Bikini and Nearby Atolls

Part 2. Oceanography (biologic)

Biologic Economy of Coral Reefs

Plankton of Northern Marshall Islands

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W. E. Wrather, *Director*

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MARSTON C. SARGENT[1] AND THOMAS S. AUSTIN[2]

ABSTRACT

The eastern reefs of Rongelap Atoll, composed of animals and attached algae, produce more organic matter than they consume. The productivity per unit area is considerably higher than that of adjacent waters or any other open marine areas. The zooxanthellae of the corals make a substantial contribution to the whole production, so that per unit of weight, actively growing reef corals may photosynthesize as fast as lithothamnia Review of work on other coral reefs indicates that these communities are generally self-maintaining.

INTRODUCTION

The coral atolls of the northern Marshall Islands are examples of a distinctive pelagic community of the Pacific Ocean. For thousands of miles in all directions they are surrounded by the communities common to all open oceans, of which the conspicuous members are plankton, fish, and birds. Only at some singular spots have a succession of crustal movements and biotic changes produced structures and biocycles strikingly different from their surroundings.

In one important respect the situation of these atolls is different from that of any coral reef where extensive studies in physiology and ecology have been conducted. Unlike fringing and barrier reefs, the reefs of these atolls are exposed to a steady one-directional wave-driven current of oceanic water as described by Von Arx (1948). As in a river, changes in the organic and inorganic content occur in this water as it crosses the reef, and if these changes are measured, conclusions can be drawn about the activities of the reef community. The most fundamental conclusion drawn from the observations recorded here is that atoll reefs are essentially self-sufficient communities, producing as much organic matter as they consume, or more. This is not necessarily true of barrier and fringing reefs where proximity of the land and stagnation of the waters overlying and adjoining the reefs may furnish conditions suitable for production of food of reef-building organisms quite independently of the presence of the reef. It may, however, be true of these reefs also, but not be easy to discern under the conditions prevailing.

In a previous brief report (Sargent and Austin, 1949) we have referred to reviews by Yonge (1940) and Shepard (1948) as covering the literature on coral biology and the geology of atolls. To these should be added several reports by Tracey, Emery, Ladd, and others on the geology of the northern Marshall Islands, which will be referred to below. Taylor's volume (1950) on the plants of Bikini Atoll also contains much unique and valuable information.

GEOGRAPHICAL SITUATION

In the present study several sets of measurements were made at two locations on the eastern reef of Rongelap Atoll and one set on the western reef. The morphology of these reefs is described by Tracey, Ladd, and Hoffmeister (1948) in a report which clearly demonstrates that it is difficult to draw a line between the geology and the biology of these structures or communities. Most measurements were made on the open reef between islands where the passage of water between sea and lagoon is unimpeded.

The eastern reef, in the classification of Tracey and others (1948), is type I-A. The smooth marginal *Lithothamnion* ridge rises only about a foot above the main reef flat and slopes gently seaward without development of high-standing buttresses. On the seaward face of the reef below low tide, spurs covered with living lithothamnia and corals and separated by grooves floored with debris reach to a depth of perhaps 15 meters. Behind the *Lithothamnion* ridge, generally 5 to 15 meters wide in these situations, is a roughly triangular zone of coral, narrow where islands approach closely to the *Lithothamnion* ridge but reaching back several hundred feet from the surf zone in the intervals between islands. The remainder of the reef to the lagoon edge is relatively barren of large fixed colonial creatures. Isolated coral colonies and small tufts of

algae project above the layer of sandy Foraminifera and inconspicuous matted algae that cover the flat. The total width of the reef at the locations studied is about 300 meters. Close to the islands on each side of an interval the reef is higher, exposed at low tide except for numerous tidepools, and largely devoid of life. This barren intertidal zone is in striking conrast with the densely populated intertidal zone of cooler seas.

The transport of water across the reef depends on the stage of the tide. The velocity change does not affect the transport as much as the change in depth. At low tide the *Lithothamnion* ridge may in spots be momentarily awash between breakers, and over the whole flat the depth may not exceed 20 centimeters. At high tide the depth on the flat may be more than a meter. The velocity over the reef flat meanwhile changes perhaps threefold with a minimum velocity around 30 centimeters per second. Depths were determined with a meter stick or, when necessary, by measurements on an observer who was carefully calibrated for the purpose. Velocities were measured by timing the passage of a small patch of fluorescein along a measured line. At this time of year (June–July) the surface of the water flowing across the reef is smooth except close to the surf zone, although no doubt at seasons of high wind it is commonly marked by whitecaps. The smoothness of flow is important for the measurements of changes in oxygen content in that it diminishes any tendency to establish equilibrium with the atmosphere. The flow occurs in pulses resulting from momentary changes of head as the breakers pile up on the face of the reef.

The western reef on which a few observations were made is type II–B–(1) according to the classification of Tracey and others (1948). The coral and algal reef with a steep front facing the sea and precipitous edges where blocks have been broken out has its highest level on the ocean side in the zone of weak surf. It gradually slopes down toward the lagoon, with larger and higher pinnacles or islands of corals growing on it as the bottom gets deeper. On the day of our measurements there was a westerly wind, rare in these latitudes, which was sufficient, together with the tidal change, to maintain a considerable current in an easterly direction. We do not therefore feel qualified to describe typical current conditions on this reef and can only refer to Von Arx (1948), who observed that the direction of the current alternates with the tides.

OBSERVATIONS

MAXIMUM RATE OF OXYGEN PRODUCTION

As the water flows across a reef, particularly at low tide, it undergoes changes in temperature and oxygen content. Table 1 shows the extent of these changes during a noon low tide north of Busch island on the eastern reef of Rongelap Atoll. The two lines were run from north to south parallel to the reef face from a point where the current near the seaward edge of the reef flowed southerly around the end of an island to a point on the other side of the interval between islands where it ran northerly around the end of the next island. It appears that the direction of flow was uniform except at the ends of the line. The velocity was highest in the middle of the interval, and less close to the islands.

At the four stations sampled near the surf zone, the temperature and oxygen content (as determined by Winkler titration) were uniform. Along the inner edge, both the temperature and the oxygen content were significantly greater. Particularly near the ends of the line where water was collected which could have run for some distance parallel to the reef before it rounded an island and crossed the reef, were high temperatures and oxygen contents found. In crossing the reef the water temperature increased, on the average, 0.4 C, the oxygen content 0.74 milliliters per liter. As the water was

TABLE 1.—*Oxygen production by a reef north of Busch island*

[Observations at 1100–1300, July 20, 1946]

	Seaward edge of reef							Lagoon edge of reef			
Station	Distance between stations (m)	Depth (cm)	Velocity (cm/sec)	True direction of current (degrees)	Water temperature (° C)	Concentration of oxygen (ml/l)	Concentration of dissolved phosphorus (mg-atoms/l)	Station	Water temperature (° C)	Concentration of oxygen (ml/l)	Concentration of dissolved phosphorus (mg-atoms/l)
1		50	19	160				1	28.7	5.28	0.51
2	122	40	25	320	28.4	4.54	0.54	2	28.6	5.04	.45
3	61	40	8	270				3	28.3	5.44	.54
4	137	35	15	270	28.4	4.50	.51	4	28.8	5.05	.47
5	146	40	34	270				5	28.7	5.06	.49
6	271	25	31	275				6	28.9	5.05	.49
7	61	35	29	260	28.3	4.53	.66	7	29.4	5.55	.48
8	70	35	34	250				8	29.0	5.77	.31
9	73	35	34	250	28.4	4.58	.51				
10	73	35	17	350				Mean	28.8	5.28	
Mean		35	24		28.4	4.54					

saturated with oxygen when it left the surf zone, the increase can be attributed only to photosynthesis by the reef organisms. The product of the mean depth in centimeters, the mean velocity in centimeters per second, and the mean change in oxygen content in milliliters per cubic centimeter,

$$35\times24\times10^{-3}\times(5.28-4.54),$$

gives the mean rate of oxygen production of the reef-top community as 0.62 milliliters per second per centimeter of reef normal to the current. This can be visualized as the oxygen production of all the organisms on a strip of reef top 1 centimeter wide running from surf to lagoon. A more elaborate calculation involving averaging individual products of depth, velocity, and oxygen change gives about the same numerical result (0.63 ml/cm/sec), but it is not otherwise justified by the nature of the data.

As the reef top is about 270 meters wide, the rate of oxygen production can be restated as 23×10^{-6} milliliters per second per square centimeter of reef surface.

The line of stations in the surf zone was on top of the *Lithothamnion* ridge; consequently, only photosynthesis by the reef-top organisms lagoonward from the line was included in the measurement. Oxygen produced by the outer portion of the ridge and by the organisms of the seaward reef face was already dissolved before the water crossed the outer station line. Because of the large volume of water available and the effectiveness of the surf in maintaining oxygen-exchange equilibrium with the atmosphere, no measurable change in oxygen content due to activity of organisms could be expected seaward of the line. The measured increase in oxygen content was therefore found in what appears to the eye as an area rather barren of plants. Besides the *Lithothamnion* of the ridge, the only other plants readily apparent are scattered small erect Rhodophyceae (*Liagora* sp.) 5 to 10 centimeters high and 20 to 50 centimeters apart. Careful search shows that matted filamentous Myxophyceae and other minute algae are common embedded in the foraminiferal sand and in other locations somewhat protected from direct sunlight (Taylor, 1950, p. 11, 102–103). The most striking oxygen-producing organisms of the reef top, however, are undoubtedly the zooxanthellae of numerous corals, tridacnids, and other animals.

By contrast, the outer portions of the *Lithothamnion* ridge and the spurs on the face of the reef appear to be almost completely paved with dark red lithothamnia and we are tempted to assume a much higher rate of oxygen production per square centimeter of reef surface than the average for the reef top. The light intensity at a depth of 15 meters is probably 20 percent of that just below the surface and is presumably adequate for

maximum photosynthesis. The circulation of water is rapid (Munk and Sargent, Prof. Paper 260–C, p. 278); consequently the supply of gases and nutrients is as good as at any point on the reef top. The assumption that the reef face is at least as productive as an equivalent area of the most productive part of the reef top is not unreasonable. The area of this zone is such that it may add another 25 to 50 percent to the total oxygen production of the reef.

Table 2 shows additional data on conditions at this station in late morning on other days. The averages from table I are included for comparison. It appears at once that individual observations on the increase in oxygen lie within the range of individual observations made nearly simultaneously along a single stretch of reef. On June 30, when observations on depth and current velocity were made, the calculated rate of oxygen production was quite comparable with that on July 20.

Data shown in table 3 for another station also support the view that this value does not vary widely for reefs of similar characteristics and dimensions.

TABLE 2.—*Oxygen production by a reef north of Busch island*

[Quantities marked by an asterisk (*) are averages]

Date	Time	Dissolved oxygen (ml/l)			Depth (cm)	Velocity (cm/sec)	Rate of oxygen production (ml/cm/sec)
		Seaward edge	Lagoon edge	Increase			
June 29	0940	4.51	5.95	1.44			
June 29	1130	4.46	4.90	.44			
June 30	1120	4.55	5.47	.92	20	49	0.90
July 20	1100–1300	*4.54	*5.28	*.74	*35	*24	.62

The single set of data for a station on the western reef shows that the oxygen content increased 0.10 milliliter per liter at noon when the water was 107 centimeters deep at a point where the velocity was 40 centimeters per second. The calculated oxygen production was 0.49 milliliters per second per centimeter of reef normal to the current. This oxygen change occurred over a considerably narrower reef than that at Busch island. In any case, the rate of production of oxygen appears to be of the same order of magnitude even on somewhat dissimilar reef areas.

DAILY COURSE OF RATE OF OXYGEN PRODUCTION AND CONSUMPTION

These measurements show the rate of oxygen production by the reef community at noon. What is the daily cycle of changes in this rate? Measurements of this kind are not easy to make except at low tide. Whenever the water on the reef is deep, and the velocity great, obtaining samples is more difficult, and the differences in oxygen content between different samples diminish until they approach the experimental errors.

Table 3 and figure 100 show the results of a set of observations made near Bokujarito island on the eastern
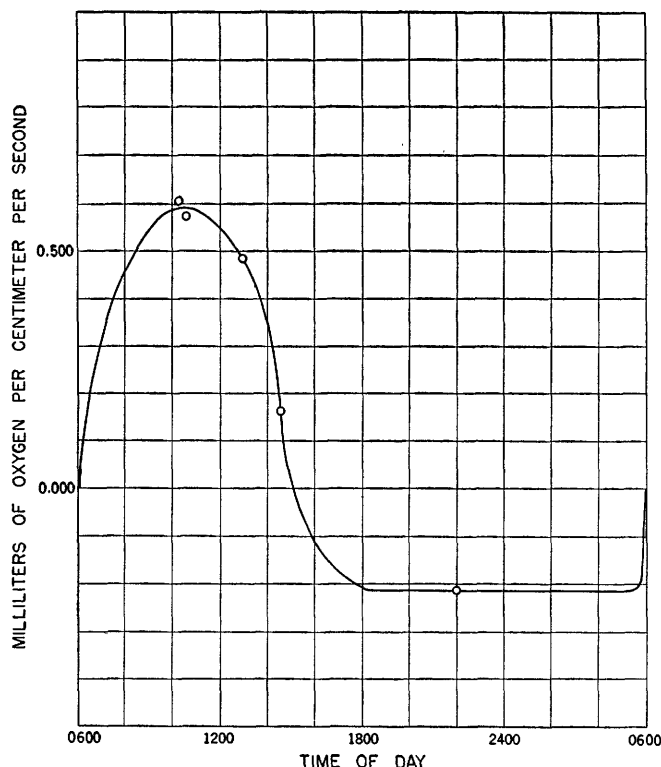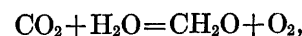

FIGURE 100.—Course of daily oxygen exchange of reef.

reef on a line of four stations across the reef throughout a period of over 24 hours. It is clear that qualitatively the cycle of events was what would be predicted. The rate of oxygen production was highest around noon, and comparable with the rate at Busch island and on the western reef, while at night there was a considerable use of oxygen by the respiration of the reef organisms. Some parts of the curve in figure 100 are drawn on the basis of reasonable assumptions such as that the rate of respiration is constant all night and photosynthesis

begins about sunrise. The diurnal variation in rate of photosynthesis, as plotted, differs from the variation in insolation in that the rate of photosynthesis is relatively lower in the afternoon hours. There are previous reports (Kostytschew *et al.* 1926, 1930) that under natural conditions, rate of photosynthesis of both land and water plants reaches a maximum before noon and then declines; Yonge, Yonge and Nichols (1932, p. 226) observed this in reef corals. Some observations of our own, described below, support this.

Graphical integration of the two arms of the curve shows that during the daylight hours 14,000 milliliters of oxygen were produced per centimeter of reef. During the night, 11,000 milliliters of oxygen were consumed. During the 24 hours there was then a slight excess of organic matter formed equivalent to 3,000 milliliters of oxygen per centimeter of reef. Table 2 shows that at Busch island the rate of oxygen production at noon was probably at least as high as at Bokujarito island. The one usable set of night observations at Busch island gives an oxygen-consumption rate of only 0.10 milliliter per centimeter per second.

