Pacific Science (1976), Vol. 30, No. 4, p. 363–372
Printed in Great Britain

Nutrient Regeneration by the Larger Net Zooplankton in the Southern Basin of Kaneohe Bay, Oahu, Hawaiian Islands[1]

JAMES P. SZYPER,[2] JED HIROTA,[2] JOHN CAPERON,[3] AND DAVID A. ZIEMANN[4]

ABSTRACT: Four experiments were performed during February 1974 with mixed zooplankton collected with .33-mm mesh in the southern basin of Kaneohe Bay. The mean specific excretion rates multiplied by the estimated average standing stocks of the animals gave estimates of addition to the bay waters of ammonia, phosphate, dissolved organic nitrogen, and dissolved organic phosphorus of 38.6, 4.0, 23.7, and 3.2 ng-at/liter/day, respectively. The specific excretion rates were not significantly affected by the concentrations of animals in experimental vessels, by the estimated concentrations of food in the environment on the days of the experiments, nor by incubation periods of up to 4.5 hours.

The rates are comparable to those obtained from zooplankton of this general size in environments that have rather different temperature and food levels, indicating that size-dependent metabolic rates are the major determinant of specific excretion rates, although feeding and temperature can affect the results of experiments.

Two collecting devices, a conical net and a purse seine made of the same plankton mesh, were used to assess possible effects of capture on the results. The animals from the net hauls excreted phosphate more slowly and dissolved organic nitrogen more rapidly than did those from the seine catches, possibly as a result of the greater initial crowding of animals in the cod-end jar of the towed net. There was no evidence that animals were damaged by collection and no observable effect of initial shock.

Although principally carnivorous, the animals in these experiments (60 to 70 percent *Sagitta*) processed dietary nitrogen and phosphorus in a way similar to that of the mainly herbivorous *Calanus*: they constructed body tissue that was richer in nitrogen relative to phosphorus than was their food and they excreted solutes that were relatively poorer in nitrogen than was their food.

REGENERATION is an important process in the cycling of essential elements in ecosystems, accounting for large proportions of the supply of the elements to the producers (Pomeroy 1970, Corner and Davies 1971). It has been recognized for some time that the excretory activity of zooplankton is the most important source of regenerated nitrogen and phosphorus in marine waters (Ketchum 1962, Johannes 1968). The purpose of the experiments reported here was to assess the contribution of the larger animal plankton to the supply of nutrient elements in Kaneohe Bay.

The use of two mesh sizes for capture of the Kaneohe Bay zooplankton resulted in an imperfect but useful separation of herbivores and omnivores from carnivores, the latter being retained on the larger .33-mm mesh (Hirota and Szyper 1976). Separation by size is even more advantageous for analysis of metabolic processes such as excretion, because the size of individual animals is known to be a major factor affecting

[1] Manuscript accepted 4 February 1976. Hawaii Institute of Marine Biology Contribution no. 503.

[2] University of Hawaii, Hawaii Institute of Marine Biology, Post Office Box 1346, Kaneohe, Hawaii 96744; and Department of Oceanography, 2525 Correa Road, Honolulu, Hawaii 96822.

[3] University of Hawaii, Department of Oceanography, 2525 Correa Road, Honolulu, Hawaii 96822.

[4] University of Hawaii, Hawaii Institute of Marine Biology, Post Office Box 1346, Kaneohe, Hawaii 96744.

turnover rates (Johannes 1964, Hargrave and Geen 1968, Conover and Corner 1968). The present experiments involved only the macroplankton, the animals retained on .33-mm mesh. Most of the experimental work on the excretion of zooplankton (reviewed by Corner and Davies 1971), particularly on nitrogen excretion, has been restricted to animals of similar or larger size. The smaller animals, those passing .33-mm mesh, are undoubtedly greater contributors to regeneration in this system, both because they can be expected to excrete at higher rates per unit body weight and because they are usually more abundant here, both in numbers and biomass. The assessment of their excretory activity, however, involved some special technical problems, which will be treated in another paper (Schell, Hirota, and Caperon, unpublished).

Excretion experiments with zooplankton can be affected by a considerable number of variables. We have investigated the effects of some of these; for example, the concentration of animals in the experimental environment, and the duration of experiments (up to 4.5 hr). For other variables, such as the size of the experimental environment and the physical condition of the animals after collection, we attempted to provide conditions as nearly optimal for the animals as possible. Some factors, such as temperature and the size of experimental animals, remained essentially constant.

