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Standing Stocks of Zooplankton Size-Classes and Trophic Levels in Kaneohe Bay, Oahu, Hawaiian Islands[1]

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ABSTRACT: Data are presented for the estimated standing stocks of nanozooplankton, microzooplankton, and macrozooplankton in the southern sector of Kaneohe Bay. Analyses of variability in the estimates due to sampling errors and spatial-temporal variations and the annual average values are also given. There is evidence that a shift has occurred in the past decade in the size-composition of the macro- and microzooplankton; during this time the total amount of zooplankton particulate nitrogen has remained nearly unchanged. The same dominant species of macro- and microzooplankton still inhabit the bay. We speculate that the historical changes in the zooplankton of southern Kaneohe Bay are the result of selection for nanophytoplankton feeders with rapid rates of metabolic turnover. The size-composition and trophic structure of the southern Kaneohe Bay zooplankton and planktivorous nekton in the ecosystem are compared with available information from the northeastern Pacific Ocean. The major differences between these ecosystems are to be found in the ratio of macrozooplankton:microzooplankton, the predominant trophic level of zooplankton captured by 0.333-mm-mesh nylon nets, and the size of the common epipelagic planktivorous nekton.

COMPONENTS of the pelagic ecosystem of Kaneohe Bay, Oahu, Hawaiian Islands, have received considerable attention in the past decade; more recently, there have been attempts to understand and to model numerically the changes in the system caused by additions of municipal waste waters (Caperon, Cattell, and Krasnick 1971; Caperon 1975). The research has necessarily had a trophic-dynamic approach, with elemental nitrogen being used as the basis for studies of transformation and mineral cycling among various particulate and dissolved components in the planktonic ecosystem.

Some of the data essential to an understanding of this ecosystem and to the applicability of an ecosystem model and its parameters are accurate estimates of the standing stocks of zooplankton for each trophic level. Estimates of absolute abundance and, where possible, estimates of time-space variability were made for three operationally defined size classes of zooplankton: (1) macrozooplankton—retained by 0.333-mm-mesh gauze, (2) microzooplankton—retained by 0.035-mm-mesh but pass through a 0.333-mm-mesh gauze and (3) nanozooplankton—pass through 0.035-mm-mesh gauze. The raw microzooplankton and macrozooplankton abundance data were modified, as described below, to give standing-stock estimates for carnivores and herbivores. The nanozooplankton (mainly athecate ciliates and tintinnids) are considered generalized heterotrophs, since it is unclear whether they feed in nature upon ultraphytoplankters, bacteria, detritus, dissolved organic matter or some or all of these varying in proportions.

In order to process as many samples as possible, we took advantage of the fact that unsorted microzooplankton and macrozooplankton catches are generally fairly good estimates of herbivore and carnivore standing stocks, respectively. Microscopic examination of the macrozooplankton made it possible for us to correct for the presence of some herbivores

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and omnivores in this catch. Adding this correction to the microzooplankton and subtracting an amount proportional to the chlorophyll-*a* content to correct for the phytoplankton retained by the 0.035-mm mesh provided us with a good herbivore estimate from the microzooplankton total catch.

Previous work on the zooplankton of Kaneohe Bay has been summarized by Clutter (1973) and Peterson (1975); these and some subsequent unpublished work were the bases that allowed Caperon (1975) to make estimates of standing stocks for an ecosystem model.

The primary purpose of this work is to provide estimates of the annual average standing stocks of heterotrophic, herbivorous, and carnivorous zooplankton trophic levels; in obtaining these data, we also gathered information regarding seasonal distributions of the three size-classes of zooplankton and this also is given here.

METHODS

Standing-stock measurements of the three size-classes were made in Kaneohe Bay at irregular time intervals, mainly between October 1973 and November 1974. Most of the data referred to the southern sector of the bay (Figure 1), although some were from stations in the northern sector. The southern sector has the most restricted circulation in Kaneohe Bay, and it is currently receiving nutrient-rich water originating from municipal waste discharge and land runoff from the surrounding urbanized watershed.

Nanozooplankton

We used a deck-mounted pump and rubber garden hose to obtain integrated samples of the nanozooplankton of the entire water column (about 12 m) and used a water bottle or bucket to obtain samples of surface and discrete depths. The seawater for integrated samples was pumped into a 20-liter carboy where it was agitated and then passed through 0.035-mm-mesh nylon gauze; 125–950 ml samples of the filtrate were preserved in 1–2 percent Formalin-seawater solution. We used the inverted microscope at 150–300 × to count the animals in the filtrate. Subsamples of 10–100 ml were settled, and in all cases the entire chamber bottom was examined for all protozoans and copepod nauplii. In preliminary work it was determined that the 0.035-mm-mesh nylon gauze allowed most ciliate protozoans to pass through, the exception being the largest, rare forms such as *Favella*. Only the earliest naupliar stages of *Oithona* and *Acrocalanus* (body width of ca. 40 μ) occasionally passed through. Hence, the nanozooplankton included ciliate protozoans, both athecate and thecate forms, plus some of the earliest larval stages of *Oithona* and *Acrocalanus*.

Protozoan and naupliar stocks were calculated as number per cubic meter and mg nitrogen or mg carbon per cubic meter. The numerical estimates derive from straightforward calculations based on numbers of organisms counted per aliquot and the subsample volume. For each taxon enumerated, appropriate linear dimensions approximating geometric solid bodies were measured for 12–28 organisms per taxon, except for three infrequently encountered taxa in which only 4–6 organisms were measured. We converted the calculated bodily volume in cubic microns to particulate nitrogen, assuming that 10^3 μ^3 equal 1 ng wet weight and 0.08 ng C (Beers and Stewart 1970) and that the C:N ratio (hereinafter always a ratio by weight) of nanozooplankton is the same as that observed for macrozooplankters and microcopepods (Bartholomew 1973), viz, 4. Total standing stocks were calculated as sums of the products of the number of organisms per cubic meter and the particulate nitrogen (PN) or particulate carbon PC) per organism, totalled for all taxa.

Microzooplankton

The microzooplankton were sampled with a 0.035-mm-mesh net that contained a 0.333-mm-mesh net zippered inside it to remove macrozooplankton (Clutter 1973: figure 6.2); the 35-cm-diameter mouth of the net was fitted with a Tsurumi-Seiki-Kosakusho Company (TSK) flowmeter to enable us to calculate the volume filtered. The net was lowered to within 1 m of the bottom and was towed vertically to provide an integrated sample over the water column.

Each live catch was divided by Folsom splitter into several aliquots: one-half was preserved in 1–2 percent Formalin-seawater solution for