Assuming that

$$CO_2 + H_2O = CH_2O + O_2,$$

where CH_2O stands for the organic matter produced by photosynthesis, and less accurately, for organic matter in general, it follows that 3,000 milliliters of oxygen produced is equivalent to 1,600 milligrams of carbon fixed as organic matter. The reef width at this point is 300 meters, and a 1-centimeter strip equals 3 square meters. The fixation of carbon as organic matter therefore amounted to 500 milligrams per day, or 190 grams per year, per square meter. As there is no indication that the reef rock contains any such proportion of organic matter as this would indicate (Ladd, Tracey, and Lill, 1948), we may suppose that this amount of material is formed on and removed from the reef annually. This removal may be continuous, in the

TABLE 3.—*Oxygen exchange on section across reef at Bokujarito island, June 17-18, 1946*

| Date and time | Station 1 (surf zone) | | | Station 2 | Station 3 | Station 4 (inner edge) oxygen content (ml/l) | Change in oxygen content (ml/l | Rate of oxygen production (ml/cm/sec) |
	Oxygen content (ml/l)	Depth (cm)	Velocity (cm/sec)	Oxygen content (ml/l)				
June 17								
1020	4.21	18	35	4.85	5.19		0.98	0.62
1150	4.25			4.50	4.77	4.80	.55	
1440	4.28	64	84	4.34	4.31	4.31	.03	.16
1750	4.31			4.23	4.27	4.29	−.02	
2200	4.09	18	[1] 35	4.03	3.94	3.74	−.35	−.22
June 18								
0100	4.19			4.27	5.02		−.17	
0400	[2] 4.26				[2] 4.25		−.01	
1030	4.49	20	73	4.57	4.67	4.88	.39	.57
1255	4.42	36	78	4.57	4.58	4.59	.17	.48

[1] Estimate.
[2] Position approximate.

form of dissolved or fine particulate organic matter, or occasional and catastrophic during storms or high waves which break off whole colonies or large blocks encrusted with living organisms. Water flowing off the reef is limpid, remarkably free of plankton or any other sediment, and has a low biochemical oxygen demand (see Johnstone's data in Sargent and Austin, 1948). We therefore incline to the belief that removal of organic matter from reef or lagoon is occasional. Loss to the outer talus slope probably does not enter our calculations because these cover only the interval from the inner edge of the surf zone to the lagoon.

One other quantity of interest is the gross rate of photosynthesis—that is, the sum of the apparent rate of formation and the concurrent rate of consumption of oxygen. We have no way of deciding how much of the measured oxygen consumption is due to animals and how much to plants. We will guess that less than half of it is due to plants, but lump it all together in estimating the gross production rate.

During the daylight hours, 14,000 milliliters of oxygen were produced per centimeter of reef. Assuming that the day lasted 12 hours, a respiration rate of 0.22 milliliters per centimeter per second concurrently consumed 9,500 milliliters of oxygen per centimeter. The gross rate of production per day was then 23,000 milliliters of oxygen per centimeter. Using the conversion factors above, the equivalent in carbon amounts to 1,500 grams per square meter per year. We have shown previously (Sargent and Austin, 1949) that this is much higher than the production rate in the adjacent ocean and lagoon waters. According to Riley's compilation (see Sverdrup, Johnson, and Fleming, 1942, p. 938) of production rates, it is higher than that of any open waters where measurements have been made. General impressions lead us to believe that some estuarine areas and, in temperate zones, rocky shores between tides and to depths of a few dekameters may be as productive as these reefs, but we have no exact observations.

OXYGEN EXCHANGE OF INDIVIDUAL REEF ORGANISMS

Oxygen was produced by all parts of the reef from the surf zone to the lagoon edge. Table 4 summarizes data taken towards midday on lines of stations crossing the reef. On each line, station 1 was on the *Lithothamnion* ridge, station 2 was well back in the zone of rich coral growth, station 3 was in the apparently barren back part of the reef, and station 4 at the lagoon edge. Although there is great irregularity in the data, it is apparent that, on the average, oxygen was produced in each zone. Although the individual plants of the

lagoonward reef flat are not conspicuous, their combined productivity is considerable.

Three sets of observations were made on the activities of individual organisms. Table 5 shows the maximum rate of oxygen production, in milliliters per gram per hour, of *Pocillopora*, *Acropora*, and *Porites*, three reef corals; *Porolithon*, the characteristic lithothamnioid of the surf zone; and *Liagora*, an alga of the reef flat.

TABLE 4.—*Oxygen content of reef waters, in milliliters per liter*

Date	Time	Oxygen content for station—			
		1	2	3	4
Bokujarito island					
June 17	1020	4.21	4.85	5.19	
	1148	4.25	4.50	4.77	4.80
June 18	1020	4.49	4.57	4.67	4.88
	1255	4.42	4.57	4.58	4.59
June 20	1220	4.28	4.34	4.44	4.41
Busch island					
June 29	0940	4.51	5.18	5.06	5.95
June 30	1120	4.55	5.32	5.04	5.47

TABLE 5.—*Rate of production of oxygen by corals and algae*

Specimen	Air-dried weight (g)	Rate of oxygen production (ml/hr) for indicated time of day			Maximum production rate (ml/g/hr)
		1015–1045	1045–1300	1300–1400	
Liagora	3.1	0.70	0.30	0.48	0.23
Porolithon	2.4	.11	.02	.09	.046
Pocillopora	11.3	.84	.16	.28	.075
Acropora	14.3	1.68	.34	.56	.118
Porites	13.2	.56	.20	.31	.042
Pocillopora	16.0	.36	.37	.56	.035
Control water		0.00	−0.04	0.02	

The method of measurement was extremely simple. Samples were selected on the reef at low tide. Water was collected in an enameled pail, and the water stirred gently but thoroughly. The samples were put in pint mason jars; these jars were filled by gradual immersion in the pail, and the caps were screwed on under water so that bubbles were excluded. Also samples of water without added organisms were bottled, and samples were taken for immediate analysis. Each mason jar was then laid on its side in flowing water on the reef and propped in place with pieces of reef rock when necessary. During the exposure the temperature in the jars did not rise significantly above the surroundings (28–29 °C). At the end of the exposure, each mason jar was shaken gently and a water sample (200 ml) siphoned off into a glass-stoppered bottle for oxygen measurement. The jars were then emptied and filled with freshly collected water for the next measurement. In order to save time and to keep the samples under as

natural conditions as possible during the whole set of measurements, all these operations were carried out on the open reef. Winkler reagents were added to the water samples within 20 minutes after they were drawn. The small activity found in the water indicates that this delay had no serious consequences.

The organisms collected as samples were selected as representatives of dominant members of the communities on different parts of the reef. The *Porolithon* was collected as far out in the surf as possible. The three species of corals—originally collected as four—occurred in the zone of abundant coral growth behind the *Lithothamnion* ridge. The *Liagora* is the most conspicuous alga of the lagoonward reef flat, where individual bushy plants a few centimeters high occur with a density of growth sometimes as high as 20 per square meter. According to Taylor (1950, p. 118), members of this genus are not as common at other times of year.

The coral samples and the *Porolithon* were in all cases single pieces taken from the tops of actively growing portions of the colony, apparently in good condition, very clean, and with no visible overgrowth of sessile organisms. The *Liagora* was essentially a whole plant about 5 centimeters high. All these samples consisted of a small amount of living tissue and a relatively massive deposit of lime. In *Liagora*, the ratio of tissue to skeleton was undoubtedly much higher than in the other organisms, and this is reflected in the relatively large oxygen production per gram.

Table 5 shows the results of a measurement of the relative maximum rates of oxygen production of the various organisms. The three measurements were made late in the morning, at noon, and early in the afternoon. Although there is no way of checking the results, we are sufficiently practiced in the technique to feel confident that the apparent differences in rate represent real differences in activity rather than inadequacies in the mechanics of measurement. For instance, the lower activity at noon appears to be real and is probably an aspect of the phenomenon, observed by Yonge and others (1932), and by us (fig. 100), that activity reaches a maximum during the morning. To what extent the differences in activity reflect responses to differences—of which we were unconscious—in our manipulation of the individual specimens, we cannot say. Yonge (1937) has pointed out that some species of corals, notably members of the genus *Acropora*, yield quantities of mucus under handling and that the rapid consumption of this material by bacteria may give spurious values for the respiratory activity of the coral. In table 5, however, *Acropora* shows a suprisingly high rate of oxygen production. Because in general our observations of this genus were over such short intervals, and because the oxygen production rates so large, correc-

tions for bacterial respiration should be only of secondary importance.

As shown in the last column of table 5, the maximum rate of oxygen evolution observed per gram of sample does not vary widely between the three species of corals or between the coral species and the alga *Porolithon*. Observations on *Liagora*, which is relatively slightly calcified, give a much higher value.

The data of Yonge and others (1932, pp. 224–228) recalculated to milliliters of oxygen per gram per hour (assuming a specific gravity of 2.5 for coral) include a range of values from 0.031 to 0.001—that is, all are somewhat lower than our values, some much lower. However, there is a clear inverse correlation between activity and size in their data, which was obtained with pieces of coral weighing from 15 to 80 grams, indicating probably that the larger pieces had lower activities because more dead coral was included. The heaviest of our pieces weighed 16 grams and all were heathy, presumably growing, tip pieces. Kawaguti (1937), using small pieces of coral, found activities as high as those we have observed. Therefore, our values for maximum rate of oxygen production by corals probably are dependable.

Only repetition of the measurements with careful selection of specimens of the alga would show how much importance should be attached to the fact that *Porolithon* had a rate of photosynthesis no higher than the corals. We also recognize, as did Yonge and others, that the activity per gram or per cubic centimeter is not a satisfactory unit for comparative studies.

Discussion.—We have previously shown (Sargent and Austin, 1949, p. 246) that the rate of consumption of organic matter by the reef community as measured by the oxygen consumption is much larger than the rate of supply of organic matter by the current driven across the reef. Neither the amount of material caught by a plankton net nor the amount available for oxidation by bacteria in the biochemical oxygen-demand measurement is sufficient to satisfy the requirements of the reef community. We have further found that between the surf zone and the lagoon the reef community as a whole produces in a 24-hour day probably somewhat more organic matter than it consumes. The picture of the reef as a self-supporting community, depending on the current only for dissolved nutrients (in a broad sense), and not for particulate or dissolved organic matter, is reasonably clean cut.

This may be true of the Great Barrier Reef, studied by Yonge and his associates, and of the coral reefs in the Bay of Batavia, studied by Verwey (1931). The absence of a steady current across the reef from the open sea at these locations makes the solution much

more difficult. In each of these cases there is an adjacent land mass and a relatively stagnant lagoon to complicate the study of the situation. The growing reef edge even here, however, might exist only in a current of open ocean water maintained by the head piled up on the reef by surf. In this case it could turn out that these reefs also are self-supporting.

Our few experiments and the more numerous and more carefully performed ones of Yonge and others (1932) show that the contribution of the zooxanthellae of the corals to the total productivity of the reef is far from negligible. There is no doubt that in many cases the rate of production of organic matter by the zooxanthellae of a coral colony is quite sufficient to support the whole colony. Yonge and others (1932, p. 234) found that 17 out of 22 colonies sealed in jars survived 14 days, and at the end of this time had not exhausted or had barely exhausted the oxygen in the jars. As long as nearly as much oxygen remained at the end of the experiment as was available in the beginning, there must have been nearly as much organic matter present at the end as at the beginning; that is, unless the original piece of coral colony was very small, or its respiratory activity very low, organic matter must have been produced by the zooxanthellae at a considerable rate or in any case almost as fast as it was consumed by the whole colony. In 6 of their 17 surviving colonies, there was more oxygen in the water and hence more organic matter in the jar at the end of the experiment than at the beginning. In another of their experiments (Yonge and others, p. 222), only 1 of 29 colonies produced more oxygen than it consumed in 24 hours. However, in another experiment (Yonge and others, p. 218) 8 of 22 specimens had a higher rate of oxygen production during 9 hours in the light than during 9 hours in the dark, and there is a reasonable possibility that 12-hour exposures would have given the same results in most cases. In other words, during a natural 24-hour day these colonies would have produced more oxygen than they consumed. Yonge and others, (1932) point out the possibility that epiphytic algae, or phytoplankton in the 14-day experiment, could have contributed to the apparent oxygen production. It should also be pointed out that bacterial activity, especially in the experiment lasting 14 days, could have consumed organic matter and oxygen at a rate sufficient to mask production by the zooxanthellae wholly or in part. Verwey (1931, pp. 175–176) found that pieces of coral colony produced as much organic matter as they consumed. The observations of Kawaguti (1937, p. 196) on the ratio of oxygen consumption to the rate of oxygen production also lend color to this view. The sum of this evidence is that the zooxanthellae of

corals produce organic matter at a rate quite comparable with its rate of consumption by the coral colony, under favorable circumstances probably exceeding it.

There is additional reason to believe that the reef corals not only could subsist on the products of their zooxanthellae but do. The product of the photosynthesis of the algae appears to remain within the coral colony. Evidence that organic matter produced on the reef remains there was presented on p. 297. In the 14-day experiments of Yonge and others (1932), no mention is made of large bacterial growth which would have indicated that the products of photosynthesis were being secreted by the coral colony. The results of these experiments strongly indicate a high rate of activity and a practically closed cycle of events within the colony.

What is true of the reef community as a whole appears now to be true of individual coral colonies. The external supply of organic nutrient is inadequate to support a coral colony on the reef, but the daily production of organic matter by its contained zooxanthellae can be sufficient. Although Yonge (1940, p. 365) has reviewed his own careful work and other data indicating that corals do not derive organic matter directly from their zooxanthellae, we believe that the weight of evidence is on the opposite side. Under conditions of growth on the eastern reef of Rongelap Atoll, the association between corals and zooxanthellae seems to be essential to the individual colonies precisely because the corals must derive organic matter from the algae or die.

This brings up another general question: zonation on the reef. As described by Tracey, Ladd, and Hoffmeister (1948), the reef top is composed of zones parallel to the edges. Behind the *Lithothamnion* ridge is a zone of rich coral development and behind this a reef flat populated principally by very small organisms. Our observations indicate that the temperature difference between the two sides of the reef even at low tide is relatively insignificant. In tide pools and backwaters around the islands large temperature differences occur, but not across the open reef between islands. The oxygen differences are likewise insignificant, and we believe that differences in carbon dioxide content and associated pH would be no greater. The possible gradient in organic matter, suspended or dissolved, is limited to a very small value by the absence of organic matter in the source water from the open sea. The difference in phosphate content (table I) is so small as not to be certainly measurable. The sediment load of the current is so small as to appear negligible.

