AGENCY FOR INTERNATIONAL DEVELOPMENT
WASHINGTON, D. C. 20523

BIBLIOGRAPHIC INPUT SHEET

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1. SUBJECT CLASSIFICATION

A. PRIMARY: Agriculture

B. SECONDARY: Fisheries

2. TITLE AND SUBTITLE

Ingestion of detritus by the lagoon pelagic community at Eniwetok Atoll

3. AUTHOR(S)

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4. DOCUMENT DATE	5. NUMBER OF PAGES	6. ARC NUMBER
1974	11 p.	ARC

7. REFERENCE ORGANIZATION NAME AND ADDRESS

International Center for Marine Resource Development
University of Rhode Island, Kingston, Rhode Island 02881

8. SUPPLEMENTARY NOTES *(Sponsoring Organization, Publishers, Availability)*

(In Limnology and oceanography, v.19, no.5, p.815-824)

9. ABSTRACT

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10. CONTROL NUMBER

PN-AAC-149

11. PRICE OF DOCUMENT

12. DESCRIPTORS

Detritus
Ingestion
Lagoons
Marine fishes
Ocean environments
Pacific islands
Reefs

13. PROJECT NUMBER

14. CONTRACT NUMBER

CSD-2455 211(d)

15. TYPE OF DOCUMENT

AID 590-1 (4-74)

INGESTION OF DETRITUS BY THE LAGOON PELAGIC COMMUNITY AT ENIWETOK ATOLL

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Reprinted from Limnology and Oceanography
Vol. 19, No. 5, September 1974
pp. 815–824
Made in the United States of America

Ingestion of detritus by the lagoon pelagic community at Eniwetok Atoll

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Abstract

The gut contents of *Undinula vulgaris* (a calanoid copepod) collected from Eniwetok lagoon consisted of about 95% detritus with only 2% of the gut material fluorescing as chlorophyll. That of *Oikopleura longicaudata* (a larvacean) consisted of about 89% detritus with only 6% fluorescing as chlorophyll. By contrast, the gut contents of the calanoid copepod, *Acartia tonsa*, from Narragansett Bay, Rhode Island, consisted of about 34% detritus with 36% of the gut material fluorescing as chlorophyll. The remaining material in the gut of all these organisms included various microorganisms and diatom frustules.

Plankton-feeding fishes from behind a reef and island were found to have consumed both zooplankton and detrital algal fragments.

[illegible] levels of particulate carbon and nitrogen in the lagoon, which had a lower C:N ratio than found in the incoming oceanic water, indicated that reef detritus enriches the lagoon environment.

Little is known of the productivity and of the food chains in lagoon waters behind coral reefs. Extremely low primary production in typical coral atoll lagoons is indicated by low chlorophyll values, by approximations of phytoplankton abundance, and by data on ^{14}C uptake (e.g. Johnson 1954; Gilmartin 1958; Jeffrey 1968; Michel 1969). Recently, various workers have been stressing the potential of organic matter exported from the reef as an additional primary food source available in lagoons. Reef export studies (e.g. Marshall 1965; Klim 1969; Qasim and Sankaranarayanan 1970; and our work in progress) indicate an abundance of particulate organic matter in the form of benthic algal fragments, fecal pellets, coral mucus, and aggregated organic matter flowing into the lagoon. Such export might support the zooplankton concentrations known to be consistently higher in lagoons than in the surrounding oceanic waters (e.g. Russell 1934; Motoda 1938). Furthermore our own underwater observations, supported by those of Johannes and Randall (personal communications) on the feeding habits of certain plankton-feeding fishes, suggested that reef detritus was being consumed in addition to zooplankton.