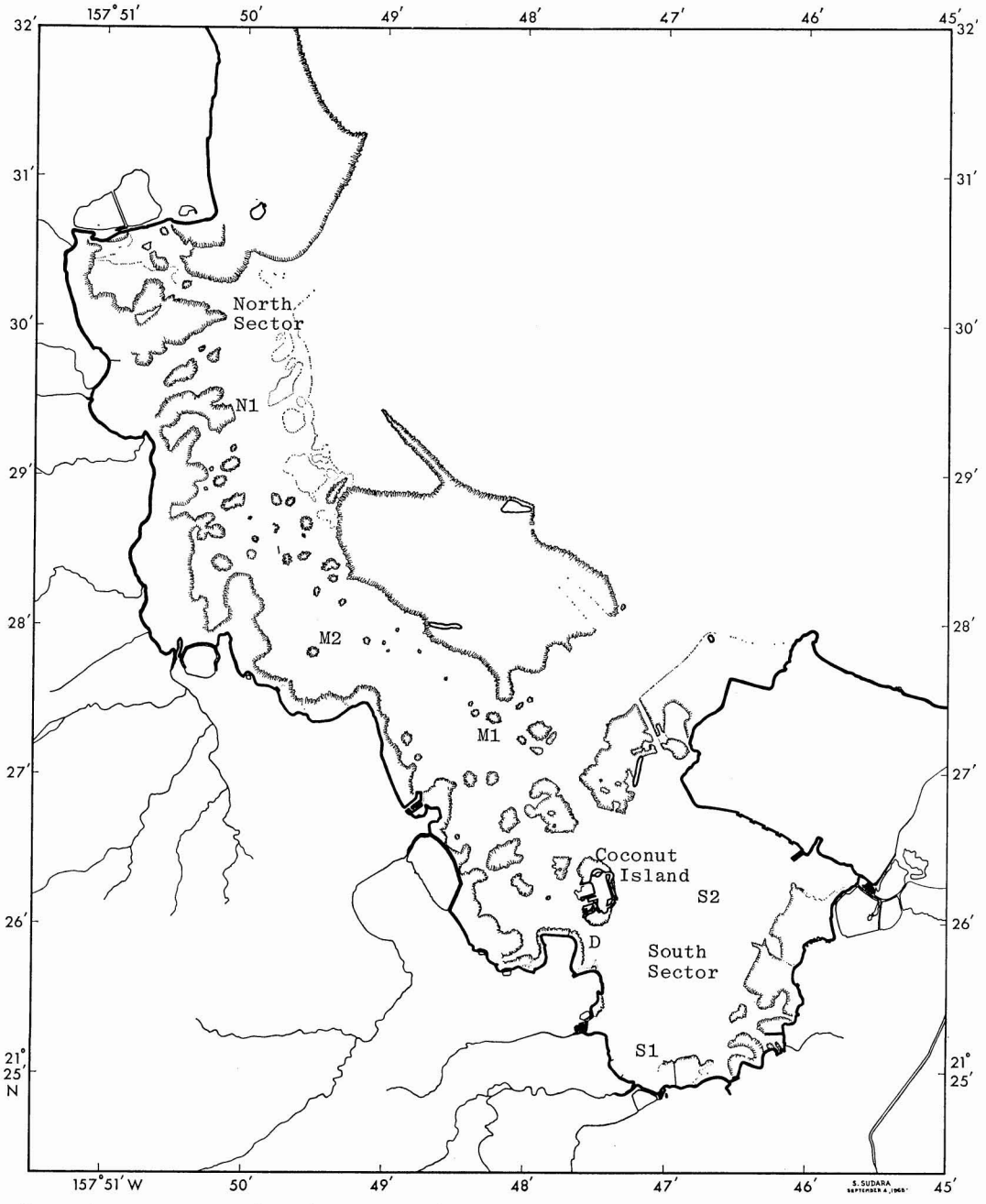

FIGURE 1. Kaneohe Bay and sampling stations. The southern sector of the bay is that portion of the bay east of Coconut Island. Five stations (S1 to N1) along the major axis of the bay were occupied for a transect survey; the diel studies were conducted at Stations D and S2; and the majority of samples for the seasonal studies were from S2.

faunistic reference, one-quarter was used for chlorophyll-*a* analysis, one-eighth was used for PC and PN analysis, and one-eighth was used for dry weight (DW) and ash-free dry weight (AFDW) determination. The chlorophyll-*a* was measured according to Strickland and Parsons

TABLE 1

POWER FUNCTION CURVE FITS FOR MICROZOOPLANKTON AND MACROZOOPLANKTON CATCHES, KANEOHE BAY, OAHU, HAWAIIAN ISLANDS

VARIABLES	MACROZOOPLANKTON	(N, r)	MICROZOOPLANKTON	(N, r)
PN versus DW	$PN = .067\ (DW)^{.998}$	(40, .98)	$PN = .292\ (DW)^{.671}$	(64, .62)
PC versus DW	$PC = .331\ (DW)^{.926}$	(40, .99)	$PC = .721\ (DW)^{.813}$	(64, .81)
PN versus AFDW			$PN = .037\ (AFDW)^{1.154}$	(38, .93)
PC versus AFDW			$PC = .336\ (AFDW)^{1.061}$	(38, .96)

NOTE: PN, particulate nitrogen; PC, particulate carbon; DW, dry weight; AFDW, ash-free dry weight; N, number of data pairs; r, correlation coefficient; all variables are in mg per m^3.

(1968) with the Parsons-Strickland trichromatic equations; however, no $MgCO_3$ was used, and the samples, which were collected on 47-mm, grade C, glass fiber filters, were placed immediately into 90-percent acetone in sample vials and then deep frozen. The one-eighth aliquots were concentrated onto 0.02-mm nylon mesh and finally collected onto tared, preweighed 21-mm, grade C, glass fiber filters. The aliquots on the filters were briefly rinsed with a few milliliters of distilled water to remove salts, and were dried at 60° C to constant weight (usually 36–48 hr at temperature). Ash-free dry weights were measured as the difference between dry weight and the ash remaining on the filter after the sample had been baked at 500° C for at least 4 hr. The other dried one-eighth aliquot was ground to a powder with a mortar and pestle before being analyzed for PN and PC in an F & M model 185 carbon-hydrogen-nitrogen (CHN) analyzer. Thus, the data on standing-stock obtained from the three sample aliquots represent total plant chlorophyll-*a*, AFDW, PN, and PC, all values being in mg/m^3.

To refine the estimated standing stock of herbivorous microzooplankton in the total catch, we made a correction for contribution to the total PN or PC by living phytoplankton plus degraded pigments (e.g., phytoplankton-associated detritus in fecal pellets of microcopepods). From the values of PN and PC an amount was subtracted equal to the value of trichromatic chlorophyll-*a* in mg/m^3 times the ratio by weight of PN:chlorophyll-*a* and PC:chlorophyll-*a*, which were taken as 11.5 and 54, respectively (Caperon, Harvey, and Steinhilper 1976), as conservative upper values.

In Kaneohe Bay over 75 percent of the chlorophyll-*a* passed through a 0.035-mm-mesh gauze (Harvey and Caperon 1976; Schell et al., unpublished data); thus most of the chlorophyll-*a* passed through the net that was used to sample microzooplankton, so that the PN and PC corrected for chlorophyll-*a* should give a good estimate of the microzooplankton stock corrected for contamination by algae and degraded pigments. This measurement will overestimate the true value of living herbivore stock by that amount of particulate detrital material that was not associated with chlorophyll-*a* or degraded pigments (e.g., crustacean moults) plus that amount of the stock which was in young stages of the carnivores that passed through 0.333-mm mesh (e.g., *Sagitta enflata* smaller than 4 mm, small ctenophores and hydroid medusae, and small eggs of all carnivores). The herbivore stock was underestimated by that proportion of the phytoplankton food in the stomachs of herbivores which would have been assimilated if the animals had survived, but which was being subtracted out by the total plant pigment correction. And finally, this measurement also underestimates the true herbivore stock by that amount of herbivores retained by the inner net of 0.333-mm mesh (e.g., barnacle and gastropod larvae, *Oikopleura*); however, a method and the procedures described below for the macrozooplankton were devised to correct for this underestimation of the herbivores in the 0.035–0.333-mm-mesh catch and overestimation of the carnivore stock in the catch by the 0.333-mm-mesh net.

After numerous PN, PC, DW, and AFDW direct measurements were made, power function curve fits were calculated for microzooplankton catches so that PN and PC could be

TABLE 2

RESULTS OF CARBON AND NITROGEN ANALYSES OF SELECTED MACROZOOPLANKTERS, KANEOHE BAY, OAHU, HAWAIIAN ISLANDS

TAXA	NUMBER OF OBSERVATIONS	μg CARBON (AVERAGE AND RANGE)	μg NITROGEN (AVERAGE AND RANGE)	CARBON:NITROGEN (AVERAGE AND RANGE)
Brachyuran Zoeae	5	8.22 6.28–8.43	2.05 1.45–2.11	4.02 3.94–4.34
Decapod Shrimp Larvae	4	5.14 4.99–5.60	1.62 1.58–1.69	3.17 3.08–3.31
Cirriped Nauplii	5	2.03 1.98–2.08	0.47 0.38– .48	4.53 4.28–5.37
Gastropod Larvae	2	4.36 4.08–4.64	0.85 0.81– .90	5.11 5.07–5.15
Oikopleura longicauda, 2.3 mm	1	4.19	1.26	3.32
Nehu (Anchovy) Egg	1	11.83	2.60	4.55
Lucifer chacei Protozoea, .8 mm	1	2.49	.56	4.42
Lucifer Schizopods, 2.8 mm	1	6.20	1.60	3.87
		REGRESSION EQUATIONS		
Lucifer chacei Juvenile–Adults (2.8–9 mm total length of body)		$\log_{10} C = -.32 + 2.54 \log_{10} L$ $\log_{10} N = -.94 + 2.53 \log_{10} L$		4.25
	$N = 15$, $r = .99$			
Lobate Ctenophore (1.7–9.5 mm polar diameter)		$\log_{10} C = .35 + 1.88 \log_{10} D$ $\log_{10} N = -.25 + 1.83 \log_{10} D$		4.29
	$N = 15$, $r = .99$			

NOTE: The carbon:nitrogen ratios are given by weight. Values given in the table are means with the range and number of observations per taxon. In the regression equations, carbon and nitrogen values are given in μg; lengths and ctenophore polar diameter are given in mm. N, number of observations; L, total body length; D, ctenophore polar diameter; r, correlation coefficient.

determined from AFDW or DW values without the necessity of performing lengthy CHN analyses (Table 1). Power functions were used instead of linear regressions because, at low concentrations of material, a linear regression overestimates the dependent variable (i.e., there is a positive y-intercept). The power functions are better fits to the data because of temporal changes in the plankton (e.g., depend on the relative contribution of ctenophores to the dry weight).

Macrozooplankton

The macrozooplankton were usually sampled in a 0.333-mm-mesh net of 0.5-m diameter simultaneously with microzooplankton but in the other side of the double-net frame (similar to a bongo net frame) that was used to tow the microzooplankton net described above. Occasionally the macrozooplankton were sampled with a separate ring net of 0.5-m diameter and 0.333-mm mesh. Calculations of filtration efficiency in which vertical distance towed and TSK flowmeter readings were used show that the 0.333-mm-mesh net sampled at 90 percent efficiency, the value used in calculating volume filtered by this net when direct flowmeter readings were not taken. These samples were also taken vertically from about 1 m above the bottom for integrated samples of the water column.