Munk and Sargent (Prof. Paper 260–C, p. 278) have suggested that *Lithothamnion* grows luxuriantly only

in the zone of violent surf because of the scrubbing action of the momentary high-velocity currents which can remove various solids and also rapidly renew the water lamina close to the surface of the algae. Almost the only factor we can imagine varying sufficiently to account for the limitation of distribution of coral colonies is also velocity of moving water. The current velocity along a line across the reef does not vary much because the depth along the line is nearly constant inside the *Lithothamnion* ridge, except close to the lagoon edge where it begins to deepen. However, the average wave height and frequency diminish with increasing distance from the seaward edge, and below some critical value for these quantities conditions for growth of coral may become extremely unfavorable.

The fact that the reefs are more productive per unit area than the surrounding waters we have previously ascribed (Sargent and Austin, 1949) to a higher overall efficiency of attached compared with planktonic algae. We have no further evidence in support of this speculation, but we can find no other ultimate reason for the flourishing of coral atolls in an empty ocean.

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Plankton of Northern Marshall Islands

By MARTIN W. JOHNSON

Bikini and Nearby Atolls, Marshall Islands

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PLANKTON OF NORTHERN MARSHALL ISLANDS

MARTIN W. JOHNSON[1]

ABSTRACT

Most of the holoplankton species found in Bikini Lagoon occur also in the surrounding open sea. The plankton fauna of the lagoon, however, is characterized by (1) a number of endemic species not found outside the lagoon except where washed out by outflowing currents, and (2) a concentration within the lagoon of many forms that occur normally also in the outside surface waters. Both features are dependent upon the degree of dispersal of the plankton and are therefore directly correlated with the semiclosed circulation which the lagoon imposes upon the water that flows in over the eastern and northeastern reefs.

A study of the vertical distribution and diurnal vertical migration of the endemic copepod *Undinula vulgaris*, and of the general plankton, reveals that much of the lagoon plankton lives mainly in the deeper, slowly (0.1 knot) eastward-moving counter current which as a water mass represents 70 to 90 percent of the living space in the lagoon. Even during the night when much of the plankton migrates toward the surface into the faster (0.3 knot) westward-moving water, about two-thirds of the plankton still remains within the deeper counter current.

Much of the oceanic plankton swept into the lagoon thrives there and becomes concentrated so that the average concentration per cubic meter of water of the 11 most common animal groups is about four times higher than in the outside northeastern area, and twice higher than the outside western-southern area of principal outflow. The increased concentration found in the outside water to the west and south indicates an outwash from the lagoon in that area and is shown especially by such forms as *Undinula vulgaris* and *Tretomphalus planus* (foraminifer), which occur abundantly in the lagoon but were not found in the area immediately to the east and north of the atoll.

The restricted water flow within the lagoon is biologically important in conserving also the transitory planktonic larval stages of lagoon and reef fishes and bottom-living animals.

A comparison of the plankton in Bikini, Eniwetok, Rongerik, and Rongelap Lagoons showed the last to be the richest for the period of the survey. Phytoplankton was exceedingly sparse in all but Rongelap, where a small "bloom" was in progress.

INTRODUCTION

By the term "plankton" is meant all the organisms, usually microscopic or semimicroscopic, that float about in the sea with little or no resistance to water currents. Thus, in general, they are dispersed and transported in a manner dependent upon the prevailing current system. The animal plankton consists not only of such forms as are permanently planktonic all of their lives (holoplanktonic), but also of the transitory young or larval stages of bottom-living forms—such as crabs, certain shrimp, clams, and others—and fishes.

In an earlier report (Johnson, 1949) the plankton was studied with a view to its use in corroborating the physical oceanographic findings relative to the water exchange between Bikini Lagoon and the surrounding sea.

From a biologist's standpoint, however, the greatest significance of the study involves an evaluation of the ecological effect of the water currents in the maintenance of a consistently endemic or concentrated population within the lagoon and on the wave-washed reefs that form its banks.

Bikini Lagoon rests as a marine lake on the summit of a coral-capped volcanic mountain which rises abruptly from the floor of the open ocean at a depth of more than 2,000 fathoms. The lagoon has a maximum depth of about 35 fathoms (Emery, Tracey, and Ladd, 1949). At low tide it is completely isolated from the sea except for a number of passages forming gaps 6 to 35 fathoms deep in the reef along the southern and southwestern periphery. (See fig. 101.) Depending upon tidal action and wind conditions, the waters of this "lake" are partially renewed daily by a flow of water over the reefs from the sparsely populated surrounding high seas.

METHODS OF COLLECTING

The quantitative plankton samples were taken in two ways in each of four lagoons:

1. Horizontal tows were made with Clark-Bumpus samplers, which give a measure of the volume of water filtered through the net. The nets used with these samplers were of No. 2 bolting silk having apertures of about 0.366 millimeter.

Inside the lagoons, two samplers were usually towed 20 to 30 minutes simultaneously at 1- and 10-fathom depths. Deeper horizontal towing within the lagoon was hazardous because of the many coral pinnacles rising from the bottom. For the 24-hour series in Bikini Lagoon, 3 samplers were towed in series at depths of 1, 10, and 25 fathoms over a course previously surveyed to assure an absence of shallower coral obstructions. Outside the
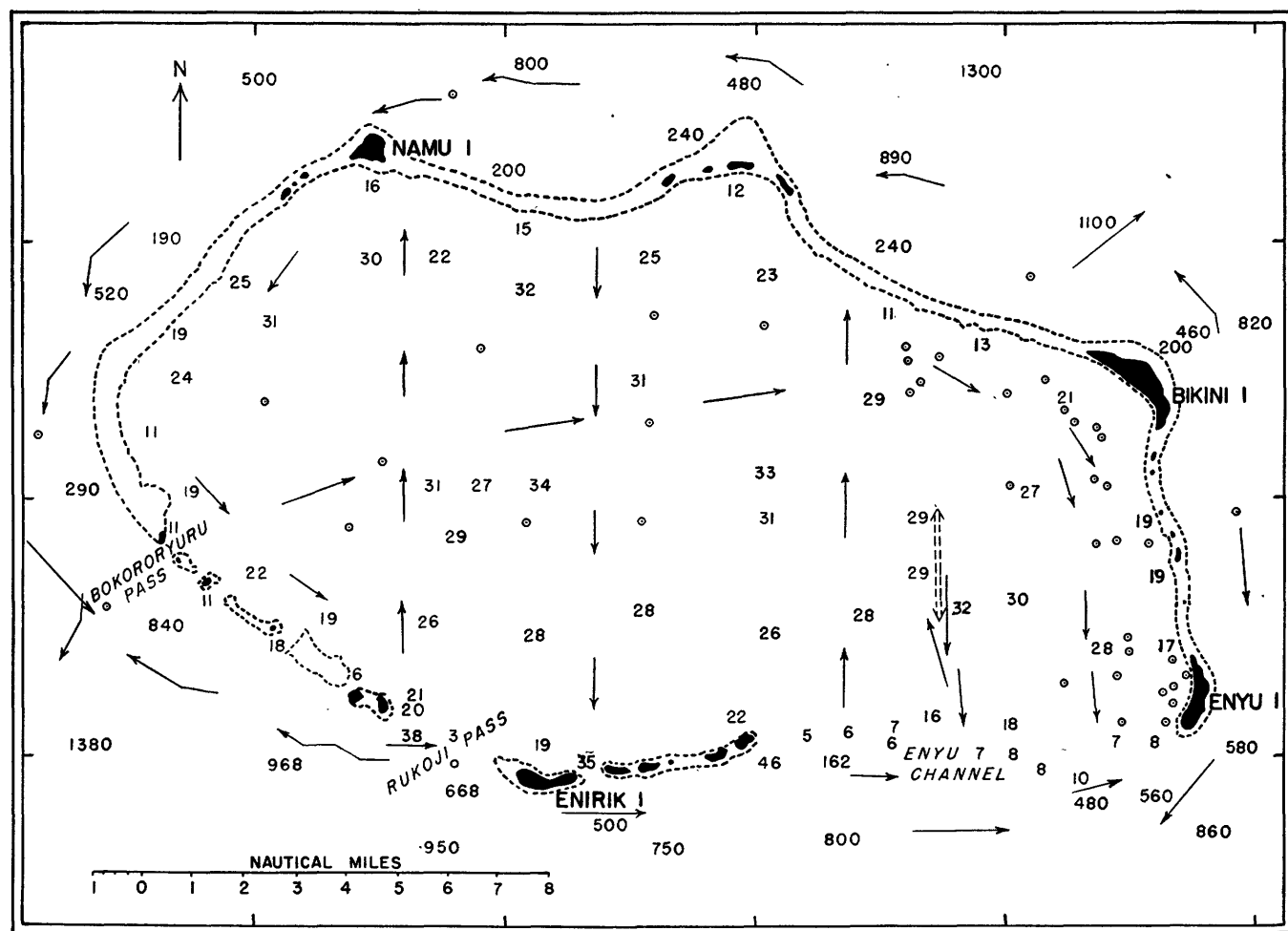
FIGURE 101.—Positions of plankton hauls taken at Bikini Atoll March 10 to May 18, 1946; the arrows indicate course of horizontal hauls; the circles indicate vertical hauls; the figures are depths in fathoms.

lagoon the samplers were towed simultaneously at 1-, 10-, and 40-fathom depths. The station positions and courses over which the Bikini samples were taken are shown in figure 101.

2. Vertical tows were made with a 10-inch net of No. 20 bolting silk having apertures of 0.076 millimeter. These nets were pulled up vertically from a depth of 50 meters or, where depths were shallower, from the bottom to the surface. The water filtered in the regular hauls was about 2.5 cubic meters. The purpose of obtaining this series was to sample the more minute organisms of the phytoplankton together with the tintinnids, copepod larvae, and clam larvae that pass through the coarser nets.

The following numbers of stations were occupied for quantitative hauls in each of the four lagoons: Bikini, 81; Eniwetok, 18; Rongelap, 35; Rongerik, 11. The No. 20 net was used at about 50 percent of the stations in each lagoon.

The regular quantitative hauls were checked qualitatively by many irregular hauls with various types of nets. A total of 437 tows are involved in the whole survey.

BIKINI LAGOON

CONCENTRATION OF PLANKTON FAUNA

Insofar as Bikini Atoll is concerned, this report deals mainly with observations made between March 10 and May 18, 1946, before the atomic-bomb tests. A few samples (not shown in fig. 101) taken outside the lagoon as late as August 8, 1946, and contrasted with the spring samples, showed no appreciable change in concentration in the plankton.

Perhaps 90 percent or more of the holoplanktonic forms found in Bikini Lagoon occur also in the outside surrounding water. The lagoon plankton fauna is, however, characterized by the following two striking features: (1) A number of the important species are endemic to the lagoon and are seldom or never found outside except at localities where they have been washed out of the lagoon over the reef or through passages; (2) there is a concentration of many forms that also occur normally in the outside surface water. In

general, the plankton concentration in the Marshall Islands area is relatively sparse, especially the phytoplankton.

CAPACITY OF THE LAGOON TO FOSTER AN ENDEMIC FAUNA

The capacity of the lagoon to foster an endemic fauna and to concentrate the fauna common to the lagoon and the outside water results largely from the same mechanism. This mechanism is inherent in the current pattern which results mainly from the retarding effect that the lagoon has on the oceanic water which it intercepts from the North Equatorial Current. This type of dependence on water currents is doubtless characteristic of other lagoons similarly constructed.

In some areas, such as the Gulf of Maine, for example, the endemic population is correlated with a large circular flow of water which produces a semiclosed system (Bigelow, 1924; Redfield, 1941). In Bikini Lagoon the current mechanism is much smaller and operates mainly in a vertical rather than horizontal plane.

Surface water in the lagoon is driven by the prevailing trade winds in a west-southwest direction, whereas the water at intermediate and greater depths flows in the opposite direction as a counter current. This gives rise to sinking in the western portion of the lagoon and to upwelling against the eastern reefs (Von Arx, 1948).

In the search for endemic species in Bikini Lagoon, the most useful thus far considered are *Undinula vulgaris* (Dana), a copepod crustacean, and *Tretomphalus planus* Cushman, a pelagic foraminifer. This foraminifer was identified by the late J. A. Cushman, who described the species originally from Samoa and stated that it occurs also in Fiji. Both species occur also in the lagoons of Eniwetok, Rongelap, and Rongerik.

Undinula vulgaris.—This is a widely distributed species which, though reported from the open ocean, appears to be preponderantly a lagoon form in this area. Large (more than 2 millimeters) and easily recognized, it occurs in varying numbers throughout most of the lagoon. During the period March 10 to
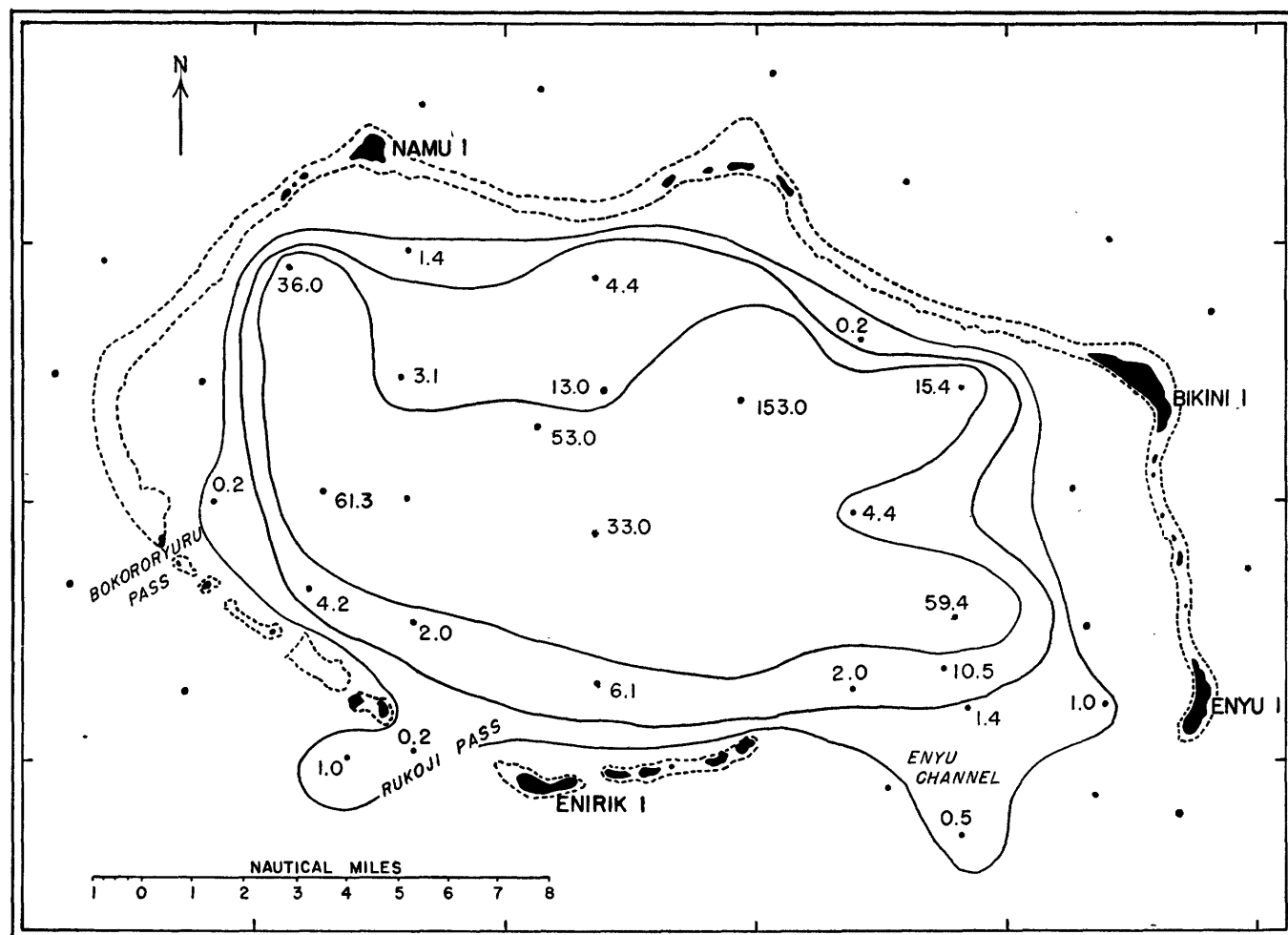

FIGURE 102.—Number of *Undinula vulgaris* per cubic meter of water, by stations (black dots).