No one has tested the suggestion that organic export from the reef is consumed by the basic consumer populations in the lagoons. To provide evidence on this matter, we have analyzed the stomach contents of two zooplankters collected from lagoon stations: a tropical filter-feeding calanoid copepod, *Undinula vulgaris*, predominately neritic and a lagoon form in these environments (Johnson 1954; E. C. Jones personal communication), and the larvacean, *Oikopleura longicaudata*. Also, several species of plankton-feeding fishes from selected patch reef or coral knoll stations were collected for gut analysis. For comparison, gut analyses were performed on the typically neritic copepod, *Acartia tonsa*, from Narragansett Bay, Rhode Island, a productive temperate area.

The relative abundance in the lagoon of reef-derived algal fragments, total particulate carbon and nitrogen, and chlorophyll were analyzed to determine the relationship between stomach contents and food available from the same stations.

We are especially indebted to P. Helfrich for his cooperation and support at Eniwetok and to J. E. Randall for his assistance in collecting the fishes. We would also like to thank M. E. Q. Pilson, T. A. Napora, S. V. Smith, and M. Fine for critical reading of the manuscript.

Materials and methods

Four stations were sampled (Fig. 1) at Eniwetok Atoll, Marshall Islands, from 31

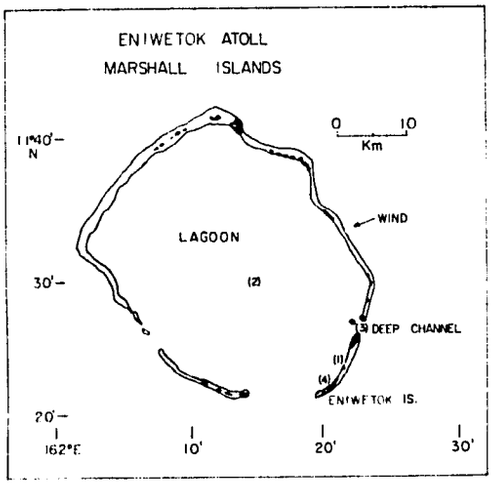

Fig. 1. Locations of sampling stations (shown in parentheses) at Eniwetok Atoll, Marshall Islands. Stippled areas indicate islands; clear outlined areas indicate reef tracts.

December 1971 to 8 February 1972. Station 1 was located along an interisland reef in the zone of larger coral heads about 200 m behind the reef crest. This station was about 8 m deep and characterized by a continuous unidirectional flow of water from in front of the reef, created by the heavy surf breaking across the reef crest. Station 2 was located about 8–10 km northwest of Eniwetok Island well into the lagoon, in about 50 m of water. Station 3 was in the southeastern pass, or deep channel, with an average depth of 31 m. A pinnacle reef or knoll on the northern side of this pass, harboring many plankton-feeding fishes, served as a collection source for these forms. Water from outside the atoll enters the lagoon via this pass. Station 4 was situated in about 6 m of water in scattered patch reefs about 200 m on the lagoon side of Eniwetok Island.

Plankton was collected with a 0.5-m No. 6 nylon plankton net (mesh 0.239 mm), having an internally mounted flowmeter, by oblique tows made from about 30 m in the deeper water and 4 m in shallow areas. Since the shallow stations, 1 and 4, were largely devoid of *U. vulgaris* and *O. longicaudata*, zooplankton gut analyses were confined to samples from stations 2 and 3. Plankton samples used for gut analysis were preserved in 5% glutaraldehyde in seawater, kept on ice and in the dark as recommended by the National Research Council, Committee on Oceanography (1969). *Acartia tonsa* from Narragansett Bay were collected and treated in the same manner.

The entire stomach contents of *O. longicaudata* and only the foregut material of the copepods were analyzed. Only specimens with full or nearly full stomachs were used. After a given specimen was teased apart, the various components of the gut contents were identified and measured under a microscope with an ocular micrometer. Then, with fluorescence microscopy (Wood 1962) and a Whipple micrometer disk, the percent by area of fluorescing (red and green) material was determined for the contents of each gut. The technique of quantifying the contents by area, as flattened on a slide, indicates the relative amounts of the various food particles ingested and potentially available for assimilation.