TABLE 3

ESTIMATES OF RELATIVE HERBIVOROUSNESS OF SELECTED ZOOPLANKTERS, KANEOHE BAY, OAHU, HAWAIIAN ISLANDS

TAXA	μg NITROGEN PER ANIMAL	NET FI (AVERAGE AND RANGE)	NUMBER OF OBSERVATIONS	MEAN FI RELATIVE TO *Sagitta*	TROPHIC ASSIGNMENT
Sagitta enflata	6.7	0.03 0–0.06	2	1	C
Brachyuran Zoeae	2.05	0.35 0.15– .55	4	12	O
Polychaete Larvae	1.26*	0.85	1	28	O
Female *Acrocalanus*	0.25	0.98 0.82–1.13	2	33	O†
Cirriped Nauplii	0.47	2.26 1.19–3.40	3	75	H
Oikopleura longicauda	1.26	3.02 2.15–3.71	3	100	H
Gastropod Larvae	0.85	7.81 4.85–10.9	3	260	H

NOTE: The mean and range of the net fluorescence index represent values at door factor 30 × with all samples having been extracted in 11 ml of 90-percent acetone. FI, fluorescence index; C, carnivority; O, omnivorousness; H, herbivorousness.

* The value for *Oikopleura* was used because of similar body volume.

† Omnivorousness indicated, but we believe that this value has been biased toward being lower than it should be; see text for explanation.

Each live catch of macrozooplankton was treated in a similar manner to that described above for the microzooplankton, except that no sample aliquot was taken for chlorophyll-*a* analysis and that the contents of the sample aliquots were preconcentrated with 0.183- or 0.202-mm-mesh nylon gauze before they were collected on glass filters.

The macrozooplankton catch was corrected for herbivores and refined for estimated carnivorous stocks in the following manner. From the uncorrected PN values an amount was subtracted which equals all herbivore PN plus 50 percent of all omnivore PN; this corrected PN value is the best estimate of that fraction of the macrozooplankton catch attributable to carnivorous species, that is, in lieu of data on the exact percentages of each omnivore's bodily PN which was sustained by plant versus animal food. The values of herbivore plus 50 percent omnivore PN as mg N/m^3 were obtained as the sum of the product of numbers per cubic meter in each taxon for herbivore and omnivore categories times bodily PN per animal. We made the counts using a dissecting microscope under 6 × –12 × magnification for aliquots of 1/32 to 1/2 of the original field sample, depending on the abundance. The values for PN and PC and for the C:N ratio were obtained by CHN analyses of selected macrozooplankters (Table 2). The technique by which taxa were determined to be herbivorous, omnivorous, or carnivorous is described below and is a modification of the methods used by Nemoto (1968).

Live animals were captured for those taxa that were expected to be omnivores and herbivores to various degrees, and the taxa were ordered or ranked by a fluorescence index relative to that of a known carnivorous chaetognath species, *Sagitta enflata*. The fluorescence readings were all standardized to door factor 30 × on a Turner model 111 fluorometer having a discrete sample cuvette and high sensitivity prism, and all samples were extracted in 11 ml of 90-percent acetone. Live specimens were collected from field samples, placed onto 0.202-mm-mesh nylon and examined under a dissecting microscope at 6 × –25 × for the degree of

stomach fullness or emptiness; only specimens with full or empty stomachs were used. The animals were counted and placed on 47-mm, grade C, glass fiber filters; the samples were placed into 90-percent acetone in vials and deep-frozen as though for standard plant pigment analysis by fluorescence. This net fluorescence index (FI) was calculated as:

$$\text{FI} = (F_f - F_e)/\mu\text{g PN/animal},$$

where F_f is the fluorescence per animal with full stomach and F_e is the value per animal with empty stomach, and this is standardized to a unit μg of bodily PN. Values of FI are shown in Table 3. For example, the fluorescence readings from animals with full stomachs are over 100 units for 25 *Oikopleura longicauda* or 25 gastropod larvae, 48 units for 30 barnacle nauplii, and 18 units for 60 female *Acrocalanus*. Values for animals with empty stomachs were found to be less than about 10 percent of the values found for animals with full stomachs.

It was decided arbitrarily that all FI values would be standardized to the value for *Sagitta* taken as unity, which would represent that relative fluorescence index for a carnivore. The high values for gastropod larvae, *Oikopleura*, and barnacle nauplii were assumed to represent herbivorousness; values for polychaete larvae, brachyuran zoeae and *Acrocalanus*, to represent omnivorousness (Table 3). Note that *Acrocalanus* females are smallest PN values, followed by cirriped nauplii. A potential bias in the FI may exist toward making small animals appear less herbivorous. This could occur because of the more rapid rates of food assimilated and because of food passage through the gut of small organisms, which may result in a larger bodily PN to be supported by a given volume of food in a full gut.

Ideally, the FI either should include a correction for rate of digestion of food or should be used on animals of nearly the same weight. *Acrocalanus* had bright green-gold gut contents when observed through a microscope, as did the other listed herbivores, and, for this reason, we suspect a bias for this organism in the FI. These crude classifications were extended for similar taxa in which no data were gathered (e.g., caridean decapod larvae were assumed to be omnivores like the zoeae) and were supplemented by literature data on known feeding habits of other taxa (e.g., adult *Lucifer chacei* can be carnivorous according to Zimmerman [1973]; and lobate ctenophores, hydroid medusae, fish larvae, fish eggs, etc., have all been classed as carnivores).

Power function regressions of data on PN and PC versus dry weight were developed from sets of field data gathered early in the study as for the microzooplankton (Table 1). On some sampling dates, estimates of the standing stock of *Sagitta enflata* alone were available from count data to assist us in completing seasonal coverage of the macrozooplankton and carnivorous stocks.

RESULTS

Nanozooplankton

The animals of the nanozooplankton are numerically abundant but constitute only a small absolute amount of particulate nitrogen and carbon per cubic meter. During the study, samples were taken to allow us to evaluate several sources of variability in nanozooplankton stocks: (1) replicate subsamples of original field samples, (2) replicate field samples, (3) diel and tidal cycle variability, (4) spatial variability over south–north transects of the entire bay, and (5) seasonal variability.

Variability due to subsampling field samples was about 10 percent for numbers of organisms (6–16 percent, $N = 4$ subsamples) and PN (3–30 percent, $N = 4$), when expressed as the range (w) divided by the mean (M) in percent ($100w/M$). The variability similarly expressed for replicate field samples is much greater, about 50 percent for numbers (35–67 percent, $N = 3$) and nitrogen (43–61 per cent, $N = 3$). The percent values differ between count data and converted nitrogen because of variation in the size-distribution of organisms in samples. The range divided by the mean of sample replicates in percent as a measure of precision can also be symbolized by the ratio of the maximum to minimum value of replicate observations. Values for $100w/M$ equal to 10, 40, and 67 percent correspond to maximum:minimum ratios of 1.105, 1.5, and 2 respectively. Although the number of pairs of observations is few, there is indicated the relative magnitude of these

TABLE 4

DIEL VARIATION IN ABUNDANCE OF NANOZOOPLANKTON, KANEOHE BAY, OAHU, HAWAIIAN ISLANDS, 27–28 NOVEMBER 1973

	27 NOVEMBER 1973				28 NOVEMBER 1973			
	1050 HOURS		2115 HOURS		0530 HOURS		1305 HOURS	
TAXA	NO. ORGANISMS PER LITER	ng NITROGEN PER LITER	NO. ORGANISMS PER LITER	ng NITROGEN PER LITER	NO. ORGANISMS PER LITER	ng NITROGEN PER LITER	NO. ORGANISMS PER LITER	ng NITROGEN PER LITER
Thecate Ciliates								
Tintinnopsis sp. 1	560	281.7	840	422.5	620	311.9	820	412.5
Tintinnopsis sp. 2	100	77.0	600	462.0	600	462.0	380	292.6
Eutintinnus sp.	280	21.3	380	28.9	220	16.7	200	15.2
Favella sp.	40	38.4	160	153.6	120	115.2	40	38.4
Codonella sp.	40	52.8	120	158.4	0	0	40	52.8
Thecate sp. G	0	0	0	0	140	38.5	200	55.0
Athecate Ciliates								
Species 1	640	90.2	300	42.3	300	42.3	200	28.2
Species 2	80	6.5	120	9.7	0	0	0	0
Species 3	200	9.6	240	11.5	420	20.2	160	7.7
Sarcodina	20	3.5	0	0	0	0	0	0
Copepod Nauplii	40	80	100	200	100	200	0	0
TOTALS	2000	661	2860	1490	2520	1200	2040	902

NOTE: Variability between subsamples of field samples was 36 percent for number of organisms per liter and 78 percent for ng nitrogen per liter, when expressed as the range (w) divided by the mean (M) in percent ($100\ w/M$).

sources of sampling and enumeration error in the stock estimates. For the stock estimates as PN the 95-percent confidence limits for a single observation (X) from an analysis of variance mean square error is $X/3.2$–$3.2X$.