May 18 it was present at about 90 percent of the lagoon stations. The largest numbers (as many as 255 per cubic meter of water) have been taken near the center of the lagoon. (See fig. 102.) In the daytime the animals seek the deeper water strata, 10 fathoms or more deep. Very few specimens were caught in the net towed at or above the 1-fathom depth except at night. It is obvious that to maintain an endemic population of an animal with a relatively long life history like that of *Undinula vulgaris*, and in such numerical concentrations, there must be a pattern of currents which leads to a relatively closed system with very slow flushing of at least a large part of the lagoon. This would require the presence of a sizable counter current or some other effective retarding system. The hydrographic study has indicated that a deep slowly moving countercurrent exists. Thus the biological and hydrographic observations support each other on this point.

During the time the animals are in the upper surface layer near the outwash of the lagoon, they are in danger of being swept out through passages or over the reef. Therefore, reproduction in the deeper layer would have to be at a rate sufficient to replenish the loss of numbers washed away by the surface layer, or where there is slow reproduction the bulk of the population would have to spend the greater part of the time in the deep, slowly moving countercurrent. That the latter occurs in Bikini Lagoon is indicated by a study of the diurnal vertical migratory journeys of *Undinula vulgaris* and a number of other planktonic forms. (See figs. 103, 104, and 105.) It will be seen from the illustrations that not only *Undinula* but the bulk of the other

FIGURE 104.—Diurnal migration of ostracodes.

FIGURE 105.—Diurnal migration of total zooplankton as represented by settling volume.

FIGURE 103.—Diurnal migration of *Undinula vulgaris;* 35-minute horizontal hauls taken at surface and at 10 and 25 fathoms at 4-hour intervals over course shown by double dashed arrow in figure 101.

planktonic forms avoid the more lighted surface waters during the day and that a goodly portion (two-thirds or more) of the population remains even at night in the slowly moving (average 0.1 knot) countercurrent. This current involves 70 to 90 percent of the water mass of the lagoon—that is, 70 to 90 percent of the living space. Nevertheless, at night much of the population must be transported towards the western and
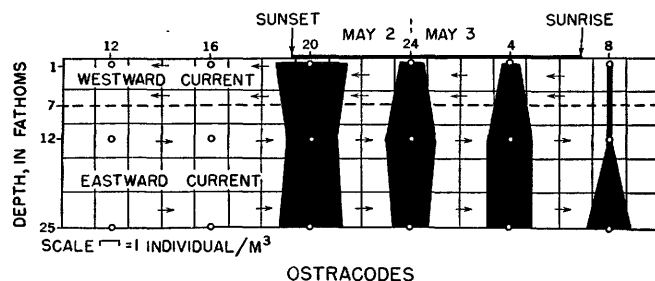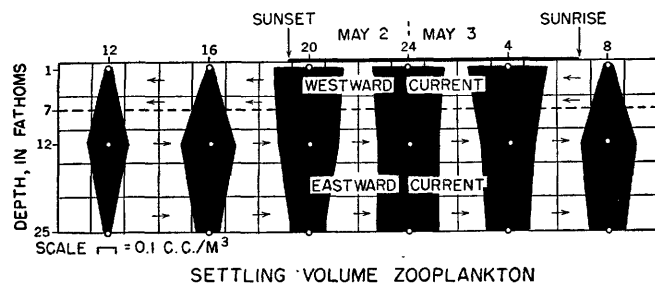
southern margins of the lagoon by the relatively fast-moving (average 0.3 knot) surface current. Depending upon wind velocity, the depth of this current varies from 2.5 to 10 fathoms, with an average of 6.5 fathoms (the maximum depth of the lagoon is about 35 fathoms). At the approach of dawn a downward movement of the animals occurs, and a slow journey eastward begins. In this manner about one-third of the distance lost during the night is recovered during the day. It is probable that this is the order of events with many larval forms of bottom-living adults in the lagoon and also with the oceanic forms swept into the lagoon over the eastern reefs. Biologically this is very important in conserving not only the holoplankton but also the transitory larvae that eventually settle to the bottom of the lagoon or on the reefs to restock the bottom-living animals.

Tretomphalus planus.—This species was found in all parts of the lagoon, sometimes in numbers up to 175 individuals or more per cubic meter of water. The average was, however, only about 25 per cubic meter. This species was present throughout the whole period of investigation (Mar. 10 to Aug. 8) and occurred at all depths within the lagoon. The greatest concentrations were in the upper 10 fathoms except in a few instances where numbers were greater in the deeper strata.

The plankton samples collected outside the lagoon yielded this species only at stations along the western and southern periphery of the atoll. The greatest outside concentrations were found near the passages, thus suggesting the main route of outwash for the species as indicated in figure 106. Apparently small
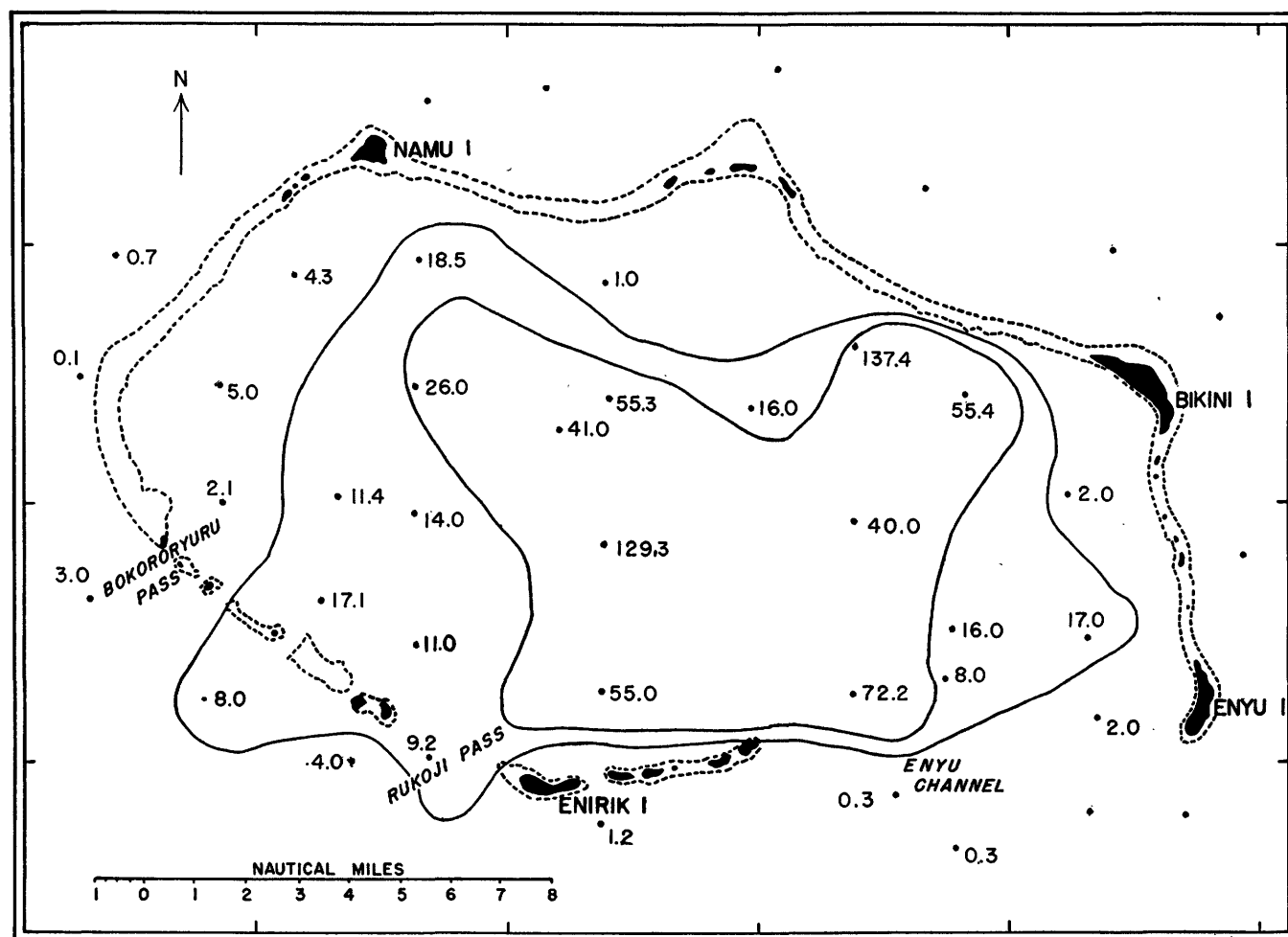
FIGURE 106.—*Tretomphalus planus*, number per cubic meter of surface water by stations (black dots).

numbers are washed out also over the long shallow reef extending from Bokororyuru Pass to Namu island. This is in keeping with the animal's habit of floating near the surface. The deeper-living lagoon animals, such as *Undinula vulgaris*, are discharged through the passages (depths varying from 6 to 35 fathoms) rather than over the reef.

From the above observations it appears that *Tretomphalus* is endemic to the lagoon, perhaps requiring shallow water during the early stages of its life history before the float chamber has been developed. This would explain its absence or scarcity in deep water outside the lagoon except where washed out on the down-current side by the prevailing flow through the lagoon. It should be pointed out here that this relationship suggests the use of *Tretomphalus* as an index of past oceanographic conditions of the atoll. Provided its tests are well preserved as fossils in the sediments, it should serve to show the general direction of currents that have swept through the lagoon in past history, for though the animal is kept suspended by the float

chamber while alive, there must be a gradual precipitation of defunct tests to the bottom along the course of the outflowing water.

MAINTENANCE AND CONCENTRATION OF OCEANIC PLANKTON IN THE LAGOON

The salinity and temperature of the water within the lagoon differ but little from that outside. The highest lagoon salinity (34.85 parts per thousand) is only about 0.1 part per thousand higher than in the open ocean, and the temperature change from about 27.02 C to 27.10 C is negligible. The vertical gradients of these factors are also insignificant. In these respects the lagoon water is essentially oceanic and would therefore not be seriously inimical to most of the surface oceanic plankton coming in over the reef.

The concentration of oceanic plankton that has drifted into the lagoon results from the semiclosed circulatory pattern in the lagoon. Presumably this circulation would operate in a mechanical manner similar to its effect on the maintenance of the endemic

fauna. In the following section it will be shown that certain forms that are common to the inside and outside may be as much as 27 times more numerous per unit of water inside the lagoon. This increased concentration doubtless results in part from better food conditions inside as a result of local production, but the reduction of dispersal must be very important.

The presence in the lagoon of many egg-bearing specimens and a large proportion of larval and juvenile stages of species common to the outside is evidence of successful reproduction inside. In the absence of wide and uninterrupted dispersal, such as occurs outside, a concentration from both reproduction inside and recruitment from outside should occur.

In summarizing the average concentration by areas of the 11 most common animal groups, it appears that the ratios of concentration per cubic meter for (a) the outside eastern-northern area, (b) the inside lagoon area, and (c) the outside western-southern area of principal outflow, are roughly a:b:c:=1:4:2.

INFLOW AND DISCHARGE OF WATER FROM THE LAGOON AS INDICATED BY THE DRIFT OF PLANKTONIC LIFE

When we compare the number of specific organisms occurring per cubic meter of water at stations occupied inside the lagoon with the number found in the surrounding water just outside the reefs and passages, it is seen that the concentration is almost invariably smallest in the waters outside the eastern and northern reefs. It is nearly always largest by far at the stations within the lagoon, and intermediate at stations just outside the western and southern passages and reefs. The largest outside catches occur near Rukoji Pass and the western portion of Enyu Channel (figs. 102, and 106 to 115). Figures 102 and 106 are especially useful since they deal with two endemic species and show clearly the route by which the species are washed out of the lagoon. According to hydrographic studies, the outflow is through these passages and over these reefs, and this is clearly corroborated by the biological evi-
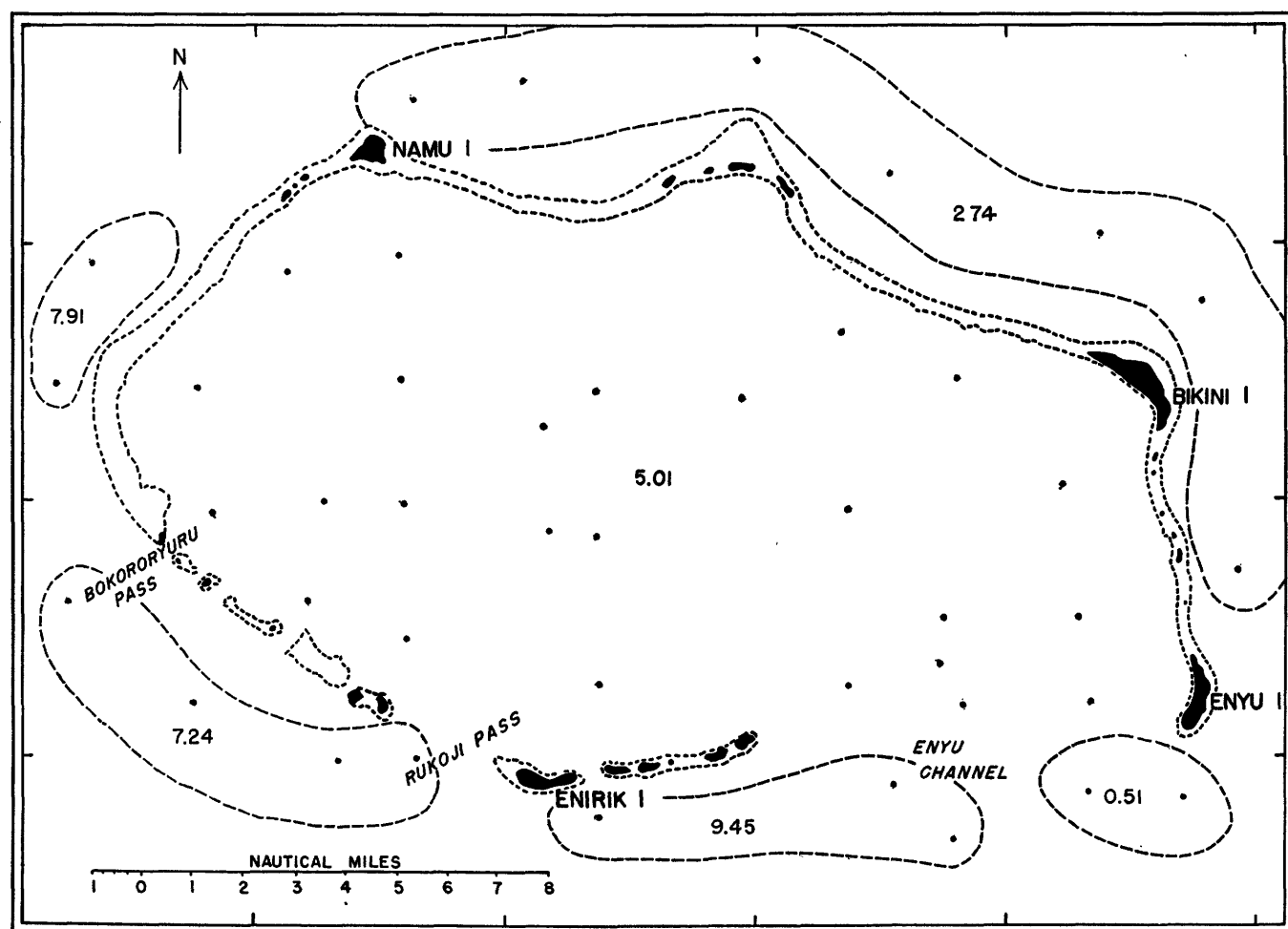