Spear-fishing, rotenone poisoning, and netting were used to collect the plankton-feeding fishes, which were also preserved in 5% gluteraldehyde and kept on ice and in the dark. Components of the gut material were identified under a dissecting microscope and their settled volume estimated with a small graduated cylinder.

Total particulate carbon was determined by filtering 9–10 liters of seawater through a pad of two Gelman type A glass-fiber filters, precombusted at 450°C for 3 hr. The filters were stored under vacuum desiccation and, using a CHN analyzer, combusted at 725°C, at which temperature carbonate interference is minimal (Telek and Marshall 1974). The top filter was assumed to collect both particulate and adsorbed organic matter whereas the lower was assumed to collect only adsorbed, and its value was deducted to give a corrected particulate value.

Chlorophyll *a* and total pheo-pigments

Table 1. Results of the zooplankton gut analyses, expressed as the percent by area of the total gut content area. (±) 95% confidence limits of the mean are shown when the item occurred in all the guts; otherwise, only the mean and the number of organisms (in parentheses) in which the item occurred are shown. Underscoring of adjacent means indicates no significant difference at the 95% level (Duncan's new multiple range test: Steel and Torrie 1960).

	U. vulgaris Midlagoon Sta 2 N=35 2.56±0.12	*U. vulgaris* Deep channel Sta 3 N-23 2.66±0.11	*O. longicaudata* Midlagoon Sta 2 N=23 7.17±0.49	F-values*	*A. tonsa* Narr. Bay, R.I. N=23 1.40±0.03
Amorphic, non-fluor.	91.8±1.7	85.5±8.6	85.0±0.2	7.74	33.9±8.8
Granular, non-fluor.	4.8±1.2	2.6±0.5	3.9±0.8	3.23	-
Large cells	1.5 (8)	1.8 (5)	1.8±0.4		1.0 (3)
Small cells	1.0 (12)	1.2 (5)	0.7±0.1		1.0 (13)
Microflag.	0.5 (3)	0.5 (4)	1.0±0.2		-
Diatoms/frag.	0.5 (6)	0.5 (4)	0.7 (13)		36.0±5.0
Radiolaria/frag.	2.4 (18)	10.5 (9)	-		-
Red fluor.	1.3±0.3	1.9±0.8	6.3±1.2	58.21	30.5±5.4
Green fluor.	0.9 (13)	1.8 (11)	1.2 (16)		-

* Original data were transformed to ARCSIN functions for analysis of variance and range test (Snedecor and Cochran 1967).

were determined by filtering 3–4 liters of seawater onto HA Millipore filters of 0.45-μ pore diameter. The filters were stored frozen and later analyzed by the method of Strickland and Parsons (1968).

Results

The results of the zooplankton analyses are summarized in Table 1. These data show a predominance of the nonfluorescing amorphic material in the guts of specimens from Eniwetok. This material appeared as a conglomerate of undifferentiated particles lacking observable structural remnants of tissues or cells. Under white light it was mostly translucent and varied from light to very dark brown. Even the gut contents of *A. tonsa* from Narragansett Bay contained a substantial amount of this amorphic material. A small undetermined amount of clear mucus, perhaps secreted by the gut lining, was occasionally noted.

Nonfluorescing granular material, occurring only in the Eniwetok specimens, did not appear to be the remains of skeletal fragments of microorganisms since the individual granules were smooth, irregular in size and shape, and lacked surface features such as pits or grooves characteristic of skeletal fragments. Some may have been small bits of calcium carbonate such as Johannes (1967) observed in the mucus flocs streaming off corals at Eniwetok.

Generally, large nonfluorescing cells (12.5–28.0 μ) without skeletal structure constituted < 2% of the gut area. Only in *O. longicaudata* did they occur regularly. Microscopic examinations of these cells suggest that some, at least, may be dinoflagellates and protozoans.

The gut contents of *U. vulgaris* and *A. tonsa* were largely devoid of small naked nonfluorescing cells (4.0–10.0 μ) and microflagellates, yet they occurred in almost every *O. longicaudata* gut analyzed. In the case of the Eniwetok specimens, these small cells were primarily coccolithophores, and perhaps some bacteria.

