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SPECIES COMPOSITION AND ABUNDANCE OF LAGOON ZOOPLANKTON AT ENIWETAK ATOLL, MARSHALL ISLANDS

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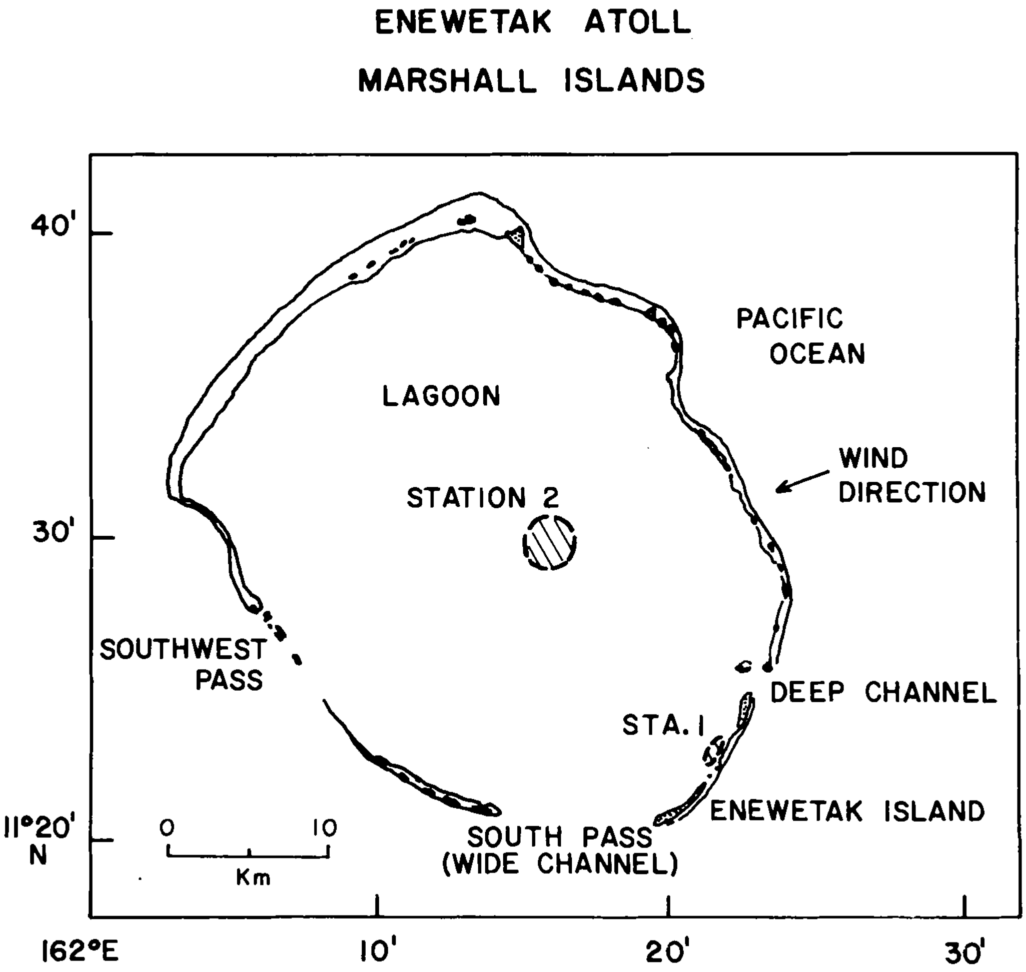

Figure 1. Enewetak Atoll, with sampling stations (1) and (2) indicated

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ABSTRACT

The species composition and abundance of lagoon zooplankton were studied from net tows made during two winters (January-February, 1972; 1974) and one summer (June-August, 1974) at a mid-lagoon station, and during the winter of 1972 at a shallow back-reef area. About 124 zooplanktonic organisms were identified, which included many species not previously reported from this lagoon.

Copepods, chaetognaths and larvaceans which dominated at the mid-lagoon station were much lower in abundance at the shallow station. At the mid-lagoon station about 56 of the more abundant species increased in abundance during the summer, while 3 species were collected only in the summer; 4 species increased in abundance during the winter, while about 4 species were collected only in the winter; and about 30 species lacked a seasonal preference. The species diversity (Shannon-Wiener and Brillouin indices) of the lagoon zooplankton, which ranged from about 3.8 to 3.9, was not significantly different for the winter and summer populations. This lack of a difference in diversity may be due to certain limitations inherent in such indices when used to describe complex communities.

INTRODUCTION

Kramer (1897) working in the lagoon at Samoa made the first quantitative study showing a greater abundance of plankton in the lagoon than in the surrounding ocean. Though rarely cited, this work was confirmed by subsequent studies of Russell (1934) at the Great Barrier Reef lagoon, Edmondson (1937) in the semienclosed waters around Oahu, Motoda (1938) in the lagoon at Palao, Johnson (1949) at Bikini and nearby atolls including Enewetak, Michel (1969) at Mururoa Atoll, Michel *et al.* (1971) at Rangiroa Atoll, and Tranter and George (1972) at

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Kavaratti and Kalpeni Atolls. Except for the study by Johnson (1949), these investigations were more concerned with the relative abundance of the total plankton or of major taxa rather than species composition. Other publications which identified zooplankton species include a preliminary survey of the more important organisms by Gilmartin (1958) at Enewetak; and studies on lagoon copepods by Mahnken (1966) from Rongelap with two additional samples from Enewetak, and by Barnett (1967) from Enewetak lagoon. Sears (1950) has reported on the siphonophores from this and other atolls in the Marshall Islands. Recently, Sale *et al.* (1976) studied the composition of the zooplankton from the Great Barrier Reef area.