FIGURE 107.—*Globigerina*, average number per cubic meter of water by areas; black dots indicate stations averaged in each area.
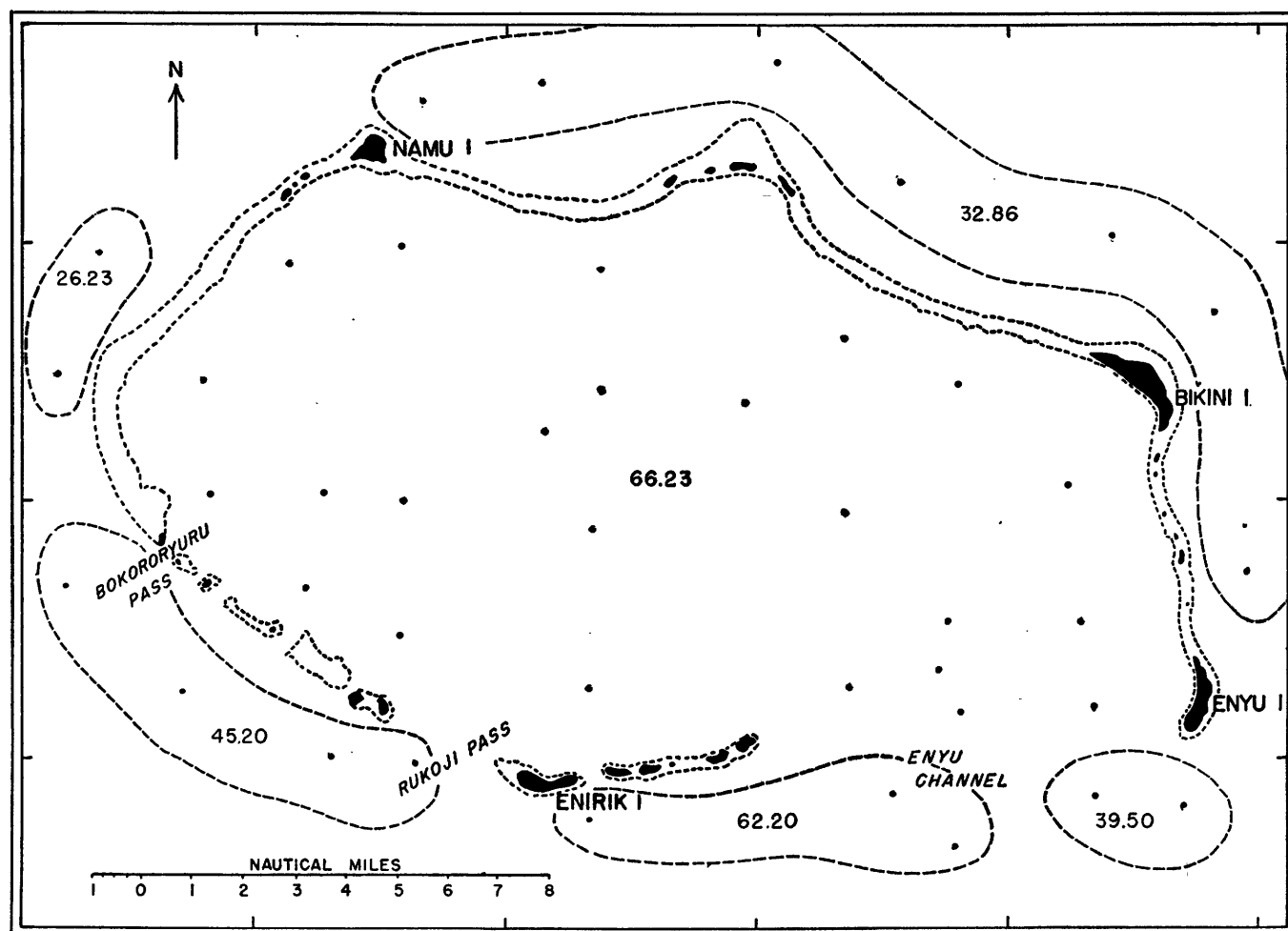
FIGURE 108.—Copepods, average number per cubic meter of water by areas; black dots indicate stations averaged in each area.

dence. The biological evidence does, however, indicate a somewhat broader outwash from Enyu Channel in the early part of the survey than the hydrographic charts indicate.

From the hydrographic survey we learn that in the open sea off Bikini Atoll there is a small northward gradient in temperature and salinity so that the water entering the lagoon from the north is about 0.1 degree (C) colder and 0.3 part per thousand more saline than that which enters the southern passes.

The plankton has not yet been studied in sufficient detail to know the extent of its usefulness in indicating other than the general routes of entry into the lagoon. The distribution of one copepod species, *Copilia mirabilis*, does, however, suggest that its center of distribution may be in the southern water with which it enters the lagoon through Enyu Channel and over the reef between Bikini and Enyu islands. Forty-four

percent of the stations in the southern half of the lagoon yielded this species; only 11 percent in the northern half. Outside the lagoon from near Bikini island around the southern periphery of the atoll to near Arriikan Pass on the west side, 75 percent of the stations yielded the species. None was taken at outside stations north of these points. Nowhere was the species found in abundance.

OTHER LAGOONS OF THE NORTHERN MARSHALL ISLANDS

Plankton surveys were made in the lagoons of Eniwetok, Rongelap, and Rongerik Atolls for comparison with Bikini Lagoon. Table 1 gives the result in type and average concentration of the more important organisms for the periods indicated.

The first part of table 1 is based on collections with the Clark-Bumpus samplers with No. 2 mesh net, the
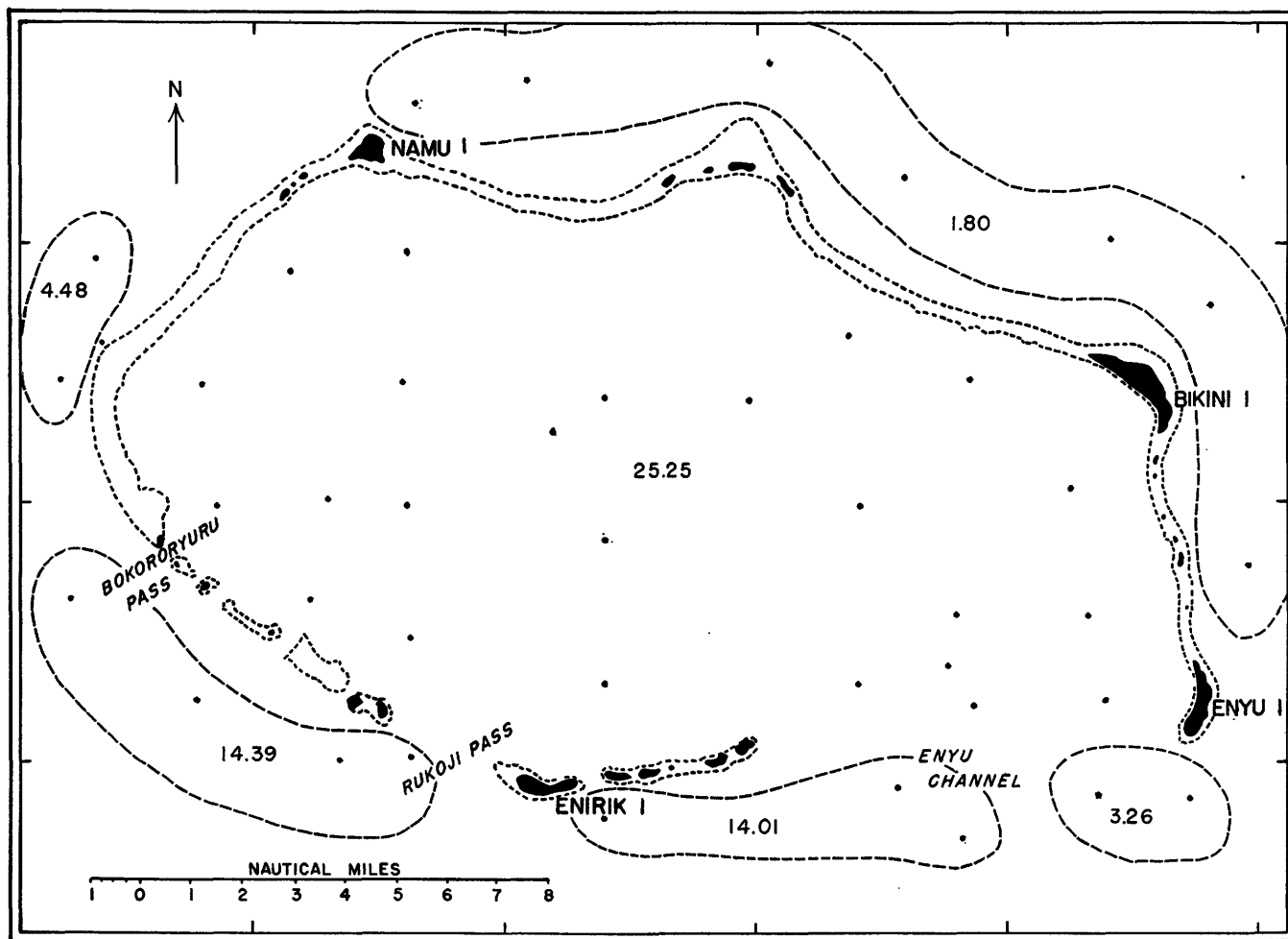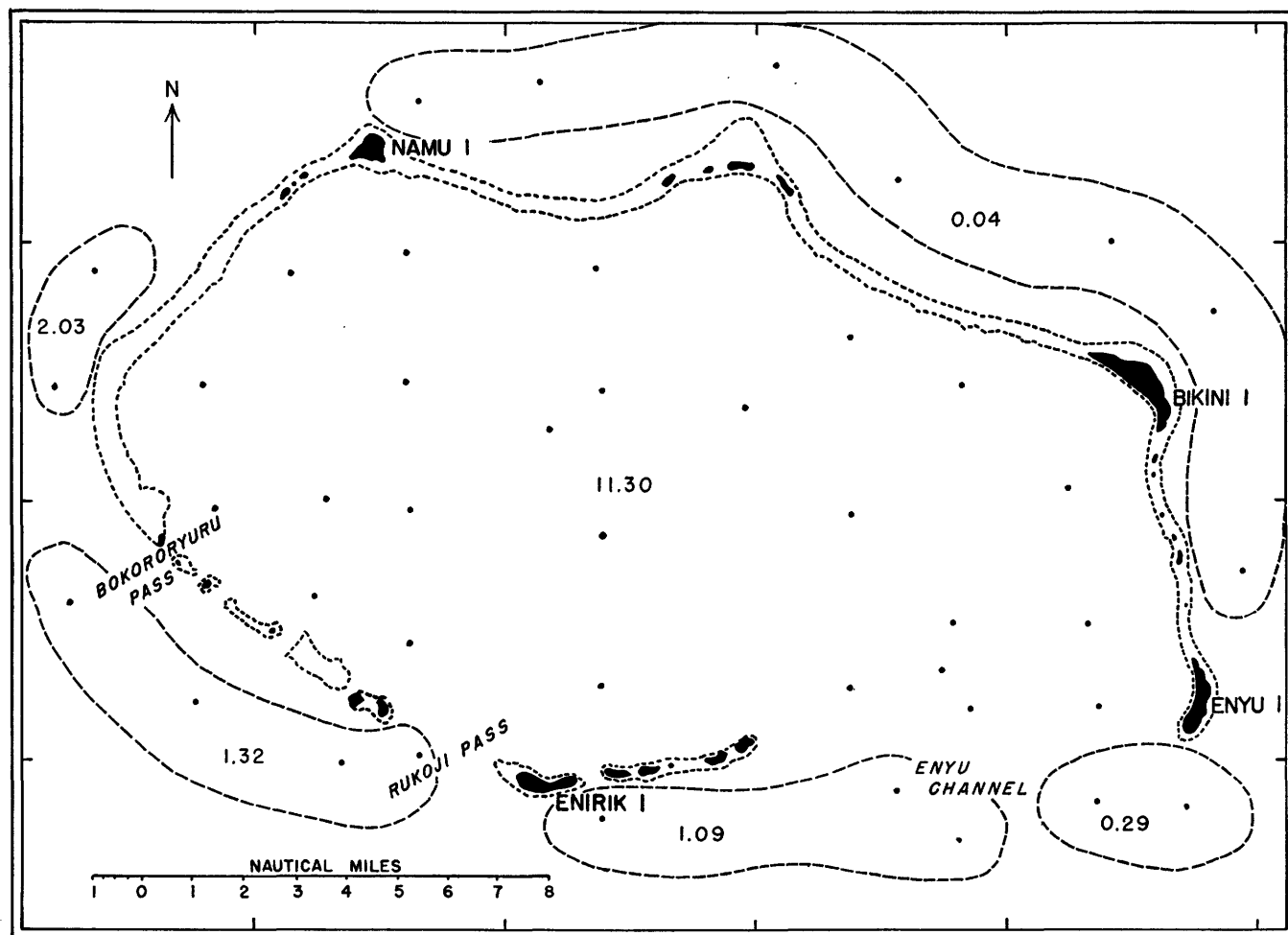
FIGURE 109.—*Appendicularia*, average number per cubic meter of water by areas; black dots indicate stations averaged in each area.