Though these foregoing cell types did not fluoresce red, it is possible that some had contained chlorophyll which was decomposed in the gut.

Table 2. The gut content analyses of plankton-feeding fishes, expressed as the percent by volume. (±) 95% confidence limits of the mean are shown when N ≥ 4; otherwise only the mean is given.

	Chromis caeruleus			*Dascyllus aruanus*		*D. reticulatus*			*Abudefduf cymatobo*		*Pomacentrus vaiuli*		*Pomacentrus pavo*	*Acanthurus thompsoni*
	Sta 1* N=11	Sta 3 N=8	Sta 4 N=20	Sta 1 N=9	Sta 4 N=5	Sta 1 N=4	Sta 3 N=4	Sta 4 N=11	Sta 1 N=1	Sta 3 N=1	Sta 1 N=2	Sta 3 N=3	Sta 4 N=2	Sta 3 N=8
	52.1±7.0	48.6±4.9	41.6±5.1	32.3±10.7	21.2±4.6	67.3±2.9	55.5±5.0	19.8±4.1	77.0	89.0	54.0	43.0	58.0	139.0
Calanoid copepods	12.8±3.5	15.3±4.4	9.7±5.3	10.8±5.7	0.6±1.0	21.5±16.6	6.3±2.9	3.6±2.1	11.0	2.0	1.0	-	8.0	24.0
Cyclopoid copepods	23.3±6.4	17.4±3.8	13.5±3.9	29.3±9.1	10.0±4.6	27.0±18.7	14.5±5.8	13.5±3.3	21.0	1.0	3.5	1.7	31.5	14.5
Harpacticoid cop.	17.5±9.1	3.6±1.7	34.7±6.7	17.0±6.5	39.2±4.1	7.5±6.5	-	41.1±3.2	-	-	4.0	14.3	3.0	0.5
Decapod larvae	3.4±3.6	3.1±2.0	1.7±1.0	1.3±1.0	1.2±1.5	4.3±2.9	4.3±6.5	2.0±1.8	17.0	-	0.5		2.0	-
Brachyura zoea	-	-	-	0.7±1.0	0.4±1.0	-	-	-	-	-	-	-	-	-
Isopods	-	-	0.4±0.5	-	-	-	-	-	-		-	-	-	-
Gammarid amph.	-	-	-	-	-	-	-	-	-	-	-	-	-	3.5
Ostracods	-	0.9±1.2	1.7±1.3	0.1±0.3	1.2±2.0	-	0.7±2.2	1.9±1.9	-	-	-	-	-	-
Crustacea frag.	-	-	-	-	-	-	-	-	11.0	-	-	-	-	11.5
Gastropod larvae	1.0±0.9	-	2.1±1.3	0.7±0.8	-	-	-	2.5±1.7	-	-	-	1.0	0.5	1.0
Pteropods	-	1.9±1.7	-	-	-	-	-	-	6.0	-	-	-	-	3.5
Round worms+	2.1±1.7	-	0.3±0.2	2.7±2.6	-	-	-	-	-	2.0	-	-	1.5	-
Polychaete larvae	-	-	2.8±4.2	-	-	1.3±2.2	-	-	-	-	-	-	-	-
Fish eggs	2.2±2.6	54.6±9.9	18.7±8.8	2.0±1.6	1.6±2.6	0.8±1.4	71.5±10.8	0.5±1.1	6.0	-	1.5	-	2.0	6.5
Fish larvae	0.2±0.4	-	-	-	-	-	-	-	-	-	-	-	-	-
Larvaceans	17.8±13.5	-	-	-	-	1.2±3.6	-	-	17.0	89.0	-	-	-	4.0
Foraminifera	2.1±0.7	3.3±2.3	4.0±1.5	1.6±0.5	2.8±1.0	1.3±0.7	1.5±2.2	3.4±1.5	3.0	5.0	2.0	2.3	1.5	3.5
Algal frag.	17.5±6.4	-	10.9±5.6	33.7±15.6	38.2±8.7	37.0±18.7	2.5±2.2	31.4±3.7	8.0	1.0	87.5	80.7	50.0	-
Fecal pellets	-	-	-	-	4.8±6.6	-	-	-	-	-	-	-	-	16.0

*Station locations: Sta 1 - near reef; sta 3 - deep channel; sta 4 - near island.
+These may be parasitic.

