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Structure and Biological Dynamics of the Oligotrophic Ocean Photic Zone off the Hawaiian Islands[1]

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ABSTRACT: The base of the photic zone, as defined by the 1-percent light depth and discontinuance of photosynthetic carbon fixation, was determined to be at 130–140 meters on stations off the Hawaiian Islands. Measurements, including radiant energy transmission, plant nutrients, and chlorophylls, were made in the depth interval 0–250 meters. The numerical vertical abundance, biomass, and the identity of phytoplankton, microzooplankton, bacteria, and fungi were determined. A discussion of the biological dynamics within this photic zone is based on these observations and on measurements of photosynthetic production, nitrogen fixation, and other microbial activities.

THE PHOTIC ZONE is frequently defined as being the body of water between the surface of the sea and the depth where the net photosynthetic assimilation of carbon dioxide reaches zero (Strickland 1960). This depth is roughly equivalent to the depth to which 1 percent of the surface incident radiant energy penetrates. In the oligotrophic ocean's photic zone, photosynthetic activity is controlled basically by the inverse gradients of light energy and plant nutrients, the latter becoming available in significant amounts only near the base of the photic zone (MacIsaac and Dugdale 1972). The biological activities and the spatial distribution of organisms in the photic zone are controlled, however, by many other factors as well: physical (temperature, position of the pycnocline, hydrostatic pressure, turbulent mixing), chemical (oxygen, nutrients, trace elements), and biological (recycling of nutrients, grazing, migrations, etc.).

During the last few years, marine biologists and oceanographers have shown increasing interest in the smaller organisms and in the dynamics of biological systems in the tropical ocean's photic zone. Numerous measurements of primary production have been carried out and many have been reviewed and discussed in a much-cited paper by Koblentz-Mischke, Volkovinsky, and Kabanova (1970). The significance of the deep chlorophyll maximum of the oligotrophic ocean has been discussed by Lorenzen (1967), Saijo (1973), Venrick, McGowan, and Mantyla (1973), and others. Phytoplankton populations have been studied by Malone (1971), Muller (1971), Semina (1972), Throndsen (1973), and others. There is increasing evidence that most of the productivity in tropical seas is due to the nannoplankton rather than to the larger phytoplankters, as previously assumed. Sorokin (1971) has shown that bacteria may play a major role as primary producers by transforming dissolved organic material to biomass and, at the same time, by fixing carbon dioxide. However, Sorokin's findings have lately been criticized and the question of bacterial production has been discussed in light of other evidence by Steemann Nielsen (1972), Skopintzev (1973), and Banse

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TABLE 1

OBSERVATIONS AND SAMPLINGS

STATION	CRUISE NUMBER	DATES 1972	DEPTH RANGE (m)	SAMPLING INTERVAL (m)	NUMBER OF CASTS	NUMBER OF OBSERVATIONS: TEMPERATURE	SALINITY	LIGHT	*p*H	ΣCO_2	O_2	PO_4	NO_2	NO_3	SiO_2	CHLOROPHYLL
B	7203	16–17 Mar	0–275	25	1	2	12	—	12	—	12	12	12	12	—	12
	7207	13–14 Jun	0–275	25	3	3	12	1	23	11	23	12	11	11	12	12
C	7204	13–14 Apr	0–275	25/50	4	3	30	—	30	6	30	30	31	31	—	10
	7210	8–9 Aug	0–199	10/25/50	2	2	—	—	—	8	—	—	—	—	—	8
	7211	20 Oct	0–217	20	1	1	—	—	—	—	—	12	12	12	—	—
	7212	18 Dec	0–158	10/20	1	1	—	—	—	—	—	12	—	—	—	—

NOTE: Station B is located in the Kealaikahiki Channel off the Hawaiian Islands at 20°41′ N, 156°55′ W; station C is located off Oahu, Hawaiian Islands, at 21°22′ N, 159°12′ W.

(1974). Extensive investigations by Beers and Stewart (1967, 1969*a*, *b*, 1970*a*, 1971), Pepipa, Pavlova, and Mironow (1970), Parsons and LeBrasseur (1970), and others have thrown new light on the zooplankton communities of the photic zone and their importance in marine food chains. The magnitude of respiration by marine organisms, which is experimentally difficult to assess, has been investigated by Pomeroy and Johannes (1968), Hobbie et al. (1972), Ivanenkov et al. (1972), and Gundersen and Corbin (in press). Nutrient regeneration, biological nitrogen fixation, and microbial transformations of nitrogen compounds have been studied by Johannes (1968), Dugdale and Goering (1967), Wada and Hattori (1971), and Mague, Weare, and Holm-Hansen (1974).

A recent paper by Eppley et al. (1973) describes work done at three stations in the oligotrophic waters of the North Pacific central gyre and is an excellent example of the usefulness of multiphasic investigations of marine ecological problems. Their study encompassed nutrient analysis, productivity, nutrient assimilation and growth rate determinations, zooplankton excretion studies, etc., and the multitude of observations made enabled this group of investigators to draw important conclusions regarding plankton dynamics and ecological interactions in the oligotrophic photic zone.

In this paper we report the results of a multiphasic study of the photic zone of the Pacific Ocean off the Hawaiian Islands. The observations were made and the experimental work performed during six cruises in 1972 of the University of Hawaii's R.V. *Teritu* to the oceanographic station Kaioli (station C) at 21°22′ N, 159°12′ W and to a station in the Kealaikahiki Channel (station B) at 20°41′ N, 156°55′ W. Tables 1 and 2 list the various cruises to these two stations, the data collected, and the experimental work done. All data and observations, whether used in the present report or not, have been deposited with the National Oceanographic Data Center, Rockville, Maryland 20852 (see also Gundersen 1974).

The authors are grateful to the officers and crew of the R.V. *Teritu* for their helpfulness and cooperation. Special thanks are due to Dr. T. K. Newbury for advice and suggestions regarding the zooplankton work.

TABLE 2

BIOLOGICAL OBSERVATIONS

ORGANISMS	CRUISE NUMBER	STATION	DEPTH RANGE (m)	NUMBER OF DEPTHS	NUMBER OF CASTS	OBSERVATION
Phytoplankton	7203	B	25–275	11	1	counts
	7207	B	0–275	8	1	counts
	7204	C	10–210	6	3	diel variation
	7210	C	10–150	8	2	primary production
Microzooplankton	7203	B	25–175	4	1	counts
	7204	C	35–120	2	2	diel variation
	7207	B	0–200	6	2	diel variation
Blue-Green Algae	7211	C	0–220	12	1	nitrogen fixation
	7212	C	0–220	12	1	nitrogen fixation
Bacteria	7203	B	125	1	1	nitrification/denitrification
	7204	C	10–200	6	2	counts
	7207	B	0–200	6	4	nitrate reducers
	7211	C	80–160	3	1	nitrate reduction
Fungi	7203	B	25–300	7	1	counts

NOTE: Station B is located in the Kealaikahiki Channel off the Hawaiian Islands at 20°41′ N, 156°55′ W; station C is located off Oahu, Hawaiian Islands, at 21°22′ N, 159°12′ W.

MATERIALS AND METHODS

Light Measurements

The downward irradiance in the photic zone was measured with a locally built color transmission metering system consisting of a floating surface cell (reference) and a weighted submersible cell. The matched selenium sensors (Weston Photronic, model 856 RR) had a spectral range of 380–1000 nm with a 50–100 percent sensitivity range from approximately 400 to 650 nm and with maximum sensitivity at 555 nm. Corning neutral density filters (Corning Glass Works, Corning, New York) were used with color filters to obtain information on the spectral distribution of light in the water column. The following color filters were used: blue (Corning CS 1-64), blue-green (Corning CS 4-70), green (Corning CS 4-74), yellow (Corning CS 3-77), and red (Corning CS 2-63).

The surface illumination, in lux, was measured with a Spectra illumination meter, model OP 400 (Photo Research Corporation). In converting the lux reading into units of radiant energy, we made use of the Smithsonian tables (Strickland 1958). The fraction of the total radiant energy transmitted by the various color filters was calculated for the range 380–650 nm and was used to determine the relative radiant energy distribution from the surface to 150 m depth.

Water Sampling

Water samples collected for the determination of salinity, dissolved oxygen, plant nutrients, *p*H, alkalinity, and chlorophyll were taken at 25-m intervals from the surface (1–5 m) down to 250 m with a set of 12 13-liter polyvinylchloride van Dorn samplers. Samples for microbiological analyses (bacteria, yeasts, and fungi) were taken with 2-liter Niskin sterile bag samplers (General Oceanics, Inc.). Microzooplankton, phytoplankton, and blue-green algae samples were taken with the van Dorn samplers.

Temperature Measurements

The water temperature was recorded with Sippican XBT probes, T-6, and the surface temperature was verified against a precision mercury thermometer.

Chemical Analysis

Salinity was determined with a laboratory salinometer (Bisset-Berman model 6230), and

standard Copenhagen seawater was used as a reference. Alkalinity, *p*H, and carbon dioxide were determined according to Strickland and Parsons (1968) with a Beckman Expandomatic *p*H meter with a Futura combination electrode (Beckman Instruments, Inc., Fullerton, California). Nitrate, nitrite, phosphate, silicate, dissolved oxygen, and chlorophylls were determined according to standard procedures (Strickland and Parsons 1968). Apparent oxygen utilization (AOU) was calculated from tables showing oxygen solubility in seawater (Green and Carritt 1967).