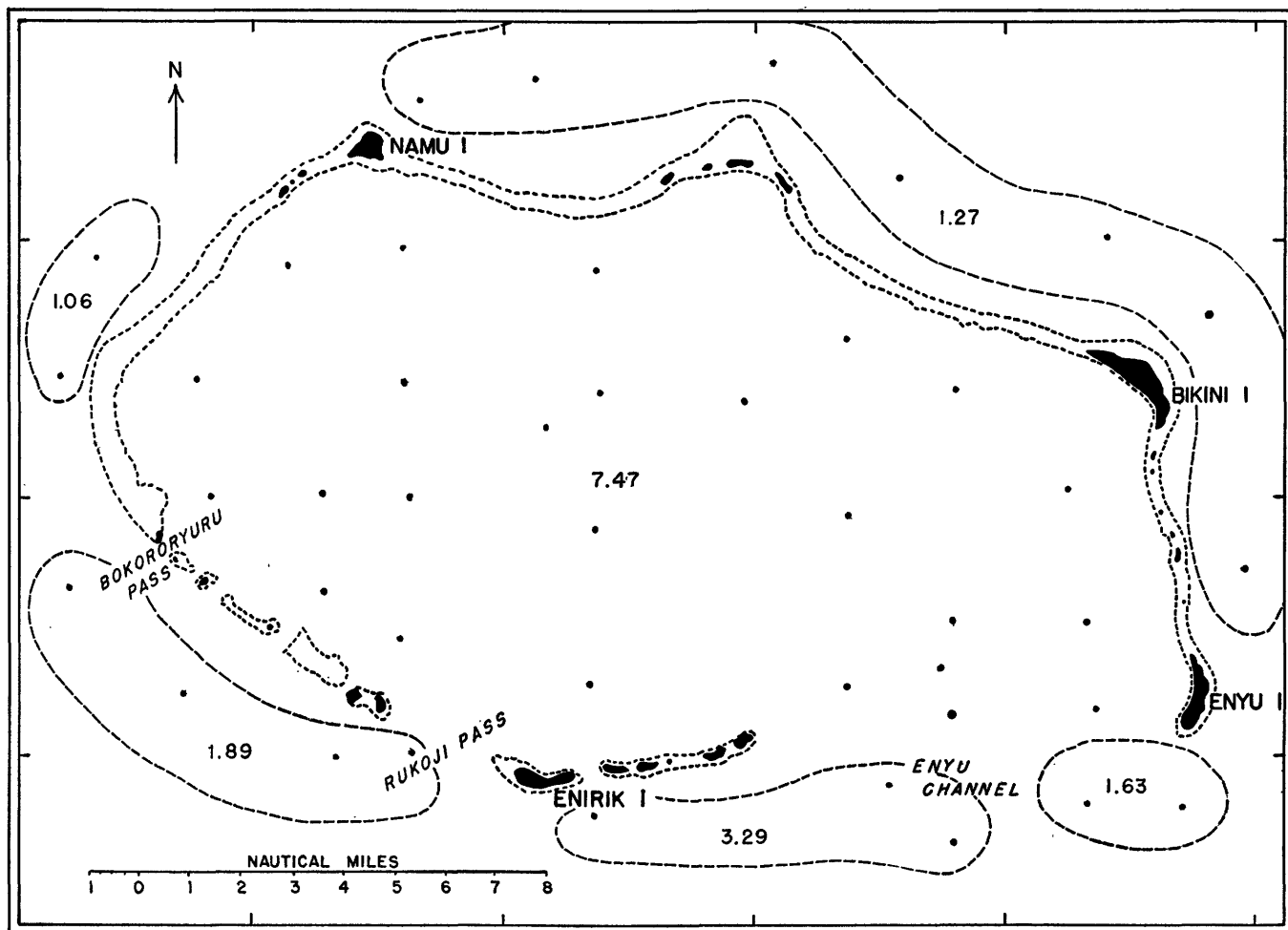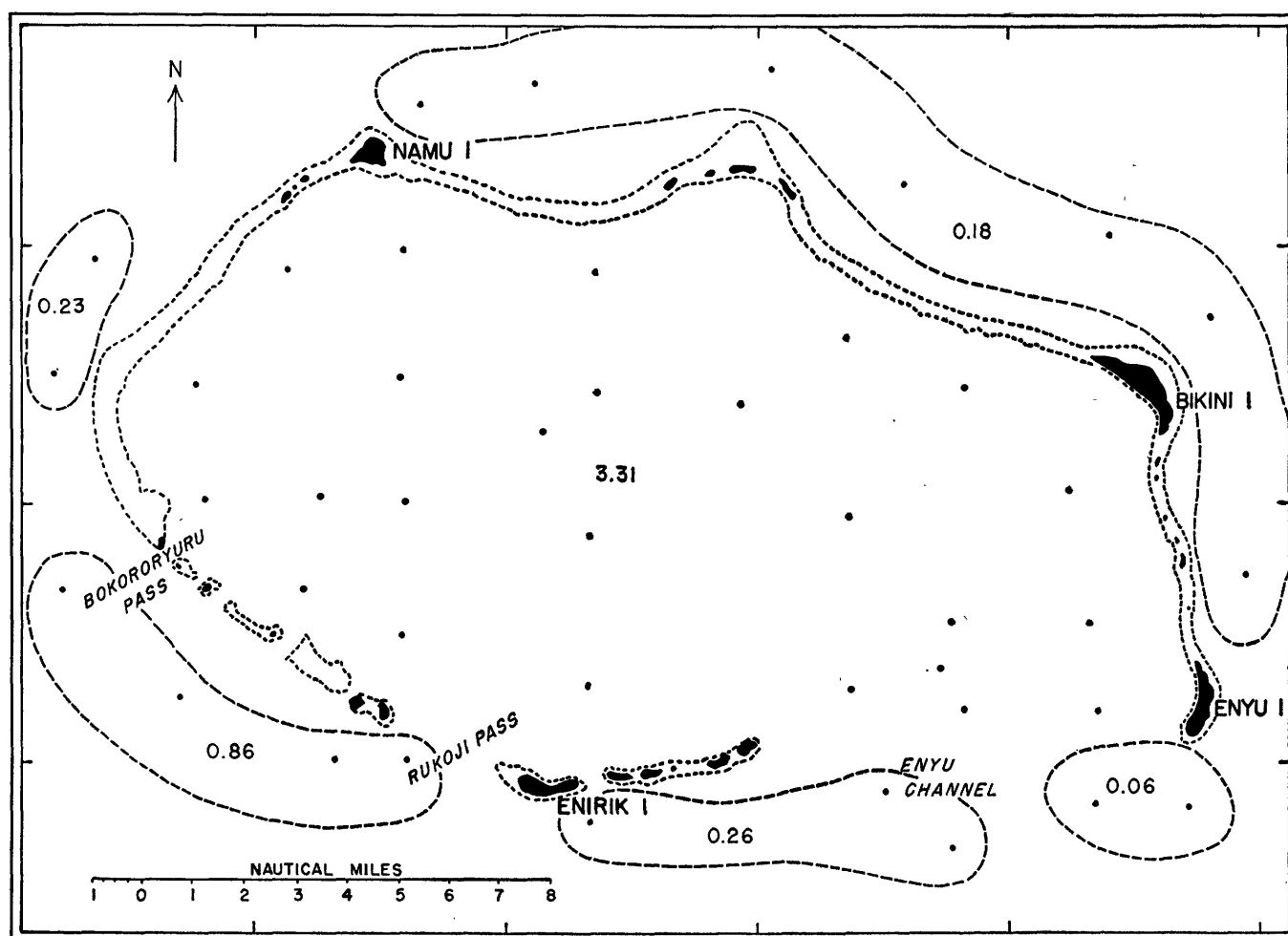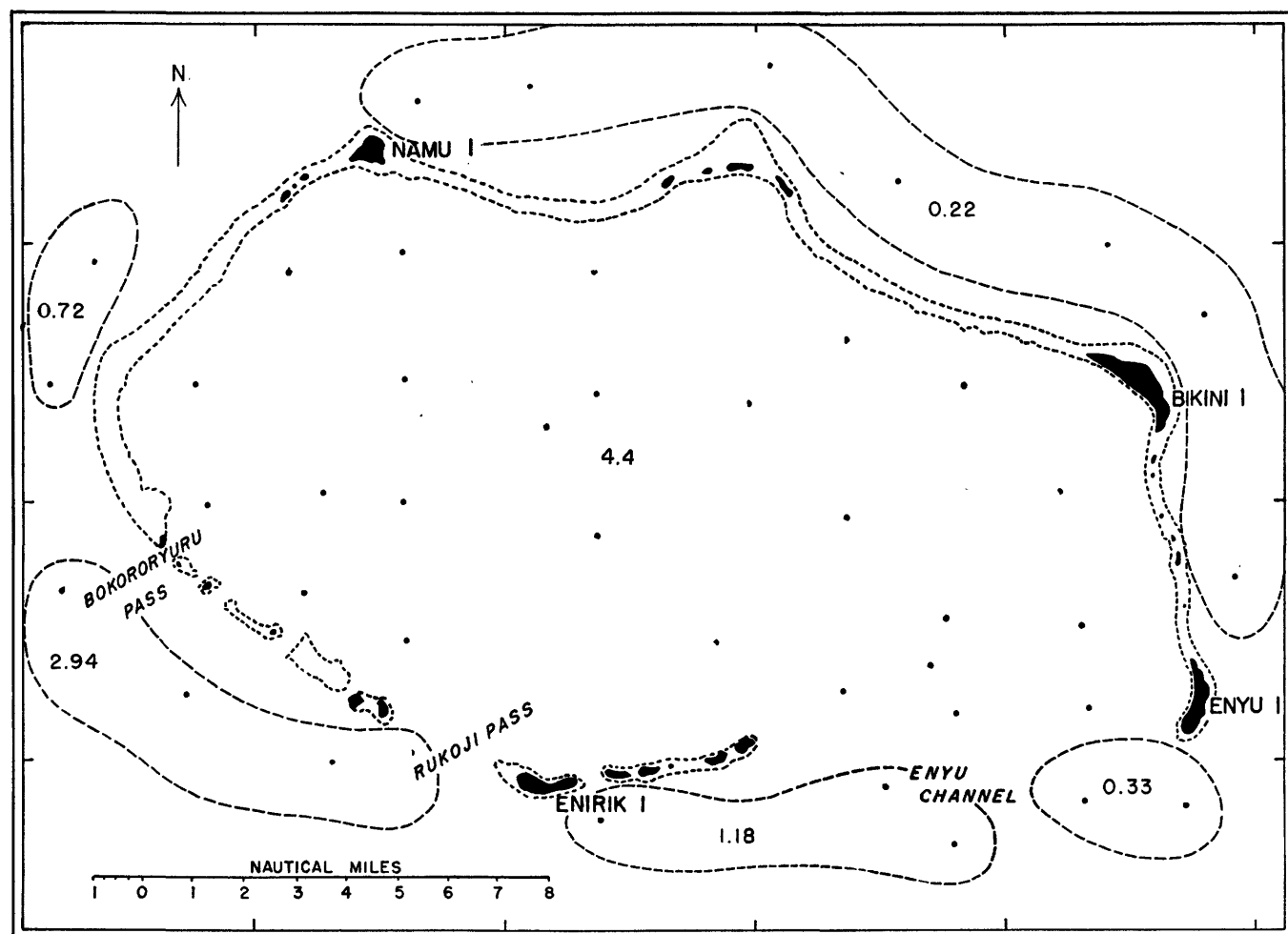TABLE 1.—*Relative number per cubic meter of certain planktonic organisms in four lagoons of atolls in the northern Marshall Islands*

Where density could not be determined, mere presence of an organism is indicated by a plus sign (+)]

	Bikini (March 25—May 18)		Eniwetok (June 2–14)	Rongelap (June 18–22)	Rongerik (June 23–24)
	Inside lagoon	Outside lagoon	Inside lagoon	Inside lagoon	Inside lagoon
Collected with Clark-Bumpus samplers—No. 2 mesh net					
Globigerina	5.01	5.56	0.41	10.88	0.62
Tretomphalus planus	25.15	1.3	2.30	6.64	3.07
Acartia hamata	5.05		8.46	3.93	4.60
Corycaeus spp	15.89		.68	16.44	3.04
Oithona spp	3.31	51.2	.38	6.17	2.31
Undinula vulgaris	18.51		4.11	(+)	1.94
Microcalanids	19.59		1.88	22.66	3.95
Crab larvae	3.31	.32	5.92	5.05	2.44
Shrimp larvae	4.41	1.08	5.06	13.84	4.78
Echinopluteus	(+)	(+)	.75	139.1	(+)
Ophiopluteus	(+)	(+)	2.30	3.50	(+)
Creseis (pteropod)	11.30	.95	.36	.34	.02
Chaetognaths	7.47	1.83	5.67	5.76	4.03
Appendicularia	25.25	7.6	1.76	26.18	47.62
Fish eggs	1.45	.66	.09	2.27	.73
Fish larvae	.61	.16	1.15	3.64	1.43
Collected with No. 20 mesh net in hauls from 50 meters to surface					
Tintinnids	95	76	271	326	309
Copepod larvae	551	298	555	1,065	483
Clam larvae	334	6	41	1,091	774
Diatoms	435	85	905	534,345	734
Dinoflagellates	1,137	273	595	1,572	631

second part on 50–0 meter hauls with the No. 20 mesh net. The amount of water filtered by the No. 20 net is subject to some error because of the drift of the ship, but this was not usually too serious since the hauls were so shallow. The numbers given for the No. 2 net hauls are doubtless minimal for some groups with small members because of the selective size of the mesh. This is especially true for the small copepods *Acartia*, *Corycaeus*, *Oithona* and for some less common cyclopoids.

On the basis of these surveys some important differences come to light relative to the standing crop within the lagoons. It is seen that Rongelap and Bikini Lagoons appear to have a somewhat richer planktonic fauna than do the other lagoons, especially Eniwetok. This was noticeable especially for the copepods as a group. For these the numbers per cubic meter of water with the No. 2 net were: Bikini, 62.37; Rongelap, 57.17; Rongerik, 18.08; and Eniwetok 15.74.

Pending further taxonomic analysis of the collections it will be useful to list the following holoplanktonic species as being among the more common for the lagoons:

Copepoda:

Acartia hamata Mori.
Calanus pauper (average 4.62 per cubic meter in Bikini Lagoon).
Calanopia minor (very common in Rongelap Lagoon).
Calocalanus pavo.
Candacia spp.
Centropages elongatus.
    sp.
Clausocalanus pungens.
Copilia mirabilis.
Corycaeus spp.
Eucalanus attenuates.
Labidocera sp.
Lubbockia squillimana.
Oithona plumifera.
Oncea venusta.
Sapphirina stellata.
Scolecithrix danae.
    sp.
Tortanus murrayi.
    gracilis.
Undinula darwini (found outside only).
    vulgaris.

The list of Copepoda is far from complete for the whole area and for the rarer species.

Chaetognaths:
    Sagitta enflata.
        robusta.
        serratodentata.

The siphonophores occurring in the samples have been discussed by Sears (1950).