More than half of the *O. longicaudata* and less than a fifth of the *U. vulgaris* from Eniwetok contained pennate diatoms but, by area, these amounted to less than 1% of the gut contents in which they occurred. The gut contents of *A. tonsa* from Narragansett Bay, on the other hand, included, by area, about 36% diatom frustules and fragments of *Skeletonema* sp., *Rhizosolenia* sp., and *Thalassiosira* sp.

Radiolarian spines and body fragments occurred in the gut contents of about half the *U. vulgaris*, yet none was observed in gut contents of *O. longicaudata*.

The amount of red fluorescence (which may include detrital chlorophyll) in the gut contents of the Eniwetok specimens was very low compared to the amount in *A. tonsa* from Narragansett Bay. The size range of the red fluorescing particles, which may include individual chloroplasts in addition to nannoplankton and small diatoms, was 5.0–25.0 μ in diameter in *U. vulgaris* and 2.5–25.0 μ in *O. longicaudata*. The red fluorescing particles in *A. tonsa* were not measured.

Green fluorescing cells from 7.5–30.0 μ in diameter occurred in at least a third of the guts of *U. vulgaris* and in more than half of the *O. longicaudata*. The exact nature of these cells was not determined; however, small (2–10 μ) green fluorescing naked flagellates were observed by Pomeroy and Johannes (1968) in the Gulf Stream and Sargasso Sea. They suggest that these cells are autotrophic and that some accessory pigment masks the red fluorescence of chlorophyll. No green fluorescing cells were found in the gut contents of *A. tonsa* from Narragansett Bay.

Table 2 summarizes the results of the gut analyses on plankton-feeding fishes. This table indicates that, in addition to their diet of zooplankton, the fish are ingesting a substantial amount of detrital algal fragments. These algal fragments were readily distinguishable filamentous types, varying in size from a few cells to large fragments about a centimeter long. The amount of algal fragments in the gut of *Chromis caeruleus*, *Dascyllus reticulatus*, and *Dascyllus aruanus* from the near-reef station 1 and the near-island station 4 were not significantly different ($P > 0.45$, "Student's" *t*-test). Except for *Pomacentrus vaiuli*, the quantity of algal fragments in the guts of fishes from the coral knoll at station 3 was exceedingly small.

The abundance of calanoid and cyclopoid copepods and decapod larvae was greatest in the guts of fishes from station 1 and over the knoll at station 3, and lowest at station 4; the reverse was true for harpacticoid copepods. This trend may reflect the influx into the lagoon of oceanic water, which contains many more calanoids and cyclopoids than harpacticoids. Ostracods, gastropod larvae, polychaete larvae, fish larvae, and larvaceans occurred infrequently and only in the guts of fishes from stations 1 and 3. The greatest abundance of fish eggs was found in the guts of fishes from station 3, with little obvious differences between stations 1 and 4. Some fish contained fairly long coiled "round worms" in their gut, which appeared to be parasitic rather than planktonic.

In addition to those listed in Table 2, gut analyses were performed on the following plankton-feeding fishes: *Caesio caeruleureux*, *Caesio* sp., *Pterocaesio tile*, *Pterocaesio marri*, *Mirolabrichthys tuka*, *Amblyglyphidon curacae*, *Chromis ternatensis*, *Chromis agilis*, *Chromis atripectoralis*, *Chromis lepidoleptris*, *Chromis* sp., *Cirrhilabrus* sp., *Pseudocoris* sp., and family Branchiostegidae (two species). The gut contents of these fishes consisted almost exclusively of zooplankton; no reef detritus was found.