Additional plankton studies have been made in close proximity to the reef and pertained to the role of plankton as an energy source for reef ecosystems (*e.g.* Glynn, 1973; and Johannes and Gerber, 1974).

The previous lagoon plankton studies at Enewetak were based on samples collected over a few days in one season; Gilmartin (1958) and Barnett (1967) took samples in the winter, and Johnson (1949) and Mahnken (1966) took samples in late summer. Since different collecting methods were used in each of these studies it is difficult to discern seasonal changes in the composition and abundance of the lagoon zooplankton.

In the present work, the lagoon plankton at Enewetak was sampled over longer periods than in the previously cited studies, and included samples from two winters and one summer. Essentially, the same methods were used throughout the study, and all the organisms in each subsample were counted and identified. These data allow consideration of seasonal patterns in the species composition and abundance of the lagoon zooplankton.

METHODS

Two lagoon stations were sampled (Fig. 1) at Enewetak Atoll, Marshall Islands during two winters (Jan.-Feb., 1972 and 1974), and one summer (June-Aug., 1974). Station 1 was located along an interisland reef about 150 m behind the reef crest and was sampled only in the winter of 1972. This station was about 2 m deep and characterized by a slight unidirectional flow of water from in front of the reef during mid to high tides. Station 2 was located about mid-lagoon, 15-20 km northwest of Enewetak Island, in about 50 m of water, and was sampled in all three periods.

Zooplankton was collected with a 1/2 m diameter, #6 mesh Nytex^R net, aperture 0.239 mm, from January 1 - January 29, 1972; and with a 1/2 m diameter, #10 mesh net, aperature 0.158 mm, from January 27 - March 3, 1974 and June 16 - August 7, 1974. Nets were equipped with internally mounted, calibrated, T.S.K. flowmeters. Each sampling consisted of oblique tows, made from about 35-40 m to the surface at Station 2, and from about 1 1/2 m at Station 1 on incoming tides.

Because Station 1 was shallow, it was necessary to make several continuous oblique tows in order to sample roughly equivalent volumes from both stations. Tows were made from about 0930 to about 0230. Station 1 was sampled ten times and only during the winter of 1972, and on the same days as the sampling of Station 2. At Station 2 during the winter of 1974 and summer of 1974 twelve samples were collected each period. All samples were preserved in 5% glutaraldehyde in sea water, kept cool and in the dark. This method of preservation retains pigmentation of the organisms better than formalin, aiding in identification and enumeration. Total volume of water filtered by the nets ranged between 15-22 m^3.

The liquid volumes in the zooplankton samples were adjusted to 100 ml, all organisms and debris larger than 4 mm were removed, and the suspended plankton subsampled using a 2 ml Stemple Pipette. Using a dissecting microscope and a gridded counting dish, all the material from five successive subsamples were identified and counted along with the larger organisms initially removed. For this 10 ml subsample the total number of individuals counted ranged from about 300 to 350 for adults, and about twice these values for juveniles and smaller organisms. It was necessary to count such large numbers of organisms since the samples often contained large amounts of mucus-like material which caused clumping of the zooplankton organisms. The presence of one individual in the subsample represented abundances ranging from about 0.5 to 1.4 organisms m^{-3}.

Seasonal changes in the lagoon zooplankton populations at the mid-lagoon station were analyzed with regard to species composition and abundance, statistically using ANOVA and Duncan's Multiple Range Test (Steel and Torrie 1960), and calculation of Shannon-Wiener and Brillouin diversity indices (Peet 1974; Pielou 1969).

RESULTS

1. Species composition and station distribution

Some 96 species of copepods, 6 chaetognaths, 7 larvaceans, 9 mysids, 1 euphausiid, 3 amphipods, 8 siphonophores, 2 pteropods, and at least 4 species of dinoflagellates were found in Enewetak lagoon in this study. Several medusae, ostracods, cladocera, isopods and various invertebrate and fish larvae were counted but not identified to species. Seven additional species of planktonic copepods (*Acartia fossae* cf. *A. hamata, Calocalanus pavoninus, Corycaeus flaccus, Corycaeus latus, Corycaeus tenuis, Eucalanus monachus,* and *Lucicutia ovalis*), twenty species of benthic harpacticoid copepods, plus the rest of the above zooplankton groups, except for the siphonophores, have not been previously reported from this lagoon.

Table 1 presents a summary of the approximate abundance levels in numbers of organisms m^{-3}, for the two lagoon stations and for the three sampling periods. The zooplankton from Station 1 (behind-reef) are characterized by a lower abundance, fewer species of typically planktonic organisms, and a greater number of benthic and meroplanktonic forms such as harpacticoid copepods, mysids, isopods and some larvae, as compared to the mid-lagoon station. Several species of presumably planktonic copepods (*Calocalanus pavoninus, Lucicutia ovalis, Macrosetella gracilis, Monstrilla* sp., *Oithona pseudofrigida* and *Scolecethricella dentata*), as well as a few possible epizooic cyclopoid copepods, were restricted to this shallow station. At the mid-lagoon station the calanoid and cyclopoid copepods predominated in terms of numerical abundance and numbers of species. Most other groups such as the larvaceans, chaetognaths, euphausiids, pteropods, and dinoflagellates were also greater in abundance, while the amphipods and siphonophores were restricted to the mid-lagoon station.