METHODS

Zooplankton was collected in the southern basin of Kaneohe Bay on the mornings of 15, 20, and 25 February 1974 by two methods. In the first method we used a purse seine 30.5 m (100 ft) in circumference and 6.4 m (21 ft) deep, constructed of .33-mm plankton mesh (Murphy and Clutter 1972). The seine was hauled in until the catch was concentrated in about 1 m^3 of water outside the boat; plankton was dipped from the catch with large (3 and 4 liter) glass beakers, which became the experimental vessels. In the other collecting method we made brief horizontal hauls near the surface with a bridled net of the same mesh, having a mouth diameter of .5 m. The catches were diluted in large beakers with surface bay water. Control vessels containing whole surface water were prepared for the 15 February experiment; and control vessels containing water that had been screened through .33-mm mesh were prepared for the others. An additional experiment was performed in the afternoon of 25 February, when only the bridled net was used for capture.

Samples for the analysis of dissolved nitrogen and phosphorus were removed from the experimental vessels immediately; the vessels were then taken to the laboratory and incubated under room light at room temperatures, which were close to those in the water (24°–25° C). Each of the four experiments involved two to five beakers containing different concentrations of plankton; the duration of experiments varied from 0.9 to 4.5 hr. The vessels were stirred gently and sampled five to seven times per hour with the probe of a Technicon Autoanalyzer II system; about 4 ml were used per sample. The sampling thus decreased the experimental volumes (2–3.5 liters) by about 2–5 percent during incubation. Analyses for ammonia and phosphate were performed according to the methods described by Schell, Ziemann, and Caperon (unpublished). Larger samples (100–250 ml) were withdrawn from some experiments at longer intervals, filtered through Whatman GF/C glass fiber filters, and analyzed for total dissolved nitrogen and phosphorus by the use of ultraviolet oxidation (Armstrong, Williams, and Strickland 1966). These samples were dipped from the vessels with small beakers, and animals were included so that the plankton concentrations in the experimental beakers remained constant.

At the end of the incubation period, the plankton in the beakers was concentrated on mesh screens, resuspended in filtered seawater, and divided in half with a Folsom splitter. Half was preserved in 2-percent Formalin: seawater for later microscopic examination, and the remaining material, further subdivided when necessary, was collected on glass fiber filters for weight determinations and chemical analyses. The volumes of water remaining in the experimental vessels after the recovery of the plankton were measured with graduated cylinders.

Dry weights and nitrogen content of plankton were determined as described by Hirota and Szyper (1976). Phosphorus content of the plankton, like nitrogen content, was determined

on aliquots of the dry plankton that had been ground in a mortar with its filter. Weighed amounts of the material were placed in 50-ml glass digestion tubes with 1 ml of 50 percent (v:v) H_2SO_4, incubated for 1 hr in a water bath at 90°–100° C, and cooled briefly in tap water. The solutions were diluted with deionized water, then approximately neutralized with 5 ml of 20 percent (w:v) KOH, made up to known volumes, and analyzed for phosphate.

Separate vertical hauls from near the bottom to the surface were taken with a fine mesh (0.035 mm) net having an inner prescreening net of .33 mm mesh, and the catch was weighed, analyzed, and corrected for the presence of plant material as described by Hirota and Szyper (1976). These estimates of the standing stocks of the microzooplankton were regarded as estimates of the concentrations of food available to the mainly carnivorous animals captured by the larger mesh.

The rates of addition of excreted substances to the waters were determined from the slopes of linear regressions of the concentrations of the substances on elapsed time. Although the rates of change of ammonia and phosphate concentrations in the control vessels were always small and with a few exceptions did not differ from zero at the 5-percent level of significance, we always subtracted these rates from the rates in the experimental vessels to obtain net changes in concentrations, because the experimental media, like the control waters, contained plants and animals that had passed the .33 mm screen. The rates of addition of dissolved organic nitrogen (DON) and dissolved organic phosphorus (DOP) were estimated by subtracting the rates of change in ammonia and phosphate from the rates of change in total dissolved N and P, respectively. We divided the net rates of change in concentrations by the concentrations of animal biomass in the vessels to obtain specific excretion rates.

