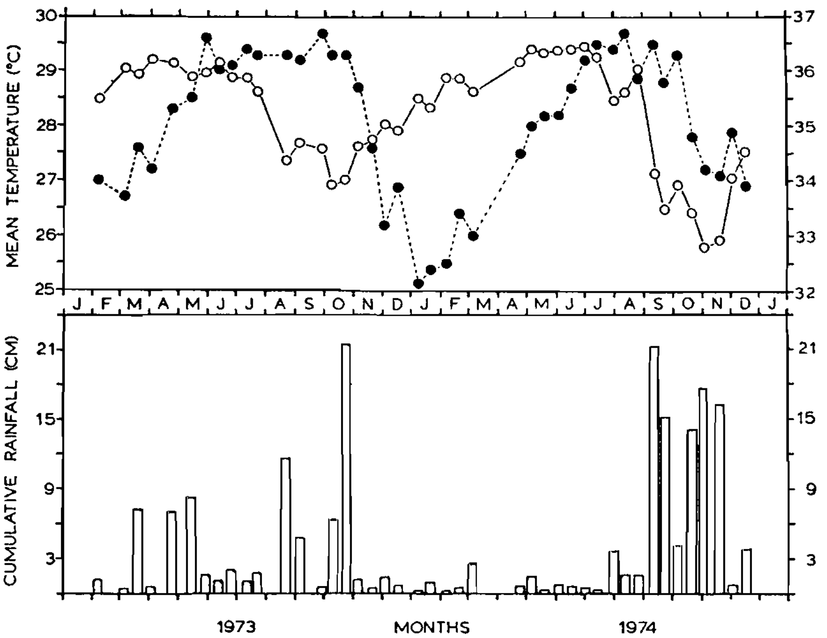

Figure 2. Mean surface temperature (●) and salinity (○) data for all stations. Rainfall data are expressed as the sum of all precipitation during a two-week period prior to each date of sampling.

Physical–chemical factors

Surface temperatures and salinities ranged from 25–30 °C and 30–37‰ (Figure 2). Temperatures plateaued each year from May to October, declined slowly from October until January or February, and then rose again toward a stable level reached in May. Salinity changes followed the seasonal cycles of rainfall. The total amounts of precipitation observed in 1973 and 1974 were similar, 97 and 110 cm, but the periods of heavy rainfall occurred at different times. In comparison with long-term records of seasonal rainfall 1973 was typical (Anonymous, 1972). The following year was drier from November through April and wetter during the period of May to October.

On the vertical scale, pronounced discontinuities of temperature or salinity were not often observed during the period of this study, i.e. differences between surface and bottom waters were usually less than 2 °C and 2‰ (Wood, 1974). Low salinity values measured in the surface waters persisted only a few days after a rain squall. Below the uppermost meter, salinities were rarely less than 32‰.

The attenuation of light varied regionally and seasonally within the bay. Judging from means of Secchi disc observations at each site, the transmission of visible light was shallowest (*ca.* 2·5 m) in the Inner Bay, somewhat deeper (*ca.* 3 m) in the Central area, and greatest (>3 m) in the Outer region. During periods of heavy rainfall and/or high wind velocity, water clarity was 1–2 m shallower than these mean values.

Phytoplankton and detritus were probably responsible for the observed variations in water turbidity. Although no measurements of phytoplankton production or diversity were made, a cursory examination of the algal populations responsible for the films that covered the nets after each tow revealed that several species of diatoms were preponderant, i.e. *Skeletonema costatum*, *Rhizosolenia fragilissima*, *Thalassionema nitzschiodes*, *Chaetoceros* spp. and *Nitzschia* spp. Filamentous blue-green forms were noted in high concentrations in some tows. Bits of turtlegrass, ash particles, and bottom sediments were common, particularly when tradewinds were strong.

Samples were collected during all tidal phases. No attempt was made to sample during consecutive tidal cycles. Fluctuations in the abundance of zooplankton were not correlated with ebb or flood tides (Stepwise multiple regression analysis). However, some groups more common in coastal waters, e.g., siphonophores, pteropods (*Creseis* spp.), sergestids (*Lucifer faxoni*), and salps, were observed in the Outer Bay more frequently in flood waters.

Sampling variability

The quantity of zooplankton collected by a net tow is an estimate. The reliability of this estimate is partly a function of the net gear and its use (Clutter & Anraku, 1968). The design of the net, the utilization of regularly calibrated flowmeters, the manner of towing the net, and the depth of each haul were defined in the *Methods* section to indicate how some field sampling errors were minimized.

Two other major factors that influence estimates of abundance are the spatial distribution (both horizontal and vertical) and avoidance behavior of zooplankton. In this study replicate samples were taken to determine a factor on which to judge differences between tows in the regions sampled or in regard to night versus day collections. The average ratio of the highest/lowest values among triplicated sets was 1·6 (median = 1·5, range = 1·1–2·7) in terms of total biomass or numbers ($n = 40$). These results suggested that most of the sample values will range within 2× of a single observed value. A more rigorous test using $\log_{10}$ transformed data has been applied to replicated data grouped into several categories (Table 1). These results indicate that mean values differing by 3× are significant in most cases ($P = 0{\cdot}05$, Steins two-stage test). Data from single tows are statistically different when values differ by 5×. When sample data from several sites within one region of the bay were pooled the variance was greater and factors of 3–5× represented significant differences.

The effects of avoidance behavior are unquantifiable in an absolute sense. Estimates of the magnitude of this factor are inconsistent for zooplankton (Clutter & Anraku, 1968). Most studies of field sampling errors have been concerned with defining the relative efficiency of gear and with demonstrating the effects of patchy distribution patterns (McGowan & Fraundorf, 1966; Wiebe & Holland, 1968). Experiments designed to examine avoidance of net gear by small zooplankton (*ca.* 0·7–5·5 mm) showed that no significant difference in density occurred between samples of copepods, e.g. *Acartia tonsa*, taken in full light or darkness (Fleminger & Clutter, 1965). Small mysids, on the other hand, were about 4× more abundant in samples collected in darkness. If these data represent the range of avoidance error for slow to fast swimming zooplankton, it seems appropriate to conclude that greater values for night/day differences are indicators of vertical migration. Furthermore, if avoidance behavior was an important source of error in this study a notably greater number

TABLE 1. The number of samples required to detect changes in the abundance of zooplankton grouped into several categories. The 30% and 50% levels are noted. Transformed ($\log_{10}$) data were used in each case

	Mean *n*-values of station replicates†		Mean *n*-values of pooled replicates‡			
	Day		Night		Day	
	30%	50%	30%	50%	30%	50%
Total biomass	2	1	3	1	4	1
Total number	2	1	4	1	4	1
Holoplankton	3	1	5	2	5	2
Copepods	3	1	5	2	5	2
Meroplankton	2	1	3	1	4	1
Cirripede nauplii	2	1	5	2	8	3
Reptantian larvae	3	1	5	2	7	3
Natantian larvae	6	2	5	2	4	1
Gastropod larvae	5	2	10	4	7	3

$n = t^2s^2/d^2$ where n is the number of samples required, t is Student's (t) for the 95% confidence level, s^2 is the sample variance based on replicate data, and d is the difference level desired (Steel & Torrie, 1960).