A Beckman ACTA II spectrophotometer was used for all colorimetric measurements. All chemical analyses were made on shipboard immediately following sampling.

Phytoplankton

Four liters of water samples from each depth were filtered through grid-marked 47-mm Millipore HA filters (Millipore Corporation, Bedford, Massachusetts) under a vacuum of about 200 mm Hg. Subsequently, aliquots of distilled water followed by solutions of 10, 25, 50, 70, 95 percent and absolute alcohol were also filtered to preserve the phytoplankton organisms. Upon drying, the Millipore filters were placed on microscope slides, covered with Histoclad (Adams Histoclad no. 3920 mounting medium), and protected by a cover slip.

We obtained phytoplankton counts by counting 100 grids under oil immersion. In general, the phytoplankters were classified to genera or groups (pennate diatoms, silicoflagellates, dinoflagellates). We calculated biomass from cell volume according to Mullin, Sloan, and Eppley (1966) and from chlorophyll *a* by using a conversion factor of 100 (Holm-Hansen 1969).

Microzooplankton

The effects of patchiness of the zooplankton on the sampling (Cassie 1963) were reduced by the use of clusters of two, three, four, or five van Dorn bottles, placed 5 or 10 m apart, to describe a depth, i.e., cluster range. After being recovered, the water samples were drained through a plankton separator constructed of a 202-μm mesh top and a 37-μm mesh bottom, both of standard Nitex netting. The most frequently filtered volume was 39 liters, but samples ranged from 26–65 liters. This procedure (Beers and Stewart 1967, 1969*b*, 1971) allowed the portion of the microzooplankton in the size range 37–202 μm to be obtained. The samples were preserved in buffered (*p*H 8.2) Formalin (Beers and Stewart 1970*b*) together with an excess of $SrCl_2$.

We developed methods for concentrating and counting the microzooplankton by following suggestions in UNESCO (1968). After being allowed to settle for 7 days, the samples were transferred to volumetric containers and adjusted to 60 ml. Two subsamples were removed with a 1-ml-capacity pipette and placed in a 2-ml-capacity gridded settling chamber for microscopic examination. Samples were stirred with a glass rod to keep them in homogeneous suspension.

The chambers were systematically examined at $\times 40$ to $\times 200$ with a Nikon inverted microscope. Photographs of unknown organisms were taken with a Nikon camera for later identification. Measurements (length and width, or diameter) were made with a calibrated ocular grid.

Only major taxonomic groups were enumerated, i.e., copepod nauplii, postnaupilar stages, other crustacean nauplii, polychaete larvae, pteropods, protozoa, tintinnids, foraminifera, and radiolaria. Naupliar and postnaupliar copepods were counted only when intact; molts were not counted. Animals with shells, tests, loricas (i.e., pteropods, foraminifera, radiolaria, and tintinnids) were counted if their shells, tests, or loricas were present. Deformation and dissolution of organisms were not problems.

Copepod nauplii and most naupliar copepods were combined and used as an index to indicate when subsampling should be stopped. After 30 organisms of this combined group had been counted, no more subsamples were taken. A total of 139 subsamples from the various casts were counted.

Variance-to-mean ratios were calculated for the individual sets of naupliar and postnaupliar copepod subsamples. A rejection criterion, i.e., nonrandom distribution, was calculated according to Greig-Smith (1964). Of 28 samples

tabulated, four, or 14 percent, departed significantly from random distribution (i.e., a nonhomogeneous suspension). These data were not eliminated from the results.

Microzooplankton biomass was calculated from numerical abundance data; methods used were based on those described by Beers and Stewart (1969*a*). The geometric shape of copepods and other planktonic crustaceans (e.g., shrimp nauplii) was assumed to be approximately cylindrical; foraminifera, pteropods, and two-thirds of the radiolaria were considered to be spherical; and the remaining radiolaria and tintinnids were assumed to be conical. Of the radiolaria, pteropods, foraminifera, and tintinnids, only 50 percent of the volume was considered to be living animal. We further assumed the living tissue to consist of 80-percent water and the dry matter to be 40-percent carbon.

Fungi

Five 100-ml aliquots of aseptically sampled seawater were filtered through 47-mm Millipore HA filters. The filter membrane was subsequently placed on Fuller's modified Vishniac agar (Fuller, Fowles, and McLaughlin 1964), prepared with 100,000 units each of potassium penicillin G and streptomycin sulfate per liter of seawater, used to control bacterial growth. All filtering was completed within 2 hours after the samples had been collected. The plates were then incubated for 14 days at 22°–25° C, and colonies of fungi were isolated in pure culture as they had appeared on the original plates.

Heterotrophic and Total Bacteria

Aliquots (10 and 100 ml) of aseptically obtained seawater were filtered through 47-mm Millipore HA filters and placed on marine agar (Difco Laboratories, Inc., Detroit, Michigan). The heterotrophic count, expressed as cfu (colony-forming units) per m^3 of seawater, was determined after the membrane and bacteria had been incubated for 10–15 days at 22°–25° C.

The total bacterial count was determined with the microscope, according to the method of Seki (1970), from the same water samples as those used for the heterotrophic count. Aliquots of 100 ml were filtered through Millipore HA filters with grids, the bacteria were then fixed in Formalin vapors, and the cells were stained with erythrosin.

The calculation of bacterial biomass was based on the total microscopic count, with an average cell volume of 1 μm^3, as determined by phase microscopy of freshly filtered seawater, being used. We assumed a specific gravity close to 1, a dry matter content of 20 percent, and a carbon content of 40 percent of the dryweight.

Nitrate-Reducing Bacteria

We used the same water for the heterotrophic count that was used for the determination of nitrate-reducing capacity and for the enumeration of nitrate-reducing bacteria. The water was diluted in a series of 1:5 sequences in a medium consisting of 0.5 percent glucose, 0.02 percent yeast extract, 0.1 percent $NaNO_3$, and trace metals in 80 percent aged surface seawater at *p*H 8. Aliquots of each dilution then were streaked on agar plates of the same composition, and replicate cultures were incubated at 22°–25° C in air, in 100 percent nitrogen, and in 100 percent oxygen. After about 1 week, colonies were picked randomly from the plates and were tested for their ability to reduce nitrate in the presence and absence of oxygen.

Nitrogen Fixation by Blue-Green Algae

Water for nitrogen fixation was taken with the van Dorn samplers, and the entire content of a bottle was filtered through a 28-μm-mesh nannoplankton net. The concentrated plankton was resuspended in 5 ml of membrane-filtered surface water and was placed in 38-ml serum bottles sealed with rubber stoppers. Nitrogen fixation was determined by the acetylene reduction method of Stewart, Fitzgerald, and Burris (1967) in the following manner. Aliquots of 5 ml of acetylene gas were injected into the bottles with a hypodermic syringe, and the excess gas pressure was released through another needle. The final partial pressure of acetylene in the reaction vessels was approximately 0.15 atm. Controls consisted of blanks containing 5 ml of filtered seawater. We incubated the serum bottles on shipboard by placing

them in a water bath with running seawater in full sunlight. After 4 hours, we removed the gas samples from the bottles with a double-end needle and with 13-by-100-mm Vacutainers (Schell and Alexander 1970). Aliquots of 0.5-ml gas samples were subsequently separated on a 5-foot by $\frac{1}{8}$-inch stainless steel Porapak R column at 60° C. The ethylene concentration was determined with an Aerograph gas chromatograph, model A-90-P, fitted with a Beckman hydrogen flame ionization detector. The amount of nitrogen fixed was calculated from the amount of ethylene formed, with a conversion factor of 3.0 being used, and was determined in separate experiments by calibration against ^{15}N (Hanson 1974).

Primary Production

Primary production was determined by the ^{14}C method in which four light-dark bottle *in situ* incubators (ISIS) (Gundersen 1973) are used simultaneously at eight depths on 2 successive days. Incubation was for 6 hours, from 0900–1500 hrs local time, during which time the ISIS were set adrift under a buoy. The water samples were enriched with 100 μCi $Na_2{}^{14}CO_3$ per liter. After being incubated, the samples were divided into 200-ml subsamples and were drained into 250-ml polyethylene bottles to which had been added 5 ml of a 10^{-4} *M*3-(3,4-dichlorophenyl)-1,1-dimethylurea solution to arrest photosynthesis. Filtration through 25-mm Millipore filters, porosity 0.45 μm, at a vacuum of 200 mm Hg, took place on shipboard. The filters containing the phytoplankton were then dried in a vacuum desiccator and ^{14}C uptake was determined in a Packard model 3320 Tri-carb scintillation spectrometer; a toluene-base fluor containing 0.4 percent naphthalene, 0.4 percent 2,5-diphenyloxazole, and 0.04 percent 2,2-*p*-phenylenebis (5-phenyloxazole) was used.

RESULTS AND DISCUSSIONS

Physical-Chemical Properties of the Photic Zone

TEMPERATURE, SALINITY, AND DENSITY: The temperature, salinity, and density (σ_T) characteristics of the photic zone of station B (7207) are shown in Table 3. The salinity profile indicates two water masses—the high salinity North Pacific central water overlaying the low salinity North Pacific intermediate water (Wyrtki et al. 1967).