Other sources of variation, which exceed those of subsampling and replicate field sampling, are diel variations and variations over mesoscale (i.e., km) horizontal transects. We studied these sources, using pump-integrated single samples of the entire water column at each station. The diel study was carried out in the channel between Coconut Island and the pier (station D, Figure 1), and the transect survey was taken at five stations ranging from near the municipal outfall to the northern sector of the bay (Figure 1).

Results from these two studies show that whereas diel variation (78-percent range: mean for PN, Table 4) was similar to that for replicate field sampling, the variability along the south–north transect was threefold greater (Table 5). The stocks decreased systematically from the eutrophic southern sector to the relatively oligotrophic northern sector by about one order of magnitude, a decrease well in excess of sampling errors or diel variability. Note that in both surveys the ciliate protozoans were the dominant nanozooplankters (except at station S-1 near the sewer outfall), and that most of the stock was contributed by the first three listed species of tintinnids and unidentified athecate species 1 and 3.

Data on seasonal variation in abundance of nanozooplankton are based on eight sampling dates in the southern sector of Kaneohe Bay. The results (Figure 2) indicate a sevenfold range in numbers and twenty-fivefold range in PN, approximately the same magnitude as observed on the transect survey from southern to northern sectors. Note that the data in Figure 2 are for protozoans only. In calculating average annual standing crops of nanozooplankton, we asssed the small copepod nauplii and protozoans separately; however, addition of naupliar abundance data would modify the numerical stock insignificantly and the PN only slightly, as indicated below.

Using the median standing stock as mg N/m^3 on a given date and applying it over one-half of

TABLE 5

Variation in Abundance of Nanozooplankton, Kaneohe Bay, Oahu, Hawaiian Islands, 21 May 1974

Taxa	Station S-1		Station S-2		Station M-1		Station M-2		Station N-1	
	no. organisms per liter	ng nitrogen per liter	no. organisms per liter	ng nitrogen per liter	no. organisms per liter	ng nitrogen per liter	no. organisms per liter	ng nitrogen per liter	no. organisms per liter	ng nitrogen per liter
Thecate Ciliates										
Tintinnopsis sp. 1	0	0	60	30.2	0	0	0	0	0	0
Tintinnopsis sp. 2	300	231.0	80	61.6	200	154.0	20	15.4	0	0
Eutintinnus sp.	100	7.6	0	0	100	7.6	80	6.1	60	4.6
Favella sp.	0	0	20	19.2	40	38.4	100	96	20	19.2
Codonella sp.	0	0	40	52.8	20	26.4	40	52.8	0	0
Thecate sp. G	0	0	0	0	0	0	0	0	0	0
Athecate Ciliates										
Species 1	1400	197.4	1400	197.4	480	67.7	460	64.9	40	5.6
Species 2	100	8.1	180	14.6	100	8.1	20	1.6	0	0
Species 3	700	33.6	440	21.1	140	6.7	340	16.3	200	9.6
Sarcodina	300	52.8	0	0	0	0	0	0	0	0
Copepod Nauplii	300	600	60	120	0	0	40	80	0	0
TOTAL	3200	1130	2280	517	1080	309	1100	333	320	39

Note: The five stations lay along a transect from the southern to the northern sectors of Kaneohe Bay. Variability between subsamples of field samples was 180 percent for number of organisms per liter and 234 percent for ng nitrogen per liter, when expressed as the range (w) divided by the mean (M) in percent ($100w/M$).

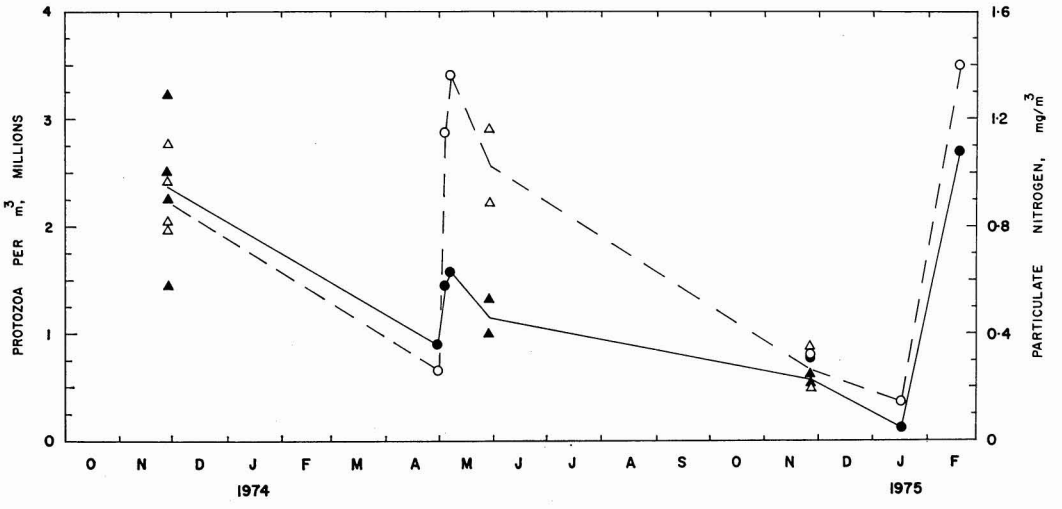

FIGURE 2. Seasonal variation of the standing stocks of protozoan nanozooplankton in numerical abundance and particulate nitrogen. Open circles, numbers in surface samples; open triangles, numbers in integrated pump samples; filled circles, particulate nitrogen of surface samples; filled triangles, particulate nitrogen of integrated pump samples.

the preceding and one-half of the following time interval, we found that linear integration over the time interval of the sampling dates gave us a value for average annual stock of 0.453 mg N/m³. The stock of protozoans plus small copepod nauplii was 0.565 mg N/m³, or about 25 percent greater. In spite of our very limited seasonal–spatial coverage of the standing stock of nanozooplankton, we believe that the seasonal variation in the southern sector was about equal to mesoscale spatial variations, and that these differences in abundance were about an order of magnitude greater than observed variations due to sampling errors or diel variations. Although the standing stock of nanozooplankton was small, about 0.5 mg N/m³, it must not be considered insignificant, for example, to the dynamics of mineral cycling rates, because of the high rates of turnover (Johannes 1964) of these small animals (the average-sized ciliate, such as athecate species, 1, contains only 0.14 ng N per individual).

Microzooplankton

Estimates of the standing stock of microzooplankton are subject to similar sources of error as for the nanozooplankton, with the additional sources of variability arising from our subsampling ground, powdered samples for CHN analyses and for total chlorophyll-*a* analysis. In our effort to describe the seasonal variation in and annual average value of the microzooplankton stock, we attempted to analyze sources of error in a nested or hierarchical classification analysis of variance (ANOVAR); (1) CHN analysis, (2) subsampling the original field sample by Folsom splitter, (3) replicate net tows, (4) stations and (5) sampling dates. In addition, special studies were carried out to evaluate: (1) diel variations, (2) spatial variation during a brief time period by synoptic areal survey sampling of the southern sector, and (3) by transect sampling from near the outfall in the southern sector up to the northern sector of the bay.

The results of the nested ANOVAR (Snedecor and Cochran 1967) show the expected general trend in the levels of variability (Table 6). The ANOVAR was performed on data transformed into logarithms and the interpretation has been adopted from Winsor and Clarke (1940). For net hauls, the value for 10^s, with s as the standard deviation obtained as the square root of the corrected mean square, is 1.169 and may also be interpreted as 16.9-percent logarithmic coefficient of variation. Comparison of this ANOVAR method with the percent range

TABLE 6

ANALYSIS OF VARIANCE TABLE FOR MICROZOOPLANKTON STANDING STOCKS AS PARTICULATE NITROGEN, KANEOHE BAY, OAHU, HAWAIIAN ISLANDS

SOURCE OF VARIATION	DEGREES OF FREEDOM	MEAN SQUARE	CORRECTED MEAN SQUARE	10^s
Dates	7	0.106	0.0245	1.434
	(23)	(0.3296)	(0.0825)	(1.937)
Stations	14	0.0416	0.0271	1.461
	(15)	(0.0408)	(0.0220)	(1.407)
Net Hauls	16	0.0046	0.0043	1.163
	(19)	(0.0073)	(0.0055)	(1.186)
Splitting	2	0.0002	0.0012	1.083
	(42)	(0.0016)	(0.0016)	(1.096)
CHN Analyses	16	0.0031	0.0031	1.137

NOTE: Numerals in parentheses represent values in dry weights in mg/m³. Numerals in the column 10^s represent measures of the variability attributable to each source of variation; s is the standard deviation obtained as the square root of the corrected mean square.

over the mean index gives similar results for PN, PC, and chlorophyll-*a* replicate haul data, in which the average indices were 14, 18 and 18 percent, respectively.