Underwater observations behind the reef at station 1 indicated a greater abundance of algal fragments than at the near-island station 4. Day net-plankton samples confirmed this observation (Table 3) and showed that remnants of *Calothrix* spp., *Asparagopsis taxiformis*, and *Dictyota* spp. made up the bulk of the samples, the zooplankton biomass (wet weight) being negligible.

Table 3. The average biomass of net plankton in mg m⁻³ (wet weight). Number of samples in parentheses.

	Sta 1 Near reef (8)	Sta 4 Near island (2)	Sta 2 Midlagoon (8)	Sta 3 Deep channel (3)
Algal frag.	23.5	15.5	-0-	-0-
Zooplankton	5.5	2.0	239.4	139.6

At the midlagoon station 2 and in the deep-channel station 3, algal fragments were not seen in underwater observations nor were any taken in plankton nets. These day samples consisted exclusively of zooplankton, of which there was more in the midlagoon than in the incoming oceanic water and the shallow areas behind the reef and island.

The data for particulate organic carbon (POC) and particulate organic nitrogen (PON) are summarized in Table 4 and treated statistically in Table 5. The concentration of POC at the near-reef station 1 was significantly higher than the deep-channel station 3, and the concentration of PON at station 1 was significantly higher than at the midlagoon station 2 and station 3. The ratio of particulate carbon to nitrogen increased from station 1 to station 3.

Table 6 indicates extremely low values for chlorophyll *a* and pheo-pigment at all stations at Eniwetok Atoll. The mean and 95% confidence limits of the combined lagoon chlorophyll *a* and total pheo-pigment samples are 0.10 ± 0.03 and 0.09 ± 0.06 mg m⁻³ respectively.

Discussion

Zooplankton nutrition

Eniwetok Atoll is located in the southern half of the North Equatorial Current in an unproductive oceanic area (Taniguchi 1972). Production in Eniwetok Lagoon and the North Equatorial Current is compared in Table 7. The slightly higher concentration of chlorophyll *a* and productivity in the lagoon than in the surrounding waters may largely reflect the input of reef algal detritus into the lagoon. Dissolved nutrients further indicate a minimal phytoplankton food base. Phosphate concentrations in the lagoon are similar to those in the North Equatorial Current and the ni-

Table 4. A comparison of the concentrations and ratios of particulate organic carbon and nitrogen in mg m⁻³. (±) 95% confidence limits of the mean shown at bottom of table along with the mean C:N ratio. Stations 1 and 2 sampled approximately every 2 days; station 3 sampled when weather permitted.

Jan 1972	Sta 1 - Near reef			Sta 2 - Midlagoon			Sta 3 - Deep channel		
	Carbon	Nitrogen	C:N	Carbon	Nitrogen	C:N	Carbon	Nitrogen	C:N
1	20.8	2.2	9:1	25.3	2.9	9:1	-	-	-
2	21.0	3.3	6:1	28.4	2.3	12:1	16.1	1.5	11:1
4	17.9	2.3	8:1	22.7	2.1	11:1	-	-	-
6	38.3	5.1	7:1	11.7	1.5	8:1	22.1	2.0	11:1
8	20.6	2.4	9:1	11.1	1.8	6:1	-	-	-
10	18.3	2.4	8:1	15.8	1.9	8:1	-	-	-
13	27.3	2.6	10:1	15.9	1.9	8:1	15.4	1.2	13:1
15	24.6	3.8	7:1	14.9	1.7	9:1	11.4	1.0	11:1
23	19.9	2.3	9:1	22.0	2.7	8:1	-	-	-
25	30.3	3.0	10:1	24.3	2.1	12:1	-	-	-
28	26.3	3.2	8:1	22.9	2.5	9:1	17.8	1.5	12:1
29	34.4	3.2	11:1	28.1	2.3	12:1	-	-	-
31	35.0	4.7	7:1	22.1	1.8	12:1	-	-	-
	25.75	3.12	8:1	20.40	2.11	10:1	16.56	1.44	12:1
	±4.15	±0.56		±3.54	±0.25		±4.82	±0.47	

Table 5. Statistical analysis of the particulate organic carbon (POC) and particulate organic nitrogen (PON) data in mg m⁻³. Underscored adjacent means = no significant difference at 95% level (Duncan's new multiple range test: Steel and Torrie 1960).