On no occasion did we observe a pronounced thermocline or pycnocline. The temperature above 250 m was always warmer than 10° C. When comparing recordings made during different cruises, we noted that the temperature variations at depth were generally more pronounced than at the surface. The mixed layer extended to 50–100 m during the various cruises. Similar depths of the mixed layer in this area were observed by Bathen (1972) and Eppley et al. (1973).

RADIANT ENERGY: Figure 1 shows the relative light energy distribution at six depths down to 150 m on station B. The measurements were made under a clear sky and with fairly calm seas between 1000–1430 hours local time. The total amount of radiant energy reaching the water surface on this occasion was 0.5 ± 0.02 cal/cm^2/min within the spectral range 380–650 nm. Readings with the submersible light cell and from data given by Jerlov (1968) allowed us to estimate that not more than 5 percent of the incident light was reflected (solar height maximum 5.6°, minimum 39.6°) by the sea surface under the conditions that prevailed during the measurements. A plot of the downward radiant energy transmission through the water column is shown in Figure 2.

Although green and blue-green light penetrate deeper than does blue light, the light transmission curve determined with the blue Corning filter 1-64 (maximum transmission at 400 nm, 15 percent transmission at 517 nm) coincided almost precisely with the radiant energy transmission curve. The two curves also coincided at all points with Jerlov's ocean water type I curve (Jerlov 1951), a type characteristic of the clearest ocean water. Eppley et al. (1973) found the 1-percent light level at 128 m in the central gyre of the North Pacific Ocean. Our measurements show that the 1-percent light level in these waters is close to 140 m.

It will be noted that the transmission curves are not straight lines, as would have been expected if the light path had passed through

TABLE 3

PHYSICAL-CHEMICAL CHARACTERISTICS OF THE PHOTIC ZONE, STATION B, CRUISE 7207

DEPTH (m)	TEMPERATURE (°C)	SALINITY (‰)	σT	pH	ΣCO_2 (mM/liter)	O_2 (ml/liter)	AOU* (ml/liter)	PO_4 (μg-at/liter)	NO_2 (μg-at/liter)	NO_3 (μg-at/liter)	SiO_2 (μg-at/liter)	CHLOROPHYLL a (mg/m^3)
0–5	25.9	34.61	22.80	8.40	2.01	4.77	+0.12	0.13	0.008	0.05	3.27	0.088
25	24.6	34.58	23.18	8.41	2.01	4.74	−0.03	0.08	0.010	0.04	2.37	0.120
50	24.3	34.91	23.51	8.42	2.01	5.16	+0.37	0.11	0.010	0.00	3.92	0.096
75	23.4	35.04	23.88	8.42	2.02	4.93	+0.06	0.04	0.008	0.04	2.83	0.084
100	21.8	35.14	24.40	8.42	2.02	4.83	−0.16	0.12	0.010	0.04	2.83	0.131
125	20.7	35.20	24.68	8.37	2.03	4.76	−0.35	0.11	0.014	0.09	2.83	0.215
150	19.5	35.13	25.02	8.36	2.08	4.49	−0.75	0.21	0.143	0.82	3.71	0.152
175	17.6	35.01	25.40	8.35	2.12	4.42	−1.07	0.25	0.127	1.84	3.82	0.102
200	16.0	34.81	25.61	8.34	2.12	4.35	−1.28	0.41	0.026	4.01	5.56	—
225	13.6	34.74	26.07	8.31	2.14	4.08	−1.83	0.45	0.034	5.05	7.74	0.046
250	12.6	34.67	26.21	8.28	2.13	4.13	−1.92	0.45	0.024	7.92	11.45	0.033

* Apparent oxygen utilization.

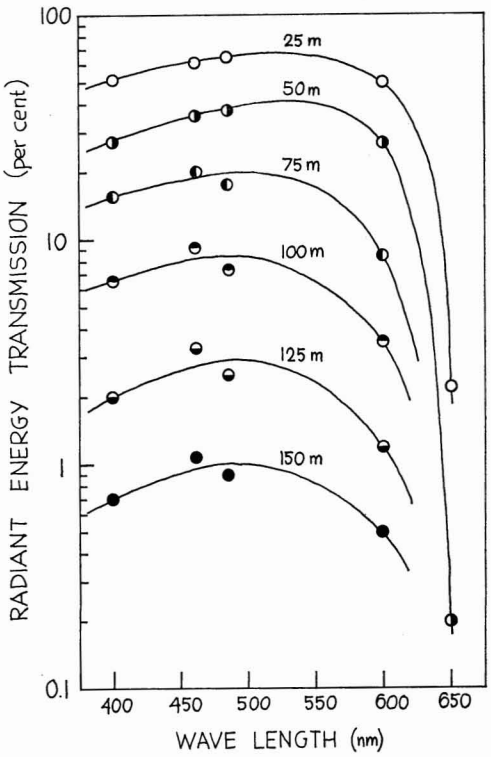

FIGURE 1. Spectral distribution of radiant energy at selected depths of the photic zone in percentage of surface radiant energy (minus 5 percent surface reflection loss). Data are based on measurements from station B.

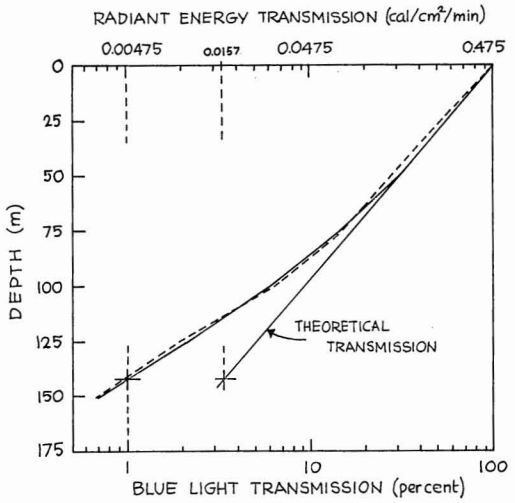

FIGURE 2. Radiant energy transmission (solid curved line) and blue light transmission (broken line) as measured on station B, 14 June 1972, 1000–1430 hours, clear skies, calm seas.

pure homogeneous water. An insignificant fraction of the curvature can be ascribed to the increasing density of the water downward through the photic zone; the better part can be accounted for by particle scattering and absorption, including the light energy absorbed by the plant pigments of the phytoplankton. As can be seen by comparing Figure 2 with Figure 5, the curvature of the light transmission curve begins at about 50 m, the depth at which a rapid increase in numbers and biomass of planktonic organisms also begins.

*p*H AND CARBON DIOXIDE: The small amount of variation in *p*H and total carbon dioxide (Table 3) that could be detected in the upper

125 m did not correlate with chlorophyll distribution or photosynthetic activity. Below 150 m, the *p*H steadily decreased and total carbon dioxide increased. These changes coincided with a decrease in dissolved oxygen and an increase in nitrate, phosphate, and silicate and probably reflected mineralization processes in the dysphotic zone.

DISSOLVED OXYGEN: A slight supersaturation of oxygen (Table 3) above 85 m and a rapidly increasing undersaturation due to respiration below this depth was observed. At 250 m, the water was only about 70 percent saturated with oxygen, corresponding to a deficit of some 1.92 ml/liter.

NITRITE: As is typical of most oceanic waters, a nitrite maximum was consistently present between 100–150 m (Hattori and Wada 1971, Eppley et al. 1973). In most cases the maximum was found to be close to 150 m, occasionally amounting to 0.15 μg-at/liter (Table 3 and Figure 9). It is characteristic that the nitrite maximum occurs at a depth where nitrate begins to appear in the water column. Also, the nitrite maximum correlated with the chlorophyll *a* distribution. Small but measurable amounts of nitrite were found to about 250 m depth but nitrite was virtually absent from the water column above 100 m.

NITRATE, PHOSPHATE, AND SILICATE: The distribution of nitrate, phosphate, and silicate (Table 3) was similar to values found in Riley and Skirrow (1965) for the photic zone of oligotrophic oceanic water. Nitrate was barely detectable in water from the surface down to about 125 m but it increased rapidly below this depth. Phosphate and silicate, on the other hand, were relatively abundant in the upper water column and probably did not limit phytoplankton growth. The relative abundance of phosphate over nitrate is reflected in the nitrate-to-phosphate ratios, which were as low as 0.5 (by atom) in the photic zone. However, below the photic zone, the nitrate and phosphate rapidly reached expected values with ratios in the range of 12–14:1. Our nitrate values agreed with those reported by Eppley et al. (1973). However, their phosphate and silicate concentrations were, in general, lower than ours.