Diel variations were studied twice at fixed stations in the southern sector of the bay (Table 7). For the first study on 27–28 November 1973, the data revealed no systematic trend relating tidal height to standing stock. Note that the range of values over this tidal cycle is about threefold to fourfold, or about twice the average range for replicate samples. In the second study on 27–28 March 1974, again no systematic variation in stock was observed as a function of tidal height; in this case the replicate samples showed less variability, and the overall range of observed values is about one-half that of the previous study (Table 7). These two diel studies indicate that neither time of day nor tidal height will create systematic bias in the estimated stock of microzooplankton; further, the data indicate in the extreme cases that any single sample may deviate from the daily mean value by less than about one-half to two times its value. This would suggest that one can either average single samples at several stations and times of day within 1 day or occupy a few stations with replicate samples.

The next source of variation in microzooplankton stock examined was spatial variation over short periods of time (i.e., the scale of hours during a given time of tide). For this study, single samples were taken at 10 stations in the southern sector of the bay (Figure 3). The stations were sampled from 0930–1230 hours, 9 January 1974, on an ebb tide from +30 cm to 0 cm tidal height, the stations being visited in a random sequence. The stock of carbon and nitrogen showed surprising uniformity over the entire area, the extremes of the range differing by only about a factor of two (Table 8). This indicates relative homogeneity in the southern sector only on this one sampling study, although we believe that on nearly all tradewind days most of the southern sector is well mixed regarding average standing stocks of the entire water column. Note that this variability for the southern sector on 1 day over a 3-hour period was approximately equal to the variation at single stations through a full diel cycle.

A sampling transect on 21 May 1974 from 0930–1300 hours was made with five stations being occupied (Figure 1). The results are similar to the previously observed order-of-magnitude decrease, south to north, in nanozooplankton stock (Table 9).

The seasonal variation in PN for the total microzooplankton catch (i.e., uncorrected for removal of plant pigment-associated nitrogen and detritus) was relatively small. The median values of sampling dates fluctuate by about a factor of two around the value of 10 mg N/m³

TABLE 7

DIEL VARIATIONS IN MICROZOOPLANKTON PARTICULATE CARBON AND PARTICULATE NITROGEN, KANEOHE BAY, OAHU, HAWAIIAN ISLANDS

LOCATION	DATE	TIME OF DAY (HAWAIIAN STANDARD TIME)	TIDAL HEIGHT, MEAN LOWER LOW WATER (cm)	PARTICULATE CARBON mg/m³	PARTICULATE NITROGEN mg/m³
Station D—					
Channel between Coconut Island and Oahu Shore	27 Nov 1973	1200	9	30.0	7.77
				15.8	3.92
„	27 Nov 1973	1600	18	13.0	5.51
„	27 Nov 1973	2100	6	23.1	7.36
„	28 Nov 1973	0100	33	16.0	5.45
„	28 Nov 1973	0500	67	16.4	4.84
				30.8	7.25
„	28 Nov 1973	0900	30	25.6	5.73
				23.5	5.00
„	28 Nov 1973	1300	12	8.0	2.74
			Mean:	18.7	5.47
			Percent Range:Mean:	123	92
			Mean C:N Ratio	3.42	
Station S-2—					
Southern Sector of Bay	27 Mar 1974	1015	12	40.7	7.29
				38.2	7.03
„	27 Mar 1974	1433	0	41.2	7.46
				51.8	9.69
„	27 Mar 1974	1843	43	45.6	8.05
				39.5	6.91
„	27 Mar 1974	2135	55	63.4	11.61
				53.5	9.73
„	28 Mar 1974	0235	18	55.2	10.10
				43.7	8.41
„	28 Mar 1974	0615	18	57.3	11.18
				50.1	9.07
„	28 Mar 1974	1015	15	49.7	9.65
				42.2	8.31
„	28 Mar 1974	1525	3	57.7	8.92
				63.8	11.56
„	28 Mar 1974	1920	43	72.7	12.94
			Mean:	52.1	9.49
			Percent Range:Mean:	66	64
			Mean C:N Ratio:	5.49	

NOTE: Values for particulate carbon and particulate nitrogen have been corrected for plant pigment carbon and nitrogen (see text, "Methods"). Pairs of values are for replicate tows.

(Figure 4), while over the entire year the ratio of maximum:minimum is 6.7. When integrated over the sampling period as described above for the nanozooplankton, the average annual standing stock was 9.85 mg N/m³ when uncorrected for nitrogen in plant pigments and 8.1 mg N/m³ when corrected. Thus, the season-weighted average of plant-associated nitrogen of the total PN being retained in the net is 18 percent. Over the year, the range of values for plant-associated PN in the total catch was 1–60 percent, with the highest median values per

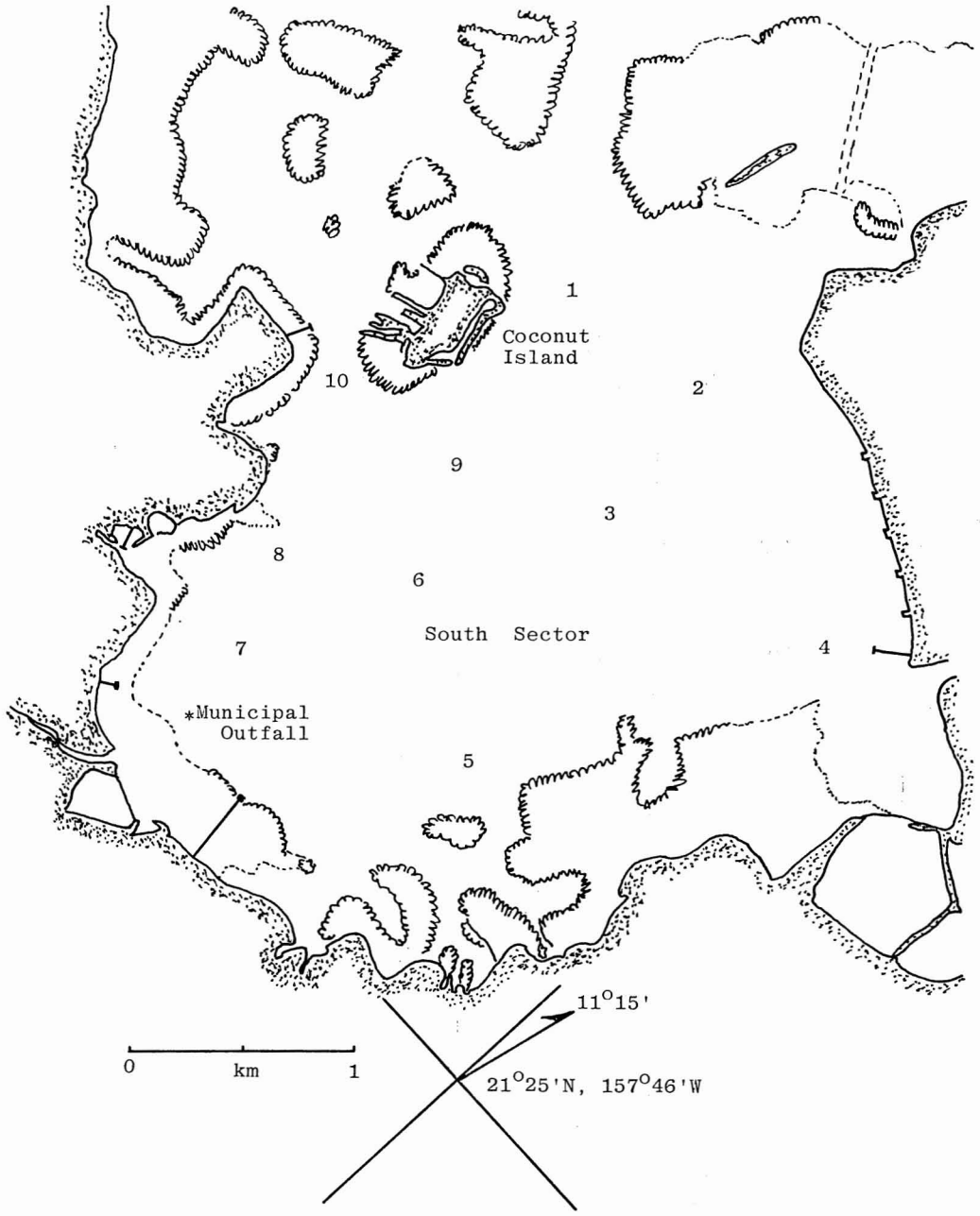

FIGURE 3. Ten station locations within the southern sector of Kaneohe Bay at which samples were taken on 9 January 1974 during a synoptic areal survey.

sampling date being 14–38 percent, and these were observed between 28 November 1973 and 21 May 1974. The corresponding estimates of the annual average stock of PC are 50.4 and 42.75 mg C/m³ for the uncorrected total catch and for the plant-corrected stock, respectively. The C:N ratio is 5.12 and 5.28 for total catch and plant corrected stock, respectively, about

TABLE 8

STANDING STOCKS OF MICROZOOPLANKTON IN SOUTHERN KANEOHE BAY, OAHU, HAWAIIAN ISLANDS, 9 JANUARY 1974

STATION SEQUENCE SAMPLED	ASH-FREE DRY WEIGHT mg/m³	PARTICULATE CARBON (mg/m³)	PARTICULATE NITROGEN (mg/m³)
5	141.8	55.2	10.30
3	133.9	49.8	8.34
6	120.7	68.3	11.46
1	165.3	72.8	11.04
7	151.0	62.1	11.15
10	159.0	70.0	13.60
9	171.6	81.1	14.00
2	196.4	71.4	11.64
8	199.0	81.7	16.90
4	185.4	98.2	14.09
Mean:	162.4	71.1	12.25
Percent Range:Mean:	48	60	70
Mean C:N Ratio:		5.80	

NOTE: Data for particulate carbon and particulate nitrogen have been corrected for living plants and detrital pigments captured in the net.