2. Seasonal distribution

Statistical analysis of the zooplankton data at the mid-lagoon station indicated considerable variability between samples collected during the same period (Table 1). Often the standard deviation of the mean is equal to or even exceeds the value of the species' mean abundance. Table 1 indicates that there is almost no difference between the species composition and abundance of the mid-lagoon zooplankton from the two winter sampling periods. Considerable differences are apparent in species composition and abundance of the mid-lagoon zooplankton between the summer and the two winter sampling periods. Fifty-six species, consisting mainly of copepods, were significantly greater in abundance, at the 0.05 probability level, during the summer compared to the previously sampled winter periods; and only 3 species, consisting of the copepods *Corycaeus tenuis* and *Temora discaudata* and one siphonophore *Lensia* sp., appeared to be restricted to the summer. In contrast 4 species of copepods, *Centropages* (copepodites), *Clausocalanus furcatus, Euchaeta rimana* and *Undinula* (copepodites), were significantly more abundant in the winter compared to the summer; and 31 species were collected only in winter. Statistical evaluation of these 31 winter species indicated that only 4 were significantly greater than zero, and consisted of the three copepods, *Acartia fossae, Acrocalanus* (copepodites), *Candacia catula,* and one dinoflagellate, *Pyrocystis fusiformis*. An additional 30 species or organisms did not exhibit any seasonal changes by statistical evaluation. The majority of the organisms in this group are of low abundance, less than 5 organisms m^{-3}, and therefore does not represent a significant portion of the total population.

3. Species diversity

Table 2 presents the Shannon-Wiener and Brillouin species diversity indices (Peet 1974; Pielou 1969), calculated for each sample collected from mid-lagoon station. The number of species per sample ranged from 56 to 77 in all the samples, while the mean number of species from the different sampling periods ranged between 62-68 species. The Shannon-Wiener and Brillouin diversity indices were very similar and the Kruskal-Wallis one-way ANOVA (Siegel 1956) indicated that there was no significant difference at the 0.05 probability level between the mean diversity indices for the three sampling periods (d.f.=2; for Shannon indices H=0.736, and for Brillouin indices H=0.655).

DISCUSSION

A more complete study on the seasonal distribution and abundance of zooplankton from Enewetak lagoon would require a series of samples collected periodically throughout one or more years. Such a study was not the intent of the present work which was confined to the summer and winter periods. These two periods, however, represent the two extremes of the seasonal cycle in terms of wind, rain and lagoon circulation patterns (Barnes *et al.*, 1948; Von Arx 1948; Smith personal communication), and it was initially felt that any seasonal change in the zooplankton population would also be most pronounced during these periods.

The low abundance of holoplanktonic zooplankton and proportionally greater abundance of meroplanktonic form found in this study at Station 1 (behind-reef), is typical of coral reef environments (e.g. Gerber and Marshall 1974, Sale *et al.*, 1976). Avoidance behaviour to this shallow area, as well as predation by the coral reef community are believed to account for this observation (Glynn 1973). Meroplanktonic organisms, such as harpacticoid copepods, in these samples were perhaps inadvertently washed from the reefs, while certain other meroplanktonic forms, such as invertebrate larvae were probably actively released from the reefs in the dispersal process. Undoubtedly these net collections of zooplankton made during the day underestimated the total shallow water zooplankton population. Emery (1968) and Sale *et al.*, (1976) both found extensive zooplankton populations in close proximity to the corals and adjacent sediment, especially at night. But these forms were mainly epibanthic resident types rather than typical open-water holoplanktonic zooplankton, which was of interest here. However, the present study collected several species of typically planktonic copepods which appeared to be restricted to this shallow area. Somehow, these species are capable of maintaining position with respect to the reef and avoid predation.

At Station 2 (mid-lagoon), the greater abundance of zooplankton in these deeper waters is evidence of an environment more apt to promote growth and reproduction of the holoplanktonic species. A deeper water column, lack of intensive predation and better food conditions are all possible explanations. Gerber and Marshall (1974 and in preparation) have found that the major food supply to the lagoon zooplankton consists of detritus exported from the surrounding reef communities. Calculations of the total supply of reef detritus available to the lagoon zooplankton was found to be more than sufficient to meet their metabolic needs.

One criticism in examining and discussing the results of the zooplankton collections from Station 2 (mid-lagoon) concerns the lack of night collections which would possibly reveal additional species, unable to avoid the towed net, and additional vertically migrating species missed because of sampling depth, as well as greater overall abundance. In Barnett's (1967) study of the vertical distribution of the copepods at Enewetak lagoon, he found 67 species with perhaps only 3 species which exhibited diel migrations. However, the total number of nonmigrating species were so great that they masked the vertical movements of the migrating species. In the present study about 78 species of planktonic copepods were recorded in the winter, and in abundances comparable to Barnett's winter collection. It is therefore felt that zooplankton collections reported here have adequately sampled the population within the limitations reported earlier

Without detailed information on the circulation patterns of the lagoon waters and the degree of exchange with the outside ocean waters an explanation for the seasonal changes in species composition and abundance of the lagoon zooplankton can only be tentative. Since the annual variation of lagoon water temperature and salinity is slight (about 0.7°C and 0.15 $^{\circ}/_{\infty}$,Barnes *et al.*, 1948), one explanation for the seasonal changes in the lagoon zooplankton may be related to the residence time of the lagoon waters. Based on temperature and salinity measurements in and around Enewetak lagoon, Smith (personal communication) calculated that the summer flushing rate is considerably longer (perhaps on the order of three months) than the winter flushing rate (which may be as short as one month). Minimal dispersal losses of the lagoon zooplankton along with an increase in phytoplankton production (Gerber and Marshall, in preparation) in summer, could account for the increased lagoon zooplankton populations observed in this study.