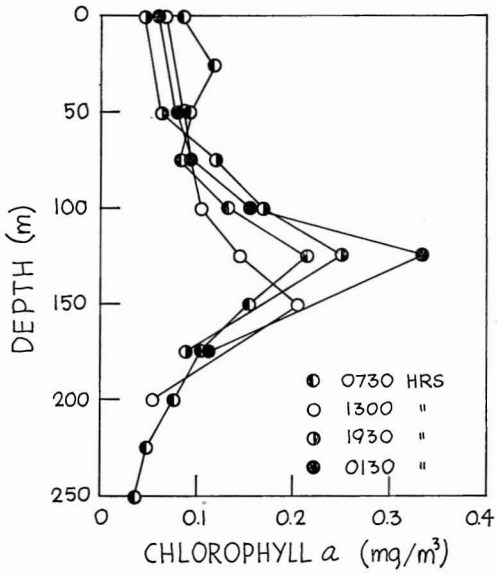

FIGURE 3. Chlorophyll *a*, diel variation, station B, cruise 7207.

CHLOROPHYLL: The chlorophyll *a* maximum (Table 3) was near 100 m, with a concentration of 0.2–0.4 mg per m³, although both deeper and shallower maxima occasionally were observed (Figures 3 and 6). Cattell and Gordon (unpublished) found 0.02–0.24 mg chlorophyll *a* per m³ at Station Gollum north of Oahu, with maxima occurring anywhere from 10–100 m throughout the year. In the central gyre of the North Pacific, Eppley et al. (1973) found chlorophyll *a* maxima from 90–120 m, with concentrations occurring from 0.04–0.23 mg/m³. Venrick, McGowan, and Mantyla (1973) reported ranges from 0.02–0.11 mg/m³, with a maximum at 105 m, and 0.02–0.13 mg/m³, with a maximum at 114 m, north of the Hawaiian Islands. Our data confirmed that deep maxima occur over most of the oligotrophic areas of the Pacific Ocean. In a total of five determinations, the total integrated amount of chlorophyll *a* from the surface to 250 m was 27.58 ± 2.61 mg/m².

Chlorophyll *a* distribution as it appeared in four determinations during a 24-hour period is shown in Figure 3. The corresponding integrated values in the depth interval 0–175 m from station B, cruise 7207, are as follows: 0730 hours, 22.31 mg/m²; 1300 hours, 19.95

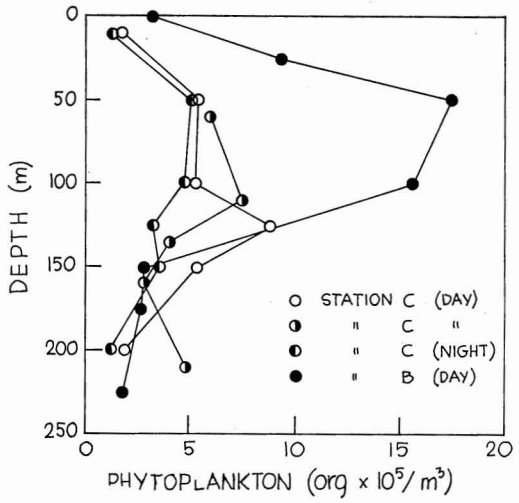

FIGURE 4. Vertical abundance of phytoplankton, all samplings.

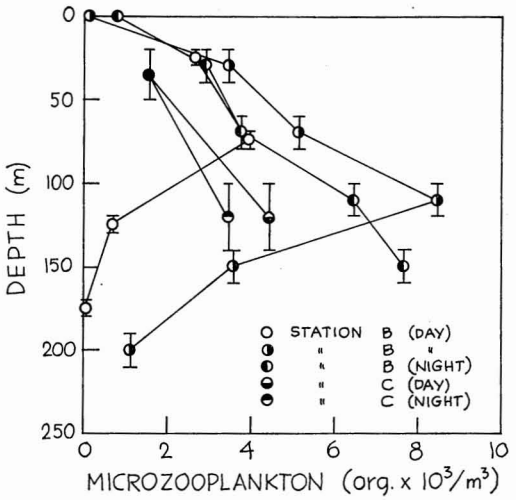

FIGURE 5. Vertical abundance of microzooplankton, all samplings. Vertical bars indicate cluster depths.

mg/m²; 1930 hours, 22.39 mg/m²; and at 0130 hours, 25.70 mg/m². The position of the maximum shifted downward from 125 to 150 m at midday and also showed its lowest value at this time. The highest value occurred after midnight. These events were probably due both to migration of the phytoplankton and to zooplankton grazing. However, our phytoplankton and zooplankton data (from the same diel cycle) only weakly support such explanations.

Very little chlorophyll *b* was present in our samples, thus indicating insignificant numbers of green algae in the phytoplankton. This was confirmed through the microscope. Chlorophyll *c*, on the other hand, made up a substantial fraction of the total chlorophyll, as would be expected from the predominance of diatoms and silicoflagellates in the phytoplankton. Chlorophyll *a*:*c* ratios in and above the chlorophyll *a* maximum usually ranged from 0.5–2.0.

Microorganisms

PHYTOPLANKTON: Silicoflagellates (Tables 4 and 5) appeared to be an important phytoplankton group in the area studied and, together with diatoms, probably constituted the base of the food chain. Muller (1971), in his studies of Hawaiian phytoplankton, considered coccolithophorids to be the dominant organisms at Station Gollum north of Oahu throughout the year but did not observe the abundance of silicoflagellates found by us. A comparison of the distribution of phytoplankton biomass as determined by cell volume measurement with distribution of phytoplankton biomass as determined by chlorophyll *a* (Table 8) indicated to us that a considerable fraction of the phytoplankton was missing in our samples. Zeitzschel (1970) pointed out the significance of very small naked flagellates in tropical waters, and Throndsen (1973) found that such organisms at stations in the Caribbean, the Sargasso Sea, and the Pacific Ocean at times constituted 80–90 percent of the total numbers of the phytoplankton and about 30 percent of the biomass. It is possible that we were not able to preserve such organisms and, if so, their presence may explain the discrepancy between biomass distribution as determined by the two different methods.

At 50 m at station B, we obtained high phytoplankton cell counts but found the diversity of organisms to be low. Here the dominant organisms were *Nitzschia* spp. Their small volume (130 μm^3/cell) accounted for the low biomass (38 percent). Pennate diatoms accounted for 88 percent of the total phytoplankton cell counts but for only 19 percent of the total biomass in the entire photic zone; whereas silicoflagellates accounted for only 3 percent of

TABLE 4

POPULATION SIZES OF PHYTOPLANKTON WITH DEPTH, STATION B, CRUISE 7207

DEPTH (m)	NUMBER OF ORGANISMS PER m^3 DIATOMS	DINOFLAGELLATES	SILICOFLAGELLATES	TOTAL
0	264,000	52,800	8,800	325,600
25	910,800	0	26,400	937,200
50	1,716,000	0	39,600	1,755,600
100	1,531,000	0	39,600	1,570,600
150	272,800	0	8,800	281,600
175	263,800	0	8,800	272,600
225	176,000	0	8,800	184,800
275	92,400	0	0	92,400

TABLE 5

RELATIVE NUMBERS OF PHYTOPLANKTON, STATION B, CRUISE 7207

DEPTH (m)	PENNATE DIATOMS (%)	*Coscinodiscus* (%)	*Chaetoceras* (%)	*Rhizosolenia* (%)	*Ceratium* (%)	*Gymnodinium* (%)	SILICOFLAGELLATES (%)
0	14	3	61	3	11	5	3
25	92	1	1	3	0	0	3
50	98	0	0	0	0	0	2
100	90	2	5	0	0	0	3
150	88	9	0	0	0	0	3
175	90	3	0	0	3	0	4
225	90	5	0	0	0	0	5
275	86	14	0	0	0	0	0

the total cell counts but 41 percent of the biomass. *Ceratium breve* was the most common dinoflagellate in the samples, and no coccolithophorids were detected.

MICROZOOPLANKTON: Comments on the microzooplankton will be restricted largely to the microcopepod fraction, which made up 78 percent (standard deviation 15 percent, $N = 28$) of the total microzooplankton for all depths sampled (Table 6). For the size fraction larger than 35 μm, copepods are the most numerous zooplankters in the epipelagic portion of the water column of most oceanic environments (Blackburn et al. 1970, Rao 1973, Marshall 1973).

During the day, the vertical distribution of microcopepods showed increasing abundance with depth, with a maximum occurring around 75–125 m and with numbers decreasing in the lower portion of the photic zone. Few microcopepods were observed either in the surface samples or in those from 200 m depth. The abundance maximum occurred within or in very close proximity to the chlorophyll *a* maximum (Figure 5, cf. Figure 3). A similar distribution pattern has been described by Beers and Stewart (1967, 1971). The numerical abundance of microcopepods at an oceanic station off California and in the tropical eastern Pacific reported by these authors was approximately equal to or double our maximum abundance.

Groups of microzooplankton other than microcopepods varied widely in number with depth. Although multiple sampling bottles were used for each depth ("cluster depth"), the patchy distribution of the protozoan and metazoan forms other than microcopepods was still evident and no clear pattern of vertical distribution was apparent from the data on these animals. Foraminifera ranged from 0–256/m^3, radiolaria from 0–803/

TABLE 6

POPULATION SIZES OF COPEPODS AND TOTAL MICROZOOPLANKTON, BY DEPTH, STATION B, CRUISE 7207

CLUSTER DEPTH (m)	NUMBER OF ORGANISMS PER m^3* COPEPOD NAUPLII	COPEPOD POSTNAUPLII	COPEPOD NAUPLII: POSTNAUPLII	TOTAL COPEPODS	TOTAL MICROZOOPLANKTON
Day					
0	103	77	1.33	180	330
20–40	2088	1428	1.46	3500	4500
60–80	4000	1231	3.25	5200	5400
100–120	5641	2821	2.00	8500	9000
140–160	2527	1099	2.30	3600	7000
190–210	282	795	0.35	1100	1200
Night					
0	615	308	2.00	920	1100
20–40	1827	1058	1.73	2900	3200
60–80	2308	1538	1.50	3800	4400
100–120	4230	2308	1.83	6500	6700
140–160	5769	1923	3.00	7700	8100

* 39 liters, filtered.