	Sta 1 Near reef	Sta 2 Midlagoon	Sta 3 Deep channel	*F-values from ANOVA
POC	25.75	20.40	16.56	4.89
PON	3.12	2.11	1.44	9.50

*Degrees of freedom - 28.

Table 6. The concentrations of chlorophyll a and total pheopigments in mg m⁻³. Stations 1 and 2 were sampled weekly; station 3 when weather permitted.

Jan 1972	Sta 1 Near reef		Sta 2 Midlagoon		Sta 3 Deep channel	
	Chl *a*	Pheo.	Chl *a*	Pheo.	Chl *a*	Pheo.
2	0.172	0.110	0.023	0.260	0.080	0.040
8	0.055	0.031	0.133	0.174	-	-
13	0.020	0.138	0.099	0.035	0.135	0.034
23	0.144	0.021	0.115	0.003	-	·

trate values recorded are less inside the atoll than in the ocean.

Hardy and Gunther (1935) suggested that radiolarians and foraminifera, which harbor symbiotic algae, assume the role of phytoplankton as primary producers and food for zooplankton in tropical oceans. This suggestion does not seem to apply to Eniwetok Lagoon where radiolarians, though the most abundant "photosynthetic" organisms found in the plankton samples, rarely occurred in the guts of *U. vulgaris* and not at all in *O. longicaudata*. The lagoon zooplankton, however, which consists of increased concentrations of oceanic forms as well as endemic types and larvae of reef fauna, is much richer than in the North Equatorial Current. The lagoon zooplankton must thus depend on some food source in addition to phytoplankton, and, as noted at the outset, the suggested source is reef detritus. This alternate food source is reflected in the higher levels of particulate organic carbon and nitrogen behind the reef and in the lagoon than in the incoming oceanic water. Typically, open ocean values for particulate organic carbon average about 10 mg m⁻³ (unpublished data), less than half that found in the lagoon.

The low carbon-to-nitrogen ratio of the suspended particulate organic matter in the lagoon also supports the concept of reef export as an alternate food source. Johannes et al. (1972) found that the C:N ratio of the suspended particulates changed from 15:1 in oceanic waters to 7:1 in the downstream end of the reef transect; they concluded that nitrogen fixation must be occurring at a high rate.

Recently Johannes (personal communication) has indicated that the blue-green algae *Calothrix*, remnants of which were abundant in our plankton samples behind the reef, is the major nitrogen fixer on the windward reefs. He believes it is a major

Table 7. Average values of parameters relating to primary production for Eniwetok Lagoon and the North Equatorial Current.

Area	Chl *a* (mg m⁻³)	Phytopl. (cell m⁻³)	Production (mg C m⁻³ hr⁻¹)	Zoopl.* (mg m⁻³)	PO_4-P (mg atom m⁻³)	NO_3-N (mg atom m⁻³)
Eniwetok Lagoon+	0.10 0.23	1.4×10^3	0.57	239	0.13	0.17
North Equatorial C‡	0.06	3.7×10^5	0.13	9	0.12	0.41

*Wet weights.
+First Chl *a* value and zooplankton wet weight, this study; second Chl *a* value and production, Doty and Capurro 1961; phytoplankton cells, Johnson 1954; PO_4-P value, Pilson and Betzer 1973; NO_3-N value, Johannes et al. 1972.
‡From Taniguchi 1972.

contributer, directly and through the food chain, to lowered C:N ratios in the lagoon.