†Means based on sets of three consecutive tows at Stations 2 and 5 ($n = 40$, day sets).

‡Means based on sets of four tows, i.e. one tow at each of the four stations within the Central Bay and the Outer Bay. ($n=29$, night sets; $n=39$, day sets).

TABLE 2. The species of copepods observed in Jobos Bay, 1973–1974

Calanoida	Cyclopoida	Harpacticoida
*Undinula vulgaris**‡	*Oithona hebes*†*‡	*Metis holothuria*†*‡
Eucalanus sewelii‡	*Oithona nana*†*‡	*Longipedia helgolandica**‡
Eucalanus monachus‡	*Oithona oculata**‡	*Euterpina acutifrons*†*‡
Acrocalanus longicornis‡	*Oithona plumifera*†*‡	*Tisbe furcata*†*‡
Calocalanus pavo‡	*Oncaea mediterranea**‡	*Macrosetella gracilis*‡
Parvocalanus crassirostris†*‡	*Oncaea venusta**‡	
Paracalanus aculeatus†*‡	*Corycaeus agilis*‡	
Paracalanus parvus†*‡	*Corycaeus amazonicus*†*‡	
Clausocalanus furcatus†*‡	*Corycaeus giesbrechti*‡	
*Temora stylifera**‡	*Corycaeus pacificus*‡	
Temora turbinata†*‡	*Corycaeus speciosus*‡	
Centropages velificatus†*‡	*Corycaeus subulatus*†*‡	
*Pseudodiaptomus coker*i†*‡	*Farranula gracilis*†*‡	
Calanopia americana†*‡		
Labidocera aestiva†*‡		
*Labidocera scotti**‡		
Acartia lilljeborgii†*‡		
Acartia spinata†*‡		
Acartia tonsa†*‡		

†Stations 1, 10 (Inner Bay).
*Stations 2, 7, 8, 9 (Central Bay).
‡Stations 3, 4, 5, 6 (Outer Bay).

of samples should be required during the day than at night to define a significant difference at a given level, i.e. a larger vaiiance between samples would be expected. Differences for n-values among night and day pooled data shown in Table 1 are small. They range from 0–3 (30% level) to 0–1 (50% level). Thus densities of zooplankton which differ by at least 3×–5× probably represent reasonable values for judging the importance of abundance changes over spatial and temporal scales.

Variability introduced by subsampling and counting in the laboratory was about ±10% since the range of variation between replicate counts of each sample was always within the range expected for randomly selected aliquots (95% confidence interval, Poisson series).

TABLE 3. The copepod species which occurred in half or more of the samples at each site. Night and day considered unless otherwise noted

	Mangrove Region	Inner Bay	Central Bay				Outer Bay			
Copepod species	10	1	9	8	2	7	5	3	6	4
Acartia tonsa	×	×	×	×	×	×	×	×	×	×
Pseudodiaptomus cokeri	×	×	×	×	×	×	×	×	×	×
*Calanopia americana**	×	×	×	×	×	×	×	×	×	×
Paracalanus parvus	×	×	×	×	×	×	×	×	×	×
Acartia lilljeborgii	×	×	×	×	×	×	×	×		
Oithona nana	×		×	×	×	×	×	×	×	×
Temora turbinata			×	×	×	×	×	×	×	×
Euterpina acutifrons			×	×	×	×	×	×	×	×
Unidentified harpacticoids			×	×	×	×	×	×	×	×
Corycaeus amazonicus						×	×	×	×	×
Acartia spinata							×	×	×	×
Oithona plumifera							×†	×	×	×
Unidentified calanoid copepodites							×†	×	×	×
Corycaeus subulatus									×	×
Farranula gracilis									×	×
Paracalanus aculeatus									×	×
Oncaea spp.									×†	×
Undinula vulgaris										×
Labidocera spp.										×
Clausocalanus furcatus										×
Oithona oculata								×		
Total number of species	**6**	**5**	**9**	**9**	**9**	**10**	**13**	**14**	**16**	**19**

*Only present in samples collected at night.
†Only present in samples collected during the day.

Species composition, relative abundance and regional differences

Throughout most of the year copepod populations formed a major portion of the zooplankton within the bay. Thirty-seven species of copepods were identified (Table 3). Of this total 22 were observed in the Inner and Mangrove sections, 28 in the Central region, and all 37 in the Outer area. These regional differences in species composition weie also evident when their frequency of occurrence and numerical abundance were considered (Tables 4 and 5). *Acartia tonsa* was always the most abundant copepod in the Inner Bay and Mangrove region, averaging 76–93% of all populations. *Pseudodiaptomus cokeri* commonly formed the next most numerous species but rarely constituted more than 10% of the total copepod density. *Acartia tonsa* usually ranked first in the Central sector. In a small portion of these samples (35/184) *Acartia lilljeborgii, Paracalanus parvus, Temora turbinata, P. cokeri,* *Calanopia americana*, *Euterpina acutifrons*, or *Oithona nana* ranked among the five most abundant species forming 10–25% of the total. In the Outer Bay *A. tonsa* was less numerous, averaging 36% of all copepod species, and often ranked below *P. parvus* and *T. turbinata* which together constituted 15–60%.

Of the 6 chaetognath species present in Jobos Bay, only 2 were often collected, *Sagitta tenuis* and *S. hispida*. *Sagitta tenuis* was the most numerous population in the Inner and Central regions. *Sagitta enflata*, *S. serratodentata*, *Khronitta mutabbii*, and *Pterosagitta draco* were more frequently collected in the Outer Bay, less so in the Central Bay, and rarely in the Inner Bay. No consistent trend in their rank order was noted. *Oikopleura dioca* and *O. longicauda* were the most abundant larvaceans. Two other species, *O. parva* and *O. fusiformis* f. *cornutogastra*, were collected in the bay during a previous study (Suarez-Caabro & Shearls, 1972). Two mysids, *Siriella chierchiae* and *Mysidopsis* sp., and 2 genera of amphipods, *Brachyscelus* and *Erichthonius*, were also noted in zooplankton samples from this earlier survey.