TABLE 7

RELATIVE NUMBERS OF MICROZOOPLANKTON, STATION B, CRUISE 7207

CLUSTER DEPTH (m)	FORAMINIFERA (%)	RADIOLARIA (%)	TINTINNIDS (%)	CRUSTACEANS (%)	PTEROPODS (%)	POLYCHAETES (%)	COPEPODS (%)
Day							
0	0	0	23	0	0	23	54
20–40	5	2	10	0	5	0	78
60–80	0	0	0	0	3	0	97
100–120	0	3	3	0	0	0	94
140–160	3	2	3	40	0	0	52
190–210	0	7	2	0	0	0	91
Night							
0	0	5	14	0	0	0	82
20–40	0	3	3	0	3	0	91
60–80	3	6	3	0	0	0	88
100–120	0	0	3	0	0	0	97
140–160	0	5	0	0	0	0	95

m^3, and tintinnids from 0–769/m^3. The maximum abundance of these groups occurred at 75 m and 125 m at station B (Table 7). Metazoans, i.e., pteropods, polychaetes, and crustaceans other than the microcopepods, occurred in only two, four, and four samples, respectively, and were comparatively rare. However, a high concentration of shrimp nauplii, 2800/m^3, was encountered in a day sample from 150 m at station B. The irregular occurrence of the metazoans no doubt reflects the inexactness of the discrete water sampling method as compared with sampling with pumps (Beers and Stewart 1967) for collecting the less abundant forms.

Microcopepods present in the samples were mostly calanoids. Rhizopodea consisted of the two subclasses Acantharia and Radiolaria, with the latter predominating. The Foraminifera were represented by Globigerinidae. Tintinnid families or subfamilies observed were Xystonellidae, Rhabdonellidae, Tintinninae,

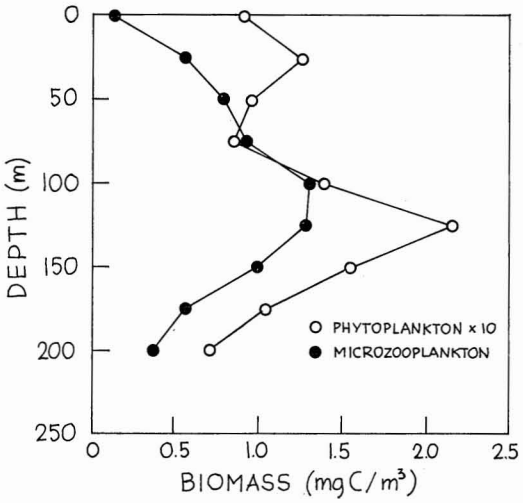

FIGURE 6. Phytoplankton and microzooplankton biomass, vertical distribution, station B, cruise 7207.

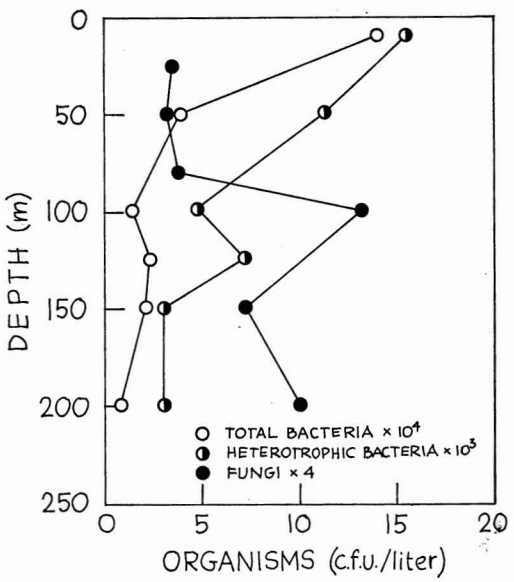

FIGURE 7. Vertical abundance of total and heterotrophic bacteria and of fungi, station B, cruise 7203, and station C, cruise 7204.

Undellidae, Cyttarocylidae, Petalotrichinae, and Coxliellidae, and pteropods were of the family Lamicinidae.

Differences in day-night casts, taken on only two of the cruises, should be viewed with caution because of the sparsity of data. However, differences between day and night abundance increased with depth, with the largest difference occurring in the 150-m sample (Figure 5). The sum of nauplii and postnauplii numbers for the upper 150 m during the day and the night (station B) was essentially the same, i.e., nauplii —day, 14,359 individuals; night, 14,749 individuals; postnauplii—day, 6656 individuals; night, 7135 individuals. These figures indicate that, if migration does occur, it is contained within the photic zone. Our results are consistent with the generally held theory that small epiplanktonic copepods remain and probably migrate within the photic zone over a 24-hour period (Lorenzen 1967).

The average nauplii-to-postnauplii ratio for all samples from above 150 m is 2.014, with a standard deviation of 0.689, $N = 17$. Beers and Stewart (1971) reported ratios of nauplii to postnauplii ranging from 2.4:1 to 7.3:1 (average 4.3) from 12 stations in the tropical eastern Pacific. However, their ratios also include copepods smaller than 35 μm. The lower value obtained by us may have been due to the absence of smaller organisms in our samples, although other causes, such as selective grazing by the next trophic level, may have affected our results.

It is apparent (Figure 6) that the distribution of primary and secondary producers follows the same pattern in the photic zone and that the bulk of their biomass was concentrated in the depth interval 100–150 m at this station. The ratio of phytoplankton biomass to microzooplankton is 15:1 (Table 8).

BACTERIA: Our count (Figure 7) of heterotrophic bacteria in the photic zone of station C was of the same order of magnitude as the "free cell" count of Hobbie et al. (1972) in the photic zone in the western Sargasso Sea and off Cape Hatteras. However, our total microscopic count was somewhat higher than their "attached cell" count. Few other reliable data on bacterial distribution in oligotrophic tropical ocean waters are available for comparison.

The number of bacteria present in the water column is a rather useless figure (Jannasch 1969), because the diverse function of bacteria and their quantitative significance as transformers of matter and energy in marine eco-

TABLE 8

BIOMASS DISTRIBUTION AT STATIONS B AND C

DEPTH (m)	BACTERIA (μg C/m^3)	FUNGI (μg C/m^3)	PHYTOPLANKTON* (mg C/m^3)	MICROZOOPLANKTON (mg C/m^3)
0	13.0	0.062	9.0	0.110
25	8.3	0.056	12.5	0.550
50	3.2	0.052	9.5	0.765
75	2.2	0.060	8.5	0.915
100	1.2	0.216	13.8	1.300
125	2.0	0.165	21.5	1.285
150	1.8	0.114	15.5	0.997
175	1.3	0.137	10.5	0.570
200	0.8	0.160	7.2	0.380
Total†	675 μg	23 μg	2497 mg	166 mg

* Calculated from chlorophyll $a \times 100$ (Holm-Hansen 1969).
† Total carbon in the water column 0–200 m per square meter of ocean surface.

systems probably are not related either to the heterotrophic or to the total counts as determined by traditional methods. The high efficiency at which organic and inorganic matter is utilized and transformed in marine food chains makes it likely that most of the bacterial activities, including mineralization, take place in the digestive tract of zooplankton and larger animals (cf. Johannes 1968) and only a very small part occurs in the water itself. The questions of how bacteria are distributed and how they function in the sea, as well as the problem of whether or not our present methodology gives accurate results, merit a critical reexamination.

As may be seen in Table 8, the bacterial biomass constituted an insignificant fraction of the total biomass in the photic zone. In sharp contrast to this finding are data reported by Sorokin (1971) on bacterial biomass in the photic zone of several stations in oligotrophic areas of the South Pacific Ocean. He found that the bacterial biomass ranged from 10 to 130 mg C/m^3, which is more than a thousandfold our figures and is in the range of our phytoplankton biomass. Although it does not seem likely that two oligotrophic tropical regions should differ this much in the size of their bacterial populations, the discrepancy cannot be resolved at this time. Banse (1974) and others also have questioned some of Sorokin's data from these stations. Seki (1970) determined the bacterial biomass in North Pacific subarctic water to be about 2 mg C/m^3, a figure also considerably higher than our values; however, a direct comparison of that nutrient-rich water mass with tropical nutrient-poor water would be pointless.

BLUE-GREEN ALGAE: We filtered surface water samples of 13 liters each through a 28-μm mesh net and found an average of 80 trichomes of the blue-green alga *Trichodesmium* sp. per sample. In subsurface water samples, *Trichodesmium* averaged five trichomes per sample. In some cases, no trichomes could be detected at all. Marumo and Asaoka (1974) found less than 100 trichomes of *T. thiebautii* per liter from surface waters at stations near the Hawaiian Islands. During a separate cruise, we observed an extensive milky discoloration of the surface water in the area of station C that was caused by *Trichodesmium*. The organism occurred in brownish green spherical bundles, 0.5–1 mm in diameter, similar to those described by Taylor et al. (1973). The bundles separated into individual trichomes when they were filtered or agitated.