Most of the copepod species which dominated the zooplankton in the lagoon and increased significantly in abundance during the summer, are also common, though reduced in abundance, in the surrounding waters of the Pacific North Equatorial Current (Scott 1909; Mori 1937; Wilson 1942; Johnson 1949; Chiba *et al.*, 1955: Mahnken 1966). This is not the case for the copepods *Corycaeus tenuis* and *Temora discaudata* which were abundant and completely restricted to the summer lagoon samples. These two copepods occur in the Indo-Pacific area (Dahl 1912; Delsman 1939; Dakin and Colefax 1940) and were possibly introduced into Enewetak lagoon by eastward moving water masses which shift slightly northward in summer (Barnes *et al.*, 1948; Mao and Yoshida 1955). As further evidence of their seasonality, these two copepods were present in the gut contents of several species of plankton feeding fishes collected at Enewetak lagoon in the summer of 1973, but were absent in the same species of fish collected the preceding winter (Gerber, unpublished data).

Despite the increase in abundance of a major portion of the lagoon zooplankton population in summer a significant change in the species diversity (Shannon-Wiener and Brillouin) was not observed. Both indices take into account the total number of species in addition to the dispersion of individual specimens among the given number species, though the Brillouin index is less sample-size dependant than the Shannon-Wiener index (Patten 1962). If as Peet (1974) argues, such indices are most sensitive to changes in the rarest species rather than in the common species, then the lack of a significant increase in the Shannon-Wiener and Brillouin indices for the summer lagoon zooplankton populations is understandable. Also, Margalef (1968) indicated that for rich tropical phytoplankton communities slight increases in diversity are poorly expressed by these indices since they asymptotically approach a maximum of around 4.5. The diversity indices for the lagoon zooplankton are close to this value, indicating that the lagoon zooplankton population has a very high biotic diversity. By contrast diversity indices fluctuate around 2.5 in coastal populations of temperate marine plankton, and range from 0.8 to 2.2 for adult fresh-water zooplankton (Margalef 1968).

It is concluded from this study that the zooplankton of Enewetak lagoon appear to exhibit an increase in abundance during the summer season. This community has a very high species diversity though a definite change in diversity between the winter and summer populations could not be shown.

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Table 1. Abundance levels of lagoon zooplankton from Enewetak Atoll lagoon.

Mean values are shown (±) one standard deviation of the mean. Underscoring of adjacent or separated means indicates no significant difference at the 0.05 probability level (ANOVA and Duncan's Multiple Range Test: Steel and Torrie 1960)

Station 1 Behind Reef	Station 2 Mid-Lagoon				
Winter 1972	Winter 1972	Winter 1974	Summer 1974	F-values	Species
					Calanoid Copepods
2.3 + 1.7	13.4 ± 10.7	8.5 ± 8.6	29.5 ± 14.3	3.68	*Acartia negligens* Dana, 1894.
5.1 ± 3.7	14.6 ± 10.7	8.1 ± 6.1	-	11.69	*A. fossae* Gurney, 1927.
1.5 ± 1.3	10.2 ± 8.6	6.7 ± 7.8	21.0 ± 15.4	4.51	*Acartia* (copepodites)
0.3 ± 0.3	2.5 ± 3.1	1.1 ± 2.6	10.8 ± 8.5	8.29	*Acrocalanus gibber* Giesbrecht, 1888.
-	11.0 ± 11.6	22.5 ± 24.0	55.8 ± 30.3	5.72	*A. gracilis* Giesbrecht, 1888.
1.0 ± 1.4	2.7 ± 4.7	3.0 ± 5.3	-	2.05	*A. longicornis* Giesbrecht, 1888.
2.2 ± 2.1	2.3 ± 5.3	0.9 ± 1.7	2.0 ± 5.1	0.29	*A. monachus* Giesbrecht, 1888.
3.1 ± 2.8	7.4 ± 9.3	16.8 ± 22.3	-	3.28	*Acrocalanus* (copepodites)
11.0 ± 10.1	165.3 ± 114.4	310.0 ± 171.7	613.8 ± 241.6	3.59	*Calanopia minor* A. Scott, 1902.
-	<0.1	-	-		*Calanus tenuicornis* Dana, 1849.
5.0 ± 6.6	96.8 ± 100.2	105.2 ± 46.6	78.4 ± 42.2	0.59	*Calocalanus pavo* (Dana, 1849).
2.3 ± 1.9	-	-	-		*C. pavoninus* Farran, 1936.
4.8 ± 6.6	5.3 ± 5.9	4.0 ± 5.4	3.3 ± 4.9	0.50	*C. plumulosus* (Claus, 1863).
-	12.6 ± 10.9	14.8 ± 13.6	38.1 ± 26.0	4.91	*C. styliremus* Giesbrecht, 1888.

Table 1. (continued)