TABLE 4. The average percent composition of those copepod species that formed the largest portion of all copepod populations among the top 90% in at least half the samples. Night and day values are separated as night/day

	Mangrove Region	Inner Bay	Central Bay				Outer Bay			
	10	1	9	8	2	7	5	3	6	4
Acartia tonsa	76/87	80/92	87/88	81/82	86/87	85/73	61/68	36/33	29/18	20/22
Pseudodiaptomus coькeri	11/0	10/0			5/0	7/0	10/0	10/6	6/10	7/9
Paracalanus parvus						0/6	4/7	18/21	20/28	26/21
Temora turbinata						0/5	0/7	6/11	13/13	10/10
Calanopia americana							6/0	7/0	7/0	7/0
Corycaeus amazonicus								0/6	6/7	5/6
Paracalanus aculeatus									0/2	0/6
Acartia spinata										7/4
Corycaeus subulatus										0/4
Clausocalanus furcatus										0/2
Total per cent	87/87	90/92	87/88	81/82	91/87	92/84	81/82	77/77	81/78	75/84
Total number of species	2/1	2/1	1/1	1/1	2/1	2/3	4/3	5/5	6/6	7/9

Hydromedusae (*Liriope tetraphyla*, *Eirene* spp.) ctenophores (*Mnemiopsis mccradyi* and *Beroe ovata*), a scyphomedusan (*Aurelia aurita*), and a cladoceran (*Evadne tergestina*) were observed. Some of these populations occasionally occurred in relatively dense swarms.

A large variety of merozooplankton was usually collected. Barnacle nauplii, primarily *Balanus amphitrite* and *B. eburneus*, generally constituted the majority of all invertebrate larvae. Although no attempt was made to quantitatively separate these species, benthic surveys indicated that adults of *B. amphitrite* were more numerous in the Mangrove area; adults of *B. eburneus* were the dominant barnacles in the Central and Outer regions (Yoshioka, 1975). Reptantian (= crab) and natantian (= shrimp) zoea as well as prosobranch veligers were common and at times quite numerous. The young stages of polychaetes, pelecypods, ectoprocts, echinoderms, isopods, sergestids, stomatopods, and ascidians appeared infrequently.

TABLE 5. A summary of the densities of several zooplankton categories observed during the two-year study. All numbers are standardized to a per m^3 basis

	Day stations									
	10 ($n = 15$)	1 ($n = 42$)	9 ($n = 28$)	8 ($n = 28$)	2 ($n = 41$)	7 ($n = 28$)	5 ($n = 43$)	3 ($n = 21$)	6 ($n = 43$)	4 ($n = 44$)
Total biomass										
mean	0·059	0·061	0·056	0·042	0·049	0·039	0·035	0·021	0·037	0·062
median	0·067	0·051	0·047	0·038	0·032	0·036	0·028	0·028	0·027	0·050
range	0·013–0·092	0·004–0·272	0·007–0·163	0·004–0·131	0·010–0·188	0·003–0·109	0·019–0·044	0·006–0·036	0·009–0·118	0·013–0·209
Total number										
mean	996	972	690	566	721	532	499	367	408	704
median	847	720	602	414	530	303	400	282	244	524
range	126–2589	105–4728	88–2021	120–1853	155–2942	49–1780	36–1917	29–1667	53–1990	47–3222
Holoplankton										
mean	470	475	353	290	417	327	253	180	262	487
median	259	274	310	188	247	187	195	79	120	356
range	96–1836	21–3480	28–1140	29–1249	18–2108	20–1357	20–1356	12–1315	20–1844	32–3222
Meroplankton										
mean	521	472	322	261	278	192	229	167	127	196
median	517	376	262	227	238	170	189	79	103	160
range	28–1684	49–1332	27–1087	36–853	33–886	15—438	36–550	18–1069	18–395	7–595
Copepods										
mean	452	433	335	266	383	307	238	169	230	446
median	255	256	320	186	234	114	187	61	100	326
range	88–1798	21–3365	25–1122	23–1143	14–2102	15–1275	20–1216	12–1278	25–1622	30–1096
Cirripede nauplii										
mean	187	206	245	183	188	105	100	27	26	32
median	149	192	152	123	168	107	90	24	16	12
range	20–517	20–707	12–1021	11–739	13–485	5–466	10–300	1–78	1–156	1–667
Fish eggs										
mean	3	15	10	10	21	10	12	10	11	12
median	1	6	4	5	15	7	8	6	8	9
range	1–11	1–65	1–95	1–98	0–158	1–34	1–58	1–29	1–56	1–41

TABLE 5.—cont.

	Night stations									
	10 ($n = 14$)	1 ($n = 28$)	9 ($n = 15$)	8 ($n = 15$)	2 ($n = 27$)	7 ($n = 17$)	5 ($n = 14$)	3 ($n = 15$)	6 ($n = 14$)	4 ($n = 14$)
Total biomass										
mean	0·188	0·196	0·145	0·119	0·119	0·184	0·081	0·102	0·083	0·131
median	0·181	0·192	0·114	0·084	0·102	0·187	0·084	0·083	0·079	0·097
range	0·119–0·314	0·079–0·421	0·055–0·353	0·044–0·324	0·027–0·397	0·041–0·466	0·044–0·107	0·056–0·185	0·041–0·185	0·038–0·366
Total number										
mean	2364	2850	1490	1384	1557	2490	923	978	1000	1082
median	1842	2346	1411	994	1142	1855	781	854	737	966
range	935–4168	446–9049	343–3743	393–3976	538–4255	367–6946	427–2769	226–2082	410–2891	225–2805
Holoplankton										
mean	1919	2552	1217	1118	1317	2100	691	694	678	679
median	1410	2217	1236	665	994	1674	510	572	534	630
range	538–3830	212–8291	266–3385	213–3607	248–4095	271–6478	311–2299	132–1719	161–2251	119–2139
Meroplankton										
mean	429	275	257	256	221	350	203	247	295	367
median	391	237	207	228	226	277	188	162	219	433
range	160–737	62–443	77–765	78–520	66–516	69–1099	103–433	83–514	68–1311	95–609
Copepods										
mean	1823	2467	1155	1067	1261	1995	610	598	544	584
median	1234	1887	1210	640	975	1488	428	522	399	537
range	518–4462	314–8144	217–3336	192–3530	242–4073	125–4541	266–1952	102–1559	129–1802	74–1984
Cirripede nauplii										
mean	189	99	133	133	133	122	42	31	18	21
median	186	87	116	117	94	96	32	13	14	12
range	70–516	27–208	32–333	29–190	14–407	21–336	10–101	1–156	1–63	1–101
Fish eggs										
mean	11	14	7	8	15	28	22	23	10	13
median	5	14	7	6	14	20	17	13	10	10
range	1–42	1–32	1–15	1–21	1–59	1–95	2–85	3–114	1–32	2–51

Fluctuations in standing stocks

Daily, seasonal, and annual differences in the standing stocks of zooplankton populations were observed. Wet volume biomass varied from 0·038–0·468 ml per m³ (night) to 0·003–0·272 ml per m³ (day). The density of all zooplankton ranged from 225–9050 per m³ (night) to 30–4700 per m³ (day). Similar statistics for other groups are listed in Table 5.