Richelia intracellularis, an endosymbiotic alga, was frequently observed in *Rhizosolenia styliformis*. Mague, Weare, and Holm-Hansen (1974) also found the heterocyst-forming blue-green alga occurring as an endosymbiont in the photic zone of several stations north and east of Hawaii. Low numbers of *Trichodesmium* and *Richelia* indicate that Cyanophyta are insignificant contributors to the total biomass in the photic zone.

TABLE 9

VERTICAL DISTRIBUTION OF FILAMENTOUS FUNGI AND YEASTS, STATION B, CRUISE 7203

ORGANISM	ORGANISMS PER LITER						
	25 m	50 m	75 m	100 m	150 m	200 m	300 m
Aspergillus sydowi	1.4*	2.6	9.4	18.0	6.0	4.0	4.0
A. niger	—	—	—	1.4	—	—	—
Aureobasidium pullulans	—	—	—	—	—	0.6	—
Cladosporium oxysporum	6.0	5.4	2.0	6.0	8.6	12.6	14.6
Cryptococcus laurentii var. *laurentii*	—	—	—	0.6	—	—	—
Curvularia lunata	—	0.6	—	0.6	—	—	—
Penicillium citrinum	0.6	—	1.4	0.6	0.6	2.6	0.6
P. lanosum	1.4	4.0	2.0	11.4	12.0	16.0	3.4
P. lilacinum	—	—	—	—	—	0.6	—
Rhodotorula glutinis var. *glutinis*	1.4	—	—	0.6	—	0.6	—
Trichoderma viridae	—	—	—	0.6	0.6	2.6	0.6
Phycomyces sp.†	1.4	0.6	0.6	—	0.6	—	—
Yeast sp. (white)†	2.0	—	—	0.6	—	—	—
Isolates/Liter	14.2	13.2	15.4	53.0	28.4	39.6	23.2
Total Species	7	5	5	10	6	8	5

* Mean of counts for three replicated depths.
† Lost from culture before being identified.

FUNGI: Although the occurrence of fungi in the marine environment has been well documented (Kohlmeyer 1963), some controversy seems to exist as to the role played by this group of microorganisms in the transformation of organic matter in the sea. Their mere presence in the water column constitutes no proof of their *in situ* activity. Viable spores of many fungi are carried worldwide through the atmosphere and may precipitate on the sea surface and slowly sediment through the water in a dormant stage. On the other hand, there is no a priori reason why fungi should not be able to grow and be metabolically active in the marine environment. Cellulose and other polysaccharides, as well as a variety of carbohydrates with which fungi are characteristically associated in other environments, are also present in the sea. Actually, strains of yeasts isolated from the sea have been found to be more versatile with respect to their nutrient requirements than are yeasts in general (van Uden and Fell 1968), a characteristic they share with marine bacteria.

The distribution pattern of fungi in the photic zone (Figure 7 and Table 8) followed closely the distribution pattern of other microorganisms. However, their low numbers and their relatively small size make this group insignificant in the total biomass. Even if their average size were approximately 100 μm^3 (the size of an average yeast cell), the fungi would constitute only some 3 percent of the bacterial biomass in the photic zone (Table 8).

The most abundant of the filamentous species found in our samples were *Aspergillus sydowi*, *Cladosporium oxysporum*, *Penicillium citrinum*, and *P. lanosum* (Table 9). The yeast *Rhodotorula glutinis* also has been found by Kriss (1964) in the Pacific Ocean.

Biological Activity

PRIMARY PRODUCTION: The light-minus-dark photosynthetic carbon fixation and the dark fixation determined at station C are shown, together with chlorophyll *a*, in Figure 8. A pronounced photosynthetic maximum was found at 50 m depth, whereas carbon fixation was low in the above 30 m and below 70 m. Positive fixation was still occurring at 130 m but was absent at 150 m. The chlorophyll *a* maximum was somewhat deeper than the photosynthetic maximum but was shallower than the chlorophyll *a* maximum found on earlier occasions at this station and at station B (Figure 3). A productivity maximum shallower

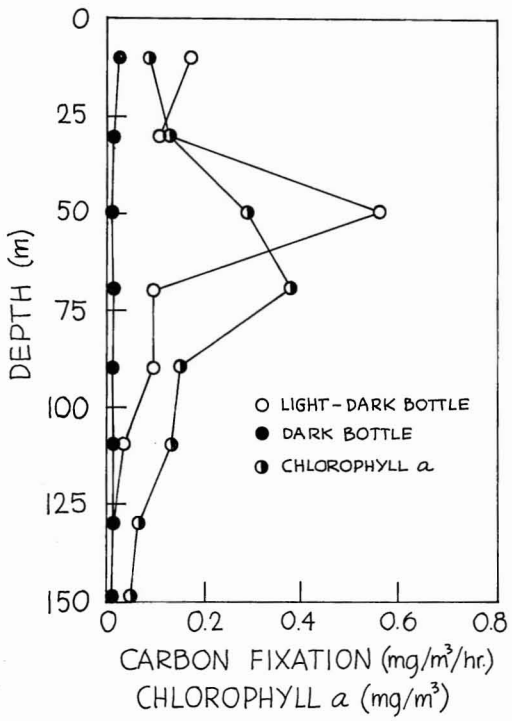

FIGURE 8. Carbon fixation and chlorophyll *a*, station C, cruise 7210.

than the chlorophyll *a* maximum is not unusual, however (Saijo 1973).

The total integrated gross carbon fixation in the photic zone was 21.4 mg C/m²/hr, or 260 mg C/m²/day (12 hrs), or 86.7 g C/m²/year. However, Gundersen and Corbin (in press) calculated from data on oxygen distribution and apparent oxygen utilization from the same water column that a total of 494 ml of oxygen were produced photosynthetically during the 12-hr light period and about 336 ml of oxygen were consumed in respiration by the phytoplankton during the 24-hr daily cycle. This means that, of the 260 mg C fixed, about 178 mg (or about 7.1 percent of the total phytoplankton biomass of 2497 mg C) were lost by respiration, resulting in a net gain of only 82 mg C/m²/day.

Our gross value of 260 mg C/m²/day compares well with the 127–318 mg C/m²/day value found by Owen and Zeitzschel (1970) during their year-long study in the tropical eastern Pacific and also with the 144–294 mg C/m²/day reported by Eppley et al. (1973) in the central gyre of the North Pacific Ocean. However, neither of these workers observed a pronounced fixation maximum. Koblentz-Mishke, Volkovinsky, and Kabanova (1970) estimated an annual mean production in subtropical oligotrophic waters of 70 g C/m² but did not consider respiratory losses which, in these warm waters, may lower the net production considerably. On the other hand, indirect determination of primary production through oxygen analysis by Ivanenkov et al. (1972) gave an average fixation of 900 mg C/m²/day (about 330 g/m²/year) in the tropical Atlantic Ocean (16.5° N, 32°–33° W). However, this estimate seems to be overly high and therefore is questionable.

The productivity index (carbon fixed per unit chlorophyll *a* per unit time) has been used as an indicator of the nutrient status of the assimilating phytoplankton (Curl and Small 1965), with low indices (<3) indicating nutrient-limiting conditions and low-fixation efficiency. Cattell and Gordon (unpublished) reported a rather wide range throughout the year (0.7–20.0) on Station Gollum north of Oahu and explained the variation in terms of changes in the stability of the water column and corresponding changes in nutrient supply. Eppley et al. (1973) found a productivity index of 4–8 in the mixed layer but only 0.3 at 120 m in the North Pacific. Our productivity indices were consistently low, the highest (2.0) occurring at the depth of the productivity maximum and at 10 m; whereas, in the photic zone as a whole, the productivity index was 0.94. It is possible that our low indices are the result of an overestimation of chlorophyll *a* in the water column, since no correction was made for possible interference by phaeophytin in the chlorophyll analysis.

Steemann Nielsen and Al Kholy (1956), Morris, Yentsch, and Yentsch (1971), and Sorokin (1971) have reported high dark fixation rates in oligotrophic tropical waters. We were not able to confirm this; dark fixation was consistently low throughout the entire 150 m of the water column in which carbon fixation was determined.

If one calculates phytoplankton biomass from the chlorophyll *a* data by using a conversion factor of 100 (Holm-Hansen 1969), then the integrated phytoplankton biomass will amount to 2497 mg/m². If the estimated respiratory loss

of 178 mg C/m²/day (Gundersen and Corbin, in press) is then subtracted from this figure, the carbon turnover time will be 30.5 days for the photic zone as a whole and 13.5 days at the photosynthetic maximum at 50 m.