Station 1 Behind Reef	Station 2 Mid-Lagoon				
Winter 1972	Winter 1972	Winter 1974	Summer 1974	F-values	Species
					Calanoid Copepods (contd.)
2.4 ± 2.9	6.2 ± 8.2	5.1 ± 6.5	3.1 ± 6.1	0.53	*Candacia aethiopica* (Dana, 1849).
-	<0.1	-	<0.1	0.01	*C. bispinosus* (Claus, 1863).
-	10.0 ± 11.1	5.3 ± 4.2	-	4.61	*C. catula* (Giesbrecht, 1889).
-	0.8 ± 1.4	0.7 ± 2.6	-	0.66	*C. truncata* (Dana, 1849).
1.8 ± 2.7	4.0 ± 4.1	6.8 ± 5.5	4.7 ± 5.0	0.19	*Candacia* (copepodites)
7.3 ± 7.1	214.4 ± 100.6	344.5 ± 151.7	789.1 ± 528.9	4.58	*Canthocalanus pauper*(Giesbrecht,1888).
1.6 ± 2.8	1.4 ± 2.7	1.8 ± 3.4	-	1.21	*Centropages calanius* (Dana, 1849).
-	2.0 ± 3.5	0.5 ± 1.7	-	0.08	*C. elongatus* Giesbrecht, 1896.
-	2.0 ± 3.4	0.8 ± 2.6	-	0.11	*C. gracilis* (Dana, 1849).
0.8 ± 1.9	45.4 ± 30.0	40.9 ± 27.6	55.3 ± 29.6	0.50	*C. orsinii* Giesbrecht, 1889.
1.9 ± 2.0	93.5 ± 66.0	109.3 ± 63.4	47.8 ± 31.5	3.70	*Centropages* (Copepodites)
2.0 ± 1.6	54.1 ± 33.5	60.8 ± 53.1	44.0 ± 21.6	0.68	*Clausocalanus arcuicornis*(Dana,1849).
-	1.8 ± 3.2	<0.1	-	0.63	*C. farrani* Sewell, 1929.
2.7 ± 2.5	23.0 ± 14.0	10.9 ± 10.8	6.1 ± 7.9	7.88	*C. furcatus* Brady, 1883.
1.3 ± 1.4	8.9 ± 9.0	5.3 ± 4.9	6.3 ± 10.2	0.76	*C. pergens* Farran, 1926.
0.5 ± 0.7	14.9 ± 12.6	23.8 ± 37.3	6.4 ± 9.4	1.17	*Clausocalanus* (Copepodites)
-	<0.1	-	1.4 ± 2.0	0.56	*Eucalanus attenuata* (Dana, 1849).
-	<0.1	-	-		*E. monachus* Giesbrecht, 1892.

Table 1 (continued)

Station 1 Behind Reef	Station 2 Mid-Lagoon				
Winter 1972	Winter 1972	Winter 1974	Summer 1974	F-values	Species
					Calanoid Copepods (contd.)
-	11.3 ± 16.9	3.0 ± 6.9	1.3 ± 4.6	3.80	*Euchaeta rimana* (Bradford, 1974.
1.3 ± 1.8	-	-	-		*Euchaeta* (copepodites)
0.9 ± 1.5	11.5 ± 12.4	16.8 ± 16.9	174.3 ± 102.8	3.16	*Labidocera laevidentata* (Brady,1883).
3.0 ± 4.16	1.6 ± 3.5	2.0 ± 4.3	-	1.66	*Lucicutia flavicornis* (Claus, 1863).
<0.1	-	-	-		*L. ovalis* Wolfenden, 1911.
-	6.5 ± 7.2	9.9 ± 10.1	57.2 ± 30.3	10.87	*Mecynocera clausi* Thompson, 1888.
2.5 ± 4.4	15.3 ± 21.2	6.9 ± 8.3	173.0 ± 88.3	17.83	*Nannocalanus minor* (Claus, 1863).
2.9 ± 2.8	531.0 ± 229.6	862.4 ± 582.1	2930.1 ± 1059.9	12.57	*Paracalanus parvus* (Claus, 1863).
16.7 ± 20.7	1188.2± 855.0	3760.5 ±2597.1	11295.3± 4814.1	11.61	*Paracalanus* (copepodites)
-	<0.1	-	2.6 ± 1.8	3.55	*Pleuromamma gracilis* (Claus,1863).
1.6 ± 3.2	0.8 ± 1.4	-	1.9 ± 4.9	0.32	*Pontellina plumata* (Dana, 1849).
1.1 ± 1.5	-	-	-		*Scolecithricella dentata* (Giesbrecht, 1892).
-	0.8 ± 1.1	0.9 ± 2.2	-	0.03	*Scolecithrix danae* (Lubbock,1856).
-	-	-	138.4 ± 53.5	25.37	*Temora discaudata* Giesbrecht,1889.
-	32.3 ± 28.2	20.2 ± 21.5	268.0 ± 206.4	7.95	*Tortanus gracilis* (Brady, 1883).
<0.1	6.0 ± 5.2	0.8 ± 1.9	1.6 ± 5.4	4.12	*Undinula darwinii* (Lubbock, 1860).

Table 1 (continued)

Station 1 Behind Reef	Station 2 Mid-Lagoon				
Winter 1972	Winter 1972	Winter 1974	Summer 1974	F-values	Species
					Calanoid Copepods (contd.)
<0.1	88.8 ± 42.4	132.7 ± 71.5	205.8 ± 59.7	2.98	*U. vulgaris* (Dana, 1849).
0.7 ± 1.3	274.8 ± 168.7	412.5 ± 271.2	132.9 ± 48.7	4.38	*Undinula* (copepodites)
					Cyclopoid Copepods
-	2.6 ± 4.2	1.0 ± 2.3	-	1.68	*Copilia mirabolis* Dana, 1852.
4.1 ± 4.2	11.1 ± 12.0	10.5 ± 10.6	54.3 ± 35.2	8.05	*Corycaeus agilis* Dana, 1849.
-	0.1	-	-		*C. asiaticus* F. Dahl, 1894.
2.1 ± 3.7	8.6 ± 6.9	21.3 ± 16.9	85.3 ± 51.5	11.84	*C. catus* F. Dahl, 1894.
1.4 ± 2.7	2.9 ± 4.2	3.3 ± 4.8	21.8 ± 28.9	3.46	*C. crassiusculus* Dana, 1849.
-	<0.1	-	<0.1	0.01	*C. flaccus* Giesbrecht, 1891.
-	1.5 ± 2.5	1.0 ± 2.3	-	0.64	*C. latus* Dana, 1848.
-	0.6 ± 0.6	0.4 ± 1.4	-	0.28	*C. lautus* Dana, 1849.
<0.1	<0.1	<0.1	-	0.01	*C. limbatus* ? Brady, 1883.
-	0.6 ± 1.9	0.8 ± 2.6	-	0.15	*C. longistylis* Dana, 1849.
9.6 ± 17.4	176.5 ± 111.1	251.3 ± 110.0	585.8 ± 385.8	6.92	*C. medius* Gurney, 1926.
0.9 ± 1.1	8.8 ± 7.2	6.4 ± 6.7	24.9 ± 18.8	5.26	*C. speciosus* Dana, 1849.
-	-	-	68.0 ± 47.9	12.86	*C. tenuis* Giesbrecht, 1891.
-	<0.1	-	-		*C. typicus* (Kroyer, 1849).