RESULTS AND DISCUSSION

Regression Analyses

The 95-percent confidence intervals for the rates of change in ammonia and phosphate in the experimental vessels (slopes) were similar, averaging ± 17.8 percent (range, 4.5–43.6 percent). Of the 12 experimental vessels used on the 3 days, only one had a rate of increase in ammonia that was not significantly different ($P > .05$) from the control; there were two such cases for phosphate. The 95-percent confidence limits for the rates of change in total dissolved N and P in the experimental vessels averaged 67.3 percent (range, 18–184 percent). The rates in the control vessels were not significantly different from zero; for nitrogen, the changes in three of eight experimental vessels were not significantly different from the controls, as was true for phosphorus in one vessel. The relatively large confidence intervals for rates of change in total N and P are probably due to the effects on the animals of being handled during sampling and filtering. Duplicate ultraviolet oxidations were performed on the samples taken from the morning experiments on 25 February. The residual variation in the five regressions for total nitrogen, i.e., the variation about the fitted line attributable to analytical error, indicated an average standard deviation of ± 19 percent of the mean concentrations analyzed.

Effects of Experimental Conditions

PREPARATION AND DURATION OF EXPERIMENTS: Our purpose in using the seine was to treat the animals as gently as possible while collecting them by minimizing mesh velocity. Of course, care was also taken in this respect with the catches of the towed net, and the animals in all vessels appeared healthy throughout incubation. There is no evidence that one collecting method treated the animals more gently than did the other. There were, however, some readily apparent differences in excretion rates between catches of the two devices (Table 1). The phosphate excretion in vessel B on 15 February (containing a seine catch) is anomalously high, probably reflecting an unhealthy condition of at least some of the animals, and we will not consider it further. Eppley et al. (1973) found that high phosphate excretion rates were characteristic of damaged animals in their experiments. The differences between net and seine catches in ammonia excretion are neither consistent nor statistically significant (Mann-Whitney test: 20), the net catches having higher

TABLE 1

EXCRETION RATES BY THE LARGER NET ZOOPLANKTON, KANEOHE BAY, OAHU, HAWAIIAN ISLANDS

DATE AND EXPERIMENTAL VESSEL	COLLECTING METHOD	ng-at/mg dry weight per hr				% body content of N or P per hr			
		AMMONIA	DON	PHOSPHATE	DOP	AMMONIA	DON	PHOSPHATE	DOP
15 Feb 74									
A	seine	–		–		–		–	
B	”	58.7		44.30		1.040		34.90	
C	net	44.8		2.56		1.170		2.08	
20 Feb 74									
A	seine	27.1	12.4	3.32	1.80	.849	.389	3.42	1.86
B	”	25.2	–	2.62	–	.730	–	2.84	–
C	net	23.7	53.6	2.06	3.55	.730	1.650	2.30	3.98
D	”	23.2	54.5	1.71	3.05	.687	1.620	1.60	2.85
25 Feb 74 AM									
A	seine	22.8	26.5	8.40	1.07	.387	.450	3.95	.50
B	”	21.9	–	5.81	4.60	.363	–	4.08	3.23
C	net	36.5	–	2.97	2.98	.888	–	2.12	2.13
D	”	35.1	50.0	2.83	1.89	.764	1.344	2.32	1.55
25 Feb 74 PM									
F	net	33.8		–		1.040		–	
Means	all*	32.1	38.4	3.59	2.71	.787	1.040	2.87	2.30
	seine*	31.1	19.4	5.04	2.49	.674	.420	3.57	1.86
	net	32.8	47.9	2.43	2.87	.882	1.340	2.08	2.63

NOTE: DON, dissolved organic nitrogen; DOP, dissolved organic phosphorus; –, indicates that the rate in a given vessel did not differ significantly from the control.

* The phosphate results for vessel B on 15 Feb have been excluded.