TABLE 9

STANDING STOCKS OF MICROZOOPLANKTON ALONG A TRANSECT FROM SOUTHERN TO NORTHERN KANEOHE BAY, OAHU, HAWAIIAN ISLANDS

STATION	ASH-FREE DRY WEIGHT mg/m³	PARTICULATE CARBON (mg/m³)	PARTICULATE NITROGEN (mg/m³)
S-1	647	112.8	20.58
S-2	202	73.0	14.62
	214	83.5	11.49
M-1	81.2	35.2	6.52
M-2	54.6	24.1	5.11
N-1	30.0	7.5	0.64
	30.2	9.2	1.15

NOTE: Transect ran from near the municipal sewer outfall in the southern portion of the bay to the northern portion. Values for particulate carbon and particulate nitrogen have been corrected for plant pigment contributions to the catch. Pairs of data represent replicate samples.

25 percent greater than the expected 4:1 ratio for *Acrocalanus* and some other zooplankters. Caperon, Harvey, and Steinhilper (1976) gave a C:N ratio of 7.3 for detritus from their study of the PC and PN passing through 102-μ-mesh gauze; Schell et al. (unpublished data) gave a C:N ratio of 10.2 as the difference between the living components (algae plus nanozooplankton plus microzooplankton) and total PC and PN. If 8.8 is taken as the C:N ratio for detritus, 4.0 for zooplankton, and 5.28 for microzooplankton plus detritus, then the amount of detrital PN in the plant-corrected catch will be 2.16 mg N/m³ (solve $4.0 = [42.75 - 8.8X]/[8.1 - X]$ for X) or 27 percent. The microzooplankton stock corrected for 27 percent nonplant detritus gave 5.9 mg N/m³ and 31.2 mg C/m³.

Only few count data were obtained for microzooplankton, except in special studies conducted for other purposes. However, in those samples and in the study of Bartholomew (1973), the overwhelming abundance of *Acrocalanus* sp.

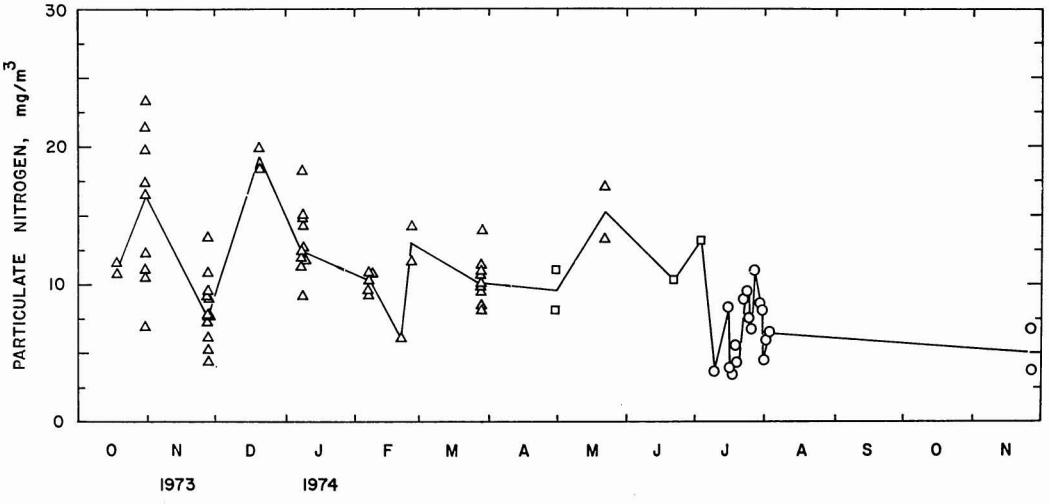

FIGURE 4. Seasonal distribution of the standing stock of microzooplankton for all stations and hauls within the southern sector of Kaneohe Bay as particulate nitrogen uncorrected for the presence of plant-pigment-associated nitrogen. Triangles, direct measurements of particulate nitrogen; squares, estimates of particulate nitrogen from ash-free dry weight regression; circles, estimates of particulate nitrogen from dry weight. The solid line connects the median stock estimate per sampling date.

TABLE 10

ANALYSIS OF VARIANCE TABLE FOR MACROZOOPLANKTON STANDING STOCKS AS PARTICULATE NITROGEN, KANEOHE BAY, OAHU, HAWAIIAN ISLANDS

SOURCE OF VARIATION	DEGREES OF FREEDOM	MEAN SQUARE	CORRECTED MEAN SQUARE	10^s
Dates	14	1.5457	0.4379	4.589
	(33)	(1.1887)	(0.4286)	(4.515)
Stations	10	0.0474	0.0376	1.563
	(17)	(0.0355)	(0.0318)	(1.508)
Net Hauls	13	0.0354	0.0316	1.506
	(16)	(0.0504)	(0.0475)	(1.655)
Splitting	(19)	(0.0083)	(0.0083)	(1.233)
CHN Analyses	12	0.0013	0.0013	1.087

NOTE: Numerals in parentheses represent values for dry weights in mg/m³. Numerals in the column 10^s represent measures of the variability attributable to each source of variation; s is the standard deviation obtained as the square root of the corrected mean square.

(Bartholomew identified it as *Paracalanus* sp. nov.) and *Oithona simplex* is evident. Other microcopepod species of lesser abundance were *Oithona nana*, *Euterpina acutifrons*, and a few species of unidentified harpacticoid copepods. There are sometimes considerable amounts of early stages of larger forms such as *Oikopleura longicauda* and barnacle, polychaete, gastropod, bivalve, and echinoderm larvae. Fortunately, these are mainly herbivores and should be included as part of the herbivorous microzooplankton stock. The numbers of such carnivores as ctenophores, hydromedusae, and chaetognaths were presumed to be small enough in the microzooplankton catch relative to the total catch to be disregarded.

Macrozooplankton

Magnitudes of variability in estimations of macrozooplankton standing stocks are in general similar to but greater than levels of variability in

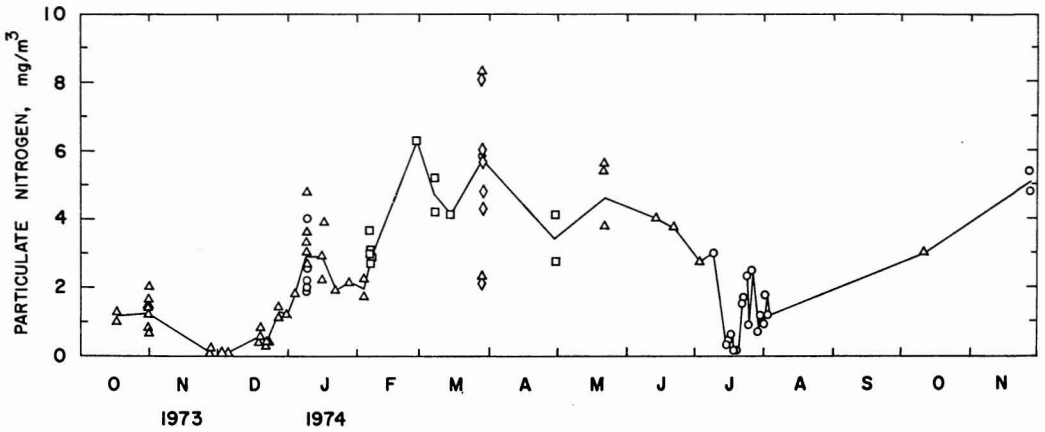

FIGURE 5. Seasonal distribution of the standing stock of macrozooplankton. Triangles, direct analyses of particulate nitrogen; circles, calculated particulate nitrogen from dry weight; diamonds, calculated particulate nitrogen with nitrogen/dry weight = 0.024 for ctenophore blooms; squares, particulate nitrogen for *Sagitta enflata* alone. The solid line connects the median stock estimate per sampling date.

the stocks of microzooplankton catches (Table 10 and cf. Table 6); it is most clearly evident that the variability among different sampling dates is much greater for macrozooplankton than for microzooplankton. The diel variability and station-to-station differences in catches of macrozooplankton within the southern sector of the bay were slightly greater than those for the microzooplankton stocks: a ratio of maximum:minimum values over a diel cycle of fourfold to sixfold for either carbon or nitrogen and a ratio of twofold to threefold for station locations. On the south–north sampling transect (21 May 1974), the macrozooplankton stock decreased by an order of magnitude, from 15 to 1 mg N/m^3 and 91 to 9 mg C/m^3. Thus, in each of the three size-classes of zooplankters it has been shown that within the southern sector of the bay over a diel cycle or over widely spaced stations sampled in a few hours (except in nanozooplankton data for which no southern sector spatial variability was examined), differences in abundance as measured by the ratio of maximum:minimum values in all sample data within a set were twofold to fourfold. Differences across the spatial gradient of the south to north sector of the bay are about an order of magnitude.