One conspicuous difference in the zooplankton of the lagoons was the relatively large number of different larval forms, including fish, in Rongelap Lagoon. Specific identification could not be made of the larvae; most of the shrimp larvae were snapping shrimp.

PHYTOPLANKTON

Another notable difference pertains to the phytoplankton caught with the No. 20 net. The standing crop of phytoplankton was exceedingly small in most of the lagoons, and this was verified by the blue color and great transparency of the water. In Rongelap Lagoon,

FIGURE 110.—Pteropod, *Creseis* sp., average number per cubic meter of water by areas; black dots indicate stations averaged in each area.

FIGURE 111.—Arrow worms, *Sagitta* spp., average number per cubic meter of water by areas; black dots indicate stations averaged in each area.

FIGURE 112.—Crab larvae, average number per cubic meter of water by areas; black dots indicate stations averaged in each area.

FIGURE 113.—Shrimp larvae, average number per cubic meter of water by areas; black dots indicate stations averaged in each area.
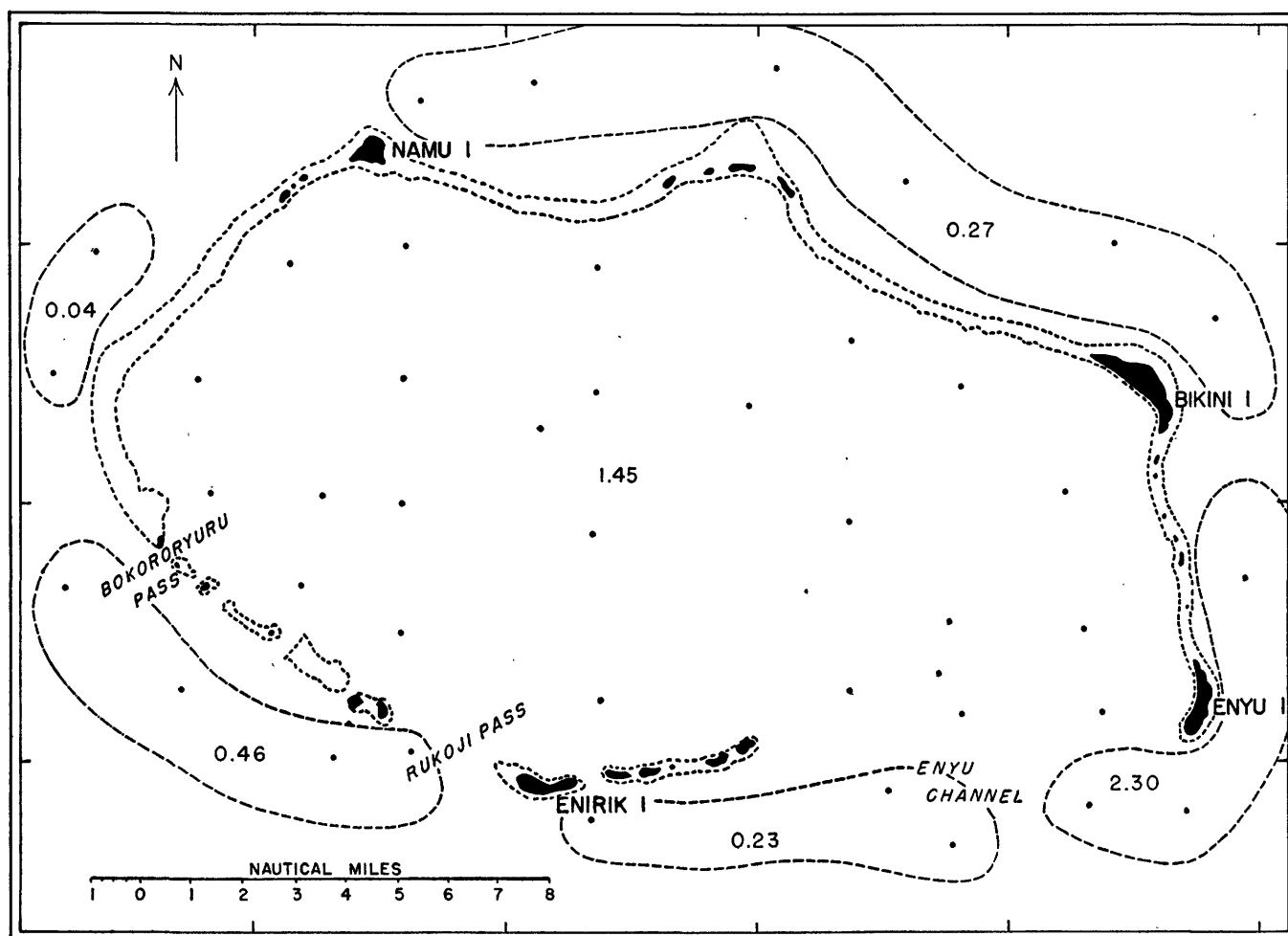
FIGURE 114.—Fish eggs, average number per cubic meter of water by areas; black dots indicate stations averaged in each area.

however, there was somewhat of a phytoplankton "bloom" in process during June 17–22. This gave a perceptible discoloration to the water in some parts of the lagoon. A second visit to the lagoon July 22 to 23 showed the phytoplankton to have diminished considerably, but it was still more abundant than observed in any of the other lagoons during the course of the survey.

The report on bottom sediments does not indicate that siliceous material was encountered. While a considerable quantity of diatom frustules may be precipitated to the bottom during the blooms, the diatoms found in the plankton were for the most part weakly silicified and therefore might add but little material to the sediments. The dominant diatom was *Rhizosolenia* sp., which constituted nearly 100 percent of the diatoms over most of the lagoon. The small northeastern bulge of the lagoon showed a similar bloom of diatoms, but these were strangely nearly all a species of *Chaetoceros*. Diatoms such as *Coscinodiscus* with heavier type of frustules were exceedingly rare in the plankton of all lagoons.

Dinoflagellates formed a substantial part of the phytoplankton and were the dominant photosynthetic forms observed in net collections in Bikini Lagoon.

Judging from the small standing crop of phytoplankton in all of the lagoons, with the possible exception of Rongelap, one is tempted to conclude that the sampling method used failed to reveal a portion of the photosynthetic forms or that production and utilization proceed at nearly the same rate. That the water must produce a fair crop of plants seems evident in view of the rather considerable concentration of zooplankton, including a substantial number of forms such as tintinnids and appendicularia that require very finely divided particulate material either as minute living cells or as detrital particles that readily pass through the meshes of the net.

Among the corals the problem of obtaining food is thought to be met by the presence of zooxanthellae that synthesize utilizable organic substance within the coral tissue. (See Prof. Paper 260–E.) However, this is controversial. Yonge (1951) is of the opinion that the

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ILLUSTRATIONS

[Plates 80 and 81 are inserted after list of references]

RECENT BRACHIOPODS

By G. A. COOPER [1]

ABSTRACT

Three genera and four species of brachiopods were found at Bikini Atoll. Some occur in the lagoon, others on the outer slopes on reef slabs at depths of 300 feet. The genera *Argyrotheca* and *Crania* have one species each of minute forms, possibly immature individuals. The genus *Thecidellina* is represented by 2 species, one new and one already described.

The extensive collecting at Bikini Atoll prior to the bomb-testing activities there produced four species of brachiopods. The specimens are all small and not easy to see. They represent three genera, none of which has so far been found commonly in Pacific waters. At Bikini Atoll, *Crania* appears as tiny yellow to orange shells that probably represent young rather than mature individuals. *Argyrotheca* occurs as small individuals one or two millimeters in width with characters that clearly indicate young shells. The two remaining species, which belong to the genus *Thecidellina* (Thomson, 1927), are fairly common. Although the first two genera may represent new species, respectively, these are not described as new because of the youthful character of the shells. Of the species of *Thecidellina* one is new, the other is a species previously described from Funafuti Atoll.

OCCURRENCE AND ASSOCIATIONS

The association of these species and their habitats are interesting. Three of the species occur together: *Crania* sp., *Argyrotheca* sp., and *Thecidellina congregata*, n. sp. This association appears on a large coralline slab about 8 by 10 inches in horizontal dimensions and about 1 inch thick. Although the life position of the slab could not be determined at the time the piece was collected, because it was dredged from 300 feet, the brachiopods are clustered on one side of the slab only. The opposite side to the one bearing the brachiopods and numerous other attached forms is rough and irregular and contains only an occassional young pelecypod (*Spondylus*) but is encrusted by nullipores. The side having abundance of life is smooth compared to the reverse side. This evidence combined with the nullipores suggests that the smooth surface is the lower side of the slab and that the brachiopods were clustered on the side where the water was quiet. The most abundant specimens on this slab are *Thecidellina congregata*. This species also appears at the northwest end of Bikini Atoll in 240 fathoms (1,440 feet) of water. The same species was taken at 180 to 200 feet in the lagoon (locality S–46–44).

Thecidellina maxilla occurs on the outer slopes of Bikini Atoll and in the lagoon as well. It does not, however, have as great a depth range as *T. congregata*. At the northwest end of Bikini Atoll *T. maxilla* ranges from 154 feet to 450 feet. In the lagoon one specimen was taken between 180 and 200 feet at the same locality as mentioned above for *T. congregata*. This particular specimen is loose, consequently its attachment surface and associates are not known.

Specimens of *Thecidellina maxilla* from K. O. Emory (Coll. 421) consists mostly of dead shells attached to the coral *Lobophyllia*. The individual shells are large and are somewhat encrusted by limy material. The entire mass may not have been found in place.

SYSTEMATIC DESCRIPTIONS

Genus CRANIA Retzius 1781

Crania sp.

Plate 80, Figures 1–5

Shell small, pale salmon-colored; pedicle valve thin, attached by its entire surface and conforming to the contours of its place of attachment; brachial valve a low, eccentric cone, the apex directed toward the posterior, which is the shorter side; apex located one-third the total shell length anterior to the posterior margin; posterior slope moderately steep, less steep than the long and gentle anterior slope. Anterior profile broadly convex with the valve narrowly pointed at the middle. Measurements of the largest specimen: length 2.8 mm, width 3.0 mm, height 0.8 mm.

Figured specimens: USNM 549272, 549273, 549274.

Locality and depth: On underside of coralline expansion, on the south side of Bikini Atoll at 300 feet.

Genus **THECIDELLINA** Thomson 1915

Thecidellina congregata Cooper, n. sp.

Plate 80, figures 6–15

Small, but of about medium size for the genus; white to blue gray; attached by nearly the entire surface of the pedicle valve; shape variable as usual with attached forms, most specimens wider than long and polygonal in outline; deepest just anterior to the beak of the brachial valve. Hinge narrow. Brachial valve marked by obscure concentric growth lines and wrinkles only.

Pedicle valve with only the apical region visible; interarea small, sharply triangular; palintrope plane, descending at an angle from the commissure ranging from 90 to about 30 degrees, but steep in most specimens. Interior of pedicle valve with large teeth buttressed by strong dental ridges; hemispondylium attached to the floor of the valve in the delthyrial chamber and consisting of two short nearly vertical plates bearing sharply pointed processes; adductor scars located in deep, elongate pits on each side of the valve just anterior to the delthyrial cavity.

Brachial valve provided with a short, broad triangular plane apical interarea. Gently convex in lateral and anterior profiles. Interior with thick narrow and strongly elevated quadrangular cardinal process; sockets moderately deep; bridge thin; septum strongly elevated; valve margin granulated; a deep, narrow trough inside the granulated margin running around the anterior side of the bridge and terminating on the flanks of the median septum at about the middle of the valve; narrow trough occupied by lophophore; posterior occupied by a chamber located just anterior to bridge and at posterior end of median septum; entrance to chamber located on anterior side of bridge at its middle and at posterior end of median septum, the "reversed spondylium" of Hayasaka; posterior side of bridge and just anterior to cardinal process marked by deep pit divided by a small septum. Area between lophophore groove and median septum occupied by a curving row of protruberances rising in height from mere nodes to erect processes which may have served as straining devices.

USNM No.	Measurements, in millimeters				
	Length	Brachial length	Maximum shell width	Hinge width	Thickness
549275a	3.3	3.1	3.4	1.4	1.2
549275c	4.9	3.9	4.5	1.9	1.1
549277	4.7	4.0	4.2	2.2	-----

Deltidial plate: The abundance of material of this species makes it possible to add some information on the generic characters of *Thecidellina*. The cover of the delthyrium is a flat plate resembling that of the Triplesiidae and suggestive of the terebratuloid symphytium. It is not known how this plate originates, but it is clear that it must have been deposited by the mantle because its growth lines are transverse to the sides of the delthyrium as in the terebratuloid symphytium. Of all the specimens studied, not one shows the deltidial plate to be punctate. Most of the specimens of *T. congregata* reveal the punctae as small white dots or in some instances as black dots. Neither of these types shows on the deltidial plate. It is therefore concluded that the deltidial plate is impunctate, although much of the remainder of the shell is strongly and coarsely punctate.

Hemispondylium: This structure, recently named by Elliott (1948), appears as two small pointed processes that extend obliquely anteriorly and are located in the delthyrial chamber. These are sharply pointed at their free end, but expand toward the floor of the valve and are attached in the apex. The floor between these plates is somewhat thickened and the plates extend posteriorly to the apex at their base so that they bound a small shallow chamber at the rear. This is quite unlike the hemispondylium of *T. maxilla*, which forms a free tube under the deltidial plates. The hemispondylium is the seat of attachment of didcutor muscles and inner adductor muscles whose other extremities are attached to the cardinal process or quadrilateral plate and the pit behind the bridge.

Teeth: The teeth are stout and are located at the base of the deltidial opening. They are buttressed by a ridge that runs along the delthyrial edge. This ridge is the growth track of the tooth.

Brachial valve: This part of *Thecidellina* is quite complicated, although the lophophore is fairly simple in form. The cardinal process or "quadrilateral plate" is fairly complex. Its external expression when the brachial valve is viewed from the exterior is that of a broad sloping, nearly smooth plate fitting under the deltidial plate. Seen from the inner side, the plate is squarish posteriorly but is buttressed by two lateral thickenings or ridges which bound an inner recess and lateral recesses. The latter serve as the deep and large sockets which receive the teeth. The lateral buttresses flare to each side at the base of the adductor attachments and bound the cavity posterior to the bridge.

The cavity just anterior to the base of the cardinal process is divided into halves by a ridge and a small septum arising from the top of the arch or vault covering the body cavity. Adductor muscle ends are attached to the upper part of the vault on either side of the septum.

The lophophore is in the schizolophus stage and is attached in the groove just inside the granulated mar-

gin, forming a big loop from the bridge and running not only down each side to curve narrowly in a posterior direction but also along each side of the median septum. The filaments of the lophophore are long and are separated in pairs or singly by thick or thin horizontal partitions that become progressively smaller toward the posterior.

The opening into the body cavity is located just posterior to the posterior end of the median septum and just anterior to the bridge, which separates it from the somewhat larger opening on the opposite side of the bridge.