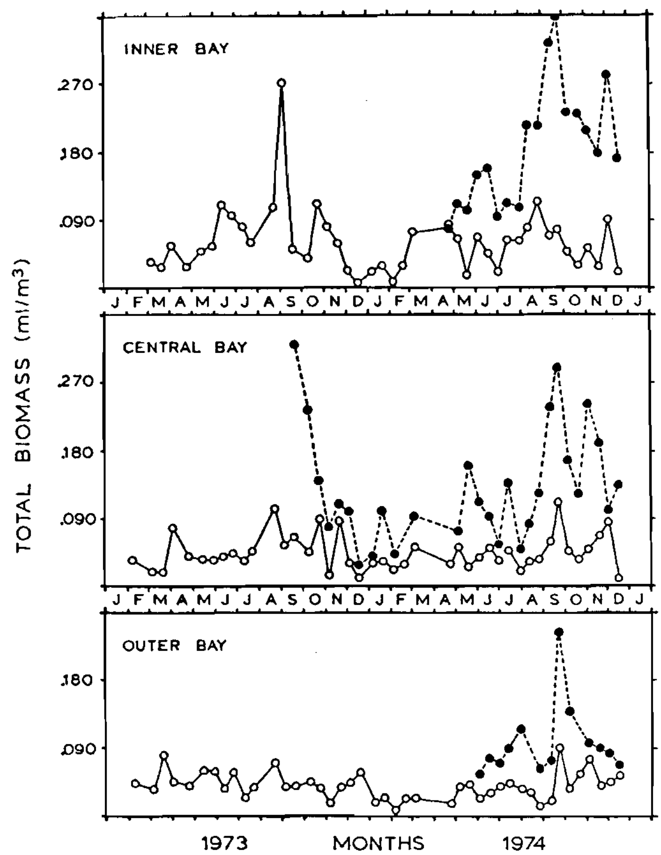

Figure 3. Night (●) and day (○) estimates of total biomass (ml/m³) for all zooplankton collected.

Night/day observations

The mean ratio of night/day densities of all zooplankton caught was 3·4× (median = 2·5×, range = 1–18×, $n = 162$). About 52% of these observations were larger than 3×, and based on statistically detectable limits between sets of samples, represent significant differences. Daily ratios of density pooled from those dates when all ten stations were sampled ($n = 14$ da) indicated that the average catch was usually at least 3× larger at night (12/14 da). A consistent relationship between these night/day ratios and the presence, absence, or phase of the moon, percent cloud cover, or tidal cycle was not apparent from regression analyses.

Copepods, commonly one of the most numerous organisms in day catches, were often an order of magnitude more abundant in night samples and invariably the dominant taxon

(Table 5). Adults and some copepodites (primarily stage V) of *A. tonsa* formed the bulk of this group. Two other species, *P. cokeri* and *C. americana*, were consistently 10–100 × more numerous in the evening collections.

Barnacle nauplii, usually the second most abundant organisms in a catch, were as numerous in day as in night samples.

Chaetognaths, larvaceans, isopods (*Excorollana* spp.), and fish larvae were often 10–100 × more numerous at night. In the periods when relatively abundant, prosobranch veligers were occasionally caught in larger numbers (5–10 ×) at night. Decapod larvae, principally reptantian and natantian zoea and mysis phases, exhibited different diel patterns of abundance. At most stations reptantian larvae were equally numerous during the day and night periods. However, when crab larvae were seasonally abundant consistently greater densities (2–27 ×) occurred in the daytime collections. Natantian larvae tended to be more abundant (2–4 ×) at night throughout the year in the Inner and Central regions. In the Outer Bay more shrimp larvae (2–50 ×) were usually caught at night. Although present in small densities (<10/m³), the juvenile stages of carideans, stomatopods, and polychaetes always occurred more frequently and generally in larger densities in the night collections.

Fish eggs were observed in low densities day and night (mostly <20/m³). Diel differences in the types of eggs present were noted. Eggs, oblong in shape, perhaps belonging to engraulid and gobiid species, were most often abundant during the day whereas large, spherical forms of unknown identity were more numerous at night.

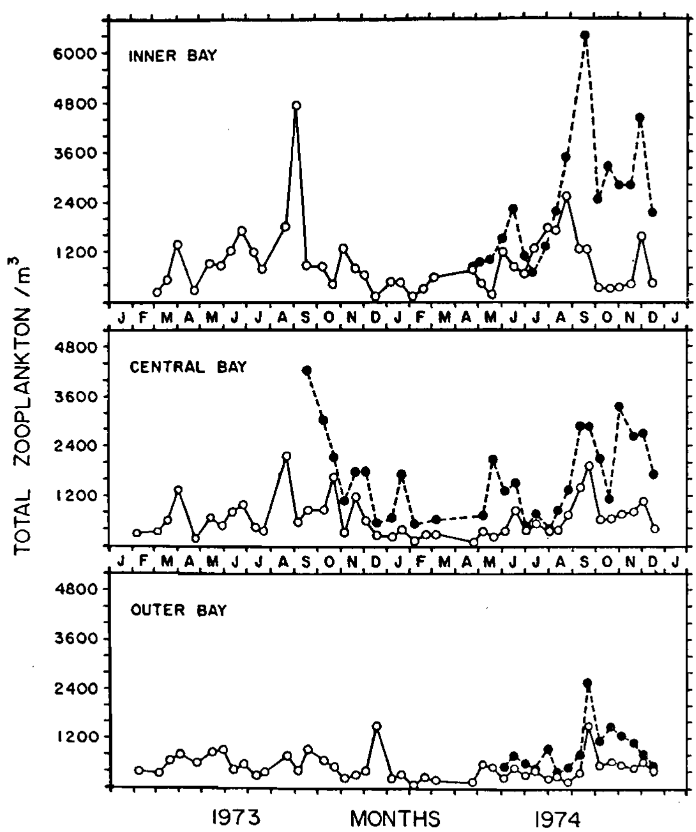

Figure 4. Night (●) and day (○) estimates of total zooplankton/m³.