Table 1. (continued)

Station 1 Behind Reef	Station 2 Mid-Lagoon				
Winter 1972	Winter 1972	Winter 1974	Summer 1974	F-values	Species
					Cyclopoid Copepods (contd.)
-	0.2 ± 0.6	0.6 ± 2.0	-	0.37	*C. vitreus* Dana, 1849.
22.0 ± 26.4	62.0 ± 37.4	186.3 ± 82.4	843.8 ± 487.2	13.93	*Corycaeus* & *Farranula* (copepodites)
3.2 ± 2.9	4.7 ± 4.4	11.3 ± 18.9	29.0 ± 22.8	5.10	*Farranula carinata* (Giesbrecht, 1891).
8.8 ± 8.9	19.5 ± 10.6	7.5 ± 8.3	28.8 ± 24.8	3.88	*F. concinna* (Dana, 1849).
9.6 ± 6.4	17.9 ± 15.8	13.9 ± 13.4	40.0 ± 21.5	4.48	*F. gibbula* (Giesbrecht, 1891).
-	<0.1	-	<0.1	0.02	*Lubbochia squillimana* Claus, 1863.
7.0 ± 8.1	1148.3 ± 1089.0	3326.3 ± 1810.1	7201.1 ± 2100.1	12.05	*Oithona nana* (Claus, 1863).
7.9 ± 6.4	17.0 ± 17.6	16.1 ± 13.6	320.9 ± 124.1	24.87	*O. plumifera* Baird, 1843.
1.3 ± 2.1	-	-	-		*O. pseudofrigida* (Giesbrecht, 1902).
2.7 ± 6.7	89.8 ± 74.3	230.1 ± 152.8	1521.8 ± 827.6	16.07	*O. rigida* Giesbrecht, 1898.
-	16.3 ± 12.3	19.0 ± 13.6	89.5 ± 62.9	8.17	*O. tenuis* Rosendorn, 1917.
13.2 ± 9.7	193.6 ± 127.5	756.6 ± 317.6	3368.8 ± 1320.5	17.95	*Oithona* (copepodites)
6.5 ± 5.2	69.3 ± 41.9	62.8 ± 35.4	134.9 ± 52.5	2.93	*Oncaea media* Giesbrecht, 1891.
3.8 ± 4.1	17.3 ± 13.7	16.6 ± 24.1	21.7 ± 17.8	0.03	*O. venusta* Philippi, 1843.
1.1 ± 2.2	1.7 ± 2.9	0.4 ± 1.4	-	0.32	*Sapphirina stellata* Giesbrecht, 1891.
	0.2 ± 0.6	3.3 ± 7.6	-	2.13	*Saphirella tropica* Wolfenden, 1905.

Table 1. (continued)

Station 1 Behind Reef	Station 2 Mid-Lagoon				
Winter 1972	Winter 1972	Winter 1974	Summer 1974	F-values	Species
					Cyclopoid Copepods (contd.)
0.7 ± 1.2	-	-	-		Unknown cyclopoids.
					Harpacticoid Copepods
4.1 ± 4.1	-	-	-		*Amphiascopsis cinctus* (Claus,1866).
2.7 ± 4.6	-	-	-		*Amphiascus coralicola* Sewell, 1940.
5.7 ± 5.1	-	-	-		*Amphiascus* sp.
4.0 ± 6.0	-	-	-		*Clytemnestra rostrata* Brady,1883.
1.6 ± 2.9	-	-	-		*C. scutellata* Dana, 1849.
1.2 ± 2.1	-	-	-		*Dactylopoda* sp.
1.9 ± 2.6	-	-	-		*Eudactylopus andrewi* Sewell, 1940.
0.9 ± 2.2	-	-	-		*E. anomala* Sewell, 1940.
1.6 ± 2.9	-	-	-		*E. fasciatus* Sewell, 1940.
1.2 ± 2.1	-	-	-		*Eudactylopus* sp.
2.3 ± 4.9	-	-	-		*Harpacticus* spp.
2.7 ± 4.0	-	-	-		*Laophonte* sp.
1.6 ± 2.9	-	-	-		*Longipedia coronata* Claus, 1866.
2.2 ± 3.0	-	-	-		*L. weberi* A. Scott, 1909.
2.7 ± 2.8	-	-	-		*Macrosetella gracilis* Dana, 1852.