The seasonal variation in particulate nitrogen of the macrozooplankton catch (i.e., the values uncorrected for herbivore and part of the omnivore stocks) was large compared to nano- and microzooplankton (Figure 5). The median values per sampling date differ by over two orders of magnitude; the minima occurred in November–December 1973 and July 1974, whereas a broad maximum occurred in March–May with a pair of high values in November 1974.

The average annual stock of macrozooplankton was 2.86 mg N/m^3; the carnivorous stock is 2.53 mg N/m^3 when the stock of herbivores plus 50 percent of the omnivores is removed if one uses data on nitrogen/animal and faunistic enumeration. The enumeration data were obtained from 37 samples spread among eight sampling dates in November 1973 and January, March, May, July, August, and November 1974. The overall average percentage carnivorous stock to total catch of PN for these eight dates was 82 percent, with a range from 55–97 percent. The average annual stock of total particulate carbon was 12.32 mg C/m^3, uncorrected for herbivores and omnivores. The C:N ratio for the total catches was 4.3 (12.32:2.86), indicating insignificant detrital material in this size range.

The faunal composition of the macrozooplankton was dominated by *Sagitta enflata*; the other important carnivorous species included a lobate ctenophore, *Lucifer chacei* adults, hydroid medusae, larval fish and fish eggs, and infre-

TABLE 11

MEANS AND RANGES OF ABUNDANCE OF SELECTED MACROZOOPLANKTERS, SOUTHERN KANEOHE BAY, OAHU, HAWAIIAN ISLANDS

TAXA	28 NOVEMBER 1973 N = 10		9 JANUARY 1974 N = 10		28 MARCH 1974 N = 9		21 MAY 1974 N = 3		9 AND 26 JULY 1974 N = 2		2 AUGUST 1974 N = 1		26 NOVEMBER 1974 N = 2	
	MEAN	RANGE	MEAN	RANGE	MEAN	RANGE	MEAN	RANGE	MEAN	RANGE	MEAN	RANGE	MEAN	RANGE
Carnivores														
Sagitta enflata	9	3–13	812	470–1438	721	382–1137	1865	1119–2323	234	230–237	127		no data	
Lobate Ctenophores	0		0		160	83–243	0		20	18–23	30		no data	
Total Medusae	18	1–56	235	8–610	28	0–63	8	0–25	8	6–10	3		no data	
Omnivores														
Brachyuran Zoeae	6	0–12	79	43–158	10	0–37	61	46–79	14	6–23	0		5	0–11
Decapod Shrimp Larvae	10	2–19	4	0–16	3	0–13	31	14–46	7	6–8	0		8	3–14
Herbivores														
Cirriped Nauplii	31	5–53	850	140–2455	9	0–36	180	20–349	42	27–56	8		60	44–75
Gastropod Larvae	0		22	0–44	147	58–327	15	6–26	34	13–55	0		494	410–578
Oikopleura longicauda	6	1–16	20	8–33	115	4–256	254	186–370	8	0–16	3		402	243–560

NOTE: Means and ranges are given in numbers of animals per cubic metre. N = number of samples per date.

quently occurring crustaceans such as adult *Evadne tergestina* and *Labidocera* sp. The macro-omnivores were brachyuran zoeae, decapod shrimp larvae, polychaete larvae, and miscellaneous copepods such as *Acartia* and *Pseudodiaptomus*. The herbivores included both holoplanktonic and several meroplanktonic forms: *Oikopleura longicauda*, larvae and juveniles of *Lucifer chacei*, larvae of gastropods, cirripeds, bivalves, and echinoderms. For several of the sampling dates for which count data were obtained, means and ranges are given for several selected macrozooplankton taxa (Table 11). Note that, although the barnacle nauplii and gastropod larvae were sometimes numerically abundant, they were about tenfold smaller in bodily PN than was the average *Sagitta*. The main characteristic of changes in abundance of macrozooplankters for all taxa seems to have been large fluctuations in abundance, up to two orders of magnitude seasonally. For *Sagitta enflata*, the main abundant carnivore in the system, its maximum seasonal abundance was very high, 1000–2000 per m^3.

Following is a summary of the mean annual standing stocks of the three size-classes of zooplankton in the bay during our study and of our best single estimates of herbivore and carnivore stocks.

1. Nanozooplankton: 0.45 mg N/m^3 and 1.8 mg C/m^3 as protozoans and 0.56 mg N/m^3 and 2.2 mg C/m^3 as all taxa including copepod nauplii (calculated assuming nitrogen:unit volume = 0.02 and carbon:unit volume = 0.08).
2. Microzooplankton: 8.1 mg N/m^3 and 42.75 mg C/m^3 as catch corrected for chlorophyll-*a* and 5.9 mg N/m^3 and 31.2 mg C/m^3 corrected for nonplant detritus; comprises principally four species of microcopepods and young stages of macrozooplankton.
3. Macrozooplankton: 2.86 mg N/m^3 and 12.3 mg C/m^3 as total catches including all taxa.
4. Carnivorous stock: 2.53 mg N/m^3 and 10.9 mg C/m^3; the C:N ratio of 4.3 has been used.
5. Herbivorous stock: 6.2 mg N/m^3 (73 percent of the 8.1 mg N/m^3 micro-+0.3 mg N/m^3 macrozooplankton stock) and 32.5 mg C /m^3 (31.2+1.3 mg C/m^3).

6. Total stocks for all zooplankton: 9.3 mg N/m³ and 45.7 mg C/m³; ratios as PN of nanozooplankton : herbivores : carnivores are 1:11:4.5; percentages nano-, micro-, and macrozooplankton of total stock as PN are 6, 63, 31.

DISCUSSION

In our efforts to describe the standing stocks of three size-categories, heterotrophic nanozooplankton and two trophic levels of zooplankton, in the southern sector of Kaneohe Bay, we gave emphasis to evaluation of relative magnitudes of variability in stock estimates as PN and PC. We gave less importance to the taxonomic composition of the zooplankton, except as it might have created biases in stock estimates of herbivores and carnivores.

The results presented above for the stocks of zooplankton are considerations of precision. Although the magnitudes of sampling and analytical variability are large, much greater precision with current methodology and the nature of sampling zooplankton appears unlikely. In addition to these problems, however, the data also contain inaccuracies. Among the size-classes and trophic levels that we sampled, we probably obtained the most accurate estimates for the nanozooplankton (mainly protozoan heterotrophs) and carnivorous macrozooplankton and the least accurate for herbivorous microzooplankton. This latter estimate involved an extra measurement of chlorophyll-*a* and subtraction of plant pigment materials from the total catch, and we had to use factors to convert to PN and PC. Moreover, in this 35–333-μ size-fraction were some variable amounts of small carnivores and nonplant detritus. However, the calculated nonplant detritus (ca. 27 percent, calculated from the observed and expected C:N ratio) in the microzooplankton stock was not very great and has been corrected for.

Other elements of subjectivity in the estimates of herbivorous and carnivorous stocks were introduced in the assignment of taxa to being herbivorous or omnivorous on the basis of relative fluorescence indices; however, these categories of taxa do in fact form a hierarchy ranging from *Sagitta* to gastropod larvae that is biologically reasonable. In addition, microscope count data and correction of the macrozooplankton catch by removal of the herbivores and omnivores changed the estimate of the carnivorous stock only very slightly from that of the uncorrected macrozooplankton catch.