Seasonal fluctuations and regional differences

The distribution, occurrence, and proportion of copepod species described in an earlier section indicated that zooplankton within this bay are probably segregated by circulation processes. The lowest number of species occurred in areas farthest from the regions where coastal waters, which harbored the greatest variety of populations, entered the bay. Stations in the Central Bay, situated between these locations, contained a mixture of species common to both regions. These observations and the fact that density levels within an area on a given day were usually quite similar provided justification for pooling data from isolated regions (Stations 1 and 10), the Central Bay, and the Outer Bay. Important differences between catches within these areas are noted when appropriate.

The largest changes in abundance appeared during the rainy season each year. Biomass values increased 2–3 × between biweekly sampling periods during this time in contrast to much smaller fluctuations during the dry season (Figure 3). Shifts in total zooplankton densities were more pronounced with pulses as great as an order of magnitude (Figure 4). These seasonal pulses were best defined in the night samples and restricted primarily to the Inner and Central sectors of the bay. In the Outer Bay fluctuations in biomass and

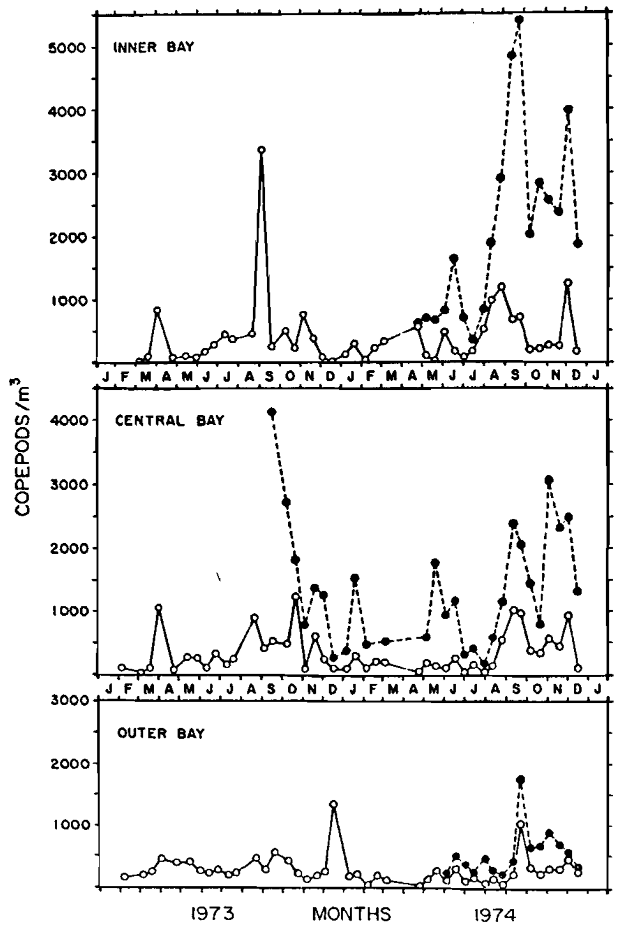

Figure 5. Night (●) and day (○) estimates of copepods/m³.

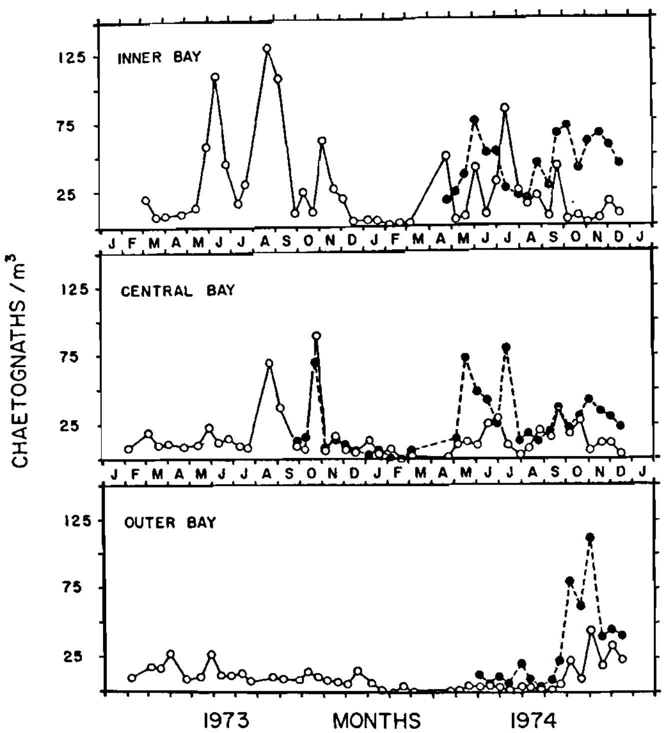

Figure 6. Night (●) and day (○) estimates of chaetognaths/m^3.

density were small throughout the year although a notable peak occurred in this area during September of the second year.

Copepod populations, particularly *A. tonsa*, formed 50–90% of the zooplankton community when the highest concentrations of zooplankton were recorded (Figure 5). Other holoplanktonic groups were also abundant when salinities were lowest. For example, cladocerans were only occasionally collected at one or two of the stations throughout the dry seasons. Densities were typically less than 2/m^3. During the wet season these animals were common at all stations, especially those in the isolated regions and the Central Bay. In late August of 1973 *E. tergestina* constituted 13 and 23%, 235 and 503/m^3, of the zooplankton caught in the Inner and Central Bays. Large concentrations of this species were not observed in the following year probably because high densities are present for only about a week.

Hydromedusae were noted throughout the bay, mainly from May through November. Large concentrations, as high as 22/m^3 (biomass = 0·397 ml/m^3), but more commonly 2–9/m^3 (biomass = 0·015–0·271 ml/m^3), appeared each year only in the Inner and Central sectors during a 3-month period extending from about 2 weeks before the end of the dry season until about 2 weeks before the end of the wet season. Very small concentrations, less than 1/100 m^3, were encountered during the remainder of the year.

Other coelenterates appeared in the wet season but only in the Outer, Mangrove, and Central areas. Densities of ctenophores, *M. mccradyi* and *B. ovata*, and the scyphozoan, *A. aurita*, were never greater than 5/100 m^3.