Table 1. (continued)

Station 1 Behind Reef	Station 2 Mid-Lagoon				
Winter 1972	Winter 1972	Winter 1974	Summer 1974	F-values	Species
					Harpacticoid Copepods (contd.)
2.3 ± 3.1	-	-	-		*Metamphiascopsis hirsutus* (Thompson & A. Scott, 1903).
1.8 ± 1.6	-	-	-		*Metis* spp.
1.4 ± 2.1	3.0 ± 3.6	18.8 ± 18.7	144.2 ± 150.1	6.47	*Microsetella rosea* (Dana, 1847).
1.5 ± 2.1	-	-	-		*Peltidium* spp.
1.1 ± 2.3	-	-	-		*Tegestes* sp.
2.3 ± 3.2	4.2 ± 4.2	4.0 ± 5.4	9.8 ± 13.1	0.82	Unknown harpacticoids
					Monstrilloid Copepods
1.2 ± 3.1	-	0.5 ± 1.7	-	1.30	*Monstrilla* sp.
56.0 ± 35.3	1290.7 ± 988.8	1623.9 ± 1085.1	5123.2 ± 1429.4	12.15	Copepod Nauplii
50.9 ± 45.1	1195.6 ± 776.2	1405.6 ± 507.1	4887.1 ± 1667.6	14.09	Copepod Copepodites
7.8 ± 4.6	1.2 ± 3.8	1.4 ± 2.1	0.8 ± 2.6	0.08	Ostracods
0.6 ± 1.4	3.6 ± 5.7	7.5 ± 12.9	0.6 ± 2.0	2.10	Cladocera
					Chaetognaths
-	0.2 ± 0.4	-	-	0.06	*Pterosagitta draco* Krohn, 1853.
-	-	0.6 ± 0.9	-	0.11	*Sagitta bipunctata* Quoy and Gaimard, 1827.
4.3 ± 5.2	298.7 ± 169.6	365.0 ± 215.6	2199.8 ± 1022.7	13.23	*S. enflata* Grassi, 1881.

Table 1. (continued)

Station 1 Behind Reef	Station 2 Mid-Lagoon				
Winter 1972	Winter 1972	Winter 1974	Summer 1974	F-values	Species
					Chaetognaths (contd.)
1.0 ± 1.7	21.6 ± 19.4	47.2 ± 26.6	90.5 ± 33.9	6.48	*S. neglecta* Aida, 1897.
8.5 ± 7.6	10.3 ± 9.5	17.6 ± 25.0	60.8 ± 47.1	4.39	*S. regularis* Aida, 1897.
-	5.9 ± 6.7	4.1 ± 5.5	3.1 ± 5.9	0.67	*S. serrafodentata* Tokioka, 1936.
8.8 ± 10.1	21.8 ± 11.7	38.9 ± 25.8	160.8 ± 68.4	13.49	Sagitta (juveniles)
					Larvaceans
3.7 ± 5.1	21.9 ± 17.1	26.7 ± 14.1	148.3 ± 121.3	6.10	*Fritillaria* spp.
6.3 ± 8.9	89.6 ± 58.4	33.7 ± 20.0	187.1 ± 124.4	5.55	*Oikopleura intermedia* Lohmann, 1896.
-	2.3 ± 3.4	2.2 ± 1.8	-	0.47	*O. fusiformis* Fol, 1872.
143.4 ± 127.9	1558.9 ± 1242.5	2098.8 ± 1683.5	5489.7 ± 2462.6	6.52	*O. longicaudata* (Vogt, 1854).
0.5 ± 0.6	1.7 ± 1.9	-	-	0.81	*O. parva* Lohmann, 1896.
5.5 ± 6.3	105.8 ± 89.2	98.7 ± 62.8	501.5 ± 245.1	12.27	*O. rufescens* Fol, 1872.
11.5 ± 14.3	21.8 ± 10.9	34.1 ± 21.0	86.4 ± 29.8	3.72	*Oikopleura* (juveniles)
					Mysiids
1.7 ± 2.5	0.6 ± 1.3	0.5 ± 1.7	1.3 ± 4.1	0.31	*Anchialina* grossa Hansen, 1910.
3.9 ± 4.8	4.6 ± 9.9	10.1 ± 15.9	2.8 ± 7.7	1.21	*A. typica* (Kroyer, 1861).
2.6 ± 3.8	0.2 ± 0.4	0.8 ± 1.6	-	1.02	*Gastrosaccus indicus* Hansen,1910.

Table 1. (continued)

Station 1 Behind Reef	Station 2 Mid-Lagoon				
Winter 1972	Winter 1972	Winter 1974	Summer 1974	F-values	Species
					Mysiids (contd.)
3.6 ± 6.8	-	-	-		*G. pacificus* Hansen, 1912.
0.6 ± 1.9	-	-	-		*G. parvus* Hansen, 1910.
2.7 ± 5.8	-	-	-		*Gastrosaccus* sp.
10.8 ± 22.9	-	-	-		*Metamblyopsis* sp.
1.7 ± 2.9	-	-	-		*Pseudanchialina inermis* Illig., 1906.
2.9 ± 4.6	-	-	-		Unknown Mysiids.
					Euphausiids
12.6 ± 25.3	82.9 ± 112.4	48.5 ± 45.8	18.3 ± 15.9	2.49	*Pseudeuphausia latifrons* (Sears, 1885)
3.4 ± 3.8	28.6 ± 40.2	28.9 ± 60.4	38.4 ± 38.1	0.01	*P. latifrons* (juveniles)
					Amphipods
-	0.2 ± 0.5	0.6 ± 1.2	-	1.24	*Hyperia dysschistus* Stebbing, 1888.
-	8.8 ± 3.7	26.3 ± 26.7	63.1 ± 33.7	10.29	*H. hydrocephalia* Vosseler, 1901.
-	2.3 ± 6.6	2.4 ± 3.4	-	1.11	*Synopia ultramarina* Dana, 1849.
9.7 ± 13.7	-	-	-		Isopods

Table 1. (continued)