We too found a low C:N ratio, and a ratio of 8:1 at the near-reef station 1. A ratio of 12:1 for the deep-channel station 3 is evidence that nitrogen enrichment affects the waters of the reef passes as well as those behind the reef proper. This may explain why we found no significant differences between the concentrations of POC and PON for stations 2 and 3. The midlagoon C:N ratio at station 2 is about halfway between the ratios at stations 1 and 3, perhaps due to mixing of the latter two sources or to a conversion of some of this detrital nitrogen to animal protein and excreta by consumer organisms.

Finally, gut analyses suggest that detritus is the most important food component of the lagoon zooplankton. Detrital material in the gut contents of the Eniwetok specimens may be composed partly of reef particulate organic matter from a wide range of possible sources, such as decomposed benthic algal fragments and fecal matter, which form the bulk of the reef detrital load (Johannes and Gerber in press), or of coral mucus flocs as suggested in Johannes (1967). It may even consist of particulate organic matter produced in the pelagic environment itself: fecal matter, or aggregated organic matter formed by mechanical and microbial processes or bacterioplankton (Baylor and Sutcliffe 1963; Sieburth 1968; DiSalvo 1970; Sorokin 1971).

Detritus is an important food source for pelagic zooplankton in other areas of the ocean. Detritus feeding is well documented for deep-sea forms and also occurs in various epipelagic open ocean areas in the tropical Pacific (Geinrikh 1958; Pomeroy and Johannes 1968; Arashkevich and Timonen 1970).

Our work suggests that detritus is also utilized by *A. tonsa* in a productive temperate zone estuary. It should be added that these copepods were collected in early November, when the phytoplankton standing crop was minimal (Smayda personal communication) and when detritus utilization would, theoretically, be at a maximum (Riley 1963).

The semiclosed circulation patterns of atoll lagoons, as interpreted from von Arx (1948), help retain endemic fauna including various larvae as well as oceanic zooplankton swept into the lagoon (Johnson 1954). The steady input to the lagoon of enriched particulate organic matter from the surrounding reefs, and to a much lesser extent from the ocean, seems to form the basis of this pelagic food web.

Plankton-feeding fishes

We have demonstrated that certain plankton-feeding fishes in reef areas consume suspended algal fragments in addition to zooplankton and show a diversified feeding habit that reflects their locality at the time of capture. For example, algal fragments were not recorded in the gut of *C. caeruleus* from stations 1 and 4 by Hiatt and Strasburg (1960). The precise location of their collection is not given, but it was presumably in an area relatively free of suspended algal fragments, as was station 3 in this study. Alternately, the lack of algal fragments could be due to a greater abundance of fish eggs, etc. in the plankton at the time of capture; these were preferred over other foods. Smith and Tyler (1973) suggested that such opportunistic feeding in reef fishes is important in maintaining community stability.

The gut contents of *D. aruanus* and *D. reticulatus* are remarkably similar to those of *C. caeruleus*, perhaps because all three species are territorial and generally feed close to the coral heads. The more or less solitary pomacentrid, *Pomacentrus pavo*, had about 50% zooplankton and 50% algal fragments in its gut. It was observed feeding on suspended particulates from the interstices of the coral branches and from midwater suspended particles. On the other hand, the gut contents of *Pomacentrus vaiuli* consisted almost exclusively of algal fragments and epibenthic harpacticoid copepods, suggesting a grazing feeding habit rather than planktonic. The gut con-

tents of *Abudefduf curacao* and *Acanthurus thompsoni* were dominated by pelagic zooplankton, with only a small amount of detrital algal fragments in *A. curacao* and none in *A. thompsoni*. However, the gut of *A. thompsoni* contained fecallike detrital material, perhaps of reef origin.

These findings further indicate that reef detritus, in the form of algal fragments, is consumed by certain lagoon fishes. The decomposition of this material by digestion within the fish may be a first step in its transformation to a form that can be readily consumed by lagoon zooplankton.

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Submitted: 18 February 1974
Accepted: 25 July 1974