TABLE 2

TAXONOMIC COMPOSITION OF THE ZOOPLANKTON IN THE EXPERIMENTAL VESSELS, KANEOHE BAY, OAHU, HAWAIIAN ISLANDS

ORGANISM	15 Feb 1974	20 Feb 1974				25 Feb 1974				
	C	A	B	C	D	A	B	C	D	F
Sagitta enflata	78.1	67.0	58.5	72.0	71.8	72.0	67.5	68.7	73.2	60.3
Ctenophores	6.7	10.2	32.6	7.2	9.4	3.2	5.6	3.3	4.4	22.4
Oikopleura	14.7	17.1	1.3	11.5	11.5	8.5	8.7	4.8	3.0	0.9
Medusae	0	1.8	0	2.3	1.2	6.0	3.2	7.3	5.9	1.7
Lucifer chacei	0	0.5	1.3	1.6	2.1	2.7	4.0	2.8	2.3	1.7
Shrimp Larvae	0	0.2	0	0.4	0	1.6	2.4	2.5	1.7	0
Crab Zoea	0	3.2	6.4	0.4	0	2.0	1.6	3.4	1.9	0.9
Barnacle Nauplii	0	0	0	0.2	0.3	0.9	2.4	5.1	4.2	2.6
Gastropod Larvae	0.3	0	0	4.3	3.6	2.1	2.4	3.3	2.1	3.4
Bivalve Larvae	0	0	0	0	0	0.9	2.4	1.4	1.3	0
Copepods	0.4	0	0	0	0	0	0	0	0	6.0
Animals/liter in Vessel	~ 1000	962	252	520	384	631	78	525	364	171

NOTE: Experimental vessels are indicated by letters of the alphabet. Taxonomic composition is given in percentages.