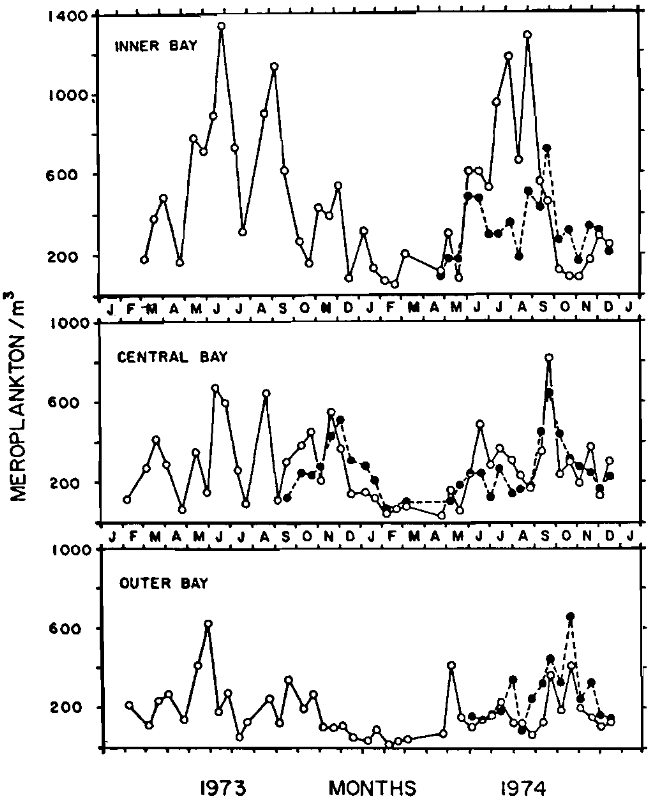

Figure 7. Night (●) and day (○) estimates of all meroplankton/m³.

Larvacean densities were typically low in all regions of the bay (mean = 23/m³, median = 10/m³, range = 1–400/m³). Peaks in abundance were infrequent and not sustained for more than 2 successive sampling periods. The largest concentrations occurred in late September and early October. These estimates of density, however, may not reflect the true abundances of this group. Preliminary comparisons of samples collected in consecutive tows with 64 and 202 μm mesh, 0·5-m diameter nets indicated that 100× to 1000× more larvaceans were present in the finer mesh catch (Owen, 1974).

Concentrations of chaetognaths were similar to those of larvaceans (mean = 23/m³, median = 18/m³, range = 1–238/m³). However, the periods when densities were highest did not always occur at the same time of year in each area (Figure 6). In 1973 three major pulses were noted in the Inner Bay, one in the dry season (late May and June) and two in the wet season (late August to early September and early November). Peaks in the Central Bay were observed only in the August–September period and in early October. Densities below the overall mean occurred throughout the year in the Outer Bay. In 1974 pulses were observed in May, June, and July in the isolated regions and the Central Bay and in all areas during the wetter months of September, October, and November.

Several organisms were responsible for major variations in the abundance of meroplanktonic fauna (Figure 7). The largest stocks, formed by barnacle nauplii and reptantian larvae, occurred in the Inner and Central Bays. Smaller densities, often 5–10× lower, were found in the Outer Bay. Natantian larvae were frequently the next most numerous

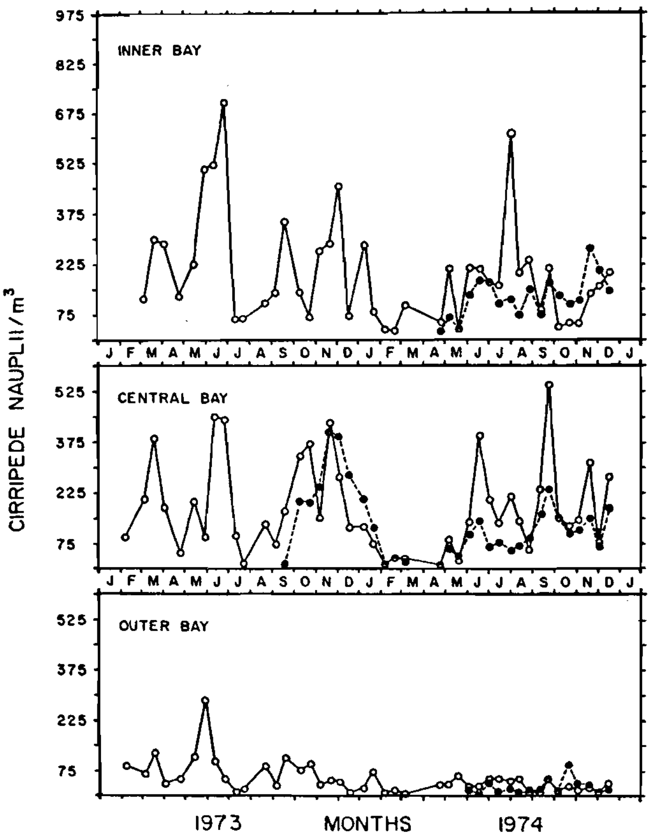

Figure 8. Night (●) and day (○) estimates of cirripede nauplii/m³.

taxon. Mean densities of shrimp larvae did not differ greatly between regions. In the Inner Bay and Mangrove region peak abundances of all three groups occurred during a 2-month period just prior to the onset of the rainy season (Figures 8–10). Large densities were also recorded during the first month of the wet season each year. Smaller pulses of barnacle nauplii and natantian larvae were noted at the end of the wet season. In the Central Bay barnacle nauplii and natantian larvae were less numerous. Concentrations of reptantian larvae were quite small. The largest densities of these groups, however, tended to co-occur with peak abundances observed in the Inner Bay. In the Outer Bay barnacle nauplii and reptantian larvae were not abundant and, except for a single peak in late May of 1973, changes in their densities were not pronounced. Shrimp larvae peaked briefly in late June and September of 1973 but reached their highest concentrations from late July through November of 1974.

The larvae of gastropods and echinoderms were occasionally quite abundant. Prosobranch (mean = 30, median = 14, range = 1–516/m³) occurred throughout Jobos Bay but were usually most numerous in the Outer Bay. These estimates of abundance are quite conservative since many of these larvae readily pass through 202 μm mesh. Echinopluteus were also most numerous in the Outer Bay but only during late October. The largest densities occurred at Stations 5 and 3 where concentrations reached 191/m³ (1973) and 891/m³ (1974), respectively.