The musculature is not easy to determine in these small shells except for the large adductor muscles that are attached at the outside base of the cardinal process. The scars of these muscles can be seen in the pedicle valve on each side of the hemispondylium on the underside of the palintrope. Two sets of muscles appear to be attached to the hemispondylium. One of these sets attaches to the posterior edge of the cardinal process and the other is attached inside the pit just anterior to the cardinal process and just behind the bridge. This is like the musculature described for *Lacazella*. (Lacaze du Thiers, 1861.)

Types: Holotye, USNM 549277; figured paratypes, USNM 549275a-d, 549276, 549278.

Locality and depth: On underside of coralline expansion, on the south side of Bikini Atoll at 300 feet.

Discussion: *Thecidellina congregata* is especially distinguished by its moderate size, irregular spreading outline; expansively adherent mode of attachment, and short, small interarea. The interior of the brachial valve has a large and conspicuous cardinal process extending far posterior to the bridge while the pedicle valve has the hemispondylium resting on the floor of the valve at the apex. The external form and interior distinguish this species readily from *T. maxilla*. The form and outline of the pedicle valve distinguish it from either *T. blochmanni* or *T. barretti* which it resembles in size.

Thecidellina maxilla Hedley

Plate 81, figures 1–10

Thecidea maxilla Hedley. Mollusca of Funafuti. pt. 2, Pelecypoda and Brachiopoda, Mem. Australian Mus., v. 3, pt. 8, p. 508–510, fig. 57, 1899.

Shell large for the genus, longer than wide and with an elongate oval outline, the beak forming the narrow end. Shell attached by the beak of the pedicle valve and usually in an upright position. Hinge slightly less than the greatest shell width, which is about at the middle. Both valves marked by concentric growth wrinkles.

Pedicle valve with interarea long, equaling more than

one-third of valve length; interaera smooth and elongate triangular. Lateral profile gently convex; anterior profile narrowly rounded; umbo more or less irregular and occupied by the scar of attachment. Median region swollen; sides narrowly rounded and steep. Teeth large and having strong, thick dental ridges; hemispondylium (Elliott, 1948) a long rounded tubular plate with two stout processes at the distal end; hemispondylium apparently free above delthyrial cavity and not attached to floor of valve.

Brachial valve with short and deeply concave cardinal process; socket ridges not well developed; granulated margin narrow, elevated toward the posterior; lophophore groove narrow and deep; bridge elevated and broad, almost hiding the cardinal process when viewed from the pedicle valve; median septum high and thin, with the lophophore groove located on its sides about midway in the direction of the brachial valve. Space between lophophore grooves occupied by elaborate nodes and irregular processes. Posterior chamber large, with smooth walls; opening into chamber at posterior end of septum small, openings just anterior to cardinal process large.

USNM No.	Measurements, in millimeters					
	Length	Brachial length	Midshell width	Hinge width	Thickness	Length of interarea
549286a	7.2	4.7	4.8	3.6	3.3	2.5
549286b	8.8	5.5	5.1	3.9	4.2	3.3
549285	8.2	5.4	5.6	3.4	4.0	2.8

Types: figured specimens, USNM 549284a, 549285, 549287, 584676.

Locality and depth: USNM 549284a and 549285, 420 to 450 feet at Bikini Atoll, lat. 10°39′10″ N., long. 165°12′59″ E.; USNM 549287, at 154 feet, Bikini Atoll, lat. 11°38′15″ N., long. 165°18′05″ E.; USNM 584676, at 180–200 feet in the lagoon, Bikini Atoll. At Funafuti Atoll in the Ellice Islands, the species was found in considerable numbers on dead coral at depths of 240 to 480 feet on the lee slope of the atoll (Hedley, 1899, p. 509).

Discussion: The specimens here referred to *T. maxilla* are the largest specimens of this genus yet found. They are identified as *T. maxilla* because of their elongate outline, erect habit of growth, long median septum and small cardinal process. These features combined with the unusually long interarea make the species easy to recognize. *Thecidellina maxilla* is entirely different from *T. congregata*, which never attains the size of *T. maxilla*, is usually attached by most of the surface of the pedicle valve, and has a more variable shape. *Thecidellina maxilla* is quite unlike *T. barretti*, an Atlantic species occurring in the waters about the West

Indies. *Thecidellina blochmanni* from Christmas Island is another small species quite unlike *T. maxilla.*

Genus THECIDELLELLA Hayasaka

Hayasaka (1938) described the genus *Thecidellella* as being very similar to *Thecidellina* but differing from that genus in having a "reversed spondylium." This latter structure is located at the posterior end of the median septum. In it is the opening just anterior to the bridge and just behind the septum. The "reversed spondylium" is present in both of the Bikini species of *Thecidellina* and also in *T. barretti,* contrary to Hayasaka's statement. Hayasaka reproduces Davidson's figure of *T. barretti* which seems to be inaccurate. All species of *Thecidellina* in the U. S. National Museum are internally like Hayasaka's species. It is therefore concluded that *Thecidellella* is a synonym of *Thecidellina.*

ARGYROTHECA

Argyrotheca sp.

Plate 81, figures 11–22

Shell minute, slighly wider than long with broadly rounded sides but indented anterior margin; hinge narrower than the midshell width; cardinal extremities rounded; subequally biconvex but with the pedicle valve having a somewhat greater depth than the brachial valve; most specimens smooth but some with about three indistinct radial costae on each side of the median-line. Coarsely punctate.

Pedicle valve gently convex in lateral profile and with maximum convexity anterior to umbo; anterior profile broadly but moderately convex, somewhat narrowly convex in the median region; umbonal region, with steep slopes; posteromedian region moderately swollen; anterior region somewhat flattened and forming a long, gentle anterior slope, sides with moderately steep slopes. Interior with ponderous teeth; apex with a moderate callosity; median ridge low, long, extending nearly to the front margin.

Brachial valve gently convex in lateral profile and with the maximum convexity just anterior to the umbonal region; anterior profile broadly and gently convex; beak small; umbo moderately swollen; median sulcus originating about one-third the valve length anterior to the beak; sulcus moderately deep, widening rapidly anteriorly to form a moderately broad indentation at the anterior margin; flanks bounding sulcus somewhat narrowly rounded to form board plicae with steep posterolateral slopes but fairly gentle lateral and antero-

lateral slopes. Interior with delicate cardinalia; socket plates erect and with narrowly rounded posterolateral boss that articulates with the teeth of the opposite valve; sockets deep, enclosed; loop short, widely divergent, attached at the base of the socket plates and extending laterally to attach to the floor at the posterolateral edge of the visceral region. Inner margin marked by seven prominent nodes on each side of the median line. Median septum arising about one-third the valve length anterior to the beak, and rising rapdily from the valve floor to extend nearly to the front margin; median septum highest near the valve middle and serrate on its anterior margin.

USNM No.	Measurements, in millimeters				
	Length	Brachial length	Midshell width	Hinge width	Thickness
549279a	1.5	1.3	1.6	0.8	0.6
549279b	1.7	1.4	1.9	1.2	2

Figured specimens: USNM 549279a, b, 549288, 549289.

Locality: 300 feet on the south side of Bikini Atoll.

Discussion: The small size, translucent shell, and coarse punctae of this species suggest the young of a larger form. However no fully grown specimens were seen. Blochmann described *A. australis* from South Australia and *A. mayi* from Tasmania, but both of these species are much larger forms with a definite costation. The Bikini specimens cannot be satisfactorily identified with either of Blochmann's species.
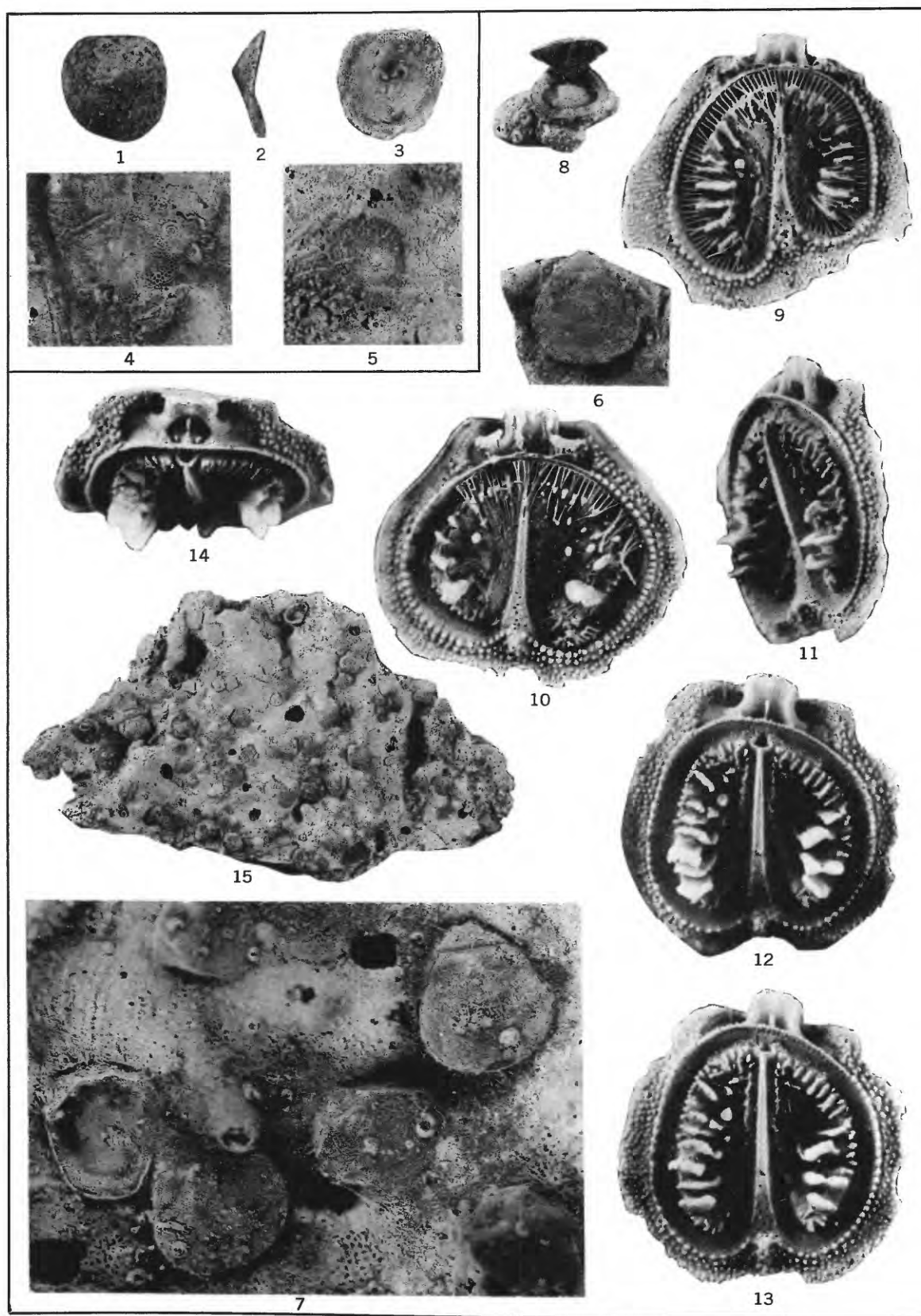
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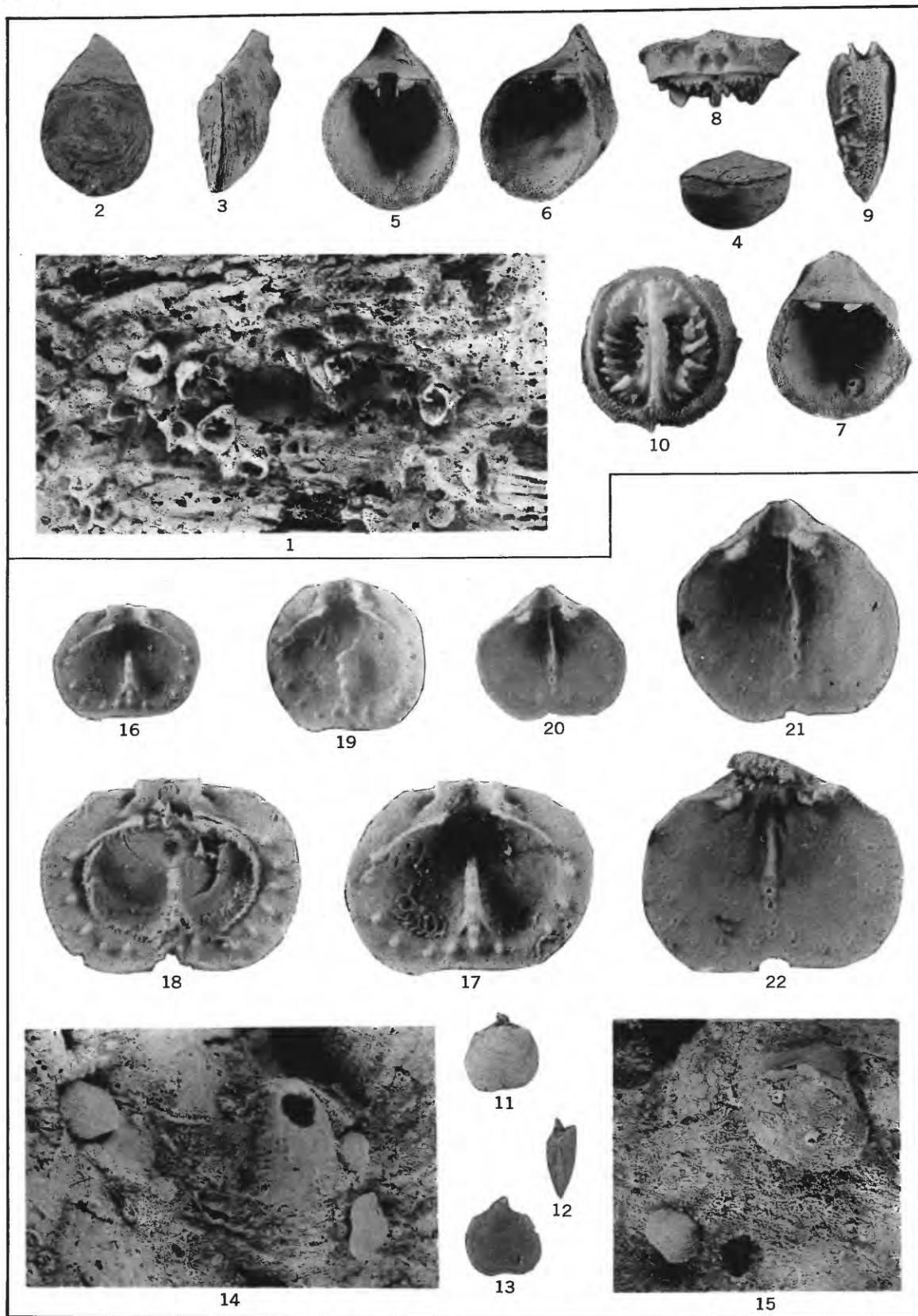
PLATES 80–81

PLATE 80

CRANIA SP. AND THECIDELLINA CONGREGATA

THECIDELLINA MAXILLA AND ARGYROTHECA SP.

PLATE 81