RECYCLING OF NUTRIENTS, GRAZING, AND FOOD CHAINS: Microcopepods showed a maximum numerical abundance that coincided with the chlorophyll *a* maximum (Figures 3 and 5). Since the numbers of organisms in the nannophytoplankton were probably underestimated in this study and since these organisms in tropical waters contain most of the chlorophyll (Malone 1971), the significance of the phytoplankton is probably not apparent from the curve showing their numerical abundance (Figure 4). If the chlorophyll distribution is taken as a measure of phytoplankton biomass distribution (Figure 6), it becomes apparent that the microcopepods are located in close proximity to their primary food source and that they remain there over a 24-hr period. Such a coupling places the metabolites of the grazing herbivores and the contents of ruptured plant cells near the phytoplankton, possibly making them a significant source of nutrients (Jawed 1973). The purposed stability of the tropical oceanic water column (Lorenzen 1967, Eppley et al. 1973) would add credence to this argument, though we have little quantitative data to support that contention.

There are, however, two disturbing observations: the location of the photosynthetic maximum and the distribution of bacteria. Maximum carbon fixation occurred somewhat higher up in the photic zone than did the chlorophyll maximum. The role of the bacteria in the mineralization and recycling processes at the depth of the chlorophyll and microcopepod maxima is not apparent from their numerical distribution (Figure 7), but, as already discussed, the bacteria probably are concentrated in the intestinal tracts and in the feces of the microcopepods and other organisms and thereby escape detection.

The net photosynthetic production within the photic zone, 82 mg C/cm²/day, indicates that the microcopepods eat their own weight every 2.2 days, if they are indeed the principal herbivore link. Pepipa, Pavlova, and Mironov (1970) estimated that consumption rates for microcopepods in the Black Sea range from around 100–200 percent of their body weight per day. Paffenhofer (1971) indicated that young stages of *Calanus helgolandicus* may consume 292 to 481 percent of their body weight per day. Our number is tenuous in that early naupliar stages of some copepods are nonfeeding and also in that other animals, such as tintinnids which were undersampled in our study, may consume large amounts of primary producers. A further objection could be raised because ingestion rates of the magnitude cited above would not manifest themselves very often in the natural environment due to the relatively low concentrations of food organisms found in tropical waters. Patchiness—concentration of the grazer and food sources into strata by physical and/or biological mechanisms—as observed in our data would, of course, tend to overcome this objection. There remains the striking indication that there is a rapid turnover of material at the first trophic level due to grazing pressure of the microzooplankton.

Utilizing existing data on the distribution and abundance of macrozooplankton (Nakamura 1967) and micronekton (Clarke 1973, and Maynard, Riggs, and Walters 1975) in Hawaiian waters and the assumptions concerning the biochemical composition of marine animals, we estimated that the total biomass (mg of carbon) of the microzooplankton, the macrozooplankton (>202 μm), and the micronekton in Hawaiian waters was about equal. Such a distribution over time could be maintained by an inverse relationship between turnover time and size (Sheldon, Prakash, and Sutcliffe 1972) and could indicate that the extended food chain postulated by Parsons and Le Brasseur (1970) and discussed in the comprehensive work of Beers and Stewart (1971), i.e., nannophytoplankton → microzooplankton → macrozooplankton → micronekton, may be a simplified structure of the food chain in the photic zone studied by us. However, short circuits, as suggested by Clarke (1973), could be responsible for the transfer of a significant portion of the biological production to higher trophic levels —from nannophytoplankton → microzooplankton → micronekton (juvenile mesopela-

TABLE 10

QUANTITY OF NITROGEN FIXED IN THE PHOTIC ZONE, STATION C

DEPTH (m)	ng/liter/hr	μg-at/liter/yr
Cruise 7211		
0–5	5.2	1.35
20	1.8	0.47
40	3.0	0.77
60	0.3	0.07
80	0.1	0.04
100	0.65	0.18
120	0.75	0.19
140	0.50	0.15
160	0.75	0.19
180	0	0
200	0	0
220	0	0
Cruise 7212		
0–5	0.85	0.22
10	1.6	0.40
20	1.8	0.47
30	1.55	0.40
40	1.55	0.40
60	0.7	0.18
80	2.3	0.58
100	1.3	0.33
110	0.6	0.15
120	0.7	0.18
140	0	0
160	0	0

gic fishes and crustacea). More extensive and comprehensive studies of the dynamics of the situation are needed to validate these speculations.

NITROGEN FIXATION: Two complete profiles of nitrogen fixation in the photic zone were obtained at station C. Fixation rates (Table 10) were generally greater in the upper water column and lesser with depth. The amount of nitrogen fixed corresponded well with the amounts reported by Goering, Dugdale, and Menzel (1966) in the tropical Atlantic Ocean and by Mague, Weare, and Holm-Hansen (1974) in the eastern and central North Pacific Ocean.

On one occasion, when a *Trichodesmium* bloom had developed in the area of station C, water from the surface microlayer was sampled with a 16-mesh fiber glass screen and was analyzed. The material showed a fixation rate of 893 ng N/liter/hr, almost three times higher than that fixed by a *Trichodesmium* bloom sampled by Goering, Dugdale, and Menzel (1966) in the Atlantic Ocean.

As has been pointed out by Mague, Weare, and Holm-Hansen (1974), nitrogen fixation by blue-green algae in tropical and subtropical oligotrophic oceans may well be of significance for the maintenance of a constant, albeit low, nitrogen level in such waters. In this study, gross photosynthetic production was found to be 86.7 g C/m²/yr. The annual fixation of nitrogen can be calculated by an integration of the two profiles shown in Table 10 to average of 0.69 g N/m². The carbon-to-nitrogen ratio of particulate organic matter in the depth interval 0–300 m in these waters was previously determined to be 4.8 by weight (Gundersen et al. 1972). If these data are accepted as being valid, the amount of combined nitrogen furnished by nitrogen-fixing organisms is about 3.8 percent of the total nitrogen required by the phytoplankton within the photic zone as a whole.

By comparing the actual nitrogen uptake by phytoplankton with the amount of nitrogen turned into combined form by the nitrogen-fixing blue-green algae, Mague, Weare, and Holm-Hansen (1974) concluded that 2–5 percent of the daily nitrogen requirement by the phytoplankton was provided by the nitrogen-fixing organisms. Some data even indicate that up to 30 percent of the nitrogen might come from fixation.

MICROBIAL ACTIVITY IN THE NITRITE MAXIMUM: The amount of nitrite present in the photic zone is almost insignificant, but the fact that most of it occurs as a distinct band, positioned immediately below the base of the photic zone and ostensibly related to the nitrate and chlorophyll *a* profiles, makes it a parameter of considerable biological interest. There are three known biochemical processes that may account for the accumulation of nitrite in the sea.

1. Ammonium may be oxidized to nitrate by aerobic chemoautotrophic nitrifying bacteria. Nitrite may, under certain conditions, appear as a metabolic intermediate in this process.
2. Nitrate may be reduced metabolically to nitrite by facultative anaerobic bacteria at the expense of organic matter. Under anoxic

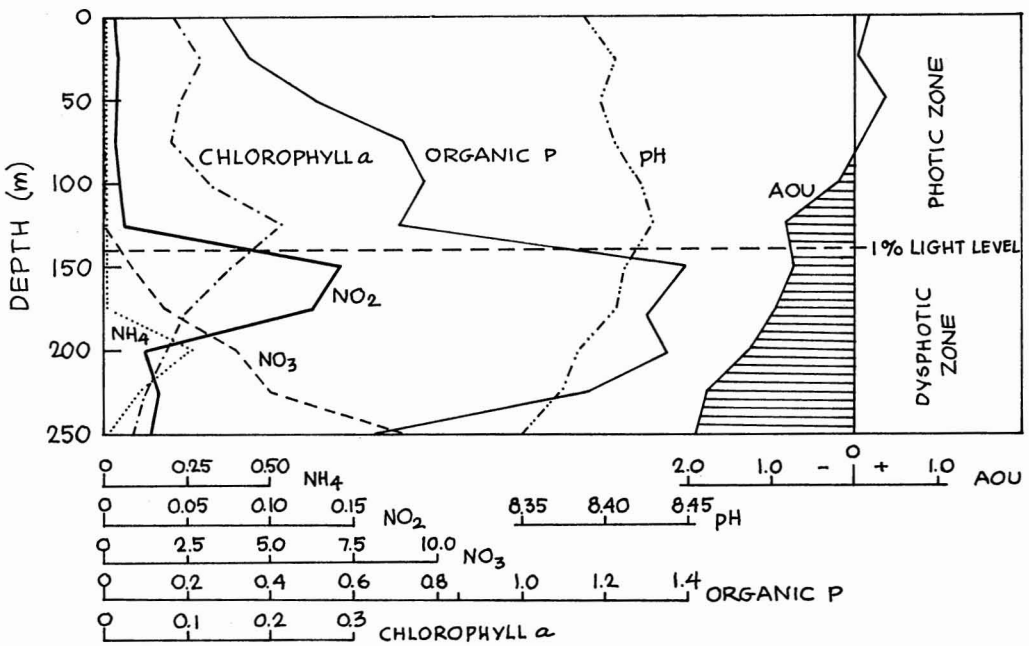

FIGURE 9. Position of nitrite maximum in relation to various other parameters, station B, cruise 7207. Chlorophyll *a* in mg/m³; apparent oxygen utilization in ml/liter; other parameters in μg-at/liter.

conditions the nitrite may become further reduced to unknown intermediates and to elemental nitrogen (denitrification).