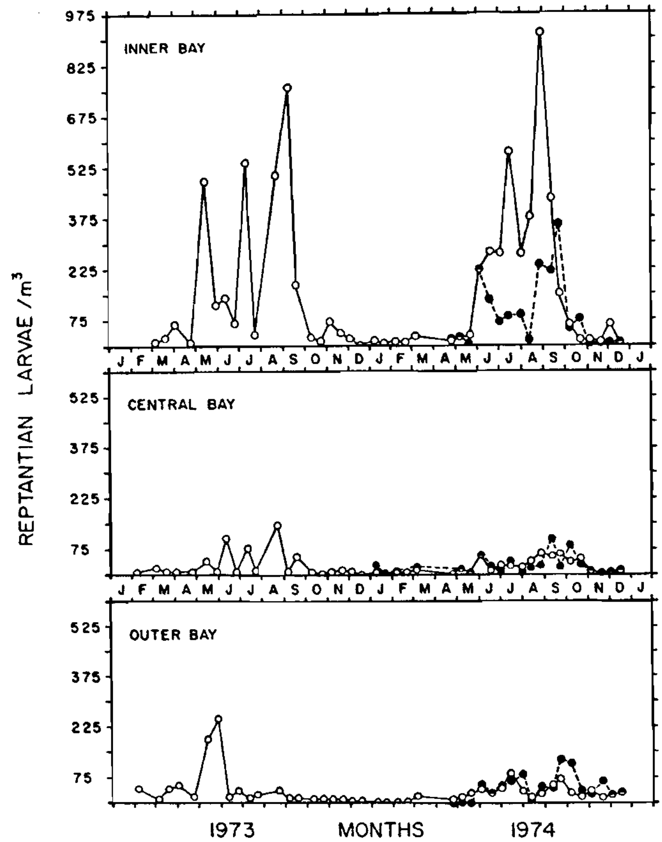

Figure 9. Night (●) and day (○) estimates of reptantian larvae/m³.

The foregoing descriptions of regional and seasonal variations in the standing stocks of zooplankton are based on diel collections. Sampling in either darkness or daylight would have underestimated the densities of some populations. A summary of these data, expressed as relative abundances of copepods and meroplankton, indicated that different proportions of zooplankton occupy the upper 3 m of the shallow water column (Figures 11 and 12). Copepods were clearly numerically dominant in the night samples from each region throughout the year. Furthermore, a greater percentage of copepods was caught in the Inner and Central regions. Meroplankton, however, were proportionately most numerous in the Outer Bay. The larvae of benthic invertebrates developed larger populations during the two months prior to the rainy period in the Inner and Central regions. Within the Outer Bay fluctuations of this group occurred every few weeks. In the day collections similar regional and seasonal patterns were noted but the relative abundance of these groups were quite different and indicate that descriptions of community structure based on percentage data can be misleading if diel sampling is not conducted.

Discussion

Major changes in the biomass, density, and variety of zooplankton within Jobos Bay occurred on diel, regional, and seasonal scales. The diel data suggest that vertical migrations, either

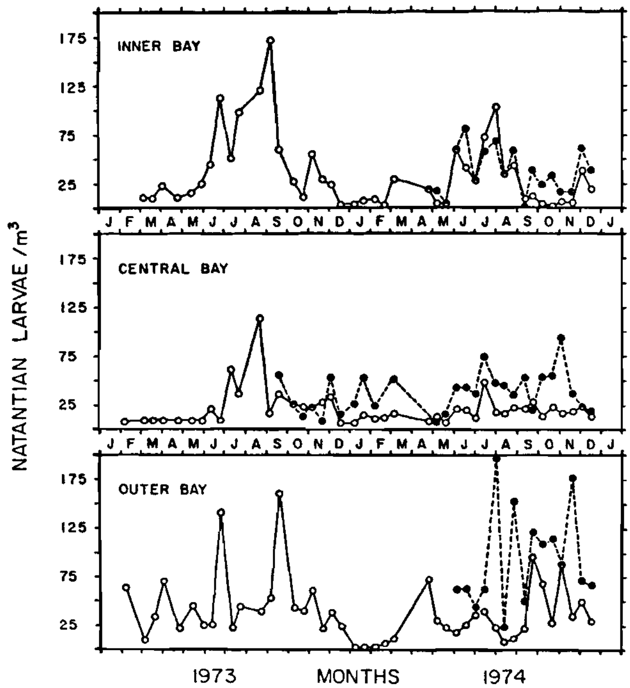

Figure 10. Night (●) and day (○) estimates of natantian larvae/m^3.

upward or downward, may occur at night and that the densities of some populations can be seriously underestimated if based solely on daytime or nighttime sampling. For example, the largest diel differences were noted during periods when the seasonal peaks of different groups were observed. At these times copepods, chaetognaths, and natantian larvae tended to be more numerous in the night samples whereas reptantian larvae, and on some occasions cirripede nauplii, were more abundant among the day collections. Similar diel shifts in density and also changes in vertical depth distributions of zooplankton have been noted in other bays (Herman & Beers, 1969; Reeve & Cosper, 1973; Trinast, 1975; Stickney & Knowles, 1975; Landry, 1978). All of these studies, however, are based on sampling conducted for only a few days and do not emphasize what appears to be a seasonal change in diel behavior which could be related to a major shift in the food consumed. Investigations in other shallow water regions suggest that several zooplankton populations are epibenthic or demersal during the day (Emery, 1968; Alldredge & King, 1977; Sameoto, 1978). Future research on zooplankton in shallow bays should design sampling programs that consider the importance of diel behavior and habitat preference to obtain better estimates of density, to determine if there are migrating and non-migrating members within the same population, and to learn the adaptive importance of this vertical positioning.

Seasonal fluctuations in the abundance of zooplankton observed in this study were determined from biweekly collections. Weekly or shorter intervals would have revealed more information about the coupling of environmental events and population growth. Biweekly collections, however, sufficed to demonstrate that major changes in density and community structure occur annually. The magnitude and duration of these seasonal pulses in density were most pronounced in the Inner and Central regions. Each year about 2 weeks after the first major rainfall population growth by copepods, primarily *A. tonsa*, was relatively rapid and during the next two months the concentrations recorded were usually several times larger than those noted in the dry season. This relationship between rainfall and subsequent development of *A. tonsa* has been observed in other tropical and subtropical bays (Woodmansee, 1958; Reeve, 1964; Youngbluth, 1976; Grahame, 1976). It is probable that this factor also acted to pulse nutrient concentrations which in turn initiated the development of phytoplankton stocks. Reduced salinities or some factor(s) related to heavy rainfall appeared to trigger spawning in echinoderms and to promote the development of cladocerans. Other zooplankton groups, e.g. cirripede nauplii, decapod larvae, hydromedusae, and chaetognaths, were numerous during the wet season but they also appeared

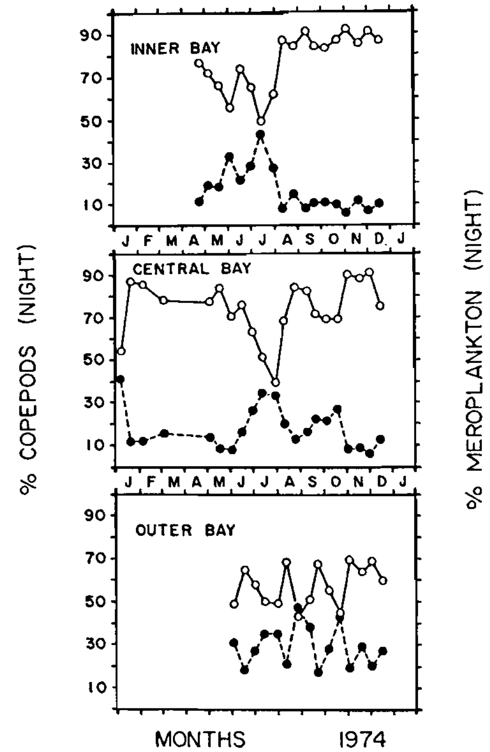

Figure 11. The relative abundance of copepods (O) and all meroplankton (●) in night collections.

in high densities as much as two months before the rainy period. The factors responsible for initiating the development of these groups are unknown. Variations in wind, tidal, and lunar conditions were not correlated with the abundance of these zooplankton. More frequent sampling, examination of food preferences among numerically important populations, identification of meroplankton to species, and a study of breeding cycles among benthic invertebrates would provide a basis for interpreting the dynamics of seasonal growth patterns.