Station 1 Behind Reef	Station 2 Mid-Lagoon				
Winter 1972	Winter 1972	Winter 1974	Summer 1974	F-values	Species
					Siphonophores
-	0.6 ± 1.3	1.1 ± 2.5	2.3 ± 5.8	0.22	*Abylopsis tetragona* Otto, 1823.
0.1 ± 0.2	0.1 ± 0.1	2.5 ± 3.3	8.3 ± 7.8	2.91	*Bassia bassensis* Quoy and Gaimard, 1834.
-	0.1 ± 0.1	0.1 ± 0.3	-	0.09	*Chelophyces contorta* Lens and Van Riemsdijk, 1908.
-	0.3 ± 0.3	-	0.2 ± 0.3	0.06	*Diphyes chamissonis* Huxley, 1858.
0.3 ± 0.9	2.8 ± 4.9	1.7 ± 2.5	5.0 ± 11.0	0.78	*D. dispar* Chamisso and Eysenhardt, 1821.
-	0.2 ± 0.6	1.6 ± 3.7	3.8 ± 7.7	1.37	*Lensia subtilis* Chun, 1885.
-	<0.1	-	-		*L. subtiloides* Lens and Van Riemsdijk, 1908.
-	-	-	4.4 ± 3.1	12.17	*Lensia* sp.
-	0.2 ± 0.2	0.7 ± 2.3	2.0 ± 2.7	0.93	Ctenophores
1.7 ± 0.4	12.9 ± 10.5	22.8 ± 18.5	98.8 ± 72.9	9.52	Medusae
					Pteropods
3.4 ± 5.3	22.6 ± 14.2	77.2 ± 29.4	1879.3 ± 1834.4	9.57	*Creseis acicula* Rang, 1828.
1.9 ± 1.6	2.9 ± 1.4	3.2 ± 3.0	14.1 ± 5.3	3.53	*Limacina* sp.

Table 1. (continued)

Station 1 Behind Reef	Station 2 Mid-Lagoon				
Winter 1972	Winter 1972	Winter 1974	Summer 1974	F-values	Species
					Larvae
63.1 ± 76.7	39.5 ± 20.8	58.3 ± 31.2	211.4 ± 84.7	13.51	Brachyura zoea
3.2 ± 6.4	1.4 ± 1.3	2.3 ± 4.4	3.1 ± 4.6	0.95	Brachyura megalopa
28.6 ± 39.5	77.0 ± 58.5	137.1 ± 83.8	357.5 ± 70.4	12.01	Decapod larvae
10.2 ± 11.7	11.1 ± 12.2	20.4 ± 14.1	9.3 ± 8.7	1.94	Echinopluteus
89.8 ± 56.5	17.5 ± 19.5	27.1 ± 24.8	43.6 ± 26.6	1.45	Fish eggs
11.9 ± 25.4	20.0 ± 13.3	7.2 ± 9.8	70.7 ± 33.2	12.16	Fish larvae
3.8 ± 4.7	0.2 ± 0.4	3.1 ± 2.6	13.4 ± 5.7	4.22	Gastropod larvae
2.9 ± 3.7	9.1 ± 16.6	5.9 ± 6.8	67.9 ± 57.5	7.53	Polychaete larvae
5.3 ± 5.5	-	-	-		Sponge gemmules
					Dinoflagellates
31.4 ± 21.1	54.5 ± 31.7	135.3 ± 75.2	993.2 ± 484.9	20.90	*Ceratium* spp.
-	<0.1	0.1 ± 0.2	<0.1	0.45	*Dissodinium lunula* (Schutt) Taylor, 1972.
3.0 ± 3.0	1.9 ± 2.7	4.0 ± 5.2	-	4.06	*Pyrocystis fusiformis* Thompson ex Murray, 1876.
46.0 ± 27.3	41.0 ± 24.5	154.2 ± 55.3	429.3 ± 160.4	16.88	*P. pseudonoctiluca* Thompson ex Murray, 1876.

Table 2. The number of species and species diversity indices (Shannon and Brillouin) for each zooplankton sample from the mid-lagoon, Station 2, at Enewetak Atoll.

WINTER 1972				WINTER 1974				SUMMER 1974			
DATE	NO. OF SPECIES	SHANN. $\bar{H}$	BRILL. $\bar{H}$	DATE	NO. OF SPECIES	SHANN. $\bar{H}$	BRILL. $\bar{H}$	DATE	NO. OF SPECIES	SHANN. $\bar{H}$	BRILL. $\bar{H}$
1/01	66	3.814	3.781	1/27	64	4.070	4.032	6/16	62	3.867	3.827
1/05	71	3.871	3.834	1/30	61	3.751	3.710	6/20	60	3.951	3.910
1/06	77	4.169	4.133	2/02	62	4.252	4.219	6/23	65	4.028	3.988
1/08	66	3.487	3.452	2/04	65	3.976	3.939	6/28	69	4.003	3.962
1/10	68	3.735	3.705	2/06	65	3.544	3.504	7/01	60	3.698	3.662
1/13	63	4.195	4.158	2/09	58	3.813	3.779	7/05	62	4.153	4.111
1/15	66	3.775	3.742	2/12	75	3.850	3.810	7/13	62	3.919	3.885
1/23	69	3.595	3.561	2/16	59	3.806	3.769	7/18	57	4.196	4.154
1/27	66	3.937	3.903	2/22	60	3.216	3.178	7/24	63	3.943	3.901
1/29	71	4.213	4.178	2/25	66	4.130	4.094	7/28	60	3.652	3.614
				2/27	56	3.325	3.289	8/02	59	3.770	3.733
				3/01	60	3.886	3.851	8/07	56	3.826	3.787
$\bar{X}$ ±	68.3±	3.879±	3.845±		62.6±	3.801±	3.765±		62.0±	3.917±	3.878±
$S_{\bar{X}}$	3.8	0.249	0.250		4.8	0.311	0.311		3.1	0.166	0.162