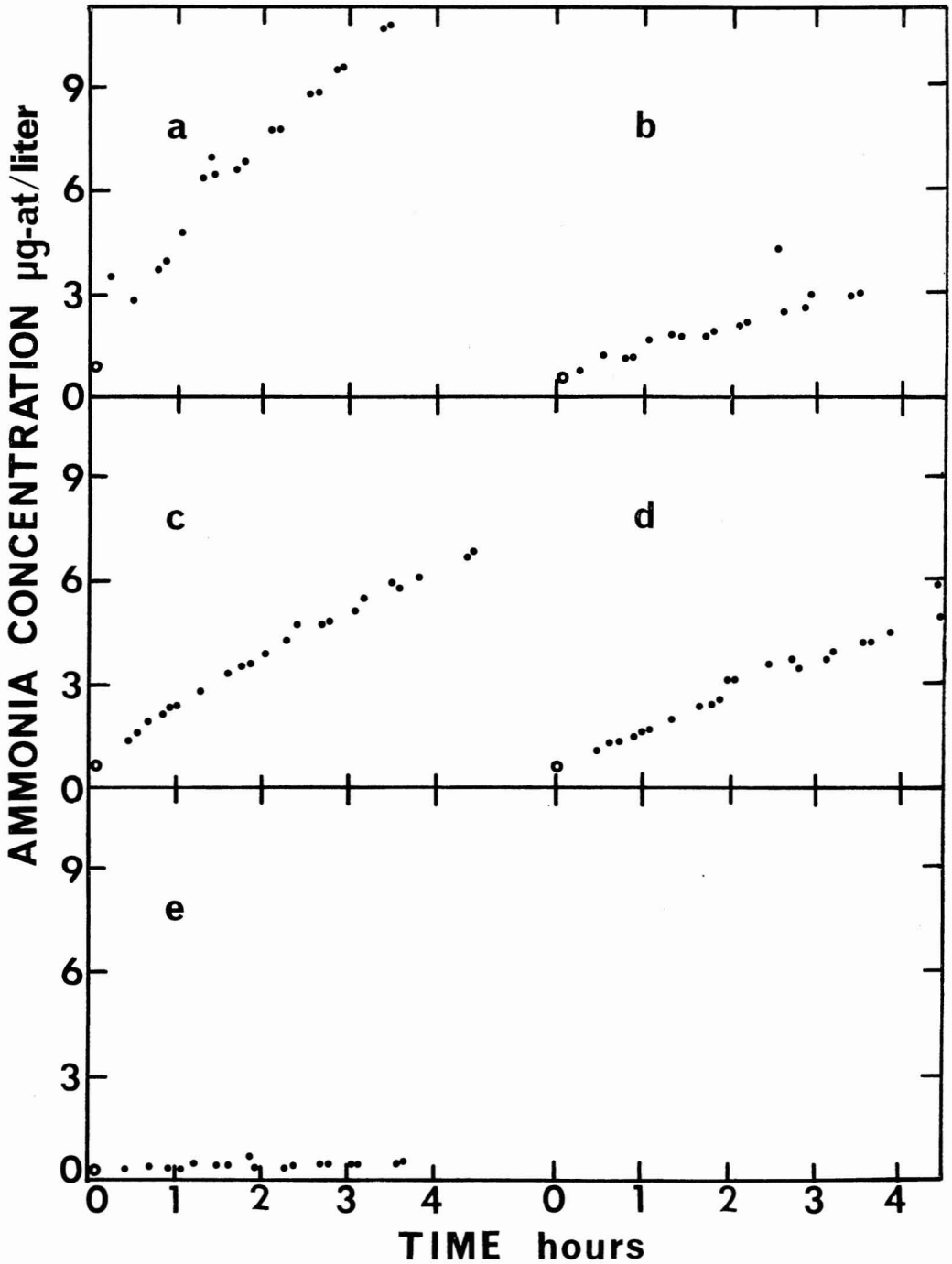

FIGURE 1. Concentrations of ammonia in the experimental (a–d) and control (e) vessels during the experiments on 20 February 1974. Open circles represent water samples taken immediately after vessels had been prepared.

rates on 15 and 25 February, the seine catches having marginally higher rates on the 20th. The seine catches excreted phosphate significantly more rapidly ($P < .05$) on the 20th and 25th, but not to the extent that damage should be suspected. Given the greater variability associated with the rates of organic excretion, we should be cautious when making comparisons involving these substances. Although neither the difference in DON nor in DOP is significant ($P \geqslant .20$), it appears that net catches excrete more DON than do seine catches, the mean for the former being about 2.5 times higher. The taxonomic compositions of catches captured by the two devices (Table 2) are closely comparable both within and among experiments, with the exception of the presence of a larger number of ctenophores in vessel B on 20 February and in vessel F on 25 February. Vessel B is notable for its lack of detectable organic excretion, but is not exceptional with respect to ammonia and phosphate. Although the proportion of organic phosphorus to total phosphorus excreted (about 44 percent) is in good agreement with earlier findings (Pomeroy, Matthews, and Min 1963; Butler, Corner, and Marshall 1970), the proportion of DON to total N (about 57 percent) is uncommonly high for zooplankton (see discussion by Corner and Newell 1967). Although, as mentioned, the confidence intervals for the rates of DON excretion are large, they were reproducible within the data set for an experimental day for each collecting method, and within collecting methods on a given day for the single comparison available. It may be noteworthy that the highest DON excretion rates and highest proportions of DON excretion were associated with the net hauls rather than with the seine catches. Plankton in the net hauls were much more concentrated (in the cod-end jar) before the preparation of experimental vessels than the seine catches were, although experimental concentrations were similar for both types of catches. This initial crowding could have stimulated increased excretion of DON, despite the subsequent reduction of densities before the animals were incubated. Corner and Newell (1967) found that extreme crowding (several grams dry weight per liter) increased organic nitrogen excretion in *Calanus*, and they invoked this result to explain the excretion of large amounts of amino acids by zooplankton in the experiments of Johannes and Webb (1965).

The addition of ammonia to the vessels in the 20 February experiment (Figure 1) was typical of the results for ammonia and phosphate, and permits several conclusions about the excretion of these substances. Since the first data point represents a sample taken in the field immediately after preparation of the vessels, and since this point is clearly included in the linear plots, there was no observable effect of the initial handling on the subsequent results. Thus, it was not necessary with the procedures used here to acclimate the animals or to permit them to recover from any initial shock; the experiments began with the animals in as "natural" a condition as possible, with the possible exception of the effect of initial crowding on excretion by the net catches. The linearity of the plots indicates that before-and-after sampling of these vessels at any interval shorter than about 4 hours would have given a good estimate of the slopes, and that neither the lengths of time the animals spent confined in the vessels nor the water-sampling procedures had any effect on the excretion rates. The animals could have fed during our experiments, since *Sagitta*, the most abundant plankter in the vessels, is known to feed both on small organisms present in the waters at natural concentrations and on some of the species in the experimental catches themselves (Piyakarnchana 1965).

EXPERIMENTAL ANIMAL CONCENTRATIONS: In order to detect changes in the concentrations of any excretory products within reasonable experimental periods, we had to concentrate the animals more than they were in nature. In our experimental vessels, animal concentrations were about 1000 times those found in the bay, and ranged from 9.4 to 93.8 mg dry weight/liter, with a mean of 44.6 (Table 3); these are low-to-medium levels compared to those employed by other workers (e.g., Corner and Newell 1967), and much lower than the levels in the experiments of Johannes and Webb (1965). The excretion rates in Table 1, expressed as ng-at element/hr/mg dry weight are uncorrelated with the animal concentrations as dry weight (Kendall's rank correlation test: $P > .20$ for all substances). Hargrave and Geen (1968) found