Surveys of zooplankton in other enclosed or semi-enclosed bays of the Caribbean region have reported communities which are similar in species composition to those found in Jobos Bay (Coker & Gonzalez, 1960; Reeve, 1964, 1970; Youngbluth, 1976). The most comparable data, with regard to collection procedures, counting techniques, and data presentation, were gathered in Guayanilla Bay, Puerto Rico, a chemically and thermally polluted embayment (Youngbluth, 1976). The mean density of most of the major zooplankton groups (Table 6) as well as the variety and abundance of copepod species closely resembled the stocks in Jobos Bay. The much smaller average density of reptantian larvae found throughout Guayanilla Bay, however, suggests that pollution levels may restrict the development of these decapod populations.

In contrast, the densities of zooplankton noted in Kingston Harbour, Jamaica were an order of magnitude larger [mean = $16261/m^3$ (Moore, 1967) and $9842/m^3$ (Grahame, 1976)] than abundance levels recorded in Puerto Rican bays and the species structure was different.

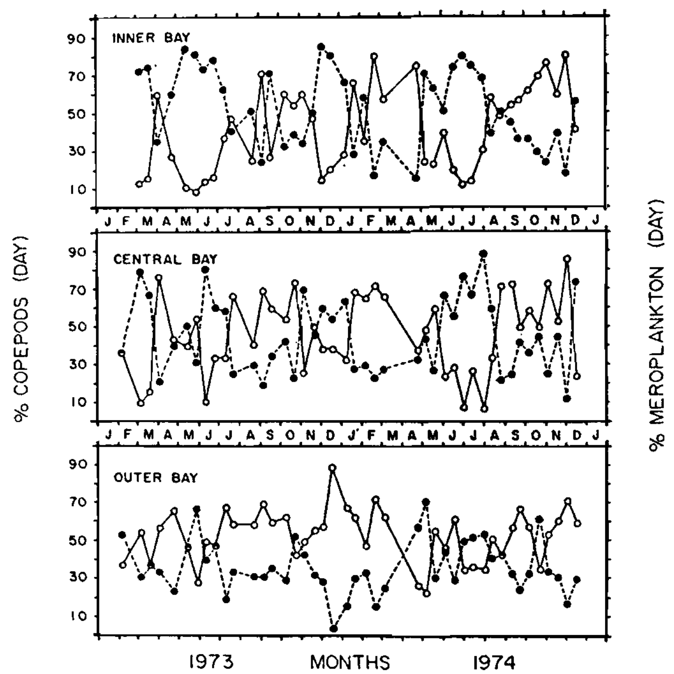

Figure 12. The relative abundance of copepods (○) and all meroplankton (●) in day collections.

Whereas, one or two copepod species (*A. tonsa* and *P. crassirostris* or *Oithona* spp.) ranked as the most dominant holoplankton in the enclosed bays of Puerto Rico, three to four populations constituted the majority in Kingston Harbour. Among these groups were *A. tonsa*, *Paracalanus* spp., *Corycaeus* spp., and *Eucalanus* sp. [*E. subcrassus* Giesbrecht auct.]. Most of these species are more commonly found in open coastal waters. In addition, a cladoceran, *Penilia avirostris*, not seen in the Puerto Rican bays, averaged from 11 to 62% of all zooplankton. The numerically dominant chaetognath in the Puerto Rican bays was *S. tenuis*. This species was not observed in Kingston Harbour and *S. enflata* was reported as the most numerous population. Meroplankton occurred in very small densities (mean $<40/m^3$). These low concentrations are not surprising judging from the large loads of organic pollution discharged into the Harbour, the presence of an extensive epibenthic

TABLE 6. A comparison of mean abundances of zooplankton groups/m^3 in Jobos Bay and Guayanilla Bay, Puerto Rico. Data based on daylight collections made from April 1973 to April 1974

	Jobos Bay (n = 69) Stations				Guayanilla Bay (n = 70) Stations			
	Inner Bay (1)	Central Bay (2)	Entrance to Bay (4)	Mean	Inner Bay (1)	Thermal Cove (2)	Entrance to Bay (3)	Mean
Total biomass (ml)	0·077	0·044	0·068	0·063	0·059	0·050	0·106	0·072
Total zooplankton	1009	712	736	819	900	490	1268	886
							(1180)	(860)
Holoplankton	482	405	565	484	464	260	883	536
Meroplankton	468	285	177	310	422	228	388*	346
							(302)	(317)
Copepods	433	364	529	442	427	257	729	471
Cirripede nauplii	220	189	47	152	332	192	235*	253
							(143)	(222)
Reptantian larvae	137	28	32	66	19	10	12	14
Natantian larvae	42	25	56	41	25	6	69	33
Gastropod veligers	13	9	29	17	8	4	31	22

*Mean number in parentheses based on all data minus one unusually large catch of barnacle nauplii.

abiotic zone in the upper basin, and the abundance of tubiculous polychaetes known to thrive in disturbed benthic environments (Wade *et al.*, 1972). These data suggest that pollutants may drastically alter the size and composition of a tropical zooplankton community but the interaction of those factors (physical, chemical, and biological) that are responsible for these differences remains undefined.

In conclusion, the zooplankton assemblages observed in Jobos Bay are probably characteristic of tropical embayment waters and are similar to subtropical zooplankton communities. The lack of wide fluctuations in temperature and salinity throughout the year, the consistency of prevailing trade winds, and the small tidal prism certainly must act to stabilize the zooplankton community but the events which underlie the relatively brief seasonal growth of some populations, e.g., copepods, cladocerans, hydromedusae, and decapod larvae, require further study. Differences in community structure and standing stocks must also be governed by predator–prey interactions. More detailed information about the size and turnover of phytoplankton and microzooplankton stocks would clarify causal relationships for production cycles, especially where water quality differs.

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