3. Assimilatory reduction may convert nitrate to nitrite by the action of phytoplankton and heterotrophic microorganisms under limiting energy conditions.

Environmental factors known to control these oxidation-reduction processes are: light energy, chemical energy (ammonium, organic matter), oxygen, and nitrate. Water temperature, density, and hydrostatic pressure may also, directly or indirectly, affect the direction and rates of these oxidation-reduction processes. Figure 9 shows the position of the nitrite maximum in relation to some of these and other parameters at station C.

In this water column, the potential for the oxidation of ammonium to nitrite was found to exist below approximately 140 m but not above this depth (Mountain 1971, Gundersen et al. 1972). However, as ammonium was barely detectable at 150 m, the depth of the nitrite maximum, it is difficult to visualize how nitrifying bacteria, which depend on ammonium as an energy source, could find sustenance there unless the ammonium is being oxidized as soon as it is formed from organic decomposition and, therefore, never accumulates to any measurable extent in the water. Apart from the apparent lack of ammonium in the nitrite maximum, all other environmental factors affecting the activities of nitrifying bacteria seem to be optimal at the depth of the nitrite maximum. The undersaturation of oxygen at this depth would not be expected to affect nitrification negatively (Gundersen 1966, Carlucci and McNally 1969).

Wada and Hattori (1971) demonstrated that water from the nitrite maximum, positioned at about 70 m at two stations in the central North Pacific, would produce nitrite in the dark but not in full sunlight if enriched with low concentrations of ammonium. Nitrite formation from ammonium was also demonstrated in the upper water column of Sagami Bay, Japan, by Miyazaki, Wada, and Hattori (1973). These authors, who used ^{15}N as a tracer, found that nitrite formation by oxidation of ammonium is of the same order of magnitude as nitrite formation by reduction of nitrate.

The distribution of nitrate-reducing bacteria

TABLE 11

INCUBATION OF ENRICHED WATER FROM THE NITRITE MAXIMUM

ENRICHMENT (μg-at/liter)	INCREASE IN NITRITE			DECREASE IN NITRATE		
	N_2	Air	O_2	N_2	Air	O_2
25 NO_3	0.14	0.08	0.18	2.60	1.43	2.00
100 NO_3	5.56	0.13	0.34	38.42	33.07	33.10
25 NO_3 and 25 NH_4	1.44	0.12	0.07	6.00	0.06	0.05
100 NO_3 and 100 NH_4	33.44	0.09	0.85	60.18	6.62	0.83

NOTE: Seawater was taken from station B at 20°41′ N, 156°55′ W; enriched with NH_4 and NO_3 in nitrogen, in air, and in oxygen; and then incubated for 7 days.

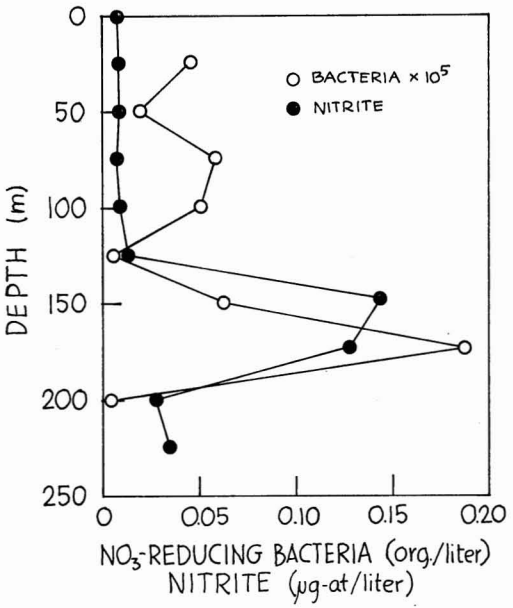

FIGURE 10. Vertical abundance of nitrate-reducing bacteria (average of four casts) in relation to the position of the nitrite maximum, station B, cruise 7207.

at station C is shown in Fig. 10. Nitrite formation in water samples enriched with 25–100 μg-at nitrate per liter and organic matter occurred only in cultures that had been incubated under anoxic conditions. No nitrite could be detected in cultures that had been incubated in air or at high oxygen tension, although nitrate disappeared from the cultures whether oxygen was present or not. However, if the water had been enriched with both nitrate and ammonium (25 μg-at/liter), the disappearance of nitrate and the accumulation of nitrite was far greater in the anoxic cultures than in the oxic ones (Table 11). In the latter, both nitrification and nitrate reduction could, of course, have occurred simultaneously and, therefore, nitrate reduction might have been masked by nitrification. Nitrate reduction may be stimulated by ammonium in anoxic cultures because ammonium is a more suitable nitrogen source than is nitrate for the nitrate-reducing bacteria.

Nitrite production by respiratory nitrate reduction seems to predominate in deep ocean water (Wada and Hattori 1972), and there can be no doubt that the extensive secondary nitrite maximum found, for example, in the oxygen-depleted intermediate water of the tropical eastern Pacific is a result of respiratory nitrate reduction and not of nitrification (Fiadeiro and Strickland 1968, Carlucci and Schubert 1969).

It is evident that the position of the chlorophyll *a* maximum is determined by the opposite gradients of light energy and nitrate. Nitrate begins to appear in the water column just below the chlorophyll *a* maximum and the nitrite maximum is positioned still farther below (Figure 9). It is tempting to conclude that the nitrite distribution is also a function of light energy and chlorophyll distribution—a hypothesis previously set forth by Vaccaro and Ryther (1960). Their hypothesis would indicate that our nitrite maximum was formed through incomplete assimilatory reduction of nitrate by the phytoplankton under light-limiting conditions. The nitrite band, which in this case had a thickness of about 75 m, received an amount of light energy equivalent to 0.001–0.01 cal/cm²/min (Figure 2).

We have on two occasions attempted to verify the Vaccaro-Ryther hypothesis by *in situ* incubation technique. After the exact depth of the nitrite maximum had first been determined in a

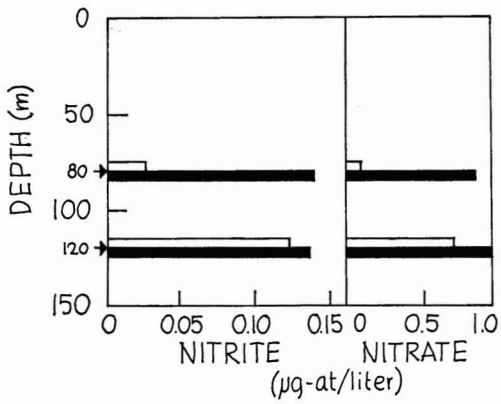

FIGURE 11. Changes in nitrate and nitrite in water from the nitrite maximum (120 m), incubated for 6 hours at that depth and at 80 m, station C, cruise 7211. Open columns, light bottles; solid columns, dark bottles.

separate hydrocast, two *in situ* incubator units were lowered to the nitrite maximum and triggered to enclose a water sample. One of the units was thereafter raised about 40 m, which brought the sample well into the photic zone. The other unit was left at the sampling depth and both units were suspended in the water for about 6 hours of incubation. After being retrieved, the water in the variously incubated light and dark bottles was analyzed for nitrite and nitrate. In one of the experiments, both the nitrate and nitrite concentrations in the light bottle which had been raised into the photic zone had dropped significantly as compared to the dark bottle from the same depth and as compared to the light and dark bottles which had remained at the low light intensity of the nitrite maximum (Figure 11). In the second experiment, these events did not occur; only insignificant changes took place in the nitrite and nitrate concentrations in the bottles, the reason for this being unknown. The first experiment suggested that if only sufficient light energy were available both nitrate and nitrite would disappear rapidly from the water and nitrite, therefore, would not accumulate. Neither experiment gave any direct evidence of further nitrite accumulation from nitrate in the dark or at low light intensity.

SUMMARY AND CONCLUSIONS

1. The depth of the photic zone was found to differ with its definition: if defined according to the 1-percent light level (in caloric units), the photic zone would extend to close to 140 m; but, if defined according to the depth at which the fixation of ^{14}C became unmeasurable, then 130 m would set the baseline. The photic zone would be considerably shallower if total respiration were taken into account, for net production then would be limited to the upper 85 m of the water column.
2. Nitrogen appeared to be the limiting nutrient for the foodchains in the photic zone, for phosphorus and silicon were present in relative abundance. Nitrogen fixation by blue-green algae may contribute significantly to nitrogen replacement in the photic zone.
3. If phytoplankton respiratory losses were not taken into account, then photosynthetic production amounted to 260 mg C/m^2/day. Net photosynthetic production was estimated to be 82 mg C/m^2/day. Although the photosynthetic maximum at 50 m coincided reasonably well with the numerical distribution of the phytoplankton, the chlorophyll *a* maximum was somewhat deeper. This may have been due to a shade-adaptive increase in chlorophyll *a* per cell. The productivity index was never higher than 2.0; the average for the entire photic zone was 0.94. The carbon turnover time was estimated to be 13.5 days at 50 m and 30.5 days for the photic zone as a whole.
4. When the phytoplankton biomass distribution was calculated from the chlorophyll *a* distribution, the microzooplankton were found to be concentrated in close proximity to their primary food source. The production at the primary trophic level would permit a biomass turnover time of 2.2 days for the microzooplankton.

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