TABLE 3

ANIMAL CONCENTRATIONS, LEVELS OF MICROZOOPLANKTON FOOD, AND NITROGEN:PHOSPHORUS RATIOS, KANEOHE BAY, OAHU, HAWAIIAN ISLANDS

DATE AND EXPERIMENTAL VESSEL	COLLECTING METHOD	ANIMAL CONCENTRATIONS			FOOD LEVELS (mgN/m³)	N:P RATIOS (ATOM:ATOM)				
		DRY WEIGHT (mg/liter)	NITROGEN (μg-at/liter)	PHOSPHORUS (μg-at/liter)		FOOD	ANIMALS	EXCRETION PRODUCTS: INORGANIC	EXCRETION PRODUCTS: ORGANIC	EXCRETION PRODUCTS: TOTAL
15 Feb 1974					3.38	27.6				
A	seine	11.2	57	1.16			49.1	–		
B	,,	19.5	110	2.48			44.4	1.32		
C	net	85.5	328	10.50			31.2	17.50		
20 Feb 1974					5.44	28.8				
A	seine	93.8	300	9.10			33.0	8.16	6.89	7.71
B	,,	25.2	87	2.32			37.5	9.62	–	–
C	net	54.9	178	4.90			36.3	11.50	15.10	13.78
D	,,	42.7	144	4.56			31.6	13.57	17.87	16.32
25 Feb 1974 A.M.					7.08	28.0				
A	seine	73.4	432	15.60			27.7	2.71	24.77	5.21
B	,,	9.4	57	1.34			42.3	3.77	–	–
C	net	37.7	155	5.27			29.4	12.29	–	–
D	,,	33.3	124	4.06			30.5	12.40	26.46	18.03
25 Feb 1974 P.M.					8.35	20.8				
F	net	49.0	158	4.71			33.5			
Means	all	44.6	178	5.50	6.06	26.3	35.5	9.28	17.05	12.13
	seine	38.8	174	5.33			39.0	5.12	15.83	6.46
	net	50.5	181	5.66			32.1	13.45	17.66	14.97

NOTE: "Inorganic" refers to ammonia and phosphate; –, no data.

that animal concentrations above about 400 animals/liter had a depressing effect on phosphate excretion. In the present study, the concentrations ranged from 78 to about 1000 animals/liter, but no such depressing effect was observed. Other differences between the two studies include, in the 1968 work, smaller vessels (275 ml), longer incubations (24 hr), and a mainly crustacean fauna. Hargarve and Geen (1968) suggested that, because the rates decreased with time in their experiments and because that decrease may well have been caused by exhaustion of food in the vessels, the decrease would be apparent sooner in the more crowded vessels. Our experiments were probably not affected by food depletion because they were shorter and because there were many animals in the beakers that are suitable food for the dominant animal, *Sagitta*. If it is crowding itself, rather than food exhaustion, that depresses phosphate excretion rates, the lower phosphate excretion by net catches might be partly explained by damage induced by crowding.

Food Levels in Nature

The mean excretion rates from each of the four experiments were uncorrelated with the natural concentrations of microzooplankton biomass determined from the hauls taken when experimental animals were being collected ($P > .70$ for all substances). The range of "food levels" observed during February 1974 was in the lower one-third to one-half of the annual range (Hirota and Szyper 1976).

Size of Individual Animals

The excretion rates reported here are comparable to those obtained by Eppley et al. (1973) and to many of the studies reviewed by Corner and Davies (1971). Rates of this magnitude are probably characteristic of zooplankton of this general size (about 100 μg dry weight/animal, in our experiments), since the reviewed studies vary widely in location, season, environmental temperature, and animal species studied. The difference in food availability for this class of plankton between Kaneohe Bay and the central Pacific waters (the site of the work by Eppley) is considerable, yet the excretion rates are similar. The rates of phosphate excretion presented here are close to what may be expected for animals of this size according to the size-rate relationships given by Johannes (1964) and by Hargrave and Geen (1968). There have been experimental comparisons of excretion rates at different temperatures and food levels (e.g., Jawed 1969, Conover and Corner 1968), demonstrating that these factors have clear effects on individual experiments. However, the long-term and worldwide correspondence of rates determined with this size-range of animals, coupled with the large effects of individual body size that have been demonstrated, argue strongly that the excretion of inorganic nitrogen and phosphorus by zooplankton is determined basically by the size-dependent metabolic rates of the animals.