There exists a considerable amount of data, mostly as enumerations of macrozooplankton from the southern sector of Kaneohe Bay, with which comparisons can be made for historical trends. For the macrozooplankton, the average annual standing stocks were 0.61, 0.68, and 3.48 ml/m³ of volume for 1963–1964, 1966–1967, and 1968–1969, respectively (Clutter 1973: table 6.2); the first two values are displacement volumes and the latter is a settled volume value. Assuming that the displacement: settled volume ratio is 1/4, a specific gravity of unity, 85-percent water content of wet weight and 6.7 percent PN:DW, these volumes correspond to 6.1, 6.8, and 8.7 mg N/m³ for the respective years cited above. These stock estimates are 2.5 times higher than the 2.86 mg N/m³ observed in our study. The count data of Peterson 1975 (Table 8) can be used to obtain additional estimates of 63 and 130 mg/m³ of dry weight, which convert to 4.2 and 8.7 mg N/m³. These latter two figures are estimates of annual average stocks for 1966–1968 and 1968–1969, both of which agree quite well with the values 6.8 and 8.7 mg N/m³ above for the same periods. However, we believe that these latter two values are too high, because Peterson used a mean value of 0.17 mg dry weight per *Sagitta* of length 9.2 mm in calculations for all individuals, a length and weight that overestimate the average-sized *Sagitta* in 0.33-mm-mesh catches. Using a 7-mm average length for *Sagitta* from annual average lengths for 1968–1969 and 1973–1974 and its corresponding 0.074 mg dry weight (Szyper, unpublished), we calculated the annual average standing stocks for 1966–1968 and 1968–1969 as 2.15 and 4.5 mg N/m³, respectively. Thus, the Peterson macrozooplankton stock estimate for 1966–1968 is just below our value for 1973–1974, but it appears that the stock from Clutter's samples of 1968–1969 was still about 60 percent higher.

It is not possible to state with reasonable certainty that any major changes in species composition or numerical abundance of selected macrozooplankters have occurred in the bay. Since the time of the work reviewed by

Clutter (1973) and Peterson (1975), the same major taxa of macrozooplankton still appear to be present, with *Sagitta enflata* often being dominant in both numbers and weight. No clear statement can be made regarding changes in rank order of species abundance within a size-class, or of average annual numerical abundance, from the few samples of macrozooplankton that have been counted and because of the enormous seasonal variability indicated by the data.

For the microzooplankton catch data, the only study for which comparison may be made is that of Bartholomew (1973), which included counts of microcopepod species converted to dry weight; the average stock over the period August 1968 to July 1969 was 15.1 mg/m³ dry weight. Using a mean PN:DW value of 0.08 (Bartholomew 1973) to convert to PN, we arrive at a figure of 1.2 mg N/m³ for the three species of microcopepods. This value is an underestimate of the total microzooplankton catch because no additional count data and weight were added for other less abundant taxa such as *Oikopleura*, larvae of gastropods, bivalves, or polychaetes. However, even increasing this estimate to 2.0 mg N/m³ and comparing it to the 5.9 mg N/m³ for microzooplankton, we estimate about a threefold increase in the stock in the 5-year period since Bartholomew's study.

In southern Kaneohe Bay, the trend of changes in the micro- and macrozooplankton stocks may be summarized as follows: whereas the total stock of micro- and macrozooplankton has been nearly unchanged at about 6–9 mg N/m³ in the last decade, there has been an apparent reversal in the relative abundance of macrozooplankton:microzooplankton stocks. In 1963–1969 there was about 2–6 mg N/m³ in macrozooplankton and probably 1.2 to 2 mg N/m³ in microzooplankton stock, while in our study respective values are 2.86 and 5.9 mg N/m³. Thus, these historical changes, if real, imply that one major consequence of the nutrient stress on the pelagic ecosystem has been change in the relative abundance of size-classes (and trophic levels) and more subtle or undetectable changes in the relative abundance or species composition within each size-class of the zooplankton community.

It may be instructive to compare the average annual stock estimates for herbivores and carnivores in the southern sector of the bay with those predicted by the ecosystem model (Caperon 1975). We estimated 6.2 mg N/m³ for herbivores and 2.5 mg N/m³ for carnivores, compared to 8.9 mg N/m³ and 7.5 mg N/m³ for respective values in a simulated one-carnivore system (Caperon 1975: table 3). The herbivore stock agreed well with the prediction, but the carnivore stock was about three times lower. Part of the first-order carnivore standing stock unaccounted for comprised planktivorous fish, for which standing stock data are presently lacking.

We have observed relatively small deviations about the annual average stock of the microzooplankton catch (herbivores) and much larger variations in values for macrozooplankton catch (carnivores). That the stock of macrozooplankton is more variable than is the stock of microzooplankton is indicated by an F-ratio test of variances. We made the test using median stock values per sampling date and calculating a variance of the medians over the period of sampling. The raw abundances were transformed into logarithms to normalize the data. The variance ratio is 11.3 with 42, 23 degrees of freedom, indicating significantly greater variance in macro- than microzooplankton catch ($P < .01$).

The average ratio of biomass or volume of macrozooplankton to microzooplankton has been found to vary from 8 at OSP (Ocean Station Papa—a weather station in the northeastern Pacific Ocean) to 21 in the Strait of Georgia (LeBrasseur and Kennedy 1972) and from 4 to 5 in coastal waters off San Diego or in the offshore California Current (Beers and Stewart 1969, 1970). LeBrasseur and Kennedy used a 44–350 μ and a > 350-μ-mesh net in their work and Beers and Stewart used nets of < 202-μ and > 202-μ mesh. Our definitions of microzooplankton (35–333 μ) and macrozooplankton (> 333 μ) are sufficiently close for comparative purposes. The ratio of macrozooplankton:microzooplankton catch observed is 0.48 (2.86/5.9 as mg N/m³), which is about 10 times less than the results of Beers and Stewart (1969, 1970) and 20 to 40 times less than those of LeBrasseur and Kennedy (1972).

There are several possible explanations for

the observed differences between the ratios observed in the northeastern Pacific versus Kaneohe Bay. First, temperature regimes are subarctic–temperate versus nearly tropical, and, therefore, the catch of macrozooplankton may be larger in the northeastern Pacific relative to Kaneohe Bay because of the presence of the abundant large forms found in cold waters. Typical dominant macrozooplankters in each area studied were *Calanus cristatus* and *C. plumchrus* (large calanoid herbivores), *C. pacificus* (medium-sized calanoid herbivore), and *Sagitta enflata* (carnivorous chaetognath) for the OSP-Strait of Georgia, the California Current, and Kaneohe Bay, respectively. In addition to the temperature difference between these systems, Kaneohe Bay is a very shallow estuary, about 12 m deep, with high insolation. The shallow water and high light-intensity would additionally exclude large, deeper-living oceanic species such as *C. cristatus* from the bay. The microcopepod species in the bay, however, are euryhaline forms (e.g., *Oithona simplex* and *O. nana*), which are probably adapted to coastal waters and fluctuating physical environments.

Although temperature and physical factors alone may be an adequate explanation for the difference between observed ratios of macro/micro stocks in the northeastern Pacific versus Kaneohe Bay, we believe also that the increase in microzooplankton and the decline in macrozooplankton in the southern sector are a result of the eutrophication process. The nutrient enrichment has not only modified the level of phytoplankton abundance and the C:N ratio of particulate matter (Caperon, Harvey, and Steinhilper 1976), but it may have caused shifts in the size-composition of the algae that favor the nanophytoplankters.

Clutter (1973) suggested that *Oikopleura* abundances have increased because of the increased abundance of nanophytoplankton, although direct evidence of changes in the ratio of net:nanophytoplankton were lacking. Since 1973 high percentages of nanophytoplankton have been found to occur in Kaneohe Bay (Harvey and Caperon 1976) and also in the eutrophic Chesapeake Bay estuary (McCarthy, Taylor, and Loftus 1974). We speculate that during the eutrophication process in Kaneohe Bay, the increase in and large crop of microzooplankters relative to macrozooplankters is a result of selection for nanophytoplankton feeders and of faster metabolic turnover rates of the microzooplankters. The low ratio of macroplankton:microplankton stocks compared to ratios obtained in the northeastern Pacific may be in part a result of the particle size spectrum of plant food available as well as a result of differences in the physical environment.

Further speculation on the importance of differences in the size spectrum of organisms in the pelagic ecosystem seems justified. It is an observable fact that in Kaneohe Bay a 0.33-mm-mesh net captures mainly carnivorous zooplankters (*Sagitta enflata*), whereas in the northeastern Pacific it would capture mainly herbivorous copepods (LeBrasseur and Kennedy 1972). The transfer of materials up a simplified food chain in Kaneohe Bay ends mainly in relatively small planktivorous fish such as the nehu (*Stolephorus purpureus*), iao (*Pranesus insularum*), and maomao (*Abudefduf abdominalis*), plus a few larger resident pelagic carangid piscivores. In contrast, the higher trophic levels occupied by epipelagic nekton in the northeastern Pacific are represented by large species of salmon and baleen whales, which feed directly upon the large copepods (LeBrasseur 1966, Nemoto 1970). Some of this difference is probably due to differences in habitat, but there is an increasing body of evidence indicating that the size-composition of species in trophic levels of communities is a critical parameter that we must examine if we are to understand the structure and functioning of ecosystems.

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NOTE ADDED IN PROOF: For the methods described in collection of microzooplankton and macrozooplankton by towed nets, the TSK flowmeter data were converted for a gain of revolutions during each net lowering (Hirota and Szyper, unpublished); a description of this volume-control bias for zooplankton sampling with vertical tows in shallow water is in preparation.