Nitrogen: Phosphorus Ratios

Ketchum (1962) pointed out that the N:P ratios of zooplankton, their food, and their excretion products are necessarily related to their assimilation and growth efficiencies. Butler, Corner, and Marshall (1969, 1970) quantified the relationships and calculated the gross efficiency of growth (material added to the body as growth: material ingested), from their data on N:P ratios for *Calanus* and its food. Their calculations in terms of nitrogen and phosphorus involve the assimilation efficiencies for these elements, which were available from earlier experimental work on the organism. We have no information on the assimilation efficiencies of the zooplankton involved in our experiments; however, using those employed by Butler, Corner, and Marshall (1969) and the mean N:P ratios obtained from our experiments, we found an efficiency for nitrogen of 45.8 percent and for phosphorus of 33.9 percent. These are higher than the mean values obtained in the work cited but are not outside the ranges tabulated by the authors from their own and other studies on gross efficiency of growth.

Given the considerable range of assimilation efficiencies that have been observed in zooplankton (Corner and Cowey 1968), we see no particular justification for the use of the values applicable to *Calanus*, and the accuracy of the efficiency estimates above is dependent on the applicability of those values to the animals in

our experiments. It is noteworthy, however, that the reasonable efficiency values were obtained from our rather different N:P ratios for all materials—food, animals, and soluble excretion products; all were roughly 25 percent higher than those in the *Calanus* work. The differences are to be expected, since the macrozooplankters here were mainly carnivores (the nutritional N:P ratio here resembles that of *Calanus* body tissue), yet the compositions of the components stand in similar relationship to one another. The animals build bodies richer in nitrogen relative to phosphorus than is their food, the excretion products being relatively poorer. The generalization seems to be valid both for herbivores and low-level carnivores.

Influence on Kaneohe Bay

The median standing stock of macrozooplankton in the southern basin during 1973–1974 was 2.86 mg N/m^3 (Hirota and Szyper 1976). The mean N:P ratio of our experimental animals, 35.5 by atoms, yields an average stock estimate of 0.18 mgP/m^3, based on the nitrogen figure. At the mean turnover rates in Table 1, the addition of ammonia and phosphate to the waters of the southern basin by the macrozooplankton may be estimated as 38.6 and 4.0 ng-at/liter/day, respectively. Although the variation in food levels in the bay during February did not affect the excretion rates, there could have been a difference between day and night rates caused by differences in the feeding behavior of the zooplankters. The dominant animal in the macrozooplankton, *Sagitta*, is known to feed more at night (Pearre 1973; Szyper, unpublished). If feeding animals excrete faster than nonfeeding ones (as Butler, Corner, and Marshall 1970, established for *Calanus*), then the above estimates would be low, depending on the occurrence and extent of feeding by our experimental animals, which were captured during the day. The excretion of DOP, as mentioned, was 44 percent of the total phosphorus excretion, and thus would add 3.2 ng-at/liter/day to the waters of the southern basin. Since the excretion of DON by the net catches may have been affected by the collecting method, the proportion of DON to total N excretion by seine catches (38 percent) can be used to estimate a DON addition to the bay of 23.7 ng-at/liter/day.

SUMMARY AND CONCLUSIONS

In addition to the above estimates of the contribution of the larger net zooplankton to the regeneration of dissolved nitrogen and phosphorus in Kaneohe Bay, the results of these experiments permit several conclusions:

1. The necessity of concentrating zooplankton for excretion experiments may well have measurable effects on the results, even when the animals are not noticeably damaged.
2. Excretion rates of zooplankton of this size-category, determined with water from the natural environment as the medium, in short-term experiments without antibiotics, are constant for several hours.
3. Experimental concentrations of animals between 9.4 and 93.8 mg dry weight/liter (78 to about 1000 animals/liter) had no effect on the observed excretion rates.
4. Despite the high temperatures (24°–25° C) and high estimated concentrations of food for larger zooplankton (3–8 mg N/m^3), the excretion rates observed here were similar to those observed in colder and less eutrophic waters, indicating that the size of the animals (about 100 μg dry weight/animal) is a major factor determining specific excretion rates.
5. The larger zooplankton here, although mainly carnivorous, process dietary nitrogen and phosphorus in a manner similar to that of the predominantly herbivorous *Calanus*: they build bodies richer in nitrogen relative to phosphorus than is their food and excrete soluble materials that are relatively poorer.

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